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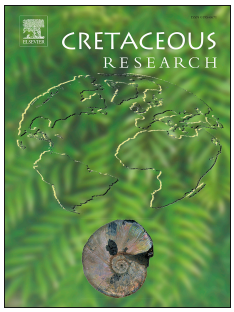

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Reassessment of *Cosmodus* Sauvage, 1879, a poorly known genus of large pycnodont fish (Actinopterygii, Pycnodontiformes) from the Cenomanian (Upper Cretaceous) of Western Europe

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ABSTRACT

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

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

Keywords: Actinopterygii; Pycnodontiformes; Coccodontidae; *Cosmodus*; Dentition; Cenomanian.

1. Introduction

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

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

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

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

2. Geological settings

2.1. Type area

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

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

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

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

3. Systematic palaeontology

Osteichthyes Huxley, 1880

Actinopterygii Cope, 1887

Neopterygii Regan, 1923

Pycnodontiformes Berg, 1937

?Coccodontidae Berg, 1940

Cosmodus Sauvage, 1879

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

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

Cosmodus carentonensis (Coquand, 1859)

Figs. 1, 3–5A

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

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

1859 *Gyrodus carentonensis* Coquand: p. 953.

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

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

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

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

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

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

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

1895 *Coelodus major* Woodward: p. 257.

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

1909 *Coelodus carentonensis* (Coquand); Priem, p. 325.

1909 *Coelodus fimbriatus* Woodward; Woodward, p. 166, fig. 47.

1912 *Coelodus* (*Gyrodus*) *carentonensis* (Coquand); Priem, p. 269.

1962 *Pycnodus* sp.; Almela and Ríos, p. 61, pl. 7, fig. 2.

1972 *Coelodus fimbriatus* Woodward; Benedetto and Sánchez, p. 61, pl. 2, fig. 7.

1997 *Gyrodus carentonensis* Coquand; Schultz and Paunović, p. 125.

1997 *Coelodus fimbriatus* Woodward; Schultz and Paunović, p. 102, 127.

2005 *Gyrodus carentonensis* Coquand; Kriwet and Schmitz, p. 53.

2005 *Cosmodus grandis* Sauvage; Kriwet and Schmitz, p. 53.

2007 "*Coelodus carentonensis*" (Coquand); Vullo, p. 79, text-fig. 3.1, pl. 4, fig. 2.

2009 "*Cosmodus carentonensis*" (Coquand); Vullo et al., p. 122, figs. 2e, 4a.

2015 *Coelodus fimbriatus* Woodward; Brignon, p. 57, fig. 32.1.

2015 *Cosmodus* cf. *grandis* (Sauvage); Vullo, p. 241, fig. 172h.

2016 "*Coelodus*" *fimbriatus* Woodward; Friedman et al., p. 171, table 1.

Neotype. MHNLR 2017.10.1, a complete vomerine dentition from "Le Puits des Insurgés", île Madame, Charente-Maritime department, France (Fig. 3A, B).

Paraneotype. MHNLR 2017.10.2, a complete left prearticular dentition from "Le Puits des Insurgés", île Madame, Charente-Maritime department, France (Fig. 3F–H).

Referred material. MHNLR 2017.10.4, a fragmentary vomerine dentition from Nersac ("Le Pas" quarry), Charente department, France (Fig. 3C–E); MHNLR 2017.10.3, a complete right prearticular dentition (juvenile) from "Le Puits des Insurgés", île Madame, Charente-Maritime department, France (Fig. 3I); MA 70-530 (type specimen of *Cosmodus grandis* Sauvage, 1879), a subcomplete left prearticular dentition from Seignelay, Yonne department, France (Fig. 4A); NHMUK PV OR 43090 (type specimen of *Coelodus fimbriatus* Woodward,

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

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

Diagnosis. Same as for genus.

3.1. Description

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

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

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

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

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

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

4. Discussion

4.1. Synonymy and designation of a neotype

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

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

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

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

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

4.2. Comparisons and affinities

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

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

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

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

4.3. Distribution and palaeoecology

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

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

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

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

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

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

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

5. Conclusions

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

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

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

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References

Almela, A., Ríos, J.M., 1962. Investigación del Hullero bajo los terrenos mesozoicos de la Costa Cantábrica (zona de Oviedo–Gijón–Villaviciosa–Infiesto). Empresa Nacional "ADARO" de Investigaciones Mineras, Madrid, 171 p.

Andrieu, S., Brigaud, B., Rabourg, T., Noret, A., 2015. The Mid-Cenomanian Event in shallow marine environments: Influence on carbonate producers and depositional sequences (northern Aquitaine Basin, France). Cretaceous Research 56, 587–607.

Barroso-Barcenilla, F., Goy, A., Segura, M., 2009. Ammonite zonation of the upper Cenomanian and lower Turonian in the Iberian Trough, Spain. Newsletters on Stratigraphy 43, 139–164.

Benedetto, J.L., Sánchez, T.M., 1972. *Coelodus toncoensis* nov. sp. (Pisces, Holostei, Pycnodontiformes) de la Formación Yacoraite (Cretácico superior) de la Provincia de Salta. Ameghiniana 9, 59–71.

499 Berg, L.S., 1937. A classification of fish-like vertebrates. Bulletin de l'Académie des
500 Sciences de l'URSS, Classe des Sciences mathématiques et naturelles (série biologique)
501 4, 1277–1280.
502 Berg, L.S., 1940. Classification of fishes, both recent and fossil. Travaux de l'Institut
503 Zoologique de l'Académie des Sciences de l'URSS 5, 87–517.
504 Brignon, A., 2015. Les débuts de la paléontologie en Normandie et dans le Boulonnais.
505 Fossiles 21, 43–62.
506 Brignon, A., 2016. L'abbé Bachelay et la découverte des premiers dinosaures et crocodiliens
507 marins dans le Jurassique des Vaches Noires (Callovien/Oxfordien, Normandie).
508 Comptes Rendus Palevol 15, 595–605.
509 Cavin, L., 2008. Palaeobiogeography of Cretaceous bony fishes (Actinistia, Dipnoi and
510 Actinopterygii). In: Cavin, L., Longbottom, A., Richter, M. (Eds.), Fishes and the
511 Break-up of Pangea. Geological Society, London, Special Publications, 295, 165–183.
512 Chen, W.-J., Santini, F., Carnevale, G., Chen, J.-N., Liu, S.-H., Lavoué, S., Mayden, R.L.,
513 2014. New insights on early evolution of spiny-rayed fishes (Teleostei:
514 Acanthomorpha). Frontiers in Marine Science 1:53.
515 Collins, J.S.H., Villier, L., Breton, G., 2013. A new etyid crab (Crustacea, Decapoda) from
516 the Cenomanian of France. Bulletin of the Mizunami Fossil Museum 39, 47–49.
517 Cope, E.D., 1887. Zittel's Manual of Palaeontology. American Naturalist 21, 1014–1019.
518 Coquand, H., 1858. Description physique, géologique, paléontologique et minéralogique du
519 département de la Charente – Tome premier. Dodivert et C^{e}, Besançon, 542 p.
520 Coquand, H., 1859. Synopsis des animaux et des végétaux fossiles observés dans la formation
521 crétacée du sud-ouest de la France. Bulletin de la Société géologique de France, 2ème
522 série 16, 945–1023.

523 Coquand, H., 1860a. Synopsis des animaux et des végétaux fossiles observés dans les
524 formations secondaires de la Charente, de la Charente-Inférieure et de la Dordogne.
525 Barlatier-Feissat et Demonchy, Marseille, 146 p.
526 Coquand, H., 1860b. Description physique, géologique, paléontologique et minéralogique du
527 département de la Charente – Tome deuxième. Barlatier-Feissat et Demonchy,
528 Marseille, 420 p.
529 Cornuel, J., 1877. Description de débris de poissons fossiles provenant principalement du
530 calcaire néocomien du département de la Haute-Marne. Bulletin de la Société
531 géologique de France, 3ème série 5, 604–626.
532 Cornuel, J., 1880. Note sur de nouveaux débris de pycnodontes portlandiens et néocomiens de
533 l'est du bassin de Paris. Bulletin de la Société géologique de France, 3ème série 8, 150–
534 162.
535 Costa, O.G., 1854–1856. Paleontologia del regno di Napoli – Parte II. Cataneo, Napoli, 380 p.
536 Dalla Vecchia, F.M., Venturini, S., Tentor, M., 2002. The Cenomanian (Late Cretaceous)
537 *Konservat-Lagerstätte* of en Nammoûra (Kesrouâne Province), northern Lebanon.
538 Bollettino della Società Paleontologica Italiana 41, 51–68.
539 Dhondt, A.V., 1984. The unusual Cenomanian oyster *Pycnodonte biauriculatum*. Geobios,
540 Mémoire spécial 8, 53–61.
541 Egerton, P., 1877. On some new pycnodonts. Geological Magazine, Decade 2, 4, 49–55.
542 Fischer, C.E., 1856. Die Fischreste aus dem Plänerschichten von Plauen, Strehlen, Weinböhla
543 und Grosssedlitz. Allgemeine deutsche Naturhistorische Zeitung 2, 134–145.
544 Floquet, M., Mathey, B., Métais, E., Emmanuel, L., Babinot, J.-F., Magniez-Jeannin, F.,
545 Tronchetti, G., 1996. Correlation of sedimentary events during the latest Cenomanian
546 from the Basque Basin to the Castilian Ramp (Northern Spain). Geogaceta 20, 50–53.

547 Francis, I.H., 1984. Correlation between the North Temperate and Tethyan Realms in the
548 Cenomanian of Western France and the significance of hardground horizons.
549 Cretaceous Research 5, 259–269.
550 Friedman, M., 2012. Ray-finned fishes (Osteichthyes, Actinopterygii) from the type
551 Maastrichtian, the Netherlands and Belgium. Scripta Geologica Special Issue 8, 113–
552 142.
553 Friedman, M., Beckett, H.T, Close, R.A., Johanson, Z., 2016. The English Chalk and London
554 Clay: two remarkable British bony fish *Lagerstätten*. In: Johanson, Z., Barrett, P.M.,
555 Richter, M., Smith, M. (Eds.), Arthur Smith Woodward: His Life and Influence on
556 Modern Vertebrate Palaeontology. Geological Society, London, Special Publications
557 430, 165–200.
558 Heckel, J., 1854. Über den Bau und die Eintheilung der Pycnodonten, nebst kurzer
559 Beschreibung einiger neuen Arten derselben. Sitzungsberichte der kaiserlichen
560 Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse 12, 433–
561 464.
562 Hemleben, C., 1977. Rote Tiden und die oberkretazischen Plattenkalke im Libanon. Neues
563 Jahrbuch für Geologie und Paläontologie, Monatschefte 1977, 239–255.
564 Hooks, G.E. III, Schwimmer, D.R., Williams, G.D., 1999. Synonymy of the pycnodont
565 *Phacodus punctatus* Dixon, 1850, and its occurrence in the Late Cretaceous of the
566 southeastern United States. Journal of Vertebrate Paleontology 19, 588–590.
567 Huxley, T.H., 1880. On the applications of the laws of evolution to the arrangement of the
568 Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological
569 Society of London 1880, 649–662.
570 Kriwet, J., 1999. Pycnodont fishes (Neopterygii, †Pycnodontiformes) from the Lower
571 Cretaceous of Uña (E-Spain) with comments on branchial teeth in pycnodontid fishes.

In: Arratia, G., Schultze, H.-P. (Eds.), Mesozoic Fishes 2 – Systematics and Fossil Record. Verlag Dr. Friedrich Pfeil, München, pp. 215–238.

Kriwet, J., 2002. *Anomoeodus pauciseriale* n. sp. (Neopterygii, Pycnodontiformes) from the White Chalk Formation (Upper Cretaceous) of Sussex, South England. Paläontologische Zeitschrift 76, 117–123.

Kriwet, J., 2005. A comprehensive study of the skull and dentition of pycnodont fishes. Zitteliana A 45, 135–188.

Kriwet, J., 2008. The dentition of the enigmatic pycnodont fish, *Athrodon wittei* (Fricke, 1876) (Neopterygii, Pycnodontiformes; Late Jurassic; NW Germany). Fossil Record 11, 61–66.

Kriwet, J., Schmitz, L., 2005. New insight into the distribution and palaeobiology of the pycnodont fish *Gyrodus*. Acta Palaeontologica Polonica 50, 49–56.

Lasseur, E., 2015. Stratigraphie et paléogéographie du Cénomanien dans le Bassin parisien. In: Morel, N. (Ed.), Stratotype Cénomanien. Muséum national d'Histoire naturelle, Paris, and Biotope, Mèze, pp. 83–98.

Lasseur, E., Guillocheau, F., Robin, C., Hanot, F., Vaslet, D., Coueffe, R., Néraudeau, D., 2009. A relative water-depth model for the Normandy Chalk (Cenomanian–Middle Coniacian, Paris Basin, France) based on facies patterns of metre-scale cycles. Sedimentary Geology 213, 1–26.

Licht, M., 2009. The relationship of prearticular length and standard length in pycnodontiform fishes. Studia Geologica Salmanticensia 45, 139–148.

Licht, M., Kogan, I., 2011. Late Cretaceous pycnodont fishes (Actinopterygii, Neopterygii) from Saxony (Eastern Germany). Freiberger Forschungshefte, C 540, 79–90.

Marramà, G., Villier, B., Dalla Vecchia, F.M., Carnevale, G., 2016. A new species of *Gladiopycnodus* (Coccodontoidea, Pycnodontomorpha) from the Cretaceous of

Lebanon provides new insights about the morphological diversification of pycnodont fishes through time. Cretaceous Research 61, 34–43.

Martín-Abad, H., Poyato-Ariza, F.J., 2013. Historical patterns of distribution in pycnodontiform and amiiform fishes in the context of moving plates. Geologica Belgica 16, 217–226.

Moreau, P., 1996. Analyse de la transgression cénomanienne sur la bordure nord-occidentale du Bassin de l'Aquitaine. Géologie de la France 1, 3–16.

Morel, N., 2015. La stratigraphie du Cénomanien de la Sarthe. In: Morel, N. (Ed.), Stratotype Cénomanien. Muséum national d'Histoire naturelle, Paris, and Biotope, Mèze, pp. 69–82.

Néraudeau, D., Thierry, J., Moreau, P., 1997. Variation in echinoid biodiversity during the Cenomanian–early Turonian transgressive episode in Charentes (France). Bulletin de la Société géologique de France 168, 51–61.

Passy, A., 1832. Description géologique du département de la Seine-Inférieure. Nicétas Periaux, Rouen, 371 p.

Philip, J., Floquet, M., Platel, J.-P., Bergerat, F., Sandulescu, M., Bara-Boshkin, E., Amon, E., Guiraud, R., Vaslet, D., Le Nindre, Y., Ziegler, M., Poisson, A., Bouaziz, S., 2000. Late Cenomanian (94.7 to 93.5 Ma). In: Dercourt, J., Gaetani, M, Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M.F., Cadet, J.-P., Crasquin, S., Sandulescu, M. (Eds.), Atlas Peri-Tethys, Palaeogeographical Maps. CCGM/CGMW, Paris, map 14.

Poyato-Ariza, F.J., Bermúdez-Rochas, D.D., 2009. New pycnodont fish (*Arcodonichthys pasiegae* gen. et sp. nov.) from the Early Cretaceous of the Basque–Cantabrian Basin, northern Spain. Journal of Vertebrate Paleontology 29, 271–275.

Poyato-Ariza, F.J., Wenz, S., 2002. A new insight into pycnodontiform fishes. Geodiversitas 24, 139–248.

622 Poyato-Ariza, F.J., Fielitz, C., Wenz, S., 1999. Marine actinopterygian fauna from the Upper
623 Cretaceous of Albaina (Laño quarry, northern Spain). Estudios del Museo de Ciencias
624 Naturales de Alava 14 (Núm. Espec. 1), 325–338.
625 Priem, F., 1897. Sur les poissons de l'Eocène du Mont Mokattam (Egypte). Bulletin de la
626 Société géologique de France, 3ème série 25, 212–227.
627 Priem, F., 1898. Sur des pycnodontes et des squales du Crétacé supérieur du bassin de Paris
628 (Turonien, Sénonien, Montien inférieur). Bulletin de la Société géologique de France,
629 3ème série 26, 229–243.
630 Priem, F., 1899. Sur des poissons fossiles éocènes d'Egypte et de Roumanie et rectification
631 relative à *Pseudolates Heberti* Gervais sp. Bulletin de la Société géologique de France,
632 3ème série 27, 241–253.
633 Priem, F., 1908. Etude des poissons fossiles du Bassin parisien. Publications des Annales de
634 Paléontologie, Masson et Cie, Paris, 144 p.
635 Priem, F., 1909. Sur un pycnodonte du Sénonien supérieur de Tunisie. Bulletin de la Société
636 géologique de France, 4ème série 9, 324–326.
637 Priem, F., 1912. Sur des poissons des terrains secondaires du Sud de la France. Bulletin de la
638 Société géologique de France, 4ème série 12, 250–271.
639 Rage, J.-C., Néraudeau, D., 2004. A new pachyostotic squamate reptile from the Cenomanian
640 of France. Palaeontology 47, 1195–1210.
641 Regan, C.T., 1923. The skeleton of *Lepidosteus*, with remarks on the origin and evolution of
642 the lower neopterygian fishes. Proceedings of the Zoological Society of London 1923,
643 445–461.
644 Sauvage, H.-E., 1879. Bulletin de la Société des Sciences historiques et naturelles de l'Yonne,
645 3ème série 1, 20–84.

Sauvage, H.-E., 1880. Notes sur les poissons fossiles (suite). Bulletin de la Société géologique de France, 3ème série 8, 451–462.

Schultz, O., Paunović, M., 1997. Der Nachweis von *Coelodus* (Osteichthyes, Pycnodontidae) im Turonien (Oberkreide) von Gams bei Hieflau, Steiermark, Österreich, und aus der Oberkreide von Kroatien und Italien. Annalen des Naturhistorischen Museums in Wien. Serie A für Mineralogie und Petrographie. Geologie und Paläontologie, Anthropologie und Prähistorie 98, 73–141.

Shimada, K., Williamson, T.E., Sealey, P.L., 2010. A new gigantic pycnodont fish from the Juana Lopez Member of the Upper Cretaceous Mancos Shale of New Mexico, U.S.A. Journal of Vertebrate Paleontology 30, 598–603.

Stumpf, S., Ansorge, J., Pfaff, C., Kriwet, J., 2017. Early Jurassic diversification of pycnodontiform fishes (Actinopterygii, Neopterygii) after the end-Triassic extinction event: Evidence from a new genus and species, *Grimmenodon aureum*. Journal of Vertebrate Paleontology 37:e1344679.

Szabó, M., Gulyás, P., Ősi, A., 2016. Late Cretaceous (Santonian) pycnodontid (Actinopterygii, Pycnodontidae) remains from the freshwater deposits of the Csehbánya Formation, (Iharkút, Bakony Mountains, Hungary). Annales de Paléontologie 102, 123–134.

Taverne, L., Capasso, L. 2014. Ostéologie et phylogénie des Coccodontidae, une famille remarquable de poissons Pycnodontiformes du Crétacé supérieur marin du Liban, avec la description de deux nouveaux genres. Palaeontos 25, 3–43.

Thurmond, J.T., 1974. Lower vertebrate faunas of the Trinity Division in North-Central Texas. Geoscience and Man 8, 103–129.

669 Van Bakel, B.W.M., 2013. Preservation of internal pleurites in a new palaeocorystid crab
670 (Crustacea, Brachyura, Raninoidia) from the Cenomanian (Upper Cretaceous) of
671 Poitou-Charentes, France. Zootaxa 3701, 322–328.
672 Videt, B., 2004. Dynamique des paléoenvironnements à huîtres du Crétacé supérieur nord-
673 aquitains (SO France) et du Moi-Pliocène andalou (SE Espagne) : biodiversité, analyse
674 séquentielle, biogéochimie. Mémoires de Géosciences Rennes 108, 1–261.
675 Videt, B., Néraudeau, D., 2007. Paléoécologie des ostréidés cénomaniens de la bordure nord
676 du Bassin aquitain (SW France). Bulletin de la Société géologique de France 178, 39–
677 50.
678 Vullo, R., 2007. Les vertébrés du Crétacé supérieur des Charentes (Sud-Ouest de la France) :
679 biodiversité, taphonomie, paléoécologie et paléobiogéographie. Mémoires de
680 Géosciences Rennes 125, 1–302.
681 Vullo, R., 2015. Les poissons. In: Morel, N. (Ed.), Stratotype Cénomanien. Muséum national
682 d'Histoire naturelle, Paris, and Biotope, Mèze, pp. 237–244.
683 Vullo, R., Courville, P., 2014. Fish remains (Elasmobranchii, Actinopterygii) from the Late
684 Cretaceous of the Benue Trough, Nigeria. Journal of African Earth Sciences 97, 194–
685 206.
686 Vullo, R., Néraudeau, D., 2009. Pterosaur remains from the Cenomanian (Late Cretaceous)
687 paralic deposits of Charentes, western France. Journal of Vertebrate Paleontology 29,
688 277–282.
689 Vullo, R., Cappetta, H., Néraudeau, D., 2007. New sharks and rays from the Cenomanian and
690 Turonian of Charentes, France. Acta Palaeontologica Polonica 52, 99–166.
691 Vullo, R., Bernárdez, E., Buscalioni, A.D., 2009. Vertebrates from the middle?–late
692 Cenomanian La Cabaña Formation (Asturias, northern Spain): Palaeoenvironmental and

palaeobiogeographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 276, 120–129.

Vullo, R., Cavin, L., Khalloufi, B., Amaghzaz, M., Bardet, N., Jalil, N.-E., Jourani, E., Khaldoune, F., Gheerbrant, E., 2017. A unique Cretaceous–Paleogene lineage of piranha-jawed pycnodont fishes. Scientific Reports 7:6802.

Walker, S.E., Brett, C.E., 2002. Post-Paleozoic patterns in marine predation: Was there a Mesozoic and Cenozoic marine predatory revolution? In: Kowalewski, M., Kelley, P.H. (Eds.), The Fossil Record of Predation. Palaeontological Society Papers 8, 119–193.

Wilmsen, M., Voigt, T., 2006. The middle–upper Cenomanian of Zilly (Sachsen-Anhalt, northern Germany) with remarks on the *Pycnodonte* Event. Acta Geologica Polonica 56, 17–31.

Wippich, M.G.E., Lehmann, J., 2004. *Allocrioceras* from the Cenomanian (mid-Cretaceous) of Lebanon and its bearing on the palaeobiological interpretation of heteromorphic ammonites. Palaeontology 47, 1093–1107.

Woodward, A.S., 1893. Some Cretaceous pycnodont fishes. Geological Magazine, Decade 3, 10, 433–436, 487–493.

Woodward, A.S., 1895. Catalogue of Fossil Fishes in the British Museum (Natural History) – Part III. Containing the Actinopterygian Teleostomi of the Orders Chondrostei (concluded), Protospondyli, Aetheospondyli, and Isospondyli) (in part). Trustees of the British Museum (Natural History), London, 544 p.

Woodward, A.S., 1909. The fossil fishes of the English Chalk – Part V. Monograph of the Palaeontographical Society, London 63, 153–184.

Woodward, A.S., 1918. The fossil fishes of the English Wealden and Purbeck formations – Part II. Monograph of the Palaeontographical Society, London 70, 49–104.

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.

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

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

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

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

768 *Anomoeodus*.

	Cosmodus (this paper)	***Coccodus*** (after Poyato-Ariza and Wenz, 2002; Kriwet, 2005)	***Coelodus*** (after Poyato-Ariza and Wenz, 2002)	***Anomoeodus*** (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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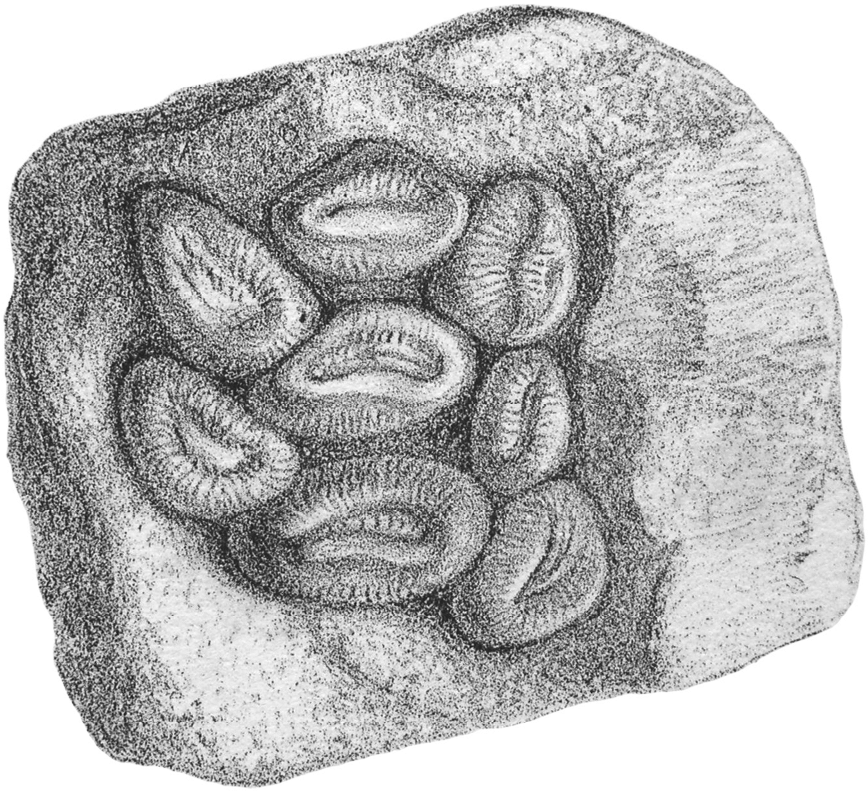

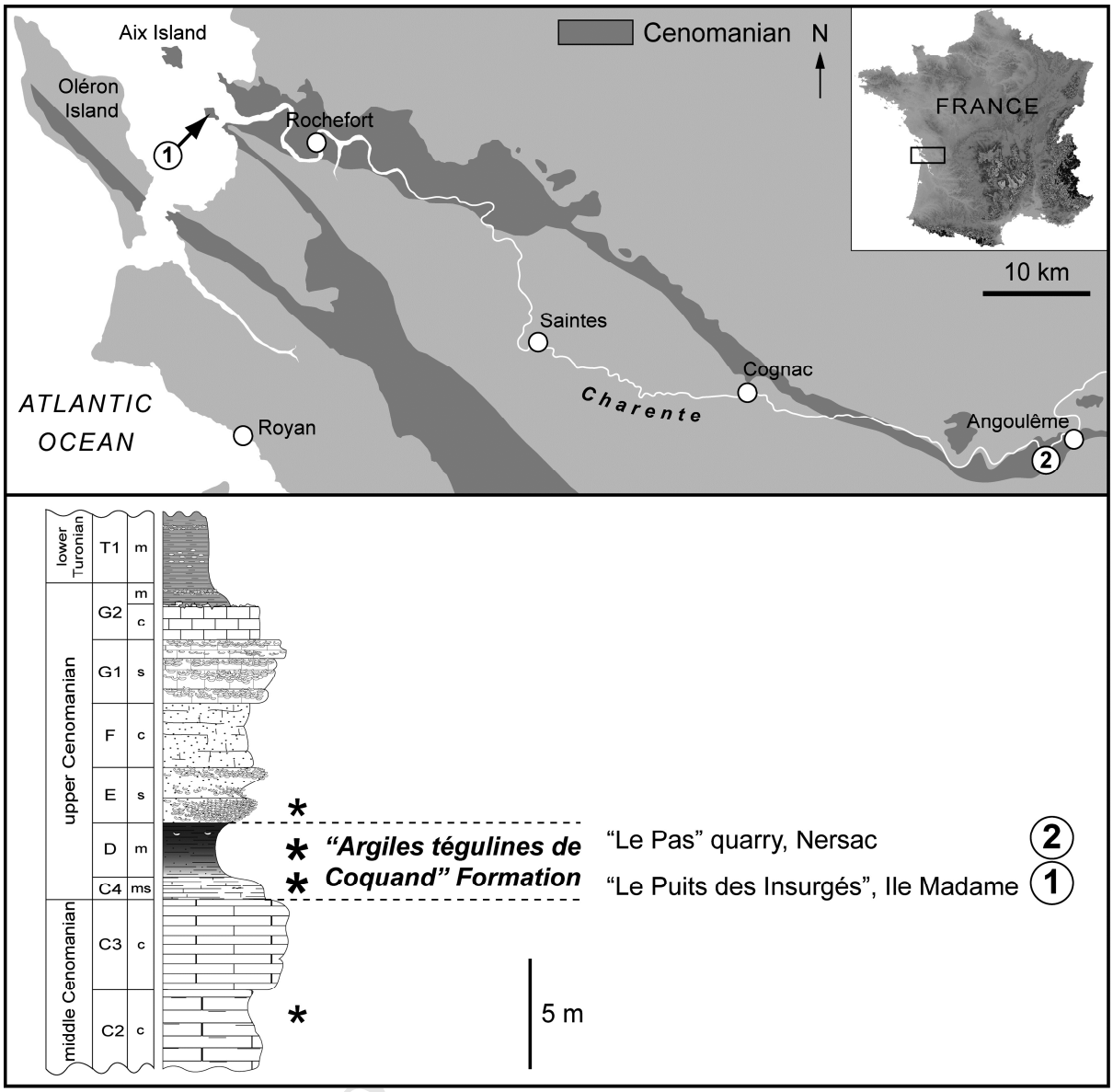
Aix Island
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upper Cenomanian
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T1
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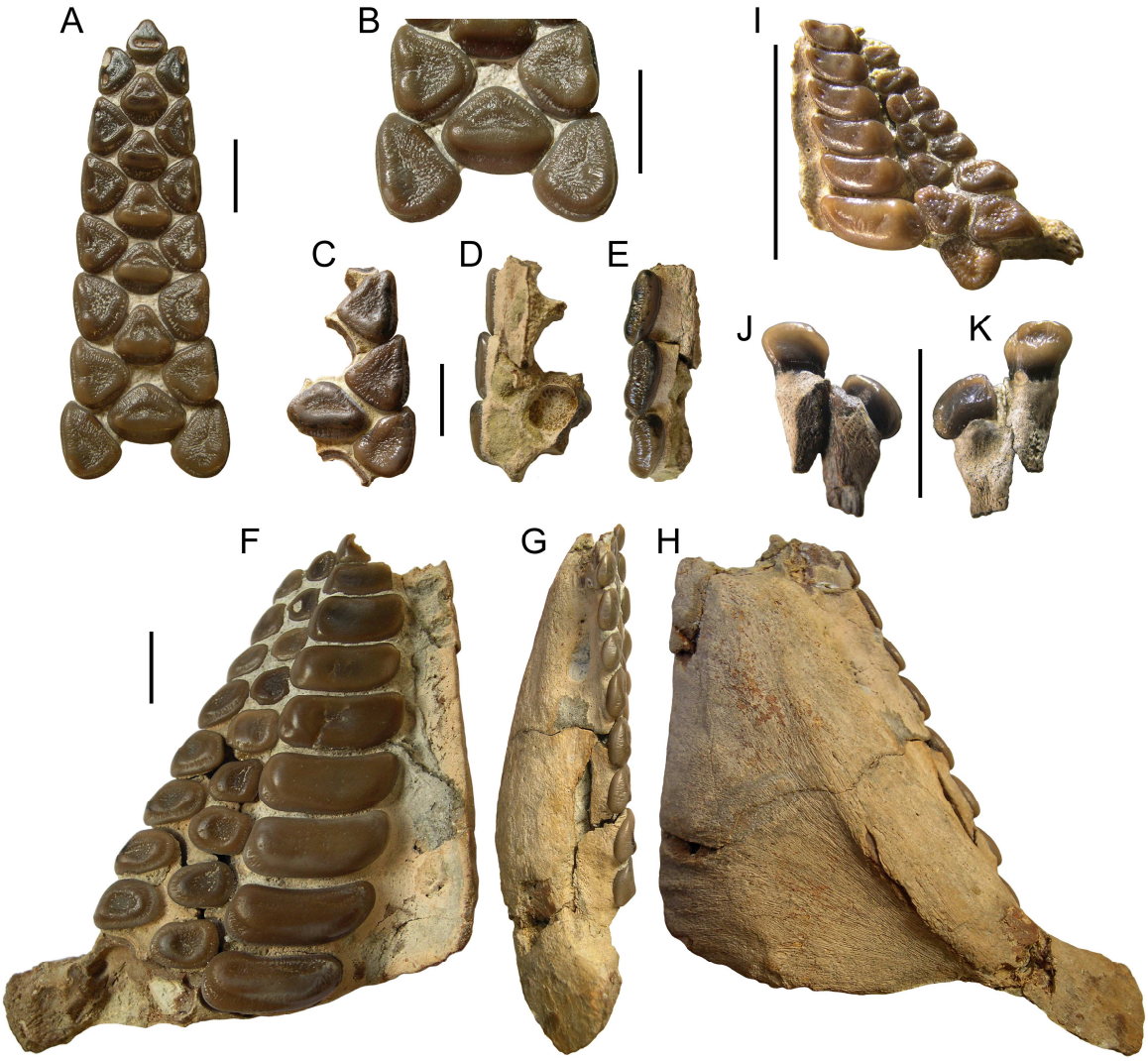
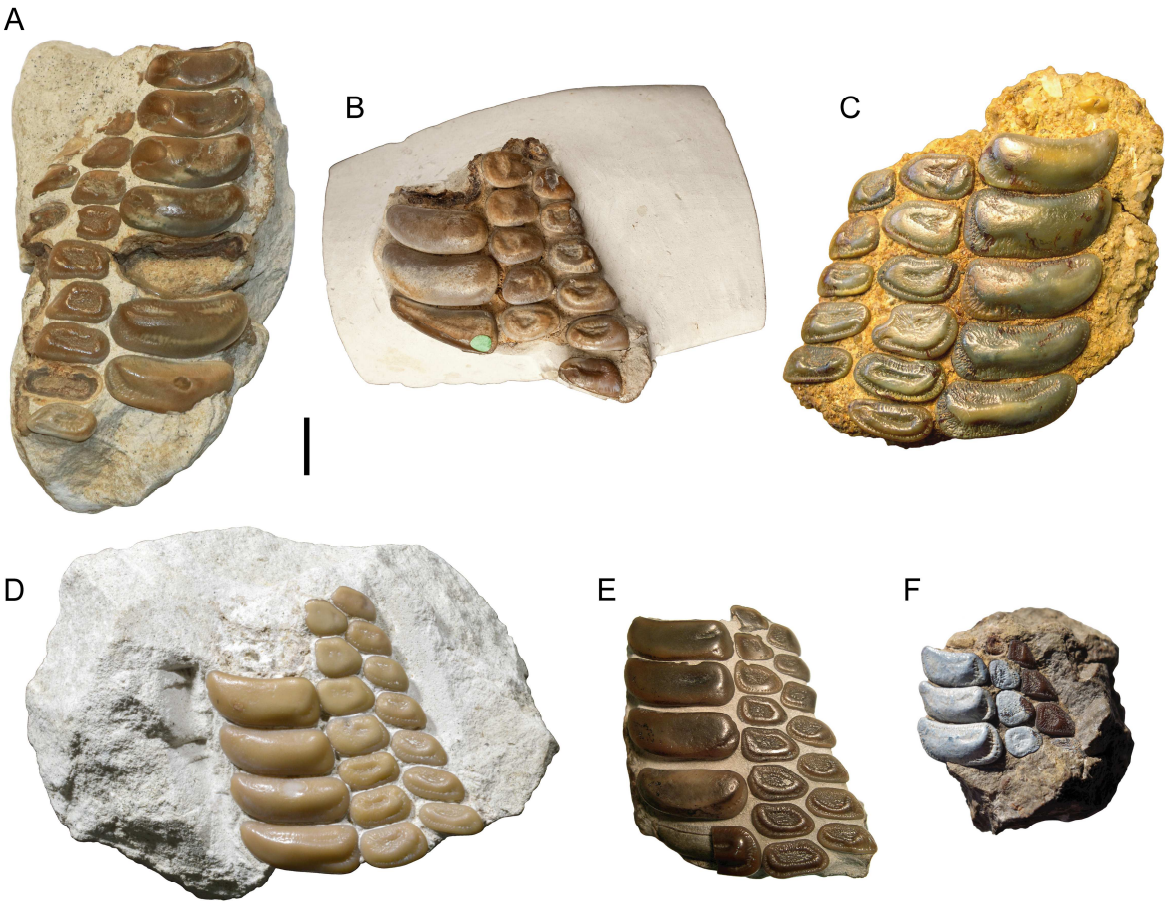
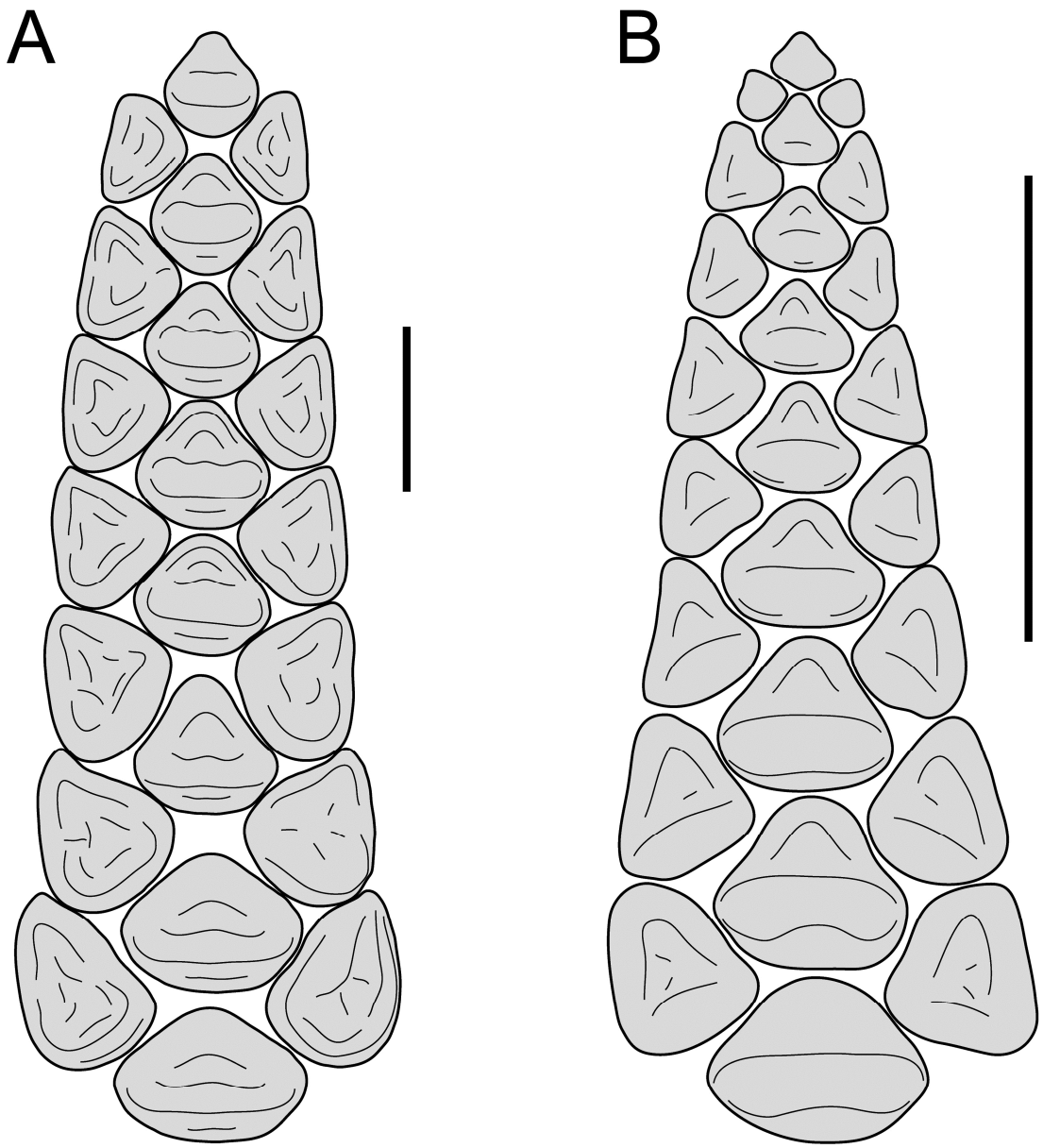
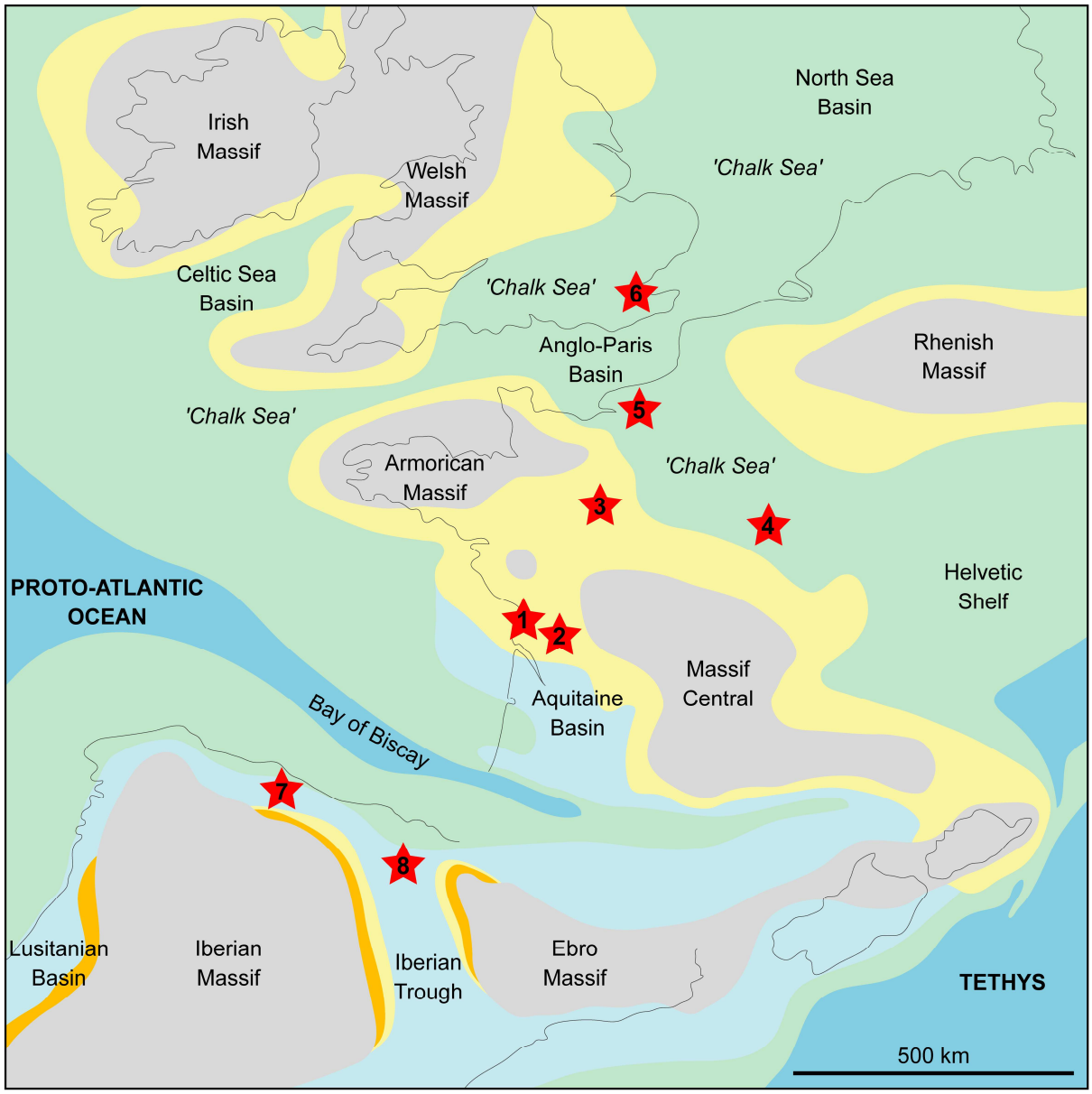
"Argiles tégulines de Coquand" Formation
"Le Pas" quarry, Nersac
"Le Puits des Insurgés", Ile Madame
5 m









DEPOSITIONAL ENVIRONMENTS

- Exposed land
- Fluvial, lacustrine
- Coastal marine, shallow marine (terrigenous shelves)
- Shallow marine carbonates (platforms, build-ups and ramps)
- Deep(er) marine carbonates (hemipelagic shelves)
- Deep marine