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QUANTIFYING A POSSIBLE MIOCENE PHYLETIC CHANGE IN *HEMIPRISTIS* (CHONDRICHTHYES) TEETH

Richard E. Chandler, Karen E. Chiswell, and Gary D. Faulkner

ABSTRACT

Using a new MATLAB-based measuring tool, teeth of the fossil shark *Hemipristis serra* from active mining sites were analyzed for changes in size and extent of serrations. Teeth were taken from disturbed sediments of the Late Oligocene – Pliocene Belgrade, Pungo River, and Yorktown Formations at two mining sites in eastern North Carolina. Four populations (approximate ages: 4.5 Ma, 15.2 Ma, 17.35 Ma, and 23.8 Ma) were analyzed and seem to differ in average size and proportion of serrated edge. Linear regression yields two plausible models for the relationship between the population age, the length of tooth edge, and the ratio of the unserrated portion to total edge length. While individual teeth vary, the average tooth length decreases with geologic age of the population. The ratio (unserrated tip length) / (total edge length) is length dependent (larger teeth have a smaller ratio on average), but is also age dependent (older populations generally have a larger ratio). To argue the soundness of these models, teeth from a chronostratigraphically better constrained Miocene deposit were also analyzed and compared to the quarry derived sample populations.

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KEY WORDS: Population statistics; *Hemipristis*; fossil shark teeth; morphological features; phyletic change; Miocene

INTRODUCTION

Fossil specimens collected from float material are usually considered less desirable for paleontological study than those collected in situ. The purpose of this study is to demonstrate that with accurate measurement and appropriate analytical techniques useful conclusions may be drawn about specimen populations, even when the samples have been obtained from active mines and quarries where operations do not permit careful in situ collecting.

The distal edge of upper teeth of the fossil shark *Hemipristis serra* is coarsely serrate with the serrations having a well-defined termination before reaching the tip of the tooth (see Figure 1). Purdy et al. (2001, p. 142) observed that "*Hemipristis* seems to increase in size through its evolutionary history...But is this size increase an evolutionary

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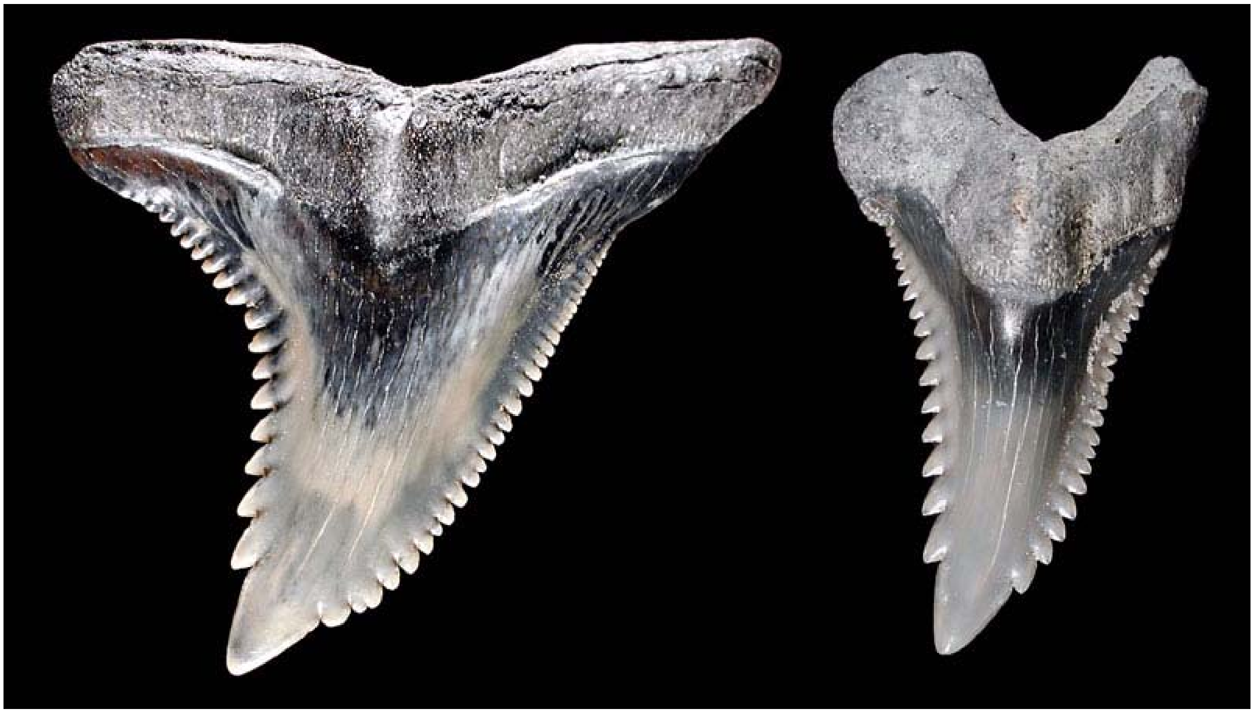

Figure 1. *Hemipristis serra* left upper lateral tooth (25 mm high, lingual view, image at left) and first left upper anterior tooth (right image).

change?" Examination of collections of teeth from the Yorktown Formation (early Pliocene), the Pungo River Formation (early – middle Miocene), and the Belgrade Formation (late Oligocene – early Miocene) of eastern North Carolina supports this observation and also suggests that the ratio (unserrated tip length) / (total edge length) decreases toward the Recent. To quantify these observations a graphics program was developed which provides quick and precise measurement of the necessarily rather small dimensions.

The goal of this study is to offer evidence of a possible phyletic change in *Hemipristis serra* upper lateral teeth which took place during the Miocene and early Pliocene. This particular change (of teeth becoming larger and more completely serrated) is difficult to confirm because it is also an ontogenic change. Several references make similar claims regarding selachian teeth but the present paper uses a statistical model to assess phyletic change in *H. serra*. Leriche (1936) states a general principle: "Lorsqu'une éspèce franchit plusieurs étages successifs, on voit généralement sa taille s'accroître à mesure que l'on s'élève dans ce groupes d'étages. C'est la «loi d'augmentation de taille dons les rameaux phylétiques» énoncée par Depéret (1907, p. 199-210)." ("When a species crosses several successive stages you generally see an increase in its size as you rise through that group of stages. This is the 'law of augmentation of size given by the phyletic branches' enunciated by Depéret."). He then mentions several species which reflect this principle, including "*Odontaspis*" *macrota* (= *Striatolamia macrota*), "*Odontaspis acutissima*" (= *Carcharias taurus*), "*Oxyrhina*" *hastalis* (= *Isurus/Cosmopolitodus hastalis*), and "*Carcharodon*" *megalodon* (= *Carcharocles megalodon*). Depéret's "law" is a variation of a similar principle, today known as Cope's law. Applegate (1986) states that Baja California *Hemipristis* teeth between the middle Oligocene and the late Miocene show a gradual increase in size but offer no evidence for this claim. The landmark paper by Naylor and Marcus (1994) lays a foundation for tracking phyletic change in the various *Carcharhinus* species, an enormously ambitious undertaking. Ward and Bonavia (2001), in a brief outline of an argument for considering *Carcharocles* to be a chronospecies, describe much more qualitatively the phyletic changes in *Carcharocles* teeth between the Eocene and Pliocene epochs.

SYSTEMATICS AND DENTITION

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Subcohort NEOSELACHII Compagno, 1977
Superorder GALEOMORPHII Compagno, 1973
Order CARCHARHINIFORMES Compagno, 1973
Family HEMIGALEIDAE Haase, 1879

Genus *HEMIPRISTIS* Agassiz, 1843
Species *H. CURVATUS* Dames, 1883 (Eocene)
Species *H. SERRA* Agassiz 1843, (Oligocene – Pleistocene)
Species *H. ELONGATA* Klunzinger, 1871 (Recent)

Synonyms for *Hemipristis elongata* include *Dirrhizodon elongatus* (Klunzinger 1871), *Carcharias ellioti* (Day 1878), *Hemipristis pingali* (Setna and Sarangdhar 1946), *Paragaleus acutiventris* (Chu 1960), *Heterogaleus ghardaqensis* (Gohar and Mazhar 1964), and *Hemipristis elongatus* (Compagno 1984) (gender mismatch). This instance is somewhat unusual because a valid fossil name (*Hemipristis*) has historical precedence over a valid extant name (*Dirrhizodon*).

Fossil and Recent teeth of many sharks of the Order Carcharhiniformes are difficult to identify at a species level (Naylor and Marcus 1994). *Hemipristis serra* upper teeth, however, are easily identifiable by anyone at all familiar with shark teeth (Cappetta 1987, p. 118, Hulbert 2001, p. 90). Baranes and Ben-Tuvia (1979) give a typical dental formula for the extant species as $\frac{14-14}{18-18}$ but without identifying the numbers of anterior, lateral, and posterior teeth. On one side of the upper jaw there are two reduced-size teeth adjacent to the midline which are designated as parasymphyseals, followed by two full-sized teeth designated as anteriors, followed by six to seven laterals, and ending with three to four posteriors. The lateral teeth are all rather similar, and it is difficult to assign a precise jaw position to fossil lateral teeth. A *Hemipristis serra* upper lateral tooth (from the Middle Miocene Pungo River Formation) which almost perfectly fits Cappetta's (1987) *Hemipristis* description is pictured on the left in Figure 1. The distal side is to the left.

The specimens used in this study were specifically chosen to be upper lateral teeth. The sacrifice that was made (in order to obtain a relatively large dataset) was the inability to test if jaw position was significant in the measurements that were taken. A better choice would have been to use only the first upper anterior teeth (see Figure 1). This tooth is unique (one on each side of the jaw) and easily identified. Unfortunately, there were statistically insignificant numbers of this tooth in the available samples.

MEASUREMENT PROCEDURES

Using MATLAB (The Mathworks, Inc.) and its included programming tool GUIDE (Graphical User Interface Development Environment) it was comparatively easy to write a macro which would:

- Read in a picture file of teeth obtained from a flatbed scanner set at a fixed resolution (600 dots per inch in this case).
- Enlarge the picture so the appropriate morphological features of the individual teeth could be selected with accuracy.
- Accept computer mouse input to specify measurement points along the edge of the tooth in the picture.
- Calculate the length of the curve through the measurement points to determine the total length of the distal edge of the tooth as well as the length of the unserrated tip.
- Determine the ratio (unserrated tip length)/(total edge length) for the distal edge of each tooth and save this as well as the distal edge length in a file.

The measuring program uses the pixels in the picture file for its coordinate system. Thus one unit in the coordinate system is one pixel in the picture. Since the resolution of the scans was 600 pixels/inch, the program had the theoretical accuracy of 1/600 inches/pixel = .04 mm/pixel. However, tooth details generally could not be resolved down to a pixel level but the measurement techniques were more than adequate for the present purpose. Scans of a precision ruler verified that the method indeed had an accuracy to at least a tenth of a millimeter. Of 10 measurements of a marked 1 cm distance on the ruler, the errors ranged between –0.0303 mm and +0.0869 mm.

Pictures of teeth were obtained from an Epson Perfection 1200 flatbed scanner with a scanning density of 600 pixels per inch. The teeth were aligned horizontally on the scanner bed, scanned one row at a time (so that the picture file size would be relatively small), and the scan saved in a TIFF file. Variations in tooth orientation would have no effect on measurement accuracy because distances were calculated using standard Euclidean geometric methods on the pixels of the picture. The picture files were next opened in a picture editing program and a number label was inserted below each tooth: the left-most tooth was assigned number 01, and the sequence continued left to right.

SPECIMENS

There were seven groups of *Hemipristis serra* teeth used in this study, examples of five are illustrated in Figure 2, with measurements detailed in Table 1. Three groups were purely float samples (collected in overburden removed by mining operations): 51 specimens from the Belgrade Formation, 102 from the Pungo River spoil piles, and 193 from

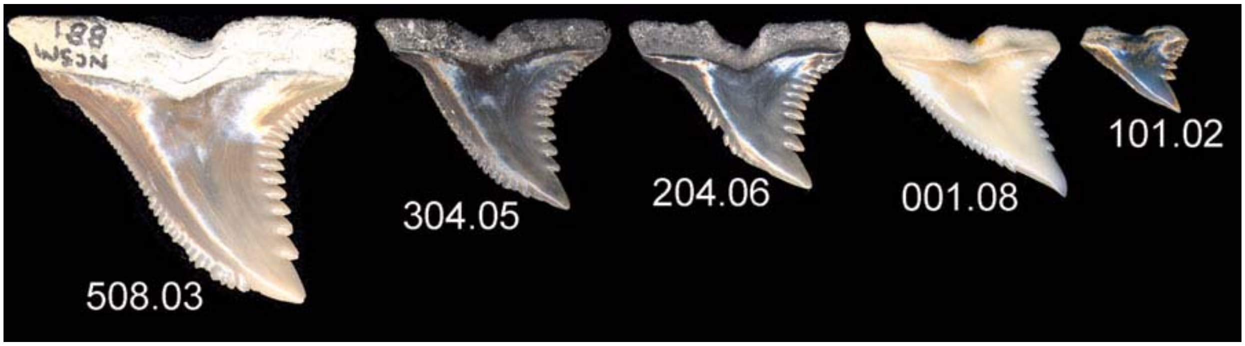

Figure 2. Examples of representative teeth from five of the studied populations (omitting the Pungo River reject and Calvert samples). Each represents an "average" tooth, that is, a tooth close to the mean length and close to the mean ratio in each sample. None of the specimens were exactly "average" but the five pictured are close. Size and locality information for these specimens is listed in Table 1.

Table 1. Measurements for the specimens in Figure 2 compared to sample averages. Specimen number is in the first column with the sample name in parentheses. Length and ratio measurements for each specimen are in the second and third columns with the sample means in parentheses.

Specimen Number	Length	Ratio
101.02 (Santee)	6.47 mm (6.50)	0.46 (0.47)
001.08 (Recent)	12.81 mm (12.65)	0.31 (0.31)
204.06 (Belgrade)	13.43 mm (12.77)	0.27 (0.27)
304.05 (Pungo River)	15.96 mm (16.72)	0.22 (0.22)
508.03 (Yorktown)	21.53 mm (22.39)	0.18 (0.18)

the Yorktown Formation spoil piles. The Pungo River and Yorktown specimens were collected in the PCS Phosphate Mine (Lee Creek) near Aurora, North Carolina, whereas the Belgrade material was collected in the Belgrade Quarry near Maysville, North Carolina.

These three float collections were obtained by experienced collectors, familiar with the appearance of the various formations' sediments. While it is thought that the overwhelming majority of each sample is pure, it is possible, perhaps even likely, that any of the three samples could be contaminated with teeth not from its labeled formation; some mixing is inevitable in mine/quarry operations. One of the points of this research is to show that useful information may be obtained even though some of the specimens likely have questionable data. However, it would be virtually impossible to collect enough specimens for this kind of study using careful, in situ screening: the mine operators would not allow the concomitant interruption of operations. There are no known surface exposures of Pungo River Foramation sediments in North Carolina; the only access is in the Lee Creek Mine. While there are a few surface exposures of the Yorktown (Snyder et al. 2001) and Belgrade Formations (Harris and Zullo 1991), specimens are not highly concentrated. The amount of excavation required to collect nearly 450 teeth in situ would be staggering.

Some familiarity with the mining operation at the Lee Creek Mine is necessary to understand the fourth collection of teeth in this study. To gain access to the ore (which lies approximately 30-35 m below sea level) the top 10 or so meters are removed using a bucket-wheel excavator and transported on a conveyor belt to a previously mined pit. The next 20-25 m are removed by large electric draglines and piled in the immediately previous cut. This "topside-down" process results in the older sediments generally being placed on top of younger ones in the spoil piles, but some mixing inevitably occurs. Once the mining equipment is removed to safe distances, specimen collecting is allowed on the spoil piles under tightly regulated conditions. These 25-30 m of spoils contain the Croatan (also known as the James City) Formation shell bed, the various levels of the Yorktown Formation, and the top level of the Pungo River Formation. This very fossiliferous level, the so-called Coquina Bed and source of the Pungo River float sample described above, consists of interbedded soft to indurated marly gray clay, a white moldic limestone, and rich black clayey phosphatic sand. The limestone's nearly white color makes it an easily recognized indicator to the dragline operators that the ore matrix has been reached. The operators are also very careful not to breach the bottom boundary of the ore matrix, a hard, dolomitic sandstone known as the caprock, as that would allow the influx of water from the underlying Castle Hayne aquifer (see Figure 3).

The ore is piled beside the dragline, sprayed with high-pressure water to break up large aggregations, and the water-ore slurry is pumped to the

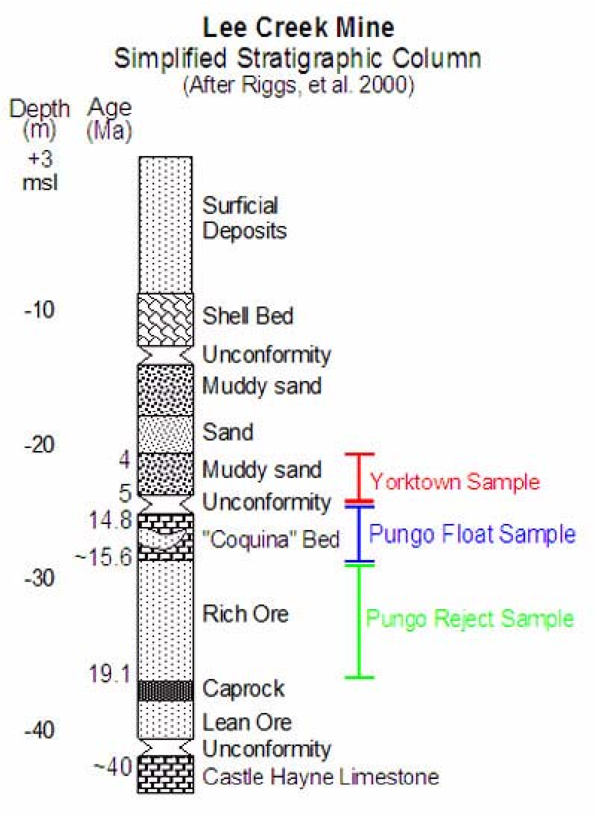

Figure 3. Simplified stratigraphic column of strata exposed in the Lee Creek Mine.

processing plant. At the plant the slurry is screened to remove the larger non-ore materials. This so-called *reject material* contains shark teeth (and other marine fossils) in great abundance. The fourth sample of 101 teeth was collected from this reject material. It is a far more homogeneous sample than the previously described float-collected Pungo River material, coming almost exclusively from the ore layer. Technically, however, it is also a float sample, its source being disturbed sediments.

A fifth collection of 32 teeth (lent by the Calvert Marine Museum) was collected in situ from various Shattuck Zones in the Calvert Formation, and fairly precise age data is available on individual teeth. The sixth sample group consisting of eight teeth from the Eocene species *Hemipristis curvatus* was collected from the Santee Limestone exposed in the Giant Cement Mine near Harleyville, South Carolina. The seventh group, 30 teeth from the Recent species, *Hemipristis elongata*, was purchased from a commercial dealer and originated in Indonesia.

Measurement data from the four float samples (Belgrade, Pungo River float, Pungo River reject, and Yorktown) are used in the statistical modeling procedures below. The Calvert sample is used in an effort to validate or refine the models. Data from the two non-*serra* species is used to discover how sensitive the models are with regard to species.

The Pungo Float, Yorktown, Santee, and Recent samples are housed in the North Carolina Museum of Natural Sciences in Raleigh. The Belgrade sample is part of the personal collection of Mr. G. Fonger of Gaithersburg, Maryland, and was collected over a period of many years in areas of the Belgrade Quarry now off-limits to collectors. The Pungo Reject sample was collected by K. and P. Young of Edward, North Carolina, during one month in the spring of 2004 from the reject pile adjacent to the PCS plant at the Lee Creek Mine. This resource is off-limits to all but a very few persons specifically permitted by PCS. After scanning, this sample was returned to the Youngs. High-resolution (600 dpi) scans of the labial side of all the specimens used in this study are available (in TIFF format) from the first-named author (REC).

IMMATURE OR ADULT?

Certain facets of phyletic tooth development in some species of sharks seem to be mirrored in their ontogenic development. One such example was given in Hubbell (1996) with his observation that some juvenile teeth of *Carcharodon carcharias* are similar in appearance to those of the late Paleocene shark *Palaeocarcharodon orientalis* (p. 13). Ward and Bonavia, (2001) outline phyletic changes, which are copied by ontogenic changes in *Carcharocles* teeth between the Eocene and Pliocene. This study attempts to identify a phyletic change in teeth of *Hemipristis serra*, which is almost certainly an ontogenic change as well. Thus, care must be taken to limit the use of juvenile specimens because they might express the earlier pattern.

Compagno (1988, pp. 269-270) has observed that in teeth of young *Hemipristis elongata* (the extant species, see Figure 4):

> "…a few distal CUSPLETS are present on upper laterals (five on fifth upper laterals of a 532 mm. specimen) but these become more numerous on adults and subadults (ten or more on fifth upper lateral) and turn into coarse serrations."

Assuming the teeth of all *Hemipristis* species behaved similarly, Compagno's (1988) description provides a means for distinguishing immature teeth. Typical features include small size, a few large distal "cusplets" (serrations), reduced or no mesial serrations, and a long unserrated tip.

Teeth of the earliest species, *Hemipristis curvatus*, might be considered as a template of the

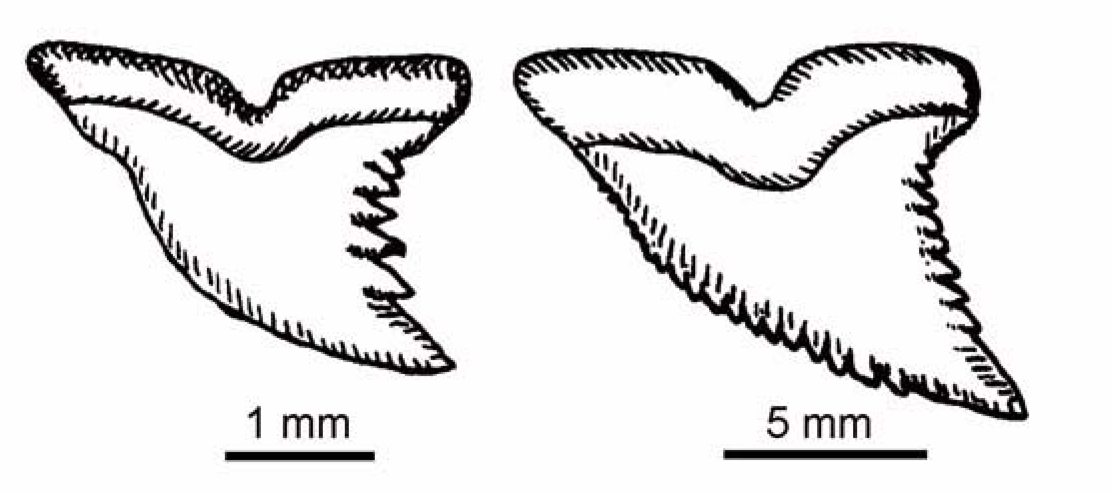

Figure 4. Outlines of immature and adult *H. elongata* teeth (redrawn from Compagno 1988).

immature form. As can be seen in Figure 5, the *H. curvatus* tooth (label 5.1) greatly resembles Compagno's (1988) immature specimen in Figure 4. Examining the scans produced very few examples of what could be considered immature teeth from the other samples. Figure 5 illustrates examples of Santee, Belgrade, Pungo Reject, and Yorktown immature-form teeth. There are no good candidates from among the Pungo Float, Calvert, or Recent samples.

Among the four samples used for statistical modeling, teeth from Belgrade were the smallest and had the fewest serrations. However, very few of the teeth from the Belgrade sample resemble the juvenile tooth figured by Compagno (1988). Of the complete Belgrade collection of more than 200 teeth, most were too fragmentary to use in this study. Several of these fragmentary teeth were of the juvenile configuration pictured by Compagno (1988). Thus, there were immature sharks in the population, which provided the Belgrade sample.

It is possible the Belgrade teeth are all from subadult individuals. There is no clear way to determine the age of the individuals, which produced the sample teeth. If distal edge length is used as a proxy for age, histograms of the four float samples used in the modeling indicate the four populations have reasonably similar distributions (see Figure 6).

As a species *Hemipristis serra* extends from the late Oligocene to the early Pleistocene (Sánchez-Villagra et al. 2000); however, examples of teeth from late Oligocene – early Miocene deposits are rare in the Atlantic coastal plain. A database search of the collection in the Florida Museum of Natural History returned 140 specimens of *Hemipristis* teeth, and only one of these was identified as being from (late) Oligocene sediments. The Chandler Bridge Formation sediments in the coastal plain of South Carolina correlate well (in age) to the Belgrade Formation (Harris and Zullo 1991) and do produce *Hemipristis* teeth. M. Havenstein, a very experienced collector in the

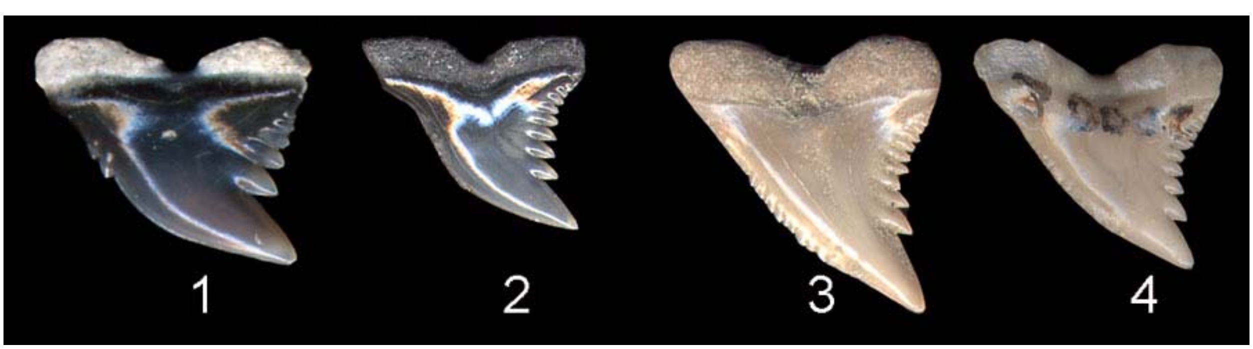

Figure 5. Examples of immature *Hemipristis* teeth, including Santee (5.1; height = 5 mm), Belgrade (5.2; height = 8 mm), Pungo Reject (5.3; height = 12 mm), and Yorktown (5.4; height = 10 mm) teeth.

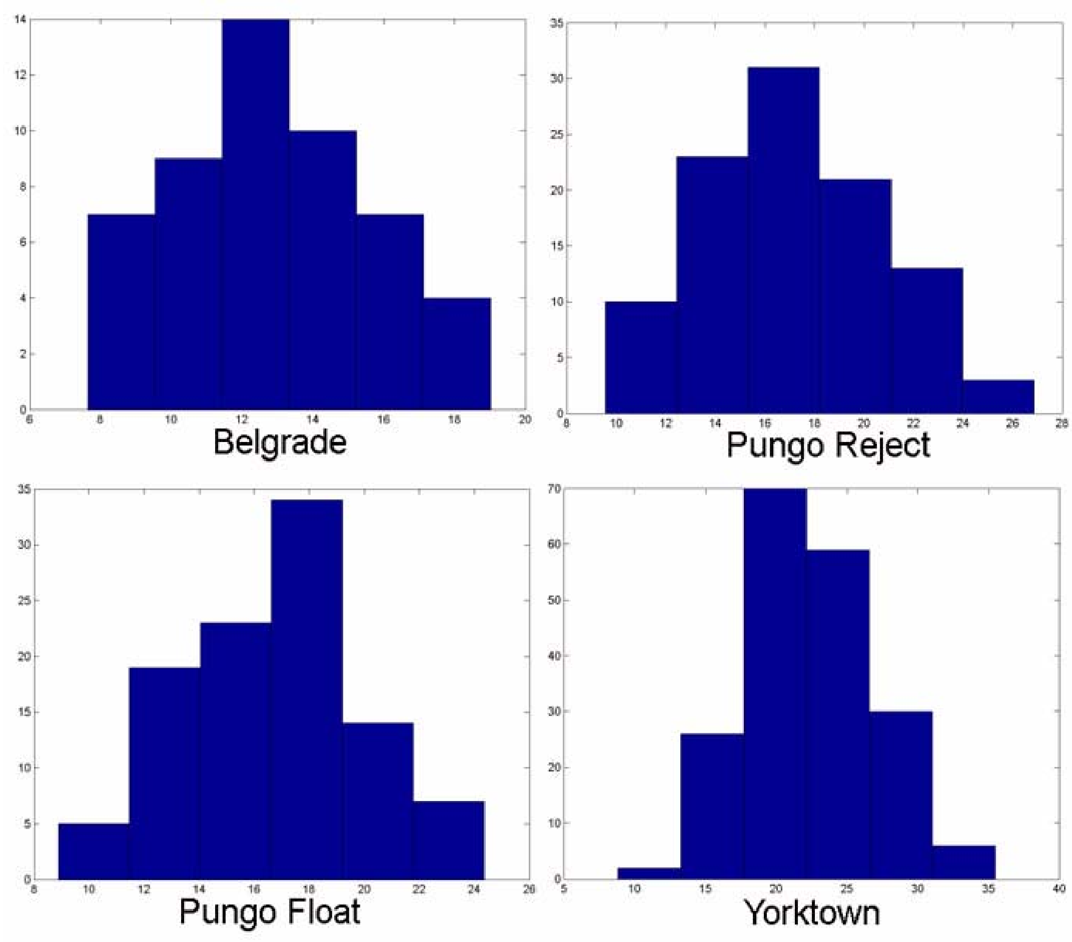

Figure 6. Histograms of edge length (x axis). Y-axis is number of specimens.

Charleston, South Carolina, area, indicated that he would consider “large” any Chandler Bridge *Hemipristis* tooth with mesial edge length in excess of 25 mm (Chandler, personal commun., 2005). By this measure there were at least four “large” teeth in the Belgrade sample. The complete absence of large teeth, the similarity in range of variation among samples, and comparison with the largest known teeth from the Belgrade Formation suggest strongly that the ontogenic distribution of the Belgrade sample is not size or age biased.

PALEONTOLOGICAL AGE ASSIGNMENT

Some range of error is almost invariably present in any attempt to determine the numerical age of paleontological specimens. For the purpose of linear regression a mean age for each sample will be assigned the individual teeth in that sample. Although perhaps somewhat contrived, this seems a better method than assigning a random age within the recognized limits of each sample.

Belgrade. Synthesizing early work, Harris and Zullo (1991) placed the Belgrade Formation as spanning the Oligocene-Miocene boundary. The age for the Belgrade float population to be used in the linear regression will be 23.8 Ma, the currently recognized age for this boundary (Berggren et al. 1995).

Pungo River. Riggs et al. (2000) divided the Pungo River Formation into four units, labeled A–D. The Pungo River float sample is from the uppermost Unit D whereas the Pungo River reject sample is from the ore matrix, Units B and C. To Unit B, Riggs et al. (2000) assigns an age range of 19.1–17.0 Ma whereas they estimate Units C and D range from 16.4 to 14.8 Ma. Because they did not resolve the geochronology in greater detail, a certain amount of arbitrariness must be used to set times for the linear regression. Choosing the midpoint of 16.4 and 14.8 gives 15.6 Ma as an approximate age for the C-D boundary. This averaging gives a range of 15.6–14.8 Ma for Unit D, and again choosing the midpoint gives a regression age of 15.2 Ma for the Pungo River float sample.

Table 2. Age assignments for Calvert teeth.

Picture File	# of Teeth	Zone	Age Range	L.R. Age
Calvert01.tif	1	19	12.0 – 12.7 Ma	12.35 Ma
Calvert02.tif	3	14	14.0 – 14.5 Ma	14.25 Ma
Calvert03.tif	6	14	14.0 – 14.5 Ma	14.25 Ma
Calvert04.tif	4	13	14.5 – 14.9 Ma	14.70 Ma
Calvert05.tif	4	12	14.9 – 15.2 Ma	15.05 Ma
Calvert06.tif	6	11	15.2 – 15.8 Ma	15.50 Ma
Calvert07.tif	5	10	15.8 – 16.5 Ma	16.15 Ma
Calvert08.tif	2	8	16.7 – 16.9 Ma	16.80 Ma
Calvert09.tif	1	3	17.5 – 18.4 Ma	17.95 Ma

The range of Units B and C (the ore body) of 19.1 Ma to 15.6 Ma gives an average regression age of 17.35 Ma for the Pungo River reject sample (Figure 3).

Yorktown. Snyder et al. (1983) identified the Yorktown Formation in the Lee Creek Mine as? contained within planktonic foraminifera zones N19 through the middle of N20. However, collecting is concentrated in the deeper material, primarily N19. This zone yields an age range of approximately 5.0–4.0 Ma. Taking the midpoint yields a regression age of 4.5 Ma.

Calvert. The 32 teeth lent by the Calvert Marine Museum had collection information assigning them to precise Shattuck Zones. Shattuck Zones have been correlated with major biostratigrafic units in de Verteuil and Norris (1996) to give the range of ages for teeth in this sample as seen in Table 2 (some ranges are interpolated).

Santee. Eight teeth of *Hemipristis curvatus*, the Eocene species, are from the Santee Formation of South Carolina. Harris and Zullo (1991) place the middle of this Formation within Foraminifera Zone P12, to which Berggren et al. (1995) assigns an age range of 43.6–40.6 Ma. Averaging gives 42.1 Ma for the linear regression age.

Recent. Thirty teeth of *Hemipristis elongata*, an Indian Ocean and western Pacific Ocean resident and the only extant species of *Hemipristis*, were also measured. Their age is 0 Ma.

STATISTICAL ANALYSIS

The relationship between five characteristics of the teeth is examined using several statistical tests. As noted, the variables of interest are (see Figure 7):

age	=	linear regression age as assigned above.
length	=	total length of tooth's distal edge = spline length A to C
ratio	=	(unserrated tip length) / (total edge length)
	=	(distance B to C) / (spline length A to C)
no. serrations	=	number of (distal) serrations between A and B
avg. serr. width	=	spline length AB / number of serrations

Descriptive summary statistics for the variables *length*, *ratio*, *number of serrations*, and *average serration width* are presented in Table 3 for each float sample.

A one-way analysis of variance (ANOVA) finds significant differences between the four samples for *length* (p-value < .0001), *ratio* (p-value < .0001), *number of serrations* (p-value < .0001), and *average serration width* (p-value < .0001). The variables *ratio*, *number of serrations*, and *average serration width* are all strongly related to the overall tooth size as quantified by *length*. The scatter plots in Figure 8 of *ratio*, *number of serrations*, and *average serration width* versus *length* strongly suggest that longer teeth have a smaller ratio, more serrations and the average width of serrations is larger.

To investigate the differences between the four float samples after adjusting for differences in tooth length, an analysis of covariance (ANCOVA) was performed for the variables *ratio*, *number of serrations*, and *average serration width*, with tooth *length* as the covariate. After taking into account variations in tooth length between the samples, there remained significant differences in *ratio* (p-value < .0001), *number of serrations* (p-value <.0001), and average serration width (p-value < .0001) between the four float samples.

There is evidence which suggests that *ratio* also is *age* dependent, specifically, that *ratio* decreases as geological *age* decreases. If a subsample (sPungo) of smaller Pungo River teeth is chosen having the same average length as the Belgrade sample, the average of *ratio* for the subsample is intermediate between the average *ratios* for the Belgrade teeth and the complete Pungo River sample (Table 4). This relationship will be explored further in the modeling below.

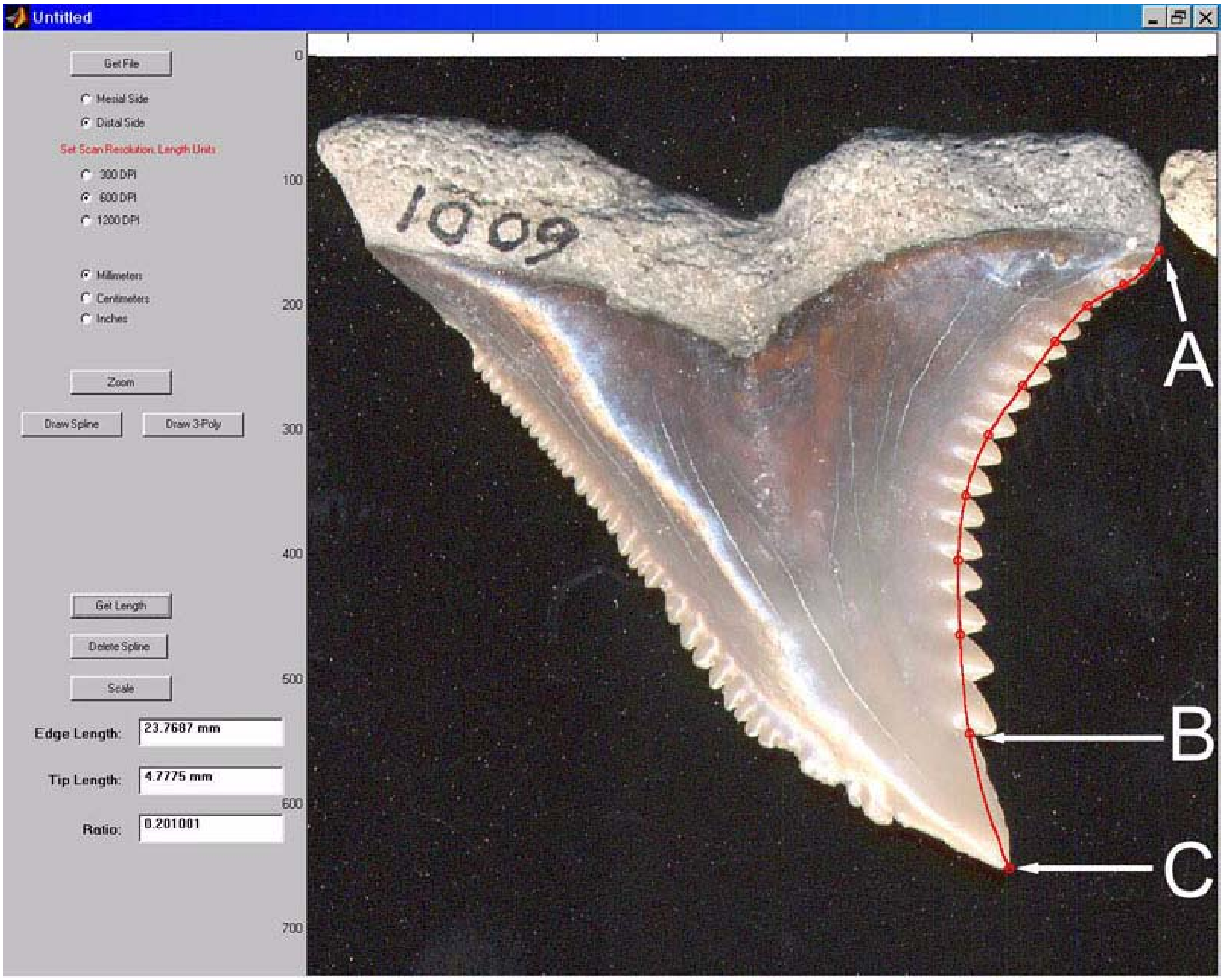

Figure 7. Screen capture: measuring a tooth. The spline curve can be seen on the distal (right) side of the tooth.

Assuming *ratio* to be a linear function of *length* and *age*,

$$ratio = b_0 + b_1{*}length + b_2{*}age + \text{error},$$

the standard least squares (linear regression) algorithm determines the coefficients given in Table 5.

Similar analysis showed a significant negative trend with geological age for *number of serrations* (b_2 = -0.062, p-value < .0001, R^2 = 0.81) and a small but significant positive change with geological age for *average serration width* (b_2 = 0.0042, p-value < .0001, R^2 = 0.59), after accounting for differences in tooth length. Note that the particularly low R^2 for this final model indicates that the trend in *average serration width* with *age* explains a relatively small portion of the overall variation in this measurement. The *number of serrations* increase as geological age decreases, and there is some evidence that *average serration width* decreases.

Note that unweighted least squares is optimal (gives minimum variance linear unbiased estimates) if the linear model is true; however, it is not necessarily optimal if the true relationship is not linear.

While any of the scatter plots in Figure 8 strongly suggest a linear relation between *ratio*, *number of serrations*, or *average serration width* and *length*, there is no such assurance regarding the relationship between *age* and the other three variables. For example, assuming *ratio* was dependent on a quadratic term in *age* would lead to a model

$$ratio = b_0 + b_1{*}length + b_2{*}age + b_3{*}age^2 + \text{error},$$

and performing a linear-in-the-parameters regression results in the coefficients given in Table 6.

Substituting the *length* and *age* information (for a given tooth) into a particular model produces a predicted value for the *ratio* of that tooth. The difference between the actual (observed) value of *ratio* and its predicted value ($ratio_o - ratio_p$) is termed the *residual*. A measure of how well the

Table 3. Descriptive statistics for each variable for the four float samples. SD is the standard deviation. Q1 is the first quartile (25% of teeth lie at or below Q1) and Q3 is the third quartile (75% of teeth lie at or below Q3).

	Belgrade (n=51)	**Pungo River reject (n=101)**	**Pungo River float (n=102)**	**Yorktown (n=193)**
Geological age (Ma)	23.8	17.35	15.2	4.5
Length (mm)				
Mean (SD)	12.8 (2.8)	17.1 (3.7)	16.7 (3.3)	22.4 (4.7)
Min, Max	7.7, 19.0	9.6, 26.9	8.9, 24.4	8.8, 35.5
median [Q1, Q3]	12.4 [10.7, 15.1]	17.2 [14.3, 19.0]	17.2 [14.2, 18.6]	22.1 [19.1, 25.4]
Ratio				
Mean (SD)	0.27 (0.03)	0.21 (0.04)	0.22 (0.03)	0.18 (0.04)
Min, Max	0.23, 0.33	0.12, 0.35	0.11, 0.30	0.10, 0.27
median [Q1, Q3]	0.26 [0.25, 0.29]	0.21 [0.19, 0.23]	0.22 [0.19, 0.24]	0.18 [0.15, 0.20]
Number of serrations				
Mean (SD)	9.1 (1.2)	12.7 (1.9)	13.1 (1.9)	15.8 (3.0)
Min, Max	7.0, 11.0	8.0, 18.0	8.0, 18.0	8.0, 28.0
median [Q1, Q3]	9.0 [8.0, 10.0]	13.0 [11.0, 14.0]	13.0 [12.0, 14.0]	16.0 [14.0, 17.0]
Avg. serr. width (mm)				
Mean (SD)	1.02 (0.18)	1.05 (0.16)	1.00 (0.15)	1.17 (0.14)
Min, Max	0.67, 1.34	0.70, 1.57	0.66, 1.45	0.74, 1.60
median [Q1, Q3]	1.01 [0.89, 1.16]	1.04 [0.95, 1.15]	1.00 [0.89, 1.10]	1.17 [1.06, 1.27]

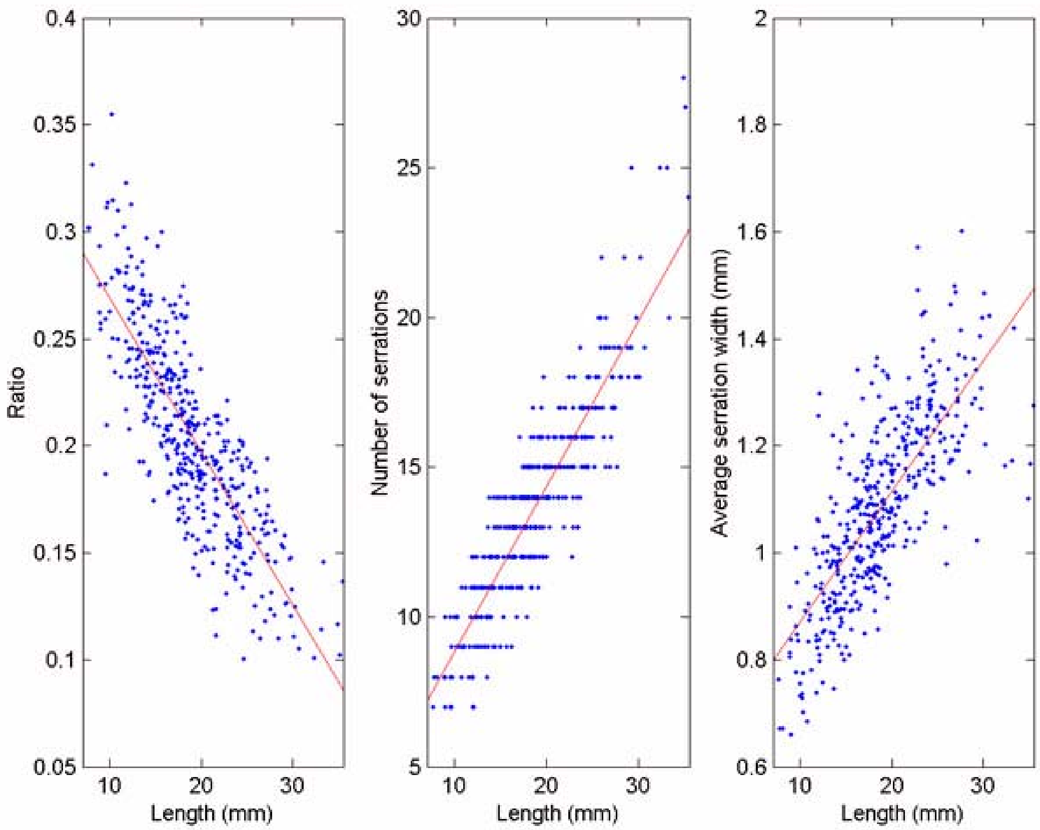

Figure 8. Scatter plot of *ratio, number of serrations* and *average serration width* versus *length* with fitted lines for the four float samples (combined).

Table 4. Means of *ratio* for Belgrade, small Pungo River, and complete Pungo River float samples.

Belgrade	sPungo	Pungo
0.2718	0.2445	0.2160

Table 5. Parameter estimates for the ordinary linear model. R^2 = 0.685.

Parameter	Estimate	Std. Err.	t-value	Pr > |t|
b_0	0.3089	0.0079	39.29	< .0001
b_1	–0.0062	0.0003	–20.42	< .0001
b_2	0.0011	0.0002	4.98	< .0001

Table 6. Parameter estimates for the linear-in-the-parameters model. R^2 = 0.706.

Parameter	Estimate	Std. Err.	t-value	Pr > |t|
b_0	0.3273	0.0083	39.53	< .0001
b_1	–0.0062	0.0003	–20.99	< .0001
b_2	–0.0034	0.0008	–4.04	< .0001
b_3	0.0002	0.0000	5.61	< .0001

model fits the data can be obtained by examining the set of residuals. Two accepted measures for error are the mean of the residuals and the mean of the squares of the residuals. These are given in Table 7. These measures for the Calvert, Santee, and Recent samples are included in the table as well (although teeth from these groups were not used to fit the model). μ_{Res} = mean of the residuals, %err = the percentage of the mean of *ratio* that μ_{Res} represents for the sample, and μ_{Sq} = mean of the squares of the residuals.

As can be seen from the mean residual columns, for the H. serra species the linear model (on average) overestimates *ratio* for both Pungo River samples and for the Calvert sample and underestimates *ratio* for the other four samples. However, the worst mean residual, 0.0154 for the Belgrade teeth, represents an error of less than 6% of the average *ratio* of the Belgrade teeth. In the quadratic model the mean residuals of all the float samples were quite small, smaller than in the linear model. For the Calvert sample this mean residual was larger than from the linear model but still represented an error of only 2.5% of the average value of *ratio* for these teeth.

For both non-*serra* species the average residual in the linear model was quite large, indicating that the linear model do not predict well for either of these species. The quadratic model does predict well for the *H. curvatus* teeth, but the sample is too small to lend much confidence to this result.

As can be seen in Figure 4, as an individual of the extant species ages, the number of distal serrations increases. Again using the distal edge length as a proxy for age, the same phenomenon occurs in the fossil species, as can be seen in the scatter plot (Figure 8) of the number of distal serrations versus the length of the distal edge.

As the geologic age of the samples decreases, the average number of serrations increases (see Table 3). For each tooth we can determine its average serration width by dividing the edge length (AB in Figure 7) by the number of serrations. Averaging over each of the float samples gives the values seen in Table 3. Curiously, the average serration width is virtually the same for all samples.

Summary of Quantitative Results

- There are significant differences in all four teeth measurements (*length*, *ratio*, *number of serrations,* and *average serration width*) between the four float samples.
- After accounting for the differences in distal length, there are still significant differences in *ratio*, *number of serrations,* and *average serration* width between the four

Table 7. Mean residuals and mean square residuals for the two models.

	Ordinary L.S.			Quadratic L.S.		
Sample	μ_{Res}	%err	μ_{Sq}	μ_{Res}	%err	μ_{Sq}
Belgrade	0.0154	5.7	0.00079	0.0011	0.4	0.00055
Pungo (R)	–0.0078	–3.6	0.00071	–0.0033	–1.5	0.00066
Pungo (F)	–0.0046	–2.1	0.00066	0.0029	1.3	0.00065
Yorktown	0.0025	1.4	0.00061	–0.0001	–0.06	0.00060
Calvert	–0.0023	–1.2	0.00057	0.0050	2.5	0.00059
Santee	0.1572	33.2	0.0253	0.0073	1.6	0.00060
Recent	0.0784	25.4	0.0078	0.0596	19.3	0.00522

samples.

- The variables *ratio*, *number of serrations,* and *average serration width* are strongly associated with *length* and with *age* (*p*-values < .0001 in the linear model).
- After having accounted for the relationship with *length*, there is still significant evidence of a decrease in *ratio* and *average serration width* and an increase in the *number of serrations* with a decrease in *geological age*.
- Examination of residuals ($ratio_o$ – $ratio_p$) from the fitted models does not show any clear deficiencies in the linear model. Fitting an additional quadratic term (age^2) in the model does improve the model. The R^2 statistic increases slightly to 0.706 (from 0.685 in the linear model), and the mean residuals improve. The quadratic term is significant ($p = 0.0041$). This suggests that although the *ratio* increases with *age*, the trend is probably not linear. Similar comments apply to the models for *number of serrations* and *average serration width*.
- The prediction errors for *ratio* in the models applied to the Calvert sample are all very small. That the model predictions for this sample are not significantly worse (than for the teeth in the samples that were used to fit the data) strongly supports the idea that analysis of the float data does provide useful insights about the dependence of *ratio* on *length* and *age*.

DISCUSSION AND CONCLUSIONS

There are numerous cases of gradual morphometric change in species over time. Because of the near-completeness of fossil records found in marine sediment core samples, some of the most convincing examples are species of shelled marine protists. Motoyama (1997) reported that the protozoan *Cycladophora davisiana* underwent a "relatively rapid decrease in thorax size with a reduction of the spongy appendage. This change occurred during about 0.4 m.y.(s/b "mya?") from 2.8 to 2.4 Ma without cladogenesis. Following this interval, a decrease in thorax size continued gradually up to the Recent, resulting in very small morphology." Kuwahara (1997) and Raffi et al. (1998) provide similar results with other species of calcareous nannofossils.

Regarding one specific genus of fossil shark teeth, Cappetta (1987, p. 108) observed:

> "*Squalicorax* represents a homogeneous group, with a lineage (*S. falcatus – S. kaupi – S. pristodontus*) showing a clear increase in tooth size, an increasingly blunt apical angle, a gradually smaller heel in relation to the cusp, with the disappearance of the notch separating the heel from the distal cutting edge of the cusp, a progressive enlargement and a more and more marked labio-lingual flattening, and finally an emphasized serration of the cutting edges."

Our data suggests there is evidence of an analogous change in the upper teeth of *Hemipristis serra* during the Miocene: they increased in size and their edges became more nearly completely serrated. While the differences do not serve to distinguish individual teeth, the differences between the various populations' samples are unequivocal. Unlike *Squalicorax*, there is no discernable change in other morphological characters, and thus no strong support for speciation events.

There are challenging problems associated with the study of specimens from disturbed sediments. As stated earlier, the possibility of contamination here was very real, given the nature of the Lee Creek mining operations. Even with a "pure" sample the assignment of a numerical value for *age* (to be used in regression modeling) necessarily requires some geochronologic compromises. In spite of these issues the statistical models give useful information.

Analysis was conducted using multiple linear regression of *ratio* on two explanatory variables: the distal edge *length* and the geologic *age* of the teeth. This showed strong evidence that geologically older teeth tended to be smaller with fewer serrations and larger teeth tend to have smaller ratio (shorter unserrated tip relative to total edge length). In addition, the regression showed strong evidence that there is some remaining variation in *ratio* (after having accounted for tooth size differences) that can be attributed to the differences in geologic age of the different samples. In other words, for teeth with similar overall size, those from the geologically older groups tend to have a larger ratio (longer unserrated tip).

The models were tested on two other species, *H. curvatus* (Eocene) and *H. elongata* (Recent). The linear model did not predict well for either of these species. The quadratic (in age) model predicted surprisingly well for the small sample of *H. curvatus* teeth, but not for the sample of *H. elongata* teeth. In future work it would be interesting to see how well this model works for a population of Lower Oligocene *Hemipristis* teeth.

We can only speculate why larger, more completely serrated teeth might confer a selective advantage. Perhaps *Hemipristis*' preferred prey changed over time. A frequently offered premise for the megatoothed shark *Carcharocles* teeth's gradual increase in size between the Eocene and Pliocene is that its preferred prey (cetaceans) increased in size during this same time frame. The extant species, *Hemipristis elongata*, today eats "a variety of fish prey, including anchovies, sea catfish, Bombay ducks (*Harpadon*), mackeral, croakers, grey sharks (*Carcharhinus*) and butterfly rays (*Gymnura*) (Compagno 1984, p. 441)."

The Belgrade Formation exposed in the Belgrade quarry is thought to have been an onshore environment (Harris and Zullo 1991). The Pungo River sediments are thought to have originated in a middle to outer shelf environment (Gibson 1983). The three members making up the Yorktown Formation in the Lee Creek Mine have been described as deposited in middle neritic, outer neritic, and middle to outer neritic environments, respectively, with ocean temperatures probably not much different from those of present-day eastern North Carolina (Snyder et al. 2001). All three of these environments (Belgrade, Pungo River, and Yorktown) would have contained the type of prey, which supports the extant species. Cappetta (1987) has described *Hemipristis* as having a cutting-clutching dentition: the spike-like lower teeth hold the prey while upper jaw teeth with their serrated edges cut like a steak knife. The Pungo River and Yorktown environments in the area where the Lee Creek Mine is now located contained large numbers of cetaceans. It is not inconceivable that *Hemipristis serra*, given its formidable dental equipment, preyed or scavenged on these as well, particularly during the Late Miocene and Pliocene. The increase in size of its teeth, with their more completely serrated edges, would surely have been advantageous for preying on cetaceans.

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