



Osteology and relationships of *Signeuxella preumonti* (Teleostei, “Pholidophoriformes”, Signeuxellidae) from the continental Middle Jurassic (Stanleyville Formation) of Kisangani (Democratic Republic of Congo)

Ostéologie et relations de *Signeuxella preumonti* (Teleostei, « Pholidophoriformes », Signeuxellidae) du Jurassique moyen continental (Formation de Stanleyville) de Kisangani (République Démocratique du Congo)

Louis TAVERNE *

Résumé : L’ostéologie de *Signeuxella preumonti* DE SAINT-SEINE, 1955 du Jurassique moyen continental (Formation de Stanleyville) de la République Démocratique du Congo est étudiée en détails. Ce poisson fossile fut initialement mais erronément rapporté aux Amiiformes. *S. preumonti* possède un vomer impair, un supraoccipital ossifié, un processus quadratique osseux et un foramen pour l’artère efférente pseudobranchiale située à la base du processus basiptérygoïde. Ces quatre caractères attestent que *S. preumonti* doit être inclus dans les Teleostei et non pas dans les Holostei. Le poisson congolais a la symphyse de la mâchoire supérieure formée par une paire de vastes dermethmoïdes latéraux dentés et soudés l’un à l’autre, les petits prémaxillaires étant situés plus latéralement. Ce caractère très particulier est partagé par trois familles de téléostéens archaïques anciennement inclus dans les “Pholidophoriformes”, les Catervariolidae, les Ichthyokentemidae et les Ankylophoridae. Cependant, quelques traits ostéologiques, par exemple le très court processus quadratique, montrent que *S. preumonti* est moins évolué que les poissons de ces trois familles. Les Signeuxellidae semblent être la branche la plus primitive au sein des multiples lignées du groupe hétérogène des “Pholidophoriformes”.

Mots-clés: Teleostei, Signeuxellidae, *Signeuxella preumonti*, ostéologie, relations, Jurassique moyen continental, Formation de Stanleyville, Kisangani, République Démocratique du Congo.

Abstract : The osteology of *Signeuxella preumonti* DE SAINT-SEINE, 1955 from the continental Middle Jurassic (Stanleyville Formation) of the Democratic Republic of Congo is studied in details. This fossil fish was initially but mistakenly assigned to the Amiiformes. *S. preumonti* exhibits an impaired vomer, an ossified supraoccipital, a quadratic bony process and a foramen for the efferent pseudobranchial artery located at the basis of the basipterygoid process. These four characters attest that *S. preumonti* must be included in the Teleostei and not in the Holostei. The Congolese fish has the symphysis of the upper jaw formed by a pair of large toothed lateral dermethmoids fused together, the small premaxillae being more laterally located. This highly peculiar feature is shared by three families of archaic teleosts formerly included in the “Pholidophoriformes”, Catervariolidae, Ichthyokentemidae and Ankylophoridae. However, a few osteological features, for instance the very short quadratic bony process, show that *S. preumonti* is less advanced than the fishes of these three families. Signeuxellidae seems to be the most primitive branch in the numerous lineages of the heterogenous “pholidophoriform” assemblage.

Key words: Teleostei, Signeuxellidae, *Signeuxella preumonti*, osteology, relationships, continental Middle Jurassic, Stanleyville Formation, Kisangani, Democratic Republic of Congo.

INTRODUCTION

The Stanleyville Formation, in the region of Kisangani (Democratic Republic of Congo), dates back to the Middle Jurassic (Aalenian-Bathonian, cf. COLIN, 1994: 34) and yields a rich continental fossil fish community.

A first study of this ichthyofauna was done more than a half century ago and published in three monographs (DE SAINT-SEINE, 1950, 1955; DE SAINT-SEINE & CASIER, 1962). A revision of these fishes in a more modern way is conducted since a few decades (TAVERNE, 1975, 2001, 2011a, 2011b, 2011c, 2014a, 2014b, 2015).

* 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

Primitive Teleostei with ganoid scales are abundant in the deposits of the Stanleyville Formation. In the past, all these archaic teleosts from the Mesozoic were ranged in the highly heterogeneous order “Pholidophoriformes”. Today, the family Pholidophoridae *sensu stricto* is considered as the unique valid lineage of a restricted order Pholidophoriformes (ARRATIA, 2013, 2017) and three new orders, Ligulelliformes, Catervarioliformes and Ankylophoriformes, were erected for three families, Ligulellidae, Catervariolidae and Ankylophoridae, formerly included in these paraphyletic “Pholidophoriformes” (TAVERNE, 2011c, 2014a, b). Ligulellidae and Catervariolidae are endemic in the Stanleyville Formation, while Ankylophoridae are recorded not only in the Jurassic deposits of Kisangani but also in the Jurassic of Europe.

The aim of the present paper is to re-describe one of these archaic teleosts from the Stanleyville Formation, *Signeuxella preumonti* DE SAINT-SEINE, 1955, in a more detailed way than previously and to determine its relationships. *S. preumonti* is known by only one specimen, the holotype. This sample was considered as a juvenile fish by DE SAINT-SEINE (1955) because of the lack of scales and of bony vertebral centra, although its skull was heavily ossified. DE SAINT-SEINE (1955) created a peculiar family for this fish, the Signeuxellidae that he considered as belonging to the holostean order Amiiformes.

It is to be noted that I use hereafter “Pholidophoriformes” when referring to all the lineages ever included in this polyphyletic order and Pholidophoridae when I consider only Pholidophoridae *sensu stricto*.

MATERIAL AND METHODS

The specimen hereafter described belongs to the paleontological collection of the Department of Geology and Mineralogy of the Royal Museum for Middle Africa (MRAC), Tervuren, Belgium.

The material was studied with a Leica MZ8 stereomicroscope. The drawings of the figures were made by the author with a camera lucida and the photos by Mr. Stéphane HANOT, from the MRAC. Aspersions with ethanol were used to improve some observations.

List of abbreviations used in the text-figures

AF	=	anal fin
AN	=	angular
APAL	=	autopalatine
APTE	=	autopterotic
ART	=	articular
ASPH	=	autosphenotic
BRSTG	=	branchiostegal ray
a. CHY	=	anterior ceratohyal
p. CHY	=	posterior ceratohyal
DETH	=	dermethmoid (= rostral)
DF	=	dorsal fin
DN	=	dentary
DPTE	=	dermopterotic
ECPT	=	ectopterygoid
ENPT	=	entopterygoid
EP 1-4	=	epurals 1 to 4
EPI	=	epiotic (= epioccipital)
FR	=	frontal
b. FU	=	basal fulcrum
HCLT	=	hypercleithrum (= supracleithrum)
HEM	=	haemal arch
HM	=	haemapophysis (= parapophysis)
HY 1, 2	=	hypurals 1, 2
HYOM	=	hyomandibula
IC	=	intercalary
IOP	=	interopercle
LDETH	=	lateral dermethmoid
LEP	=	lepidotrichium (= fin ray)
LETH	=	lateral ethmoid
MX	=	maxilla
NEUREP	=	neural spine
NP 8, 17	=	eighth and seventeenth neural spines
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PHY	=	parhypural

PMX	=	premaxilla
POP	=	preopercle
PORB 1-2	=	postorbitals (= suborbitals) 1 to 2
PS	=	parasphenoid
PSPH	=	pleurosphenoid (= pterosphenoid)
PT	=	posttemporal
QU	=	quadrate
RAD	=	pterygiophore (= radial)
RI	=	ribs
SAN	=	surangular
SCU	=	caudal scute
SMX	=	supramaxilla
SN	=	supraneural
SOC	=	supraoccipital
SOP	=	subopercle
SORB	=	supraorbital
VO	=	vomer
a. g.	=	aortic groove on the parasphenoid
b. h. c.	=	bucco-hypophyseal canal
b. pr.	=	basiperygoid process of the parasphenoid
f. e. p. a.	=	foramen for the efferent pseudobranchial artery
g. t. h. VII	=	groove for the <i>truncus hyoideomandibularis</i> of the facial nerve (VII)
ot. c.	=	otic sensory canal
pop. c.	=	preopercular sensory canal
qu. pr.	=	quadratic bony process
sorb. c.	=	supraorbital sensory canal

SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii KLEIN, 1885

Series Neopterygii REGAN, 1923

Division Teleostei MÜLLER, 1845

Order « Pholidophoriformes » BERG, 1940 (not *sensu* ARRATIA, 2013, 2017)

Family Signeuxellidae DE SAINT-SEINE, 1955

Emended diagnosis

The same as the genus (monogeneric family)

Genus *Signeuxella* DE SAINT-SEINE, 1955

Emended diagnosis

The same as the species (monospecific genus)

Species *Signeuxella preumonti* DE SAINT-SEINE, 1955

Emended diagnosis

Small archaic teleost. Large ovoid toothed vomer. Supraoccipital present. Toothless parasphenoid. Foramen for the efferent pseudobranchial artery located at the basis of the basipterygoid process. Small orbitosphenoid and pleurosphenoids present. Short jaws. Fused lateral dermethmoids forming a broad toothed plate at the symphysis of the upper jaw, before the dermethmoid (= rostral). Small toothed premaxilla laterally located. Toothed maxilla, broader posteriorly than anteriorly. Only one small supramaxilla. Toothless autopalatine. Ectopterygoid narrow, elongate and toothless. Large entopterygoid, with a toothed anterior region. Quadrate with a short claw-like bony process located at the posterior ventral corner of the bone. At least two postorbitals (= suborbitals). Small crescent-like preopercle, not reaching the margin of the skull roof. Elongate hypercleithrum (= supracleithrum) and posttemporal. No ossified vertebral centra. Paired neural spines and haemapophyses (= parapophyses) in the abdominal region. Unpaired neural and haemal spines in the caudal region. Short supraneurals in the abdominal region. No intermuscular bones. No fringing fulcra on fins. Pectoral fin with two large basal fulcra and four rays. Ventral fin with one large basal fulcrum and five rays. Dorsal and anal fins located at the same level, near the tail. Dorsal fin with two basal fulcra and nine rays. Anal fin with two

basal fulcra and nine rays. Four epurals. Ural neural spines not forming uroneurals. One caudal scute in each lobe of the caudal fin. Enlarged plate-like first hypural. No scales.

Holotype and only specimen

Specimen MRAC RG 7541a: an almost nearly complete specimen, with the skull preserved in dorsal-ventral orientation (Fig. 1). Total length: 38 mm. It is to be noted that RG 7541b is not the counter-part of RG 7541a.

Formation and locality

Stanleyville Formation, level 4 (black bituminous shales), Mekombi river, 50 km South-East of Kisangani, Democratic Republic of Congo.



Figure 1. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Holotype MRAC RG 7541a.

Osteology

The skull (Figs 2-4)

The skull roof is seen from its inner side as it is clearly shown by the presence of well visible vomer and parasphenoid lying on the frontals and parietals and not from its upper side as thought by DE SAINT-SEINE (1955: fig. 61). In the visible parts of the skull roof, the bones are not fused but clearly separated from each other. The bones of the endocranium are individualized.

The anterior margin of the skull is formed by two broad toothed lateral dermethmoids fused together at the symphysis. The bone bears a series of small conical teeth. The rounded anterior region of the dermethmoid (= rostral) is visible just behind the lateral dermethmoid. The posterior region of this dermethmoid is hidden by a wide ovoid vomer that is a little broader than long. This vomer is covered with conical teeth and dental sockets. There is a pair of large lateral ethmoids located under and behind the vomer and on both sides of the parasphenoid. The nasals are not visible and we do not know if they separated the dermethmoid from the frontals or not.

The parasphenoid is a strong toothless and rod-like bone. The bucco-hypophyseal canal opens in the middle of the bone. The basiptyergoid process is broken but the foramen of the efferent pseudobranchial artery is clearly visible at the basis of the process. There is a short aortic groove at the posterior extremity of the parasphenoid. The small orbitosphenoid is located between the lateral ethmoids and the pleurosphenoids but is partly hidden by the parasphenoid. The basisphenoid is not visible, being also covered by the parasphenoid. The two pleurosphenoids are located on each side of the parasphenoid, at the same level as the bucco-hypophyseal canal.



Figure 2. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Head region of holotype MRAC RG 7541a. Scale in mm.

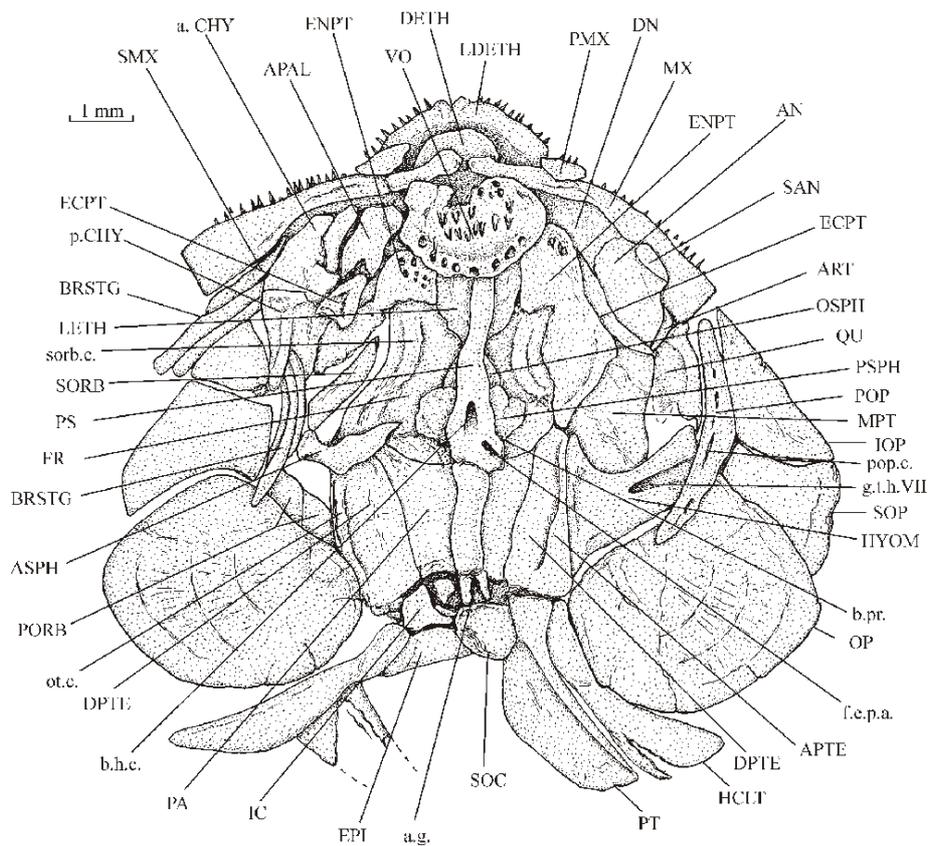


Figure 3. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Skull and pectoral girdle of holotype MRAC RG 7541a.

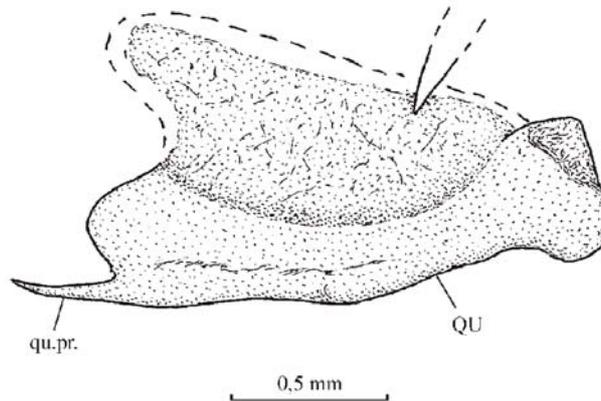


Figure 4. *Signeuxella preumonti* DE SAINT-SEINE, 1955. The right quadrate.

The right autosphenotic is preserved. It is a small bone, with a knob-like postorbital process. The supraoccipital is a small but well individualized bone. The right epiotic (= epioccipital) and a part of the right intercalary are also preserved. The prootics, the exoccipitals and the basioccipital are missing, a loss due to an artefact of fossilization.

The autopalatine is short and massive. It articulates on the lateral margin of the vomer. No toothed dermopalatine is visible. The most anterior part of the two entopterygoids is preserved. They are broad bones that bear a few small conical teeth and dental alveoli on their anterior region. The ectopterygoid is long, narrow and toothless. The quadrate is more or less triangular in shape, with a strongly swollen ventral margin and a well developed knob-like articular condyle. There is a short acuminate claw-like bony quadratic process at the posterior ventral corner of the quadrate. This small process is posterior to the body of the bone and reaches the ventral margin of the hyomandibula. The large metapterygoid is visible above the quadrate and before the hyomandibula.

The upper jaw and the mandible have the same length and both are rather short. The premaxilla and the maxilla bear small conical pointed teeth. As already said, the symphysis of the upper jaw is occupied by the fused toothed lateral dermethmoids. The small premaxillae are more laterally positioned. The maxilla has a narrow anterior half but deepens in its posterior half. The two maxillae are in contact under the dermethmoid. The posterior margin of both maxillae is slightly damaged and it is not possible to determine if this margin was concave, rectilinear or convex. There is only one short and narrow supramaxilla. An important part of the left mandible is preserved but not its oral margin that remains hidden by the left maxilla. The presence of a leptolepid notch is thus uncertain. The dentary, the angular, a small portion of the articular and a reduced surangular, forming a coronoid process, are visible. The presence of an autogenous retroarticular is uncertain. The articulation between the lower jaw and the quadrate is located at the level of the anterior margin of the orbit.

The orbital bones are unknown but a small part of two postorbitals (= suborbitals) is visible just before the right opercle.

The preopercle is small, narrow and crescent-like. Dorsally, it does not reach the lateral margin of the skull roof. Traces of the preopercular sensory canal are visible. The opercle is ovoid and rather wide. Both opercles bear a few concentric growth ridges and some short and feebly marked wrinkles perpendicularly oriented in regard to the growth ridges. The right and left subopercles and interopercles have not the same shape. The left interopercle is much larger than the right one. The anterior margin of the right subopercle is longer than that of the left bone. Such an asymmetry between the left and the right sides of the skull is not rare in fishes.

The left hyomandibula is seen from its inner side. The bone has a very broad head that forms a long undivided articular condyle. The ventral branch is broad but not very deep. The groove for the *truncus hyoideomandibularis* of the facial nerve (VII) is well marked. The symplectic is not visible. The bone probably is lost or covered by the quadrate.

The girdles (Figs 3, 5, 6)

The cleithra, the postcleithra, the possible clavicle and the scapular endochondral elements are not preserved. The posttemporal is a long and broad bone. Its anterior margin is bulged. The hypercleithrum (= supracleithrum) is a little longer but narrower than the posttemporal. The right pectoral fin is incompletely

preserved. Four rays are visible but a few others probably are missing. The distal extremity of the rays is lost. There are two long and pointed basal fulcra. The first one is free but the second one is fused with the basis of the first ray. There are no fringing fulcra.

The pelvic bones are not preserved. The right ventral fin contains five rays and one basal fulcrum. The distal extremity of the rays is lost. The basal fulcrum has a broad basis and a long pointed distal region. There are no fringing fulcra.

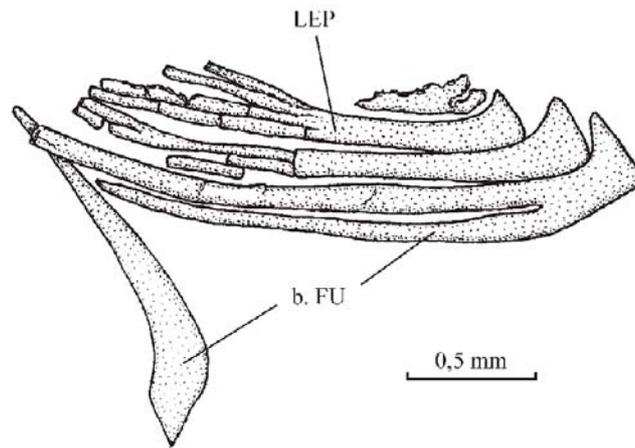


Figure 5. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Righth pectoral fin of holotype MRAC RG 7541a.

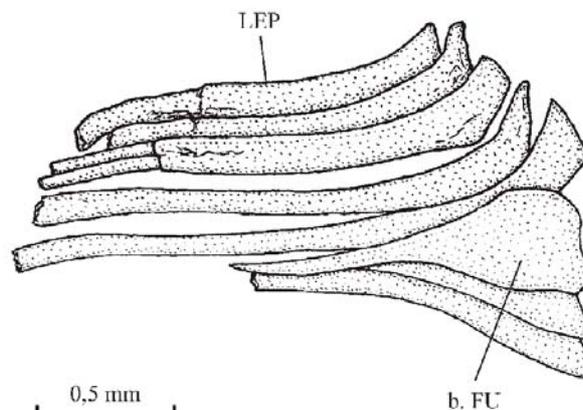


Figure 6. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Righth ventral fin of holotype MRAC RG 7541a.

The axial skeleton (Fig. 7)

Ossified ring-like centra are missing. The total number of vertebral segments is unknown but there are 22 pairs of neural spines in the abdominal region, between the head and the level of the dorsal and anal fins. The paired neural spines are moderately long, with a broad basis. These neural pieces are devoid of fused epineurals. Other free intermuscular bones are also missing. A small triangular haemapophysis (= parapophysis), articulated with a rib, is preserved on the left side of the fish, at the level of the 14th and 15th neural spines. No other haemal elements are visible in the abdominal region but at least two haemal spines, including the parhypural, are present in the tail region. The caudal neural and haemal spines are unpaired.

There is a series of short rod-like supraneurals associated to the neural elements anterior to the level of the dorsal and anal fins. One supraneural is associated to each pair of neural spines.

A few moderately long and rectilinear ribs are preserved on both sides of the axial skeleton.

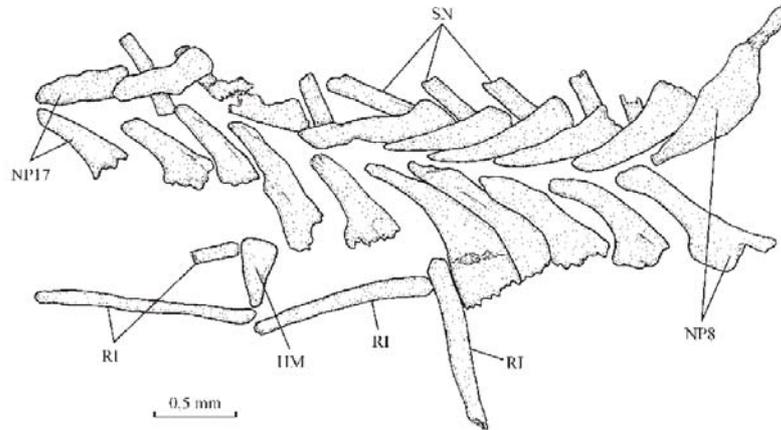


Figure 7. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Neural arches in the abdominal region of holotype MRAC RG 7541a.

The dorsal and anal fins (Fig. 8)

The dorsal fin begins with 2 pointed basal fulcra that are followed by fragments of 9 rays. There are no fringing fulcra. Four dorsal pterygiophores are preserved. The first one is broad and supports the two basal fulcra. The three other pterygiophores are rod-like. The origin of the dorsal fin is slightly posterior to that of the anal fin.

The anal fin contains 2 pointed basal fulcra and fragments of 9 rays. The fin is devoid of fringing fulcra. The pterygiophores are not preserved.

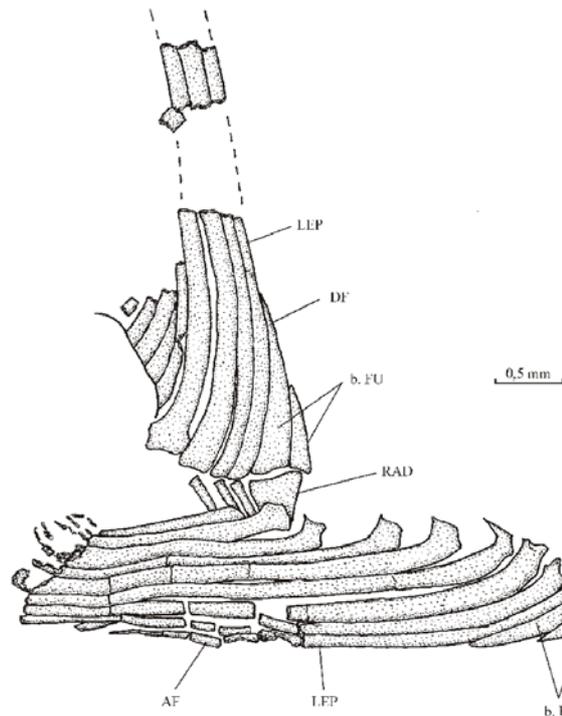


Figure 8. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Dorsal and anal fins of holotype MRAC RG 7541a.

The caudal skeleton and fin (Figs 9, 10, 11)

A great part of the caudal endoskeleton is preserved. The last preural and ural neural spines are elongate, pressed together but they are not transformed into true uroneurals. Traces of four epurals are observable. The parhypural and its haemal arch are visible. The first hypural is strongly enlarged, with a broad articular head. Such a large ventral hypural plate probably results from the fusion of at least two or three hypurals. A fragment of another hypural is also visible.

The two long lobes of the caudal fin are fossilized the one over the other. It is not possible to count the principal caudal rays. The articulation between the segments of the rays is straight. A large arrow-head-like basal scute is present at the basis of each lobe. The dorsal scute is still larger than the ventral one. The basal fulcra are long, narrow, with a thin pointed posterior extremity and a bifid anterior region. Only one basal fulcrum is present in the lower lobe against seven basal fulcra in the upper lobe. There are no traces of fringing fulcra.



Figure 9. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Tail region of holotype MRAC RG 7541a. Scale in mm.

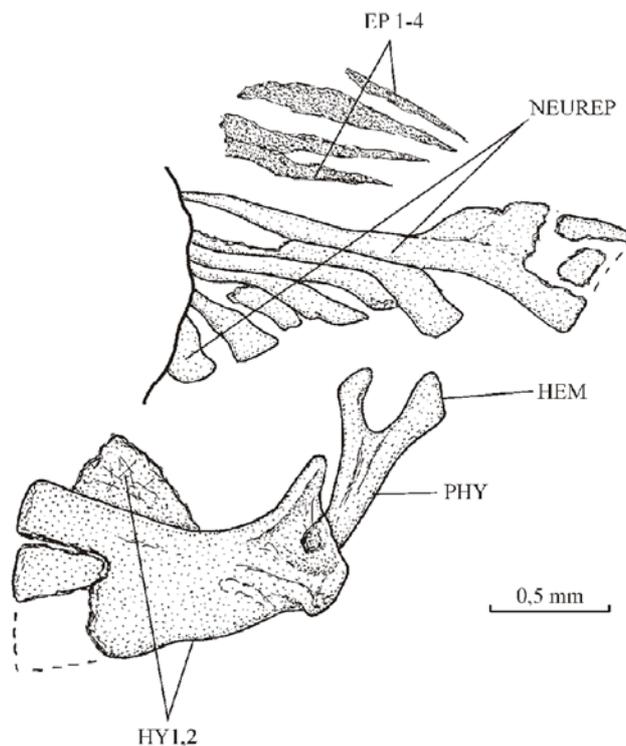


Figure 10. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Caudal endoskeleton of holotype MRAC RG 7541a.

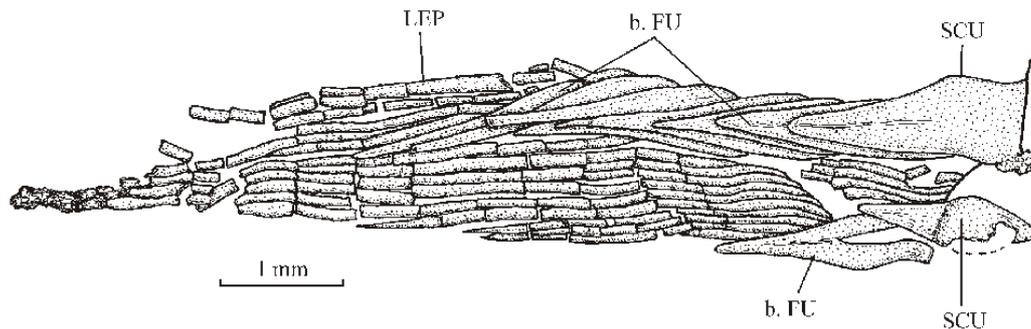


Figure 11. *Signeuxella preumonti* DE SAINT-SEINE, 1955. Caudal fin of holotype MRAC RG 7541a.

The squamation

No scale is present but large fragments of a thick dark skin are preserved in a few places. The absence of scales perhaps could be normal if the specimen really is a juvenile.

DISCUSSION

The relationships of *Signeuxella* within Neopterygii

As previously written, *Signeuxella preumonti* and the family Signeuxellidae were originally included in the holostean order Amiiformes by DE SAINT-SEINE (1955), an opinion followed by ARAMBOURG & BERTIN (1958: 2189), while LEHMAN (1966: 134) ranged the genus in the order Parasemionotiformes, but with some doubt, and PATTERSON (1973: 295) left it halecostome *incertae sedis*. The analysis of the five following characters can bring some light to solve the problem of the relationships of *S. preumonti*.

(1) The premaxilla of Holostei is a large bone located at the symphysis of the upper jaw. It bears a nasal process that partly covers the floor of the endocranial nasal capsule (ALLIS, 1898: fig. 4; BJERRING, 1972: fig. 1; among others). This nasal process or rhinal occurs independently of the premaxilla in the young embryo (PEHRSON, 1940: fig. 49; BJERRING, 1972: fig. 3 A, B1) but the two bones fuse together later in the embryonic development. The snout morphology is quite different in some advanced Halecostomi and in a few archaic Teleostei. In these fishes, the primitive holostean premaxilla is divided in two toothed elements, a lateral dermethmoid, comprising the nasal process and occupying the symphysis of the upper jaw, just before the dermethmoid (= rostral), and a secondary premaxilla located more laterally on the jaw (TAVERNE, 2011a: fig. 20B). That is the pattern found in *S. preumonti*. Such a specialized character appears for the first time in Pachycormiformes, a fossil fish order closely related to the teleosts. However, in these fishes, the lateral dermethmoids are partially fused to the inner side of the dermethmoid and thus are hidden under this bone; only their teeth are visible, giving so the false impression that the dermethmoid is toothed (PATTERSON, 1975: fig. 139; MAINWARING, 1978: fig. 3). A lateral dermethmoid located at the symphysis, with the premaxilla laterally positioned, is an anatomical feature that also occurs in Ligulellidae (TAVERNE, 2011c: figs 2, 3) and in three families of ganoid teleosts, Catervariolidae (TAVERNE, 2011b: figs 8-12, 15, 17, 19, 2014a: figs 4-7, 2015: fig. 2), Ichthyokentemidae (PATTERSON, 1975: fig. 126; GRIFFITH, 1977: fig. 26) and Ankylophoridae (PATTERSON, 1973: fig. 14, 1975: figs 82, 121, 124, 125, 145; ARRATIA, 1999: fig. 6C, 2000: fig. 15, 2013: fig. 49A, B; TAVERNE, 2011a: figs 4, 5, 2014b: figs 4, 6; TAVERNE & CAPASSO, 2017: fig. 4). In some “pholidophoriform” fishes and in most primitive teleosts with cycloid scales, such as *Leptolepis coryphaenoides* (BRONN, 1830), the lateral dermethmoids are fused to the dermethmoid and the three united bones form the exoskeletal covering of the mesethmoid endoskeleton (PATTERSON, 1975: fig. 127a-e, 128a, 129; TAVERNE, 2011a: fig. 20D; among others). There are also some evolved “pholidophoriform” fishes that keep independent but toothless lateral dermethmoids that are no more involved in the upper jaw dentition (TAVERNE & STEURBAUT, 2017: figs 10, 16).

(2) The development of a bony process on the quadrate (ARRATIA, 1999: fig. 5A, B) is one of the principal features characterizing Teleostei. Such a bony process is absent in Holostei and in Ligulellidae (TAVERNE,

2011c: fig. 20). However, a small cartilaginous process exists in the Recent *Amia calva* LINNAEUS, 1766 (GRANDE & BEMIS, 1998: fig. 48). A very small pointed bony process appears on the posterior ventral corner of the quadrate in at least some Pachycormiformes (PATTERSON, 1973: fig. 18; MAINWARING, 1978: figs 8, 9). A true quadratic bony process exists in *S. preumonti* but remains rather short though quite longer than in pachycormid fishes. A well developed bony process on the quadrate also occurs in many “Pholidophoriformes” (PATTERSON, 1973: fig. 7; GAUDANT, 1978: pl. 2, fig. 1, pl. 3, fig. 2, TAVERNE, 2011a: fig. 6, 2011b: figs 21, 24, 2014a: fig. 10) but is missing in Pholidophoridae *sensu stricto* (ARRATIA, 2013: numerous figs). However, a tiny quadratic process exists in one sample of *Pholidophorus gervasuttii* ZAMBELLI, 1980 that she illustrates (*ibid.*, 2013: fig. 15). The absence of bony quadratic process in Pholidophoridae perhaps is an apomorphic loss and not a plesiomorphic missing.

(3) *S. preumonti* exhibits a single median vomer, an osteological apomorphy present in Ligulellidae (TAVERNE, 2011c: figs 9, 17) and in Teleostei, including “Pholidophoriformes” (GRIFFITH & PATTERSON, 1963: fig. 3; PATTERSON, 1975: figs 84, 122a-c; TAVERNE, 2011b: figs 11, 17, 23, 2014: fig. 9). There is a pair of vomers in Holostei (GRANDE & BEMIS, 1998: figs 24C, 28, 34; GRANDE, 2010: fig. 38; among others) and also in Pachycormiformes (MAINWARING, 1978: fig. 6).

(4) *S. preumonti* has a small but clearly visible and well individualized supraoccipital. The presence of an autogenous supraoccipital is one of the major apomorphies of the teleosts and this bone is also present in most “Pholidophoriformes” (GRIFFITH & PATTERSON, 1963: fig. 4; PATTERSON, 1975: numerous figs; ARRATIA, 2000: figs 5, 7; TAVERNE, 2011b: figs 9-11, 19; TAVERNE & CAPASSO, 2017: figs 3, 8; TAVERNE & STEURBAUT, 2017: figs 10, 13). However, a bony supraoccipital is missing in Pholidophoridae *sensu stricto* (ARRATIA, 2013: numerous figs; TINTORI *et al.*, 2015: figs 4a, 7c; TAVERNE & CAPASSO, 2015: fig. 5) but it seems that the endocranium of these fishes remains essentially cartilaginous. This character could explain the absence of a bony supraoccipital in Pholidophoridae. A bony supraoccipital also exists in Ligulellidae (TAVERNE, 2011c: figs 7-9, 12, 14). In many Holostei and in Pachycormiformes, the region between the epiotics is unossified (GRANDE & BEMIS, 1998: fig. 36A, B, C; GRANDE, 2010: Fig. 40A, B, C; MAINWARING, 1978: fig. 20; among others). In a few Holostei, the occipital region does ossify but remains fused to the epiotics and thus an independent supraoccipital does not exist (GARDINER, 1960: figs 37-39; SCHAEFFER, 1971: figs 1-3; PATTERSON, 1975: fig. 113; SCHAEFFER & PATTERSON, 1984: fig. 9; among others).

(5) A foramen for the efferent pseudobranchial artery is present at the basis of the basiptyergoid process of the parasphenoid in *S. preumonti*. Such a foramen is missing in Holostei (GRANDE & BEMIS, 1998: figs 24C, 28, 34; GRANDE, 2010: fig. 38) and in Pachycormiformes (MAINWARING, 1978: fig. 5) but exists in a few basal teleosts, such as “Pholidophoriformes” (RAYNER, 1948: fig. 29B; GRIFFITH & PATTERSON, 1963: fig. 3; PATTERSON, 1975: figs 141 (above), 142a, c, 150) and Leptolepididae (RAYNER, 1937: figs 9-11; PATTERSON, 1975: figs 141 (below), 142b, d, 143, 144). This foramen disappears in most other teleosts.

The character analyzed in point (1) indicates that *S. preumonti* belongs to a fish assemblage grouping Pachycormidae, Ligulellidae, Catervariolidae, Ichthyokentemidae and Ankylophoridae. The character discussed in point (2) shows that the Congolese fish is more evolved than Holostei, Pachycormidae and Ligulellidae and that it belongs to the Teleostei. This inclusion within the Teleostei is confirmed by the characters considered in points (3), (4) and (5). These five osteological features lead to the conclusion that the systematic position of *S. preumonti* is to be found somewhere in the lineages formerly grouped in the heterogenous order “Pholidophoriformes” and more especially in the subgroup that exhibits symphyseal lateral dermethmoids. Thus, I shall examine hereafter the possible relationships of *S. preumonti* with the three concerned families.

***Signeuxella* and Ankylophoridae**

Ankylophoridae have two supramaxillae, a preopercle with an expended ventral region and only one large postorbital lying above an enlarged third infraorbital (TAVERNE, 2011A: fig. 4, 2014b: figs 4-6). *Ankylophorus* GAUDANT, 1978 and *Lehmanophorus* GAUDANT, 1978, both from the Upper Jurassic of France, and *Siemensichthys* ARRATIA, 2000, from the Upper Jurassic of Germany, offer a more evolved pattern. These fishes have the infraorbitals 4 and 5 fused together and with the postorbital, forming a very large infraorbital bone (DE SAINT-SEINE, 1949: fig. 94; GAUDANT, 1978: pl. 1, fig. 2; ARRATIA, 2000: fig. 9). There is no more a free postorbital. Moreover, *Siemensichthys* exhibits only one supramaxilla. But this very long supramaxilla probably represents two fused supramaxillae (ARRATIA, 2000: figs 7-9, 14, 15C). *Signeuxella preumonti* exhibits only one small supramaxilla, a crescent-like preopercle and at least two postorbitals. The Congolese fish keeps thus a more primitive condition for these three characters and can not be included in Ankylophoridae. The short jaws of *S. preumonti* also differ from the elongate jaws of Ankylophoridae.

***Signeuxella*, Ichthyokentemidae and Catervariolidae**

Signeuxella, Ichthyokentemidae and Catervariolidae have preserved a few primitive features, such as the presence of only one small supramaxilla over the maxilla and of a crescent-like preopercle (GRIFFITH & PATTERSON, 1963: fig. 6; TAVERNE, 2011b: figs 8, 35, 2014a: fig. 4, 2015: fig. 3). They also share a specialized character, the presence of a broad and strongly toothed vomer (GRIFFITH & PATTERSON, 1963: figs 2, 3; PATTERSON, 1975: fig. 126; TAVERNE, 2011b: figs 10, 11, 17, 23, 34, 2014a: figs 6, 8). In Pachycormiformes, the paired vomers are long and edentulous (LEHMAN, 1949: fig. 4; MAINWARING, 1978: fig. 6). In Ligulellidae, the unpaired vomer is also toothless (TAVERNE, 2011c: figs 9, 17). In “Pholidophoriformes”, the vomer is elongate and sometimes it bears a patch of small teeth in the anterior region (PATTERSON, 1975: fig. 122a, b, c).

However, Catervariolidae and Ichthyokentemidae differ from *Signeuxella* by a few other osteological characters, such as for instance the presence of a heavily toothed parasphenoid (GRIFFITH & PATTERSON, 1963: figs 2, 3; PATTERSON, 1975: fig. 126; TAVERNE, 2011b: figs 10, 11, 18, 34, 2014a: figs 6, 9). Catervariolidae have a toothed dermopalatine and epineurals associated to the neural arches in the abdominal region (TAVERNE, 2011b: figs 19, 22, 23, 43). *Signeuxella* and Ichthyokentemidae are devoid of dermopalatine and of epineurals (GRIFFITH & PATTERSON, 1963: 27, figs 10, 12). Both Catervariolidae and Ichthyokentemidae possess ossified ring-like vertebrae (GRIFFITH & PATTERSON, 1963: fig. 12; TAVERNE, 2011b: figs 41-46), another difference with *Signeuxella*. Catervariolidae and *Signeuxella* exhibit more than one postorbital (TAVERNE, 2011b: figs 8, 35, 2014a: fig. 4, 2015: fig. 3). Ichthyokentemidae and many other “Pholidophoriformes” share a more advanced pattern of this region. Only the dorsal postorbital is preserved while the ventral one is captured by the third infraorbital that becomes a much larger bone (GRIFFITH & PATTERSON, 1963: fig. 6).

But the major difference between these fishes is located on the quadrate. Catervariolidae and Ichthyokentemidae possess a typically teleostean quadrate, with an elongate rod-like bony process attached to the anterior corner of the bone and lying all along its ventral margin (GRIFFITH & PATTERSON, 1963: fig. 10; TAVERNE, 2011b: figs 21, 24). The morphology of the quadrate is different in *Signeuxella*. The bony process is short, thin, claw-like and fused to the posterior ventral corner of the bone. Such a shape represents a more primitive pattern in the development of the quadratic bony process than that of Catervariolidae and Ichthyokentemidae.

All these anatomical features do not allow the inclusion of *Signeuxella* either in Catervariolidae or in Ichthyokentemidae and indicate that the Congolese fish is less advanced than the members of these two families. The preservation of a peculiar family, the Signeuxellidae, for *Signeuxella* seems thus completely justified.

TAVERNE (2011a, b, 2014a, 2015) considers the Catervariolidae as the most primitive lineage within the heterogenous “pholidophoriform” assemblage. *Signeuxella* probably represents a still less advanced taxon within that “pholidophoriform” group.

Many osteological features of *Signeuxella* remain unknown. It is why I prefer to let this fossil fish as a member of the polyphyletic “Pholidophoriformes” rather than to erect a peculiar order for it.

ACKNOWLEDGMENTS

I greatly thank Dr. Thierry DE PUTTER and Dr. Florias MEES, from the Department of Geology and Mineralogy of the MRAC, for allowing me the access to the specimen studied in the present paper. I also thank Mr. Stéphane HANOT, from the MRAC, and Mr. Adriano VANDERSYPEN, from the Belgian Royal Institute for Natural Sciences, for their technical help. I am grateful to the anonymous reviewers who have read and commented the present text.

REFERENCES

- ALLIS, E. P., 1898. On the morphology of certain of the bones of the cheek and snout of *Amia calva*. *Journal of Morphology*, 14: 425-466.
- ARAMBOURG, C. & BERTIN, L., 1958. Super-ordres des holostéens et des halécostomes (Holostei et Halecostomi). In: *Traité de Zoologie*, 13 (3), GRASSÉ, P. (ed.), Masson et Cie, Paris: 2173-2203.
- ARRATIA, G., 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. In: ARRATIA, G. & SCHULTZE, H. P. (eds) *Mesozoic Fishes 2 – Systematics and Fossil Record*, Verlag Dr. F. Pfeil, München: 265-334.
- ARRATIA, G., 2000. New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the « pholidophoriforms ». *Paläontologische Zeitschrift*, 74(1/2): 113-143.
- ARRATIA, G., 2013. Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes (Actinopterygii, Teleostei). *Journal of Vertebrate Paleontology*, 33, Supplement to Nr 6, *Memoir* 13: 1-138.

- ARRATIA, G., 2017. New Triassic teleosts (Actinopterygii, Teleostomorpha) from northern Italy and their phylogenetic relationships among the most basal teleosts. *Journal of Vertebrate Paleontology*, DOI: [10.1080/02724634.2017.1312690](https://doi.org/10.1080/02724634.2017.1312690): 24 p.
- BJERRING, H. C., 1972. The rhinal bone and its evolutionary significance. *Zoologica Scripta*, 1 (5): 193-201.
- COLIN, J.-P., 1994. Mesozoic-Cenozoic lacustrine sediments in Zaire Interior Basin. In: GIERLOWSKI-KORDESCHAND, E. & KELTTZ, K. (eds), Global Geological Record of Lake Basins, I.G.C.P. Project 324, Cambridge University Press, Cambridge, 1: 31-36.
- DE SAINT-SEINE, P., 1949. Les poissons des calcaires lithographiques de Cerin (Ain). *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, 2 : I-VII and 1-357.
- DE SAINT-SEINE, P., 1950. Contribution à l'étude des vertébrés fossiles du Congo Belge. *Annales du Musée Royal du Congo Belge*, Tervuren (Belgique), Série in-8°, *Sciences Géologiques*, 5: 1-32.
- DE SAINT-SEINE, P., 1955. Poissons fossiles de l'étage de Stanleyville (Congo belge). Première partie. La faune des argilites et schistes bitumineux. *Annales du Musée Royal du Congo Belge*, Tervuren (Belgique), Série in-8°, *Sciences Géologiques*, 14: 1-126.
- DE SAINT-SEINE, P. & CASIER, E. 1962. Poissons fossiles de l'étage de Stanleyville (Congo). Deuxième partie. La faune marine des Calcaires de Songa.. *Annales du Musée Royal de l'Afrique Centrale*, Tervuren (Belgique), Série in-8°, *Sciences Géologiques*, 44: 1-52.
- GARDINER, B. G., 1960. A revision of certain actinopterygian and coelacanth fishes, chiefly from the Lower Lias. *Bulletin of the British Museum (Natural History)*, *Geology*, 4 (7): 239-384.
- GAUDANT, J., 1978. Essai de révision taxonomique des « *Pholidophorus* » (poissons actinoptérygiens) du Jurassique supérieur de Cerin (Ain). *Nouvelles Archives du Musée d'Histoire Naturelle de Lyon*, 16 : 101-121.
- GRANDE, L., 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *Copeia*, supplementary issue, 10 (2A): 1-871.
- GRANDE L., BEMIS W. E., 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Journal of Vertebrate Paleontology*, 18 (Suppl. 1, Memoir 4): 1-690.
- GRIFFITH, J., 1977. The Upper Triassic fishes from Polzberg bei Lunz, Austria. *Zoological Journal of the Linnean Society*, London, 60 (1): 1-93.
- GRIFFITH, J. & PATTERSON, C., 1963. The structure and relationships of the Jurassic fish *Ichthyokentema purbeckensis*. *Bulletin of the British Museum (Natural History)*, *Geology*, 8 (1): 1-43.
- LEHMAN, J.-P., 1949. Etude d'un *Pachycormus* du Lias de Normandie. *Kungliga Svenska Vetenskapsakademiens Handlingar*, Fjärde Serien, 1 (2) : 1-44.
- LEHMAN, J.-P., 1966. Actinopterygii. In: *Traité de Paléontologie*, 4 (3), PIVETEAU, J. (ed.), Masson et Cie, Paris : 1-242.
- MAINWARING, A. J., 1978. Anatomical and systematic review of the Pachycormidae, a family of Mesozoic fossil fishes. Ph. D. thesis (unpublished), University of London: 1-162.
- PATTERSON, C., 1973. Interrelationships of holosteans. *Zoological Journal of the Linnean Society*, London, 53 (Supplement 1): 233-305.
- PATTERSON, C., 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London, series B, Biological Sciences*, 269(899): 275-579.
- PEHRSON, T., 1940. The development of dermal bones in the skull of *Amia calva*. *Acta Zoologica*, 21: 1-50.
- RAYNER, D. H., 1937. On *Leptolepis bronni* Agassiz. *Annals and Magazine of Natural History*, series 10, 19: 46-74.
- RAYNER, D. H., 1948. The structure of certain Jurassic holosteans fishes, with special reference to their neurocrania. *Philosophical Transactions of the Royal Society of London, series B, Biological Sciences*, 233 (601): 287-345.
- SCHAEFFER, B., 1971. The braincase of the holostean fish *Macrepistius*, with comments on neurocranial ossification in the Actinopterygii. *American Museum Novitates*, 2459: 1-34.
- SCHAEFFER, B. & PATTERSON, C., 1984. Jurassic fishes from Western United States, with comments on Jurassic fish distribution. *American Museum Novitates*, 2796: 1-86.
- TAVERNE, L., 1975. Étude ostéologique de *Leptolepis caheni*, téléostéen fossile du Jurassique supérieur (Kimméridgien) de Kisangani (ex-Stanleyville, Zaïre) précédemment décrit dans le genre *Paraclupavus*. *Revue de Zoologie Africaine*, 89 (4): 821-853.
- TAVERNE, L., 2001. Position systématique et relations phylogénétiques de *Paraclupavus* (« *Leptolepis* ») *caheni*, téléostéen marin du Jurassique moyen de Kisangani (Calcaires de Songa, Étage de Stanleyville), République Démocratique du Congo. *Musée Royal de l'Afrique Centrale*, Tervuren, Belgique, *Département de Géologie et Minéralogie, Rapport Annuel 1999-2000*: 55-76.
- TAVERNE, L., 2011a. Ostéologie et relations phylogénétiques de *Steurbaulichthys* (« *Pholidophorus* ») *aequatorialis* gen. nov. (Teleostei, « Pholidophoriformes ») du Jurassique moyen de Kisangani, en République

- Démocratique du Congo. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 81: 129-173.
- TAVERNE, L., 2011b. Ostéologie et relations de *Catervariolus* (Teleostei, « Pholidophoriformes ») du Jurassique moyen de Kisangani (Formation de Stanleyville) en République Démocratique du Congo. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 81: 175-212.
- TAVERNE, L., 2011c. Ostéologie et relations de *Ligulella* (Halecostomi, Ligulelliformes nov. ord.) du Jurassique moyen de Kisangani (Formation de Stanleyville) en République Démocratique du Congo. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 81: 213-233.
- TAVERNE, L., 2014a. Ostéologie et position systématique de *Songanella callida* (Teleostei, Catervarioliformes nov. ord.) du Jurassique moyen de Kisangani (Formation de Stanleyville, Calcaires de Songa) en République Démocratique du Congo. *Geo-Eco-Trop*, 37 [2013] (1): 1-32.
- TAVERNE, L., 2014b. Osteology and relationships of *Songaichthys luctacki* gen. and sp. nov. (Teleostei, Ankylophoriformes ord. nov.) from the Middle Jurassic (Songa Limestones) of Kisangani (Democratic Republic of Congo). *Geo-Eco-Trop*, 37 [2013] (1): 33-52.
- TAVERNE, L., 2015. Osteology and relationships of *Kisanganichthys casieri* gen. and sp. nov. (Teleostei, Catervariolidae) from the Middle Jurassic (Stanleyville Formation) of Kisangani (Congo R. D.). Comments on the systematic position of Catervarioliformes. *Geo-Eco-Trop*, 38 [2014] (2): 241-258.
- TAVERNE, L. & CAPASSO, L., 2015. Osteology and relationships of *Ceneichthys zambellii* gen. and sp. nov. (Teleostei, Pholidophoridae) from the Late Triassic of northern Italy. *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, 9: 13-26.
- TAVERNE, L. & CAPASSO, L., 2017. Comments on the phylogenetic relationships of *Pholidorhynchodon malzannii* and of *Eurycormus speciosus* (Teleostei, “Pholidophoriformes”), two Mesozoic tropical fishes. *Geo-Eco-Trop*. 40 (4) [2016]: 305-316, 8 fig.
- TAVERNE, L. & STEURBAUT, E., 2017 (in press). Osteology and relationships of *Luxembourgichthys* (« *Pholidophorus* ») *friedeni* gen. nov. (Teleostei, “Pholidophoriformes”) from the Lower Jurassic of Belgium and the Great Duchy of Luxemburg. *Geologica Belgica*, 20 [2017] (1-2): 15 p.
- TINTORI, A., ZUOYU, S., PEIGANG, N., LOMBARDO, C., DAYONG, J. & MOTAN, R., 2015. Oldest stem Teleostei from the Late Ladinian (Middle Triassic) of southern China. *Rivista Italiana di Paleontologia e Stratigrafia*, 121(3): 285-296.