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TOOTH TERMINOLOGY AND VARIATION IN SHARKS WITH SPECIAL REFERENCE TO THE SAND SHARK, *CARCHARIAS TAURUS* RAFINESQUE.

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TOOTH TERMINOLOGY AND VARIATION IN SHARKS WITH SPECIAL REFERENCE TO THE SAND SHARK, *CARCHARIAS TAURUS* RAFINESQUE.

By SHELTON P. APPLEGATE[1]

ABSTRACT: Heterodonty in teeth is common in sharks. The use of three new terms is advocated: alternates, medials and posteriors. Dental formulae can be used in classifying recent and fossil sharks. In *Carcharias taurus* Rafinesque, tooth length was found to be proportional to total length of the shark. Unassociated fossil teeth may be identified through the erection of artificial tooth sets if the teeth can reasonably be referred to a single species.

INTRODUCTION

In current studies of recent sharks the implications of the tooth terminology and dental formulae which were proposed and used by Maurice Leriche (1905, 1910, 1926) have not yet received the attention and use which they warrant. This is due to a need to demonstrate that these tooth types and dental formulae are truly significant characters that can, in fact, be useful in classifying species and higher taxa. Once the approach pioneered by Leriche has been validated, as attempted in this paper, it should be possible to project the results obtained from studying fossil and recent shark dentition into higher and higher taxonomic categories. This will lead, hopefully, to a better understanding of generic and familial characters and to a better comprehension of selachian evolution.

The aims of this paper are to give a general discussion of the use of tooth types and dental formulae in sharks and to attempt to analyze the range of variation in the teeth of the sand shark *Carcharias taurus* Rafinesque. If tooth morphology and number varied widely between individuals of the same species then the use of tooth characters to delineate species of fossil carchariids and related sharks would be unwise and the whole rationale behind the use of tooth types and dental formulae would be weakened. However, the variation within the sample of *Carcharias taurus* is not of the magnitude that would cast doubt on the validity of using tooth types or formulae in this shark. I therefore contend that it is possible to distinguish species of fossil carchariids by their teeth alone once the proper tooth type and probable position in the jaws of the fossil teeth has been determined.

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DISCUSSION OF HETERODONTY

The basis for tooth terminology and dental formulae in sharks rests on the widespread occurrence of heterodonty among fossil and recent sharks. Heterodonty, although normally not applied to sharks' teeth, is the logical term used to express the radical change in size and shape of the teeth found in a shark's jaw. The normal reduction in size alone from the front to the rear of the mouth does not indicate heterodonty.

A heterodont condition as is here defined is well documented for the older Paleozoic and early Mesozoic sharks, particularly the hybodonts (Woodward, 1891). On the other hand, the older cladodonts and their relatives need a more detailed investigation before any similar generalization can be made. One major factor in studying the occurrence of heterodonty in Paleozoic sharks is that many of the species are described from a single tooth, a fact that can be demonstrated by an examination of Woodward, 1891. Such a state of affairs would tend to support an early appearance of homodonty whether it ever existed in these sharks or not.

In recent and fossil sharks true homodonty, *i.e.,* where the teeth in a jaw are all the same shape and show no abrupt change in size, is a rare phenomena. It may exist in recent *Rhincodon* and *Cetorhinus.* There is some evidence for this condition in the Orectolobidae and to a lesser extent in the Scyliorhinidae. *Chlamydoselachus,* the primitive fringed-gilled shark, has what could be considered a homodont condition except that it has a single row of medial teeth which are unique. If a true homodont tooth condition ever preceded a heterodont condition it has yet to be demonstrated in the fossil record.

Heterodonty in sharks involves a number of distinct variations. A primary type of heterodonty occurs when the upper teeth are quite different from the lower teeth. In the family Pseudotriakidae and in some Scyliorhinidae not only

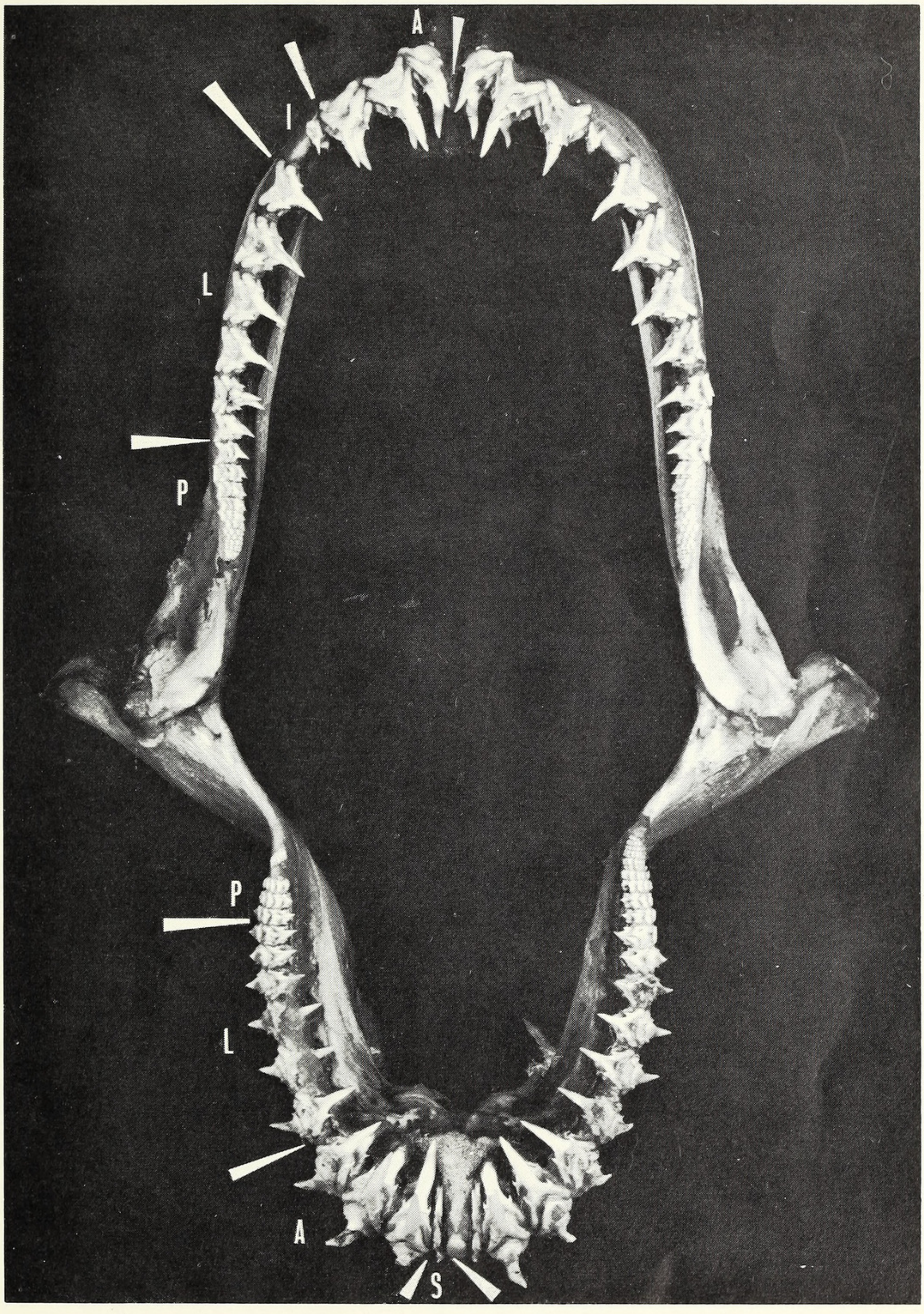

Figure 1. Jaw of *Carcharias taurus,* field number 7, LACM number F 105, total length 205 cm, from Sandy Hook Bay, New Jersey. A = anteriors, I = intermediate, L=laterals, P=posteriors, S=symphyseal. Approximately half natural size.

is the tooth shape distinct in different positions but the teeth of the lower jaw are arranged in a completely different manner (*see* Bigelow and Schroeder, 1948: fig. 40). In the Hexanchidae the lower teeth are long, flat and blade-like, while the upper teeth are needle-like. A similar and possibly related condition exists in the majority of species now placed in the families Squalidae and Dalatiidae. The reverse condition exists when the upper teeth are blade-like and the lower teeth are more narrowly pointed. This condition is well displayed in the majority of the Carcharhinidae and in all of the Sphyrnidae. The latter type of heterodonty has been developed independently in *Carcharodon* and in some of the fossil species of *Isurus*—*I. hastalis* Agassiz for example. An even more fundamental type of heterodonty occurs when individual teeth in an upper or lower jaw vary widely in size and shape from their neighbors. This common condition exists in the Heterodontidae, Hexanchidae, Carchariidae (including the family Scapanorhynchidae), Isuridae, Alopidae, Carcharhinidae and Sphyrnidae. Slight tooth differentiation occurs in Chlamydoselachidae as has been discussed. Tooth differentiation is weakly defined in the Orectolobidae, Scyliorhinidae, Squalidae, Dalatiidae, Echinorhinidae, Squatinidae, and Pristophoridae.

Such regional differences in the shark jaws as has just been noted can be best treated through the use of terms of a positional nature. A nomenclature of this type already exists, for in 1905 Leriche coined such terms for the teeth that occur in *Carcharias ferox* and later (1905, 1908, 1910, 1926), he extended the use of these names to species belonging to other families, *i.e.*, Isuridae, Alopiidae, Hexanchidae, Squatinidae, Scyliorhinidae, and Carcharhinidae. Leriche did not exhaust the applications of these terms nor their possible modifications. There has been a wide use of Leriche's names since 1905 by British and French paleontologists; therefore any attempt to completely abandon Leriche's terms, no matter how technically desirable, would only confuse the already lengthy literature. There is no reason why these names may not be modified and new terms added if there is a real need for them. In time the terminology of tooth types should become stable and will with common usage give us a valuable tool in working with both recent and fossil sharks.

Leriche (1905) used the tooth names *symphysaires antérieures, intermédiaires,* and *laterales* to describe the different teeth in *Carcharias ferox* (Risso). An approximate English translation of these terms would be symphyseals, anteriors, intermediates and laterals. It is suggested that the term posteriors be substituted for the posterior laterals as used by White in 1931. In considering the teeth in the Scyliorhinidae, Triakidae, Pseudotriakidae, Carcharhinidae, Sphyrnidae, Hexanchidae, Squalidae, Dalatiidae and Heterodontidae it has become apparent that there is a need for another term to designate the median teeth which occur in the symphyseal area and are distinct from the symphyseal teeth as used in the Carchariidae. Obvious terms for these teeth are median or medial teeth definable as small teeth of the symphyseal

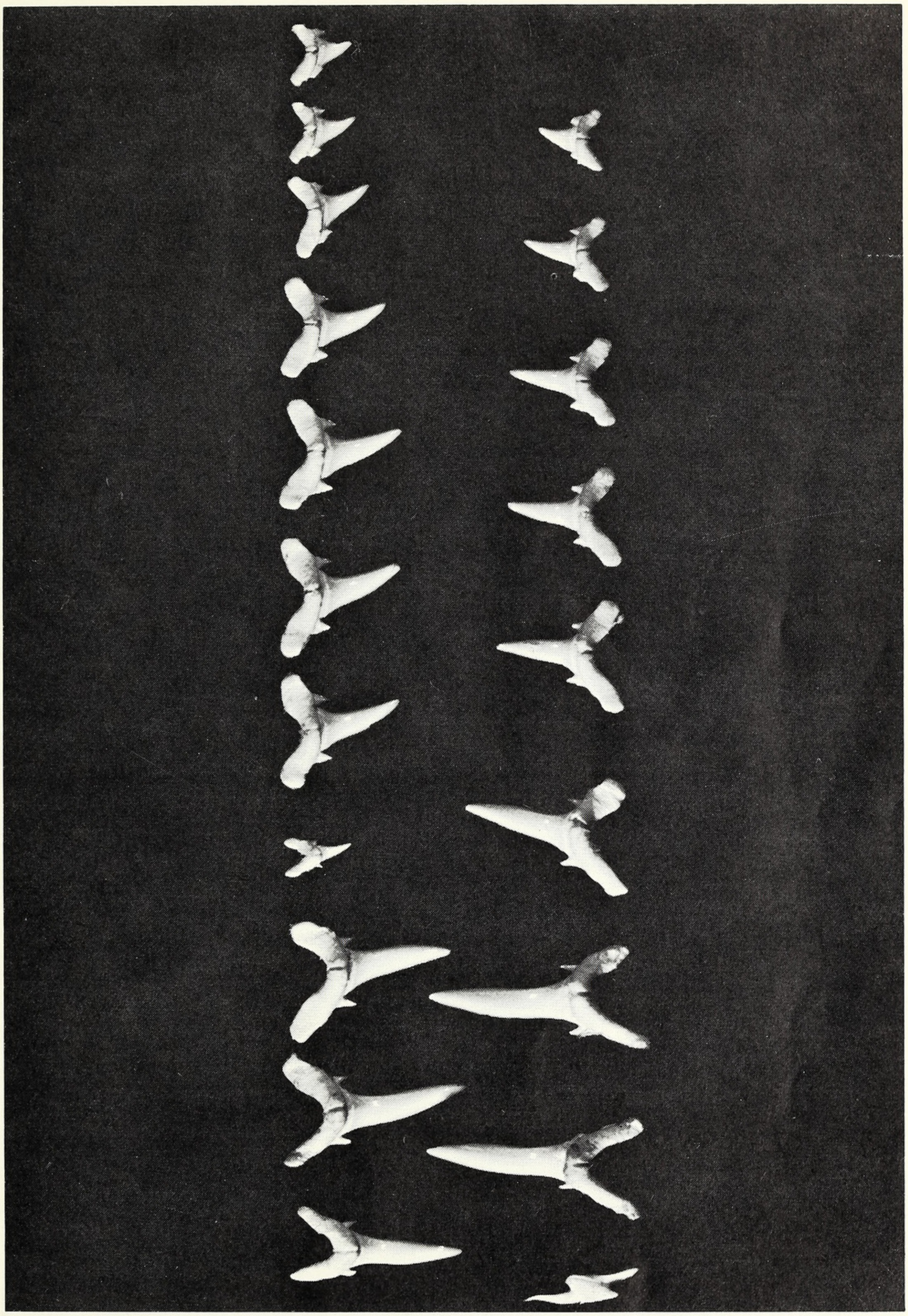

Figure 2. Symphyseal, anteriors, intermediates, and laterals of *Carcharias taurus* number 11, LACM F 106, adult female caught off of Lewes, Delaware. The teeth are from the right side and are shown in an internal view. Approximately .8 natural size.

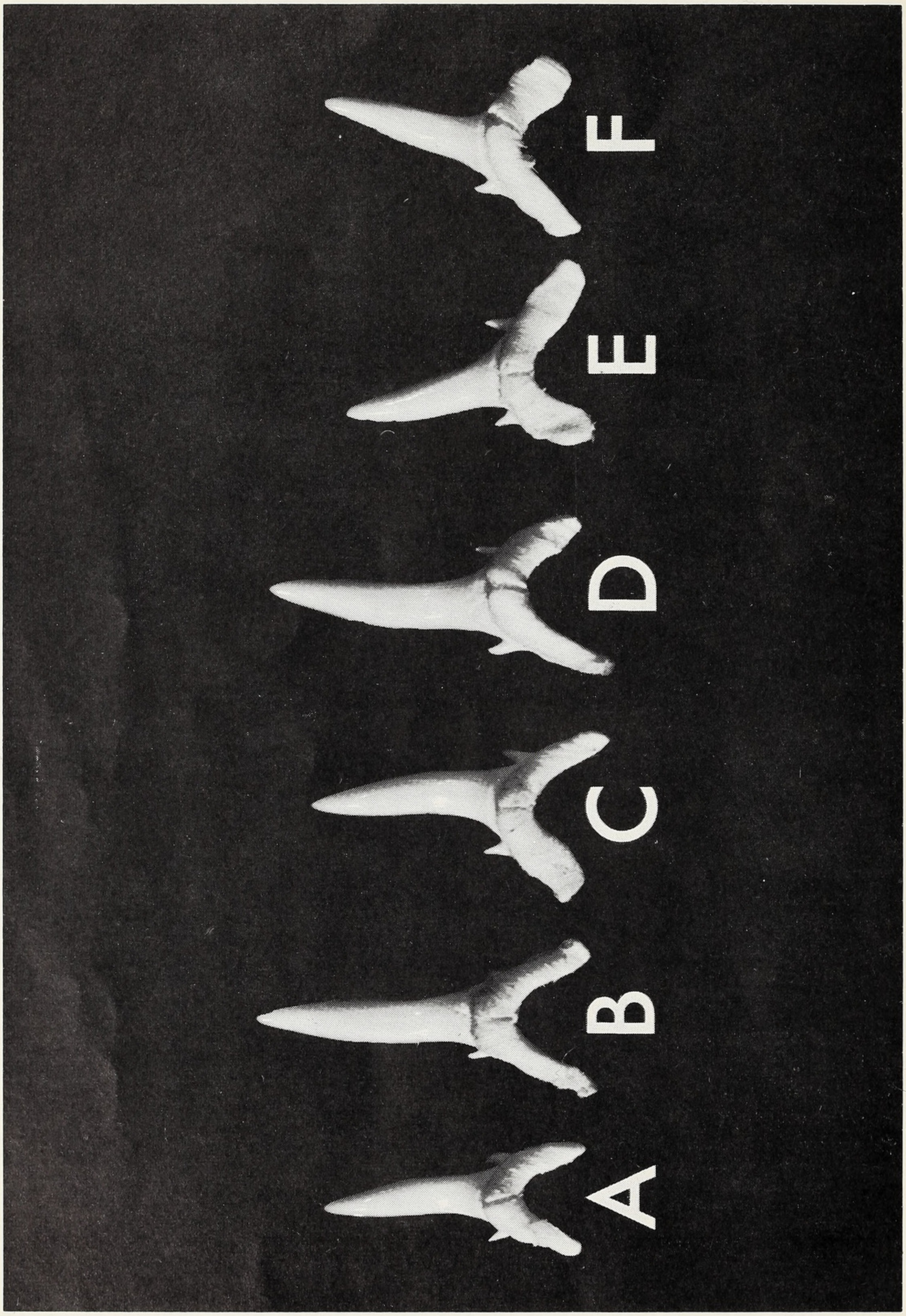

Figure 3. LACM F 106. A=first upper anterior, B=first lower anterior, C=second upper anterior, D = second lower anterior, E = third upper anterior, F = third lower anterior. Approximately natural size.

area with at least one tooth in a medial position and the other teeth, if present, identical to this median tooth. If the teeth adjacent to the median tooth are similar in size and shape they should be considered median teeth also. Median teeth may be symmetrical, or asymmetrical as in the recent *Prionace glauca,* and then be oriented to the left or right.

In many of the Carcharhinidae there are small teeth which occur in the symphyseal area that are neither medial, nor symmetrically arranged as the symphyseals. These small teeth occur in oblique tooth rows of 2, 3, 4, or 5 teeth. Since there is an alternation of these teeth in the last position, the term alternate tooth is suggested to cover these teeth.

Symphyseal teeth are the small asymmetrical teeth which lie on either side of the symphysis (Fig. 2) and never in the center of the jaw. In *Carcharias taurus* such teeth are limited to the lower jaw. The teeth which might be called upper symphyseals are here interpreted as being first upper anterior teeth as they resemble these teeth in both shape and size.

Anterior teeth are situated on both sides of the upper and lower jaws in *Carcharias;* these teeth differ widely from the symphyseals (Figs. 2 and 3). In *C. taurus,* there are three upper rows of anteriors. The smallest anterior is borne in the first or more medial upper row or file (the latter term was used by Leriche). The lower jaw also possesses three rows of anteriors on either side of the symphysis; these teeth lie to the outside of the symphyseals. The largest tooth in the jaws of *C. taurus* is the second lower anterior tooth. The total height of the anteriors is approximately twice their greatest root width. The lateral edges of the tooth crown of the anteriors are nearly parallel for a short distance before narrowing to an attenuated point. When these teeth are viewed from the side there is a pronounced S-shaped curve of the crown. The total anterior tooth even when it is in the first position in a file or row inclines inward into the mouth. The two roots of the anteriors form an acute angle which is greater than that of the symphyseals, but less than in the lateral teeth. In the anteriors the largest root points toward the symphysis; in the symphyseals on the other hand the larger root points away from the symphysis.

In the small immature specimens at hand the first upper anterior lacks denticles, confirming the observation of Bigelow and Schroeder (1948: 99).

In the upper jaw the teeth termed intermediates occur just lateral to the anteriors; there is only a single file of intermediates on each side of the upper jaw. This tooth (Fig. 2) has a small triangular crown. The roots are asymmetrical. The longest branch of the two roots points toward the symphysis. There are apparently no denticles on this tooth in very young specimens, a feature shared with the first upper anterior as discussed above.

The teeth designated as laterals occur to the rear and lateral to the intermediates in the upper jaw and to the rear and lateral to the anteriors in the lower jaw. Laterals are shown in Figure 2. Seen in side view the crown of the laterals is straight; seen in anterior view the crowns are lower than those

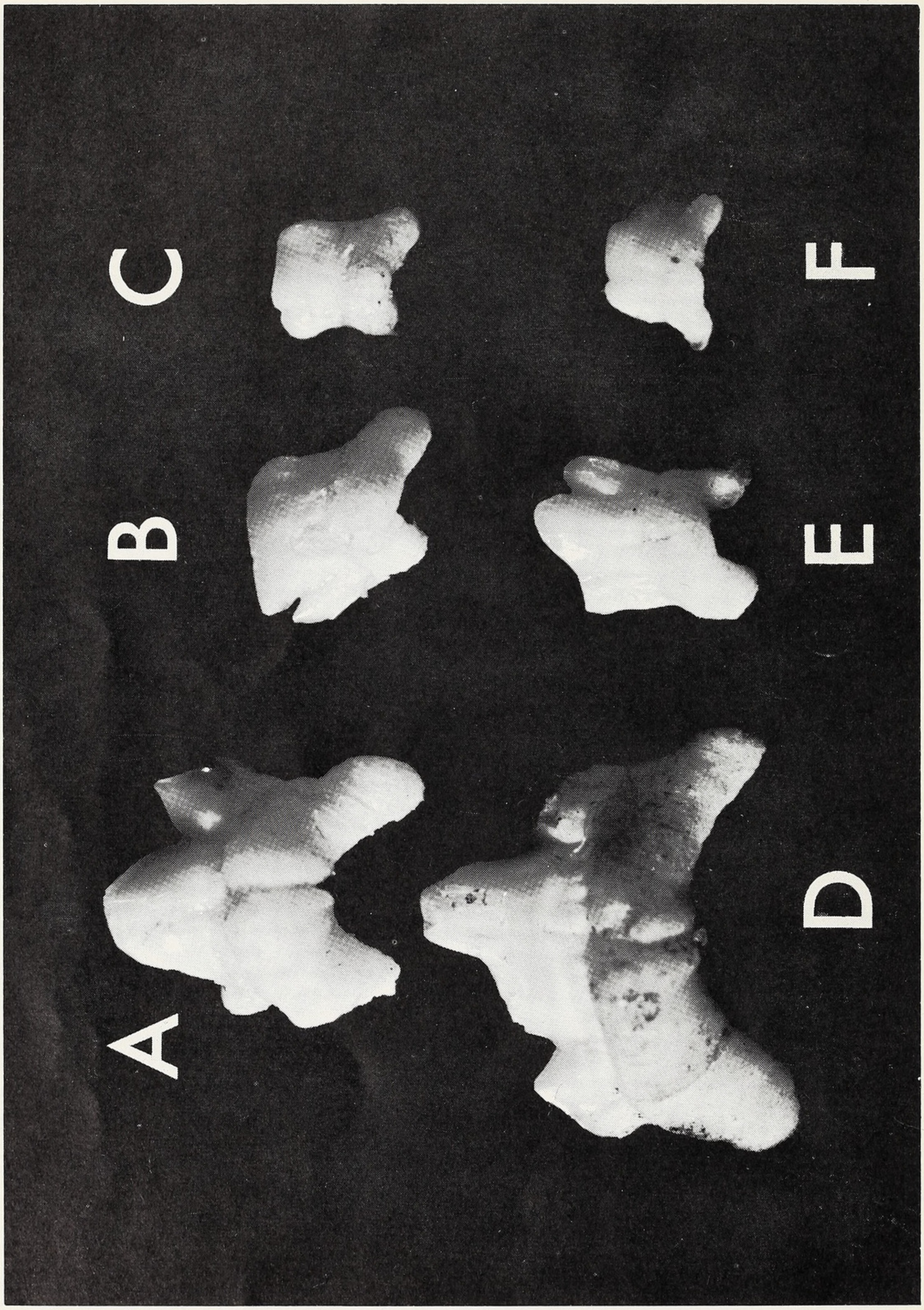

Figure 4. Posteriors of LACM F 106. Upper teeth, A=number 1, B=number 6, C=number 11. Lower teeth, D=number 1, E=number 5, F=number 10. One should note the great amount of chipping and wear in these teeth. Approximately 10 times natural size.

of the anteriors. The roots of the laterals characteristically form obtuse angles with each other. The total tooth height is almost equal to the greatest width. The lower lateral teeth, when viewed anteriorly have a straight axis. The upper laterals have crowns with a curved axis; this curve is directed toward the corners of the jaw. Occasionally the lower posterior laterals may show a marked posterior curving of the crown axis. There is a tendency in *C. taurus* for the upper laterals to bear two denticles on each side of the tooth in contrast to the usual one.

The small teeth in back of the laterals are called posteriors (Fig. 4). They are the most variable of the teeth in *Carcharias*. The crown may have a straight or curved axis. The denticles may even rival the crown in size. The greatest width of the roots is frequently more than the height of the tooth. There is no marked extension of the root beyond the base of the crown as occurs in the laterals.

In order to compare the tooth types mentioned in the sand shark (such as alternates and medials) with those seen in other shark families, it may be said that in 16 families of living sharks, excluding the Rhincodontidae and Cetorhinidae, medials are lacking in only four, the Carchariidae, Isuridae, Alopiidae and Echinorhinidae. Alternate teeth are known only from the Scyliorhinidae, Triakidae, Carcharhinidae, Sphyrnidae and Echinorhinidae. Anteriors are lacking in the Echinorhinidae. Intermediates are known only in the Carchariidae, Isuridae and Alopiidae. Laterals are lacking in *Heterodontus* for in this species the anteriors are followed by flat posterior teeth. Posterior teeth occur in all of the families.

FUNCTIONAL RELATIONSHIPS

The teeth in *C. taurus* serve to puncture, slice and crush the fish on which this shark feeds. In feeding on its prey the shark must hold, immobilize (often sever in half) and move its food to the stomach via the pharyngeal cavity through the short esophagus.

The anteriors serve to puncture and kill or stun the prey; their strong inward inclination makes it easy for food to be held and moved into the mouth. A turn of the head or body would place the prey under the laterals where it would be sliced and swallowed. The posteriors must serve to hold and crush the food. The latter action is indicated by the great amount of wear that the posteriors receive.

I believe that the symphyseals and intermediates function mainly to break up the anterior teeth into patches; this would reduce the number of teeth puncturing the prey, a factor making for both rapid and deep penetration of these fangs as well as quick removal of the prey after it has been caught and killed. Lack of serrations may be a factor in freeing prey from the teeth.

It is interesting to note that an examination of the articulation of the two jaws in *C. taurus* leads to the conclusion that lateral movement of one jaw in relation to another is all but impossible. Food must be moved by the movement of the whole jaw, or turning the head or the whole body in relation to the food.

Most of the fishes taken from the stomachs of twelve sand sharks were menhaden (*Brevoortia tyrannus,* between 8 and 10 inches long). Each had been chopped into two parts, the tails of each fish showing punctures that, from their size and spacing, were made by the anteriors. The severing of the fish must have been accomplished by the laterals as the cut in each case was straight and clean.

REPLACEMENT AND NUMBER OF TEETH

In *Carcharias* there is continuous replacement of teeth throughout the life of the shark (Breder, 1942; Cadenat, 1962). As the teeth in the last position fall out they are replaced by those behind; the last part of a tooth to calcify is the tip of the root. Complete roots indicate that the tooth had reached the last position; therefore, the paleontologist can be sure that he is examining mature teeth by inspecting the tips of the roots. The tooth bud and the teeth in the process of formation are hidden by a gum-like membrane through which the teeth rupture. Once they have passed through this membrane, the teeth may be considered to be functional. At any given time there are usually two functional rows of anteriors, intermediates and laterals followed by from 4 to 6 rows of small posteriors. The large number of posterior teeth no doubt add appreciably to the total crushing area of these teeth.

In the present *Carcharias* sample the number of teeth in the upper jaw varies from 38 to 55 and in the lower jaw from 34 to 44. This is a greater variation in tooth number than has been reported in the past (Garman, 1913; Bigelow and Schroeder, 1948). The use of total tooth number as a taxonomic character in the Carchariidae therefore has little validity.

DENTAL FORMULA AND TERMINOLOGY

A more helpful tool is the variation in the number of teeth in the different tooth types; this can be best revealed by the use of a dental formula similar to that used by Leriche (1905, 1910, 1926), Desbrosses (1930) and Dartvelle and Casier (1943). Such a formula uses the first letter of each tooth type followed by the number of teeth of this type in the first row (Fig. 1). If a tooth is missing in the first position the one behind it is counted.

A horizontal line separates the teeth in the upper jaw from those of the lower. As an example let us take the teeth of *Carcharias taurus* as figured by Bigelow and Schroeder (1948: 95). This left portion of the jaw would be written as follows:

A3	I1	L7	P16
S1	A3	L5	P13

The total numerical variation of the tooth types in the series of twelve specimens of *Carcharias taurus* used in the present study may be expressed by the following formula.

P6-19	L6-7	I1	A3	A3	I1	L6-8	P8-15
P4-14	L5-6	A3	S1	S1	A3	L5-6	P8-13

From this formula it is evident that neither the symphyseals, intermediates and or the anteriors varied in number. The variation of the laterals and posteriors is shown in Table 1.

TABLE 1

The variation in the number of lateral and posterior teeth in *Carcharias taurus*.

	Laterals				Posteriors			
	Upper		Lower		Upper		Lower	
Specimen No.	Right No.	Left No.	Right No.	Left No.	Right No.	Left No.	Right No.	Left No.
1.	6	6	5	5	8	10	8	9
2.	6	6	5	6	10	10	9	9
3.	7	6	5	5	9	8	9	9
4.	6	6	5	5	10	10	9	8
5.	6	6	5	5	10	9	8	8
6.	6	6	5	5	19	15	14	11
7.	6	7	6	6	11	15	4	11
8.	6	6	5	5	12	12	12	12
9.	6	7	5	6	9	10	10	8
10.	7	7	5	6	8	10	10	9
11.	7	8	5	5	13	11	13	13
12.	7	7	5	6	9	10	12	12

The mode of the lower laterals is five per side and in the upper laterals it is six per side. These modes occur in 79% and 66% of the sample respectively. The upper posteriors vary from 8 to 19, which is a range of 11 teeth as opposed to a range of 3 teeth for the laterals. The upper posterior teeth average 10.7 per side; the mode per side is 10. The lower posteriors have an average of 9.8 per side with a variation from 4 to 14 with a range of 10.

In some of the specimens of *C. taurus* the addition of posterior teeth during the life of the shark may be demonstrated; several single teeth were followed in the replacement series by a double row of immature teeth. The deletion of teeth in a jaw is more difficult to demonstrate although a case of deletion may be reflected in a specimen in the comparative anatomy collections at Duke University in which no intermediates are present even though a space for these teeth exists. Since this specimen lacks data one cannot be sure the intermediates have not been removed; however close examination suggests that this is unlikely.

In reconstructing the dentition of fossil sharks several terms were needed.

First "tooth set"; that is, a single complete row of all types of mature teeth from both sides of the upper and lower jaws, arranged in their natural order as they occurred in life. A "natural tooth set" is one which shows the natural order of tooth arrangement. Such a "natural tooth set" occurs obviously in living sharks; in fossils it occurs only under exceptional conditions of preservation where the teeth are still in place in the jaws. It is, of course, more likely that a partial "natural tooth set" will be found with only a few teeth in place. An "associated tooth set" occurs when a number of tooth types are found which can be referred to one specimen. An "artificial tooth set" may be erected when a number of tooth types from one locality may be considered to belong to one species. In doing this, comparisons are made with known related natural sets as well as associated sets. As with the "associated tooth set" tooth positions can only be inferred. Occasionally material from more than one locality may be used in "artificial sets" when the chance of confusion with a closely related species is negligible.

Once we know what tooth types exist for a set of a fossil species then we can assess more accurately the specific limits of these types and the likelihood of calling different tooth types from the same set different species becomes more remote. If carefully used and applied, the use of "sets" should allow more exactitude in determination of species.

BODY LENGTH AND TOOTH HEIGHT

It is evident from an examination of Table 2, that there is a general increase in total tooth height which coincides with a similar increase in the total length of the shark. In this case total length is the measurement from the tip of the snout to the tip of the tail, and total tooth height is that measurement from the tip of the tooth to the tip of the largest root. These measurements of tooth height and fish length were plotted against each other. A definite linear relationship was found in all cases. An example of such a plot is shown in Figure 5. The total height of the second lower anterior tooth was plotted against the total length of 10 sharks having these teeth. It may be added that the second anterior is the largest tooth in the jaws although the third anterior is slightly larger in one jaw. The constancy of this linear relationship at once suggests the possibility of being able to predict the total length of a shark once the total height of a particular tooth of one of the tooth types is known. Once his procedure has been established in recent sharks then it might be possible to compute the total length of fossil sharks such as *Isurus hastalis* (Agassiz), *Hemipristis serra* Agassiz and *Carcharodon megalodon* Agassiz.

One might conclude that the tooth bud or even earlier germinal layer increases in size as the shark grows larger, so that at any one time the functional tooth size is a reflection of the size of the fish.

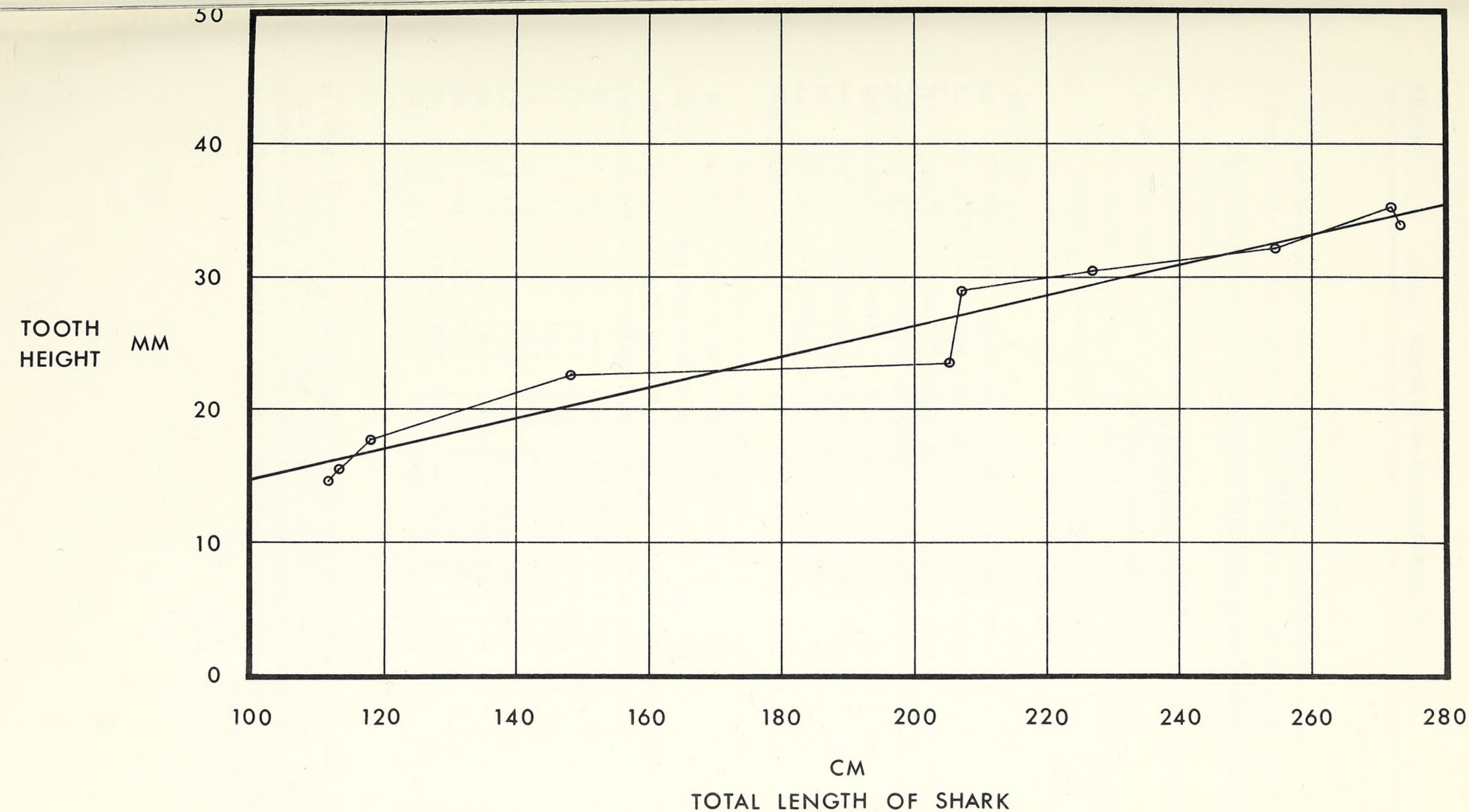

Figure 5. Relationship of total height of the second right anterior to the total length of the whole shark. The line represents a linear interpretation of the data.

TABLE 2

Total length of ten sand sharks compared with total tooth height

LOWER JAW

Total tooth height in cm.

Total length in cm.			right						left			
No.	P1	L1	A3	A2	A1	S1	S1	A1	A2	A3	L1	P1
1. 112	.27	.71	1.23	1.49	1.46	.65	.79	1.46	1.53	.98	.71	.30
2. 113	.26	.86	1.27	1.55	1.61	.79	.78	1.52	1.65	1.25	.82	.23
4. 118	.35	.99	1.27	1.77	1.51	.79	.75	1.52	1.66	1.25	.88	.35
6. 148	.41	1.21	1.50	2.27	2.18	1.13	.98	2.22	2.14	1.77	1.35	.41
7. 205	.35	1.38	1.73	2.38	2.21	1.13	1.12	2.16	2.34	1.85	1.48	.62
8. 207	.45	1.52	2.36	2.90	2.78	1.28	1.25	2.73	2.85	—	1.52	.34
9. 227	.71	1.81	2.64	3.03	3.00	1.70	1.74	2.98	3.06	2.66	1.88	—
10. 252	.70	1.62	2.15	3.20	2.88	1.50	1.55	2.53	3.00	—	1.46	.85
11. 272	.60	2.27	2.69	3.54	3.50	1.78	1.64	3.35	3.27	2.95	2.01	.69
12. 273	.62	1.89	2.61	3.44	3.33	1.89	1.82	(2.69)	3.02	—	2.00	.50

UPPER JAW

			right						left			
No.	P1	L1	A3	A2	A1	S1	S1	A1	A2	A3	L1	P1
1. 112	.30	.81	.33	1.07	1.35	1.02	1.03	1.35	1.19	.31	.66	.31
2. 113	.37	.85	.41	1.28	1.30	1.11	1.20	—	1.29	.40	.89	.38
4. 118	.37	1.09	.50	1.23	1.44	—	1.19	1.45	—	.51	.91	.38
6. 148	.42	1.12	.69	1.60	1.71	1.59	1.69	1.69	1.72	.73	1.21	.43
7. 205	.49	1.27	.75	1.83	2.04	1.70	1.70	2.00	1.77	.81	1.31	.52
8. 207	.69	1.42	.98	1.82	2.46	2.10	2.10	2.47	—	.89	1.29	.52
9. 227	—	1.80	1.07	2.32	2.99	2.23	—	2.93	—	.92	1.69	.65
10. 252	.79	1.70	.83	2.55	2.72	2.31	2.28	2.55	2.50	.84	1.80	.66
11. 272	.65	2.02	1.15	2.64	2.93	—	2.54	2.99	2.43	1.11	1.95	.88
12. 273	1.06	2.22	1.17	2.75	—	2.60	2.65	3.11	2.70	1.06	2.06	1.02

The total tooth height (greatest distance from tip of root to tip of tooth) is measured in centimeters. It should be noted that sharks number 3 and 5 with total lengths of 113 and 140 centimeters were not used in this chart for they were broken. The capital letters at the top of each column stand for the respective tooth types as described in the text.

CONCLUSIONS

Leriche's terminology and dental formulae give the student of fossil and recent sharks a meaningful method of describing and studying sharks' teeth.

Heterodont dentition as defined in this paper is a common phenomena in recent and fossil sharks.

To Leriche's tooth terms should be added medials, alternates and posteriors as distinctive tooth types.

The restrictive nature of tooth types above a familial level suggests a natural grouping of sharks which may be phyletic.

The functional use of teeth in *Carcharias taurus* can be correlated with tooth type.

Completely formed root tips indicate mature teeth.

In *Carcharias taurus,* total tooth number for the upper and lower jaw is not a reliable specific character; however the number of the symphyseals, anteriors and intermediates is constant. Numerical variation is confined to the laterals and posteriors.

In *C. taurus* tooth length is directly proportional to total length.

The use of artificial tooth sets is an effective way to treat unassociated fossil teeth.

The results of this study of tooth variation in *C. taurus* suggest that there is much information to be gained by extending such studies to other recent species of sharks. Essential to such studies are collections of jaws accurately identified with reliable locality, sex, and size data. For each species as many jaws as is practical should be examined.