



**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**

**Ostéologie et relations de *Kisanganichthys casieri* gen. et sp. nov. (Teleostei, Catervariolidae) du Jurassique moyen (Formation de Stanleyville) de Kisangani (R.D.Congo)**  
**Commentaires sur la position systématique des Catervarioliformes.**

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**Résumé :** L'ostéologie de *Kisanganichthys casieri* gen. et sp. nov., un petit poisson catervariolidé de la Formation de Stanleyville (Jurassique moyen), Kisangani, République Démocratique du Congo, est étudiée en détails. *K. casieri* gen. et sp. nov. possède une paire de petits latérodermethmoïdes triangulaires dentés qui sont situés à la symphyse de la mâchoire supérieure, avec les prémaxillaires dentés positionnés plus latéralement. Les frontaux présentent une large extrémité antérieure qui est suturée avec le dermethmoïde (= rostral). Il n'y a qu'un supramaxillaire. Les nasaux sont séparés l'un de l'autre par le dermethmoïde et de l'orbite par l'anthorbitaire. Il y a deux supraorbitaires et deux vastes postorbitaires (= suborbitaires). Le préoperculaire montre une forme en croissant avec une très courte partie dorsale. Le sous-operculaire est beaucoup plus grand que l'operculaire. Parmi les Catervariolidae, *K. casieri* gen. et sp. nov. semble être apparenté de plus près à *Songanella callida* qu'à *Catervariolus hornemani*. Les relations systématiques des Catervariolidae au sein des lignées « pholidophoriformes » sont rediscutée et une position basale est confirmée.

**Mots-clés:** Teleostei, Catervariolidae, *Kisanganichthys casieri* gen. et sp. nov., Ostéologie, Relations, Jurassique moyen, Formation de Stanleyville, Kisangani, R.D. Congo.

**Abstract :** The osteology of *Kisanganichthys casieri* gen. and sp. nov., a small catervariolid fish from the Stanleyville Formation (Middle Jurassic), Kisangani, Democratic Republic of Congo, is studied in details. *K. casieri* gen. and sp. nov. has a pair of small triangular toothed lateral dermethmoids located at the symphysis of the upper jaw, the toothed premaxillae being more laterally positioned. The frontals have a broad anterior extremity that is sutured with the dermethmoid (= rostral). There is only one supramaxilla. The nasals are separated from each other by the dermethmoid and from the orbit by the antorbital. There are two supraorbitals and two large postorbitals (= suborbitals). The preopercle is crescent-like but with a very short dorsal part. The subopercle is much larger than the opercle. Within Catervariolidae, *K. casieri* gen. and sp. nov. seems more closely allied to *Songanella callida* than to *Catervariolus hornemani*. The systematic relationships of Catervariolidae in the "pholidophoriform" lineages are re-discussed and a basal position is confirmed.

**Key words :** Teleostei, Catervariolidae, *Kisanganichthys casieri* gen. and sp. nov., osteology, relationships, Middle Jurassic, Stanleyville Formation, Kisangani, Democratic Republic of Congo.

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## INTRODUCTION

The continental Middle Jurassic (Aalenian-Bathonian, cf. COLIN, 1994) Stanleyville Formation, in the Democratic Republic of Congo, yields an important ichthyofauna that was firstly studied in three small monographs more than a half-century ago (DE SAINT-SEINE, 1950, 1955; DE SAINT-SEINE & CASIER, 1962) and is now re-studied in a more detailed and a more modern way (TAVERNE, 1975, 2001, 2011a, b, c, 2014a, b).

The fossil fish fauna from the Stanleyville Formation contains many archaic teleosts, with ganoid scales and a peg-and-socket articulation.

Traditionally, these Mesozoic primitive teleosts from all around the world are ranged in “Pholidophoriformes”. This highly heterogenous order groups a few families and many genera and species not closely allied together but however osteologically close to the “classical” primitive teleosts with cycloid scales (PATTERSON, 1973; ARRATIA, 2000, 2013; TAVERNE, 2011a).

The break-up of this polyphyletic assemblage is now begun. TAVERNE (2011c, 2014a, b) has recently erected three new orders, Ligulelliformes for the family Ligulellidae, Catervarioliformes for the family Catervariolidae and Ankylophoriformes for an enlarged family Ankylophoridae, and ARRATIA (2013) has restricted the Pholidophoriformes to the unique family Pholidophoridae *sensu stricto*.

Among the Congolese Middle Jurassic ganoid teleosts, the family Pleuropholidae is particularly well represented, with 131 specimens ranged in four genera and six species (TAVERNE, work in progress). One specimen seen by DE SAINT-SEINE was labelled by him as a member of the pleuropholid species *Parapleuropholis olbrechtsi* DE SAINT-SEINE, 1955. However, this sample is not a pleuropholid fish. Its middle flank scales are not as deep as in Pleuropholidae and they bear the lateral line sensory canal. In all Pleuropholidae, the middle flank scales are extremely deep and the lateral line is deflected into the scale-row just below these deep flank scales. Moreover, this peculiar specimen exhibits two separated toothed lateral dermethmoids at the symphysis of the upper jaw, while *P. olbrechtsi* has the two premaxillae, fused together, located at the same place and no toothed lateral dermethmoid.

The aim of the present paper is thus to study in details this new ganoid teleost fish and to determine its relationships. The systematic position of Catervariolidae within the “pholidophoriform” lineages is also re-discussed.

## MATERIAL AND METHODS

The specimen hereafter described belongs 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

CLT	=	cleithrum
DETH	=	dermethmoid (= rostral)
DPTE	=	dermopterotic
DSPH	=	dermosphenotic
ENPT	=	entopterygoid
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HCOR	=	hypocoracoid
HEMAP	=	haemapophysis
HYOM	=	hyomandibula
IOP	=	interopercle
IORB 1-5	=	infraorbitals 1 to 5
LDETH	=	lateral dermethmoid
LEP	=	fin ray (= lepidotrichia)

MX	=	maxilla
NA	=	nasal
NEUR	=	neural arch
OP	=	opercle
PA	=	parietal
PMX	=	premaxilla
POP	=	preopercle
PORB 1, 2	=	dorsal and ventral postorbitals (= suborbitals)
PT	=	posttemporal
QU	=	quadrate
RAD	=	pectoral pterygiophore (= radial)
SC	=	scale
SCA	=	hypercoracoid (= scapula)
SCU	=	caudal scute
SMX	=	supramaxilla
SOP	=	subopercle
SORB 1, 2	=	supraorbital 1 and 2
ST	=	supratemporal (= extrascapular)
SY	=	symplectic
V	=	vertebral centrum (= chordacentrum)
b. fu.	=	basal fulcra
ex. c.	=	extrascapular sensory canal
fr. fu.	=	fringing fulcra
l. l.	=	lateral line sensory canal
ot. c.	=	otic (= postorbital) sensory canal
p. l.	=	pit-line
sorb. c.	=	supraorbital sensory canal

## SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii KLEIN, 1885

Series Neopterygii REGAN, 1923

Division Teleostei MÜLLER, 1845

Ordre Catervarioliformes TAVERNE, 2014

Family Catervariolidae DE SAINT-SEINE, 1955

Genus *Kisanganichthys* gen. nov.

**Type species:** *Kisanganichthys casieri* gen. and sp. nov. (here designated)

### Diagnosis

The same as the species (monospecific genus).

### Etymology

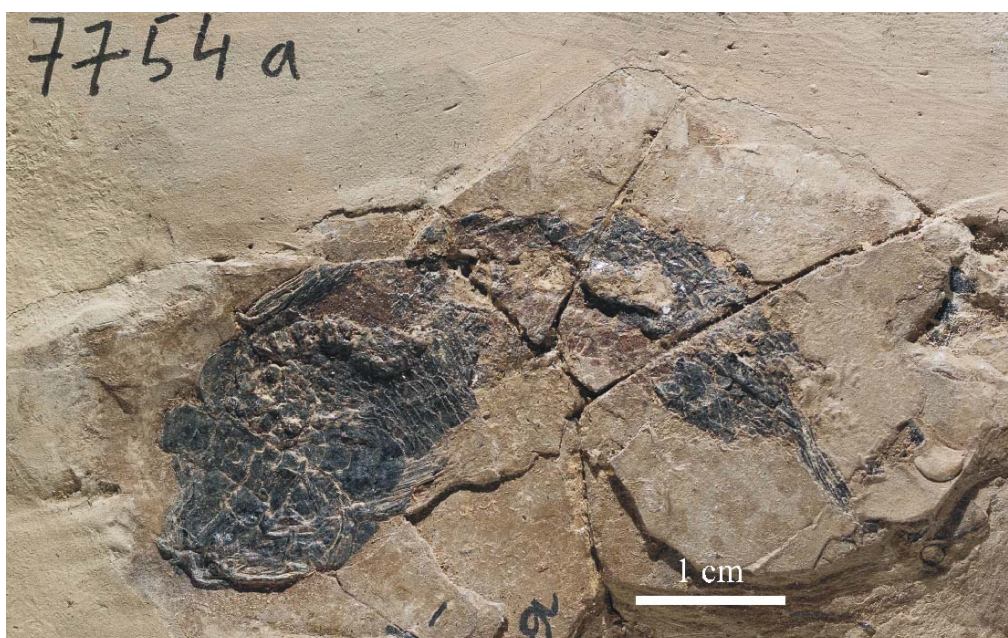
The generic name refers to Kisangani, formerly Stanleyville, in the Democratic Republic of Congo, the region where the new fossil fish genus was discovered. The Greek word *ichthys*, fish, is added.

*Kisanganichtys casieri* gen. and sp. nov.

### Diagnosis

Small catervariolid fish of about 7 cm of total length. Dermal bones of the skull covered by ganoin, with a smooth surface or very weakly ornamented. Triangular dermethmoid (= rostral),

devoid of rostral sensory commissure. Small nasals separated from each other by the dermethmoid and from the orbit by the antorbital. Frontal with a broad anterior extremity sutured with the dermethmoid. Long quadrangular parietals meeting on the mid-line. Supraorbital and otic sensory canals not connected. A vertical pit-line lying on the dermopterotic. Supratemporal (= extrascapular) deep and narrow. Paired small toothed triangular lateral dermethmoids positioned at the symphysis of the upper jaw. Lateral dermethmoid without dorsal wing-like expansion. Long toothed premaxilla laterally located. Long maxilla. Only one elongate supramaxilla. Quadrate without bony quadratic process. Two supraorbital. Five infraorbitals. Third and fourth infraorbitals narrow. Dermosphenotic with a small posterior bony process. Two large postorbitals (= suborbitals). Preopercle crescent-like, with a very short dorsal part. Small opercle. Subopercle much larger than the opercle. Broad posttemporal. Curved cleithrum. Pectoral fin with one basal fulcrum fused to the first ray. Fringing fulcra lying along the first pectoral ray. Dorsal fin located at mid-length of the body and beginning with three impaired basal fulcra. Three caudal scutes, paired basal fulcra and fringing fulcra in the dorsal lobe of the caudal fin. Ganoid scales with a peg-and-socket articulation, a smooth surface and a smooth posterior margin. Lateral line scales deep and located at mid-depth of the flank.



**Figure 1 :** *Kisanganichthys casieri* gen. and sp. nov. Holotype MRAC RG 7754a.

### **Etymology**

The specific name is dedicated to the Belgian paleontologist Edgar Casier (1904-1976), in honour of his numerous papers and monographs on the fossil fishes from the Congo area.

### **Holotype and only specimen**

Sample MRAC RG 7754a: a nearly complete specimen with a well preserved skull (Fig. 1). A small part in the middle of the body, the pelvic girdle, the anal fin and almost all the caudal fin are missing. Total length: 63 mm (the distal part of the caudal fin is missing). This slab also bears the caudal region of a small pleuropholid fish.

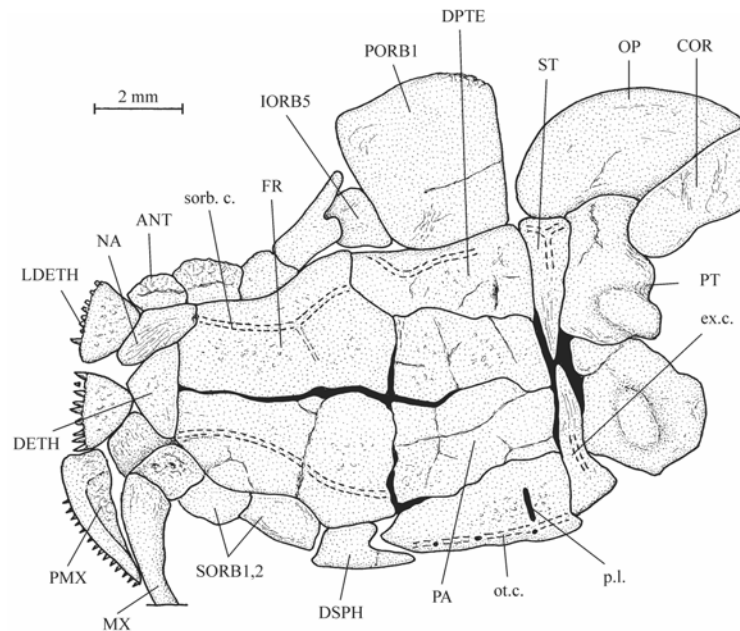
### **Formation and locality**

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

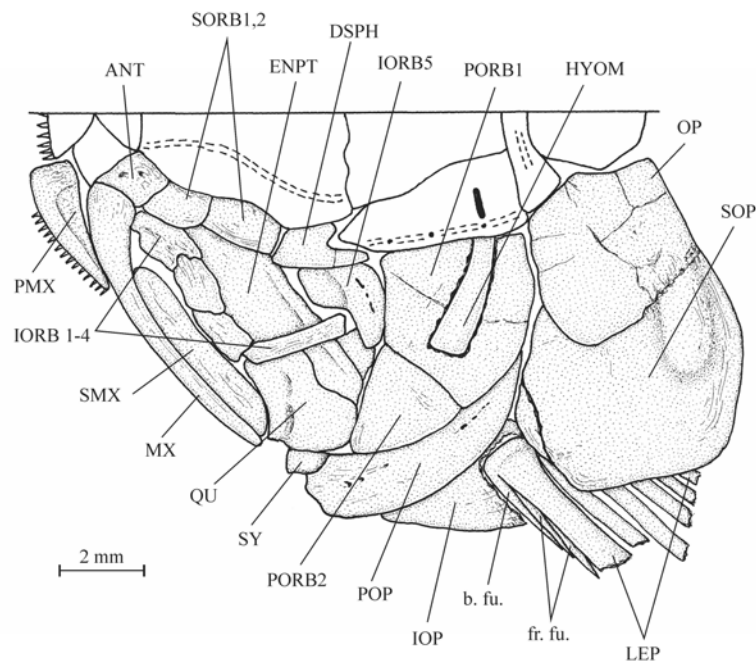
## Osteology

### *The skull* (Figs 2, 3)

The skull is strongly ossified. The cranial dermal bones have a smooth surface or are weakly ornamented with a few small, irregular and poorly developed tubercles. No endocranial bone is visible.



**Figure 2 :** *Kisanganichthys casieri* gen. and sp. nov. Skull roof of holotype MRAC RG 7754a.



**Figure 3 :** *Kisanganichthys casieri* gen. and sp. nov. Suspensorium of holotype MRAC RG 7754a. The left pectoral fin is displaced below the subopercle, due to the fossilisation. The rod-like ventral branch of the hyomandibula has cracked the dorsal postorbital (= suborbital).

All the bones of the skull roof are sutured together. There is no trace of fusion between them.

The dermethmoid (= rostral) is small and triangle-shaped. Its broad posterior margin reaches the frontals in a rectilinear suture that is perpendicular to the sagittal axis of the cranium. A sensory rostral commissure is not visible on the dermethmoid. Two separated and toothed lateral dermethmoids are located at the symphysis of the upper jaw, just before the dermethmoid. This lateral dermethmoid is a narrow triangular bone with the top reaching the dermethmoid. Its oral margin bears 8 or 9 small conical acute teeth. The nasals are rather small. They are separated from each other by the dermethmoid and from the orbit by the antorbital. The vomer and the parasphenoid are not visible. The frontals, the parietals and the dermopterotics are large bones. The frontals are broadened in their posterior region but even their anterior part is wide, with a broad anterior border. The skull is medio-parietal and the parietals are longer than broad. The supratemporals (= extrascapulars) are narrow, triangular and their acuminate medial tips meet on the mid-line. The supraorbital sensory canal on the frontal and the otic (= postorbital) sensory canal on the dermopterotic are not connected. In the specimen studied, the left supraorbital canal ends at the level of the suture between the frontal and the parietal but the right canal reaches the dermopterotic and not the parietal. On the right frontal, a thin epiphyseal commissure rises out of the supraorbital canal. A vertical pit-line is present on the left pterotic, just above the otic canal. No pit-line is visible on the parietal. The otic canal crosses the supratemporal that also bears the extrascapular sensory commissure.

The quadrate is almost quadrangular. No bony quadratic process is visible. A large entopterygoid is present between the supraorbitals, the first three infraorbitals and the quadrate.

Only the left half of the upper jaw is preserved. The premaxilla is located laterally on the jaw, the symphysis being occupied by the lateral dermethmoid. The premaxilla is a rather long bone, deeper at its anterior extremity than posteriorly. Its oral border bears at least fourteen small conical teeth well visible when sprinkled with ethanol. The maxilla is seen by its upper margin and the shape of its external face remains unknown. The anterior articular head of the maxilla is broadened. The supramaxilla is elongated, rather narrow and it covers most of the dorsal margin of the maxilla. The lower jaw is unknown.

The orbital bony ring completely surrounds the orbit and contains an antorbital, five infraorbitals, a dermosphenotic, two supraorbitals and two postorbitals (= suborbitals). The antorbital connects the first infraorbital and the first supraorbital. The first three infraorbitals are moderately narrow and not very elongated. The fourth one is a long and narrow bone, reduced to its neurodermic component. The fifth infraorbital is rather large, triangular, with a broadened upper part. The two supraorbitals lie along the frontal. The well developed dermosphenotic exhibits a thin bony process on its posterior lower corner. The upper postorbital is a very large bone, as large as the opercle. The lower postorbital is smaller and triangle-shaped, with a broad upper part and a pointed ventral corner. A small portion of the infraorbital sensory canal is visible on the fourth infraorbital.

The preopercle is moderately crescent-shaped, with a very short acuminate upper part and a broader lower part. Its dorsal portion remains far from the lateral margin of the skull roof. The opercle is rather small when compared to the skull size, and more or less rounded. The subopercle is much larger than the opercle. Its anterodorsal process is well marked. The suture between the opercle and the subopercle is obliquely oriented. The interopercle is a triangular bone located below the preopercle. The branchiostegal rays and the gular plate are unknown. A few traces of the preopercular main sensory canal are visible on the preopercle but no accessory tubule.

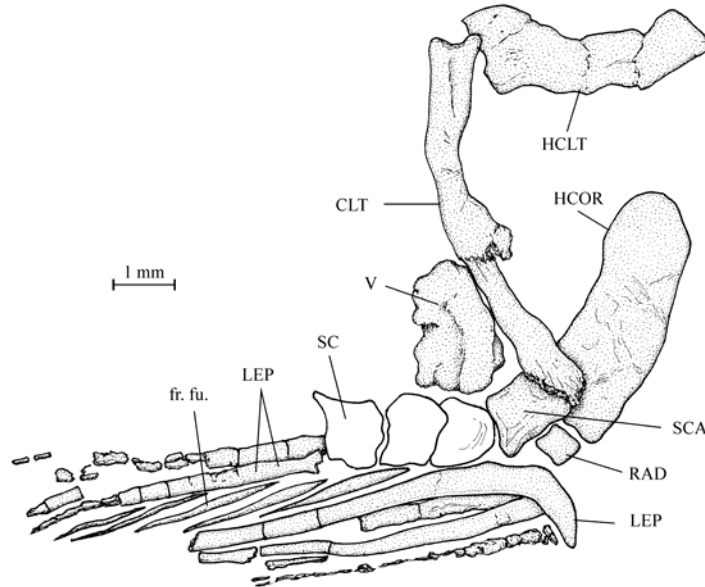
### ***The hyoid and branchial skeleton*** (Fig. 3)

The articular head of the left hyomandibula is hidden under the skull roof. Its rod-like ventral branch has pierced the left dorsal postorbital and is thus apparent. The anterior part of the symplectic is visible under the quadrate and before the preopercle. We do not know if this symplectic was articulated with the lower jaw or not.

### ***The girdles*** (Figs 2, 4)

The left half of the pectoral girdle is covered by the opercle and the subopercle. A small part of the left cleithrum forms a large swelling under the subopercle and the proximal parts of six pectoral rays are visible below the subopercle. The first ray is larger than the others and a basal fulcrum is fused to its basis. Two fringing fulcra lie against this ray. The right half of the girdle contains a crescent-shaped cleithrum, a large hypercleithrum (= supracleithrum), a small hypercoracoid (= scapula), a long and broad hypocoracoid, one pterygiophore, fragments of a few pectoral rays and some fringing fulcra. Both posttemporals are preserved. They are large bones.

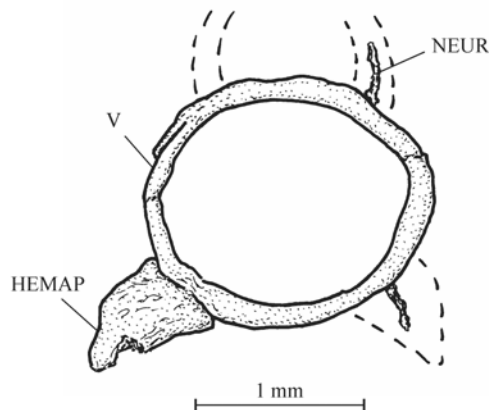
The pelvic girdle and the ventral fins are lost, due to the fossilisation.



**Figure 4** : *Kisanganichthys casieri* gen. and sp. nov. Right pectoral fin of holotype MRAC RG 7754a.

### ***The axial skeleton*** (Fig. 5)

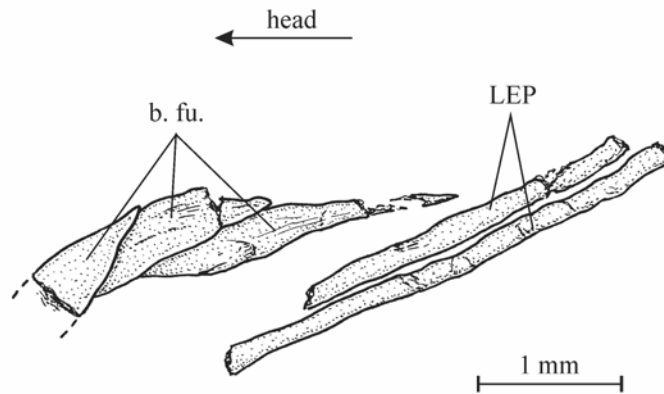
The vertebrae are covered by the scales, except the first ones. Their number is unknown. One isolated abdominal vertebra is thin, ring-like (chordacentrum) and bears a pair of small haemapophyses and a very small fragment of neural arch.



**Figure 5** : *Kisanganichthys casieri* gen. and sp. nov. Abdominal vertebra of holotype MRAC RG 7754a.

***The dorsal and anal fins*** (Fig. 6)

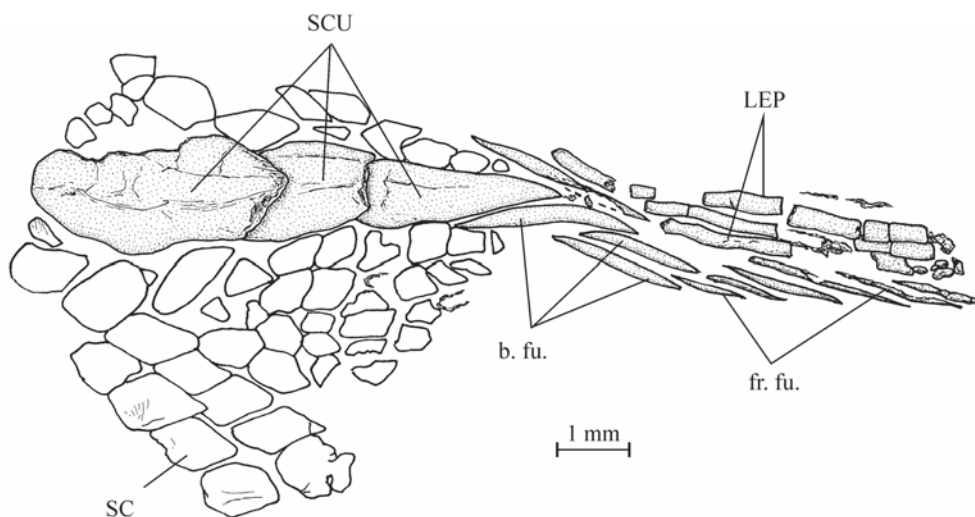
The badly preserved and incomplete dorsal fin is located at mid-length of the body. The fin begins with three impaired basal fulcra of progressive length. Fragments of two long rays are also visible. The anal fin is missing.



**Figure 6 :** *Kisanganichthys casieri* gen. and sp. nov. Anterior part of the dorsal fin of holotype MRAC RG 7754a.

***The caudal skeleton*** (Fig. 7)

The caudal skeleton is not preserved but a part of the upper lobe of the caudal fin is visible. The fin begins with three large pointed caudal scutes that are followed by three paired basal fulcra. A series of fringing fulcra is lying along the first ray. The rays have a straight segmentation.

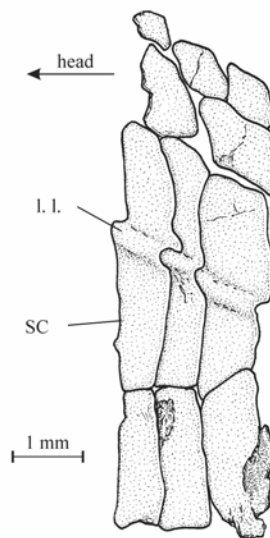


**Figure 7 :** *Kisanganichthys casieri* gen. and sp. nov. Dorsal lobe of the caudal fin of holotype MRAC RG 7754a



### ***The squamation*** (Fig. 8)

The scales are ganoid and the peg-and-socket articulation is present. It is not possible to count the scales in lateral line, some parts of the body being missing. Generally, the scales have a smooth surface but a few ones are feebly ornamented with some weakly marked ridges or tubercles. The posterior margin of the scales is smooth. The middle flank scales are deep, but not as deep as in Pleuropholidae, and they bear the lateral line sensory canal. The scales of the row just below are deep too. The scales dorsally located are smaller and lozenge-in shaped.



**Figure 8** : *Kisanganichthys casieri* gen. and sp. nov. Flank scales in the abdominal region of holotype MRAC RG 7754a.

## **DISCUSSION**

### **The relationships of *Kisanganichthys* gen. nov. within Neopterygii**

*Kisanganichthys* gen. nov. exhibits a pair of toothed lateral dermethmoids occupying the symphysis of the upper jaw, the premaxillae being more laterally located.

Such a structure of the upper jaw is the result of the division of the neopterygian primitive premaxilla into two different toothed bones, a symphyseal lateral dermethmoid and a lateral “secondary” premaxilla (PATTERSON, 1975: 496-515; TAVERNE, 2011a: fig. 20A, B). This peculiar morphology appears in the Pachycormidae where the toothed lateral dermethmoids are fused to the inner face of the dermethmoid (PATTERSON, 1975: fig. 139; MAINWARING, 1978: figs 2, 3). Symphyseal toothed lateral dermethmoids also occur in Ligulellidae (TAVERNE, 2011c: figs 6-9) and in three families of ganoid teleosts, Ichthyokentemidae (PATTERSON, 1975: fig. 126; GRIFFITH, 1977: fig. 26), Ankylophoridae (PATTERSON, 1973: fig. 14, 1975: figs 82, 121, 124, 125, 145; ARRATIA, 1999: fig. 6C, 2000: fig. 15, 2013: figs 49A, B; TAVERNE, 2011a: figs 4, 5, 2014b: figs 4, 6) and Catervariolidae (TAVERNE, 2011b: figs 8-12, 15, 17, 19, 2014a: figs 4-7). The situation is different in more advanced ganoid teleosts and in primitive cycloid teleosts. In these fishes, the “secondary” premaxilla re-occupies the symphysis and covers the underlying lateral dermethmoid that becomes toothless and is frequently fused with the dermethmoid (TAVERNE,

2011a: fig. 20C, D). The relationships of *Kisanganichthys* are thus to be sought in the five families that exhibit this remarkable upper jaw morphology.

The osteology of *Kisanganichthys* gen. nov. greatly differs from that of Pachycormidae (LOOMIS, 1900; LEHMAN, 1949; MAINWARING, 1978; LAMBERS, 1988; among others) and of Ligulellidae (TAVERNE, 2011c). It is clear that the new African genus does not belong to these two families.

The skeleton of Ichthyokentemidae is rather well known (GRIFFITH & PATTERSON, 1963; PATTERSON, 1975; GRIFFITH, 1977). The family contains two genera, *Ichthyokentema* WOODWARD, 1941 from the Late Jurassic of England and *Elpistioichthys* GRIFFITH, 1977 from the Late Triassic of Austria. *Elpistioichthys* exhibits paired toothed lateral dermethmoids at the upper jaw symphysis, as in *Kisanganichthys* gen. nov., whereas these two bones are fused together in *Ichthyokentema*. Ichthyokentemidae also retain the primitive number of three or four supraorbitals and have only one supramaxilla. Their nasals meet on the mid-line. *Ichthyokentema* has a crescent-shaped preopercle, with its dorsal extremity reaching the dermopterotic. In *Elpistioichthys*, the preopercle has a much shorter dorsal branch but the ventral part of the bone is enlarged and bears a series of long tubules associated with the preopercular sensory canal. Ichthyokentemidae share with the more evolved archaic teleosts an important apomorphy concerning the orbital bony ring. The dorsal postorbital is preserved as a free bone but the ventral postorbital is captured by the third or the fourth infraorbital that becomes very wide elements. *Kisanganichthys* gen. nov. retains the plesiomorphic condition of having narrow third and fourth infraorbitals and two large independent postorbitals. Thus, the new Congolese fossil fish genus cannot be ranged within Ichthyokentemidae.

The family Ankylophoridae was erected by GAUDANT (1978) for two genera from the Late Jurassic of France, *Ankylophorus* GAUDANT, 1978 and *Lehmanophorus* GAUDANT, 1978. Later, ARRATIA (2000) has ranged *Ankylophorus* in her new *Siemensichthys*-group near the genera *Eurycormus* WAGNER, 1863 and *Siemensichthys* ARRATIA, 2000. More recently, TAVERNE (2011a, 2014b) has still considerably enlarged the family, with the inclusion of “*Pholidophorus*” *germanicus* QUENSTEDT, 1858, *Pholidophoristion* WOODWARD, 1941, *Pholidorhynchodon* ZAMBELLI, 1980, *Neopholidophoropsis* TAVERNE, 1981, *Eopholidophorus* ZAMBELLI, 1989, *Sturbautichthys* TAVERNE, 2011 and *Songaichthys* TAVERNE, 2014. However, ARRATIA (2013) has kept a more restricted view of the family, with only the genera *Ankylophorus*, *Lehmanophorus* and *Siemensichthys*. Today, the osteology of some ankylophorid species is more or less adequately known (PATTERSON, 1973, 1975; GAUDANT, 1978; ARRATIA, 1999, 2000, 2013; ARRATIA & SCHULTZE, 2007; TAVERNE, 2011a, 2014b) but the skeleton of a few ones is still to be studied. The lateral dermethmoid of Ankylophoridae has a dorsal wing-like expansion extending on the floor of the olfactory fossa. Such an expansion is not present on this bone in *Kisanganichthys* gen. nov. Their preopercle exhibits a broader ventral part than that of the new Congolese genus and with numerous tubules on the preopercular sensory canal. Ankylophoridae possess a wide dorsal postorbital, an enlarged third infraorbital and no free ventral postorbital as in Ichthyokentemidae. Some of them even lose the free dorsal postorbital that becomes part of a broadened fourth infraorbital. Thus, *Kisanganichthys* gen. nov. is less specialized than Ankylophoridae and can not be included in this family.

Catervariolidae contain two genera, *Catervariolus* DE SAINT-SEINE, 1955 and *Songanella* DE SAINT-SEINE and CASIER, 1962, both from the Stanleyville Formation. Their skeleton has been recently re-studied in a detailed way (TAVERNE, 2011b, 2014a). They have the nasal separated from the orbit by the antorbital. Their toothed lateral dermethmoid is devoid of dorsal wing-like process. Only one supramaxilla is present. The third and the fourth infraorbitals are narrow bones. There are two or three large postorbitals, with the lower one triangle-shaped and ventrally pointed. The preopercle is crescent-shaped. These characters also occur in *Kisanganichthys* gen. nov. The placement of the new Congolese fish genus in the family Catervariolidae seems therefore justified.

#### **The generic validity and the relationships of *Kisanganichthys* gen. nov.**

*Kisanganichthys* gen. nov. differs from the two other catervariolid genera by many characters. The two lateral dermethmoids are independent (*versus* fused). The dermethmoid is devoid of a

rostral sensory commissure (*versus* rostral commissure present). The suture between the dermethmoid and the frontals is broad (*versus* the three bones contacting in only one point or no contact at all). The nasals are separated from each other by the dermethmoid (*versus* nasals meeting on the mid-line). There are two supraorbitals (*versus* three). The premaxilla is rather long and deeper at its anterior extremity (*versus* short and triangular). The upper part of the preopercle is very short and remains far from the skull roof lateral margin (*versus* preopercle reaching the skull roof lateral margin). The supramaxilla is elongated (*versus* short). The subopercle is much larger than the opercle (*versus* opercle much larger than subopercle).

These differences clearly show that *Kisanganichthys* gen. nov. deserves its peculiar generic status. *Kisanganichthys* gen. nov. seems more closely related to *Songanella* than to *Catervariolus*. Indeed, the new genus and *Songanella* share two characters differing from those of *Catervariolus*. Their dermethmoid reaches the frontals. They have only two large postorbitals. The dermethmoid of *Catervariolus* is separated from the frontals by the two nasals and this fish exhibits three large postorbitals.

Only two supraorbitals are present in *Kisanganichthys* gen. nov. and its crescent-shaped preopercle has a very short dorsal part that does not reach the lateral margin of the dermopterotic. These two features announce the morphological situation found in Ankylophoridae and in Pholidophoridae. The quadrate of *Kisanganichthys* gen. nov. seems devoid of bony process as in Pholidophoridae.

### **The systematic position of Catervarioliformes within archaic teleosts (Fig. 9)**

The family Catervariolidae was erected by DE SAINT-SEINE (1955) who ranged it in the order Amiiiformes, a systematic position accepted by GARDINER (1966), while LEHMAN (1966) included the family in the order Parasemionotiformes. PATTERSON (1973) was the first to suggest a relationship with the “Pholidophoriformes” and the archaic teleosts, a point of view shared by subsequent authors. The detailed osteological study of *Catervariolus* by TAVERNE (2011a, b) has plainly confirmed this systematic position.

In the hypothesis of phylogeny proposed by TAVERNE (2011a, b, 2014a, b), Catervariolidae are considered as the most primitive lineage within the “pholidophoriform” assemblage. This position is occupied by Pholidophoridae in the hypothetical phylogenetic tree built by ARRATIA (2013, Node C), *Catervariolus* being located two levels “higher” (Nodes D and E).

I give hereafter some comments about the most important characters used by these two authors to construct their respective hypotheses. The data concerning Catervariolidae come from TAVERNE (2011a, b, 2014a, present paper) and those concerning Pholidophoridae from ARRATIA (2013). I do not include *Pholidorhynchodon* in the following comments because I consider that this fossil fish does not belong to the Pholidophoridae (I will discuss this point in a forthcoming paper). Comparisons also are made with Pachycormidae and Ligulellidae, two plesiomorphic sister-groups of “Pholidophoriformes”. *Hulettia americana* (EASTMAN, 1899) from the Lower Jurassic of the U.S.A. and *Prohalicetes porroi* (BELLOTTI, 1957) from the Late Triassic of Italy, two halecostomid fishes close to the teleosts, are also used for some comparisons. Some data concerning more primitive halecomorph fishes are also invoked.

(1) In *Catervariolus*, the sutures between the cartilage bones of the braincase are preserved throughout life (ARRATIA, 2013, Node E, character 18[1]). That is not the case in Pholidophoridae (character 18[0]). However, this condition does not necessary indicate a more primitive state than in Catervariolidae. Indeed, ARRATIA (2013) never mentions an endocranial bone in the numerous pholidophorid specimens that she describes, with the possible exception of the ethmoid region and the autosphenotic in *Zambellichthys bergamensis* ARRATIA, 2013 (ARRATIA, 2013: fig. 29). Apparently, the endocranium of Pholidophoridae seems to remain unossified in adult, and thus evidently without bony sutures. In Pachycormidae, the endocranium is ossified and sutures are present (LOOMIS, 1900: pl. 19; STENSIÖ, 1935: fig. 6; LEHMAN, 1949: fig. 12, 13; MAINWARING, 1978: fig. 22, 26). Ligulellidae and *Hulettia americana* also have a sutured bony endocranium (TAVERNE, 2011c: fig. 8, 9; SCHAEFFER & PATTERSON, 1984: fig. 8A, B). Even in some primitive halecomorph fish, the braincase could be ossified and the bones sutured (MAISEY, 1991: fig. p. 159 [bottom]; SCHAEFFER, 1971: fig. 2-7; etc.). So, in place of being

considered as plesiomorphic, the unsutured condition of the endocranium in Pholidophoridae can be interpreted as an autapomorphy of the family.

(2) *Catervariolus* has an ossified supraoccipital (Node E, character 13[1]), a bone absent (character 13[0]) in Pholidophoridae and in Pachycormidae (MAINWARING, 1978: fig. 20), the region comprised between the epiotics probably remaining cartilaginous in that last family. However, an ossified supraoccipital exists in Ligulellidae (TAVERNE, 2011c: fig. 7-9, 12, 14). In *Hulettia americana*, the supraoccipital region is ossified but not separated by a suture from the epiotics (SCHAEFFER & PATTERSON, 1984: fig. 9). An ossified supraoccipital even exists in more primitive halecomorph fishes, such as for instance the semionotiform *Dapedium* LEACH, 1822 (WOODWARD, 1893: pl. 50, fig. 3, 3a; GARDINER, 1960: fig. 37-39) or the ionoscopiform *Macrepistius* COPE, 1894 (SCHAEFFER, 1971: fig. 1-3). The absence of a bony supraoccipital is not astonishing in Pholidophoridae seeing that their adult endocranium seems essentially cartilaginous. Once again, in this precise case, this character is not necessary an indication that Pholidophoridae occupy a more plesiomorphic position than Catervariolidae.

(3) The presence of a bony process on the quadrate is considered as one of the major apomorphies of teleosts (Node D, character 78[1]). Such a process lies along the ventral margin of the quadrate in *Catervariolus* (TAVERNE, 2011b: fig. 21, 24). ARRATIA (2013) describes the quadrate of Pholidophoridae as lacking such a bony process (character 78[0]) and, therefore, representing a more primitive state of evolution. Nevertheless, the quadrate is partly or totally covered by the infraorbitals or by the preopercle in most pholidophorid samples studied by ARRATIA (2013). She also writes that in most cases the quadrate remains partly cartilaginous in Pholidophoridae. However, an extremely reduced bony quadratic process exists in one specimen of *Pholidophorus gervasuttii* ZAMBELLI, 1980 (ARRATIA, 2013: fig. 15). The situation is thus uncertain. We could consider that the apparent absence of this bony structure in Pholidophoridae perhaps is the result of the shortening or the loss of the process because of the partial ossification of the quadrate in these fishes, *i. e.*, an autapomorphy rather than a plesiomorphy. The quadratic process has a long story within Neopterygii. A small cartilaginous quadratic process is already present in the Recent holostean species *Amia calva* LINNAEUS, 1766 (GRANDE & BEMIS, 1998: fig. 48). In Aspidorhynchidae, the ventral margin of the quadrate often is swollen, forming a sort of bony pad (BRITO, 1997: fig. 15A) and a true bony quadratic process could even be individualized (TAVERNE, 1981: fig. 5). In Pachycormidae, some samples also seem to develop an individualized bony process (MAINWARING, 1978: fig. 8, 9). Ligulellidae do not possess such a process (TAVERNE, 2011c: fig. 20). It is also to be noted that this process is reduced or lost independently in members of many teleost lineages, such as Mormyridae (TAVERNE, 1972: num. fig.), Tselfatiidae (TAVERNE, 2000a: fig. 5A, 2000b: fig. 8, 9), Clupeidae (TAVERNE, 2011d: fig. 6), Enchodontoidei (GOODY, 1969: num. fig.), Alepisauroides (GOODY, 1969: num. fig.; TAVERNE, 2004: fig. 3), Siluroidei (FINK & FINK, 1981: 321, fig. 11), etc.

(4) ARRATIA (2013) considers that the symplectic of *Catervariolus* is not articulated with the lower jaw (Node D, character 79[1]), whereas this bone reaches the lower jaw in Pholidophoridae, a more primitive condition (character 79[0]). However, the symplectic of *Catervariolus* is always partly hidden by the quadrate (TAVERNE, 2011b: 196-197 and fig. 24) and we do not know if it reaches or not the lower jaw. In *Songanella* and *Kisanganichthys*, two other catervariolid fishes, the symplectic is not preserved (TAVERNE, 2014a and the present paper). In Pholidophoridae, both articulated and not articulated conditions exist. Some specimens of *Pholidophorus gervasuttii* have the symplectic articulated to the lower jaw (ARRATIA, 2013: fig. 15, 16), other samples of the same species not (ibid., 2013: fig. 18A, B). The articulation is present in *Parapholidophorus nybelini* ZAMBELLI, 1975 (ibid., 2013: fig. 59B) but absent in *Knerichthys* ARRATIA, 2013 (ibid., 2013: fig. 39) and *Pholidoctenus* ZAMBELLI, 1977 (ibid., 2013: 102). The situation is unknown in *Pholidophorus latiusculus* AGASSIZ, 1832, *Zambellichthys* ARRATIA, 2013, *Annaichthys* ARRATIA, 2013, *Parapholidophorus caffii* (AIRAGHI, 1908) and *Pholidophoretetes* GRIFFITH, 1977. In the Pachycormidae, the symplectic does not articulate with the lower jaw (MAINWARING, 1978: 27, fig. 8, 9). The articulation is present in *Ligulella* (TAVERNE 2011c: fig. 20).

(5) ARRATIA (2013) includes *Catervariolus* in the group of teleosts having only four pectoral pterygiophores sustaining the pectoral fin (Node E, character 110[1]), Pholidophoridae

being positioned at a more plesiomorphic level in her phylogenetic tree (Node C). However, the exact number of pectoral pterygiophores is unknown either in Catervariolidae or in Pholidophoridae, and some Pachycormidae already possess four pectoral radials (JESSEN, 1972: pl. 25, fig. 1; MAINWARING, 1978: fig. 29).

(6) Pholidophoridae have chordacentra but do not possess autocentra (character 96[0]). ARRATIA (2013) quoted *Catervariolus* as having each vertebral centrum of the caudal region composed of a chordacentrum surrounded by an autocentrum (Node E, character 96[1]). The vertebrae of *Catervariolus* are thin ring-like bony structures. When seen in transversal view, only one bony layer is visible. Generally, those vertebrae have a smooth lateral surface without any relief. But a few rare vertebrae exhibit a feebly marked median crest (TAVERNE, 2011b: fig. 43). That could be due to deformations induced by the fossilisation or to the presence of an autocentrum associated with the chordacentrum. The presence of autocentra is often considered as an autapomorphy shared by *Leptolepis coryphaenoides* (BRONN, 1830) and the more specialized teleosts (see for instance ARRATIA et al., 2001: 147). However, many halecomorph fishes, much more primitive than Pholidophoridae, exhibit crests and fossae on the lateral face of the vertebrae (MAISEY, 1991: fig. p. 166; GRANDE & BEMIS, 1998: num. fig.; etc.). A few ionoscopiform fishes possess two ring-like bony layers surrounding the notochord and separated from each other by a small interspace (DE SAINT-SEINE, 1950: fig. 4). There is no direct contact between the notochord and the external bony layer because of that interspace. Some authors have understood these two bony layers as a perichondral ossification surrounded by the chordacentrum but others have considered these two ossified layers as associated autocentra and chordacentra (BARTRAM, 1975: 185, fig. 3A).

(7) Some neural arches of *Catervariolus* bear epineurals (Node D, character 102[1]) (TAVERNE, 2011b: fig. 43), while Pholidophoridae are described as devoid of such intermuscular bones (character 102[0]). However, epineurals are already present in some Pachycormidae (MAINWARING, 1978: 79) and even in *Huletia americana* (SCHAEFFER & PATTERSON, 1984: fig. 17C) and in *Prohalicetes porroi* (TINTORI, 1990: 163). So, the absence of epineurals in Pholidophoridae must be understood as an apomorphic loss and not as a plesiomorphic character.

(8) The fishes located by ARRATIA (2013) in her Node E, as *Catervariolus*, possess epipleurals (character 103[1]), a structure absent in Pholidophoridae (character 103[0]). However, epipleurals also are missing in *Catervariolus* (TAVERNE, 2011b: 202).

(9) ARRATIA (2013) ranges *Catervariolus* within the primitive teleosts with 7 or more uroneurals (Node D, character 132[1]), Pholidophoridae being considered as having the ural neural arches not changed into uroneurals (character 132[0]). However, the ural neural arches are only known in one specimen of *Parapholidophorus nybelini* ZAMBELLI, 1977 and in one specimen of *Pholidoctenus serianus* ZAMBELLI, 1977 (ARRATIA, 2013: fig. 68, 84), not in other Pholidophoridae. Concerning Catervariolidae, *Songanella* exhibits 6 uroneurals (TAVERNE, 2014a: fig. 17) and *Catervariolus* no more than 4 true uroneurals, but with the preural neural arch 1 also transformed, forming the first element in a series of five pieces (TAVERNE, 2011b: fig. 50-53). The transformation of neural arches in uroneurals is a homoplastic character in Neopterygii and occurred several times, at different systematic levels. In Aspidorhynchidae, for instance, some species possess broad and short uroneurals still resembling closely to neural arches (TAVERNE, 1998: fig. 4; BRITO, 1999: fig. 4B, 5B; TAVERNE & CAPASSO, 2012: fig. 3) but other species develop elongated uroneurals (ARRATIA & LAMBERS, 1996: fig. 15; TAVERNE, 1998: fig. 3; BRITO, 1999: fig. 1B, 3B). In Pachycormidae too, the last neural arches are elongated in uroneurals (PATTERSON, 1973: fig. 19; MAINWARING, 1978: fig. 28; ARRATIA & LAMBERS, 1996: fig. 3A, 4B, 8B, 11) and Ligulellidae also exhibit long uroneurals (TAVERNE, 2011c: fig. 31). On the other hand, *Dorsetichthys bechei* (AGASSIZ, 1837), placed by ARRATIA (2013: fig. 95) in a more apomorphic position in regard to *Catervariolus* and to her *Siemensichthys*-group, exhibits short first ural neural arches not yet transformed into uroneurals (PATTERSON, 1968: fig. 2A, B, 5).

(10) ARRATIA (2013) places *Catervariolus* with the teleosts having only ural neural arches modified as uroneurals (Node E, character 131[1]). But we have just seen in the preceding paragraph 9 that the preural neural arch 1 of *Catervariolus* is also modified and joined to the uroneural series (character 131[0]).

(11) In ARRATIA's phylogenetic tree, the presence of a diastema between hypurals 2 and 3 (character 141[1]) is a feature of her Node D, a group that contains *Catervariolus* and some evolved "Pholidophoriformes". Pholidophoridae are located at a lower level in the tree (Node C). However, this diastema is very feebly marked in *Catervariolus* (TAVERNE, 2011b: fig. 50-53) and the same sort of small diastema already exists in *Parapholidophorus nybelini* and *Pholidoctenus serianus* (ARRATIA, 2013: fig. 68, 84), the two Pholidophoridae for which the caudal skeleton is partly known.

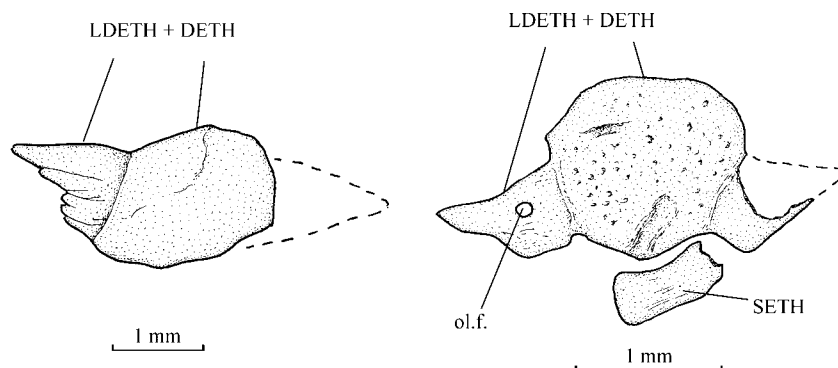
(12) As is stated above, ARRATIA (2013) places *Catervariolus* in her Node D, an assemblage of genera having a Z-like segmentation of the principal caudal rays (character 151[1]). Pholidophoridae are more primitive and they have the principal caudal rays with a straight segmentation (character 151[0]). That is once again an erroneous position for Catervariolidae. Indeed, *Catervariolus*, *Songanella* and *Kisanganichthys* possess principal caudal rays with a straight segmentation (Fig. 7; TAVERNE, 2011b: fig. 57, 2014a: fig. 18).

Thus, all these twelve characters are not really relevant to decide that Catervariolidae are more specialized than Pholidophoridae, the more so as that some characters assigned to *Catervariolus* in the matrix used by ARRATIA (2013) are erroneously quoted.

On the other hand, the phylogeny proposed by ARRATIA (2013) does not really take in account a few osteological characters for which *Catervariolus* seems obviously more primitive than Pholidophoridae.

(1) The upper jaw symphysis is occupied by the toothed lateral dermethmoids in Catervariolidae, with the small toothed premaxillae laterally placed (TAVERNE, 2011b: fig. 8-12, 17, 19, 2014a: fig. 4-7), as in Pachycormidae (PATTERSON, 1975: fig. 139; MAINWARING, 1978: fig. 2, 3) and in Ligulellidae (TAVERNE, 2011c: fig. 6-9). A pair of small premaxillae is located at the symphysis in Pholidophoridae.

(2) As stated above, Catervariolidae have a large dermethmoid and two independent lateral dermethmoids that are fused together or not (Fig. 2; TAVERNE, 2011b: fig. 8-18, 13, 17, 2014a: fig. 5). In Pholidophoridae, the dermethmoid (= rostral in ARRATIA, 2013) bears paired lateral triangular processes (Fig. 9, left) and no lateral dermethmoid is mentioned. The same situation occurs in Pleuropholidae (Fig. 9, right), another "pholidophoriform" family considered as close to the primitive teleosts with cycloid scales. In his comments on these fishes, PATTERSON (1973: 269) has considered the two lateral processes of their dermethmoid as possible fused lateral dermethmoids, an opinion that I can confirm (TAVERNE, study in progress on the Middle Jurassic Pleuropholidae from the Democratic Republic of Congo). Such a fusion of the two lateral dermethmoids with the dermethmoid is one of the most important apomorphies of the "classical" primitive teleosts (*Leptolepis coryphaenoides* (BRONN, 1830) and the more advanced species). The rostral morphology of Pholidophoridae could be so an argument to remove them from a basal to a higher position on the phylogenetic tree of the "Pholidophoriformes".



**Figure 9** : Rostral region of (left) *Pholidophorus gervasuttii* ZAMBELLI, 1980 (modified from ARRATIA, 2013: fig. 7C) and (right) undetermined pleuropholid fish, specimen MRAC RG 10233 from the continental Middle Jurassic (Stanleyville Formation) of the Democratic Republic of Congo.

(3) Catervariolidae possess only one supramaxilla (TAVERNE, 2011b: fig. 8, 26B, 2014a: fig. 4, 11), as in Pachycormidae (LEHMAN, 1949: fig. 2; WENZ, 1967: fig. 53; MAINWARING, 1978: fig. 2) and many holostean fishes, whereas Pholidophoridae already have two supramaxillae as in more specialized “Pholidophoriformes” and in primitive teleosts with cycloid scales.

(4) There are two or three supraorbitals in Catervariolidae (TAVERNE, 2011b: fig. 8, 9, 13, 16, 2014a: fig. 4, 5). Three supraorbitals are present in *Hulettia americana* (SCHAEFFER & PATTERSON, 1984: fig. 11) and *Prohalicetes porroi* (TINTORI, 1990: fig. 2). The supraorbitals are fused with the dermosphenotic in Pachycormidae, forming one long bone lying along the frontal (LEHMAN, 1949: fig. 2; MAINWARING, 1978: figs 1, 2). Ligulellidae possess only one small supraorbital located at the nasal level (TAVERNE, 2011c: fig. 6, 7, 23). This loss of the posterior supraorbitals in *Ligulella* is probably due to the presence of strong spines on the lateral margin of the frontal. Pholidophoridae have generally two supraorbitals.

(5) Catervariolidae exhibit two or three large postorbitals (= suborbitals) behind the posterior infraorbitals (TAVERNE, 2011b: fig. 8, 2014a: fig. 4), as in Pachycormidae (LEHMAN, 1949: fig. 2; WENZ, 1967: fig. 53; MAINWARING, 1978: fig. 2), *Hulettia americana* (SCHAEFFER & PATTERSON, 1984: fig. 11) and *Prohalicetes porroi* (TINTORI, 1990: fig. 2). In Ligulellidae, the postorbitals are fused to the posterior infraorbitals (TAVERNE 2011c: fig. 6). In Pholidophoridae, there is only one large postorbital that sometimes is reduced to a series of smaller elements.

(6) Pholidophoridae exhibit a well developed leptolepid notch in the upper margin of the dentary. Such a notch is absent or very feebly marked in *Catervariolus* (TAVERNE, 2011b: fig. 27, 28). Pachycormidae and Ligulellidae do not possess a leptolepid notch (MAINWARING, 1978: fig. 4; TAVERNE, 2011c: fig. 22B, C). A leptolepid notch also is missing in *Hulettia americana* (SCHAEFFER & PATTERSON, 1984: fig. 13) and in *Prohalicetes porroi* (TINTORI, 1990: fig. 4).

(7) There are three toothed coronoids associated with the lower jaw in *Catervariolus* (TAVERNE, 2011b: fig. 28), a situation similar to that of Pachycormidae with their series of toothed coronoids above the prearticular and all along the inner face of the dentary (MAINWARING, 1978: fig. 4). No coronoid bone has been mentioned in Pholidophoridae.

(8) The preopercle is narrow and crescent-shaped in Catervariolidae (TAVERNE, 2011a: fig. 8, 35, 2014a: fig. 4), exactly as in Ligulellidae (TAVERNE, 2011c: fig. 6), *Hulettia americana* (SCHAEFFER & PATTERSON, 1984: fig. 11) and many holostean fishes. Pachycormidae also possess a crescent-shaped preopercle but much broader (LEHMAN, 1949: fig. 2; MAINWARING, 1978: fig. 2). Pholidophoridae exhibit a more specialized preopercle, with an enlarged ventral part and a short dorsal branch.

Unless to invoke many reversions, this second series of eight characters, allied to those of the first series, clearly show that Catervariolidae occupy a more basal place than Pholidophoridae in the phylogeny of “Pholidophoriformes” (*contra* ARRATIA, 2013).

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