Geo-Eco-Trop., 2018, 42, 1 : 89-116

The Mesozoic fish genus *Pholidophorus* (Teleostei, Pholidophoriformes), with an osteological study of the type-species *Pholidophorus latiusculus*. Comments on some problems concerning the "pholidophoriform" fishes

Le genre *Pholidophorus* (Teleostei, Pholidophoriformes), poisson du Mésozoïque, et ostéologie de l'espèce-type *Pholidophorus latiusculus*. Commentaires sur quelques problèmes concernant les poissons « pholidophoriformes »

Louis TAVERNE [1]

Abstract : The story of *Pholidophorus*, the most famous genus within the fossil basal teleosts, is evocated. The osteology of its type-species, *Pholidophorus latiusculus* from the Upper Triassic of Austria, is studied in details. Comparisons are done with *Lombardichthys gervasuttii* from the Upper Triassic of Italy, a species formerly included in the genus *Pholidophorus* and considered as closely related to *Ph. latiusculus*. The systematic position of *Ph. latiusculus* within Pholidophoridae is discussed. Comments are done on the validity of the pholidophorid genus *Ceneichthys* that is confirmed, on the bony quadratic process and on the evolution of the orbital bones and of the preopercle within "Pholidophoriformes". The analyzed characters strengthen the idea that Pholidophoridae occupy a more advanced systematic position than Catervariolidae within the lineages formerly included in the polyphyletic order « Pholidophoriformes ».

Key words: Teleostei, Pholidophoriformes, Pholidophoridae, *Pholidophorus*, *Ph. latiusculus*, history, osteology, relationships. Upper Triassic, Seefeld, Tyrol, Austria.

Résumé : L'histoire de *Pholidophorus*, le genre le plus célèbre parmi les téléostéens basaux fossiles, est évoquée. L'ostéologie de son espèce-type, *Pholidophorus latiusculus* du Trias supérieur d'Autriche, est étudiée en détails. Des comparaisons sont faites avec *Lombardichthys gervasuttii* du Trias supérieur d'Italie, une espèce précédemment incluse dans le genre *Pholidophorus* et considérée comme voisine de *Ph. latiusculus*. La position de *Ph. latiusculus* au sein des Pholidophoridae est discutée. Des commentaires sont faits sur la validité du pholidophoridé *Ceneichthys* qui est confirmée ainsi que sur le processus quadratique osseux et l'évolution des os orbitaires et du préoperculaire au sein des « Pholidophoriformes ». Les caractères analysés renforcent l'idée que les Pholidophoridae occupent une position systématique plus avancée que les Catervariolidae parmi les lignées rapportées anciennement à l'ordre polyphylétique des « Pholidophoriformes ».

Mots-clés: Teleostei, Pholidophoriformes, Pholidophoridae, *Pholidophorus*, *Ph. latiusculus*, histoire, ostéologie, relations, processus quadratique osseux, os orbitaires, préoperculaire, Trias supérieur, Seefeld, Tyrol, Autriche.

INTRODUCTION

The Mesozoic genus *Pholidophorus* AGASSIZ, 1832 is one of the most cited fossil fishes in the paleontological literature, as it was considered during a long time as a hinge-genus between Holostei and Teleostei. *Pholidophorus* is become also the type-genus of the family Pholidophoridae WOODWARD, 1890 and later of the order Pholidophoriformes BERG, 1940 (not *sensu* ARRATIA, 2013, 2017), a lineage of ganoid fishes firstly ranged in the Halecostomi but now considered as basal Teleostei (PATTERSON, 1973; ARRATIA, 2013, 2015, 2017; among others). Dozens of species were progressively included in *Pholidophorus* since its erection almost two centuries ago.

---

[1] Royal Institute of Natural Sciences of Belgium (IRSNB), Directorate Earth and History of Life, Vautierstreet, 29, B-1000 Brussels, Belgium. E-mail: louis.taverne@gmail.com

In spite of the importance of such a genus, its diagnosis was until now never really satisfactory, a fact certainly linked to the long, strange and difficult story of this fossil fish (ARRATIA, 2013: 116, 118; TAVERNE & STEURBAUT, 2017: 13).

The aim of the present paper is to remember a few historical data concerning the genus *Pholidophorus*, to re-study the osteology of *Pholidophorus latiusculus* AGASSIZ, 1832, the type-species, and to give more accurate figures of its skull. Indeed, the two drawings in NYBELIN (1966: figs 3, 4) are very schematic and the one shown by ARRATIA (2013: fig. 5) is based on the neotype, a beautiful specimen but with a very incomplete cranium. My own description rests essentially on specimens from the Natural History Museum (London) having a much better preserved skull than that of the neotype. A so important species as *Ph. latiusculus* certainly deserves a more detailed osteological description than those already existing.

It is to be noted that the order Pholidophoriformes *sensu lato* is now considered as polyphyletic (ARRATIA, 2000, 2013, 2015, 2017; TAVERNE, 2011a, b, c, 2014a, b, 2015). ARRATIA (2013) limited the order to the family Pholidophoridae only. Recently, she also added to the Pholidophoriformes *sensu stricto* the newly erected family Eurycormidae (ARRATIA, 2017), a lineage containing only the genus *Eurycormus* WAGNER, 1863 from the Late Jurassic of Germany. However, another systematic position for *Eurycormus* is proposed by TAVERNE & CAPASSO (2017).

MATERIAL AND METHODS

The three specimens described in the present paper belong to the paleontological collections of the Natural History Museum of London (NHM) and were studied with a stereomicroscope Wild M 5. The drawings of the figures were made by the author with a camera lucida and the photos by Mr. Thierry HUBIN, from the Belgian Royal Institute of Natural Sciences. Razing light and aspersion with ethanol were used to improve some observations.

Material from the Royal Museum of Central Africa (MRAC), the National Museum of Natural History of Luxembourg (MNHNL), the Belgian Royal Institute of Natural Sciences (IRSNB) and the CAPASSO collection in Chieti (CLC) is also used in the part “Discussion”.

List of abbreviations used in the text-figures

AN = angular
ANT = antorbital
ART = articular
AX = pectoral axillary process
CLA = clavicle
CLT = cleithrum
DETH = dermethmoid (= rostral)
DN = dentary
DPTE = dermopterotic
DSPH = dermosphenotic
ECPT = ectopterygoid
ENPT = entopterygoid (= endopterygoid)
EPI = epiotic (= epioccipital)
FR = frontal
HCLT = hypercleithrum (= supracleithrum)
HCOR = hypocoracoid
HYOM = hyomandibula
IOP = interopercle
IORB 1-5 = infraorbitals 1 to 5
LDETH = lateral dermethmoid
LEP = fin ray (= lepidotrichia)
MPT = metapterygoid
MX = maxilla
NA = nasal
NEUR = neural arch

OP = opercle
PA = parietal
PCLT 1-3 = postcleithra 1 to 3
PMX = premaxilla
POP = preopercle
PORB 1, 2, 3 = postorbitals (= suborbitals) 1, 2, 3
PORB a. = accessory postorbitals
PRO = prootic
PS = parasphenoid
PT = posttemporal
QJ = quadratojugal
QU = quadrate
RAD = pterygiophores (= radials)
RART = retroarticular
SAN = surangular
SC = scale
SCA = hypercoracoid (= scapula)
SCL = sclerotic bone
SCU = caudal scute
SMX 1, 2 = supramaxillae 1 and 2
SOC = supraoccipital
SOP = subopercle
SORB 1, 2, 3 = supraorbitals 1, 2, 3
ST = supratemporal (= extrascapular)
SY = symplectic
VO = vomer
a. pr. = ascending process of parasphenoid
b. fu. = basal fulcra
b. pr. = basipterygoid process of parasphenoid
br. = broken
cr. = crest on the dentary separating the dental and the splenial regions
e. ps. n. (?) = notch for the efferent pseudobranchial artery (?)
ex. c. = extrascapular sensory commissure
fr. fu. = fringing fulcra
i. c. f. (?) = foramen for the internal carotid (?)
iorb. c. = infraorbital sensory canal
l. = left
l. l. = lateral line sensory canal
l. n. = “leptolepid” notch
m. c. = mandibular sensory canal
no. = nostril
ol. f. = olfactive foramen
ot. c. = otic sensory canal
p. = peg
p. l. = pit-line
pop. c. = preopercular sensory canal
ps. t. = patch of minute teeth on the parasphenoid
q. pr. = bony process of the quadrate
r. = rigth
ro. c. = rostral sensory commissure
sorb. c. = supraorbital sensory canal
sy. d. = depression for the symplectic on the inner face of the quadrate

HISTORICAL DATA

Pholidophorus was erected in 1832 by Louis AGASSIZ in a short paper written in German. The definition he gave at that time of this new Mesozoic fish was very succinct, no more than five lines. He described *Pholidophorus* as a herring-like fish, with ganoid scales, opposite dorsal and ventral fins and small anal fin (AGASSIZ, 1832:145). He included two species in his new genus: *Pholidophorus latiusculus* AGASSIZ, 1832 (ibid., 1832: 145) and *Pholidophorus pusillus* AGASSIZ, 1832 (ibid., 1832: 146), both from the Norian (Upper Triassic) of Seefeld in Tyrol, Austria. He wrote that *Ph. latiusculus* had larger scales than *Ph. pusillus* but did not give any other information on these two species. No specimen was figured and no holotype named. Following the actual rules of the code of zoological nomenclature, *Ph. latiusculus* and *Ph. pusillus* would be considered as *nomina dubia*.

In his monumental monograph in five volumes and atlas "Recherches sur les Poissons Fossiles », AGASSIZ re-defined *Pholidophorus* as a fish with an elongate body, a small dorsal fin opposite to the ventral fins, a forked caudal fin with the two lobes of equal length, scales slightly extending on the basis of the dorsal lobe of the caudal fin ant teeth "en brosse" (AGASSIZ, 1833-43, vol. 2, part 1: 9). He described and figured twenty species in the genus (ibid., 1833-1843, vol. 2, part 1: 271-288, atlas, vol. 2: pl. 36-43) and cited *Pholidophorus latiusculus* and *Pholidophorus pusillus* (ibid., 1833-1843, vol. 2, part 1: 9, 287) but once again without adequate descriptions and figures. However, he wrote that *Ph. pusillus* had very small scales. He also mentioned a third Austrian species from Seefeld, *Pholidophorus dorsalis* AGASSIZ, 1833, with a very succinct description and no figure (ibid., 1833-1843, vol. 2, part 1: 9, 287), a fish reported later to the genus *Allolepidotus* DEECKE, 1889 by WOODWARD (1895: 316).

KNER (1866: 328-334: pl. 3, figs 2, 3, pl. 6, fig. 2) was the first to describe and figure *Pholidophorus latiusculus* and *Pholidophorus pusillus*. Unfortunately, he did not give an osteological description of the skull of these two species. In a second paper, he gave once again a few data concerning the two species and figured another specimen of *Ph. latiusculus* (KNER, 1867: 803-804, pl. 2, fig. 1).

A first attempt to define *Pholidophorus* in a more detailed and precise way was done by WOODWARD (1895: 447-449). At that time, he numbered already 41 species in the genus. Unfortunately, his new diagnosis was based on general characters and plesiomorphies, not on apomorphies. Moreover, he considered the English Lower Jurassic *Pholidophorus bechei* AGASSIZ, 1844 as the type-species of the genus and not the Austrian Upper Triassic *Pholidophorus latiusculus*, the first species mentioned by AGASSIZ (1832). The new definition of the genus given a half-century later by WOODWARD (1941) in a short paper did not improve his former diagnosis as it was entirely based on *Ph. bechei*. Today, *Ph. bechei* is referred to the genus *Dorsetichthys* ARRATIA, 2013 and is no more included in the family Pholidophoridae (ARRATIA, 2013: 118) but in the new family Dorsetichthyidae and the new order Dorsetichthyiformes (NELSON *et al*., 2016; ARRATIA, 2017).

In a small monograph, NYBELIN (1966) studied nine species ranged in four different genera that he reported to the Pholidophoridae. Unfortunately, the figures joined to his text were rather schematic. Four species included in *Pholidophorus* were taken into account: *Pholidophorus bechei*, considered as the type-species of the genus, *Pholidophorus latiusculus* and *Pholidophorus pusillus*, the two species firstly described in the genus by AGASSIZ (1832), and *Pholidophorus caffii* AIRAGHI, 1908 from the Rhaetian (Upper Triassic) of northern Italy, a species now ranged by ARRATIA (2013: 86) in the genus *Parapholidophorus* ZAMBELLI, 1975. His new diagnosis of *Pholidophorus* did not really differ from that of WOODWARD (1895, 1941), except for the mention that the nasals were separated from each other by the frontals. NYBELIN (1966: 386) also wrote that the original material of *Ph. latiusculus* and *Ph. pusillus* was lost, probably destroyed in 1942 during World War 2. As no holotype was designated for *Ph. latiusculus* by AGASSIZ (1832), he chose the best preserved specimen studied by KNERR (1866: pl. 3, fig. 3) as neotype (NYBELIN, 1966: pl. 15, figs 1, 2; ARRATIA, 2013: fig. 1 A, B). Untowardly, this neotype exhibits an incomplete and crushed skull. So, he based principally his study of the cranium on a specimen from Seefeld in the collections of the Natural History Museum of London (NHM) with a well better preserved skull. He also studied *Ph. pusillus*, using for his description another specimen from Seefeld present in the collections of the NHM and previously attributed to *Ph. latiusculus* by WOODWARD (1895). This sample was badly preserved and its braincase was missing (NYBELIN, 1966: fig. 6, pl. 6, fig. 2).

Twenty years later, in his sixth paper on the Italian Late Triassic pholidophorid fishes, ZAMBELLI (1986: 7-9) restricted the genus *Pholidophorus* to only two species, *Pholidophorus latiusculus* and *Pholidophorus bechei*. He considered the species *Pholidophorus gervasuttii* ZAMBELLI, 1980 as a simple subspecies, *Pholidophorus latiusculus gervasuttii* (ibid., 1986: 8).

This point of view was followed by ARRATIA (2000). She specified however that *Ph. latiusculus* was the type-species of the genus and not *Ph. bechei*. She also gave on that occasion the first cladistic diagnosis of *Pholidophorus* based on four characters (her Node C1): frontals broad in the posterior region but elongate and narrow in the anterior part (character 126[1]), lepisosteid flank scales higher than long and with a smooth surface and posterior margin (character 136[1], nasals disjoined, separated by the frontals (character 138[1] and anterior acuminate extremities of the frontals contacting the rostral in a restricted region (character 139[1]).

In her recent monograph on the marine Upper Triassic Pholidophoridae from northern Italy and Austria, ARRATIA (2013) re-studied the skeleton of *Pholidophorus* and provided a new emended diagnosis for that fish. She maintained only two species in the genus, *Pholidophorus latiusculus*, the type-species, and *Pholidophorus gervasuttii* ZAMBELLI, 1980. She rejected the other species ever ranged in *Pholidophorus*. Unfortunately, specimens of *Ph. latiusculus* are rare. In most samples, including the neotype, the skull is incomplete and badly preserved. So, she based her new diagnosis principally on *Ph. gervasuttii* that was known by more and better preserved specimens. Once again, the new definition mentioned only one autapomorphy for the genus. The anterior extremities of the frontals ("parietals" in ARRATIA's monograph), that separate the two nasals, are elongated and very narrow, with a width of about one-fifth or one-sixth of the postorbital skull width (ARRATIA, 2013: 15; node C1b, character 5[1]). She considered that feature as one of the most important characters of the genus. However, there was a problem with a diagnosis of *Pholidophorus* resting essentially on *Pholidophorus gervasuttii*. Indeed, in the phylogenectic tree that she proposed, this species shared with *Knerichthys* ARRATIA, 2013 and *Pholidorhynchodon* ZAMBELLI, 1980 a few characters (ARRATIA, 2013, node C1d) unknown in *Pholidophorus latiusculus*. Such a strange situation implied that the genus *Pholidophorus* was paraphyletic, a fact that ARRATIA (2013: 116, 118) willingly conceded.

In her last paper on pholidophorid fishes (ARRATIA, 2017), she finally solved the problem by erecting a new genus, *Lombardichthys* ARRATIA, 2017, for *Pholidophorus gervasuttii*. So, *Pholidophorus latiusculus* is presently not only the type-species of *Pholidophorus* but also the only valid species belonging to this genus.

The generic status of *Pholidophorus pusillus*, the other pholidophorid fish from Seefeld, is uncertain as the major part of its skull remains unknown (NYBELIN, 1966: fig. 6).

SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii KLEIN, 1885
Series Neopterygii REGAN, 1923
Division Teleostei MÜLLER, 1845
Ordre Pholidophoriformes BERG, 1940 *sensu* ARRATIA, 2013, 2017
Family Pholidophoridae WOODWARD, 1890 *sensu* ARRATIA, 2013, 2017
Genus ***Pholidophorus*** AGASSIZ, 1832

Type-species: *Pholidophorus latiusculus* AGASSIZ, 1832

Species ***Pholidophorus latiusculus*** AGASSIZ, 1832

Emended diagnosis

Small ganoid teleost. Dermic cranial bones weakly ornamented. Maxilla and supramaxillae ornamented with strongly marked longitudinal ridges. Bones of the skull roof partially or totally fused together. Dermethmoid (= rostral) ovoid, with a pair of short lateral processes. Nasal ovoid, narrow, with a slightly pointed anterior tip and devoid of foramen for the nostril. Nasals separated from each other by the frontals but reaching the dermethmoid. Anterior region of frontals elongate, narrow, strip-like, slightly acuminate and reaching dermethmoid. Postorbital region of skull roof very broad. Supraorbital and otic sensory canals not in contact. A long middle pit-line present on the dermopterotic. Posterior margin of enlarged infraorbital 3 reaching the preopercle. Infraorbitals 3 and 5 reduced. Large postorbital (= suborbital) resting on the upper margin of the infraorbital 3. One accessory postorbital. Posterior margin of the maxilla oblique and slightly outpacing the orbital posterior border. First supramaxilla very small. Dorsal branch of the preopercle short and not reaching the lateral border of the skull roof. Opercle ovoid. Large subopercle located below and posterior to the opercle. Cleithrum divided in two branches, an acuminate dorsal one and a broad ventral one. Three postcleithra. Pectoral fin with 3 basal fulcra and 17 to 19 rays. Pectoral axillary process present. Ventral fins with 10 rays, devoid of fringing fulcra. First ventral fin ray short, thick and acuminate. Dorsal and ventral fins located at the same level. Caudal fin with 22 principal rays and a concave posterior margin. Pectoral, dorsal, anal and caudal fins bearing fringing fulcra. Scales with smooth external surface and posterior margin. 38 or 39 vertical rows of scales along the body. Dorsal margin of caudal fin preceeded by some small scales and not by a large scute.

Specimens studied

Sample P. 1063. An almost complete specimen, with a well preserved skull (Fig. 1). Collection EGERTON.

Figure 1. *Pholidophorus latiusculus* AGASSIZ, 1832. Specimen NHM P. 1063. The scale is in millimetres.

Sample P. 1063a. An almost complete specimen, with a moderately well preserved skull (Fig. 2). Collection EGERTON.

Figure 2. *Pholidophorus latiusculus* AGASSIZ, 1832. Specimen NHM P. 1063a. The scale is in millimetres.

Sample P. 11.780. A mandible, some isolated cranial bones, articulated scales and some isolated scales (Fig. 3).

Figure 3. *Pholidophorus latiusculus* AGASSIZ, 1832. Specimen NHM P. 11780. The scale is in millimetres.

These three specimens from Seefeld were determined as *Pholidophorus latiusculus* by A. S. WOODWARD. This determination probably is based on the large scales that these three fossil fishes exhibit. The other pholidophorid fish present in Seefeld, *Pholidophorus pusillus*, has very small scales (AGASSIZ, 1833-1843, vol. 2, part 1: 9; KNER, 1866, pl. 6, fig. 2).

Formation and locality

Norian (Upper Triassic) of Seefeld, Tyrol, Austria.

Osteology

The skull (Figs 4-12)

The dermethmoid (= rostral) of specimen P. 1063a is complete but badly preserved. The ganoid layer is lost and only a thin bony layer is visible. The bone is rather large, more or less ovoid, with a short lateral process on each side. It is in contact with the two premaxillae. In specimen P. 1063, the dermethmoid is broken and only a small part of the bone is present. The nasals are visible on P. 1063. They are more or less ovoid, rather narrow, with a rounded posterior margin and a slightly pointed anterior extremity. There is no aperture in the bone for the nostril. The two nasals are separated from each other by the frontals but they reach however the dermethmoid. The nasal forms the major part of the anterior orbital border. A great part of the vomer is preserved on P. 1063a in association with the parasphenoid. The bone seems toothless. However, its most anterior region is missing. The eventual endochondral ethmoid ossifications are unknown. No independent lateral dermethmoid is visible.

The skull roof is more or less triangular in shape and contains three paired bones that are partially or totally fused together, the frontal (= parietal, according to the cranial bone nomenclature of SCHULTZE, 2008), the parietal (= postparietal) and the dermopterotic The thin layer of ganoin that covers these bones is slightly ornamented with feebly marked tubercles and ridges. The cranial vault of P. 1063 and P. 1063a is divided by a long medial suture in right and left halves. Anteriorly, this medial suture is straight but becomes strongly sinuous at the orbital level. On P. 1063a, this median suture disappears at the level of the parietals. On P. 1063, there is a breaking line between the two parietals and the presence of the suture at that level is thus uncertain. In each half of the skull roof, the frontal, the parietal and the dermopterotic are fused together. However, a partial suture is present between the parietal and the dermopterotic on the left side in P. 1063a. The sutures between these three bones shown in NYBELIN (1966: fig. 4) are irregular fractures due to the fossilisation and not real sutures. In the neotype, there is no trace of suture at all on the skull roof (ARRATIA, 2013: fig. 5). The anterior part of the frontals is elongate, narrow, strip-like and slightly acuminate. Each frontal contacts the dermethmoid in only one point. Posteriorly, the skull roof progressively broadens and reaches its maximal breadth at the postorbital level. A large supratemporal (= extrascapular) overlaps the posterior region of the dermopterotic and the parietal. The bone reaches the mid-line of the skull roof.

Figure 4. *Pholidophorus latiusculus* AGASSIZ, 1832. Head region of specimen NHM P. 1063. The scale is in millimetres.

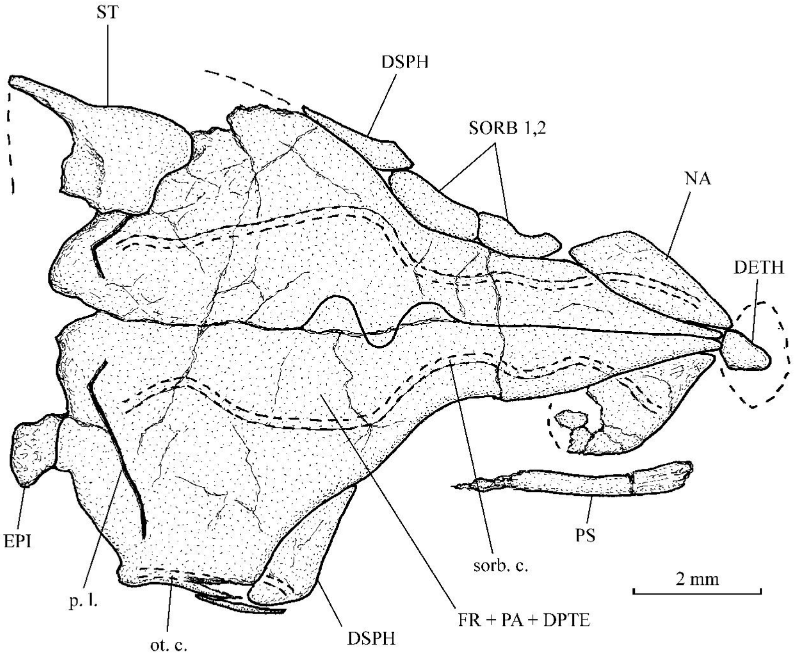

Figure 5. *Pholidophorus latiusculus* AGASSIZ, 1832. Skull roof of specimen NHM P. 1063.

The tube-like supraorbital sensory canal goes through the nasal, the frontal and the parietal and has no junction with the otic sensory canal that lies at the external margin of the dermopterotic. The supraorbital canal exhibits a sigmoid curve in the postorbital region of the skull roof. There are no secondary tubules and apparently no pores along the course of the canal. A long and narrow middle pit-line crosses the dermopterotic and the parietal. The supraorbital canal ends posteriorly near the middle pit-line but there is no real junction between them.

Figure 6. *Pholidophorus latiusculus* AGASSIZ, 1832. Head region of specimen NHM P. 1063a. The scale is in millimetres.

No part of a possible bony endocranium is visible. However, in P. 1063, a small bone is sutured with the posterior margin of the right dermosphenotic but is located at a slightly lower level. This bony element seems to be a part of the right epiotic (= epioccipital).

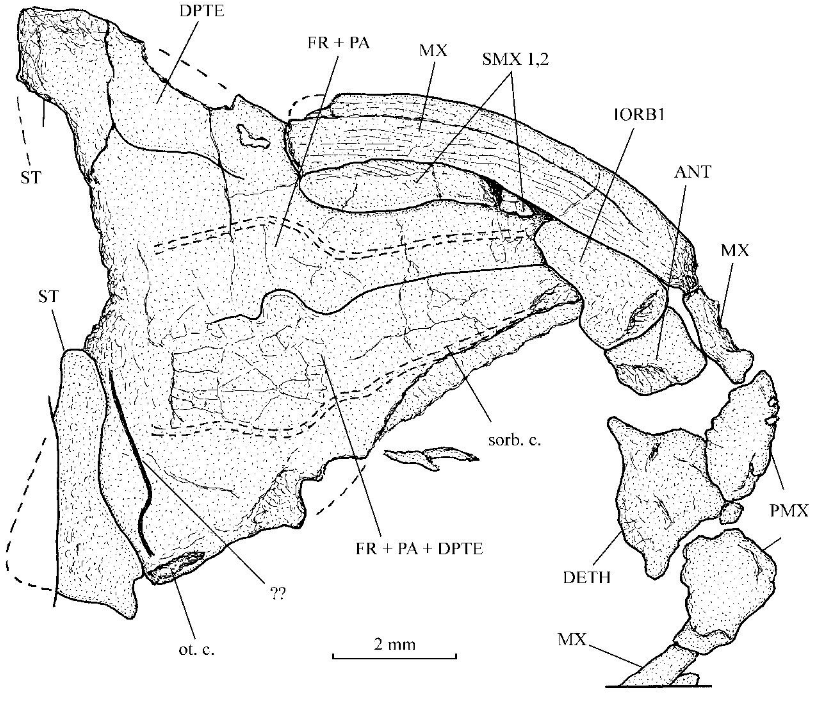

Figure 7. *Pholidophorus latiusculus* AGASSIZ, 1832. Skull roof of specimen NHM P. 1063a.

A fragment of the trabecular portion of the parasphenoid is preserved on P. 1063. A more complete but badly preserved parasphenoid is visible on P. 1063a. The bone is elongate, narrow and toothless. It bears a pair of long basipterygoid processes and a pair of smaller ascending processes. There is no trace of a foramen for the efferent pseudobranchial artery on the basipterygoid process itself. It seems that this artery passes through a notch at the basis of the anterior margin of the process. A more posteriorly located trace, at the level of the ascending process, could be the foramen for the internal carotid.

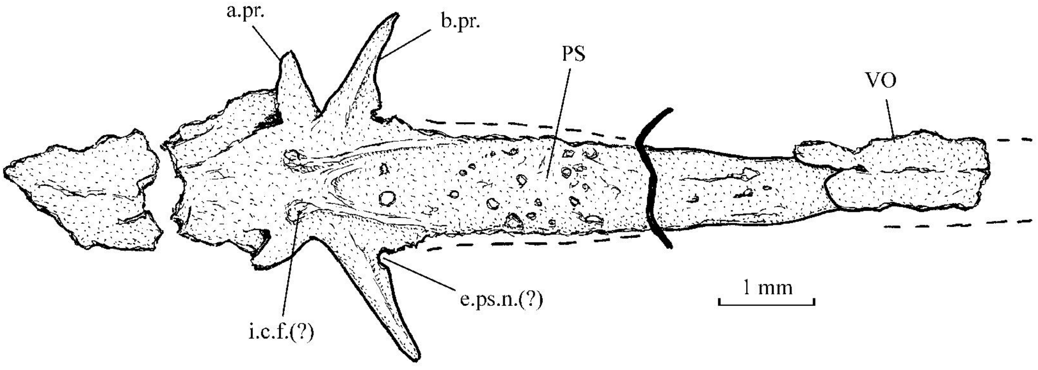

Figure 8. *Pholidophorus latiusculus* AGASSIZ, 1832. Parasphenoid of specimen NHM P. 1063a.

The quadrate and the symplectic are intimately associated. Both pieces are well preserved in bones and in imprints on specimen P. 11780. The quadrate is a triangular bone, longer than deep, and devoid of bony process. Its articular head is strongly developed. The rod-like symplectic lies along the ventral margin of the quadrate but is longer and has an acuminate posterior extremity.

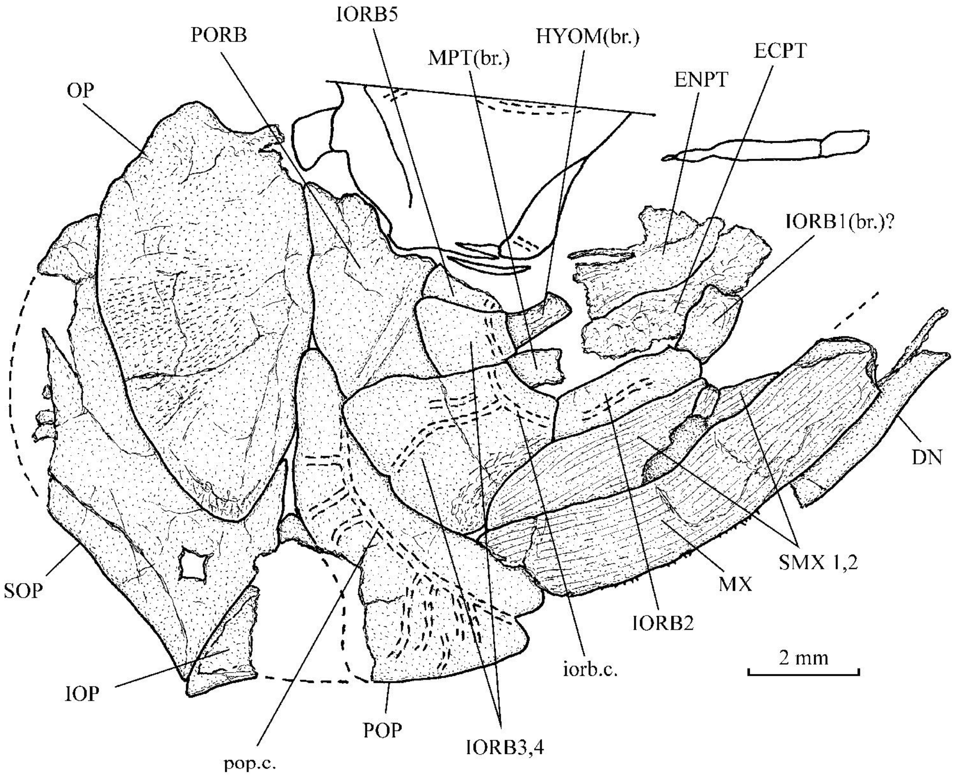

Figure 9. *Pholidophorus latiusculus* AGASSIZ, 1832. Suspensorium of specimen NHM P. 1063.

Its anterior extremity is expanded and pressed against the articular head of the quadrate, forming a big composed condyle. Both bones articulate with the lower jaw. A large portion of the entopterygoid and of the ectopterygoid is present on P. 1063. The two bones seem toothless.

The premaxillae are present neither on the neotype (ARRATIA, 2013: fig. 5) nor on P. 1063. However, the two bones are visible on P. 1063a but badly preserved. They are rather small bones with a more or less rounded upper margin. They are devoid of marked ascending processes. They occupy the symphysis of the upper jaw, just anterior to the dermethmoid. Two fragments of very small conical teeth are visible on the oral margin of the left premaxilla. The maxilla is elongate and rather broad, except at its anterior extremity that is narrow. The posterior margin is oblique on the neotype (ibid., 2013: fig. 5) and on P. 1063. A few very small conical teeth are preserved on the oral margin of the bone in P. 1063. There are two supramaxillae, the first one being very small and triangular in shape. The second supramaxilla is elongate, with a rounded posterior extremity and a short pointed antero-dorsal process that slightly overlaps the first supramaxilla. The maxilla and the two supramaxillae are ornamented with long and well marked ridges. The posterior extremity of the upper jaw reaches the level of the posterior margin of the orbit in the neotype (ARRATIA, 2013: fig. 5) and is a little posterior to this level in P. 1063.

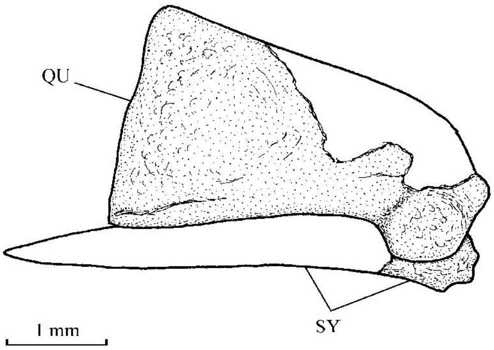

Figure 10. *Pholidophorus latiusculus* AGASSIZ, 1832. Quadrate and symplectic of specimen NHM P. 11780. The parts shaded are preserved in bones and those left “in white” are preserved as imprints.

Specimen P. 11780 exhibits a complete right lower jaw that is moderately well preserved and is seen by its external face. This mandible is triangle-shaped, with a narrow symphysis and high coronoid region, and contains the dentary, the angular and the surangular. The posterior portion of the articular is also visible at the postero-ventral corner of the jaw. There is no autogenous retroarticular. The oral margin is almost rectilinear and raises up regularly from the symphysis to the coronoid area formed by the surangular. There is a long and strongly marked ridge that separates the dental and splenial portions of the dentary.

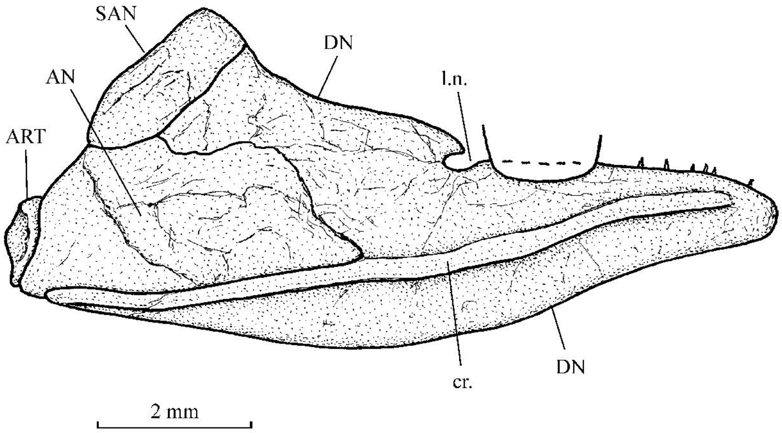

Figure 11. *Pholidophorus latiusculus* AGASSIZ, 1832. Lower jaw of specimen NHM P. 11780.

A well visible “leptolepid” notch is located at mid-length of the oral border. The dentary bears a few very small conical teeth anterior to the “leptolepid” notch. The internal face of the mandible is not visible and the possible presence of a prearticular and of one or more coronoid bones is thus uncertain.

The antorbital and the first infraorbital are preserved in P. 1063a. The other circumorbital bones are visible in P. 1063. There are two small supraorbitals. The well developed antorbital is sutured to the anterior margin of the first infraorbital (= lachrymal) that is a more elongate bone, with an expanded antero-dorsal region. The second infraorbital is still longer but remains rather narrow. The third infraorbital is extremely enlarged and reaches the anterior margin of the preopercle. The fourth and fifth infraorbitals and the dermosphenotic are smaller. There is only one large postorbital (= suborbital). It is located behind the fourth and fifth infraorbitals. Its broad lower margin lies on the upper border of the third infraorbital and its posterior margin rests on the opercle. No accessory postorbital is visible in P. 1063 and P. 1063a. Accessory postorbitals are also missing in the neotype (ARRATIA, 2013: 17). However, in P. 11780, the postorbital is seen in inner view, with a crushed fragment of the ventral branch of the hyomandibula, and a small triangular accessory postorbital is associated to the principal postorbital. In P. 1063, the infraorbital sensory canal is visible from the second to the fifth infraorbital and on the dermosphenotic that realizes the connection with the otic canal borne by the dermopterotic. The canal bears secondary tubules at the level of the third infraorbital.

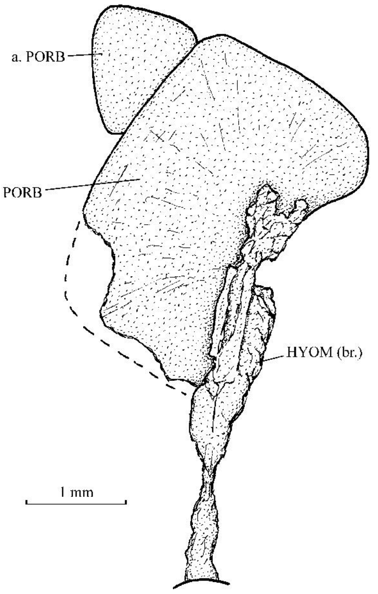

Figure 12. *Pholidophorus latiusculus* AGASSIZ, 1832. Postorbital (= suborbital) and accessory postorbital of specimen NHM P. 11780.

The preopercle is more or less triangle-shaped, slightly curved, with an enlarged ventral region and a short dorsal limb that does not reach the lateral margin of the skull roof. The preopercular sensory canal runs all along the bone and bears a series of ventral secondary tubules. A few short secondary tubules are also present in the dorsal branch of the bone. There is a shallow notch in the inferior part of the posterior margin of the preopercle (ARRATIA, 2013: fig. 5) and another smaller notch at the ventral ending of the preopercular canal. Both the opercle and the subopercle are large bones. The ovoid opercle is broader in its upper region than in the ventral one. The upper margin is rounded and the lower region a little more acuminate. A few feebly marked ridges are visible. The subopercle is obliquely oriented. Its posterior region extends dorsally along the posterior margin of the opercle. There is a well developed ascending pointed process at the antero-dorsal corner of the subopercle. Only the posterior part of the interopercle is preserved on P. 1063. The gular plate and the branchiostegal rays are not visible on the available specimens.

The girdles (Figs 13-15)

The exoskeleton of the shoulder girdle is almost complete in P. 1063, except the posttemporal that is missing and the hypercleithrum (= supracleithrum) that is incompletely preserved. The cleithrum is divided in two branches, a dorsal one with an acuminate tip and a broader ventral one obliquely oriental along the subopercle. The bone exhibits a posterior triangular bony wing at the junction of the two branches. There are three postcleithra, two large dorsal elements positioned against the upper branch of the cleithrum and a small ventral piece.

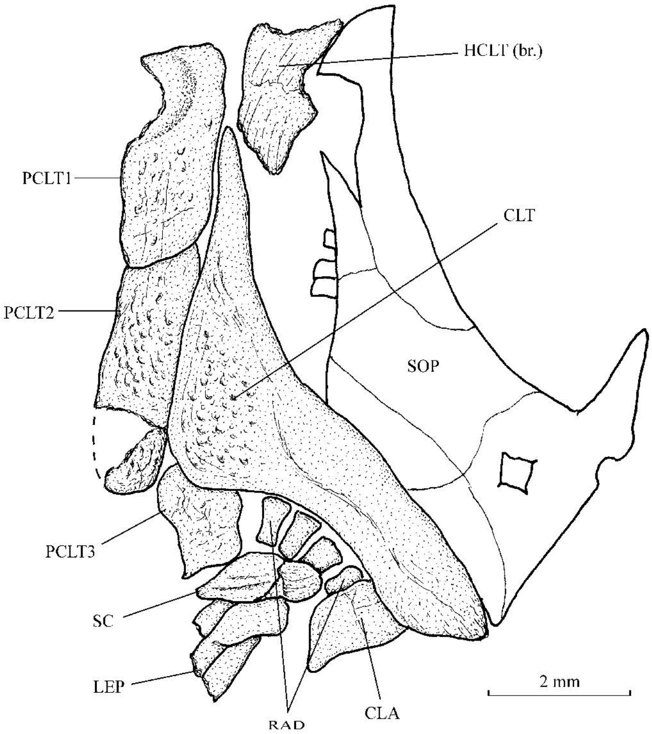

Figure 13. *Pholidophorus latiusculus* AGASSIZ, 1832. Pectoral girdle of specimen NHM P. 1063.

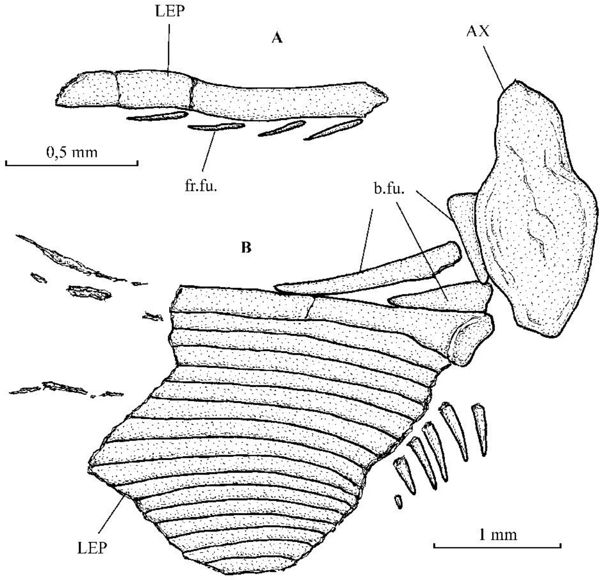

Figure 14. *Pholidophorus latiusculus* AGASSIZ, 1832. (A) Distal extremity of the first pectoral ray of specimen NHM P. 1063, showing the fringing fulcra. (B) Pectoral fin of specimen NHM P. 1063a.

The two dorsal postcleithra and the bony wing of the cleithrum are ornamented with weakly marked tubercles. The pectoral endoskeleton is not visible. The pectoral fin is supported by at least four pterygiophores and contains 19 rays in P. 1063 and 17 rays in P. 1063a. There are 3 basal fulcra in P. 1063a. A few small fringing fulcra are visible along the distal part of the first ray in P. 1063. A large pectoral axillary process is present in P. 1063a.

The pelvic bones are not visible on the available specimens. However, parts of the ventral fins are present but badly preserved in P. 1063 and P. 1063a. The proximal region of the fins is missing in both fishes. In P. 1063, fragments of 10 rays are preserved. The first ray is thicker and shorter than the following ones. Its distal extremity forms a strong acuminate point that is articulated with the basal part of the ray. The other rays are segmented and branched. Fringing fulcra are not present. In P. 1063a, fragments of 6 rays are visible.

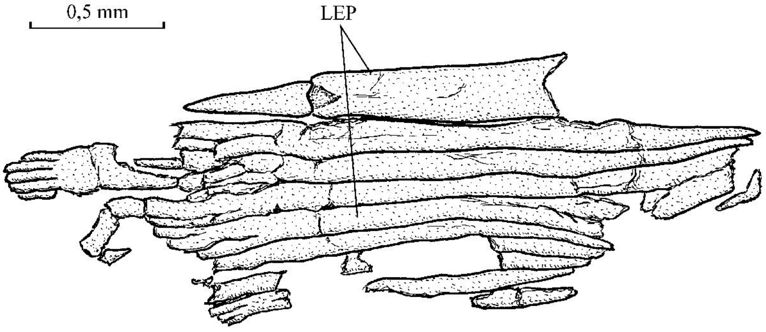

Figure 15. *Pholidophorus latiusculus* AGASSIZ, 1832. Distal part of the ventral fin of specimen NHM P. 1063, with the tick, short and pointed first ray.

The axial skeleton

The number of vertebrae is unknown, most of the axial skeleton being hidden under the scales in all the samples. A few fragments of ring-like chordacentra are visible on P. 1063. We do not know if diplospondyly was present in the caudal region or not.

The dorsal and anal fin

The dorsal and anal fins are missing or poorly preserved on all the available specimens. The dorsal fin is positioned anterior to the anal fin and approximately at the same level as the ventral fins (KNER, 1867: pl. 2, fig. 1; ARRATIA, 2013: 18). In a specimen studied by ARRATIA (2013: 18), the dorsal fin begins by a few basal fulcra followed by 18 rays. The anal fin is short and located closer to the tail than to the ventral fins. Fringing fulcra are present on both the dorsal and anal fins.

The caudal skeleton and fin (Fig. 16)

The caudal endoskeleton is unknown, being always covered by the scales. The caudal fin is incomplete in all specimens. ARRATIA (2013: 18) mentions 22 principal caudal rays in one of the specimens she studied. In sample P. 1603a, a few fringing fulcra are visible on both margins of the fin and the first epaxial basal fulcrum is narrow and unpaired. The dorsal and ventral scales preceding the fin are small. *Pholidophorus latiusculus* is devoid of the large caudal scutes present in other pholidophorid fishes.

The squamation (Fig. 17)

Specimens P. 1063 and P. 11.780 have an incomplete squamation. There are 39 vertical rows of scales along the body in P. 1063a and 38 rows in the neotype (ARRATIA, 2013: 19). The scales of *Pholidophorus latiusculus* are well described and figured by SCHULTZE (1966: fig. 37a) and

ARRATIA (2000: fig. 2D, 2013: fig. 6). The scales are moderately deep on the flanks but of smaller size in the dorsal and ventral regions. The external face and the posterior margin are smooth. The peg and socket system of articulation is well developed.

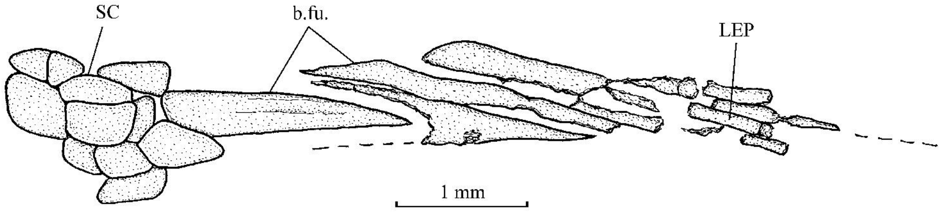

Figure 16. *Pholidophorus latiusculus* AGASSIZ, 1832. Specimen NHM P. 1063a. Beginning of the dorsal margin of the caudal fin, with the unpaired first basal fulcrum preceded by a few small scales.

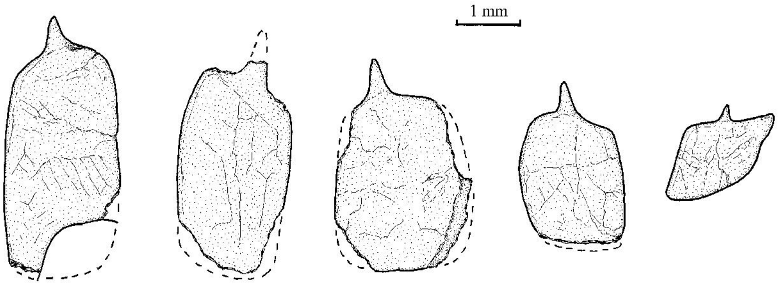

Figure 17. *Pholidophorus latiusculus* AGASSIZ, 1832. Specimen NHM P. 11780. A few scales, showing the variability of shape and size between the flank scales (left) and those of the dorsal and ventral regions (right).

DISCUSSION

Pholidophorus and *Lombardichthys*

As already written, *Lombardichthys gervasuttii* was erected by ZAMBELLI (1980) as a valid species of the genus *Pholidophorus* but later considered by him (ZAMBELLI, 1986) as a simple subspecies of *Pholidophorus latiusculus*. *Pholidophorus gervasuttii* was treated again as a valid species belonging to the genus *Pholidophorus* but differing from *Ph. latiusculus* by ARRATIA (2013) and still more recently as a peculiar monospecific genus, *Lombardichthys* in ARRATIA (2017). It is thus interesting to enhance the differences that separate the two fishes. The data on *L. gervasuttii* hereafter used come from ZAMBELLI (1980) and ARRATIA (2013).

(1) The nasal of *L. gervasuttii* is broader anteriorly than posteriorly and is pierced by a large foramen for the posterior nostril. That of *Ph. latiusculus* has a more acuminate anterior extremity and is devoid of foramen for the nostril.

(2) The skull roof of *L. gervasuttii* is strongly ornamented with ridges and tubercles of ganoine, while that of *Ph. latiusculus* is very weakly ornamented.

(3) The posterior margin of the maxilla is rounded or notched in *L. gervasuttii* but is oblique in *Ph. latiusculus*.

(4) The first supramaxilla is proportionally much larger in *L. gervasuttii* than in *Ph. latiusculus*.

(5) The leptolepid notch of the dentary upper margin is located anterior to the mid-length of the lower jaw in *L. gervasuttii* and at the mid-length level in *Ph. latiusculus*.

(6) The first infraorbital of *L. gervasuttii* is larger than that of *Ph. latiusculus* and seems partially or totally separate the nasal from the orbital anterior margin (ARRATIA, 2013: figs 10A, B, 13C, 14).

(7) In *L. gervasuttii*, the pointed lower part of the postorbital (= suborbital) goes down along the posterior margin of the third infraorbital. In *Ph. latiusculus*, the broad rectilinear lower margin of the postorbital lies on the upper margin of the third infraorbital.

(8) The cleithrum has a completely different shape in the two fishes. The cleithrum of *L. gervasuttii* has a long and broad dorsal branch and a short ventral branch. *Ph. latiusculus* exhibits a cleithrum with a rather short and acuminate dorsal branch and a long ventral branch.

(9) The ventral fin of *L. gervasuttii* bears fringing fulcra and does not possess the long and strong pointed first ray present in *Ph. latiusculus*.

(10) A large caudal scute precedes each margin of the caudal fin in *L. gervasuttii* and the first unpaired epaxial basal fulcrum has a broad basis. In *Ph. latiusculus*, the dorsal margin of the caudal fin is not preceded by a large scute but by a few small scales and the first unpaired epaxial basal fulcrum is narrow.

(11) The layer of ganoine covering the scales is devoid of ornamentation in *Ph. latiusculus* but is ornamented with tubercles in *L. gervasuttii*.

ARRATIA (2013: 116) cotes three other differences (her node C1d) between *Ph. latiusculus*, on the one hand, and *Ph. gervasuttii,* on the other hand, these differences being shared by *Pholidorhynchodon malzanii* ZAMBELLI, 1980 and *Knerichthys bronni* ARRATIA, 2013. She mentions an elongate maxilla reaching behind the orbit (character 56[0]), the quadrate-mandibular articulation located posterior to the orbit (character 62[0]) and a notch at the posteroventral margin of the preopercle (character 89[1]). The posterior margin of the maxilla is slightly crushed in specimens P. 1063 and P. 1063a of *Ph. latiusculus*. However, the posterior region of this maxilla clearly outpaces the level of the orbit in these two fishes. The mandible of *Ph. latiusculus* is partially exposed, missing or isolated in all the available samples. It is not possible to determine the exact level of the articulation between the quadrate and the lower jaw in this species. A notch is present in the posteroventral border of the preopercle in *Ph. latiusculus* (ARRATIA, 2013: fig. 5). So, it seems that these three differences are not really consistent.

However, the differences between all the pholidophorid genera are not very important. So, those that separate *Ph. latiusculus* and *L. gervasuttii* (the preceding characters 1 to 11) are largely sufficient to justify the erection by ARRATIA (2017) of the new genus *Lombardichthys* for the species *gervasuttii*.

The validity of *Ceneichthys*

Ceneichthys TAVERNE & CAPASSO, 2015 is a recently described monospecific pholidophorid genus from the Upper Triassic of northern Italy. It differs sufficiently from the other known genera of the family to justify its peculiar generic status and seems more closely allied to *Lombardichthys* than to the other members of the Pholidophoridae (TAVERNE & CAPASSO, 2015: 21-23).

However, ARRATIA (2017: 21) does not recognize this fish “as a valid taxon because its diagnosis is based on one specimen deposited in a private collection” and “because its characters are ambiguous and unclear due to the poor preservation”. These three assertions deserve some comments.

Many fossil fish species and genera are described on the basis of a unique specimen. That is not exceptional in the paleontological field and even in the zoological field. ARRATIA herself, in her long and productive career, has erected some new fossil fish species and genera with the holotype as only known sample, for instance the primitive ostariophysan fish *Tischinglerichthys* ARRATIA, 1997 from the Upper Jurassic of Germany (ARRATIA, 1997: 90).

The holotype and unique specimen of *Ceneichthys* belongs to the CAPASSO collection in Chieti (Italy), considered as a private one by ARRATIA. However, a private archaeological or paleontological collection is illegal in Italy (law 1089/39). The CAPASSO collection is legally registered by a decree of the “Ministerio per I Beni e le Attivita Culturali ”, dated of October 11th, 1999, and is in no case a private one. The real owner of the collection is the Italian State and Prof.

CAPASSO is only the curator of the collection. Samples from the CAPASSO collection have been described since many years in scientific papers and some of them are become holotypes and paratypes.

Both sides of the holotype of *Ceneichthys* are preserved. Side "a" is almost complete, while side "b" is mostly preserved as an imprint (TAVERNE & CAPASSO, 2015: figs 1, 2). The orbital bones series, the supramaxillae and a great part of the preopercle are missing but the other regions of the skull are clearly visible (ibid., 2015; fig. 5). *Ceneichthys* exhibits a well better preserved skull than some other Upper Triassic Italian Pholidophoridae, such as *Knerichthys bronni* ARRATIA, 2013 and *Parapholidophorus caffii* (AIRAGHI, 1908) (ARRATIA, 2013: figs 37, 39, 72), two species that are however considered as valid by ARRATIA (2013)

So, the three arguments invocated by ARRATIA (2017: 21) to consider *Ceneichthys* as an invalid taxon are clearly not pertinent. Obviously, there are no good reasons to contest the validity of *Ceneichthys*.

***Pholidophorus* within Pholidophoridae (Fig. 18)**

Prohalicetes porroi (BELLOTTI, 1857), a small fossil fish from the Middle Triassic of Italy, is considered by ARRATIA (2013, 2015, 2017) as the direct plesiomorphic sister-taxon of Teleostei, including Pholidophoridae *sensu stricto* and other "Pholidophoriformes". I completely agree with the systematic position proposed by ARRATIA for this Italian fish. I also consider that *Catervariolus hornemani* DE SAINT-SEINE, 1955, from the continental Middle Jurassic of the Democratic Republic of Congo, and the other Catervariolidae represent a more primitive lineage than Pholidophoridae within the "pholidophoriform" assemblage (TAVERNE, 2011a, b, 2014a, 2015) *contra* ARRATIA (2013, 2015, 2017) who expresses an opposed point of view.

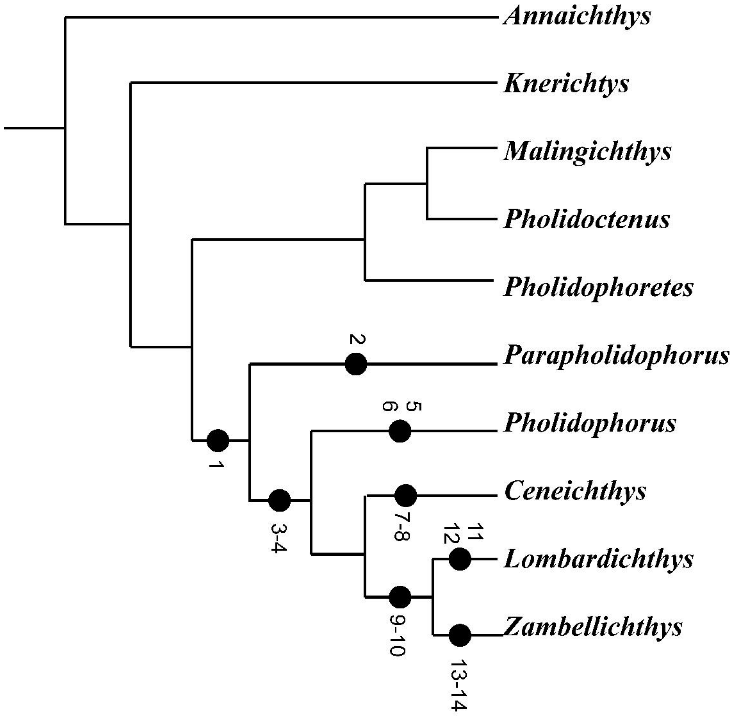

Figure 18. The phylogeny within Pholidophoridae.

Members of the family Pholidophoridae *sensu stricto* differ from *P. porroi* and *C. hornemani* by acquiring a series of new advanced characters, for instance the nasal forming a part of the orbital border, the presence of two supramaxillae, the well marked "leptolepid" notch on the upper margin of the dentary, the strong crest separating the dental and splenial parts of the dentary, the important broadening of the ventral region of the preopercle, the reduction of the number of the principal postorbitals (= suborbitals), etc.

ARRATIA (2013: figs 95, 96A, 2017: figs 9, 11A, B) places the genus *Annaichthys* ARRATIA, 2013 as the less specialized member of the family Pholidophoridae. This fish exhibits a moderately broad postorbital region of the skull roof, nasals separated by the frontals and bearing a foramen for the nostril, frontals with a broad anterior extremity that reaches the dermethmoid, rather short jaws ending at the level of the mid-length of the orbit and weakly ornamented maxilla and supramaxillae (ARRATIA, 2013: fig. 32).

Other pholidophorid fishes have a much broader postorbital region, elongate jaws and maxilla and supramaxillae ornamented with strongly marked longitudinal ridges.

In *Knerichthys* ARRATIA, 2013, the frontals reach the dermethmoid but the anterior extremity of the bone is broad and the dermethmoid separates the two nasals (ARRATIA, 2013: fig. 37). The strong ornamentation of the upper jaw already exists (ibid., 2013: fig. 39). The postorbital region of the skull is broader than in *Annaichthys* but, however, less important than in all the other pholidophorid genera (ibid., 2013: fig. 37). *Knerichthys* seems intermediate between *Annaichthys*, on the one hand, and the other members of the family, on the other hand. ARRATIA (2013: figs 95, 96A) has another opinion concerning the systematic position of *Knerichthys* that is positioned as the sister genus of *Pholidorhynchodon*. However, *Knerichthys* is not taken in account by ARRATIA (2017: fig. 11B) in her most recent phylogenetic tree of the Pholidophoridae.

In her latest hypothesis concerning the phylogeny within Pholidophoridae, ARRATIA (2017: fig. 11B) divides the remaining members of the family in two subgroups.

One subgroup (her Node C4) contains the genera *Pholidoctenus* ZAMBELLI, 1977, *Pholidophoretes* GRIFFITH, 1977 and *Malingichthys* TINTORI et al., 2015. Frontals with a broad anterior region and nasals meeting on the mid-line and separating the dermethmoid (= rostral) from the frontals are the main features characterizing that assemblage.

The other subgroup (her Node C5) gathers the genera *Pholidophorus*, *Lombardichthys, Parapholidophorus* ZAMBELLI, 1975 and *Pholidorhynchodon* ZAMBELLI, 1985. They have the anterior region of the frontals elongate and acutely sharp, reaching the dermethmoid in only one point and separating the two nasals (character 5[1]). That is the most striking feature of the lineage. Another mentioned feature is the presence of two or three accessory postorbitals (= suborbitals) (character 54[1]).

Zambellichthys ARRATIA, 2013 and *Ceneichthys* exhibit exactly the same morphology of the snout (ARRATIA, 2013: 40; TAVERNE & CAPASSO, 2015: fig. 5) and obviously belong to this second subgroup, even if they are not taken in account by ARRATIA (2017). On the other hand, some osteological arguments are developed in TAVERNE & CAPASSO (2017) leading to the exclusion of *Pholidorhynchodon* from Pholidophoridae and to the placement of this fossil fish in the family Ankylophoridae. ARRATIA (2017) herself points out the peculiar snout anatomy of *Pholidorhynchodon* (ibid., 2017: fig. 6A) that differs from the one of all the other pholidophorid fishes (ibid., 2017: fig. 6B, C, D, E) by the presence of toothed lateral dermethmoids and rostral.

Within the second subgroup (Node C5), ARRATIA (2017: fig. 11B) puts *Parapholidophorus* in the less specialized position. In her phylogenetic scheme, *Pholidophorus*, *Lombardichthys* and *Pholidorhynchodon* differ from that genus by four features: the nasal with a large opening for the nostril (character 25[1]), the long maxilla ending posterior to the orbit (characters 62[0]), the quadrate-mandibular articulation located posterior to the orbit (character 70[0]) and a notch at the posterior ventral border of the preopercle (character 98[1]). However, some comments must be done about character 25[1]. Indeed, this character is missing in *Pholidophorus*, this fish being devoid of aperture for the nostril in the nasal (Fig. 5). On the contrary, character 25[1] is not really absent in *Parapholidophorus*. This fish has a nasal with an enlarged aperture for the nostril and this marked enlargement induces a breaking in the nasal margin. This opening in the margin of the bone changes the nostril aperture into a wide and deep notch (ARRATIA, 2013: figs 61, 62). A well marked foramen in the nasal for the nostril already exists in the primitive pholidophorid *Annaichthys* (ARRATIA, 2013: fig. 32). In *Prohalicetes porroi*, the nasal is devoid of foramen and the nostril probably opened at the slightly concave external margin of the bone (TINTORI, 1990: fig. 3A, B, C). In *Catervariolus hornemani*, the nostril was probably located between the lateral margin of the nasal and the antorbital (TAVERNE, 2011b: fig. 9).

I propose hereafter a more complete phylogenetic tree for the genera of the Node C5 to which I add *Zambellichthys* and *Ceneichthys*. But I exclude *Pholidorhynchodon* from the scheme as I do not consider this fish as a member of the Pholidophoridae *sensu stricto* (cf. TAVERNE & CAPASSO, 2017). The phylogeny within the subgroup C4 is not part of my following analysis. For that point, I just refer the reader to the comments of ARRATIA (2017).

As already written, one main feature characterizes the pholidophorid fishes of the subgroup C5.

(1) The elongate and acuminate anterior extremities of the frontals reach the dermethmoid (= rostral) and separate the two nasals (character 5[1] in ARRATIA, 2017).

Parapholidophorus occupies the most basal position within the clade. Its nasal has a peculiar character not present in the other members of the family.

(2) The lateral margin of the nasal is open and the enlarged foramen for the nostril becomes a deep notch bored into the bone (ARRATIA, 2013: figs 61, 62).

The other members of the subgroup chiefly differ from *Parapholidophorus* by two characters probably linked together.

(3) The maxilla is elongate and its posterior extremity slightly outpaces the level of the orbit (character 62[0] in ARRATIA, 2017).

(4) The lower jaw is elongate and its articulation with the quadrate is located posterior to the orbit (character 70[0] in ARRATIA, 2017).

The remaining genera are divided in two branches, *Pholidophorus* on the one hand and *Ceneichthys*, *Lombardichthys* and *Zambellichthys* on the other hand. *Pholidophorus* differs from the three preceding genera by at least two main characters.

(5) The nasal exhibits a narrow anterior extremity and is devoid of foramen for the nostril (Fig. 5).

(6) The caudal fin is preceded by a few small scales and not by large caudal scutes (Fig.15).

The nasal foramen for the nostril and the caudal scutes, lost in *Pholidophorus* but present in *Annaichthys* and *Parapholidophorus*, are preserved in *Ceneichthys*, *Lombardichthys* and *Zambellichthys*. *Ceneichthys* exhibits two peculiar characters in the pectoral girdle that are present neither in *Lombardichthys* and *Zambellichthys* nor in other pholidophorid fishes.

(7) The cleithrum has a very elongate and horizontally oriented ventral branch (TAVERNE & CAPASSO, 2015: fig. 5).

(8) There are two large postcleithra as deep as the dorsal branch of the cleithrum and located the one behind to other (ibid., 2015: fig. 5).

Lombardichthys and *Zambellichthys* share some new characters absent in the preceding genera.

(9) The postorbital is deep, with a narrow and pointed ventral extremity that extends along the upper part of the posterior margin of the third infraorbital (ARRATIA, 2013: figs 10A, B, 11B, 13, 14, 28, 29).

(10) The ventral region of the cleithrum is strongly shortened (ibid., 2013: figs 19B, C, 20, 28, 29)

Lombardichthys is characterized by a few peculiar features.

(11) The first infraorbital and the antorbital are greatly enlarged and separate almost totally the nasal from the orbit (ibid., 2013: figs 7, 9B, 10A, B, 13C, 14).

(12) The thick layer of ganoine that covers the bones of skull roof, the fin rays and the scales is strongly ornamented with ridges and tubercles.

Zambellichthys differs from *Lombardichthys* and from the other pholidophorid genera by at least two characters.

(13) The postorbital is divided in a series of small elements (ibid., 2013: figs 28, 29).

(14) The dorsal branch of the preopercle is elongate and comes close to the lateral margin of the skull roof (ibid., 2013: fig. 29).

Quadrate, quadratojugal and bony quadratic process (Figs 19-21)

The absence of bony quadratic process and the very close association between the quadrate and the symplectic in *Pholidophorus latiusculus* lead me to re-examine the problem of the quadratojugal and of the bony process of the quadrate in archaic teleosts.

The quadratojugal is an independent bone from the ventral part of the cheek region, close to the quadrate and the symplectic. It is present in many actinopterygians and sarcopterygians. For a very long period, the bony quadratic process of teleosts was considered as a quadratojugal fused to the quadrate during the embryological development of these fishes (JOLLIE, 1975, 1984; WILEY, 1976; among many others).

More recently, ARRATIA & SCHULTZE (1991) and ARRATIA (1999) clearly demonstrated that the bony quadratic process of the modern teleosts appeared during the early ontogeny of the quadrate. The process was not a free bone that fused later to the quadrate. On the contrary, from the origin, it was continuous with the small bone that developed in the ventral region of the still cartilaginous quadrate.

After the publication of these two papers, the scientific community was convinced that the bony quadratic process was not a fused quadratojugal but a peculiar autapomorphy characterizing teleosts.

In teleosts, the first ossification of the embryonic cartilaginous quadrate appears along its ventral margin, posterior to the articular condyle that remains cartilaginous at that stage. At the first onset, the bony process is attached to this perichondral bone, forming a long and thin stalk (ARRATIA & SCHULTZE, 1991: fig. 44B, 45C; ARRATIA, 1999: fig. 5A, B). The process is not pressed against the body of the quadrate but is largely separated from it by the symplectic. At an older stage in the embryonic development, the bone progresses vertically along the body of the cartilaginous quadrate. The bony process broadens but remains separated from the lower margin of the quadrate by the symplectic. The articular head is still cartilaginous and ossifies later but the bony process is not involved in the ossification of that quadratic articular condyle (VERRAES, 1977: fig. 3; ARRATIA & SCHULTZE, 1991: fig. 15B, 26A, 28B).

In adult teleosts, this bony process wedges the symplectic against the quadrate. On a functional point of view, the process sets a sort of joining link between the palatoquadrate and the hyosymplectic arches. The same link is realized by a short cartilage in some primitive Neopterygii, as for instance in the Amiidae (ARRATIA & SCHULTZE, 1991: fig. 14; GRANDE & BEMIS, 1998: fig. 48).

In the Middle Triassic *Prohalicetes porroi*, the wedging mechanism between the quadrate and the symplectic is still strengthened by an independent quadratojugal (Fig. 17; TINTORI, 1990: fig. 4).

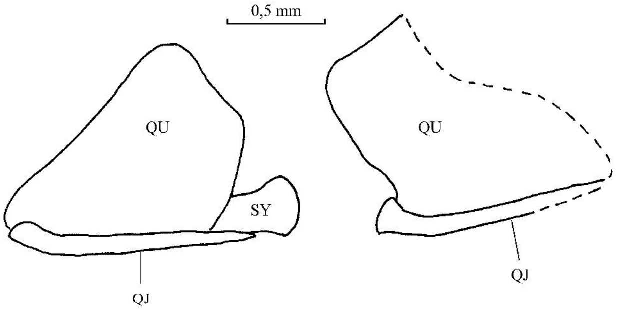

Figure 19. *Prohalicetes poroi* (BELLOTTI, 1857). Quadrate, quadratojugal and symplectic (modified from TINTORI, 1990: figs 2A, 4A).

Until now, an independent quadratojugal was never mentioned in teleosts. Thus, as already written, it seems that the lost of the quadratojugal in fishes more advanced than *Prohalicetes porroi* and its replacement by a quadratic bony process really are two of the most important autapomorphies of Teleostei. However, the situation could be more complex than it seems at first sight. Another scenario is perhaps possible as I will explain hereafter.

The bony quadratic process is missing in Pholidophoridae (ARRATIA, 2013: numerous figs). HEINEKE (1907: pl. 5, fig. 2) described and figured the quadrate of *Eurycormus speciosus* WAGNER, 1863 also as devoid of bony process. However, a very short process located at the posterior ventral corner of the bone does exist in this species (Fig. 20; ARRATIA, 2017, Appendix 2, fig. S2A). The quadrate of the advanced “pholidophoriform” *Dorsetichthys bechei* (AGASSIZ, 1844) is also described and figured by RAYNER (1948: fig. 27A) without any bony process. But ARRATIA (2017, Appendix 3: 4, character 78[1]) codes the bony process as present in this species. The process is reduced or lost in some lineages of living teleosts.

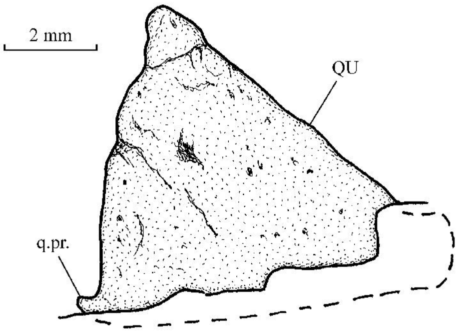

Figure 20. *Eurycormus speciosus* WAGNER, 1863. Quadrate of specimen CLC S-1234, from the Tithonian (Upper Jurassic) of Solnhofen, Germany.

The presence of a bony quadratic process in *Catervariolus hornemani* DE SAINT-SEINE, 1955 (TAVERNE, 2011b: fig. 24) and its absence in Pholidophoridae was one of the arguments invocated by ARRATIA (2013) for considering Catervariolidae as more specialized than Pholidophoridae in the phylogenetic tree she proposed for the "Pholidophoriformes" (ibid., 2013: fig. 95) *contra* TAVERNE (2011a, b, 2014a, 2015) who placed Catervariolidae at a more plesiomorphic level than Pholidophoridae in his own phylogenetic hypothesis.

The Congolese Middle Jurassic ganoid teleost *Catervariolus hornemani* is represented by almost 600 specimens. An important variability in the shape of numerous bones is observed (TAVERNE, 2011b: 207). That is also the case for the quadrate. This bone is well visible in only five more or less complete samples, the specimens MRAC RG 7485a (right quadrate, inner side), RG 7591 (left quadrate, external side), RG 7725 (right quadrate, external side), RG 8000a (right quadrate, inner side) and RG 10.152 (left quadrate, external side). Each of these five quadrates differs from the others. The general shape of the bone is triangular. In specimen RG 7485a (Fig. 19A), the articular condyle is divided in two distinct parts, one dorsal and the other ventral, that are sutured together. The upper condylar part is in perfect continuity with the body of the quadrate. On the contrary, the lower condylar part is in continuity with the quadratic process and is also fused postero-dorsally with the body of the quadrate. The process is not longer than the quadrate itself and is pressed against the ventral margin of the bone. The symplectic is not preserved in this sample but an elongate gutter is visible in the posterior ventral region of the quadrate to accommodate this bone. The situation is different in specimen RG 7591 (Fig. 19D). There is a unique articular condyle. The bony process is narrow, separated from the body of the bone, a little longer than the quadrate itself and anteriorly fused with the condyle. In specimen RG 7725 (Fig. 19C), the condyle is partly preserved and the bony process is completely fused to the quadrate, forming a strong thickening of the ventral margin of the bone. Only the most posterior part of the bony process outpaces the body of the quadrate. The morphology is once again different in specimen RG 8000a (Fig. 19B). The quadrate has only one big articular condyle. The bony quadratic process is broad, longer than the quadrate and with a pointed posterior extremity. It is sutured with the ventral margin of the bone and forms with this margin a deep gutter in which lies a fragment of a broken symplectic. In specimen RG 10.152 (Fig. 19E), the quadrate is incomplete, the articular condyle being broken away due to an artefact of fossilization. The process is longer than the quadrate itself and has an acuminate posterior extremity. Anteriorly, the process is completely fused to lower margin of the quadrate but posteriorly, a well marked suture is visible between the process and the posterior ventral corner of the bone. The symplectic is not preserved.

A similar morphology of the quadrate as that of sample RG 7485a, with a double condyle and the ventral condyle linked to the quadratic process, is known in *Ichthyokentema purbeckensis* (DAVIES, 1887) (GRIFFITH & PATTERSON, 1963: fig. 10) and in *"Pholidophorus" germanicus* QUENSTEDT, 1858 (PATTERSON, 1973: fig. 7).

Such a pattern of the condyle and of the process seems better correspond to a fused quadratojugal than to a true teleostean bony quadratic process.

In this hypothesis, Catervariolidae could exhibit the plesiomorphic state of the quadrate within teleosts, a state in which the quadratojugal is still present and fused with the quadrate. Pholidophoridae could represent a more apomorphic state in which the quadratojugal is lost but the teleostean type of bony process not yet developed. A true bony process of teleostean type could be present in some more advanced "Pholidophoriformes", such as *Luxembourgichthys friedeni* (DELSATE, 1999) (TAVERNE & STEURBAUT, 2017: fig. 16).

Pachycormidae is a fish lineage grouping around a dozen of Jurassic genera and one Cretaceous genus. The family is considered by some as halecostomes closely related to the teleosts (PATTERSON, 1973) or as basal teleosteomorphs by others (ARRATIA, 2017). PATTERSON (1973: fig. 18) described and figured the quadrate of a specimen (NHM P. 32434) of *Pachycormus curtus* AGASSIZ, 1844. The articular condyle is double, one part being externally located and the other internally. The symplectic is fused to the inner face of the quadrate by its anterior extremity. There is no process separated from the body of the quadrate but the ventral border of the bone is particularly thickened. PATTERSON considered this important thickening as a possible fused quadratojugal. A separated process sutured to the body of the bone was already illustrated by RAYNER (1948: fig. 17) in the same species. MAINWARING (1978: 27, figs 8, 9) described and figured the quadrate of three specimens (NMH P. 10146, P. 24410 and P. 32432) of *Pachycormus macropterus* (DE BLAINVILLE, 1818). The quadrate exhibits an individualized process that is fused with a part of the double articular condyle and is pressed against the lower margin of the bone. The anterior extremity of the symplectic is also fused to the inner side of the quadrate. So, Pachycormidae could be another family that has a true quadratojugal fused to the quadrate and not a process of teleostean type.

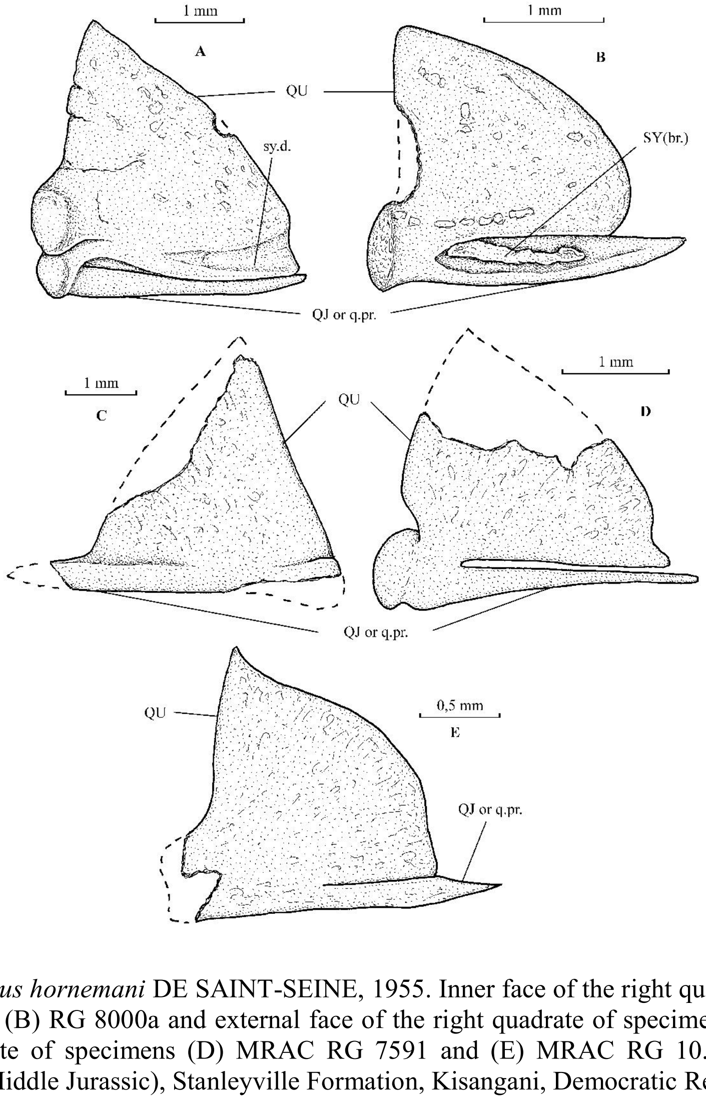

Figure 21. *Catervariolus hornemani* DE SAINT-SEINE, 1955. Inner face of the right quadrate of specimens (A) MRAC RG 7485a and (B) RG 8000a and external face of the right quadrate of specimen (C) MRAC RG 7725 and of the left quadrate of specimens (D) MRAC RG 7591 and (E) MRAC RG 10.153. All five from the Aalenian-Bathonian (Middle Jurassic), Stanleyville Formation, Kisangani, Democratic Republic of Congo.

Ligulellidae is a family of endemic fishes from the Congolese continental Middle Jurassic containing only one species, *Ligulella sluysi* DE SAINT-SEINE, 1955. It was described with an elongate symplectic lying along the quadrate, both bones being articulated with the lower jaw (TAVERNE, 2011c: fig. 20). This “symplectic” is unusually long and its posterior extremity is acuminate. That is not a normal shape for a true symplectic. The bone could be a quadratojugal reaching the mandible as in some other neopterygian fishes (ARRATIA & SCHULTZE, 1991: fig. 13B) and not a true symplectic.

Signeuxellidae is another endemic family from the continental Middle Jurassic of the Democratic Republic of Congo. The lineage contains a unique species, *Signeuxella preumonti* DE SAINT-SEINE, 1955, and is ranged within “Pholidophoriformes”. The quadrate of *S. preumonti* has a small claw-like process fused to the posterior ventral corner of the bone (TAVERNE, 2017: fig. 4). This fossil fish could be one of the oldest teleosts having a true bony quadratic process and not a fused quadratojugal.

The orbital series in “Pholidophoriformes” (Figs 22-24)

There are fundamentally two principal morphologies of the orbital bones within the lineages formerly included in the “Pholidophoriformes”. One pattern is present in Catervariolidae. The second one is found in Pholidophoridae in the other groups ranged in that polyphyletic order.

Catervatiolus hornemani has an antorbital, three infraorbitals, a dermosphenotic, three supraorbitals, three postorbitals (= suborbitals) and, at least in some specimens, two small dorsal accessory postorbitals in its orbital bony series. The antorbital is well developed, located just anterior to the first infraorbital and is more or less L-shaped. Its ventral branch prolongs the infraorbital sensory canal towards the dermethmoid. Its dorsal branch carries the antorbital sensory commissure and joins the first supraorbital. The infraorbitals 1 and 2 are rather small. The infraorbitals 3, 4 and 5 (IORB 3-5) are fused, forming a long angular bone that occupies the postero-ventral corner and the posterior margin of the orbit. The bone is not posteriorly expanded. The three very wide postorbitals completely separate IORB 3-5 from the narrow crescent-shaped preopercle.

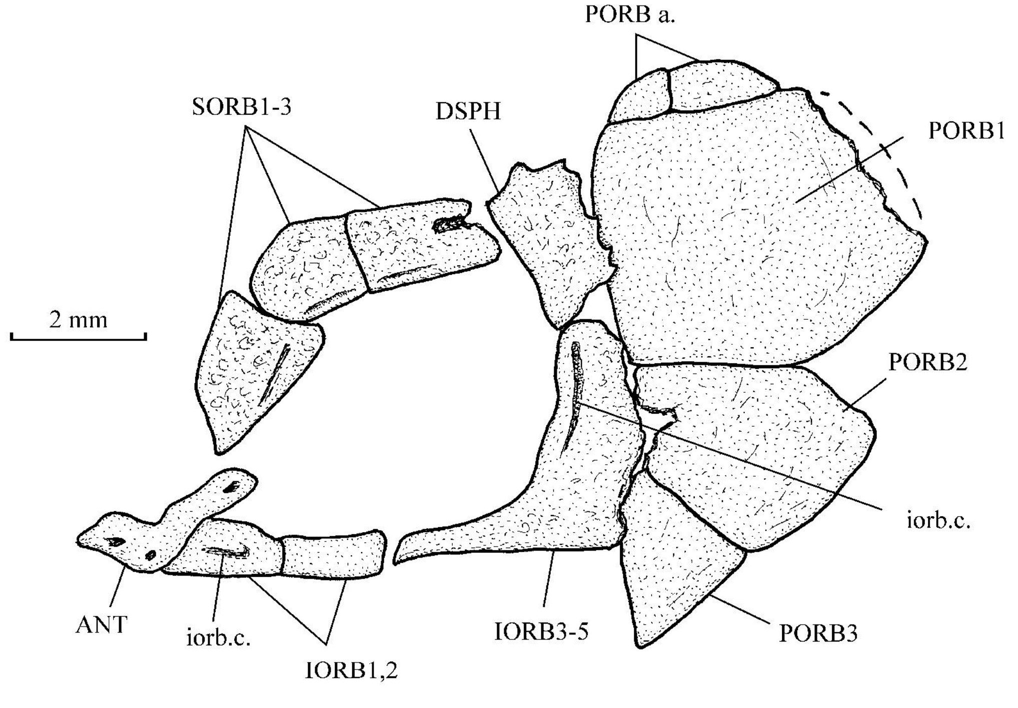

Figure 22. *Catervariolus hornemani* DE SAINT-SEINE, 1955. Orbital bones of specimen MRAC RG 7485a (Aalenian-Bathonian [Middle Jurassic], Stanleyville Formation, Kisangani, Democratic Republic of Congo).

This orbital morphology of *Catervariolus hornemani* is rather similar to that of the Italian Middle Triassic *Prohalicetes porroi* (TINTORI, 1990: fig. 2A).

In Pholidophoridae and most other "pholidophoriform" fishes, the architecture of the orbital bony ring is different. Generally, the number of supraorbitals is reduced to two. In some very rare cases, a small third supraorbital is present. The large dorsal postorbital is the only one preserved. It is positioned posterior to IORB 4 and 5. IORB 3 becomes by far the largest bone of the infraorbital series. Its posterior margin reaches the preopercle. This enlargement of IORB 3 is the result of the capture of the ventral postorbitals. In some Ankylophoridae, there is no more a free postorbital. The dorsal postorbital is fused with IORB 4 that becomes also a very wide bone reaching the preopercle and the opercle (GAUDANT, 1978: pl. 1, fig. 2; ARRATIA, 2000: figs 7-9A, B).

The same evolved orbital bony pattern, with two supraorbitals, one dorsal postorbital and a large IORB 3 that reaches the preopercle, is preserved in some primitive teleosts with cycloid scales, such as Leptolepididae and Vasarichthyidae (ARRATIA, 1981: fig. 4).

The evolution of the circumorbital bony series in "Pholidophoriformes" and Pholidophoridae is thus a strong argument in favour of a less advanced position of Catervariolidae in the phylogeny of those basal Teleostei than that of Pholidophoridae.

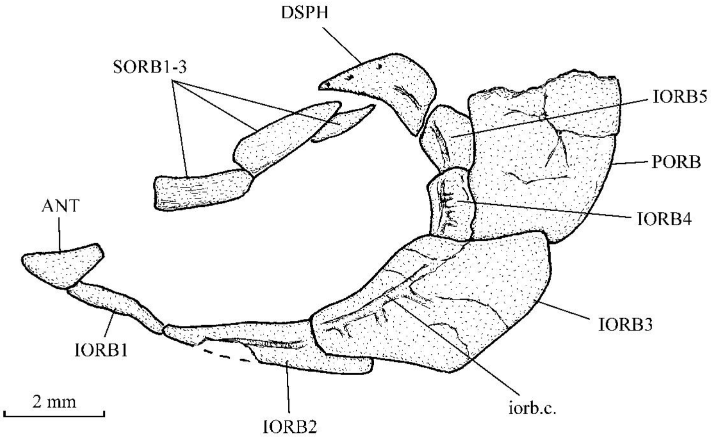

Figure 23. *Luxembourgichthys friedeni* (DELSATE, 1999). Orbital bones of holotype MNHNL N° TU 998B (former MF 17B) (Toarcian [Lower Jurassic), Schouweiler, Grand Duchy of Luxembourg).

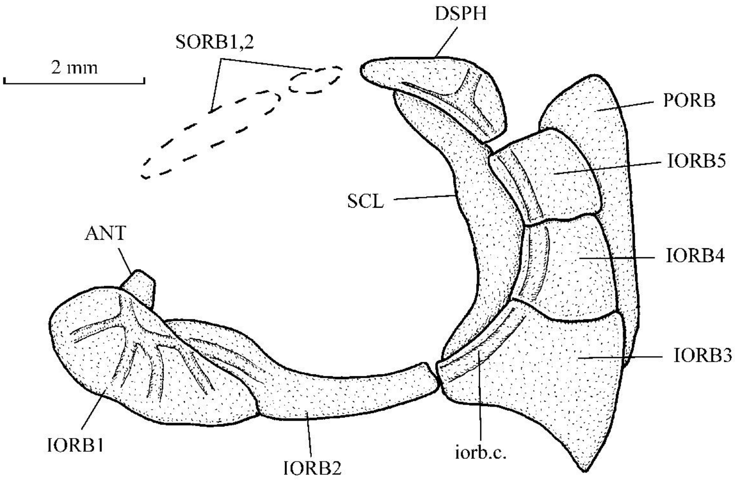

Figure 24. *Leptolepis normandica* NYBELIN, 1962. Orbital bones of specimen IRSNB P 9908 (former I.G. 22.448 N° 108-25) (Toarcian [Lower Jurassic], Athus, Belgium).

The preopercle in "Pholidophoriformes" (Fig. 25)

The preopercle of *Catervariolus hornemani* and of other Catervariolidae is crescent-like and narrow (TAVERNE, 2011b: figs. 8, 35, 2014a: fig. 4, 2015: fig. 3). It strongly resembles that of many halecostome fishes. It is close to the preopercle of *Prohalicetes porroi* that is also crescent-shaped (TINTORI, 1990, fig. 2A). However, in this Middle Triassic Italian fish, the preopercle is specialized and divided in two parts, a short ventral region that has retained a membranic bony component and a long dorsal region reduced to the sensory canal tube.

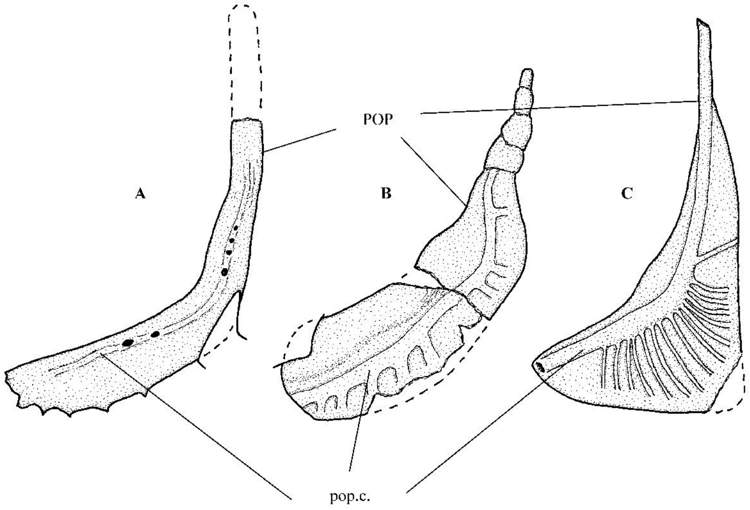

Figure 25. Preopercles of (A) *Catervariolus hornemani* DE SAINT-SEINE, 1955, paratype MRAC RG 7490, (B) *Luxembourgichthys friedeni* (DELSATE, 1999), holotype MNHNL N° TU 998B, and (C) *Leptolepis normandica* NYBELIN, 1962, specimen IRSNB P 9909 (former I. G. 22.917 N° 211) (reversed).

In Pholidophoridae and in many other "Pholidophoriformes", the preopercle has a more specialized shape, with an enlarged basal region, a narrower dorsal branch that is often but not always shortened and some well developed secondary tubules on the preopercular sensory canal. This peculiar morphology seems to announce the classical preopercle of primitive cycloid teleosts, with two well developed branches and many secondary tubules associated to the preopercular canal.

The evolution of the preopercle seems once again an argument favouring a more basal position for Catervariolidae than for Pholidophoridae within the teleostean phylogeny.

ACKNOWLEDGMENTS

I greatly thank Dr. Emma BERNARD, curator of the paleontological collections of the Natural History Museum of London, for the loan of the three specimens studied in the present paper. I am also grateful to Mr. Thierry HUBIN and Mr. Adriano VANDERSYPEN, both from the Belgian Royal Institute for Natural Sciences of Brussels, for their technical help and to the anonymous colleagues who reviewed my text.

REFERENCES

AGASSIZ, L., 1832. Untersuchungen über die fossilen Fische der Lias-Formation. *Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, 3: 139-149.

AGASSIZ, L., 1833-1844. Recherches sur les Poissons Fossiles. Five volumes + Atlas, imprimerie de Petitpierre, Neuchatel, Suisse: 1798 p.

ARRATIA, G., 1981. *Varasichthys ariasi* n. gen. et sp. from the Upper Jurassic of Chile (Pisces, Teleostei, Varasichthyidae n. fam.). *Palaeontographica*, A, 175 (4-6): 107-139.

ARRATIA, G., 1997. Basal teleosts and teleostean phylogeny. *PalaeIchthyologica*, 7: 1-168.

ARRATIA, G., 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. *In*: ARRATIA & G., SCHULTZE, H. P. (eds) *Mesozoic Fishes 2 – Systematics and Fossil Record*, Verlag Dr. F. Pfeil, München: 265-334.

ARRATIA, G., 2000. New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the « pholidophoriforms". *Paläontologische Zeitschrift*, 74 (1/2): 113-143.

ARRATIA, G., 2013. Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes (Actinopterygii, Teleostei). *Journal of Vertebrate Paleontology,* 33, Supplement to Nr 6, *Memoir 13*: 1-138.

ARRATIA, G., 2015. Complexities of early Teleostei and the evolution of particular morphological structures through time. *Copeia*, 103 (4): 999-1025.

ARRATIA, G., 2017. New Triassic teleosts (Actinopterygii, Teleosteomorpha) from northern Italy and their phylogenetic relationships among the most basal teleosts. *Journal of Vertebrate Paleontology*, DOl: 10.1080/02724634.2017.1312690.

ARRATIA, G. & SCHULTZE, H.-P., 1991. Palatoquadrate and its ossifications: development and homology within osteichthyans. *Journal of Morphology*, 208: 1-81.

GAUDANT, J. 1978. Essai de révision taxonomique des « *Pholidophorus* » (Poissons Actinoptérygiens) du Jurassique supérieur de Cerin (Ain). *Nouvelles Archives du Musée d'Histoire Naturelle de Lyon*, 16: 101-121.

GRANDE, L. & BEMIS, W. E., 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Journal of Vertebrate Paleontology*, 18 (Suppl. 1, Memoir 4): 1-690.

HEINEKE, E., 1907. Die Ganoiden und Teleostier des Lithographischen Schiefers von Nusplingen. *Geologische und Palaeontologische Abhandlungen*, Iena, Neue Folge, 8 (3): 159-214.

JOLLIE, M., 1975. Development of the head skeleton and pectoral girdle in *Esox*. *Journal of Morphology*, 147: 61-88.

JOLLIE, M., 1984. Development of the head skeleton and pectoral girdle of salmons, with note on the scales. *Canadian Journal of Zoology*: 62: 1757-1778.

KNER, R., 1866. Die fossilen Fische der Asphaltschiefer von Seefeld in Tirol. *Sitzungsberichte der mathematisch-naturwissenchaftlichen Classe der kaiserlichen Akademie der Wissenschaften*, Wien, 54 (1): 303-334.

KNER, R., 1867. Nachtrag zur fossilen Fauna der Asphaltschiefer von Seefeld in Tirol. *Sitzungsberichte der mathematisch-naturwissenchaftlichen Classe der kaiserlichen Akademie der Wissenschaften*, Wien, 56 (1): 898-909.

NELSON, J. S., GRANDE, T. & WILSON, M. V. H., 2016. Fishes of the World. Fifth edition. WILEY and Sons edit., New York: 707 p.

NYBELIN O., 1966. On certain Triassic and Liassic representatives of the family Pholidophoridae s. str. *Bulletin of the British Museum (Natural History)*, *Geology*, 11 (8): 351-432.

PATTERSON, C., 1973. Interrelationships of holosteans. *Zoological Journal of the Linnean Society*, London, 53, Supplement No. 1: 233-305.

RAYNER, D. H., 1948. The structure of certain Jurassic holostean fishes with special references to their neurocrania. *Philosophical Transactions of the Royal Society of London*, Series B, *Biological Sciences*, 233 (601): 287-345.

SCHULTZE H.-P., 1966. Morphologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid- zu Rundschuppen). *Neues Jahrbuch der Geologie und Paläontologie Abhandlungen*, 126: 232-314.

SCHULTZE, H.-P., 2008. Nomenclature and homologization of cranial bones in actinopterygians. *In*: ARRATIA, G., SCHULTZE, H. P. and WILSON, M. V. H. (eds) *Mesozoic Fishes 4 – Homology and Phylogeny*, Verlag Dr. F. Pfeil, München: 23-48.

TAVERNE, L., 2011a. Ostéologie et relations phylogénétique de *Steurbautichthys* (« *Pholidophorus* ») *aequatorialis* gen. nov. (Teleostei, « Pholidophoriformes ») du Jurassique moyen de Kisangani, en République Démocratique du Congo. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, *Sciences de la Terre*, 81: 129-173.

TAVERNE, L., 2011b. Ostéologie et relations de *Catervariolus* (Teleostei, « Pholidophoriformes ») du Jurassique moyen de Kisangani (Formation de Stanleyville) en République Démocratique du Congo. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, *Sciences de la Terre*, 81: 175-212.

TAVERNE, L., 2011c. Ostéologie et relations de *Ligulella* (Halecostomi, Ligulelliformes nov. ord.) du Jurassique moyen de Kisangani (Formation de Stanleyville) en République Démocratique du Congo. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, *Sciences de la Terre*, 81: 213-233.

TAVERNE, L., 2014a Ostéologie et position systématique de *Songanella callida* (Teleostei, Catervarioliformes *nov. ord.*) du Jurassique moyen de Kisangani (Formation de Stanleyville, Calcaires de Songa) en République Démocratique du Congo. *Geo-Eco-Trop*, 37 [2013] (1): 1-32.

TAVERNE, L., 2014b. 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). *Geo-Eco-Trop*, 37 [2013] (1): 33-52.

TAVERNE, L., 2015. 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. *Geo-Eco-Trop*, 38 [2014] (2): 241-258.

TAVERNE, L., 2017. Osteology and relationships of *Signeuxella preumonti* (Teleostei, "Pholidophoriformes", Signeuxellidae) from the continental Middle Jurassic (Stanleyville Formation) of Kisangani (Democratic Republic of Congo). *Geo-Eco-Trop*, 41 [2017] (1): 85-
98, 11 fig.

TAVERNE, L. & CAPASSO, L., 2015. Osteology and relationships of *Ceneichthys zambellii* gen. and sp. nov. (Teleostei, Pholidophoridae) from the Late Triassic of northern Italy. *Bollettino del Museo Civico di Storia Naturale*, *Geologia Paleontologia Preistoria*, 39: 13-26.

TAVERNE, L. & CAPASSO, L., 2017. Comments on the phylogenetic relationships of *Pholidorhynchodon malzannii* and *Eurycormus speciosus* (Teleostei, "Pholidophoriformes"), two Mesozoic tropical fishes. *Geo-Eco-Trop*, 40 [2016] (4): 305-316.

TAVERNE, L. & STEURBAUT, E., 2017. Osteology and relationships of *Luxembourgichthys* (« *Pholidophorus* ») *friedeni* gen. nov. (Teleostei, "Pholidophoriformes") from the Lower Jurassic of Belgium and the Great Duchy of Luxemburg. *Geologica Belgica*, 20 (1-2): 15 p.

TINTORI, A. 1990. The actinopterygian fish *Prohalicetes* from the Triassic of northern Italy. *Palaeontology*, 33 (1): 155-174.

VERRAES, W., 1977. Postembryonic ontogeny and functional anatomy of the ligamentum mandibulo-hyoideum and the ligamentum interoperculo-mandibulare, with notes on the opercular bones and some other cranial elements in *Salmo gairdneri* Richardson, 1836 (Teleostei: Salmonidae). *Journal of Morphology*, 151 (1): 111-119.

WILEY, E. O., 1976. The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). *Miscellaneous Publications*, *Museum of Natural History*, *University of Kansas*, 64: 1-111.

WOODWARD, A. S., 1895. Catalogue of the fossil fishes in the British Museum (Natural History). Part III. Trustees of the British Museum (Natural History), London: I-XXXIX + 1-544.

WOODWARD, A. S., 1941. The Mesozoic ganoid fishes of the genus *Pholidophorus* Agassiz. *Annals and Magazine of Natural History*, series 11, 8(8): 88-91.

ZAMBELLI, R., 1980. Note sui Pholidophoriformes. III contributo. *Pholidophorus gervasuttii* sp. n. *Revista del Museo Civico di Scienze Naturali "Enrico Caffi",* Bergamo, 2: 5-44.

ZAMBELLI, R., 1986. Note sui Pholidophoriformes. VI contributo. Pholidophorinae subfamiglia nuova del Triassico Superiore. *Revista del Museo Civico di Scienze Naturali "Enrico Caffi",* Bergamo, 10: 1-32.

ADDENDUM

During the time the present paper was in press, a book has been published concerning the Late Triassic world. Chapter 9 gives an interesting restatement of the modern knowledge on the fossil fishes from the Zorzin Formation, Norian, northern Italy (TINTORI & LOMBARDO, 2018). These two authors mention *Ceneichthys* and the paper of TAVERNE & CAPASSO (2015) but they follow the arguments of ARRATIA (2017) and thus consider the genus as non valid. I have already exposed why the arguments presented by ARRATIA (2017) concerning the non validity of *Ceneichthys* were not pertinent (see "Discussion, subchapter 2").

TINTORI & LOMBARDO (2018) also write the following sentence: "In our opinion, it (*Ceneichthys*) is probably a *Pholidorhynchon* (misspelling of *Pholidorhynchodon* I presume) specimen, quite common in the Cene assemblage". It is easy to show that such a synonymy is incorrect. *Ceneichthys* exhibits long toothed premaxillae meeting at the symphysis of the upper jaw, an edentulous dermethmoid (= rostral) not reaching the symphysis, no visible lateral dermethmoid, rather small opercle and subopercle, a cleithrum with a long ventral and a broad dorsal branch, two elongate postcleithra positioned the one behind the other, weakly ornamented scales and only 34 scales along the lateral line (TAVERNE & CAPASSO, 2015). On the other hand, *Pholidorhynchodon* has toothed dermethmoid and lateral dermethmoids located at the symphysis of the upper jaw, small premaxillae positioned posterior to the symphysis, large opercle and subopercle, a cleithrum with a narrow dorsal and a short ventral branch, only one large dorsal postcleithrum, scales ornamented with tubercles and 39 or 40 scales along the lateral line (ARRATIA, 2013; TAVERNE & CAPASSO, 2017). With such an amount of differences, it is really difficult to consider *Ceneichthys* and *Pholidorhynchodon* as synonyms.

TINTORI, A. & LOMBARDO, C., 2018. The Zorzino Limestone actinopterygian fauna from the Late Triassic (Norian) of the Southern Alps. *In*: TANNER, L. H. (ed.), *The Late Triassic World. Earth in a Time of Transition*, Series "Topics in Geobiology", 46, Springer edit., New York: 315-350.

For ARRATIA (2013, 2017) and TAVERNE & CAPASSO (2015, 2017) see the "References".