# New sharks and rays from the Cenomanian and Turonian of Charentes, France

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New or so far poorly known neoselachians from the Cenomanian and Turonian of SW France are described. The material studied herein comes from nine localities in the Charentes region, comprising palaeoenvironments ranging from coastal to open marine environments, and consists of two orectolobiforms, six lamniforms, and four rajiforms. The new taxa are *Squalicorax coquandi* sp. nov. and *Roulletia bureaui* gen. et sp. nov. within lamniforms, and *Hamrabatis bernardezi* sp. nov., *Archingeayia sistaci* gen. et sp. nov., and *Engolismaia couillardi* gen. et sp. nov. within rajiforms. New specimens of *Odontaspis rochebrunei* Sauvage, 1880 from the type area allow redescription of this taxon, assigned herein to the genus *Cenocarcharias*. Occurrences of *Squalicorax baharijensis*, *S.* cf. *intermedius*, and *Archaeolamna* sp., previously unrecorded from this region, and *Almascyllium*, a genus generally described from younger strata, are also noted, and improve knowledge of mid-Cretaceous selachian faunas from Western Europe.

Key words: Chondrichthyes, Neoselachii, Orectolobiformes, Lamniformes, Rajiformes, Cretaceous, France.

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## Introduction

The Cenomanian deposits of the Charentes region (administrative departments of Charente and Charente-Maritime), in the northern part of the Aquitaine Basin (SW France), display successions of coastal marine rocks rich in isolated vertebrate remains, especially selachian teeth. As early as the 19th Century, Coquand (1859) and Sauvage (1880) mentioned and described a few specimens, then largely assigned to new species (*Corax elongatus* Coquand, *C. parallelus* Coquand, *C. trapezoidalis* Coquand, *Lamna trigeri* Coquand, *Otodus michoni* Coquand, *Odontaspis rochebrunei* Sauvage, *Galeocerdo tremauxi* Sauvage). The five nominal species created by Coquand, very briefly described, without figures and based on presumed lost material, may constitute nomina dubia. In comparison, the two species established by Sauvage were illustrated: *O. rochebrunei* seems to be a valid taxon, but needing redefinition, whereas *G. tremauxi* might be a junior synonym of *Cretolamna appendiculata* (Agassiz, 1843). Thereafter, in an article enumerating some fish remains from the Mesozoic of Southern France, Priem (1912) recognized with certainty only *C. appendiculata* and *Squalicorax falcatus* (Agassiz, 1843). Since the works of these former authors, very few studies have dealt with the selachians from the Cenomanian of Charentes. Recently, Landemaine (1991), in an article devoted to the Late Cretaceous elasmobranchs from several localities of SW France, established for the site of "Les Renardières", near to Tonnay-Charente (Charente-Maritime), a list of 21 taxa of which seven were new species included in four new genera. Recent systematic study of new or previously ignored deposits has yielded abundant material (Vullo et al. 2003, 2005; Vullo 2005). In addition to the re-description and illustration of *O. rochebrunei* Sauvage, 1880, the new forms of selachians are described here.

*Institutional abbreviation*.—UM, Université de Montpellier II (France).

*Other abbreviations*.—AMA, l'Amas; FBN, Font-de-Benon; FVN, Fouras-Vauban; LMS, Le Mas; MTG, Montagan; PDB, Port-des-Barques; PDI, Le Puits des Insurgés; RND, Les Renardières; TLM, Traslemaine.

## Geological settings

Cenomanian deposits occur largely on the northern edge of the Aquitaine Basin, where they outcrop along a NW-SE axis connecting the Armorican Massif with the Central Massif (Fig. 1A). Within the region, the Cenomanian transgression represents the return to marine conditions after the Late Jurassic–Early Cretaceous regressive period. The various

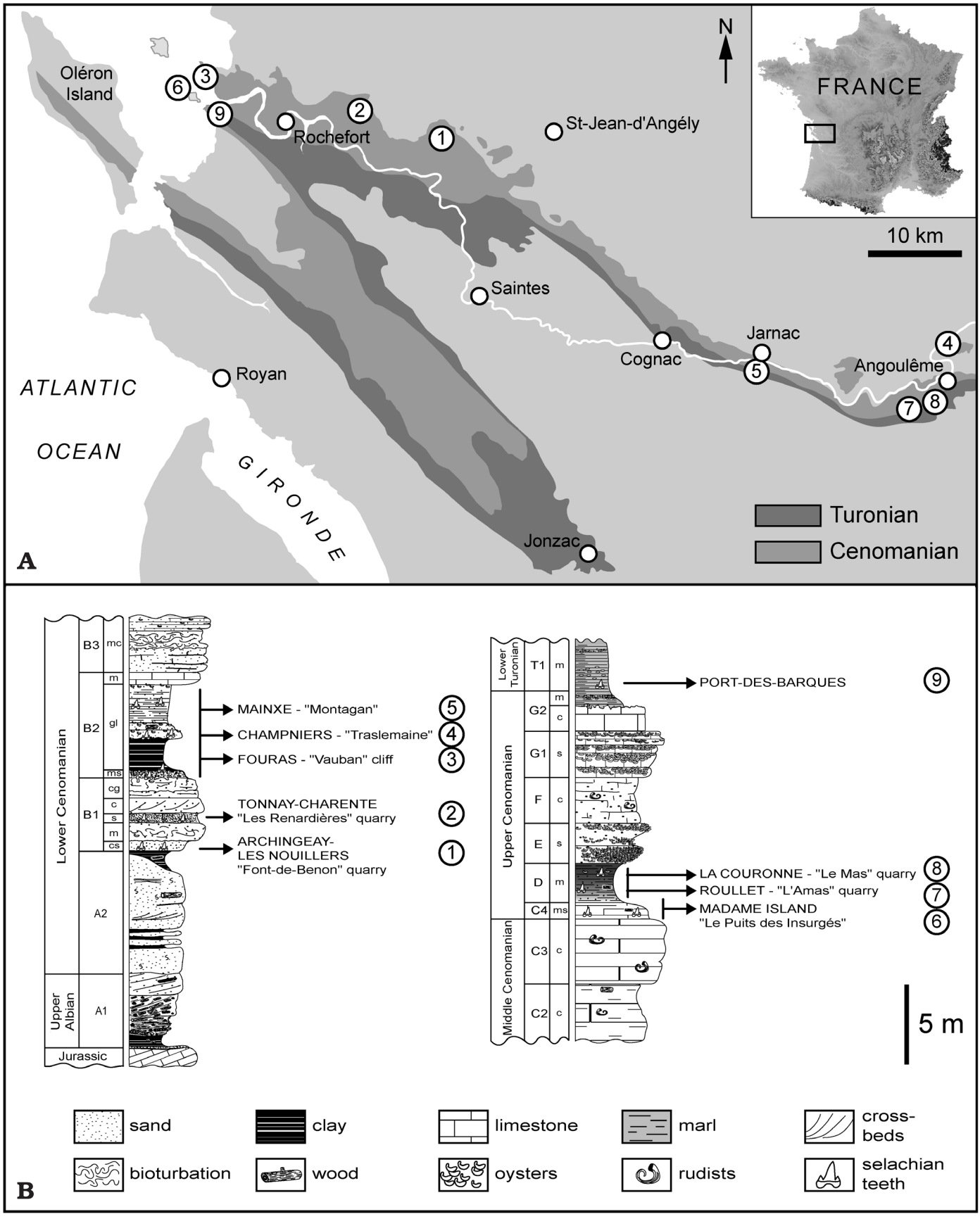


Fig. 1. **A**. Map of the Charentes region showing the Cenomanian and Turonian outcrops and the geographical position of the localities which have yielded the selachian teeth studied in this paper. **B**. Stratigraphical positions of the localities.

Table 1. List and relative abundance of selachian taxa from each locality (after Landemaine 1991; Vullo et al. 2003, 2005; Vullo 2005). Abbreviations: A, abundant; C, common; R, rare; Tur., Turonian; AMA, l'Amas; FBN, Font-de-Benon; FVN, Fouras-Vauban; LMS, Le Mas; MTG, Montagan; PDB, Port-des-Barques; PDI, Le Puits des Insurgés; RND, Les Renardières; TLM, Traslemaine.

| Taxa / Localities | Lower Cenomanian | | | | | Upper Cenomanian | | | Tur. |
|---|---|---|---|---|---|---|---|---|---|
| | FDB | RND | FVN | TLM | MTG | PDI | AMA | LMS | PDB |
| *Hybodus* sp. | C | C | C | R | R | – | – | – | – |
| *Polyacrodus maiseyi* Landemaine, 1991 | – | R | R | R | – | – | – | – | – |
| *Polyacrodus levis* (Woodward, 1887) | – | R | – | – | – | – | – | – | – |
| *Polyacrodus* sp. | R | – | – | – | – | – | – | – | – |
| *Tribodus morlati* (Landemaine, 1991) | A | A | C | C | C | – | – | – | – |
| *Heterodontus paucicarinatus* (Landemaine, 1991) | – | R | – | C | R | – | – | – | – |
| *Cederstroemia* sp. | – | R | – | R | – | – | – | – | – |
| *Almascyllium* sp. | R | – | – | – | – | – | – | – | – |
| *Cantioscyllium* spp. | A | R | C | C | C | – | R | – | – |
| *Chiloscyllium* sp. | C | – | R | R | R | – | – | – | – |
| "*Carcharias*" *amonensis* (Cappetta and Case, 1975) | A | A | A | A | A | R | C | – | – |
| *Roulletia bureaui* gen. et sp. nov. | – | – | – | – | – | – | R | – | – |
| *Scapanorhynchus minimus* Landemaine, 1991 | A | A | A | C | A | R | R | – | – |
| *Squalicorax baharijensis* (Stromer, 1927) | – | R | – | – | – | R | – | R | – |
| *Squalicorax coquandi* sp. nov. | – | – | – | – | – | – | – | – | R |
| *Squalicorax* cf. *intermedius* Glückman in Glückman and Shvazhaite, 1971 | – | – | – | – | – | R | – | – | – |
| *Squalicorax* sp. | R | C | C | R | R | R | R | – | – |
| *Cenocarcharias tenuiplicatus* (Cappetta and Case, 1975) | R | R | R | R | R | – | – | – | – |
| *Cenocarcharias rochebrunei* (Sauvage, 1880) | – | – | – | – | – | R | R | R | – |
| *Cretodus semiplicatus* (Münster in Agassiz, 1843) | R | C | C | R | R | – | R | R | – |
| *Archaeolamna* sp. | – | R | R | R | – | – | R | – | – |
| *Protolamna compressidens* (Herman, 1977) | – | C | R | – | R | – | R | – | – |
| *Protolamna* sp. | – | R | R | R | R | – | R | R | – |
| *Cretolamna appendiculata* (Agassiz, 1843) | – | – | – | – | – | – | R | R | R |
| *Protoscyliorhinus magnus* Landemaine, 1991 | R | R | R | R | R | – | – | – | – |
| *Pseudohypolophus mcnultyi* (Thurmond, 1971) | A | C | A | R | C | – | – | R | – |
| *Turoniabatis cappettai* Landemaine, 1991 | C | R | C | R | R | – | – | – | – |
| *Onchopristis dunklei* McNulty and Slaughter, 1962 | R | C | C | – | R | – | – | – | – |
| *Ptychotrygonoides pouiti* Landemaine, 1991 | R | C | C | C | C | – | – | – | – |
| *Ptychotrygon* spp. | A | R | C | R | C | – | – | – | – |
| Sclerorhynchid-like indeterminate genus and species | – | – | – | – | – | – | R | – | – |
| *Archingeayia sistaci* gen. et sp. nov. | R | – | – | – | – | – | – | – | – |
| *Engolismaia couillardi* gen. et sp. nov. | – | – | – | R | R | – | – | – | – |
| *Hamrabatis bernardezi* sp. nov. | R | – | C | R | C | – | R | – | – |
| "*Rhinobatos*" sp. | – | – | R | R | R | – | – | – | – |
| *Squatirhina* sp. | – | – | – | R | – | – | – | – | – |

localities treated here are dated from the basal Cenomanian to the basal Turonian (Fig. 1B). The first facies of the series correspond to very paralic, coastal environments (littoral, lagoons, mangroves, estuaries) (Néraudeau et al. 2002; Vullo et al. 2003) changing to more distal and pelagic environments (outer shelf) at the end of the stage (Moreau 1996). The Cenomanian deposits of the Charentes area are divided into seven lithological units (A to G), themselves subdivided into subunits (e.g., subunits B1, B2, and B3 for unit B), each subunit consisting of one or several lithological levels (e.g., B2gl for the glauconitic upper part of the subunit B2) (Néraudeau et al. 1997).

*Locality 1*.—"Font-de-Benon" quarry at Archingeay – Les Nouillers, Charente-Maritime (Lower Cenomanian; subunit B1, lithological level B1cs): this locality, originally exploited and studied for its levels with insect-bearing amber (Néraudeau et al. 2002), contains in the higher part of the section a condensed sandy layer (60 cm thick), very rich in vertebrate microremains and yielding a diverse invertebrate fauna (orbitolinids, oysters, echinoids) (Vullo et al. 2003). This level, located towards the top of the section, corresponds to the very first clearly marine siliciclastic facies deposited at the beginning of the Cenomanian transgression.

*Locality 2*.—"Les Renardières" quarry at Tonnay-Charente, Charente-Maritime (Lower Cenomanian; subunit B1, lithological level B1s): within a cutting now landscaped, this rich vertebrate microremain deposit corresponds to a 40 to 50 cm thick condensed bed, consisting of phosphatic silty sands. The stratigraphy and the palaeontological characteristics of that locality, sometimes also mentioned in the literature as "Lussant", have recently been described by Néraudeau et al. (2005), after the selachian fauna had been previously studied by Landemaine (1991).

*Locality 3*.—"Vauban" cliff at Fouras, Charente-Maritime (Lower Cenomanian; subunit B2, lithological level B2ms): this locality occurs as a condensed level deposited on a hard ground marking the top of the subunit B1. It comprises 50 cm thick sandy clayey lenses bearing many gravels, encrusting algal concretions, oysters, echinoderms, bone pebbles, and small limonitized wood fragments. The vertebrate remains accompanying the selachian teeth are represented by actinopterygians (pycnodontiforms, *Enchodus* sp.), chelonians, crocodilians, pterosaurs, and dinosaurs (Vullo et al. 2005).

*Locality 4*.—"Traslemaine" at Champniers, Charente (Lower Cenomanian; subunit B2, lithological levels B2ms–B2gl): this site was a temporary section exposed in 2004 by the construction of a new road and is now landscaped. There was here no real distinction between lithological levels B2ms and B2gl. The vertebrate-bearing layer corresponded to an alternation of shelly glauconitic sands and sandstones (50 cm to 3 m thick). The fauna is rather similar to that recovered from Fouras-Vauban.

*Locality 5*.—"Montagan" at Mainxe, Charente (Lower Cenomanian; subunit B2, lithological levels B2ms–B2gl): this site corresponds to a temporary exposure caused in 2005 by the construction of a new road, just south of the city of Jarnac. The glauconitic subunit B2 is lenticular (0 to 4 m thick) and consists of very fine green sands and of an alternation of millimetres-thick clay lenses. Vertebrates and wood microremains are locally highly concentrated. Invertebrate remains are rare and comprise poorly preserved fine shell fragments.

*Locality 6*.—"Le Puits des Insurgés" at Madame Island, Charente-Maritime (Upper Cenomanian; subunits C4–D, lithological levels C4ms–Dm): the cliff of this small island exposes at this place a mound of silty marls (2 m thick), basally indurated (C4ms), and resting in discontinuity on the top of the Middle Cenomanian. In the Angoulême region, this transgressive sequence shows an appreciably different facies, described below. As regards the vertebrate fauna, Madame Island and Angoulême formations have numerous taxa in common but differ from each other in respective proportions of the various groups. The selachian teeth, relatively rare at Madame Island, are associated with common pycnodontiform fish remains as well as vertebrae of a marine aigialosaur varanoid, *Carentonosaurus mineaui* (Rage and Néraudeau, 2004).

*Locality 7*.—"L'Amas" quarry at Roullet–Saint-Estèphe, Charente (Upper Cenomanian; subunit D, lithological level Dm): this layer, originally called "argiles tégulines" by Coquand (1859), is exposed in numerous cement quarries just south of Angoulême. In Angoumois, this unit shows a particular facies characterized by distinctive bluish clay deposits, 5 metres thick, slightly silty-sandy at their base and very rich in oysters (*Ceratostreon flabellatum*). The selachian teeth were collected throughout the whole thickness of the layer.

*Locality 8*.—"Le Mas" quarry at La Couronne, Charente (Upper Cenomanian; subunit D, lithological level Dm): localized close to "l'Amas", this quarry shows the same levels and facies, and has yielded a similar fauna (see Table 1). Among the vertebrate fauna, pycnodont fish are predominant here.

*Locality 9*.—Port-des-Barques, Charente-Maritime (basal Turonian; subunit T1, lithological level T1m): visible in the northern cliff of the village, the layer that has yielded the unique specimen of *Squalicorax* described below is 1.5 m above the base of a series of beige marls marking the maximum flooding of the Cenomanian–Turonian boundary. The macrofauna is very poor and not very diverse, but contains rare Upper Cenomanian ammonites (*Metoicoceras geslinianum*) in the underlying marls of the subunit G2 (lithological level G2m). Since the publication of the synthetic section by Néraudeau et al. (1997), the discovery of a few Lower Turonian ammonites (*Pseudotissotia* sp. gr. "*P. inopinata*" Kennedy and Bayliss, 1977) (Philippe Courville personal communication 2004) only one metre above the base of the marls allows us to recognize a slightly lower position of the Cenomanian–Turonian boundary. Consequently, it is here presumed that the tooth has been collected in the earliest Turonian beds.

# Material and methods

Most teeth examined for this study were obtained between 2002 and 2005 using bulk sampling and screen-washing method (sieve sizes used: 0.35–0.71–1 mm), especially for the condensed sandy layers of the Early Cenomanian localities (about 500 kg to 1 t of sediment per locality). The larger teeth, mainly from the Late Cenomanian and Turonian localities, have been surface-collected, mostly since 2000. All numbered and figured specimens are housed in the palaeontological collections of the University of Montpellier II, France. Unnumbered material is housed in the University of Rennes I. The tooth terminology follows that of Cappetta (1987).

# Systematic palaeontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Subcohort Neoselachii Compagno, 1977
Order Orectolobiformes Applegate, 1972

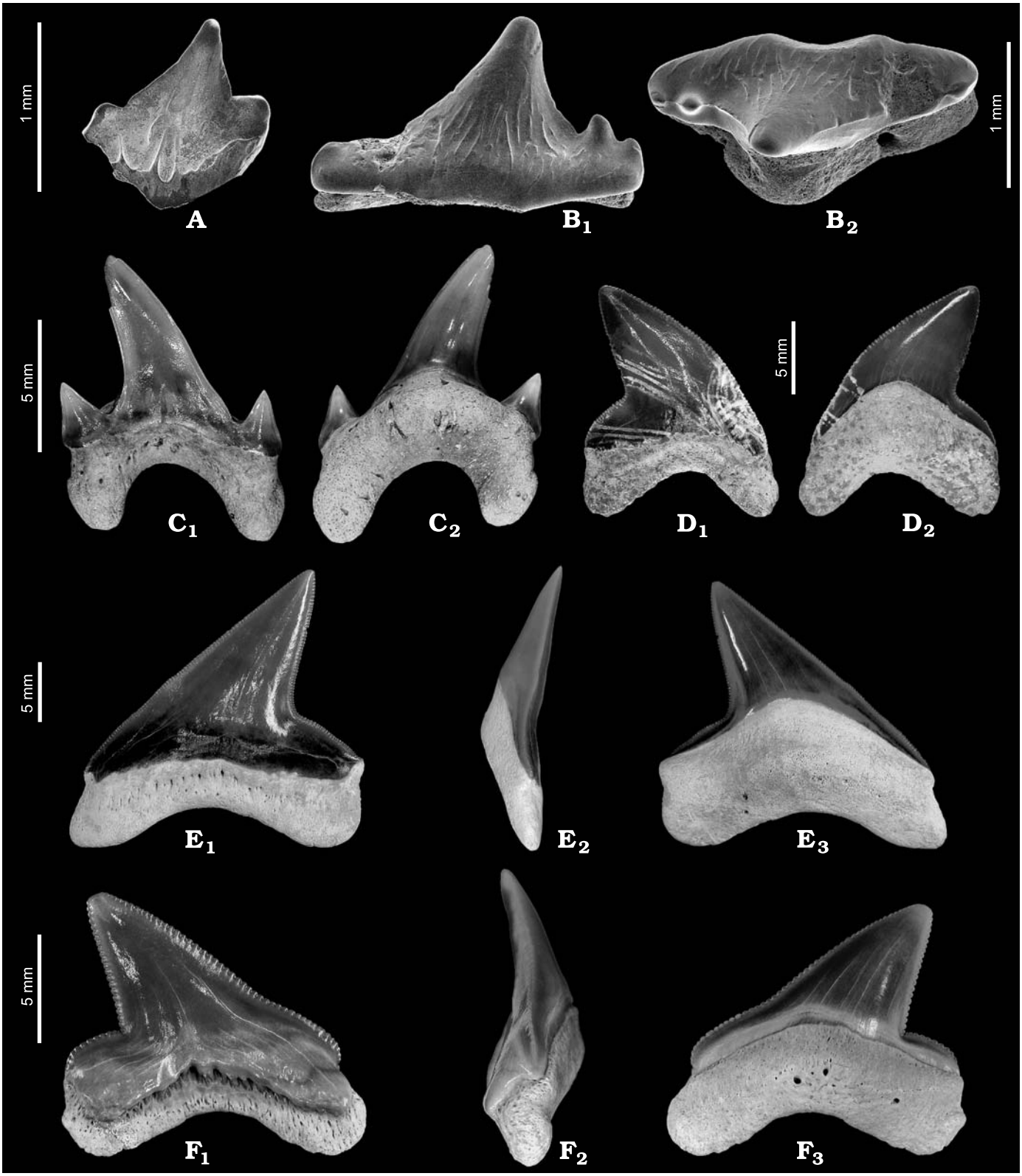


Fig. 2. Teeth of the hemiscylliid *Almascyllium* Cappetta, 1980a, the ginglymostomatid *Cantioscyllium* Woodward, 1889, the cretoxyrhinid *Archaeolamna* Siverson, 1992 and the anacoracid *Squalicorax* Whitley, 1939 from the Cenomanian and Turonian of Charentes, SW France. **A**. *Almascyllium* sp., Font-de-Benon, Lower Cenomanian; labial view of UM FBN 1. **B**. *Cantioscyllium* cf. *decipiens* Woodward, 1889, l'Amas, Upper Cenomanian; labial ($B_1$), and occlusal ($B_2$) views of UM AMA 1. **C**. *Archaeolamna* sp., l'Amas, Upper Cenomanian; labial ($C_1$), and lingual ($C_2$) views of UM AMA 2. **D**. *Squalicorax baharijensis* Stromer, 1927, Le Mas, Upper Cenomanian; labial ($D_1$), and lingual ($D_2$) views of UM LMS 1. **E**. Holotype of *Squalicorax coquandi* sp. nov., Port-des-Barques, basal Turonian; labial ($E_1$), distal ($E_2$), and lingual ($E_3$) views of UM PDB 1. **F**. *Squalicorax* cf. *intermedius* Glückman *in* Glückman and Shvazhaite, 1971, Le Puits des Insurgés, Upper Cenomanian; labial ($F_1$), mesial ($F_2$), and lingual ($F_3$) views of UM PDI 1.

## Family Hemiscylliidae Gill, 1862

### Genus *Almascyllium* Cappetta, 1980a

*Type species*: *Chiloscyllium cheikheliasi* Signeux, 1949 from the Santonian of Lebanon.

#### *Almascyllium* sp.

Fig. 2A.

*Material*.—A single isolated tooth crown (UM FBN 1) from Font-de-Benon, Archingeay-Les Nouillers, Lower Cenomanian, base of subunit B1.

*Description*.—The unique specimen corresponds to a lateral tooth devoid of its root. The crown displays a rather slim and pointed cusp, with clearly concave edges in labial view. We observe a pair of relatively rounded lateral cusplets. The distal one is at right angle to the cusp, whereas the smaller mesial one is separated from the main cusp by a slight notch. The basal edge of the apron is damaged. The ornamentation is reduced to five spaced labial folds and not exceeding the height of the cusplets. The three central folds follow the alignment of the cusp whereas each lateral fold is directed towards the respective cusplet.

*Remarks*.—This tooth is morphologically very close to that of *Almascyllium cheikheliasi* (Santonian) illustrated by Cappetta (1980a: 120, fig. 24a–c) in his study on the selachians from the Cretaceous of Lebanon. It differs only from this one by its relatively larger mesial cusplet, as well as by its lower and twice less numerous folds. Bernardez (2002) assigned with doubt a few teeth from the Lower Turonian of the Northern Spain to the genus *Almascyllium*. Those teeth, devoid of lateral cusplets and showing a practically smooth labial face, clearly differ from the tooth here described. Although the specimen UM FBN 1 might be a parasymphyseal or a lateral tooth of *Cantioscyllium* displaying a unusual morphology, like those described by Cappetta and Case (1999: pl. 15: 12–?13) from the Upper Cenomanian of Texas, we assign it to *Almascyllium* sp. because of its rather concave labial face and its salient basal crests parallel to the labial edge of the crown.

## Family Ginglymostomatidae Gill, 1862

### Genus *Cantioscyllium* Woodward, 1889

*Type species*: *Cantioscyllium decipiens* from the Cenomanian of England.

#### *Cantioscyllium* cf. *decipiens* Woodward, 1889

Fig. 2B.

*Material*.—A single isolated tooth (UM AMA 1) from l'Amas, Roullet–Saint-Estèphe, Upper Cenomanian D.

*Description*.—This is a complete lateral tooth, broader than high. The triangular main cusp bears on its labial face a few enameloid folds. They are not very strong, and are restricted to the basal half of the crown. The apron is very broad, not prominent, and slightly bifid. There are two pairs of small, blunted, lateral cusplets (damaged on the mesial side). In occlusal view, the medio-lingual protuberance is not very well developed. The hemiaulacorhize root displays one pair of large margino-lingual foramina.

*Remarks*.—Teeth of *Cantioscyllium* are relatively common in the Lower Cenomanian of Charentes, and even can be very abundant locally, like in the sands of the "Font-de-Benon" quarry at Archingeay-Les Nouillers (Vullo et al. 2003). Despite this, the tooth described herein represents the first occurrence of this genus in the Upper Cenomanian of the Charentes region. Although the labial face of the crown is less densely folded than in *C. decipiens*, this tooth is morphologically close to the specimens figured by Cappetta (1973) and Cappetta and Case (1999), and can be tentatively assigned to the type species. Furthermore, a comparison can also be made with very similar teeth, described by Bernardez (2002) as "*Cantioscyllium* sp. B", from the Upper Cenomanian of northern Spain. Conversely, the specimen UM AMA 1 differs from the two other Upper Cretaceous species, *C. meyeri* Case and Cappetta, 1997 and *C. nessovi* Ward and Averianov, 1999, which have narrower and more folded lateral teeth. It also differs from the Lower Cretaceous species *C. alhaulfi* Kriwet, 1999, which has teeth with a single pair of cusplets and very few labial folds. Finally, our tooth fits well with the type specimen from the Turonian of England described by Woodward (1889) and illustrated in 1911 (pl. 42: 7–11).

## Order Lamniformes Berg, 1958

## Family Cretoxyrhinidae Glückman, 1958

Actually, the extent and the content of this family are rather imprecise and subject to discussion. So, a serious revision of this family is needed, but out of the scope of the present article. This problem will be treated by one of us (HC) in a forthcoming study. The assignment of the genus *Archaeolamna* to this family is provisional.

### Genus *Archaeolamna* Siverson, 1992

*Type species*: *Odontaspis kopingensis* Davis, 1890 from the Campanian of Sweden.

#### *Archaeolamna* sp.

Fig. 2C.

*Material*.—One tooth (UM AMA 2) from l'Amas, Roullet–Saint-Estèphe, Upper Cenomanian D; a few unnumbered incomplete teeth from Les Renardières, Tonnay-Charente, Lower Cenomanian B1, and from Vauban cliff, Fouras and Traslemaine, Champniers, Lower Cenomanian B2.

*Description*.—The illustrated lateral tooth (UM AMA 2) shows a relatively narrow cusp curved toward the commissure. The lingual face of the cusp is convex, and the labial face is flat. Both faces are smooth. There is one pair of strong, triangular lateral cusplets. The root is thick and has a well-developed medio-lingual protuberance. The lingual neck is narrow, nearly as much at the centre of the cusp as near the margins. The two lobes are clearly distinct, separated by a rounded basal notch. In the anterior files, the teeth have a more erect cusp and a less laterally expended root.

*Remarks*.—The genus *Archaeolamna* was originally erected by Siverson (1992) for the reassignment of the Davis' species *Odontaspis kopingensis*, from the Campanian of Sweden. This genus occurs commonly from the Albian to the Maastrichtian in numerous regions (Siverson 1992, 1996, 1997; Biddle 1993). A second species, *A. haigi* Siverson, 1996, has been recently described from the Cenomanian of Australia, beside teeth tentatively referred to *A. kopingensis* (Siverson 1996). Conversely to *A. kopingensis*, *A. haigi* have lingually folded teeth. Zhelezko (1990) has described three species and subspecies, *Archaeolamna aduncata*, *A. aduncata suberecta*, and *A. arcuata orica* from the Santonian of western Kazakhstan, under the generic name of *Protolamna* Cappetta, 1980c. Due to the poor quality of the Zhelezko's illustrations, it is difficult to evaluate the validity and mainly the morphological differences between species. According to Mikael Siverson (1996, personal communication 2006), this material entirely corresponds to the type species *A. kopingensis*. The specimen UM AMA 2 is also similar to the lateral teeth of *Dwardius* Siverson, 1999, but it cannot be assigned to this monospecific genus owing to its relatively slenderer cusp and its narrower neck at the centre of the cusp (see Siverson 1999). In *Dwardius woodwardi* (Herman, 1977), the neck is indeed much more developed below the cusp than marginally. Due to the scarcity of the Charentes material, it is here considered preferable to leave the specimens in open nomenclature, as *Archaeolamna* sp.

## Family Anacoracidae Casier, 1947

## Genus *Squalicorax* Whitley, 1939

*Type species*: *Corax pristodontus* Agassiz, 1843 from the Maastrichtian of the Netherlands.

### *Squalicorax baharijensis* (Stromer, 1927)

Fig. 2D.

1927 *Corax baharijensis* Stromer, 1927: 5, pl. 1: 25–27.
1969 *Squalicorax kaupi*; Bilelo 1969: 342, text-fig. 2l–o (?p, ?q).
1974 *Squalicorax baharijensis*; Slaughter and Thurmond 1974: 32, figs. 2b, c.
1974 *Squalicorax curvatus*; Meyer 1974: 298, 300, text-fig. 89.
1989 *Squalicorax baharijensis*; Werner 1989: 35, text-fig. 13, pl. 14: 1–9, pl. 15: 1–3.
1993 *Squalicorax curvatus*; Welton and Farish 1993: 116, figs. 1, 2, and 4 (?fig. 3).
1999 *Squalicorax baharijensis*; Cappetta and Case 1999: 12, pl. 3: 6–9.
2001 *Squalicorax baharijensis*; Case 2001: 106, pl. 2: 3.
2002 *Squalicorax baharijensis*; Bernardez 2002: 279, pls. 42, 43. Unpublished PhD.

*Material*.—Four teeth from Le Puits des Insurgés, Madame Island, l'Amas, Roullet–Saint-Estèphe and Le Mas, La Couronne (UM LMS 1), Upper Cenomanian C4-D; a few teeth from Les Renardières, Tonnay-Charente, Lower Cenomanian B1.

*Description*.—The most characteristic tooth corresponds to an anterior element and is 15.7 mm high (UM LMS 1; Fig. 2D). It is higher than wide, with a crown that is narrow and sharp. The mesial cutting edge shows a regular and distinct convexity, while the distal one is completely straight. The distal notch and heel are well developed. The cutting edges are finely serrated. The root is rather thick, with the distal lobe more developed than the mesial one and a deep basal notch.

*Remarks*.—This rather large species of *Squalicorax*, restricted to the Cenomanian, displays a broad geographical distribution. It occurs in Egypt (Werner 1989), in North America (Texas, Minnesota) (Cappetta and Case 1999; Case 2001) and in Europe, where it has been recently described from Spain (Bernardez 2002). Its discovery in Charentes is thus not surprising. This species was not recognized by Landemaine (1991) among the *Squalicorax* teeth from the Lower Cenomanian of Les Renardières, all assigned (without illustrations) by this author to *S. falcatus*. Cappetta and Case (1999) and Antunes and Cappetta (2002) noted that the status of the species *S. falcatus* is poorly defined, and Landemaine's assignment thus remains doubtful. However, we collected a few teeth that might correspond to *S. baharijensis*. It is interesting to note that *S. baharijensis* is always accompanied by "*Carcharias*" *amonensis* (Cappetta and Case, 1975), an abundant species occurring in all the Cenomanian localities studied in Charentes (Landemaine 1991; Vullo et al. 2003, 2005; Vullo 2005; Table 1). This association is characteristic of the peri-Tethyan and North American Cenomanian shallow water deposits.

### *Squalicorax coquandi* sp. nov.

Fig. 2E.

*Holotype*: Specimen UM PDB 1.

*Derivation of the name*: Species named in memory of Henri Coquand (1811–1881), for his work on the palaeontology of the Cretaceous of Charentes (1859).

*Type locality*: Port-des-Barques, Charente-Maritime.

*Type horizon*: Lowermost Turonian, base of subunit T1, lithological unit T1m.

*Material*.—One complete tooth. Only known from the type locality.

*Diagnosis*.—This large-sized species of *Squalicorax* is easily distinguishable from all other species of the genus by its tooth morphology, characterized by an acute, slim cusp showing subrectilinear edges (according to the single available specimen). The cutting edges are very finely and regularly serrated. There is a clear and rounded distal notch.

*Description*.—The single but perfectly preserved specimen (UM PDB 1; Fig. 2E) is 22 mm high and probably corresponds to an antero-lateral tooth, slightly broader than high. This tooth has a narrow, slim and acute cusp, bent toward the rear. The edges are practically straight: the mesial one is very slightly convex and the distal one very slightly sigmoid. The distal notch is rather open (110°) and is both clear and slightly rounded. The distal heel, well developed, is long, oblique, and almost rectilinear. The cutting edge serrations are very fine and very regular. The basilo-labial bulge of the crown is not very prominent and disappears laterally. The root is rather high and not very thick, with lobes separated by

a broad median concavity. It displays a series of foramina under the labial bulge of the crown.

*Remarks*.—It is sure that the definition of a new species based on a single tooth can be discussed and criticized. However, it is important to note that the species of *Squalicorax* are generally characterized by a weak gradient monognathic and dignathic heterodonty (see Welton and Farish 1993). Thanks to this relative homodonty, one tooth can be enough to display the diagnostic dental features of a species. In this precise case, the holotype is perfectly preserved and clearly different from all other previously described species. A second specimen, unfortunately lost, has also been studied. This large-sized species seems to be very rare. Collecting additional specimens may take a lot of time. So, it seems to us that the description of this new taxon is justified.

By its tooth morphology, *Squalicorax coquandi* sp. nov. differs clearly from the other described species of the genus. However, Antunes and Cappetta (2002: pl. 7: 6–8) have figured, under the name of *Squalicorax* sp., some teeth from the Upper Turonian of Iembe (Angola) showing similarities with *S. coquandi* sp. nov. (narrow and acute cusp, subrectilinear edges). These teeth, however, differ in their smaller size and in having a more acute and angular distal notch. The large size of teeth of *S. pelagicus* sp. nov. is unlike that of other *Squalicorax* of earliest Turonian age. The analogy existing between the teeth of *Squalicorax* and the upper teeth of some large pelagic species of *Carcharhinus* Blainville, 1816 was underlined by Cappetta and Case (1999). If the teeth of *S. falcatus*, with a broader and more robust crown, can be compared for example with those of *C. longimanus* Poey, 1861, *S. coquandi* sp. nov. reminds by its more sharp teeth another oceanic species, *C. falciformis* Müller and Henle, 1841. It also reminds the tooth morphology of the genus *Sphyrna* Rafinesque, 1810.

### *Squalicorax* cf. *intermedius* Glückman in Glückman and Shvazhaite, 1971

Fig. 2F.

*Material*.—A single isolated tooth (UM PDI 1) from Le Puits des Insurgés, Madame Island, Upper Cenomanian, unit D, lithological level Dm.

*Description*.—This tooth is broader than high and rather thick. The cusp is sharp and distally inclined at an angle of about 45°. The mesial cutting edge is relatively straight, with a light concave sinuosity on its lower third. The distal cutting edge is rectilinear and oblique. The distal heel is not very high and slightly convex. The cutting edges are rather strongly but regularly serrated. The distal notch makes an angle of about 90°. In profile view, the tooth is clearly concave labially. The labial face of the crown overhangs the root by a strong and salient bulge cut out by some irregular foraminae that are larger medially. The root is thick and very well separated lingually from the crown; its lingual face shows three irregularly placed foramina.

*Remarks*.—By its size and morphology, our specimen can be related to the *Squalicorax falcatus* "species-group". This "group" probably contains numerous undescribed species and requires revision, out of the scope of this article. One species has been described from the Upper Turonian of western Kazakhstan, *S. intermedius* Glückman in Glückman and Shvazhaite, 1971. The original illustration is rather poor but a dozen of well preserved specimens from Kazakhstan have been studied by one of us (HC). Our specimen shows a dental morphology that is similar to *S. intermedius*, especially in respect to the basal labial bulge of the crown. In *S.* cf. *intermedius*, however, the cutting edges of the cusp, and particularly the distal one, are straight, when they are clearly convex in *S. intermedius*.

## Family Odontaspididae Müller and Henle, 1839

### Genus *Roulletia* nov.

*Type species*: *Roulletia bureaui* sp. nov.

*Derivation of the name*: From the name of the type locality.

*Diagnosis and comparisons*.—Small Odontaspididae, characterized by rather bulbous teeth with a cusp showing a strong labial bulge. The lingual and labial faces are completely smooth. There is only one pair of divergent, very small sized, sometimes incipient, lateral cusplets. An additional minute distal cusplet can develop. The mesial edge is slightly concave in antero-lateral teeth. The teeth of this genus have a more bulbous labial face and one pair of proportionally smaller cusplets than in other odontaspidids. They are also distinguished from teeth of "*Carcharias*" *amonensis*, the morphologically closest taxon, by a thicker crown and root (labio-lingually compressed in "*C.*" *amonensis*), and in having fewer and smaller lateral cusplets (generally two pairs in "*C.*" *amonensis*). The teeth of *Roulletia* gen. nov. mainly differ from those of *Cenocarcharias* Cappetta and Case, 1999 by a smooth crown. From the teeth of the cretoxyrhinid? *Dallasiella* Cappetta and Case, 1999 they are distinguished by their weaker lateral cusplets and their clear, well developed nutrient groove on the lingual protuberance of the root.

*Remarks*.—Relatively few odontaspidid genera have been reported in Cretaceous deposits: *Carcharias* Rafinesque, 1810, *Cenocarcharias* Cappetta and Case, 1999, *Hispidaspis* Sokolov, 1978, *Johnlongia* Siverson, 1996, and *Odontaspis* Agassiz, 1838. The genera *Cenocarcharias* and *Hispidaspis* have teeth whose base of the cusp is strongly folded labially, and even lingually for the first one. The teeth of *Roulletia* gen. nov. have a completely smooth enamel and so can be easily separated from *Cenocarcharias* and *Hispidaspis*. *Roulletia* gen. nov. has teeth with cutting edges which are in continuity between the cusp and the cusplets, that separates it from the genus *Odontaspis* in which the cutting edges do not reach the base of the cusp nor of the cusplets, mainly in the anterior files. Moreover, the teeth of *Odontaspis* have sharp and high cusplets, often duplicated, that is not the case of *Roulletia* gen. nov. in which they are simple and low. The teeth of the genus *Johnlongia* have a very particular morphology, mainly in the anterior files whose root shows a very salient lingual protuberance, much more developed than in *Roulletia* gen. nov. In the lateral files, the cusplets are


Fig. 3. Teeth of the odontaspidid *Roulletia* gen. nov. from the Cenomanian of Charentes, SW France. *Roulletia bureaui* gen. et sp. nov., l'Amas, Upper Cenomanian. **A**. Specimen UM AMA 3; in labial view. **B**. Specimen UM AMA 4; in labial ($B_1$), mesial ($B_2$), and lingual ($B_3$) views. **C**. Specimen UM AMA 5; in labial ($C_1$), and lingual ($C_2$) views. **D**. Holotype, specimen UM AMA 6; in labial ($D_1$), mesial ($D_2$), and lingual ($D_3$) views. **E**. specimen UM AMA 7; in labial ($E_1$), and lingual ($E_2$) views. **F**. specimen UM AMA 8; in labial ($F_1$), mesial ($F_2$), and lingual ($F_3$) views. **G**. specimen UM AMA 9; in labial ($G_1$), and lingual ($G_2$) views.

sometimes duplicated mesially and the base of the labial face is often folded. The teeth of *Roulletia* gen. nov. are characterized by a not very high cusp compared to the root. In lingual view, the cusp is indeed practically as high as the root. By this feature, *Roulletia* gen. nov. is distinguished easily from *Carcharias* whose teeth, mainly in the anterior files, have a cusp clearly higher than the root. Moreover, as already noted, the teeth of *Roulletia* gen. nov. have a completely smooth enamel, while in *Carcharias* the lingual face of the teeth bears more or less numerous and marked folds.

## *Roulletia bureaui* gen. et sp. nov.

Fig. 3A–G.

*Derivation of the name*: Species named after Mr. Michel Bureau, the amateur palaeontologist who collected the material.

*Holotype*: Specimen UM AMA 6.

*Paratypes*: Specimens UM AMA 3–5, UM AMA 7–9.

*Type locality*: L'Amas quarry, Roullet–Saint-Estèphe, Charente.

*Type horizon*: Upper Cenomanian, unit D, lithological level Dm.

*Material*.—Seven teeth. Only known from the type locality.

*Diagnosis*.—Same as for genus.

*Description*.—The holotype (UM AMA 6; Fig. 3D) is a lateral tooth, 10 mm high and distally inclined. The smooth crown is relatively narrow, and displays a pair of small cusplets. A second, minute cusplet, can be observed distally. The labial face is slightly swollen. The root is asymmetrical, with a distal lobe stronger than the mesial one. The basilar notch of the root is angular. The lingual protuberance is very developed, and is marked by a deep and relatively broad groove. One of the paratypes (UM AMA 9; Fig. 3G) is an anterior tooth, 9 mm high. It is almost symmetrical, with an erect, sharp cusp, and slightly concave edges. The crown is devoid of ornamentation, and shows convex labial and lingual faces. It bears one pair of very reduced but sharp, acute, marginal cusplets. The root is rather thick, with strong lobes separated by an angular notch. Some specimens, like UM AMA 7 (Fig. 3E), display a rounded root notch.

*Remarks*.—Among odontaspidids, the more reminiscent species is "*Carcharias*" *amonensis* (mainly for some teeth of antero-lateral files), whose very distinctive teeth have been found in association with the teeth of *Roulletia bureaui* gen. et sp. nov. in the type locality. So, one could question about the separation of the two taxa at the generic level. Yet, a close study of the material allows us to reject this possibility. In *R. bureaui* gen. et sp. nov., the cutting edge of the crown is in continuity between the cusp and the lateral cusplets, as well in the anterior as in the lateral files. The cusplets are minute and not duplicated, and the root is rather thick with a deep groove. In "*C*." *amonensis*, in the anterior and antero-lateral files, the teeth lack cutting edges at the base of the cusp and of the cusplets. The teeth of "*C*." *amonensis* have one to three pairs of lateral cusplets, generally more developed. They are also more labio-lingually compressed, and the crown displays a flatter labial face. The root is more expanded transversally and more flattened labio-lingually (Cappetta and Case 1975; Landemaine 1991). The association of these morphological features allows to separate *R. bureaui* gen. et sp. nov. and "*C*." *amonensis* at the generic level. It must be also noted that teeth of *R. bureaui* gen. et sp. nov. have never been collected in localities where "*C*." *amonensis* is abundant, as for instance in the Cenomanian of Texas or in the locality of "Les Renardières", at Tonnay-Charente. Therefore, *R. bureaui* gen. et sp. nov. cannot be considered as a scarce morphological variation of "*C*." *amonensis*.

## Genus *Cenocarcharias* Cappetta and Case, 1999

*Type species*: *Odontaspis tenuiplicatus* Cappetta and Case, 1975 from the Cenomanian of Texas.

## *Cenocarcharias rochebrunei* (Sauvage, 1880)

Fig. 4.

1880 *Odontaspis rochebrunei*, Sauvage 1880: 457, pl. 13: 3.

*Type locality*: L'Amas quarry, Roullet–Saint-Estèphe, Charente.

*Type horizon*: Upper Cenomanian, unit D, lithological level Dm.

*Material*.—Three teeth (UM AMA 10–12) from l'Amas, Roullet–Saint-Estèphe, and one tooth from Le Mas, Upper Cenomanian, unit D.

*Revised diagnosis*.—Odontaspidid with relatively robust, narrow teeth, whose crown displays a strongly folded basal bulge on its labial face, and very reduced ornamentation on lingual face. There is one or two pairs of acutely pointed lateral cusplets, rather linked to the main cusp. The root is rather thick and has a strong lingual protuberance, with a clear groove. This species of *Cenocarcharias* differs from the only other species of the genus, *Cenocarcharias tenuiplicatus* (Cappetta and Case, 1975), by its larger, more robust, and more strongly folded teeth.

*Description*.—An anterior tooth (UM AMA 10; Fig. 4A), 11 mm high, shows a sharp and erect main cusp, relatively narrow and slightly bent distally. The labial face is almost flat whereas the lingual face is convex. The labial face is strongly folded at its base, and the basal ledge is very concave, forming a bulge overhanging the root. The enamel of the lingual face displays a slight granular texture around the root contact. There is one pair of erect marginal cusplets, closely linked to the main cusp. The root shows a strong medio-lingual protuberance bearing a deep groove. A lateral tooth (UM AMA 12; Fig. 4C) has a main cusp very inclined distally, with two pairs of erect lateral cusplets.

*Remarks*.—The original description of this species by Sauvage (1880) was based on only three teeth of the same position (anterior teeth), coming from the "argiles tégulines de la tranchée de Pisani" (locality located on the commune of L'Houmeau-Pontouvre, surroundings of Angoulême). These specimens are currently lost but the discovery of a series of teeth coming from the same area enables us to redefine this taxon. The combination of morphological characters suggests that this species should be referred to the genus *Cenocarcharias* Cappetta and Case, 1999. It is very similar to *Cenocarcharias tenuiplicatus*, a species with slenderer teeth never exceeding 7 or 8 mm (Welton and Farish 1993; Cappetta and Case 1999). However, *Cenocarcharias rochebrunei* may be distinguished from *C. tenuiplicatus* by its larger (up to 11.5 mm), more robust teeth and by its relatively narrower anterior teeth, showing a more pronounced ornamentation on the labial bulge, but a less marked ornamentation on the lingual face of the cusp. It is interesting to note that distinctive teeth of *C. tenuiplicatus* occurs in the Lower Cenomanian of Charentes (Landemaine 1991; Vullo et al. 2005). A tooth from the Cenomanian of Bahariya (Egypt), figured


Fig. 4. Teeth of the odontaspidid *Cenocarcharias* Cappetta and Case, 1999 from the Cenomanian of Charentes, SW France. *Cenocarcharias rochebrunei* (Sauvage, 1880), L'Amas, Upper Cenomanian. **A**. Neotype, specimen UM AMA 10; in labial ($A_1$), mesial ($A_2$), and lingual ($A_3$) views. **B**. Specimen UM AMA 11; in labial ($B_1$), distal ($B_2$), and lingual ($B_3$) views. **C**. Specimen UM AMA 12; in labial ($C_1$), and lingual ($C_2$) views.

by Slaughter and Thurmond (1974: fig. 2j) as *Odontaspis* sp. could be referred to *Cenocarcharias* sp.

## Superorder Batomorphii Cappetta, 1980b

## Order Rajiformes Berg, 1940

## Family *incertae sedis*

## Genus *Hamrabatis* Cappetta, 1991

*Type species*: *Hamrabatis ornata* Cappetta, 1991 from the Maastrichtian of Egypt.

### *Hamrabatis bernardezi* sp. nov.

Fig. 5A–C.

1991 ?*Dasyatis* sp.; Landemaine 1991: 35, pl. 15: 8, 9.

2002 *Hamrabatis sanchezi*; Bernardez 2002: 313, pls. 55, 56, pl. 57: 1. Unpublished Ph.D.

2005 *Hamrabatis* sp.; Vullo et al. 2005: 99, fig. 2.7.

*Derivation of the name*: Species named after Mr. Enrique Bernardez, who originally recognized and described this new species within his unpublished Ph.D. thesis.

*Holotype*: Specimen UM FVN 1.

*Paratypes*: Specimens UM FVN 2, UM MTG 1.

*Type locality*: Vauban cliff, Fouras, Charente-Maritime.

*Type horizon*: Lower Cenomanian, subunit B2, lithological level B2ms.

*Material*.—Two teeth from Font-de-Benon, Archingeay-Les Nouillers, Lower Cenomanian, subunit B1; numerous teeth from Vauban cliff at Fouras, Traslemaine at Champniers and Montagan at Mainxe, Lower Cenomanian, subunit B2; four teeth from l'Amas, Roullet–Saint-Estèphe, Upper Cenomanian, unit D.

*Diagnosis and comparisons*.—Small species of *Hamrabatis* characterized by its teeth with a rhombic crown in occlusal view, slightly wider than long. Ornamentation consisting of shallow alveoli located at the periphery of the labial face which is rather convex, with a clear but not sharp transverse keel. Lingual face very angular in profile view, with an almost vertical part, below the lingual margin of the labial face. This small-sized species of *Hamrabatis* is easily distinguished from the two other species previously described from Maastrichtian deposits (*Hamrabatis ornata* Cappetta, 1991 from Egypt, and *H. weltoni* Case and Cappetta, 1997 from Texas) by its smaller teeth, displaying a crown less elongated mesio-distally and with a more rhombic outline.

*Description*.—In occlusal view, the holotype (UM FVN 1; Fig. 5A) has a rhombic crown, slightly elongated mesio-distally. A weak transverse keel is developed. The apex of the crown is worn in this specimen. The ornamentation consists of irregular alveoli located on the margins of the occlusal face. The root is nearly half as wide as the crown. In basal view, the root is marked by a deep groove. Some teeth (UM FVN 2 and UM MTG 1; Fig. 5B, C) are narrower in occlusal view, with a crown as wide as long. They are dorso-ventrally less compressed.

*Remarks*.—In his unpublished Ph.D. thesis, Bernardez (2002) recently described a new species of *Hamrabatis* ("*H.*

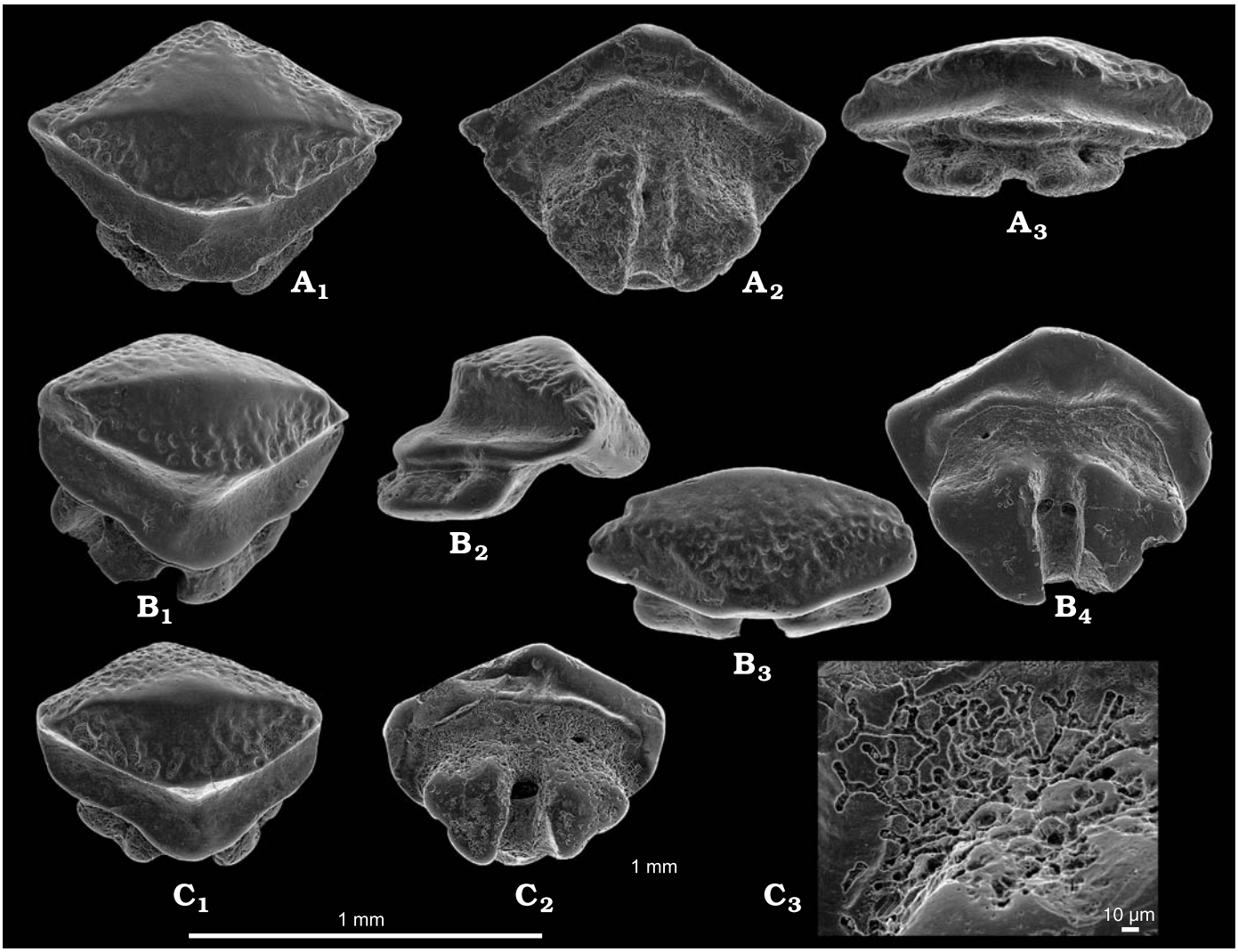


Fig. 5. Teeth of the rajiform *Hamrabatis* Cappetta, 1991 from the Cenomanian of Charentes, SW France. *Hamrabatis bernardezi* sp. nov., Fouras-Vauban (**A**, **B**) and Montagan (**C**), Lower Cenomanian. **A**. Holotype, specimen UM FVN 1; in occlusal ($A_1$), basal ($A_2$), and lingual ($A_3$) views. **B**. Specimen UM FVN 2; in occlusal ($B_1$), lateral ($B_2$), labial ($B_3$), and basal ($B_4$) views. **C**. Specimen UM MTG 1; in occlusal ($C_1$), and basal ($C_2$) views. $C_3$: enlargement of the root showing the endolithic microborings (ichnotaxon *Abeliella riccioides* Mägdefrau, 1937) near the crown-root junction.

*sanchezi*") from abundant material from the Cenomanian of Asturias (northern Spain). The teeth from the Lower Cenomanian of Charentes are similar to the Spanish form although they show a more pronounced ornamentation on both crown faces. Indeed, the Spanish specimens show an enamel very slightly alveolated only at the level of the labial area of the crown. The small differences between these two populations are maybe the result of a preservational bias, and the creation of a further new taxon would not be justified. The original description of this new Cenomanian species by Bernardez (2002) has not been published and "*Hamrabatis sanchezi*" therefore qualifies as a *nomen nudum*, so we herein name this taxon. The genus *Hamrabatis* was originally described from the Maastrichtian of Egypt (Cappetta, 1991), then reported from the contemporary deposits of Texas (Case and Cappetta 1997), Syria (Bardet et al. 2000), and Morocco (Pierre Zennaro personal communication 2003). It also occurs in the Coniacian of Morocco (HC unpublished data). This Cenomanian species of *Hamrabatis* is distinguished from the Maastrichtian species *Hamrabatis ornata* and *H. weltoni* by its smaller and narrower teeth. This new species was previously assigned to a dasyatid by Landemaine (1991) owing to its tooth morphology, but its histologic tooth type (orthodont) indicates that it corresponds to a rajiform.

## Rajiformes Family *incertae sedis* or Family ?Sclerorhynchidae Cappetta, 1974

## Genus *Archingeayia* nov.

*Type species*: *Archingeayia sistaci* sp. nov.

*Derivation of the name*: From the name of the type locality of the type species.

*Diagnosis and comparisons*.—Genus with "*Ptychotrygon*-like" minute teeth with a high, triangular, and clearly cuspi-

date crown in labial (or lingual) view; ornamentation absent or very reduced labially, corresponding generally to a basal marginal ridge; a simple medial vertical labial fold can be developed, bifurcating downward and thus delimiting the apron; one or two pairs of slight vertical lingual folds; relatively strong labio-lingual compression. The root is relatively low, half to third as high as the crown.

Among oral teeth of Sclerorhynchidae, *Ptychotrygon* sensu scricto and closely related forms, *Archingeayia* gen. nov. is firstly well differentiated from the "cross-like crown" group bearing a well developed apron (*Dalpiazia* Checchia-Rispoli, 1933, *Ischyrhiza* Leidy, 1856, *Kiestus* Cappetta and Case, 1999, *Onchopristis* Stromer, 1917, *Pucapristis* Schaeffer, 1963, *Plicatopristis* Cappetta, 1991, *Renpetia* Werner, 1989). It is closer to *Bahariprístis* Werner, 1989, *Biropristis* Suarez and Cappetta, 2004, *Borodinopristis* Case, 1987, *Celtipristis* Kriwet, 1999, *Ctenopristis* Arambourg, 1940, *Ganopristis* Arambourg, 1935, *Libanopristis* Cappetta, 1980b, *Micropristis* Cappetta, 1980b, *Ptychotrygon* Jaekel, 1894, *Ptychotrygonoides* Landemaine, 1991, *Sclerorhynchus* Woodward, 1889, and *Texatrygon* Cappetta and Case, 1999. However, teeth of the species of *Ptychotrygon* are generally low cusped, well ornamented and not strongly labio-lingually compressed. *Ptychotrygonoides*, *Sclerorhynchus*, *Ganopristis*, *Biropristis*, and *Borodinopristis* have a radial labial ornamentation. *Celtipristis* shows a strong constriction between the crown and the root. Teeth of *Libanopristis* and *Micropristis* have a rather similar reduced ornamentation but are both relatively low cusped. Teeth of *Texatrygon* have either a completely smooth crown or numerous short vertical labial folds. Anterior teeth of *Ctenopristis* show a more distinct and high cusp. Anterior teeth of *Bahariprístis* have a hooked crown strongly bent labio-lingually.

## *Archingeayia sistaci* gen. et sp. nov.

Fig. 6A–C.

*Derivation of the name*: Species named after Mr. Paul Sistac, geologist, for his valuable assistance in the field.

*Holotype*: Specimen UM FBN 4.

*Paratypes*: Specimens UM FBN 2–3.

*Type locality*: Font-de-Benon quarry, Archingeay-Les Nouillers, Charente-Maritime, western France.

*Type horizon*: Lower Cenomanian, subunit B1, lithological level B1cs.

*Material*.—Ten teeth. Only known from the type locality.

*Diagnosis*.—Same as for genus.

*Description*.—The holotype (UM FBN 4; Fig. 6C) has a rather high, triangular cusp, slightly worn at its apex. The labial face is smooth, except the presence of a basal horizontal ridge delimiting a bulge. The medio-labial protuberance is not well developed. The lingual face is more steep in profile view and shows three oblique folds not reaching the apex. There is a distinct basal lingual bulge. The uvula above the root notch is rather well differentiated and bears a weak interlocking hollow. The root is relatively low (about one quarter of the total tooth height). It is slightly narrower than the crown and shows typical triangular lobes in basal view.

*Remarks*.—*Archingeayia* gen. nov. is based on isolated oral teeth. The systematic affinities of this new genus thus remains uncertain because of its unique tooth morphology. In the locality of Archingeay-Les Nouillers, *Archingeayia* gen. nov. occurs in association with *Ptychotrygonoides* and small teeth of *Ptychotrygon* spp. However, the presence of a true Sclerorhynchidae is attested by the discovery of numerous small rostral teeth that seem to belong to a single taxon. For the moment, it is reasonable not to attempt to link these rostral teeth to any oral ones.

Teeth of *Archingeayia* gen. nov. display a particular morphology, with a straight and well cusped triangular crown. However, they are close to some other Cenomanian forms, especially from the Bahariya Formation, Egypt. Werner (1989: pl. 22: 1, 2) incorrectly linked to the rostral teeth of *Onchopristis numidus* some oral teeth showing clear resemblances with teeth of *Archingeayia* gen. nov. (well developed cusp; ornamentation pattern). However, these teeth are characterized by their larger size, their root wider than the crown, and by their cusp bent labio-lingually. The set of teeth described by Werner should be assigned to the genus *Kiestus*, recently defined from the Turonian–Coniacian boundary of Texas (Cappetta and Case 1999). The teeth of *Archingeayia* gen. nov. also show affinities with a few teeth (lateral ones) of *Bahariprístis* (Werner 1989: pl. 29: 2). But, as mentioned above in the "Diagnosis and comparisons", *Bahariprístis* shows a strong monognathic heterodonty and remains clearly different from *Archingeayia* gen. nov.

## Family, genus, and species indet.

Fig. 7E.

*Material*.—One single tooth (UM AMA 13) from l'Amas, Roullet–Saint-Estèphe, Upper Cenomanian D.

*Description*.—This unique specimen corresponds to a small "*Ptychotrygon*-like" tooth, with a cusped crown. In occlusal view, the medio-labial protuberance is broad and not detached from the general outline. The labial face displays a very reduced ornamentation, with a single vertical ridge linking the apex to the apron A weak fold is also present along one of the two of the basilo-labial margins. The lingual face is smooth, with a shallow central depression not well delimited. The root is slightly broader than the crown, with a very flat basal face.

*Remarks*.—This tooth represents the only occurrence of a sclerorhynchid-like rajiform in the Upper Cenomanian of Charentes. This contrast with the abundance of teeth of this group in the lower part of the stage (subunits B1 and B2) (Landemaine 1991; Vullo et al. 2003, 2005). The lack of a transverse ridge along the middle of the lingual face separates this specimen from the genus *Ptychotrygon*. It also differs from the genus *Ptychotrygonoides* in lacking radiating labial ridges. A very similar form (small size, cusped crown, same reduced ornamentation) has been described by Ber-

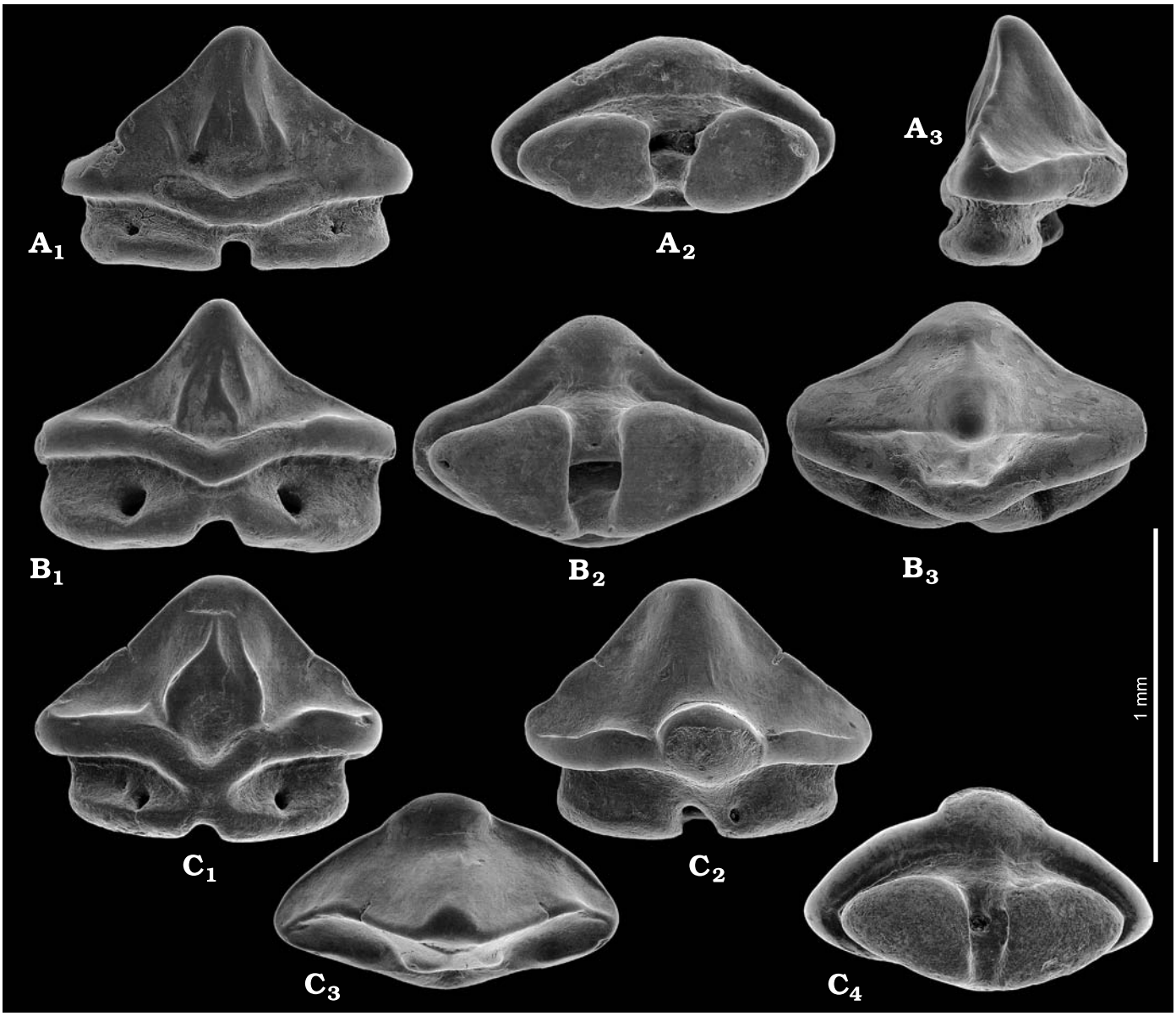


Fig. 6. Teeth of the rajiform *Archingeayia* gen. nov. from the Cenomanian of Charentes, SW France. *Archingeayia sistaci* gen. et sp. nov., Font-de-Benon, Lower Cenomanian. **A**. Specimen UM FBN 2; in lingual ($A_1$), basal ($A_2$), and lateral ($A_3$) views. **B**. Specimen UM FBN 3; in lingual ($B_1$), basal ($B_2$), and occlusal ($B_3$) views. **C**. Holotype, specimen UM FBN 4; in lingual ($C_1$), labial ($C_2$), occlusal ($C_3$), and basal ($C_4$) views.

nardez (2002) from the Middle–Late Cenomanian of northern Spain, for which he proposed a new species, "*Ptychotrygonoides lamoldai*" (unpublished, *nomen nudum*). The assignment of the Spanish species to this genus, based mainly on the cuspidate crown, remains doubtful as these teeth are clearly different from those of the type species, *P. pouiti* Landemaine, 1991.

## Genus *Engolismaia* nov.

*Type species*: *Engolismaia couillardi* sp. nov.

*Derivation of the name*: Derived from *Engolisma*, the Latin name of the town of Angoulême.

*Diagnosis and comparisons*.—Small rajiform genus, characterized by minute (up to 1 mm wide), cuspidate teeth, of which the transverse keel develops one to two distinct and blunt pairs of cusplets, slightly lower than the main cusp. The rather prominent medio-labial protuberance bears a single pustule developed from a vertical medial ridge. The root is relatively high.

*Engolismaia* gen. nov. differs from all other Rajiformes by its well-cusped crown displaying one or two pairs of well-developed rounded lateral cusplets, and by the ornamentation of the apron consisting of one single pustule. Another monospecific sclerorhynchid genus, *Baharipristis*, can also display a pair of lateral cusplets (Werner 1989: pl. 26: 4), but these cusplets remain very reduced compared to the main cusp. Moreover, the main cusp of *Baharipristis bastetiae* is not erect, but clearly inclined labio-lingually.

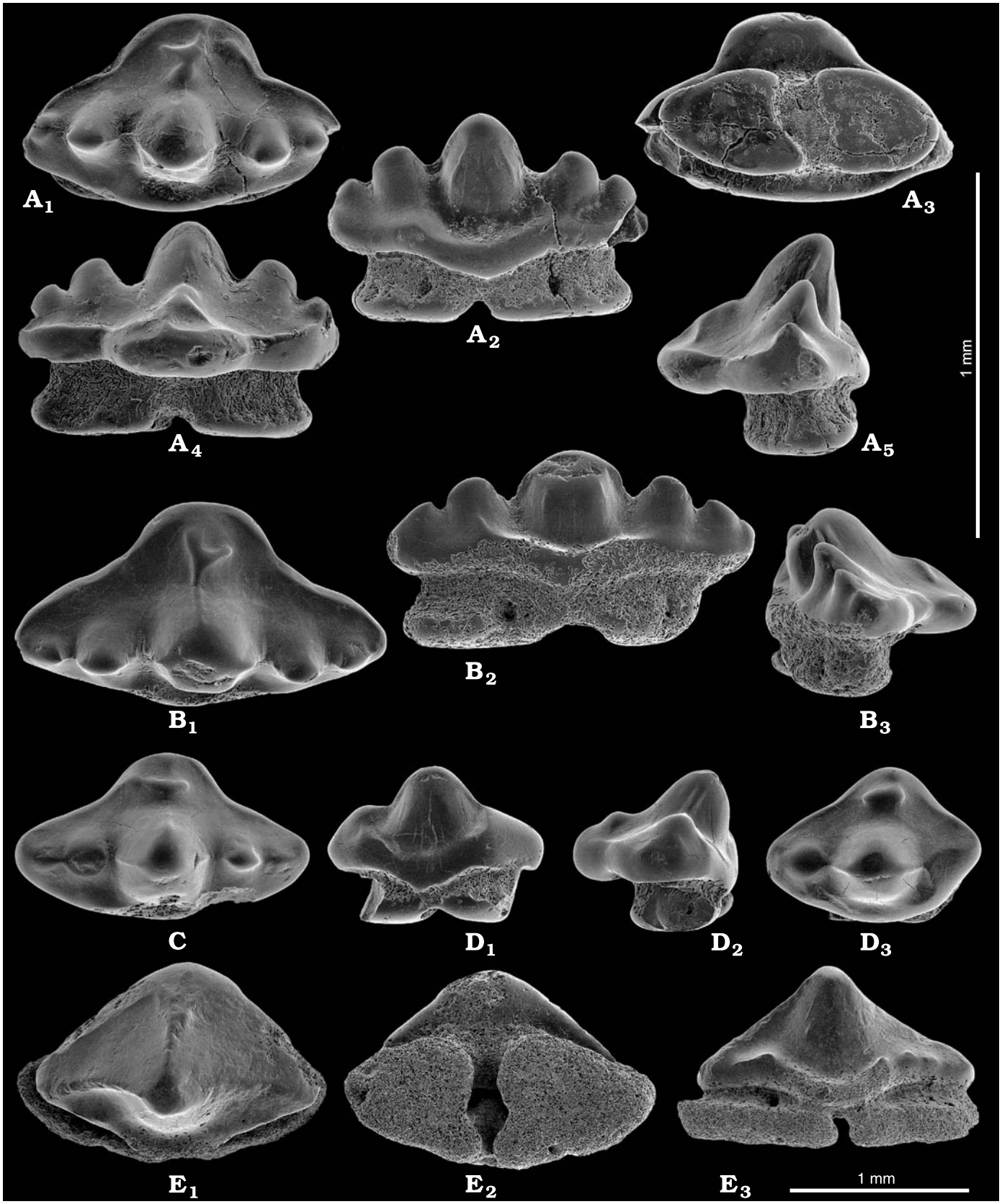


Fig. 7. Teeth of the rajiform *Engolismaia* gen. nov. from the Cenomanian of Charentes, SW France. *Engolismaia couillardi* gen. et sp. nov., Traslemaine, Early Cenomanian. **A**. Holotype, specimen UM TLM 1; in occlusal ($A_1$), lingual ($A_2$), basal ($A_3$), labial ($A_4$), and lateral ($A_5$) views. **B**. Specimen UM TLM 2; in occlusal ($B_1$), lingual ($B_2$), and lateral ($B_3$) views. **C**. Specimen UM TLM 3; in occlusal view. **D**. Specimen UM TLM 4; in lingual ($D_1$), lateral ($D_2$), and occlusal ($D_3$) views. **E**. Rajiformes indet., l'Amas, Late Cenomanian; occlusal ($E_1$), basal ($D_2$), and lingual ($D_3$) views of UM AMA 13.

*Engolismaia couillardi* gen. et sp. nov.

Fig. 7A–D.

*Derivation of the name*: Species named after Mr. Alain Couillard, for his valuable assistance in the field.

*Holotype*: Specimen UM TLM 1.

*Paratypes*: Specimen UM TLM 2–4.

*Type locality*: Traslemaine, Champniers near Angoulême, Charente.

*Type horizon*: Lower Cenomanian, subunit B2, lithological level B2gl.

*Material*.—Fifteen teeth from Traslemaine, Champniers, and three teeth from Montagan, Mainxe, Lower Cenomanian, subunit B2.

*Diagnosis*.—Same as for genus.

*Description*.—The holotype (UM TLM 1; Fig. 7A) is a presumed antero-lateral tooth, 0.9 mm wide. In occlusal view, the crown shows a broad, rounded, well-defined apron. The two pairs of cusplets are symmetrically developed on each side of the main cusp. All the cusps have a rounded apex. The basilo-labial ridge is well distinct. The main cusp bears two subvertical folds on its lingual face. The lingual central depression is rather deep. The root, slightly narrower than the crown, displays a flattened basal face, and bears two well-marked foramina on its lingual face. An anterior (or posterior?) tooth (UM TLM 4; Fig. 7D) is narrow, with only one poorly defined lateral cusplet widely united to the base of the main cusp. The other side corresponds to a simple heel. The apron bears a single, oval pustule. The root is relatively high (about one third of the total tooth height).

*Remarks*.—*Engolismaia* gen. nov. is a very characteristic element of the Charentes selachian fauna because of its unusual tooth morphology. It is currently known only to occur in the eastern part of the Charentes region (Montagan and Traslemaine localities) and is restricted to the middle part of the Lower Cenomanian.

# Comments on palaeoecology and palaeobiogeography

Adding to the systematic results previously supplied by Landemaine (1991), the present study increases our knowledge of the selachian faunas from shallow detrital and terrigenous Cenomanian facies of SW France. In addition, a new species of *Squalicorax* is also described from the deeper basal Turonian chalky marls. The selachian species lists are given for the different localities in the Table 1.

Combined with previous works (Landemaine 1991; Vullo et al. 2003, 2005; Néraudeau et al. 2005), these new data allow to refine the palaeoecological and palaeobiogeographical interpretations for the selachian faunas of this area. The shallow sandy deposits of the Lower Cenomanian indicate coastal paralic habitats that seem to have been favourable to the development of small orectolobiforms and rajiforms. Numerous extant species (e.g., bamboo and nurse sharks) are known to grow, mate, and live in such environments, like mangroves (Compagno 2001). By analogy, the existence of nursery grounds has been suggested by Vullo et al. (2003) for the earliest Cenomanian of Charentes. Small sclerorhynchid sawfishes (or closely related forms) are abundant in these detrital and terrigenous sediments, as it can be also observed in numerous localities from the Cenomanian of Texas (Welton and Farish 1993; Cappetta and Case 1999), Spain (Bernardez 2002), and Egypt (Werner 1989). In the Upper Cenomanian Bahariya Formation, Egypt, where the selachian fauna and other vertebrates is very similar to the Charentes fauna, the palaeobotanical content and the depositional environment indicate a *Weichselia*-dominated mangrove (Lacovara et al. 2001). Interestingly, this mangrove tree fern occurs in the Early Cenomanian deposits of Charentes (Bernard Gomez, personal communication 2005), as some gymnosperms (*Frenelopsis*, *Glenrosa*) and angiosperms (*Pseudoasterophyllites*) characterizing salt marshes (Gomez et al. 2004; Fejfar et al. 2005). All these data show that palaeoecological conditions existing in Southern Tethys may have extended northward up to the Aquitaine Basin. The Charentes selachian fauna differs mainly from Northern European (England, Belgium, Germany) deeper water assemblages by the lack of squaloid, palaeospinacid, and scyliorhinid sharks, common in the Boreal realm (Herman 1977; Müller and Diedrich 1991; Underwood and Mitchell 1999).

During the Late Cenomanian, deeper and more open marine environments ("argiles tégulines" and chalky marl facies) tend to develop in Charentes, with the proliferation of large lamniforms (e.g., *Squalicorax*) and the local appearance of some cosmopolitan taxa (e.g., *Cretolamna*). This contrasts with the strong decrease of the abundance and the diversity of small benthic forms, like orectolobiforms.

In conclusion, these new data confirm that the selachian fauna from the Cenomanian of Charentes shares numerous affinities with those recovered from North America (Texas, Minnesota) (Cappetta and Case 1999; Case 2001), Southern Europe (Spain) (Bernardez 2002), and Northern Africa (Egypt) (Werner 1989), as previously noted by Landemaine (1991), Cappetta and Case (1999) and Vullo et al. (2005). This suggests, in combination with sedimentological and synecological data, similar climatic conditions and depositional environments, like warm tropical shallow coastal waters.

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# References

Agassiz, L. 1833–1843. *Recherche sur les Poissons fossiles*, 5 vols. 1420 pp. Imprimerie de Petitpierre, Neuchâtel et Soleure.

Antunes, M.T. and Cappetta, H. 2002. Sélaciens du Crétacé (Albien–Maastrichtien) d'Angola. *Palaeontographica A* 264: 85–146.

Applegate, S.P. 1972. A revision of the higher taxa of orectolobids. *Marine Biological Association of India Publication* 14: 743–751.

Arambourg, C. 1935. Note préliminaire sur les vertébrés fossiles des phosphates du Maroc. *Bulletin de la Société géologique de France, série 5* 5: 413–439.

Arambourg, C. 1940. Le groupe des Ganopristinés. *Bulletin de la Société géologique de France, série 5* 10: 127–147.

Bardet, N., Cappetta, H., Pereda Suberbiola, X., Mouty, M., Al Maleh, A.K., Ahmad, A.M., Khrata, O., and Gannoum, N. 2000. The marine vertebrate faunas from the Late Cretaceous phosphates of Syria. *Geological Magazine* 137: 269–290.

Berg, L.S. 1940. Classification of Fishes both Recent and Fossil [in Russian; English translation: J.W. Edwards (ed.), Ann Arbor, Michigan, 1947]. *Trudy Zoologičeskogo Instituta, Akademiâ Nauk SSSR, Leningrad* 5: 87–517.

Berg, L.S. 1958. *System der rezenten und fossilen Fischartigen und Fische*. 310 pp. VEB Verlag der Wissenschaften, Berlin.

Bernardez, E. 2002. *Los dientes de selaceos del Cretacico de la Depresion Central Asturiana*. 476 pp. Unpublished Ph.D. thesis, University of Oviedo, Oviedo.

Biddle, J.-P. 1993. Les Elasmobranches de l'Albien inférieur et moyen (Crétacé inférieur) de la Marne et de la Haute-Marne (France). *In*: J. Herman and H. Van Waes (eds.), Elasmobranches et Stratigraphie. *Belgian Geological Survey Professional Paper* 264: 191–239.

Bilelo, A.M. 1969. The fossil shark genus *Squalicorax* in North-Central Texas. *Texas Journal of Science* 20: 339–348.

Blainville, H. de 1816. Prodrome d'une nouvelle distribution systématique du règne animal. *Bulletin de la Société Philomatique de Paris* 8: 105–112.

Bonaparte, C.L.J.L. 1838. Selachorum tabula analytica. *Nuovi Annali delle Scienze Naturali* 1: 195–214.

Cappetta, H. 1973. Selachians from the Carlile Shale (Turonian) of South Dakota. *Journal of Paleontology* 47: 504–514.

Cappetta, H. 1974. Sclerorhynchidae nov. fam., Pristidae et Pristiophoridae: un exemple de parallélisme chez les sélaciens. *Comptes Rendus de l'Académie des Sciences, Paris* 278: 225–228.

Cappetta, 1980a. Les sélaciens du Crétacé supérieur du Liban. 1: Requins. *Palaeontographica A* 168: 69–148.

Cappetta, 1980b. Les sélaciens du Crétacé supérieur du Liban. 2: Batoïdes. *Palaeontographica A* 168: 149–229.

Cappetta, 1980c. Modification du statut générique de quelques espèces de sélaciens crétacés et tertiaires. *Palaeovertebrata* 10: 29–42.

Cappetta, H. 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. *In*: H.-P. Schultze (ed.), *Handbook of Paleoichthyology 3B*, 1–193. Gustav Fischer Verlag, Stuttgart.

Cappetta, H. 1991. Découverte de nouvelles faunes de sélaciens (Neoselachii) dans les phosphates maastrichtiens de la Mer Rouge, Egypte. *Münchner Geowissenschaftliche Abhandlungen A* 19: 17–56.

Cappetta, H. and Case, G.R. 1975. Sélaciens nouveaux du Crétacé du Texas. *Geobios* 8: 303–307.

Cappetta, H. and Case, G.R. 1999. Additions au faunes de sélaciens du Crétacé du Texas (Albien supérieur–Campanien). *Palaeo Ichthyologica* 9: 5–111.

Case, G.R. 1987. *Borodinopristis schwimmeri*, a new ganopristine sawfish from the Upper Blufftown Formation (Campanian) of the Upper Cretaceous of Georgia. *Bulletin of the New Jersey Academy of Sciences* 32: 25–33.

Case, G.R. 2001. A new selachian fauna from the Corelaine Formation (Upper Cretaceous / Cenomanian) of Minnesota. *Palaeontographica, Abteilung A* 261: 103–112.

Case, G.R. and Cappetta, H. 1997. A new Selachian fauna from the late Maastrichtian of Texas (Upper Cretaceous/Navarroan; Kemp formation). *Münchner Geowissenschaftliche Abhandlungen, Reihe A* 34: 131–189.

Casier, E. 1947. Contribution et évolution de la racine dentaire des Euselachii, II; Étude comparative des types. *Bulletin du Musée royal d'Histoire naturelle de Belgique* 23: 1–32.

Checchia-Rispoli, B. 1933. Di un nuevo genere di "Pristidae" del Cretaceo superiore della Tripolitania. *Memorie della Reale Accademia italiana, Classe Scienze Fisiche Mathematiche e Naturale* 4: 1–6.

Compagno, L.J.V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist* 17: 303–322.

Compagno, L.J.V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2: Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). *FAO Species Catalogue for Fishery Purposes 1*. 269 pp. FAO, Rome.

Coquand, H. 1859. Synopsis des animaux et des végétaux fossiles observés dans la formation crétacée du sud-ouest de la France. *Bulletin de la Société Géologique de France, série 2* 16: 945–1023.

Davis, J.W. 1890. On the fossil fish of the Cretaceous formations of Scandinavia. *Scientific Transactions of the Royal Dublin Society* 4: 363–434.

Fejfar, O., Košťák, M., Kvaček, J., Mazuch, M., and Moučka, M. 2005. First Cenomanian dinosaur from Central Europe (Czech Republic). *Acta Palaeontologica Polonica* 50: 295–300.

Gill, T. 1862. Analytical analysis of the order of Squali; and revision and nomenclature of genera. Squalorum generum novorum descriptions diagnosticae. *Annals of the Society of Natural History of New York* 1862: 367–413.

Glückman, L.S. 1958. Rates of evolution in Lamnoid sharks. *Doklady Akademii Nauk SSSR* 123: 568–572.

Glückman, L.S. and Shvazhaite, R.A. [Švažaite, R.A.] 1971. Sharks of the family Anacoracidae from the Cenomanian and Turonian of Lithuania, Pre-Volga's Region and Middle Asia [in Russian]. *Paleontologiâ i Stratigrafiâ Pribaltiki i Belorussii* 3: 185–192.

Gomez, B., Daviero-Gomez V., Perrichot, V., Thévenard, F., Coiffard, C., Philippe, M., and Néraudeau, D. 2004. Assemblages floristiques de l'Albien–Cénomanien de Charente-Maritime (SO France). *Annales de Paléontologie* 90: 147–159.

Hay, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. *Bulletin,United States Geological Survey* 179: 1–868.

Herman, J. 1977. Les sélaciens des terrains néocrétacés et paléocènes de Belgique des contrées limitrophes. Eléments d'une biostratigraphie intercontinentale. *Mémoires pour servir à l'Explication des Cartes Géologiques et Minières de la Belgique* 15: 1–401.

Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 1880: 649–662.

Jaekel, O. 1894. *Die eocänen Selachier vom Monte Bolca*. 176 pp. Verlag Julius Springer, Berlin.

Kennedy, W.J. and Bayliss, O.H. 1977. The earliest tissotiid ammonite. *Palaeontology* 20: 901–906.

Kriwet, J. 1999. Neoselachier (Pisces, Elasmobranchii) aus der Unterkreide (unteres Barremium) von Galve und Alcaine (Spanien, Provinz Teruel). *Palaeo Ichthyologica* 9: 113–142.

Lacovara, K.J., Smith, J.R., Smith, J.B., Lamanna, M.C., and Dodson, P. 2001. Coastal depositional environments along the Cretaceous Tethys Seaway of Egypt. *Geological Society of America Abstracts with Program* 33 (6): 1–195.

Landemaine, O. 1991. Sélaciens nouveaux du Crétacé supérieur du sud-ouest de la France. Quelques apports à la systématique des élasmobranches. *Société Amicale des Géologues Amateurs* 1: 1–45.

Leidy, J. 1856. Notice of remains of extinct vertebrated animals of New-Jer-

sey, collected by Prof. Cook of the State Geological Survey under the direction of Dr. W. Kitchell. *Proceedings of the Academy of Natural Sciences of Philadelphia* 8: 220–221.

Mägdefrau, K. 1937. Lenesspuren fossiler "Bohr"-Organismen. *Beiträge zur naturkundlichen Forschung in Süd-westdeutschland* 2: 54–67.

Meyer, R.L. 1974. *Late Cretaceous Elasmobranches from the Mississippi and East Texas Embayments of the Gulf Coastal Plain*. 419 pp. Unpublished Ph.D. thesis, Southern Methodist University, Dallas.

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.

Müller, A. and Diedrich, C. 1991. Selachier (Pisces, Chondrichthyes) aus dem Cenomanium von Ascheloh am Teutoburger Wald (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen* 20: 1–105.

Müller, J. and Henle, F.G.J. 1839–1841. *Systematische Beschreibung der Plagiostomen*. i–xxii + 200 pp. Berlin.

Néraudeau, D., Perrichot, V., Dejax, J., Masure, E., Nel, A., Philippe, M., Moreau, P., Guillocheau, F., and Guyot, T. 2002. Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). *Geobios* 35: 233–240.

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

Néraudeau D., Vullo R., Gomez B., Perrichot V., and Videt, B. 2005. Stratigraphie et paléontologie (plantes, vertébrés) de la série paralique Albien terminal–Cénomanien basal de Tonnay-Charente (Charente-Maritime, France). *Comptes rendus Palevol* 4: 79–93.

Poey, F. 1861. Memorias sobre la historia natural de la Isla de Cuba, acompañadas de sumarios Latinos y extractos en Francés. *La Habana* 2: 337–342.

Priem, F. 1912. Sur des Poissons des terrains secondaires du Sud de la France. *Bulletin de la Société géologique de France, série 4* 12: 250–271.

Rage, J.-C. and Néraudeau, D. 2004. A new pachyostotic squamate reptile from the Cenomanian of France. *Palaeontology* 47: 1195–1210.

Rafinesque, C.S. 1810. *Caratteri di alcuni nuovi generi e nuove specie di animali e pinate della Sicilia, con varie osservazioni sopra i medisimi. Part 1*. i–iv + 3–69. San Filippo, Palermo.

Sauvage, H.E. 1880. Sur quelques Squales de la craie des Charentes. *Bulletin de la Société géologique de France, série 3* 8: 455–458.

Schaeffer, B. 1963. Cretaceous fishes from Bolivia, with comments on Pristid evolution. *American Museum Novitates* 2159: 1–20.

Signeux, J. 1949. Notes paléoichthyologiques II; Sur les genres *Isurus*, *Chiloscyllium* et *Triakis* trouvés à l'état fossile dans le gisement Sénonien de Sahel-Alma. *Bulletin du Muséum d'Histoire naturelle de Paris* 21: 635–638.

Siverson, M. 1992. Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. *Palaeontology* 35: 519–554.

Siverson, M. 1996. Lamniform sharks of the mid Cretaceous Alinga Formation and Beedagong Claystone, Western Australia. *Palaeontology* 39: 813–849.

Siverson, M. 1997. Sharks from the mid-Cretaceous Gearle Siltstone, Southern Carnarvon Basin, Western Australia. *Journal of Vertebrate Paleontology* 17: 453–465.

Siverson, M. 1999. A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late Cretaceous) of Western Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 90: 49–66.

Slaughter, B.H. and Thurmond, J.T. 1974. A lower Cenomanian ichthyofauna from the Bahariya Formation of Egypt. *Annals of the Geological Survey of Egypt* 4: 25–40.

Sokolov, M.I. 1978. *Zuby akul kak rukovodâŝie iskopaemye pri zonal'nom rasčlenenii melovyh otloženij Turanskoj plity*. 60 pp. Nedra, Moskva.

Stromer, E. 1917. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharaje-Stufe (unterstes Cenoman). 4. Die Sägen der Sägehaie. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftlichen Abteilung, Neue Funde* 28: 1–28.

Stromer, E. 1927. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägypten. II. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 9. Die Plagiostomen mit einem Anhang über Käno- und mesozoische Rückenflossenstacheln von Elasmobranchiern. *Abhandlungen der Bayerischen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Abteilung, Neue Funde* 31: 1–64.

Suarez, M. and Cappetta, H. 2004. Sclerorhynchid teeth (Neoselachii, Sclerorhynchidae) from the Late Cretaceous of the Quiriquina Formation, central Chile. *Revista Geologica de Chile* 31: 89–103.

Underwood, C.J. and Mitchell, S.F. 1999. Albian and Cenomanian selachian assemblages from north-east England. *Special Papers in Palaeontology* 60: 9–56.

Vullo, R. 2005. *Les vertébrés du Crétacé supérieur des Charentes (Sud-Ouest de la France): biodiversité, taphonomie, paléoécologie et paléobiogéographie*. 302 pp. Unpublished Ph.D. thesis, University of Rennes 1, Rennes.

Vullo, R., Néraudeau, D., and Videt, B. 2003. Un faciès de type falun dans le Cénomanien basal de Charente-Maritime (France). *Annales de Paléontologie* 89: 171–189.

Vullo, R., Néraudeau D., Allain R., and Cappetta H. 2005. Un nouveau gisement à microrestes de vertébrés continentaux et littoraux dans le Cénomanien inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). *Comptes Rendus Palevol* 4: 95–107.

Ward, D.J. and Averianov, A.O. 1999. A new ginglymostomatid shark (Chondrichthyes, Orectolobiformes) from Late Cretaceous of Kyzylkum Desert. *Russian Academy of Sciences Proceedings of the Zoological Institute* 277: 89–93.

Welton, B.J. and Farish, R.F. 1993. *The Collector's Guide to Fossil Shark and Rays from the Cretaceous of Texas*. 204 pp. Before Time Edition, Lewisville.

Werner, C. 1989. Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation (Obercenomanan) der Oase Bahariya, Ägypten. *Palaeo Ichthyologica* 5: 5–112.

Whitley, G.P. 1939. Taxonomic notes on sharks and rays. *Australian Zoologist* 9: 227–262.

Woodward, A.S. 1889. *Catalogue of the Fossil Fishes in the British Museum (Natural History). Part I: Elasmobranchii*. xlvii + 474 pp. British Museum (Natural History), London.

Woodward, A.S. 1911. The fossil fish of the English Chalk. Part VI. *Monographs of the Palaeontographical Society* 64 (313): 185–224.

Zhelezko, V.I. [Železko, V.I.] 1990. Pisces (Selachii) [in Russian]. *In*: G.N. Papulov, V.I. Železko, and A.P. Levina (eds.), *Verhnemelovye otloženiâ Ûžnogo Zaural'â (rajon verhnego Pritobol'â)*, 122–133. Ural'skoe Otdelenie AN SSSR, Sverdlovsk.