Upon the Importance of the Fossil Sharks in the Establishment of the Isochronisms of Formations at Great Distances and Upon the Stratigraphic and Geographic Distribution of Some Tertiary Species.*

by
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The Lamnidae and the Carcharidae are eminently nectonic sharks that frequent indifferently the coastal zone and the high seas, and of which the area of dispersion is nearly always very extended.

Of the geologic epochs, their area distribution was often very vast, and some Tertiary species, like *Oxyrhina hastalis* L. Agassiz and *Carcharodon megalodon* L. Agassiz, have lived in all the seas, with the exception of the frigid seas.

The fossil sharks have, for the geologist, a capital importance, principally with that which concerns the Tertiary Era, because the great groups of pelagic animals of the previous epochs have disappeared, and better than the other Tertiary fossils, they permit one to establish synchronisms among the formations greatly separated from one another.

Nevertheless, geologists have disregarded for a long time their advantage, and the reputation of the "bad fossils" that they gave them survives still in some recent works.

This misconception of the stratigraphic value of the fossil sharks has several causes. It is due, on the one part, to the complexity of the denture in this class of fishes and to the fact that the teeth of fossil sharks are nearly always dispersed in the deposits, the species, established upon insufficient elements of the denture have not been defined, from the beginning, in a sufficiently precise manner. It is due, on another part, to that other fact that the species more formerly described – that are, in general, the more common – have been founded upon the teeth whose provenance is either unknown or indicated in a vague manner or even erroneous.

[p. 740]

The complexity of the denture of the sharks and errors committed in the establishment of fossil species. – Necessity, for defining exactly the fossil species, by reconstructing their denture.

The jaws of sharks are furnished with a great number of teeth, of which the characters (general form and dimensions) varies according to the jaw that bears them, often the place that they occupy in them, often the age and sometimes the sex of the individual.

The skeleton of the shark is cartilaginous, the fossil species are only scarcely known by their teeth, that one finds often in great number, but nearly always disseminated in the strata.

Several of the fossil species have been established only upon a small number of teeth, that belong either to the lower jaw, or to the upper jaw, and that are either the anterior teeth or else the lateral teeth; so that, in many the case, the specific characters have been confused with the characters that are only some function of the situation that the teeth occupy upon the jaws. The teeth of one same species, but coming from different parts of the jaws , have been so described as those of distinct species, and, inversely, the teeth of different species, but occupying, in the

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denture, an identical position, have been represented as those of one same species.

An uninformed paleontologist will not discover inevitably the greater differences among the teeth occupying the different positions upon the jaws of one same species than among the teeth occupying a similar position in the different species.

This confusion of the characters has had in effect the assignment of an extreme longevity to species artificially established.

Among many of the examples, I cite this one of *Odontaspis macrota* L. Agassiz, that is one of the commonest sharks of the Eocene Epoch. L. Agassiz had described some lateral teeth from the upper jaw under the name of "*Otodus macrotus*", then the anterior teeth of the two jaws and the anterior lateral teeth of the lower jaw, under that, much more known to geologists, of "*Lamna elegans*". But, A. Rutot[1] has insisted upon the great vertical extension of "*Lamna elegans*", that, according to him, could have appeared in the Upper Cretaceous, in order to only become extinct at last in the Rupelian.[2]

[p. 741] in reality, *Odontaspis macrota* is not known in the Upper Cretaceous, nor in the Rupelian. The only specimens of this species that have been encountered in the Oligocene come from the base of the Tongrian, where they are found very probably in the altered state.

Odontaspis macrota is an essentially Eocene species. It first appears in the Paleocene as a small permutation, "*Otodus striatus*" of Winkler.

The typical form appears in the Ypresian, and its size increases in proportion as one rises in the properly Eocene.

In order to characterize exactly the fossil species it is entirely necessary to reconstruct the denture. It is then possible to isolate clearly the specific characters that are tied to the position of the teeth upon the jaws.

To discharge the authors that have confused all these characters, it is well known that description of the denture of the living sharks has nearly always been neglected by zoologists, and, in the more recent works to which these sharks have been given place, the denture, that offers however the specific characters of the first order, is still, most often, only very imperfectly described and figured. So that the paleontologists often has the only other recourse the direct study of the denture of the living sharks. This study just for the reconstruction of the denture of the fossil sharks will make evident, in the individuals of one same species, the rather obvious differences, that are due to age.

In the Lamnidae and Carcharidae, these differences appear especially in the form of the more or less slender teeth: those of the young individuals are relatively more slender than the corresponding teeth of older individuals.

It is still by the reconstruction of the denture that one is able to determine the limits of variability of the species and characterize the races.

The Neogene of California contained an oxyrhine which Agassiz has described the teeth of

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[1] A. Rutot, Note upon the extension of *Lamna elegans*, AG. to traverse the Cretaceous and Tertiary terrains. *Annales de la Sociêtê gêologique de Belgique*, t. II, Mêmoires, pp. 34-41; 1875

[2] In reuniting to *Lamna elegans* the *Lamna contortidens* of Agassiz, – that is to say *Odontaspis acutissima*, which had lived in part of the Oligocene until the Pliocene, – Le Hon made *Odontaspis macrota* even endure until the end of Tertiary time. (see H. Le Hon, *Preliminaires d'un memoire sur les Poissons tertiaires de Belgique*, p. 12, Brussels, 1871).

the upper jaw and of the lower jaw respectively under the names of *Oxyrhina plana* and *O. tumula*. Held separately, these teeth are not different or can hardly be distinguished from the teeth of the corresponding jaws of *O hastalis* of the Neogene of Europe. But if one reconstructs its denture, one perceives some very slight differences between the Oxyrhine of California and that of Europe[3]. In the former, the teeth of the lower jaw are, in general, a little more stocky, and the crown of the lateral teeth of the upper jaw are sometimes a little more recurved toward the corner of the mouth.

[p. 742] These differences are too little importance in order to give them a specific value, and *Oxyrhina plana* of California, that lives in the same epoch that *O. hastalis*, are able to be considered as a rare race of this latter species.

The Insufficient Information upon the Deposit of the Types of the Species of the Older Descriptions. – The Types of Louis Agassiz.

Nearly all the most common fossil sharks have been named by Louis Agassiz, a century ago.

The illustrious founder of paleoichthyology had visited the numerous of Europe, where he had drawn the materials used in his celebrated work.

But, the bases of these museums are for a great part constituted by the collections, – the natural history cabinets of the late 18th Century and the collections of amateurs – the formation of which was often directed by mere curiosity or a simple whim. Moreover, in this epoch, the stratigraphy is still only rough shaped, and most of the collectors attached only a secondary interest to the age of the deposits that yielded their fossils.

One must not however be astonished if the exact origin of most of Agassiz's types is unknown or only indicated in a very vague manner. And in the case where the descriptions of Agassiz are accompanied with apparently precise data about the provenance of the types or about the age of the formation that had furnished them, one must not be surprised either by the errors that these data are able to contain.

I am not multiplying here the examples; one finds them in the *memoires* that I have devoted to the Tertiary fishes. The sole example of "*Otodus apiculatus*" will show even to what point one is able to continue the confusion, as to the stratigraphic point of view and the systematic point of view.

This name has been given by Agassiz to one lot of teeth that are preserved in the paleontological collections of the Museum of Natural History, in Paris, and that I have had the occasion to study. Two of these teeth, that L. Agassiz regarded as the types of the species, are the teeth of *Oxyrhina hastalis*; they probably come from the Miocene of the Department of Landes. Among the others are found the teeth of the Eocene species [*Odontaspis macrota* Agassiz, *Lamna verticalis* Agassiz, *L. vincenti* (Winkler) A. Smith Woodward] that were collected in the Paris Basin, notably in the "Coarse limestone" (Lutetian) of Vetheuil (Seine-et-Oise). It is this last provenance that is indicated by Agassiz for "*Otodus apiculatus*." So that, according to the indications of origin given [p. 743] by Agassiz, one is able to conclude that *Oxyrhina hastalis* appears in the Eocene, whereas, this species is, as one will see, exclusively Neogene.

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[3] See the reconstruction of the denture of *Oxyrhina hastalis* in M. Leriche ... 1926 ..... I have been able to reconstruct the denture of the California Oxyrhine, thanks to numerous materials that were sent to me by Mr. Charles Morrice, secretary of a petroleum company at Oil City (California). These materials come from a deposit, Shark-tooth Hill, situated on the North of the Kern River at four miles to the East of Oil City.

The Area of Dispersion of Some Tertiary Species.

The reconstruction of the denture of fossil sharks, while making evident the artificial character of a great number of formerly established species, gives to the true species the precise criteria that make them easy to recognize. It permits one to set aside, in the establishment of species, the geographic factor, that has sometimes motivated, by itself, the creation of new specific names.

One recognizes as well a certain number of species, particularly among the Lamnidae, have had a very great area of dispersion.

In the maps that accompany the present work, I have endeavored to determine, according to the documents and the materials used in works up to now, the area of distribution of some of the commonest Tertiary species.

This attempt is based: 1 upon the synonymies established for the species in the memoires already published or that presently will be published; 2 upon some indications, unaccompanied by figures; 3 upon the materials of which the study is in progress.

***Odontaspis macrota* L. Agassiz (map n. 1)**. – One has seen, above, as a consequence of these confusions this species has been able to be considered as having lived at the end of the Cretaceous and during all of the Tertiary era. It is, in reality, limited to the Eocene proper (Ypresian to Bartonian inclusively), but it was preceded, during the Paleocene, by a permutation (*O. striata* Winkler).

The teeth of *O. macrota* that have been noted in the formations more recent than the Eocene are nearly always rolled. They are found in these formations in the altered state.

[p. 744]

***Odontaspis cuspidata* L. Agassiz (map n. 2).** – It is under two distinct names that this species is described in the work of Agassiz: "*Lamna cuspidata*," – that is applied to the anterior teeth of the two jaws and to the lateral teeth of the lower jaw; "*Lamna denticulata*," – that designated the lateral teeth of the upper jaw.

Odontaspis cuspidata is a species of great size that has lived during the Oligocene and the Miocene. It was preceded in the Eocene proper (from the Ypresian to the Bartonian inclusively) by a permutation of smaller size, "*Lamna* (*Odontaspis*) *hopei*" of Agassiz.

Odontaspis acutissima L. Agassiz (map no. 3). – Agassiz has first described under the name of "*Lamna* (*Odontaspis*) *acutissima*," the lateral teeth of the lower jaw, then, under another, more well known, of "*Lamna* (*Odontaspis*) *contortidens*," the anterior teeth of the two jaws and the lateral teeth of the upper jaw.

The *Odontaspis acutissima* appears in the Oligocene, where its size is relatively small. It becomes common in the Lower and Middle Miocene, begins to become scarce in the Sahelian (Upper Miocene) and disappears in the Pliocene, where it is soon replaced by one mutation of greater size, the "*Lamna* (*Odontaspis*) *vorax*" of Le Hon.

***Lamna cattica* Philippi (map n. 4).** – This species, of which the type comes from the Chattian (Upper Oligocene), is encountered especially in the Miocene.

Its small size and fragmentary state – owing to its fragility – under which one encounters it generally causes it to pass often unnoticed.

One is aware of it from the Miocene of Central and Western Europe. It has been collected in the Patagonian (Lower Miocene) of Patagonia. Its area of dispersion must have been very extended.

***Oxyrhina hastalis* L. Agassiz (map n. 5)**. – The synonymy of this species, common in the Neogene, is extremely rich. A whole series of names have been proposed in order to designate the teeth from the diverse parts of the jaws and the teeth that only differ by size or by provenance.

In order to make known this species, Agassiz himself has not employed less than eight names: *Otodus apiculatus*, *O. recticonus*, *Oxyrhina hastalis*, *O. xiphodon*, *O. leptodon*, *O. crassa*, *O. trigonodon*, *O. plicatilis*.

The obvious errors that include the information given by Agassiz on the stratigraphic levels from where could arise the types he refers to these different names are the principal cause of the mistakes of authors on the vertical extension of *Oxyrhina hastalis*.

The "Limestone of Vêteuil," which is, according to Agassiz, the deposit of "*Otodus apiculatus*" comes from, [p. 745] according to all probability, the Miocene of Landes. It goes without saying that not one tooth of *Oxyrhina hastalis* has been found in the Tertiary terrain of the Paris Basin since the collections of fossils were made in a methodical fashion.

The types of "*Oxyrhina xiphodon*" are noted, in the work of Agassiz, as coming from the gypsum in the vicinity of Paris. But, the formations of gypsum of the Paris Basin, that is a lagoon-lake formation dating from the end of the Eocene and the beginning of the Oligocene, has yielded up to now not one remain of a shark.

But, with reason, Agassiz cited, as it were other deposits of "*O. xiphodon*," the vicinity of Dax (Landes) and the Isle of Malta, where the Miocene contains, in effect, *O. hastalis*.

Concerning the deposits of *O. hastalis*, *O. crassa*, *O. trigonodon*, Agassiz mentioned the Tertiary deposits of the Rhine Valley. Several authors believed that the formations which Agassiz made allusion to are the Oligocene deposits of the Mayence Basin. Not only *O. hastalis* has not been collected in the Oligocene of the Mayence Basin, but it was never found in the Oligocene of the neighboring regions (Belgium, Switzerland, Paris Basin), that had been particularly well explored.

There are reasons to believe that, under the vague designation of "Tertiary deposits of the Rhine Valley," sometimes employed by Agassiz, it must mean the Miocene sandstone of the Rhine region, upstream from Bàle.

***Oxyrhina retroflexa* L. Agassiz (map n. 6)**. – This species, which is one of the better characterized, has been often confused with *Oxyrhina hastalis*. It is very clearly distinguished from it.

It is, like *O. hastalis*, an exclusively Neogene species.

It is less common than *O. hastalis*. Its deposits, actually well known, without being as numerous as those of this latter species are very scattered, with the result that its area of expansion seems as having been very vast.

***Carcharodon megalodon* L. Agassiz (map. n. 7)**. – The teeth of this giant species appear in nearly all the old cabinets of natural history. Scill has represented some of the specimens coming from the Isle of Malta, and collectors from the end of the 18th Century and to the beginning of the 19th Century designated these teeth, which was their origin, under the name of Maltese teeth.

It is also under multiple names that this species has been described. *Carcharodon*

rectidens, *C. subauriculatus*, *C. productus*[4], *C. polygyrus*, *C. semiserratus*, [p. 746] in order to cite only the names proposed by Agassiz, there are as many synonyms of *C. megalodon*.

Like *Oxyrhina hastalis*, *Carcharodon megalodon* is a Neogene species, that one finds, nearly as common as *O. hastalis*, in the marine Neogene of nearly of all the regions of the world.

It appears in the Aquitanian. Its size, which is relatively small in the Aquitanian and the Burdigalian, grows progressively in proportion to its height in the Miocene: it becomes very large in the Upper Miocene (Sahelian = Anversian) and in the Pliocene.

Carcharodon megalodon probably still lived in the Pleistocene Epoch. The dredges executed in the course of the "Challenger" and "Albatross" expeditions have brought back the teeth coming from the red clay that coats the great depths of the Pacific.

The map of the distribution of *C. megalodon* (map no. 7) – like the one, moreover, that indicates the distribution of *Oxyrhina hastalis* (map no. 5) – shows, in a striking manner, the deposits marking out the ancient Tethys. A breach of continuity – that corresponds to a gap in our knowledge – is present in the region of Iran. One must expect to find in the marine Miocene of this region *Carcharodon megalodon*, *Oxyrhina hastalis* therefore the whole cortege of sharks (*Oxyrhina retroflexa*, *Galeocerdo aduncus*, *Hemipristis serra*, etc.) that accompany them in the Miocene deposits in other Tethyan regions.

***Carcharodon rondeleti* Müller and Henle (map no. 8).** – This living species, that lives in all the tropical and subtropical seas, resembles *Carcharodon sulcidens* of Agassiz, of which the type comes from the "Upper Tertiary" (very probably the Pliocene) of Italy.

Carcharodon rondeleti appeared in the Miocene, where it is rare; it is common in the Pliocene, where it tends to supplant *C. megalodon*.

L. Agassiz has noted "*C. sulcidens*" in the Eocene formations near Soissons (Aisne). This indication based upon a tooth in the "Voltz collection" is only able to result from a mistake upon the provenance of the fossil, because no tooth of this species has been recovered, after Agassiz, in the marine formations of the Paris Basin, of which the latest – the Fontainebleau Sands – belong to the Middle Oligocene (Rupelian).

***Galeocerdo aduncus* L. Agassiz (map no. 9)**. – *Galeocerdo latidens* L. Agassiz and *G. aduncus* L. Agassiz are the two commonest species of the genus. [p. 747] They were often confused. The reconstruction of their denture shows that very clear differences separate them.
They characterize two different epochs: *G. latidens*, the Eocene proper (Ypresian to Bartonian inclusively); *G. aduncus*, the Neogene and more particularly the Miocene.

The geographic distribution of *G. aduncus* seems to have been the same as that of *Oxyrhina hastalis* and of *Carcharodon megalodon*.

***Hemipristis serra* L. Agassiz (map no. 10).** – The genus *Hemipristis* is represented, in the present day epoch, only by a single species, *Hemipristis* (*Dirrhizodon*) *elongatus* Klunzinger. This one is itself known only by the holotype, which was captured in the Red Sea and is found

[4]There is without a doubt an error in the mention by Agassiz (*Recherches sur les Poissons fossiles*, t. III, p. 253) of the presence of "*C. productus*" in Alzey (Mayence Basin), either that the teeth that he refers to this species belong to another form, or that the error bears upon the indicated provenance. No tooth of *C. megalodon* has been found in the Oligocene of the Mayence Basin, and also, not in Oligocene of the adjacent recent (Belgium, Switzerland, Paris Basin).

preserved in the Stuttgart Museum.

Hemipristis serra is a species characteristic of the Miocene, where it is common. It has however been noted, by Lawley, in the Pliocene of Tuscany, where it is very rare, and, by Jordan and Hannibal, in the Pleistocene of San Diego (California). It is possible that it is reworked in San Diego.

This species has lived only in the warm seas, tropical and subtropical.

In the northern hemisphere, its limit of expansion , toward the north, hardly exceeds the 49 parallel: its northernmost deposits are those of the West of France and southern Germany.

Hemipristis serra has not been encountered in the Miocene of the north [southeastern England, northern France, Belgium, Netherlands, northwestern Germany, Denmark]. Its frequency in the Miocene of Brittany, opposed to its absence in the Miocene of Belgium, shows that no direct communication, by the English Channel, existed, in the Miocene Epoch, between the sea of Brittany and that of Flanders.

Most of the Neogene sharks studied, on the preceding pages, from double point of view of their stratigraphic distribution and their geographic distribution: *Oxyrhina hastalis*, *Carcharodon megalodon*, *Galeocerdo aduncus*, *Hemipristis serra*, have been noted by Gibbes, in 1848-1849, in the Eocene of South Carolina. These indications of Gibbes have been faithfully repeated by authors, and in the recent works, one sees still the appearance of these species referred to the Eocene.

A priori, the attribution to the Eocene strata of South Carolina that have yielded these fossils could be inexact, but it is difficult to admit that the fish so cosmopolitan as the sharks have been able to remain confined to a single point on the globe, during the Eocene, that they may be later refugees in [p. 748] another place, unknown, during the Oligocene, in order to disperse only in all seas in the Miocene Epoch.

The research with which I am supplied, in the course of a recent voyage to the United States, has shown me that the data of Gibbes, concerning the deposits of the previously cited species, result effectively from an error in the determination of the age of the strata of South Carolina that have furnished these fossils. These strata proper containing the Eocene fossils and Cretaceous fossils, but these fossils, Eocene and Cretaceous, are found in the reworked state.