New Carcharhiniformes (Chondrichthyes, Neoselachii) from the Ypresian of the Paris Basin*

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[Abstract provided in English in the original]

Introduction

The selachians of the Eocene Paris Basin have been the subject of some now outdated publications (Priem, 1906, 1911; Leriche 1905, 1906, 1923) based on surface collecting, which explains why few small species were reported. More recently, Cappetta and Nolf (1981) reported a Bartonian age fauna collected by sieving in the Ronquerolles region, yielding species of small size. A faunal list summarizing the available data has been published (Cappetta, 1988).

The discovery of an important Late Ypresian deposit at the former Premontre abbey about twenty kilometers to the NNE of Soissons has enabled us to sample a rich and diverse vertebrate fauna containing both mammals and selachians (Degremont et al., 1985). Thanks to intensive fine-mesh screenwashing (down to 360 microns) a significant number of species of selachians, of which many are new for the Paris Basin, have been identified. The whole fauna will be the subject of a future study. This preliminary work limits itself to the description of two new taxa recognized at Premontre.

- a new genus and species of scyliorhinid
- a new genus of triakid traditionally described under the name *Galeorhinus lefevrei* (Daimeries, 1891)

A section of the deposit has already been published and the reader is invited to consult Degremont et al. (1985). The fossils described below originated from Bed 2 of this section. The sediment consists of very fine, slightly ferruginous and highly decalcified sand.

Systematics

Class Chondrichthyes
Subclass Elasmobranchii
Cohort Euselachii
Subcohort Neoselachii
Superorder Galeomorphii
Order Carcharhiniformes Compagno 1973
Family Scyliorhinidae Gill 1862

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Genus *Premontreia* nov. gen.
Type species *Premontreia degremonti* nov. gen. nov. sp.
Name derivation: from the name of the type locality.

Diagnosis:
Scyliorhinid with rather large teeth (up to 6mm in total height); teeth with a high, rather compressed cusp – also quite narrow and sharp with prominent and fine cutting edges; convex lingual face with completely smooth enameloid; labial face weakly convex bearing numerous very short, vertically parallel folds at its base – the folds never extending past the height of the heels; labial enameloid boundary is rectilinear, often very slightly concave medially; labial crown face barely overhangs the root without a differentiation of a bulge; a pair of sharp lateral cusplets are broadly united to the cusp – sharp but quite broad and low – or they are absent with short fine-edged oblique heels instead with rounded marginal edges in labial view; medio-basal part of the labial crown face is depressed.

Root is high and thick with a broad flat basal face divided by a deep, omega-shaped median groove; main foramen in an entirely lingual position; the well-developed, oblique lingual face bears numerous elliptical foramina; the labial face is high and concave with lobes extending widely in occlusal view; rather numerous foramina are observed above the basal labial edge.

Premontreia degremonti nov. gen., nov. sp.: pl. 1, fig. 1-12
Material: more than 150 well-preserved teeth
Type locality: Bed 2 of the section at the former Premontre abbey near Anizy-Le-Chateau, Soissons region, Aisne, France.
Age: Late Ypresian
Name derivation: in honor of Mr. E. Degremont, now deceased, who made known the deposit.
Holotype: Pl. 1, fig. 4a-b (PRE 4)
Diagnosis: Same as that for the genus
Dimensions: (taken in lingual view and expressed in millimeters; H = total height; l = total width)*

	H	l
PRE 1	5.19	2.86
PRE 2	4.52	3.30
PRE 3	3.98	2.78
PRE 4	5.15	3.85
PRE 5	4.49	4.15
PRE 6	4.92	3.91
PRE 7	4.00	3.73
PRE 8	4.65	4.62
PRE 9	3.05	3.42

* French word for “width” is “largeur,” hence “l” [JS]

PRE 10 3.09 3.99
PRE 11 1.85 2.82
PRE 12 1.09 1.84

Description:

The holotype (pl. 1, fig. 4) is an anterior tooth. It is symmetrical with a high, straight cusp and a sharp slightly lingually-directed tip. On either side of the crown base are high, fine-edged, weakly extended, and rather abrupt heels with a rounded contour in labial view. The lingual face is somewhat convex; the labial face is subrectilinear in profile and slightly less convex.

The crown base overhangs the root labially without forming a bulge and the enameloid boundary is rectilinear. The base of the labial face bears numerous short vertical folds, the longest ones not reaching the height of the heels. The folds are situated medially in a zone where the crown is slightly compressed.

The root is high, wider than it is long and broadly borders the crown base in labial view. Its labial face is high, quite developed and in profile concave. Its basal margin projects labially, particularly visible in occlusal view. Numerous elliptical foramina are observable above this basal margin. On the oblique margino-lingual faces numerous foramina are present on either side of the lingual protuberance, which is split by a medial groove. The main foramen opens lingually. The basal face is wide, flat, and mesiodistally well-developed.

On the more lateral teeth, which lack cusplets, the cusp is lower and wider at its base. The heels are more extended mesiodistally. The folds of the crown's labial face may almost completely disappear (pl. 1, fig. 5a).

Other teeth exhibit the same characters but the heels bear a pair of low, blunt cusplets; on rare occasions a second cusplet forms from a split mesial cusplet.

The anteriormost teeth (pl. 1, fig. 1) are mesiodistally compressed, especially the root. They exhibit an upright cusp with the labial base being distinctly plicated and flanked by a pair of sharp, narrow, and clearly divergent cusplets. The root is almost as long as it is wide with a pinched groove labially.

In the lateral files (pl. 1, fig. 7-10) the cusp is lower and inclines distally. The root extends mesiodistally. In the lateralmost files (pl. 1, fig. 11) the cusp is very low and the heels are relatively developed, extended, and high with very low, weakly-differentiated cusplets. A posterior tooth (pl. 1, fig. 12) exhibits a reduced lamniform crown, in which the medial cusp is hardly more developed than the lateral cusplets. The root remains high and of a morphology very close to that of the lateral teeth.

The teeth of juvenile individuals (pl. 1, fig. 3) present the same characters but with a more slender cusp and a more sigmoidal profile (pl. 1, fig. 3b).

Discussion

The family Scyliorhinidae includes 15 modern genera containing between 91 and 95 species according to authors and assigned to four subfamilies (Compagno, 1988). It is therefore an important and diverse group representing a little more than one-fourth of all modern shark species.

This family is equally well-represented in the fossil record with about thirty species scattered from the Middle Jurassic to the Pliocene (Cappetta, 1987).

The direct examination of the dentitions of most of the modern genera (with the exception of *Pentanchus* Smith & Radcliffe 1912) and the excellent recently-published illustrations of all the modern genera of the family (Herman et al., 1990) allow a better approach to the group and a more precise interpretation of the fossil species.

The modern scyliorhinids were the subject of several reviews and monographs (Nakaya, 1975; Springer, 1979; Compagno, 1988), of which the most documented and most complete remains that of Compagno. This author grouped the modern genera into four subfamilies: Atelomycterinae White 1936, Schroederichthyinae Compagno 1988, Scyliorhininae Gill 1862, and Pentanchinae Smith & Radcliffe 1912 with the last subdivided into two tribes, Galeini Fowler 1934 and Pentanchini Smith & Radcliffe 1912. In any case it is important to note that these groupings, based on the study of numerous morphological and anatomical characters are supported by dental morphology as well.

Within the Atelomycterinae the teeth are characterized by their high, slender lateral cusplets (sometimes, an extra pair of cusplets is present) and their rather low root featuring a very low labial face with a broad, flat basal face. The root's lingual protuberance bears deep depressions.

Within the Schroederichthyinae the teeth are extended with a prominent apron ranging from coarsely serrated (*Schroederichthys maculatus* Springer 1966) to almost smooth (*S. bivius* Mueller & Henle 1838). The lateral cusplets are rather low and broadly united to the base of the cusp.

The Scyliorhininae possess teeth with a rather high root and a cusp bearing folds on both faces as well as a well-differentiated apron. The lateral cusplets are quite distinct with two pairs often present or they can be absent on adult anterior teeth.

Within the Pentanchinae the lateral cusplets are relatively well-developed compared to the main cusp with two to several pairs present. The labial and lingual faces of the crown bear strong folds and the root is rather flat.

Herman et al. (1990) separated the genus *Cephalurus* Bigelow & Schroeder 1941 from other scyliorhinids but the dental material figured by these authors was so damaged that it

is difficult to make any definitive determination. They also joined the genera *Schroederichthys* Springer 1966 and *Halaelurus* Gill 1862. This grouping, however, shows very different dental morphologies in agreement with separate subgenera. For example, *Halaelurus* (*Bythaelurus*) *canescens* (Guenther 1878) is more closely related to the genus *Scyliorhinus* Blainville 1816 than to *Schroederichthys*. The teeth of the other subgenus *Halaelurus* (*Halaelurus*) *buergeri* Mueller & Henle 1838 are quite distinctive in their transverse development, low cusp, extended heels, and very low or more often absent lateral cusplets. This species presents a quite unique dental morphology, separating it even from other species of the Scyliorhinidae.

Based on their dental scheme modern scyliorhinids therefore present great morphological diversity but nearly all species possess a cusp flanked by one or more pairs of lateral cusplets except where noted above - *Halaelurus* (*H.*) *buergeri* and the anterior teeth of certain species of *Scyliorhinus*, *S. stellaris* Linnaeus 1758 and *S. canicula* Linnaeus 1758, among adults at least, in particular.

All species feature an anaulacorhizous or hemiaulacorhizous root (in other words, lacking a groove or with a partially open groove labially), except *Halaelurus canescens*, of which certain teeth show a completely open groove. All also possess a crown with enameloid folds labially and lingually.

In the fossil record numerous species of the Scyliorhinidae bear holaulacorhizous roots – that is, the groove is completely open. These species are traditionally attributed to the genus *Scyliorhinus*. I have stressed (Cappetta, 1976; 1987), however, that the assignments of numerous fossil species to the genus *Scyliorhinus* have resulted from insufficient knowledge of the dentitions of modern genera.

In fact, in the fossil record the scyliorhinids with holaulacorhizous roots are largely represented, while at present it can be seen that this group, known from the Pliocene as "*Scyliorhinus*" *dachiardi* Lawley 1876, has completely disappeared. It is necessary, however, to stress an important point: it is quite probable that numerous fossil species with an open groove do not belong to a homogeneous group, at least at the generic level, this character having certainly appeared repeatedly across different lineages. This character can be considered as apomorphic compared to the plesiomorphic condition corresponding to the closed (completely or partially) groove stage, though some authors (Herman et al., 1991) consider the groove to be secondarily closed within the Scyliorhinidae. The discovery of plesiomorphic-type scyliorhinids from the Middle Jurassic (pers. obs. unpubl.) would tend to prove that this dental type is quite ancient, dating back before the open groove type, which did not appear until the Late Cretaceous (*Pteroscyllium* Cappetta 1980).

Therefore, from the study of the dentition of modern genera it is possible to group different genera at the subfamilial level according to their dental morphology, even if the exact position of certain species is not easy to establish. Therefore, the same criteria can be used to attempt subfamilial groupings for fossil species.

The new scyliorhind from Premontre presents a quite unique dental morphology unlike that of any modern genus. The genus *Premontreia* is distinguished from all the other known scyliorhinid genera, modern or fossil, by its relatively high cusp, its weakly convex labial face (not presenting a differentiated basal bulge), the absence of any lingual folds, its holaulacorhizous root with a broad, flat basal face, and its weakly-developed, or often absent, lateral cusplets. It is related to certain Tertiary species with teeth of the holaulacorhizous stage such as "*Scyliorhinus*" *subulidens* Arambourg 1952, "*S.*" *dachiardi* Lawley 1876 or "*S.*" *gilberti* Casier 1946. If it seems premature to assign these species to the genus *Premontreia*, their assignment to a new subfamily Premontreinae (see below) is more probable.

With the genus *Premontreia* not being attributable to any of the subfamilies defined by Compagno (1988), based on dental characters, its highly derived root in particular, I propose to include it in the new subfamily, Premontreinae, which can be defined as follows:

- scyliorhinid with teeth presenting a high, sharp labiolingually compressed main cusp with smooth cutting edges; labial and lingual faces bearing numerous folds of variable size; lateral cusplets totally absent or with 1-2 pairs more or less distinct and developed; high root of derived morphology with a broad, flat basal face of a generally cordiform shape and divided by a distinct, deep groove.

In 1984 Pfeil proposed the new family Megascyliorhinidae for the genus *Megascyliorhinus* Cappetta & Ward 1977. On the sole basis of its general dental morphology there is no reason to exclude this genus from the Scyliorhinidae. However, it can be placed into its own subfamily, Megascyliorhininae Pfeil 1984 nov comb. because of some particular characters (large tooth size, high conical cusp with very weakly-marked cutting edges, clear folds on the labial and lingual faces of the cusp, lateral cusplets often absent, holaulacorhizous root).

There remains one group of Cretaceous scyliorhinids, represented by a single genus, *Pteroscyllium*, known from the Cenomanian to the Maastrichtian. The species of this genus possess teeth of a very unique odontaspoid-type morphology. Furthermore, on the basis of this morphological convergence with the teeth of the Odontaspididae, Maisey (1984) placed *Pteroscyllium* into the Lamniformes! This genus is also distinguished from other scyliorhinids by its well-developed, sharp-tipped pectoral fins (Cappetta, 1980), so I propose to assign the genus *Pteroscyllium* to the new subfamily Pteroscylliinae, defined as follows:

- scyliorhinid characterized by well-developed, falciform, sharp-tipped pectoral fins (based on skeletons from the Santonian of Lebanon); teeth of a very derived odontaspoid-type morphology; sharp, slender cusp with clear folds on the labial and lingual faces and smooth cutting edges; cusp flanked by one to several pairs of slender lateral cusplets; root with narrow elongated lobes and a prominent lingual protuberance bearing a well-marked groove.

Family Triakidae Gray, 1851
Genus *Pachygaleus* nov.
Type species: *Galeus lefevrei* Daimeries 1891
Name derivation: from the Greek *pachys* (=thick), alluding to the morphology of the teeth of this genus, and *galeos* (=shark).

Diagnosis:
Teeth can exceed 1cm in total width, characterized by a thick crown and root, clearly curved in labial view.

The crown is rather high but always wider than high, overhanging the root labially with a distinct bulge, quite convex in profile. The labial crown boundary is concave differentiated by a sort of broad median bulb, hardly prominent yet quite distinct.

The main cusp is strongly inclined distally with a long, generally highly convex mesial cutting edge, which can be very lightly serrated or even bear some coarse serrations on its lower third. The distal heel is well-developed, bearing up to seven distally-directed serrations of regularly-decreasing size. The enameloid is generally completely smooth but can bear some labial folds, sometimes well-developed in the more lateral files of adults or juveniles.

The root is very thick, clearly bulging lingually on either side of a wide, deep groove, which is more broadly open labially. In general there is a large central foramen and some well-developed paracentral foramina. The labial face is concave in profile. Numerous aligned foramina are present above the basal edge along with numerous margino-lingual foramina.

The basal face is well-developed and broadly united to the lingual face without a marked basal lingual edge.

Discussion

The family Triakidae contains nine modern genera within two subfamilies (Compagno, 1988):

- Triakinae with *Triakis* Mueller & Henle 1838, *Mustelus* Linck 1790 and *Scylliogaleus* Boulanger 1902.
- Galeorhininae – subdivided into two tribes: Iagini with *Hemitriakis* Herre 1923, *Furgaleus* Whitley 1951, *Iago* Compagno & Springer 1971, and *Gogolia* Compagno 1973; Galeorhinini with *Galeorhinus* Blainville 1816 and *Hypogaleus* Smith 1957.

Four fossil genera must be added here: *Palaeogaleus* Gurr 1962 and *Paratriakis* Herman 1977, the dental morphologies of which permit their assignment to the Triakinae along with *Archaeotriakis* Case 1978 and *Squatigaleus* Cappetta 1989, of which the subfamilial and even familial position has not been definitively determined. For comparison, all

modern and fossil genera were able to be directly examined. In addition, the dentitions of the modern genera were figured by Herman et al. (1988).

Pachygaleus nov. gen. is directly comparable only to the Galeorhinini and certain genera of the Iagini such as *Hemitriakis* and *Furgaleus*.

In *Hemitriakis* the cusp is narrower than in *Pachygaleus* with a tip sometimes straightened. The mesial cutting edge of the crown is much more rectilinear. There are up to three distal serrations. The root is flatter and not as wide as the crown base in labial view while in *Pachygaleus*, the root is always wider than the crown.

The genus *Furgaleus* possesses a dentition with strong dignathic heterodonty, recalling what is seen among the Hemigaleidae, so only its upper teeth can be compared to those of *Pachygaleus*. They are, however, not as thick, less curved, bearing a thinner, irregular labial bulge while the tips of the cusp and the distal serrations follow a clear concavity. In *Pachygaleus* they are generally aligned.

The other two genera of the Iagini, *Iago* and *Gogolia*, possess teeth with a morphology that differs greatly from that of *Pachygaleus* (see Herman et al., 1988).

Without question, the teeth of *Pachygaleus* share the most similarities with those of *Galeorhinus* and *Hypogaleus*. In *Pachygaleus*, however, the teeth are thicker with a less-upright cusp, which is more broadly united to a higher number of distal serrations.

The teeth of *Pachygaleus* also differ noticeably from the upper teeth of hemigaleids in their greater thickness, their well-marked labial bulge, and their less slender and shorter main cusp.

The species *lefevrei* was described without figures by Daimeries (1891) from the Ypresian of Saint-Gilles in Belgium under the generic name *Galaeus* (sic). Later, this well-known, easily-identified species was correctly described and figured (Leriche o.c.; Casier 1946, 1966), so there is no reason to review it here.

If this species is well-represented in the Early-Middle Eocene of the Anglo-Franco-Belgian Basin, it is in contrast totally absent from contemporaneous deposits, though rich in selachians, in North and West Africa. It has not been reported in North America either (Ward & Wiest, 1990), but it is possible that it existed there. The inventory of faunas of that vast region is far from completion.

Conclusions

Thanks to the discovery of the Premontre deposit, the selachian fauna of the Ypresian of the Paris Basin has turned out to be much more diverse than previously thought, based on previously published works on the subject. In fact, it is virtually as varied, if not more so, than contemporaneous or subcontemporaneous faunas of Belgium and England.

The family Scyliorhinidae is enriched by a new genus and a new species, *Premontreia degremonti*, of which the dental morphology differs from all that is known of this family.

The examination of modern genera allowed the re-evaluation of the subfamilial position of several fossil genera and three new subfamilies are proposed:

Premontreinae nov.
Pteroscylliinae nov.
Megascyliorhininae Pfeil 1984 nov. comb.

The study of the dentition of all the modern and fossil genera of the Triakidae also allowed a review of the systematic position of a well-known species, traditionally assigned to the genus *Galeorhinus*: *G. lefevrei* Daimeries 1891. Based on its unique dental characters, this species cannot be assigned to any known genus of the family which necessitated the creation of the new genus *Pachygaleus*.

The absence of *Premontreia degremonti* in contemporaneous deposits in Belgium and England is to be emphasized. These deposits have been well-sampled so this absence can be considered significant. It is possible that the Premontre fauna corresponds to a faunal stratum not represented (or not yet discovered!) in England and Belgium.

The age of the deposit has been discussed already (Degremont et al., o.c.) and its attribution to the terminal Ypresian is most probable. Some samplings have been taken in search of calcareous nannofossils and are currently under study (E. Steurbaut). The highly decalcified vertebrate-bearing layer does not contain calcareous nannofossils. In contrast, the beds that succeed it without an apparent gap are attributable to the zone NP14, in other words, to the Early Lutetian (Steurbaur, *in litt*.). The vertebrate-bearing layer, which is immediately below can be therefore attributed to the Late or terminal Ypresian. These results are a little contradictory to certain published findings by Steurbaut (1988), which made evident a significant gap in sedimentation in the Paris Basin, corresponding to NP12, NP13, and part of NP14. The Ypresian deposits in the Premontre region are particularly thick and therefore could be much more complete than elsewhere in the Paris Basin.

Thus, the Premontre deposit reveals itself to be particularly interesting not only because of its rich vertebrate fauna, but also for the stratigraphic questions it raises. In any case the selachian fauna seems younger than the classic faunas of the Belgian Ypresian which originate from the Sands of Forest-les-Bruxelles, equivalent to the middle part of the Sands of Mons-en-Peleve, corresponding to the base of Zone NP12 (Steurbaut, 1990).

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