Notes on West African Ichthyology

XXXVIII. - Documents to serve the research of the displacement and replacement mechanisms of teeth in sharks.

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Summary

FIRST PART

In 1784 W. Andre on the occasion of the description of the teeth of two teleosts of the genera *Anarhichas* and *Chaetodon*, described an anomalous dentition among the tiger shark: *Galeocerdo arcticus* Faber, designated them under the name of *Galeus* and attempted also for the first time to demonstrate that the teeth among sharks carried over in a continuous motion, being perpetually renewed[1]

After the above was published by Andre (Fig. 2), the anomaly observed concerning *Galeocerdo* corresponds exactly to one of the types of anomalies that we have observed in other species. It is not a question of a deformation due to the simple implantation of a *Dasyatis* spine between the dental units, but that of what we will call farther on an anomaly of type 2, that is to say caused **[552]** by the penetration of a foreign body (caudal spine of a species of *Dasyatis* in this particular case) in the deep zone of the jaw where it has sectioned the of germs of a dental unit and has divided them into two separate parts having given rise to each a series of half teeth.

Later authors have admitted that the teeth developing upon the internal side of the jaw were replaced regularly by rotation around these and that this rotation is singular among all the elasmobranchs.

If the movement placed in evidence is admitted by different authors, its mechanism remains unknown and its causes are discussed.

The point of view more commonly admitted is that the fibrous tissue to which the teeth

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[1] André, W. 1784, *Phil. Trans. Roy. Soc. London*, **74**, 274-282.

are fixed acts as a moving body, a kind of rolling rug, carrying the teeth with it.

It has been expressed and defended by Owen, R.[2], and although it is perhaps not perfectly satisfactory to grasp easily the mode of displacement and replacement of the teeth among the sharks, because as a matter of fact, all pass along exactly as if the ensemble constituted by all the dental units being carried along toward the edge of the jaws in a continuous motion in a vertical plane, and upon the internal side of the jaws.

In 1953-54, W. Warwick James, in a work laid down in June 1952 takes up again the problem and searches histologically the causes of the displacement and replacement of the selachian teeth.[3]

According to him, the explanation of a running band (*tapis roulant*) of fibrous tissue carrying along the teeth is difficult to understand and to accept because the fibrous tissue alone is not able to exert traction.

On the contrary the examination of the histological sections has permitted him to detect the existence of a mass of dental epithelium between the formed teeth and above this the ones that are in the courses of development and it appears that it is the only tissue capable of exerting a pressure.

It is the study of these structures that has led Warwick James to the following conclusions concerning the movement of the teeth:

– there is no muscular motion.

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– The action of the fibrous tissue is limited to that of alignment controlling the movement of the rotation of the teeth, but on the contrary assures the stability of the latter and maintains the directions of movement.

– The displacement of the teeth: vertical displacement of the whole dental unit and rotation of each tooth in order to assume its functional position, are owing principally to an osmotic phenomenon resulting from the increase in number and in volume of the constituent cells, promoted by the high pressure of the cellular and intercellular liquids due to the strong content of urea in the blood of selachians.

Recall first of all the knowledge acquired concerning the origin and the formation of teeth in the selachians. We will cite for the brief résumé that which is given by L. Burtin in the tome XIII (fasc. I) of the *Traité de Zoologie* published under the direction of Professor Grassé, p. 518, and of which we utilize the terminology.

"The teeth of selachians originate at the expense of the epidermal fold (dental crest or lamina), that is deep tangentially to the lingual side, on the interior dermis of the gum. On the internal face this fold form the dental germs that resemble exactly those of the cutaneous denticles.

Recall the stages of this formation:

a) Accumulation on a point of the dermis, under the limit, of large mesenchymal cells destined to become odontoblasts.

b) Rising from the epidermal generatrix at the contact of this blastema and differentiation of

[2]Owen, R. 1839. Research upon the structure and the formation of the teeth of squaloids and application of the facts observed to a new theory of the development of teeth. *Ann. Sc. Paris*, **9**, 784-788.

Owen R., unteersuchungen über ddie struktur und entwickelung der zähne squaloiden. *Neue notizen (Froriep),* 1840, **13**, n. 270, *ibid*., 1841, **17**, n. 358.

[3]W. Warwick James, the succession of teeth in elasmobranchs. *Proceed. Zool. Soc. London*, vol. **123**, (1953-54), p. 419-474, 12 pl., 11 text-fig.

these cells into ameloblasts.

c) Peripheral depression of the epidermis around the blastema that it caps as in a cap named adamantine sac.

d) Secretion of the dentine by the odontoblasts and of the enamel by the ameloblasts.

e) Realization of a pulp cavity that is able to be encroached upon secondarily by the osteodentine.

f) connection of the dental cone with a basal plate produced on the interior of the dermis."

The process of ontogenesis is not exactly the same in all selachians. There exists the requiems with "hollow teeth" such as Carcharhinidae and Sphyrnidae. (See Pl. XX, XXI, XXII, [554] XXIV and XXV) among which the pulp cavity remains more or less large whereas the linings are formed by pseudodentine (toward the exterior) and orthodentine (toward the interior), and the sharks with "solid teeth," such as *Carcharias* and *Isurus* (Pl. XXIII) among which the pulp cavity is completely filled by an osteodentine cone.

Concerning the deep dental lamina, they are relatively constant in number for a determined species but very variable according to the species considered, in the formation zones of the dental buds or "germs."

Among many requiems, Carcharhinidae in particular, these zones are separated from one another in sort of alveoli placed in evidence by the sections and X-rays especially those in plates XVII, XIX, XX and XXII.

In each of these alveoli numerous growing teeth continue their development as their displacement toward the edge of the jaw.

The ensemble of teeth (from rough shaped to functional teeth) comes from one same alveolus that which one calls a *dental unit* ("dental unit" of Warwick James).

These dental units are displaced more or less parallel to one another at a practically equal speed in normal conditions, because the forces of osmotic pressure that constitute the principal mover are the same.

Nevertheless for different reasons (possibly being accidental) a certain inequality in the rapidity of the displacement of the teeth of a dental unit is able to occur and is manifested by an irregularity in the position of the functional teeth upon the edge of the jaws, those functional teeth can be in general different according to the units considered, even in the case where the disposition of the completely formed teeth carrying along a certain interdependence of the units between them as for example for the teeth in quincunx of the Carcharhinidae (Pl. XIII) and Mustelidae (Pl. XVI, fig. 45), or the imbricated teeth that one observes among the Squalidae (Pl. XIV and XV).

In the same manner the number of dental units from one species to another likewise the number of teeth of a dental unit is able to vary, although by much narrower limits, according to the sharks considered. The highest numbers are encountered in the species of the families Orectolobidae and Mustelidae.

From the zone of formation of the dental germs to the edge of the jaw where they are functional, the teeth of different generations [555] succeed one another regularly and proportionally with their growth.

At first completely buried in the mass of dental epithelium, which maintains them in a position more or less parallel to the external side of the jaw, the extremity of the cusp is directed toward the zone of formation of the germs, the teeth free up themselves little by little, the basal region appears first to the exterior. Liberated also by the action of this pressure that maintained them against the external wall of the jaw, the teeth will be able to begin their rotation movement under the interplay of the growth that continues to exercise itself on bases for them, and the one of the epithelium masses dental that have penetrated between the extremity of the released tooth and the base of the one of the following generation (as that which is still visible upon the section of Plate XIX). The whole thing is assisted moreover by the form even of basilar part of the tooth, moving like a lifter around the extremity of the cartilaginous skeleton of the jaw.

The observation of an important series of dental anomalies in several species of requiems and other West African selachians (anomalies in the deep zones of the jaws), make obvious the very clear manner of this continuous motion of dental units, and although our macroscopic study is not accompanied by histological documents, we have the idea that this documentation can be advantageously deposited in the file of the study of the dentition among selachians.

Let us note first of all that the forces analyzed by Warwick James, exerting themselves upon each tooth taken separately, can have different effects along the same order of teeth upon the jaw. One can distinguish 4 principal types of dispositions of the teeth among the selachians.

1st The teeth of one same dental unit are clearly independent of the teeth of the neighboring units: their width at the base is less greater than the space separating the extremities of the bases of the teeth of the two closest dental units, the one to the right and the one to the left.

The pressure exerted upon a tooth can only react with the other teeth in the same unit and is not able to have direct influence upon the movement of the teeth of neighboring units.

This type of arrangement of the teeth particularly evident among the Squatinidae and among *Carcharodon carcharias* (Pl. XII, fig. 36-37) is observed equally among a certain number of other requiems **[556]** and especially among the other Isuridae, the Alopiidae and the Carchariidae.

2nd The teeth of one same unit overlays in part those of the neighboring rank in the direction of the commissures, and are themselves in part overlain by the teeth of another adjacent series in the direction of the symphysis.

All the pressure exerted upon a tooth is automatically transmitted partially to the adjacent tooth unit that overlies it in part, and it reacts in the same manner with the other units of the same side.

This disposition of the teeth imbricated as the tiles of a housetop is observed particularly in the lower jaw for the most part in the representatives of the family Squalidae; it is illustrated by the figures 40 to 42 in Plates XIV and XV that show this peculiar disposition and the rocker movement of the teeth assuming their functional position, normally (fig. 40) and abnormally following an unspecified accident (fig.42).

3rd The teeth are more or less clearly arranged in quincunx; there exists generally only a single functional tooth per dental unit. The basal part of the teeth of one same unit is wider than the space separating the extremities of the bases of the two adjacent units: a pressure exerted upon one tooth is in part rebounded upon the teeth of the right and left by means of the extremities of their basal parts.

This disposition illustrated by the figures 39 and 39, PL. XIII, is observed among most of the modern sharks and especially among the Carcharhinidae and the Sphyrnidae.

4th The teeth are very clearly arranged in quincunx forming sort of a pavement or mosaic; a number more or less raised ranks are functional; each tooth is dependent on the ensemble which appears to be displaced in a unit.

This arrangement, characteristic of the requiems of the family Mustelidae (especially *Mustelus),* is the rule among the Hypotremata among which the dental rug is able to be detached entirely upon dried specimens after insufficient fixation.

This disposition is illustrated by the figures 43 to 47 of Plates XV and XVI and by the anomalies of Plates IX and X.

Material examined:

The ensemble of our observations are supported by more than 1,300 selachians jaws (rays and sharks), in the Department of Biology of the IFAN at Gorée.

[557]

The "useful" observations have been made nearly solely upon sharks of average or large size belonging more often to the families Carcharhinidae and Sphyrnidae.

In his 1937 work[4] upon the anomalies of the dentition among sharks, Gudger, in recalling or describing different cases observed upon 20 specimens belonging to 8 species: *Chlamydoselachus anguineus, Heterodontus philippi, Gyropleurodus* sp., and 5 species of Carcharhinidae of which the tiger shark (recalling the case described by Andre and new observations upon three other jaws). A total of 24 abnormal dental units are described. In three cases only, the cause of the anomaly (implantation of a spine of the Dasyatidae in the jaw) has been exactly defined, at first among *Galeocerdo arcticus* (case observed by Andre) and in two cases described among a specimen of *Carcharhinus limbatus* from the Gulf of Aden. In all other cases described, even those with beautiful anomalies that we designate in the following under the name of "anomalies of type 2" (dental units divided into a double rank of half teeth) and represented in particular in figures 11 (*Carcharhinus commersoni*), 13 (*Carcharhinus limbatus*) 15 (*Carcharhinus* sp.) and 19 (*Galeocerdo arcticus*, the actual cause of the anomaly is not apparent and cannot be stated precisely. It is possible that the radiographs of these jaws could show the presence of strange bodies (probably remains of a spine of the Dasyatidae or of other fishes) in the zone of formation of the dental germs.

It is first upon the 50 jaws of tiger sharks (*Galeocerdo arcticus*), that is to say the species upon which W. Andre has made his first authentications, that we have searched for , without success, a dental anomaly comparable to that described.

Although the feeding regimen of this species is extremely varied and includes the elements of a nature to induce the injuries of the deep zones of the jaw, we have not detected the slightest malformation of teeth that which permits one to consider as entirely fortuitous (at least along the coast of Senegal, and upon this species), a case comparable to those observed by Andre and Gudger.

On the contrary we have found the case of dental anomalies:

– among certain selachian hypotremes: Pristidae, Rhinobatidae (*Rhinobatus)* and Dasyatidae (*Taeniura* and *Dasyatis*), for which the cause has not been defined;

[558]

– among several Squalidae (*Centrophorus* and *Lepidorhinus*) probably caused by the wounds due to fish hooks;

– among diverse Carcharhinidae (*Carcharhinus* and *Negaprion*) and especially in a species of the family of the Sphyrnidae, the great hammerhead shark, that we designate here still under the name of *Sphyrna tudes* (sensu Bigelow and Schroeder, 1948).

They are all particularly the observations made upon the jaws of this species that we

[4] Gudger, F. W. Abnormal dentition in sharks (Selachii). *Bull. Amer. Mus. Nat. Hist*., **73**.

analyze below.

They are due in nearly all cases to damage caused by the implantation of foreign bodies in the jaws during the process of nutrition.

As we have indicated previously[5], the feeding regimen of this hammerhead shark along the coast of Senegal is basically fish bearing formidable arms: rays of the families Dasyatidae and Myliobatidae, with a tail armed with barbed spines (in 85% of the stomach contents inventoried), and Siluridae of the genus *Arius* (figuring nearly 24% of the stomach inventories carried out). All of the observations made since 1957 have given exactly comparable results.

The ingestion of these fishes does not go on without some danger of very numerous spines penetrating deeply into the tissues of sharks in particular in the jaws where they remain most often stuck after having been broken.

Not one of the prepared jaws is exempt from such spines and we have succeeded in enumerating up to 72 in a single one.

If the wounds so inflicted do not seem to impede the hammerhead shark and if not one wound is visible when the spine has penetrated into only the muscular masses, it is not the same when the spines proceed to penetrate into the jaws properly where they are able to involve the anomalies more or less imprints on the dentition more especially when there is a lesion in the zone of the formation of dental germs.

We have recently proceeded with a reexamination of the 43 jaws of *Sphyrna tudes* in the collection at Goree, coming from individuals of all sizes, and we have summarized the observations made below:

Jaws of *Sphyrna tudes* examined 43
with spines of Dasyatidae or of *Arius* 43
[559]
without dental anomaly 17
presents at least one dental anomaly 26
upper jaws present at least one dental anomaly . 10
Total of anomalies verified upon the upper jaws. 14
lower jaws present at least one dental anomaly . 21
Total of anomalies verified upon the lower jaws
(2 jaws presenting up to 6 abnormal dental
series) 46

Most of the individuals upon which the anomalies have been verified are from females of average size (between 2.75 m and 3.25 m).

Most of the wounds are made by the spines penetrating from the interior toward the exterior, that is to say while the prey is already in the mouth of the shark. Some spines, however, have penetrated in the jaws from the exterior toward the interior, that is to say when the prey (or at least the wounding part of this one) is still outside of the mouth of the shark.

If this seems rather easily explainable in the case of rays with spines, a satisfactory explanation is much more difficult to find for that which concerns the wounds of this type produced by the spines of *Arius*.

It seems in this case that the sufficient force in order to permit the deep penetration of a

[5] Cadenat, J., 1957, *Bull. IFAN*, **XIX**, A, 1.

spine of *Arius* in the jaw of a hammerhead shark is produced by the shark itself, coming literally impaled by the prey that it desires when it rests upon the bottom and can be at that time considered as a fixed point.

Although *Arius* may be consumed in less greater quantity than *Dasyatis* (we have found up to 17 *Dasyatis margarita* in one same stomach and we have seen that this species appears in more than 80% of the stomachs inventoried, whereas the number of *Arius* recognized in less than 25% of the cases, generally does not exceed 2), the majority of the dental anomalies observed and particular most important, are due to the spines of *Arius*.

This reversal of the proportions is much more apparent than real; it is necessary not to forget in reality that each ray is armed with a single spine whereas each *Arius* bears three of them nearly always much more robust and of a volume very perceptibly more massive than those of *Dasyatis*. The injuries that they cause are more serious, the mass of the tissues penetrated is considerably **[560]** more. Besides being given the form of the two kinds spines, the wounds produced by those of rays can compared to those made with a well rounded probe (section without wrenching of tissues), those due to the spines of *Arius* operate in the manner of a rugose awl causing dilaceration and pulling up of the tissues.

Analysis of the classification of the principal types of dental anomalies observed according to their probable cause

A. A foreign body implanted in the jaw has attained and injured the zone of formation of the dental germs.

This zone is able to have been:

a) completely destroyed. There is a stoppage in the formation of new teeth, the previously formed teeth continue their migration and disappear, **Type 1.**

b) fragmented, generally in 2 parts giving each source a succession of teeth of size and form different from those of the teeth of normal units,
. . . . **Type 2.**

c) amputated in a more or less large fraction, the remaining part gives origin to a single series of smaller teeth of different form from those of the normal units, **Type 3.**

d) superficially injured: it gives then origin to a dental unit with the teeth of nearly normal but presents a slight deformation **Type 4.**

B. The foreign body implanted in the jaw has not injured the zone of formation of the dental germs, the formation of the teeth continues, but their development or their transfer can be constrained more or less considerably by the obstacle that constitutes the foreign body.

This last can be implanted

a) either behind the zone of formation of dental germs in the most internal part of the jaw, or, according to its inclination, it is an impediment to the normal development of the teeth, providing the anomalies of **Type 5.**

[561]

b) or having it in front of the zone of the formation of the dental germs, that is to say in the anterior part of the jaw, where it may constitute a fixed obstacle impeding more or less the progression of the teeth in one or several series.

One can even here establish several cases, according to whether:

1st the obstacle is able to be neither deflected nor surmounted; there is then a crushing of the newly formed teeth against the obstacle, and disappearance of the teeth that are found in front of the obstacle at the moment of its implantation **Type 6.**

2nd the obstacle can be shunned by deflection by the sides **Type 7.**

Or by passing **Type 8.**

All these types of dental anomalies have been discovered upon the jaws of sharks and some on those of some species of rays from the coast of Senegal in the collection at Goree. They are abundantly illustrated by a series of direct photos by the author, and from remarkable radiographs owing to the kindness and the high technicality of Dr. Pineau.

Commentaries relating to the figures in Plates I to XVI.

(The Plates I to VII inclusive refer to the examples observed upon the jaws of *Sphyrna tudes*); those numbered from VIII to XI show some types of anomalies observed concerning several other species of selachians: "Requiems" and "Rays". The Plates XII to XVI illustrate the different types of disposition of the teeth.

Plate I.

Fig. 1. – Middle left of the lower jaw of a large hammerhead shark with normal dentition, viewed from the inside, after removal of the soft tissue.

Fig. 2-3 – Two cases where a ray spine of *Arius* is driven into a jaw of the great hammerhead shark, between two dental units, without provoking the perturbation in the development or the displacement of the teeth (fig. 2., portion of the lower jaw, fig. 3, portion of the upper jaw).

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Fig. 4 – left half viewed from the internal face of the lower jaw of another specimen of the great hammerhead shark showing several abnormal dental units.

Plate II.

Fig. 5-7. – Portion of the lower jaw representing the first type of anomaly considered (Type 1: total absence of a dental unit, the 5th), due probably to the destruction of the zone of formation of dental germs. The teeth already formed at the moment of the accident eventually have been carried along and lost, according to the process described apropos to the explanation of figures 16 and 17. (See also Pl. XXV, fig. 60d).

One observes on the side of the commissure a normal unit and on the side of the symphysis another, abnormality of type 5: the generatrix zone producing normally the teeth that are hindered in their development by a fixed obstacle implanted behind the latter. This obstacle here is constituted by a group of 5 spines (4 of *Arius* and 1 of *Dasyatis*) solidly driven down in the jaw and oriented within the axis of the dental unit, paralleling the anterior edge of the jaw (particularly well visible in figure 7). (See equally

Pl. XXV, fig. 60e.)

Fig. 6-8. – Portion of the lower jaw of *Sphyrna tudes* presenting an anomaly of type 3 preceding on the 7th dental unit a type 1 anomaly, to the side of an anomaly of type 5 presented by the 8th unit. A strong spine of *Arius* (see Pl. XXIV, fig. 59-b) has probably injured the zone of the formation of the dental germs of the 7th unit which since then has given birth to the deformed teeth of reduced dimensions and of which the 3 last are still visible in the direction of the edge of the jaw; subsequently a 2nd spine of *Arius* and one of *Dasyatis* have completely destroyed the remains of the zone of formation of the teeth and all new formation of teeth has ceased.

These broken spines flush with the cartilaginous part of the jaw are not visible in the photos but are clearly visible in the X-ray in Plate XXIV, figure 59-a.

The type 5 anomaly which is affecting the 8th unit is caused by the presence in the zone of appearance of the dental germs another spine of *Arius*.

[563]

Plate III

Fig. 9-11. – Three cases of anomalies of type 2. The spine has divided the formation zone of the dental germs into two parts, each of them continues to produce for its part a unit of half-teeth of variable size and forms, the figures 9 and 11 show for examples one complete unit of two half-teeth nearly similar, differently inclined and perfectly independent, the speed of advancement of each of the half-teeth can be perceptibly different, which is clearly emphasized by the relative position of the oldest half-teeth upon the edge of the jaw (fig. 11). This figure shows, moreover, beside the “units” of half-teeth, an anomaly of type 5 very clearly comparable to that of figures 5 and 7 of Plate II: the formation zone of the tooth germs has not been harmed, it has had a constraint in development but not in displacement of the dental unit: the teeth have been constrained from adopting an abnormal form and inclination.

Upon the photo one sees clearly the fragment of spine of *Arius* cause of this deformation, penetrating the jaw. (See also fig. 15, Pl. V.)

Upon the figure 10, the two half-teeth of the abnormal unit are very different, the ones are short and wide with the cusp strongly inclined, the others long and narrow with a perfectly straight cusp.

Plate IV.

Fig. 12. – Several spines having penetrated into the dental germs have provoked the type 4 anomalies upon 3 neighboring units, for which the teeth are diverse and irregularly deformed.

Fig. 13 – Type 3 anomaly. The generatrix zone has been injured and has produced the teeth of identical form with a regularly shorter cusp than that of normal teeth of neighboring units.

Fig. 14. – Another anomaly of type 4, but here the generatrix zone seems to have been destroyed in a great part, the part remaining produces a unit of deformed teeth , of small size, with cusp and base very straight.

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Plate V.

Fig. 15. – The figure reproduces the anomalies of types 2 and 5 already illustrated by figure 11 of Plate III; it shows moreover in the posterior part of the Meckel's cartilage a zone where one counts no less than 5 spines (*Arius* and *Dasyatis*) more or less deeply penetrating, without having injured the dental zone.

Fig. 16 and 17. – Type 6 anomaly: the generative zone is not affected, it continues to produce teeth normally, but these are arrested in their procession toward the edge of the jaw. In the case represented, a spine of *Arius* piercing completely through the jaw has penetrated a young tooth (at the moment of the accident) and it is literally pinned.

The tooth has been therefore solidly fixed; one can state:

– on the one hand, that the new teeth, in proportion as to their formation, are arising crushed against the bumper formed by the immobilized tooth and its spine of fixation;

– on the other hand, that at the same time, and without undergoing the growth of the younger teeth of the same unit, the upper teeth, that is to say from the more ancient formation, have continued their displacement toward the functional position, the last one has not entirely reached "the shedding zone."

One notices that this last tooth, is in reality represented only by two halves of its single basal part. One can then suppose that the cusp has been destroyed at the moment of the injury having immobilize the tooth following.

One notices moreover that the teeth with lateral unity have been a little have been a little constrained in their movement of progression. In the course of the movement , one of the extremities at the base of these lateral teeth are coming to rest against temporarily upon the opposite extremity of the base of the fixed tooth, and each happened as if a breakage is being exercised upon a single extremity of the base of the tooth, this last has been brought to pivot slightly on the side where it developed resistance. Figure 17 shows well this slight deformation, in the areas of the opposing bands, the teeth of the two units framing that of the immobilized tooth.

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Plate VI.

Fig. 18 to 20. – Type 7 anomaly: The generatrix zone for the teeth is not injured, the teeth are simply obstructed in their displacement by a fixed obstacle, but which can be overflowed laterally.

The figures present at different angles a large spine from *Arius* deeply driven in (from the exterior to the interior) in the jaw between two dental units. In their movement to the front the teeth (by means of one of the lateral extremities of their basal part) are coming to rest against the fixed point of the spine. The resistance to the advancement is exerted on only one side of the teeth, it followed from there a deviation of those until the moment where their degree of inclination toward the original direction of advancement has been rather great in order to permit them to overflow the obstacle border, with a tendency to be put back in a normal plane once the obstacle is cleared.

In short all happened as in the preceding case of the type 6 anomaly represented in Plate V, figures 16 and 17, with only the following differences: a) there has been no complete stopping of the progression of the teeth of one complete dental unit (type 6).

b) The dental units, momentarily deflected, are two contiguous units whereas in the preceding case it moves in two separated one from the other by a third, stopped in its progression toward the edge of the jaw.

Plate VII.

Fig. 21 – This figure represents a case of type 8 anomaly that can be considered as a variant of type 6. We see therein a complete unit of teeth completely deformed, rolled into the form of a horn.

The foreign body (spine of *Arius*) is driven just in front of the generatrix zone and it has probably compressed it probably without injuring it seriously probably obliging it to follow its contour. The teeth formed in these conditions have followed equally the form of the margin of the obstacle.

After a more or less long period of time of stopping the advancing movement, comparable to the case represented by anomaly 6 (P. V, Fig 16 and 17), the obstacle has been able to be surmounted or the portion to surmount had been naturally of slight length at the moment of the accident, or the spine has been **[566]** broken under the increasing pressure of the newly formed teeth.

In this case no trace of deviation in the vicinity of the dental units is apparent. If the time of arrest marked by the dental unit has been rather long in order to provoke a deviation in the unit areas, the moment when the deformed teeth have been able to surmount the obstacle and continue their displacement at a normal speed is already rather old in order that the teeth must have had the time to disappear or take again a normal position.

Fig. 22. – We see a tooth pierced by a foreign body that has been eliminated by the following, either that it has not penetrated rather deeply into the jaw in order to become fixed and constitute a durable obstacle, or that it had been immediately broken. The attacked tooth presents a simple perforation, but it developed practically without any other deformation; furthermore, there has not been repercussions upon the following teeth of the same unit.

The neighboring units each present an anomaly of the type 4 probably without relation with the cause of the perforation.

Plate VIII

The three figures represent a case of the anomaly discovered upon the lower jaws of *Negaprion brevarostris* (3 jaws present anomalies out of 18 in the collection). Among this species we have discovered that the *Dasyatis* figures in 16.6% of the stomach contents inventories and *Arius* in 39.4%.

In one case, an anomaly of the type 2 (fig. 25) has been provoked by a spine of *Dasyatis*; in the two other cases, anomalies of types 3 and 4 (fig. 23 and 24), the anomalies are provoked by the spines of *Arius.* These diverse spines broken at the level of the cartilage are not visible upon the photographs.

Plate IX.

Portions of lower jaws of three specimens of sawfish (*Pristis pectinatus*) show that the lesions provoked probably in the generative zone **[567]** of the teeth have caused an abnormal growth in these several units. As among the requiems, all the teeth of one same unit for which the generative layer has been injured presents the same deformations but continues their displacement at the same speed.

The figure 28 shows, however, that the lesion, deeper , has destroyed the different layers of tissue even in the cartilage itself in such a manner that it causes the separation of the "dental blanket" into distinctive parts showing a clear tendency to move away from one another with anarchistic growth of the teeth nearest to the axis of the wound.

The cause of this anomaly has not been recognized.

Plate X.

Fig. 29. – Jaw of the Rhinobatidae (*Rhinobatus cemiculus*) shows a slight anomaly concerning only one dental unit and probably due to a very superficial lesion to the generatrix layer during the course of feeding (with a base of fish and crustaceans). The teeth of this unit are less wide and less high than the those of the others and their succession is manifested by the formation of a narrow groove.

The figure 31 shows an anomaly of the same type upon a lower jaw of *Dasyatis hastata*: the groove seems deeper by the fact that the teeth of the neighboring units seem themselves elevated in relation to the following dental belts.

Upon the figure 30, which represents the jaw of another species of Dasyatidae (*Taeniura grabata*), we find again much more clearly an anomaly of the same type as that represented in Plate IX, figure 28. There has been destruction to the generatrix layer entailing the total disappearance of at least one dental unit (comparable to the anomaly of the type 1 described among *Sphyrna tudes*).

There has been another deformation of the teeth in the units immediately near by (anomaly of types 3 and 4 observed among the requiems), and distortion of the units formed normally on both sides of the dead zone, under the effect of the rupture in equilibrium of the pressure exerted upon a normal dental belt (tapis). It has not been disclosed to us the cause of this anomaly.

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Plate XI.

Fig. 32. – Upper jaw of *Lepidorhinus squamosus* from Madère completely deformed by a grave wound to the jaw provoked probably by the fish hook of a fisherman.

Fig. 33. – Lower jaw of *Centrophorus granulosus* from Madère showing two neighboring units of teeth clearly cuspidate different from that of the teeth of other units.

Fig. 34. – Lower jaw of *Centrophorus granulosus* from Madère where the teeth of two median units have their cusp directed in an opposite direction from that which they

should have.

Fig. 35. – lower jaw of *Centrophorus granulosus* from Madère presenting two types of anomalies:

1st (a) Anomaly of type 2 (the generatrix layer of the second unit to the left of the symphysis has been divided in 2 parts each giving birth to a half-tooth of different form from those of the normal teeth).

2nd (b) The oldest tooth in the 3rd dental unit to the left of the symphysis is bicuspid while the other teeth of the same unit (of which one is visible in the photo) are normal.

Plate XII.

– Two types of jaws with dental units clearly separated from one another, independent: the pressure exerted upon the teeth of the one is not transmitted directly to the teeth of nearby units.

Fig. 36. – *Squatina aculeata,* upper jaw.

Fig. 37. – *Carcharodon carcharias*, upper and lower jaws.

Plate XIII.

– Two types of jaws with teeth disposed in quincunx: the width of the base of the teeth in one unit is greater than the space separating the teeth in lateral units: the pressure that is exerted upon the teeth in one of these units is rebounded upon those of the neighboring units, and equally distributed on each side.

Fig. 38. – *Carcharhinus leucas*, upper jaw.

Fig. 39. – *Carcharhinus limbatus*, upper jaw.

[569]

Plate XIV.

Jaws of Squalidae (*Centrophorus*) showing the teeth disposed in very condensed units becoming covered in part as in imbricated tiles; the pressures exerting upon the teeth of a dental unit are transmitted to those of only one of the close units (this situated on the side of the symphysis), of which the teeth cover in part those of the unit considered initially. The figure 40 shows the teeth of a group of a nearby unit making their movement following a normal curve.

Plate XV.

Fig. 42. – Lower jaw of a *Centrophorus granulosus* from Madère showing the movement of straightening of the teeth of the same generation belonging to a group of neighboring units, following an abnormal curve, for an imprecise cause.

Fig. 43-44. – Two types of dentition “in mosaic.” Fig. 43 among *Pteromylaeus bovina*; one notices traces of wear provoked by the crushing of particularly resistant foods (mollusks, and shells inhabited by hermit crabs).

Fig. 44: among *Rhinoptera marginata.*

Plate XVI.

Three types of teeth disposed in quincunx and forming veritable "dental carpet."

Fig. 45 among a requiem: *Mustelus canis*.

Fig. 46 and 47, among a ray: *Taeniura grabata* with very clear dental sexual dimorphism (fig. 46: adult male; fig. 47: adult female).

SECOND PART

In the first part of these Notes, we have recalled the different stages in the formation in the selachians just as they rise from the histological studies that have been made of them.

The radiographic and photographic documents that we publish in this second part place in evidence this formation from dental germs in the basin-shaped valleys or separated alveoli, **[570]** situated in the deep zone of the jaws, and the continued growth of the teeth proceeding regularly during the whole time of their movement until the moment of their shedding.

They in addition help to understand in what manner it occurs, after a certain of functioning, the phenomenon of their disappearance of their replacement.

In 1936-1938, P. Budker studied and described a phenomenon of the destruction of certain dermal spicules in selachians following a process exactly inverse to that of the formation of teeth.[6]

He wanted to see a demonstration of a more general phenomenon and believed to be able to extend it to the teeth of the jaws his conclusions concerning the spicules.

He based it particularly upon his observation of the teeth of *Carcharias (Odontaspis)* of which the basal part is more or less developed, in truth totally absent, and which he considers as the successive stages of destruction.

This opinion is still expressed today under the pen of L. Bertin (after Budker) in the Traité de Zoologie published under the direction of P. Grassé (t. XIII, 1958, fasc. I, p. 521).

He has written: "the disappearance of the teeth after a certain time of functioning is not simply a phenomenon of use, but a necrosis comparable to that of the cutaneous denticles. Budker (1938) has verified it among a great number of species. The destruction proceeds from the root of the basal plate up to the extremity (fig. 324, p. 520). it takes place tooth after tooth and not simultaneously for all the teeth of one same longitudinal rank."

In our opinion this point of view is erroneous and the phenomenon of the disappearance of the teeth among the sharks is totally different from that which has been described for the spicules.

It is evident first of all that the teeth of *Carcharias* having caused the error of interpretation, have not been retained "in place" upon the edge of the jaw where they ought to be found for a duration of a more or less long time of functioning. It is a question of teeth not belonging all to the same dental unit and of very different generations coming from all levels of the jaw.

Besides there exists fundamental differences between the **[571]** phenomena of

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[6] P. Budker. 1936. Upon an osteoclast determining the falling out of placoid scales or cutaneous teeth of sharks. *C. R. Acad. Sciences, Paris*, **202**, 1936, p.505-507

P. Budker. 1938. Sensory crypts and cutaneous denticles of the Plagiostomes. Thesis, Masson et Cie edit, Paris.

disappearance and of replacement of dermal spicules and of the teeth.

The primary of these fundamental differences is that spicules originate, grow, are destroyed, and replaced from a fixed position. There is on the contrary a migration of the teeth in the course of their development. The place where the destruction of the spicule occurs, according to osteoclastic processes, is the same as that which has seen its birth and the same equally as that where it will form later on the germ of the replacement spicule. For the teeth a more or less great distance always separates the points where the teeth are becoming functional and are near to their disappearance.

It seems besides that the phenomenon of destruction and the replacement of the spicules are very limited in time and are produced in reality only among the individuals not yet having attained their sexual maturity. It is characterized by the fact that the replacement spicules have a different form (sometimes rather perceptible) from that of the spicules of the previous generation.

Concerning the teeth, it seems well by contrast that the formation of new generations are pursued during all the existence of the shark and that, apart from some few exceptions moreover still poorly known[7], all the teeth come from one same dental unit conserving practically the same form.

There exists finally one other difference between the spicules and the teeth, a nature difference to make more obvious the one of the mechanism of replacement of the spicules on the one hand, the teeth on the other: the functional role of the spicules is limited to the protection of the animal; they occupy always the same position with relation to the skin; no force is exerted normally on them being able to involve their fall or their wrenching.

The teeth have on the contrary an important alimentary function, they can be grinders, cutters, adapted for catching hold. They are likewise driven by a slow and continuous movement; their degree of inclination upon the edge of the jaw is variable; in that case, always pushed by the more juvenile teeth of their dental unit, they **[572]** have taken a position of a "false door" upon the extreme edge of the jaw, it is easy to understand the importance which the succession of the "forces" can have then exerted upon these teeth each time that the animal grasps sections or grinds it food and that this is in consequence, the feeding even of the shark that is the principal cause of the dropping of its teeth.

At the moment of their drop these teeth are always completely formed and perfectly sound.

We have proceeded to examine more than 1,300 jaws belonging to the majority types of selachians, more particularly west African.

We have made numerous sections at all the levels in the numerous jaws belonging to a dozen different species of sharks.

We have examined finally a certain number of radiographs of the jaws of the following species: *Carcharias taurus, Isurus oxyrhynchus, Ginglymostoma cirratum, Galeocerdo arcticus, Hypoprion bigelowi, Galeorhinus laevis, Carcharhinus limbatus, Sphyrna tudes, Centrophorus granulosus.*

We have each time been able to prove the processes of generation from birth and to

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[7]Sexual dimorphism has been noted in the teeth of some *Deania* in particular, dimorphism manifested only from the premier sexual maturity. It has equally been noted that the teeth of the term fetus of *Carcharias* is deprived of denticles at their base. One has observed also that among certain Carcharhinidae (*Prionace* notably), the teeth of young individuals are little different from those of adults.

definitive formation of the teeth, that they are "full" or that they remain "hollow", always the same since the appearance of the enamel at the extremity of the cusp (at the level of the formation zone of the dental germs) until it arrived in a functional position upon the edge of the jaws and to its final disappearance.

The illustrations of Plates XVII to XXV are particularly instructive in this regard. We have on the contrary never observed the least case of necrosis and never the least trace of destruction upon the teeth of the functional ranks, with the exception of some very rare teeth accidentally broken, or for those presenting the traces of use as one is able to observe among several grinder species such as *Mustelus, Ginglymostoma* among the sharks among the hypotreme families Rhinobatidae, Myliobatidae and Rhinopteridae.

That they are dental units in place (and we have observed more than 50,000 upon more than 1,300 jaws), that they are sections, that they are X-rays, one [of them] has never allowed us to find any tooth from any level of the jaw that is in a more advanced state of construction than the older teeth of the generation (that is to say closer to the edge of the jaw), or a less advanced state of construction **[573]** than the teeth of the younger generation (that is to say nearer the zone of formation of the dental germs).

These series of considerations has led us to consider that among the sharks the dropping of the teeth is not due to a necrosis and cannot be compared to the particularly well studied phenomenon of the destruction and replacement of the dermal spicules, and that happens “in a fixed position,” but that it is simply the result diverse combined actions exerted upon the elements in movement, the principles of these actions are of purely mechanical order.

It is indeed not easy to follow the phenomenon of crossing and of replacement of the teeth among the sharks, in order to demonstrate the experimental cogency of our point of view.

We however could make a particularly interesting observation personally showing well that teeth, after they fall, are always as solidly constituted as the functional teeth (and others) in place.

It is at Gorée, the 23-XII-1955, that we have captured a gravid female of *Carcharias taurus* bearing still its two young (one on each side), each of which measured 1.10 m in total length. These young, for which the teeth have attained upon the jaws the functional position, present the characteristic denticles of the species on both sides at the base of the cusp, have, however, already lost those anterior generations deprived of denticles. We have found several of these lost teeth in the uterine pouches of the mother. They all have the roots particularly well developed, compact, of uniform density, does not present the least trace of decay, necrosis or other indication of any process of destruction (P. XXVI, fig. 61), (See also Cadenat, 1956, p. 1255, fig. 3).

This sole observation seems to us of a nature to confirm our conclusions issuing from our research upon the dried jaws.

Relative remarks on the figures of plates XVII to XXVI

Plate XVII.

Section in a jaw of *Carcharhinus.*

In this particular case (as in the other sections moreover), all the first outlines of the teeth of the **[574]** last generations, which are extremely fragile, have been destroyed during the operations of preparation of the sections, it is even so of the X-rays in Plates XXIII (fig. 57), XXIV, and XXV, done after the specimens upon which the connective tissue constitutes the internal part of the "gums" have been removed, not without provoking some destruction of the teeth of the last generations. On the contrary the X-rays in Plates XX, XXI, and XXII upon which this removal of the fibrous tissue has not been done, showing the dental units in all their integrity.

Fig. 48 – Longitudinal section of a dental unit showing the series of successive tooth generations, more and more "formed" in proportion as it goes away from the zone appearance in the dental germs. The enamel cap grows longer, the pulp cavity reduces in volume at the same time as it thickens the deposition of pseudo and orthodentine and as it appears and develops the basal plaque or "root."

Fig. 49. – A slightly oblique section enlarged, at the level of the dental germs zones, showing the first rough shapes of the teeth in four contiguous "alveoli." The section being oblique one notes that the wall of separation of the alveoli is so much less thick and solid as one goes away from the base of these alveoli and as a consequence one approaches the edge of the jaw. This is so because the first septum to the right presents a median part constituted of compact cartilage, the average septum is practically constituted only by a dense fibrous connective tissue, but remains still united to the wall of the jaw; the septum more to the left (at a level approaching more the edge of the jaw), without the least trace of cartilaginous tissue, is already practically no longer united to the external wall of the jaw. At this level the rough shaping of the teeth are still widely separated the one from the other, it is a question in effect only of the terminal part (the point) of the teeth, the formation takes place from the point toward the basal part. Little by little the basal parts are developed, the total width becomes greater than the space separating the bases of the teeth of two contiguous series, in order to result in the quincunx disposition illustrated in Plate XIII. (The section is carried out following a plan that would pass almost by the line X, Y, of the figure 48.)

[575]

Plate XVIII.

Longitudinal sections follow the median axis of the dental units showing clearly the elongation and the progressive thickening of the sides of the cusp and the subsequent appearance among the two species with "hollow" teeth.

Fig. 50 and 51. – *Carcharhinus limbatus*

Fig. 52. – *Galeocerdo arcticus*

Plate XIX.

Fig. 53. – Transverse section at the level of the median plane, of one dental unit of a jaw of *Carcharhinus limbatus*. In addition to the particularly clear progressive formation of the teeth, we have already remarked upon the preceding figures (48 to 52), one sees a thin plate of connective tissue on the internal part of the jaw, inserted under the preterminal tooth of the unit in order to add probably a supplementary force to the thrust exerted already upon its base, and contributes to in particular to the rotation and erection of this tooth into a functional position upon the edge of the jaw.

Plate XX.

Fig. 54. – Radiograph in natural size of the right jaw, in internal view of a *Carcharhinus limbatus*, with functional said “hollow” teeth, showing in a particularly clear manner the process of formation of the teeth in the different dental units, the extremity of the point appears at once with gradual development of the external layer of enamel, then formation of the pseudo internal tissues and orthodentine, appearance finally of the basal part.

The successive alveoli where appears the dental germs are particularly very visible upon the Meckel’s cartilage.

Plate XXI.

Enlargement of a part of the preceding X-ray (upper jaw) showing in a particular manner the functional “hollow” teeth at the basal part **[576]** uniformly opaque with the exception of the median furrow where opens the central foramen through which penetrates the nutritive vessels.

Plate XXII.

Fig. 56 – Radiograph of a portion of a jaw of *Galeocerdo arcticus*, another species with “hollow” teeth, showing so clearly the process of formation of the teeth and the succession of the alveoli, vaults of the tooth germs.

Plate XXIII.

Radiograph magnifying the isolated dental units of the two jaws of sharks with “filled” teeth.

Fig. 57. – *Isurus oxyrhynchus*, upper jaw, 1st unit to the left of the symphysis.

Fig. 58. – *Carcharias (Odontaspis) taurus* 6th unit to the right.

One sees very clearly that the most internal teeth, that is to say the youngest generations, are still hollow, limited to a sheath of enamel lengthened little by little and of which the partitions double themselves in a layer of pseudodentine while the cavity is filled by a mass of osteodentine at the same time that it forms the basal part to which it finally unites.

The teeth brought to the edge of the jaw have the roots (basal part), uniformly opaque never presenting a trace of destruction.

Plate XXIV.

Fig. 59. – Radiograph of the lower left half jaw, in internal view, of a great hammerhead shark (species with “hollow” teeth, showing always the same process of formation and growth of the teeth, and in addition a certain number of spines of the Dasyatidae and of the Siluridae implanted in the jaw having provoked diverse types of dental anomalies described and figured (photos) in the first part of these Notes.

a) Remains of spines having destroyed the zone of formation of germs of dental units (type 1 anomaly): the teeth already formed and still in the course of migration will

present [577] anteriorly an anomaly of type 3 provoked by the spine b. (See photos Pl. II, fig. 6 and 8).
b), c) Broken spines having provoked the anomalies of types 3 and 5 (See photos Pl. II, fig. 6 and 8).
d) Simple arrest by bony fish implants in front of the zone of formation of dental buds and not having involved the anomaly.

Plate XXV.

Radiograph of the lower right half jaw, in internal view of the same hammerhead shark, presenting the same characteristics of the other half.
a) spine implanted between 2 dental units for which it constrains the displacement (anomaly no. 7, photos Pl. VI, fig. 18 to 20).
b) Spine implanted between 2 dental units at the level of the zone of formation of the germs but without injury to the latter and having provoked not one anomaly (photo Pl. VI, fig. 18).
c) Remains of a spine not having provoked any deformation.
d) Remains of a spine having completely destroyed the zone of formation of the dental germs and having provoked the stoppage of the formation of new teeth at a time sufficient for those formed anteriorly to the accident having already ended their migration and their period of functional activity (photos Pl. II, fig. 5 and 7). Anomaly of the type 1.
e) A number of spines of *Arius* and of *Dasyatis* not having injured the zone of formation of dental germs, but having constrained the normal development of teeth: anomaly of type 5 (photos Pl. II, fig. 5 and 7).

Plate XXVI.

Teeth of *Carcharias (Odontaspis) taurus*.
Fig. 61. – Four very thick teeth all of the first generations, without basal denticles, lost before it gave birth and found in the uterine pouches of the mother.
Fig. 62. – Two functional teeth from the mother with basal denticles.
In the two cases the roots (basal part) present not one trace of necrosis or indication of destruction of any sort.

[578]

SUMMARY

The examination of an important collection of selachian jaws has permitted us to establish a certain number of cases of dental anomalies more especially among the great hammerhead sharks *Sphyrna tudes*.

A classification essay of these abnormalities after their probable causes is attempted.

The observation of the causes fully explains the different types of anomalies encountered, placing in evidence the movement of displacement of the teeth from their point of formation toward their functional position, emphasizing the importance of the forces of pushing that are exerted upon each dental unit and their effects upon the movement of other dental units.

Furthermore the examination of a series of photographs of macroscopic sections and of radiographs competes the illustration, making it become clearly evident the process of formation and the crossing of the teeth commencing with the cusp (enamel) continuing by the formation of the filling of the dentine, the basal part appearing only last. This process is constantly even, and we never observed inverse phenomenon of destruction as that produces itself for the spicules with the young Sharks for example, before the replacement of the premier form by spicules of definitive form.
Two of the X-rays complete moreover the specific documentation relating to the injuries of the jaw and to their consequences.

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