Osteology and relationships of *Songaichthys luctacki* gen. and sp. nov. (Teleostei, Ankylophoriformes ord. nov.) from the Middle Jurassic (Songa Limestones) of Kisangani (Democratic Republic of Congo)

Ostéologie et relations de *Songaichthys luctacki* gen. et sp. nov. (Teleostei, Ankylophoriformes ord. nov.) du Jurassique moyen (Calcaires de Songa) de Kisangani (République Démocratique du Congo)

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Abstract: The osteology of *Songaichthys luctacki* gen. and sp. nov., an archaic teleost with ganoid scales from the Middle Jurassic (Stanleyville Formation, Songa Limestones) of the Democratic Republic of Congo, is studied in details. Its large lateral dermethmoid located at the upper jaw symphysis, its two supramaxillae, the elongated shape of its lower jaw and its other cranial characters show that it belongs to the family Ankylophoridae. It notably differs from *Steurbautichthys* (« *Pholidophorus* ») *aequatorialis*, another ankylophorid fish from the same Congolese deposits, and from the other genera of the family. It deserves thus its peculiar generic status. The break-up of the polyphyletic order "Pholidophoriformes" into monophyletic lineages is continued by the creation of the new order Ankylophoriformes for the family Ankylophoridae.

Key words: Teleostei, Ankylophoriformes ord. nov., Songaichthys luctacki gen. and sp. nov., osteology, relationships, Middle Jurassic, Stanleyville Formation, Songa Limestones, Democratic Republic of Congo.

Résumé: L'ostéologie de Songaichthys luctacki gen. et sp. nov., un téléostéen archaïque à écailles ganoïdes du Jurassique moyen (Formation de Stanleyville, Calcaires de Songa) de la République Démocratique du Congo, est étudiée en détails. Son vaste latérodermethmoid situé à la symphyse de la mâchoire supérieure, ses deux supramaxillaires, la forme allongée de sa mandibule et ses autres caractères crâniens montrent qu'il appartient à la famille des Ankylophoridae. Il diffère notablement de Steurbautichthys (« Pholidophorus ») aequatorialis, un autre poisson ankylophoridé du même gisement congolais, et des autres genres de la famille. Il mérite donc son statut générique particulier. Le démembrement de l'ordre polyphylétique des « Pholidophoriformes » en lignées monophylétiques est poursuivi par la création du nouvel ordre des Ankylophoriformes pour la famille des Ankylophoridae.

Mots-clés: Teleostei, Ankylophoriformes ord. nov., Songaichthys luctacki gen. et sp. nov., ostéologie, relations, Jurassique moyen, Formation de Stanleyville, Calcaires de Songa, République Démocratique du Congo.

INTRODUCTION

The Stanleyville Formation (Kisangani) in the Democratic Republic of Congo (DRC), originally reported to the Kimmeridgian (Late Jurassic), is now considered as Aalenian-Bathonian (Middle Jurassic) on the basis of its ostracode fauna and palynological assemblages (COLIN, 1994: 34).

The Stanleyville Formation contains an important fossil fish fauna that was firstly studied more than a half century ago in three small monographs (DE SAINT-SEINE, 1950, 1955; DE SAINT-SEINE & CASIER, 1962) and is progressively revised in a more detailed anatomical way (TAVERNE, 1975, 2001, 2011a, b, c, in press).

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This ichthyofauna is particularly rich in archaic teleosts with ganoid scales. Six families and nine genera are present in the Middle Jurassic deposits of the DRC, i. e. Catervariolidae with *Catervariolus* DE SAINT-SEINE, 1955 and *Songanella* DE SAINT-SEINE & CASIER, 1962, Ankylophoridae with *Steurbautichthys* TAVERNE, 2011, Pleuropholidae with *Pleuropholis* EGERTON, 1858, *Parapleuropholis* DE SAINT-SEINE, 1955 and *Austropleuropholis* DE SAINT-SEINE, 1955, Lombardinidae with *Lombardina* DE SAINT-SEINE, 1955, *Signeuxellidae* with *Signeuxella* DE SAINT-SEINE, 1955 and Majokiidae with *Majokia* DE SAINT-SEINE, 1955.

Until now only the catervariolid *Catervariolus* and *Songanella* and the ankylophorid *Steurbautichthys* have been re-studied in a modern manner (TAVERNE, 2011a, b, in press). The other Congolese ganoid teleosts still need a revision.

The Mesozoic teleosts with ganoid scales from all around the world are traditionally ranged within "Pholidophoriformes", a polyphyletic and highly heterogenous order containing many genera not always closely related together but close to the "classical" primitive teleosts with cycloid scales, i. e. *Leptolepis coryphaenoides* (BRONN, 1830) and more advanced species. Recent papers (ARRATIA, 2000; ARRATIA & SCHULTZE, 2007; TAVERNE, 2011a, b, in press) slowly allow a better understanding of the "pholidophoriform" taxonomic problems. The break-up of this polyphyletic and artificial order in monophyletic lineages is now necessary. TAVERNE (in press) has begun that dismemberment by removing Catervariolidae from the "Pholidophoriformes" and innovating for this primitive family the new order Catervarioliformes. The present paper continues that needed break-up by the creation of the new order Ankylophoriformes for the Ankylophoridae (*sensu* TAVERNE, 2011a), another "pholidophoriform" family.

One specimen of archaic teleost seen by DE SAINT-SEINE and CASIER was not included in their monograph (1962) because of a rather bad preservation. They simply wrote on the accompanying label that it could probably be a juvenile sample of the species *Pholidophorus aequatorialis* DE SAINT-SEINE & CASIER, 1962, now the type-species of the genus *Steurbautichthys*. The aim of the present paper is to describe that specimen, to compare with *Pholidophorus sensu stricto* and *Steurbautichthys aequatorialis* and to determine its true relationships.

MATERIAL AND METHODS

The sample of *Songaichthys luctacki* belongs to the paleontological collections of the Department of Geology of the Royal Museum for Central Africa (MRAC), Tervuren, Belgium. It has been studied with a stereomicroscope Leica MZ8. The drawings of the figures were made by the author with a *camera lucida*. Aspersions with ethanol were used to improve the observations.

SYSTEMATIC PALEONTOLOGY

Division Teleostei MÜLLER, 1845
Ordre Ankylophoriformes nov.

Diagnosis
The same as the family (unifamilial order).
Family Ankylophoridae GAUDANT, 1978 sensu TAVERNE, 2011a

Emended diagnosis
Small archaic teleosts formerly ranged within "Pholidophoriformes". Dermal bones of the skull roof and endochondral bones of the braincase individualized. Enlarged lateral dermethmoids (fused together or not, toothed or not) forming the upper jaw symphysis.

Ossified hypoethmoid associated to vomer. Dermethmoid (= rostral) with ethmoidal sensory commissure. Wide nasals in contact medially or separated by the frontals. Medioparietal skull. Toothed area of parasphenoid reduced. Parasphenoid teeth very small, if present. Prootic and intercalar connected, forming a bony bridge over the subtemporal fossa. Ossified supraoccipital. Premaxillae laterally located on the upper jaw. Two supramaxillae. Lower jaw elongated and articulation with the quadrate placed posterior to orbit. Upper margin of the dentary ascending progressively. "Leptolepid" notch present but not deep and posteriorly located on the dentary. Surangular present, forming a weakly developed coronoid process. Prearticular present. Retroarticular fused to angular-articular or autogenous. Antorbital present. Large third infraorbital. Two supraorbitals. One large postorbital (= suborbital), sometimes fused with the posterior infraorbitals. Small accessory postorbitals sometimes present. Ventral part of the preopercle enlarged. Only one gular plate. Ural vertebrae weakly or not ossified. Ganoid scales with a peg-and-socket articulation.

Genera and species included

Following TAVERNE (2011a), Ankylophoridae comprise the following genera and species:

Pholidophorus AGASSIZ, 1832
"Pholidophorus" germanicus QUENSTEDT, 1858 [Lower Jurassic, England, Germany; not a true *Pholidophorus*]

Eurycormus WAGNER, 1863
Eurycormus speciosus WAGNER, 1863 [Upper Jurassic, Germany]

Pholidophoristion WOODWARD, 1941
Pholidophoristion ornatus (AGASSIZ, 1844) [Upper Jurassic, England, France; Lower Cretaceous, Germany]
Pholidophoristion micronyx (AGASSIZ, 1844) [Upper Jurassic, Germany]
Pholidophoristion ovatus (WAGNER, 1860) [Upper Jurassic, France and Germany]
Pholidophoristion spaethi (TAVERNE, 1981) [Lower Cretaceous, Germany]

Ankylophorus GAUDANT, 1978
Ankylophorus similis (WOODWARD, 1895) [Upper Jurassic, France]

Lehmanophorus GAUDANT, 1978
Lehmanophorus segusianus (DE SAINT-SEINE, 1949) [Upper Jurassic, France]

Neopholidophoropsis TAVERNE, 1981
Neopholidophoropsis serrata TAVERNE, 1981 [Lower Cretaceous, Germany]

Siemensichthys ARRATIA, 2000
Siemensichthys macrocephalus (AGASSIZ, 1844) [Upper Jurassic, Germany]
Siemensichthys siemensi ARRATIA, 2000 [Upper Jurassic, Germany]

Steurbautichthys TAVERNE, 2011
Steurbautichthys aequatorialis (DE SAINT-SEINE & CASIER, 1962) [Middle Jurassic,Democratic Republic of Congo]

TAVERNE (2011a: 164) considers *Pholidorhynchodon malzannii* ZAMBELLI, 1980 and *Eopholidophorus forojuliensis* ZAMBELLI, 1989, both from the Late Triassic of Italy, as probable candidates for an inclusion within Ankylophoridae. Indeed, they are described with a toothed rostral (= dermethmoid) occupying the upper jaw symphysis, the two premaxillae being located laterally (ZAMBELLI, 1980b: fig. 1, 2, 1989: fig. 2, 3). These "rostral" teeth

probably belong to the lateral dermethmoids completely covered by the rostral, i. e. the usual upper symphysis anatomy in Ankylophoridae. The two fishes also have an elongated lower jaw, with the upper margin more or less rectilinear (ibid., 1980b: fig. 1, 5B, 1989: fig. 2), another character separating Ankylophoridae from the remaining "Pholidophoriformes". However, a revision of these two species is needed before taking a formal decision concerning their relationships.

<center>Genus Songaichthys gen. nov.</center>

Derivatio nominis
The generic name refers to the Songa Limestones, a subdivision of the Stanleyville Formation. The Greek *ichthys*, fish, is added.

Type-species
Songaichthys luctacki sp. nov. (by monospecificity)

Diagnosis
The same as the species (monospecific genus).

<center>Species Songaichyhys luctacki sp. nov.</center>

Derivatio nominis
The specific name is dedicated to the Belgian geologist Luc TACK, from the Royal Museum of Central Africa, in honour of his numerous works on the geology of the Democratic Republic of Congo and of Burundi.

Holotype
MRAC N° 8096a, b, the two faces of a complete specimen, very slightly curved, from the Songa Limestones of the Stanleyville Formation, Democratic Republic of Congo (Fig. 1-2). Total length: 98 mm.
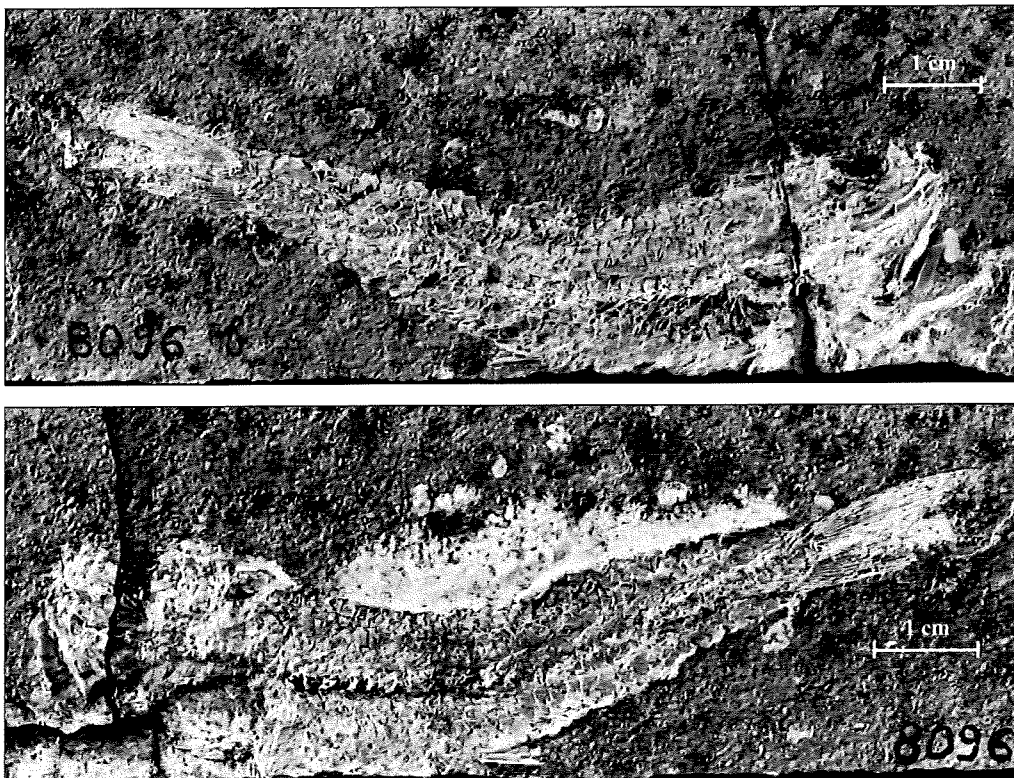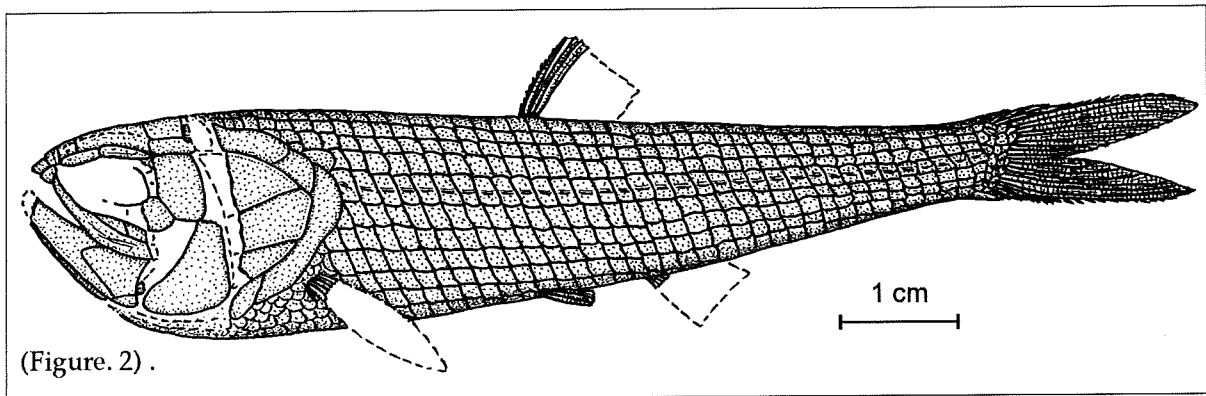

Figure 1.

(Figure. 2) .

Diagnosis

Small ankylophorid fish of about 10 cm of total length. Small braincase and large suspensorium. Dermal bones of the skull covered by a thin smooth layer of ganoin. Broad median lateral dermethmoid occupying the symphysis of the upper jaw. Small premaxillae laterally located. Wide dermethmoïd (= rostral) bearing the ethmoidal sensory commissure. Broad nasals in contact medially and separating the frontals from the dermethmoid. Foramen in the nasal for the posterior nostril. Frontals without sharp and narrow anterior processes. Large quadrangular parietals meeting on the mid line. Toothless jaws. Quadrate-mandible articulation located behind the orbit level. Long maxilla with a gently curved lower margin. Two supramaxillae. Large dentary with a more or less rectilinear upper border. Enlarged third infraorbital. Two large supraorbitals. One large postorbital (= suborbital). Preopercle with a broad ventral branch. Subopercle larger than opercle. Suture between opercle and subopercle horizontally oriented. Long and narrow gular plate. Posttemporal triangular. Short hypercleithrum (= supracleithrum). Curved cleithrum. Clavicle present. One postcleithrum. Ventral fins with 3 rays each and no fringing fulcra. About 40 vertebrae ossified as thin bony cylinders. Caudal centra monospondylous. Short autogenous neural and haemal spines. Supraneurals in the predorsal region. Epineurals associated to the neural arches. Origin of the dorsal fin located a little before that of the ventral fins. Dorsal fin with fringing fulcra. Anal fin located closer to the pelvic girdle than to the tail. No bony ural centra. At least 5 hypurals. Hypurals 1 to 3 fused into a broad hypural plate. Long forked caudal fin, with 16 principal rays and fringing fulcra on each leading margin. Scales of lepisosteid-type, with the peg-and-socket articulation, a smooth surface and a smooth posterior margin. About 34 scales along the lateral line.

Morphometric data

The morphometric characters are given in % of the holotype standard length (81 mm).

Head length (with the opercle)	29.5 %
Head depth (in the occipital region)	24.3 %
Maximum body depth (just behind the head)	23.8 %
Body depth (at the level the ventral fins)	19.8 %
Body depth (at the level of the anal fin)	16.4 %
Caudal peduncle depth	9.3 %
Prepelvic length	43.2 %
Predorsal length	42.0 %
Preanal length	54.3 %

Osteology

1. - The skull (Fig. 3-6)

The braincase is rather small compared to the size of the suspensorium. The dermal bones of the skull are covered by a thin unornamented layer of ganoin.
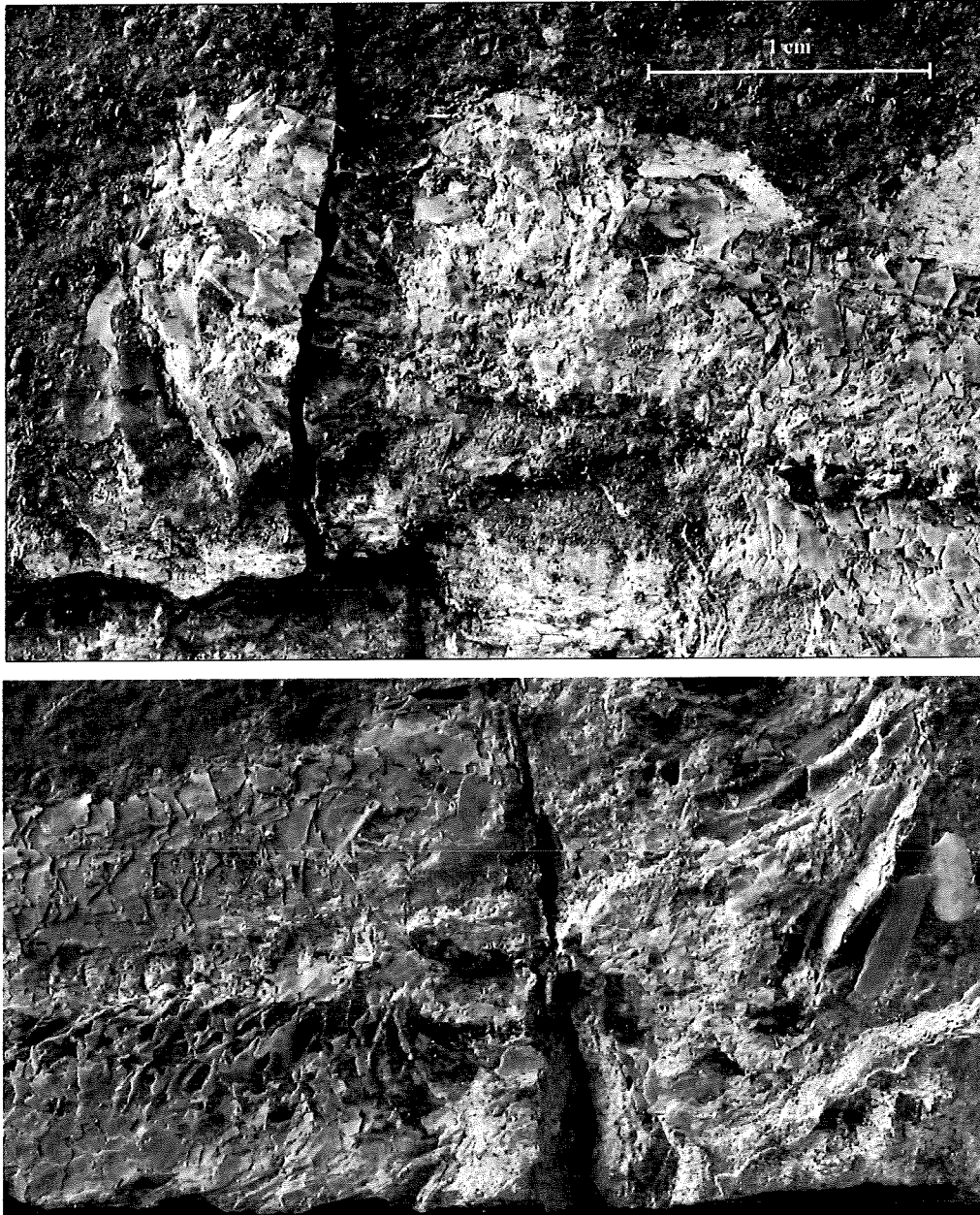

Figure 3:

The endochondral mesethmoid and the lateral ethmoids are not visible. The ethmoid region perhaps was entirely cartilaginous and so not fossilised. The dermethmoid (= rostral) is short but very wide. The ethmoidal (= rostral) sensory commissure crosses the dermethmoid from one lateral border to the other. A large fragment of broad paired lateral dermethmoids fused together is located at the symphysis of the upper jaw just before the dermethmoid but the bone is badly preserved and it is not possible to say if its anterior border was toothed or toothless. However, the jaws being toothless, there is a great probability that the lateral dermethmoid was also toothless.
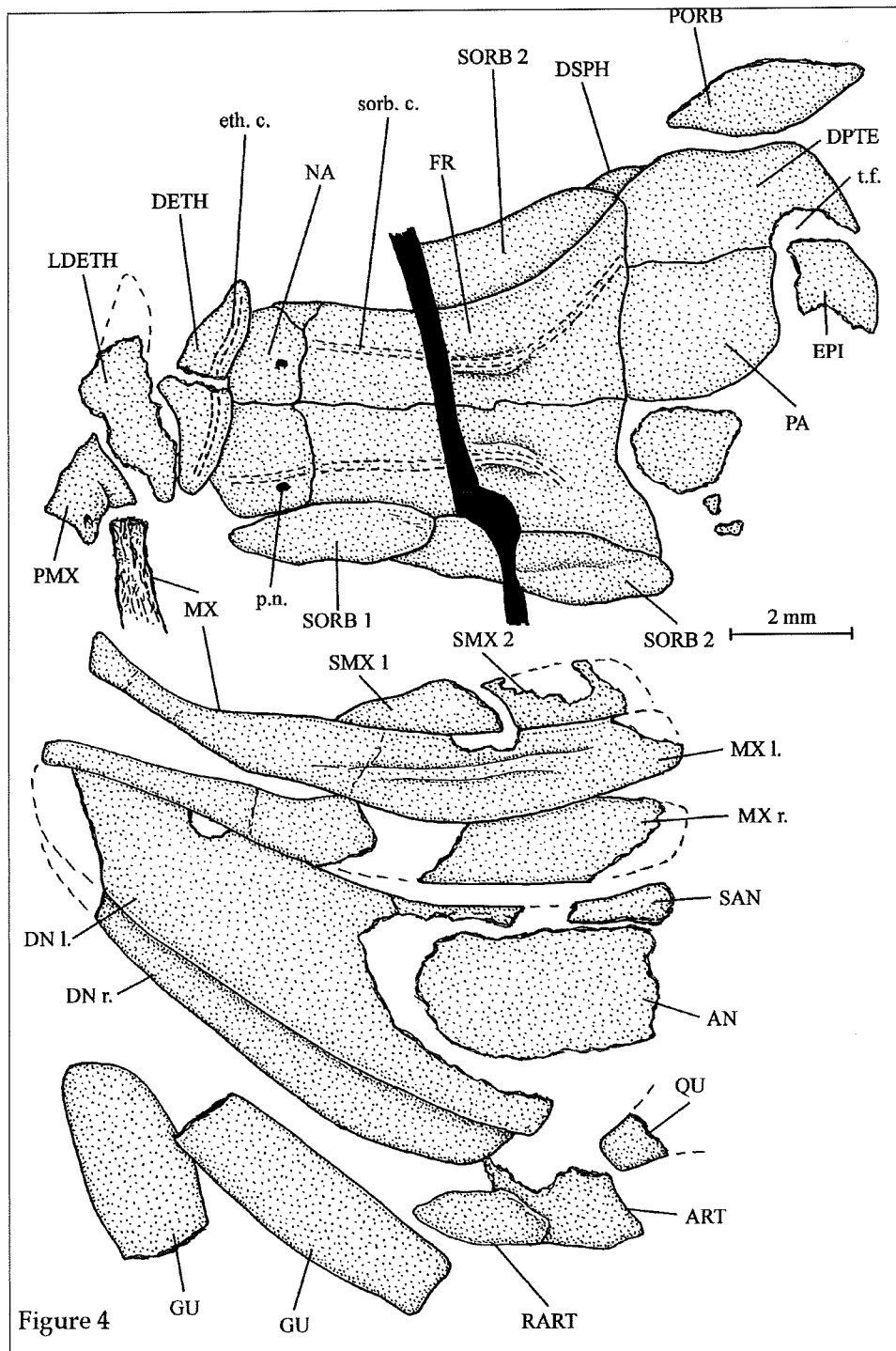
Figure 4

Behind the rostral region, the skull roof is composed by paired nasals, frontals, parietals, pterotics and epiotics. There is no fontanelle in the skull roof. The two more or less quadrangular nasals are in contact together all along their median margins, completely separating the dermethmoid from the frontals. The nasal is pierced by a foramen for the posterior nostril. The suture between the frontal and the nasal is straight and the frontal does not possess a narrow anterior process as it is the case in many "pholidophoriform" fishes (Nybelin, 1966; among others). The frontal is rather wide in the orbital region and still broadens at its posterior extremity. The supraorbital sensory canal is visible on the nasal and the frontal. The parietal is a large quadrangular bone and the skull is medioparietal. The dermopterotic is longer but less deep than the parietal. The epiotic (= epioccipital) is well developed. The supraoccipital and the supratemporal are unknown. The temporal (= post-temporal) fossa is open between the dermopterotic and the epiotic. Neither sensory canals nor pit-lines are visible on the parietal and the dermopterotic but that could be due to the bad preservation.

The cranial bones of endochondral origin and the parasphenoid are not preserved. The condylar head of the quadrate is the only visible part of the palatoquadratic arch.

The palatine and the pterygoid bones are not preserved.

The large toothless jaws are practically as long as the skull roof. The premaxilla is small, very short and laterally rejected by the median lateral dermethmoid. The long maxilla is narrow in its anterior first third but becomes broader in its posterior two other thirds. Its lower margin is gently curved. Its posterior margin is partly broken, so the exact shape of this margin remains unknown. There are two well developed supramaxillae. They are less deep than the maxilla. The dentary is a very large bone with a more or less rectilinear upper border progressively rising up till a weakly developed coronoid region. The presence of a "leptolepid" notch in the upper branch margin of the dentary is uncertain. If present, this notch must be located very posteriorly because no trace of such a notch is visible on the pre-served part of the bone. Fragments of a large plate-like angular, of a small surangular, of an articular and of a retroarticular are also preserved. The quadrate-mandible articulation is located behind the orbit level.

There are two long and wide supraorbitals. They are running along the lateral margin of the skull roof from the anterior extremity of the nasal to the posterior extremity of the

Figure 5

Figure 6
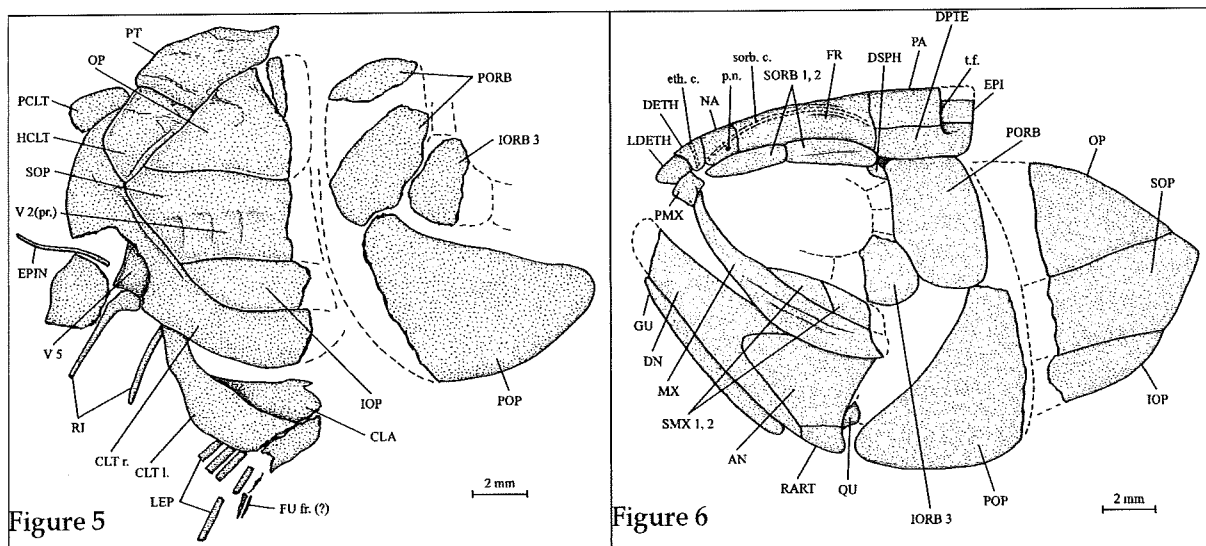
frontal. Fragments of a large third infraorbital and of a very large postorbital (= suborbital) are visible. A small part of the right dermosphenotic is preserved at the level of the suture between the frontal and the pterotic, just behind the posterior supraorbital. The other orbital bones were lost during the fossilisation.

Only the very broad ventral region of the preopercle is preserved but the preopercular sensory canal is not visible. The dorsal branch of the preopercle is missing. So, we do not know if this branch was reaching the dermopterotic level or not. The bones of the opercular series are placed posteriorly to the posterior margin of the braincase. The subopercle is longer than the rather small triangular opercle and almost as deep. The suture between the opercle and the subopercle is horizontally oriented and not very obliquely as in many "Pholidophoriformes". A well developed interopercle is located just under the subopercle. There is a long and narrow gular plate. The branchiostegal rays are not preserved. The hyomandibula, the symplectic, the hyoid bar and of the branchial skeleton are not visible.

2. - The girdles (Fig. 5, 7)

The posttemporal is a large triangular bone. The hypercleithrum (= supracleithrum) is broad but rather short. The cleithrum is well developed with a ventral branch longer than the dorsal one. A large clavicle is present before the cleithrum. There is a small postcleithrum. The

endochondral bones of the pectoral girdle are not visible. That region remained perhaps entirely cartilaginous. Only small fragments of the fins are preserved. It is not possible to determine the number of the rays composing the fin. A small ventrally located bony element seems to be a fringing fulcrum.

The pelvic bones are hidden by scales. Each ventral fin contains 3 rays. There are no traces of fringing fulcra.

3. - The axial skeleton (Fig. 8)

The vertebral column is not visible in its entirety because of the scales partly covering the vertebrae. However, when comparing the length of the preserved centra to the length of the complete vertebral axis, it is possible to determine that the axial skeleton is composed of

Figure 7

Figure 8
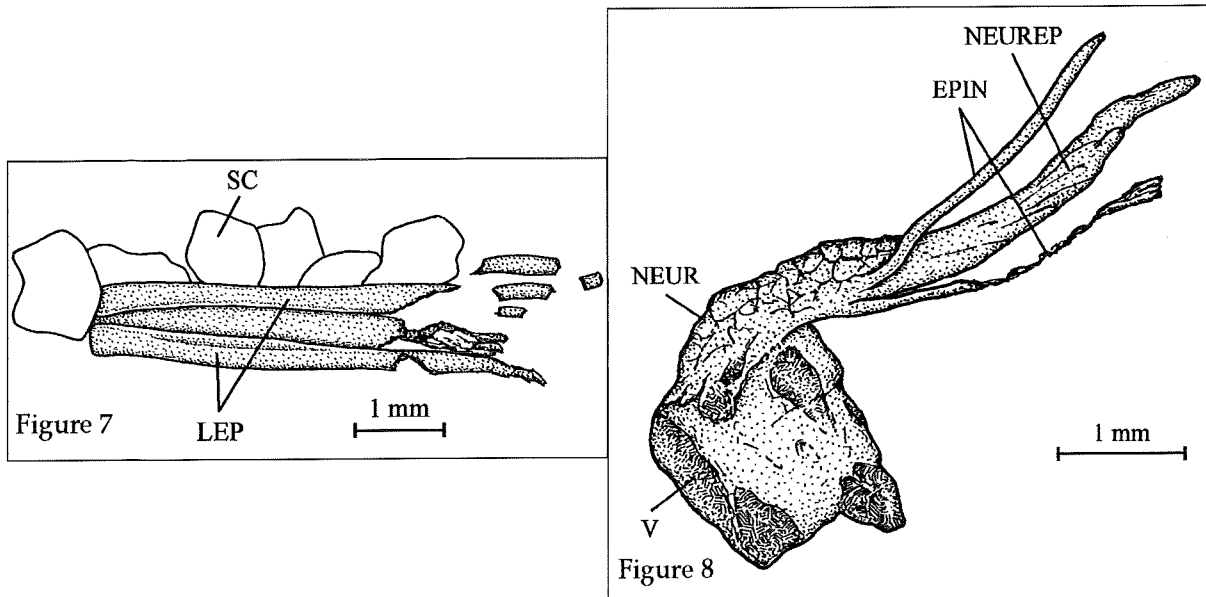
about 40 vertebrae. The first four vertebrae are seen as slight prints on the subopercle. The centra are completely ossified, forming thin bony cylinders. Short autogenous haem apophyses are associated with at least some centra in the abdominal region. The neural and haemal spines are autogenous and rather short. Fragments of nine pairs of strong ribs are preserved. The first rib is attached to the fourth vertebral centrum. A few fragments of supraneurals are visible between the scales in the predorsal region. A pair of epineurals fused to the corresponding neural arch is visible on one abdominal vertebra of face 8096a. An isolated epineural is preserved just behind the cleithrum and the fifth vertebra on face 8096b.

4. - The dorsal and anal fin (Fig. 9)

Only parts of the first three rays of the dorsal fin are preserved. The origin of the fin is located a little in front of that of the ventral fins. Three small fringing fulcra are preserved at the basis of the first dorsal fin ray.

Only a few very small fragments of the anal fin are visible. The origin of the fin is nearer to the ventral fins than to the tail.

5. - The caudal skeleton (Fig. 10-12)

The caudal skeleton is severely crushed on face 8096a but the outlines of the caudal bones are however clearly visible. The most posterior part of the caudal skeleton is missing on that face but is rather well preserved on face 8096b. When combining information from the two faces, it is possible to reconstruct almost entirely that caudal complex.

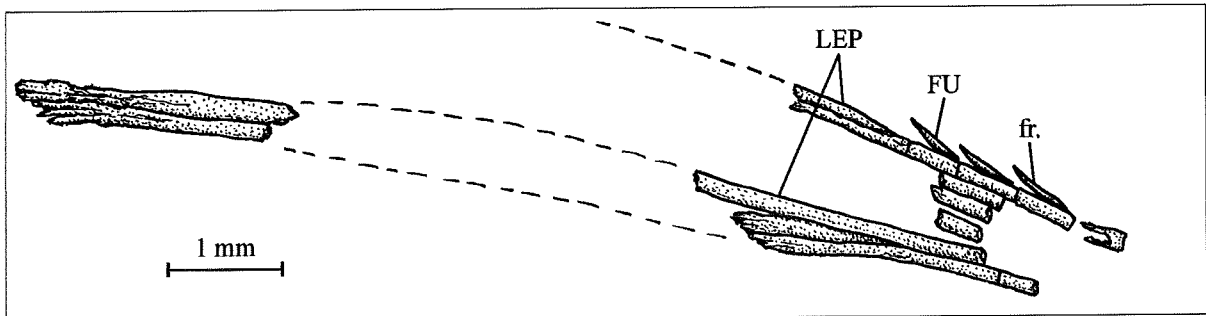The last centra of the preural series are monospondylous and well ossified. Preural

Figure 9

centrum 1 (PU 1) is the last one but is greatly reduced when compared with preural centrum 2 (PU 2). There is no bony ural centrum. The last neural and haemal spines are autogenous and inclined to the vertebral axis. The neural spines are shorter than the haemal spines. The neural spine of PU 2 is the last one. The haemal spine of PU 2 and the parhypural of PU 1 are rather broad. The first three hypurals (HY 1-3) are fused in a wide and more or less triangular hypural plate well preserved on face 8096b. The larger part of the plate is
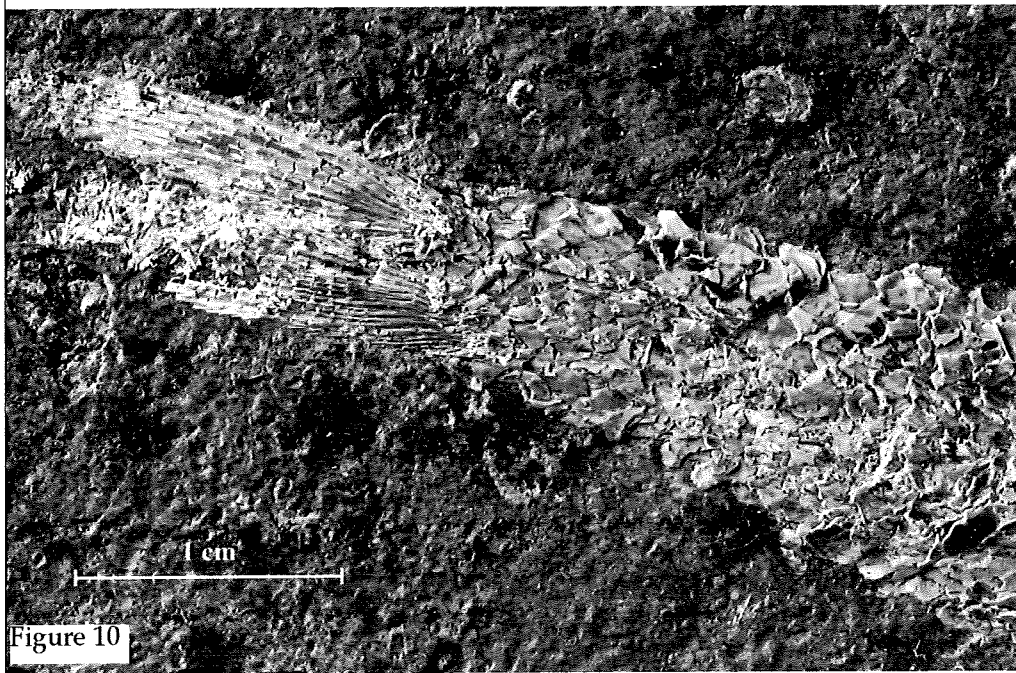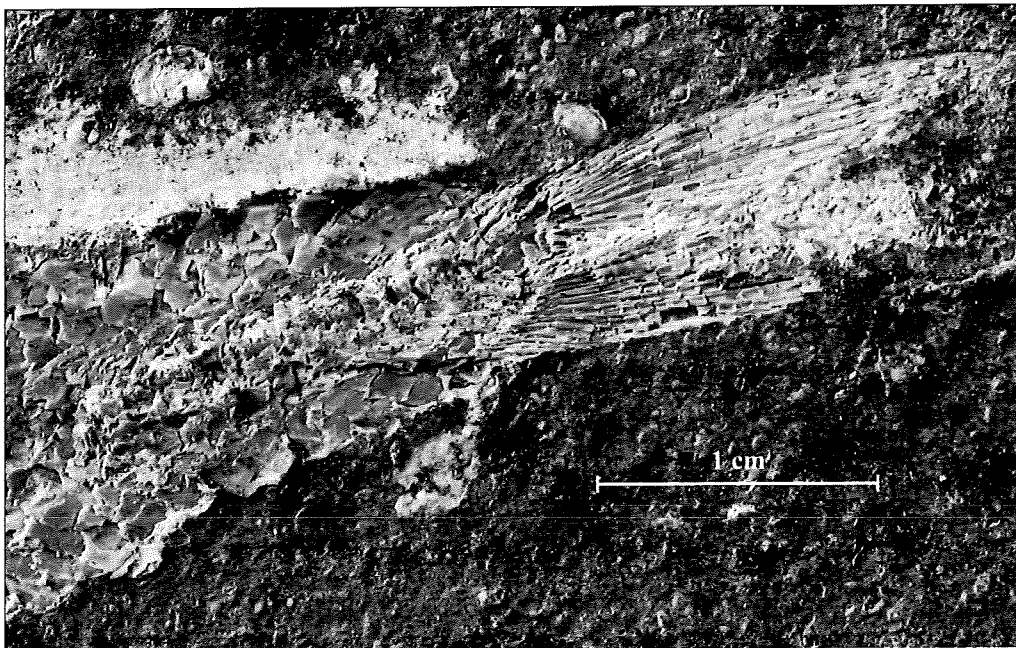

Figure 10

42

associated with the ventral lobe of the caudal fin but its upper part corresponds to the most ventral rays of the dorsal lobe. Small fragments of the fourth and the fifth hypurals are visible on face 8096b. Epurals, uroneurals and urodermals are not preserved.

The caudal fin is long, forked and contains 16 principal segmented rays, 9 in the dorsal lobe and 7 in the ventral lobe. The outermost principal ray in each lobe is unbranched. The other rays are branched. There are 4 unsegmented procurrent rays in the dorsal lobe and 5 in the ventral lobe of which the two longest are segmented. Both leading margins of the caudal fin bear numerous small fringing fulcra. The longest ventral procurrent ray forms the proximal extremity of the ventral leading margin and bears the first five ventral fringing fulcra.
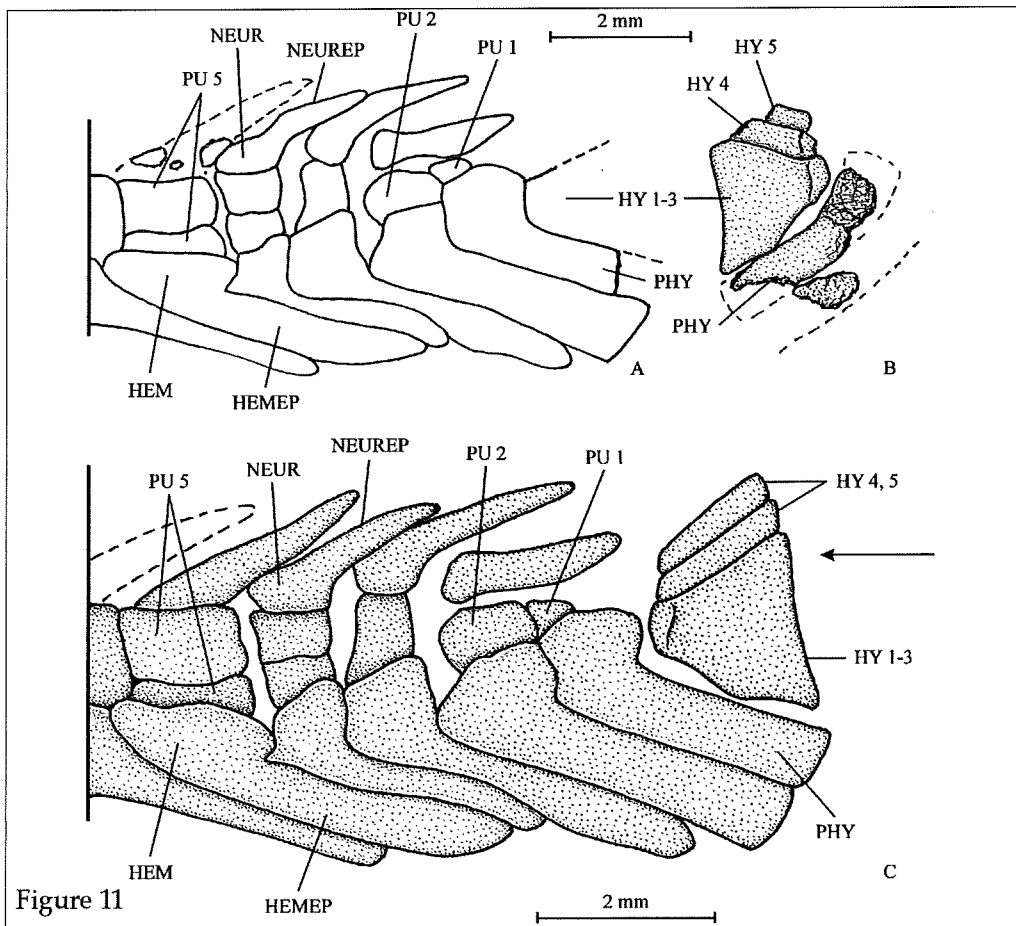
6. - The squamation (Fig. 13)

Figure 11

The scales are severely crushed. Only a few ones are well preserved. They are of lepisosteid type with a thin ganoid superficial layer and a weakly developed peg-and-socket articulation. The surface is smooth and the posterior margin not serrated. The flank scales are more or less rectangular and much deeper than long. The scales become lozenge-shaped in the dorsal and ventral regions and near the tail. The middle flank row consists of about 34 scales.
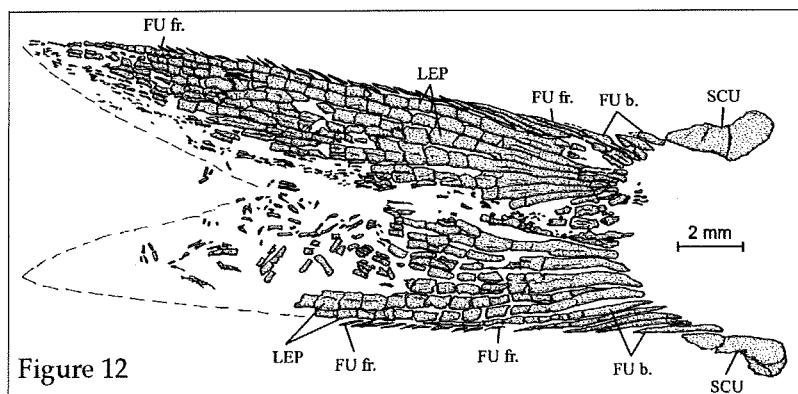

Figure 12

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There are 9 scales in a vertical row at the level of the anal fin. A large arrow head-shaped scale is present just before the procurrent rays of each caudal fin lobe. The lateral line sensory canal is clearly visible on the scales all along the body.

DISCUSSION

1. - *Songaichthys luctacki* within Neopterygii

Songaichthys luctacki has fused lateral dermethmoids that occupies the upper jaw symphysis, rejecting laterally the two premaxillae. Within Neopterygii, such a peculiar character is shared only by Pachycormiformes, Ligulelliformes, Catervarioliformes, Ankylophoriformes and Ichthyokentemidae. No other neopterygian fish, including the remaining "Pholidophoriformes", exhibits this character.
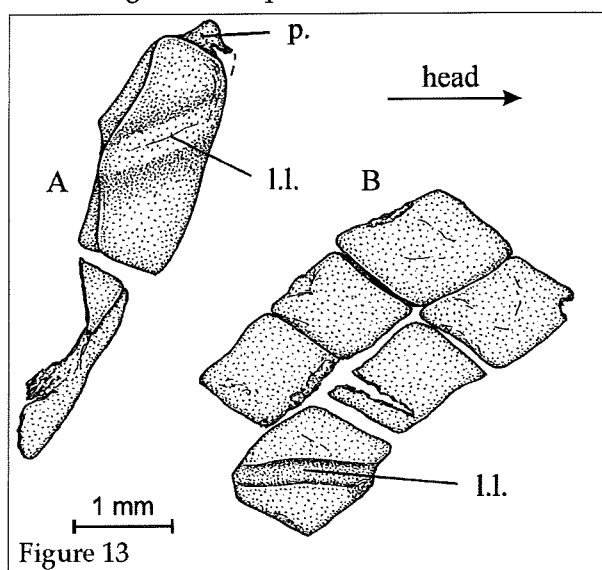
Figure 13

It is clear that *S. luctacki* does not possess the numerous autapomorphies of the Pachycormiformes (MAINWARING, 1978; LAMBERS, 1992) and of the Ligulelliformes (TAVERNE, 2011c) and can not belong to these two orders. Moreover, *S. luctacki* has ossified epineurals, a structure present in Catervarioliformes, Ankylophoriformes, "Pholidophoriformes" and more evolved teleosts but absent in Pachycormiformes and Ligullelliformes.

Catervarioliformes are a recently erected new order containing only the Catervariolidae and their two genera *Catervariolus* and *Songanella* (TAVERNE, 2011b, in press). This family was formerly ranged within "Pholidophoriformes" and considered as the most primitive lineage of this order (ibid., 2011a, b). *S. luctacki* appears more advanced than these two fishes. Indeed, Catervarioliformes have toothed jaws, only one small supramaxilla, a narrow crescent-like preoperde, three supraorbitals, two or three postorbitals, a pair of lateral posterior gulars and a series of ossified ural centra. *S. luctacki* differs from them for all those characters and, thus, can not be a member of that order.

On the other hand, *S. luctacki* has two well developed supramaxillae over the maxilla, a character linking the Congolese fossil fish to Ankylophoriformes and to the remaining members of the "Pholidophoriformes".

2. - *Songaichthys and Pholidophorus sensu stricto*

DE SAINT-SEINE and CASIER thought that sample MRAC 8096a, b, herein described, belonged to the genus *Pholidophorus*.

ARRATIA (2000: 143, fig. 20, 21) is the first author to propose a cladistic definition of *Pholidophorus sensu stricto*, the type-genus of the order "Pholidophoriformes". This definition is based on four characters (her "Node C1"): the frontals are distinctly broader posteriorly, but long and narrow anteriorly (character 126[1]), the flanks are covered by lepisosteid-type of scales, deeper than long, smooth surface and smooth posterior margin (character 136[1]), the nasals are separated by the frontal bones (character 138[1]) and the frontals are acutely sharp anteriorly and sutured with the rostral by a very narrow contact (character 139[1]).

Songaichthys does not share characters 126[1], 138[1] and 139[1] and, thus, does not belong to the genus *Pholidophorus sensu stricto*.

3. - *Songaichthys luctacki* and *Steurbautichthys aequatorialis*

As already written, sample MRAC 8096a, b was considered as a possible juvenile specimen of *Steurbautichthys* ("*Pholidophorus*") *aequatorialis* by DE SAINT-SEINE and CASIER. A comparison between the two fishes is thus necessary to confirm or infirm that hypothesis.

Steurbautichthys aequatorialis has toothed jaws, a small premaxilla longer than deep, a reduced dermethmoid, a frontal with an anterior triangular process, two small supraorbitals, a large opercle deeper than long, ventral fins with about 10 rays and fringing fulcra, a dorsal fin located behind the level of the ventral fins, an anal fin located at mid-distance between the ventral fins and the tail and a caudal fin with 23 principal rays (TAVERNE, 2011a).

On the contrary, *Songaichthys luctacki* has toothless jaws, a small premaxilla as long as deep, a very broad dermethmoid, a frontal without anterior triangular process, two large supraorbitals, a small opercle longer than deep, ventral fins with 3 rays and no fringing fulcra, a dorsal fin located above the ventral fins, an anal fin close to the ventral fins and a caudal fin with 16 principal rays.

Both species possess a wide hypural plate in their caudal skeleton. However, in *Steurbautichthys aequatorialis*, that plate is formed by the fusion of the dorsal hypurals (HY 3 + X) and is associated with the upper lobe of the caudal fin (ibid., 2011a: fig. 17), whereas the plate is principally located at the level of the lower lobe and represents the fused three first hypurals (HY 1-3) in *Songaichthys luctacki*.

Songaichthys luctacki is thus clearly different from *Steurbautichthys aequatorialis*.

4. - *Songaichthys*, *Ankylophoriformes* and "*Pholidophoriformes*"

As previously said, *Songaichthys luctacki* has large lateral dermethmoids fused together, located at the symphysis of the upper jaw, the premaxillae being laterally located. Within the remaining ganoid teleosts, only two families, the Ankylophoridae and the Ichthyokentemidae, share this primitive character (PATTERSON, 1973: fig. 4, 1975: fig. 82, 121, 124-126; ARRATIA, 1999: fig. 6, 2000: fig. 15A; TAVERNE, 2011a: fig. 4, 5, 20B, 2011b: fig. 12). The two symphyseal lateral dermethmoids can be fused together or separated from each other. In the more evolved "Pholidophoriformes", the premaxillae join at the symphysis and cover the lateral dermethmoids (TAVERNE, 2011a: fig. 20C).

The upper margin of the dentary is more or less rectilinear in Songaichthys luctacki as in Ankylophoridae (ARRATIA, 2000: fig. 8, 15E, F; TAVERNE, 2011a: fig. 8, 2011b: fig. 27, 28). In Ichthyokentemidae and in more specialized "Pholidophoriformes", the dentigerous part of the upper border of the dentary, before the leptolepid notch, is shortened and depressed, in opposition to the coronoid region of the mandible that becomes often abruptly deeper (RAYNER, 1948: fig. 27D; GRIFFITH & PATTERSON, 1963: fig. 8, 9; NYBELIN, 1966: pl. 3, fig. 1, 5, pl. 15, fig. 5-8; ZAMBELLI, 1978: fig. 5; TAVERNE, 2011a: fig. 21B-E). *Songaichthys luctacki* is thus less evolved than Ichthyokentemidae and the more advanced "Pholidophoriformes".

These few characters clearly indicate that *Songaichthys luctacki* belongs to Ankylophoridae, the unique family of the new order Ankylophoriformes.

5. - *Songaichthys within* Ankylophoriformes

The most primitive Ankylophoridae, such as *Eurycormus* Wagner, 1863 and *Steurbautichthys*, have the dorsal fin located posteriorly on the back, only a little before the anal fin level (GRANDE & BEMIS, 1998: fig. 421A; TAVERNE, 2011a: fig. 3). In *Songaichthys luctacki* and in the five more specialized ankylophorid genera, i. e. "*Pholidophorus*" *germanicus*, *Pholidophoristion*, *Siemensichthys*, *Ankylophorus* and *Lehmanophorus*, the dorsal fin is brought forward, above the ventral fins or even a little before them (ARAMBOURG, 1935: pl. 3, fig. 3; DE SAINT-SEINE, 1949, pl. 23, fig. B; GAUDANT, 1978: pl. 4, fig. 1).

However, these five more evolved Ankylophoridae, share two apomorphic characters

not present in *Eurycormus*, *Steurbautichthys* and *Songaichthys*. The toothed margin of their maxilla is no more curved but becomes more or less rectilinear (ARAMBOURG, 1935, pl. 3, fig. 3; WOODWARD, 1941: 90; DE SAINT-SEINE, 1949: fig. 96; GAUDANT, 1978: pl. 1, fig. 2, pl. 2, fig. 1, pl. 4, fig. 2; ARRATIA, 2000: fig. 7-9). The posterior infraorbitals are considerably enlarged, probably by the fusion with the postorbital (DE SAINT-SEINE, 1949: fig. 96; GAUDANT, 1978: pl. 1, fig. 2, pl. 4, fig. 2; ARRATIA, 2000: fig. 7-9). It is to be noted that the posterior infraorbitals of *"Pholidophorus" germanicus* are not known.

Thus, within the Ankylophoridae, *Songaichthys* occupies an intermediate position between *Eurycormus* and *Steurbautichthys*, on the one hand, and the five more specialized genera, on the other hand.

The phylogenetic relationships within Ankylophoridae are analyzed in TAVERNE (2011a: 164-166, fig. 39).

6. - The position of Ankylophoriformes within archaic ganoid teleosts (Fig. 14)

TAVERNE (2011a, b, in press) has shown that Catervarioliformes are the most primitive lineage within the archaic teleosts with ganoid scales.

Ankylophoriformes and the remaining "Pholidophoriformes" share a series of specialized characters not present in Catervarioliformes.

(1) An ossified hypoethmoid is associated with the vomer. PATTERSON (1975: 485, fig. 84) described this bone in the ankylophorid *Siemensichthys macrocephalus*. In the ankylophorid *"Pholidophorus" germanicus*, there is only a small perichondral ossification fused to the vomer that forms two thin processes supporting the ventral part of a cartilaginous mesethmoid (ibid., 1975: 478, fig. 122 a-c). The presence of a bony hypoethmoid
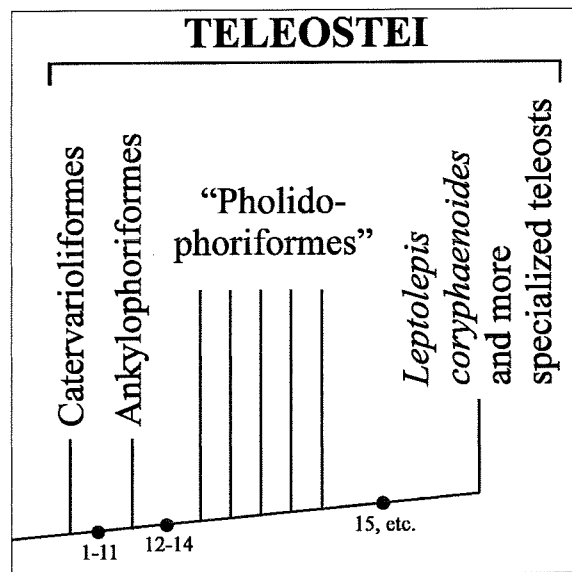
seems to be the rule within other "Pholidophoriformes" and in the primitive "classical" teleosts (ibid., 1975: 473-516). (2) Two supramaxillae overlie the maxilla (NYBELIN, 1966: fig. 1, 3, 6, 7, 9, 12-14; ZAMBELLI, 1975: fig. 1, 1978: fig. 1; 1980a: fig. 1, 1980b: fig. 1, 1986: fig. 1, 1989: fig. 2). In *Siemensichthys*, the two supramaxillae are fused (ARRATIA, 2000: fig. fig. 7-9, 14, 15C) and only the posterior supramaxilla is present in Ichthyokentemidae (GRIFFITH & PATTERSON, 1963: fig. 6). (3) The "leptolepid" notch of the dentary is well marked (TAVERNE, 2011a: fig. 8, 21). The notch is weakly developed in Catervarioliformes (TAVERNE, 2011b: fig. 27, 28).

(4) The toothed coronoids of the lower jaw are lost or their number is reduced to one (GRIFFITH & PATTERSON, 1963: fig. 9; ARRATIA, 2000: fig. 15 F; TAVERNE, 2011: fig. 8).
(5) There is only one large dorsal postorbital (= suborbital), the ventral one being lost (NYBELIN, 1966: fig. 1, 3, 6, 7, 9, 12-14). In some rare cases, the postorbital is fused to the posterior infraorbitals. Two small accessory postorbitals sometimes are present.
(6) The number of supraorbitals is reduced from three to two (NYBELIN, 1966: fig. 1, 3, 4; GAUDANT, 1978: pl. 1, fig. 2, pl. 2, fig. 1, pl. 3, fig. 2; ZAMBELLI, 1978: fig. 1, 2, 1989: fig. 2 et 3; GRANDE & BEMIS, 1998: fig. 421C; TAVERNE, 2011a: fig. 4), except in Ichthyokentemidae where the number of supraorbitals increases to four (GRIFFITH & PATTERSON, 1963: fig. 1, 6) and in Pleuropholidae in which the number of all the circumorbital bones is greatly multiplied (PATTERSON, 1973: fig. 16).

(7) The prootic and the intercalary are connected and form a bony bridge over the subtemporal fossa (PATTERSON, 1975: fig. 46, 56, 67, 68, 71, 84).

(8) The vomer bears some small teeth distributed on a reduced part of its ventral surface (ibid., 1975: fig. 84, 122a-c), except in Ichthyokentemidae where the vomer is completely toothed (GRIFFITH & PATTERSON, 1963: fig. 2, 3). In Catervarioliformes, the vomerian teeth cover an important area of the bone (TAVERNE, 2011b: fig. 10, 11, 17, 23, in press: fig. 6, 9).

(9) The toothed area of the parasphenoid is reduced and the teeth, if present, are small (RAYNER, 1948: fig. 28 et 29; PATTERSON, 1975: fig. 62, 84, 142a). However, Ichthyokentemidae retain a strongly toothed parasphenoid (GRIFFITH & PATTERSON, 1963: fig. 2 et 3).

(10) The preopercle is no more crescent-like and its ventral part is greatly broadened (NYBELIN, 1966: fig. 1, 3, 5-7, 9, 12, 13; ZAMBELLI, 1975: fig. 1, 1978: fig. 1, 1980a: fig. 1, 1980b: fig. 1, 1989: fig. 9; ARRATIA, 2000: fig. 8, 9, 14, 15B; etc.).

(11) The ural vertebrae do not exist or are weakly ossified and reduced in number (PATTERSON, 1968: fig. 1-4, 1973: fig. 15, 17; ARRATIA & SCHULTZE, 2007: fig. 12; TAVERNE, 2011a: fig. 17).

The remaining "Pholidophoriformes" differ from the Ankylophoriformes by some new apomorphies.

(12) The premaxillae form the symphysis of the upper jaw. The lateral dermethmoids are covered by dermethmoid, the nasals and the premaxillae (TAVERNE, 2011a: fig. 20C). In some evolved "Pholidophoriformes", such as the Pleuropholidae, the lateral dermethmoids are fused to the dermethmoid (pers. obs. on *Pleuropholis lannoyi* DE SAINT-SEINE, 1955, specimen MRAC RG 10233; PATTERSON, 1973: 269).

(13) The "leptolepid" notch deepens and separates abruptly the mandible in a low anterior part and a high coronoid region (RAYNER, 1948: fig. 27D; GRIFFITH & PATTERSON, 1963: fig. 8, 9; NYBELIN, 1968: pl. 3, fig. 1, 5, pl. 15, fig. 5-8; GAUDANT, 1978: pl. 3, fig. 2; ZAMBELLI, 1978: fig. 5).

(14) The anterior toothed part of the dentary upper margin is strongly shortened (RAYNER, 1948: fig. 27D; GRIFFITH & PATTERSON, 1963: fig. 8, 9; NYBELIN, 1968: pl. 3, fig. 1, 5, pl. 15, fig. 5-8; GAUDANT, 1978: pl. 3, fig. 2; ZAMBELLI, 1978: fig. 5).

Leptolepis coryphaenoides and the primitive "classical" teleosts share many new specialized characters absent in "Pholidophoriformes".

(15, etc.) These apomorphies are analyzed in a detailed way in TAVERNE (2001: 69-71, fig. 9).

ACKNOWLEDGMENTS

LIST OF ABBREVIATIONS USED IN TEXT-FIGURES

AN: angular
ART: articular
CLA: clavicle
CLT (l., r.): cleithrum (left, right)
DETH: dermethmoid (= rostral)
DN (l., r.): dentary (left, right)
DPTE: dermopterotic
DSPH: dermosphenotic
EPI: epiotic (= epioccipital)
FR: frontal
FU b.: basal fulcrum (= procurrent ray)
FU fr.: fringing fulcrum
GU: gular plate
HCLT: hypercleithrum (= supracleithrum)
HEM: haemal arch
HEMEP: haemal spine
IOP: interopercle
IORB 3: infraorbital 3
LDETH: lateral dermethmoid
LEP: fin ray
MX (l., r.): maxilla (left, right)
NA: nasal
NEUR: neural arch
NEUREP: neural spine
OP: opercle
PA: parietal
PCLT : postcleithrum
PHY: parhypural
PMX: premaxilla
POP: preopercle
PORB: postorbital (= suborbital)
PU 1-5: preural vertebrae 1 to 5
QU: quadrate
RART: retroarticular
RI : rib
SAN: surangular
SC: scale
SCU : caudal scute
SMX 1, 2: supramaxilla 1 and 2
SOP: subopercle
SORB 1, 2: supraorbital 1 and 2
V, V 2 (pr.), 5: vertebral centrum, vertebrae 2 (print) and 5
eth. c.: ethmoidal (= rostral) sensory commissure
l. l.: lateral line sensory canal
p.: peg
p. n.: posterior nostril
sorb. c.: supraorbital sensory canal
t. f.: temporal (= posttemporal) fossa

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Figures in the text

Figure 1. *Songaichthys luctacki* gen. and sp. nov. Holotype MRAC RG 8096a (above) and 8096b (below).

Figure 2. *Songaichthys luctacki* gen. and sp. nov. General reconstruction based on the two faces of holotype MRAC RG 8096a, b.

Figure 3. *Songaichthys luctacki* gen. and sp. nov. Head region of holotype MRAC RG 8096a (above) and 8096b (below).

Figure 4. *Songaichthys luctacki* gen. and sp. nov. Holotype, skull roof of face MRAC RG 8096a (above) and jaws (reversed) of face 8096b (below).

Figure 5. *Songaichthys luctacki* gen. and sp. nov. Holotype, opercular region and pectoral girdle of face MRAC RG 8096b.

Figure 6. Songaichthys luctacki gen. and sp. nov. Reconstruction of the skull based on the two faces of holotype MRAC RG 8096a, b.

Figure 7. *Songaichthys luctacki* gen. and sp. nov. Left ventral fin of holotype MRAC RG 8096a.

Figure 8. Songaichthys luctacki gen. and sp. nov. One vertebra of the abdominal region.

Figure 9. *Songaichthys luctacki* gen. and sp. nov. Fragments of the dorsal fin of holotype MRAC RG 8096b.

Figure 10. *Songaichthys luctacki* gen. and sp. nov. Caudal region of holotype MRAC RG 8096a (above) and 8096b (below).

Figure 11. *Songaichthys luctacki* gen. and sp. nov. Holotype, (A): outlines of the components of the caudal skeleton of face MRAC RG 8096a, (B) fragments of the caudal skeleton of face 8096b, and (C) reconstruction of the caudal skeleton based on the two faces 8096a, b. The arrow indicates the middle of the caudal fin.

Figure 12. *Songaichthys luctacki* gen. and sp. nov. Caudal fin of holotype MRAC RG 8096b.

Figure 13. *Songaichthys luctacki* gen. and sp. nov. Holotype, (A) flank scale with the lateral line at the level of the anal fin on face MRAC RG 8096b and (B) scales of the caudal peduncle on face 8096b.

Fig. 14. Systematic position of Ankylophoriformes ord. nov. within archaic Teleostei. Numbers refer to the characters discussed in the text.

ADDENDUM

An important and remarkable monograph dealing with the osteology and relationships of the Late Triassic « Pholidophoriformes » from North Italy and Austria has been published very recently (ARRATIA, 2013), during the time the present paper was in press.

ARRATIA (2013) proposes a new hypothesis of the relationships among the most basal Teleostei. Her phylogenetic tree (ibid., 2013: fig. 95) includes fourteen genera traditionally ranged within the "Pholidophoriformes" and some other archaic teleosts. She also gives a new description of *Pholidophorus* AGASSIZ, 1832, a genus that she restricts to *Pholidophorus latiusculus* AGASSIZ, 1832, the poorly known type-species, and *Pholidophorus gervasuttii* ZAMBELLI, 1980, a well better known species. She excludes *Pholidophorus bechei* AGASSIZ, 1837 from the genus and creates for it the new taxon *Dorsetichthys* ARRATIA, 2013, a genus that she places as the plesiomorphic sister-group of *Ichthyokentema* WOODWARD, 1941, *Leptolepis coryphaenoides* (BRONN, 1830) and the more advanced teleosts. She refers *Pholidophorus, Parapholidophorus* ZAMBELLI, 1975, *Pholidophoretes* GRIFFITH, 1977, *Pholidoctenus* ZAMBELLI, 1077, *Pholidorhynchodon* ZAMBELLI, 1980 and the new genera *Annaichthys* ARRATIA, 2013 and *Knerichthys* ARRATIA, 2013 to the family Pholidophoridae.

The phylogenetic conclusions regarding the "Pholidophoriformes" in ARRATIA (2013) differ on some points from those in TAVERNE (2011a, b, in press). For instance, she considers the Pholidophoridae as the most primitive lineage within the Teleostei. TAVERNE (2011a: fig. 39) gives that position to the Catervariolidae. She includes *Pholidorhynchodon* in the Pholidophoridae. In opposition to such a systematic position, TAVERNE (2011a: 164) suggests that this genus is a member of the Ankylophoridae. ARRATIA (2013) also places *Eurycormus* WAGNER, 1863 in a plesiomorphic position regarding to *Catervariolus* DE SAINT-SEINE, 1955, while TAVERNE (2011a) considers this last genus as more primitive than the first one, *Eurycormus* being regarded by him as the most primitive member of the Ankylophoridae.

These divergences are essentially the result of our choices of characters and our different manners to apply the cladistic method. ARRATIA (2013) uses a great number (167) of characters to elaborate a matrix. Then, a computer constructs on this basis a most parsimonious phylogenetic tree of the "Pholidophoriformes". However, in these 167 characters, some are important, others are not very significant and some of them present a homoplasic evolution. That could partly "drown" the more important characters. Moreover, a few important ones are not mentioned. In my own reconstruction of the "Pholidophoriformes" phylogeny, I have preferred to emphasize on some characters seeming less open to a homoplasic evolution, such as the bipartition of the primitive neopterygian premaxilla into a symphyseal toothed lateral dermethmoid and a "secondary" premaxilla, the progressive migration of this "secondary" premaxilla from a lateral position towards the symphysis and over the lateral dermethmoid, the development of the leptolepid notch, the shortening of the toothed part of the dentary upper margin anterior to the leptolepid notch, the abrupt depression of this toothed portion in opposition to the deeper coronoid region of the mandible, the progressive lost of the coronoids, the reduction in number of the supraorbitals and of the postorbitals (= suborbitals) or the evolution of the preopercle shape.

I have not the possibility in the limited pages of this addendum to analyse in a detailed way the differences between the phylogenies proposed by TAVERNE (2011a, b, in press) and ARRATIA (2013). But I shall do so in my forthcoming papers on the "Pholidophoriformes" from the Stanleyville Formation.

ARRATIA, G., 2013. Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes (*Actinopterygii, Teleostei*). *Journ. Vert. Paleont.*, 33 (Suppl. to 6, Mem. 13):1-138.
For TAVERNE (2011a, b, in press), see References.