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Osteology and phylogenetic relationships of *Congophiopsis lepersonnei* gen. nov. (Halecomorphi, Ionoscopiformes) from the Songa Limestones (Middle Jurassic, Stanleyville Formation), Democratic Republic of Congo

Ostéologie et relations phylogénétiques de *Congophiopsis lepersonnei* gen. nov. (Halecomorphi, Ionoscopiformes) des Calcaires de Songa (Jurassique moyen, Formation de Stanleyville), République Démocratique du Congo

Louis TAVERNE [(*)]

Résumé: L'ostéologie et les relations phylogénétiques de *Congophiopsis lepersonnei* gen. nov., un poisson ionoscopiforme du Jurassique moyen (Calcaires de Songa, Formation de Stanleyville) de Kisangani en République Démocratique du Congo, sont étudiées en détails. *C. lepersonnei* diffère de tous les autres Ionoscopiformes connus par deux caractères importants. Son dermosphénotique et sont autosphénotique occupent une position postérieure et sont suturés uniquement avec le dermoptérotique et non pas avec le frontal. Son premier infraorbitaire (= lacrymal) est réduit, disjoint du maxillaire et il forme un pont entre le premier supraorbitaire et le deuxième infraorbitaire. Au sein des Ionoscopiformes, *C. lepersonnei* appartient à la famille des Ophiopsidae. En effet, il possède un pariétal aussi long que le dermoptérotique, un faible nombre de supraneuraux (moins que 15), des vertèbres dont les faces latérales sont dépourvues de fossettes et des écailles ganoïdes. Parmi les Ophiopsidae, *C. lepersonnei* occupe une position intermédiaire entre le genre plésiomorphe *Ophiopsis*, d'une part, et les genres apomorphes *Archaeosemionotus*, *Macrepistius*, *Teoichthys* et *Ophiopsiella*, d'autre part.

Mots-clés: Ionoscopiformes, Ophiopsidae, *Congophiopsis lepersonnei* gen. nov., ostéologie, relations phylogénétiques, Jurassique moyen, Calcaires de Songa, Formation de Stanleyville, République Démocratique du Congo.

Abstract: The osteology and the phylogenetic relationships of *Congophiopsis lepersonnei* gen. nov., an ionoscopiform fish from the Middle Jurassic (Songa Limestones, Stanleyville Formation) of Kisangani in the Democratic Republic of Congo, are studied in details. *C. lepersonnei* differs from all other known Ionoscopiformes by two important characters. Its dermosphenotic and its autosphenotic are posteriorly located and sutured with only the dermopterotic and not with the frontal. Its reduced first infraorbital (= lacrimal) is disjoined from the maxilla and forms a bridge between the first supraorbital and the second infraorbital. Within Ionoscopiformes, *C. lepersonnei* belongs to the family Ophiopsidae. Indeed, it has the parietal as long as the dermopterotic, a low number of supraneurals (less than 15), the lateral faces of the vertebrae devoid of fossae and ganoid scales. Within Ophiopsidae, *C. lepersonnei* occupies an intermediate position between the plesiomorphic genus *Ophiopsis*, on the one hand, and the apomorphic genera *Archaeosemionotus*, *Macrepistius*, *Teoichthys* and *Ophiopsiella*, on the other hand.

Key words: Ionoscopiformes, Ophiopsidae, *Congophiopsis lepersonnei* gen. nov., osteology, phylogenetic relationships, Middle Jurassic, Songa Limestones, Stanleyville Formation, Democratic Republic of Congo.

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INTRODUCTION

Ionoscopiformes are an order of marine Mesozoic halecomorph fishes. This fossil lineage contains about a dozen of genera ranged in two families, Ionoscopidae and Ophiopsidae. Sometimes, the South American genus *Oshunia* WENZ & KELLNER, 1986 is considered as forming a third family, Oshuniidae (GRANDE & BEMIS, 1998). But more generally, this genus is ranged within Ionoscopidae.

Ionoscopiformes are known from the Middle Triassic to the Early Cretaceous. Their oldest occurrence is located in the Anisian deposits (Middle Triassic) of China, in the Palaeotethys Ocean, with *Robustichthys* XU *et al*., 2014 and *Panxianichthys* XU & SHEN, 2015, two primitive genera (XU et al., 2014; XU & SHEN, 2015). They reach Europe as early as the Ladinian (Late Triassic), with *Archeosemionotus* DEECKE, 1889 and perhaps some other species in need of revision (DEECKE, 1889; DE ALESSANDRI, 1910; LÓPEZ-ARBARELLO *et al*., 2014). During the Jurassic and the Early Cretaceous, Ionoscopiformes spread into the European realm of the Mesogea and adjacent regions. Three genera with various species are present, *Ophiopsis* AGASSIZ, 1834, *Ionoscopus* COSTA, 1853 and *Ophiopsiella* LANE & EBERT, 2015 (STUETZER, 1972; BARTRAM, 1975; GRANDE & BEMIS, 1998; LANE & EBERT, 2012, 2015; among others). That is also during the Early Cretaceous that Ionoscopiformes invade the seas of North, Central and South America. Five American genera are known, *Macrepistius* COPE, 1894, *Oshunia*, *Teoichthys* APPLEGATE, 1988, *Placidichthys* BRITO, 2000, *Quetzalichthys* ALVARADO-ORTEGA & ESPINOSA-ARRUBARRENA, 2008 (SCHAEFFER, 1960, 1971; WENZ & KELLNER, 1986; APPLEGATE, 1988; MAISEY, 1991a, 1999; BRITO, 2000; ALVARADO-ORTEGA & ESPINOSA-ARRUBARRENA, 2008; BRITO & ALAVARADO-ORTEGA, 2008; MACHADO *et al*., 2013).

DA SILVA SANTOS & VALENCA (1968) mentioned *Ophiopsis* in the Early Cretaceous of Brazil. But the presence of this genus in South America is highly doubtful (MAISEY, 1991b; BRITO, 2000; LANE & EBERT, 2015). A possible Early Cretaceous Australian ionoscopiform fish, *Canaryichthys* BARTHOLOMAI, 2015 has been recently described but only its braincase is known (BARTHOLOMAI, 2015). A few other genera, *Callopterus* THIOLLIÈRE, 1858, *Brachyichthys* WINKLER, 1861, *Osteorhachis* EGERTON, 1868, *Heterolepidotus* EGERTON, 1872, *Spathiurus* DAVIS, 1887 and *Neorhombolepis* WOODWARD, 1888 have been cited as possible ionoscopiform candidates but they need all to be re-studied before their eventual inclusion in the order. "*Furo*" *longiserratus* (AGASSIZ, 1843) from the Late Jurassic of Germany, with its strongly marked maxillary sensory canal (LAMBERS, 1998: fig. 2), is very probably also an ionoscopiform fish.

The aim of the present paper is to study in a detailed way and to precise the systematic position of a new ionoscopiform genus from the Songa Limestomes, one of the most basal layers of the Stanleyville Formation (Aalenian-Bathonian, Middle Jurassic, cf. COLIN, 1994) in the Democratic Republic of Congo. This fossil fish was previously described as *Ophiopsis lepersonnei* DE SAINT-SEINE, 1950 (DE SAINT-SEINE, 1950; DE SAINT-SEINE & CASIER, 1962) and was later ranged in the genus *Ophiopsiella* (LANE & EBERT, 2015). However, both generic attributions are erroneous (see "Discussion, point 2"). This new genus is the only occurrence of an ionoscopiform fish in Africa (LÓPEZ-ARBARELLO *et al*., 2008) and in a continental environment. Indeed, the Songa Limestones are now considered as deposits from a Jurassic salt lake and no more from a Congolese interior sea (TAVERNE, 2011a).

The present paper is the ninth of a series dealing with the revision of the Middle Jurassic ichthyofauna from the Stanleyville Formation in the Democratic Republic of Congo (TAVERNE, 1975, 2001, 2011a, b, c, 2014a, b, in press).

MATERIAL AND METHODS

The specimens hereafter described belong to the paleontological collection of the Department of Geology 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. Aspersions with ethanol were used to improve the observations.

List of abbreviations used in the text-figures

AN	=	angular
ANT	=	antorbital
ASPH	=	autosphenotic
BRSTG	=	branchiostegal ray
CBR	=	ceratobranchial
CHY	=	ceratohyal
CLT	=	cleithrum
DETH	=	dermethmoid (= rostral)
DN	=	dentary
DPTE	=	dermopterotic
DSPH	=	dermosphenotic
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
IOP	=	interopercle
IORB 1-4	=	infraorbitals 1 to 4
LEP	=	fin ray (= lepidotrichia)
LETH	=	lateral ethmoid
MX	=	maxilla
NA	=	nasal
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PCLT 1-3	=	postcleithra 1 to 3
PMX	=	premaxilla
POP	=	preopercle
PORB	=	postorbitals (= suborbitals)
PS	=	parasphenoid
PSPH	=	pleurosphenoid
PT	=	posttemporal
QU	=	quadrate
RAD 1-18	=	dorsal pterygiophores (= radials) 1 to 18
RART	=	retroarticular
SAN	=	surangular
SC	=	scale
SCA	=	hypercoracoid (= scapula)
SCU	=	caudal scute
SMX	=	supramaxilla
SOP	=	subopercle
SORB 1-3	=	supraorbital 1 to 3
ST	=	supratemporal (= extrascapular)
SY	=	symplectic
V	=	vertebral centrum
VO	=	vomer
a.	=	anterior
ant. c.	=	antorbital sensory commissure
b. cy.	=	vertebral bony cylinders surrounding the notochord
b. fu.	=	basal fulcra
ch.	=	notochord
ex. c.	=	extrascapular sensory canal
fr. fu.	=	fringing fulcra

iorb. c.	=	infraorbital sensory canal
l.	=	left
l. l. c.	=	lateral line sensory canal
m. c.	=	mandibular sensory canal
mx. c.	=	maxillary sensory canal
ot. c.	=	otic (= postorbital) sensory canal
p.	=	posterior
p. l.	=	pit-line
r.	=	right
sorb. c.	=	supraorbital sensory canal

SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii KLEIN, 1885
Series Neopterygii REGAN, 1923
Division Holostei MÜLLER, 1845
Subdivision Halecomorphi COPE, 1871
Order Ionoscopiformes GRANDE & BEMIS, 1998
Family Ophiopsidae BARTRAM, 1975
Genus ***Congophiopsis*** gen. nov.

Diagnosis (autapomorphies indicated with an asterisk)

Small to medium-sized Ophiopsidae characterized by the following unique combination of features. Small dermethmoid (= rostral) with lateral horns. Parietal equal in length to the dermopterotic. Toothed jaws with strong conical teeth. Maxilla not reaching the level of the posterior border of the orbit. One large supramaxilla. Four infraorbitals. Three supraorbitals, the first one enlarged. Antorbital not reaching the orbit. *Reduced first infraorbital (= lacrimal) dorsally located, separated from the maxilla, and forming a bridge between the second infraorbital and the first supraorbital. *Second infraorbital reaching the premaxilla. A notch in the ventral margin of the second infraorbital for the supramaxilla. Large third infraorbital. Small fourth infraorbital inclined posterodorsally. Postorbitals (= suborbitals) well developed. *Dermosphenotic and autosphenotic posteriorly located and sutured with the dermopterotic only. Crescent-like preopercle reaching dorsally the skull roof lateral margin. Pectoral fin with 14 rays, no fringing fulcra. Ventral fin with 6 rays and a few fringing fulcra. Origin of ventral fin located at the bottom of 16th scale row. Vertebrae composed of two bony cylinders surrounding the notochord and devoid of lateral fossae. About 10 supraneurals. Dorsal fin with 3 basal fulcra and 18 principal rays, without fringing fulcra. Origin of dorsal fin located at the top of the 18th scale row. Origin of anal fin located at the bottom of the 25th scale row. Caudal fin forked, with about 18 principal rays. Fringing fulcra in the dorsal lobe. Scales thick, rhomboid, with a serrated posterior border, as deep as long on the flanks, longer than deep ventrally. 47 scales along the lateral line. 20 scales in a vertical row at the maximum body depth. Lateral line sensory canal not prolonged into the caudal fin rays.

Derivatio nominis

The generic name refers the Democratic Republic of Congo and to *Ophiopsis*, the genus in which the fossil fish was originally ranged.

Species : ***Congophiopsis lepersonnei*** (DE SAINT-SEINE, 1950)

Diagnosis

The same as the genus (by monospecificity).

Holotype

MRAC RG N° 2979: a nearly complete large specimen (right face, a small part of the caudal fin is missing) (Fig. 1). Total length: 161 mm.

Paratype

MRAC RG N° 8518: a nearly complete small specimen (left face, a great part of the caudal fin is missing) (Fig. 2). Total length: 70 mm.

Other material

MRAC RG N° 8107a, b: part and counterpart of a small incomplete specimen. The snout and the caudal fin are missing. Length: 60 mm.

MRAC RG N° 8546a, b: part and counterpart of a large incomplete specimen. The head and a great part of the caudal fin are missing. Length: 105 mm.

Formation and locality

Songa Limestones (Stanleyville Formation), Lualaba river, 55 km South-East of Kisangani, Democratic Republic of Congo.

Morphometric data (Fig. 3)

The morphometric data are based on the holotype, the best and the more completely preserved specimen, and are given in percentage (%) of its standard length (137 mm).

Head length (with opercle) ……. 25.5 %
Head depth (in the occipital region) ……... 21.9 %
Maximum body depth (between the head and the dorsal fin) …… 26.3 %
Body depth at the dorsal fin level …….. 21.9 %
Caudal peduncle depth ……... 13.9 %
Predorsal length ……. 48.2 %
Prepelvic length ……. 56.9 %
Preanal length …… 74.5 %

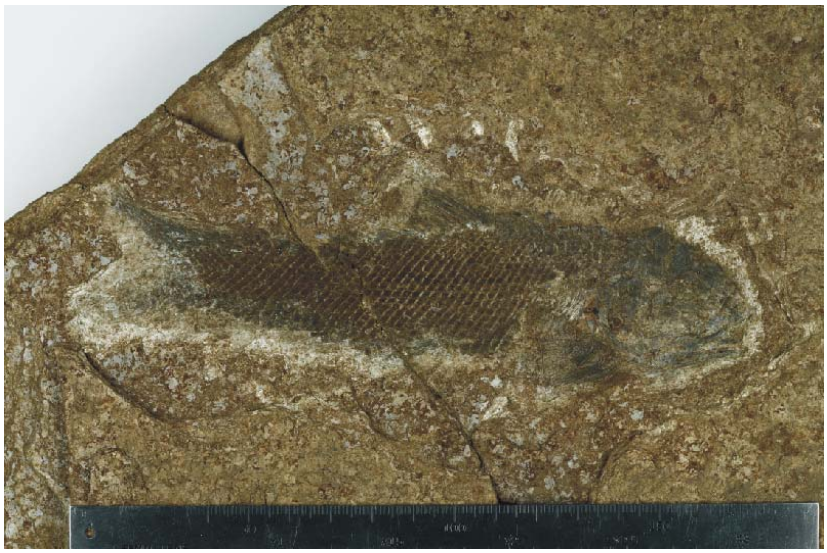

Figure 1. *Congophiopsis lepersonnei* gen. nov. Holotype MRAC RG 2979 (copyright Africamuseum).

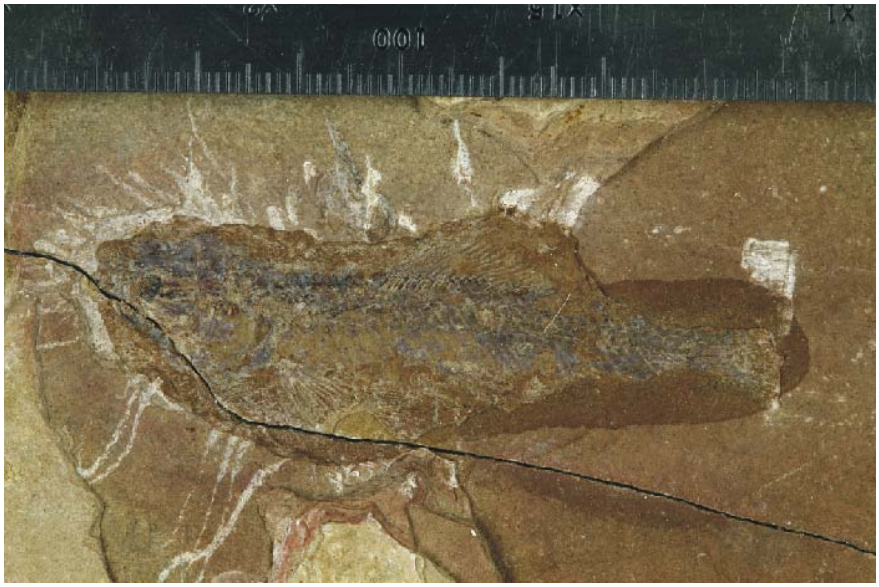

Figure 2. *Congophiopsis lepersonnei* gen. nov. Paratype MRAC RG 8518 (copyright Africamuseum).

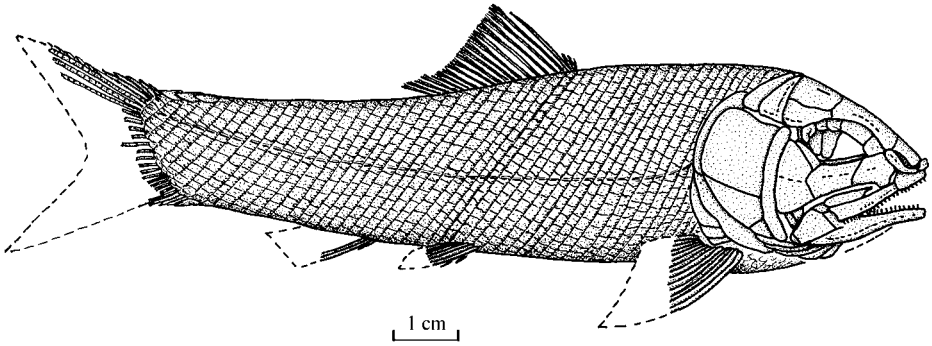

Figure 3. *Congophiopsis lepersonnei* gen. nov. Genral reconstruction. The scale refers to holotype MRAC RG 2979.

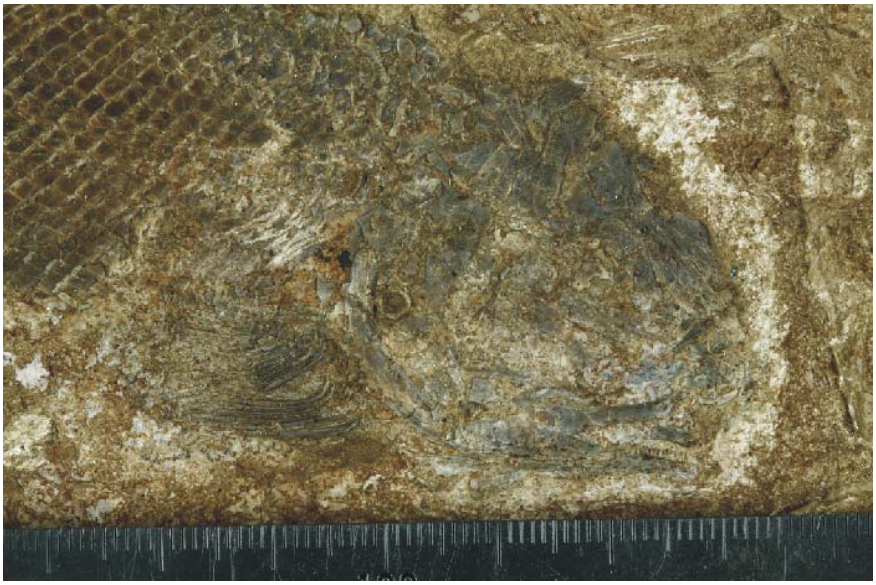

Figure 4. *Congophiopsis lepersonnei* gen. nov. Head region of holotype MRAC RG 29 (copyright Africa Museum).

Osteology

The skull (Figs 4-10)

The bones of the skull roof are rather thick, with a layer of ganoin. They are feebly ornamented with some poorly marked tubercles.

The dermethmoid (= rostral) is preserved on the holotype. It is a small, V-shaped bone with a pair of short lateral horny process. No endochondral component of the mesethmoid is present, this region remaining cartilaginous in Ionoscopiformes (MAISEY, 1999: fig. 1A, B) as in Amiidae. A small part of the right lateral ethmoid is visible on the holotype, between the first infraorbital and the nasal. On the holotype, the left nasal is not present. Its right nasal is displaced due to the fossilisation and is seen by its lateral margin. That orientation gives a false narrower aspect to the bone. However, a part of the left nasal is visible in dorsal view on the paratype. The bone is rather large and reaches the mid-line, separating the dermethmoid from the frontals. The anterior part of the right vomer is visible on the holotype, the posterior part of the bone being covered by the right frontal.

The frontals are elongated. They have a marked constriction between the orbits, as usual in ionoscopiform fishes. The supraorbital sensory canal lies along the external margin of the frontal. The parietals are large bones meeting on the mid-line. They are a little longer than wide. A sagittal pit-line is visible on the right parietal of the paratype. The same region is damaged on the right parietal of the holotype, the bone being fissured. The dermopterotics bears the otic (= postorbital) sensory canal and have the same length as the parietals. The right autosphenotic is visible on the holotype. The bone forms a sort of large ventral spur appended to the posterior region of the dermopterotic. The supratemporals (= extrascapulars) are large triangular-shaped bones with a broad lateral margin. The two bones meet on the mid-line. The supratemporal bears the extrascapular sensory commissure and the beginning of the lateral line sensory canal.

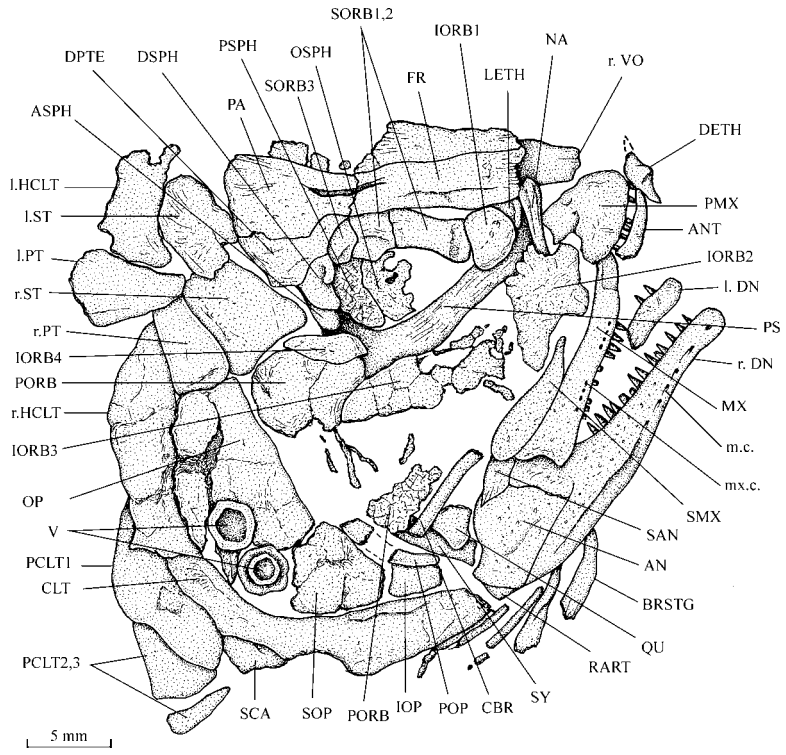

Figure 5. *Congophiopsis lepersonnei* gen. nov. Skull of holotype MRAC RG 2979.

The sphenoid bones are visible on the holotype. The orbitosphenoid and the pleurosphenoids are located in the posterior part of the orbit. They reach the parasphenoid ventraly. There is no contact between the orbitosphenoid and the lateral ethmoid. The trabecular portion of the parasphenoid is long, broad and toothless.

The articular head is the only preserved part of the quadrate on the holotype. It covers a part of the strong rod-like symplectic. Both the quadrate and the symplectic are articulated with the lower jaw. The pterygoid bones and the palatine are not visible.

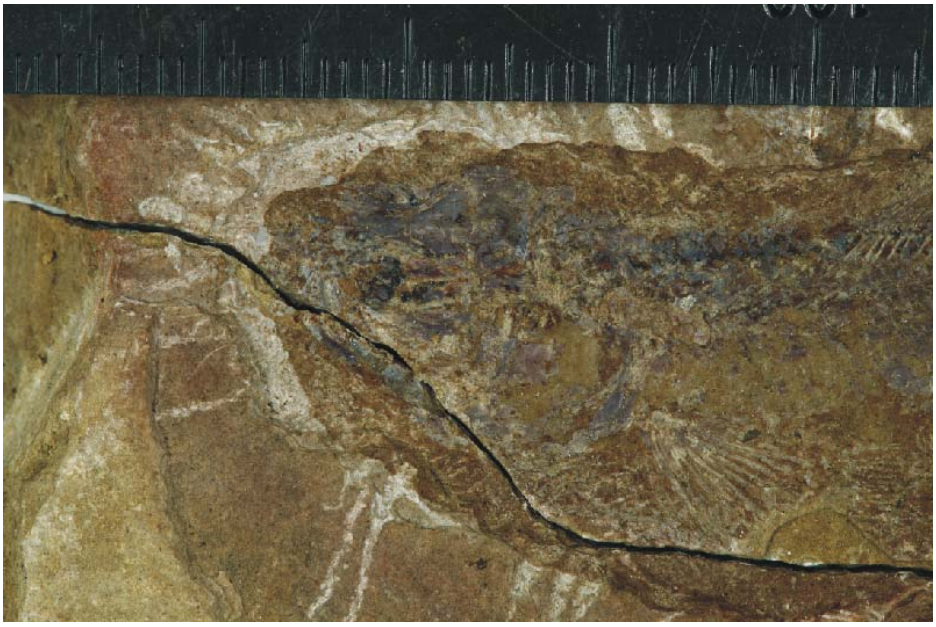

Figure 6. *Congophiopsis lepersonnei* gen. nov. Head region of paratype MRAC RG 8518 (copyright Africamuseum).

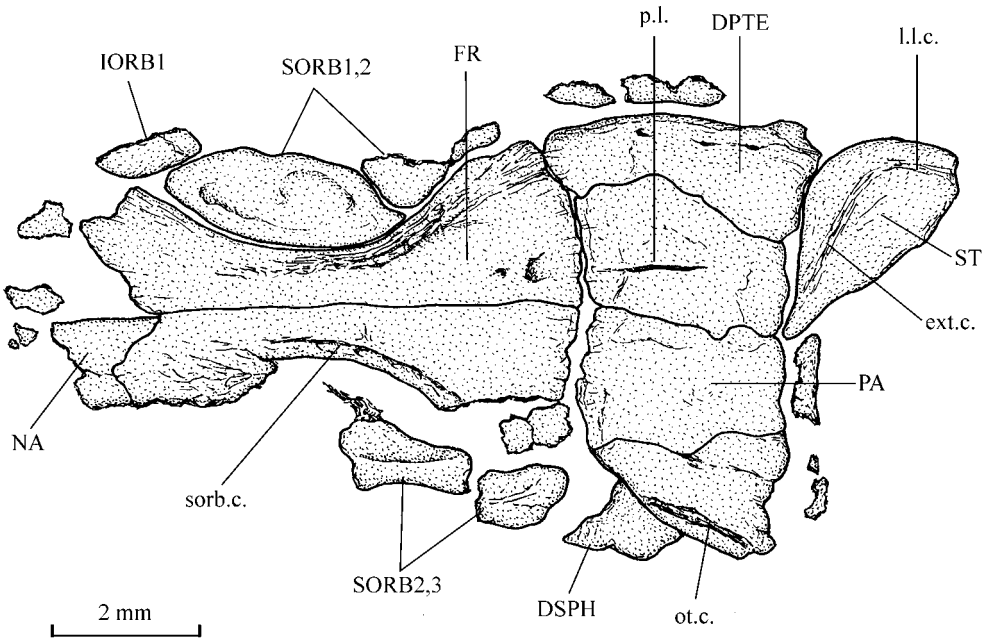

Figure 7. *Congophiopsis lepersonnei* gen. nov. Skull roof of paratype MRAC RG 8518.

The jaws are toothed. The teeth are conical and rather robust. The upper jaw contains the premaxilla, the maxilla and one supramaxilla. The premaxilla is a large bone that bears a well developed wing-like nasal process. The maxilla is moderately elongate and much shorter than the lower jaw. The bone is deeper posteriorly than anteriorly. It does not reach the level of the orbit posterior border. Its anterior extremity bears an external facet that articulates with the inner face of the premaxilla. The posterior margin of the maxilla is concave. The dorsal border of the bone is more or less rectilinear and there is no notch for the supramaxilla. A series of small pores located all along the ventral border of the bone indicates the presence of a maxillary sensory canal. The supramaxilla is long and represents the half of the maxilla length. The lower jaw is elongated and is formed by the dentary, the angular, a small surangular and an autogenous retroarticular. The articular, the prearticular and the coronoids, located on the inner face of the mandible, are not visible. The toothed part of the dentary is narrow but the posterior region of the mandible deepens abruptly. The articulation with the quadrate and the symplectic is positioned at the level of the posterior margin of the orbit.

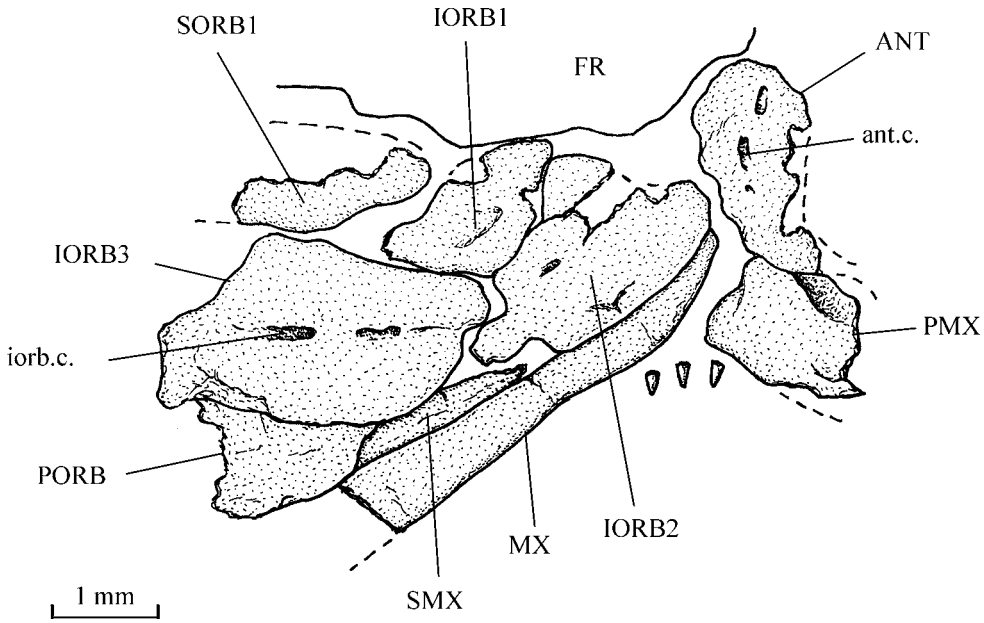

Figure 8. *Congophiopsis lepersonnei* gen. nov. Snout region of specimen MRAC RG 8107a.

The orbital bony ring contains three supraorbitals, the antorbital, four infraorbitals, the dermosphenotic and some postorbitals (= suborbitals). The first supraorbital is much larger the two posterior elements of the series. The dermosphenotic is incorporated into the skull roof. It is a small bone sutured to lateral margin of the dermopterotic and located just behind the third supraorbital. The bone bears a ventral flange that covers a part of the autosphenotic. The preservation is not good enough to see the presence of a sensory canal on the bone. The ventral tubular part of the antorbital is preserved on the holotype but the remaining portion of the bone is missing on this specimen. However, the enlarged dorsal region of the bone is visible on sample MRAC RG N° 8107a. This upper part of the bone bears some pores of the antorbital sensory canal. The antorbital does not reach the orbit. The first infraorbital is rather small and more or less ovoid. It has no contact with the maxilla and is located much more dorsally, above the second infraorbital, forming a sort of bridge between this second infraorbital and the first supraorbital. The second infraorbital is a larger bone that occupies a more anterior position than in other ionoscopiform fishes. It lies on the maxilla just behind the premaxilla. The ventral margin of the bone bears a large notch for the supramaxilla. Such a notch for the supramaxilla in the ventral border of the second infraorbital is known in a few ionoscopiform fishes (ALVARADO-ORTEGA & ESPINOSA ARRUBARRENA, 2008: fig. 5;

LÓPEZ-ARBARELLO *et al*., 2014: fig. 6; LANE & EBERT, 2015: fig. 9B). The third infraorbital is a very large bone but severely crushed and incomplete on the three available specimens. The fourth infraorbital is much smaller, elongated, more or less triangular and its posterior margin, sutured to the postorbital, is obliquely oriented. The postorbitals (= suborbitals) cover a wide area before the preopercle. The dorsal postorbital is a rather large bone. More ventrally, the bone is very crushed and fragmented. It is not possible to know if there are fragments of one or two large ventral postorbitals or if there is a mosaic of small bones as in *Teoichthys* (APPLEGATE, 1988: fig. 5; MACHADO *et al*., 2013: fig. 2B, D). No sclerotic bone is present.

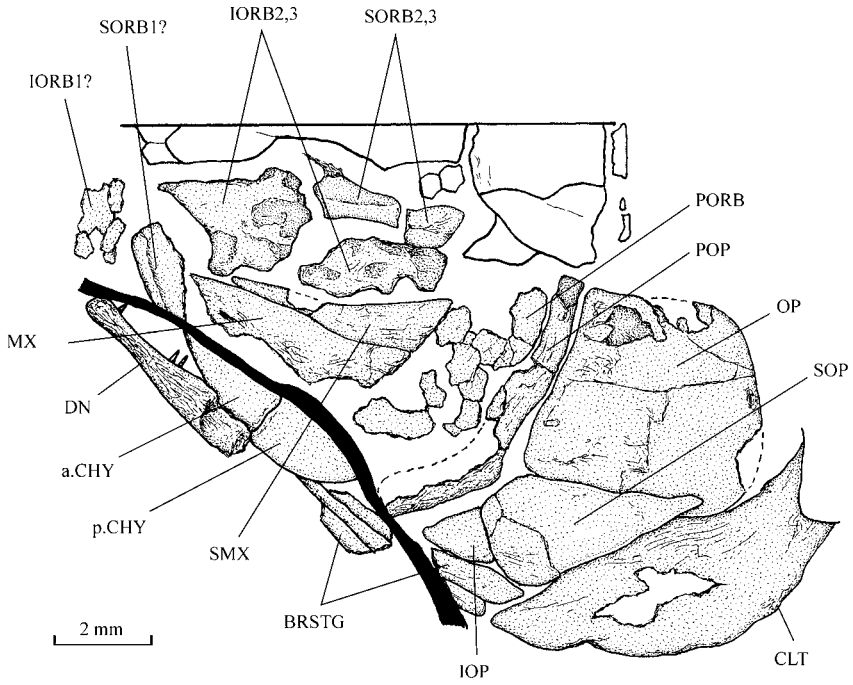

Figure 9. *Congophiopsis lepersonnei* gen. nov. Suspensorium of paratype MRAC RG 8518.

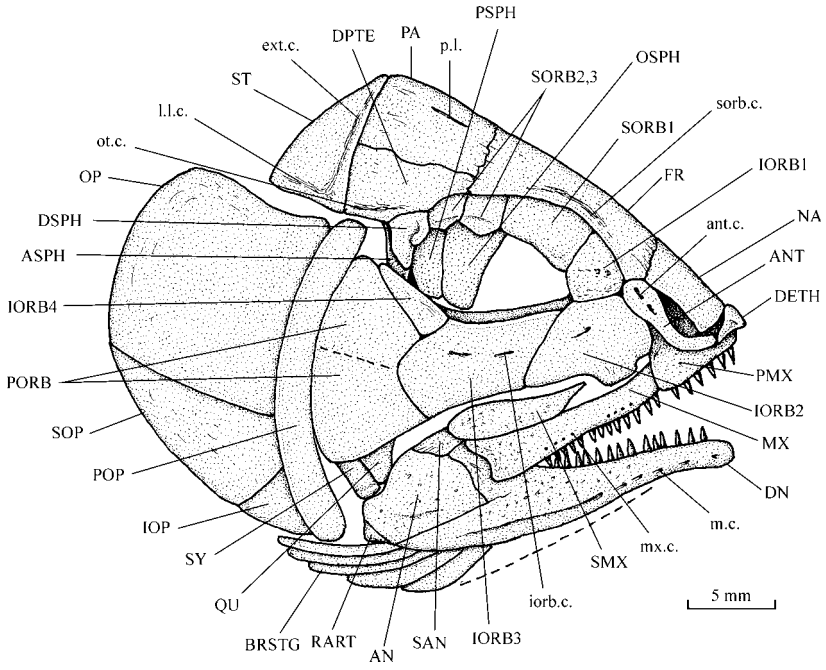

Figure 10. *Congophiopsis lepersonnei* gen. nov. Reconstruction of the skull in right lateral view. The scale refers to holotype MRAC RG 2979.

The preopercle is well visible on the paratype though severely crushed. It is a long, narrow and crescent-shaped bone. On the holotype, only two small fragments of the ventral extremity of the bone are preserved. The opercle is large and as deep as long. On the holotype, the posterior border of the opercle is lost, giving a false narrower shape to the bone. The subopercle is well developed, triangle-in-shape, with a broad anterior margin and an acuminate posterior corner. The interopercle is a small triangular bone. The gular plate is not preserved. Fragments of some branchiostegal rays are visible on the holotype and the paratype.

The hyoid and branchial skeleton (Figs 6, 9)

A large part of the hyoid bar is present on the paratype, with a portion of the anterior ceratohyal and the complete posterior ceratohyal. The symplectic and a rod-like fragment of a ceratobranchial are visible on the holotype.

The girdles (Figs 6, 9, 11, 12)

The posttemporal is triangular in shape and deeper than broad. The hypercleithrum (= supracleithrum) is a large elongated element positioned behind the posttemporal and the opercle. The cleithrum is a massive bone, with a short dorsal branch and a long and broad ventral branch. There are three postcleithra. The dorsal one is the larger and the ventral one the smaller. The scapula is preserved on the holotype. The pectoral fin has 14 rays that are unbranched and unsegmented in their proximal region but the most distal part of the rays is missing in all specimens. The fin is devoid of fringing fulcra.

On the holotype, the ventral fins origin is located at the bottom of the 16th row of scales and the fin contains 6 rays, the first two being much broader than the following four. Two fringing fulcra are visible.

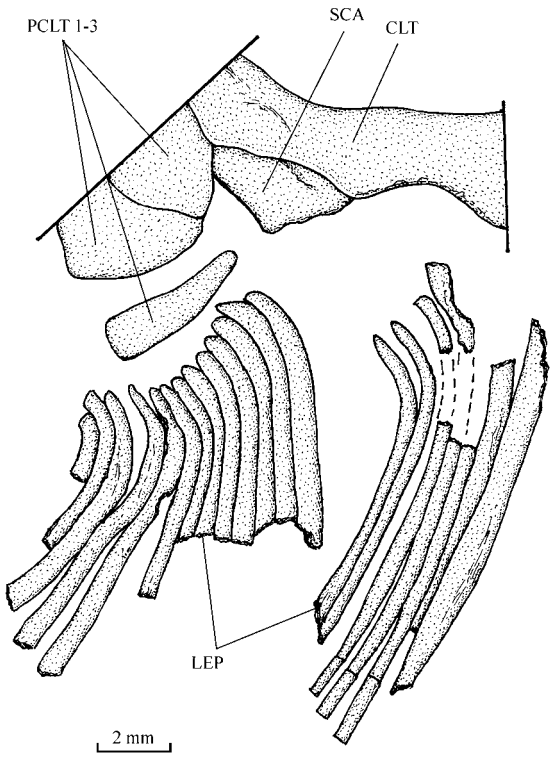

Figure 11. *Congophiopsis lepersonnei* gen. nov. Pectoral fins of holotype MRAC RG 2979

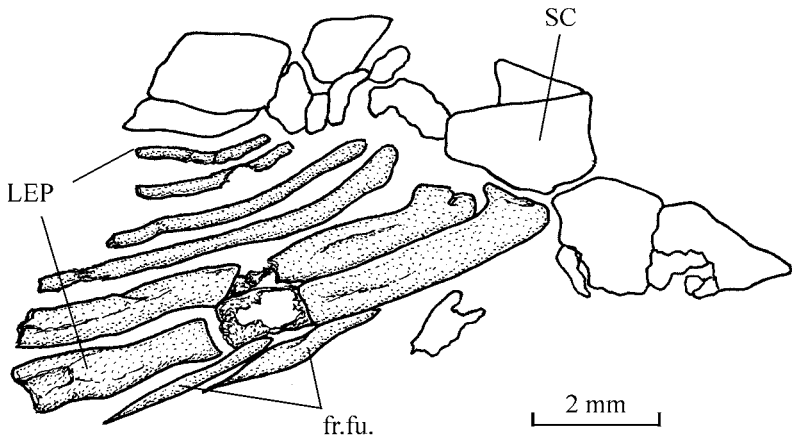

Figure 12. *Congophiopsis lepersonnei* gen. nov. Ventral fin of holotype MRAC RG 2979.

The axial skeleton (Fig. 13)

The axial skeleton or at least its major part is hidden by the scales on the four available specimens. The number of vertebra is not determinable as is unknown the possible presence of the diplospondyly in the caudal region of the fish. One of the first vertebrae is displaced under the opercle on the holotype and is seen by its anterior or posterior face. This vertebra shows that the notochord is surrounded by two concentric bony cylinders. Bartram (1975: 192, fig. 3A) considered the internal bony layer as a chordacentrum and the external one as an arcocentrum. But more generally, the internal cylinder is seen as a perichordal ossification. The few visible vertebrae have smooth lateral faces devoid of any fossa.

Traces and fragments of 8 supraneurals are visible on the holotype, between the pectoral girdle and the dorsal fin. The total number of supraneurals probably was around 10.

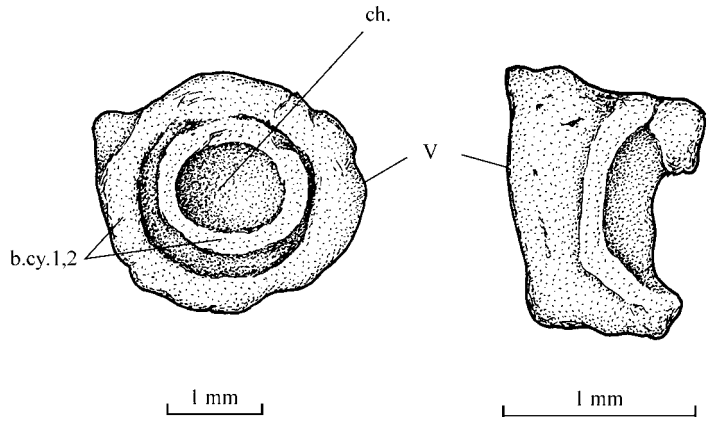

Figure 13. *Congophiopsis lepersonnei* gen. nov. Vertebral centrum of holotype MRAC RG 2979 in anterior or posterior view (left) and of specimen MRAC RG 8107b in right lateral view (right).

The dorsal and anal fins (Figs 14, 15)

On the holotype, the dorsal fin origin is located at the top of the 18th row of scales, well before the level of the ventral fins origin. The dorsal fin is better preserved on the paratype than on the holotype. There are 18 pterygiophores that support 3 short spiny rays (= basal fulcra) and 18 principal rays. The fin is devoid of fringing fulcra. The first pterygiophore is the largest of the series

and it bears the three spiny rays and the first principal ray. This first principal ray is shorter than the following ones. The principal rays are segmented at their distal extremities. At least the last rays are branched.

Only the holotype has preserved a small part of the anal fin. One basal fulcrum and long fragments of the first two principal rays are visible. The anal fin origin is positioned at the bottom of the 25th row of scales. There is no trace of fringing fulcra.

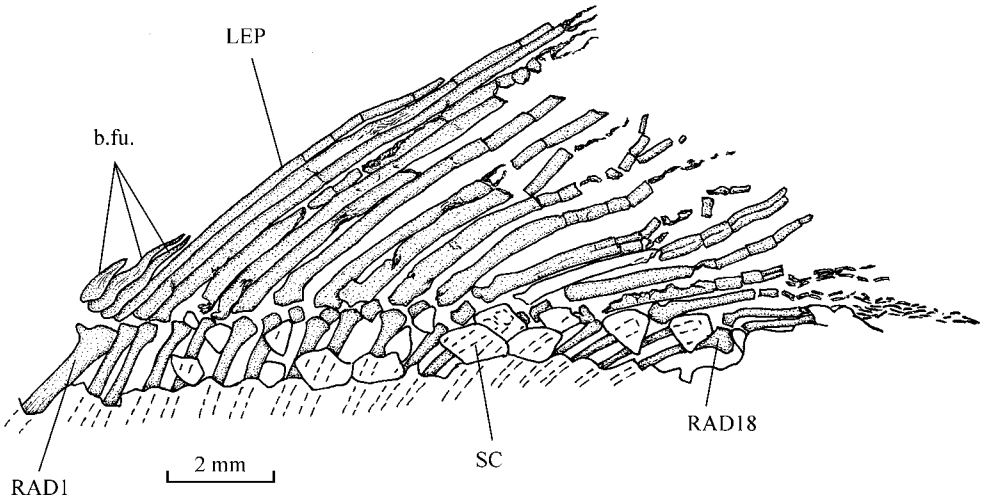

Figure 14. *Congophiopsis lepersonnei* gen. nov. Dorsal fin of paratype MRAC RG 8518.

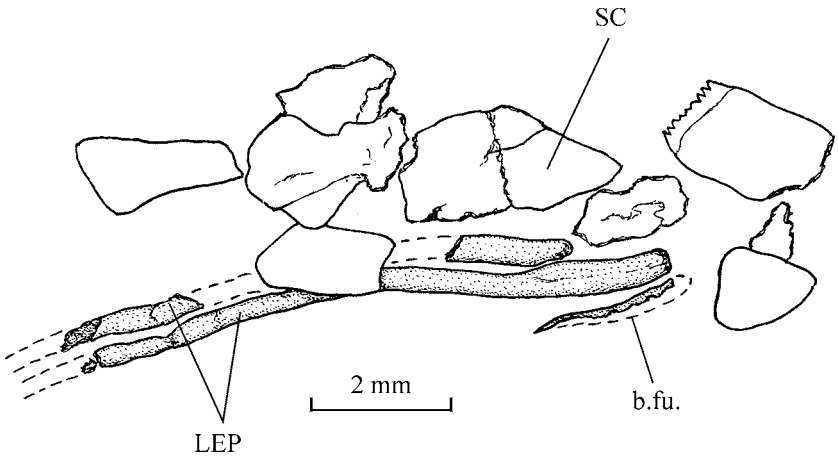

Figure 15. *Congophiopsis lepersonnei* gen. nov. Beginning of the anal fin of holotype MRAC RG 2979.

The caudal skeleton and the tail (Fig. 16)

The caudal skeleton is unknown, being hidden by the scales on the four available specimens. The caudal fin is forked but always badly and incompletely preserved. The number of principal caudal rays is around 18. On the holotype, the dorsal limb begins with 3 caudal scutes and a few basal fulcra. There is a series of fringing fulcra along the most external principal ray of this dorsal lobe.

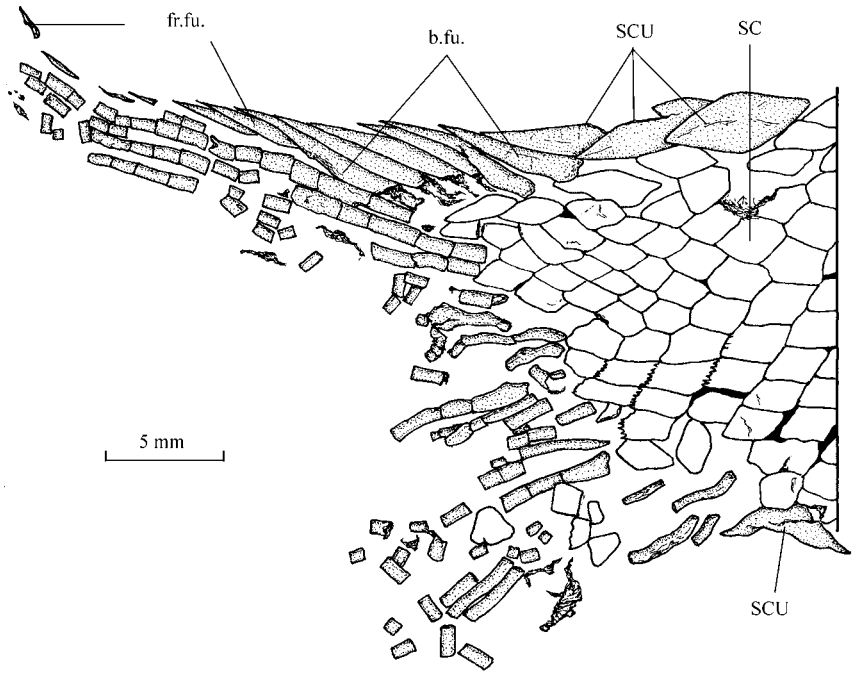

Figure 16. *Congophiopsis lepersonnei* gen. nov. Caudal fin of holotype MRAC RG 2979.

The squamation (Fig. 17)

The body is entirely covered by small, thick, rhomboid ganoid scales. The surface is smooth, except near the dorsal and the ventral borders where a few very thin ridges are often visible. The posterior margin is serrated. The flank scales are as deep as long. But ventrally, the scales become longer than deep. There are 47 scales along the lateral line on the holotype and 20 and 13 scales in a vertical row respectively just before the dorsal fin and on the caudal peduncle. A canal is visible on the scales that bear the lateral line. This lateral line is not continued by a chain of small ossicles in the dorsal lobe of the caudal fin as it is the case in some ionoscopiform fishes (BARTRAM, 1975: fig. 6; among others).

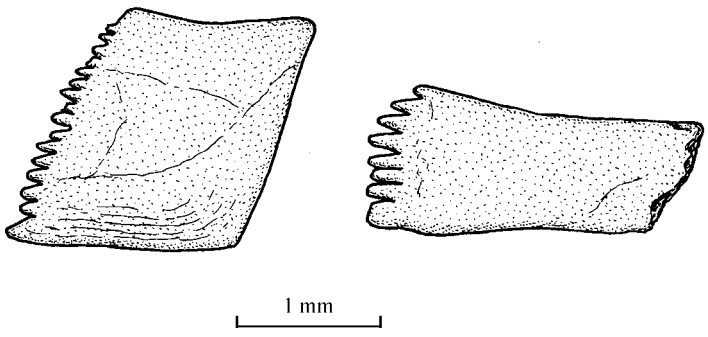

Figure 17. *Congophiopsis lepersonnei* gen. nov. Scales of holotype MRAC RG 2979.
Left: a scale from the abdominal region at the level of the dorsal fin.
Right: a scale from the ventral area of the abdominal region near the ventral fin.

DISCUSSION

The systematic position of *Congophiopsis lepersonnei* within Neopterygii

Congophiopsis lepersonnei exhibits the three synapomorphies that support the monophyly of Halecomorphi, *i. e.*, a concave notch in the posterior margin of the maxilla, a supramaxilla and a double articulation for the mandible (GRANDE & BEMIS, 1998). The Congolese fish also possesses the two synapomorphies that characterize the lineage grouping *Cipactlichthys* BRITO & ALVARADO-ORTEGA, 2013, Amiiformes and Ionoscopiformes, *i. e.*, a V-shaped dermethmoid with lateral horns and a crescent-shaped preopercle. It presents the synapomorphy of the amiiform-ionoscopiform assemblage, the presence of a dermosphenotic sutured to the skull roof (GRANDE & BEMIS, 1998; BRITO & ALVARADO-ORTEGA, 2013). *Congophiopsis lepersonnei* has also a sensory canal on the maxilla [(*)] and an innerorbital flange on the dermosphenotic, two typical characters of Ionoscopiformes (ALVARADO-ORTEGA & ESPINOSA-ARRUBARRENA, 2008; LANE & EBERT, 2012, 2015; LÓPEZ-ARBARELLO *et al*., 2014; etc.), an order in which the Congolese fossil fish can be confidently ranged, as was already done by DE SAINT-SEINE (1950) and DE SAINT-SEINE & CASIER (1962).

Congophiopsis, *Ophiopsis* and *Ophiopsiella*

As previously written, *Congophiopsis lepersonnei* was originally described as belonging to *Ophiopsis* (DE SAINT-SEINE, 1950; DE SAINT-SEINE & CASIER, 1962), a well known European genus. However, *Ophiopsis* is now split into two different genera. Today, *Ophiopsis* contains only its type-species, *Ophiopsis* ("*Furo*") *muensteri* AGASSIZ, 1834 from the Late Jurassic of Germany and France (LANE & EBERT, 2012, 2015). The other species previously ranged in this genus, *O. lepersonnei* included, are now transferred to the new genus *Ophiopsiella* (LANE & EBERT, 2015). A short comparison of the Congolese ionoscopiform fish with these two genera is thus necessary to see if it can be effectively ranged in one of these two generic taxons. Data on *Ophiopsis* and *Ophiopsiella* hereafter cited come from LAMBERS (1998) and LANE & EBERT (2012, 2015).

Both European genera exhibit a very large first infraorbital located before the second infraorbital and lying on the maxilla. Their dermosphenotic is sutured with the frontal lateral margin or at the junction between the frontal and the dermopterotic. Their dorsal and anal fins possess fringing fulcra. Moreover, *Ophiopsis* has an elongate body, 61 scales along the lateral line, only two supraorbitals, 26 or 27 scales in vertical row at the maximum body depth level, only 12 principal rays in the dorsal fin and its antorbital reaches the orbit. *Ophiopsiella* has a series of small ossicles that continues the sensory lateral line into the caudal fin.

For all these characters, the Congolese ionoscopiform completely differs from *Ophiopsis* or *Ophiopsiella*. It is clear that it does not belong to these two genera.

The generic validity of *Congophiopsis*

Congophiopsis also differs from all other known ionoscopiform fishes by at least two remarkable characters. Data used hereafter and concerning these two characters in Ionoscopiformes come from SCHAEFFER (1960), APPLEGATE (1988), MAISEY (1991a), LAMBERS (1998), GRANDE & BEMIS (1998), BRITO (2000), ALVARADO-ORTEGA & ESPINOSA-ARRUBARRENA (2008), LANE & EBERT (2012, 2015), BRITO & ALVARADO-ORTEGA (2013), MACHADO *et al.* (2013), LÓPEZ-ARBARELLO et al. (2014), XU *et al*. (2014) and XU & SHEN (2015).

[(*)] A sensory canal on the maxilla is one of the major apomorphies of Ionoscopiformes. No other holostean fish exhibits such a character. However, a maxillary pit-line is present in the semionotid *Lepidotes elvensis* (BLAINVILLE, 1818) from the Lower Jurassic of Germany (THIES, 1989). In Lepisosteidae, the highly specialized and fragmented maxilla captures the infraorbital sensory canal, forming a bridge between the first infraorbital (= lacrimal) and the antorbital (GRANDE, 2010) but that is not a real maxillary sensory canal different from the infraorbital canal as in ionoscopiform fishes.

The wide second infraorbital reaches the premaxilla. The first infraorbital is reduced and has no more contact with the maxilla. The bone is located more dorsally, forming a bridge between the first supraorbital and the second infraorbital. In Ionoscopiformes, the first infraorbital is a large element, lying on the maxilla and separating the premaxilla from the second infraorbital. There is only one exception, the ionoscopid *Quetzalichthys*. This genus exhibits a large first infraorbital that reaches the maxilla in only one point and that is located between the first supraorbital and the second infraorbital (ALVARADO-ORTEGA & ESPINOSA-ARRUBARRENA, 2008: fig. 5).

The autosphenotic and dermosphenotic are sutured to the lateral margin of the dermopterotic and do not contact the frontal. That is a more posterior position than in other ionoscopiform fishes where the dermosphenotic is sutured to the lateral margin of the frontal or at the junction between the frontal and the dermopterotic.

These two characters amply justify the peculiar generic status of *Congophiopsis*.

The relationships of *Congophiopsis lepersonnei* within Ionoscopiformes

Congophiopsis lepersonnei has the parietal as long as the dermopterotic, a low number of supraneurals (less than 15), the lateral faces of the vertebrae devoid of fossae and ganoid scales. These four characters clearly place the Congolese fish in the family Ophiopsidae.

Ionoscopidae have the parietal shorter than the dermopterotic, 15 or more supraneurals, the vertebrae ornamented with lateral fossae and their scales are amioid-like.

The systematic position of *Congophiopsis lepersonnei* within Ophiopsidae

The phylogenetic relationships within Ionoscopiformes have been investigated several times in the recent years (ALVARADO-ORTEGA & ESPINOSA-ARRUBARRENA, 2008: fig. 8; LÓPEZ-ARBARELLO *et al*., 2014: fig. 10; XU & SHEN, 2015: fig. 6). I use hereafter the ionoscopiform phylogeny proposed by XU & SHEN (2015) that is the most recent and most complete provided today. However, I add to their scheme *Archaeosemionotus*, a genus that these two authors do not take in account. The skull of the ophiopsid *Placidichthys* is insufficiently known because a bad preservation and this genus can not be included in the discussion.

Ophiopsis is considered as the most plesiomorphic Ophiopsidae. This fish still possesses an antorbital that contributes to the orbital margin and a low second infraorbital (LANCE & EBERT, 2012: fig. 4B). *Congophiopsis* and the four remaining ophiopsid genera have a smaller antorbital that does not reach the orbit and a deeper second infraorbital. *Archaeosemionotus*, *Macrepistius*, *Teoichthys* and *Ophiopsiella* share a very peculiar character not present in *Ophiopsis* and *Congophiopsis*. A series of small scale-like ossicles extends the lateral line sensory canal between the rays of the caudal fin dorsal lobe (BARTRAM, 1975: fig. 6; APPLEGATE, 1988: fig. 7A; LÓPEZ-ARBARELLO *et al*., 2014: fig. 9).

Thus, within Ophiopsidae, *Congophiopsis* occupies an intermediate position between the plesiomorphic *Ophiopsis*, on the one hand, and the apomorphic *Archaeosemionotus*, *Macrepistius*, *Teoichthys* and *Ophiopsiella*, on the other hand.

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