Selachians from the Miocene of the Montpellier region

by

Henri Cappetta*

Hexanchus primigenius (Agassiz, 1843)

[p. 16]

Material: Two complete upper teeth and some fragments of lateral teeth from the two jaws.

Provenance: Loupian.

Description:

A very anterior tooth (fig. 12) possess a nearly straight cusp with internal and external faces rather convex; the root is stocky and thick; the basal face is of subtrapezoidal contour.

One upper anterior tooth (fig. 13) presents a single cusp rather straightened with internal face more convex than the external face. The mesial and distal heels, this latter more developed, each beares a short denticle inclined toward the commissure. The root, of subrectangular form, is slightly less high on its distal part; the basal face, very developed, bears numerous foramina that are prolonged often by a narrow vertical furrow; its lower edge is cut off.

A fragment of an upper lateral tooth (fig. 14) shows a principal cone rather straightened, slightly inclined toward the interior of the mouth with the anterior denticles reduced in number and dimensions.

An incomplete symphseal tooth (fig. 11) shows four cones of decreasing size beginning with the center, diverging and turning toward the exterior.

[p. 17] The lower teeth are incomplete (fig. 16-19); they possess a principal cone inclined toward the commissure; it bears on its mesial edge six to seven denticles, of which the size increases from front to rear; the accessory cones diminish regularly in size toward the rear. The internal and external faces are moderately and equally convex.

Remarks:

---

* Original citation: Cappetta, H. 1970. Les selaciens du Miocène de la région de Montpellier. *Palaeovertebrata* 1970:1-139. Translated by Robert Purdy, Smithsonian Institution.

The species *N. repens* Probst, from the German Miocene, is indistinguishable from this species.

Joleaud has figured (1912, pl. IV, fig. 1-2) two teeth that he refers to *Notidanus repens* of Probst but that, in fact, must belong to the genus *Heptranchias*.

The species of Joleaud, *N. avenionensis* from the Miocene of Comtat (1912, pl. IV, fig. 4) must equally be referred to the genus *Heptranchias*.

The teeth figured by E. Menesini (1969, pl. I, fig. 1-5) under the name of *N. primigenius* are the teeth entirely typical of *Hexanchus gigas*. It is moreover rather difficult to distinguish the two species apart by their size, and it is not impossible that *N. primigenius* and *N. gigas* represent one same species, very near the living *H. griseus*.

Family Isuridae

This family includes the living genera *Isurus*, *Lamna*, *Carcharodon* and the fossil genera *Palaeocarcharodon* and *Procarcharodon*.

These forms are distinguished from the Odontaspidae by the absence of differentiated symphyseal teeth; moreover, the intermediate teeth are lacking or are reduced to a single rank (*Isurus*, *Lamna*); the crown is in general larger and more compressed. Certain genera possess the lateral denticles (*Lamna*, *Palaeocarcharodon*, and *Procarcharodon* in part), others are as a rule deprived (*Alopias*, *Isurus*).

Genus *Isurus* Rafinesque, 1810

This genus is known since the Cretaceous; it is represented in our deposits by 3 species. The teeth are distinguished from those of the genus *Lamna* by the absence, as a rule, of lateral denticles.

[p. 18]

Isurus hastalis (Agassiz), 1843

Plate 5, fig. 1-13

Material collected: about thirty teeth, of whcih many are broken

Provenance: Loupian.

Description:

The teeth of this species is of rather great size and compressed. The upper anteriors are the most characteristic.

Upper Teeth:

The anterior teeth have a rather narrow crown with a flat external face and a moderately convex internal face, separated by sharp edges. [p. 19] The cusp is lying slightly toward the commissure and the tip turned toward the exterior, which confers to the tooth a sigmoidal profile. The not very thick root has massive branches, not very high and very spread apart; the internal protuberance is not very marked. The external profile is concave.

The lateral teeth (fig. 1-5) have a more massive crown, more inclined toward the corner of the mouth; the external face is slightly convex and it can develops heels. The root, much higher than in the anterior teeth, possesses a large basilar face; its mesial part is more developed than its distal part.

Lower teeth:

The anteriors (fig. 6-8) have a less higher, more massive crown, with a slightly convex external face; they present a sigmoidal profile and contour. The branches of the root, which is thicker than in the upper teeth, are more lengthened and determine a more acute angle.

The lateral teeth (fig. 9-12) have a straight crown, slightly inclined toward the interior of the mouth; the branches of the high and massive rootbear oblique enamel heels. A little below the extremities of the heels, the root presents a more or less marked narrowing. A posterior tooth (fig. 13) shows a slender, straight crown with a very developed root bearing the sharply defined heels.

Close to the typical forms, one encounters the teeth, rather rare and of rather small size, with a much flatter and slimmer crown with an equally less thick root (fig. 5 and 8). The same differences one observes among juvenile and adult individuals of living *Isurus oxyrhynchus*, we attribute these fossil forms to the young of *O. hastalis* Ag. S. Jonet, on the contrary, has created a variety *lusitanica* for designating these forms, for the material coming from the Miocene of Portugal.

Isurus desori (Agassiz), 1844

Plate 2, fig. 17

[p. 20]

Material collected: an incomplete anterior tooth

Provenance: Loupian.

Description:

This species is only represented by an incomplete anterior tooth. The branches of the root and the tip of the crown are broken; one is able however to attribute this tooth to the species *desori*. The crown presents a sigmoidal profile; the cutting edge, very individualized, descends very much lower; the external face is practically flat; the internal face is rather strongly and regularly convex. The root presents a strong internal protuberance that bears a badly formed nutritive foramen.

Remarks:

The distinction between the anterior teeth of this species and the corresponding elements of young individuals of *Isurus hastalis* Ag. is rather fine; it is sometimes very difficult to differentiate. The upper anterior teeth present a sigmoidal crown that is not present in the uppers of *I. hastalis*.

Isurus retroflexus (Agassiz), 1843

Plate 6, fig. 1

Material collected: one anterior tooth

Provenance: Loupian.

Description:

This species, very characteristic, is represented in our material by a complete lower anterior tooth but of which a branch of the root has been displaced in the course of fossilization.

The tooth is of very stocky form and the root is nearly as high as the crown that is of triangular form, wide at the base, rather short, with obtuse tip.

The base of the external face is slightly convex transversely, but presents a triangular median depression that attains about the middle of the height of this face, of which the tip is equally transversely convex. The internal face, much more convex at the base than at the tip, presents a concave profile, while the external face presents a convex profile; the crown is inclined toward the interior of the mouth.

The cutting edge is very individulalized, especially on the lower part of the cusp, where it is separated from the internal face by a depression.

The root, that shows two well developed branches and terminating in a point, possesses a strong inrernal protuberance. It bears, a little to the rear of the of the internal limit of the enamel and parallel to this latter, a distinct swelling.

The branches are rather strongly flattened transversely and determine between them a rather acute angle. They bear on their lower anterior part a deep furrow; hence the external face of the crown overhangs greatly the anterior region of the root.

Remarks:

The species has been established upon an incomplete lower lateral tooth of uncertain origin, Molasse of southern Germany or from Switzerland (fide Leriche).

A tooth from southern Australia, referred by N. Pledge to *Lamna* cf. *crassidens* Ag. belongs to the species *I. retroflexus* Ag.

[p. 21] Genus *Alopias* Rafinesque, 1810

This genus, known from the Oligocene, is represented in our deposits by two species.

Alopias latidens (Leriche), 1908

Plate 6, fig. 3-8

Material collected: Seven teeth all incomplete.

[p. 22]

Provenance: Loupian

This species is represented by a very small number of teeth.

The crown is stocky, of triangular form, inclined toward the commissure in the lateral teeth.

The external face rather flat but all the same very slightly convex presents a triangular depression in its medio-lower part. The anterior cutting edge, at first nearly straight, incurves rather rapidly toward the commissure and the posterior cutting edge delineates a more or less marked concavity according to the position of the tooth upon the jaw. The internal face is regularly convex.

The branches of the root, which are not very massive, are very divergent and bear the enamel heels.

The external face of the crown overhangs slightly the root. a symmetrical tooth (fig. 3), of triangular form, with straight cutting edges represents certainly an anterior tooth.

Relations and differences:

This species is very near to *A. subexigua* Darteville and Casier from the Miocene of the Bololo (Lower Congo), it is distinguished from it by a wider crown. Casier considered this African form as intermediate between *A. latidens* and *A. exigua*.

The species *A. grandis* described by Leriche from the Atlantic Coastal Plain of the U.S.A. is morphologically very near *A. latidens* but is distinguished immediately from it by its much greater dimensions; it is moreover possible that the teeth of *A. grandis* are only the intermediate teeth of the genus *Isurus* which they strangely resemble.

Remarks:

This species, of which the type comes from the Oligocene of Belgium (Boom Clay) seems rare in the Miocene. M. Leriche, in 1927, has figured an anterior tooth of the Burdigalian from Switzerland; E. Menesini, in 1969, has figured a tooth in a bad state of preservation from the Italian Miocene.

Alopias exigua (Probst), 1879

Plate 6, fig. 9-11

[p. 23]

Material collected: three incomplete teeth.

Provenance: Loupian.

Description:

The root is very developed in comparison with the crown that is straight, short, pointed, and wide at the base. The external face is flat or slightly convex; the internal face is rather strongly convex, especially at its base.

The massive root shows the branches rather separated; there is not a trace of a furrow upon the internal protuberance. The crown sends out upon the two branches oblique heels.

On the external face, the crown clearly overhangs the root. The teeth having all three having a straight and rather low crown and the lobes of the roots are certainly lateral elements.

Relations and differences:

This species is distinguished immediately from *A. latidens* and the closely related forms by the gracility and the narrowness of the crown that is often very low in the lateral teeth. It is

differentiated from the the closest species *A. acutidens* Casier from the Miocene of Bissix Hill (Isle of Barbado, Antilles) by a less slencer crown and the rather marked cutting cutting edges.

Remarks:

The three large teeth figured by E. Menesini (1969, pl. V, fig. 7-8-9) under this name, only fig. 8 represents a tooth of *Alopias exigua* (Probst); fig. 7 is probably a tooth of *Odontaspis acutissima* that has lost its denticles; as for fig 9 it represents an incomplete lower tooth of *Carcharhinus priscus*.

Genus *Lamna* Cuvier, 1817

This genus, known after the Cretaceous, flouishes particularly in the Eocene with numerous species, is only represented in present day nature by a very small number of species (2 or 3). The Neogene terains have yielded only a single species, *Lamna cattica* (Philippi).

Lamna cattica (Philippi), 1846

Pl. 2, fig. 18-19 and Pl. 4, fig. 1-9

[p. 24]

Material collected: about twenty teeth.

Provenance: La Paillade, Caunelle, Loupian.

Description:

This species presents teeth of very particular and perfectly recognizable form, because it is practically the only species of the genus known in the Neogene terrains.

The teeth have a triangular, very compressed crown, entirely smooth with a pair of large lateral denticles, inclined toward the commissure, except for the anterior teeth.

The external face of the very flat crown, presents at its base a rather vague triangular depression; the internal face with a weak convexity shows sometimes at its base a rather distinct flattening. The cutting edges are accentuated by its slight thickness of the crown. The lateral denticles, one pair in number, are very developed, of triangular form, wide at the base, acuminate at the tip; like the rest of the tooth, they are flat divergent and slightly warped toward the interior of the mouth with reference to the crown.

The root possesses very spread out branches in the lateral teeth. Under the limit of the enamel, its external face shows a depression subparallel to the anterior edge of the basal face that bears a rather distinct nutritive groove.

Between the crown and the root, one is able to see, on the internal face a narrow non-enamel band, of darker color and slightly depressed with respect to the crown.

In the very lateral teeth, the crown inclines toward the commissure; upon these teeth is able to exist, at the base of the external face, vertical plications of the enamel; this character observed frequently in the posterior teeth of *Odontaspis*. It happens that the denticles tend to double.

On each side of these typical teeth, one encounters the symmetrical teeth with a straight crown or of slightly sigmoidal profile (Pl. 4, fig. 1-3); the denticles, less massive, are more erect and parallel.

The branches of the root are divergent. these teeth, which represent probably the anterior elements, are identical to those figured by Leriche (1927) from the Swiss Molasse. Two teeth from the Paillade that I have [p. 25] ranked in the genus *Odontaspis* are probably the anterior teeth of *Lamna cattica*.

The first tooth (Pl. 2, fig. 18) has a slender crown with sigmoidal profile; the internal face is regularly and rather strongly convex; the external face, nearly flat, is depressed toward the base. The distinct cutting edges stop rather high upon the crown that is flanked by a pair of sharp-edged, straight, conical, lateral denticles of circular section at the base, sharp at the tip; each possesses, upon its lower lateral edge, an enamel ridge.

The branches of the root are rather short and spread apart.

The second specimen (Pl. 2, fig. 19) shows a wider, less thick crown. The cutting edges reach lower down on the cusp, the equal, very developed denticles are tranchant upon all their height. The root possesses short branches and spread far apart.

Concerning the two specimens, the crown is absolutely smooth and brilliant.

Ramarks:

The tooth figured by Priem (1911) under the name of *Carcharoides totuserratus* Ameghino, from the Patagonian of the Republic of Argentina, presents the general contours of *Lamna cattica*; it is distinguished from it only by finely serrated cutting edges. The three teeth from La Paillade are clearly larger than the teeth from Caunelle and from Loupian.

Dartevelle and Casier have figured (1959, pl. XXX, fig. 8, 9, 12) from the Miocene of the Lower Congo the teeth that they have attributed to *O. acutissima* Ag. and that seem very near the two anterior teeth collected at La Paillade.

Relations and differences:

If the lateral teeth are easy to identify, the anterior teeth on the contrary present a greater resemblance with the anterior teeth of *Odontaspis*; they are distinguished however by their thinner crown, with clearly less marked sigmoidal profile, with a smooth internal face, and with the external face overhanging the root; and by their lateral denticles, relatively more developed and straight.

[p. 26]

Genus *Procarcharodon* Casier, 1960

In 1960, Casier has separated from the genus *Carcharodon* two new genera *Palaeocarcharodon* and *Procarcharodon*.

This author has in effect demonstrated that the genus *Carcharodon* is polyphyletic.

The genus *Palaeocarcharodon* Casier, 1969 (*sic*), that is comprised of only one species -- *P. landanensis* (Leriche) from the Paleocene of Landana -- is derived from *Lamna appendiculata* of which the variations are numerous and large in the Paleocene, epoch that corresponds to the disappearance of this species.

The principal characters are: very compressed teeth, irregularly serrated on their edges, serrated lateral denticles, root weakly developed.

The only species of the genus in known only from the African Paleocene: Congo and Morocco.

The genus *Procarcharodon* Casier, 1960, appeared in the Eocene is know up until the Pliocene. It derives indirectly from *Lamna appendiculata* through the intermediary of *Lamna obliqua* of which a "mutation" *Lamna obliqua subserrata* known from the Ypresian of the Anglo-Belgian Basin, foretells this second group of Carcharodonts.

The principal characters of this genus are: large and wide teeth, slightly compressed, with generally regular marginal serrations, sometimes, pectinate; the denticles, present in the Eocene and

Oligocene forms, disappear in the more recent forms; the root is very developed. The type of the genus is *P. angustidens* (Ag.), 1843.

This genus includes the following species:

P. auriculatus (de Blainville)	Eocene of Europe.
P. disauris (Ag.)	Eocene of Europe.
P. debrayi (Leriche)	Eocene of Europe & Nigeria.
P. stromeri (D. and C.)	Eocene of Egypt and the Congo.
P. angustidens (Ag.)	Oligocene, Miocene of Europe.
P. megalodon (Ag.)	Cosmopolitan.
P. megalodon indicus (Leriche)	Miocene of India.

The genus *Carcharodon* Muller and Henle is represented by the unique species *C. carcharias* confined within the warm seas.

This third type derived probably from *Isurus hastalis*, of which a Pliocene variety, *Isurus escheri*, which presents the serrations, pointing out how one has been able to differentiate the genus *Carcharodon* s. st.

This genus is known from the Miocene to present day; however, Casier (1960) in his phyletic table of *Carcharodon* s. l. has it commence only in the Pliocene.

From Casier, one is able to diagrammatize the evolution of *Carcharodon* in the following fashion:

In *Palaeocarcharodon*, there is an acquisition of serrations without loss of the denticles.

In *Procarcharodon*, there is the appearance of serrations, afterward the secondary loss of the denticles.

In *Carcharodon* s. st. there is the appearance of serrations preceded by the loss of denticles.

Procarcharodon megalodon (Agassiz), 1343

Plate 6, fig. 2

[p. 27]

Material collected: an incomplete lateral tooth.

Provenance: Loupian.

Description:

Although widely represented in most of the Miocene deposits, this cosmopolitan species seems to have been rather rare in our regions; in effect, only the Loupian deposits has yielded an incomplete lateral tooth and of average size.

The crown is wide, triangular, slightly inclined toward the commissure; the internal face is convex; the external face, bears at its base a triangular depression where originates a crest that reaches the tip of the tooth. The cutting edges are rather strongly but very regularly serrated. The root is broken.

[p. 28]

Family Odontaspidae (*sic*)

This family containing the living genera *Odontaspis* and *Scapanorhynchus* (= *Mitsukirina*) and the fossil genus *Anomotodon*.

The teeth are straight, slender, and possess normally on both sides of the base of the crown the acute lateral denticles. The denture of these sharks is characterized by the presence of differentiated parasymphyseal teeth and reduced and deformed intermediate teeth.

The forms present in our deposits belong to the genus *Odontaspis* Ag.

Genus *Odontaspis* Agassiz, 1838

The living species of this genus are not very abundant and are able to be divided into two groups:

species group of *O. ferox*;

species group of *O. taurus*.

The morphologic variability of the teeth is poorly known in these species.

Odontaspis ferox possess the reduced parasymphyseal teeth in the two jaws; the intermediate files in the upper jaws are numerous; the teeth with smmooth crowns possess two pairs of large lateral denticles.

Odontaspis taurus presents the reduced and deformed parasymphseals in lower jaw only; the intermediate files are less numerous; the teeth, with crown sometimes wrinkled upon the internal face, possess a pair of lateral denticles.

White in 1931 has proposed to divide the genus *Odontaspis* into three subgenera:

Odontaspis s. st., having for the type *O. ferox*.

Synodontaspis, having for the type *O. taurus*.

Parodontaspis, having for the type *O. platensis*.

Giltay has shown in 1937 that *O. platensis* must be placed in synonomy with *O. taurus*, the last subgenus of White is no longer able to utilized. Certain authors however (Gurr, 1962) have adopted it just as it is.

The distinction of the living subgenera is easy when one possesses the complete dentures; on the contrary, when one has recourse to fossil material, always fragmentary and more or less abundant according to the deposits, the distinction is much less easy: in effect, the forms of the Oligocene and the Lower Miocene *Odontaspis acutissima* Ag. (which is practically identical to *O. taurus*, therefore it must be ranked in the subgenus *Synodontaspis*) possess two pairs of lateral denticles, that is as a rule a character of the subgenus *Odontaspis* s. s. It is therefore because of the imprecision of certain characters of fossil forms that I utilize in the systemmatic portion the genus *Odontaspis* without distinguishing the subgenera proposed by White.

The genus *Odontaspis* is known since the Cretaceous.

[p. 29]

Odontaspis acutissima Agassiz, 1844

Material collected: very numerous teeth.

Provenance: La Paillade, Caunelle, Loupian.

Description:

This species is widely represented in the Miocene of Herault where it attains a large size.

[p. 30]

The parasymphyseal teeth (Pl. I, fig. 1-3) are sometimes deprived of lateral denticles; they are rather small and the stocky root possessing a strong internal protuberance, has its branches fused and transversely flattened. The crown has a fairly defined sigmoidal profile and the cutting edges stop high up. The external and internal faces of the crown are very convex at the base that, from this fact, presents a subcircular section.

Certain parasymphyseals possess the more or less deformed denticles of which the mesial is very reduced and of which the distal, normally developed, is flat near the base of the crown. The

root, always flattened transversely, possesses a strong internal protuberance. The branches of the root are in part fused; the free extremity of the anterior branch is very reduced.

The anterior teeth (Pl. 1, fig. 4-6) are slender, pointed, awl-shaped in form; they have a very marked and clearly defined sigmiodal profile.

The internal face of the strongly convex crown bears flexuous, irregular, and vertical wrinkles able to rise rather high up; among the older individuals, these wrinkles rise toward the middle of the internal face that presents often a characteristic flattening. Among the young individuals (Pl. 2, fig. 6-12), on the contrary, these wrinkles are very marked and occupy more of half of the height of the crown. The external face is slightly convex transversely and is depressed along the tranchant that, hence, is very marked, except at the base of the tooth where it is able to disappear sometimes.

The root, very swollen on its internal face, possesses two branches very developed and rather close together. The Internal protuberance bears a shallow but very visible furrow. The crown is flanked at its base by a pair rather large, very pointed, strongly recurved to the rear, lateral denticles; they are clearly thicker at the base, of circular section, than at the tip that is provided with a tranchant.

Certain anterior teeth (Pl. 1, fig. 6) present, at the base of the external face of the crown, a median, vertical depression where one observes a carina can cover the lower third of the cusp.

The lower lateral teeth (Pl. 1, fig. 1-5) have a straight and very slightly slanted toward the interior of the mouth crown; the upper laterals (pl. 1, fig. 8-17) have a wider, triangular crown, at the base, more flattened, and so much the more inclined toward the commissure than the element occupying a more lateral position; the lobes of the roots are more spread out than in the lower laterals.

The basal face of the root takes on importance and flattens; the nutritive furrow that is rather poorly marked upon the anterior teeth becomes deep.

In the more lateral elements, the denticles become large and assume a triangular form; from this fact, certain teeth resemble much the teeth of the genus *Lamna*.

The posterior teeth (pl. 1, fig. 18-22) have a very large root, which is able even to be larger than the crown; the latter is very inclined [p. 31] toward the commissure; the mesial denticle may disappear; sometimes the crown is reduced to a simple enamel plate. The external face, that can be parallel to the basiliar face of the root, bears very often at its base strong, vertical, enamel folds.

The intermediate teeth (Pl. 1, fig. 7) are very small, deformed and strongly flattened in the labio-lingual sense. The root is as large as the crown, which is often of synuous contour.

Relations and differences:

It is sometimes difficult to differentiate teeth of small size of *O. cuspidata* from those of *O. acutissima* particularly when one possesses incomplete teeth. The distinction is easy if one has the forms of *O. acutissima* with striated internal face; otherwise, the teeth of *O acutissima* can be distinguished by their narrower crown, with a more pronounced sigmoidal profile, with internal face slightly flattened in the anterior teeth and by their more developed and pointed lateral denticles, rarely doubling in the lateral teeth.

Remarks:

The teeth that we have just described are extremely near to those of the living species of *O. taurus* Rafinesque. In particular, it is difficult to establish the differences between our teeth and the teeth of *O. taurus* figured by S. Applegate (1965). C. Arambourg, in 1927, has already noted the great similarity existing between the two species, and he does not hesitate to rank the fossil forms of the Oran region in the present day species.

In the deposits of the La Paillade and of Caunelle, the teeth that I attributed to *O. acutissima* (Pl. 2, fig. 14-16) are characterized by a doubling of the lateral denticles; only this character, other than their rather distinctly smaller size, permits one to distinguish the typical forms.

The specimens of *O. acutissima* from the Boom Clay, that I was able to examine, are on the contrary very different from those of the Miocene Heraultais.

They posssess two pairs of lateral denticles of which the first is relatively more developed than in the Miocene forms of Herault; these denticles, furthermore, are warped toward the interior face of the mouth; the second smaller pair is however well individualized; the lateral teeth bear at the base of the external face numerous, vertical, short enamel folds but very short; this character is observed in the Loupian species only in the posterior teeth.

It seems in all cases evident that, under the same specific name, one has ranked different forms; in effect, it is clear that the forms of the Boom Clay do not correspond with the species *acutissima* of our region. It is possible that the differences observed are of an evolutionary order, it

is equally possible that these differences are only geographic variations; it is regretable that one has no one studied the geographic variations of the actual *O. taurus* Raf. that has a wide distribution.