ANALYSIS OF DENTAL INSERTION ANGLES
IN THE SAND TIGER SHARK, *CARCHARIAS TAURUS*
(CHONDRICHTHYES: LAMNIFORMES)

by

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ABSTRACT.!-!Differences in insertion angles of each tooth type of *Carcharias taurus* are described and analyzed within a functional framework. Upper anterior teeth show a more pronounced inward inclination than upper lateral and lower anterior ones that would be related to initial puncturing of prey. Lower anterior teeth have an outward inclination, probably related to a function of initial prey grasping by these teeth while the upper anteriors puncture prey. The upper lateral teeth are more inclined than the lower lateral. Upper and lower lateral teeth would be adapted to hold prey. A ventral inclination of the anterior part of the palatoquadrate is present in *C.!taurus*, and it is likely to facilitate the puncturing work of the upper anterior and to enhance the patchiness of these teeth. We also report some dental anomalies such as intermediate tooth reversal, reduced first and second lower anterior teeth, presence of hook-like anterior and lateral teeth, and the absence of a lower lateral tooth. These latter two anomalies are described for the first time in *C.!taurus*. Our results agree with previously published interpretations based on tooth shape. The results here presented can be considered as a working hypothesis for future experimental research.

RÉSUMÉ.!-!Analyse des angles d'insertion des dents chez le requin taureau, *Carcharias taurus* (Chondrichthyes!: Lamniformes).
        Les différences entre les angles d'insertion de chaque type de dents de *Carcharias taurus* sont décrites et analysées dans une perspective fonctionnelle. Les dents antérieures supérieures montrent une inclinaison vers l'intérieur plus prononcée que celle des dents latérales supérieures ainsi que celle des dents antérieures inférieures. Ceci pourrait être lié à leur capacité de perforer la proie. Les dents antérieures inférieures ont une inclinaison vers l'extérieur liée probablement à leur fonction initiale de saisie de la proie. Les dents latérales supérieures sont plus inclinées que les dents latérales inférieures. Les deux types de dents seraient adaptés à la rétention des proies. Il existe une inclinaison ventrale dans la région antérieure du palatocarré de *C.!taurus*, qui facilite le travail de perforation des dents antérieures supérieures et augmente leur irrégularité. Quelques anomalies dentaires ont été également observées: réversion des dents intermédiaires, réduction des première et seconde dents antérieures inférieures, présence de dents latérales et de dents antérieures en forme de crochet et absence d'une dent latérale inférieure. Ces deux dernières anomalies sont décrites pour la première fois chez le *C.!taurus*. Nos résultats s'accordent avec les interprétations publiées par d'autres auteurs, fondées sur l'aspect des dents. Ces résultats peuvent être considérés comme hypothèse de travail pour une recherche expérimentale prochaine.

Key!words.!- Elasmobranchii - *Carcharias taurus* - Teeth - Morphology - Feeding - Mechanics.

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Several studies have shown the relationship between tooth shape and function in elasmobranchs. Piscivorous forms have narrow and long teeth, while species that prey on marine mammals and reptiles have large, serrated teeth. Elasmobranchs that feed on crabs, molluscs and other hard-shelled organisms have pavement-like dentitions (Budker, 1971; Lagler *et al.*, 1977; Cailliet *et al.*, 1986; Tricas *et al.*, 1997). However, these generalisations have some exceptions. For example the narrownose smoothhound shark, *Mustelus schmitti* (Carcharhiniformes), has a pavement-like dentition but fish is an important prey item of its diet (Menni *et al.*, 1986).

Teeth with different shape and/or size play different roles during prey catching and handling in elasmobranchs (Applegate, 1965). For instance, in species with heterodonty such as the horn sharks *Heterodontus* spp. (Heterodontiformes) and the bonnethead shark *Sphyrna tiburo* (Carcharhiniformes), anterior teeth are sharp and efficient in grasping food, while posterior teeth are molariform and crush the food (Tricas *et al.*, 1997). Some authors have also acknowledged the importance of Dental Insertion Angles (DIA), an angle between the long axis of a jaw and the axis of a tooth, in elasmobranchs. For example, Frazzetta (1988) studied the biomechanics of serrated and smooth-edged shark teeth and found a relationship between the DIA and the cutting capability of teeth. Kajiura and Tricas (1996) described a reproduction-linked seasonal change of DIA in the Atlantic stingray, *Dasyatis sabina* (Rajiformes).

The sand tiger shark, *Carcharias taurus*, is a common shark found in warm temperate coastal waters of both sides of the Atlantic, Mediterranean, Red Sea, western Indian Ocean, western Pacific, and southern Australia (Compagno, 1984; Last and Stevens, 1994). It feeds primarily on small to medium-sized fishes (Compagno, 1984; Sauer and Smale, 1991; Lucifora *et al.*, 1999). The dentition of the sand tiger shark consists mainly of narrow, long, and large teeth well suited for prey grasping (Bigelow and Schroeder, 1948; Springer, 1961).

The aims of this paper are: (1) to describe and quantitatively analyse DIAs of the sand tiger shark; (2) to compare our functional interpretations of DIA analysis with the previously published hypothesis of differential use of teeth based on tooth shape (Applegate, 1965); and (3) to describe some dental anomalies (=!deformed teeth) in *C.!taurus*.

MATERIAL AND METHODS

For practical purposes, we use a tooth type nomenclature similar to that proposed by Applegate (1965) (Fig.!1), although it may not reflect homologies among teeth of different species (Shimada, 1999). In this study we examined 15 randomly sampled jaw specimens of *Carcharias taurus* from the Province of Buenos Aires coast (~!36°S to ~!41°S, Argentina); samples are kept by the senior author. The jaws were obtained from commercial fishermen and they were already excised from the shark when available to us. Then, size of sharks could not be measured. However, crown height of the second lower anterior tooth (La2) ranged from 15.5 to 29!mm, which corresponds to sharks measuring between 143 and 281!cm in total length (TL), according to the regression equation presented by Shimada (1999) (i.e., TL!(cm)!=!10.189 x La2 (mm) - 14.28).

All measurements were taken from the left side. The DIA for each tooth were defined as the angle between the long axis parallel to the ventral border of the palatoquadrate and an imaginary line running through the tip of the tooth and the midpoint of the tooth base (Fig.!2). DIAs were measured with a pair of compasses and translated to paper by imposing the compasses on the paper and drawing a short line on the compasses'arms. The DIA was completely drawn by continuing and intercepting the lines on the paper. A right-angled triangle including
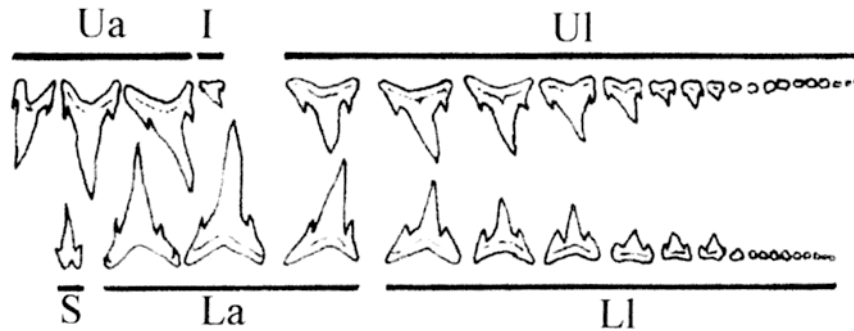
Fig.!1.!-!Tooth types of the sand tiger shark, *Carcharias taurus*. Ua: upper anterior; I: intermediate; Ul:!upper lateral; S: symphyseal; La: lower anterior; Ll: lower lateral. Tooth nomenclature modified from Applegate (1965); illustration modified from Compagno (1984). Not to scale.

the DIA was then constructed, and the DIA value was obtained from the triangle by trigonometric calculus. The right-angled triangle's leg adjacent to the DIA was fixed at 5!cm. We also experimented with different leg lengths (e.g., 10 and 15!cm), but the differences in calculated DIA were always less than 0.06%. Thus, we assumed that there was no bias related to triangle size in measuring the DIA. Obtuse angle measurements were obtained by substracting the supplementary angle value of the DIA to 180°. DIAs from lower teeth were measured in the same manner but with regard to an axis parallel to the dorsal border of the Meckel's cartilage.

We could not take some measurements from some specimens due to the absence or breakage of some teeth. Also, anomalous teeth were not used in measurements of DIAs. However, the sample size was always higher than ten.

By using the one-tailed Wilcoxon paired rank test (Zar, 1984), we statistically evaluated the differences in DIAs for the following pairs of teeth: First Upper Anterior (Ua1) *vs*. First Lower Anterior (La1), Second Upper Anterior (Ua2) *vs*. Second Lower Anterior (La2), Third Upper Anterior (Ua3) *vs*. Third Lower Anterior (La3), Ua1 *vs*. First Upper Lateral (Ul1), Ua2 *vs*. Second Upper Lateral (Ul2), Ua3 *vs*. Third Upper Lateral (Ul3), Ul1 *vs*. First Lower Lateral (Ll1), Ul2 *vs*. Second Lower Lateral (Ll2), and Ul3 *vs*. Third Lower Lateral (Ll3). The null hypotheses were that there are no differences in DIA between each tooth type compared. The alternative hypotheses were that the first-mentioned tooth type in each comparison has a lower value of DIA than the second-mentioned tooth type.

The angle of the Ventral Inclination of the anterior part of the Palatoquadrate (VIP) was measured and its value calculated just like obtuse DIAs. The mean VIP was compared with the value of 180° (=!no inclination) using the one-tailed Student's t test (Zar, 1984). The null hypothesis was that the inclination of the anterior part of the palatoquadrate does not differ from 180° (i.e., VIP does not occur). The alternative hypothesis was that the anterior part of the palatoquadrate has an angle less than 180°.

All jaws were examined seeking dental anomalies. A non-normal tooth was considered to be anomalous when the entire row (i.e., functional and replacement teeth) had the same deformity.
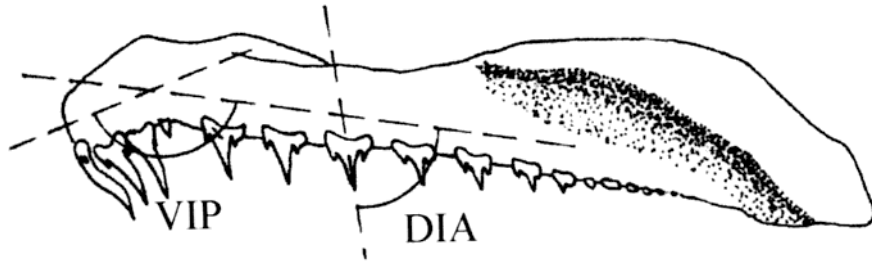
Fig. 2. - Left view of palatoquadrate of sand tiger shark *Carcharias taurus*. Dashed lines show Dental Insertion Angle (DIA) of third upper lateral tooth, and Ventral Inclination of the Palatoquadrate (VIP). Not to scale.

RESULTS

Mean DIAs for each tooth type were as follows (mean ± standard deviation in decimal scale): $Ua1 = 49.05° \pm 18.05°$, $Ua2 = 39.98° \pm 16.99°$, $Ua3 = 35.83° \pm 13.84°$, $La1 = 97.04° \pm 18.17°$, $La2 = 88.85° \pm 16.52°$, $La3 = 79.70° \pm 16.79°$, $Ul1 = 47.01° \pm 11.58°$, $Ul2 = 54.30° \pm 10.10°$, $Ul3 = 58.65° \pm 7.56°$, $Ll1 = 89.83° \pm 0.62°$, $Ll2 = 87.64° \pm 4.68°$, and $Ll3 = 83.52° \pm 6.80°$. Statistically significant differences were found in all comparisons except for the comparison between the Ua1 and Ul1 (Table I).

The VIP ranges between 122°41' and 154°14' and was significantly less than 180° (Student's t test, $t = 4.131$, $p < 0.001$, $d.f. = 13$).

Four kinds of dental anomalies were observed: 1) intermediate tooth reversal, an opposite orientation of the tooth tip with regard to the neighbouring teeth, $n = 2$ (Fig. 3A); 2) sharp inward hook-like curvature of teeth, $n = 2$ (Fig. 3B); 3) anterior teeth reduced in size, $n = 1$ (Fig. 3C); 4) absence of a lower lateral tooth (Ll3) which leaves an empty space, $n = 1$, this anomaly was associated to a hook-like Ll2 (Fig. 3D).

Table I. - Comparisons of dental insertion angles between different teeth of *Carcharias taurus* using the one-tailed paired Wilcoxon rank test. $T_+ = $ test statistic. For null and alternative hypotheses see text. For abbreviations see figure 1.

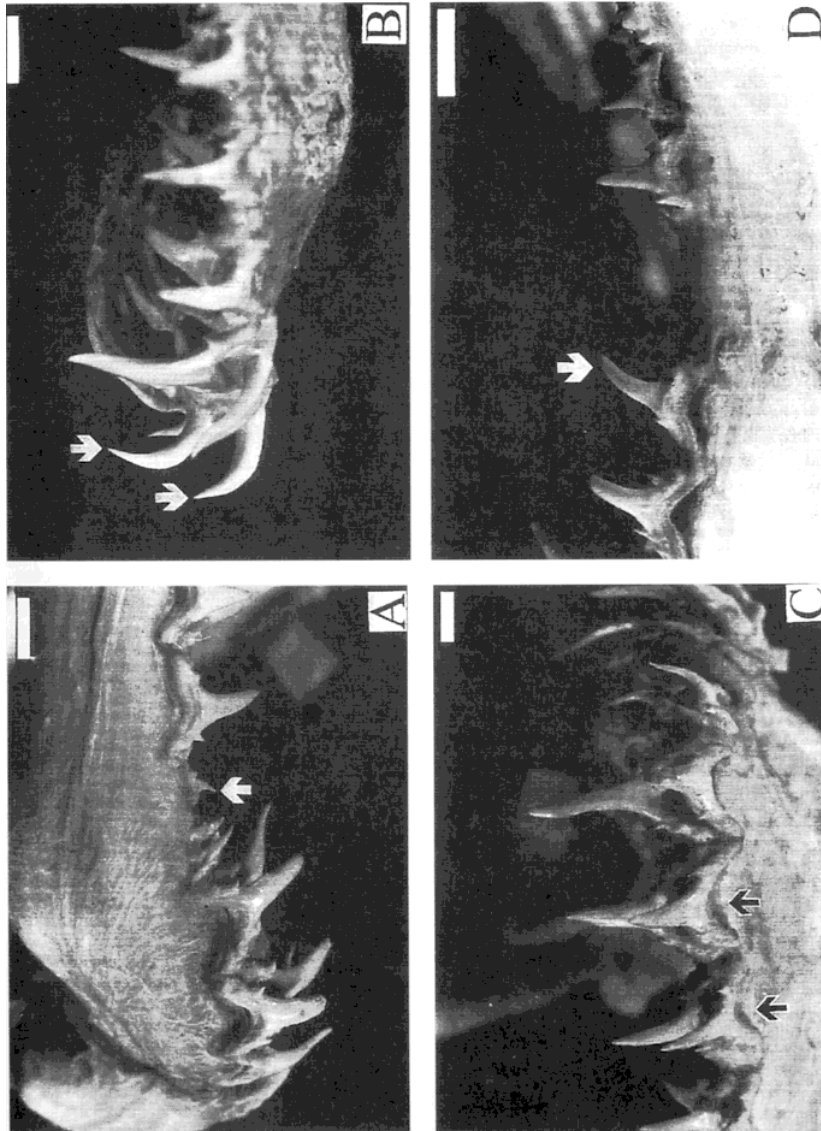| Comparison	Value of T+	Sample size	Significance level
Ua1 vs La1	0	13	p < 0.0005
Ua2 vs La2	0	15	p < 0.0005
Ua3 vs La3	1	14	p < 0.0005
Ua1 vs Ul1	69	14	p > 0.0500
Ua2 vs Ul2	6	13	p < 0.0025
Ua3 vs Ul3	3	14	p < 0.0005
Ul1 vs Ll1	0	12	p < 0.0005
Ul2 vs Ll2	0	10	p < 0.0025
Ul3 vs Ll3	0	13	p < 0.0005

Fig.!3.!:!Dental anomalies of sand tiger sharks, *Carcharias taurus*, from the SW Atlantic. Scale bars!=!1cm. **A**: Reversed left intermediate tooth (arrow). **B**:!Hook-like lower anterior teeth (arrows). **C**: Reduced lower anterior teeth (arrows). **D**: Hook-like lower lateral tooth (arrow) followed by an empty space.

DISCUSSION

The results of our DIA analysis are in accordance with Applegate's (1965) tooth-shape-based findings in that different tooth types may play different roles. Ua teeth have a sharper DIA than lower anterior ones. This difference produces the La being procumbent (Frazzetta, 1994) and the Ua being pointed inward. Consequently, the Ua may be useful in the initial stabbing of prey (Applegate, 1965; Shimada, 1997), and in preventing prey to escape. La teeth would mainly grasp prey. This grasping function of lower anterior teeth has been observed in the lemon shark *Negaprion brevirostris* (Carcharhiniformes) (Frazzetta and Prange, 1987). In *N.!brevirostris*, upper teeth play an important role in prey manipulation while lower teeth hold prey (Frazzetta and Prange, 1987). These tooth functions are aided by palatoquadrate protrusion which allows to expose the upper anterior and to puncture prey better (Moss, 1972; Tricas and McCosker, 1984; Frazzetta and Prange, 1987; Motta *et al.*, 1997).

Sadowsky (1970) noted a greater inclination of the Ua compared to that of the Ul in embryos of *Carcharias taurus*. We propose that Ul teeth may help to hold prey after anterior teeth punctured them. A similar difference in the DIA between Ua and Ul teeth in a dried jaw of a porbeagle shark, *Lamna nasus* and in published photographs (Samper, 1979) of the short-fin mako, *Isurus oxyrinchus* (Lamniformes) was observed. *C.!taurus*, *L.!nasus* and *I.!oxyrinchus*, have similar adult dentitions (narrow, long, large teeth) and are mainly piscivorous (Compagno, 1984). However, Ul of *I.!oxyrinchus* seem to have a cutting function because this species may feed occasionally on larger prey (e.g., marine mammals) compared to *C.!taurus* (see Compagno, 1984, and Cliff *et al.*, 1990 for feeding data of *I.!oxyrinchus*; Sauer and Smale, 1991, and Lucifora *et al.*, 1999 for diet of *C.!taurus*). Thus, the Ul in *C.!taurus* are more likely to have a holding function rather than a cutting one. A triangular shape of "upper lateral" was observed in *C.!taurus* embryos (Gilmore *et al.*, 1983) suggesting a cutting function of these teeth during the adelphophagic (i.e., cannibalistic) embryonic phase. The "upper lateral" become narrower and longer when embryos leave the adelphophagic phase and enter the oophagic (i.e., oocyte consuming) phase of embryonic development (Gilmore *et al.*, 1983; Gomes and Fernandes dos Reis, 1990).

Inward transport of prey may be carried out by hydraulic mechanisms and teeth would be less important in transport as observed in several sharks as in other aquatic vertebrates (Reilly and Lauder, 1990; Motta *et al.*, 1997; Wilga and Motta, 1998).

The shape of the palatoquadrate and of Meckel's cartilage as well as the position of the hyomandibular, allow variation in feeding mechanisms among elasmobranchs (Tricas, 1985). In *C.!taurus*, the VIP accentuates the inward inclination of the Ul. Functionally, the VIP helps the Ua in puncturing of prey and accentuates the distinctiveness of the Ua aided by adjacent, small intermediate and symphysial teeth (Applegate, 1965). These postulated functions of the VIP are strongly related to the ability of jaw protrusion of a species (see Waller and Baranes, 1991). Although the protrusion ability of *C.!taurus* remains to be experimentally tested, it seems to be high based on observations of fresh specimens (L.O.L., pers. obs.).

A dental differentiation similar to that of *C.!taurus* may occur in the angel sharks *Squatina* spp. (Squatiniformes) (Cadenat, 1962). In the angular angel shark, *Squatina guggenheim*, the anteriorly located upper teeth occur in a patch (L.O.L., pers. obs.). The three first upper teeth of each half of the palatoquadrate are much closer to each other than to the posteriorly located teeth. Another similarity between teeth of *C.!taurus* and *S.!guggenheim* is that the tips of anterior teeth are inclined outward (Applegate, 1965; Frazzetta, 1988). An extensive palatoquadrate protrusion occurs in the Pacific angel shark, *Squatina californica* (Fouts

and Nelson, 1999). Main food items of both *C.!taurus* and *S.!guggenheim* are fishes (Cousseau, 1973; Sauer and Smale, 1991; Lucifora *et al.*, 1999) and this may help to explain, at least in part, the described similarities.

Teeth are usually the only fossil remains for elasmobranchs. Thus, most fossil species are described on the basis of their teeth, including extinct *Carcharias* (e.g., Long, 1992). Knowledge of the range of variation (including anomalies) in teeth are useful to correctly identify fossil and extant elasmobranch species (Shimada, 1997). Among the dental anomalies found in this study are two cases of intermediate tooth reversal (Fig.!3A). Tooth reversal is known in the Pacific sleeper shark *Somniosus pacificus* (Dalatiiformes), the smooth hammerhead shark *Sphyrna zygaena*, the school shark *Galeorhinus galeus* (Compagno, 1967), and the night shark *Carcharhinus signatus* (Carcharhiniformes) (Raschi *et al.*, 1982). Within Lamniformes, anomalous tooth reversal has been reported from embryos of *C!taurus* (Gomes and Fernandes dos Reis, 1990). Intermediate tooth reversal usually occurs in the great white shark *Carcharodon carcharias* (Applegate and Espinosa-Arrubarrena, 1996; Hubbell, 1996).

Our observation on size-reduction in the La in *C.!taurus* (Fig.!3C) is based on the dental homologies established by Shimada (1999). On the basis of their shape, these two reduced La could be interpreted as two Ll replacing the last two La. However, Shimada (1999) states that in extant lamniform sharks tooth types can not be identified on the basis of their shape or size and that tooth homologies can be determined based on the topographic correspondence among teeth. The main character used to recognise dental homologies is the position of the teeth in relation to the inflated hollow dental bulla, which supports the symphysial, anterior, and intermediate teeth in most macrophagous lamniforms (Shimada, 1999). We observed that the two reduced teeth are supported by the dental bulla. Then, it is more parsimonious to consider them as reduced La rather than Ll.

Lucifora and Menni (1998) reported a specimen of *Lamna nasus*, in which an intermediate tooth was absent. We report the absence of the Ll3 in one *C.!taurus* specimen, where the tooth was not replaced by any other one, leaving an empty space, and a hook-like Ll2 was placed before the empty space (Fig.!3D). The developmental relationship (see Reif, 1976), if any, between these two anomalies is uncertain.

In conclusion, different teeth of *C.!taurus* have different DIAs. This fact agrees with previous views of different use of teeth in this species. Our results can be used as a working hypothesis for future experimental work which allow to elucidate the actual tooth use during feeding by *C.!taurus*.

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