New data on *Pleuropholis decastroi* (Teleostei, Pleuropholidae), a "pholidophoriform" fish from the Lower Cretaceous of the Eurafrican Mesogea

Nouvelles données sur *Pleuropholis decastroi* (Teleostei, Pleuropholidae), un poisson "pholidophoriforme" du Crétacé inférieur de la Mésogée eurafricaine

Louis TAVERNE [1] & Luigi CAPASSO [2]

Résumé: Le crâne et le corps de *Pleuropholis decastroi*, un poisson fossile de l'Albien (Crétacé inférieur) du sud de l'Italie, sont redécrits en détails. *P. decastroi* diffère des autres espèces du genre par ses deux nasaux en contact médian et qui séparent complètement le dermethmoïde (= rostral) des frontaux. Avec son maxillaire extrêmement élargi qui couvre la mâchoire inférieure et son supramaxillaire fortement réduit, *P. decastroi* semble plus nettement apparenté avec *Pleuropholis cisnerosorum*, du Jurassique supérieur du Mexique, qu'avec les autres espèces du genre. Par ses mâchoires raccourcies et ses nombreux os orbitaires, *Pleuropholis* apparaît également comme le genre le plus spécialisé de la famille. La position systématique des Pleuropholidae au sein du groupe des « pholidophoriformes » est discutée.

Mots-clés: *Pleuropholis decastroi*, Albien, Italie du sud, *Pleuropholis*, Pleuropholidae, "Pholidophoriformes", ostéologie, position systématique.

Abstract: The skull and the body of *Pleuropholis decastroi*, a fossil fish from the marine Albian (Lower Cretaceous) of southern Italy, are re-described in details. *P. decastroi* differs from the other species of the genus by their two nasals that are in contact along the mid-line, completely separating the dermethmoid (= rostral) from the frontals. With its extremely broadened maxilla that covers the lower jaw and its strongly reduced supramaxilla, *P. decastroi* seems more closely related to *Pleuropholis cisnerosorum*, from the Upper Jurassic of Mexico, than to the other species of the genus. With its shortened jaws and its numerous orbital bones, *Pleuropholis* also appears to be the most specialized genus of the family. The systematic position of Pleuropholidae within the "pholidophoriform" assemblage is discussed.

Key words: *Pleuropholis decastroi*, Albian, southern Italy, *Pleuropholis*, Pleuropholidae, "Pholidophoriformes", osteology, systematic position.

INTRODUCTION

The family Pleuropholidae was erected by DE SAINT-SEINE (1949) to contain the genus *Pleuropholis* EGERTON, 1858, a small fossil "pholidophoriform" fish known at that time by a few species present only in the marine Upper Jurassic and the continental Lower Cretaceous of Europe (EGERTON, 1858; WAGNER, 1861-1863; SAUVAGE, 1883; WOODWARD, 1895, 1919; TRAQUAIR, 1911; BIESE, 1927; DE SAINT-SEINE, 1949) and in the continental Lower Cretaceous of Lebanon (JANENSCH, 1925). This genus has a small head, an elongate body and is characterized by its short upturned lower jaw, the multiplication of its circumorbital bones, the presence of extremely deep flank scales and the deflection of its lateral line sensory canal into the scale row just below the deep scales.

Other species attributed to *Pleuropholis*, some undetermined pleuropholid fragments and new pleuropholid genera were described later during the 20th century and the beginning of the 21st century (DE SAINT-SEINE, 1955; DA SILVA SANTOS, 1974; SANZ *et al.*, 1988; BRAVI, 1988; CHIAPPE *et al.*, 1998; LAMBERS, 1999; ORTEGA *et al.*, 1999; BRITO & GALLO, 2002; BONDE & CHRISTIANSEN, 2003; POYATO-ARIZA, 2005; SUCCAR & GIORDANO, 2012; BRAVI *et al.*, 2014; EBERT *et al.*, 2015; SCHULTZE & ARRATIA, 2015; ALVARADO-ORTEGA *et al.*, 2014; ARCUCCI *et al.*, 2015; ALVARADO-ORTEGA & BRITO, 2016; GIORDANO *et al.*, 2018).

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[1] Royal Institute of Natural Sciences of Belgium, Directorate Earth and History of Life, Vautierstreet, 29, B-1000 Brussels, Belgium. E-mail: louis.taverne@gmail.com
[2] Museo Universitario dell'Universita "G. d'Annunzio" di Chieti-Pescara, Piazza Trento et Trieste, 1, I-661000 Chieti, Italy. E-mail: lcapasso@unich.it

Today, in addition to *Pleuropholis*, four other genera are included in the Pleuropholidae, *Parapleuropholis* DE SAINT-SEINE, 1955 and *Austropleuropholis* DE SAINT-SEINE, 1955, both from the continental Middle Jurassic of the Democratic Republic of Congo (Africa), *Gondwanapleuropholis* BRITO & GALLO, 2002, from the continental Upper Jurassic of Brazil and *Zurupleuropholis* GIARDONO *et al.*, 2018, from the continental Lower Cretaceous of Argentina (DE SAINT-SEINE, 1955; BRITO & GALLO, 2002; GIORDANO *et al.*, 2018). All four have small head, a long body and they exhibit the same specialisations of their body scales and lateral line as *Pleuropholis*. But some of them have longer jaws, less circumorbital bones and a shorter ventral branch of the preopercle.

Members of the family are presently recorded from the Middle Jurassic to the Lower Cretaceous in deposits from marine and freshwater origin. They are known in Europe, the Near East, Africa, North, Central and South America.

The Pleuropholidae of the Middle Jurassic from the Democratic Republic of Congo represent the oldest occurrence presently known for the family. A revision of the concerned material is actually conducted. It appears that the Congolese material contains not only the genera *Pleuropholis*, *Parapleuropholis* and *Austropleuropholis* but also two other new genera (TAVERNE, monograph in preparation).

Pleuropholis decastroi BRAVI, 1988, from the marine Albian of Pietraroja (southern Italy) (Fig. 1), and *Zurupleuropholis quijadensis* GIORDANO *et al.*, 2018 and *Zurupleuropholis decollavi* GIORDANO *et al.*, 2018, both from the continental Albian of Argentina (San Luis Province), are the youngest pleuropholid fishes ever described.

Until now, *Pleuropholis decastroi* was known by the holotype only (BRAVI, 1988). Three other specimens from the same Italian locality were discovered recently. Two of them are well preserved (CAPASSO, 2007). They give new interesting information on the cranial anatomy of this species and of the genus *Pleuropholis*.

The aim of our paper is thus to re-study *Pleuropholis decastroi* by the light of the four specimens presently available, to allow a better osteological knowledge of the genus *Pleuropholis* than previously, to compare this genus with the other pleuropholid genera and to comment about its bearing on the systematic position of the family Pleuropholidae within the "pholidophoriform" lineages.

Figure 1: Location map of the Pietraroja village, Province of Benevento, Campania, southern Italy.
1: Naples, 2: Pietraroja, 3: Benevento.

MATERIAL AND METHODS

The material hereafter studied belongs to the collections of the Museum of Paleontology of the Università degli Studi di Napoli Federico II (MPUN) and to the CAPASSO registered collection (CLC) in Chieti.

The specimens were studied with two stereomicroscopes, a Nikon SMZ 1500 and a Leica Wild M 8. The figures were drawn by the first author (L. T.) with a camera lucida and photos. Aspersions with ethanol were

used to improve some observations. The photos were made by Mr. Luciano LULLO, from the Università "G. d'Annunzio" di Chieti-Pescara.

The CAPASSO collection (CCL) in Chieti (Italy) is legally registered by a decree of the Ministero per I Beni e le Attività Culturali under the date of October 11th 1999, following the disposition of the Italian law 1089/39. The Soprintendenza per I Beni Archeologici dell'Abruzzo-Chieti has authorized the authors to study this collection by two letters bearing the dates of May 5th, 2011 (ref.: MBAC-SBA-ABR PROT 0004537 05/05/2011 Cl. 34.25.01/2.1) and July 30th, 2014 (ref.: MBAC-SBA-ABR PROT 0005618 31/07/2014 Cl. 34.25.01/2.1).

Some Middle Jurassic Congolese pleuropholid remains from the collection of the Royal Museum of Middle Africa (MRAC), Tervuren, Belgium, are used for comparisons.

List of abbreviations used in the text-figures

AN	=	angular
ANT	=	antorbital
APAL	=	autopalatine
ART	=	articular
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 1-6	=	infraorbitals 1 to 6
LDETH	=	lateral dermethmoid
LETH	=	lateral ethmoid
MPT	=	metapterygoid
MX	=	maxilla
NA	=	nasal
NEUR	=	neural arch
OP	=	opercle
PA	=	parietal
PMX	=	premaxilla
POP	=	preopercle
PORB	=	postorbital (= suborbital)
PT	=	posttemporal
QU	=	quadrate
RAD	=	pterygiophores (= radials)
RART	=	retroarticular
SAN	=	surangular
SC	=	scale
SCA	=	hypercoracoid (= scapula)
SCL	=	sclerotic bone
SMX	=	supramaxilla
SOC	=	supraoccipital
SOP	=	subopercle
SORB 1-6	=	supraorbitals 1 to 6
ST	=	supratemporal (= extrascapular)
a. p. l.	=	anterior pit-line
br.	=	broken
ex. c.	=	extrascapular sensory commissure
iorb. c.	=	infraorbital sensory canal
l. l. c.	=	lateral line sensory canal
l. n.	=	"leptolepid" notch
m. c.	=	mandibular sensory canal
m. p. t.	=	middle pit-line
ot. c.	=	otic sensory canal
pop. c.	=	preopercular sensory canal
q. pr.	=	bony process of the quadrate

ro. c.   =   rostral sensory commissure
sorb. c.   =   supraorbital sensory canal

SYSTEMATIC PALEONTOLOGY

Division Teleostei MÜLLER, 1846
  Order "Pholidophoriformes" BERG, 1940 (not *sensu* ARRATIA, 2013)
   Family Pleuropholidae DE SAINT-SEINE, 1949
    Genus *Pleuropholis* EGERTON, 1858
     Type-species: *Pleuropholis attenuata* EGERTON, 1858.

Species *Pleuropholis decastroii* BRAVI, 1988

Emended diagnosis

    Pleuropholis characterized by the following characters. Small dermethmoid crossed by the rostral sensory commissure. Nasals meeting in the mid-line, all along their length, and completely separating the frontals from the dermethmoid. Six infraorbitals. Six supraorbitals. One small postorbital. Well developed antorbital joining the first infraorbital and the first supraorbital. Jaws toothless. Two premaxillae. Extremely broadened maxilla, with a straight upper margin and covering entirely the lower jaw. One reduced supramaxilla. Short and deep lower jaw. "Leptolepid" notch on the upper margin of the dentary, near the symphysis. Five branchiostegal rays. Small gular plate. Pectoral fin with 8 rays. Ventral fin with 5-6 rays. Dorsal fin with 8 rays. Anal fin with 12 rays. Dorsal fin origin a little posterior to the anal fin origin. Forked caudal fin with 16 principal rays. Fringing fulcra on all the fins. A row of 36 to 38 deep flank scales. Some ventral keel scales bearing one spine.

Holotype

MPUN N° M 19432 (former N° 139), a complete specimen (Fig. 2; BRAVI, 1988: fig. 3). Total length: 81 mm. Standard length: 65 mm.
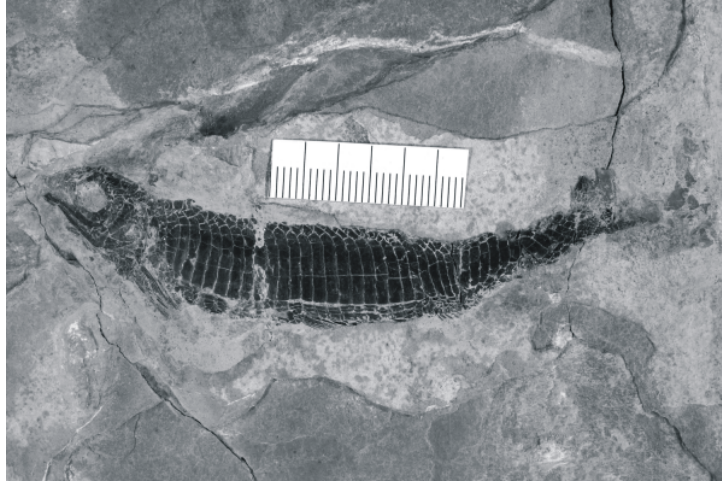

Figure 2: *Pleuropholis decastroi* BRAVI, 1988. Holotype MPUN M19432 (former Nr 139 in BRAVI, 1988). Total length: 81 mm.

Other material

MPUN N° M 19313, an incomplete specimen, with a crushed and partial head.
CLC I-61, an almost complete specimen (Fig. 3; CAPASSO, 2007: fig. 143). A part of the caudal fin is missing. Total length: 95 mm. Standard length: 85 mm.
CLC I-86a, b: the two sides of an almost complete specimen (Fig. 4; CAPASSO, 2007: fig. 142). The skull roof is missing. Total length: 105 mm. Standard length: 89 mm.

Figure 3: *Pleuropholis decastroi* BRAVI, 1988. Specimen CLC I-61.
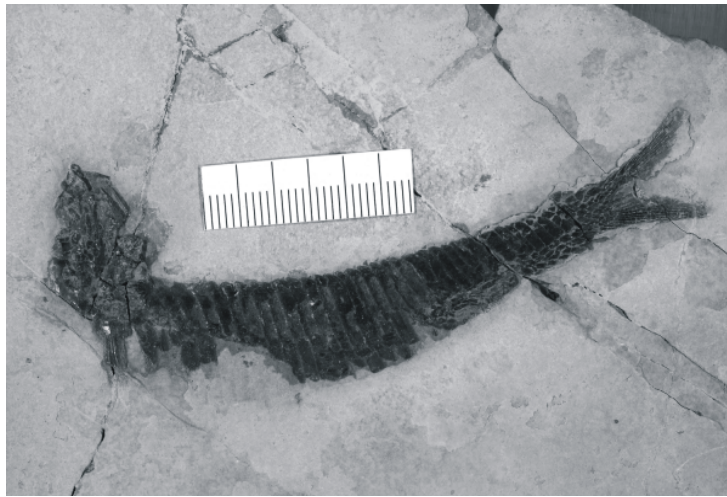
Figure 4: P*europholis decastroi* BRAVI, 1988. Specimen CLC I-86a.

Formation and locality

Limestones of Pietraroja, marine Albian (Early Cretaceous), around the village of Pietraroja, province of Benevento, Campania, southern Italy.

**Osteology**

The skull (Figs 5-7)

The skull roof is composed by an impaired bone, the dermethmoid (= rostral), and four paired bones, the nasal, the frontal, the parietal and the dermopterotic. All these bones are sutured together. There is no trace of fusion between them. However, a partial fusion between the bones of the skull roof exists in some pleuropholid specimens (BIESE, 1927: pl. 5, fig. 1b, pl. 6, fig. 1b; TAVERNE & CAPASSO, 2015: fig. 10 [right]). The dermethmoid is a small bone, broader than long and with two pointed lateral extremities. It bears the rostral sensory commissure. The nasals are missing on the holotype but well preserved on specimen CLC I-61. They are long and broad bones that meet on the mid-line and completely separate the frontals from the dermethmoid. The parietals are large bones. The skull is medio-parietal. The supraobital sensory canal goes through the nasal and the frontal, and ends on the parietal, forming there a small anterior pit-line. There is also a short middle pit-line on the parietal. The dermopterotic lies laterally, against the frontal and the parietal. The bone exhibits a pointed posterior corner. The dermopterotic bears the otic sensory canal. The supraorbital and the otic canals remain completely separated. There is a small triangle-shaped supratemporal (= extrascapular, scalebone) that reaches the mid-line. The extrascapular sensory commissure is not visible.

Figure 5: *Pleuropholis decastroi* BRAVI, 1988. The head region of specimen CLC I-61.

A great part of the endochondral braincase is hidden by the dermal bones. A massive lateral ethmoid is visible just below the nasal in specimen CLC I-86a. Fragments of the orbitosphenoid and the pleurosphenoid are preserved on specimen CLC I-61. A complete bony interocular septum is formed by these two bones. Such a septum also exists in some Middle Jurassic Pleuropholidae from the Democratic Republic of Congo (L. T., pers. observ.).

The palatine arch is almost complete on sample CLC I-86a. The quadrate is triangular in shape, with a well developed articular condyle for the jaw and a long quadratic bony process oriented parallel to the ventral margin of the bone. The ectopterygoid and the entopterygoid are small toothless bones. The ectopterygoid is sutured with the posterior part of the upper margin of the quadrate. The entopterygoid overhangs the quadrate. The metapterygoid is elongate and rather narrow. It lies on the ventral branch of the hyomandibula, just behind the ectopterygoid. A very small bone located just between the first infraorbital and the entopterygoid could be the palatine.

The jaws are extremely short and edentulous. The premaxilla is small and deeper than long. The maxilla is short but extremely broadened and covers almost entirely the mandible. The dorsal margin is straight but dug by two small notches. The maxilla bears numerous very thin ridges. A strongly reduced supramaxilla lies on the maxilla. The lower jaw is completely preserved and well visible on sample CLC I-86a. The jaw is almost as deep as long. The oral margin of the dentary raises up abruptly to form the coronoid region. A well marked "leptolepid" notch is visible in the oral margin of the bone, near the symphysis. The articular, angular and retroarticular seem fused together. A well developed surangular is present but does not participate to the coronoid region. The mandibular sensory canal is visible along the lower margin of the dentary.

Figure 6: *Pleuropholis decastroi* BRAVI, 1988. Reconstruction of the skull and the pectoral girdle based on holotype MPUN M19432 and specimens CLC I-61 and I-86a, b. The scale refers to specimen CLC I-61.

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Fifteen elements compose the orbital bony ring. They surround completely the orbit, as seen on specimen CLC I61 that is more completely preserved in that region than the holotype. There are an antorbital, six infraorbitals, one dermosphenotic, six supraorbitals and a postorbital (= suborbital). A small fragment of a narrow sclerotic bone is also visible just above the second infraorbital. The antorbital is a rather large bone that reaches the first infraorbital ventrally and the first supraorbital dorsally. The first infraorbital is the longer bone of the series. The fifth infraorbital and the lower part of the sixth one are slightly broadened. The dermosphenotic is small. The infraorbital sensory canal goes through the six infraorbitals, the dermosphenotic and joins the otic canal on the dermopterotic. A short secondary tubule of the canal is visible on the fourth infraorbital. The first supraorbital is the larger bone of the supraorbital series. The postorbital is a moderately developed bone located under the dermopterotic and behind the dermosphenotic and the sixth infraorbital. It has a more or less pyriform shape, with a pointed ventral extremity.

The preopercle is composed of two branches. The ventral one is strongly elongated. The dorsal branch is shorter and does not reach the level of the skull roof margin. The preopercular sensory canal runs over all the length of the bone. Three short secondary tubules of the canal are visible at the ventral posterior corner of the preopercle in specimen CLC I-61. The interopercle is a large bone still a little longer than the ventral branch of the preopercle. The opercle is a wide bone with a straight anterior margin and a rounded posterior one. The subopercle is small and triangular in shape. Five short branchiostegal rays and a small gular plate are visible on specimen CLC I-61.

The hyomandibula is preserved on sample CLC I-86a. The articular head is large, with a rounded upper border. The ventral branch is elongate, broad and very obliquely oriented. The *processus opercularis* is not developed.
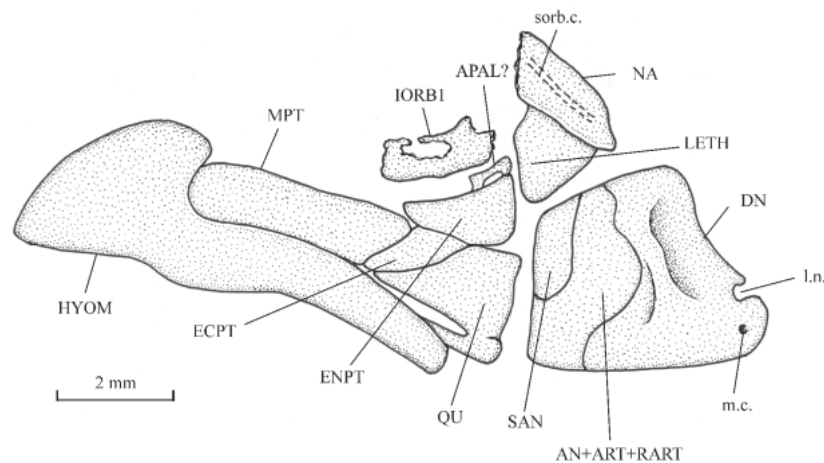
Figure 7: *Pleuropholis decastroi* BRAVI, 1988. Part of the suspensorium of specimen CLC I-86a.

The girdles (Figs 5, 6)

The posttemporal is large and almost quadrangular in shape. The hypercleithrum (= supracleithrum) is broad and ovoid. The cleithrum is divided in two long branches, its ventral member being longer than the dorsal one. There is a small wing-like expansion on the ventral region of its posterior border. The hypercoracoid (= scapula) is small but the hypocoracoid (= coracoid *sensu stricto*) is a very wide and triangular bone. The pectoral fin contains 8 rays. The first one is elongate, robust, pointed and not segmented. It bears fringing fulcra all along its length. The other rays are thinner, segmented and branched at their distal extremities. Two pectoral pterygiophores are visible on specimen CLC I-61 but they were probably more numerous.

The pelvic bones are hidden by the scales. The ventral fins are well preserved in holotype and specimen CLC I-61. In sample CLC I-86a, only the proximal fragment of the first ray is visible. Each ventral fin is composed by 5 or 6 rays. The first ray is broad, not segmented, acuminate and it bears fringing fulcra. The following rays are thinner, segmented and branched at their distal extremity. The origin of the ventral fins is located at the level of the thirteenth row of scale in specimen CLC I-86a and the fourteenth row in holotype and specimen CLC I-61.

The axial skeleton

The axial skeleton is completely hidden by the scales. However, small fragments of two cylindrical centra are visible on specimen CLC I-86b, near the pectoral region.

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The dorsal and anal fins

The dorsal fin contains 8 segmented and branched rays in the holotype. There are fringing fulcra. In specimen CLC I-61, the dorsal fin is pressed against the dorsal ridge and the rays can not be counted. In specimen CLC I-86a, b, the dorsal fin is lost The origin of the dorsal fin is located at the level of the twenty-seventh row of scales in holotype and the twenty-eighth row in specimen CLC I-61.

The anal fin of the holotype is composed of 12 segmented and branched rays. The fringing fulcra are present. In sample CLC I-61, only six rays are preserved. The anal fin is lost in ample CLC I- 86a, b. The origin of the anal fin is located at the level of the twenty-fourth row of scales in holotype and the twenty-fifth row in specimen CLC I-61.

The caudal skeleton and fin (Fig. 8)

The caudal endoskeleton is entirely covered by the last scales in all the available specimens and remains unknown.

The forked caudal fin is well preserved in holotype and in specimen CLC I-86a. A great part of the tail is missing in sample CLC I-61. There are 16 principal rays, 8 in each lobe. The most external ray of each lobe is segmented and pointed. The other fourteen principal rays are segmented and branched. The segmentation is straight. There are 4 basal fulcra in each lobe. Those of the upper lobe are scale-like, with a long and strongly acuminate posterior extension. In the lower lobe, the first two basal fulcra are also scale-like but the third and the fourth ones look like short rays and they are segmented. In each lobe, a series of numerous fringing fulcra follows the basal fulcra.
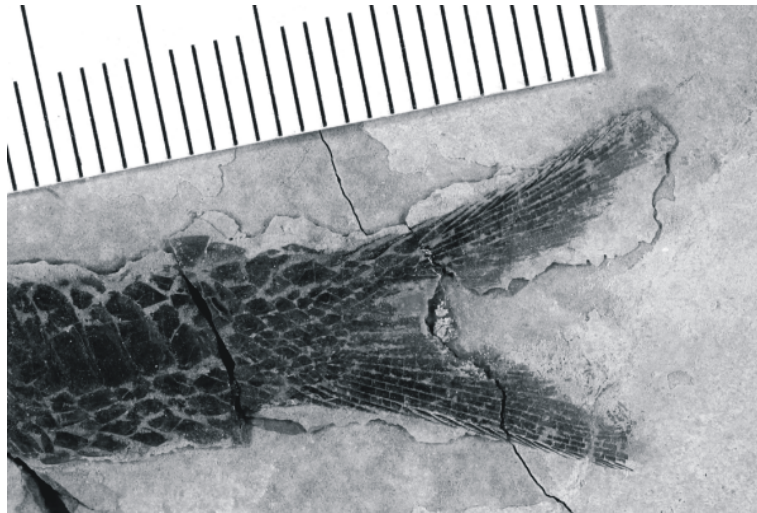
Figure 8: *Pleuropholis decastroi* BRAVI, 1988. Caudal fin of specimen CLC I-86a.

The squamation (Fig. 9)

All the scales have a smooth surface. Two rows of rhombic scales are located along the dorsal region. The flanks are covered by a row of excessively deep scales that become less deep in the posterior region of the fish. There are respectively 36, 37 and 38 deep scales before the small rhombic scales covering the tail region, in specimen CLC I-86a, in holotype and in specimen CLC I-61. The posterior margin of these deep flank scales is ornamented with a series of tiny denticles. A weakly developed peg-and-socket articulation is visible in imprint on some flank scales in specimen CLC I-86b. Because of the fossilization, some flank scales are broken in their middle, giving the false impression that there are two scales in place of one. A few scales are even broken in three or four parts. Three rows of rectangular scales occupy the ventral region. Between the ventral and the anal fins, the scales of the ventral keel bear one well developed spine.

There are three lateral sensory lines. One of them is short and dorsally located on the first rhombic scales of the second row. The first deep flank scales bear a short second line. The third and principal line runs all along the fish. It begins on the flank scales but is quickly deflected in the first row of rectangular scales below the deep flank scales.
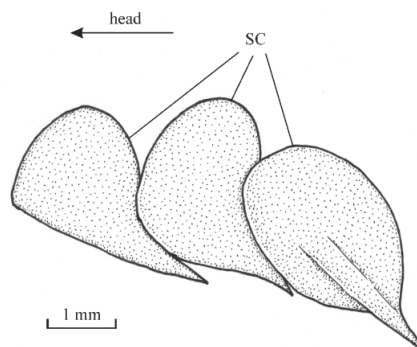
Figure 9: *Pleuropholis decastroi* BRAVI, 1988. Three spiny ventral scales of specimen CLC I-86b.

DISCUSSION

Pleuropholis decastroi and the other species of *Pleuropholis*

Pleuropholis is a short-jawed pleuropholid genus, with an elongate ventral branch of the preopercle. The type-species, *Pleuropholis attenuata*, was found in the deposits of the English Purbeckian (Tithonian-Berriasian). Its original description was rather superficial and its skeleton was never really studied. A small drawing of the holotype is given by EGERTON (1858: pl. 7, fig. 1) and by WOODWARD (1919: fig. 35A). The figure shows that *P. attenuate* has a moderately shortened and not markedly broadened maxilla. Another Purbeckian species, *Pleuropholis crassicauda* EGERTON, 1858, also exhibits a rather narrow maxilla (WOODWARD, 1895, pl. 14, fig. 5).

Besides *Pleuropholis decastroi*, the skull is only known in four other species of the genus, *Pleuropholis longicauda* EGERTON, 1858, from the Purbeckian of England, *Pleuropholis thiollieri* SAUVAGE, 1883, from the Kimmeridgian of France, *Pleuropholis jamotti* DE SAINT-SEINE, 1955, from the Middle Jurassic of Congo, and *Pleuropholis cisnerosorum*, from the Kimmeridgian of Mexico. The data on these fishes used hereafter come from DE SAINT-SEINE (1949, 1955), PATTERSON (1973), ALVARADO-ORTEGA & BRITO (2016) and from the still unpublished observations of the first author (L. T.) on *P. jamotti*.

P. longicauda and *P. jamotti* have a short but moderately broadened maxilla, with a curved dorsal margin, and a well developed supramaxilla. *P. decastroi*, *P. thiollieri* and *P. cisnerosorum* differ from these two species by one new apomorphy. Their maxilla is extremely broadened, with an almost straight upper border, and it covers almost entirely the lower jaw. *P. decastroi* and *P. cisnerosorum* share another apomorphy. Their supramaxilla is strongly reduced. *P. decastroi* seems thus more closely related to *P. cisnerosorum* than to *P. longicauda*, *P. thiollieri* and *P. jamotti*. *P. decastroi* also differs from the other species of the genus by its two nasals that meet in the mid-line all along their length, separating completely the dermethmoid from the frontals. In *P. longicauda*, *P. thiollieri* and *P. jamotti*, the nasals meet only in one point or are completely separated by the frontals and the dermethmoid. The position of the nasals is unknown in *P. cisnerosorum*, the skull roof being not preserved in this fish.

Pleuropholis and the other pleuropholid genera

As already mentioned, the family Pleuropholidae contains today five genera, *Pleuropholis*, *Parapleuropholis*, *Austropleuropholis*, *Gondwanapleuropholis* and *Zurupleuropholis*. The information on the last four genera comes from DE SAINT-SEINE (1955), BRITO & GALLO (2002), GIORDANO *et al.* (2018) and from the still unpublished study of the Middle Jurassic Pleuropholidae of Congo by the first author (L. T.).

Austropleuropholis is a monospecific genus. It has short jaws and a preopercle with a long ventral branch as in *Pleuropholis*. DE SAINT-SEINE (1955: 99) justifies the erection of his new genus essentially by the presence of strong spines on the dermosphenotic and on the lateral margin of the dermopterotic. However, a spiny dermosphenotic is known in *Pleuropholis longicauda* (PATTERSON, 1973: fig. 16) and some specimens of *Pleuropholis jamotti* exhibit spines on the lateral margin of the dermopterotic (Fig.10). Therefore, it seems reasonable to put *Austropleuropholis* in synonymy with *Pleuropholis*.

Parapleuropholis, *Gondwanapleuropholis* and *Zurupleuropholis* differ from *Pleuropholis* by their long jaws and their preopercle with a short ventral branch. *Parapleuropholis* is also characterized by the lost of the supramaxilla and by the fusion of the two premaxillae in only one median bone, a unique apomorphy among Pleuropholidae. *Parapleuropholis* and *Zurupleuropholis* do not exhibit the multiplication of the orbital bones that is present in *Pleuropholis*. The condition of the orbital bony ring is unknown in *Gondwanapleuropholis*.

With its reduced jaws and its numerous infraorbitals and supraorbitals, *Pleuropholis* is thus the most specialized genus of the family.
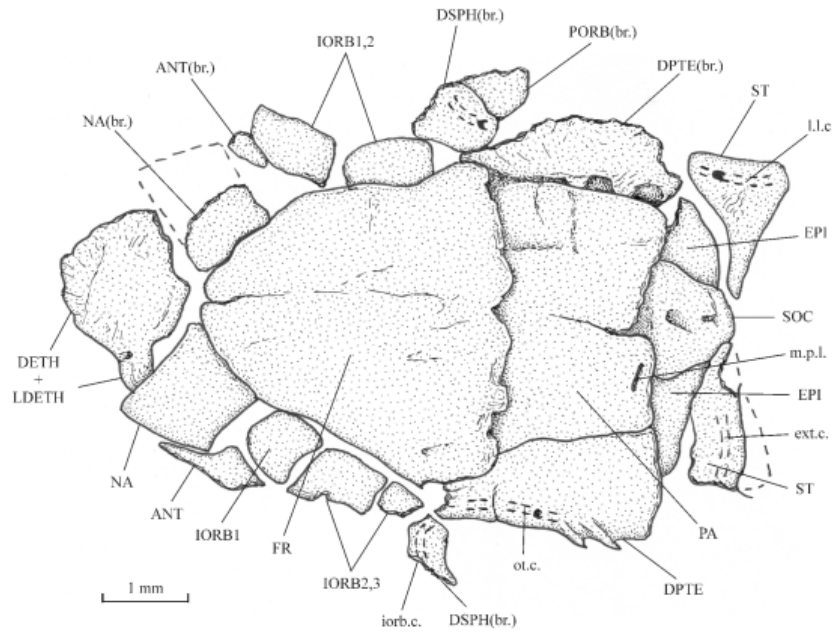
Figure 10: *Pleuropholis jamotti* DE SAINT-SEINE, 1955 (Middle Jurassic of the Democratic Republic of Congo). Skull roof of specimen MRAC RG 10.063.

Pleuropholidae within "Pholidophoriformes"

The order "Pholidophoriformes" was erected by BERG (1937) to group many lineages of ganoid fishes considered at that time to be close to the teleosts. All the subgroups of "Pholidophoriformes" are now included in the Teleostei. Today, the break-up of that highly heterogenous order is begun. The Pholidophoriformes *sensu stricto* (ARRATIA, 2013) are restricted to the family Pholidophoridae. ARRATIA (2017) also includes the Eurycormidae in the Pholidophoriformes *sensu stricto* but that systematic position is challenged by TAVERNE & CAPASSO (2017). Several new orders were recently erected: Liguelliformes, Catervarioliformes, Ankylophoriformes and Dorsetichthyiformes (TAVERNE, 2011a, b, c, 2014a, b; NELSON *et al.*, 2016). However, some genera and families in need of revision are still confined in the "Pholidophoriformes" (*sensu lato*) or left order *incertae sedis*. That is the case of the Pleuropholidae.
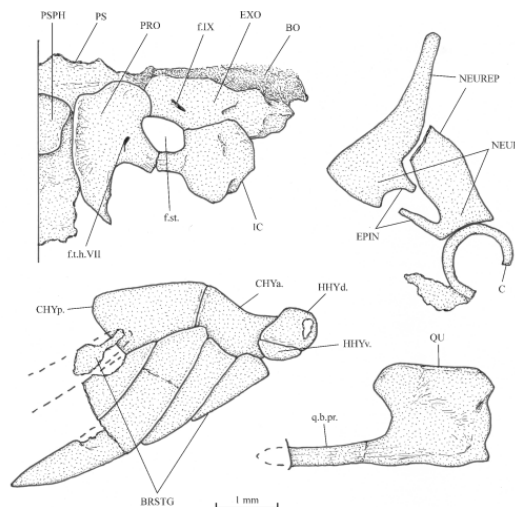
Figure 11: *Pleuropholis jamotti* DE SAINT-SEINE, 1955. (A) Subtemporal fossa and bony bridge between the prootic and the intercalary in specimen MRAC RG 10.072. (B) One vertebra in specimen MRAC RG 10.056.

(C) Hyoid bar in paratype MRAC RG 10.063. *Pleuropholis* (*Austropleuropholis*) *lombardi* DE SAINT-SEINE, 1955 (Middle Jurassic of the Democratic Republic of Congo). (D) Quadrate of paratype MRAC RG 10.034.

In his brief comments on the family, PATTERSON (1973: 268-270) concludes that pleuropholids are effectively related to the teleosts. We give hereafter some comments on the possible systematic position of Pleuropholidae within "Pholidiphoriformes" based on the analysis of a few characters.

(1) The quadrate of Pleuropholidae bears a well marked bony process (Fig. 11D; PATTERSON, 1973: 269; BRITO & GALLO, 2002: 701, fig. 2).

Since the papers of ARRATIA & SCHULTZE (1991) and ARRATIA (1999), the quadratic bony process of the modern teleosts is no more considered as a fused quadratojugal but as a process that developed in the ventral region of the still cartilaginous quadrate. The quadratic bony process is now regarded as one of the major apomorphies of teleosts. In the Middle Triassic "pre-teleost" *Prohalicetes porroi* (BELLOTTI, 1857), the quadrate is devoid of bony process and an independent quadratojugal is still present (TINTORI, 1990: fig. 4). An ossified quadratic process is present in most "pholidophoriform" lineages (GRIFFITH & PATTERSON, 1963: fig. 10; GAUDANT, 1978: pl. 1, fig. 2, pl. 2, fig. 1, pl. 3, fig. 2; ARRATIA, 2000: figs 8, 14, 15D; TAVERNE, 2011a: figs 6, 9, 2011b: figs 21, 24, 2014a: fig. 10; among others)., but not in Pholidophoridae (ARRATIA, 2013: numerous figs). However, ARRATIA (2013; fig. 15) figured a very small process in a specimen of *Lombardichthys gervasuttii* (ZAMBELLI, 1980). A very short process located at the posterior ventral corner of the quadrate also exists in Eurycormidae (ARRATIA, 2017, Appendix 2, fig. S2A; TAVERNE, in press: fig. 20).

(2) Pleuropholid fishes have a well developed supraoccipital located between the two epiotics (Fig. 10) as in Teleostei.

Pachycormiformes, Aspidorhynchiformes and Ligulelliformes are three orders closely allied to Teleostei. In Pachycormiformes, the supraoccipital does not exist (PATTERSON, 1975: fig. 107; MAINWARING, 1977: fig. 20). In Aspidorhynchiformes, a well developed supraoccipital is present but not separated from the epiotics (BRITO, 1992: fig. 5; BOGAN *et al.*, 2011: fig. 6). Ligulelliformes also exhibit a supraoccipital (TAVERNE, 2011c: fig. 7). Many fossil fishes attributed to the "Pholidophoriformes" have an ossified supraoccipital. That is the case of *"Pholidophorus" limbata* AGASSIZ, 1844, *Dorsetichthys bechei* (AGASSIZ, 1844), *Siemensichthys macrocephalus* (AGASSIZ, 1844), *"Pholidophorus" germanicus* QUENSTEDT, 1858, *Eurycormus speciosus* WAGNER, 1863, the Callovian *"Pholidophorus"* sp., *Ichthyokentema purbeckensis* (DAVIES, 1887), *Catervariolus hornemani* DE SAINT-SEINE, 1955, *Songanella callida* DE SAINT-SEINE & CASIER, 1962, *Pholidorhynchodon malzannii* ZAMBELLI, 1980, *Luxembourgichthys friedeni* (DELSATE, 1999) and still a few others (GRIFFITH & PATTERSON, 1963: figs 1, 2, 4 ; PATTERSON, 1975: figs 44, 55, 70, 82, 145, 151; ARRATIA, 2000: fig. 5; TAVERNE, 2011b: figs 9, 10, 2014a: figs 5, 6; TAVERNE & CAPASSO, 2017: figs 3, 8; TAVERNE & STEURBAUT, 2017: figs 10, 11, 13). A bony supraoccipital is unknown in Pholidophoridae (ARRATIA, 2013, 2017) but their endocranium seems weakly ossified. That is perhaps the explanation of this apparent missing of the supraoccipital in these fishes.

(3) The two lateral dermethmoids are fused to the dermethmoid (= rostral) in Pleuropholidae. They form a small lateral process on each side of the bone (Fig. 10; PATTERSON, 1973: 269; TAVERNE, 2015: fig. 9 [right]).

The same evolved morphology is present in *Leptolepis coryphaenoides* (BRONN, 1830) and in some other primitive teleosts with cycloid scales (PATTERSON, 1975: fig. 127a-e, 128a). A more primitive pattern occurs in Pachycormiformes and in a few lineages formerly ranged within "Pholidophoriformes". A pair of lateral dermethmoids occupies the symphysis of the upper jaw, just before the dermethmoid. The premaxillae are located more laterally on the jaw. Such a peculiar morphology is known in Ligulellidae (TAVERNE, 2011c: figs 2, 3), Catervariolidae (TAVERNE, 2011b: figs 8-12, 15, 17, 19, 2014a: figs 4-7, 2015: fig. 2), Ichthyokentemidae (PATTERSON, 1975: fig. 126; GRIFFITH, 1977: fig. 26), Ankylophoridae (PATTERSON, 1975: figs 82, 121, 124, 125, 145; ARRATIA, 2000: fig. 15A, 2013: fig. 49A, B; TAVERNE, 2011a: figs 4, 5, 2014b: figs 4, 6; TAVERNE & CAPASSO, 2017: fig. 4), Signeuxellidae (TAVERNE, 2017: fig. 3) and Eurycormidae (PATTERSON, 1973: fig. 14; ARRATIA, 1999: fig. 6C). However, in Pachycormiformes, the lateral dermethmoids are not visible externally. They are partially fused to the inner side of the dermethmoid and hidden by this bone (PATTERSON, 1975: fig. 139; MAINWARING, 1978: fig. 3). Pholidophoridae seem devoid of lateral dermethmoid (ARRATIA, 2013; TAVERNE & CAPASSO, 2015; TINTORI *et al.*, 2015). However, ARRATIA (2017: fig. 3C) considers the anterior part of the mesethmoid floor in *Pholidoctenus sanpellegrinensis* ARRATIA, 2017, from the Upper Triassic of Italy, as a lateral dermethmoid. But nothing is written about this bone in her text (ibid., 2017: 4). The presence of lateral dermethmoids in this Italian species seems uncertain. There are also some evolved "Pholidophoriformes", for instance *Luxembourgichthys friedeni*, that keep independent lateral dermethmoids that are not involved in the upper jaw margin (TAVERNE & STEURBAUT, 2017: figs 10, 16).

(4) A bony bridge between the prootic and the intercalar that overhangs a subtemporal fossa is present in Pleuropholidae (Fig. 11A).

A contact between the prootic and the intercalar exists in some Holostei but, in this case, these two bones do not form a bony bridge over a subtemporal fossa (GRANDE & BEMIS, 1998: fig. 22B, C, 24B, C; PATTERSON, 1975: figs 99, 102; among others). In Pachycormidae, Catervariolidae and Ichthyokentemidae, there are neither a subtemporal fossa nor a bony bridge formed by the intercalary and the prootic (GRIFFITH & PATTERSON, 1963: figs 2, 3; PATTERSON, 1975: fig. 106; MAINWARING (1978: fig. 22; TAVERNE, 2011b: figs 10, 11, 19). The condition is unknown in Pholidophoridae and Eurycormidae. But such a bony bridge and a subtemporal fossa appear in some "pholidophoriform " fishes: *Dorsetichthys bechei*, the Callovian "*Pholidophorus*", *Siemensichthys macrocephalus* and "*Pholidophorus*" *germanicus* (PATTERSON, 1975: figs 56, 67, 68, 71, 84). The same morphology is preserved in a few primitive cycloid teleosts, for instance *Tharsis dubius* DE BLAINVILLE, 1818 (PATTERSON, 1975: fig. 92), the families Elopidae, Megalopidae (FOREY, 1973: figs 3, 5, 22, 23, 30), Osteoglossidae (TAVERNE, 1977: figs 43, 45, 72, 74, 125, 127), Notelopidae (FOREY, 1977: fig. 2) and some others.

(5) Pleuropholidae have only one supramaxilla.

The presence of only one supramaxilla is the rule in many holostean fishes, in Pachycormiformes (LEHMAN, 1949: fig. 2; WENZ, 1967: fig. 53; MAINWARING, 1978: fig. 2) and in Catervarioliformes (TAVERNE, 2011b: figs 8, 26B, 2014a: figs 4, 11). Pholidophoridae have a more evolved pattern with two supramaxillae (ARRATIA, 2013: num. figs) as in most "Pholidophoriformes" and in primitive teleosts with cycloid scales.

(6) A well marked leptolepid notch is present in the upper margin of the dentary in *Pleuropholis decastroi* but is weakly developed in *Pleuropholis jamotti*. The condition is unknown in the other Pleuropholidae.

A leptolepid notch is missing in *Hulettia americana* (EASTMAN, 1899) (SCHAEFFER & PATTERSON, 1984: fig. 13), in *Prohalicetes porroi* (TINTORI, 1990: fig. 4), in Pachycormiformes (MAIWARING, 1978: figs 4, 7, 8) and in Ligulelliformes (TAVERNE, 2011c: fig 22B, C). Such a notch is absent or feebly marked in Catervarioliformes (TAVERNE, 2011b: figs 27, 28). Most "pholidophoriform" fishes, including Pholidophoridae, exhibit a well developed leptolepid notch in the upper margin of the dentary (GRIFFITH & PATTERSON, 1963: figs 8, 9; NYBELIN, 1966: pl. 3, figs 1, 5, pl. 15, figs 5-7; ARRATIA, 2013: num. figs; among others). The leptolepid notch is preserved in some primitive fossil teleosts with cycloid scales, for instance the Leptolepididae (TAVERNE & STEURBAUT, 2017: fig. 17 [right]), the Varasichthyidae (ARRATIA, 1981: figs 7, 8) and a few others.

(7) The preopercle of Pleuropholidae is divided in two branches, one dorsal and one ventral.

In Catervarioliformes, the preopercle is crescent-like as in most Holostei (TAVERNE, 2011a: figs 8, 35, 2014a: fig. 4, 2015: fig. 3). Pholidophoridae and some other "pholidophoriform" fishes have a preopercle 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 (NYBELIN, 1966: num. figs; GAUDANT, 1978: pl. 1, fig. 2, pl. 2, fig. 1, pl. 3, fig. 2, pl. 4, fig. 2; ARRATIA, 2013: num. figs, 2017: figs 2, 4B, C; TAVERNE & STEURBAUT, 2017: figs 8, 10, 16; among others). Many teleosts exhibit a preopercle with two well developed branches.

(8) Pleuropholidae have only one large postorbital (= suborbital) located behind the uppermost infraorbital and the dermosphenotic.

Catervarioliformes exhibit two or three large postorbitals (= suborbitals) behind the posterior infraorbitals (TAVERNE, 2011b: fig. 8, 2014a: fig. 4), as in Pachycormiformes (LEHMAN, 1949: fig. 2; WENZ, 1967: fig. 53; MAINWARING, 1978: fig. 2), *Hulettia americana* (SCHAEFFER & PATTERSON, 1984: fig. 11) and *Prohalicetes porroi* (TINTORI, 1990: fig. 2). In Ligulelliformes, the postorbitals are fused to the posterior infraorbitals (TAVERNE, 2011c: fig. 6). In Pholidophoridae, there is only one large postorbital that sometimes is reduced to a series of smaller elements (ARRATIA, 2013: num. figs, 2017: figs 2B, 4A, B, C; TINTORI *et al.*, 2015: figs 4, 7b; TAVERNE & CAPASSO, 2015: fig. 5). Most other "pholidophoriform" fishes also exhibit only one large postorbital (NYBELIN, 1966: num. figs; TAVERNE & STEURBAUT, 2017: figs 8, 10). The postorbital disappears in recent teleosts.

(9) The anterior certohyal is devoid of "beryciform" fenestra in Pleuropholidae (Fig. 11 C).

In Pachycormiformes, in Ligulelliformes and in most "Pholidophoriformes", the "beryciform" fenestra is missing (BIESE, 1927: fig. 8; LEHMAN, 1949: fig. 17; GRIFFITH & PATTERSON, 1963: fig. 11; NYBELIN, 1966: pl. 3, fig. 5; MAINWARING, 1978: fig. 11; TAVERNE, 2011a: fig. 10, 2011b: fig. 34, 2011c: fig. 25, 2014a: fig. 12; ARRATIA, 2013: fig. 15). The only exception is the "pholidophoriform" *Luxembourgichthys friedeni* (DELSATE, 1999) that has the anterior ceratohyal pierced by a small beryciform fenestra (DELSATE, 1999: fig. 12). The "beryciform" fenestra is an apomorphy that appears for the first time in a few Jurassic teleosts with cycloid scales, such as *Leptolepis coryphaenoides*, *Tharsis dubius*, *Leptolepides sprattiformis* (DE BLAINVILLE, 1818), *Paraclupavus caheni* DE SAINT-SEINE & CASIER, 1962 and *Varasichthys ariasi*

ARRATIA, 1981 (RAYNER, 1937: fig. 6; NYBELIN, 1974: figs 24, 25, 31B-E; TAVERNE, 1975: fig. 7, 1981: fig. 6; ARRATIA, 1981: fig. 13, 1997: fig. 42A, B, 43A). This fenestra in the anterior ceratohyal is also present in some modern teleosts.

(10) The hyoid bar of Pleuropholidae contains a dorsal and a ventral hypohyals (Fig. 11C).

Holostei have a unique hypohyal on each hyoid bar (GRANDE & BEMIS, 1998: figs 55, 56; among others). The same pattern, with only one hypohyal, also occurs in *Hulettia americana* (SCHAEFFER & PATTERSON, 1984: fig. 14), in Pachycormiformes (LEHMAN, 1949: fig. 17; MAINWARING, 1978: fig. 11) and in Catervarioliformes (TAVERNE, 2011b: fig. 34, 2014a: fig. 12). In Ligulelliformes, there is no ossified hypohyal (TAVERNE, 2011c: fig. 25). Information on the hypohyal of "pholidophoriform" fishes is extremely poor. Indeed, the hyoid bar is generally covered by other bones. In the pholidophorid *Lombardichthys gervasuttii*, there is only one partially ossified hypohyal in the hyoid bar (ARRATIA, 2013: fig. 15). A unique hypohyal also exists in *Dorsetichthys bechei* (NYBELIN, 1966: pl. 3, fig. 5) but two hypohyals, one dorsal and one ventral, are present in *Siemensichthys macrocephalus* (BIESE, 1927: fig. 8). Some primitive Jurassic teleosts with cycloid scales, for instance *Leptolepis coryphaenoides* and *Paraclupavus caheni*, have only one ossified hypohyal (RAYNER, 1937: fig. 6; TAVERNE, 1975: fig. 7) but other Jurassic teleosts, such as *Tharsis dubius* and *Varasichthys ariasi*, possess two well developed hypohyals (NYBELIN, 1974: fig. 24; ARRATIA, 1981: fig. 13). In *Leptolepides sprattiformis*, some specimens have only one ossified hypohyal (TAVERNE, 1981: fig. 6) while other samples have a large ventral hypohyal and a small dorsal hypohyal (ARRATIA, 1997: figs 42A, B, 43A). Usually, in modern teleosts, there are two hypohyals (McALLISTER, 1968: num. figs; among others).

(11) Very short ossified epineurals fused to the neural arches are present at least in *Pleurpholis jamotti* (Fig. 11B). The eventual presence of intermuscular bones in other Pleuropholidae is unknown.

Short ossified epineurals fused to the neural arches already exist in some "palaeonisciform" fishes, such as *Boreosomus* STENSIÖ, 1921and *Australosomus* PIVETEAU, 1930 (NIELSEN, 1949: figs 41-43, 47, 48), in the amiiform *Caturus chirotes* AGASSIZ, 1842 (GARDINER, 1960: fig. 33), in the neopterygian *Hulettia americana* (SCHAEFFER & PATTERSON, 1984: fig. 17C), in Pachycormiformes (MAINWARING, 1977: 79) and in Eurycormidae (ARRATIA & SCHULTZE, 2007: fig. 9C). Elongated epineurals are known in the "pre-teleost" *Prohalicetes porroi* (TINTORI, 1990: 163), in many "pholidophoriform" lineages, for instance Catervariolidae (TAVERNE, 2011b: fig. 43; ARRATIA, 2017, Appendix 2: fig. 18A, B) and Dorsetichthyidae (LUND, 1966: figs 1, 2; SCHAEFFER & PATTERSON, 1984: fig. 17D), and in most teleosts. Ossified intermuscular bones are missing in Pholidophoridae (ARRATIA, 2013, 2017; TINTORI *et al.*, 2015), in Ichthyokentemidae (GRIFFITH & PATTERSON, 1963: 27) and in Signeuxellidae (TAVERNE, 2017: fig. 7).

(12) The caudal skeleton is known in only two pleuropholid species, *Pleuropholis serrata* EGERTON, 1858 and *Gondwanapleuropholis longimaxillaris* BRITO & GALLO, 2002. In both fishes the ural neural arches are elongated, forming a series of four to six uroneurals (PATTERSON, 1973: fig. 17; BRITO & GALLO, 2002: fig. 4) as in some primitive cycloid teleosts. Long uroneurals are frequent in Teleostei.

All these twelve characters confirm that the family Pleuropholidae belongs to the ganoid lineages of the teleosts formerly ranged in the "pholidophoriform" assemblage

Unfortunately, the detailed analysis of those twelve anatomical data leads to conflicting results in regard to the systematic position of Pleuropholidae within "Pholidophoriformes". Characters (5) and (11) seem to place the family in a primitive phylogenetic position within the group, whereas characters (3) and (10), on the contrary, militate for a highly evolved position. Characters (4), (6), (7) and (8) indicate a more advanced position than the one of Catervarioliformes. Character (7) also seems to place Pleuropholodae above the phylogenetic level of Pholidophoriformes *sensu stricto* and of most other "pholidophoriform" fishes, including *Luxembourgichthys friedeni*. For character (3), pleuropholid fishes also are more advanced than *L. friedeni* but, once again, character (9) gives a different result, with *L. friedeni* appearing more evolved than Pleuropholidae.

However and despite those uncertain results, an evolved position is the one privileged here, essentially on the basis of characters (3), (7) and (10).

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