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# A comparison of isolated teeth of early Eocene *Striatolamia macrota* (Chondrichthyes, Lamniformes), with those of a Recent sand shark, *Carcharias taurus.*

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**Abstract:** A comparison of positional similarities between isolated fossil shark teeth of *Striatolamia macrota* Agassiz, 1843, from the Potapaco Member of the Nanjemoy Formation, Virginia, USA, and teeth extracted from the jaw of a Recent sand shark, *Carcharias taurus* Rafinesque, 1810, is made using text and photographs. A new method of arranging fossil teeth for the study of positional tooth-form variation is proposed. An artificial tooth set for *S. macrota* is constructed, suggesting three upper anterior tooth positions.

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## INTRODUCTION

Many Recent lamniform sharks possess sufficiently similar dentitions to allow them to be used as a template for the construction of artificial dentitions for fossil species. This technique was employed by Agassiz (1835-1843), Leriche (1902, 1905), Applegate (1965), Cappetta (1987), Ward (1988) Applegate & Espinosa-Arrubarrena (1996), Siverson (1999) and Kent & Powell (1999)

Applegate (1965) demonstrated that in Recent *Carcharias taurus*, positional variation and functional relationships of the teeth remained reliably constant for the species. He then suggested that similar characters might be found in fossil species, thus enabling the reconstruction of their dentitions.

Welton & Farish (1993) defined three different types of tooth sets. A **natural tooth** set is the rare situation where the teeth are still in place in the jaws (see Shimada, 1997). An associated **tooth** set, is one from a single individual, where the teeth are displaced from their original positions. The arrangement is open to alternative interpretations (see Siverson, 1999) An **artificial tooth** set is based on isolated teeth, usually from a single locality and horizon, single species and from individuals of a similar size (ontogenetic stage). The sample must be large enough for all tooth positions to be identified and to allow ontogenetic variation to be recognized. Usually a Recent species is used as a model. In this paper the Recent sandshark *Carcharias taurus* is used to construct an artificial tooth set from isolated fossil teeth of *S. macrota*.

## TERMINOLOGY

The tooth position terminology is based on that of Applegate, (1965), Cappetta (1985) and Siverson (1999) which includes anterior, intermediate, lateral, and posterior tooth positions. Anterior teeth of the upper and lower jaw are numbered from the midline of the jaw, distally.

## MATERIAL

*Striatolamia macrota* was chosen as a large number of these teeth were collected by the author between July 1995 and January 1997 from early Eocene (Ypresian) Potapaco Member of the Nanjemoy Formation. The locality, referred to as "Fisher/Sullivan Site" or "Muddy Creek," is located in an unnamed tributary to Muddy Creek in Stafford County, Virginia (Weems & Grimsley, 1999). The teeth were collected from one small lens of matrix; a 0.7m thick layer of dark-gray, sandy clay, 3m above the stream, and within 4m horizontal proximity. This correlates to the lower part of Bed B of the Potapaco Member (Ward, 1985) equivalent to "zone" 11 of Clark & Martin (1901). The horizon is early Eocene, early Ypresian, approximately NPll, mid-P6 in age.

Approximately 450kg of matrix were sieved through 1.5mm mesh window-screen material. The residue was later dried and sorted under magnification. Of the larger shark species, the most abundant teeth were those of *S. macrota*. The presence of striations, lateral denticles and consistent inclusion into positional groups were the primary means by which they were sorted from other species. Of the *S. macrota* teeth collected, 270 had excellent preservation and advanced root development and were selected to represent positional variation (Table 1). While all of the *S. macrota* teeth collected were checked against position, a few striated teeth, possibly pathological or from other species, did not conform to the positional grouping and were excluded.

The isolated teeth of *S. macrota* were assigned their respective positions using characters observed in *C. taurus.* Long, narrow teeth were separated from shorter blade-like teeth and assigned to **anterior** positions. The upper and lower anterior teeth were grouped according to the amount of lingual curvature, recurvature of the crown-tip, and angle of root-lobe divergence (measured from the bottom of the root-lobe interspace to the tips of the lobes). Of six rows established, those with the greatest lingual curvature and

| Position | *C. taurus* | *S. macrota* |
|---|---|---|
| First upper anterior | 9 | 1 |
| Second upper anterior | 10 | 13 |
| Third upper anterior | 10 | 11 |
| Intermediate | 10 | 2 |
| Upper lateral | 58 | 74 |
| Upper posterior | 49 | 16 |
| First lower anterior | 6 | 3 |
| Second lower anterior | 8 | 14 |
| Third lower anterior | 8 | 13 |
| Fourth lower anterior | 8 | 13 |
| Lower lateral | 7 | 11 |
| Lower posterior | 44 | 89 |
| | 62 | 13 |
| Total | 281 | 270 |

**Table 1.** Number of teeth compared in study

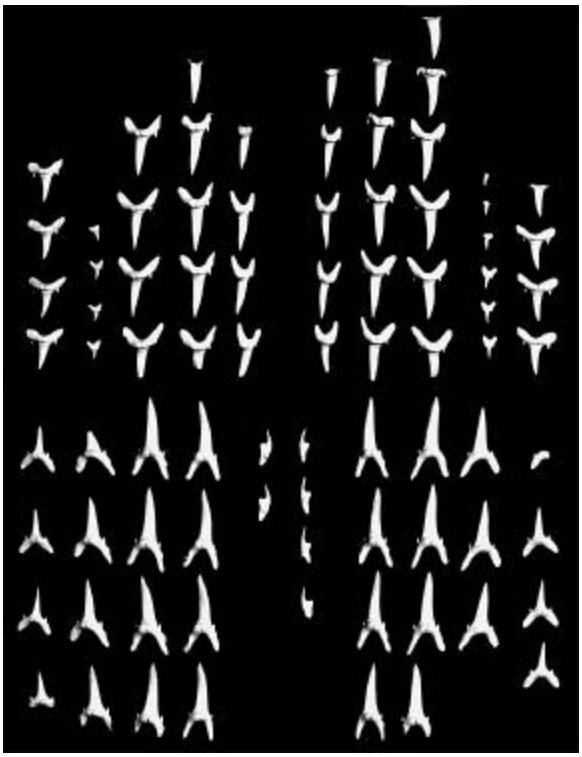


**Plate 1.**
**Partial *C. taurus* dentition in "life" position**

Traditional arrangement of an incomplete natural *C. taurus* dentition. lingual view. This arrangement includes the anterior, intermediate and first lateral files of teeth of the left and right side of the upper and lower jaw. The remaining lateral and posterior files of teeth are not shown. Teeth of the upper jaw are on the top half pointing down, and teeth of the lower jaw are on the bottom half pointing up. Teeth of the left side of the upper and lower jaw are on the left half and teeth of the right side of the upper and lower jaw are on the right half.

The first rows of teeth above and below the horizontal centerline are the foremost teeth in the files of the upper and lower jaw. The remaining teeth above and below the foremost teeth are progressively younger teeth in each file. The teeth that are furthest from the horizontal centerline are the youngest teeth in each file and have not fully developed.

x 0.60.

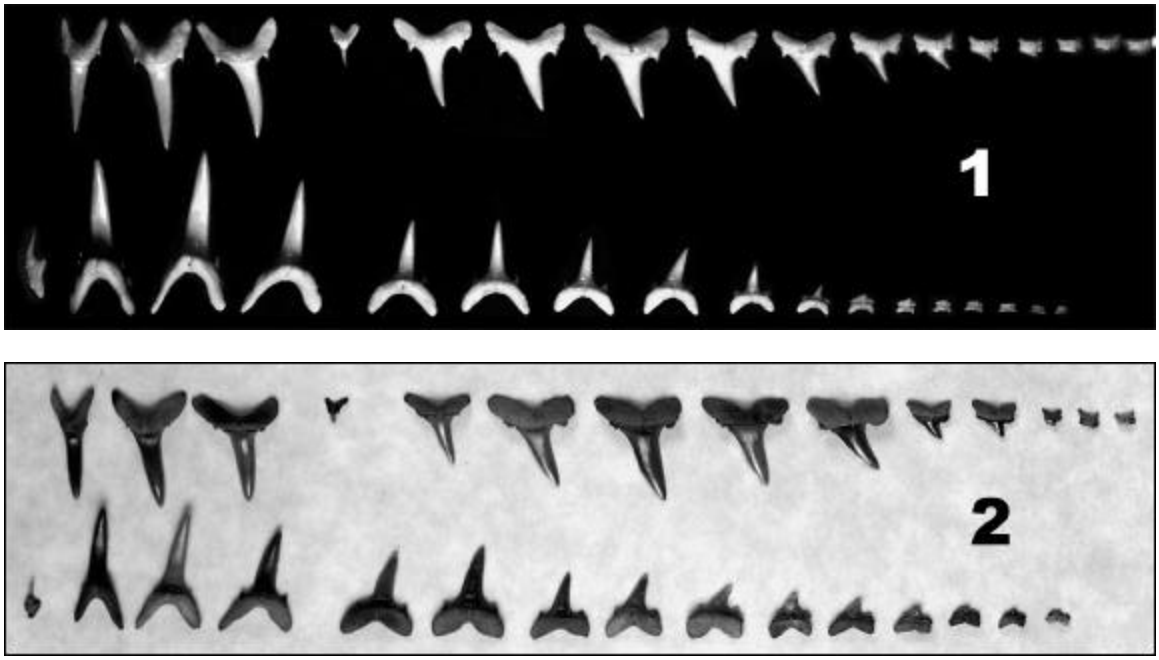



**Plate 2. Traditional Shark Tooth Sets**

**1.** *C. taurus* traditional natural set of the right upper and lower jaw, lingual view. This arrangement includes the most fully developed tooth of each file of the entire right side of the upper and lower jaw. Anterior teeth are on the left and posterior teeth are on the right. x O.66.

**2.** *S. macrota* traditional artificial set of the right upper and lower jaw, lingual view. These teeth are arranged the same as fig. 2, except that they are isolated teeth from numerous individuals. This artificial tooth set shows positional attributes but does not demonstrate the degree of variation for each tooth position. x 0.66.

strongest lingual protuberance were assigned to the lower jaw. The remaining three rows (all having strongly recurved crown-tips) were assigned to the upper jaw. Their positions were then determined by the angle of root-lobe divergence. As the upper and lower anterior positions progress away from the midline of the jaw, this angle increases.

The **lateral** teeth, having shorter, triangular crowns, were sorted according to curvature of the labial side of the crown; those with a nearly straight labial surface, from the base of the enamel to the crown-tip were assigned upper jaw positions, and those with a convex surface to lower jaw positions. When the upper laterals are laid labial side down, only the crown-tip and root contact the surface on which they rest, or lay flat, unlike lower lateral teeth, the crowns of which curve away from the surface.

**Posterior** teeth were separated from small lateral teeth according to the definition of the lateral denticles and presence of strong inflation and coarse wrinkling of the basal portion of the labial enamel. They were then assigned to upper and lower jaw in the same manner as lateral teeth; the labial side of the crown is straight on the upper posterior teeth, and the lower posterior teeth exhibit a lingually directed curvature.

**Intermediate** teeth are discussed below.

A *C. taurus* jaw, from the southern coast of Brazil (gender unknown), was cleaned of skin and muscle tissue. Some of the youngest teeth in each file were missing due to their weak attachment in the early stages of development, and several of the remaining teeth were broken, probably from feeding damage. The teeth were extracted after soaking the jaw in hot water, and the roots scraped of recalcitrant tissue. Those of each file were put in a separate cup labeled by position, then treated with 3% hydrogen peroxide solution to remove stains. After drying, the teeth of each file were arranged in separate rows. Extraction was necessary to expose roots, normally obscured by jaw tissue. All of the teeth extracted were retained, regardless of the degree of root development or condition.

## TOOTH SET ARRANGEMENT

Traditionally, shark teeth, when separate from the jaw, are displayed aligned to the dorsal-ventral orientation of a shark's jaw (Plate 1). The files of first anterior teeth are in the middle, and those of posterior teeth are to the left and right. Each row represents the various tooth positions from the midline to the articulation of the jaw, and files of teeth are represented vertically. Teeth from the upper jaw point down and are positioned directly above teeth from the lower jaw, which point up, as in life position. This natural arrangement offers a good perspective of the way the teeth are aligned and positioned in the jaw of one individual and allows the study of developing teeth if they are present in the display. The teeth of the upper and lower jaw are pointing in different directions, however, which makes positional differences of similar looking teeth difficult to detect. The tooth files of each position of the left and right side of the jaw are separated by the vertical centerline of the layout and as corresponding files progress to the posterior, they are separated by greater distance.

Another traditional arrangement of teeth, often used to show an abbreviated version or a dentition, is a positional study set (Pl. 2, figs 1, 2). One tooth from each file of one side of the upper and lower jaw, aligned to life position, is shown to represent positional attributes. This arrangement also offers a good perspective of how the teeth are arranged in the jaw assuming the opposing side is a mirror image. This arrangement, however, does not allow the study of tooth-form variation within each position.

When trying to construct an artificial tooth set, using isolated fossil teeth, each position, or artificial file, includes teeth from numerous individuals and can show variation of size and slight variation of tooth-form for each position. Sufficient numbers of isolated teeth are needed to establish a position with reasonable certainty.

When sorting isolated teeth it is easier to compare those with positional similarities in a horizontal row, with teeth of the upper and lower jaw pointing in the same direction, so that the eye has less distance to travel and fewer perspective differences while comparing their attributes. Therefore, a new method of arranging isolated fossil teeth for the purpose of studying slight tooth-form variation for each position, the "horizontal dentition" is proposed (Pl. 4, figs 1, 2).

In this arrangement, a natural or artificial tooth set is displayed with the first anterior teeth of the upper and lower jaw at the top of the layout, and the posterior teeth at the bottom. Teeth of the upper jaw are grouped on the left half, and teeth from the lower jaw are grouped on the right. Teeth of the upper and lower jaw are again separated into left and right halves that are, essentially, mirror images of each other. The centermost tooth of each half represents the actual position, the foremost tooth in the file of teeth. The teeth to the right or left of the centermost teeth are progressively younger teeth, in line to replace the foremost tooth when it is shed by the shark. The separation between the centermost teeth represents the separation of the jaw into left and right halves. Thus, the files of teeth on either side of the midline of the jaw, for any given position, are arranged in a single horizontal row. The teeth of corresponding positions of the upper and lower jaw are also arranged in a single row and pointing in the same direction which eliminates perspective changes while comparing the teeth of each position. Even though the teeth in Pl. 4, fig. 1 are from one individual, variation of tooth-form can be observed within any given file, especially in the youngest teeth which have not fully developed.

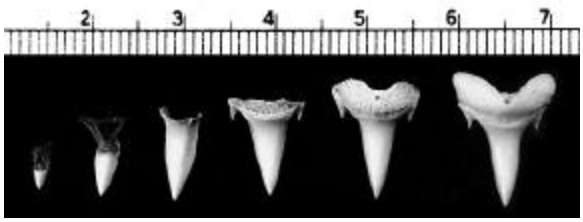
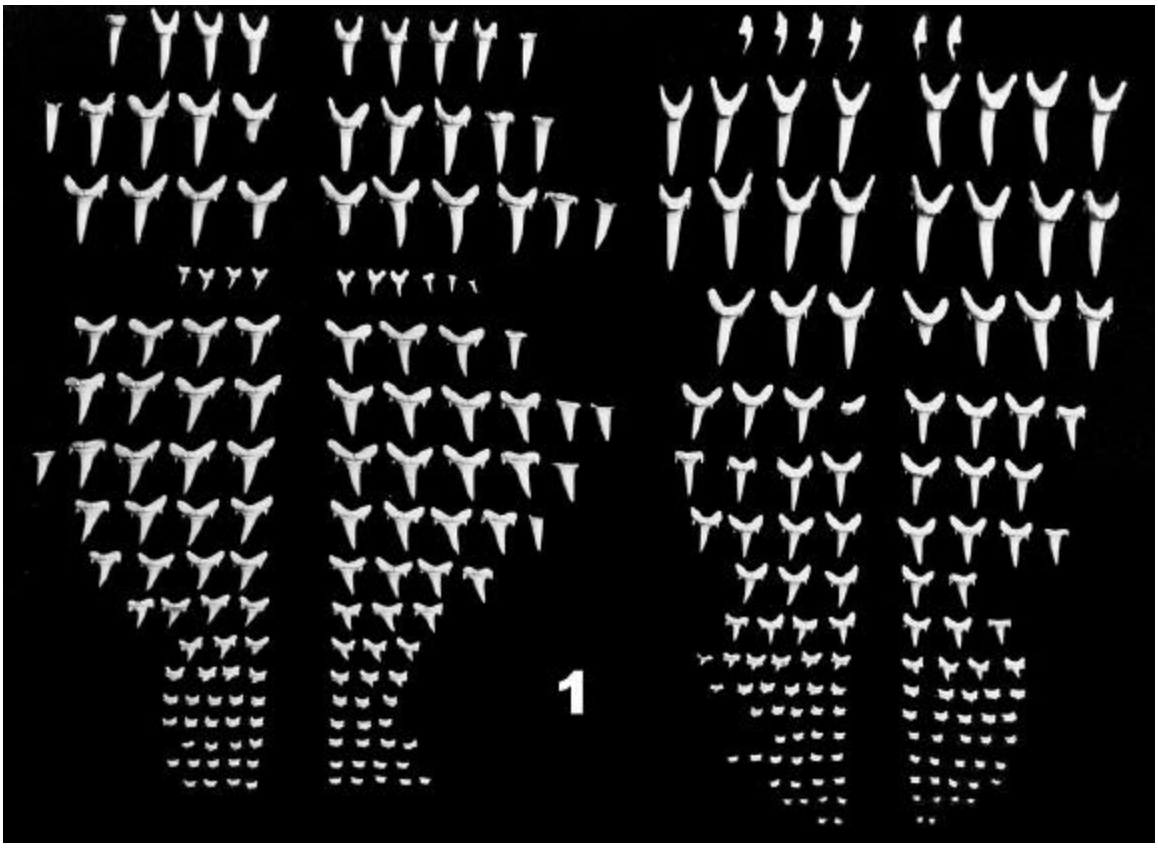



**Plate 3. Tooth development**
The youngest teeth of the left first lower anterior file extracted from a Recent *Lamna nasus* Bonnaterre, 1788, lingual view. *L. nasus* is shown here because of excellent tissue preservation of the developing teeth. Three more fully developed teeth were present in the file, but not shown. The teeth appear to be, in part, the same size.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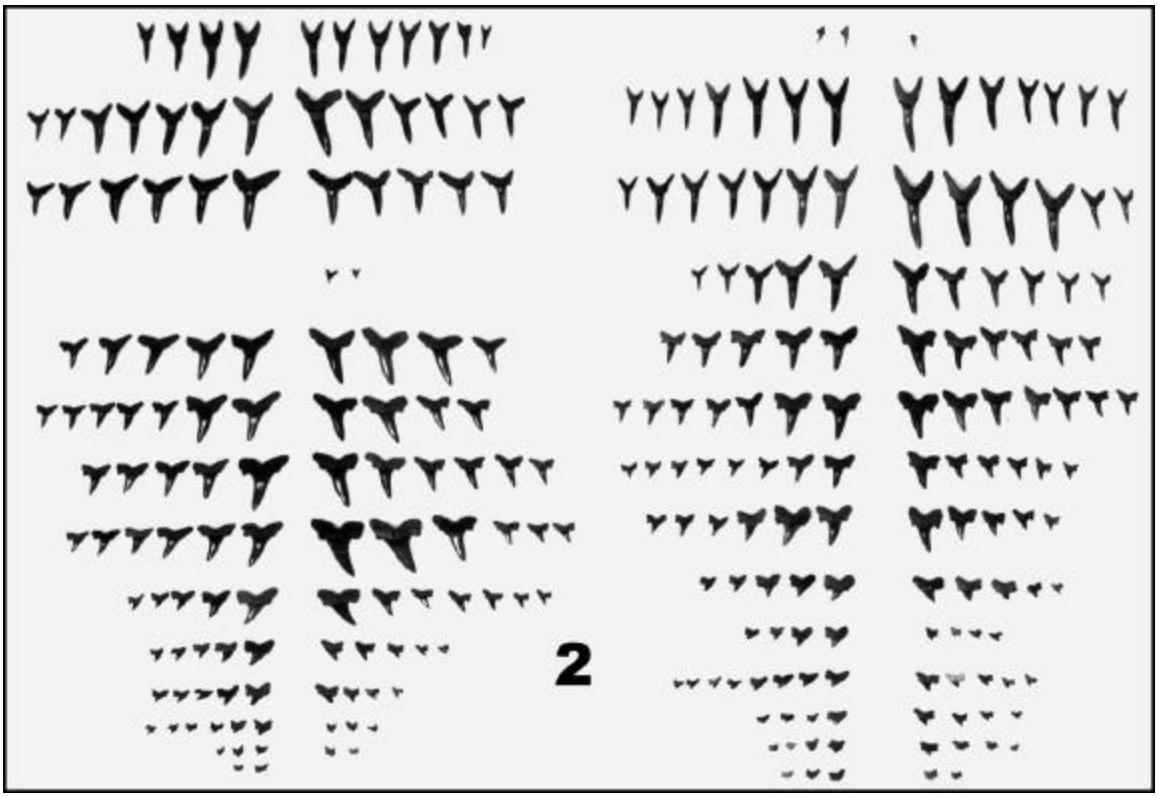
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The teeth comprising each file of *C. taurus* appear to be the same size, unlike artificial files of isolated fossil teeth (Pl. 4, fig. 2). When the tissue of a shark's jaw produces a new tooth, the crown-tip starts to form first (Pl. 3). Most of the crown is developed before the root starts to calcify. The teeth do not grow bigger as they move forward in the file; instead, they complete their development as they move toward functional rank. While the shark grows, the jaw grows, and so do the teeth, requiring the youngest tooth of each file to be slightly larger than the previously formed tooth, but the size difference of the teeth in each file is imperceptible for any given time. The files in the artificial horizontal dentition of *S. macrota*, however, include isolated teeth that share the same positional attributes, but vary in size. The teeth to the left or right of the centermost teeth of each half of the upper and lower jaws are from progressively younger (smaller) individuals.

**PHOTOGRAPHIC LAYOUT**

Teeth are photographed lingual side up except for some examples of posteriors (as noted). The teeth of the upper and lower jaw are oriented with the crowns pointing down to facilitate their comparison. Photographs of teeth in the anterior and intermediate positions include two teeth from each side of the jaw for each position, to demonstrate consistent positional characteristics in spite of slight individual variation. Photographs of lateral and posterior teeth include only one tooth for each position, from one side of the jaw, as their exact lateral or posterior position is less definable for isolated teeth, and there is a greater degree of individual variation than in anterior positions. Photographs of posterior teeth include examples from opposing sides of the jaw, labial side up, to show inflation and wrinkling of the base of the enamel. Measurements shown in photographs are in metric units.

**POSITIONS OF THE UPPER JAW**

**First upper anterior position**

Previously described as a “symphyseal” (White, E.I,. 1931:61), these teeth, although smaller than the second and third anteriors are sufficiently similar to them to be regarded as "anteriors" rather than "symphyseals". The use of the word "symphyseal" was proposed by Leriche, 1905, and has been widely used to describe the file of teeth closest to the symphysis (midline where the left and right halves connect) of the jaw. Applegate, 1965, proposed additional terms to satisfy these arrangements; "medial" for teeth growing on the midline of the jaw, or median, and any identical adjacent teeth; "alternate" for teeth that are next to the midline, but are not symmetrically arranged on either side of the midline; and "symphyseal" for highly compressed, asymmetrical teeth, symmetrically arranged on either side of the midline, that depart in appearance from adjacent anterior teeth. These terms have not been generally adopted. The term "parasymphyseal" is sometimes used in order to distinguish between those teeth that origination or straddle the symphysis, and those that are placed alongside it. More recently Siverson (1999: 55) restricted the term "symphysial" to those teeth developing on and between the symphysial bars. Those teeth arising within the anterior hollows, become, by definition anterior teeth.

The teeth of the first upper anterior position in *C. taurus* (Pl. 5, fig. 1) are nearly bilaterally symmetrical, similar in appearance to the second lower anteriors, thus making it difficult to sort the teeth of these two positions. Excluding size, they appear to be the same tooth. Both are well curved lingually, and measure the same angle of root-lobe divergence, but the crown-tip of the second upper anterior is strongly recurved labially, unlike the first lower anterior, the crown-tip of which is just slightly recurved (Pl. 5, fig. 3). This is the most useful diagnostic feature when comparing teeth of the two positions. Less obvious, but also diagnostic, is the depth of the interspace between the root-lobes; which is deeper in the second lower anterior teeth than in the first upper anterior teeth.

The root-lobes of the first upper anterior teeth are almost the same length, but careful observation will determine the distal lobe to be longer.

The cutting edges of the teeth in the first upper anterior position are nearly complete. Even though the edge fades, a distinct line can be traced to the base of the enamel. The cutting edge separates the weakly inflated labial side of the crown from the strongly inflated lingual side.

Additional inflation is present at the base of the labial side of the enamel. This inflation is bisected by a short, perpendicular ridge, present on all of the anterior teeth and the larger lateral teeth of the upper and lower jaw. The basal area of the labial enamel, in the interspace between the root-lobes, shows fine, hair-like wrinkles where the enamel blends into the root.

When sorting isolated *S. macrota* teeth, especially when individual variation is present, these characters are most reliable for separating first upper from second lower anterior teeth.

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**Plate 4. The horizontal dentition**

**1.** *C. taurus* natural horizontal dentition of the entire upper and lower jaw, lingual view. This arrangement includes all of the teeth extracted from the *C. taurus* jaw used for this study. Some of the teeth are broken or have not fully developed. Teeth of the left and right side of the upper jaw are on the left half of the layout and teeth of the right and left side of the lower jaw are on the right half. The files of teeth are organized horizontally. The first anterior files of teeth for the upper and lower jaw are at the top of the layout and subsequent files are organized beneath the previous files. Posterior files of the upper and lower jaw are at the bottom of the layout. All of the teeth are pointing down. While the positions are represented vertically, the files of the left and right side of the jaw, for each position, are organized in a single horizontal row. The eye has fewer perspective changes and less distance to travel while studying tooth variation and positional attributes. Developed for the study of isolated fossil teeth. the horizontal dentition is used for *C. taurus* to aid in comparing the teeth with those of *S. macrota*. Note that the teeth of each file in a natural dentition (from a single individual) appear to be the same size. Mag. x 0.66.

**2.** *S. macrota* artificial horizontal dentition. lingual view. Arranged the same as Pl. 4, fig. 1, the isolated fossil teeth of each horizontal file are from progressively younger (smaller) individuals. unlike a natural dentition (from a single individual) in which the teeth of each file appear to be the same size. Developed for the study of tooth variation for each position, the horizontal dentition offers a broader reference for species identification than the traditional study set (Pl. 2. figs 1,2). Mag. x 0.66.

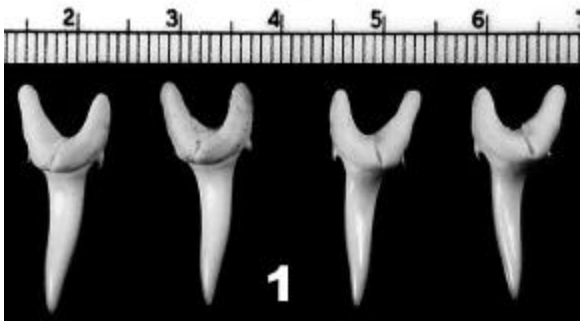
The first upper and second lower anterior teeth are so similar in appearance that the first upper anteriors could easily be included as small second lower anteriors while constructing an artificial tooth set, thus eliminating the first upper position altogether. While *S. macrota* first upper and second lower anterior teeth exhibit less curvature lingually than *C. taurus*, the same distinctive recurvature of the crown-tip is present on all of the first upper anterior teeth (Pl. 5, fig. 4), as is the deeper interspace on second lower anterior teeth. The cutting edges are nearly complete on the first upper anteriors. The root-lobes of each first upper anterior are nearly equal in length, but the distal lobe is longer on the best preserved teeth.

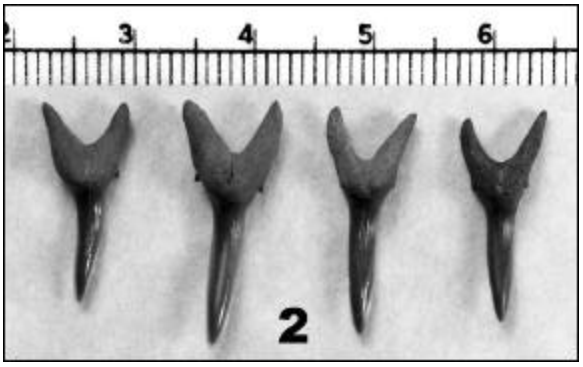
As in *C. taurus*, there is additional mild inflation of the basal part if the labial side of the enamel followed by the same fine, hair-like wrinkles in the area where the enamel blends into the root on some teeth. The tiny perpendicular ridge bisecting the inflated portion of the base of the labial enamel, is variable; on some teeth it is missing or replaced by a depression or fold in the enamel.

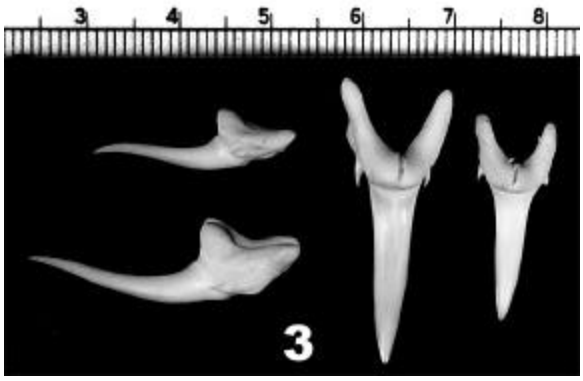
The high degree of variation of this ridge on isolated teeth make this a poor positional feature. Wrinkles in the area at the root/crown junction are also variable; some teeth do not clearly show them. However, when present, their coarseness can offer positional clues. Wrinkling of the labial base of the enamel becomes exaggerated in more distal tooth files.

**Second upper anterior position**

The teeth of the second upper anterior position in *C. taurus* (Pl. 6, fig. 1) are clearly different from the first upper anteriors. While the first upper anterior teeth are nearly bilaterally symmetrical, the second upper anteriors are not. The second upper anteriors are, in *Carcharias* and *Striatolamia*, so distinctive that they can be separated at a glance from isolated teeth. The mesial root-lobe and crown-edge form an almost straight line, but the distal lobe and crown-edge form an obtuse angle. The crowns and cutting edges of the first two upper anterior teeth are similar in appearance, but the roots are distinctly different. The mesial root-lobe of the second upper anterior is compressed



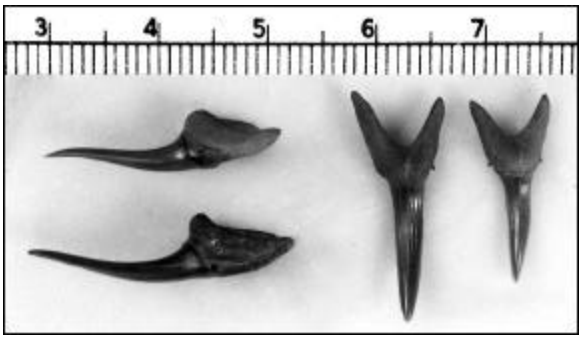



**Plate 5. First upper anterior position (with comparison to first lower anterior)**

**1.** *C. taurus* teeth of the first upper anterior position, lingual view. The two leftmost teeth are from the left side of the upper jaw, and the two teeth on the right are from the right side.

**2.** *S. macrota* teeth of the first upper anterior position, lingual view. The two leftmost teeth are from the left side of the upper jaw, and the two teeth on the right are from the right side.

**3.** *C. taurus* teeth of the first upper and second lower anterior positions, profile and lingual view. Top left and far right are first upper anterior teeth. Bottom left and middle are second lower anterior teeth. Note the extent of labial recurvature of the crown-tip on the first anterior tooth, top left. The second lower anterior tooth, bottom left, has very little labial recurvature.

**4.** *S. macrota* teeth of the first upper and second lower anterior positions, profile and lingual view. Top left and far right are first upper anterior teeth. Bottom left and middle are first lower anterior teeth. Note the extent of labial recurvature of the crown-tip on the first upper anterior tooth. top left. The second lower anterior tooth , bottom left, has very little labial recurvature. The recurvature of the crown tip is the most consistent difference between these two positions.

mesio-distally and the distal root-lobe is compressed labio-lingually. Unlike the first upper anterior teeth, the mesial root-lobe is longer.

The crown is curved lingually with the same strong recurvature of the crown-tip as in the first upper anteriors, and the cutting edges are nearly complete. The angle of root-lobe divergence is greater than that of the first upper anterior teeth (Pl. 6, fig. 3). The labial base of the enamel is inflated, followed by, in the area of the bottom of the interspace were the enamel blends into the root, the same fine, hair-like wrinkles as on the first upper anterior teeth.

The second upper anterior teeth in *S. macrota* (Pl. 6, fig. 2) are even more distinctive than in *C. taurus.* Neither the broad crown nor the root resemble the first upper anterior teeth.

The longer mesial root-lobe of *S. macrota* second upper anterior shows individual variation. Some of these lobes are compressed mesio-distally, while some do not appear compressed at all. This variation might be due to erosion and wear, although the distal lobe is reliably compressed labio-lingually, as in *C. taurus.* In large adults a hump is often present on the dorsal edge of the distal root-lobe (Pl. 6, fig. 3, second from right).

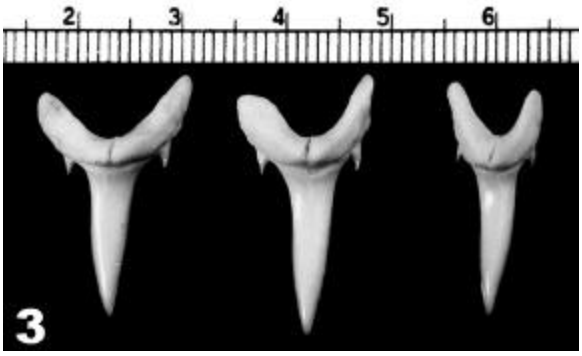
The crown is only slightly curved lingually and is so strongly recurved that when laid on its labial face, the crown-tip contacts the surface on which it rests. The cutting edges are nearly complete.

The angle of root-lobe divergence is much greater than that of the first upper anterior teeth (Pl. 6, fig. 4) and consistent, regardless of the variation of the root-lobes. The root-lobes of the second upper and third upper anterior teeth of *S. macrota* are so divergent, it challenges the imagination to find enough room for three upper anterior positions in the jaw. However, root-lobes do not complete their development until well forward in the file (Pl. 3), at which time the root-lobes slightly overlap in an alternating pattern with adjacent teeth in anterior positions.

There is mild inflation on the base of the labial enamel, followed by the same hair-like wrinkles, on some teeth, as in *C. taurus.*

**Third upper anterior position**

The unusual teeth of the third upper anterior position defy positional assignment when learning to construct artificial dentitions. Most teeth in a shark's jaw slant distally (away from the midline) of the jaw, but the crown of the third



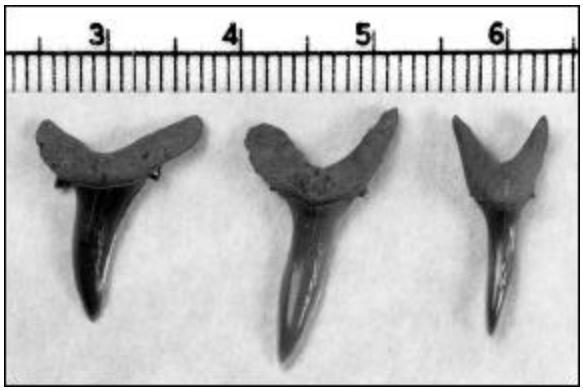


**Plate 6. Second upper anterior position and root-lobe divergence in upper anterior positions**

**1.** *C. taurus* teeth of the second upper anterior position. lingual view. Two teeth from the left side of the upper jaw, on left, and two teeth from the right side. Note the flattened distal root-lobe on each tooth. The tip of the first tooth on the right is broken, probably from feeding damage.

**2.** *S. macrota* teeth of the second upper anterior position, lingual view. Two teeth from the left side of the upper jaw, on left, and two teeth from the right side. The second tooth from the right shows a variation of the distal root-lobe typical of large adult teeth.

**3.** *C. taurus* teeth of the left upper anterior positions, lingual view. Rightmost tooth is the first upper anterior, middle is second, and third from the right is the third upper anterior. The angle of root-lobe divergence increases as the positions progress further from the midline of the jaw (starting from the right).

**4.** *S. macrota* teeth of the left upper anterior positions, lingual view. First position is on the right, second in the middle and third upper anterior on the left. The angle of root-lobe divergence increases as the positions progress away from the midline of the jaw (starting from the right).

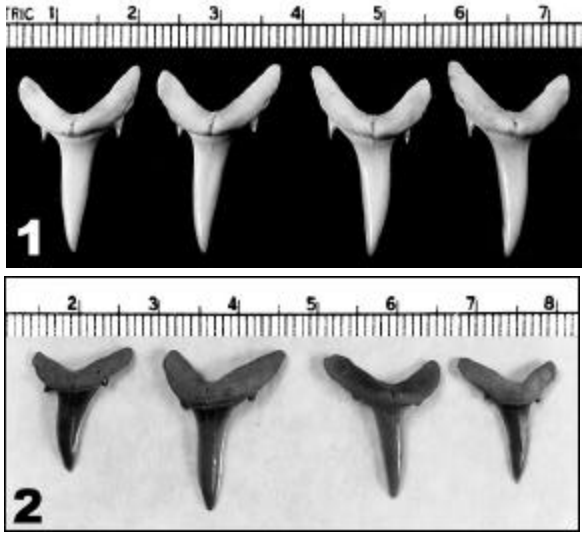


**Plate 7. Third upper anterior position**

**1.** *C. taurus* teeth of the third upper anterior position, lingual view. Two teeth from the left side of the upper jaw, on left, and two from the right side. Note that the concave mesial edge and convex distal edge make these teeth appear to curve toward the midline of the jaw.

**2.** *S. macrota* teeth of the third upper anterior position, lingual view. Two teeth from the left side of the upper jaw, on left, and two from the right side. As in *C. taurus,* these teeth appear to curve toward the midline of the jaw.

upper anterior, has a straight or slightly concave mesial edge and a convex distal edge, appears to curve mesially. This is to conform to the distal margin of the anterior hollow in the palatoquadrate (Siverson 1999: fig 3a).

The longer mesial root-lobe of the third upper anterior of *C. taurus* is just slightly compressed labio-lingually, while the distal lobe is so compressed that the distal side of the lingual protuberance and distal lobe appears collapsed.

The crown has a slight lingual curve and a strong recurvature, as in the first and second upper anterior teeth. Unlike the first and second upper anteriors, the cutting edges are complete. The angle of root-lobe divergence is greater than that of the previous two anterior teeth (Pl. 6, fig. 3). The inflation and hair-like wrinkles on the labial base of the crown are the same as on the first two upper anterior teeth.

The mesial and distal root-lobes of the third upper anterior teeth of *S. macrota* (Pl. 7, fig. 2) are compressed labio-lingually as in *C. taurus.* The mesial root-lobe is longer than the distal. The crown is not curved lingually, but does show a strong recurvature of the crown-tip. Thus, when placed labial side down, the tip of the crown prevents the remaining enamel from contacting the surface on which it rest. As in *C. taurus,* the cutting edges appear complete, unlike the not quite complete edges of the first two upper anterior teeth. The angle of root-lobe divergence is greater than that of the teeth in the previous two positions (Pl. 6, fig. 4). Mild inflation of the labial base of the enamel is present, followed by fine wrinkles on some teeth.

**Intermediate position**

Intermediate teeth are teeth that originate on the intermediate bar between the anterior hollow and the lateroposterior hollow of the palatoquadrate (Siverson, 1999: fig 3a). They are generally small labio-lingually flattened teeth. The term "intermediate" is also used, incorrectly, for reduced upper anterior teeth in other lamniform genera, for example, *Isurus* and *Carcharodon*.

The *C. taurus u*sed here had one intermediate tooth position on each side between the third upper anterior and first upper lateral files (Pl. 8, fig. 1).

The intermediate teeth measure about one third the vertical height of the third upper anterior teeth. The vertical height of the root is approximately equal to that of the crown, and the root-lobes are highly compressed labio-lingually, rendering them thin and delicate. The tips of the root-lobes are rounded and the lingual surface of the lobes is flat. The interspace between the lobes is shallow, and the trend of ever increasing root-lobe divergence is broken here, the angle being less than that of the third upper anterior teeth. The crown is narrow and lingually curved, the cutting edges are complete, and there is very weak inflation of the labial base of the enamel followed by fine wrinkles in the area of the interspace were the enamel blends with the root.

Of the fossil material collected, two teeth (Pl. 8, fig. 2) were found that resemble the intermediate teeth of *C. taurus.* Their inclusion into the *S. macrota* artificial dentition is supported by the presence of striations on the lingual side of the crown. The vertical height of the roots is approximately equal to that of the crowns, the root-lobes are highly

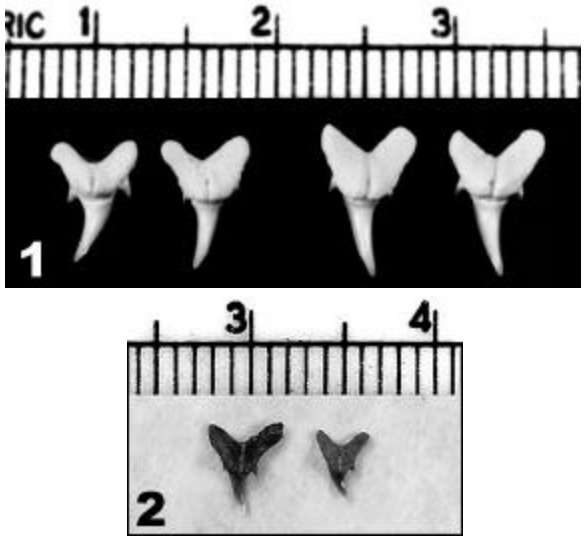


**Plate 8. Intermediate position**

**1.** *C. taurus* teeth of the intermediate position, lingual view. Two teeth from the left side of the upper jaw, on left, and two from the right side. This position is between the third upper anterior and the first upper lateral files of teeth. Note the flattened root-lobes. Even though these teeth came from one individual, they show variation of form and size.

**2.** *S. macrota* intermediate teeth, lingual view. Two from the right side of the upper jaw were the only ones collected. Note their similarity to *C. taurus*' intermediate teeth.

compressed labio-lingually, flattened in appearance, and the interspace is shallow, as in *C. taurus*. The tiny crown is lingually curved with complete cutting edges.

A problem occurs, however, with the number of teeth collected. Except for the intermediate (and 1st lower anterior) teeth, sufficient numbers of *S. macrota* teeth were collected from the fossil material to establish a reasonable certainty of their positional assignments. Only two intermediate teeth were collected suggesting that this position may not always be present. Alternatively, the delicate nature of these tiny teeth may result in few being preserved in the fossil record.

Case (1994) described two "species" of odontaspid: *Pseudodontaspis lauderdalensis* and *P. mississippiensis* on dentitions based on solely isolated intermediate teeth.

**Upper lateral positions**

Lateral and posterior teeth are those that originate in the lateroposterior hollow of the palatoquadrate. Their separation is gradational and thus somewhat arbitrary.

The upper lateral teeth of *C. taurus* (Pl. 9, fig. 1) differ markedly from anterior teeth. Their root-lobes have a very wide angle of divergence, greater than that of the upper anterior and intermediate teeth, with less of a lingual protuberance. The angle of root-lobe divergence remains constant throughout the upper lateral files. In the most anterior files of lateral teeth the mesial root-lobe is longer than the distal. The distal lobe tends to be broader and more rounded at the tip. However, as the lateral files progress toward the articulation of the jaw, the lobes tend to be more bilaterally symmetrical.

The crowns become shorter than those of the anteriors, relative to the width of the root-lobes. The lingual surface is less inflated and broader at the base of the enamel, giving the lateral teeth a somewhat flattened appearance. The cutting edges are complete on the upper lateral teeth. As the files progress toward the articulation of the jaw, the vertical height of the crown increases through the third lateral tooth, after which the height decreases, and the crowns become more distally slanted. But for a mild labial curve of the crown-tip, all of the upper lateral teeth lay flat when placed labial side down. Inflation of the labial base of the enamel is mild in the most anterior lateral files, as on teeth in the anterior positions, but becomes more pronounced as the laterals progress toward the posterior.

The wrinkles in the labial area where the enamel blends with the root become more pronounced during this progression, and extend into the inflated base of the enamel.

The first upper laterals form a distinctive, easily recognized, file in having a lower, more distally directed crown, and a longer mesial root lobe. This is to accommodate the tooth in the mesial margin of the lateroposterior hollow.

The upper lateral teeth of *S. macrota* (Pl. 9. fig. 2), while being bulkier in appearance than those of *C. taurus*, progress distally in a similar fashion to those of *C. taurus*. Unlike *C. taurus*, the mesial lateral denticle diminishes in size during this progression until, in the most posterior lateral files, it is almost absent. This progression aids in placing the teeth in their respective rows. Individual variation makes it difficult to determine the number of lateral files for *S. macrota*.

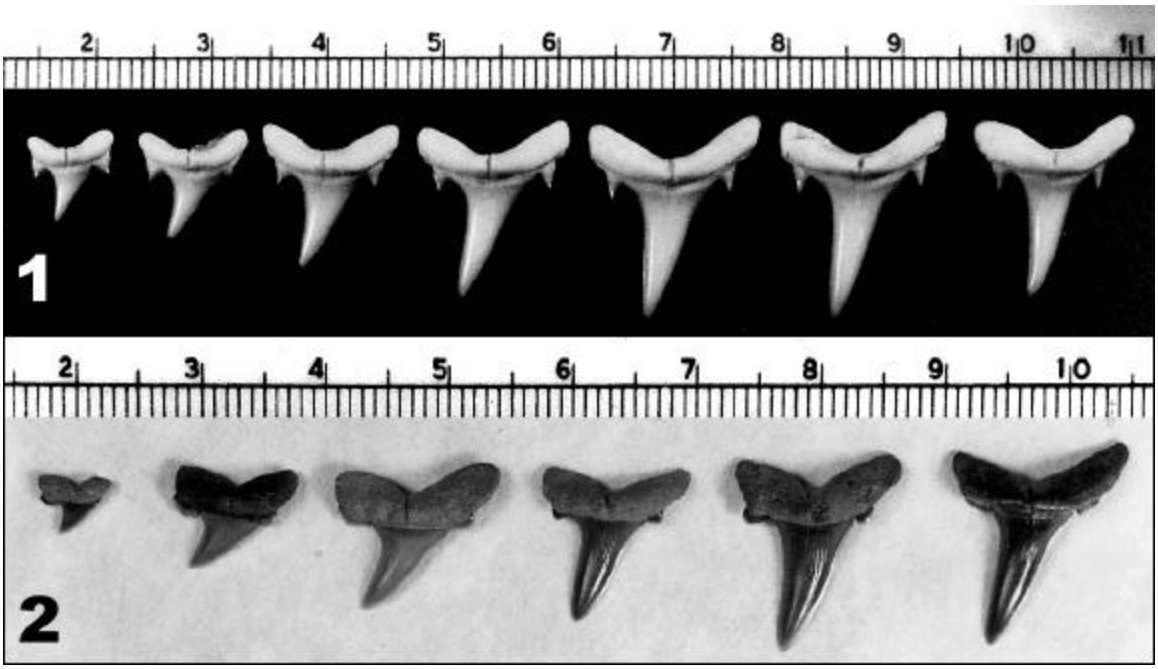



**Plate 9. Upper lateral positions**

**1.** *C. taurus* left upper lateral teeth. lingual view. In this arrangement only one tooth from each upper lateral file is shown. The tooth to the right is the first lateral file.

**2.** *S. macrota* left upper lateral teeth. lingual view. One tooth from each artificial upper lateral file is shown. Note that the mesial denticle diminishes in size as the teeth progress to the left (toward the posterior).

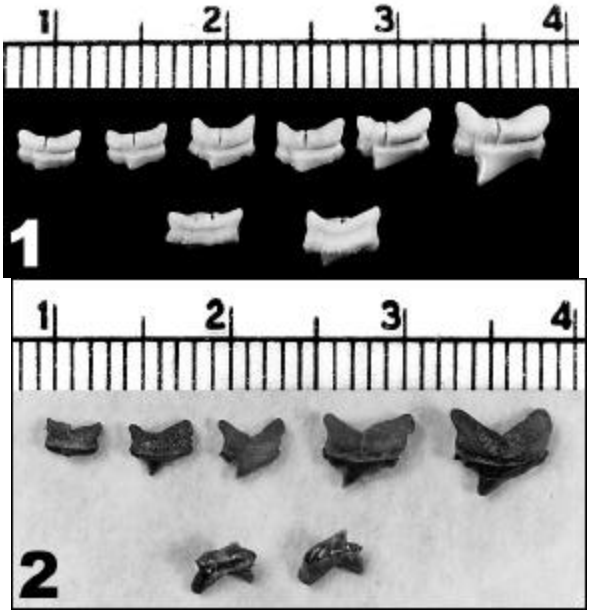



**Plate 10. Upper posterior positions**
**1.** *C. taurus* upper posterior teeth. One tooth from each posterior file of the left side of the upper jaw is included on the top row, lingual view. The bottom row includes two teeth from the right side of the upper jaw, labial view, to show inflation and wrinkling of the labial face of the enamel.

**2**. *S. macrota* upper posterior teeth. Top row includes one tooth from each of the artificial posterior files of the left side of the upper jaw, lingual view. Bottom row includes two teeth from the right side of the upper jaw, labial view, to show inflation and wrinkling of the labial face of the enamel.

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On the most anterior lateral teeth, the labial face of the crown and root form an angle, so that when they are placed labial side down, only the crown-tip and root-lobe tips make contact with the surface on which they rest. In the most posterior lateral positions, the teeth lay flat.

The cutting edges are complete on all of the upper lateral teeth. As in *C. taurus*, the most anterior lateral teeth have a longer mesial lobe, and often broader and more rounded distal lobe. As the laterals progress toward the articulation of the jaw, the lobes maintain this differentiation and are less bilaterally symmetrical than those of *C. taurus*.

In the larger middle lateral teeth, the narrow interspace becomes an abrupt "U" shape on some specimens. The wrinkling on the labial base of the enamel becomes very pronounced as the artificial files progress to the articulation of the jaw, often appearing as distinct folds or ridges. On some specimens the folds extend halfway up the labial surface of the enamel. Some of the lateral teeth show no wrinkling at all.

**Upper posterior positions**

The posterior teeth of *C. taurus* (Pl. 10, fig. 1) exhibit a change of attributes distinguishing them from the upper laterals. After (in this example) the seventh file of upper lateral teeth, the lateral denticles lose most of their definition from the crown, becoming shoulder-like in appearance.

The complete cutting edges continue onto the lateral denticles. The vertical height of the root is approximately equal to that of the crown and the lateral extension of the root-lobes is reduced.

On the most posterior files of teeth, the lateral extension of the lobes disappears, becoming even with the base width of the crown. The angle of divergence of the root-lobes appears less than in the lateral teeth and the lobes are nearly bilaterally symmetrical. The labial base of the enamel becomes strongly inflated with the inclusion of well defined, coarse wrinkles (Pl. 10, fig. 1, bottom row). The amount of inflation and coarseness of the wrinkles help distinguish the posterior teeth from small laterals.

The crown-tip becomes very short relative to the width of the crown and in the most posterior files the crown-tip almost disappears. The root-lobes form a broad "V" shape with a shallow interspace.

As in *C. taurus*, the upper posteriors of *S. macrota* (Pl. 10, fig. 2) show a similar change in attributes from lateral teeth; however, the root-lobes appear more "V" shaped than in *C. taurus*. The distal lateral denticle retains its definition from the crown, but the mesial lateral denticle becomes shoulder-like in appearance. Similar to upper lateral teeth, the labial side of the short crown is straight on upper posterior teeth.

The complete cutting edges continue onto the lateral denticles, as in *C. taurus*. The vertical height of the crown is approximately equal to that of the root, and the lateral extension of the lobes becomes even with the base width of the crown. The root-lobes are nearly bilaterally symmetrical, and there is strong inflation and coarse wrinkling of the labial base of the crown on most of the upper posterior teeth.

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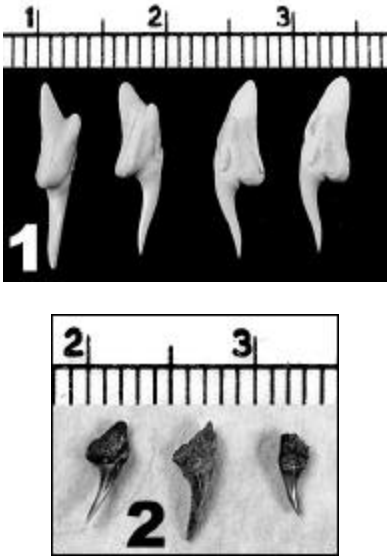


**Plate 11. First lower anterior position**
**1.** *C. taurus* teeth of the first lower position. Two from the right side of the lower jaw, on left, and two from the left side. First tooth on left is lingual view, the rest are profile view. Note the longer distal root-lobe.

**2.** *S. macrota* first lower teeth, in profile view. Two teeth from the right side of the lower jaw, on left, and one from the left side. These teeth are similar in appearance to those of *C. taurus*.

**POSITIONS OF THE LOWER JAW**

**First lower anterior position**

*C. taurus* has one file of small, highly laterally compressed teeth on each side of the midline of the lower jaw (Pl. 11**,** fig. 1). The size and asymmetry distinguish them from adjacent lower anterior teeth. The root-lobes are so convergent and compressed mesio-distally that they are pressed together except at the ends. The distal root-lobe is almost twice the length of the stunted mesial lobe.

Confusion concerning the terms "symphysial" and "intermediate" is a result of two different perspectives; positional and functional. A positional viewpoint allies the compressed, stunted teeth on either side of the lower symphysial bar of *C. taurus* with the lower anterior files, as they share a common origin in the lower anterior palatoquadrate hollow, regardless of their function, while a functional viewpoint clearly distinguishes these teeth as different. However, fossil evidence suggests that the function of sharks' teeth is in constant evolutionary transition. Therefore, deriving tooth terminology from a functional point of view may be less reliable considering that, in evolutionary terms, any given file of teeth can change function while maintaining the same position in the jaw.

Previously these have been referred to as symphysials, but using the same criteria as with the 1st upper anterior, we must refer to this file as 1st lower anteriors.

The total vertical height of the first lower anterior teeth is about half of the second lower anteriors, and the vertical height of the root is approximately equal to that of the crown.

The crown curves lingually with a labially directed recurvature of the crown-tip. The lingual protuberance is so strong that it overhangs the base of the lingual enamel. There is inflation at the labial base of the enamel, but the wrinkles in the area where the enamel blends with the root were not detected on any of the teeth.

The cutting edges are nearly complete. The overall appearance of these teeth is that of compressed and stunted anteriors.

Three fossil teeth were found (Pl. 11, fig. 2) corresponding to *C. taurus* first lower anterior teeth. As with the intermediates, these teeth are not supported by sufficient numbers (see intermediate position). Nevertheless, as in *C. taurus* the root-lobes appear convergent and mesio-distally compressed even though the tips of the lobes have been worn off.

The lingual protuberance is strong and overhangs the base of the enamel (Pl. 11, fig. 2, left most tooth). Weak striations appear on the lingual surface of the enamel, and the cutting edges are nearly complete.

There is inflation of the labial base of the enamel, but no wrinkles are present. The crown is lingually directed with a mild labial recurvature of the crown-tip. As in *C. taurus*, the overall appearance of these teeth is of stunted and compressed lower anteriors.

**Second lower anterior position**

With the exception of the similarities between first upper and second lower anterior teeth, the crowns of the lower anterior teeth in *C. taurus* and *S. macrota* appear narrower, more inflated and more lingually curved than do their upper counterparts. As in the upper anteriors, the root-lobes become more divergent as the lower anterior files progress further from the midline of the jaw.

The second lower anterior teeth of *C. taurus* (Pl. 12, fig. 1) are strongly curved lingually, with a mild labial recurvature.

The lingual protuberance is strong, and each root-lobe is compressed mesio-distally, with an angle of divergence equal to that of the teeth of the first upper anterior position.

The distal root-lobe is just slightly longer than the mesial, adding to the difficulty of sorting these teeth from the first upper anteriors (see first upper anterior position). The only teeth that have a longer distal root-lobe, in the entire jaw, are the first upper anterior, first and second lower anterior teeth. Except for the longer distal lobe, and slight distal slant of the crown, the second lower anterior teeth appear bilaterally symmetrical.

The cutting edges are nearly complete. The labial base of the enamel shows stronger inflation than the upper anterior teeth, with coarser wrinkles in the area of the interspace where the enamel blends with the root.

The teeth of the second anterior position of *S. macrota* (Pl.

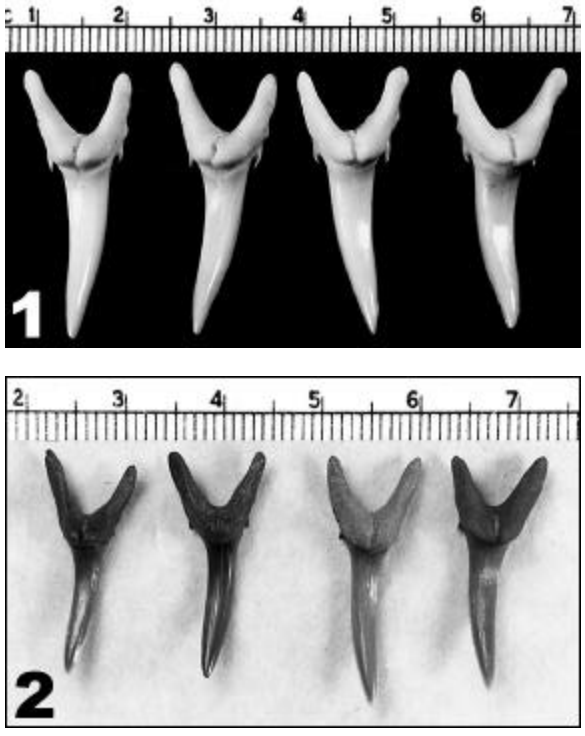


**Plate 12. Second lower anterior position**

**1.** *C. taurus* teeth of the second lower anterior position, lingual view. Two teeth from the right side of the lower jaw, on left, and two teeth from the left side. These teeth are similar in appearance to the first upper anterior teeth (compare with PI 5, fig. I).

**2.** *S. macrota* teeth of the second lower anterior position, lingual view. Two teeth from the right side of the lower jaw, on left, and two teeth from the left side. The teeth are very similar in appearance to the first upper anterior teeth (compare with PI. 5, fig. 2).

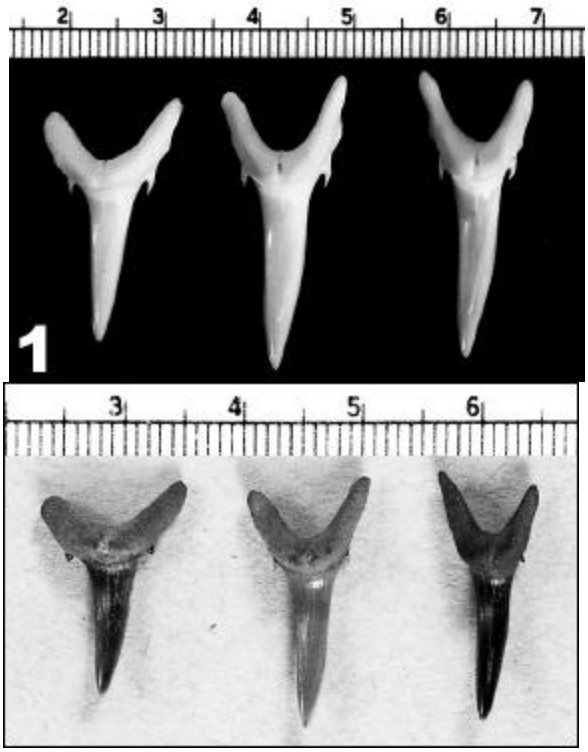

**Plate 13. Root-lobe divergence in lower anteriors**

**1.** *C. taurus* teeth of the right lower anterior positions. lingual view. The rightmost tooth is the second lower anterior. middle is the third. and leftmost is the fourth lower anterior tooth. As with the upper anterior teeth. the angle of root-lobe divergence increases as the positions progress away from the midline of the jaw (starting from the right).
**2.** *S. macrota* teeth of the right lower anterior positions. lingual view. The rightmost tooth is the second lower anterior. middle is the third. and leftmost is the fourth lower anterior. As in *C. taurus*. the angle of root-lobe divergence increases distally (starting from the right).

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12, fig. 2) bear a strong resemblance to those of *C. taurus*. If both species were extant today, the second lower anterior teeth of each would be indistinguishable.

The crown is strongly curved lingually, with a mild recurvature, and the cutting edges are nearly complete. The root-lobes are compressed mesio-distally, and have an angle of divergence equal to those of the first upper anterior teeth.

The teeth of the lower anterior positions show the same increase in the angle of root-lobe divergence as in *C. taurus* (Pl. 13, figs 1, 2). In Pl. 12, fig. 2, left most tooth, the distal root-lobe is longer than the mesial, as in *C. taurus* but, due to the possibility of erosion and wear, this may not be a good diagnostic factor in isolated fossil teeth.

The inflation of the labial base of the enamel and wrinkles in the area where the enamel blends with the root are similar in appearance to teeth of the upper anterior positions.

**Third lower anterior position**

The teeth of the third lower anterior position of *C. taurus* (Pl. 14, fig. 1) are very similar in appearance to those of the second lower anterior position. The mesial root-lobe is longer and thinner than the distal on the third lower anterior teeth, and the angle of root-lobe divergence is greater than the second lower anterior teeth.

These teeth have the largest vertical height and the strongest lingual protuberance of the *C. taurus* anteriors. The crown is strongly curved lingually with a mild labial recurvature, and the cutting edges are nearly complete.

The inflation of the labial base of the enamel is present and, like the second lower anterior teeth, the wrinkles are more pronounced than on those of the upper anterior positions.

The corresponding teeth of *S. macrota* (Pl. 14, fig. 2) also are similarly recurved, and have a strong lingual protuberance. These teeth account for some of the longest *S. macrota* teeth found. The cutting edges are nearly complete.

The mesial root-lobe is longer and thinner than the distal lobe on well preserved teeth and the angle of root-lobe divergence is greater than in teeth of the second lower anterior position (Pl. 13, fig. 2). This increase of divergence, even though it is slight, helps distinguish these teeth from the similar looking second lower anteriors.

The inflation at the base of the labial enamel and subsequent wrinkles where the enamel blends with the root, are similar to the upper anterior teeth.

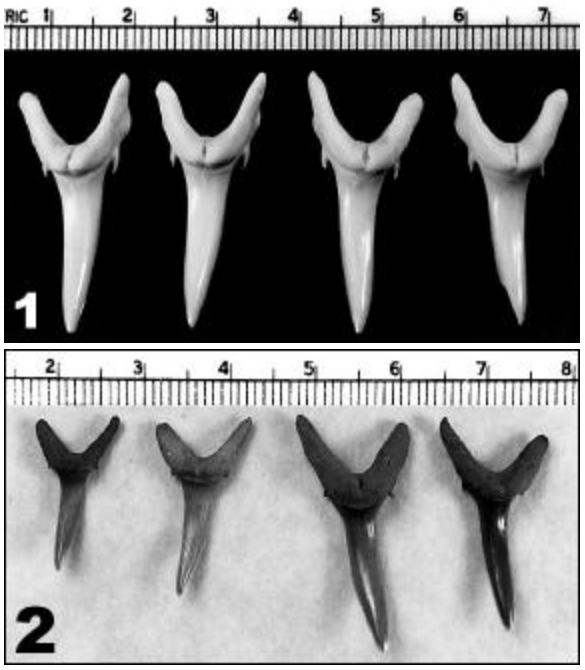

**Plate 14. Third lower anterior position**

**I.** *C. taurus* teeth of the third lower anterior position, lingual view. Two teeth from the right side of the lower jaw, on left, and two teeth from the left side.

**2.** *S. macrota* teeth of the third lower anterior position, lingual view. Two teeth from the right side of the lower jaw, on left, and two teeth from the left side.

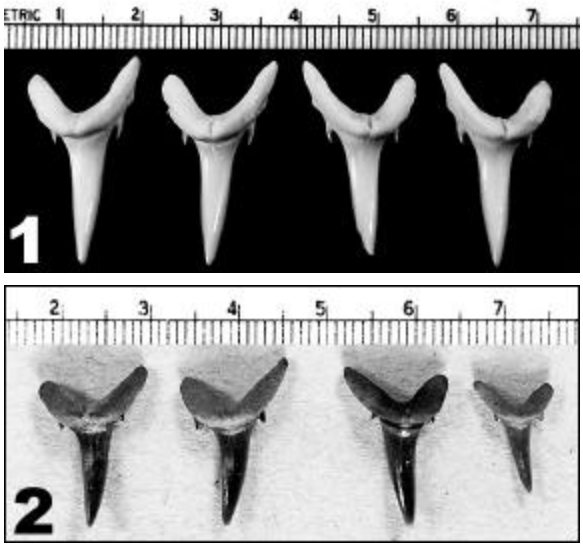

**Plate 15. Fourth lower anterior position**
**1.** *C. taurus* teeth of the fourth lower anterior position, lingual view. Two teeth from the right side of the lower jaw. on left. and two teeth from the left side. The tip of the tooth second from the right is broken, probably from feeding damage.
**2.** *S. macrota* teeth of the fourth lower anterior position, lingual view. Two teeth from the right side of the lower jaw, on left, and two teeth from the left side.

**Fourth lower anterior position**

The teeth of the fourth lower anterior position of *C. taurus* (Pl. 15, fig. 1) show more variation of the root-lobes than those of the second and third lower anteriors.. The longer mesial lobe is somewhat compressed mesio-distally, and the distal lobe is compressed labio-lingually. The angle of divergence is greater than that of the third lower anterior teeth, and the lingually curved crown is more labially recurved and slanted more distally than those of the second and third lower positions. The cutting edges are nearly complete and the inflation on the labial base of the crown, and subsequent wrinkles, are similar to the second and third lower anteriors.

Except for a bulkier appearance of the root, the fourth lower anterior teeth of *S. macrota* (Pl. 15, fig. 2) look very much like those of *C. taurus*. The longer mesial root-lobe is compressed mesio-distally, and the distal lobe is compressed labio-lingually. The angle of root-lobe divergence is greater than the third lower anterior teeth. The lingually curved crown shows more recurvature of the crown-tip than the second and third lower anteriors, similar to *C. taurus*. The cutting edges are complete and the swelling at the labial base of the enamel is stronger, with coarser wrinkles below, than the first two lower anteriors. As in *C. taurus*, the teeth of this position show more positional uniqueness than the teeth of the second and third lower anterior positions.

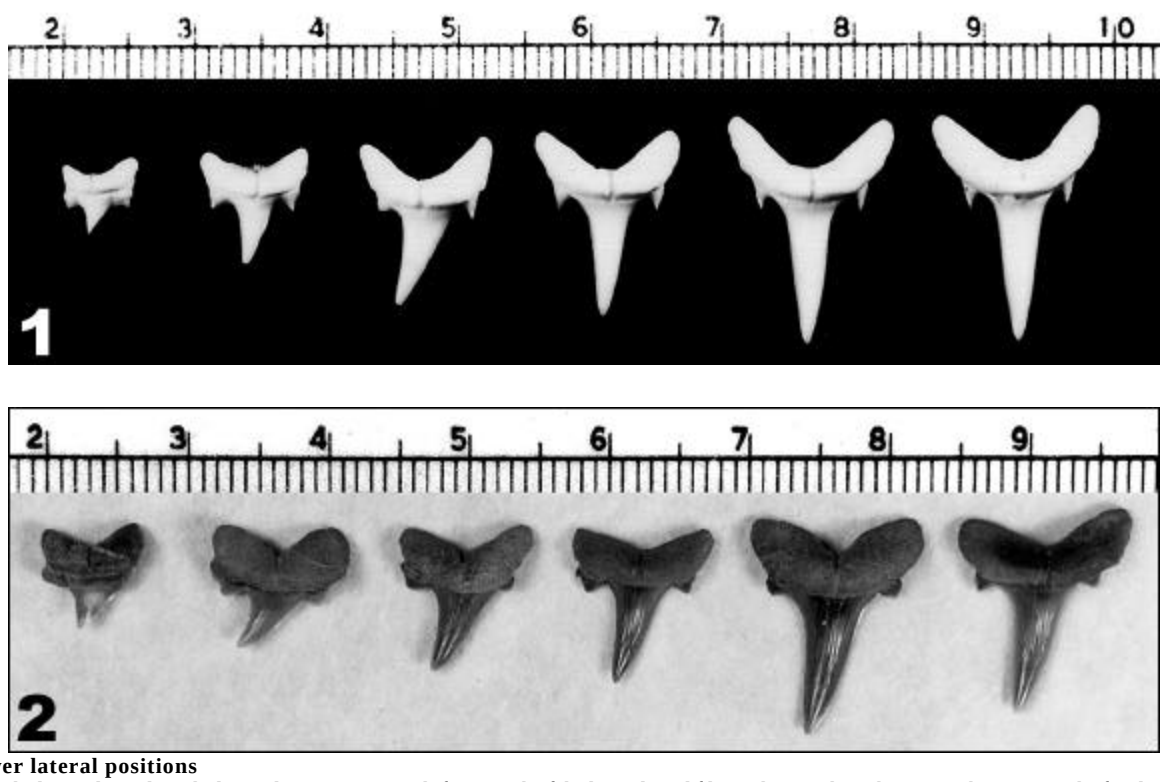

**Plate 16. Lower lateral positions**
**1.** *C. taurus* right lower lateral teeth. lingual view. One tooth from each of the lower lateral files is shown. The rightmost tooth represents the first lower lateral file.
**2.** *S. macrota* right lower lateral teeth, lingual view. One tooth from each of the artificial lower lateral files is shown. The three teeth with the unusual double distal lateral denticles could be from the same individual. These teeth represent the greatest departure from the overall appearance of the *C. taurus* dentition. The rightmost tooth represents the first lower lateral file.

**Lower lateral positions**

The lower lateral teeth in *C. taurus* (Pl. 16, fig. 1) are not as flattened as the upper laterals. They all have shorter crowns, relative to the width of the roots, than the lower anterior teeth.

The root-lobes, equal in length, are somewhat compressed labio-lingually and the narrow crowns tend to be less distally slanted as they progress toward the articulation of the jaw than those of the upper laterals. The angle of divergence of the root-lobes, constant throughout the lower lateral files, is approximately equal to that of the third lower anterior teeth. The lower lateral teeth appear to be bilaterally symmetrical except in the most posterior files, where the crowns become more distally slanted.

The crowns are lingually curved with a mild recurvature of the crown-tip and, when placed labial side down, arch away from the surface on which they rest. The cutting edges are complete.

The base of the labial enamel shows inflation and, in the most posterior files of lateral teeth, becomes very pronounced with coarse wrinkles in the area where the enamel blends into the root.

The lower lateral teeth of *S. macrota* (Pl. 16, fig. 2) maintain the same blade-like appearance as the upper lateral teeth, making them difficult to distinguish from their upper counterparts. The easiest way to sort them is by placing them labial side down. As in *C. taurus,* the crown-tips of the lower lateral teeth arch away from the surface on which they rest.

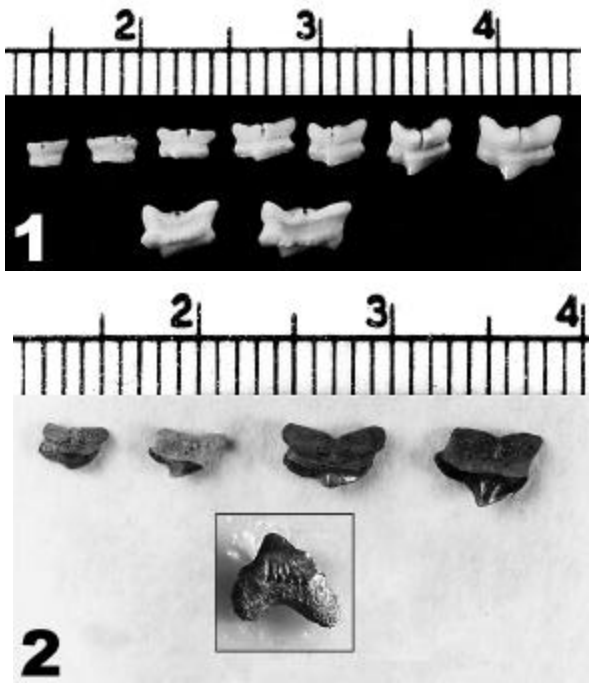


**Plate 17. Lower posterior positions**

**I.** *C. taurus* lower posterior teeth. Top row shows one tooth from each of the right lower posterior files, lingual view. Bottom row includes two teeth from the left lower posterior files, labial view, to show inflation and wrinkling of the labial enamel.

**2.** *S. macrota* lower posterior teeth. Top row includes one tooth from each of the artificial right lower posterior files, lingual view. Inset (same scale) includes one tooth from the right side, labial view, to show wrinkling of the labial enamel.

The lateral denticles of the teeth tend to be more triangular than on the upper laterals, and the mesial lateral denticle is reduced in size as the artificial files progress to the posterior positions.

The root-lobes are bulkier than those of the upper laterals. Unlike *C. taurus* lower laterals, the mesial lobe is longer on the most anterior lateral files, similar to the upper laterals. However, in the most posterior lower lateral files the root-lobes become equal in length. The crowns are lingually curved with a very mild labial recurvature of the crown-tip and the cutting edges are complete.

The swelling of the labial base of the enamel becomes more pronounced as the artificial files progress toward the articulation of the jaw, the basal wrinkles extend through the inflation and, in some specimens, continue onto the labial surface of the crown. As in the upper laterals, some specimens showed no wrinkling at all.

As with the first upper lateral, the first lower lateral is easily recognized in having a lower, more distally directed crown, and a longer mesial root lobe. The first lower lateral in *C. taurus* is not distally inclined (see Pl. 16).

Lower posteriors The lower posterior teeth of *C. taurus* (Pl. 17, fig. 1) differ in appearance from the lower lateral teeth, in the same way as those of the upper jaw. The lateral denticles loose their definition from the crown and the teeth become broad and squat, with roots and crowns of approximately equal vertical height. They are very similar in appearance to the upper posteriors, except for a lingual curvature of the tiny crown. The complete cutting edges are not interrupted as they continue onto the shoulder-like lateral denticles. As the posterior files progress toward the articulation of the jaw, the lateral extension of the root-lobes is equal to the base of the crown and the interspace becomes very shallow.

The lingual curvature of the crown is the criterion for separating the lower posterior teeth of *S. macrota* (Pl. 17, fig. 2) from the upper posterior teeth. The interspace between the root-lobes is shallower and more "U" shaped than those of the upper posteriors and the lobes are bulkier in appearance. The lateral extension of the lobes is equal to the width of the base of the crown as in *C. taurus.* As on the upper posteriors, the mesial lateral denticle disappears in the most posterior files. The complete cutting edges continue onto the lateral denticles without interruption. The swelling at the labial base of the enamel, and coarse wrinkling, becomes very pronounced on most of the lower posterior teeth.

**CONCLUSIONS**

When sufficient numbers of isolated fossil shark teeth are collected from the same locality, their positions in the jaw can be deduced with reasonable certainty when they are grouped according to similar characters, *i.e.* shapes, and compared with those of Recent sharks. It is easier for the eye to compare shapes when files of teeth are arranged in horizontal rows with teeth of the upper and lower jaw pointing in the same direction. Examination of the variation of fully developed roots, as well as the crowns of shark teeth, is necessary to help determine position. The nature of inflation and wrinkles on the base of the labial enamel offer positional clues when present; as the positions progress to the

posterior, the inflation becomes more pronounced and wrinkles become coarser on most of the teeth.

Though *S. macrota* is extinct, the positional variation and dental morphology of the teeth closely resemble those of recent *C. taurus.* Isolated *S. macrota* teeth can be arranged in files and form an artificial tooth set similar to the natural dentition of *C. taurus.* The angle of root-lobe divergence in upper and lower anterior teeth increases in both species as the positions progress away from the midline of the jaw. The upper anterior teeth in both species have noticeably stronger labial recurvature of the crown-tip than the lower anterior teeth; The teeth of the lower jaw of both species are curved more lingually than their upper counterparts.

Although this method is a powerful tool for determining phylogenetic relationships, comments on the phylogeny and ontology of *S. macrota* have not been considered.

The positional variation of isolated teeth often leads to taxonomic problems.. Efforts to construct artificial tooth sets for fossil shark species would help eliminate many of these taxonomic problems and help demonstrate the validity of phylogenic conclusions based solely on the study of isolated fossil shark teeth.

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