



**Osteology and phylogenetic relationships of *Majokia brasseuri* (Teleostei, Majokiiformes nov. ord.) from the continental Middle Jurassic (Stanleyville Formation) of Kisangani (Democratic Republic of Congo)**

**Ostéologie et relations phylogénétiques de *Majokia brasseuri* (Teleostei, Majokiiformes nov. ord.) du Jurassique moyen continental (Formation de Stanleyville) de Kisangani (République Démocratique du Congo)**

Louis TAVERNE \*

**Résumé :** L'ostéologie de *Majokia brasseuri*, un téléostéen ganoïde du Jurassique moyen continental (Formation de Stanleyville) de la République Démocratique du Congo, est décrite en détails. La région du museau est extrêmement spécialisée, avec un appareil de morsure qui implique la mâchoire inférieure, les os palatins et le dermobasihyal mais pas la mâchoire supérieure édentée. Les deux os nasaux les dermethmoïdes latéraux et le dermethmoid (= rostral) reposent sur un gigantesque mésethmoïde endochondral. Le supraoccipital est ossifié. L'épiotique porte une fosse dorsale. Le carré possède un processus osseux très développé. La série orbitaire comprend l'antorbitaire, cinq infraorbitaires porteurs d'un méplat suboculaire, le dermosphénotique et deux petits supraorbitaires mais pas de postorbitaire (= suborbitaire). La branche ventrale du préoperculaire est plus allongée que la dorsale. Les vertèbres sont complètement ossifiées et ornementées d'alvéoles. Il y a des épineuraux ossifiés. Les nageoires pectorales et ventrales portent des fulcres frangeants. Le squelette caudal est composé de quatre hypuraux dont les trois premiers sont hypertrophiés. Les flancs sont couverts par une série de 32 écailles ganoïdes très hautes. La ligne latérale passe dans la rangée de petites écailles directement sous-jacentes aux hautes écailles des flancs. Les caractères très particuliers et très spécialisés de *Majokia brasseuri* sont inconnus dans les autres lignées de « Pholidophoriformes » *sensu lato* et justifient amplement l'érection pour ce poisson d'un nouvel ordre téléostéens ganoïdes: les Majokiiformes.

Mots-clés: Teleostei, Majokiiformes *nov. ord.*, *Majokia brasseuri*, ostéologie, relations phylogénétiques, Jurassique moyen continental, Formation de Stanleyville, Kisangani, République Démocratique du Congo.

**Abstract :** The osteology of *Majokia brasseuri*, a ganoid teleost from the continental Middle Jurassic (Stanleyville Formation) of the Democratic Republic of Congo, is studied in details. The snout region is extremely specialized, with a biting apparatus involving the lower jaw, the palatine bones and the dermobasihyal but not the toothless upper jaw. The two nasals, the fused lateral dermethmoids and the dermethmoid (= rostral) are lying on a gigantic endochondral mesethmoid. The supraoccipital is ossified. There is a dorsal fossa on the epiotic. The quadrate bears a strongly developed bony process. The orbital series contains the antorbital, five infraorbitals with a subocular shelf, the dermosphenotic and two small supraorbitals but no postorbital (= suborbital). The ventral branch of the preopercle is more elongate than the dorsal one. The vertebrae are completely ossified. There are bony epineurals. The pectoral and ventral fins bear fringing fulcra. The caudal skeleton contains four hypurals, the first three being hypertrophied. The flanks are covered by a series of 32 very deep scales. The lateral line is deflected into the scale row located just below the deep scales. The very peculiar and very specialized characters of *Majokia brasseuri* are unknown in the other lineages of "Pholidophoriformes" and amply justify the erection of a new order of ganoid teleosts for this fish: the Majokiiformes.

Key words: Teleostei, Majokiiformes *nov. ord.*, *Majokia brasseuri*, osteology, phylogenetic relationships, continental Middle Jurassic, Stanleyville Formation, Kisangani, Democratic Republic of Congo.

## INTRODUCTION

The continental Middle Jurassic Stanleyville Formation (Aalenian-Bathonian, cf. COLIN, 1994: 34) is located in the southern neighbourhood of Kisangani, a city of the north-eastern region of the Democratic Republic of Congo. These geological layers have revealed one of the world richest ichthyofaunas for the Jurassic period. These fossil fishes were firstly studied more than a half century ago. Three monographs were edited at that time (DE SAINT-SEINE, 1950, 1955; DE SAINT-SEINE & CASIER, 1962). A more detailed study of this fish community is conducted since a few decades. Eleven papers are today published in this new series (TAVERNE, 1975, 2001, 2011a, b, c, 2014a, b, 2015a, b, 2017, 2019).

\* 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)

Numerous primitive Teleostei with ganoid scales are present in the fish fauna of the Stanleyville Formation. During almost a century, these Mesozoic ganoid teleosts from all over the world were ranged in the polyphyletic order “Pholidophoriformes” *sensu lato*. Today, the Pholidophoriformes *sensu stricto* contains only one family, the Pholidophoridae *sensu stricto* (ARRATIA, 2013).

Recently, ARRATIA (2017) erected the new family Eurycormidae for *Eurycormus speciosus* WAGNER, 1863 from the Late Jurassic of Germany. She included this new family in the Pholidophoriformes *sensu stricto* near the Pholidophoridae. At the same time, another systematic position for this German fossil fish was expressed by TAVERNE & CAPASSO (2017). In their recent study of the neopterygian phylogeny, LOPEZ-ARBARELLO & SFERCO (2018: fig. 8) also consider *Eurycormus speciosus* as not closely allied to the Pholidophoridae.

One small ganoid teleost from the Stanleyville Formation, *Majokia brasseuri*, exhibits a very peculiar skull. It is a small long-snouted fish known by only one specimen. The aim of the present paper is to re-describe this strange little fish in a more detailed way than previously and to determine its phylogenetic relationships.

## MATERIAL AND METHODS

The specimen hereafter described belongs to the paleontological collection of the Department of Geology and Mineralogy of the Royal Museum for Middle Africa (MRAC), Tervuren, Belgium. The material was studied with a Leica MZ8 stereomicroscope. The drawings of the figures were made by the author with a camera lucida and the photos by Mr. Stéphane HANOT, from the MRAC.

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

|           |   |  |
|-----------|---|--|
| ANT       | = | antorbital                                       |
| APAL      | = | autopalatine                                     |
| BR        | = | branchial bones                                  |
| BRSTG     | = | branchiostegal rays                              |
| CH        | = | notochord  |
| CLT       | = | cleithrum  |
| DBHY      | = | dermobasihyal                                    |
| DETH      | = | dermethmoid (= rostral)                          |
| DN        | = | dentary  |
| DPAL      | = | dermopalatine                                    |
| DPTE      | = | dermopterotic                                    |
| DSPH      | = | dermosphenotic                                   |
| EPI       | = | epiotic (= epioccipital)                         |
| EPIN      | = | epineural  |
| FR        | = | frontal  |
| HCLT      | = | hypercleithrum (= supracleithrum)                |
| HP        | = | haemal spine                                     |
| HY 1-4    | = | hypurals 1 to 4                                  |
| HYOM      | = | hyomandibula                                     |
| IOP       | = | interopercle                                     |
| IORB 1-5  | = | infraorbitals 1 to 5                             |
| LDETH     | = | lateral dermethmoid                              |
| LEP       | = | fin ray (= lepidotrichia)                        |
| METH      | = | mesethmoid                                       |
| MPT       | = | metapterygoid                                    |
| MU        | = | muscles  |
| MX        | = | maxilla  |
| NA        | = | nasal  |
| OP        | = | opercle  |
| PA        | = | parietal   |
| PCLT 1, 2 | = | postcleithra 1 and 2                             |
| PMX       | = | premaxilla                                       |
| POP       | = | preopercle                                       |
| PT        | = | posttemporal                                     |
| QU        | = | quadrate   |
| SC        | = | scale  |
| SCA       | = | hypercoracoid (= scapula)                        |
| SCU       | = | caudal scute of the upper lobe of the caudal fin |
| SMX 1, 2  | = | supramaxillae 1 and 2                            |
| SOC       | = | supraoccipital                                   |
| SOP       | = | subopercle                                       |

|           |   |                                  |
|-----------|---|----------------------------------|
| SORB 1, 2 | = | supraorbitals 1 and 2            |
| ST        | = | supratemporal (= extrascapular)  |
| SY        | = | symplectic                       |
| V         | = | vertebra                         |
| b. fu.    | = | basal fulcra                     |
| br.       | = | broken                           |
| ep. f.    | = | dorsal fossa on the epiotic      |
| ex. c.    | = | extrascapular sensory commissure |
| fr. fu.   | = | fringing fulcra                  |
| gr.       | = | grooves on the autopalatine      |
| iorb. c.  | = | infraorbital sensory canal       |
| l.        | = | left                             |
| l. l. c.  | = | lateral line sensory canal       |
| ot. c.    | = | otic sensory canal               |
| p. l.     | = | pit-line                         |
| pop. c.   | = | preopercular sensory canal       |
| q. pr.    | = | bony process of the quadrate     |
| r.        | = | right                            |
| sorb. c.  | = | supraorbital sensory canal       |

## SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii KLEIN, 1885  
 Series Neopterygii REGAN, 1923  
 Division Teleostei MÜLLER, 1845  
 Order Majokiiformes *nov. ord.*

### **Diagnosis**

The same as the family (only one family in the order)

Family Majokiidae DE SAINT-SEINE, 1955

### **Diagnosis**

The same as the genus (monogeneric family)

Genus *Majokia* DE SAINT-SEINE, 1955

### **Diagnosis**

The same as the species (monospecific genus)

Species *Majokia brasseurii* DE SAINT-SEINE, 1955

### **Emended diagnosis**

Small ganoid teleost. Dermal bone of the skull covered by a thin layer of ganoin but not ornamented. Endochondral mesethmoid strongly hypertrophied. Fused toothless lateral dermethmoids, dermethmoid (= rostral) and nasals lying on the mesethmoid. No rostral sensory commissure on the dermethmoid. Nasals large and not meeting on the mid-line. Biting apparatus involving the lower jaw, the palatine bones and the dermobasihyal but not the upper jaw. One large symphyseal tooth on the dentary. Two large teeth on the dermopalatine. Autopalatine very elongate and bearing grooves for muscles insertion. Upper jaw short, deep and toothless. First supramaxilla reduced. Second supramaxilla hypertrophied. Medio-parietal skull. Supraoccipital ossified. A dorsal fossa present on the epiotic. Quadrate with a strongly developed bony process. One antorbital, five short infraorbitals, one dermosphenotic, two small supraorbitals and no postorbital (= suborbital). Infraorbitals with a wide subocular shelf. Preopercle with an elongate ventral branch. Opercle large and ovoid. Spines on the preopercle, the interopercle and the subopercle. Supraorbital and otic sensory canals not in contact. A vertical pit-line on the dermopterotic. Dermobasihyal elongate, narrow, toothed and reaching the symphysis. Small cleithrum triangular in shape. Two postcleithra. Pectoral fin elongate, with one impair basal fulcrum. First pectoral ray segmented in the distal region, with fringing fulcra fused to the basal portion and free fringing fulcra associated to the segmented region. Vertebrae completely ossified, ornamented with alveoli (autocentra present).

Ossified epineurals. Caudal skeleton with 4 hypurals, three strongly enlarged and one narrow. Flank scales of the middle region extremely deep, some with weakly marked denticles on the posterior margin. 32 deep scales along the body. Lateral line canal deflected into the scale row just below the deep scales.

### Holotype and only specimen

Specimen MRAC RG 7871: a nearly complete specimen (Fig. 1). The caudal fin is missing. Total length: 60 mm.



**Figure 1.** *Majokia brasseurii* DE SAINT-SEINE, 1955. Holotype MRAC RG 7871. The scale is in centimetre.

### Other material

DE SAINT-SEINE (1955: 107) also mentions a paratopotype (specimen MRAC RG 7545a, b) from the Mekombi river. However, this badly preserved sample differs from *Majokia brasseurii* by the shape of its preopercle and of its cleithrum and by its ring-like vertebrae. This specimen does not belong to *Majokia brasseurii* but to the family Pleuropholidae, one of the numerous lineages of “pholidophoriform” fishes.

### Formation and locality

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

### Osteology

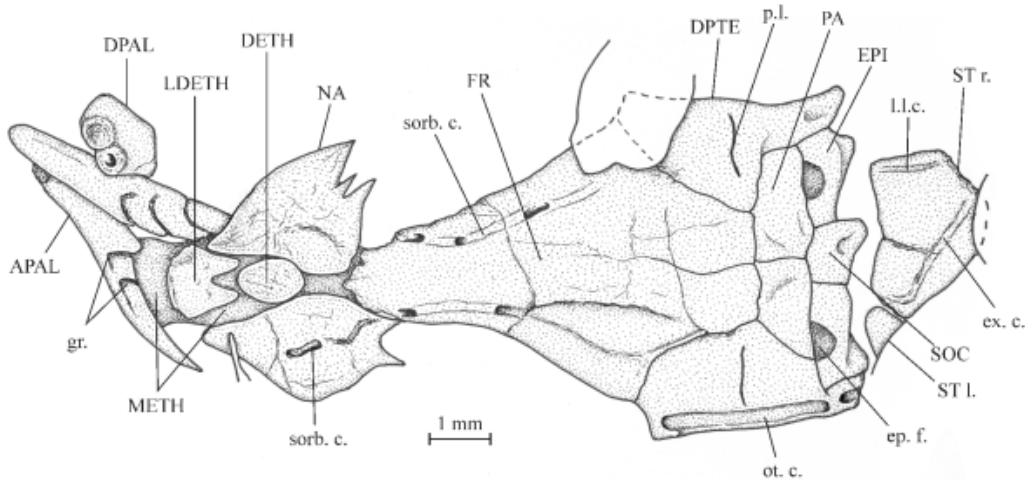
#### *The skull* (Figs 2-5)

The skull is preserved in dorsal view. The dermal bones are covered by a thin layer of ganoine but are not ornamented. The bones of the endocranium are not visible, except the mesethmoid.



**Figure 2.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Head region of holotype MRAC RG 7871. The scale is in millimetre.

The very elongate snout is highly specialized and was completely misunderstood by DE SAINT-SEINE (1955). A long, broad, massive endochondral mesethmoid occupies the middle of the snout region and is partly covered by the two nasals on its lateral sides and by the frontals posteriorly. Two small dermal bones are lying on the dorsal face of this mesethmoid. The anterior bone is formed by a pair of small, fused and toothless lateral dermethmoids, with a rounded anterior margin and two short posterior processes. The posterior bone is the ovoid dermethmoid (= rostral). This small dermethmoid is devoid of rostral sensory commissure. The tip of the snout is formed by the highly specialized palatine bones that are located between the two halves of the upper jaw and anterior to the mesethmoid. This anterior and well exposed position of the palatine bones is totally unusual. The two autopalatines (“rostraux latéraux” in DE SAINT-SEINE, 1955: fig. 85) are pressed the one against the other. They are very elongate and thick bones, with a long acuminate posterior extremity. They bear two or three well marked groves on their external side, just at the level of the anterior margin of the mesethmoid. The right dermopalatine is the only one visible. It is an ovoid massive bone much smaller than the autopalatine. It is turned upside down due to the fossilisation and is located against the right autopalatine. But its normal position certainly was just below the autopalatine. The oral side of this right dermopalatine bears two large tooth sockets but the fang-like teeth are not preserved. The nasals are wide bones, with a pointed anterior extremity and two or three spines on their posterior margin. The two bones do not meet on the mid-line, a small part of the subjacent mesethmoid remaining visible between them posterior to the dermethmoid. The anterior part of the supraorbital sensory canal is clearly visible on the left nasal. The vomer and the lateral ethmoids are hidden by the other bones of the snout. It is possible that the lateral ethmoids are integrated in the extremely massive mesethmoid. A hypothesis concerning the functional morphology of this strange snout is proposed in the chapter “Discussion”.



**Figure 3.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Ethmo-palatine region and skull roof of holotype MRAC RG 7871.

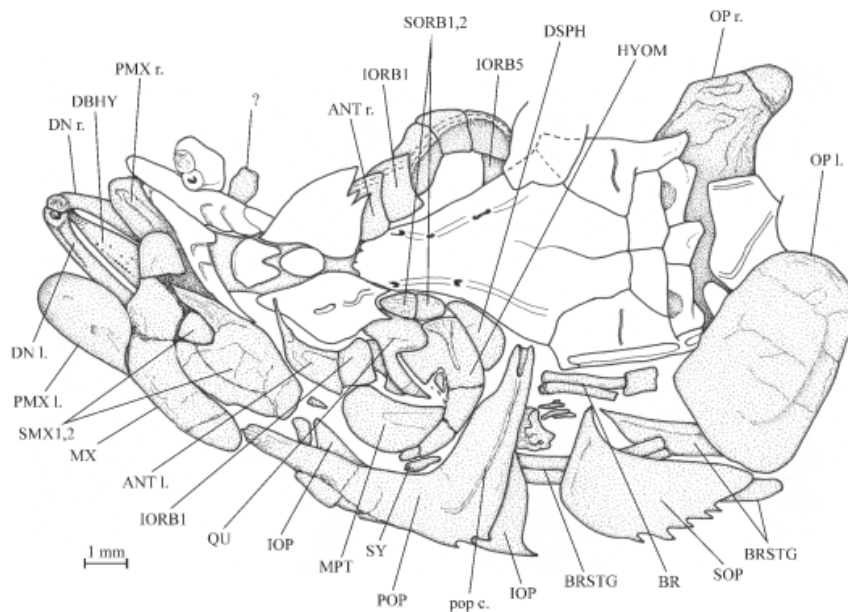
The skull roof is composed of three paired bones, the frontal, the parietal and the dermopterotic. The anterior region is narrow but the width of the skull roof increases posteriorly and the postorbital region is much broader. The two frontals are fused together in the anterior region but a suture between the two bones subsists in the posterior area. Anteriorly, the two bones are rather narrow but they broaden at the level of their middle

region. The posterior region of the frontals is narrower and surrounded by the dermopterotics. The supraorbital sensory canal is visible on the frontal. It bears a few pores. The two parietals meet on the mid-line (medioparietal skull). They do not bear pit-lines. The dermopterotic is a large bone. It has a process at its posterior external corner. An open otic sensory canal is visible along the external margin of the left dermopterotic. There is no connexion between the supraorbital and the otic canals. The dermopterotic also bears a vertical pit-line.

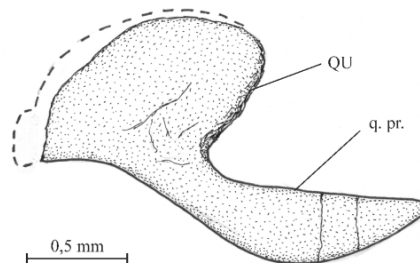
Three bones, the two epiotics (= epioccipitals) and the supraoccipital, are visible behind the parietals. A small fossa is present on the dorsal side of each epiotic as in many fossil osteoglossid fishes (TAVERNE, 1978: figs 3, 4, 16, 21, 22; among others). The supraoccipital is smaller than the epiotic and it forms a slightly marked posterior protuberance.

A small part of the left supratemporal and the complete right supratemporal are preserved behind the braincase. It is a large triangular bone bearing the extrascapular sensory commissure and the beginning of the lateral line sensory canal located along its basal margin.

Two elements of the palato-quadrate arch are visible on the left side of the skull. The quadrate is displaced in the orbit, due to the fossilization. Its articular condyle and its anterior margin are hidden by the nasal and the supraorbitals. A long and strong bony process is fused with the posterior ventral corner of the bone. The metapterygoid, located just before the hyomandibula and above the ventral branch of the preopercle, is longer than deep.



**Figure 4.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Skull and suspensorium of holotype MRAC RG 7871. The captions of the bones shown in Fig. 3 are not mentioned in Fig. 4.



**Figure 5.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Left quadrate of holotype MRAC RG 7871.

The toothless upper jaw is well preserved on the left side of the skull. The premaxilla is a large and deep bone, with a straight lower margin and rounded anterior and dorsal borders. There is no symphyseal upper process. The maxilla is broken in three fragments. The bone is rather short, deep and curved. There are two supramaxillae. The first one is very small and almost completely surrounded by the hypertrophied second supramaxilla that bears a long pointed anterior process. The anterior region of the two dentaries is the only

visible part of the lower jaw. This dentary is narrow and toothless, except at its symphyseal extremity that bears a large socket for a lost fang-like tooth.

The orbital series contains one antorbital, five infraorbitals, one dermosphenotic and two supraorbitals but no postorbital (= suborbital). The right antorbital is partly covered by the nasal but the left antorbital is complete though partly broken. The anterior part of the bone is elongated in a long and thin process that reaches the rostral region. The five infraorbitals are rather short and they exhibit a wide subocular shelf. The third and the fourth infraorbitals are not larger than the other pieces of the series. The dermosphenotic is well developed. The two supraorbitals are small. The first one is ornamented with weakly marked ridges. The infraorbital sensory canal is visible on the antorbital and the first four infraorbitals on the right side of the skull.

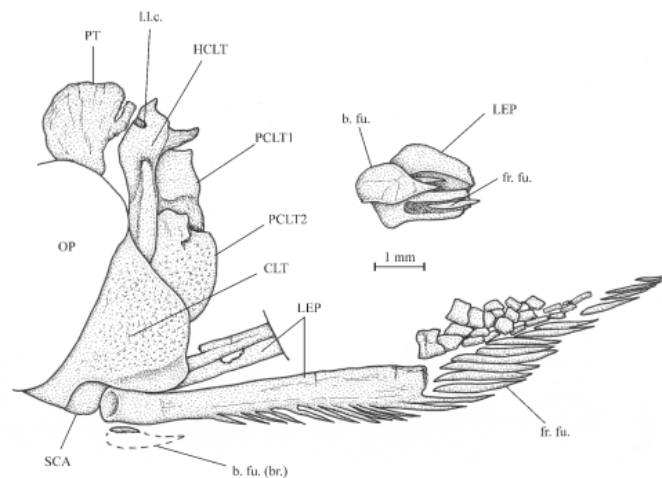
The preopercle is composed of two long branches, the lower one being very elongate. The bone bears three small spines on its posterior ventral corner. The preopercular sensory canal is visible on the dorsal branch. The opercle is a large bone, more or less ovoid and a little broader in its lower region than more dorsally. The subopercle is wide, with a small ascending process on its anterior dorsal corner and five spines on its ventral margin. The interopercle is a long element partly covered by the preopercle. It has a spine on its posterior ventral corner. Some fragments of branchiostegal rays are visible but no gular plate.

The hyomandibula is a rather large bone. Its articular head is partly hidden by the dermosphenotic. There is a small anterior wall in its upper region. Its ventral branch is curved and the lower extremity is acuminate. A small bone located between the lower extremity of the hyomandibula and the upper margin of the preopercle probably is a fragment of the symplectic. A long and narrow dermobasihyal (= dermentoglossum), bearing a few small teeth sockets, is visible between the two dentaries. The bone reaches the symphysis. There are some fragments of branchial bones and branchiospines preserved below the left dermosphenotic.

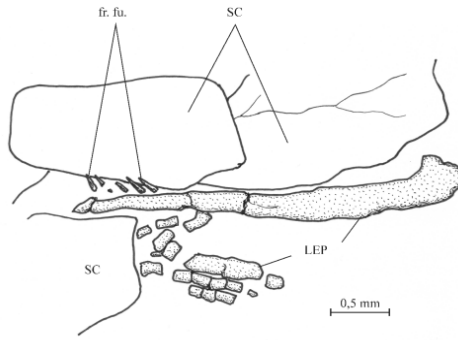
### ***The girdles*** (Figs 6, 7)

The left pectoral girdle is almost completely preserved. The posttemporal is a large bone. The hypercleithrum is deep and narrow, with a median crest in its lower part and a small posterior process in its upper region. The lateral line sensory canal is visible at the top of the bone. There are two postcleithra, the ventral one being wider than the dorsal. The cleithrum is triangular in shape but rather small. It bears a notch in its lower margin in which a small knob-like hypercoracoid (= scapula) is visible. The lower postcleithrum and the cleithrum are ornamented with small tubercles. No trace of a hypocoracoid (= coracoid *sensu stricto*) is visible. If this bone exists, it would be strongly reduced and completely hidden by the cleithrum. There is no clavicle. A small part of the right pectoral fin is displaced on the right margin of the skull, at the level of the suture between the frontal and the dermosphenotic. The fin begins with a short impar basal fulcrum with a broad basis and an acuminate dorsal extremity. The first three rays and a small fragment of the basal fulcrum of the left pectoral fin are also preserved. The first ray is stronger than the two following ones. Its distal part is segmented. A series of fringing fulcra are fused to the basal part of the ray. The fringing fulcra are free at the level of the segmented part of the ray.

The pelvic bones are hidden by the scales. The ventral fins are incompletely preserved. Only one complete ray and some fragments of another ray are visible. The complete ray is not segmented and it bears a few small fringing fulcra.



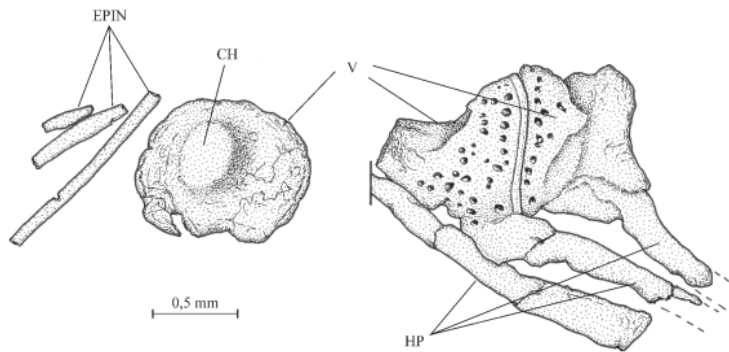
**Figure 6.** *Majokia brasseuri* DE SAINT-SEINE, 1955. (A) Left pectoral girdle of holotype MRAC RG 7871. (B) The small displaced part of the right pectoral fin showing the basal fulcrum.



**Figure 7.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Fragment of the ventral fin of holotype MRAC RG 7871.

***The axial skeleton*** (Fig. 8)

Two vertebrae are visible between the scales, above the anal fin. A third vertebra is preserved a little before that level. These vertebrae are strongly ossified. The notochord is slightly constricted. The lateral face is ornamented with numerous small alveoli. This well marked ornamentation indicates that autocentra surround the chordacentra. Strong haemal spines are fused to the centra. Fragments of long and thin bones, the epineurals, are visible near the first preserved vertebra.

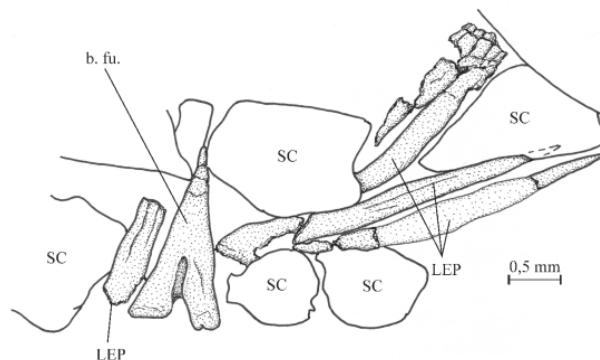


**Figure 8.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Three vertebrae of holotype MRAC RG 7871.

***The dorsal and anal fins*** (Fig. 9)

No trace of a dorsal fin is visible. The fin perhaps was lost during the fossilization. It is also possible that *Majokia* was devoid of dorsal fin.

Some fragments of the anal fin are preserved below the eighteenth, the nineteenth and the twentieth rows of scales. There is one impar basal fulcrum, with a large and bifid base and an acuminate upper extremity and fragments of at least five rays. The first two long rays are pointed and not segmented. No fringing fulcrum is present but this apparent absence perhaps is due to the bad preservation of the fin.

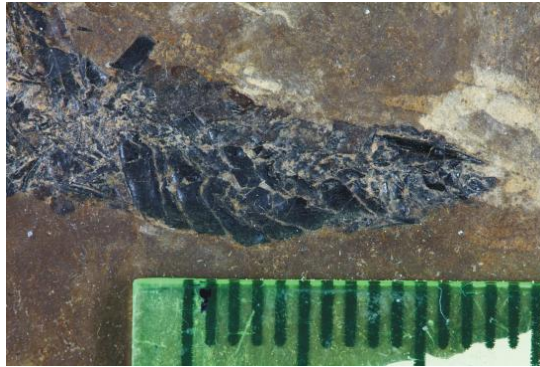


**Figure 9.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Beginning of the anal fin of holotype MRAC RG 7871.

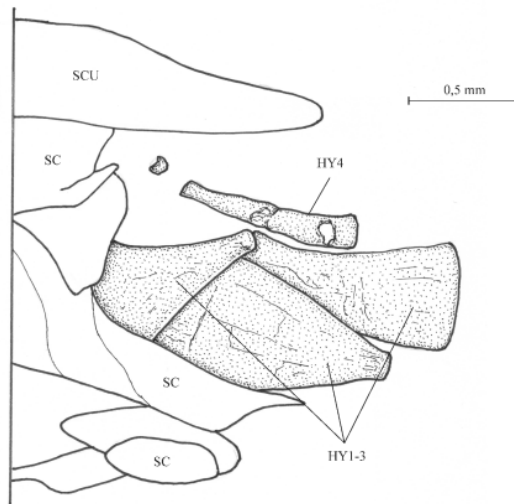


**The caudal skeleton** (Figs 10-12)

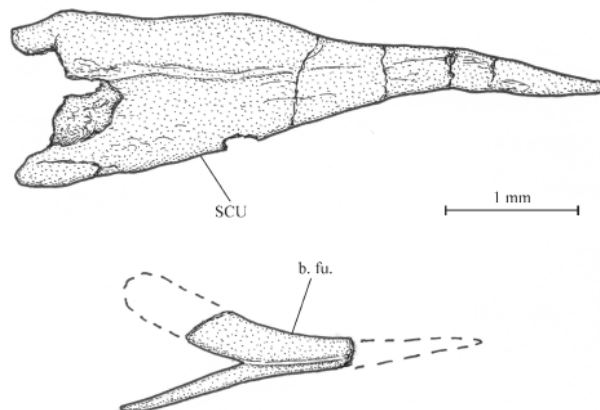
Four hypurals are preserved but they are displaced because of the fossilization. The first three are strongly broadened, while the fourth one remains narrow. The other caudal bones and the caudal fin are missing.



**Figure 10.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Caudal region of holotype MRAC RG 7871. The scale is in millimetre.



**Figure 11.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Caudal endoskeleton of holotype MRAC RG 7871.

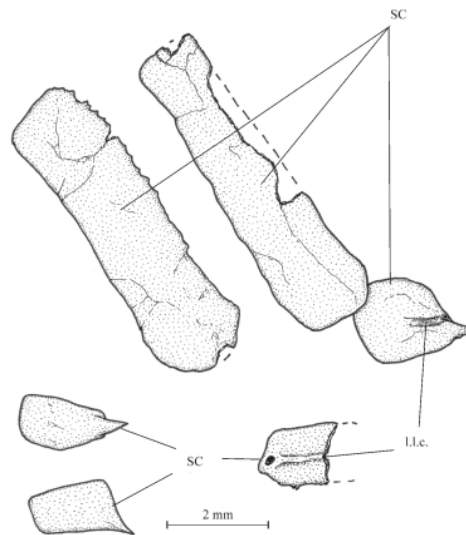


**Figure 12.** *Majokia brasseuri* DE SAINT-SEINE, 1955. (A) Dorsal caudal scute and (B) ventral basal fulcrum of the caudal fin of holotype MRAC RG 7871.

### *The squamation* (Fig. 13)

All scales are covered by a layer of ganoine and exhibit a smooth surface. No trace of a peg-and-socket system of articulation is visible. The scales of the middle region of the flanks are extremely deep but do not bear the lateral line sensory canal, as is the case in the Pleuropholidae. Weakly marked denticles are visible on the posterior margin of some of these deep scales. There are 32 deep scales along the body. The other scales are much smaller and often have a spine at their posterior ventral corner. The lateral line canal crosses the rank of small ventral scales that are located immediately under the deep flank scales.

An elongate and broad caudal scute, with an acuminate posterior extremity, is preserved in the dorsal region of the tail. Ventrally, a large basal fulcrum, with a bifid posterior extremity, is also visible.



**Figure 13.** *Majokia brasseuri* DE SAINT-SEINE, 1955. (A) Flank scales. (B) Dorsal scales. (C) Ventral scale bearing the lateral line sensory canal.

## DISCUSSION

### The relationships of *Majokia* within Neopterygii

The presence of a well developed interopercle attests that *Majokia* belongs to Neopterygii.

*Majokia* has two supraorbitals, two supramaxillae, the lateral dermethmoids separated from the premaxillae, an interopercle almost totally covered by the preopercle, a bony endochondral mesethmoid partly covered by the dermethmoid (= rostral), the fused lateral dermethmoids and the nasals, a well developed supraoccipital, a toothed dermobasihyal, a large bony process on the quadrate, epineurals and ganoid scales. The mixed presence of these osteological features indicates that the relationships of the Congolese fish are to be found within the basal teleosts of the “pholidophoriform” assemblage.

### *Majokia* and the Pleuropholidae

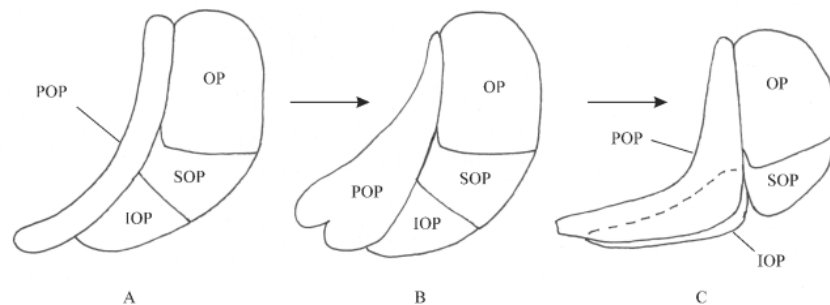
*Majokia* and Pleuropholidae share a very peculiar character unknown in other “Pholidophoriformes”. Their flank scales are extremely deep but do not bear the lateral line sensory canal, except for the first ones. The canal is deflected into the scale-row just below these deep flank scales. Moreover, *Majokia* exhibits short jaws, a deep upper jaw and a preopercle with the ventral branch longer than the dorsal one as in *Pleuropholis* EGERTON, 1858, the type-genus of the family Pleuropholidae (PATTERSON, 1973, fig. 16).

However, in this case, these specialized features seem to be homoplasies and not synapomorphies that would unit the two lineages. Indeed, *Majokia* and Pleuropholidae differ by many important characters and could not be close relatives. Pleuropholidae exhibit a normal morphology of the snout (PATTERSON, 1973: fig. 16; TAVERNE & CAPASSO, 2015: fig. 10 [right], 2019: figs 6, 7, 10). Their lateral dermethmoids are reduced and fused to the dermethmoid (= rostral), forming a pair of lateral processes (TAVERNE, 2015b: fig. 9). They have one large postorbital (= suborbital), only one reduced supramaxilla, ring-like vertebrae and narrow hypurals in

the caudal endoskeleton (PATTERSON, 1973: figs 16, 17; BRAVI, 1988: fig. 3; BRITO & GALLO, 2002: fig. 4; ALVARADO-ORTEGA & BRITO, 2016: figs 1B, 3).

#### The systematic position of *Majokia* within “Pholidophoriformes” (Fig. 14)

In the hypotheses of phylogeny proposed by TAVERNE (2011a, b, 2014a, b, 2015b) and by LÓPEZ-ARBARELLO & SFERCO (2018) for the “Pholidophoriformes” *sensu lato*, Catervariolidae are positioned as the most basal lineage of the all group. Fishes of this family still have toothed lateral dermethmoids occupying the symphysis, premaxillae located posterior to the symphysis, only one small supramaxilla, a weakly marked “leptolepid” notch on the dentary, three coronoids in the lower jaw, three supraorbitals, two or three large postorbitals completely separating the infraorbitals from the opercular series, a crescent-like preopercle and a few other primitive characters (TAVERNE, 2011b, 2014a, 2015b).



**Figure 14.** Opercular series (A) in the ganoid teleosts with a crescent-like preopercle (Catervariolidae, Ichthyokentemidae, Signeuxellidae), (B) in ganoid teleosts with a preopercle ventrally enlarged (Pholidophoridae and most “pholidophoriform” fishes) and (C) in teleosts with a preopercle divided in two branches and covering the interopercle (*Majokia*, Pleuropholididae, teleosts with cycloid scales).

Ichthyokentemidae are joined to Catervariolidae in LÓPEZ-ARBARELLO & SFERCO (2018: fig. 8). Indeed, they share many of the primitive characters known in Catervariolidae but have the ventral postorbital fused to the fourth infraorbital, only one coronoid and a well marked “leptolepid” notch (GRIFFITH & PATTERSON, 1963; GRIFFITH, 1977; PATTERSON, 1975).

Signeuxellidae also have fused toothed lateral dermethmoids located at the symphysis, small premaxillae laterally positioned, only one supramaxilla and a crescent-like preopercle (TAVERNE, 2017).

Ankylophoridae, Pholidophoridae, Eurycormidae, Dorsetichthyidae and most other “pholidophoriform” fishes represent a more evolved subgroup in which there are two supramaxillae, only two supraorbitals, an enlarged third infraorbital reaching the preopercle, never more than one large postorbital and a preopercle that is no more crescent-like (RAYNER, 1948; NYBELIN, 1966; PATTERSON, 1973; TAVERNE, 2011a, 2014b, 2018; TAVERNE & CAPASSO, 2017; TAVERNE & STEURBAUT, 2017; ARRATIA, 2013, 2017; among others). The osteological characters of *Majokia* show that the genus belongs to this subgroup.

Pholidophoridae and most “pholidophoriform” fishes exhibit a preopercle that has a narrow upper region and a broadened lower region and, thus, that is not crescent-like. However, the interopercle is always completely or almost completely exposed below the preopercle and the supraopercle in the ganoid teleosts with a crescent-like preopercle as in those with a ventrally enlarged preopercle (Fig. 14 A, B). In teleosts with cycloid scales, the morphology of the opercular series is more advanced. The preopercle is generally composed of two branches, one ventral and one dorsal, and a major part of the interopercle is covered and hidden by the ventral branch of the preopercle (Fig. 14 C). *Majokiidae* and *Pleuropholididae* share this apomorphic character. Within the “pholidophoriform” assemblage, these two families seem thus more closely related to the cycloid teleosts than are the other lineages of the group.

*Pleuropholididae* have ring-like vertebrae that are devoid of autocentra as in other “pholidophoriform” fishes. *Majokia* exhibits strongly ossified vertebrae that constrict the notochord. Such a shape of the centra is closer to that of the cycloid teleosts than to the vertebral morphology of the other “Pholidophoriformes”. Moreover, autocentra are present in the vertebrae of *Majokia*. The presence of autocentra is generally considered as an apomorphy shared by *Leptolepididae* and the more evolved teleosts (ARRATIA *et al.*, 2001: 147).

The conclusion seems clear. Within all the ganoid fishes of the “pholidophoriform” assemblage, *Majokia* is the most closely related genus to the teleosts with cycloid scales.

#### The “Pholidophoriformes” and the erection of the new order *Majokiiformes*

The break-up of the old polyphyletic and heterogenous order “Pholidophoriformes” is now largely begun. Today, Pholidophoriformes *sensu stricto* are restricted to the unique family Pholidophoridae (ARRATIA, 2013). ARRATIA (2017) also includes the Eurycormidae in the Pholidophoriformes *sensu stricto* but, as previously mentioned, that systematic position is challenged by TAVERNE & CAPASSO (2017) and by LÓPEZ-ARBARELLO & SFERCO (2018). Several new orders were recently erected to accommodate some subgroups formerly ranged in the “Pholidophoriformes” *sensu lato*: Ligulelliformes, Catervarioliformes, Ankylophoriformes and Dorsetichthyiformes (TAVERNE, 2011a, b, c, 2014a, b; NELSON *et al.*, 2016).

However, many genera and families in need of revision or incompletely known are still confined in the “Pholidophoriformes” *sensu lato* or left order *incertae sedis* (cf. KONWERT & HORNIG, 2018; among others).

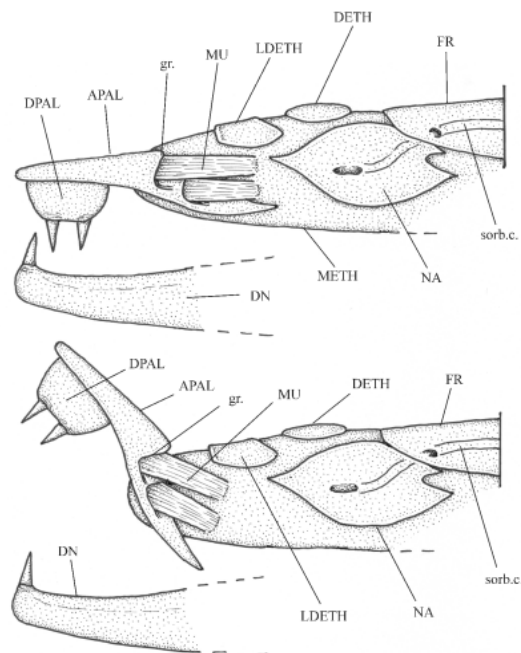
That was the case of *Majokia* until now. But, today, we know that *Majokia* greatly differs from all the other known lineages of the “pholidophoriform” assemblage. The anatomy of its snout and of its biting apparatus is absolutely unique within the group. Its strongly ossified vertebrae with autocentra, the shape of its infraorbitals, the loss of the postorbitals and its three hypertrophied hypurals are other major differences.

*Majokia* is already the unique member of a peculiar family, the Majokiidae. But all these highly specialized features characterizing this Congolese fossil fish clearly show that the genus certainly deserves the erection of a peculiar order, the Majokiiformes.

### Functional morphology of the snout of *Majokia* (Fig. 15)

As already written, *Majokia* has a highly specialized snout and a peculiar biting apparatus involving the lower jaw, the dermopalatines and the dermobasihyal but not the upper jaw.

A large tooth is present at the symphyseal extremity of each dentary and two large teeth on each dermopalatine. The two dental and the four palatine teeth form a double hook-like gripper. The grooves on the dorsal side of the autopalatines allow the insertion of muscles also attached to the gigantic mesethmoid. When these muscles are contracted and shortened, they raise up the all palatal complex. When the contraction stops, the palatal complex abruptly comes down and the preys are harpooned between the dental and the palatine fang-like teeth. The work of these muscles needs to be attached on a very strong piece. That explains the extreme hypertrophy of the mesethmoid. After the capture, the smaller teeth of the dermobasihyal, perhaps coupled with vomerian teeth, could tear up the preys in pieces. The short, toothless but extremely deep upper jaw could operate as the blade of an axe, carving bigger preys in smaller fragments easier to gulp down.



**Figure 15.** *Majokia brasseuri* DE SAINT-SEINE, 1955. Reconstruction of the snout region. The action of the palatine bones during the capture of preys is shown. Above: the rest position. Below: the erected position. The upper jaw is removed to allow a better view of the mechanism.

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