



## Osteology and relationships of *Lombardina decorata* (Holostei, Parasemionotidae), a fossil fish from the continental Middle Jurassic of Congo (D. R. C.)

### Ostéologie et relations de *Lombardina decorata* (Holostei, Parasemionotidae), un poisson fossile du Jurassique moyen continental du Congo (R. D. C.)

Louis TAVERNE <sup>1</sup>

**Résumé:** L'ostéologie de *Lombardina decorata* DE SAINT-SEINE, 1955, un petit poisson fossile du Jurassique moyen continental (Formation de Stanleyville) de la République Démocratique du Congo, est étudiée en détails. Ses relations systématiques sont analysées. Un interopercle est présent. Le maxillaire est mobile. Il y a deux vomers. L'endocrâne est ossifié d'une seule pièce, sans os individualisés. Un os mentomeckelien est présent dans la mâchoire inférieure. Il n'y a pas de basihyal ossifié ni d'os intermusculaires. Le préoperculaire est réduit à une branche dorsale élargie avec un bord postérieur arrondi. Ces caractères indiquent que *L. decorata* appartient aux Neopterygii, aux Holostei et aux Parasemionotidae, une famille de poissons holostéens marins primitifs du Trias inférieur. *L. decorata* est donc le plus jeune genre de la famille et le seul à avoir été découvert dans des gisements continentaux. Des comparaisons sont faites avec les Parasemionotidae de Madagascar. Deux spécimens du Trias malgache, erronément rapporté au genre *Watsonulus*, possèdent un parasphénoïde identique à celui de *L. decorata* et pourrait être le prédécesseur de l'espèce congolaise.

Mots-clés: Holostei, Parasemionotidae, *Lombardina decorata*, ostéologie, relations, Jurassique moyen continental, Formation de Stanleyville, République Démocratique du Congo.

**Abstract:** The osteology of *Lombardina decorata* DE SAINT-SEINE, 1955, a small fossil fish from the continental Middle Jurassic (Stanleyville Formation) of the Democratic Republic of Congo, is studied in details. Its systematic relationships are analyzed. An interopercle is present. The maxilla is mobile. There are two vomers. The endocranium is ossified in one piece, without individualized bones. An elongate mentomeckelian bone is present in the lower jaw. No ossified basihyal is present. Intermuscular bones are missing. The preopercle is reduced to a very broad vertical limb with a rounded posterior margin. These characters indicate that *L. decorata* belongs to the Neopterygii, to the Holostei and to the Parasemionotidae, a family of marine primitive holostean fishes from the Lower Triassic. *L. decorata* is thus the youngest genus of the family and the only one discovered in continental deposits. Comparisons are done with the Parasemionotidae from Madagascar. Two Triassic Madagascan specimens, erroneously reported to the genus *Watsonulus*, have a parasphenoid similar to the one of *L. decorata* and could be the predecessor of the Congolese species.

Key words: Holostei, Parasemionotidae, *Lombardina decorata*, osteology, relationships, continental Middle Jurassic, Stanleyville Formation, Democratic Republic of Congo.

## INTRODUCTION

The Stanleyville Formation is located in the southern neighbourhood of Kisangani, a city of the north-eastern region of the Democratic Republic of Congo and is constituted by a series of lacustrine deposits. This geological formation dates back to the Aalenian-Bathonian (Middle Jurassic) (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. Three monographs were published at that time (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, b, c, 2014a, b, 2015a, b, 2017, 2019a, b).

<sup>1</sup>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](mailto:louis.taverne@skynet.be)

The aim of the present paper is to re-describe one of these numerous fossil fishes from the Stanleyville Formation, *Lombardina decorata* DE SAINT-SEINE, 1955, in a more detailed way than previously and to determine its relationships. *L. decorata* is a small fish, with an elongate body and lozenge-shaped ganoid scales. The largest specimens reach a total length of about 10 cm.

## MATERIAL AND METHODS

The specimens hereafter described belong to the paleontological collection of the Department of Geology and Mineralogy of the Africa Museum (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.

*Lombardina decorata* is represented by eight specimens. The holotype (MRAC RG 10.197) and four paratypes (MRAC RG 10.198, 10.199, 10.200a, b, 10.201) come from Mikaeli, on the upper Lualaba, at 200 km up-stream of Kisangani. Two samples, named paratopotypes (MRAC RG 7748, 7777), come from the Majoki river, at 50 km South-East of Kisangani. An eighth sample (MRAC RG 10.238) was labelled *L. decorata* by DE SAINT-SEINE but not mentioned in his monograph. It was found on the Sangi river, a tributary of the Lomami, at 350 km South of Kisangani.

The identification of all the available specimens as *L. decorata* is based on the presence of the highly characteristic ganoid scales of the species. All these samples were found in the black bituminous shales of the level 4, also named Minjaro-Mekombi-Kewe layer.

### List of abbreviations used in the text-figures

AN	=	angular
ANT	=	antorbital
APAL	=	autopalatine
ART	=	articular
BBR 1, 2	=	basibranchial 1 and 2
BO	=	basioccipital region of the endocranium
BRSTG	=	branchiostegal rays
CHY a.	=	anterior ceratohyal
CHY p.	=	posterior ceratohyal
CLA	=	clavicle
CLT	=	cleithrum
CO	=	coronoid
DETH	=	dermethmoid (= rostral)
DN	=	dentary
DPTE	=	dermopterotic
DSPH	=	dermosphenotic
ENCR	=	endocranium
ECPT	=	ectopterygoid
ENPT	=	endopterygoid
EPI	=	epiotic (= epioccipital) region of the endocranium
FR	=	frontal
GU	=	gular plate
HAP	=	haemapophysis (= parapophysis)
HCLT	=	hypercleithrum (= supracleithrum)
HHY	=	hypohyal
HYOM	=	hyomandibula
IOP	=	interopercle
IORB 1-4	=	infraorbitals 1 to 4
LEP	=	fin ray (= lepidotrichia)
MMK	=	mentomeckelian bone
MPT	=	metapterygoid
MX	=	maxilla
NA	=	nasal
OP	=	opercle
PA	=	parietal
PCLT	=	postcleithrum
PELV	=	pelvic bone
PMX	=	premaxilla
POP	=	preopercle
PORB	=	postorbital (= suborbital)

PS	=	parasphenoid
QU	=	quadrate
RART	=	retroarticular
RI	=	rib
SAN	=	surangular
SC	=	scale
SCU	=	caudal scute
SN	=	supraneural
SOC	=	supraoccipital region of the endocranium
SOP	=	subopercle
SORB 1, 2	=	supraorbitals 1 and 2
SY	=	symplectic
V, V1-3	=	vertebra, vertebrae 1 to 3
b. fu.	=	basal fulcra
br.	=	broken
c. m.	=	mandibular sensory canal
fr. fu.	=	fringing fulcra
g. a. p. a.	=	groove for the afferent pseudobranchial artery
iorb. c.	=	infraorbital sensory canal
l.	=	left
l. l. c.	=	lateral line sensory canal
ot. c.	=	otic sensory canal
p. l.	=	pit-line
r.	=	right
sorb. c.	=	supraorbital sensory canal

### SYSTEMATIC PALEONTOLOGY

Subclass: Actinopterygii KLEIN, 1885  
Series: Neopterygii REGAN, 1923  
Division: Holostei MÜLLER, 1844  
Order: Parasemionotiformes LEHMAN, 1966  
Famille: Parasemionotidae STENSIÖ, 1932

Genus : *Lombardina* DE SAINT-SEINE, 1955

#### Diagnosis

The same as the species (monospecific genus)

Species : *Lombardina decorata* DE SAINT-SEINE, 1955

#### Emended diagnosis

#### Holotype

MRAC RG 10.197: a nearly complete specimen (Fig. 1) from Mikaeli. The snout region and a part of the caudal fin are missing. Length: 103 mm.

#### Paratypes

MRAC RG 7748: a specimen from the Majoki river, reduced to the head and the anterior part of the body (Fig. 2). Length: 80 mm.

MRAC RG 7777: a specimen from the Majoki river, reduced to the head and the anterior region of the body (Fig. 3). Length: 75 mm.

MRAC RG 10.198: a specimen from Mikaeli, reduced to the body. Length: 66 mm.

MRAC RG 10.199: a specimen from Mikaeli, reduced to the posterior region of the body, with a part of the caudal fin. Length: 53 mm.

MRAC RG 10.200a, b: the two sides of a specimen from Mikaeli, reduced to the middle region of the body. Length of side "a": 48 mm, and of side "b": 60 mm.

MRAC RG 10.201: a nearly complete specimen (Fig. 4) from Mikaeli. The caudal fin is missing. Length: 98 mm.



**Figure 1:** *Lombardina decorata* DE SAINT-SEINE, 1955. Holotype MRAC RG 10.197.



**Figure 2:** *Lombardina decorata* DE SAINT-SEINE, 1955. Paratype MRAC RG 7748.



**Figure 3:** *Lombardina decorata* DE SAINT-SEINE, 1955. Paratype MRAC RG 7777.



**Figure 4:** *Lombardina decorata* DE SAINT-SEINE, 1955. Paratype MRAC RG 10.201.

### Other material

MRAC RG 10.238: an incomplete specimen, the head and the upper lobe of the caudal fin being missing (Fig. 5), from the Sangi river, at 350 km South of Kisangani. Length: 70 mm. The identification as *Lombardina decorata* is based on the presence of a few spiny scales typical of the species.



**Figure 5:** *Lombardina decorata* DE SAINT-SEINE, 1955. Specimen MRAC RG 10.238.

### Formation and locality

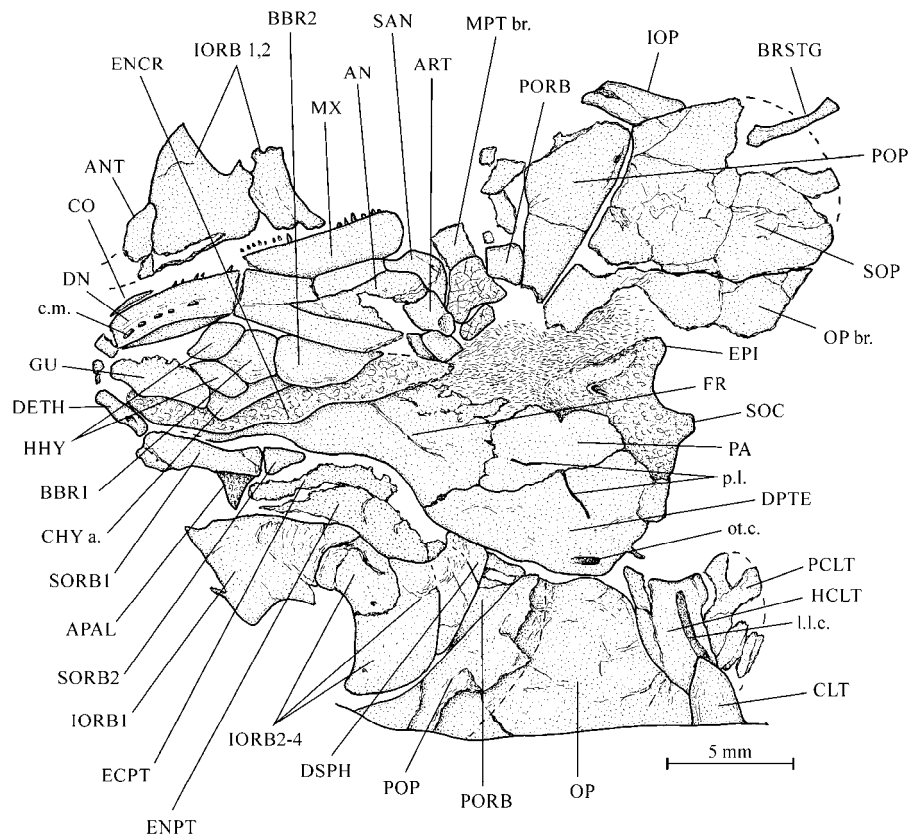
Stanleyville Formation, level 4 (black bituminous shales, Minjaro-Mekombi-Kewe layer), at the Majoki river, 50 km South-East of Kisangani, at Mikaeli, on the upper Lualaba, 200 km up-stream of Kisangani and at the Sangi river, 350 km South of Kisangani. Democratic Republic of Congo.

### Osteology

#### *The skull* (Figs 6-10)

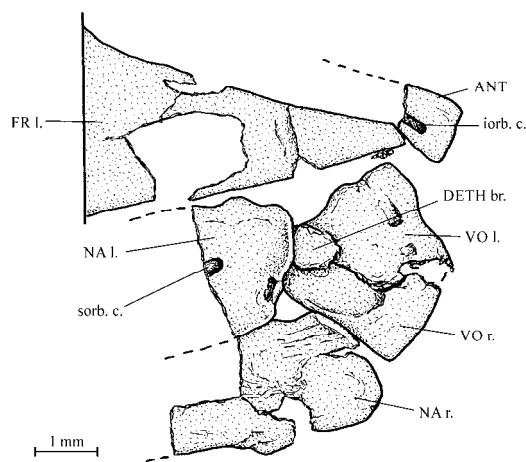
Paratype MRAC RG 7748, from the Majoki river, has the best preserved and more complete skull of all the specimens. The skull is less complete and more crushed on paratype MRAC RG 7777, the other sample from

Majoki. The heads of the holotype and of the other specimens from Mikaeli are incomplete and very badly preserved. Only coaly traces are visible.



**Figure 6:** *Lombardina decorata* DE SAINT-SEINE, 1955. Skull of paratype MRAC RG 7748.

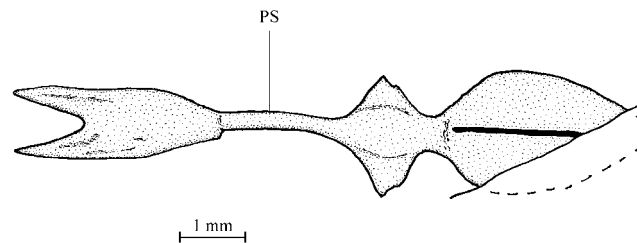
The dermethmoid (= rostral) is present on paratype MRAC RG 7748. It is a small and narrow bone. The nasals are wide. They meet on the mid-line and separate the dermethmoid from the frontals. They bear the anterior part of the supraorbital sensory canal. The anterior parts of the two vomers are visible in dorsal view on paratype MRAC RG 7777, just before the two nasals and under a broken fragment of the dermethmoid.



**Figure 7:** *Lombardina decorata* DE SAINT-SEINE, 1955. Snout region of paratype MRAC RG 7777.

The frontal is long, rather narrow in its anterior part and at the orbital level but it broadens in the postorbital region. The supraorbital sensory canal is not visible on the frontal. The parietal is well developed. It bears a short anterior pit-line. The skull is medioparietal. The dermopterotic is a wide bone. Its anterior extremity outpaces only slightly the level of the anterior margin of the parietal. The dermopterotic bears a long middle pit-line and the otic sensory canal. The middle pit-line does not enter on the parietal. There is no posterior pit-line on the parietal.

The parasphenoid is preserved on sample MRAC RG 10.238 and is especially well visible when sprinkled with ethanol. The bone is displaced by the fossilization and is located above and a little behind the skull region. The most anterior part is broad and divided in two lobes that probably were connected to the two vomers. The middle portion is extremely narrow and toothless. There is short ascending process on each side of the bone. The parachordal part of the parasphenoid is enlarged and separated in two parts by a long median slit, the probable posterior opening of the myodome.



**Figure 8:** *Lombardina decorata* DE SAINT-SEINE, 1955. Parasphenoid of specimen MRAC RG 10.238.

The endocranium is ossified in one piece, without individualized bones. The epiotic (= epioccipital) region, the supraoccipital region and the basioccipital region form marked protuberances on the rear of the endocranium.

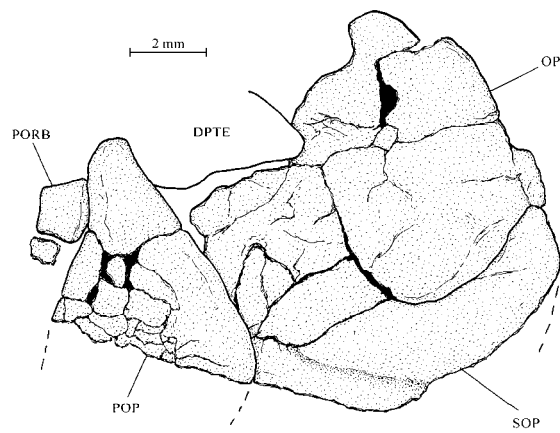
Large parts of palato-quadrate arch are present on paratype MRAC RG 7748. The entopterygoid and of the ectopterygoid are preserved between the frontal and the infraorbitals. The two bones seem toothless. A triangular endochondral bone is visible just below the first supraorbital and before the two pterygoids. This bone probably is the autopalatine. Both the quadrate and the symplectic are articulated with the lower jaw. A small fragment of the metapterygoid is also present.

The jaws are partly preserved on paratype MRAC RG 7748. They are toothed, the teeth being small and conical. The premaxilla and the supramaxilla are missing. Only the posterior part of the maxilla is visible. The posterior margin of the bone is rounded. The maxilla is free, *i. e.*, not connected to the preopercle. The lower jaw is moderately elongated, rather narrow in the symphyseal extremity but a little deeper in the coronoid region formed by the surangular. The articular is independent from the angular. There is a small autogenous retroarticular. A long mentomeckelian bone is present on the inner side of the lower jaw. A series of five small pores of the mandibular sensory canal are visible on the anterior part of the dentary. A small fragment of a coronoid is present just above the dentary.

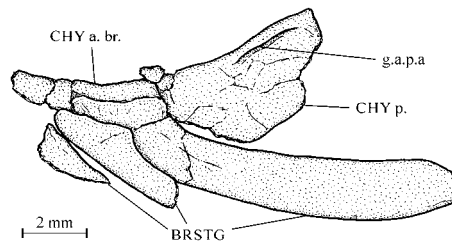
A fragment of the antorbital is visible on sample MRAC RG 7748. There are four infraorbitals and a small dermosphenotic. The first infraorbital is large, with an expended triangular dorsal region. The second and the fourth infraorbitals are smaller bones, while the third one is also a wide element. There is a long triangular postorbital (= suborbital) located between the preopercle and the posterior infraorbitals. There are two supraorbitals. The first one is elongate, while the second one is short.

The preopercle is very broad, vertically oriented and devoid of ventral branch. The anterior margin is rectilinear and the posterior margin rounded. Both the opercle and the subopercle are large bones. They have approximately the same size. A small interopercle is present. There are branchiostegal rays. The last ones are long and broad elements. There is only one gular plate that is long and moderately broad.

A part of the hyoid bar, with three attached branchiostegal rays is preserved on paratype MRAC RG 7748. A groove for the hypobranchial artery (= afferent pseudobranchial artery) is visible on the posterior ceratohyal.



**Figure 9:** *Lombardina decorata* DE SAINT-SEINE, 1955. Opercular region of paratype MRAC RG 7777.

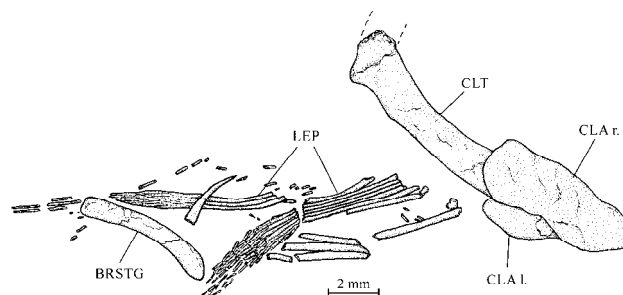


**Figure 10:** *Lombardina decorata* DE SAINT-SEINE, 1955. Hyoid bar and branchiostegal rays of paratype MRAC RG 7748.

**The girdles** (Figs 6, 11, 12)

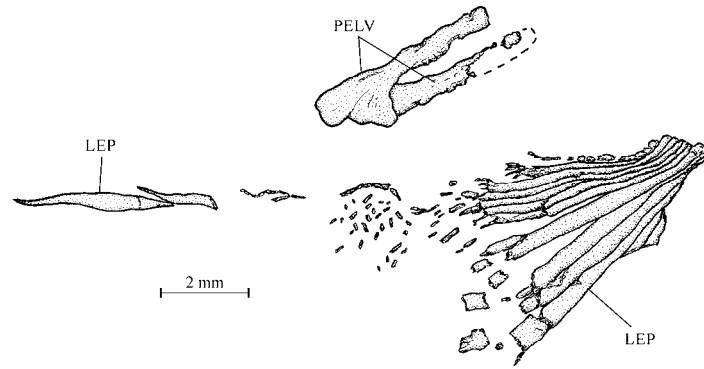
A part of the pectoral girdle and of the ventral fins is preserved on sample MRAC RG 10. 238. A large clavicle is visible at the anterior extremity of the lower limb of the cleithrum. The long pectoral fin contains about ten rays and almost reaches the level of the origin of the ventral fins. The hypercleithrum (= supracleithrum) is preserved on paratype MRAC RG 7748. The bone bears the beginning of the lateral line sensory canal. A large posttemporal is present.

The ventral fins are also preserved on specimen MRAC RG 10.238. They are extremely elongated and are located at the same level of the dorsal fin. Each fin is composed of about a dozen of rays. Two strong pelvic bones are visible on paratype MRAC RG 10.201. They are located in the middle of the lower border of the body.



**Figure 11:** *Lombardina decorata* DE SAINT-SEINE, 1955. Pectoral girdle and fin of specimen MRAC RG 10.238. A displaced branchiostegal ray is present along the fin.

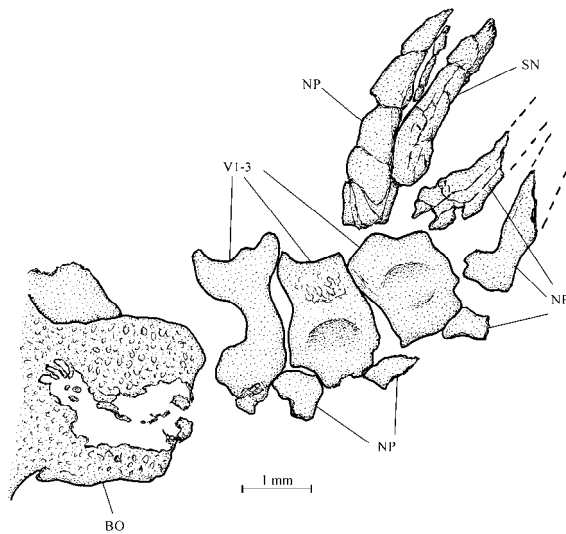




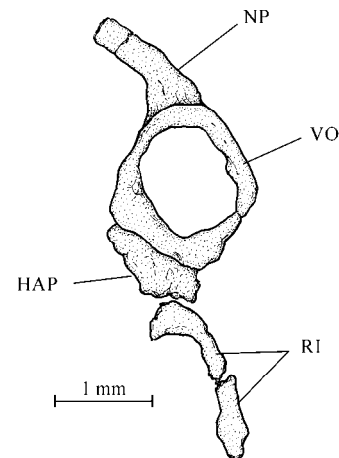
**Figure 12:** *Lombardina decorata* DE SAINT-SEINE, 1955. (A) Pelvic bones of paratype MRAC RG 10.201. (B) ventral fin of specimen MRAC RG 10.238.

**The axial skeleton** (Figs 13, 14)

The body is elongated but no specimen allows a precise count of the vertebrae, the number being between 45 and 50. The centra are ring-like, with a wide median space for the notochord. The lateral faces of the centra are not ornamented. The first vertebrae bear a pair of broad but moderately long neural spines. These spines are articulated but not fused to centra. There are well developed supraneurals. Small haemapophyses (= parapophyses) bearing ribs are articulated on the centra in the abdominal region. Haemal spines are visible in the caudal region. There is no trace of diplospondyly. The last caudal vertebrae have the same size than the abdominal ones. Intermuscular bones are missing.



**Figure 13:** *Lombardina decorata* DE SAINT-SEINE, 1955. First three vertebrae of paratype MRAC RG 7777.



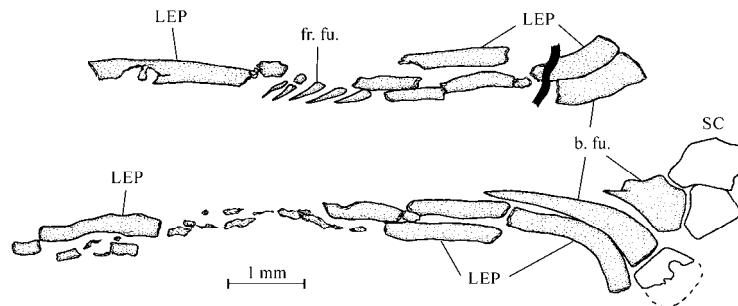
**Figure 14:** *Lombardina decorata* DE SAINT-SEINE, 1955. A vertebra of paratype MRAC RG 10.198.

**The dorsal and anal fins** (Fig. 15)

A part of the long dorsal fin is visible on sample MRAC RG 10. 238. Weak traces of the dorsal fin are also present on the holotype and on paratype MRAC RG 10.198. The fin is located in the middle of the upper border of the body, approximately at the same level of the ventral fins. The first ray of the dorsal fin is preserved

on paratype MRAC RG 10.200a, b. This ray is very long, segmented and branched. Two unsegmented basal fulcra precede the ray. The first one is short and broad, with a small spine. The second one is longer and spiny. Fringing fulcra are present.

The anal fin is not visible. But the first anal pterygiophore is preserved on sample MRAC RG 10.238.

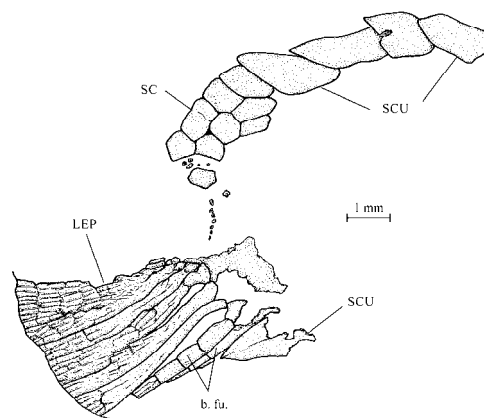


**Figure 15:** *Lombardina decorata* DE SAINT-SEINE, 1955. First dorsal fin ray of paratype MRAC RG 10.200 a (above) and b (below).

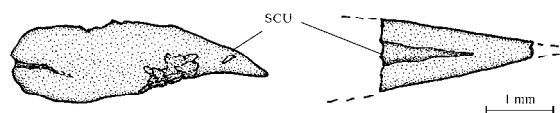
**The caudal fin and skeleton** (Figs 16, 17)

The caudal endoskeleton is covered by the scales and is thus unknown.

The caudal fin is forked but badly preserved. A part of its dorsal lobe is visible on the holotype and a part of the ventral lobe on paratype MRAC RG 10.199 and on specimen MRAC RG 10.238. The rays are segmented and branched. No fringing fulcra are present. There are two segmented basal fulcra (= procurrent rays) on each lobe. A series of caudal scutes precede the dorsal lobe of the fin. There is only one caudal scute in the ventral lobe.



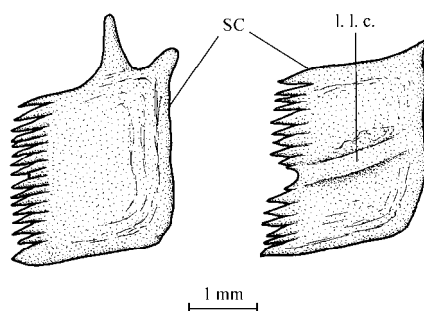
**Figure 16:** *Lombardina decorata* DE SAINT-SEINE, 1955. Preserved part of the caudal fin of paratype MRAC RG 10.199.



**Figure 17:** *Lombardina decorata* DE SAINT-SEINE, 1955. Dorsal (left) and ventral (right) caudal scutes of holotype MRAC RG 10.197.

### *The squamation* (Fig. 18)

The scales are more or less quadrangular and covered by a thick layer of ganoine. Generally, the surface is smooth but small tubercles and weakly marked wrinkles are visible on some scales. The posterior margin of the scales exhibits a series of strongly marked spines. The most ventral spine of each scale is broader than those located above. These long spines are typical of *Lombardina decorata*. No other ganoid fossil fish from the Stanleyville Formation has scales with so developed spines on the posterior border. There are a little more than 40 scales along the flank but no specimen allows a precise count. The peg-and-socket system of articulation is present. The lateral sensory line crosses the scales positioned at mid-height of the flanks. There is a recess in the posterior margin of the lateral line scales at the level of the sensory canal.



**Figure 18:** *Lombardina decorata* DE SAINT-SEINE, 1955. Two scales of paratype MRAC RG 7777.

## DISCUSSION

### *Lombardina* within Actinopterygii

DE SAINT-SEINE (1955: 73) erected the family Lombardinidae for *Lombardina decorata* and reported this new lineage to the order Amiiformes. ARAMBOURG & BERTIN (1958: 2189) ratified this point of view while LEHMAN (1966: 134) ranged *L. decorata* in the family Catervariolidae, giving it a peculiar subfamilial status, the Lombardinae. At that time, he included the Catervariolidae in the order Parasemionotiformes. Today, Catervariolidae are considered as archaic teleosts and no more as holostean fishes (TAVERNE, 2011b). Moreover, the skull of Catervariolidae completely differs from the one of *L. decorata*, their endocranium being completely ossified in individualized bones (TAVERNE, 2011b, 2014a, 2015b). Obviously, a close relationship between *L. decorata* and the Catervariolidae is not possible. No other scientist has discussed the systematic affinities of *L. decorata* since more than a half century. Now, the cranial skeleton of *L. decorata* is known in a more detailed way than previously. That allows a better understanding of the relationships of this Congolese fossil fish.

An interopercle is present in the opercular series of *L. decorata* and the maxilla is mobile. These two characters attest that this fish belongs to the Neopterygii.

The endocranium is ossified in one piece, without individualized bones. There are two vomers. An elongate mentomeckelian bone is present in the lower jaw. The right and left hypohyals are pressed the one against the other and there is no bony basihyal between them. Intermuscular bones are missing. These five features indicate that *L. decorata* must be ranged within the Holostei and not within the Teleostei.

The preopercle of *L. decorata* is not crescent-like as in most Holostei but is reduced to a deep and very broad vertical limb with a rounded posterior margin. Within holostean fishes, this character is the typical autapomorphy of the family Parasemionotidae.

Parasemionotidae is an extinct lineage of primitive Holostei. The family contains about twenty genera. Unfortunately, most of them are poorly known. They are present in the Lower Triassic marine deposits of Madagascar, Canada, Greenland and South China (see references in LI, 2009).

### Chronological and zoogeographical implications

*Lombardina* is thus and by far the youngest genus of the family and the only one found in a lacustrine environment. It is probable that an unknown parasemionotid population from Madagascar survived after the Lower Triassic in the Mozambique Chanel that began to separate the island from Africa. One of these

parasemionotid fish migrated via the regional hydrographic net from the African east coast into the large lake that occupied the region of Kisangani during the Jurassic to become there *Lombardina decorata*.

### ***Lombardina* and the other Parasemionotidae**

The geographic localization of *Lombardina* in Congo (D. R. C) and its highly probable origin from the Madagascan parasemionotid assemblage led us to compare the Congolese genus more particularly with the parasemionotid genera present in the Lower Triassic deposits of Madagascar.

*Parasemionotus* PIVETEAU, 1929 is the first described Madagascan parasemionotid genus. Its body is much deeper (LEHMAN, 1952: fig. 123) than the one of *Lombardina*. The dermal skull of *Parasemionotus* (ibid., 1952: fig. 116) seems rather similar to the one of the Congolese genus but the sketch of the pit-lines is different. The parietal bears not only the anterior pit-line but also a posterior pit-line and the middle pit-line crosses both the parietal and the dermopterotic (ibid., 1952: fig. 117). The middle part of the parasphenoid is rather narrow but bears a long patch of minute teeth (BELTAN, 1968: pl. 36 A, B) contrarily to *Lombardina*. The presence of two gular plates in *Parasemionotus* (LEHMAN, 1952: fig. 122 B) is another difference between the two fishes. The dorsal fin of *Parasemionotus* is positioned in the caudal region of the fish (ibid., 1952: fig. 123) and is not located in the abdominal region, at the same level of the ventral fins as in *Lombardina*. Obviously, the two genera are different.

*Ospia* STENSIÖ, 1932 and *Broughia* STENSIÖ, 1932 were originally described from the Lower Triassic of Greenland (STENSIÖ, 1932) but they are also present in the Lower Triassic of Madagascar (BELTAN, 1968). Both genera differ from *Lombardina*. They possess a broad parasphenoid with elongate ascending processes (STENSIÖ, 1932: figs 78, 87, 88, pl. 26, fig. 3, pl. 33, figs 1, 2; BELTAN, 1968: fig. 24, pl. 28B). The basidorsals and basiventrals are disjoined in *Ospia* and do not form ring-like centra (STENSIÖ, 1932: fig. 85, pl. 31, fig. 1). The dorsal fin of *Broughia* is positioned in the caudal region of the fish and is just a little before the level of the anal fin (ibid., 1932: pl. 30, fig. 1). There is clearly no close relationships between these two parasemionotid fishes and the Congolese genus.

*Jacobulus* LEHMAN, 1952, *Thomasinotus* LEHMAN, 1952 and *Lehmanotus* BELTAN, 1968 share a highly specialized character. Their preopercle is divided in three or four elements, with a posterior crescent-like component that contains the preopercular sensory canal (LEHMAN, 1952: figs 126, 129; BELTAN, 1968: fig. 34). *Lombardina* has preserved the primitive condition, *i. e.*, a preopercle in one piece, and thus is certainly not a descendant of these three genera.

*Stensiönotus* LEHMAN, 1952 is characterized by two specialized features, the multiplication of the supraorbitals, five elements on each side of the skull, and the presence of a series of small anamestic bones between the posterior infraorbitals and the preopercle (LEHMAN, 1952: fig. 124, pl. 41, fig. C), a different morphology than that of *Lombardina*.

*Devillersia* BELTAN, 1968 differs from *Lombardina* by a few cranial features. The skull is especially broad, with a strongly marked lateral process on the dermopterotic, and the parasphenoid is a large bone (BELTAN, 1968: fig. 27, pl. 43, 44). A close relationship between these two genera seems not possible.

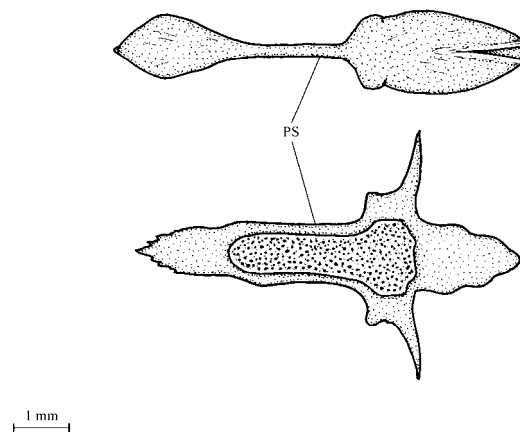
*Piveteaunotus* BELTAN, 1968 is only known by its endocranium (BELTAN, 1968: fig. 41) and can not be compared with *Lombardina*.

*Lombardina* exhibits elongate pectoral, ventral and dorsal fins. This specialized character is shared by the genus *Icarealcyon* BELTAN, 1984, another parasemionotid fish from the Lower Trias of Madagascar (BELTAN, 1984: fig. 2, pl. 3A, B). It is possible that the two genera are close relatives. However, *Icarealcyon* has wider fins, a shorter and deeper body than *Lombardina* and its skull is unknown. No cranial comparison is thus possible between the two fishes.

*Watsonulus* BROUGH, 1939 is the best known of all the parasemionotid genera (PIVETEAU, 1934, 1939-40; LEHMAN, 1952; BELTAN, 1968; OLSEN, 1984). However, it seems clear that the genus is not homogenous, different morphotypes being present in the taxon (PIVETEAU, 1934: 58). *Watsonulus* differs from *Lombardina* by its broad and toothed parasphenoid, with a pair of elongate ascending processes, by its dermopterotic that strongly outpaces the anterior margin of the parietal, by the middle pit-line that extends not only on the dermopterotic but also on the parietal and by its very broad gular plate (LEHMAN, 1952: fig. 122 A; BELTAN, 1968: fig. 26, pl. 30; OLSEN, 1984: figs 2, 3, 7, 8). Moreover, the notochord is free in *Watsonulus* and there is no complete centrum, the basidorsals and basiventrals remaining separated the ones from the others (LEHMAN, 1952: 170).

One specimen (Mus. Nat. Hist. Nat. Paris, I. P. 126) erroneously attributed to *Watsonulus eugnathoides* (PIVETEAU, 1934) has a parasphenoid completely differing from the one of the true *W. eugnathoides* and of the other parasemionotid genera but similar to the parasphenoid of *Lombardina*, with a broad anterior extremity, an extremely narrow and toothless middle section, short ascending processes and an enlarged posterior region with a split for the posterior myodome (Fig. 19; BELTAN, 1968: fig. 27). This unnamed Madagascan Triassic

parasemionotid fish probably is the precursor of *Lombardina decorata* and perhaps already belongs to the genus *Lombardina*.



**Figure 19:** Above: the *Lombardina*-like parasphenoid of specimen Mus. Nat. Hist. Nat. Paris, I. P. 126 from the Lower Triassic of Madagascar, a sample erroneously reported to *Watsonulus eugnathoides* (PIVETEAU, 1934) but probably belonging to a Madagascan species of *Lombardina* (modified from BELTAN, 1968: fig. 27). Below: reconstruction of the parasphenoid of the true *Watsonulus eugnathoides* (modified from BELTAN, 1968: fig. 26 and OLSEN, 1984: fig. 8).

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