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Romain Vullo, Jean-Pierre Archambeau, Gilles Bailly, Pierre Bénéfice. Reassessment of *Cosmodus Sauvage*, 1879, a poorly known genus of large pycnodont fish (Actinopterygii, Pycnodontiformes) from the Cenomanian (Upper Cretaceous) of Western Europe. *Cretaceous Research*, 2018, 91, pp.217-228. 10.1016/j.cretres.2018.05.019 . insu-01819797

HAL Id: insu-01819797

<https://insu.hal.science/insu-01819797>

Submitted on 21 Jun 2018

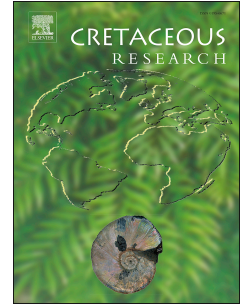
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Accepted Manuscript

Reassessment of *Cosmodus* Sauvage, 1879, a poorly known genus of large pycnodont fish (Actinopterygii, Pycnodontiformes) from the Cenomanian (Upper Cretaceous) of Western Europe

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PII: S0195-6671(18)30109-5

DOI: [10.1016/j.cretres.2018.05.019](https://doi.org/10.1016/j.cretres.2018.05.019)

Reference: YCRES 3893

To appear in: *Cretaceous Research*

Received Date: 21 March 2018

Revised Date: 7 May 2018

Accepted Date: 30 May 2018

Please cite this article as: Vullo, R., Archambeau, J.-P., Bailly, G., Bénéfice, P., Reassessment of *Cosmodus* Sauvage, 1879, a poorly known genus of large pycnodont fish (Actinopterygii, Pycnodontiformes) from the Cenomanian (Upper Cretaceous) of Western Europe, *Cretaceous Research* (2018), doi: [10.1016/j.cretres.2018.05.019](https://doi.org/10.1016/j.cretres.2018.05.019).

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1 **Reassessment of *Cosmodus* Sauvage, 1879, a poorly known genus of large pycnodont fish**
2 **(Actinopterygii, Pycnodontiformes) from the Cenomanian (Upper Cretaceous) of**
3 **Western Europe**

4
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15
16 Declaration of interest: none.

17
18 **ABSTRACT**

19 The large pycnodontiform fish genus *Cosmodus* Sauvage, 1879 is redescribed on the basis of
20 both historical material and new specimens, and a formal diagnosis is proposed. The vomerine
21 and prearticular dentitions of *Cosmodus* show a unique combination of characters, including
22 the morphology and ornamentation of the tooth crowns and the number of tooth rows.
23 *Cosmodus* is thus recognized as a valid distinct genus, restricted to the middle–upper
24 Cenomanian of Western Europe (France, England, Spain, and possibly Germany) and
25 including a single species, *C. carentonensis* (Coquand, 1859). *Cosmodus* shares some peculiar

26 dental features with *Coccodus* (e.g., vomerine dentition with three rows of subtriangular teeth)
27 and is therefore tentatively interpreted as a gigantic member of the Coccodontidae, a family of
28 highly specialized pycnodont fishes so far known only from the middle–upper Cenomanian of
29 Lebanon.

30
31 *Keywords:* Actinopterygii; Pycnodontiformes; Coccodontidae; *Cosmodus*; Dentition;
32 Cenomanian.

35 **1. Introduction**

36
37 The order Pycnodontiformes is a widespread group of ray-finned fishes known from
38 the Upper Triassic to the Eocene (e.g., Martín-Abad and Poyato-Ariza, 2013). Although
39 pycnodontiform genera and species should be preferably defined and diagnosed on the basis
40 of complete, articulated skeletons (Poyato-Ariza and Wenz, 2002), isolated vomerine and
41 prearticular dentitions with unique features (or unique combinations of characters) are still
42 regularly used to erect new taxa (e.g., Poyato-Ariza and Bermúdez-Rochas, 2009; Shimada et
43 al., 2010; Stumpf et al., 2017; Vullo et al., 2017).

44 The Cenomanian genus *Cosmodus*, based on isolated dentitions, was erected by
45 Sauvage (1879) to accommodate a large pycnodontiform species that had been previously
46 assigned to the genus *Gyrodus* (*G. carentonensis* Coquand, 1859). Subsequently, the genus
47 *Cosmodus* has been unanimously regarded as a junior synonym of the widespread genus
48 *Coelodus* Heckel, 1854 (Woodward, 1895, 1909, 1918; Priem, 1908, 1909, 1912; Kriwet and
49 Schmitz, 2005), although it clearly appears that the former possesses distinctive dentitions
50 with a unique combination of characters. Here, the genus *Cosmodus* is reassessed and

51 redescrbed on the basis of material coming from the type region (Charentes, northern
52 Aquitaine Basin, southwestern France) and from other parts of Western Europe (Anglo-Paris
53 Basin and northern Spain). This material is used here to designate a neotype, to provide a
54 formal diagnosis of the type and only species, *Cosmodus carentonensis* (Coquand, 1859), and
55 to discuss, by comparison with other taxa, the systematic affinities of the genus.

56
57 **Institutional abbreviations.** APVSM, Association Paléontologique de Villers-sur-Mer; MA,
58 Muséum d’Auxerre; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz ; MGM,
59 Museo Geominero, Madrid; MHNLM, Musée Vert, Muséum d’Histoire Naturelle, Le Mans;
60 MHNLR, Muséum d’Histoire Naturelle de La Rochelle; NHMUK, Natural History Museum,
61 London, UK.

64 2. Geological settings

66 2.1. Type area

67
68 The lost type specimen (Fig. 1) described by Coquand (1859, 1860a, b) and Sauvage
69 (1879, 1880) was collected by the naturalist Alphonse T. de Rochebrune at Pont-de-Basseau
70 in Angoulême, Charente department (northern Aquitaine Basin). In their respective
71 descriptions, Coquand (1859, 1860a, b) and Sauvage (1879, 1880) did not provide any
72 information on the exact stratigraphic position of the specimen within the Cenomanian series,
73 indicating only “étage carentonien” [Carentonian Stage] or “étage à *Caprina adversa*”
74 [*Caprina adversa* Stage] (see Francis, 1984). Since 2000, intensive collecting of Cenomanian
75 vertebrates in the surrounding area of Angoulême has allowed to precisely locate the

76 stratigraphic position of *Cosmodus* (Vullo, 2007). It appears that isolated teeth and
77 fragmentary dentitions (MHNLR 2017.10.4) of *Cosmodus* commonly occur in the marls and
78 clays (“argiles tégulines” of Coquand, 1858) of the lower upper Cenomanian lithological units
79 C4 and D (*Calycoceras guerangeri* Zone; Moreau, 1996; Néraudeau et al., 1997) outcropping
80 in several clay pits (“Le Pas”, “Le Mas” and “L’Amas” quarries) opened in a small area
81 southwest of Angoulême (towns of Nersac, La Couronne and Roulet–Saint-Estèphe) (Vullo,
82 2007) (Fig. 2). These shallow marine deposits have yielded a rich and diverse fossil
83 assemblage (Moreau, 1996), including abundant oysters (*Rhynchostreon suborbiculatum*,
84 *Rastellum diluvianum*, *Pycnodonte biauriculata*, *Ceratostreon flabellatum*) (Videt, 2004;
85 Videt and Néraudeau, 2007), rare ammonites (*Thomelites* cf. *lattense*; Moreau, 1996),
86 brachyuran crabs (Collins et al., 2013; Van Bakel, 2013), echinoids, and common vertebrate
87 remains (Rage and Néraudeau, 2004; Vullo, 2007; Vullo et al., 2007; Vullo and Néraudeau,
88 2009).

89 In the Charente-Maritime department, about 100 km west of Angoulême, the île
90 Madame cliffs expose the beds of the lower upper Cenomanian lithological units C4 and D
91 (*Calycoceras guerangeri* Zone) at the place called “Le Puits des Insurgés” (Fig. 2). The fossil
92 assemblage recovered from these shallow transgressive marine deposits is roughly similar to
93 that found in the Angoulême area. However, oysters are less abundant, ammonites are
94 represented by *Pseudocalycoceras* sp. and plant fragments (conifers) are present (Videt and
95 Néraudeau, 2007). Besides numerous isolated teeth, complete dentitions of *Cosmodus*
96 (MHNLR 2017.10.1, MHNLR 2017.10.2, MHNLR 2017.10.3) have been collected at “Le
97 Puits des Insurgés”. In the île Madame Cenomanian series, a few teeth of *Cosmodus* have
98 been also found in the underlying marly limestone deposits of the middle Cenomanian subunit
99 C2 and in the overlying sandy oyster bed located at the base of the upper Cenomanian unit E
100 (Fig. 2).

101

102 2.2. Other localities

103

104 Outside the type area (Charentes region), three additional French *Cosmodus* specimens
105 are known from the Cenomanian of the Paris Basin. They all correspond to historical
106 specimens that were collected with more or less precise stratigraphic data. The first specimen
107 (unnumbered specimen from the APVSM collection), probably found by Charles Bacheley at
108 the end of the 18th century (Brignon, 2016: 599) and subsequently communicated by Auguste
109 Le Prévost to Antoine Passy at the beginning of the 19th century, comes from the lower part of
110 the côte Sainte-Catherine in Rouen (Seine-Maritime department, Normandy) (Passy, 1832).
111 This famous locality, which has provided many fossils since the end of the 18th century,
112 exposes chalky deposits of middle to late Cenomanian age corresponding to the “Craie de
113 Rouen” Formation (Lasseur et al., 2009; Lasseur, 2015). It is very likely that this specimen
114 was collected from the middle Cenomanian phosphatic “Horizon de Rouen” (*Acanthoceras*
115 *rhotomagense* Zone), although it might also have been found in one of the overlying strata of
116 the *Acanthoceras jukesbrownei* Zone. The second specimen (MA 70-530) comes from the
117 middle–upper Cenomanian glauconitic chalk (“Craie glauconieuse”) of Seignelay (Yonne
118 department, Burgundy) (Sauvage, 1879). The third specimen (MHNLM 2013.0.2.21) comes
119 from Coulaines near Le Mans (Sarthe department, Maine), a classic fossil-rich locality which
120 was exposing the middle Cenomanian Jalais sandstone and hardground, at the top of the
121 “Sables et grès du Mans” (*Acanthoceras jukesbrownei* Zone) (Morel, 2015; Vullo, 2015).

122 Geographic and stratigraphic information about the previously published specimens
123 from England and Spain is provided by Friedman et al. (2016) and Vullo et al. (2009),
124 respectively. The specimen from Halling (Kent, southeastern England), which is the type of
125 *Coelodus fimbriatus* Woodward, 1893 (NHMUK PV OR 43090), comes from the *Holaster*

126 *subglobosus* Zone (Lower Chalk, Grey Chalk Group; middle part of the Zig Zag Chalk
127 Formation; upper middle to lower upper Cenomanian) according to Friedman et al. (2016).
128 Specimen MGM-2504C from Tiroco (Asturias, northern Spain) comes from the La Cabaña
129 Formation, which is middle?–late Cenomanian in age. Interestingly, MGM-2504C was found
130 in association with the ammonite *Neolobites vibrayeanus* (Almela and Ríos, 1962). This
131 ammonite is the index species of a zone partially equivalent to the lower upper Cenomanian
132 *Calycoceras guerangeri* Zone (Barroso-Barcenilla et al., 2009). In Asturias, some jaw
133 fragments and isolated teeth of *Cosmodus* have also been collected from coeval beds of the La
134 Cabaña and El Toral quarries near Oviedo (Vullo et al., 2009). An additional, previously
135 unpublished specimen (MCNA registration number pending) comes from the upper
136 Cenomanian of Sóbron (Álava, Basque Country, northern Spain). The geological setting of
137 this area and the Sóbron section are described in detail in Floquet et al. (1996).

138

139 **3. Systematic palaeontology**

140

141 Osteichthyes Huxley, 1880

142 Actinopterygii Cope, 1887

143 Neopterygii Regan, 1923

144 Pycnodontiformes Berg, 1937

145 ?Coccodontidae Berg, 1940

146

147 *Cosmodus* Sauvage, 1879

148

149 **Type and only species.** *Gyrodus carentonensis* Coquand, 1859.

150

151 **Diagnosis.** Large-sized pycnodont fish genus that differs from all other pycnodont genera in
152 having the following combination of characters: elongated, narrow vomerine dentition with
153 three rows of seven or eight subtriangular teeth; teeth of the medial row of the vomer slightly
154 smaller than corresponding adjacent lateral teeth; robust prearticular bone bearing three rows
155 (one main row located medially and two secondary rows located laterally) of large curved
156 drop-shaped teeth (main row) and smaller suboval to subrectangular teeth (secondary rows);
157 complex tooth ornamentation, with a sculpted crown surface (central depression present in all
158 teeth except teeth of the prearticular main row) showing a rugose texture and irregular
159 wrinkles arranged in a more or less pronounced radiating pattern.

160

161 *Cosmodus carentonensis* (Coquand, 1859)

162 Figs. 1, 3–5A

163

164 1832 “Palais de poisson”, “Appareil dentaire de poisson”; Passy, p. 179, pl. 15, fig. 1.

165 ?1856 *Gyrodus Münsteri* Agassiz; Fischer, p. 138, fig. 21.

166 1859 *Gyrodus carentonensis* Coquand: p. 953.

167 1860a *Gyrodus carentonensis* Coquand; Coquand, p. 41.

168 1860b *Gyrodus carentonensis* Coquand; Coquand, p. 97.

169 1879 *Cosmodus carentonensis* (Coquand); Sauvage, p. 49.

170 1879 *Cosmodus grandis* Sauvage: p. 49, pl. 3, fig. 29.

171 1880 *Cosmodus carentonensis* (Coquand); Sauvage, p. 459, pl. 14, fig. 1.

172 1893 *Coelodus fimbriatus* Woodward: p. 491, pl. 17, fig. 6.

173 1895 *Coelodus carentonensis* (Coquand); Woodward, p. 257.

174 1895 *Coelodus major* Woodward: p. 257.

175 1908 *Coelodus major* Woodward; Priem, p. 48.

- 176 1909 *Coelodus carentonensis* (Coquand); Priem, p. 325.
- 177 1909 *Coelodus fimbriatus* Woodward; Woodward, p. 166, fig. 47.
- 178 1912 *Coelodus (Gyrodus) carentonensis* (Coquand); Priem, p. 269.
- 179 1962 *Pycnodus* sp.; Almela and Ríos, p. 61, pl. 7, fig. 2.
- 180 1972 *Coelodus fimbriatus* Woodward; Benedetto and Sánchez, p. 61, pl. 2, fig. 7.
- 181 1997 *Gyrodus carentonensis* Coquand; Schultz and Paunović, p. 125.
- 182 1997 *Coelodus fimbriatus* Woodward; Schultz and Paunović, p. 102, 127.
- 183 2005 *Gyrodus carentonensis* Coquand; Kriwet and Schmitz, p. 53.
- 184 2005 *Cosmodus grandis* Sauvage; Kriwet and Schmitz, p. 53.
- 185 2007 “*Coelodus carentonensis*” (Coquand); Vullo, p. 79, text-fig. 3.1, pl. 4, fig. 2.
- 186 2009 “*Cosmodus carentonensis*” (Coquand); Vullo et al., p. 122, figs. 2e, 4a.
- 187 2015 *Coelodus fimbriatus* Woodward; Brignon, p. 57, fig. 32.1.
- 188 2015 *Cosmodus* cf. *grandis* (Sauvage); Vullo, p. 241, fig. 172h.
- 189 2016 “*Coelodus*” *fimbriatus* Woodward; Friedman et al., p. 171, table 1.
- 190
- 191 **Neotype.** MHNLR 2017.10.1, a complete vomerine dentition from “Le Puits des Insurgés”,
- 192 île Madame, Charente-Maritime department, France (Fig. 3A, B).
- 193 **Paraneotype.** MHNLR 2017.10.2, a complete left prearticular dentition from “Le Puits des
- 194 Insurgés”, île Madame, Charente-Maritime department, France (Fig. 3F–H).
- 195 **Referred material.** MHNLR 2017.10.4, a fragmentary vomerine dentition from Nersac (“Le
- 196 Pas” quarry), Charente department, France (Fig. 3C–E); MHNLR 2017.10.3, a complete right
- 197 prearticular dentition (juvenile) from “Le Puits des Insurgés”, île Madame, Charente-
- 198 Maritime department, France (Fig. 3I); MA 70-530 (type specimen of *Cosmodus grandis*
- 199 Sauvage, 1879), a subcomplete left prearticular dentition from Seignelay, Yonne department,
- 200 France (Fig. 4A); NHMUK PV OR 43090 (type specimen of *Coelodus fimbriatus* Woodward,

201 1893), a fragmentary right prearticular dentition from Halling, Kent, England (Fig. 4B);
202 MHNLM 2013.0.2.21, a subcomplete left prearticular dentition from Coulaines, Sarthe
203 department, France (Fig. 4C); APVSM unnumbered specimen, a subcomplete right
204 prearticular dentition from Rouen, Seine-Maritime department, France (Fig. 4D); MGM-
205 2504C, a subcomplete right prearticular dentition from Tiroco, Asturias, Spain (Fig. 4E);
206 MCNA (registration number pending), a fragmentary right prearticular dentition from Sóbron,
207 Álava, Spain (Fig. 4F); MHNLR 2017.10.5, a left dentary (or left premaxilla?) from Nersac
208 (“Le Pas” quarry), Charente department, France (Fig. 3J, K).

209 **Type locality and horizon.** “Le Puits des Insurgés”, île Madame, Port-des-Barques,
210 Charente-Maritime department, France. Lower upper Cenomanian lithological units C4 and D
211 (*Calycoceras guerangeri* Zone), “Argiles tégulines de Coquand” Formation (Moreau, 1996;
212 Néraudeau et al., 1997; Andrieu et al., 2015).

213 **Diagnosis.** Same as for genus.

214

215 3.1. Description

216

217 The vomer is an elongate, relatively narrow bone. MHNLR 2017.10.1 (Fig. 3A, B) is a
218 complete vomerine dentition (65 mm in length) showing 21 teeth closely arranged in three
219 well-defined longitudinal rows. Seven teeth are preserved in each row. The posteriormost
220 tooth of the medial row is missing. In cross-sectional view, the three rows are in the same
221 plane. With the exception of the anterior teeth of the medial row with a diamond-shaped
222 contour, all the teeth show a subtriangular contour in occlusal view. The teeth of the medial
223 row alternate with those of the lateral rows. The teeth have a central depression, which is
224 larger and more rugose and wrinkled in the crowns of the lateral rows. The ornamentation
225 shows a more or less pronounced radiating pattern. The teeth of the medial row show a thick

226 transverse bulge posterior to the central depression. MHNLR 2017.10.4 (Fig. 3C–E) is a
227 vomer fragment bearing four teeth. The preserved portion corresponds to the posterior part of
228 the vomer. It shows the second posteriormost tooth of the medial row, and the three
229 posteriormost teeth of the left lateral row. In left lateral view, the bone shows a well-
230 developed subvertical oral border above the tooth row. In dorsal view, the bulged lateral
231 margin of the lateral teeth can be seen.

232 The prearticular corresponds to a massive, well-ossified bone. MHNLR 2017.10.2
233 (Fig. 3F–H) is a large, complete left prearticular with a well-preserved dentition showing
234 three tooth rows. The main row has nine curved drop-shaped teeth that are devoid of central
235 depression. The largest teeth are 20 mm in width. Nine and eight teeth are preserved in the
236 inner and outer lateral rows, respectively. However, there were originally ten teeth in each of
237 the two lateral rows, as indicated by empty tooth spaces. The lateral row teeth show a suboval
238 to subrectangular contour and display an ornamentation similar to that of vomerine teeth (i.e.,
239 central depression, rugose texture and irregular wrinkles showing a more or less pronounced
240 radiating pattern). The symphysis is thin and long. There is a relatively narrow edentulous
241 area between the main tooth row and the symphysis, corresponding to a medioventral lamina.
242 In cross-sectional view, this lamina is rather thin and concave dorsally. The coronoid process
243 is thick, rather low, and shows a slightly convex dorsal margin. The ventrolateral surface of
244 the prearticular shows a salient coronoid ridge. A large foramen is present laterally, just below
245 the third anterior tooth of the outer lateral row. MHNLR 2017.10.3 (Fig. 3I) is a complete
246 right prearticular belonging to a juvenile. Six teeth are preserved in the main row. The tooth
247 arrangement and tooth morphology are rather similar to those observed in larger specimens,
248 indicating that ontogenetic heterodonty in *Cosmodus* was very weak. The two main
249 differences with adult dentitions are 1) the proportionally larger size of posterior teeth of

250 lateral rows and 2) the higher angle between medial and lateral margins of the dentition. In
251 addition, anterior teeth of the two lateral rows are fused in MHNLR 2017.10.3.

252 MHNLR 2017.10.5 (Fig. 3J, K) is a small subtriangular, flattened bone bearing two
253 incisiform prehensile teeth. This element, interpreted as a left dentary (or, alternatively, a right
254 premaxilla), is tentatively assigned to *Cosmodus* because of the presence of unusual
255 ornamentation on the tooth crowns. Both teeth are wider than high and not strongly
256 compressed labiolingually. The lingual faces are irregularly wrinkled and show a basal bulge,
257 whereas the labial faces are smooth.

258 All the *Cosmodus* specimens previously described from the Anglo–Paris Basin (Passy,
259 1832; Sauvage, 1879; Woodward, 1893; Vullo, 2015) and northern Spain (Almela and Ríos,
260 1962; Vullo et al., 2009) correspond to large prearticular dentitions (Fig. 4A–E). They are less
261 complete than MHNLR 2017.10.2, all lacking the anterior portion of the dentition. However,
262 they clearly show the same tooth arrangement and morphological features that the material
263 from Charentes, displaying a main row with drop-shaped teeth and two secondary rows with
264 smaller suboval to subrectangular teeth ornamented by irregular radiating wrinkles. The new
265 Spanish specimen from Sóbron is a smaller fragment corresponding to the anterior portion of
266 a right prearticular dentition (Fig. 4F). It is also morphologically consistent with the Charentes
267 material.

268

269 4. Discussion

270

271 4.1. Synonymy and designation of a neotype

272

273 In his synopsis of the Cretaceous fossils of southwestern France (*“Synopsis des*
274 *animaux et des végétaux fossiles observés dans la formation crétacée du sud-ouest de la*

275 France”), Coquand (1859) provided a brief description without illustration of a new species
276 of pycnodont fish, *Gyrodus carentonensis*, from the upper Cenomanian of the Angoulême
277 area, Charente department. Coquand’s original description of *Gyrodus carentonensis* was
278 based on a single fragmentary vomer (now lost) bearing six teeth characterized by a peculiar,
279 complex ornamentation (Fig. 1). Later, Sauvage (1879, 1880) figured this specimen (Fig. 1),
280 discussed the affinities of this species, found that it was clearly distinct from the other species
281 of *Gyrodus*, and finally concluded that it should be assigned to a new genus. Thus, Sauvage
282 (1879) erected the genus *Cosmodus*, in which he also placed a new species, *Cosmodus*
283 *grandis*, from the Cenomanian of Seignelay, Yonne department, northeastern France (Fig.
284 4A). Sauvage (1879, 1880) also placed the species *Pycnodus imitator* Cornuel, 1877 and
285 *Pycnodus sculptus* Cornuel, 1877 (Lower Cretaceous of Wassy, Haute-Marne department,
286 northeastern France; Cornuel, 1877, 1880) in his new genus *Cosmodus*, but these two species
287 must be assigned to the genus *Gyrodus* (Woodward, 1895). The type specimens of *Gyrodus*
288 *imitator* and *Gyrodus sculptus* are prearticular dentitions which display the same features that
289 those of *Gyrodus* sp. described from the Lower Cretaceous of Germany (Kriwet and Schmitz,
290 2005). Because neither *Gyrodus imitator* nor *Gyrodus sculptus* displays diagnostic features,
291 these two species must be considered as *nomina dubia* and the type material is here referred to
292 *Gyrodus* sp.

293 Woodward (1893) described a new large species of *Coelodus*, *C. fimbriatus*, on the
294 basis of an incomplete prearticular dentition from the Lower Chalk of Halling, Kent,
295 southeastern England (Fig. 4B). The dental morphology and tooth arrangement of this
296 prearticular dentition clearly indicate that this species belongs to the genus *Cosmodus*. Both
297 *Cosmodus grandis* Sauvage, 1879 and *Cosmodus fimbriatus* (Woodward, 1893) are
298 undistinguishable from the type species (known by several vomerine and prearticular
299 dentitions), and these two taxa are therefore regarded here as junior synonyms of *Cosmodus*

300 *carentonensis* (Coquand, 1859). In the present study, we select the complete vomerine
301 dentition MHNLR 2017.10.1 from the “Argiles tégulines de Coquand” Formation of the
302 Charentes region (type horizon and area) as the neotype of *Cosmodus carentonensis*,
303 consistently with the type specimen originally described by Coquand (1859). In addition, the
304 complete prearticular dentition MHNLR 2017.10.2, collected from the same locality that
305 yielded the neotype (i.e., “Le Puits des Insurgés”, île Madame), is designated as paraneotype.

306 A prearticular dentition from the middle–upper Cenomanian of the côte Sainte-
307 Catherine in Rouen (Normandy, northwestern France), originally figured by Passy (1832: pl.
308 15, fig. 1) as “appareil dentaire de poisson” [dental apparatus of fish] and recently referred to
309 *Coelodus fimbriatus* by Brignon (2015), can be confidently assigned to *Cosmodus*
310 *carentonensis* (Fig. 4D).

311

312 4.2. Comparisons and affinities

313

314 The genus *Cosmodus* shares some dental features with a few other pycnodont genera.
315 Several authors have considered the genus *Cosmodus* as a subjective junior synonym of the
316 genus *Coelodus* (Woodward, 1895, 1909, 1918; Priem, 1908, 1909, 1912; Kriwet and
317 Schmitz, 2005). Woodward (1895: 257) even proposed the replacement name *Coelodus major*
318 for *Coelodus grandis* (Sauvage, 1879), which consequently became a junior homonym of
319 *Coelodus grandis* (Costa, 1856). Like *Cosmodus*, *Coelodus* typically has three prearticular
320 tooth rows (Woodward, 1909; Schultz and Paunović, 1997; Poyato-Ariza and Wenz, 2002;
321 Szabó et al., 2016). However, *Cosmodus* clearly differs from *Coelodus* by the tooth shape, the
322 tooth ornamentation, and the number of vomerine tooth rows (Woodward, 1909; Schultz and
323 Paunović, 1997; Poyato-Ariza and Wenz, 2002) (Table 1). As in *Cosmodus*, the prearticular
324 of the genus *Anomoeodus* also shows a main tooth row with comma-shaped crowns.

325 However, the vomerine and prearticular dentitions of *Anomoeodus* display more tooth rows
326 than those of *Cosmodus*. In addition, the teeth of *Anomoeodus* are generally smooth or less
327 ornamented than those of *Cosmodus* (Kriwet, 1999, 2002; Poyato-Ariza and Wenz, 2002;
328 Friedman, 2012) (Table 1). As *Cosmodus*, the much smaller coccodontid (*sensu lato*) genera
329 *Coccodus* and *Ichthyoceros* also have a vomer bearing three rows of subtriangular teeth
330 (Poyato-Ariza and Wenz, 2002: fig. 22d; Fig. 5B). However, the prearticular dentition of
331 *Coccodus* shows only two tooth rows (Poyato-Ariza and Wenz, 2002; Kriwet, 2005: fig. 44)
332 (Table 1). In *Ichthyoceros*, there are three prearticular tooth rows as in *Cosmodus*, but the two
333 secondary rows are located medially and laterally to the main row (Poyato-Ariza and Wenz,
334 2002: fig. 23a). The presence of three tooth rows in both the vomerine and prearticular
335 dentitions is known in several other pycnodontiform taxa (e.g., *Arcodonichthys*,
336 *Paramicrodon*, *Phacodus*, *Proscinetes*, *Neoproscinetes*), but the teeth of the main vomerine
337 tooth row are never triangular in contour and are always larger and wider than those of lateral
338 rows (Thurmond, 1974; Hooks et al., 1999; Poyato-Ariza et al., 1999; Poyato-Ariza and
339 Wenz, 2002; Poyato-Ariza and Bermúdez-Rochas, 2009). Lastly, it is worth noting that a
340 rugose tooth crown ornamentation rather similar to that of *Cosmodus* is convergently present
341 in the large Eocene species *Pycnodus mokattamensis*, an otherwise distinct pycnodont with
342 five vomerine tooth rows and suboval teeth (Priem, 1897, 1899). The new material described
343 here confirms the validity of the genus *Cosmodus*, which can be clearly distinguished from
344 *Coelodus* and other pycnodontiforms by its unique combination of characters.

345 As *Cosmodus* is known only by isolated dentitions, caution is needed when attempting
346 to determine the systematic affinities of this genus. However, unusual dental features of
347 *Cosmodus* provide clues regarding its familial assignment. Interestingly, Poyato-Ariza and
348 Wenz (2002) found that subtriangular vomerine teeth represent an autapomorphic character of
349 the clade *Coccodus* + *Ichthyoceros* within the Coccodontidae (*sensu lato*), a highly

350 specialized family of small-sized, well-armored pycnodonts so far restricted to the middle–
351 upper Cenomanian of Lebanon (Poyato-Ariza and Wenz, 2002; Martín-Abad and Poyato-
352 Ariza, 2013; Taverne and Capasso, 2014). In addition, *Cosmodus* shares with *Coccodus* a
353 suite of characters, including the number and relative width of vomerine tooth rows (three
354 rows of subequal widths), the slenderness of the vomer (high length/width ratio), the tooth
355 crown ornamentation (e.g., vomerine teeth with wrinkled central depression and peripheral
356 bulges), the morphology of main prearticular teeth (curved drop-shaped contour), and the
357 number of teeth in main rows of vomerine and prearticular dentitions (less than 10) (Poyato-
358 Ariza and Wenz, 2002; Kriwet, 2005; Taverne and Capasso, 2014) (Fig. 5). As far it is
359 known, *Cosmodus* mainly differs from *Coccodus* by its much larger size, its more marked
360 tooth crown ornamentation, and the presence of an additional lateral tooth row in the
361 prearticular dentition. In conclusion, dental features of *Cosmodus* indicate that this genus is
362 more closely related to *Coccodus* than to any other pycnodontiform genus, and *Cosmodus* is
363 therefore tentatively referred to the Coccodontidae.

364

365 4.3. Distribution and palaeoecology

366

367 Outside the Aquitaine Basin, where the type area is located (Coquand, 1859; Sauvage,
368 1880; Vullo, 2007), the genus *Cosmodus* is known from the Anglo-Paris Basin (Passy, 1832;
369 Sauvage, 1879; Woodward, 1893; Vullo, 2015) and from the Asturian Central Depression in
370 the northern margin of the Iberian Peninsula (Almela and Ríos, 1962; Vullo et al., 2009) (Fig.
371 6). An additional Spanish occurrence is reported here, based on a previously unpublished
372 specimen coming from the upper Cenomanian of Sóbron (Álava, Basque Country) in the
373 Basque–Cantabrian Basin (Fig. 6). Lastly, a single tooth from the upper Cenomanian
374 (*Metoicoceras geslinianum* Zone; Dölzschen Formation) of Plauen (Saxony, eastern

375 Germany), originally described as “*Gyrodus Münsteri*”, shows a suboval contour, a central
376 depression and short radiating wrinkles (Fischer, 1856; Licht and Kogan, 2011). This
377 specimen, about 6 mm in largest diameter and likely corresponding to an anterior tooth of a
378 prearticular lateral row, may be referred to *Cosmodus*. However, this assignment, based on
379 Fischer’s original figure (Fischer, 1856: fig. 21), must be considered as highly tentative.

380 *Cosmodus* therefore appears to be well distributed in Western Europe, from chalky
381 facies with boreal influences (as observed in Kent, Seine-Maritime and Yonne; e.g., Lasseur
382 et al., 2009) to more detrital facies with Tethyan influences (as observed in Charentes, Sarthe,
383 Basque Country and Asturias; e.g., Moreau, 1996) (Fig. 6). This indicates that *Cosmodus*
384 probably lived in a wide range of habitats, from shallow marine to deeper outer shelf
385 environments. However, the material from Charentes, which is abundant, well-preserved and
386 comes from both juvenile and adult individuals, suggests that *Cosmodus* preferentially
387 inhabited shallow coastal areas such as lagoons and bays. In the type area, *Cosmodus* co-
388 occurs with other medium-sized to large-sized pycnodont taxa, such as *Coelodus*,
389 *Anomoeodus*, *Phacodus*, and cf. *Neoproscinetes* (Coquand, 1859, 1860a, b; R. Vullo, pers.
390 obs.). However, the latter are somewhat smaller and *Cosmodus* corresponds to the largest
391 form of the Charentes pycnodont assemblage, as also observed in the Anglo-Paris Basin and
392 Asturias (Vullo et al., 2009; Vullo, 2015; Friedman et al., 2016). Mid-Cretaceous pycnodont
393 fishes include some particularly large forms, as exemplified by *Coelodus ellipticus* and
394 *Coelodus gyrodoides* from the Albian of southern England (Egerton, 1877). With an
395 estimated maximum standard length of about 80 cm (according to the correlation existing
396 between prearticular length and standard length; see Licht, 2009) and an inferred total length
397 of around one meter, the putative coccodontid *Cosmodus carentonensis* is one of these large-
398 sized pycnodonts that flourished during the mid-Cretaceous and strongly contrasts with the
399 small-sized Lebanese coccodontid taxa (around 10 cm in total length for *Coccodus*; Taverne

400 and Capasso, 2014). The observed distribution of *Cosmodus* in Western Europe can be partly
401 correlated with the middle–late Cenomanian development of oysters such as the gryphaeid
402 species *Pycnodonte biauriculata* (*Pycnodonte* Event; Dhondt, 1984; Videt, 2004; Wilmsen
403 and Voigt, 2006). These abundant, robust bivalves may have represented a major food
404 resource for such powerful-jawed fishes with a grinding dentition.

405 If correct, the familial assignment of *Cosmodus* proposed here considerably extends
406 the palaeogeographic range of the Coccodontidae, a group so far considered endemic to
407 Lebanon (Cavin, 2008; Martín-Abad and Poyato-Ariza, 2013; Taverne and Capasso, 2014;
408 Marramà et al., 2016). The presence of a single coccodontid species in Europe would contrast
409 with the relatively high diversity of Lebanese coccodontids (*sensu lato*), usually regarded as
410 the result of a local radiation event due to peculiar ecological conditions (Cavin, 2008;
411 Marramà et al., 2016). In addition, this would support the hypothesis that collecting and
412 taphonomic biases (i.e., “Lagerstätten effect”) may be responsible for the so far observed
413 geographic restriction of this peculiar lineage to the Middle East, as previously suggested by
414 Marramà et al. (2016). Lebanese coccodontids (*sensu lato*) mostly come from the lower upper
415 Cenomanian strata of Hâqel and Hjoûla (Taverne and Capasso, 2014). The late Cenomanian
416 age of these two fossil-Lagerstätten was first proposed on the basis of an assemblage of
417 planktonic foraminifera from contiguous deposits (Hemleben, 1977) and subsequently
418 confirmed by the occurrence of the ammonite *Allocrioceras* cf. *annulatum*, a species
419 occurring in the *Metoicoceras geslinianum* Zone (Wippich and Lehmann, 2004).
420 Coccodontids are also present in the En Nammoûra locality (Taverne and Capasso, 2014),
421 which is late middle Cenomanian in age as indicated by associations of benthic foraminifera
422 (Dalla Vecchia et al., 2002). *Cosmodus* is known from the middle to the upper Cenomanian,
423 occurring from the *Acanthoceras jukesbrownei* Zone (or possibly the underlying
424 *Acanthoceras rhotomagense* Zone) to the *Calycoceras guerangeri* Zone (or possibly the

425 overlying *Metoicoceras geslinianum* Zone). Therefore, *Cosmodus* shows a restricted
426 stratigraphic distribution that is roughly consistent with that of Lebanese coccodontids.

427 During the latest Cenomanian, *Cosmodus* apparently became extinct and several
428 equivalent-sized taxa appeared in Europe, North America and Africa during the Turonian.
429 These taxa include some particularly large species of the widespread pycnodontid genus
430 *Coelodus* (e.g., Woodward, 1909; Priem, 1898; Schultz and Paunović, 1997), the poorly
431 known pycnodontid genus *Acrotemnus* (= *Macropycnodon*) (e.g., Woodward, 1909; Shimada
432 et al., 2010; Vullo and Courville, 2014), and the bizarre serrasalmimid genus *Polygyrodus*
433 (Vullo et al., 2017). It can be assumed that this trend to gigantism in various distinct lineages
434 (reported here for the first time within the Coccodontidae), with some forms exceeding one
435 meter in total length, is one aspect of the explosive early Late Cretaceous diversification
436 observed in pycnodont fishes (Marramà et al., 2016). As early as the Cenomanian, new
437 morphological innovations with obvious defensive functions (e.g., horns, spines, armor)
438 evolved independently in several marine fish lineages (e.g., pycnodonts, acanthomorphs),
439 probably in response to the increased levels of predation characterizing the Mesozoic Marine
440 Revolution (Chen et al., 2014; Marramà et al., 2016). On the basis of the available material
441 (i.e., isolated dentitions), it is not possible to know whether *Cosmodus* was a well-armored
442 form like small-sized, spinous coccodontids from Lebanon (Taverne and Capasso, 2014).
443 Nevertheless, it is worth noting that the remarkably large size of some mid-Cretaceous
444 pycnodonts such as *Cosmodus* may have represented an alternative or additional physical
445 defensive adaptation in ecosystems with increasing predation rates.

446

447 **5. Conclusions**

448

449 Our study shows that the pycnodont fish *Cosmodus*, occurring in the mid-Cretaceous
450 (Cenomanian) of Western Europe and previously thought to be a junior synonym of
451 *Coelodus*, is actually a monospecific genus that can be clearly distinguished from all other
452 taxa. The tooth arrangement and tooth morphology of *Cosmodus* suggest that this large-sized
453 genus is closely related to *Coccodus*, a small armored form endemic to Lebanon. *Cosmodus* is
454 therefore tentatively assigned to the Coccodontidae, a highly specialized family of pycnodonts
455 known so far only from the famous Lagerstätten of Lebanon. This new taxonomic
456 interpretation of *Cosmodus* would extend the palaeogeographic distribution of coccodontids
457 to the European archipelago. Interestingly, the stratigraphic range of *Cosmodus* is equivalent
458 to that of Lebanese coccodontids (middle–upper Cenomanian).

459 *Cosmodus*, as well as other large mid-Cretaceous pycnodonts (i.e., *Coelodus*,
460 *Acrotemnus*, *Polygyrodus*), probably fed on robust hard-shelled organisms and may have been
461 preyed upon by large top predators such as lamniform sharks and marine reptiles. The
462 gigantism observed in these pycnodont taxa can be interpreted as a direct consequence of an
463 important phase of predator–prey escalation in Cretaceous marine ecosystems (Walker and
464 Brett, 2002).

465 Our results confirm the important contribution of diagnostic isolated dentitions to our
466 knowledge of the palaeodiversity, palaeobiogeography and palaeoecology of pycnodontiform
467 fishes (e.g., Kriwet and Schmitz, 2005; Kriwet, 2008; Szabó et al., 2016; Stumpf et al., 2017).

468

469 **Acknowledgments**

470

471 We thank Arnaud Brignon for providing information concerning the whereabouts of
472 the Rouen specimen. We are grateful to Horst Gödicke, Jean-Marie Guégan, Bernard Pierson
473 (Association Paléontologique de Villers-sur-Mer), Damien Gendry (Université de Rennes 1),

474 Gaëlle Labonne (Muséum d'Auxerre), Nicolas Morel (Musée Vert, Le Mans), Kevin Webb
475 (Natural History Museum, London), José J. Moratalla and María José Torres (Instituto
476 Geológico y Minero de España, Madrid) for photographs of some specimens, to Didier
477 Néraudeau (Université de Rennes 1) for providing specimen MHNLR 2017.10.3, and to
478 Enrique Bernárdez (Universidad de Atacama, Copiapó) for providing information about the
479 material from Asturias. Access to the Tiroco specimen was kindly provided at the Museo
480 Geominero (IGME, Madrid). Ramiro López Medrano (Ponferrada) is warmly thanked for
481 providing photographs of the specimen from Sóbron and for kindly donating it to the Museo
482 de Ciencias Naturales de Álava. Finally, we wish to thank Giuseppe Marramà and Márton
483 Szabó for their thorough reviews and constructive comments.

484

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Figure captions:

Fig. 1. Reproduction of the original drawing of the lost type specimen of *Gyrodus carentonensis* Coquand, 1859 from the upper Cenomanian of Angoulême (Charente department, northern Aquitaine Basin, France) (after Sauvage, 1880). Scale bar equals 1 cm.

Fig. 2. Map and synthetic section showing the geographic locations and stratigraphic positions (asterisks) of *Cosmodus carentonensis* (Coquand, 1859) in the type area (Charentes region, northern Aquitaine Basin). Most of the specimens were collected from the lower upper Cenomanian “Argiles tégulines de Coquand” Formation (type horizon).

Fig. 3. *Cosmodus carentonensis* (Coquand, 1859) from the type region (Charentes, northern Aquitaine Basin, France). A, B, complete vomerine dentition (MHNLR 2017.10.1) from île Madame, Charente-Maritime department, in occlusal view (A) and close-up occlusal view (B) of posteriormost teeth showing the detail of the crown ornamentation. C–E, fragmentary vomerine dentition (MHNLR 2017.10.4) from Nersac, Charente department, in occlusal (C), dorsal (D) and left lateral (E) views. F–H, complete left prearticular dentition (MHNLR 2017.10.2) from île Madame, Charente-Maritime department, in occlusal (F), ventrolateral (G) and dorsolateral (H) views. I, complete right prearticular dentition of juvenile individual (MHNLR 2017.10.3) from île Madame, Charente-Maritime department, in occlusal view. J, K, left dentary (or right premaxilla?) (MHNLR 2017.10.5) from Nersac, Charente department, in labial (J) and lingual (K) views. Scale bars equal 1 cm.

742 **Fig. 4.** *Cosmodus carentonensis* (Coquand, 1859) from localities outside the type region. A,
743 subcomplete left prearticular dentition (MA 70-530; type specimen of *Cosmodus grandis*
744 Sauvage, 1879) from Seignelay, Yonne department, France. B, fragmentary right prearticular
745 dentition (NHMUK PV OR 43090; type specimen of *Coelodus fimbriatus* Woodward, 1893)
746 from Halling, Kent, England. C, subcomplete left prearticular dentition (MHNLM
747 2013.0.2.21) from Coulaines, Sarthe department, France. D, subcomplete right prearticular
748 dentition (APVSM unnumbered specimen) from Rouen, Seine-Maritime department, France.
749 E, subcomplete right prearticular dentition (MGM-2504C) from Tiroco, Asturias, Spain. F,
750 fragmentary right prearticular dentition (MCNA registration number pending) from Sóbron,
751 Álava, Spain. All specimen in occlusal view. Scale bar equals 1 cm.

752
753 **Fig. 5.** Comparison between the vomerine dentitions of *Cosmodus* and *Coccodus*. A,
754 vomerine dentition of *Cosmodus carentonensis* (reconstruction based on MHNLR 2017.10.1
755 and MHNLR 2017.10.4). B, vomerine dentition of *Coccodus armatus* (reconstruction based
756 on Poyato-Ariza and Wenz, 2002: fig. 22d). Note the subtriangular teeth closely arranged in
757 three rows and the ornamented crowns with a central depression and peripheral bulges. Scale
758 bars equal 1 cm (A) and 5 mm (B).

759
760 **Fig. 6.** Middle-late Cenomanian palaeogeographic map showing the distribution of *Cosmodus*
761 *carentonensis* (red stars) in the epicontinental seas of Western Europe (after Philip et al.,
762 2000). This marine pycnodontiform taxon occurs in Charente-Maritime (1), Charente (2),
763 Sarthe (3), Yonne (4) and Seine-Maritime (5) in France, Kent (6) in England, and Asturias (7)
764 and Álava (8) in Spain; the possible occurrence of *Cosmodus* in Saxony (eastern Germany) is
765 not taken into account here.

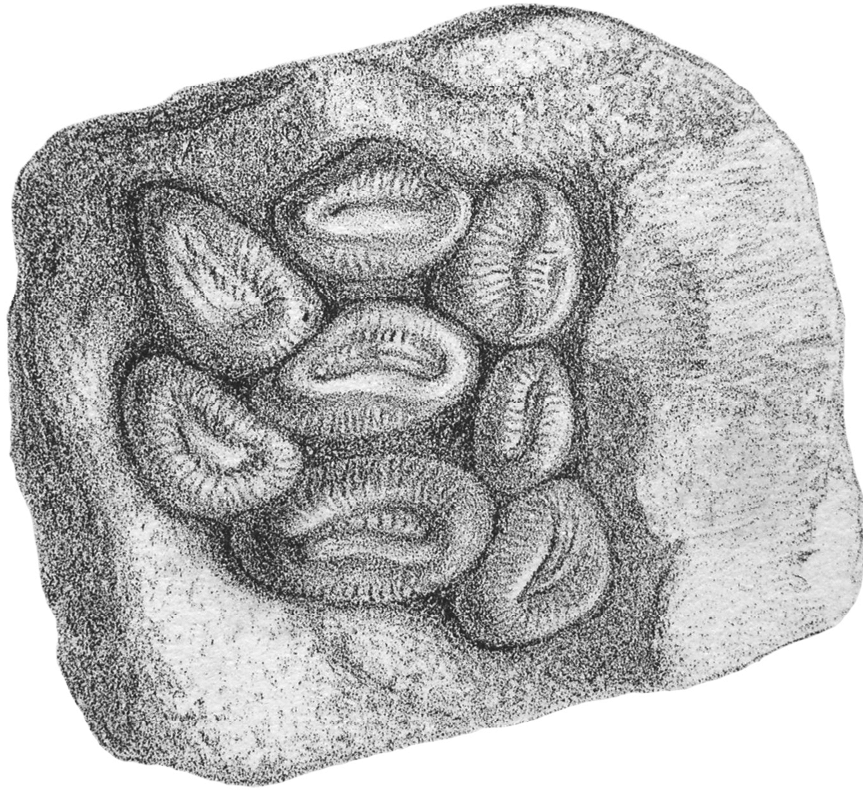
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767 **Table 1.** Comparison between the dentitions of *Cosmodus*, *Coccodus*, *Coelodus* and
 768 *Anomoeodus*.

	<i>Cosmodus</i> (this paper)	<i>Coccodus</i> (after Poyato-Ariza and Wenz, 2002; Kriwet, 2005)	<i>Coelodus</i> (after Poyato-Ariza and Wenz, 2002)	<i>Anomoeodus</i> (after Kriwet, 1999, 2002; Poyato-Ariza and Wenz, 2002)
Morphology of vomerine teeth	subtriangular contour	subtriangular contour	suboval contour	subcircular to suboval
Morphology of prearticular teeth (main row)	curved drop-shaped (comma-shaped) contour	suboval to curved drop-shaped (comma-shaped) contour	transversally (mediolaterally) elongated (capsule-shaped) contour	sigmoid to curved drop-shaped (comma-shaped) contour
Tooth crown ornamentation	complex, irregular surface (central depression, bulges) with wrinkled and rugose texture	irregular surface (transversal groove, central depression, bulges); weak crenulations and wrinkles occasionally present	smooth or transversal groove	smooth or transversal groove; teeth occasionally mammilated
Number of vomerine tooth rows	three	three	five	five
Number of prearticular tooth rows	three	two	three	four to eight
Number of teeth on main tooth row of vomerine and prearticular dentitions	less than 10	less than 10	10 or more	variable (generally 10 or more)

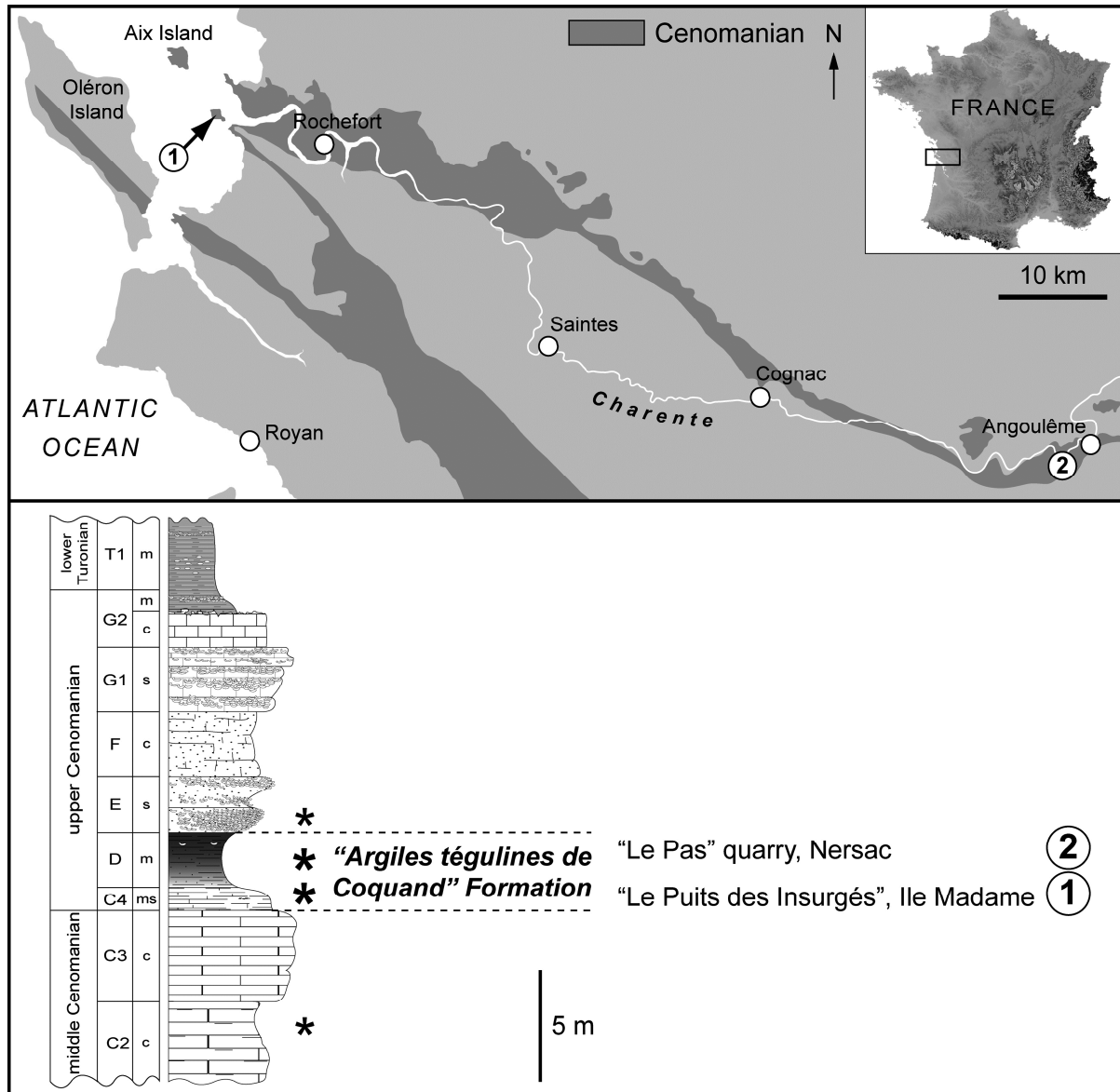
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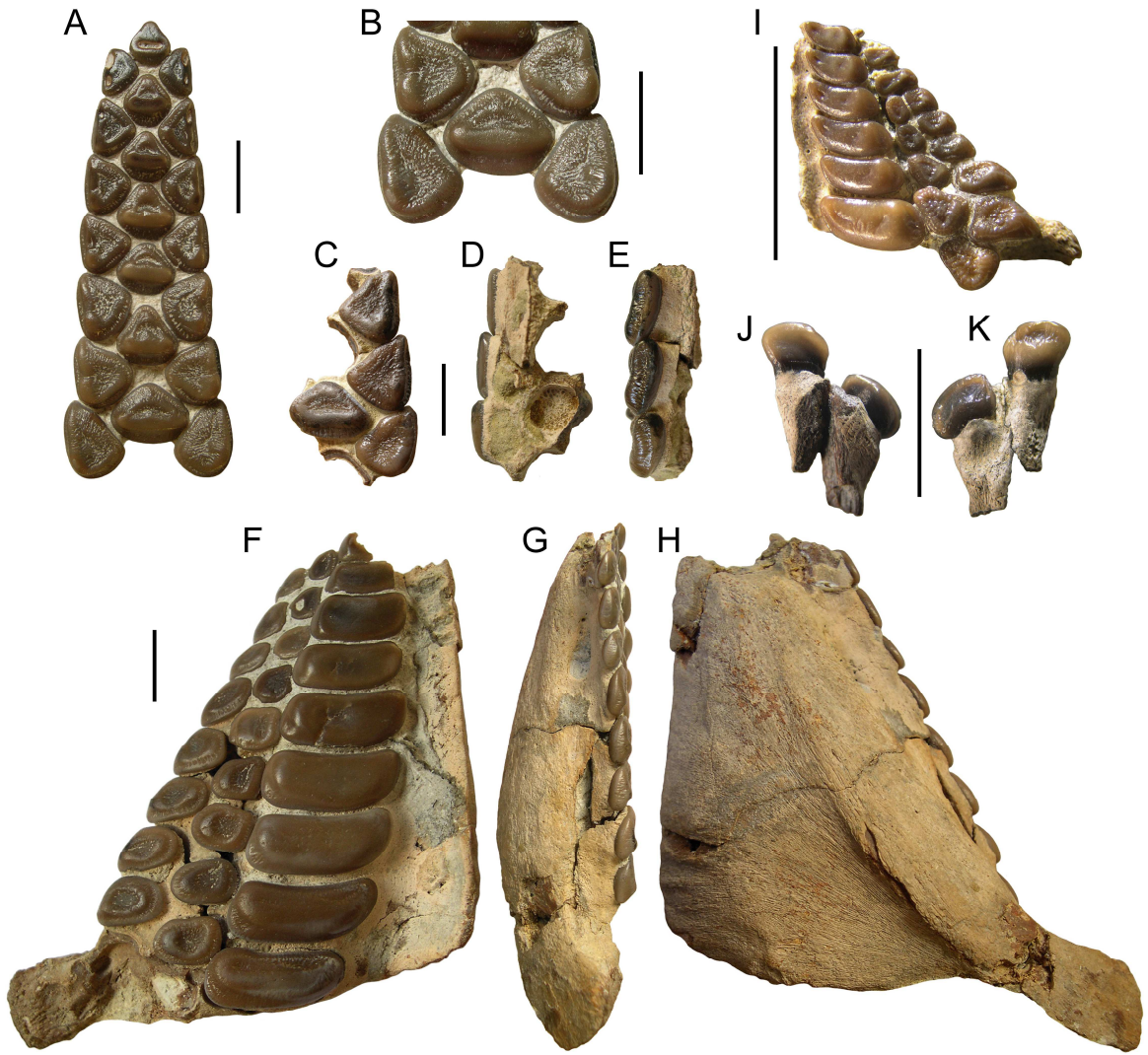
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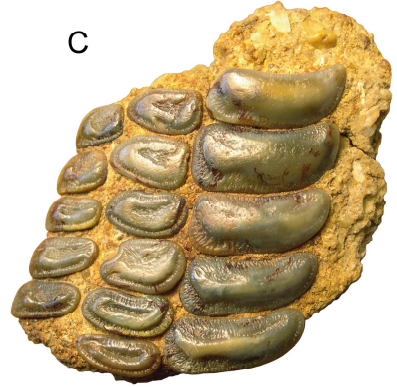
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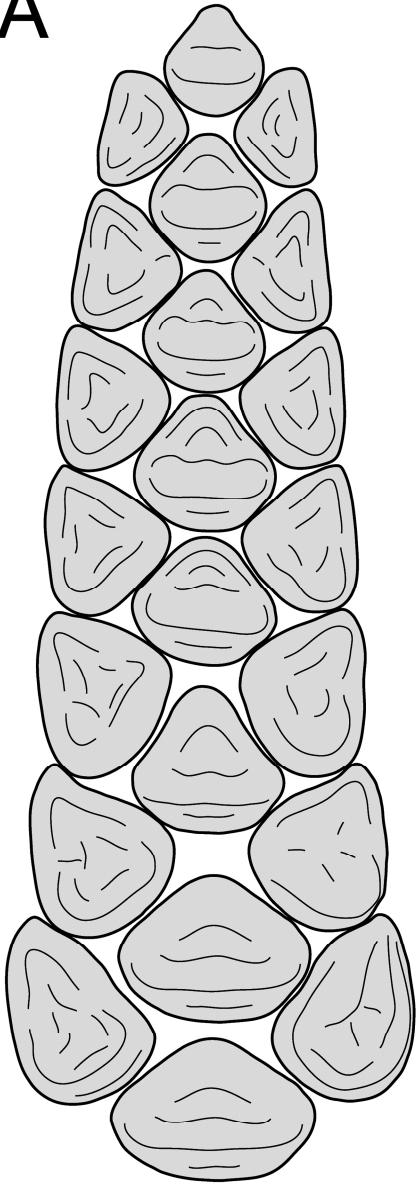


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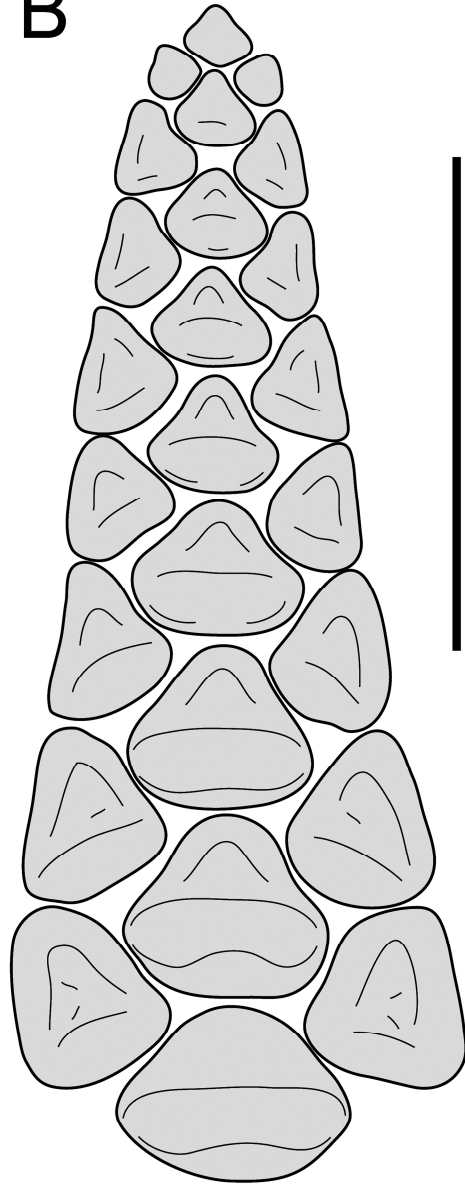


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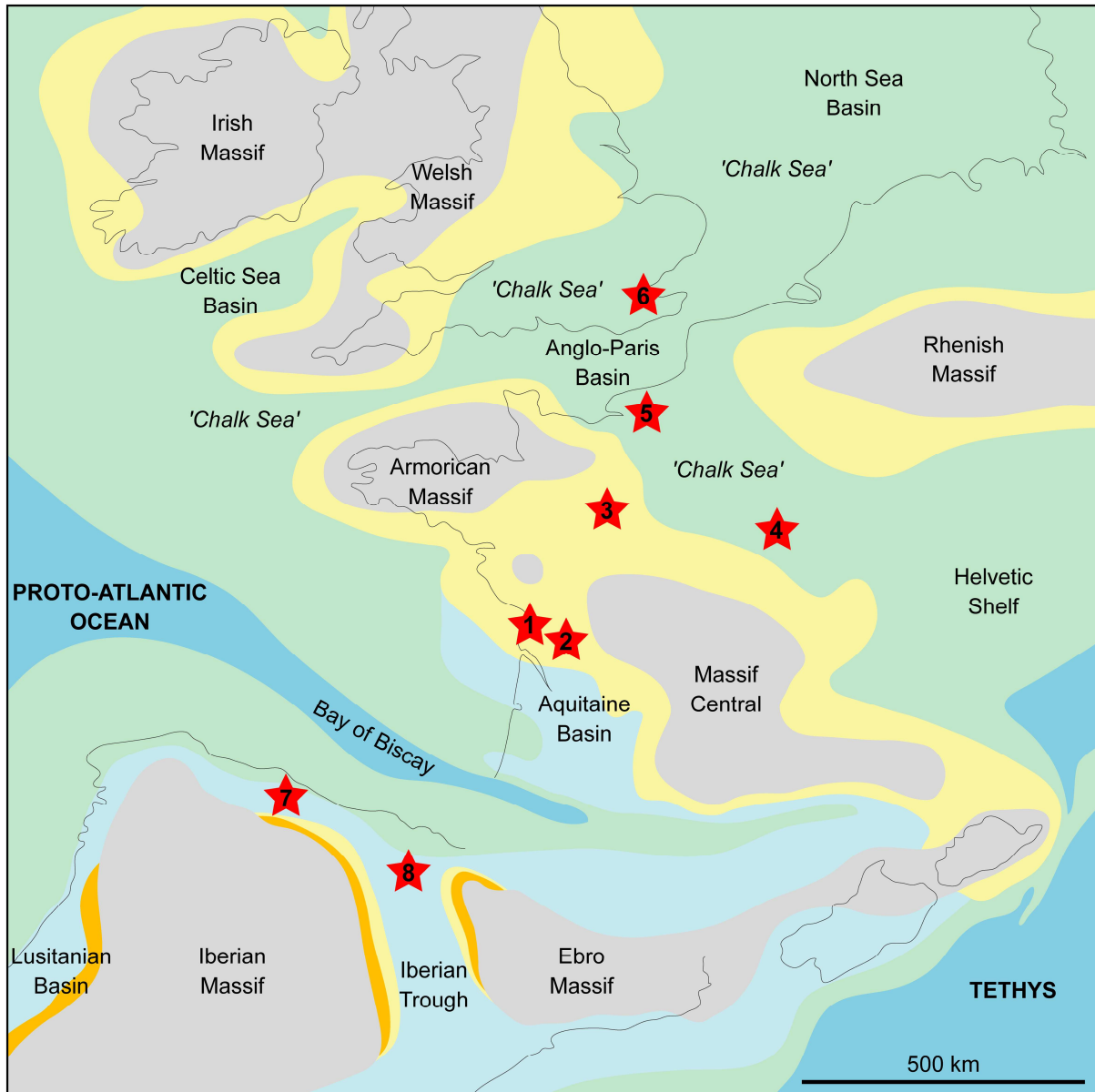
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