New Fossil Triakid Sharks from the Early Eocene of Prémontré, France, and Comments on Fossil Record of the Family

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New fossil triakid sharks from the early Eocene of Prémontré, France, and comments on fossil record of the family

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During the last two decades, an abundant selachian assemblage has been collected from the late Ypresian (NP12) fossiliferous sands of Prémontré (Aisne, northern France) but has received little attention. Sharks of the family Triakidae (Carcharhiniformes) are particularly well represented and all are described and figured herein. Among them, two new species of the genus *Galeorhinus* are described: *G. duchaussoisi* sp. nov. and *G. louisi* sp. nov.; these are compared to the common Paleogene *G. ypresiensis* which is refigured. Another triakid taxon, the genus *Gomphogaleus* gen. nov., is described. Most of the triakids have been recorded elsewhere in the North Atlantic region, suggesting a wider distribution than expected for these small sharks during the Paleogene. The present paper updates the list of selachians from Prémontré, bringing the number of taxa from 19 to 33 (including 22 sharks and 11 batoids) and improving our knowledge of the ancient North Atlantic Ypresian selachian fauna. Despite this vastly improved record, it is clear that fossil data are still very incomplete and insufficient for calibrating phylogenetic hypotheses of living forms. Review of the Prémontré fauna shows that the Triakidae were much more diverse and broadly distributed than at present, suggesting that the limited distribution and low diversity of living forms is probably a recent phenomenon.

Key words: Chondrichthyes, Triakidae, *Galeorhinus*, *Gomphogaleus*, Eocene, France.

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Introduction

Although our knowledge of Cenozoic selachians from the Paris Basin has increased as a result of considerable collecting during the nineteenth and twentieth centuries, almost all of the small species have received scant attention due to inappropriate collecting techniques. Study of the microichthyofauna therefore requires additional investigations, especially in European fossil localities excavated before the 1970s.

Discovered in 1980, fossil bearing levels of Prémontré (Paris Basin) have been extensively excavated and exploited by the members of the local "Société Laonnoise et Axonaise de Paléontologie" for its important accumulation of fossil vertebrates, and especially for its rich and varied mammal fauna. The mammal remains occur in an estuarine deposit and are associated with selachians which are essentially restricted to isolated but numerous and well preserved teeth. The first faunal list (selachians included) was published by Dégrémont et al. (1985), followed by many studies focusing on the mammal fauna (Godinot et al. 1992; Lecomte 1994; Sudre and Erfurt 1997; Escarguel 1999) and the reptilian remains (Augé et al. 1997; Augé and Smith 2002; Augé 2003). In the selachian faunal lists, a number of systematic mistakes occurred, some of them have been subsequently corrected (Cappetta 1992) but no updated faunal list had been published during the last two decades. Large quantities of sediment have been carefully processed and sieved with meshes as fine as 0.4 mm. The residue was concentrated by heavy liquids, allowing the study of micro-selachian fauna, missing from the work of Dégrémont et al. (1985). Currently, the selachian fauna from Prémontré far exceeds the 19 species previously recorded in Dégrémont et al. (1985) and contains several new selachian taxa under study. Among sharks, Carcharhiniformes and Lamniformes are particularly well represented and diversified. Two Carcharhiniformes, *Premontreia* and *Pachygaleus*, were the subject of a previous paper (Cappetta 1992). Among the Carcharhiniformes, the family Triakidae is one of the most diversified families recovered in Prémontré, with five species belonging to four genera. One of these (*Pachygaleus*) has been previously described; the present note aims to record the others and to review and update the entire list of fossil selachians discovered in Prémontré.

Institutional abbreviations.—UM-PRE (Prémontré, France) and UM-FLP (Forest-lez-Bruxelles, Belgique), vertebrate paleontology collections of the Paleontology Department, University of Montpellier (UM II), France.

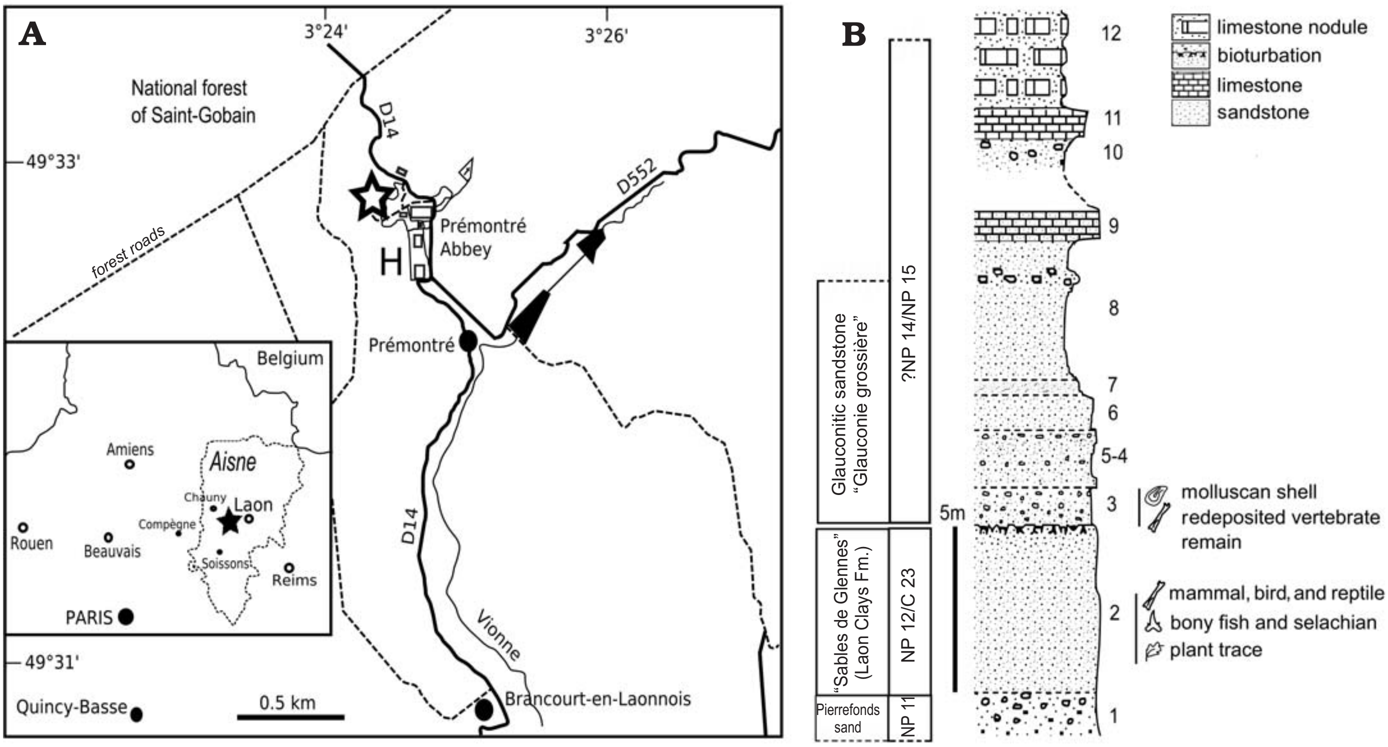


Fig. 1. **A**. Location of the Prémontré Abbey (Aisne, northern France). **B**. Simplified stratigraphic column of Prémontré with fossiliferous (2–3) and non-fossiliferous (4–12) levels (from Dégrémont et al. 1985: 12).

Geographical and geological setting

Prémontré is located in the north-eastern Paris Basin, at 20 km north of Soissons (Fig. 1A), in the Aisne department of France. The material described here comes from a restricted escarpment located in the northwest of the Prémontré Abbey (now reconverted to the psychiatric department of the hospital of Aisne), still accessible on request.

Dégrémont et al. (1985) have informally divided the Prémontré deposits (Fig. 1B) into 12 lithologic levels (Dégrémont et al. 1985: fig. 1). Located at the base of the escarpment, level 2 consists of at least four meters of unconsolidated fine yellow sands, slightly iron-stained, which have yielded all fossil remains (plants, invertebrates, and vertebrates). These highly fossiliferous sands are interpreted as representing accumulations in a nearshore, high-energy marine environment. All the shark material described in this paper was collected from this level. There has been considerable controversy over the age of the Paleogene sands of the Paris Basin. The age of the deposits outcropping at Prémontré (belonging to the "Glennes" Sand Formation as proposed by Dégrémont et al. 1985) has been discussed on different occasions and according to various stratigraphic (Pomerol and Feugeur 1974; Megnien 1980) or paleontological arguments (see Escarguel et al. 1997; Escarguel 1999). The assemblage and evolutionary state of the terrestrial fauna has suggested an Ypresian age (MP10, following Aguilar et al. 1997). As previously noted the fossiliferous sands from level 2 of Prémontré are considered to be a lateral equivalent of the Laon Clays, dated as late Ypresian (upper Cuisian, NP12) according to Steurbaut (1998). The data summarized in this study strongly supports this.

The terminology used here for selachian teeth follows Cappetta (1987). The systematic classification follows Cappetta (1987, 2006) and Compagno (1999) for fossil and Recent taxa respectively. All the taxa from Prémontré are listed in the Appendix 1; they will be studied and figured in detail in a forthcoming work.

Updated list of the selachians from Prémontré

Dégrémont et al. (1985) reported 19 taxa of fossil elasmobranchs from level 2 of the Prémontré Abbey. Further discoveries, improved sampling methods and more work on the material have resulted in revision of the previous list and the recognition of many additional taxa. Cappetta (1992) first reattributed some of those which were partially misidentified. Here we give the first updated list of the entire selachian fauna from Prémontré (Appendix 1). Dégrémont et al. (1985) indicated the occurrence of hexanchid remains (*Notidanus* in text); but no specimen which could be referred to this genus occurs in the studied material. In the same work, *Raja* sp. probably corresponds to *Jacquhermania* or *Ouledia* sp. of our updated list, and *Galeocerdo latidens* corresponds to *Physogaleus* herein. A number of taxa are reported for the first time in the late Ypresian of Prémontré (Appendix 1). Some of them are probably new and will be described in detail in a forthcoming publication.

The updated list includes 33 species of sharks and rays. The selachian fauna of Prémontré appears as diverse as the other contemporaneous fossil-bearing sites from the North Sea Basin (Paris Basin, Hampshire Basin, London Basin, Belgian Basin) and more broadly, from both sides of the North Atlantic (Casier 1946, 1966; Bor 1985; Ward 1980; Nolf 1988; Ward and Weist 1990; Kemp 1994; Kent 1999a, b; Müller 1999). All the determined taxa are common in the Ypresian and Lutetian deposits around the North Atlantic. Some of these taxa (e.g., *Eomobula stehmanni*, *Ginglymostoma* aff. *G. angolense*, *Nebrius thielensi*, *Rhinobatos bruxelliensis*) are nevertheless also distributed in equatorial seas (Dartevelle and Casier 1943; Kruckow and Thies 1990; Noubhani and Cappetta 1997; Tabuce et al. 2005). The occurrence of Heterodontidae, Rhinobatidae, Orectolobiformes and the predominance of dasyatids and small Carcharhiniformes are all indicative of an extreme littoral habitat in tropical latitude. As pointed out by Dégrémont et al. (1985), such a selachian fauna associated with a large and diverse terrestrial fauna (especially mammals and reptiles) indicates that these fossiliferous sands were correctly interpreted as representing accumulations by fluvial flows in a near shore, high-energy marine environment under a warm climate. However, the presence of a significant component of large predators (Odontaspididae) or pelagic forms (Squalidae, Rhincodontidae, Mobulidae) inhabiting more open seas, suggest more marked episodic marine influences than formerly supposed (Dégrémont et al. 1985).

Systematic paleontology

Order Carcharhiniformes Compagno, 1973

Family Triakidae Gray, 1851

Genus *Galeorhinus* Blainville, 1816

Type species: *Squalus galeus* Linnaeus, 1758, Recent. "European seas".

Galeorhinus duchaussoisi sp. nov.

Fig. 2A–J.

2006 *Galeorhinus*? sp. nov.; Adnet 2006: 74–76, pl. 25: 1–7.

Etymology: Species named in honour of François Duchaussois, from the "Société Laonnoise et Axonaise de paléontologie", for his contribution to paleontological research in Prémontré.

Holotype: UM-PRE 5, an upper antero-lateral tooth, (Fig. 2E), collected by HC.

Type locality: Prémontré Abbey, Prémontré (Aisne, Northern France).

Type horizon: "Sables de Glennes" (Laon Clays Fm.), Level 2, late Ypresian (NP12), Eocene.

Material.—86 teeth.

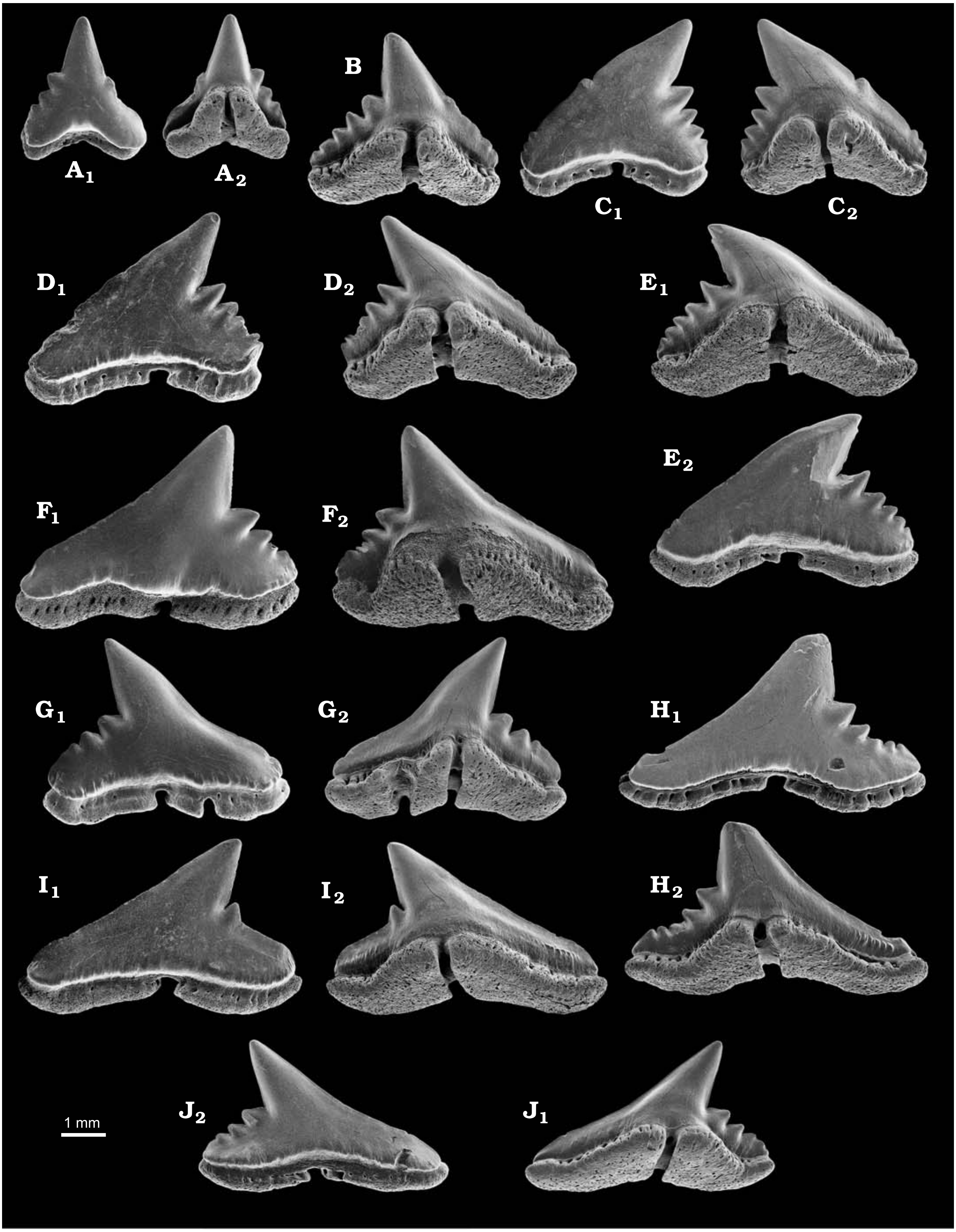
Diagnosis.—Fossil species of *Galeorhinus* distinguished from the majority of *Galeorhinus* species (*Galeorhinus louisi* sp. nov. included) in having thick, medium-sized teeth up to 7 mm in total width with a combination of a series of up to 6 large, divergent distal denticles. *Galeorhinus duchaussoisi* sp. nov can be distinguished from the closest fossil species *G. ypresiensis* by its reduced or absent mesial denticles or serrations and a strong thickness of the root, even in anterior and antero-lateral rows.

Description.—The dignathic heterodonty is moderate and concerns especially the shape and size of the cusp. The holotype (Fig. 2E) is an upper latero-anterior tooth, broader than high. The enamel is mainly smooth. The cusp is high, well individualized, distally inclined with an angle close to 45°; its mesial cutting edge is rectilinear on the whole, slightly concave and oblique. The distal cutting edge is straight, long and oblique. The distal heel is well-developed, oblique and bears five denticles with a size which decreases distally. The distal angle (formed by the distal cutting edge of cusp and the mesial edge of the first denticle of the heel) is acute. The lingual face of the crown is rather convex transversely, especially on the median part and it sometimes bears some parallel folds at the base of the mesial extremity (Fig. $2E_1$). The labial face is rather convex, especially at the level of the cusp. Its basal limit is medially concave and clearly overhangs the root without forming a true transversal bulge. The root is thick; the lobes have very flat basal faces and are separated by a broad and deep nutritive groove that reaches the crown-root boundary on the lingual face (Fig. $2E_1$). A large foramen opens in the median part of the groove. The lingual protuberance of the root is well-marked but not salient. The two margino-lingual faces of the root show many and rather large foramina, especially towards the ends of the lobes. In lingual view, the basal edge of the root is medially concave and marginally raised. The labial face of the root is low, with a slightly concave profile and bears many foramina, irregularly spaced and aligned parallel to the basal edge. Other antero-lateral teeth show a similar morphology with moderate change in cusp shape (Fig. 2D) and number of distal denticles.

In the anterior teeth, the mesial cutting edge of the cusp bears few serrations on its basal and median part (Fig. 2B, C). The distal heel is abrupt and cut out by five denticles. The nutritive groove is narrower (Fig. $2C_2$) than on the holotype.

A lower symphyseal tooth is almost symmetrical (Fig. 2A). The tooth is rather narrow, with an almost vertical erected cusp. The mesial edge is concave, with a blunt denticle in its median half part. The distal edge is very abrupt and bears three denticles; distal angle is close to 90°. The lower boundary of the enamel is medially concave.

The lower teeth (Fig. 2F–J) are relatively broader than the upper ones, with a more erect cusp, leading to a more concave mesial cutting edge. On an anterior tooth (Fig. 2G), the mesial cutting edge is medially concave to slightly convex near the apex of the cusp; the distal cutting edge is long and oblique and the distal heel has three denticles. This tooth is remarkable by the presence of a broad and probably abnormal supplementary nutritive groove across the mesial lobe of


A1
A2
B
C1
C2
D1
D2
E1
F1
F2
E2
G1
G2
H1
I1
I2
H2
1 mm
J2
J1

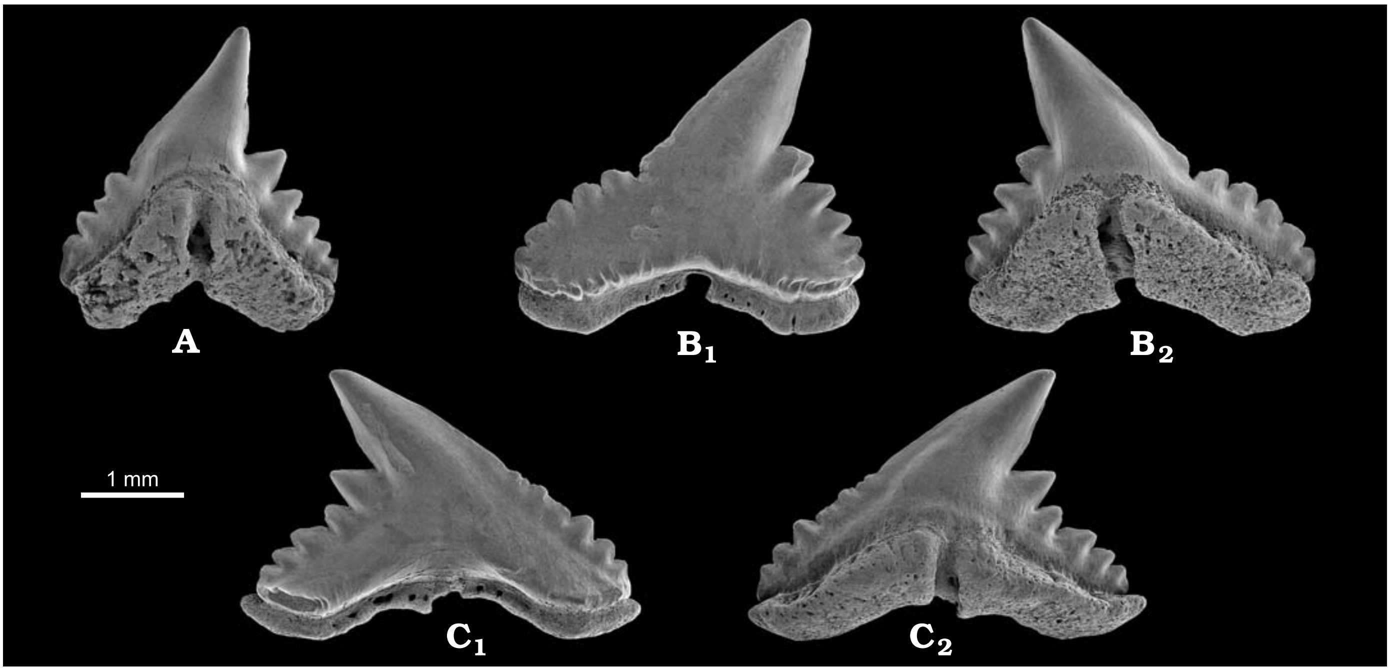


Fig. 3. Triakid shark *Galeorhinus ypresiensis* (Casier, 1946). Forest-lez-Bruxelles, Belgique. **A**. UM-FLB 1, anterior tooth, lingual face. **B**. UM-FLB 2, anterior tooth, labial (B_1) and lingual (B_2) faces. **C**. UM-FLB 3, anterior tooth, labial (C_1) and lingual (C_2) faces.

root (Fig. $2G_2$). In more lateral files, the mesial cutting edge is more concave. The distal heel bears from three to five denticles according to the tooth position. One tooth (Fig. 2I) shows only one denticle followed by a rather straight heel, except in its distal part where it bends. The labial crown-root boundary is slightly concave in the median part, except on a very massive tooth (Fig. 2F) which has a median convexity. The root is massive and thick as in the upper teeth.

Comments.—Many species have been attributed to the triakid genus *Galeorhinus*, but, in fact, a close examination of their dentitions show that most of them belong to the carcharhinid genus *Physogaleus*. This is the case for the species *G. cuvieri* (Agassiz, 1835), from the Ypresian of Monte Bolca, northern Italy (still assigned to *Galeorhinus* in Cappetta 2006), for the widespread species *G. minor* (Agassiz, 1835) noted in the Paleocene and the Eocene from the English-French-Belgian Basin (Leriche 1905, 1906; Casier 1946 ,1966; Herman 1972, 1977; Ward 1980; Kemp 1994) to the East coast of the USA (Ward and Weist 1990; Cvancara and Hoganson 1993; Case 1996) and for the species *G. falconeri* White, 1926 from the Lutetian of Nigeria. The species *G. huberiensis* Case, 1981, from the late Eocene of Georgia, is clearly different from all the others in its large size (10 mm in width), high number of secondary denticles or serrations on the mesial cutting edge of the cusp and a labio-lingually compressed root which resembles the morphology of the large carcharhinid genus *Galeocerdo*. Teeth of the Belgian *G. ypresiensis* (Casier, 1946), well-known from the Ypresian–Lutetian stages in the English-French-Belgian basin (Bor 1985; Dutheil 1991; Kemp 1994) and the U.S. Atlantic Coast (Ward and Weist 1990; Kent 1999a), is related to *Galeorhinus duchaussoisi* sp. nov. but despite a certain resemblance, the teeth of the new species can be easily separated from *G. ypresiensis* by their larger size, their more important thickness and the usual lack of denticles or serrations on the mesial cutting edge from anterior to antero-lateral files. As the tooth morphology of *G. ypresiensis* is relatively confused in the literature, typical teeth of *G. ypresiensis* from Forest-lez-Bruxelles (the type locality) have been refigured here (Fig. 3A–C) for comparison.

Galeorhinus duchaussoisi sp. nov. is clearly separated from the other fossil species of the genus in having thick teeth with a crown bearing numerous denticles (up to 6) on the distal heel. In fact, most Paleogene species of *Galeorhinus* have teeth with no more than 3 distal denticles, as seen in *G. mesetaensis* Noubhani and Cappetta, 1997 and *G. minutissimus* (Arambourg, 1935) from Morocco. Moreover, *G. mesetaensis* has teeth always bearing folds at the base of the labial face of the crown, mainly under the heels. *G. minutissimus* has much smaller teeth with a more slender cusp.

The species *G. loangoensis* Dartevelle and Casier, 1943 (pl. 12: 32–36) was described from the Lutetian of Landana,

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← Fig. 2. Triakid shark *Galeorhinus duchaussoisi* sp. nov. Prémontré Abbey, late Ypresian. **A**. UM-PRE 1, parasymphyseal tooth, labial (A_1) and lingual (A_2) faces. **B**. UM-PRE 2, anterior tooth, lingual face. **C**. UM-PRE 3, anterior tooth, labial (C_1) and lingual (C_2) faces. **D**. UM-PRE 4, anterior tooth, labial (D_1) and lingual (D_2) faces. **E**. UM-PRE 5, holotype, antero-lateral tooth, lingual (E_1) and labial (E_2) faces. **F**. UM-PRE 6, lower antero-lateral tooth, labial (F_1) and lingual (F_2) faces. **G**. UM-PRE 7, lower antero-lateral tooth, labial (G_1) and lingual (G_2) faces. **H**. UM-PRE 8, lower lateral tooth, labial (H_1) and lingual (H_2) faces. **I**. UM-PRE 9, lower lateral tooth, labial (I_1) and lingual (I_2) faces. **J**. UM-PRE 10, lower lateral tooth, lingual (J_1) and labial (J_2) faces.

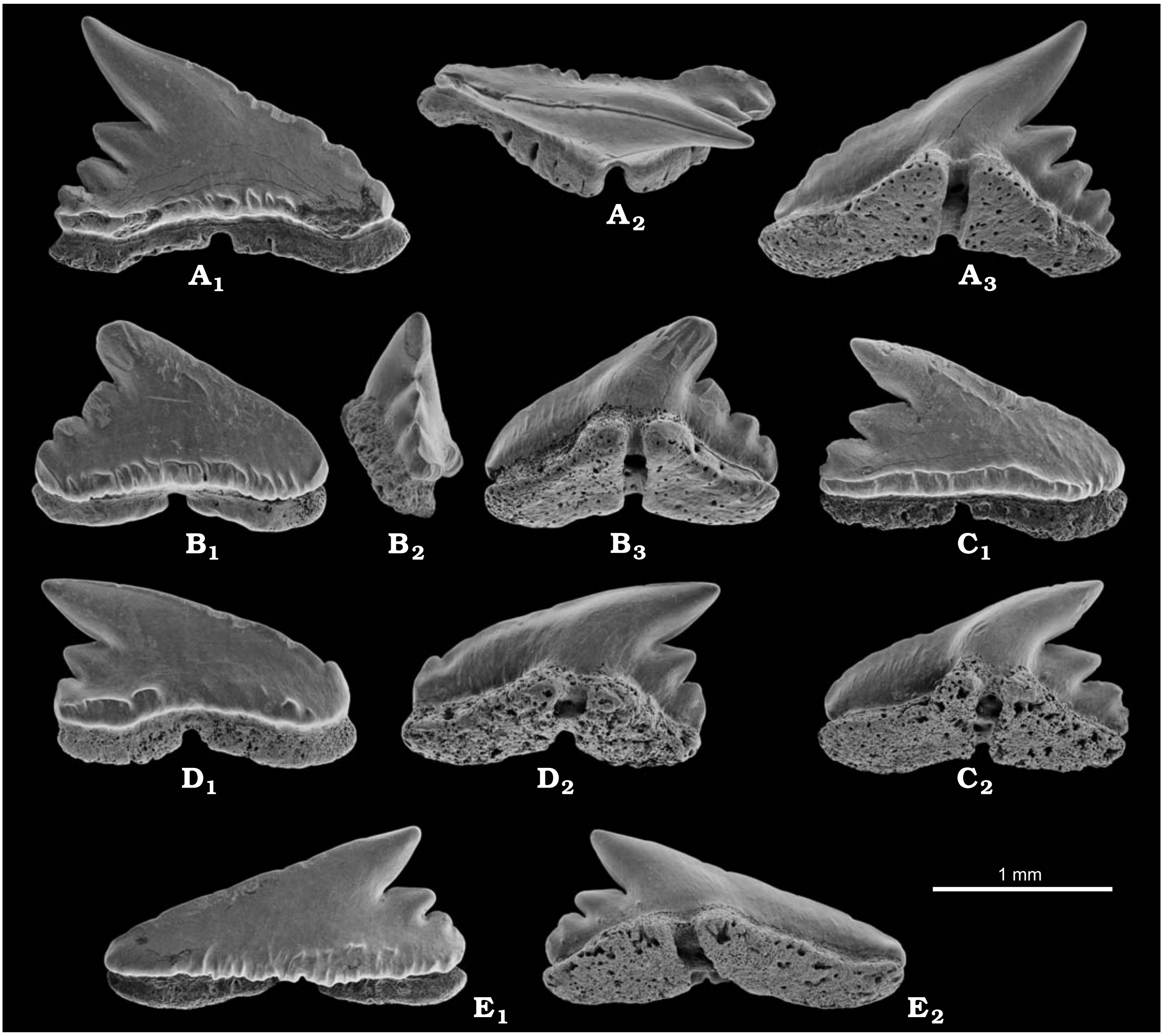

Fig. 4. Triakid shark *Galeorhinus louisi* sp. nov. Prémontré Abbey, late Ypresian. **A**. UM-PRE 11, holotype, antero-lateral tooth, labial face (A$_1$), apical view (A$_2$), and lingual face (A$_3$). **B**. UM-PRE 12, antero-lateral tooth, labial face (B$_1$), profile view (B$_2$), and lingual face (B$_3$). **C**. UM-PRE 13, lateral tooth, labial (C$_1$) and lingual (C$_2$) faces. **D**. UM-PRE 14, lateral tooth, labial (D$_1$) and lingual (D$_2$) faces. **E**. UM-PRE 15, more lateral tooth, labial (E$_1$) and lingual (E$_2$) faces.

Angola. The type series is not homogeneous and the teeth of their figs. 34 and 35, and maybe 33, can be attributed to the genus *Physogaleus*. Only fig. 32, depicting a symphyseal tooth, and fig. 36, which shows posterior tooth, represent the genus *Galeorhinus*. This material is quite insufficient to correctly define a species, but these teeth, mainly the symphyseal one, differ clearly from the teeth of *G. duchaussoisi* sp. nov.

Adnet (2006: pl. 25: 1–7) figured an unnamed species (as *Galeorhinus*? sp. nov.) from the late Ypresian of St Géours-d'Auribat (Landes, southwestern France) which can now be assigned to the new species *G. duchaussoisi*.

Stratigraphic and geographic distribution.—Late Ypresian (NP12) of north and southwestern France.

Galeorhinus louisi sp. nov.

Fig. 4A–F.

Etymology: Species named in honour of Pierre Louis from the local "Société Laonnoise et Axonaise de paléontologie" for his contribution to palaeontological research in the Reims region.

Holotype: UM-PRE 11, a lower antero-lateral tooth (Fig. 4A) collected by HC.

Type locality: Prémontré Abbey, Prémontré (Aisne, northern France).

Type horizon: "Sables de Glennes" (Laon Clays Fm.), Level 2, late Ypresian (NP12), Eocene.

Material.—Nine teeth.

Diagnosis.—Small species of *Galeorhinus*, teeth up to

2.2 mm in total width, with a reduced number of denticles on the distal edge of crown (up to 4) and lacking denticles and serrations on the mesial cutting edge, except sometimes a very small basal one. *G. louisi* differs from all other *Galeorhinus* species in having the base of the labial face of the crown (overhanging the labial crown-root junction) with several marked irregular folds and associated notches on the entire width, forming sometimes a horizontal, straight transversal bulge in labial view. Root not very thick, with lobes always clearly separated, even in the anterior files.

Description.—The holotype (Fig. 4A) is a lower antero-lateral tooth. The cusp is acute, well individualized, and distally inclined with an angle close to 45°. Its mesial cutting edge is sigmoid, slightly convex at the base to concave near the apex. The distal edge of the cusp is short, very oblique and convex. The distal heel is abrupt and bears three large denticles. The labial crown-root boundary is concave in labial view. The basal edge of the crown, overhanging the crown-root junction, is deeply incised by several vertical notches and folds on its entire width. Limited in height, these delimit a horizontal, straight and salient bulge. In apical view (Fig. $4A_2$), the labial face is convex under the cusp and concave at its extremities, especially under the distal heel. The enamel of the lingual face of the crown is smooth. The root is moderately thick; its lobes have flat basal faces and are separated by a deep and large nutritive groove (Fig. $4A_3$). The margino-lingual faces of the root are well-separated from the basal face and bear some elliptic foramina on their surface. The large principal foramen opens in the lingual part of the nutritive groove. The labial face of the root is low; its profile is concave and largely overhung by the crown enamel in occlusal view (Fig. $4A_2$).

The lateral teeth (Fig. 4C–E) show a cusp with a more buckled enamel compared to the anterior ones, especially on the lingual face. The distal heel bears from one to three denticles. The labial crown-root boundary is generally straight and its basal transversal bulge may be very prominent and irregular, showing many folds and associated notches except on its mesial extremity (Fig. $4B_1$, C_1). In some more lateral files (Fig. 4E), the cusp is distally elongated with an apex being above the distal extremity of the root. The mesial cutting edge is long, slightly but regularly convex, with an unique small mesial serration. The distal heel is short and bears only two denticles. The labial crown-root boundary is medially concave.

A probably upper anterior tooth (Fig. 4B) appears less mesio-distally developed than the lower teeth. The mesial cutting edge of the crown is straight and the labial transversal bulge is medially underlined by many short and vertical folds. On the upper lateral tooth (Fig. 4E), the diagnosic labial transversal bulge is always developed and folded.

Comments.—The tooth morphology is definitily that of *Galeorhinus* but the shape of the peculiar labial crown-root boundary recalls that of a contemporaneous species such as *Triakis wardi* Cappetta, 1976 and justifies the description of this new species. The closest species seems to be *G. mesetaensis* Noubhani and Cappetta, 1997 from the Thanetian of Morocco. Yet, *G. louisi* sp. nov. can be clearly separated from the latter in having a more continuous and irregular bulge at the base of the labial face of the crown. Compared with *G. mesetaensis*, this basal bulge is lacking in the median part of the crown.

Musick et al. (2004) discussed the historical zoogeography of *Galeorhinus* and noted that the origin and paleoenvironment of the ancestors of the unique living species *G. galeus* (Linnaeus, 1758), worldwide distributed, suggest similar thermal preferences to the cold waters as for the extant species (Compagno et al. 2005). However, Paleogene fossil localities of North Atlantic where numerous species of *Galeorhinus* are recorded (such as *G. louisi* sp. nov.) correspond to warm climatic conditions, implying an obvious environmental change in the Recent distribution of this genus.

Stratigraphic and geographic distribution.—Late Ypresian (NP12), known only from the type locality.

Genus *Gomphogaleus* nov.

Type species: *Mustelus rodgersi* Case, 1994, by monotypy; Meridian, Lauderdale County, Mississippi, USA, Ypresian, lower Eocene.

Etymology: From Greek *gomphos* = "thick" referring to the great thickness of teeth.

Diagnosis.—Fossil genus differing from all other triakid genera in having small, thick teeth with short distal cusplets and completely smooth enamel. Compared to all genera with cuspidate teeth (*Galeorhinus*, *Kouribgaleus*, *Pachygaleus*, *Triakis*, among others), the cusp is shorter, rather erect, little detached from the rest of the crown and its mesial cutting edge is clearly concave in labial view. The labial face is convex in profile and strongly overhangs the root. Only one short denticle emerges from the distal heel of the crown. The root is stocky and reduced in size; its lingual protuberance is well developed, prominent, rounded and the two lobes are largely separated by a broad and deep nutritive groove.

Gomphogaleus rodgersi (Case, 1994)

Fig. 5A, B.

1994 *Mustelus rodgersi* sp. nov.; Case 1994: 118, pl. 13: 276–281.

Material.—Four teeth.

Description.—The best preserved specimen (Fig. 5B) is a latero-anterior tooth. The enamel is smooth on both faces. The cusp is little detached from the rest of the crown, short and slightly erect. The crown is broader than high. The mesial cutting edge is concave except in the mesial base where it is rather strongly rounded. The distal heel is well developed, high and bears a strong, short denticle. The distal cutting edge of the cusp is short, subvertical and slightly longer than the mesial edge of the distal denticle. The distal angle is close to 90°. The marginal part of the distal heel is rather long and slightly convex; its lateral extremity is very rounded. The labial face of the crown is nearly flat. Its basal edge is marked by a well individualized transverse bulge above the crown-root junction. Not very salient, this bulge is

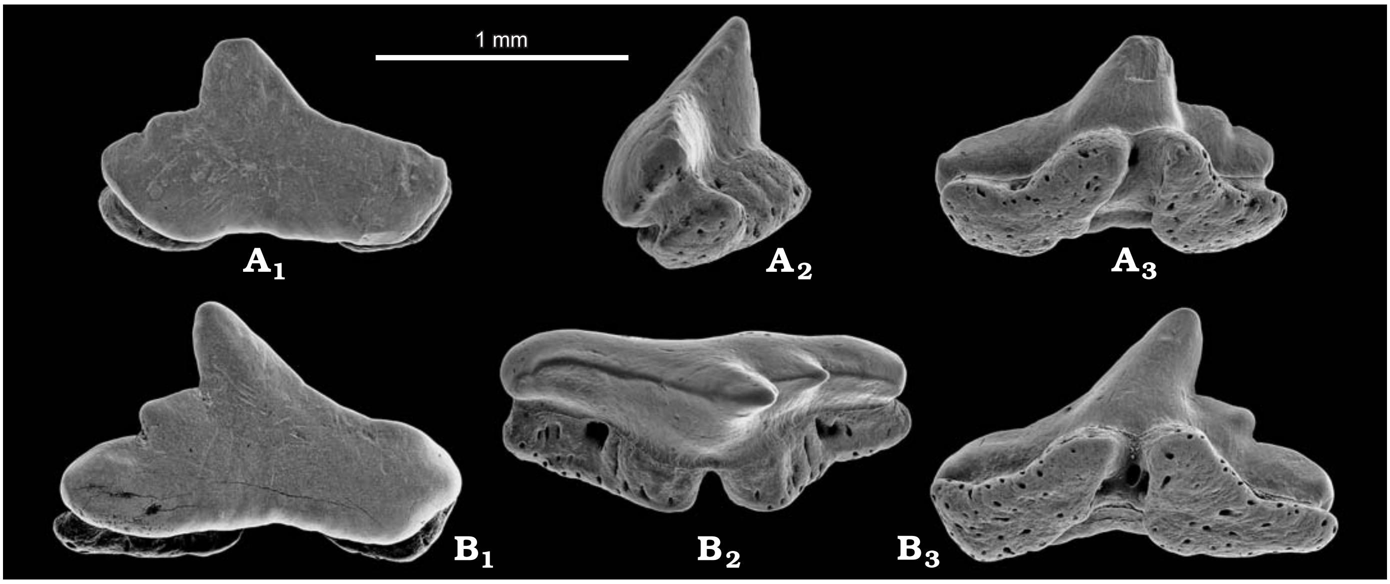

Fig. 5. Triakid shark *Gomphogaleus rodgersi* Case, 1994. Prémontré Abbey, late Ypresian. **A**. UM-PRE 16, anterior tooth, labial face (A_1), profile view (A_2), and lingual face (A_3). **B**. UM-PRE 17, holotype, antero-lateral tooth, labial face (B_1), apical view (B_2), and lingual face (B_3).

rounded in profile view and strongly overhangs the root. The root is thick. The two lobes are separated by a broad and deep nutritive groove that is broader labially than distally. There is a pair of large margino-lingual foramina on each side of the lingual protuberance (Fig. 5B_2). The labial face of the root is low and concave (Fig. 5B_2) , bearing a set of small foramina that open above its basal edge. A second specimen (Fig. 5A) has a broken cusp and a very low and blunt denticle on the distal heel. As for the holotype, the basal bulge of the labial face is well-rounded in profile (Fig. 5A_2) and the lingual protuberance of the root is medially salient in lingual view (Fig. 5A_3). The axial groove is deep and very broad, with large foramina in variable number.

Comments.—The species *G. rodgersi*, described by Case (1994) from the Tuscahoma Formation of Meridian, Mississippi, USA, was erronneously interpreted and assigned to the genus *Mustelus*. The single specimen figured by Case (1994) is slightly larger than our teeth, not perfectly preserved but is morphologicaly very similar to our material. The age of the Tuscahoma Formation is considered as Thanetian in the work of Case (1994). Yet its selachian assemblage, particularly its richness and diversity in carcharhinids, is more consistent with an Ypresian age. *G. rodgersi* is also represented in the Ypresian deposits from Egem, Belgium (HC unpublished data) and in the early Ypresian of Khouribga, Basin of Ouled Abdoun, Morocco (HC unpublished data), though it is uncommon there.

Stratigraphic and geographic range.—Ypresian, French-Belgian Basin, Morocco, and Mississippi, USA.

Genus *Mustelus* Linck, 1790

Type species: *Squalus mustelus* Linnaeus, 1758; Recent.

Mustelus aff. *M. vanderhoefti* Herman, 1982

Fig. 6A.

2006 *Mustelus* sp.; Adnet 2006: 76–78: pl. 26: 1–3.

Material.—Two teeth.

Description.—The species of this genus are characterised by a crushing-type dentition. The lateral tooth figured here (Fig. 6A) is slightly asymmetrical and transversely elongated, with a reduced, distally directed cusp. The enamel of the crown is strongly wrinkled, especially on the labial and lingual faces. The crown is as high as the root. Its occlusal face is flat and relatively smooth except on its labial edge, where it bears deep folds. The labial face of the crown broadly overhangs the root in profile (Fig. 6A_2) and the lingual face bears a salient uvula located under the cusp (Fig. 6A_1, A_3). The root is thick with a flat basal face. The lingual protuberance of the root is well-developed under the uvula and several marginal foramina open on both sides. The nutritive groove is broad, straight and the principal nutritive foramen opens on it lingual edge.

Comments.—The fossil record of the genus *Mustelus* is poorly documented. The oldest record seems to be from the Thanetian of the Paris Basin (Bault and Genault 1995) but this genus remains scarce in deposits until the Neogene, during which it becomes more abundant (Herman 1982: 191; Bault and Genault 1995: 207). *Mustelus* is currently one of the most diverse triakid genera, including 22 living species, and inhabits mainly the neritic zone (up to 200 m depth) of the cold to tropical areas of most of the seas and oceans (e.g., Compagno 1984; Compagno et al. 2005). The tooth morphology of *Mustelus* species is very homogeneous and species are hardly differentiable on the basis of dental characters (Herman et al. 1988, 1990), which partly explains why paleontologists hesitate to refer fossil *Mustelus* teeth to precise

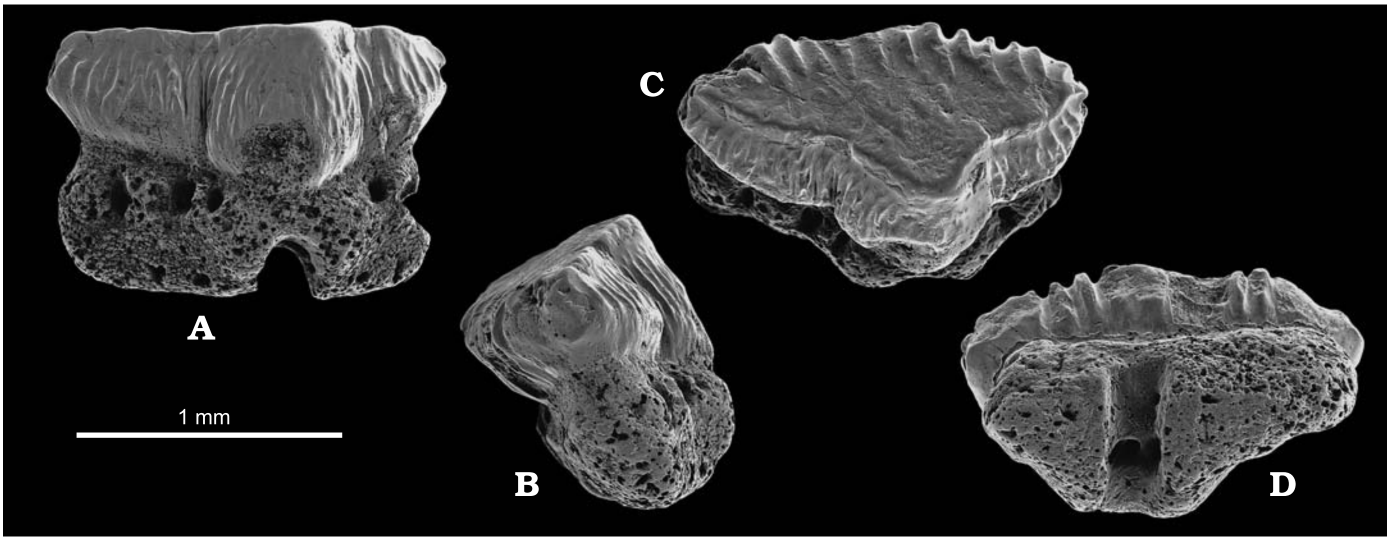

Fig. 6. Triakid shark *Mustelus* aff. *M. vanderhoefti* Herman, 1982. Prémontré Abbey, late Ypresian. UM-PRE 18, lateral tooth, lingual face (**A**), profile view (**B**), occlusal face (**C**), and basal face (**D**).

species (Cappetta and Cavallo 2006). As a result, only three fossil species of *Mustelus* have been described and considered as valid (Cappetta 2006): *Mustelus biddlei* Bault and Genault, 1995 (Thanetian of Ressons-sur-Matz , northern France); *Mustelus whitei* Cappetta, 1976 (lower Ypresian of Burnham-on Crouch, London Clay, England) and *Mustelus vanderhoefti* Herman, 1982 (Ypresian of Egem, Belgium). The teeth of Premontré, like those from the middle Lutetian of southwestern France (Adnet 2006), are closely similar to those of *Mustelus vanderhoefti*, known until the middle Eocene of England (Kemp 1994).

Genus *Pachygaleus* Cappetta, 1992

Type species: *Galaeus lefevrei* Daimeries, 1891; Saint-Gilles, Belgium, Ypresian.

Pachygaleus lefevrei (Daimeries, 1891)

Fig. 7A–C.

1891 *Galaeus lefevrei* sp. nov.; Daimeries 1891: 74 (no figure).
1905 *Galeus lefevrei* (Daimeries, 1891); Leriche 1905: pl. 11: 54–58.
1946 *Eugaleus lefevrei* (Daimeries, 1891); Casier 1946: pl. 1: 13.
1992 *Pachygaleus lefevrei* (Daimeries, 1891); Cappetta 1992: 644–645.
1994 *Galeorhinus lefevrei* (Daimeries, 1891); Kemp 1994: pl. 16: 7, 8.
1994 *Galeorhinus lefevrei* (Daimeries, 1891); Case 1994: pl. 8: 165, 166.
1995 *Pachygaleus lefevrei* (Daimeries, 1891); Bault and Genault 1995: pl. 7: 5, 6, pl. 8: 1, 2.
1999 *Galeorhinus lefevrei* (Daimeries, 1891); Müller 1999: pl. 5: 2.
1999 *Pachygaleus lefevrei* (Daimeries, 1891); Kent 1999a: pl. 2.2: P.

Material.—65 teeth.

Description.—This species has been frequently described and illustrated, so detailed treatment here is unnecessary. The teeth are medium sized (up to 10 mm width) with an oblique, compressed crown having generally smooth enameloid. The mesial cutting edge is slightly convex and usually lacks cusplets or serrations, though serrations may occur on some teeth (Fig. 7B). The distal heel, very long and

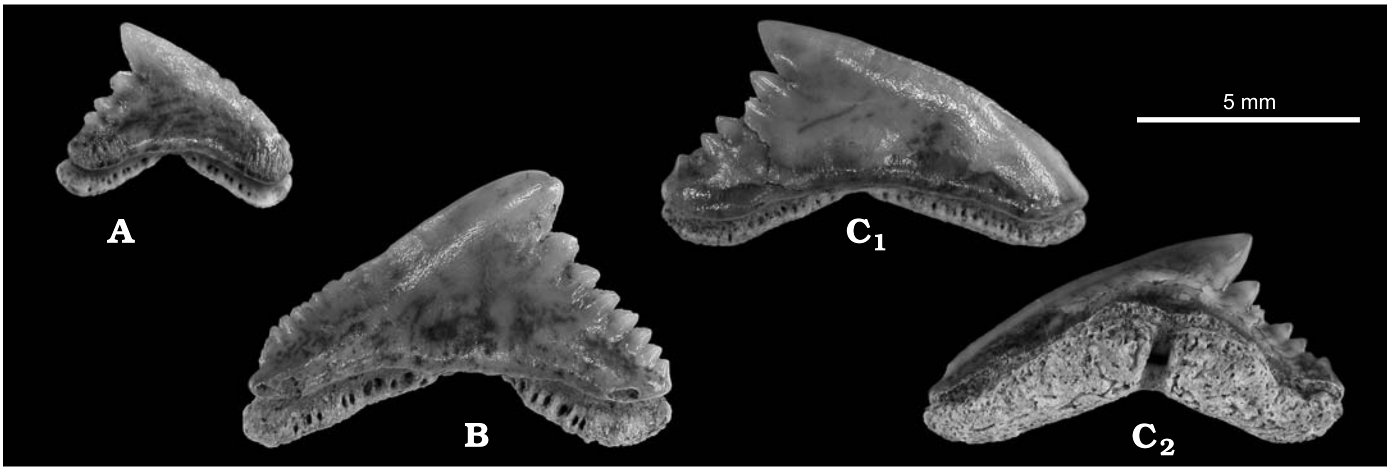

Fig. 7. Triakid shark *Pachygaleus lefevrei* (Daimeries, 1891). Prémontré Abbey, late Ypresian. **A**. UM-PRE 19, anterior tooth, labial face. **B**. UM-PRE 20, antero-lateral tooth, labial face. **C**. UM-PRE 21, lateral tooth, labial (C_1) and lingual (C_2) faces.

oblique, bears numerous well-developed cusplets that become smaller distally. The root is wide, moderately robust, expanding basally in two lobes with rounded extremities. It is overhung by the labial bulge of the crown which may sometimes present irregular wrinkles.

Comments.—The type species was originally described from material of the Saint-Gilles locality (Belgium, Ypresian) by Daimeries (1891), who attributed it to the invalid genus *Galaeus* (typological mistake). Cappetta (1992) amended the diagnosis of this species with the description of the new genus *Pachygaleus*, characterized by the large size and the very peculiar thickness of their teeth. *Pachygaleus lefevrei* is known from Thanetian to Lutetian deposits of the of the U.S. Atlantic Coast to west European basins including south England, Belgium, northern and southwestern France (Casier 1946, 1966; Dutheil 1991; Cappetta 1992; Kemp 1994; Bault and Genault 1995; Kent 1999a; Müller 1999; Adnet 2006). As Cappetta (1992) noted, the distribution of this triakid shark seems to have been restricted to the North Atlantic coasts during the Paleogene.

Overview on family Triakidae

The fossil record of Triakidae is documented from the Cenomanian of Ukraine (Popov and Lapkin 2000) and the lineage can be traced back to the Hauterivian (northeast England: Triakidae? indet.: Underwood et al. 1999). Based on the revision of Cappetta (1992), we present herein an updated list of fossil (†) and Recent triakid genera (Appendix 2), with information about temporal and geographical distributions extracted from literature (e.g., Cappetta 1987, 1992, 2006; Compagno 1984, 1999; Compagno et al. 2005; Musick et al. 2004) and from our own data.

Currently, the family Triakidae is one of the largest families of sharks in term of diversity, with over 40 living species (Compagno 1999) belonging to 9 genera. They are distributed world-wide in warm and temperate coastal seas, where they principally frequent the continental slope below 200 m in depth. Living triakid species show a relatively well specialized feeding type according to their prey spectrum (see Cortes 1999). Consequently, their teeth morphologies are particularly heterogeneous, including clutching-cutting type (genera: *Galeorhinus*, *Hypogaleus*, *Furgaleus*, *Iago*, *Hemitriakis*, and *Gogolia*), clutching-type (*Triakis*) or crushing-type dentition (*Mustelus*, *Scylliogaleus*), with many species intermediate in dental morphology (Compagno 1970).

Herman et al. (1988) have extensively figured teeth of all Recent triakid genera and defined some odontological keys. Later, Herman et al. (1990) assigned the genus *Furgaleus* to Hemigaleidae on the presence of strong dignathic heterodonty, lacking in Triakidae, and considered *Galeorhinus* and *Hypogaleus* as congeneric based on their dental morphology.

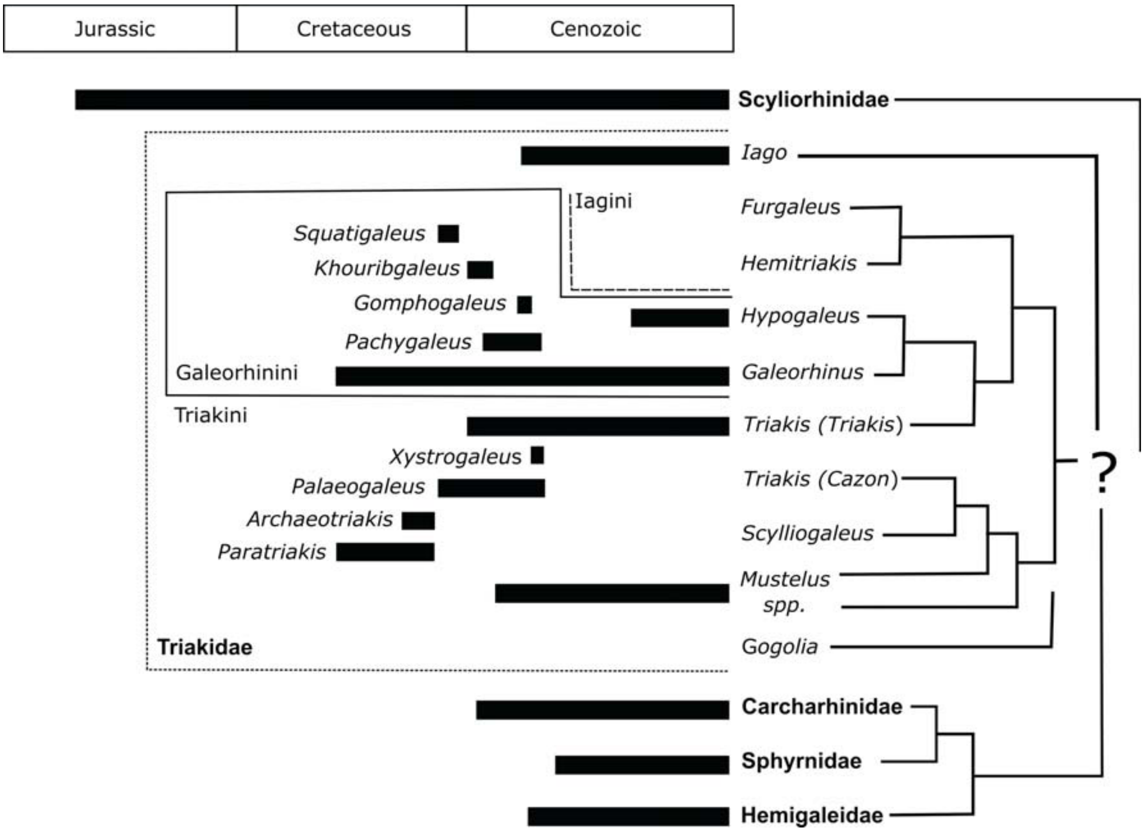

Fig. 8. Fossil record of triakid genera plotted against simplified phylogenetic relationships of extant Triakidae (from Lopez et al. 2006 in part). See text and Appendix 2 for discussion and details.

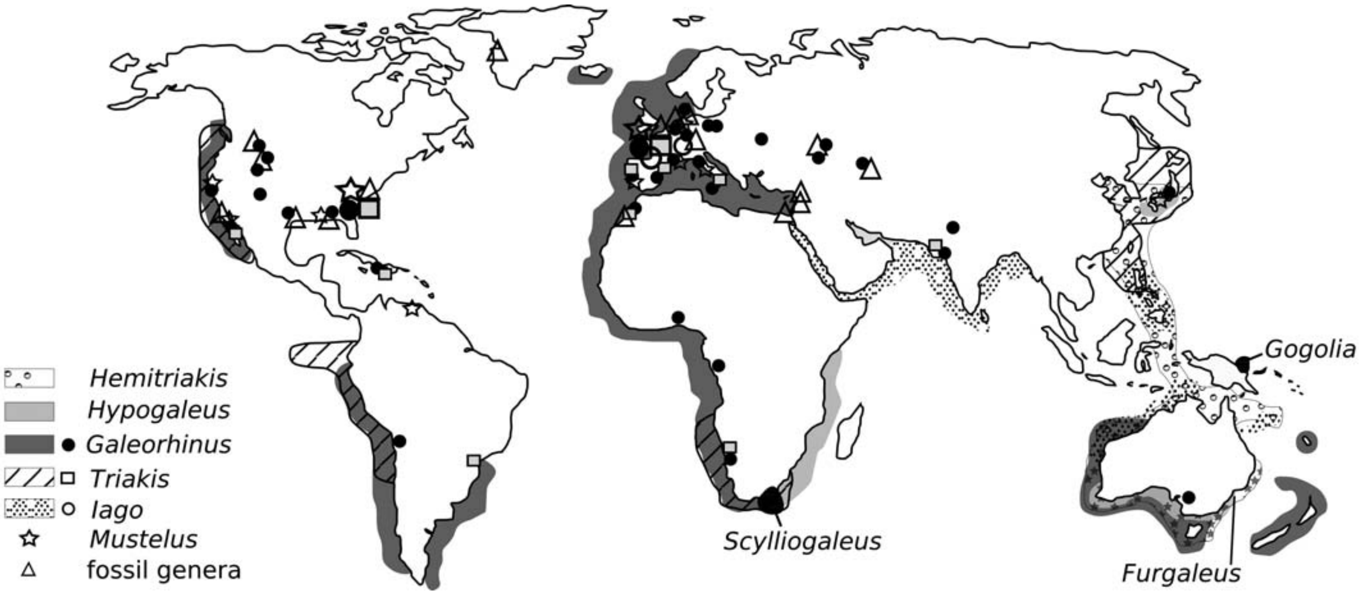

Fig. 9. Distribution of living triakid genera (areas) and their fossil relatives (geometric symbols) compiled from the literature. The number of symbols (plotting the fossil evidence) is intentionally reduced for western Europe and southeastern USA. Living *Mustelus* is circumglobal in all temperate and tropical seas and is not figured on the map.

Cappetta (1992: 644) discussed the systematics and dental characters of fossil and Recent triakid genera. He pointed out the triakid subdivisions (subfamily and tribe) usually reported in literature devoted to Recent Carcharhiniformes (Compagno 1988). Two subfamilies are commonly recognized on their general morphology: the subfamily Triakinae (*Triakis*, *Mustelus*, and *Scylliogaleus*) and Galeorhininae for the others. This last subfamily is subdivided into two tribes: the Iagini (*Iago*, *Hemitriakis*, *Furgaleus*, and *Gogolia*) and the Galeorhinini (*Galeorhinus* and *Hypogaleus*). Based on dental morphology, Cappetta (1987, 1992) attributed some fossil genera to one or the other subfamily groups, relegating, for example, *Palaeogaleus* and *Paratriakis* to Triakinae and *Pachygaleus* to Galeorhininae (tribe Galeorhinini). Noubhani and Cappetta (1997) supported this point of view and attributed the fossil genus *Kouribgaleus* to the Galeorhinini. However, family and subfamily positions of *Archaeotriakis*, *Squatigaleus*, and *Xystrogaleus* remain undefined. Even if these subfamilies seem homogeneous on the basis of tooth morphology, they did not appear in the more recent systematic works (e.g., Compagno 1999). The main reason is that the phylogenetic relationships of Recent species became unclear and that Triakidae are suspected as comprising a paraphyletic group. The principal argument for paraphyly is the branching of the family Carcharhinidae from within the triakid clade (Maisey 1984; Compagno 1988; Winchell et al. 2004; Iglésias et al. 2005). Lopez et al. (2006) recently tested the monophyly of living triakids based on molecular data. These authors do not clearly reject monophyly even if they have no evidence to support it. If the genera *Mustelus* and *Triakis* are paraphyletic and polyphyletic respectively, results support the previously proposed triakid subdivisions with modifications. The position of some genera inside Triakidae remains, however, unclear (e.g., for *Iago*, initially considered to be morphologically intermediate between carcharhinids and triakids by Compagno and Springer 1971) according to choices of methods and gene sequences. The hypothesis of a possible origination of *Mustelus* from the *Triakis* pool (Compagno 1970) is unverified so far as their tooth morphologies are concerned. A provisional hypothesis of relationships among Triakidae (from Lopez et al. 2006 and based on the single most parsimonious tree from analysis of combined mtDNA and RAG1 sequences) is shown in Fig. 8, juxtaposed with a chart depicting the updated fossil record for the family. Data from the fossil record are contradictory and do not help to resolve conflicts or provide insights as to relationships. The first record of *Galeorhinus* complicates the situation because it suggests a deep-water origin of numerous extant genera without fossil evidence (e.g., *Furgaleus*, *Hemigaleus*), as based on the phylogenetic hypothesis of Lopez et al. (2006). At the moment, the paucity of the fossil record does not allow one to reasonably test its agreement with different phylogenetic hypotheses.

The diversity of triakid sharks in the North Atlantic during the early Eocene was clearly higher than now, with eight triakid genera (*Triakis*, *Mustelus*, *Galeorhinus*, *Iago*, *Pachygaleus*, *Palaeogaleus*, *Xystrogaleus*, *Gomphogaleus* gen. nov.) versus only two at present. Except for *Galeorhinus* and *Mustelus*, all the extant and fossil genera (recovered in fossil deposits of both sides of the North Atlantic) have totally disappeared from this area (Fig. 9). Musick et al. (2004) pointed out that the genus *Triakis* became extinct in the North Atlantic after the late Miocene. An similar situation occurs for species of the genus *Iago*, currently confined to the Indo-Pacific area. Their ancestors frequented the North Atlantic realm during the middle Eocene (southwest France: Adnet 2006) and the Mediterranean realm from the early Miocene with *Iago angustidens* (Cappetta 1973, originally assigned to *Triakis*; Barthelt et al. 1991; Bollinger et al. 1995) to the early Pliocene with *I. costamagnai* (Cappetta and Nolf 1991). This suggests a relatively modern distributional shift of *Iago* species in response to post-Pliocene environmental changes, as suspected for the Mediterranean selachian faunal turnover (Cappetta and Nolf 1991; Valsecchi et al. 2005). The unique and widespread species of *Galeorhinus* inhabits all the coastal waters of the Atlantic Ocean, from North Europe to Patagonia, except for eastern North America. The disappearance of *Galeorhinus* in deposits of the east coast of North America can be dated to the early Miocene (Case 1980; Müller 1999) or perhaps the early Pliocene (Purdy et al. 2001). On the contrary, *Mustelus* is relatively uncommon in the coastal sediments before the Miocene (Herman 1982; Bault and Genault 1995) compared to the current situation, where living species are diversified, widespread and particularly abundant. All these facts strongly support the hypothesis of a Recent reorganisation in triakid distribution. The global and intense cooling in the Pliocene epoch (Ravalo et al. 2004) probably led to a spreading or a shifting of taxa respectively adapted (e.g., *Galeorhinus*) or not (e.g., *Iago*) to the cold temperate coastal waters. Coupled with the final closure of the Panamanian seaway (Haug et al. 1998; Bartoli et al. 2005), these paleoenvironmental changes were important in shaping the present-day distribution of triakids. However, they do not explain the drastic decrease in diversity of Triakidae in the Atlantic area including the Caribbean. As noted by Musick et al. (2004), the historical zoogeography of the Triakidae as well as their interrelationships remain poorly understood and further speculation on the subject requires more complete phylogenetic analysis and review of the fossil record. These last questions are partially answered in the present work but the evolutionary history of triakid sharks still remains peculiar and unclear.

Conclusion

Only a few localities in the Paris Basin have yielded a high taxonomic diversity in selachian species of early Eocene age. The description of 3 new taxa and the updating of the fossil list of the well-dated locality of Prémontré improve our knowledge of the small selachian communities that frequented the European sea and which remain often underestimated in fossil samples. This work emphasises the wide distribution of these small fossil sharks living in the North Sea Basin during the early Eocene.

Although this systematic work significantly improves our knowledge of fossil triakid sharks, the fossil record of this shark group emphasises that it remains unfortunately incomplete, extremely disparate and cannot be presently useful for confidently dating the phylogenetic hypotheses of the extant forms. However, the fossil record reveals that this family was more diverse and more widely distributed than to date on both sides of the North Atlantic in the past, as the present review of Prémontré fauna testifies. Such differences suggest that the distribution and the low diversity of living triakids in the North Atlantic and Mediteranean Sea apparently correspond to relatively recent paleoclimatological and paleogeographical events.

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Appendix 1

An updated list of fossil selachians from Level 2 of the Prémontré Abbey, Prémontré (late Ypresian, NP12).

- Squaliformes
  - Squalidae
    - *Squalus* sp.
- Squatiniformes
    - *Squatina* sp.
- Orectolobiformes
  - Ginglymostomatidae
    - *Ginglymostoma* aff. *G. angolense* Dartevelle and Casier, 1943
    - *Nebrius thielensi* (Winkler, 1874)
  - Hemiscylliidae
    - *Chiloscyllium* sp.
  - Rhincodontidae
    - *Palaeorhincodon wardi* Herman, 1974
- Heterodontiformes
    - *Heterodontus* sp.
- Lamniformes
  - Odontaspididae
    - *Brachycarcharias lerichei* (Casier, 1946)
    - *Hypotodus verticalis* (Agassiz, 1843)
    - *Sylvestrilamia teretidens* (White, 1931)
    - *Odontaspis winkleri* Leriche, 1905
    - *Striatolamia macrota* (Agassiz, 1838)
- Carcharhiniformes
  - Triakidae
    - *Galeorhinus duchaussoisi* sp. nov.
    - *Galeorhinus louisi* sp. nov.
    - *Gomphogaleus rodgersi (*Case, 1994)
    - *Mustelus* aff. *vanderhoefti* Herman, 1982
    - *Pachygaleus lefevrei* (Daimeries, 1891)
  - Carcharhinidae
    - *Physogaleus* sp.
    - *Rhizoprionodon* sp.
- Carcharhiniformes indet.
    - *Foumtizia pattersoni* (Cappetta, 1976)
    - *Casieria* sp.
  - Scyliorhinidae
    - *Premontreia* (*Premontreia*) *degremonti* Cappetta, 1992
- Rajiformes
  - Pristidae
    - *Pristis* sp. or *Anoxypristis* sp.
  - Rhinobatidae
    - *Rhinobatos bruxelliensis* (Jaekel, 1894)
  - Rhynchobatidae
    - *Rhynchobatus* sp.
- Myliobatiformes
  - Dasyatidae
    - *Dasyatis* sp. 1 to 4
  - Dasyatoidea incert. fam.
    - *Coupatezia* sp.
  - Myliobatidae
    - *Leidybatis* sp.
    - *Myliobatis* sp.
  - ?Gymnuridae
    - *Ouledia* sp.
    - *Jacquhermania duponti* (Winkler, 1876)
  - Mobulidae
    - *Burnhamia* sp.
    - *Eomobula stehmanni* Herman, Hovestadt-Euler, and Hovestadt, 1989

Appendix 2

An updated list of fossil (†) and extant triakid genera. Systematics from Compagno (1988, 1999), amended according to Lopez et al. (2006).

Triakinae

Triakis Müller and Henle, 1838: 36 [Magazine of Natural History]; Danian–Recent.

Type species: *Triakis scyllium* Müller and Henle, 1838: Recent species. This genus is known since the Danian of Morocco (Noubhani and Cappetta 1997). Eight fossil species (Cappetta 2006) have been described on the both sides of Atlantic and East Pacific. Today it is restricted to the north to central Pacific (subgenus *Triakis*) and east Pacific to south Atlantic and west Indian Ocean (subgenus *Cazon*).

Scylliogaleus Boulenger, 1902: 51 [Annals and Magazine of Natural History]; Recent.

Type species: *Scylliogaleus quecketti* Boulenger, 1902: Recent species. Not yet recorded in the fossil record and its distribution is currently limited to the South African coast. Fossil teeth are possibly confused with those of *Mustelus*.

Mustelus Linck, 1790: 31 [Magazin Neueste aus der Physik und Naturgeschichte, Gotha]; Thanetian–Recent.

Type species: *Squalus mustelus* Linnaeus, 1758: Recent species. With more than twenty living species, this genus is distributed worldwide. It is recorded in the fossil record from the Thanetian of the North Atlantic (Bault and Génault 1995; Smith 1999) and the Neogene of the Pacific (Pledge 1967).

†*Palaeogaleus* Gurr, 1962: 428 [Proceedings of the Geological Association, London]; Campanian–Ypresian.

Type species: *Scyllium vincenti* (Daimeries, 1888): Selandian (= Heersian); Maret, Orp-le-Grand, Belgium. This genus ranges from the Campanian of Belgium (Herman 1977) to the Ypresian in a large area including north to central Atlantic seas (e.g., Noubhani and Cappetta 1997; Cappetta and Corral 1999).

†*Paratriakis* Herman, 1977: 265 [Mémoires pour servir à l'explication des Cartes géologiques et minières de la Belgique, 1975 (in 1977)]; Turonian–Campanian.
Type species: *Paratriakis bettrechiensis* Herman, 1977: Turonian (marl with *T. rigida*); Bettrechies (old quarry, near the Railway Station), northern France. The genus is known in the late Santonian and Campanian of Lebanon and Belgium respectively.

Galeorhininae, Tribe Galeorhinini

Hypogaleus Smith, 1957: 589 [Annals and Magazine of Natural History]; Recent.
Type species: *Galeorhinus* (*Hypogaleus*) *hyugaensis* (Miyosi, 1939): Recent species. Its distribution is limited to the Indo-west Pacific. It has been cited from the lower Miocene of North America (Purdy et al. 2001) but it is probably confused with *Galeorhinus*.

Galeorhinus Blainville, 1816: 121 [Bulletin de la Société Philomatique de Paris] (= *Protogaleus* Molin, 1860); Cenomanian–Recent.
Type species: *Squalus galeus* (Linnaeus, 1758): Recent species. Monotypic and worldwide distributed at the present day, fossil species are relatively diverse (at least 15 species are described) and distributed worldwide since the Cenomanian (Popov and Lapkin 2000).

†*Khouribgaleus* Noubhani and Cappetta, 1997: 82 [Palaeo Ichthyologica]; Thanetian.
Type species: *Galeorhinus gomphorhiza* (Arambourg, 1952) (pars): Thanetian; "Recette IV", South of Delpit, level 2a, Ouled Abdoun Basin, Morocco. This genus is only known from Paleocene deposits of Morocco.

†*Pachygaleus* Cappetta, 1992: 644 [Geobios]; Thanetian–Lutetian.
Type species: *Galaeus* (sic!) *lefevrei* (Daimeries, 1891): Ypresian; Saint-Gilles, Belgium. This fossil genus is restricted to the Thanetian –Lutetian of the North Sea Basin (Europe to eastern USA).

†*Gomphogaleus* gen. nov.; the present work.

Galeorhininae, Tribe Iagini

Hemitriakis Herre, 1923: 70 [Phillipine Journal of Science]; Recent.
Type species: *Hemitriakis leucoperiptera* Herre, 1923: Recent species. Not yet recorded in the fossil record; Recent distribution is limited today to waters off northern Australian and the Philippines.

Furgaleus Whitley, 1951: 61–68 [Proceedings of the Royal Zoological Society of New South Wales]; Recent.
Type species: *Furgaleus macki* (Whitley, 1943): Recent species. Not yet recorded in the fossil record and the distribution of the Recent species is restricted to the west and south Australian coasts.

Subfamily indet.

Gogolia Compagno, 1973: 383 [Proceedings of the California Academy of Sciences]; Recent.
Type species: *Gogolia filewoodi* Compagno, 1973: Recent species. Not yet recorded in the fossil record and the unique living species is confined to the coastal waters off northern New Guinea.

Iago Compagno and Springer, 1971: 616 [Fish. Bull.]; Lutetian–Recent.
Type species: *Eugaleus omanensis* Norman, 1939: Recent species. This genus is recorded since the Ypresian/Lutetian of Southwest France (Adnet 2006); at the present day, the genus is restricted to the Indian-West Pacific area.

†*Xystrogaleus* Adnet 2006: 81 [Palaeo Ichthyologica]; early Lutetian.
Type species: *Xystrogaleus cappettai* Adnet 2006: Lutetian; Level 0, Miretrain, Angoumé (Landes, southwestern France). Only known in the type locality.

†*Archaeotriakis* Case, 1987: 191 [Palaeontographica, Abt.A]; Campanian.
Type species: *Archaeotriakis rochelleae* Case, 1987: Campanian (Judith River Fm.); Site 1, Suction Creek, Rattle Snake Creek and Site 5, Timber Ridge, SW of Suction Creek, Blaine Co., Montana, U.S. The assignment of this genus to the Triakidae remains hypothetical. Restricted to Montana and Wyoming (Case 1987).

†*Squatigaleus* Cappetta, 1989: 12 [Mesozoic Research]; Campanian –Maastrichtian.
Type species: *Squatigaleus atlasi* Cappetta, 1989: Lower Maastrichtian.; Oued Erguita (lower level), north of Taroudant, Morocco. As for the previous genus, the assignment of this genus to the Triakidae remains hypothetical. The genus is also known in the Maastrichtian of Egypt (Cappetta 1991).