

# Contribution of Eocene sharks and rays from southern France to the history of deep-sea selachians

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## ABSTRACT:

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Fossil deep-sea selachians are rare and their diversity underestimated as a consequence of the scarcity of available outcrops of sediments containing them. Here we report a new fossil locality from the Middle Eocene of south-western France and give a first synthesis of the deep-sea deposits of this area which have yielded one of the richest fossil selachian faunas ever to have inhabited the continental slope. The fossil records of deep-sea sharks and rays are discussed in the context of these new fossil occurrences, a literature review and the recent phylogenetic hypothesis.

**Key words:** SW France, Eocene, Deep-sea selachians, Fossil record.

## INTRODUCTION

Deep-sea and freshwater habitats may be considered as secondarily invaded by some untypical sharks and rays as evidenced by the fact that living deep-sea and freshwater taxa are distributed within most of the orders. Although the adaptation of some Chondrichthyes to freshwater occurred relatively early (e.g. Xenacanthiformes) and recurred throughout the history of the Mesozoic–Cenozoic Elasmobranchs, including Neoselachii (see SWEETMAN & UNDERWOOD 2006), little is known about the Neoselachian lineages that invaded the deep-water marine environment (from mesopelagic to bathybenthic zones). However, almost 48 % of living selachian species actually inhabit marine waters deeper than 200 m (KYNE & SIMPFENDORFER 2007) and 24 % may be considered as completely adapted to the deep-sea zone because they do not occur on the continental or insular shelves, or in the epipelagic zone (down to 200 m depth). The diversity of deep-sea selachians in the

fossil record is significantly lower but is broadly underestimated. This is not only because the fossil record is inherently imperfect, but also because the conditions of fossilization in deep-sea habitats are unfavourable for the preservation of selachians, and outcrops of deep-sea sediments are in any case relatively rare. It also remains difficult to determine the factors responsible for the invasion of modern sharks and rays into the deep-sea waters and to date when certain lineages occupied the deep-sea environment, with the exception of the Squaliformes, whose history seems to be relatively well linked to major global events (ADNET & CAPPETTA 2001).

## EOCENE RECORD FROM SW FRANCE

Several localities in south-western France revealed a rich selachian fauna deposited in deep-sea sediments of the Aquitaine basin at the end of the Pyrenean orogen. This fauna includes some modern deep-sea taxa that

were previously unknown in the fossil record (see ADNET 2006, p. 116-117). The new locality of Peyrehorade (south-western France, Landes), currently dated at least as Bartonian (Text-fig. 1A) yielded a new selachian association, of which a preliminary list of taxa is given here: *Chlamydoselachus* sp., *Hexanchus agassizi*, *Echinorhinus* sp., *Centrophorus* cf. *granulosus*, *Centroscymnus* spp., *Scymnodalatias cigalafulgosii*, *Somniosus* sp., *Isistius* cf. *triturratus*, *Eosqualiolus aturensis*, *Squaliodalatias* sp. *Acrosqualiolus mirus*, *Paraetmopterus nolfi*, *Squaliformes* indet., *Pristiophorus* aff. *lacipidiniensis*, *Squatina prima*, *Heterodontus vincenti*, *Hemiscyllium tailedisensis*, *H.* cf. *bruxeliensis*,

*Pararhincodon* aff. *germaini*, *Eostegostoma* aff. *angustum*, *Orectoloboides reyndersi*, *Mitsukurina* cf. *maslinensis*, *Striatolamna* sp., *Isurolamna affinis*, *Abdounia* sp., *Physogaleus* sp., *Triakis* sp., *Galeorhinus* cf. *duchaussoisi*, *Iago* sp., *Mustelus* sp., *Premontreia gilberti*, *Apristurus sereti*, *Scyliorhinus* spp., *Rhinobatoidei* indet., *Raja marandati*, *Dasyatis* spp., *Coupagezia* spp., *Gymnura* spp. and *Torpedo* aff. *acarinata*.

As in present-day seas, the bulk of the fossil deep-sea fauna of Landes comprises squaloid and scyliorhinid sharks and rajoid batoids. Several taxa not previously recorded from the two nearby localities of Saint-Géours-d'Auribat and Angoumé (e.g. the oldest occurrence of

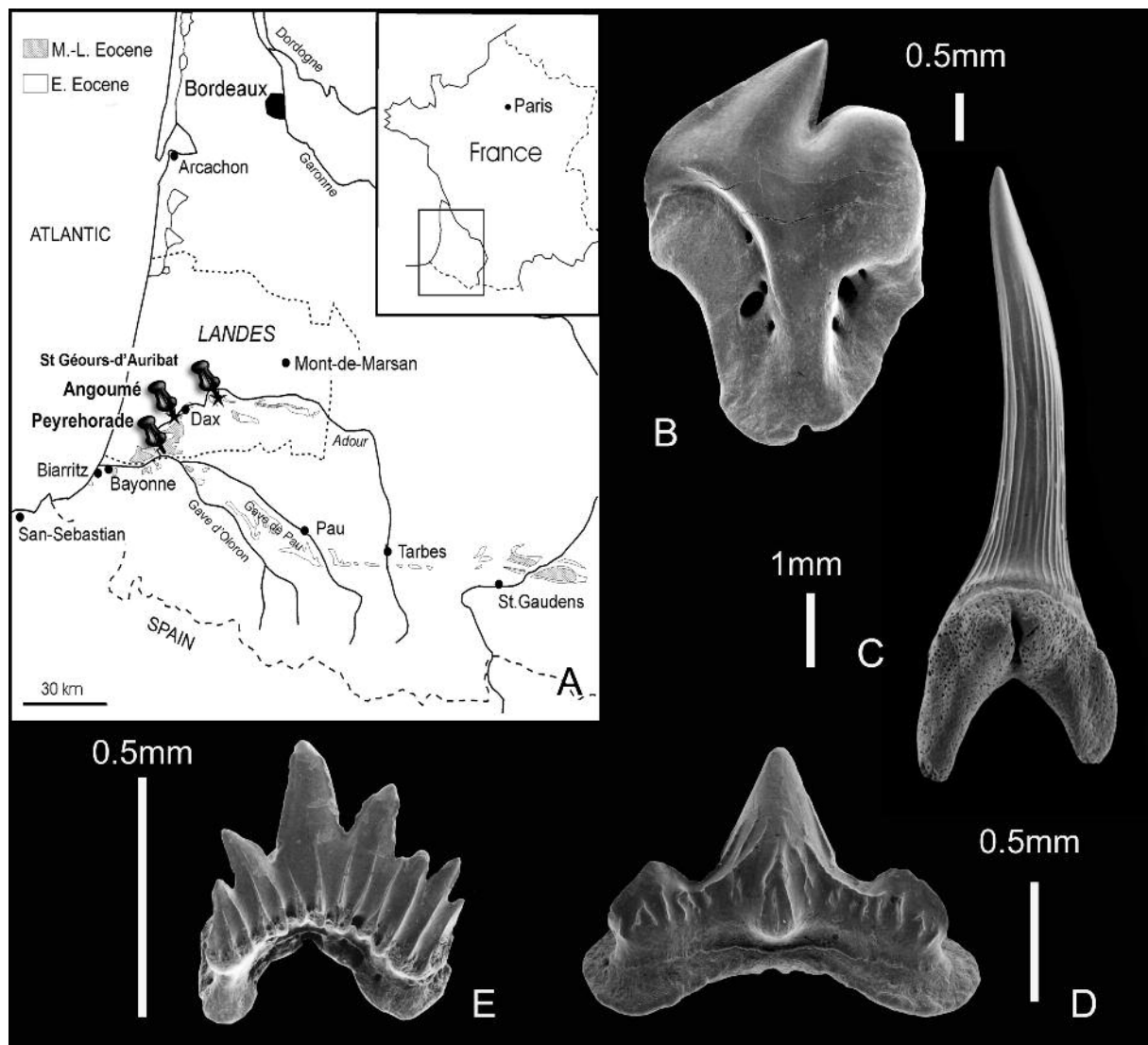


Fig. 1. A. Location of fossil sites of Landes (SW France) where the reported fossil deep-sea selachians have been found (including the new locality of Peyrehorade). B-E – Isolated fossil teeth from the marl of Peyrehorade (Bartonian, SW France); B – *Somniosus* sp. – PEY001: labial view of antero-lateral lower tooth; C – *Mitsukurina* aff. *maslinensis* (PLEDGE 1967) – PEY030: lingual view of anterior tooth; D – *Orectoloboides reyndersi* ADNET, 2006 – PEY050: labial view of antero-lateral tooth; E – *Apristurus sereti* ADNET, 2006 – PEY060: labial view of lateral tooth

the extant genus *Somniosus*, new species of *Centroscymnus* and *Triakis*, new Rhinobatoidei and Squaliformes genera) are currently under study. This first synthesis of the fossil selachian fauna from Landes emphasizes the high diversity of deep-sea selachians, with at least forty species considered as frequenting the deep-sea zone on the basis of comparison with closely related extant taxa. Moreover, some of them belong either to fossil taxa that are supposedly extinct (e.g. the latest occurrence of the early Cretaceous genus *Orectoloboides* – Text-fig. 1D) or to taxa absent from a large part of the fossil record (e.g. *Apristurus* – Text-fig. 1E) or to taxa that would be unexpected in such a deep water environment (e.g. *Heterodontus*, *Orectolobiformes* and some *Myliobatiformes*), increasing actually the proportion of Lazarus taxa in the Neoselachii, which is already considered to be relatively high (UNDERWOOD 2006).

A stratigraphical range chart for the modern deep-sea shark and ray genera (including those present in our three localities) was compiled for the first time (Text-fig. 2) and updated with respect to the new occurrences (e.g. *Somniosus*, see Text-fig. 1 B) observed in our sites and/or deduced from our personal data base and the recent literature (e.g. CAPPETTA 2006, UNDERWOOD 2006, ADNET & CAPPETTA 2008, ADNET & *al.* 2008). As expected, completeness of the deep-sea selachian fossil record is relatively low (less than 70% of Recent shark genera and only about 15% of Recent skate and rays genera are known in the fossil record), inducing several ghost lineages in the context of the usually accepted phylogenetic relationships of living taxa (fossils unknown from supposed speciation dated by comparison with the oldest evidence of the sister group, equivalent to the calculation of RCI (Relative Completeness Index, see BENTON & STORRS 1994). These new discoveries in the deep-sea deposits of Landes allowed the fossil record of many extant genera to be extended, thereby filling several large gaps (see Text-fig. 2) in the restricted stratigraphical range of many modern deep-sea taxa. Palaeogene occurrences of these taxa are totally consistent with, but not yet sufficient to prove, the most consensual phylogenetic hypotheses concerning extant genera, such as: *Scymnodalatias*, *Trigonognathus*, *Euprotomicroides*, *Apristurus* and *Iago* or modern *Parascylliidae* and *Hexatrygonidae*, which are commonly considered as “primitive” among their respective families or orders.

In considering phylogenetic hypotheses in the context of fossil ranges of taxa (Text-fig. 2), it appears that the fossil record of Squaloid sharks is relatively well documented in comparison with that of the other deep-sea selachian groups within the *Carcharhiniformes* and

*Rajiformes*, probably because the evolutionary history of this group is the oldest. On the other hand, there remain several peculiar gaps, such as those concerning the very well-diversified living genus *Centroscyllium* within the Squaloids (supposedly a primitive Etmopterid), most of the deep-sea *Scyliorhinid* sharks (e.g. the genera *Pentanchus* and *Parmaturus*) and almost all the deep-sea rajoid genera (*Arhynchobatidae*, *Anacanthobatidae* and *Rajidae*). With the exception of *Centroscyllium*, most of those listed above are actually barely distinguishable on tooth morphology from *Scyliorhinus* and *Raja*, which are more frequently recorded from fossiliferous localities. Such misidentification is due in part to our poor knowledge of the tooth morphology of living deep-sea species and to the paucity of fossil material (due to the scarcity of deep-sea sedimentary deposits, even in the Cenozoic). Whilst it is currently impossible to explain why only some major lineages (e.g. *Squaliformes*, *Carcharhiniformes* and *Rajiformes*) invaded the deep water marine environment, we strongly suspect a radiation in the mid-Cretaceous for several of the more important deep-sea selachian groups (*Squaloids*, *Scyliorhinoids* and perhaps *Rajiids*), as shown in Text-fig. 2. The causes (e.g. major global event) of such adaptive radiation in these diverse lineages remain unknown and are probably both numerous and exclusive to each selachian group according to its own evolutionary history. The fossils from the Landes testify unequivocally that most of the Recent taxa frequenting the deep-sea environment were present and well-diversified from as early as the Eocene. Most future new discoveries concerning occurrences of Recent shark and ray taxa in the fossil record will probably be in deep-sea deposits and investigations need to be focused on pre-Eocene deposits.

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