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Pleuropholis germinalis n. sp., a new Pleuropholidae (Neopterygii, Teleostei) from the Early Cretaceous of Bernissart, Belgium

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ABSTRACT
The Barremian–Aptian (Cretaceous) locality of Bernissart, Belgium, yielded an assemblage of various actinopterygians. Among them, is the pleuropholid *Pleuropholis germinalis* n. sp., initially described as *Pleuropholis* sp. by Traquair at the beginning of the 20th century. Here, *P. germinalis* n. sp. is revised and fully described, and its assignment to pleuropholids confirmed. This new species is supported by a novel combination of characters, i.e. a robust preopercle with the horizontal limb as wide and high as the vertical limb, an entirely smooth posterior edge of the preopercle, a preopercular canal at equal distance from the dorsal and ventral borders of the preopercle ventral branch (autapomorphy of *P. germinalis* n. sp.), a short and upturned maxilla, a leptolepid notch in the median-dorsal part of the dentary, the quadrato-mandibular articulation lying anteriorly to the orbit, and a smooth posterior edge of flank scales.

KEY WORDS
Actinopterygian assemblage, Barremian-Aptian, coal-mine paleontology, Province of Hainaut, Traquair, new species.

RÉSUMÉ
Pleuropholis germinalis *n. sp., un nouveau Pleuropholidae (Neopterygii, Teleostei) du Crétacé inférieur de Bernissart, Belgique.*
La localité d'âge barrémien-aptien (Crétacé) de Bernissart, Belgique, a produit un assemblage varié d'actinoptérygiens. Parmi ceux-ci se trouve le pleuropholidé *Pleuropholis germinalis* n. sp., décrit en tant que *Pleuropholis* sp. par Traquair au début du 20ème siècle. Le présent article étudie de manière détaillée l'ostéologie de *P. germinalis* n. sp. Son appartenance aux pleuropholidés est confirmée. Cette nouvelle espèce se caractérise par la combinaison unique de caractères suivante : un préoperculaire robuste avec la branche horizontale aussi haute et large que la branche verticale, un préoperculaire avec le bord postérieur lisse, un canal préoperculaire qui court au milieu de la branche ventrale du préoperculaire (autapomorphie de *P. germinalis* n. sp.), un maxillaire court et retourné, un dentaire avec un « leptolepid notch » dans sa partie médiane dorsale, une articulation du carré et de la mandibule localisée antérieurement à l'orbite, un bord postérieur lisse des écailles du flanc.

MOTS CLÉS
Assemblage d'actinoptérygiens, Barrémien-Aptien, paléontologie dans les mines de charbon, Province du Hainaut, Traquair, espèce nouvelle.

INTRODUCTION

The Cretaceous locality of Bernissart in Belgium is well-known for the fossils of *Iguanodon* it yielded (e.g. Godefroit 2012), whereas the more than 3000 actinopterygian specimens found in the same coalmine are less known. Traquair (1911) was the first to study the actinopterygian assemblage from this locality, followed by various studies investigating the different taxa: chondrosteans (Olive *et al.* 2017, 2019), pycnodontiformes (Poyato-Ariza & Wenz 2004), ginglymodians (Olive *et al.* 2017; Cavin *et al.* 2020), halecomorphes (Grande & Bemis 1998), and teleosteans (Gaudant 1966; Taverne 1981, 1982, 1999). The revision of the pleuropholids from this site, described as *Pleuropholis* sp. by Traquair (1911), was still pending and is the purpose of this study.

The family Pleuropholidae was created by Saint-Seine (1949) for a group of small fishes, easily distinguishable because of the presence of a single row of extremely deepened ganoid scales covering almost the whole side of the body (e.g. Brito & Gallo 2002; López-Arbarello *et al.* 2008). Its phylogenetic relationship within Teleostei is still unclear. This family was alternatively placed within the groups Isospondyli (Woodward 1895), Halecostomi (Saint-Seine 1949, 1955) or Holostei (Wenz 1968). The term "halecostome" is confusing, with various authors using the term to describe different concepts. Saint-Seine (1949) and others such as Arambourg & Bertin (1958) contrasted it with the term holostean and used it to bring together intermediate forms between these and the true Teleostei. Patterson (1973) applied the term to bring together *Amia* Linnaeus, 1766 and affine forms (which correspond to the Halecomorphi) and Teleostei. He considered Pleuropholidae to be basal teleosts and later (Patterson 1977) as the sister group of *Ichthyokentema* Woodward, 1941 and more derived teleosts. However, resolving the phylogenetic position of Pleuropholidae is beyond the scope of this study, which only aims to bring new data on a new species of *Pleuropholis* Egerton, 1858.

Pleuropholidae had a very large distribution from the Middle Jurassic to the Early Cretaceous. They are found in North America (Alvarado-Ortega *et al.* 2014; Alvarado-Ortega & Brito 2016), South America (Chiappe *et al.* 1998; Brito & Gallo 2002; Arcucci *et al.* 2015; Giordano *et al.* 2018), Africa (Saint-Seine 1955; Lehman 1966; Taverne & Capasso 2019) and Europe (Sauvage 1883; Egerton 1858; Traquair 1911; Woodward 1919; Saint-Seine 1949; Bravi 1988; Lambers 1999; Bonde & Christiansen 2003; Poyato-Ariza 2005; Bravi *et al.* 2014; Schultze & Arratia 2015; Ebert *et al.* 2015). Pleuropholids are found in both marine (e.g. Woodward 1919; Bravi 1988; Alvarado-Ortega *et al.* 2014) and freshwater (e.g. Saint-Seine 1955; Brito & Gallo 2002) environments, throughout their stratigraphic range.

In this study, we re-describe the taxon studied by Traquair (1911), erect a new species and consider its affinities with regard to other Pleuropholidae.

MATERIAL AND METHODS

Geological settings

Bernissart is situated in the northwestern part of the Mons Basin (western Belgium), an east-west synclinal structure filled with Meso-Cenozoic deposits (Fig. 1). Its sedimentation started in a continental environment at the beginning of the Cretaceous period (during the so-called Wealden) due to an active subsidence, mainly controlled by intrastratal dissolution of deep evaporite beds in the Mississippian (Carboniferous) basement. This led to the creation of sinkholes, or natural pits, in various parts of the basin (Spagna 2010; Quinif & Licour 2012). Once these natural pits are connected to the surface, they act as a sediment trap including the accumulation of local faunal and floral remains. At Bernissart, the fossil remains were found in a lacustrine clay, which was defined as the Sainte-Barbe Clays Formation (Cornet & Schmitz 1898; Cornet 1927). The age of this formation was determined based on palynologic data as late Late Barremian to earliest Aptian (Yans *et al.* 2006; Dejax *et al.* 2007; Yans *et al.* 2012). The environment at the top of the *Iguanodon* pit of Bernissart was formerly interpreted as lacustrine (Van den Broeck 1898) and now lacustrine to swampy (Yans 2007; Schnyder *et al.* 2009; Spagna 2010; Spagna *et al.* 2012).

Material

Fishes have been recovered in the *Iguanodon* sinkhole through a lateral tunnel, starting at the Sainte-Barbe mine shaft, at depth of –322 m (Fig. 1D). They were deposited alongside chelonians and crocodiles in one or two bonebeds mainly (bonebeds III and/or IVb) but also found isolated within dinosaur bone beds (I, II, IV, and V) (Baele *et al.* 2012a). Unfortunately, the information on the exact stratigraphic provenance of these fossil fishes is lost as the specimens were mixed before labelling during the excavation process.

The specimens were prepared at the beginning of last century. No record was found regarding the preparation protocol at this time, but it was most likely done mechanically. Additional mechanical preparations were performed on several specimens for the scope of this study. The general body outlines and the outlines of some of the skull bones are recognizable, but in most specimens, bones were damaged, resulting in the skull roof pattern to be poorly preserved. Four specimens of *Pleuropholis* sp. were mentioned in Traquair's work (1911) and are redescribed here. We noticed that two specimens described by Traquair, i.e. IRSNB P.1236 and IRSNB P.1235, are actually the same specimen (part and counterpart). For curatorial reasons, the specimen numbers were not changed accordingly.

Abbreviations

Institutional abbreviation

IRSNB Institut royal des Sciences naturelles de Belgique.

Anatomical abbreviations

an.f anal fin;
Ang angular;
Cl cleithrum;

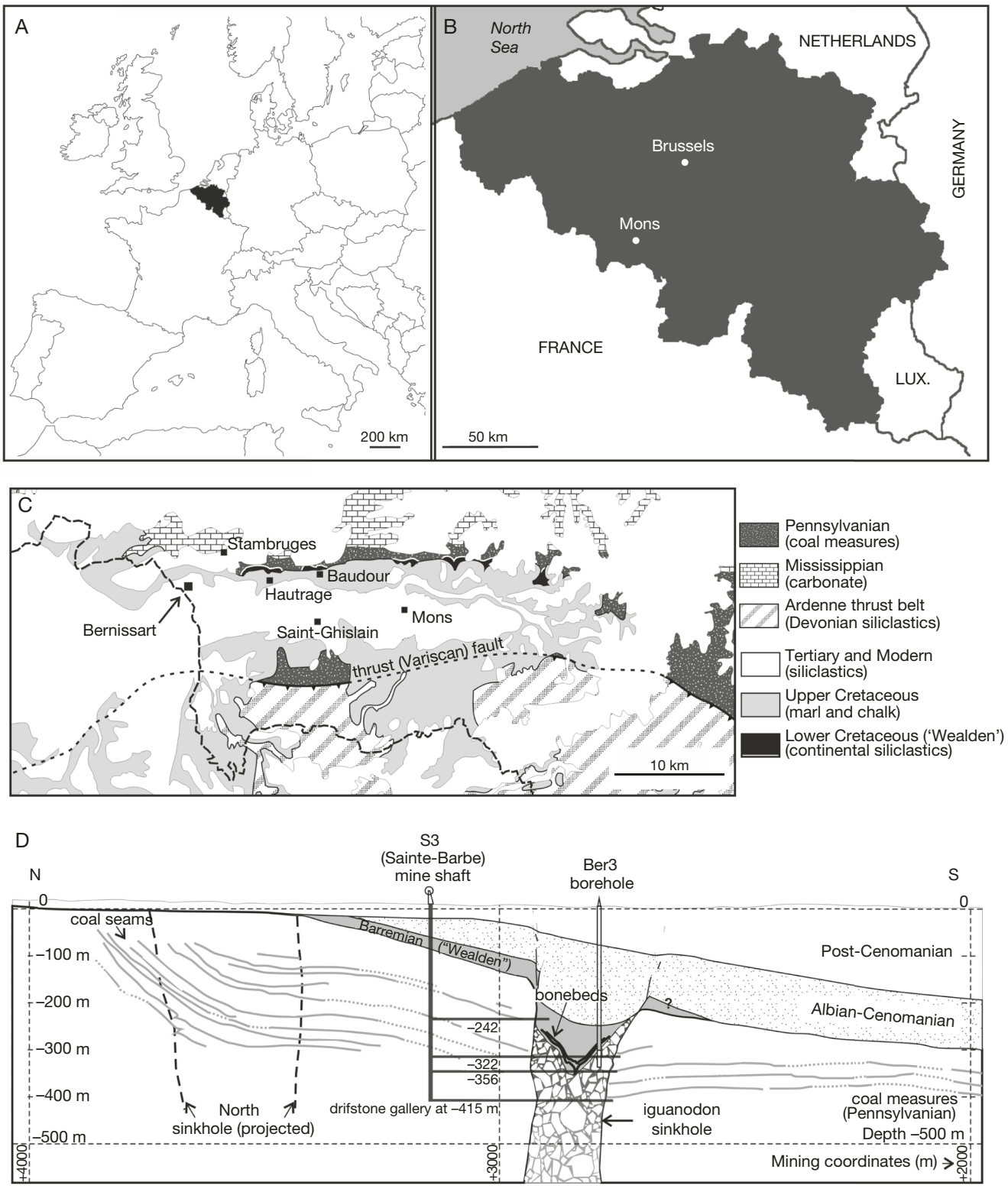

FIG. 1. — Location and geological framework of the Bernissart locality: **A**, localisation of Belgium in western Europe; **B**, localisation of Mons within Belgium; **C**, localisation of Bernissart within the Mons Basin, from Baele *et al.* (2012b); **D**, cross section of the Bernissart area showing the geological setting of the *Iguanodon* Sinkhole, modified from Baele *et al.* (2012b), who adapted the figure from Delmer & Van Wichelen (1980). Abbreviation: **Lux.**, Luxemburg.

D	dentary;	Fr	frontal;
d.f,	dorsal fin;	Io	infraorbital;
Dpt	dermopterotic;	io.c	infraorbital canal;
Dsph	dermosphenotic;	Iop	interopercle;
Exsc	extrascapular;	l.n	leptolepid notch;

Mx	maxilla;
m.c	mandibular canal;
Na	nasal;
Op	opercle;
Pa	parietal;
pec.f	pectoral fin;
Pop	preopercle;
pop.c	preopercle canal;
Pt	posttemporal;
pt	pterygiophore;
Ro	rostral;
Scl	supracleithrum;
Smx	supramaxillar;
So	supraorbital;
Sop	subopercle.

SYSTEMATIC PALAEONTOLOGY

Superclass ACTINOPTERYGII Cope, 1887
Subclass NEOPTERYGII Regan, 1923
Infraclass TELEOSTEI *sensu* Arratia (1999)
Order *incertae sedis*
Family PLEUROPHOLIDAE Saint-Seine, 1949
Genus *Pleuropholis* Egerton, 1858

Pleuropholis germinalis n. sp.
(Figs 2-5)

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Pleuropholis sp. indet. – Traquair 1911: 45, pl. IX, figs 1-3.

DIAGNOSIS. — Small sized actinopterygian (SL of roughly 64 mm) with the dorsal fin located posteriorly and at the same level as the anal fin. Species of *Pleuropholis* with the following unique combination of characters: robust preopercle with the horizontal limb as wide and high as the vertical limb; preopercle with the posterior edge entirely smooth; preopercle canal placed at equal distance from the dorsal and ventral borders of the horizontal branch (autapomorphy of *P. germinalis* n. sp.); short and upturned maxilla; dentary with leptolepid notch in its median-dorsal part; quadrato-mandibular articulation lying anteriorly to the orbital margin; smooth posterior border of flank scales.

HOLOTYPE. — IRSNB P.1236 and 1235 (part and counterpart; Figs 2, 3).

PARATYPE. — IRSNB P.1234 (Fig. 4).

OTHER SPECIMENS. — IRSNB Vert-01680-00651 (Fig. 5).

ETYMOLOGY. — The specific name refers to the novel of Emile Zola, Germinal. The novel focuses on the coalmine work and the harsh conditions of miners. Without miners, fossils from Bernissart would have never been extracted and this specific assignment consequently honors them.

TYPE LOCALITY AND HORIZON. — Bernissart, Province of Hainaut, Belgium. Sainte-Barbe Clays Formation, uppermost Barremian to lowermost Aptian (Yans *et al.* 2006, 2012; Dejax *et al.* 2007).

DESCRIPTION

With a standard length of approximately 64 mm (specimen IRSNB P.1234, Fig. 4), this is a small sized actinopterygian, although one of the largest within Pleuropholidae. The highest part of the fish is located in the mid-length of the body (Fig. 3). The head, from the anterior part of the rostral to the posterior part of the opercle, is roughly one fourth of the standard length. The dorsal fin is situated well posteriorly, at the same level as the anal fin. The dermal bones and the scales are covered with ganoin.

Skull

The skull is fragmented in all specimens exhibiting it. The skull roof is preserved in right lateral view on specimen IRSNB P.1236 (Fig. 2) and is partially preserved in left lateral view, where it is somewhat distorted, in IRSNB P.1234 (Fig. 4). Regarding IRSNB vert-01680-00651 (Fig. 5), only the posterior part of the skull, in lateral view, is preserved. The following description of the skull is therefore mainly based on specimen IRSNB P.1236 (Fig. 2).

The rostral is not well preserved in any of the specimens and its posterior suture with the nasals is not clearly discernible. The nasals are longer than wide, located anteriorly to the frontals. Frontals are the longest bones of the skull roof. Like in other species of teleosts (e.g. *Pleuropholis*, *Ichthyokentema, Siemensichthys* Arratia, 2000*, Eurycormus* Wagner, 1863, and *Gondwanapleuropholis* Brito & Gallo, 2002) the frontals are broad, and do not display the anterior narrowing found in more advanced teleosts (Arratia 2000; Brito & Gallo 2002). The parietals (Fig. 2) are subrectangular, slightly longer than wide and their length represents approximately two thirds of the length of the frontals. The extrascapulars are located posteriorly to the parietals and are barely distinguishable in the available material. Only the impression of the right dermopterotic is present in the specimen IRSNB P.1236 (Fig. 2). The dermopterotic is a subrectangular bone, that widens in its posterior part.

The circumorbital series, as well as the posterior cheek region, are not well preserved in any of our specimens. The circumorbital series is formed by at least four infraorbitals, the dermosphenotic, and at least two supraorbitals. The infraorbital series is very fragmented in the specimen IRSNB P.1236 (Fig. 2). The dermosphenotic is in contact with the dorsal edge of the most posterior infraorbital; it is a somewhat rectangular bone that participates in the posterodorsal corner of the orbit, below the frontal and the dermopterotic.

The preopercle is a "L-shaped" robust bone in which the horizontal limb is as wide and high as the vertical limb. These limbs are placed perpendicular to each other (Fig. 2). The posterior edge of the preopercle is totally smooth (Figs 2; 5). The preopercular canal is placed at equal distance from the dorsal and ventral borders of the horizontal limb of the preopercle (Figs 2; 5). The opercular series is formed by a slightly deeper than wide opercle, a subtriangular subopercle, and an interopercle (incomplete on IRSNB P.01236).

The maxilla is upturned, rather narrow and short, but badly preserved (Fig. 2). The oral margin of the maxilla is not preserved here. The single supramaxilla is a moderately large bone placed posteriorly to the maxilla and along the

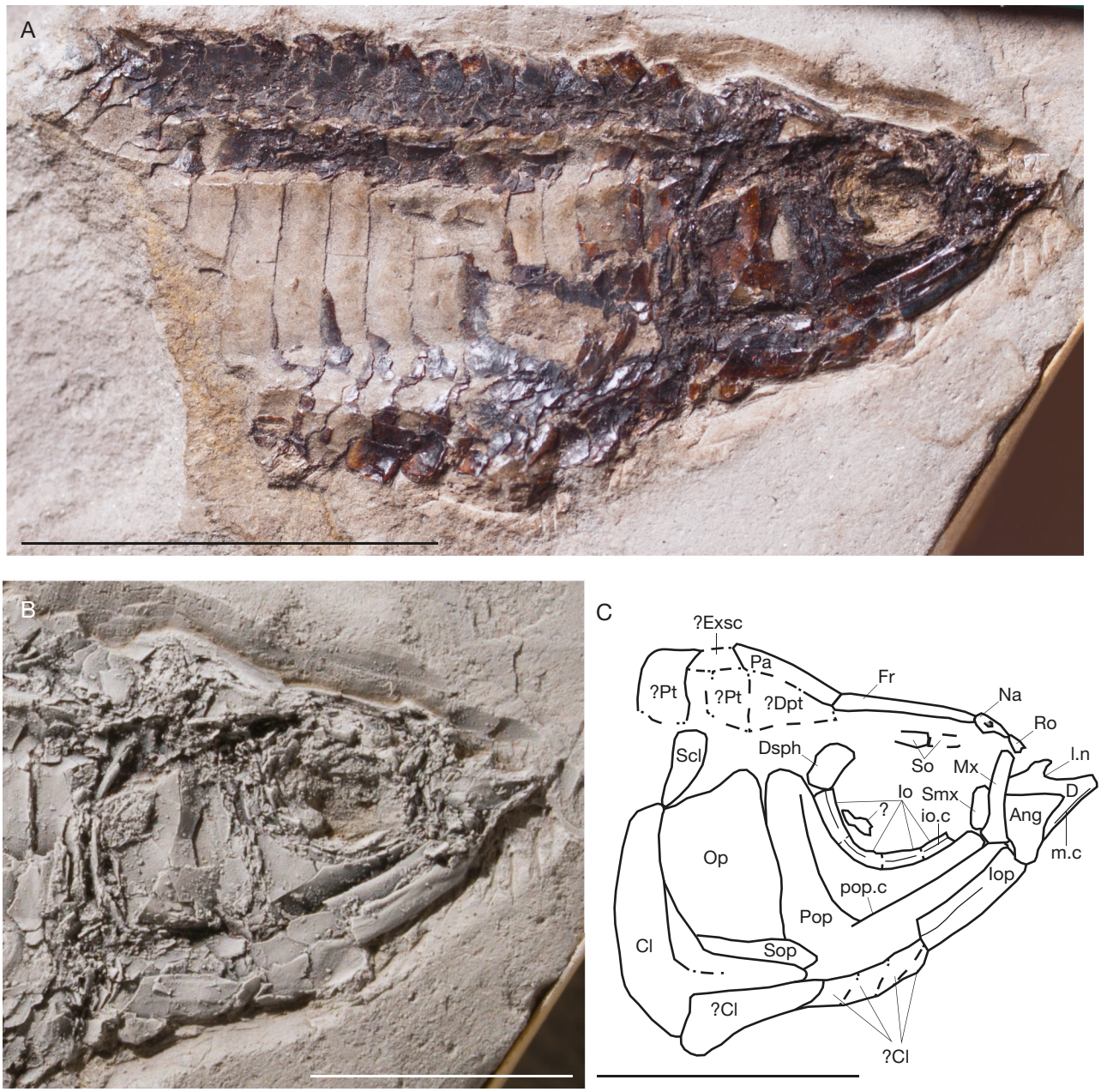

FIG. 2. — Skeleton of *Pleuropholis germinalis* n. sp., IRSNB P.01236, holotype: **A**, photograph; **B**, close-up on the head whitened with ammonium chloride; **C**, line drawing reconstruction. Scale bars: A, 1 cm; B, C, 0.5 cm.

anterior margin of the orbit (Fig. 2). No premaxilla is preserved in the available specimens.

Dentary and angular are exposed laterally. The dentary is a short stout subsquare bone that increases in height posteriorly. The dentary presents, in its median-dorsal part, a leptolepid notch, like in *P. decastroi* Bravi, 1988, from the Early Cretaceous of Italy (Taverne & Capasso 2019). The dentary is traversed by the mandibular sensory canal, which extends along its ventral border. Posteriorly, the dentary sutures with the angular that is partially exposed in IRSNB P.1236 and forms the posterior corner of the lower jaw (Fig. 2). Other bones of the lower jaw are not exposed in the specimens studied here. No teeth have been observed in the available material.

Vertebral column

Only few vertebral elements of the abdominal region are exposed where some scales are displaced or lost (Fig. 4).

Paired girdles and fins

Some elements of the pectoral girdle are preserved as fragmented elements, impressions in the matrix, or are hidden by the presence of displaced scales (Figs 2-4). The cleithrum is a robust bone located ventrally to the short and small supracleithrum. It is smooth, and anteriorly underlies the subopercle. Fragmented and displaced elements of the putative ventral branch of the cleithrum are found in IRSNB P.1236 (Fig. 2). The pectoral fin

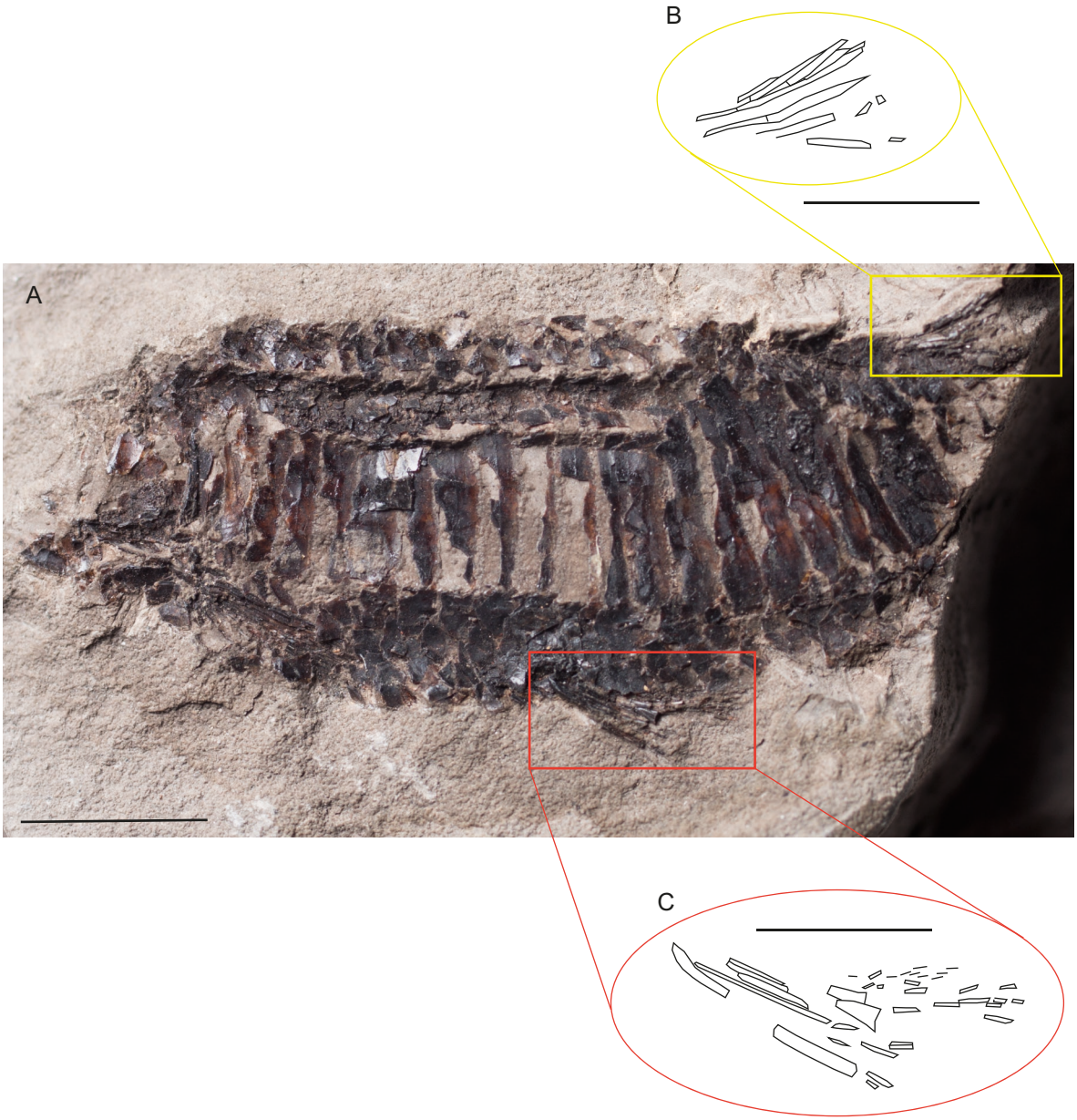

Fig. 3. — Skeleton of *Pleuropholis germinalis* n. sp., IRSNB P.01235, holotype, counterpart of IRSNB P.01236: **A**, photograph; **B**, line drawing close-up on the dorsal fin; **C**, line drawing close-up on the pelvic fin. Scale bars: A, 0.5 cm; B, C, 0.25 cm.

is positioned close to the ventral margin of the body and below the large scales of the body flank in IRSNB P.1234 (Fig. 4). At least nine rays are preserved. In IRSNB P.1235, a pelvic fin is preserved, in which roughly seven rays are preserved (Fig. 3). No bones of the pelvic girdle are exposed in any of the studied specimens.

Dorsal and anal fins

The dorsal fin (Figs 3; 4) counts at least 9 dorsal fin rays on IRSNB P.1235 (Fig. 3) whereas the anal fin (Fig. 4) displays at least 11 fin rays. The anterior margin of the anal fin displays at least 7 fringing fulcra. Elongated pterygiophores, supporting the anal fin, are observed anteriorly.

Caudal fin

The caudal pedicle is slender and covered with rhombic caudal scales (Figs 4; 5). The caudal endoskeleton is covered by scales and not visible for analysis. Although the posterior tip of the caudal fin is not preserved, the caudal fin is almost complete in IRSNB P.1234 (Fig. 4). The caudal fin is hemiheterocercal and includes at least 19 evenly segmented rays. On the dorsal margin of the caudal fin, there are at least 4 dorsal caudal fulcra. The ventral margin of the caudal fin is preserved in none of the specimens.

Scales

The scales are thick and of ganoid type (Figs 2-5). Those along the flank are rectangular in shape, 5-6 times deeper

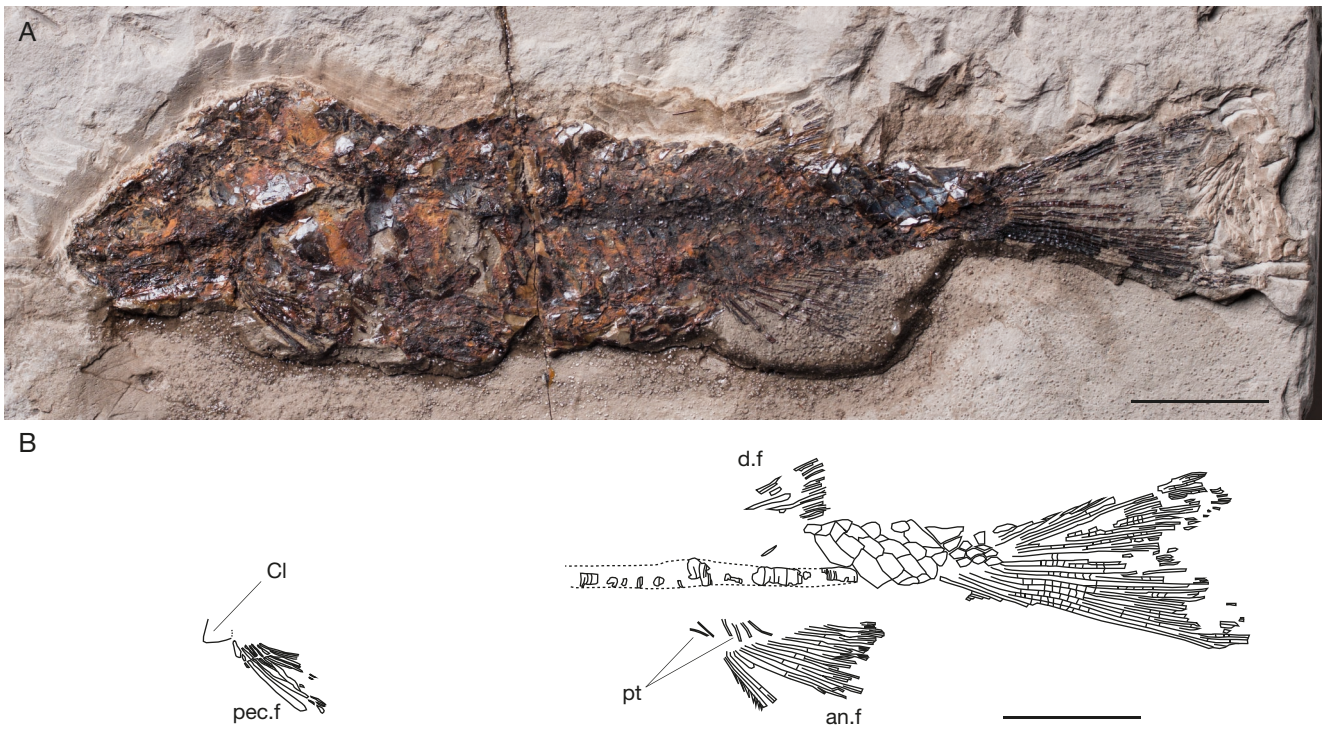

FIG. 4. — Skeleton of *Pleuropholis germinalis* n. sp., IRSNB P.01234, paratype: **A**, photograph; **B**, line drawing of the vertebral skeleton and of fins. Scale bars: 1 cm.

than long, with anterior and posterior borders being slightly curved. The entire posterior border of all flank scales is smooth. Dorsally to the flank scale row, two rows of rhomboidal scales are observed. The most dorsal scales, anterior to the dorsal fin, could potentially be pair scute-like elements. However, the preservation of this feature is not good enough to be conclusive. Ventrally to the flank scale row, at least two scale rows (probably three) are present. Scales are relatively small and rhomboidal. The lateral line is not observable through the body flank scales; pores or thickenings revealing the course of branch of the lateral line system are not observable probably due to a lack of preservation.

DISCUSSION

Although the Bernissart material are limited to somewhat fragmentary specimens, their distinctive morphology presenting deepened flank scales, an edentulous mouth, and an orbital series formed by numerous infraorbital and supraorbital bones, support the identification of this taxon as a Pleuropholidae (Saint-Seine 1949; Brito & Gallo 2002).

Pleuropholis germinalis n. sp., shares with the other species of *Pleuropholis* the presence of a short, upturned maxilla and the quadrato-mandibular articulation lying anteriorly to the orbit (Woodward 1919; Saint-Seine 1949; Patterson 1973; Bravi 1988; Taverne & Capasso 2019). Also, the two branches of the preopercular are similar in height and width, and this seems to be a common characteristic in all *Pleuropholis* species.

Currently, one of the biggest problems in the taxonomy of the basal teleosts is the validity of the innumerable species of the genus *Pleuropholis*. These species are often based on body proportions from imperfectly preserved specimens (c.f. Patterson 1973; Alvarado-Ortega & Brito 2016; Taverne & Capasso 2019). Despite this issue, the new species described here differs from the other species of *Pleuropholis* by a combination of characters that include the presence of a leptolepid notch in the median-dorsal part of the dentary, the middle (at equal distance from the dorsal and ventral borders) position of the preopercle canal in the horizontal branch of this bone (autapomorphy of *P. germinalis* n. sp.), the smooth posterior edge of the preopercle, and the smooth posterior edge of flank scales.

A well-marked leptolepid notch in the median-dorsal part of the dentary is present in *P. decastroi* from the Albian of southern Italy, and weakly developed in *P. jamotti* Saint-Seine, 1955, from the Middle Jurassic of Congo (Taverne & Capasso 2019: 46). The presence of a leptolepid notch is unknown in the other Pleuropholidae (Taverne & Capasso 2019). Although partially preserved, the maxilla of *P. germinalis* n. sp. appears to be narrow, like seen in *P. attenuata* Egerton, 1858, and *P. longicauda* Egerton, 1858 from the Upper Jurassic of England (Egerton 1858; Woodward 1919). Three species, *P. thiollieri* Sauvage, 1883, *P. decastroi* and *P. cisnerosorum* Alvarado-Ortega & Brito, 2016, share the condition of an extremely broad maxilla that covers almost entirely the lower jaw. This feature is not present in *P. germinalis* n. sp. The absence of serrations in the posterior edge of the preopercle differentiates *Pleuropholis germinalis* n. sp. from *P. cisnerosorum*. The absence of serrations in the

FIG. 5. — Photograph of the skeleton of *Pleuropholis germinalis* n. sp. with a close-up on the preopercle, IRSNB vert.01680-0065. Scale bars: A, 1 cm; B, 2 mm.

posterior edge of flank scales distinguishes *P. germinalis* n. sp. from *P. serrata* Egerton, 1858, *P. jamotti*, *P. cisnerosorum* and *P. decastroi*. The presence of an unserrated posterior edge on the scales is known in all nominal species from the Purbeckian [Tithonian] deposits of England (i.e. *P. longicauda*, *P. formosa* Woodward, 1919, *P. attenuata*, *P. crassicauda* Egerton, 1858), apart from *P. serrata*.

CONCLUSIONS

In the past few years, our knowledge of the actinopterygian assemblage from the Cretaceous locality of Bernissart, Belgium, has known a considerable impetus (Olive *et al.* 2017, 2019; Cavin *et al.* 2020) and resulted in a clearer view of the different components present. In this paper, a detailed morphological study of material, last described by Traquair (1911), has resulted in the erection of a new species, *Pleuropholis germinalis* n. sp. This new species is supported by a novel combination of morphological characteristics, i.e. a robust preopercle with the horizontal limb as wide and high as the vertical limb, an entirely smooth posterior edge of the preopercle, the preopercular canal at equal distance from the dorsal and ventral borders of the preopercle ventral branch (autapomorphy of *P. germinalis* n. sp.), a short and upturned maxilla, a leptolepid notch in the median-dorsal part of the dentary, the quadrato-mandibular articulation lying anteriorly to the orbit and smooth posterior edges of flank scales. The family Pleuropholidae includes several doubtful species, poorly described and/or described on the basis of badly preserved material. Thus, an overall and detailed revision of the whole family would be necessary to assess its validity, its content, and to build a solid setting for evaluating the phylogenetic relationships in this family.

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REFERENCES

ALVARADO-ORTEGA J. & BRITO P. M. 2016. — A Jurassic pleuropholid fish (Teleostei, Pleuropholidae) in the Tethys Sea domain of North America. *Journal of Vertebrate Paleontology* 36 (5): e1201767. https://doi.org/10.1080/02724634.2016.1201767

ALVARADO-ORTEGA J., BARRIENTOS-LARA J. I., ESPINOSA-ARRUBARRENA L. & MELGAREJO-DAMIÁN M. DEL P. 2014. — Late Jurassic marine vertebrates from Tlaxiaco, Oaxaca state, southern Mexico. *Palaeontologia Electronica* 17 (1): 12A. https://doi.org/10.26879/454

ARAMBOURG C. & BERTIN L. 1958. — Super-ordre des Holostéens et des Halecostomi (Holostei et Halecostomi). *Traité de Zoologie : Anatomie, Systématique, Biologie* 13: 2173-2203.

ARCUCCI A. B., PRAMPARO M. B., CODORNIÚ DOMINGUEZ L. S., GIORDANO P. G., CASTILLO ELÍAS G., PUEBLA G. G., MEGO N., GOMEZ M. A. & BUSTOS ESCALONA E. L. 2015. — Biotic assemblages from Early Cretaceous lacustrine systems in the San Luis Basin, mid-western Argentina. *Boletín Geológico Minero* 126 (1): 109-128.

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. https://doi.org/10.1007/BF02987957

ARRATIA G. 2001. — The sister-group of Teleostei: consensus and disagreements. *Journal of Vertebrate Paleontology* 21 (4): 767-773. https://doi.org/bqt2j5

ARRATIA G. 2013. — Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes (Actinopterygii, Teleostei). *Journal of Vertebrate Paleontology* 33 (suppl. 1): 1-138. https://doi.org/10.1080/02724634.2013.835642

ARRATIA G. 2015. — Complexities of early Teleostei and the evolution of particular morphological structures through time. *Copeia* 103 (4): 999-1025. https://doi.org/10.1643/CG-14-184

BAELE J.-M., GODEFROIT P., SPAGNA P. & DUPUIS C. 2012. — A short introduction to the geology of the Mons Basin and the Iguanodon sinkhole, Belgium, *in* GODEFROIT P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems.* Indiana University Press, Indiana: 35-42. http://www.jstor.org/stable/j.ctt16gzfhx.8

BAELE J.-M., GODEFROIT P., SPAGNA P. & DUPUIS C. 2012. — Geological model and cyclic mass mortality scenarios for the Lower Cretaceous Bernissart Iguanodon Bonebed, *in* GODEFROIT P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems.* Indiana University Press, Indiana: 155-171. http://www.jstor.org/stable/j.ctt16gzfhx.19

BONDE N. & CHRISTIANSEN P. 2003. — New dinosaurs from Denmark. *Comptes Rendus Palevol* 2 (1): 13-26. https://doi.org/10.1016/S1631-0683(03)00009-5

BRAVI S. 1988. — Contributo allo studio del giacimento ad ittioliti di Pietraroja (Benevento). I: *Pleuropholis decastroi* n. sp. (Pisces, Actinopterygii, Pholidophoriformes). *Memorie della Società Geologica Italiana* 41: 575-586.

BRAVI S., GARASSINO A., BARTIROMO A., AUDO D., CHARBONNIER S., SCHWEIGERT G., THÉVENARD F. & LONGOBARDI C. 2014. — Middle Jurassic Monte Fallano Plattenkalk (Campania, southern Italy): first report on terrestrial plants, decapod crustaceans and fishes. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 272 (1): 79-107. https://doi.org/10.1127/0077-7749/2014/0398

BRITO P. M. 1997. — Révision des Aspidorhynchidae (Pisces-Actinopterygii) du Mésozoïque : ostéologie, relations phylogénétiques, données environnementales et biogéographiques. *Geodiversitas* 19 (4): 681-772.

BRITO P. M. & GALLO V. 2002. — A new pleuropholid, *Gondwanapleuropholis longimaxillaris* n. g., n. sp. (Actinopterygii: Teleostei) from the Jurassic of north east Brazil. *Comptes Rendus Palevol* 1 (8): 697-703. https://doi.org/10.1016/S1631-0683(02)00080-5

CAVIN L., DEESRI U. & OLIVE S. 2020. — *Scheenstia bernissartensis* (Actinopterygii: Ginglymodi) from the Early Cretaceous of Bernissart, Belgium, with an appraisal of ginglymodian evolutionary history. *Journal of Systematic Palaeontology* 18 (6): 513-527. https://doi.org/10.1080/14772019.2019.1634649

CHIAPPE L., RIVAROLA D., CIONE A., FREGENAL-MARTÍNEZ M., SOZZI H., BUATOIS L., GALLEGO O., LAZA J., ROMERO E. & LÓPEZ-ARBARELLO A. 1998. — Biotic association and palaeoenvironmental reconstruction of the "Loma del Pterodaustro" fossil site (Early Cretaceous, Argentina). *Geobios* 31 (3): 349-369. https://doi.org/10.1016/S0016-6995(98)80018-1

CORNET J. 1927. — L'époque wealdienne dans le Hainaut. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie* 50: 89-104.

CORNET J. & SCHMITZ G. 1898. — Note sur les puits naturels du terrain houiller du Hainaut et le gisement des iguanodons de Bernissart-Bull. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie* 12: 196-206 (https://www.biodiversitylibrary.org/page/45195268), 301-318 (https://www.biodiversitylibrary.org/page/45195829).

DEJAX J., PONS D. & YANS J. 2007. — Palynology of the dinosaur-bearing Wealden facies in the natural pit of Bernissart (Belgium). *Review of Palaeobotany and Palynology* 144: 25-38. https://doi.org/10.1016/j.revpalbo.2005.10.004

DELMER A. & VAN WICHELEN P. 1980. — Répertoire des puits naturels connus en terrain houiller du Hainaut. *Professional Paper, Publication du Service géologique de Belgique* 172: 1-79.

EBERT M., KÖLBL-EBERT M. & LANE J.A. 2015. — Fauna and predator-prey relationships of Ettling, an actinopterygian fish-dominated Konservat-Lagerstätte from the Late Jurassic of Southern Germany. *PLoS One* 10 (1): e0116140. https://doi.org/10.1371/journal.pone.0116140

EGERTON P. M. G. 1858. — British fossils. *Memoirs of the Geological Survey of the United Kingdom*, Decade IX: 1-32.

GAUDANT J. 1966. — Sur la nécessité d'une subdivision du genre *Anaethalion* White (Poisson Téléostéen). *Compte Rendu sommaire des Séances de la Société géologique de France* 8: 308-310.

GIORDANO P. G., SUCCAR C. A., CODORNIÚ L., CIONE A. L. & ARRATIA G. 2018. — *Zurupleuropholis* gen. nov. (Teleostei, Albian, Argentina), first pleuropholids from the Cretaceous of South America. *Cretaceous Research* 84: 223-239. https://doi.org/10.1016/j.cretres.2017.11.017

GODEFROIT P. 2012. — *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*. Indiana University Press, Indiana, 629 p. https://www.jstor.org/stable/j.ctt16gzfhx

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): 1-696. https://doi.org/10.1080/02724634.1998.10011114

LAMBERS P. H. 1999. — The actinopterygian fish fauna of the Late Kimmeridgian and Early Tithonian 'Plattenkalke' near Solnhofen (Bavaria, Germany): state of the art. *Geologie en Mijnbouw* 78 (2): 215-229. https://doi.org/10.1023/A:1003855831015

LEHMAN J.-P. 1966. — Actinopterygii, *in* PIVETEAU J. (ed.), *L'origine des vertébrés. Leur expansion dans les eaux douces et le milieu marin*. Masson et Cie Éditeurs, Paris, 242 p. (Traité de Paléontologie; Tome IV.)

LÓPEZ-ARBARELLO A., RAUHUT O. W. M. & MOSER K. 2008. — Jurassic fishes of Gondwana. *Revista de la Asociación Geológica Argentina* 63 (4): 586-612.

OLIVE S., TAVERNE L., CAVIN L. & DEESRI U. 2017. — Systematic revision of the Cretaceous actinopterygian fauna from Bernissart, Belgium. *Research & Knowledge* 3 (1): 43-46. https://doi.org/10.14456/randk.2017.11

OLIVE S., TAVERNE L. & LÓPEZ-ARBARELLO A. 2019. — A new genus of coccolepidid actinopterygian from the Cretaceous Iguanodon-bearing locality of Bernissart, Belgium. *Cretaceous Research* 95: 318-335. https://doi.org/10.1016/j.cretres.2018.11.020

PATTERSON C. 1973. — Interrelationships of holosteans, *in* GREENWOOD P. H., MILES R. S. & PATTERSON C. (eds), *Interrelationships of Fishes*. Academic Press, London: 233-305.

PATTERSON C. 1977. — The contribution of paleontology to teleostean phylogeny, *in* HECHT M. K., GOODY P. C. & HECHT B. M. (eds), *Major Patterns in Vertebrate Evolution.* Springer, Boston: 579-643. https://doi.org/10.1007/978-1-4684-8851-7_21

POYATO-ARIZA F. J. 2005. — Palaeoecology of the fishes from the Early Cretaceous lake of Las Hoyas, Cuenca, Spain, with a hypothesis of sexual dimorphism for the chanidae *Rubiesichthys*. *Bulletin of the Kitakyushu Museum of Natural History and Human History, series A (Natural History)* 3: 153-168.

POYATO-ARIZA F. J. & WENZ S. 2004. — The new pycnodontid fish genus *Turbomesodon*, and a revision of *Macromesodon* based on new material from the Lower Cretaceous of Las Hoyas, Cuenca, Spain, *in* ARRATIA G. & TINTORI A. (eds), *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity*. Verlag Dr. Friedrich Pfeil, Munich: 341-378.

QUINIF Y. & LICOUR L. 2012. — The karstic phenomenon of the Iguanodon sinkhole and the geomorphological situation of the Mons Basin during the Early Cretaceous, *in* GODEFROIT P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems.* Indiana University Press, Indiana: 51-61. http://www.jstor.org/stable/j.ctt16gzfhx.10

SAINT-SEINE P. DE 1949. — Les poissons des calcaires lithographiques de Cerin (Ain). *Publications du Musée des Confluences* 2 (1): 3-79.
SAINT-SEINE P. DE 1955. — Poissons fossiles de l'étage de Stanleyville (Congo Belge). *Annales du Musée royal du Congo belge Tervuren (Belgique). Sciences géologiques* 14: 1-126.
SAUVAGE H. E. 1883. — Notes sur les poissons fossiles. *Bulletin de la Société géologique de France,* série 3, 11: 475-503. https://www.biodiversitylibrary.org/page/47193837
SCHNYDER J., DEJAX J., KEPPENS E., TU T. T. N., SPAGNA P., BOULILA S., GALBRUN B., RIBOULLEAU A., TSHIBANGU J. -P. & YANS J. 2009. — An Early Cretaceous lacustrine record: organic matter and organic carbon isotopes at Bernissart (Mons Basin, Belgium). *Palaeogeography, Palaeoclimatology, Palaeoecology* 281 (1): 79-91. https://doi.org/10.1016/j.palaeo.2009.07.014
SCHULTZE H.-P. & ARRATIA G. 2015. — Knochenfische im weiteren Sinne (Osteichthyes oder Osteognathostomata), *in* ARRATIA G., SCHULTZE H.-P., TISCHLINGER H. & VIOHL G. (eds), *Solnhofen ein Fenster in die Jurazeit*. Verlag Dr. Friedrich Pfeil, München: 360-409.
SPAGNA P. 2010. — *Les faciès wealdiens du Bassin de Mons (Belgique) : paléoenvironnements, géodynamique et valorisation industrielle*. Faculté polytechnique de l'Umons, 138 p.
SPAGNA P., YANS J., SCHNYDER J. & DUPUIS C. 2012. — The Paleoenvironment of the Bernissart Iguanodons: Sedimentological Analysis of the Lower Cretaceous Wealden Facies in the Bernissart Area, *in* GODEFROIT P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems.* Indiana University Press, Indiana: 87-96. http://www.jstor.org/stable/j.ctt16gzfhx.14
TAVERNE L. 1981. — Ostéologie et position systématique d'*Aethalionopsis robustus* (Pisces, Teleostei) du Crétacé inférieur de Bernissart (Belgique) et considérations sur les affinités des Gonorynchiformes. *Bulletin de l'Académie royale de Belgique, Classes des Sciences*, série 5, 67: 958-982.
TAVERNE L. 1982. — Sur *Pattersonella formosa* (Traquair, RH, 1911) et *Nybelinoides brevis* (Traquair, RH, 1911) : Téléostéens salmoniformes argentinoides du Wealdien inférieur de Bernissart, Belgique, précédemment attribués au genre *Leptolepis* Agassiz, L., 1832. *Bulletin de l'Institut royal des Sciences naturelles de Belgique – Sciences de la Terre* 54 (3): 1-27.
TAVERNE L. 1999. — Ostéologie et position systématique d'*Arratiaelops vectensis* gen. nov., téléostéen élopiforme du Wealdien (Crétacé inférieur) d'Angleterre et de Belgique. *Bulletin de l'Institut royal des Sciences naturelles de Belgique – Sciences de la Terre* 69: 77-96.
TAVERNE L. & CAPASSO L. 2019. — New data on *Pleuropholis decastroi* (Teleostei, Pleuropholidae), a "pholidophoriform" fish from the Lower Cretaceous of the Eurafrican Mesogea. *Geo-Eco-Trop* 43 (1): 35-51.
TRAQUAIR R. H. 1911. — Les poissons wealdiens de Bernissart. *Mémoires du Musée royal d'Histoire naturelle de Belgique* 6: 1-65. https://www.biodiversitylibrary.org/page/42309609
VAN DEN BROECK E. 1898. — Les coupes du gisement de Bernissart. Caractères et dispositions sédimentaires de l'argile ossifère du Cran aux Iguanodons. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie* 12: 216-243. https://www.biodiversitylibrary.org/page/45195288
WENZ S. 1968. — Note préliminaire sur la faune ichthyologique du Jurassique supérieur du Montsech (Espagne). *Bulletin de la Société géologique de France* 7 (1): 116-119. https://doi.org/10.2113/gssgfbull.S7-X.1.116
WILEY E. O. & JOHNSON G. D. 2010. — A teleost classification based on monophyletic groups, *in* NELSON J. S. SCHULTZE H.-P. & WILSON M. V. H (eds), *Origin and Phylogenetic Interrelationships of Teleosts*. Verlag Dr. Friedrich Pfeil: 123-182.
WOODWARD A. S. 1895. — *Catalogue of the Fossil Fishes in the British Museum (Natural History), Part III*. British Museum of Natural History, London, 544 p.
WOODWARD A. S. 1919. — The Fossil Fishes of the English Wealden and Purbeck Formations. Part III. *Monographs of the Palaeontographical Society* 71 (340): 105-148.
YANS J. 2007. — Lithostratigraphie, minéralogie et diagenèse des sédiments à faciès wealdien du Bassin de Mons (Belgique). *Mémoires de la Classe des sciences, Académie royale de Belgique*, série 3, 9: 1-179.
YANS J., DEJAX J., PONS D., TAVERNE L. & BULTYNCK P. 2006. — The iguanodons of Bernissart are middle Barremian to early Aptian in age. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 76: 91-95.
YANS J., DEJAX J. & SCHNYDER J. 2012. — On the age of the Bernissart Iguanodons, *in* GODEFROIT P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems.* Indiana University Press, Indiana: 79-84. http://www.jstor.org/stable/j.ctt16gzfhx.13

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