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DEFINING FUNCTIONAL TOOTH MORPHOTYPES IN EXTANT AND EXTINCT
CROCODYLIANS, WITH DIETARY AND FEEDING IMPLICATIONS

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By

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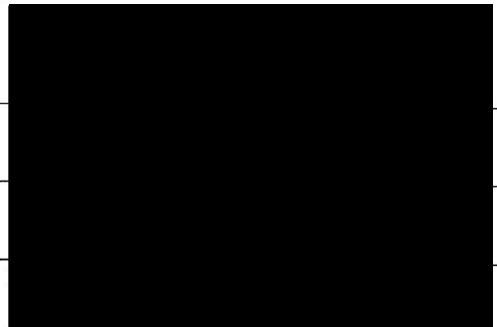
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A THESIS APPROVED FOR THE DEPARTMENT OF ZOOLOGY



Acknowledgments

I would like to thank I. [unclear] for the generous loan of four specimens. Next, I am grateful to the staff of Smith's [unclear] for providing my presence in their care. Thanks also to Alan [unclear] and his assistants for [unclear] allowing me valuable time in the [unclear], and for answering all my questions.

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ABSTRACT

Crocodylians have traditionally been considered to have homodont dentitions (eg., Kälin, 1933; Langston, 1973). Although all the teeth in these species are cone-shaped, there is a large amount of morphological variation present, which has prompted some authors to describe crocodylian dentitions as heterodont (eg., Kieser et al., 1993; Aoki, 1989). Furthering such observations, ten modern crocodylian species were sampled and their teeth measured in four aspects. These data were processed using principal components and cluster analyses, and functional tooth morphs were defined within each species. Tooth morphs (here termed “functional morphotypes”) were then correlated with dietary and feeding information gleaned from other studies. An ontogenetic series of *Alligator mississippiensis* skulls was used to test for ontogenetic changes in the dentition. While many have reported that crocodylian teeth change shape ontogenetically (eg., Langston, 1973; Westergaard, 1990), no significant ontogenetic changes in tooth shape were found to occur. This finding lends greater importance to all research concerning crocodylian tooth morphology. Finally, a random sample of Cretaceous age crocodyliform teeth from the Cedar Mountain Formation in Utah (OMNH site V695) was tested using the preceding methodology to discover the number of tooth morphotypes and species present in this sample. Based on the large number of morphotypes defined, at least three species are represented. The low degree of clarity gleaned from this part of the study, however, urges caution in applying generic and family-level designations to isolated fossilized teeth. Moreover, the high degree of heterodonty present in fossil taxa suggests that only the most conservative identifications be attempted until more is known about the dentitions of fossil crocodyliform taxa.

INTRODUCTION

The teeth of modern crocodylians are all variably cone-like in shape, but there is considerable intraspecific and interspecific variation in tooth widths, lengths and curvatures. This variation has been noted by many authors (eg., Aoki, 1989; Edmund, 1969; Iordansky, 1973), while others have insisted on defining the dentition of crocodylians as homodont or isodont (eg., Simpson, 1937; Langston, 1973 ; Larsson and Sidor, 1999). Attempts to define the dentition patterns of crocodylians have resulted in a wealth of confusing terminology. Iordansky (1973) supplied the term “pseudoheterodont” to describe the crocodylian dentition, noting that the “height and thickness” of teeth varies from region to region within the jaw. This term was applied later specifically to the American Alligator (Ferguson, 1981). Another term applied to the dentition patterns of crocodylians is “anisodont” (Westergaard, 1990). The implication in this definition seems to be that the teeth are not identical, but are not truly heterodont.

Heterodonty is usually only attributed to mammals and those reptiles ancestral to them. Indeed, the term “incipient heterodonty” has been applied to certain Permian therapsids which possess only an enlarged first maxillary and dentary tooth in an otherwise very regular homodont dentition (Simpson, 1936). “Incipient heterodonty” is a qualified version of true heterodonty, but is apparently applicable nevertheless. Though most authors refer to crocodylians as homodont, some have recognized a few exceptionally differentiated dentition patterns (eg., Aoki, 1989; Edmund, 1962; Kieser, 1993). For example, Simpson (1930) reported that the teeth of the Cretaceous crocodylomorph *Allognathosuchus* were quite typical anteriorly but were very blunt and

flattened posteriorly. Like many authors (eg., Langston, 1965; Steel, 1973; Buffetaut, 1979), Simpson mistakenly attributed this dental characteristic of durophagy solely to the alligatorids.

Recently, several fossil crocodylomorphs from Africa have been recovered which possess very heterodont teeth, some of which may indicate herbivory (Clark, 1989; Gomani, 1997; Larsson, 1999). While modern crocodylians do not possess the strongly differentiated teeth of these early African species, some researchers have bravely applied the term heterodont to modern crocodylians (Aoki, 1989; Kieser, 1993). These authors and the research herein will show that all modern crocodylians do indeed possess differently shaped teeth which likely perform different functions within the jaws.

Crocodylomorphs with a very similar body plan to modern crocodylians have existed since at least the Late Jurassic and all belong to a group now known as “mesoeucrocodylia” (Molnar, 1994). Since the Late Jurassic, these animals have shown progressive vertebral and cranial advancements leading to the modern *bauplan* which has existed since the Early Cretaceous (Brochu, 1997a; Norell, 1990). These animals are called “eusuchians” which means literally “true crocodiles” (Brochu, 1997b). Eusuchia contains many fossil taxa, as well as the modern forms, called “crocodylians.” Crocodylia includes the Alligatoridae, Crocodylidae, and Gavialidae (Brochu, 1997c).

Modern crocodylians are semiaquatic predators which consume a variety of prey types (Guggisberg, 1972). They have evolved for an aquatic environment, but have directed the majority of their senses towards the terrestrial world (Neill, 1971). Using cryptic coloration and discrete behavior, they are able to avoid detection by most prey animals and larger predators (Magnusson, 1991). Since their early introduction into this

ecological niche, they have dominated it for many millions of years (Langston, 1973; Guggisberg, 1972; Steel, 1973). Other diapsid reptiles, such as phytosaurs, champsosaurs, and aetosaurs, convergently evolved similar *bauplane* (Carroll, 1988) and also utilized a semiaquatic ambush-predator niche. No other taxa, however, have persisted and thrived in this niche to the extent that crocodylians have. Indeed, crocodylians have been common predators of tropical freshwater environments around the world for over 100 million years (Molnar, 1994).

The overwhelming success of the crocodylian clade appears to be due, in part, to several specific adaptations of the skull and associated musculature (Iordansky, 1964). Modern crocodylians possess the most extensive secondary palate of all vertebrates, including mammals (Carroll, 1988). This secondary palate is composed primarily of medial extensions of the premaxillary and maxillary bones which contact the palatine bones near the anterior margins of the large infraorbital foramina (Langston, 1973). The palatine and pterygoid bones are fused and form the posterior portion of the secondary palate (Iordansky, 1973). This has allowed for a very posterior placement of the internal nares, or choanae. In eusuchians, the choanae are surrounded by the pterygoid bones, while earlier forms incorporated the palatines into the border of the internal nares (Langston, 1973). Thus, the modern crocodylian secondary palate provides for a sufficiently posterior position of the internal nares to allow for easy breathing while the mouth is occupied by a prey item (Langston, 1973). Another advantage of an extensive bony palate is structural. Compared to the majority of their archosaurian relatives, crocodylians have a highly dorsoventrally compressed skull (Iordansky, 1973; Langston, 1973). The acquisition of vertical cranial compression likely aided sensory and feeding

abilities within the crocodylian ecological niche, at the cost of cranial integrity. The secondary palate strengthens the elongate and flattened crocodylian rostrum to the extent that Langston (1973) argues this to be its primary function.

Like their primitive archosaurian ancestors, crocodylians possess akinetic skulls (Gans, 1969). The parietal bones are fused along the midline and form the majority of the post-orbital "skull roof" (Busbey, 1989). Within the skull roof, the supratemporal fenestrae form attachment surfaces for large jaw-closing musculature (Chiasson, 1962). The size of these fenestrae is correlated with relative bite force (Iordansky, 1964; Busbey, 1989). Posteriorly, the quadrate bones are more highly fused and incorporated into adjacent skull elements than in other reptiles (Iordansky, 1973). The quadrates are also more inclined and posteriorly located than in other reptiles. This weakens bite force, which is compensated by enlarged retroarticular processes on the mandible (Brochu, 1999). These processes provide for greater mechanical advantage via the insertion of large pterygoideus muscles at this point (Chiasson, 1962). The mechanics of this anatomy produce the greatest amount of force when the jaws are in maximum gape position (Iordansky, 1964; Busbey, 1989; Cleuren and De Vree, 1992).

Because of the lack of cranial and mandibular kinesis that is common in squamates, crocodylians are "inertial feeders" (Gans, 1969). This involves the use of inertia and gravity for manipulating items within the jaws (Busbey, 1989; Gans, 1969). Unlike that of mammals, the crocodylian tongue does not appear to be of much assistance during the feeding process (Busbey, 1989; Iordansky, 1964). Several authors have observed crocodylians feeding and noted that these animals use different regions of the jaws for different purposes, or at different times during the feeding process (eg., Cleuren

and De Vree, 1992; Busbey, 1989; McIlhenney, 1976). Without the aid of a mobile jaw joint, kinetic skull, or protrusible tongue, crocodylians use rapid head jerking and rotating movements in order to manipulate prey. This form of prey manipulation is more effective than might be expected, as crocodylians are capable of consuming a huge variety of prey animals (Guggisberg, 1972).

Crocodylians vary their feeding methods considerably based on what prey is being utilized (Thorbjarnarson, 1990, 1993). For example, crocodylians consume fishes during all phases of ontogeny with the exception of very early adolescence (eg., Cott, 1960; Forsyth, 1910). After acquiring and subduing a fish, the crocodylian will unerringly swallow the fish head-first (Thorbjarnarson, 1990). Crustaceans, however, are usually crushed in the posterior region of the jaws and reduced to smaller pieces prior to swallowing (Thorbjarnarson, 1993). Any prey animal which is too large to be consumed whole (usually a mammal) is held by the “maxillary canine tooth” (McIlhenney, 1976), while the head is rotated around the long axis to remove portions sufficient for swallowing (Cott, 1960). This process is seen best in larger species of crocodiles feeding on large mammals, in which case the crocodylian initiates a “death roll,” rotating its entire body for multiple revolutions in order to retrieve manageable pieces of the prey animal (Neill, 1971; Webb, 1991; Tamarack, 1993). Surprisingly, insects are consumed during all crocodylian life stages, with smaller animals selecting individual insects (Corbet, 1959; Delany, 1990), and larger animals often snapping at clouds of flying insects (Forsyth, 1910 ; McIlhenney, 1976). Certainly, though, insects do not compose a significant part of the diet of larger crocodylians (Taylor, 1979).

Busbey (1989) noted a feeding “routine” that consists of four stages: acquisition,

holding, manipulation (as well as biting and crushing), and swallowing. During the acquisition phase, he observed that prey items were bitten first by using the most anterior teeth. This observation was confirmed by Cleuren and De Vree (1992). Next, prey items were repositioned into the mid-jaw line using rapid head movements. Multiple workers have noted the prey item being held by the large maxillary tooth in the middle of the upper jaw (Busbey, 1989; McIlhenney, 1976). Presumably because the prey animal is alive and struggling, crocodylians safeguard their catch by maintaining a firm grip, using what is usually the largest tooth in the dentition. In Busbey's next phase of consumption termed "manipulating, biting, and crushing," he observed that the prey item (in this case a large rat) was then inertially or gravitationally moved to the posterior region of the tooth row where it was given a series of quick crushing and killing bites. If the rat continued to struggle, it was moved again to the mid-jaw line to be held again by the large maxillary tooth (Busbey, 1989). This process was repeated until the animal was apparently dead, at which time it was swallowed.

Recent research on some of the more obviously heterodont crocodylians, such as *Crocodylus niloticus*, includes attempts to define functional tooth sets within the dentition of this animal (Kieser et al, 1993). Similar studies on tooth form and function have been conducted with the goal of defining tooth morphotypes (Aoki, 1989; Massare, 1987). While such investigations have focused on functional tooth morphotypes, this information was assumed to be applicable to complete dentitions, instead of functional regions or individual teeth in the jaws. Heterodonty, then, has rarely been a consideration of studies focusing on tooth morphotypes.

Studies such as those of Busbey (1989) and Cleuren and De Vree (1992), along

with field observations from multiple authors (eg., McIlhenney, 1976; Cott, 1960; Magnusson, 1991) confirm that modern crocodylians are very versatile predators despite the limitations of kinetic inertial feeding (Gans, 1969). Moreover, the morphotyping techniques used by Massare (1987) and others make it possible to better understand tooth types and realistically speculate on their specific functions. The research contained herein furthers such work by attempting to define the types of teeth in various crocodylian species which perform different functions for these animals. Moreover, by defining multiple “morphotypes” of teeth present in different species, direct correlations can be made with known dietary and feeding adaptations. This goal constitutes the first part of my study.

In order to add meaning and importance to the first part of this research, an analysis of the potential for change in tooth shape during ontogeny was performed. Several authors have indicated that crocodylian teeth change shape (are replaced by successively different-shaped teeth) during ontogeny (eg., Kälin, 1933; Langston, 1973). However, no study so far has involved an analysis of measured crocodylian tooth shapes in an attempt to find ontogenetic changes. Westergaard (1990) reported an “increasing anisodonty with age.” His otherwise thorough study did not expand much on this statement, as the focus of his research was the dental changes occurring just before and after hatching. Along with Edmund (1962), Westergaard reported that very young crocodylians (less than 5-7 weeks old) have teeth set not in individual alveoli, but instead in a common groove. This situation changes quickly after the first set of replacement teeth erupts, with interdental septae and subsequent alveoli forming in an anterior to posterior direction during aging (Westergaard, 1990; Sato, 1990).

Older crocodylians often exhibit a reduced number of teeth, as well as very rounded and blunt teeth (Guggisberg, 1972; McIlhenney, 1976). Instead of being indicative of ontogenetic tooth shape change, this in fact results from infrequent replacement of teeth in old age, while subsequent tooth wear changes the original shape of the teeth (Edmund, 1962). Tooth replacement actually ceases in very old crocodylians, and completely edentulous American alligators have been reported (Erickson, 1996). Comparisons made between the teeth of old adult crocodylians and younger animals, therefore, would likely give the mistaken impression of ontogenetic change in tooth shape.

Considerable intraspecific conservatism of dental patterns can be seen in crocodylians (Edmund, 1969). The number of teeth in any individual of a species varies so minimally that this number can be expected to change little outside of the loss of one or (uncommonly) two teeth as an animal ages. These teeth are often lost from the posterior end of the maxilla and dentary and are accompanied by a loss of the alveolus (Edmund, 1962).

Several authors have described an ontogenetic dietary change in crocodylians, with prey choices originally including arthropods and molluscs and later comprising mainly vertebrates (eg., Taylor, 1979; Magnusson, 1987; Perez-Higareda, 1989). It may be because of this that many researchers expect ontogenetic change in tooth shape to occur. The variety of tooth shapes in the dentitions of most crocodylian species (Aoki, 1989), though, likely makes consumption of a variety of prey types feasible at all life stages. The second part of this study, then, is an attempt to quantify ontogenetic tooth shape change.

Tooth replacement plays a role in tooth-shape change, due to a decreasing rate of replacement with increasing age (Edmund, 1969). In very young crocodylians, the rate of tooth replacement is higher, simply because of the need for larger teeth in a skull which is rapidly increasing in size (Monteiro, 1997; Edmund, 1962; Westergaard, 1990). Edmund (1962) produced an excellent and highly referenced work on crocodylian tooth replacement, in which he surmised that teeth are replaced in successive waves called *Zahnreihen*. These replacement waves appear to have a regular periodicity, with one tooth replaced at a time (simultaneously on both sides of the jaw). The *Zahnreihen* occur from back to front in young animals, with a shift occurring when the animals reach about 60 cm in overall length (in *Alligator mississippiensis*) to front-to-back replacement. Edmund (1962) reported that the irregularity of this pattern increases with age. Thus, the likelihood of older animals retaining a single tooth much longer than average, or replacing a tooth too rapidly with its next larger successor would account for the “snaggleteethed” appearance of older crocodylians reported by several authors (eg., Erickson, 1996; Neill, 1971).

The average rate of tooth replacement in crocodylians is about 1 year in adult animals (Edmund, 1962). More posterior teeth generally require several more months between successive replacements than do the anterior teeth. Westergaard (1990) studied the dental development of embryonic through juvenile alligators and found that tooth replacement in the first two years of life had a very high average rate of about 1 month between replacements. Presumably, this replacement rate decreases gradually as overall growth rate slows, eventually reaching Edmund’s (1962) replacement rate of 1 year per tooth during adulthood.

Because crocodylians have dominated tropical freshwater environments worldwide for millions of years (Neill, 1971), and their teeth are replaced so regularly (Westergaard, 1990; Edmund, 1962), crocodylian teeth are very common fossils throughout the world. Indeed, the fossil record provides researchers with copious quantities of rootless, shed crocodylian teeth which would be difficult or impossible to recover from modern environments. So far, many fossil teeth have been grouped based on gross morphological similarity, and bravely assigned to mesoeucrocodylian families (Pomes, 1988; Estes and Sanchíz, 1982). Entire new species have been erected on the basis of a few fossil crocodyliform teeth (Steel, 1973). However, taxonomic designations based on a small number of isolated teeth should be viewed with healthy scepticism (Langston, 1973; Brochu, pers. comm.) because of the variety of tooth types present in crocodylian jaws.

In order to understand the origin of the thousands of shed teeth in museum collections, it is important to consider crocodylian population structure. Several such studies have been performed (eg., Cott, 1960; Campos, 1996; Thorbjarnarson, 1994), providing very similar results throughout. Crocodylian species surveyed show that juveniles and subadult animals are the most numerous members of any given population. This is not readily apparent to the casual observer, since crocodylians commonly separate geographically into different size-classes (Da Silveira, 1997; Hutton, 1989). This behavior is probably an instinctive attempt by smaller individuals to avoid the predation of cannibalistic adults (Webb, 1991; Cott, 1960). Because of the predominance of younger members in crocodylian populations, fossilized remains of ancient species should be strongly skewed towards smaller individuals. Moreover, because of the much

higher rate of tooth replacement in juveniles, collections of fossil crocodylian teeth are very likely to contain an inordinate number of teeth from immature individuals.

The collections of the Oklahoma Museum of Natural History (OMNH) contain several thousand well-documented isolated, crocodylian or mesoeucrocodylian teeth from a number of fossil localities. With the implications just discussed in mind, and using the functional tooth morphotyping methods utilized in the first part of this study, it should be possible to estimate the numbers and types of species present from a well-collected fossil locality. This research constitutes the final part of this investigation. Any reasonable results gained from this part of my research will greatly improve the value and utility of isolated fossilized crocodylian teeth.

MATERIALS AND METHODS

Tooth morphotype analyses

For the functional morphology portion of this study, skulls of healthy adult specimens of 10 species of modern crocodylians were acquired. The example of *Alligator mississippiensis* used was a personally-owned specimen measuring 294 mm from the anterior premaxilla to the back of the “skull table,” at the supraoccipital. The next species, *Crocodylus acutus*, was represented by a 355 mm specimen (TMM M-6040) borrowed from the Texas Memorial Museum at Austin. Two other specimens representing *Crocodylus niloticus* and *Crocodylus moreleti* were borrowed from TMM; these measured 435 mm (TMM M-1786) and 260 mm (TMM M-4980), respectively. The *Gavialis gangeticus* data was taken from an accurate Bone Clones® replica belonging to the Oklahoma Museum of Natural History. The remaining species studied,

Alligator sinensis, *Paleosuchus palpebrosus*, *Paleosuchus trigonatus*, *Caiman crocodilus*, and *Crocodylus porosus* were studied on-site at the Field Museum of Natural History in Chicago, Illinois. Their measurements and specimen numbers are as follows (respectively): 216 mm, FMNH 31303; 191 mm, FMNH 69867; 205 mm, FMNH 69882; 220 mm, FMNH 73440; 320 mm, FMNH 15231.

Four measurements were made for all teeth in each modern skull (see Figure 1). These measurements included two widths (anterior/posterior and lingual/labial widths) as well as two lengths (lingual side and labial side) for each tooth. Differences between widths of teeth account for lateral tooth compression, while differences in lengths account for tooth curvature and provide valuable comparisons with width measurements. Two groups of statistical tests comprised the morphotype analysis, both with the goal of defining functional morphotypes within individual specimens. All analyses were performed using NTSYSpc, version 2.02i (Copyright © 1986-1998 Applied Biostatistics Inc., All Rights Reserved worldwide). The first of these tests involved the generation of phenetic dendrograms starting with non-standardized data, as each data set was derived from one specimen. Principal components analyses were then performed on standardized versions of these data sets.

The data sets in this case consisted of rectangular matrices which were first transformed into triangular similarity matrices using the Penrose Shape Coefficient. This dissimilarity coefficient was used because it contains an internal correction that removes the tendency for larger values to weigh more heavily in an analysis (Rohlf, 1999). This technique was designed to minimize size factors. Next, cluster analyses were performed on the matrices with the default un-weighted pair group method, using arithmetic

averages (UPGMA). This overall technique tends to produce trees with a minimal number of ties.

The principal components analyses were performed on the same data matrices as were used in the previous analyses, each matrix in this case being standardized by characters. Each value was subtracted from the average for that character, then divided by the standard deviation for that character. Next, the product-moment correlation similarity coefficient was applied, creating triangular matrices based on the four measured variables. The first three principal components for each specimen were then projected onto each standardized data matrix. Results were displayed in two-dimensional plots of the first two principal components.

Final analyses of tooth form were conducted using 2-dimensional plots of variable ratios. This simple methodology was derived from McGhee's (1999) work on theoretical morphology. First, a ratio of the labial/lingual width to anterior/posterior width was calculated for each tooth and plotted against the ratio of anterior/posterior width to tooth length on the labial side of the tooth. This technique was designed to account for the maximum amount of shape variation and to support results from preceding analyses.

Ontogenetic tooth shape study

A study of possible ontogenetic tooth shape change was done next, using seven skulls of *Alligator mississippiensis*. Two personally-owned specimens of this species were used, measuring 146 mm and 294 mm. A large *A. mississippiensis* specimen belonging to the Oklahoma Museum of Natural History (OMNH 39-1-54) was also used, measuring 540 mm. The remaining four specimens were measured on-site at Skulls

Unlimited® in Oklahoma City, Oklahoma. This business sells museum and teaching-quality skulls of several vertebrate species to private and institutional collections. The four skulls utilized from this store were selected to represent a wide variety of ages and measured 80 mm, 208 mm, 292 mm, and 469 mm. Based on these skull sizes, we can estimate the ages (McIlhenney, 1976) of the youngest (80 mm skull) animal to be 2-3 years of age, a young juvenile, and the oldest (540 mm-skull) animal to be at least 10 years of age, a mature adult.

The same measurements were made on the teeth of these alligator skulls as were used in the tooth morphology study (see Figure 1), except that only the labial length of each tooth was recorded. The lingual length was not included in this phase of the work because curvature has not been reported by any previous researchers as a factor in tooth-shape change in *Alligator mississippiensis*. To simplify the process, only the upper teeth were used in this study, based on the assumption that ontogenetic changes in the maxilla and premaxilla would be mirrored in the dentary. An average value was calculated for the sixty measurements per specimen (3 variables, 20 teeth). Skull dimensions were not used for standardization purposes in the analysis, as these are known to vary based on ecological and genetic variables (Brochu, 1999; Monteiro, 1997). All tooth measurements of the skulls were multiplied by the ratio of the median skull's (292 mm specimen) average of measurements to the average of all measurements for that specimen. Individual variation was preserved in this way, while the effects of size were essentially removed from the analysis.

A Bonferroni paired t-test was performed on the standardized data from these seven alligator skulls using SYSTAT version 8.0 statistical software (Copyright © SPSS

Inc., 1998. All Rights Reserved). This particular version of the t-test was used due to the need for multiple comparisons and corrected P-values based on this factor. All data for each skull were arranged vertically in one matrix with the three variables for each tooth in repeating series of two widths and one length. In this way, each variable for each tooth in all specimens could be compared horizontally. Because of the goal of this analysis and the arrangement of the data, opposite values to those usually needed were desired in this case. Thus, the goal was to achieve complete failure in all 21 comparisons (among the seven skulls), thereby showing a lack of significant difference among the teeth of the individuals tested.

The same data used in the paired t-test were used to graphically test for differences among the seven specimens, as well as to display the maxillary tooth “signature” for *Alligator mississippiensis*. Each tooth variable was represented by a single line produced by the average of values. Error bars were calculated for each variable and graphed in order to represent the standard error at each tooth locus. Graphing and calculation for this exercise was performed with SigmaPlot version 5.0 (Copyright© SPSS Inc., 1986-1999, All Rights Reserved).

Cretaceous tooth sample

The final portion of this research consisted of testing a random sample of Cretaceous age mesoeucrocodylian teeth by applying the methodology used in the first part of this study to hopefully estimate the numbers of species present at a single fossil locality. The teeth used were selected from one sample of unsorted and unassociated crocodylian teeth (OMNH 34573) collected from the Cedar Mountain Formation in

Emery County, Utah. These teeth were used because no previous attempt had been made to assign these specimens to any existing families. The Cedar Mountain Formation is of Aptian/Albian age and has yielded a diverse fauna of Early Cretaceous microvertebrates (See Pomes, 1988; Cifelli et al., 1997; Cifelli et al., 1999). The crocodylian teeth studied were found at OMNH locality V695. Hundreds of teeth from this locality have been sorted and assigned to mesoeucrocodylian families such as Atoposauridae, Goniopholididae, and Bernissartiidae. While little skeletal evidence for these families exists from this location, there are precedents (Pomes, 1988; Estes and Sanchíz, 1982) for this methodology, and teeth of this age with certain distinctive shapes are commonly assigned to these families (Langston, pers. comm.).

The very small size of the 137 Cedar Mountain teeth measured (average crown height of 2.3 mm) precluded the use of calipers. Instead, the teeth were measured microscopically using a reflex microscope (see MacLarnon, 1989 for an explanation of reflex microscopy). Three variables (anterior/posterior width, labial/lingual width, and greatest length) were recorded for each tooth. The data matrix created was then processed using a principal components analysis and a cluster analysis using the same methods described for the first set of analyses. The only exception to this methodology was to standardize the data set prior to the cluster analysis, because these teeth were not derived from the same individual. A final analysis using the same 2-dimensional graphing technique discussed earlier was performed. The graphical results from this test were combined with those of appropriate extant species in order to better describe the shape-space defined.

Institutional abbreviations used in this paper are as follows: TMM= Texas

Memorial Museum, Austin, TX; OMNH= Oklahoma Museum of Natural History, Norman, OK; FMNH= Field Museum of Natural History, Chicago, IL.

RESULTS

Tooth morphotype analyses

Cophenetic correlation coefficients for the cluster analyses varied from 0.64 to 0.75. These numbers indicate a moderately good match between the trees produced and the original Penrose shape coefficient similarity matrices (Rohlf, 1999). From these dendrograms based on individual specimens, 2 to 4 valid morphotypes (varying among the species) appear to be present. These morphotypes were based on tree clusters of significant branch length to indicate viable groups of similarly-shaped teeth. To save space and reduce redundancy, graphs of cluster analysis results and those from the proceeding analyses will display only maxillary and premaxillary tooth information. The cluster analysis results are displayed in Figures 2 and 4.

The principal components analyses showed principal component 1 accounting for an average of 77% of the variance of characters among the ten trials, while principal component 2 accounted for 22% of the remaining variance. For this reason, two dimensional plots were deemed sufficient to display the pertinent information of each analysis. Loadings for the first principal component were over 0.75 in an average of three out of the four variables, while the second principal component usually showed loadings over 0.5 for one or two of the variables. In all of the analyses, principal component 1 reflects greater tooth size with higher loadings, while principal component 2 reflects increasing squatness and robustness of the tooth at the higher loading values,

whereas lower values indicate a more slender and round-based tooth.

All principal components analyses defined the same 2-4 morphotypes that were seen in the cluster analyses. While the strengths of groups defined within these tests varied considerably, the actual distances between points in shape-space were within reasonable parameters when compared with dendrogram results. Graphical principal components analysis results are shown in Figures 3 and 5. All results for each species are displayed with a common letter and consecutive numbers in the figures. The results for *Alligator mississippiensis*, for example, are shown in Figures 2a and 3a.

Ontogenetic tooth shape study

The Bonferroni paired t-test, used to analyze the ontogenetic data, yielded the predicted results. Adjusted Bonferroni P-values were 1.00 for 19 out of the 21 comparisons made among the seven *Alligator mississippiensis* skulls. That is, >90% of comparisons showed a significant lack of difference between the teeth of the different-aged skulls. Thus, significant ontogenetic change in tooth shape does not occur in *Alligator mississippiensis*. Because of the experimental design in this case, P-values as far away from 0.00 (or .05 in normal significance tests) were desired. P-values of 1.00 therefore showed no significant difference between the dentitions. The two unsuccessful comparisons made were between the 469 mm skull and the 80 mm and 292 mm skulls. The 469 mm skull possessed a greater degree of tooth wear than the other specimens, which probably accounted for the non-significant comparisons.

The ontogenetic data set was graphed, and errors bars included. Standard error was calculated at each tooth locus and found to have an average value of 0.12. This low

value for standard error can be seen graphically in Figure 6. Standard error was highest in the tooth length comparisons. The ratio of length to width appears to increase very slightly (not significantly) with increasing age of the animal, while tooth widths remain very constant, increasing isometrically with age.

Cretaceous tooth sample

The random sample of teeth from OMNH V695 provided some ambiguous and some positive results. The principal components analysis yielded results within the parameters described in the first part of this study in terms of component variance and loadings for characters. Successful morphotype definition based on the results of this test proved impossible, however, due to overlap of data points. Fortunately, the cluster analysis (cophenetic correlation coefficient of 0.65) did provide multiple possible morphotypes. Conservatively, this analysis defined at least 9 separate morphotypes. This interpretation is represented in Figure 7 by the gray broken vertical bar of possible morphotypes to the left of the dendrogram. The black broken vertical bar represents another scenario, in which as many as 14 morphotypes can be distinguished. Based on the number of tooth morphotypes present in modern species and both possible interpretations of this cluster analysis, the sample of Cretaceous-age mesoeucrocodylian teeth likely represents at least three species.

Graphical results of ratio-based comparisons of form for the Cretaceous teeth supported the previous results when these data points were overlaid with those of modern species (see Figure 8). Interestingly, the portion of shape-space occupied by modern forms versus that taken up by the OMNH V695 teeth represents approximately 40% of

the whole (compare with Figure 9). This factor indicates that the Cretaceous species from this sample were considerably more heterodont in their dentitions than modern species. Moreover, the ability to fit multiple modern dentition patterns within the space occupied by these Cretaceous teeth supports the results of the cluster analysis, which suggest that at least three species are present in the random OMNH V695 sample. Figure 8 shows example tooth shapes to aid in understanding the variety of shapes addressed. These tooth outlines represent only the lingual or labial views of these teeth, and vary in the horizontal component of the figure. The vertical axis of Figure 8 depicts variation in tooth roundness. This factor is not represented by the tooth outlines, but accounts for a large component of the overall variation.

A final test was performed that compared the average tooth shapes of all species and the Cretaceous teeth in terms of previous ratio comparisons (see Figure 10). This figure summarizes the shapes of all teeth studied and provides morphological information which can be interpreted phylogenetically as well as in reference to dietary specializations. In this case, the sample from OMNH locality V695 shows that these teeth represent species with a higher degree of durophagous specialization. Phylogenetic interpretation of this information should be avoided, however, because this singular data point probably represents multiple species. Good separation between modern crocodylids and alligatorids can also be seen in Figure 10, as well as a fairly isolated position for the distinctive *Gavialis gangeticus*. This figure also displays the relatively different average tooth shapes for those species studied.

DISCUSSION

Tooth morphotype analyses

Functional tooth morphotypes were named in this study based on feeding information from several authors (eg., Gans, 1969; Busbey, 1989; Cleuren and De Vree, 1992), and on the tooth morphotype work of Massare (1987). The most informative feeding observations were those in which care was taken to note the regions of jaws used during different phases of the feeding process in crocodylians, as in Busbey's work (1989). Massare (1987) defined morphotypes of marine reptile teeth which performed specific functions based on comparisons with the dentitions of modern cetaceans. Borrowing liberally from both sources, all modern crocodylian teeth were categorized as one of the following morphotypes.

The first morphotype defined is the most obvious type of crocodylian tooth, often called a "caniniform" tooth (Brochu, 1999; Guggisberg, 1972; McIlhenney, 1976). This tooth type is here termed a "hold/pierce" tooth. A two-part name is used to address the (at least) dual function of these teeth. Observers of feeding in crocodylians have often noted the use of these teeth to maintain a firm hold on the prey. Based on the shape of this tooth, however, it certainly performs a piercing function due to its very high narrow crown with a pointed apex and fairly round base (Massare, 1987). Other tooth morphotypes defined in this study were given two-part names to better describe their functions.

Most modern crocodylians possess smaller and more robust versions of the preceding morphotype on either side of the hold/pierce teeth in the jaws. These teeth are defined here as "pierce/cut" teeth. Pierce/cut teeth are more laterally and longitudinally

compressed, and possess the most prominent carinae (anterior and posterior cutting edges) of any teeth in the dentition. For this reason, they are assumed to perform a cutting function as a secondary role to their overall piercing shape. When crocodylians remove pieces of a large prey animal by holding it with the hold/pierce teeth and rotating the body about the longitudinal axis (Hutton, 1987; Forsyth, 1910), the sharper carinae and appropriate position of the pierce/cut teeth permit them to remove pieces of the prey animal. No other teeth in the dentition are shaped or positioned as appropriately to perform this function.

Prior to swallowing a small to medium-sized prey animal, the prey is usually processed by the most posterior teeth in the jaws (Cleuren and De Vree, 1992; Busbey, 1989; Carpenter and Lindsey, 1980). The distinctive tribodont (blunt and rounded) shapes of posterior teeth in several modern species have been noted repeatedly (Aoki, 1989; Kieser, 1993; McIlhenney, 1976). Massare (1987) reported that mosasaur teeth of this shape likely performed a crushing function and were found in species thought to subsist primarily on hard-shelled ammonites and other cephalopods. Indeed, such teeth are commonly associated with durophagy. These crocodylian teeth are defined here as the “crush/smash” morphotype. The “smash” portion of the name points to the fact that many of the teeth assigned to this morphotype possess somewhat higher crowns than the most posterior and tribodont teeth observed.

The remaining teeth in the dentition belong to the “pierce/smash” morphotype. This morphotype includes very round-based teeth with pointed crowns of medium height. The majority of these teeth are located just anterior to the crush/smash teeth, and here likely perform a large part of the prey killing and reducing functions (Busbey, 1989).

These teeth are also located in the first and second premaxillary alveoli of many species and also act in initial prey acquisition. Their shape places them midway between the pierce and smash morphotypes defined by Massare (1987). These teeth probably also help with repositioning maneuvers after prey acquisition (Busbey, 1989).

The results of this tooth morphotype analysis are designed to be interpreted descriptively, rather than as infallible new truths. As seen in Figure 9, there is considerable morphotype overlap between species. For this reason, morphotypes were assigned only within individual species. The work herein is an attempt to better understand the variable patterns of crocodylian dentitions noted by several authors (eg., Aoki, 1989; Guggisberg, 1972; Westergaard, 1990), and correlate this information with diet.

Alligatoridae- The two species of *Alligator* showed more similar results in the morphotype analyses than did any other two members of this family. Both have large and morphologically distinct hold/pierce teeth in upper tooth row positions 4 and 9 (see Figures 2a, 3a, 4a, and 5a). The hold/pierce teeth and associated alveoli are obvious enough features of the dentition to make them useful in phylogenetic analyses recently (Brochu, 1999), and are considered to be of some taxonomic weight (Norell, 1989). Given this factor, note that only *Caiman crocodylus* shares the 4 and 9 hold/pierce position (with the addition of tooth number 3) with members of *Alligator*.

Alligator sinensis has more teeth devoted to the pierce/smash and crush/smash morphotypes than does *Alligator mississippiensis*. This supports observations that *A. sinensis* has one of the most durophagous dentitions known among modern species

(Aoki, 1989). Little is known about the diet of *A. sinensis* except for reports of turtle-eating (Barbour, 1922). In terms of average tooth shape (see Figure 10), this species most resembles *Caiman crocodilus* (Figures 3b and 4b), which is known to consume more arthropods and molluscs than other amazonian crocodylians (Magnusson, 1987; Magnusson, 1995). Indeed, *A. sinensis* and *C. crocodilus* possess the most tribodont teeth studied other than those of Cretaceous species from OMNH V695. This evidence supports the theory that *A. sinensis* occupies a durophagous feeding niche.

Alligator mississippiensis is perhaps the most studied crocodylian (Busbey, 1989), yet there are few generalizations that can be made about the diet of this animal (Chabreck, 1971). As E. A. McIlhenny (1976, p. 41) said, American Alligators eat "...every living thing coming within range of its jaws that flies, walks, swims, or crawls that is small enough for them to kill..." Such observations are not limited to this species (eg., Neill, 1971; Cott, 1960), and Magnusson et al. (1987) suggest that much of what alligatorids consume depends on the habitats they frequent most often. Given this observation, it is not surprising that alligators consume a large number of fish, turtles, mammals, and snails in their most commonly occupied habitats of bayous, lakes, and rivers (Chabreck, 1971; McIlhenny, 1976). *Alligator mississippiensis*, then, appears to be a generalist and opportunist in its feeding habits, and consumes prey animals based on size and availability rather than any specific preferences. The variety of distinct morphotypes defined in this study for *A. mississippiensis* presumably make such a varied diet possible.

In Brochu's (1999) recent phylogenetic study of alligatorids, the two modern members of *Paleosuchus* constitute a sister group to other modern and extinct members

of Alligatoridae within a group defined as Caimaninae. *Paleosuchus palpebrosus* (Figure 3c and 4c) and *Paleosuchus trigonatus* (Figure 3d and 4d), then, likely diverged from the group leading to the modern genus *Caiman* during the Late Cretaceous. This fairly distant relationship to other South American alligatorids is supported in this study by the quite different results gleaned from these two genera (see Figures 5c and 5d). Three morphotypes were identified in the two species of *Paleosuchus*, versus the four defined for other alligatorids. Five upper teeth were assigned to the hold/pierce morphotype in all analyses performed for the two members of *Paleosuchus*. Instead of the usual alligatorid positions of 4 and 9 for these teeth, both members of the genus have teeth 3 and 8 assigned for this purpose, as well as three other anterior teeth (different positions in the two species). This condition, based on phylogenetic analyses (Brazaitis, 1998; Brochu, 1999), may represent an ancestral condition within Caimaninae.

The two species of *Paleosuchus* are the smallest living crocodylians, neither of which generally exceeds 1.5 m in overall length (Magnusson, 1991; Guggisberg, 1972). *Paleosuchus palpebrosus* was shown by Magnusson et al. (1987) to have a diet very similar to that of *Caiman crocodilus*, subsisting on a variety of fish, molluscs, and crustaceans as adults, with a larger number of snails and insects consumed by juveniles. Conversely, *Paleosuchus trigonatus* was observed in the same study to consume primarily terrestrial vertebrates, even as juveniles. This species has been observed most commonly inhabiting small shallow streams under dense forest canopy (Magnusson, 1987, 1991, 1992), which helps explain the large number of vertebrates in its diet. Other unusual observations concerning this species include subadults wandering great distances through the jungle in search of new territories and perhaps prey sources. Based on

known ecological information, *Paleosuchus trigonatus* can be considered the most terrestrial of modern crocodylians.

Upon gross observation of the teeth of both species of *Paleosuchus*, one notices the especially large and posteriorly (instead of lingually) recurved anterior teeth. These anterior teeth also possess unusually strong carinae. Unfortunately, these unusual features could not be addressed analytically in this study. Along with unusual curvature and strong carinae, the hold/pierce teeth of both species of *Paleosuchus* are considerably more laterally compressed than is usual for alligatorids (see Figures 5c, 5d, and 10). Because *Paleosuchus trigonatus* apparently does most of its feeding in terrestrial environments, I propose that the genus *Paleosuchus* has lost its pierce/cut teeth in favor of more hold/pierce teeth in order to adapt to this environment. Without the mechanical advantages of water resistance while feeding (Thorbjarnarson, 1990), these animals may have evolved (or retained) larger, more caniniform teeth to better control struggling prey in a non-aquatic environment. This theory requires and deserves further investigation.

Crocodylidae- *Crocodylus acutus* (Figures 2b and 3b), *Crocodylus porosus* (Figures 4e and 5e), and *Crocodylus niloticus* (Figures 2c and 3c) will be discussed together here because of the overall similarity of their tooth patterns. Like members of *Alligator* and *Caiman*, four functional tooth morphotypes were defined in these species. These animals all possess 19 total premaxillary and maxillary teeth. Unlike the alligatorids, these members of *Crocodylus* show tooth numbers 4 and 10 to be the hold/pierce teeth. Only those teeth immediately anterior to the hold/pierce teeth were successfully grouped as pierce/cut teeth in *Crocodylus niloticus*, with a surprisingly large number of teeth (13-19)

being resolved as crush/smash teeth. *Crocodylus acutus* possessed four pierce/cut teeth, eight pierce/smash teeth, and five crush/smash teeth. *Crocodylus porosus* has more teeth devoted to the pierce/cut morphotype than does any other member of its genus.

Conversely, there were fewer pierce/smash and crush/smash teeth defined in this species.

While much has been learned about the diets of crocodiles in the wild (eg., Hutton, 1987; Webb, 1991; Cott, 1960), little of this information is helpful in discerning the subtle dental differences between these three species. All of these animals eat large numbers of insects, crustaceans, and molluscs as juveniles (Corbet, 1959; Webb, 1991), and consume more vertebrates with increasing size (Taylor, 1979; Cott, 1960; Guggisberg, 1972). As stated before, it appears that the food most crocodylians consume is primarily a function of prey size and availability (Taylor, 1979; Perez-Higareda, 1989; Magnusson, 1987). Conversely, it is possible that the more common prey items in the varied habitats of these species have allowed for the evolution of slight morphological differences.

Cott (1960) observed that *Crocodylus niloticus* ate fish at all stages of life, but mostly within the 1.5 to 3.5 m size range, while smaller individuals relied primarily on molluscs and other invertebrates. Larger members of the populations he surveyed ate primarily mammals and reptiles. Similar observations were made by Thorbjarnarson (1988) concerning *Crocodylus acutus*, with the caveat that a greater number and variety of fish made up the diet of this species compared to *C. niloticus*. Multiple authors who have surveyed the food and feeding habits of *Crocodylus porosus* reported a surprisingly high number of crustaceans being consumed at all life stages (Taylor, 1979; Webb, 1991). Both authors reported, however, that this was likely due to sampling of

crocodylians in an estuarine environment. Given that the majority of prey choices are so similar, its not surprising that there is little difference among the dentitions of these species.

Crocodylus moreleti (Figures 2d and 3d) is the most brevirostrine living member of *Crocodylus* (Langston, pers. comm.), and so represents an interesting study animal. Magnusson et al. (1987) suggested that short snouts and broad, flat heads are an adaptation for swamp environments, while adaptations for riverine environments include longer narrower heads. This may be the case, since the alligatorid-shaped head (like that of *C. moreleti*) has evolved multiple times within Crocodylidae and Alligatoridae (Langston, 1973; Brochu, 1999). From the results displayed in Figure 10 we can see that short-snoutedness does not appear to affect dental morphology. Moreover, the assumption that brevirostrine forms tend to be more durophagous (McIlhenney, 1976) certainly does not appear to hold true (again, see Figure 10).

Despite unusual head morphology, *Crocodylus moreleti* has a fairly standard crocodylian dentition. Probably because there are only 17 upper teeth present, the hold/pierce teeth of this species are shifted forward one alveolus to positions 3 and 9 (from the usual 4 and 10 of *Crocodylus*). Like *Crocodylus niloticus*, the pierce/cut teeth of this species are those immediately anterior to the hold/pierce teeth. There are eight teeth assigned to the pierce/smash morphotype and 5 teeth assigned to the crush/smash group. Like other members of its genus, *C. moreleti* appears to be a generalist feeder. In one study, a population of this species was observed consuming 26 different taxa, including several dogs and goats (Perez-Higareda, 1989). In support of the theory of Magnusson et al., (1987) this species inhabits swamps and lakes of Central America.

Gavialis gangeticus- The Indian gharial exhibits extreme piscivorous specialization (Guggisberg, 1972; Neill, 1971). It has a very long and narrow snout, and is likely the most aquatically adapted modern crocodylian, having apparently lost the ability to perform the “high walk” (Thorbjarnarson, 1990). Although bird and mammal prey are occasionally taken by this species (Neill, 1971), the diet is composed primarily of fish (Thorbjarnarson, 1990).

Twenty-eight teeth are present in the upper dentition of *Gavialis gangeticus* (Figures 2e and 3e), and among these only 2 morphotypes were defined. The anterior twenty-four teeth were assigned to the pierce/cut morphotype. Although these teeth occupy similar shape-space to the hold/pierce teeth of other modern species (see Figure 9), they possess strong carinae and more lateral compression than do the hold/pierce teeth of other species. The remaining posterior teeth were assigned to the pierce/smash group, as they certainly could not be described as tribodont. According to most phylogenetic analyses including this animal (eg., Norell, 1989; Brochu, 1997), the gharial is distantly related to other modern crocodylians. This work supports these findings, as no crocodylid or alligatorid dental features were noted in the dentition. Moreover, the results displayed in Figure 10 show a very divergent position for *G. gangeticus* compared to other modern species.

Ontogenetic tooth shape study

Reports of “increasing anisodonty with age” (Westergaard, 1990), and other statements supporting ontogenetic tooth shape change (Kälin, 1933; Langston, 1973; Mook, 1921) were shown to be inaccurate in the second part of this study. Although a

slight increase in length versus width with age occurs (see Figure 6), there is no significant overall ontogenetic change in shape in the teeth of *Alligator mississippiensis*. Since this species is commonly used as a model for all other modern crocodylians (Busbey, 1989; Edmund, 1962; Sato, 1990), the same can probably be said for all modern species. These results lend greater importance to the morphotype analyses in the first part of this study, and all other observations of crocodylian and mesoeucrocodylian dentitions (see eg., Aoki, 1989; Larsson, 1999; Williamson, 1996).

Cretaceous tooth sample

Descriptions of mesoeucrocodylian dentitions are very often brief (Steel, 1973; Williamson, 1996). We know, however, that the teeth of early crocodylomorphs were at least as heterodont as those of modern forms (Joffe, 1967; Buffetaut, 1979; Simpson, 1937). *Bernissartia*, for example, is well known for its blunt crushing teeth, but also possessed narrow high crowned anterior teeth (Norell, 1990), not unlike those often assigned to the family Goniopholididae (Brochu, pers. comm.).

Pomes (1988) attempted to define morphotypes from the same Cretaceous formation studied in this research. He used gross morphological features of the teeth to define two to three morphotypes within certain mesoeucrocodylian families and genera, without the aid of complete dental information for any of these taxa. Estes and Sanchíz (1982) performed similar work in which isolated teeth were assigned to families and genera based on such features as carina strength, gross shape, and irregular features of the enamel (termed “ribs” or “striations”). While such work is important and aids in our understanding of early biodiversity, too many of the features used to classify these teeth

are subject to wear and irregularity. Features of the enamel, for example, vary considerably within the same animal, as do carinae.

Without comparison to complete dentitions, it is impossible to know the numbers and shapes of tooth morphotypes present within the teeth of a given Cretaceous species. For this reason, identification of isolated teeth based on incomplete dentitions of fossil forms should be viewed with scepticism. Moreover, there is considerable overlap of morphotypes in modern species (see Figure 9) and this is certainly the case in fossil forms. Indeed, even using complete dentitions for comparison, resolution between the same morphotype in different species proves challenging.

The mesoeucrocodylian species potentially represented in this sample of teeth are mostly considered to be diminutive forms (Joffe, 1967; Buffetaut, 1979; Buffetaut, 1983; Norell and Clark, 1990). Specifically, Pomes (1988) reported that the majority of teeth he recovered, derived from the families Atoposauridae and Bernissartiidae, were very small. According to the population surveys performed on modern species by Cott (1960) and Taylor (1979), the majority of individuals in any crocodylian population are juveniles. This fact, in combination with what others (Westergaard, 1990; Edmund, 1962; Poole, 1961) have discovered about the much higher rates of tooth replacement in young crocodylians, leads one to the assumption that the majority of teeth shed in any crocodylian population will be derived from immature individuals. This hypothesis was supported by the very small average crown height (2.3 mm) of the teeth measured from OMNH V695. Even from a population of very small crocodylians, this appears to be a low value for average tooth size.

This study has shown that it is likely the sample of teeth taken from OMNH V695

represents at least three species. The limitations of applying principal components and cluster analyses to such data became apparent in this study, however, because of the variety of possible interpretations of such results (see Figure 6). Pomes (1988) identified five families of mesoeucrocodylians from this formation. This study supports his finding that several taxa are represented in this formation. The methodology he used to arrive at his conclusions, however, can not be endorsed. With better fossil data pertaining to the producers of these teeth, it will eventually be possible to learn more from isolated fossilized teeth.

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Tooth Measurements

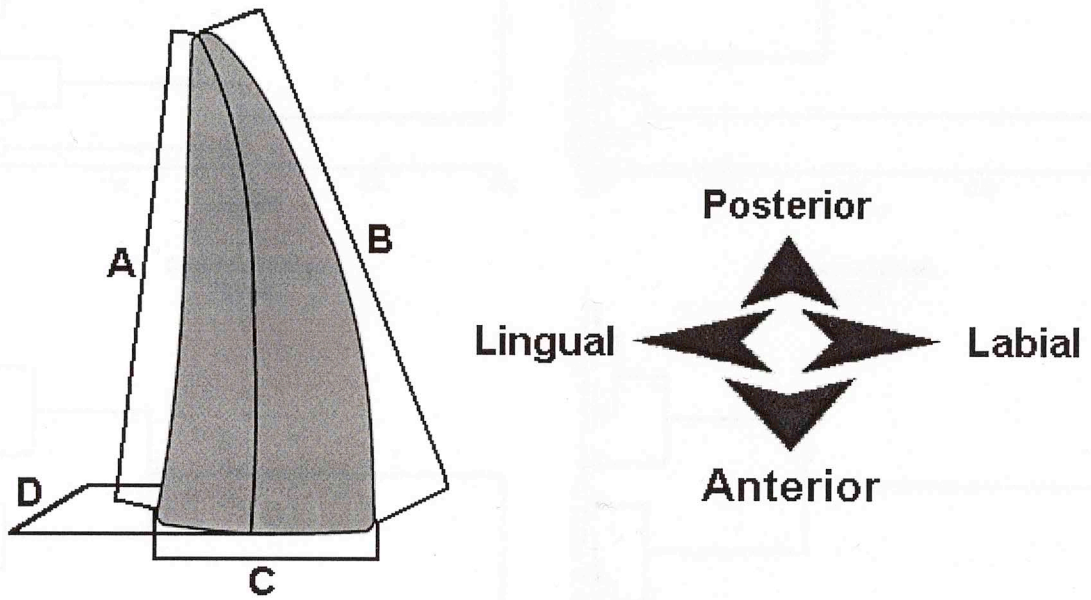
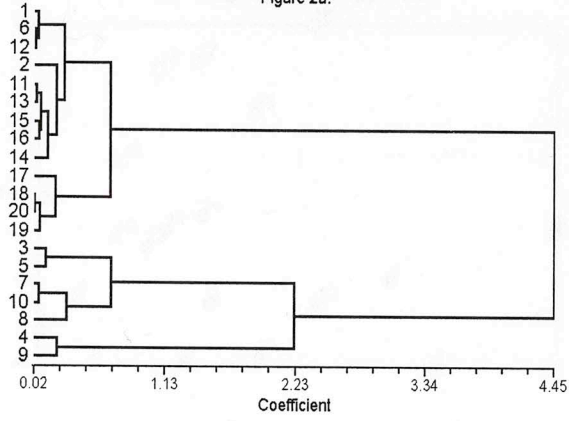
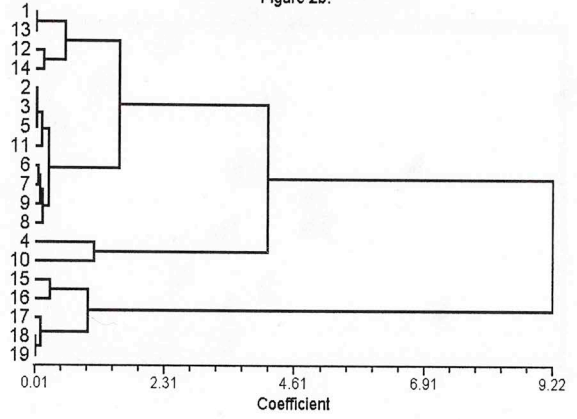


Figure 1.

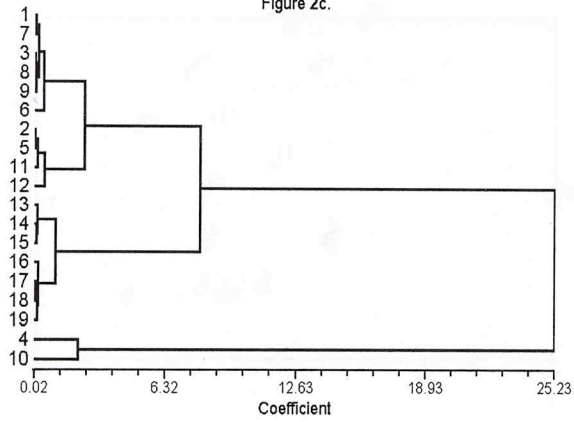
Alligator mississippiensis
Figure 2a.



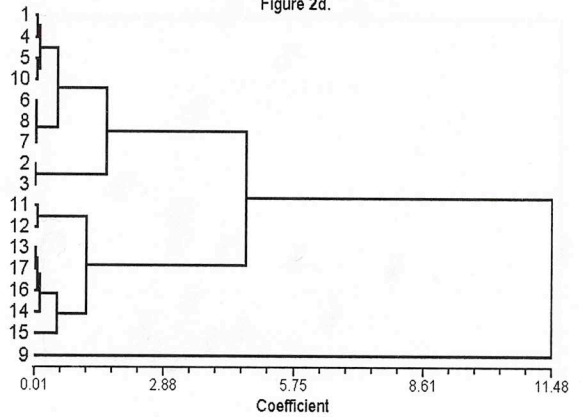
Crocodylus acutus
Figure 2b.



Crocodylus niloticus
Figure 2c.



Crocodylus moreleti
Figure 2d.



Gavialis gangeticus
Figure 2e.

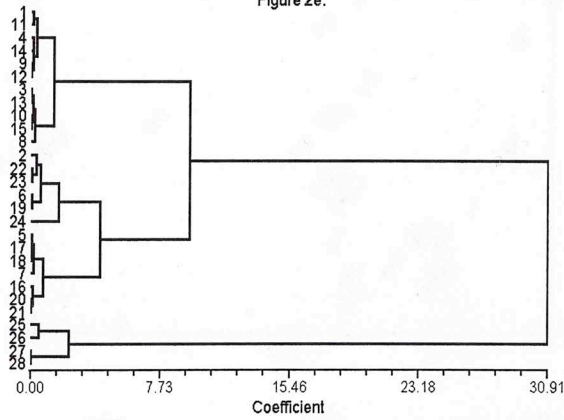


Figure 2a-e.

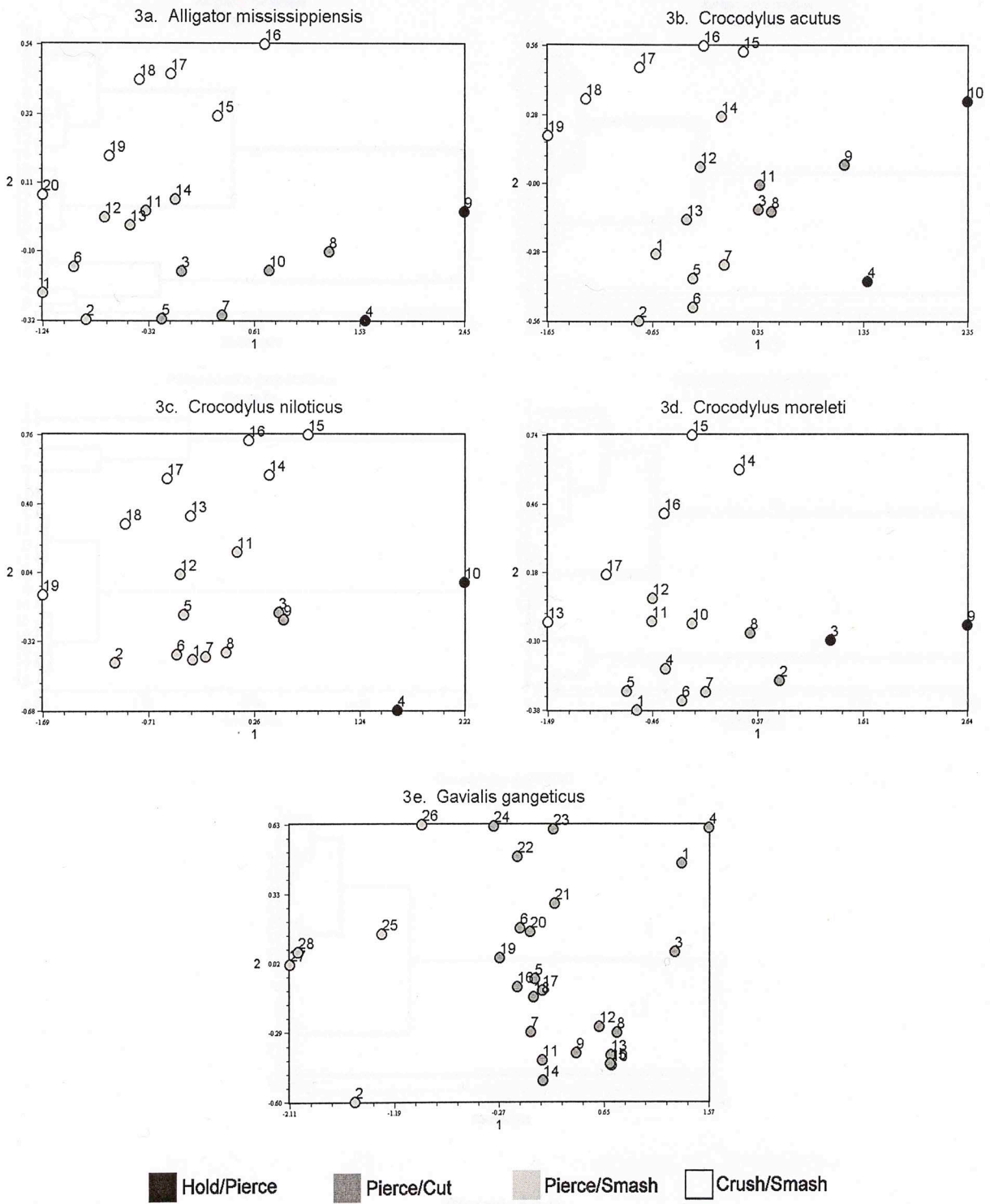
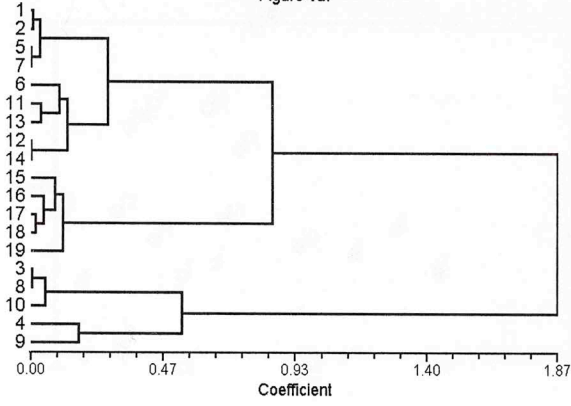
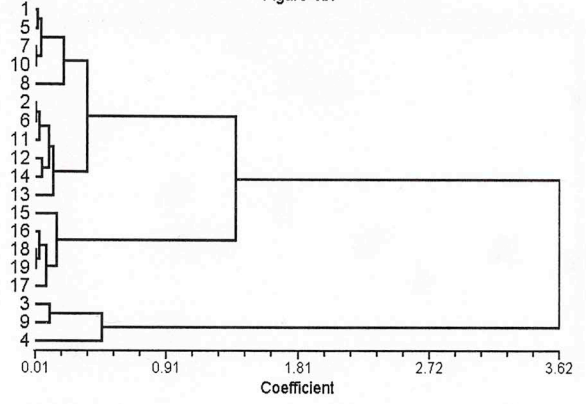


Figure 3a-e.

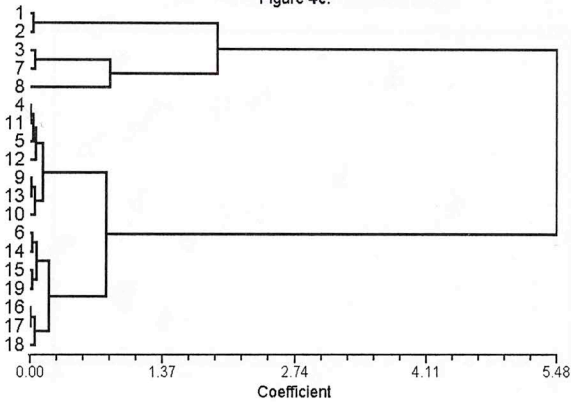
Alligator sinensis
Figure 4a.



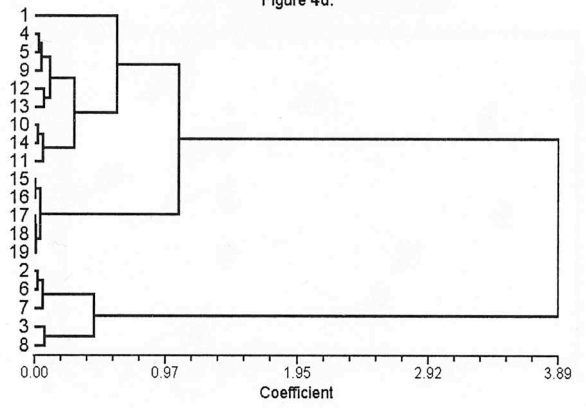
Caiman crocodilus
Figure 4b.



Paleosuchus palpebrosus
Figure 4c.



Paleosuchus trigonatus
Figure 4d.



Crocodylus porosus
Figure 4e.

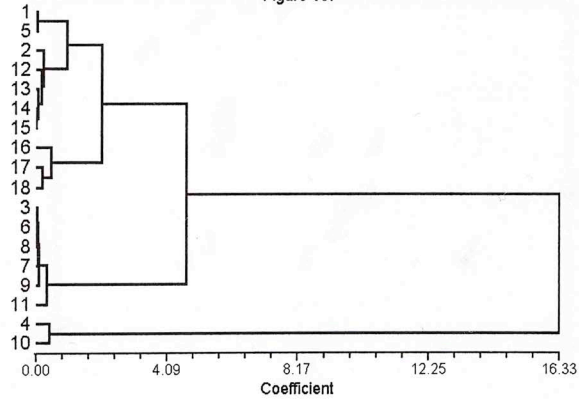


Figure 4a-e.

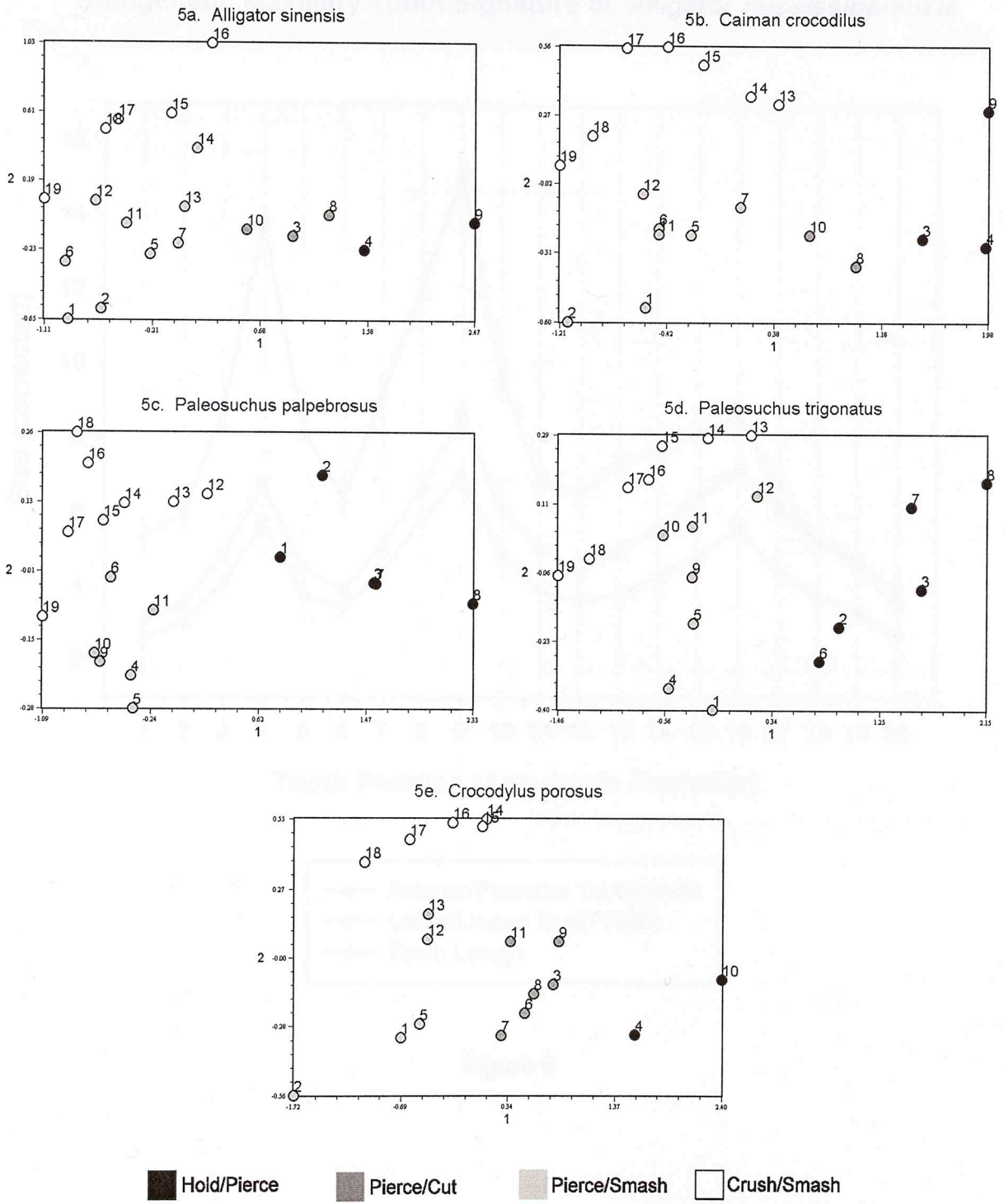


Figure 5a-e.

Ontogenetic Maxillary Tooth Signature of *Alligator mississippiensis*

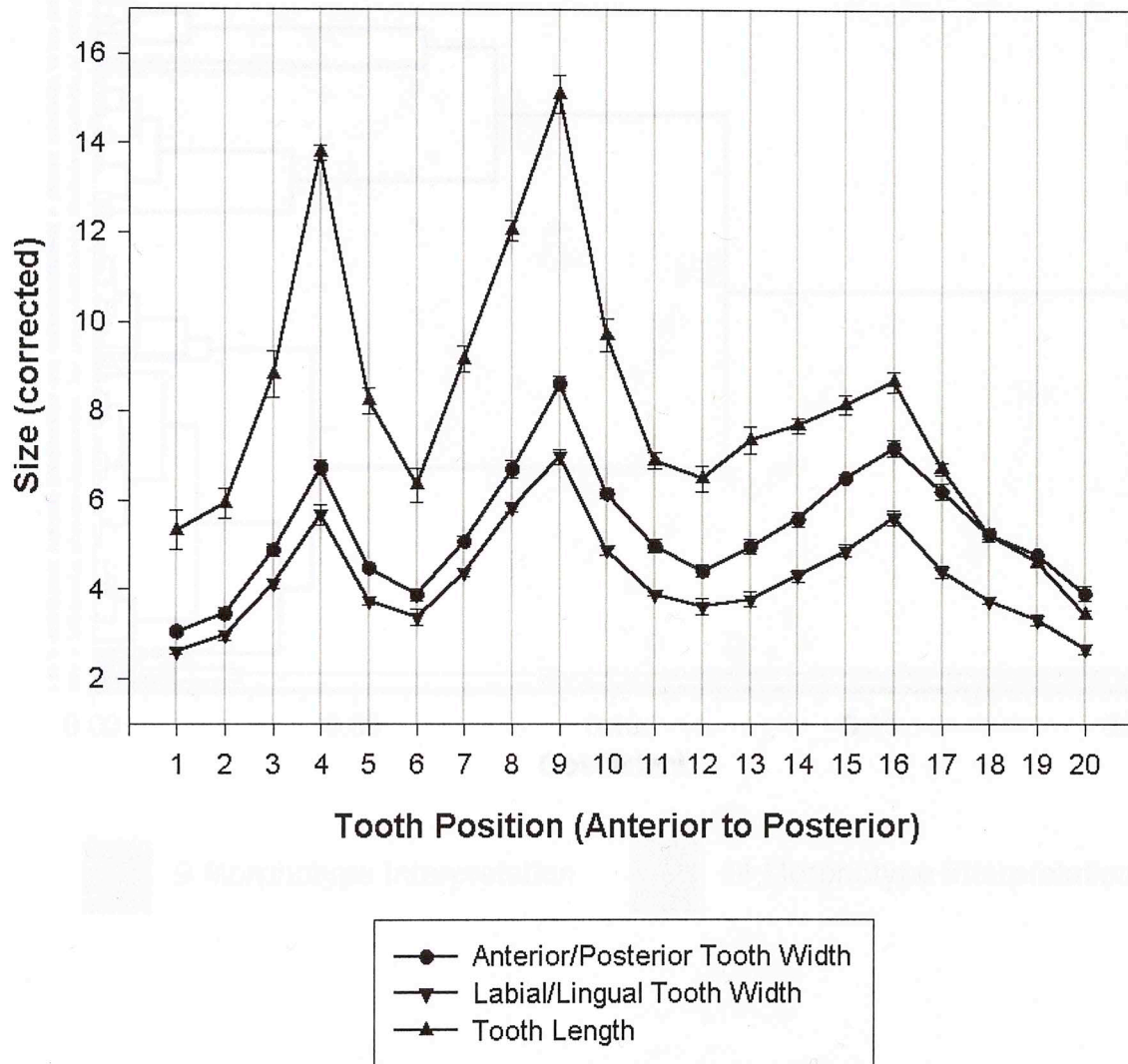


Figure 6.

Truncated UPGMA Tree from Standardized OMNH V695 Teeth

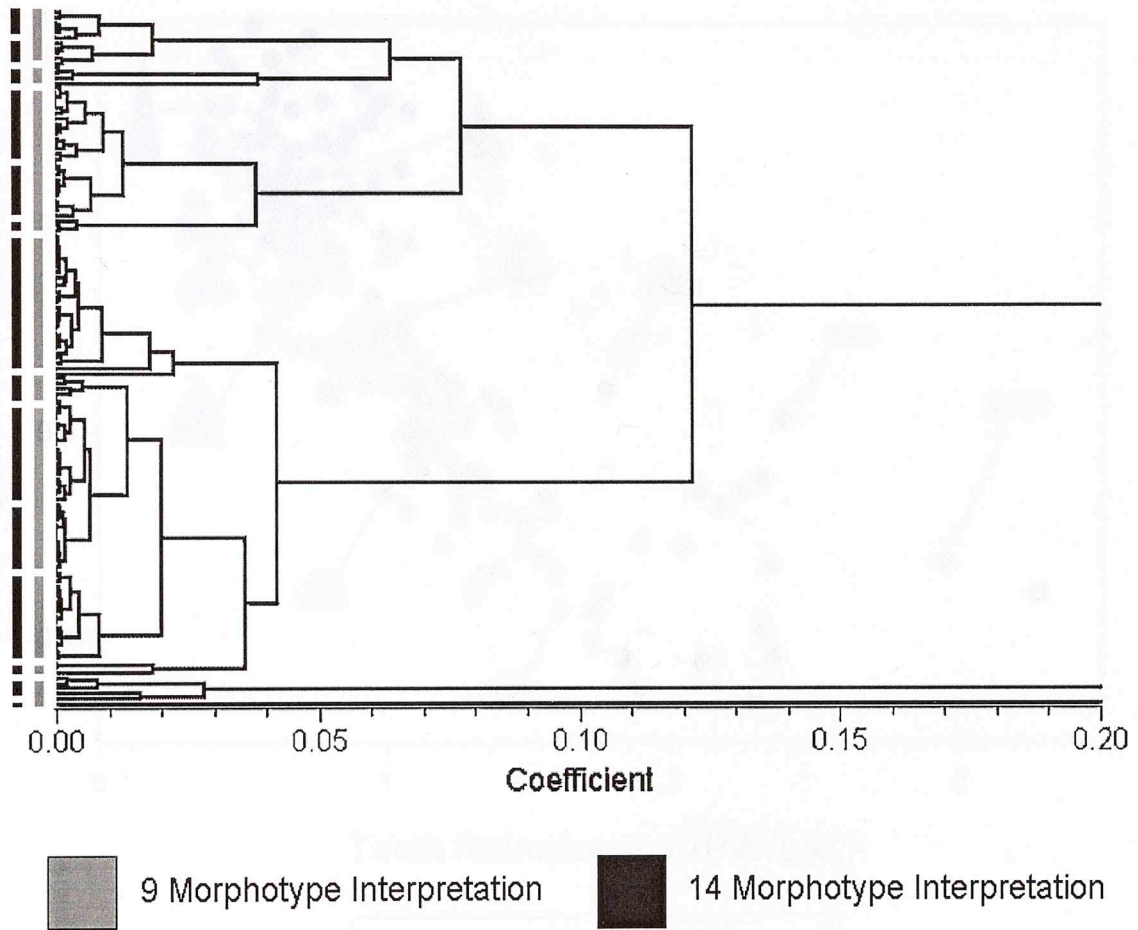


Figure 7.

Modern vs. Cretaceous Tooth Shape Summary

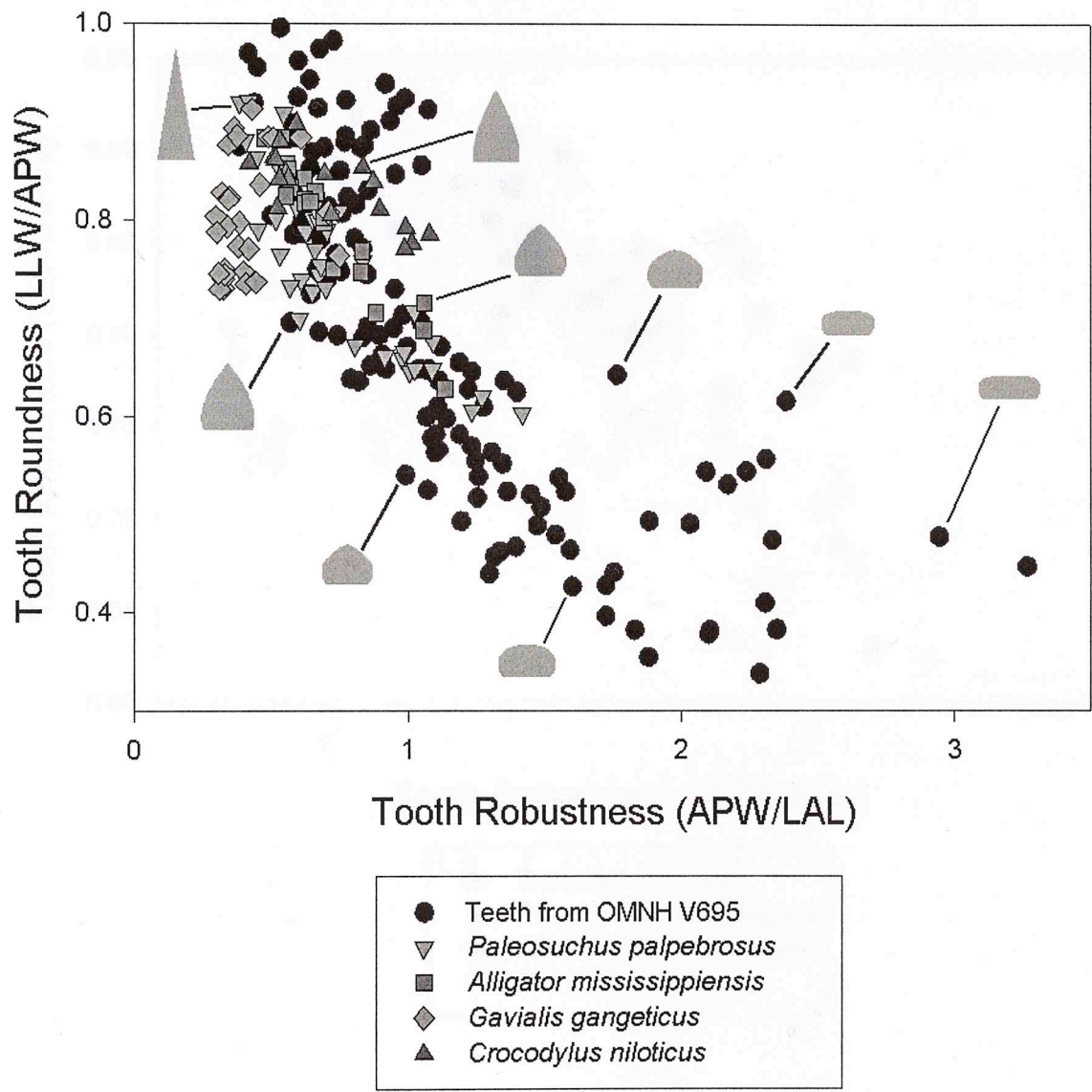


Figure 8.

Modern Crocodylian Tooth Shape Summary

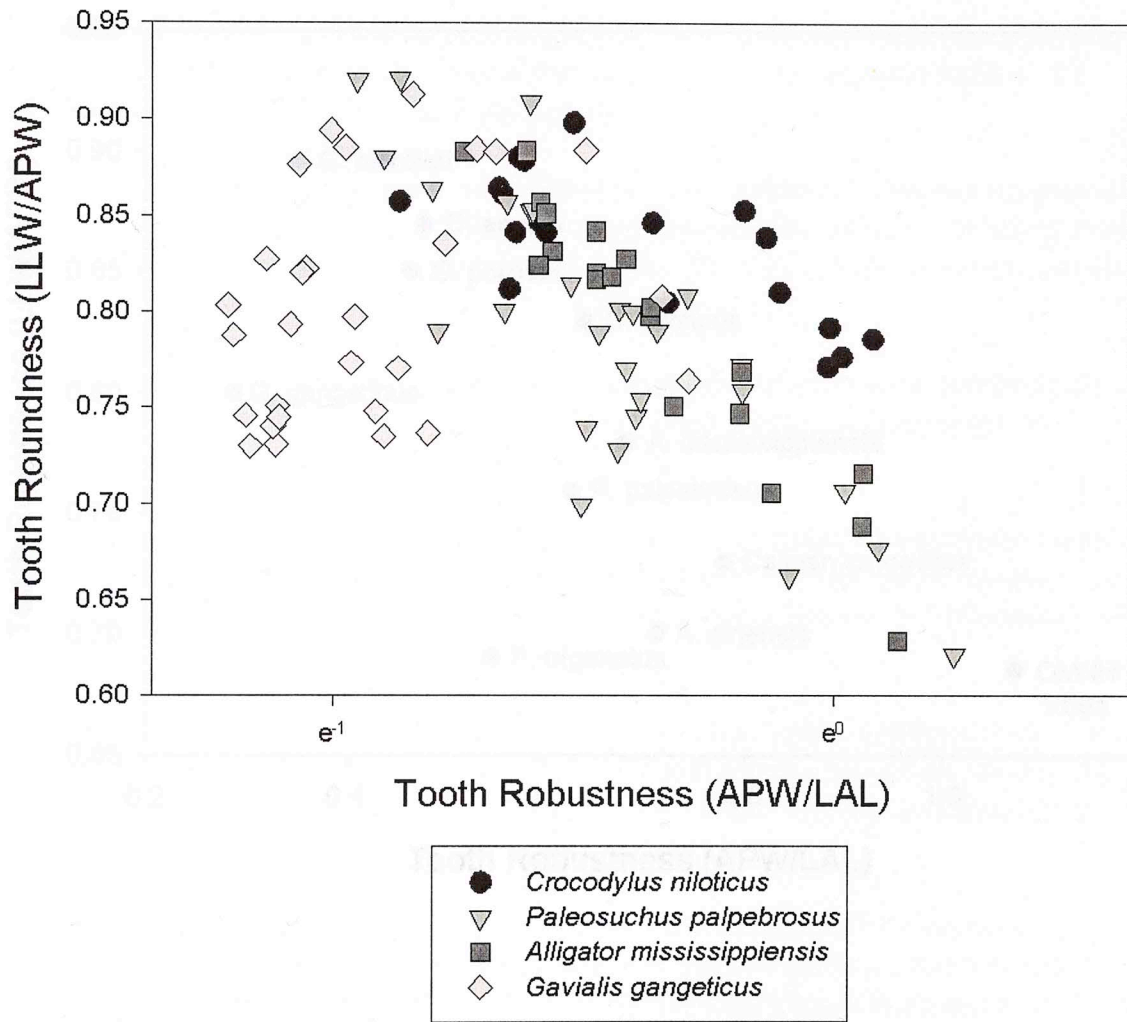


Figure 9.

Combined Tooth Shape Summary

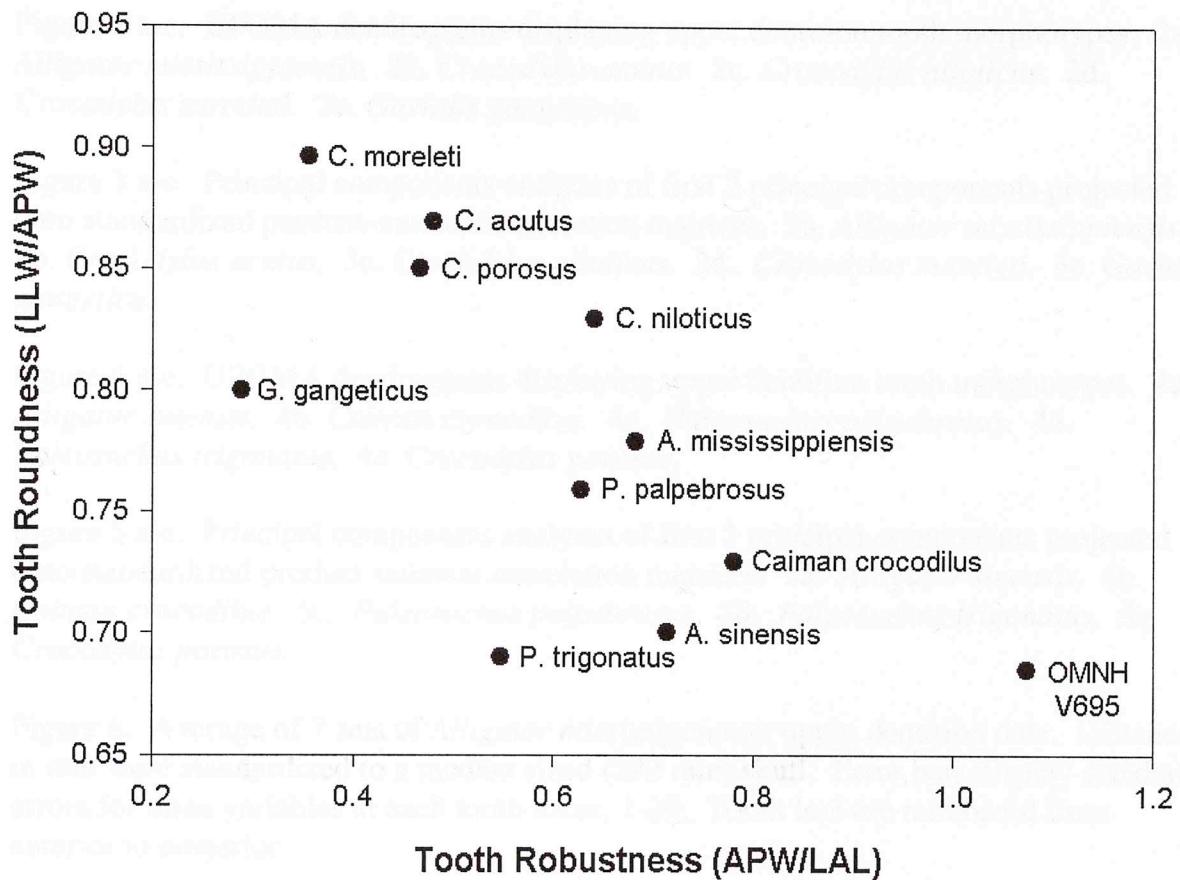


Figure 10.

Figures

Figure 1. Tooth measurements. A- Tooth length on lingual side; B- Tooth length on labial side; C- Labial/lingual tooth width; D- Anterior/posterior tooth width.

Figure 2 a-e. UPGMA dendrograms displaying upper dentition tooth morphotypes. 2a. *Alligator mississippiensis*. 2b. *Crocodylus acutus*. 2c. *Crocodylus niloticus*. 2d. *Crocodylus moreleti*. 2e. *Gavialis gangeticus*.

Figure 3 a-e. Principal components analyses of first 2 principal components projected onto standardized product-moment correlation matrices. 3a. *Alligator mississippiensis*. 3b. *Crocodylus acutus*. 3c. *Crocodylus niloticus*. 3d. *Crocodylus moreleti*. 3e. *Gavialis gangeticus*.

Figure 4 a-e. UPGMA dendrograms displaying upper dentition tooth morphotypes. 4a. *Alligator sinensis*. 4b. *Caiman crocodilus*. 4c. *Paleosuchus palpebrosus*. 4d. *Paleosuchus trigonatus*. 4e. *Crocodylus porosus*.

Figure 5 a-e. Principal components analyses of first 2 principal components projected onto standardized product-moment correlation matrices. 5a. *Alligator sinensis*. 5b. *Caiman crocodilus*. 5c. *Paleosuchus palpebrosus*. 5d. *Paleosuchus trigonatus*. 5e. *Crocodylus porosus*.

Figure 6. Average of 7 sets of *Alligator mississippiensis* upper dentition data. Distances in mm were standardized to a median sized (292 mm) skull. Error bars display standard errors for three variables at each tooth locus, 1-20. Tooth loci are numbered from anterior to posterior.

Figure 7. UPGMA dendrogram based on three variables for 137 Cretaceous age teeth from OMNH locality V695. Tree diagram is shortened to show a greater resolution of possible morphotypes. Gray vertical bar shows a 9-morphotype interpretation while the black bar shows a less conservative 14-morphotype interpretation.

Figure 8. Shape-space defined by tooth measurement ratios. Tooth roundness is labial/lingual width divided by anterior/posterior width. Tooth robustness is anterior/posterior width divided by tooth length on labial side. Tooth outlines included to show range of shapes represented in this plot.

Figure 9. Shape-space defined by tooth measurement ratios. Tooth roundness is labial/lingual width divided by anterior/posterior width. Tooth robustness is anterior/posterior width divided by tooth length on labial side. X-axis natural log transformed to improve resolution among teeth of modern species.

Figure 10. Summary of all data taken. Each species/sample has been averaged to show overall tooth shape within each dentition. Plot displays possible overall feeding preferences as well as potential phylogenetic information. Shape space defined by tooth

measurement ratios. Tooth roundness is labial/lingual width divided by anterior/posterior width. Tooth robustness is anterior/posterior width divided by tooth length on labial side.

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