



**HAL**  
open science

**A new species of Pleuropholis (Teleostei:  
Pleuropholidae) from the Upper Cretaceous Akrabou  
Formation of southeastern Morocco, with comments on  
the evolutionary history of the genus**

Paulo M Brito, Romain Vullo

► **To cite this version:**

Paulo M Brito, Romain Vullo. A new species of Pleuropholis (Teleostei: Pleuropholidae) from the Upper Cretaceous Akrabou Formation of southeastern Morocco, with comments on the evolutionary history of the genus. *Cretaceous Research*, 2023, 148, pp.105500. 10.1016/j.cretres.2023.105500 . insu-03997427

**HAL Id: insu-03997427**

**<https://insu.hal.science/insu-03997427v1>**

Submitted on 20 Feb 2023

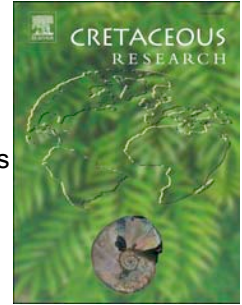
**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Journal Pre-proof

A new species of *Pleuropholis* (Teleostei: Pleuropholidae) from the Upper Cretaceous Akrabou Formation of southeastern Morocco, with comments on the evolutionary history of the genus

Paulo M. Brito, Romain Vullo



PII: S0195-6671(23)00028-9

DOI: <https://doi.org/10.1016/j.cretres.2023.105500>

Reference: YCRES 105500

To appear in: *Cretaceous Research*

Received Date: 13 December 2022

Revised Date: 3 February 2023

Accepted Date: 3 February 2023

Please cite this article as: Brito, P.M., Vullo, R., A new species of *Pleuropholis* (Teleostei: Pleuropholidae) from the Upper Cretaceous Akrabou Formation of southeastern Morocco, with comments on the evolutionary history of the genus, *Cretaceous Research*, <https://doi.org/10.1016/j.cretres.2023.105500>.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2023 Published by Elsevier Ltd.

**Credit Author Statement**

**Authors' contribution.** P.M.B. and R.V. conceived the study, determined and assessed morphological traits, discussed the results, wrote the manuscript and made the figures.

Journal Pre-proof

1 **A new species of *Pleuropholis* (Teleostei: Pleuropholidae) from the Upper Cretaceous**  
2 **Akrabou Formation of southeastern Morocco, with comments on the evolutionary history of**  
3 **the genus**

4

5 Paulo M. Brito<sup>a,b</sup>, Romain Vullo<sup>c,\*</sup>6 <sup>a</sup>*Departamento de Zoologia, Instituto de Biologia, Universidade do Estado do Rio de Janeiro,*  
7 *20559-900 Rio de Janeiro, Brazil*8 <sup>b</sup>*BOREA, UMR 8067, Département Adaptations du vivant, Muséum national d'Histoire naturelle,*  
9 *75231 Paris, France*10 <sup>c</sup>*Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France*

11

12 \*Corresponding author.

13 E-mail addresses: pbritopaleo@yahoo.com.br (P. M. Brito); romain.vullo@univ-rennes.fr (R. Vullo).

14

15 **ABSTRACT**

16 A pleuropholid fish is described for the first time from the Upper Cretaceous (Cenomanian)  
17 Akrabou Formation, Agoult locality, southeastern Morocco. The new material, consisting of a  
18 single complete specimen, is attributed to a new species, *Pleuropholis danielae*, and is diagnosed by  
19 its slender body shape, the absence of a leptolepid notch in the dentary, a broad maxilla, covering  
20 almost the entirely lower jaw, and flank scales with an unserrated posterior margin. This species  
21 represents the last known occurrence of Pleuropholidae, a group so far unknown from the Late  
22 Cretaceous.

23

24 *Keywords:*

25 Actinopterygii; Neopterygii; Pleuropholid fish; New taxon; Cenomanian; Africa.

26

27 **1. Introduction**

28

29 Pleuropholidae is an extinct family erected by Saint-Seine (1949), with a  
30 chronostratigraphic range of Middle Jurassic to Lower Cretaceous (Olive et al., 2022). Known from  
31 marine and continental strata in Europe (e.g. Egerton, 1858; Sauvage, 1883; Woodward, 1919;  
32 Biese, 1927; Bravi, 1988; Lambers, 1999; Bonde, 2004; Bravi et al., 2014; Schultze and Arratia  
33 2015; Poyato-Ariza and Martín-Abad, 2016; Olive et al., 2022), North America (Alvarado-Ortega  
34 and Brito, 2016), South America (Brito and Gallo, 2002; Chiappe et al., 1998; Giordano et al.,  
35 2018), Africa (Saint-Seine, 1955) and the Middle East (Janensch, 1925; Basse et al., 1954; El Hajj  
36 et al., 2021), pleuropholids are currently accepted as basal teleosts (Patterson, 1973, 1977; Pinna,  
37 1996) although their phylogenetic relationships within Teleostei are still unclear (López-Arbarello  
38 et al., 2008). Today, pleuropholids are represented by five genera (i.e. *Pleuropholis* Egerton, 1858,  
39 *Parapleuropholis* Saint-Seine, 1955, *Austropleuropholis* Saint-Seine, 1955, *Gondwanapleuropholis*  
40 Brito and Gallo, 2002, and *Zurupleuropholis* Giordano et al., 2018) and about 24 nominal species  
41 comprising relatively small (usually < 10 cm in total length), slender fishes, readily recognized by  
42 their small and upturned mouth, the numerous supra and infraorbital bones, and the presence of a  
43 single row of deep (i.e. dorsoventrally elongated) flank scales covering almost the whole side of the  
44 body (Brito and Gallo, 2002; López-Arbarello et al., 2008; Arratia, 2013).

45 In the present paper we describe a new species of *Pleuropholis* from the Akrabou  
46 Formation, which is clearly distinguishable from all the other known species. In addition to the  
47 inherent importance of this discovery, the presence of this taxon in the Upper Cretaceous of  
48 Morocco increases the distribution and diversity of pleuropholids and represents the youngest  
49 member of this family.

50 The specimen described here comes from the Plattenkalk Konservat-Lagerstätte of Agoult,  
51 located at the top of the Gara Sbâa hill, in the Kem Kem region of southeastern Morocco (Cavin et  
52 al., 2010: fig. 2; Martill et al., 2011: fig. 1). These transgressive laminated limestones (Gara Sbâa

53 Member) correspond to the base of the Akrabou Formation and assigned to the upper Cenomanian–  
54 ?lower Turonian (Cavin et al., 2010; Martill et al., 2011). This site has mainly yielded a rich and  
55 diverse actinopterygian assemblage (Cavin and Dutheil, 1999; Murray and Wilson, 2009, 2011,  
56 2013, 2014; Murray et al., 2013; Taverne and Capasso, 2021); the assemblage also includes  
57 ichnofossils, plants, worms, arthropods, echinoderms, elasmobranchs, and an undescribed lizard  
58 specimen (Garassino et al., 2008; Guinot et al., 2008; Martill et al., 2011; Engel et al., 2012;  
59 Krassilov and Bacchia, 2013; Vullo et al., 2016; Lamsdell et al., 2020). The Agoult fossil  
60 assemblage, consisting of both marine and terrestrial organisms, indicates that these laminated  
61 carbonates were deposited in a shallow marine coastal environment, most likely a quiet muddy  
62 lagoon (Garassino et al., 2008; Cavin et al., 2010; Martill et al., 2011; Ibrahim et al., 2020).

63

## 64 **2. Material and methods**

65

66 The specimen is cataloged in the collections of the Muséum d’Histoire naturelle de  
67 Marrakech, Morocco (MHNM), but is currently housed at the Muséum national d’Histoire naturelle  
68 of Paris, France (MNHN), for study, within an agreement between both museums. Photographs  
69 were taken using ultraviolet light, following the technique proposed by Tischlinger and Arratia  
70 (2013).

71 General anatomical terminology follows Brito (1997). For the anatomy of the caudal region,  
72 we used the terminology proposed by Arratia (2008).

73 The publication and the newly described species are registered in Zoobank. The LSID (Life  
74 Science Identifier) for the publication is: urn:lsid:zoobank.org:pub:93E130B3-AFBE-480F-BA42-  
75 9EA726DDD0E8; the LSID for the new species is: urn:lsid:zoobank.org:act:21F4D5D2-06E9-  
76 4846-8504-F43B230DABC6.

77

## 78 **3. Results**

79

80 *3.1. Systematic palaeontology*

81

82 Infraclass Teleostei Müller, 1846 (*sensu* Arratia, 1999)83 Order *incertae sedis*

84 Family Pleuropholidae Saint-Seine, 1949

85 Genus *Pleuropholis* Egerton, 185886 Type species: *P. attenuata* Egerton, 185887 ***Pleuropholis danielae*** sp. nov.

88 LSID: urn:lsid:zoobank.org:act:21F4D5D2-06E9-4846-8504-F43B230DABC6.

89 Figs. 1–5

90 *Diagnosis.* Large-sized pleuropholid differing from all other species of the genus by its slenderer  
91 body shape, the absence of a leptolepid notch in the dentary, a broad maxilla, covering almost the  
92 entirely lower jaw, and flank scales with an unserrated posterior margin.

93 *Holotype.* MHNM.KK.393, complete flattened specimen preserved in left lateral view.

94 *Etymology.* The specific epithet is dedicated to Daniela Vullo, the mother of one of us (R.V.), who  
95 passed away in May 2022, for her constant support.

96 *Type-locality and horizon.* The specimen comes from outcrops of the Gara Sbaa hill, near the  
97 locality of Agoult, in the Kem Kem region of southeastern Morocco. Gara Sbaa Member of the  
98 Akrabou Formation, Upper Cretaceous (Cenomanian).

99

100 *3.2. Description*

101

102 This is a large-sized *Pleuropholis* (115 mm in standard length and about 130 mm in total  
103 length) and by far one of the largest known pleuropholid fishes. The body is very elongated and  
104 slender (standard length/body height = 7.7) (Fig. 1). The deepest part of the body is constant

105 between the pectoral and the anal fin (body height = 15 mm). The head, including the opercular  
106 series, measures approximately 1/6 of the standard length. The dermal bones and scales are covered  
107 with ganoin.

108 The description of some skull elements is difficult due to poor preservation. Most of the  
109 skull bones are recognizable, but in some cases, some elements are damaged. This situation makes  
110 it difficult to interpret the shape of several bones, especially in the upper jaw.

111 Only a small fragment of the rostral is preserved and both its shape and suture with the  
112 posterior bones are not clearly discernible. The nasal is longer than wide, with its anterior half  
113 slightly thinner than the posterior one. The nasal overlaps the frontal posteriorly, and contacts the  
114 antorbital antero-laterally. The frontal lies just behind the nasal, and is the longest element of the  
115 dermal skull, having a length approximately three times that of the nasal. It extends posteriorly to  
116 the parietal and dermopterotic. The parietal is a well-developed bone, slightly longer than wide and  
117 having approximately half of the length of the frontal. The lateral border of the parietal is almost  
118 linear and contacts ventrally the dermopterotic. The dermopterotic is a subrectangular bone, placed  
119 lateral to the parietal and posterior to the frontal. This bone is directed backwards, narrowing at its  
120 most posterior part. The extrascapular is much smaller than the parietal. The occipital sensory canal  
121 passes through the mid-length of the extrascapulars. Anteriorly, the extrascapular partly overlaps  
122 the posterior margins of the parietal and the dermopterotic; posteriorly, it overlaps the anterior  
123 margin of the posttemporal, and laterally, it is in contact with the dorsal part of the opercle.

124 The orbital series is formed by one antorbital, the lacrimal, four infraorbitals, the  
125 dermosphenotic, and at least two supraorbitals (Figs. 2, 3). The antorbital is a subtriangular bone;  
126 this bone is positioned above the lacrimal. The lacrimal is an elongated bone with the infraorbital  
127 canal extending into it. Both antorbital and lacrimal form the anterior margin of the orbit. The first  
128 two infraorbitals border the orbit ventrally, followed by two covering the postorbital region of the  
129 orbit. The infraorbital canal extends in the middle part of the bones. The posterior infraorbitals  
130 border the anterior edge of the vertical limb of the preopercle. Although not very well preserved,



131 the dermosphenotic is a somewhat diamond-shaped bone that borders the posterior dorsal angle of  
132 the orbit. It is in contact with the anterior part of the dorsal edge of infraorbital 4. At least two  
133 supraorbitals are preserved, forming the dorsal margin of the orbit.

134 As a characteristic of the genus, the jaws are short, upturned, and positioned ahead of the  
135 orbit. The maxilla is poorly preserved with only few fragments present. However, these fragments  
136 point to an extremely broadened bone that covers almost entirely the lower jaws. It has a straight  
137 dorsal edge. The supramaxilla is not preserved.

138 The lower jaw seems to be somewhat triangular; the dentary and the angular bones are  
139 exposed laterally (Figs. 2, 3). The dentary is a short stout subtriangular bone that presents a rounded  
140 symphysis. The mandibular sensory canal extends along the ventral border of the bone. Contrary to  
141 the pattern found in *Pleuropholis decastroii* Bravi, 1988, from the Albian of Italy (cf. Taverne and  
142 Capasso, 2019) and *P. germinalis* Olive, Taverne and Brito, 2022 from the Barremian–Aptian of  
143 Belgium the new species does not present a leptolepid notch in the median-dorsal part of the  
144 dentary. Posteriorly, the dentary sutures with the angular. The jaw looks toothless.

145 The preopercle is an L-shaped bone in which the horizontal limb is slightly larger than the  
146 vertical limb. These limbs are placed perpendicular to each other (Figs. 2, 3). The preopercular  
147 canal is close and parallel to the ventral and dorsal borders of the bone. The opercular series consists  
148 of the large opercle, a subtriangular subopercle and an elongated interopercle. Only part a relatively  
149 narrow branchiostegal ray is preserved.

150 The posttemporal bone is somewhat oval and located behind the skull; the posterior edge  
151 overlies the dorsal end of the supracleithrum. The supracleithrum laterally overlaps the dorsal end  
152 of the cleithrum. The cleithrum has an elongated lower arm, less developed than the dorsal one. The  
153 pectoral fin is well developed and nine rays are preserved. It is positioned close to the ventral  
154 margin of the body, on the lower border between the flank scales and the scales immediately below.  
155 The pelvic fin is located at the level of the 15th transverse row of scales. Only four branched rays  
156 are preserved. No bones of the pelvic girdle are visible.

157 Both the dorsal and the anal fins are triangular and located posteriorly in the body, at the  
158 level of the 29th and 26th transversal row of scales, respectively (Figs. 1, 4). The dorsal fin presents  
159 two short, unsegmented procurrent ray followed by seven principal rays. The first ray is segmented,  
160 longer and thicker than the preceding procurrent rays. The longest ray of the dorsal fin is the second  
161 principal ray, which is segmented and branched. Elongated fringing fulcra are placed in the anterior  
162 margin of the first and the second principal rays.

163 The anal fin is larger than the dorsal fin. Procurrent rays are not preserved in the specimen  
164 that has about 13 branched principal rays. The first and the second rays seem to have the same  
165 length. The main leading ray is preceded by numerous fringing fulcra. After the third ray, they  
166 decrease in size and width.

167 The vertebrae as well as the caudal endoskeleton are completely hidden by the scales and  
168 thus not observable in the studied specimen. The caudal fin is almost completely preserved,  
169 although some few elements are broken.

170 The caudal fin has a forked outline. As in other species of the genus (e.g. Egerton 1858: pl.  
171 7, fig. 4; Woodward, 1919: text-fig. 36; Taverne and Capasso, 2019: fig. 8), the upper lobe is  
172 slightly longer than the lower lobe (Figs. 1, 5). There are about fourteen epaxial basal fulcra, a  
173 series of elongated, small, epaxial fringing fulcra, 15 to 16 principal rays, a series of hypaxial  
174 fringing fulcra, segmented procurrent rays, and two hypaxial basal fulcra.

175 The epaxial basal fulcra are elongated, unsegmented leaf-like elements, partially covering  
176 the next fulcra. The epaxial fringing fulcra are associated with the first and second principal rays.  
177 The first principal ray is shorter than the following segmented-and-branched principal ray. Both,  
178 together form the dorsal leading margin of the fin.

179 In the lower lobe, the hypaxial procurrent rays are segmented with their terminal segment  
180 resembling the fringing fulcra; fringing fulcra extend along the ventral margin of the last principal  
181 rays. As in the upper lobe, the last principal ray is shorter than the following segmented-and-  
182 branched principal ray (Fig. 5).

183           There are at least 39 lateral rows of thick, ganoid-type scales, from the supracleithrum to the  
184 base of the caudal fin (Fig. 5). These scales have different shapes according to the region of the  
185 body. The flank scales are deeper than long, progressively decreasing in size posteriorly and  
186 becoming diamond-shaped in the caudal region. They present no serrations in the posterior edge.  
187 Dorsal to the flank scales there are two rows of small scales. Ventral to the flank scales, there are  
188 three rows of small, rectangular scales.

189

#### 190 **4. Discussion**

191

192           *Pleuropholis danielae* sp. nov. possesses synapomorphies of the family Pleuropholidae,  
193 including: the presence of a single row of deepened ganoid scales covering almost the whole side of  
194 the body, an edentulous mouth, and a complete orbital series formed by infraorbital and supraorbital  
195 bones (cf. Saint-Seine, 1949; Brito and Gallo, 2002; Olive et al., 2022).

196           The presence of an upturned maxilla and a jaw articulation lying anterior to the orbit (cf.  
197 Woodward, 1919; Saint-Seine, 1949; Patterson, 1973; Bravi, 1988; Alvarado-Ortega and Brito,  
198 2016; Taverne and Capasso, 2019; Olive et al., 2022) places the new taxon in the genus  
199 *Pleuropholis*.

200           One of the biggest problems concerning the genus *Pleuropholis* is the validity of most of its  
201 contained species, especially those from the Jurassic. Therefore, a comprehensive revision of all  
202 these taxa would be necessary, especially because many of them lack any autapomorphies to sustain  
203 their taxonomic status, or they are based on body proportions from imperfect or distorted specimens  
204 (e.g. Patterson, 1973; Alvarado-Ortega and Brito, 2016; Taverne and Capasso, 2019; Olive et al.,  
205 2022).

206           Despite these problems, *P. danielae* sp. nov. clearly differs from the other species of  
207 *Pleuropholis* by its considerably more slender body shape. The absence of a leptolepid notch in the  
208 dentary distinguishes *P. danielae* n. sp from *P. jamotti* Saint-Seine, 1955 (a species, like *P. lannoyi*

209 from the same locality, that needs taxonomic revision and does not appear to belong to the genus  
210 *Pleuropholis*), *P. decastroi* Bravi, 1988, and *P. germinalis* Olive, Taverne and Brito, 2022.  
211 Although not well preserved, the maxilla of *P. danielae* sp. nov. seems to be broad, almost entirely  
212 covering the lower jaw, a condition also known in *P. thiollieri* Sauvage, 1883, *P. decastroi* and *P.*  
213 *cisnerosorum* Alvarado-Ortega and Brito, 2016. Finally, flank scales with an unserrated posterior  
214 margin are known in *P. germinalis*, *P. longicauda* Egerton, 1858, *P. formosa* Woodward, 1919, *P.*  
215 *attenuata* Egerton, 1858, and *P. crassicauda* Egerton, 1858.

216 From a palaeobiogeographical point of view, the evolution and distribution of *Pleuropholis*  
217 appear to have been centered in the Tethyan realm (Fig. 6). So far, the only unambiguous Middle  
218 Jurassic occurrence of *Pleuropholis* is from the Bajocian–Bathonian of southern Italy (Bravi et al.,  
219 2014); this single occurrence, representing the oldest known record of *Pleuropholis*, is indicative of  
220 a low taxic diversity at that time and probably reflects a restricted distribution at the beginning of  
221 the evolutionary history of the lineage (neoendemism; see Cowman et al., 2017). The genus  
222 *Pleuropholis* reached its apparent highest diversity during the Late Jurassic–earliest Cretaceous (an  
223 observation possibly partly due to a preservational bias; see Cavin, 2010), resulting in several  
224 European species described from Cerin and the Meuse department in France (Sauvage, 1883; Saint-  
225 Seine, 1949), Bavaria in Germany (Egerton, 1858; Biese, 1927), and the English Purbeck and  
226 coeval beds in Denmark (Egerton, 1858; Woodward, 1919; Bonde, 2004). Two additional species,  
227 *P. cisnerosorum* from the Kimmeridgian of southern Mexico (Alvarado-Ortega and Brito, 2016)  
228 and *P. bassei* Lehman in Basse et al., 1954 from the Tithonian–Berriasian of Yemen (Basse et al.,  
229 1954), indicate westward dispersal to the Hispanic Corridor and eastward dispersal to the Arabian  
230 platform, respectively; furthermore, pending a revision of *P. jamotti* and *P. lannoyi* Saint-Seine,  
231 1955, the genus also occurs in Upper Jurassic freshwater deposits of the Democratic Republic of  
232 Congo (Saint-Seine, 1955; Caillaud et al., 2017). During the Early Cretaceous, the genus  
233 *Pleuropholis* appears to have been decreasing in diversity and less widely distributed; it is known  
234 from five localities in the Middle East and Western Europe: the Barremian of Lebanon (Janensch,

235 1924; El Hajj et al., 2021), the Barremian of El Montsec and Las Hoyas in eastern Spain (Wenz,  
236 1968; Sanz et al., 1988; Poyato-Ariza and Martín-Abad, 2016), the Barremian–Aptian of Belgium  
237 (Olive et al., 2022), and the Albian of southern Italy (Bravi, 1988); with the exception of the latter,  
238 all these occurrences are from continental localities, indicating that *Pleuropholis* was a euryhaline  
239 genus that colonized brackish and freshwater environments at many times between the Late Jurassic  
240 and the middle Early Cretaceous. The present study reports the first Upper Cretaceous occurrence  
241 of *Pleuropholis*; therefore, *P. danielae* sp. nov. from the Cenomanian of Agoult, southeastern  
242 Morocco, represents the youngest known member of the genus and the last known occurrence of  
243 pleuropholid fishes (Fig. 6). The narrowly distributed species *P. decastro* (Albian of Italy) and *P.*  
244 *danielae* sp. nov. suggest a range contraction for this formerly widespread genus, with the  
245 Mediterranean Tethys as a center of survival (paleoendemism; see Cowman et al., 2017). The new  
246 discovery extends the stratigraphic range of this group by about 15 million years and makes  
247 *Pleuropholis* one of the most temporally long-lived actinopterygian genera of all time, with a fossil  
248 record spanning ~75 million years. Based on 1108 time ranges calculated from Cavin et al.’s  
249 (2021a) database, Cavin et al. (2021b: fig. 7) found that the average time duration of the ray-finned  
250 fish genera having their first occurrence in the Devonian–Palaeocene interval is 13.3 million years  
251 all environments combined, with only a dozen genera having a longer range than that of  
252 *Pleuropholis*.

253 The discovery of *P. danielae* sp. nov. confirms that several relictual lineages of fishes that  
254 had been flourishing during the Late Jurassic persisted until the early Late Cretaceous (a period  
255 during which they were probably severely affected by competition with diversifying modern  
256 teleosts; Guinot and Cavin, 2016), and apparently became extinct at the end of the Cenomanian,  
257 possibly in relation to the Cenomanian–Turonian Boundary Event (CTBE). These forms include  
258 some holosteans such as the ionoscopiforms *Spathiurus* (Ionoscopidae) and *Petalopteryx*  
259 (?Ophiopsiellidae) from Lebanon and *Agoultichthys* (?Ophiopseliidae) from Morocco (Ebert, 2018;  
260 El Hossny et al., 2020), the probable ionoscopiform *Aphanepygus* (?Ophiopsiellidae) from Croatia

261 and Lebanon (Bartram, 1977), and some basal teleosts such as the newly described *Pleuropholis*  
262 (Pleuropholidae) species from Morocco. It is likely that these declining groups, known from very  
263 few specimens in Lebanese, Moroccan, and Croatian Cenomanian Konservat-Lagerstätten, were  
264 relatively rare in early Late Cretaceous (pre-CTBE) fish faunas and palaeoendemic, i.e.  
265 geographically restricted to small areas of the Mediterranean Tethys (Levant Platform, Atlas Gulf  
266 of the Saharan Platform, Apulian terrane). This suggests that the apparent absence in Cenomanian  
267 strata of other groups of ray-finned fishes with last known occurrences being from Albian deposits  
268 (e.g. macrosemiids and callipurbeckiid semionotiforms) could be due to problems with the  
269 detection of rare species in the fossil record (rarity bias), especially in undersampled Plattenkalk  
270 localities and understudied areas (collecting bias).

271

## 272 **5. Conclusions**

273

274 The Cenomanian beds of the Akrabou Formation of southeastern Morocco yielded a single  
275 specimen of pleuropholid fish, which is recognized as belonging to a new species of *Pleuropholis*.  
276 Interestingly, *P. danielae* sp. nov. is the first Late Cretaceous Pleuropholidae and thus represents  
277 the youngest known member of this family of basal teleosts. This discovery contributes to our  
278 understanding of the mid-Cretaceous turnover of marine fish faunas, which is a significant  
279 biological event characterized by the apparent extinction of relictual lineages such as pleuropholids  
280 and the diversification of modern groups such as neoteleosts.

281

## 282 **Acknowledgements**

283

284 We wish to express our gratitude to D. Martill and D. Dutheil for their comments on the  
285 manuscript and to L. Cazes and P. Loubry for the photographs. We are grateful to N.-E. Jalil for  
286 providing a MHNM collection number. We also thank E. Koutsoukos as well as L. Cavin and an

287 anonymous reviewer for their helpful comments that improved the manuscript. P.M.B. was partially  
288 supported by the CNPq (#305118/2021-8) and FAPERJ (#E-26/201.172/2022).

289

## 290 **References**

291

292 Alvarado-Ortega, J., Brito, P.M., 2016. A Jurassic pleuropholid fish (Teleostei, Pleuropholidae) in  
293 the Tethys Sea domain of North America. *J. Vert. Paleontol.* 36, e1201767.

294 Arratia, G., 1999. The monophyly of Teleostei and stem group teleosts. In: Arratia, G., Schultze,  
295 H.-P. (Eds.), *Mesozoic Fishes 2 – Systematics and Fossil Record*. Verlag Dr. Friedrich Pfeil,  
296 München, pp. 265–334.

297 Arratia, G., 2008. Actinopterygian postcranial skeleton with special reference to the diversity of fin  
298 ray elements, and the problem of identifying homologies. In: Arratia, G., Schultze, H.-P.,  
299 Wilson, M.V.H. (Eds.), *Mesozoic Fishes 4 – Homology and Phylogeny*. Verlag Dr. Friedrich  
300 Pfeil, München, pp. 49–101.

301 Arratia, G., 2013. Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes  
302 (Actinopterygii, Teleostei). *Soc. Vert. Paleontol. Mem.* 13, *J. Vert. Paleontol.* 33 (suppl. to 6),  
303 1–138.

304 Bartram, A.W.H., 1977. The Macrosemiidae, a Mesozoic family of holostean fishes. *Bull. Brit.*  
305 *Mus. (Nat. Hist.), Geol.* 29, 137–234.

306 Basse, E., Karrenberg, H., Lehmann, J.-P., Alloiteau, J., Lefranc, J.-P., 1954. Fossiles du Jurassique  
307 supérieur et des "Grès de Nubie" de la région de Sana (Yémen). *Bull. Soc. Géol. Fr., Sér.* 6, 4,  
308 655–688.

309 Biese, W., 1927. Über einige Pholidophoriden aus den lithographischen Schieferen Bayerns. *N. Jb.*  
310 *Min. Beilage, Abt.* 58, 50–100.

311 Bonde, N., 2004. An Early Cretaceous (Ryazanian) fauna of "Purbeck-Wealden type" at Robbedale,  
312 Bornholm, Denmark. In: Arratia, G., Tintori, A. (Eds.), *Mesozoic Fishes 3 – Systematics*,

- 313 Paleoenvironments and Biodiversity. Verlag Dr. Friedrich Pfeil, München, pp. 507–528.
- 314 Bravi, S., 1988. Contributo allo studio del giacimento ad ittioliti di Pietraraja (Benevento). I.
- 315 *Pleuropholis decastroi* n. sp. (Pisces, Actinopterygii, Pholidophoriformes). Mem. Soc. Geol.
- 316 Ital. 41, 575–586.
- 317 Bravi, S., Garassino, A., Bartiromo, A., Audo, D., Charbonnier, S., Schweigert, G., Thévenard, F.,
- 318 Longobardi, C., 2014. Middle Jurassic Monte Fallano Plattenkalk (Campania, southern Italy):
- 319 first report on terrestrial plants, decapod crustaceans and fishes. N. Jb. Geol. Paläont. Abh. 272,
- 320 79–107.
- 321 Brito, P.M., 1997. Révision des Aspidorhynchidae (Pisces, Actinopterygii) du Mésozoïque :
- 322 ostéologie, relations phylogénétiques, données environnementales et biogéographiques.
- 323 Geodiversitas 19, 681–772.
- 324 Brito, P.M., Gallo, V., 2002. A new pleuropholid, *Gondwanapleuropholis longimaxillaris* n. g., n.
- 325 sp. (Actinopterygii: Teleostei) from the Jurassic of north east Brazil. C. R. Palevol 1, 697–703.
- 326 Cavin, L., Dutheil, D.B., 1999. A new Cenomanian ichthyofauna from southeastern Morocco and
- 327 its relationships with other early Late Cretaceous Moroccan faunas. Geol. Mijnb. 78, 261–266.
- 328 Cavin, L., Tong, H., Boudad, L., Meister, C., Piuz, A., Tabouelle, J., Aarab, M., Amiot, R.,
- 329 Buffetaut, E., Dyke, G., Hua, S., Le Lœuff, J., 2010. Vertebrate assemblages from the early
- 330 Late Cretaceous of southeastern Morocco: an overview. J. Afr. Earth Sci. 57, 391–412.
- 331 Cavin, L., 2010. The Late Jurassic ray-finned fish peak of diversity: biological radiation or
- 332 preservational bias? In: Nelson, J.S., Schultze, H.-P., Wilson, M.V.H. (Eds.), Origin and
- 333 Phylogenetic Interrelationships of Teleosts. Verlag Dr. Friedrich Pfeil, München, pp. 111–121.
- 334 Cavin, L., Piuz, A., Ferrante, C., Guinot, G., 2021a. Giant Mesozoic coelacanths (Osteichthyes,
- 335 Actinistia) reveal high body size disparity decoupled from taxic diversity. Sci. Rep. 11, 11812.
- 336 Cavin, L., Toriño, P., Van Vranken, N., Carter, B., Polcyn, M.J., Winkler, D., 2021b. The first Late
- 337 Cretaceous mawsoniid coelacanth (Sarcopterygii: Actinistia) from North America: Evidence of
- 338 a lineage of extinct ‘living fossils’. PLoS ONE 16, e0259292.



- 339 Chiappe, L., Rivarola, D., Cione, A.L., Fregenal-Martínez, M., Sozzi, H., Buatois, L., Gallego, O.,  
340 Laza, J., Romero, E., López-Arbarello, A., Buscalioni, A., Marsicano, C., Adamonis, C.,  
341 Ortega, F., McGehee, S., Di Iorio, O., 1998. Biotic association and palaeoenvironmental  
342 reconstruction of the “Loma del *Pterodaustro*” fossil site (Early Cretaceous, Argentina).  
343 *Geobios* 31, 349–369.
- 344 Cowman, P.F., Parravicini, V., Kulbicki, M., Floeter, S.R., 2017. The biogeography of tropical reef  
345 fishes: endemism and provinciality through time. *Biol. Rev.* 92, 2112–2130.
- 346 Ebert, M., 2018. *Cerinichthys koelblae*, gen. et sp. nov., from the Upper Jurassic of Cerin, France,  
347 and its phylogenetic setting, leading to a reassessment of the phylogenetic relationships of  
348 Halecomorphi (Actinopterygii). *J. Vert. Paleontol.* 38, e1420071.
- 349 El Hajj, L., Baudin, F., Gèze, R., Cavin, L., Dejax, J., Garcia, G., Horne, D.J., Maksoud, S., Otero,  
350 O., Azar, D., 2021. *Dysodiles* from the lower Barremian of Lebanon: Insights on the fossil  
351 assemblages and the depositional environment reconstruction. *Cret. Res.* 120, 104732.
- 352 El Hossny, T., Maksoud, S., Azar, D., Abi Saad, P., Cavin, L., 2020. *Spathiurus dorsalis* Davis,  
353 1887, from the Upper Cretaceous of Haqel, Lebanon, and the evolutionary history of  
354 *Ionoscopiformes*. *Cret. Res.* 120, 104619.
- 355 Egerton, P.M.G., 1858. *British fossils – Pleuropholis*. Figures and Descriptions Illustrative of  
356 *British Organic Remains*. *Mem. Geol. Surv. U.K.*, Dec. 9, Pl. 7, 1–7.
- 357 Engel, M.S., McKellar, R.C., Gibb, S., Chatterton, B.D.E., 2012. A new Cenomanian–Turonian  
358 (Late Cretaceous) insect assemblage from southeastern Morocco. *Cret. Res.* 35, 88–93.
- 359 Garassino, A., De Angeli, A., Pasini, G., 2008. New decapod assemblage from the Upper  
360 Cretaceous (Cenomanian–Turonian) of Gara Sbaa, southeastern Morocco. *Atti Soc. Ital. Sci.*  
361 *Nat. Mus. Civ. Stor. Nat. Milano* 149, 37–67.
- 362 Giordano, P.G., Succar, C.A., Codorníu, L., Cione, A.L., Arratia, G., 2018. *Zurupleuropholis* gen.  
363 nov. (Teleostei, Albian, Argentina), first pleuropholids from the Cretaceous of South America.  
364 *Cret. Res.* 84, 223–239.

- 365 Guinot, D., De Angeli, A., Garassino, A., 2008. Marocarcinidae, a new eubrachyuran family, and  
366 *Marocarcinus pasinii* n. gen., n. sp. from the Upper Cretaceous (Cenomanian–Turonian) of  
367 Gara Sbaa, southeastern Morocco (Crustacea, Decapoda, Brachyura). *Atti Soc. Ital. Sci. Nat.*  
368 *Mus. Civ. Stor. Nat. Milano* 149, 25–36.
- 369 Guinot, G., Cavin, L., 2016. ‘Fish’ (Actinopterygii and Elasmobranchii) diversification patterns  
370 through deep time. *Biol. Rev.* 91, 950–981.
- 371 Ibrahim, N., Sereno, P.C., Varricchio, D.J., Martill, D.M., Dutheil, D.B., Unwin, D.M., Baidder, L.,  
372 Larsson, H.C.E., Zouhri, S., Kaoukaya, A., 2020. Geology and paleontology of the Upper  
373 Cretaceous Kem Kem Group of eastern Morocco. *ZooKeys* 928, 1–216.
- 374 Janensch, W., 1925. Fische aus dem Dysodil des Wealden vom Libanon. *Z. Dtsch. Geol. Ges.* 76,  
375 54–59.
- 376 Krassilov, V., Bacchia, F., 2013. New Cenomanian florule and a leaf mine from southeastern  
377 Morocco: palaeoecological and climatological inferences. *Cret. Res.* 40, 218–226.
- 378 Lambers, P.H., 1999. The actinopterygian fish fauna of the Late Kimmeridgian and Early Tithonian  
379 ‘Plattenkalke’ near Solnhofen (Bavaria, Germany): state of the art. *Geol. Mijnb.* 78, 215–229.
- 380 Lamsdell, J., Tashman, G., Pasini, A., Garassino, A., 2020. A new limulid (Chelicerata,  
381 Xiphosurida) from the Late Cretaceous (Cenomanian–Turonian) of Gara Sbaa, southeast  
382 Morocco. *Cret. Res.* 106, 104230.
- 383 López-Arbarello, A., Rauhut, O.W.M., Moser, K., 2008. Jurassic fishes of Gondwana. *Rev. Assoc.*  
384 *Geol. Argent.* 63, 586–612.
- 385 Martill, D.M., Ibrahim, N., Brito, P.M., Baidder, L., Zouhri, S., Loveridge, R., Naish, D., Hing, R.,  
386 2011. A new Plattenkalk Konservat Lagerstätte in the Upper Cretaceous of Gara Sbaa, south-  
387 eastern Morocco. *Cret. Res.* 32, 433–446.
- 388 Müller, J., 1846. Über den Bau und die Grenzen der Ganoiden und über das natürliche System der  
389 Fische. *Abh. Königl. Akad. Wiss. Berlin* 1844, 117–216.
- 390 Murray, A.M., Wilson, M.V.H., 2009. A new Late Cretaceous macrosemiid fish (Neopterygii,

- 391 Halecostomi) from Morocco, with temporal and geographical range extensions for the family.  
392 Palaeontology 52, 429–440.
- 393 Murray, A.M., Wilson, M.V.H., 2011. A new species of *Sorbinichthys* (Teleostei: Clupeomorpha:  
394 Ellimmichthyiformes) from the Late Cretaceous of Morocco. Can. J. Earth Sci. 48, 1–9.
- 395 Murray, A.M., Wilson, M.V.H., 2013. Two new paraclupeid fishes (Clupeomorpha:  
396 Ellimmichthyiformes) from the Upper Cretaceous of Morocco. In: Arratia, G., Schultze, H.-P.,  
397 Wilson, M.V.H. (Eds.), Mesozoic Fishes 5 – Global Diversity and Evolution. Verlag Dr.  
398 Friedrich Pfeil, München, pp. 267–290.
- 399 Murray, A.M., Wilson, M.V.H., 2014. Four new basal acanthomorph fishes from the Late  
400 Cretaceous of Morocco. J. Vert. Paleontol. 34, 34–48.
- 401 Murray, A.M., Wilson, M.V.H., Gibb, S., Chatterton, B.D.E., 2013. Additions to the Late  
402 Cretaceous (Cenomanian/Turonian) actinopterygian fauna from the Agoult locality, Akrabou  
403 Formation, Morocco, and comments on the palaeoenvironment. In: Arratia, G., Schultze, H.-P.,  
404 Wilson, M.V.H. (Eds.), Mesozoic Fishes 5 – Global Diversity and Evolution. Verlag Dr.  
405 Friedrich Pfeil, München, pp. 525–548.
- 406 Olive, S., Taverne, L., Brito, P.M., 2022. *Pleuropholis germinalis* n. sp., a new Pleuropholidae  
407 (Neopterygii, Teleostei) from the Early Cretaceous of Bernissart, Belgium. Geodiversitas 44,  
408 505–514.
- 409 Patterson, C., 1973. Interrelationships of holosteans. In: Greenwood, P.H., Miles, R.S., Patterson,  
410 C. (Eds.), Interrelationships of Fishes. Academic Press, London, pp. 233–305.
- 411 Patterson, C., 1977. The contribution of paleontology to teleostean phylogeny. In: Hecht, M.K.,  
412 Goody, P.C., Hecht, B.M. (Eds.), Major Patterns in Vertebrate Evolution. Plenum Press, New  
413 York, pp. 579–643.
- 414 Pinna, M.C.C. de, 1996. Teleostean monophyly. In: Stiassny, M.L.J., Parenti, L.R., Johnson, G.D.  
415 (Eds.), Interrelationships of Fishes. Academic Press, San Diego, pp. 147–162.
- 416 Poyato-Ariza, F.J., Martín-Abad, H. 2016. Osteichthyan fishes. In: Poyato-Ariza, F.J., Buscalioni,

- 417 A.D. (Eds.), *Las Hoyas: A Cretaceous Wetland*. Verlag Dr. Friedrich Pfeil, München, pp. 114–  
418 132.
- 419 Saint-Seine, P. de, 1949. Les poissons des calcaires lithographiques de Cerin (Ain). *Nouv. Archs.*  
420 *Mus. Hist. Nat. Lyon* 2, 3–357.
- 421 Saint-Seine, P. de, 1955. Poissons fossiles de l'étage de Stanleyville (Congo Belge) – Première  
422 partie : La faune des argilites et schistes bitumineux. *Ann. Mus. R. Congo Belge, Sér. in-8, Sci.*  
423 *Géol.* 14, 1–126.
- 424 Sanz, J.L., Wenz, S., Yebenes, A., Estes, R., Martinez-Delclos, X., Jimenez-Fuentes, E., Diéguez,  
425 C., Buscalioni, A.D., Barbadillo, L.J., Via, L., 1988. An Early Cretaceous faunal and floral  
426 continental assemblage: Las Hoyas fossil site (Cuenca, Spain). *Geobios* 21, 611–635.
- 427 Sauvage, H.E., 1883. Note sur le genre *Pleuropholis*. *Bull. Soc. Géol. Fr., Sér. 3*, 11, 496–503.
- 428 Schultze, H.-P., Arratia, G., 2015. Knochenfische im weiteren Sinne (Osteichthyes oder  
429 Osteognathostomata). In: Arratia, G., Schultze, H.-P., Tischlinger, H., Viehl, G. (Eds.),  
430 Solnhofen – Ein Fenster in die Jurazeit 2. Verlag Dr. Friedrich Pfeil, München, pp. 360–409.
- 431 Taverne, L., Capasso, L., 2019. New data on *Pleuropholis decastroi* (Teleostei, Pleuropholidae), a  
432 “pholidophoriform” fish from the Lower Cretaceous of the Eurafrikan Mesogea. *Geo-Eco-Trop*  
433 43, 35–51.
- 434 Tischlinger, H., Arratia, G., 2013. Ultraviolet light as a tool for investigating Mesozoic fishes, with  
435 a focus on the ichthyofauna of the Solnhofen archipelago. In: Arratia, G., Schultze, H.-P.,  
436 Wilson, M.V.H. (Eds.), *Mesozoic Fishes 5 – Global Diversity and Evolution*. Verlag Dr.  
437 Friedrich Pfeil, München, pp. 549–560.
- 438 Vullo, R., Guinot, G., Barbe, G., 2016. The first articulated specimen of the Cretaceous mackerel  
439 shark *Haimirichia amonensis* gen. nov. (Haimirichiidae fam. nov.) reveals a novel  
440 ecomorphological adaptation within the Lamniformes (Elasmobranchii). *J. Syst. Palaeontol.* 14,  
441 1003–1024.
- 442 Wenz, S., 1968. Note préliminaire sur la faune ichthyologique du Jurassique supérieur du Montsech

- 443 (Espagne). Bull. Soc. Géol. Fr., Sér. 7, 10, 116–119.
- 444 Woodward, A.S., 1919. The fossil fishes of the English Wealden and Purbeck formations. Part III.
- 445 Monogr. Palaeontogr. Soc. 71, Issue 340, 105–148.
- 446

Journal Pre-proof

447 **Figure Captions**

448

449 **Fig. 1.** *Pleuropholis danielae* sp. nov., holotype MHNM.KK.393 photographed under natural light  
450 (A) and UV light (B), in left lateral view. Scale bar equals 10 mm.

451

452 **Fig. 2.** *Pleuropholis danielae* sp. nov., holotype MHNM.KK.393, detail of the head region  
453 (photograph under UV light) (A) and interpretative line drawing (B). Abbreviations: Ang, angular;  
454 Ao, antorbital; Cl, cleithrum; De, dentary; Dsp, dermosphenotic; Dpt, dermopterotic; Ex,  
455 extrascapular; Fr, frontal; Io, infraorbital; Iop, interopercle; La, lacrimal; Mx, maxilla; Na, nasal;  
456 Op, opercle; Pa, parietal; Pmx, premaxilla; Pop, preopercle; Pt, posttemporal; Ro, rostral; Scl,  
457 supracleithrum; So, supraorbital; Sop, subopercle. Scale bar equals 10 mm.

458

459 **Fig. 3.** Reconstruction of the skull of *Pleuropholis danielae* sp. nov. Abbreviations: Ang, angular;  
460 Ao, antorbital; De, dentary; Dsp, dermosphenotic; Dpt, dermopterotic; Ex, extrascapular; Fr,  
461 frontal; Io, infraorbital; Iop, interopercle; La, lacrimal; Mx, maxilla; Na, nasal; Op, opercle; Pa,  
462 parietal; Pmx, premaxilla; Pop, preopercle; Pt, posttemporal; Ro, rostral; Smx, supramaxilla; So,  
463 supraorbital; Sop, subopercle. Scale bar equals 10 mm.

464

465 **Fig. 4.** *Pleuropholis danielae* sp. nov., holotype MHNM.KK.393, detail of the dorsal and anal fins  
466 (photograph under UV light). Scale bar equals 10 mm.

467

468 **Fig. 5.** *Pleuropholis danielae* sp. nov., holotype MHNM.KK.393, detail of the caudal region  
469 (photograph under UV light) (A) and interpretative line drawing (B). Abbreviations: 1st PR, first  
470 principal ray; ebfu, epaxial basal fulcra; f.f, fringing fulcra; hbfu, hypaxial basal fulcra; l. PR, last  
471 principal ray; v.pr, ventral procurrent rays. Scale bar equals 10 mm.

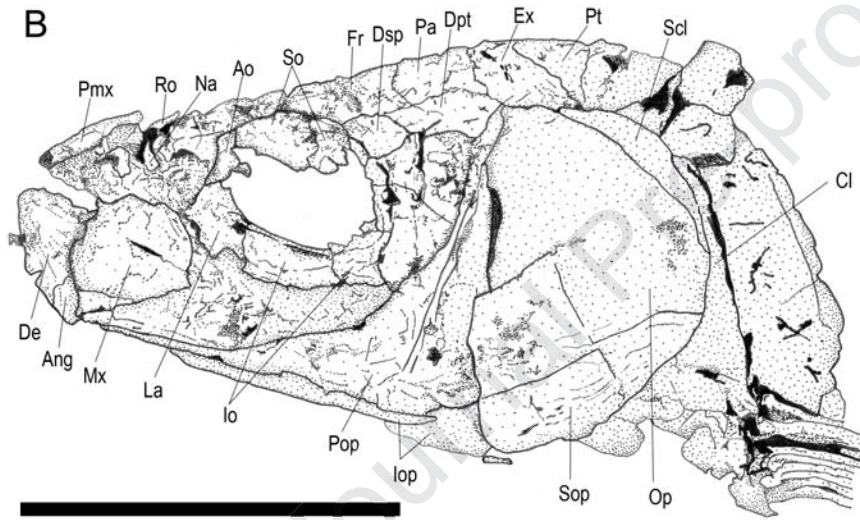
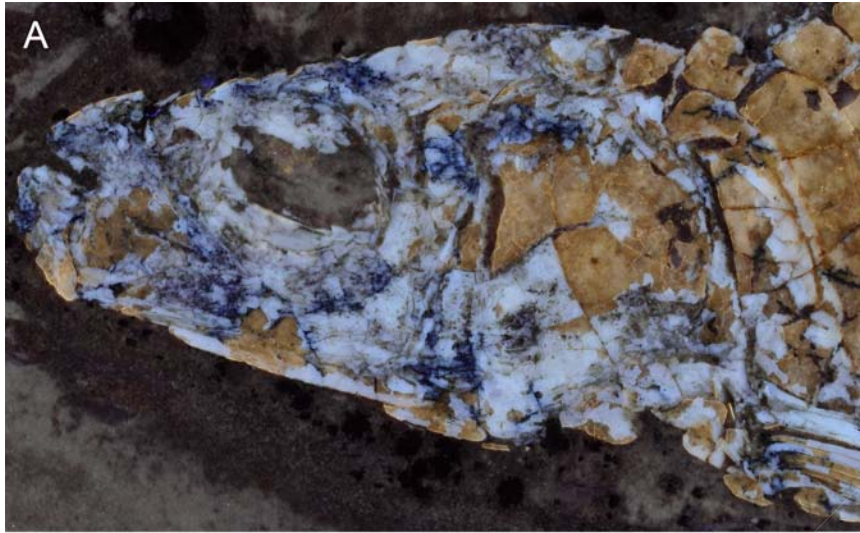
472

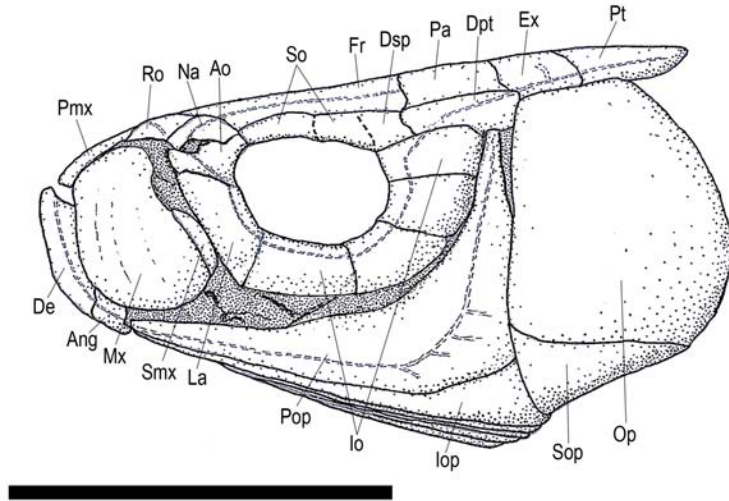
473 **Fig. 6.** Simplified time-scaled distribution of the genus *Pleuropholis*, showing the various known  
474 occurrences from the Middle Jurassic to the early Late Cretaceous (see text for details and  
475 references). Some nominal species (i.e. *P. lannoyi* from the Kimmeridgian–Tithonian of the  
476 Democratic Republic of Congo, *P. egertoni* and *P. obtusirostris* from the Kimmeridgian of France,  
477 *P. pompecki* and *P. wagneri* from the Kimmeridgian–Tithonian of Germany, and *P. crassicauda*  
478 and *P. longicauda* from the Berriasian of England), co-occurring with some of those presented here,  
479 are not included.

Journal Pre-proof

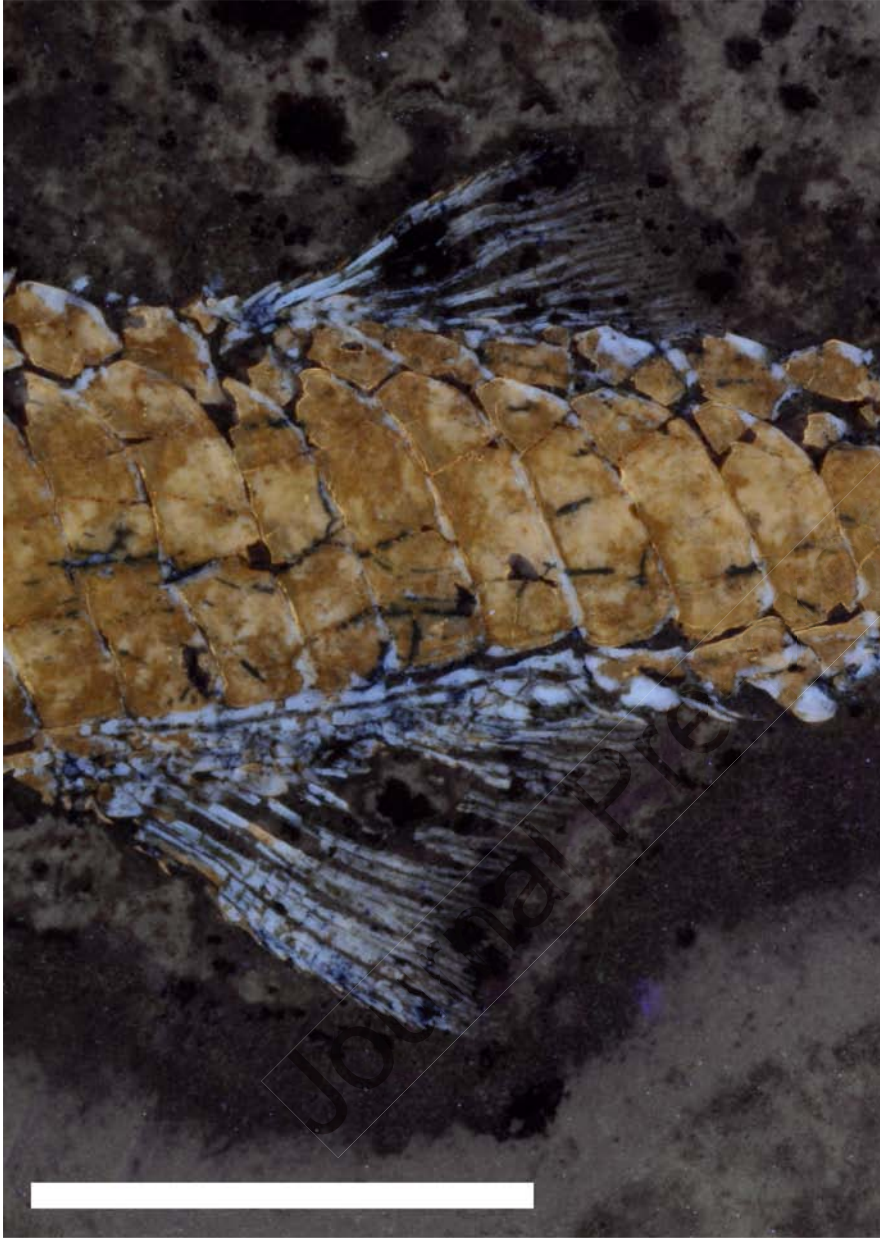


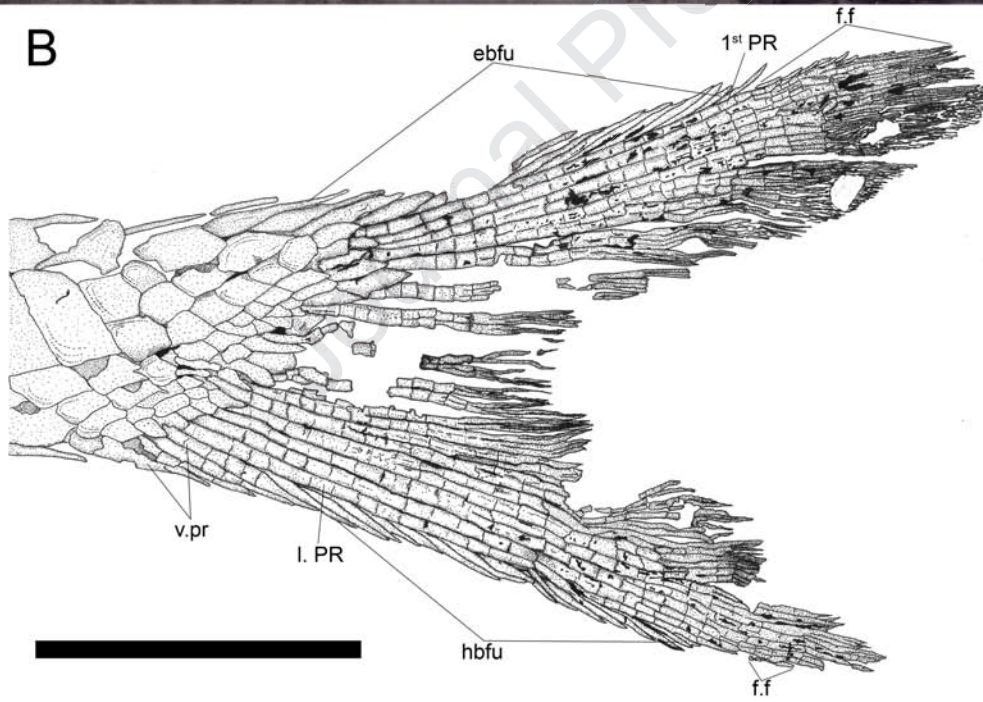
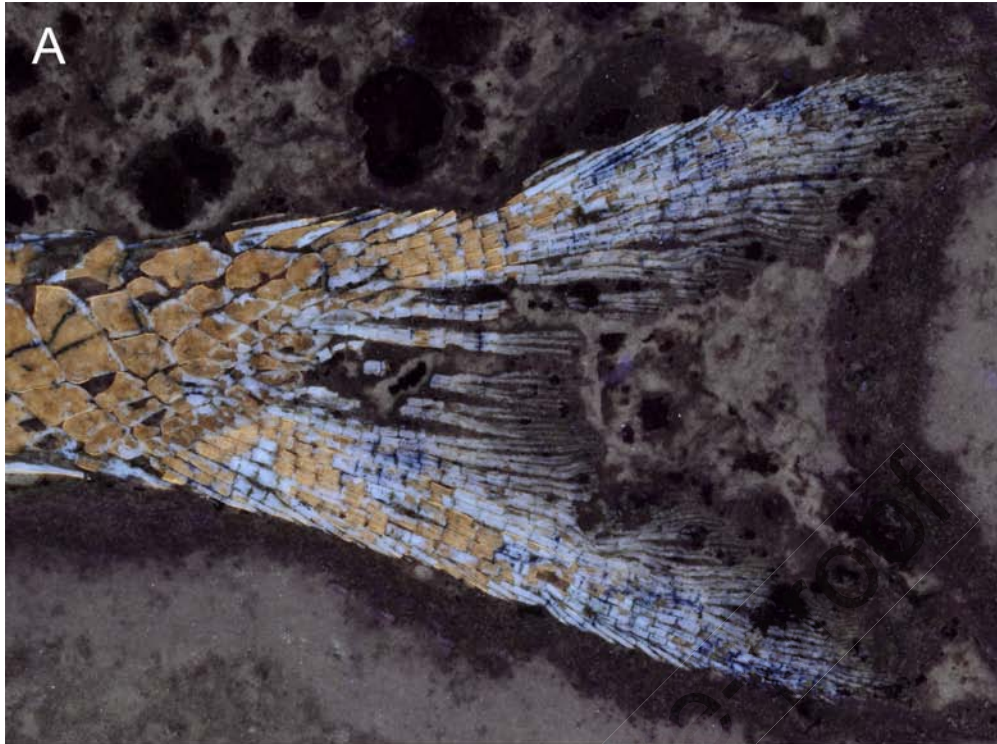


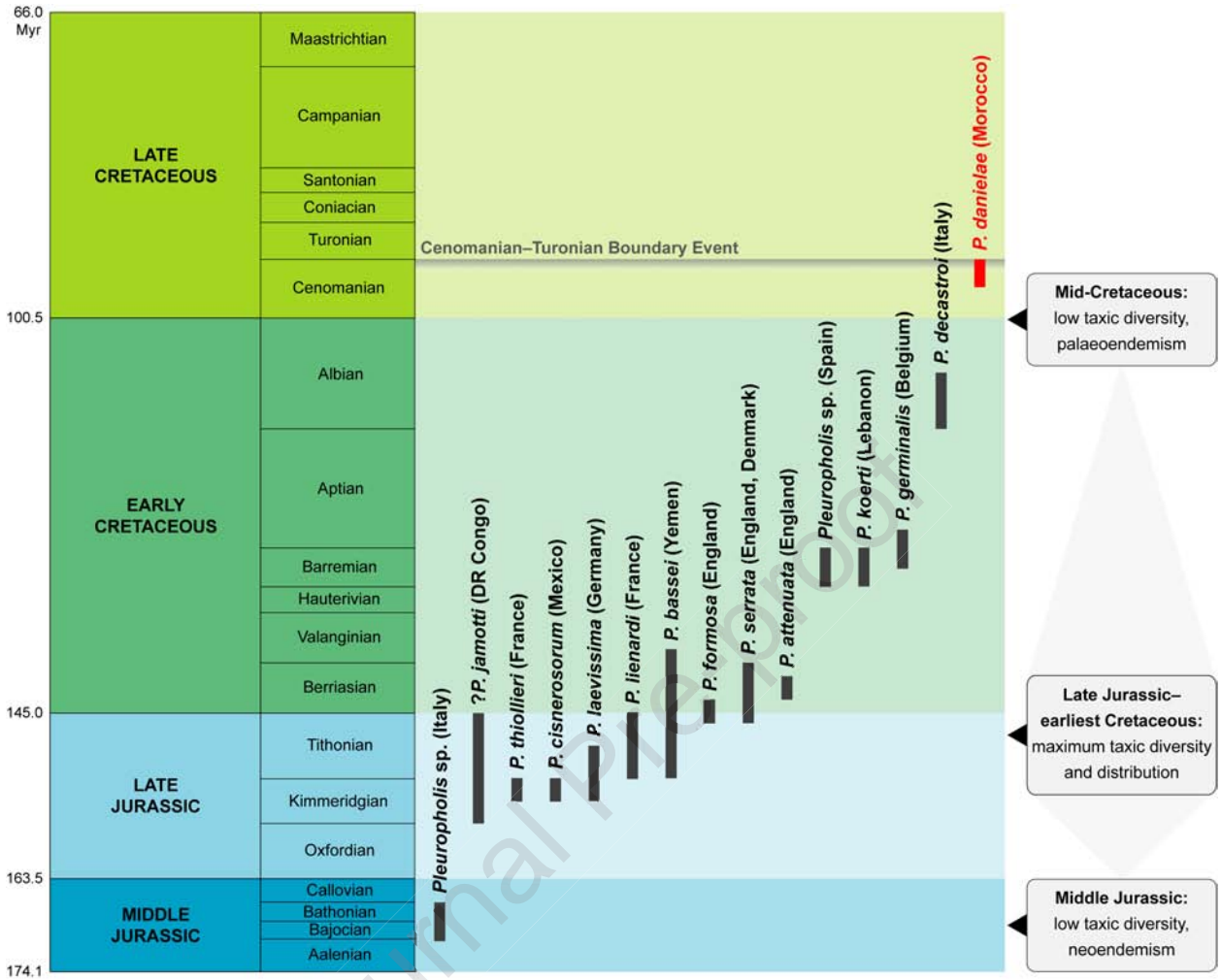




Journal Pre-proof







A pleuropholid fish specimen is described from the Cenomanian of Agoult, SE Morocco.

The specimen is assigned to a new species of the genus *Pleuropholis*, *P. danielae*.

This is the first known occurrence of Pleuropholidae in the Upper Cretaceous.

Pleuropholid fishes may have become extinct at the Cenomanian–Turonian boundary.

This adds to our understanding of the mid-Cretaceous turnover of marine fish faunas.

Journal Pre-proof

**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Journal Pre-proof