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Community structure and paleoecology of crocodyliforms from the upper Hell Creek Formation (Maastrichtian), eastern Montana, based on shed teeth

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Community structure and paleoecology of crocodyliforms from the upper Hell Creek Formation (Maastrichtian), eastern Montana, based on shed teeth

George E. Bennett , III [1,2]

ABSTRACT

Modern crocodilian populations display a distinct attritional age class frequency distribution, with each age class corresponding roughly to size. Hatchlings constitute the largest age class, with each successive age class containing fewer individuals. This pattern reflects the continuous growth and natural mortality rate in crocodilians.

Screen washing of microvertebrate localities in the upper Hell Creek Formation of eastern Montana has produced several hundred shed crocodyliform teeth. Two dominant species of Hell Creek crocodyliforms, *Borealosuchus sternbergii* and *Brachychampsa montana*, possess indistinguishable anterior teeth and have been combined in this study. The sample of shed teeth represents a temporally averaged and spatially constrained assemblage, whereby the effects of stochastic events that affected hatching rates in the original populations during a single season are muted.

Using a modeled population and measured tooth replacement rates through ontogeny of the extant *Alligator mississippiensis*, it was found that both the extant and extinct crocodyliforms studied shed proportionally similar numbers of teeth in each size category into the environment. Results indicate that: (1) the size and age structures of ancient and extant crocodyliform communities are similar; (2) microvertebrate localities in channel sands are size-sorted and should be used with caution in studies of population demographics; and (3) using unbiased collecting techniques, the community structures of other extinct vertebrates that lack modern analogues can be established.

INTRODUCTION

Community structure can embrace any number of concepts pertaining to the ecology of living systems, but is defined herein as either the age or size distribution of a group of individuals in either a true population or multiple closely related species. Although age cannot often be ascertained from the fossil record (but see below), in certain cases size can be used as a proxy for age. The patterns of histograms derived from size distributions are associated with physiological modes of life. Many ectotherms decline in numbers of individuals in each successive size-class because of large clutch size, high infant mortality, and continuous, though progressively diminished, bone growth throughout the life of the animal. In such taxa size can be cautiously used to approximate the relative age of the individual. Endotherms often have a normal size distribution among adults of the population resulting from determinate bone growth that results in a narrow adult size range; in endotherms, size cannot be used as a proxy for age. While the fixed adult size of endotherms means that the number of individuals drops off abruptly beyond a certain size, ectotherms may also show this pattern (e.g., Cree et al., 1995; Olsson and Shine, 1996). Due to differences in reproductive strategies (i.e., lack of, or reduced

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parental care) many ectotherms tend to produce more offspring with a higher mortality rate; however, endotherm populations may also be skewed toward the smaller size classes. The majority of population studies on modern vertebrates suffer from collection bias, whereby the smallest individuals are poorly represented in the sample because of the difficulties in finding and capturing them (Cree et al., 1995; Olsson and Shine, 1996).

Age classes are usually assessable in modern populations, and the aging of some fossil taxa has been successfully attempted. Newbrey and Bozek (2003) compiled an age distribution of a Paleocene osteoglossid fish using scale annuli, and Newbrey and Wilson (2005) and Newbrey et al. (2007) used annuli on hiodontid fish centra to determine age classes. Size distributions of fossil fishes have also been documented using standard lengths upon the recovery of large numbers of skeletons (Wilson, 1984; Dietze, 2007). However, the lack of a satisfactorily unbiased method for obtaining complete skeletons (such that all individuals, regardless of size or other factors, have the same likelihood of being preserved and collected) precludes the specimens from revealing a typical community structure. Furthermore, skeletons represent death assemblages (thanatocoenoses), rather than living populations. A more satisfactory method of obtaining size distributions of extinct taxa is by the use of trackways, which by their nature preserve records of living populations (biocoenoses). Lockley (1994) compiled a record of ornithopod dinosaur trackways from Korea which reveal a normal size distribution paralleling patterns of modern endotherms, and also a series of sauropod trackways that record an abundance of juveniles and relatively few adults. Lockley (1994) postulated that juvenile ornithopods are rare because of rapid growth but another possibility is the poor preservation potential for tracks of small, light-weight animals (Avanzini and Lockley, 2002). The sauropod community may be enriched in juveniles because of the proximity to a nesting area (Lockley, 1994). Triassic archosaur tracks from a social group of animals were examined by Avanzini and Lockley (2002) which yielded a normal size distribution, however the sample size was relatively small (n = 15). Erickson et al. (2006) determined ages and survivorship curves for several theropod dinosaurs based on growth lines in the fibulae and metatarsals of individuals from a single monospecific site and museum collections from multiple sites. Each of the aforementioned studies incorporates some element of preservational or collection bias, and may or may not represent a typical community structure for the respective taxon. Single tracksites or skeletal localities indicate an isolated event or snapshot of a portion of the population which would not be representative of the overall population. The present study does not ascribe absolute ages to size classes, but based on the assumption that size is reflective of age, creates a size distribution for late Cretaceous crocodyliforms of the Western Interior based on tooth size. The application of this method to other taxa is assessed.

Size distributions of modern crocodilian populations based solely on field measurements of total body length (TL) of individuals are unreliable as a means to determine a general population structure for two reasons. First, stochastic environmental events such as hurricanes, or human related events such as cullings or ecological disturbance can disrupt nesting behavior in a given season (Taylor, 1989; Lutterschmidt and Wasko, 2006). Thus, the timing of data collection can skew the results. Second, field censuses do not always yield consistent results. Measuring the small size-classes can be misleading because hatchlings of some species often stay within 300 m of the nest (Rodda, 1984), so the location of data collection affects the survey. The largest crocodilians are more adept at avoiding human contact by submerging when approached by boat, preventing field workers from visually estimating body length (Lutterschmidt and Wasko, 2006). Both issues result in one or more size classes being underrepresented in the sample. To overcome this problem, Taylor and Neal (1984) modeled a population of *Alligator mississippiensis* to determine an idealized size distribution for purposes of resource management (Figure 1). Their model incorporated such field-measured factors as sex ratio, percentage of females nesting annually,

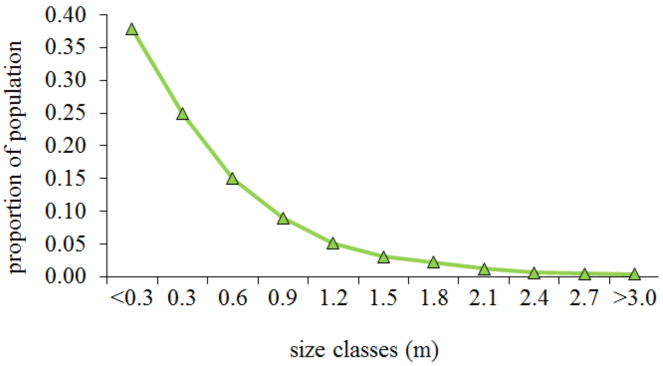

Figure 1. Size distribution of *A. mississippiensis*. Model based on field data from a population in Louisiana with an estimated 2002 individuals. Data from Taylor and Neal (1984).

average number of eggs per nest, and average hatching rate (Taylor and Neal, 1984; Taylor, 1989). The model generates an ectothermic pattern with many small individuals and progressively fewer individuals in larger size classes due to continuous growth and attrition throughout life. The size distribution of *A. mississippiensis* is logarithmic with a progressively more moderate decrease in number of individuals from one class to the next.

In this paper the size distribution of shed crocodyliform teeth from the Upper Cretaceous Hell Creek Formation of Montana will be compared to the shed teeth from a modeled population of *A. mississippiensis* to determine the population structure of extinct crocodyliforms and test the accuracy of the microvertebrate fossil record. The teeth of most non-mammalian vertebrates are polyphyodont, i.e., teeth are replaced successively during the life of the animal. Resistant to abrasion and breakage, enamel covered shed teeth are one of the most common fossils in many Cretaceous formations (Erickson, 1996a). Crocodyliform teeth, in particular, can make up more than 50% of all isolated teeth recovered in a unit (Bennett, unpublished data) and are diagnostic to the appropriate taxonomic level (but in this case not to the generic level; see below). Ideally the skeletal element used for a size-frequency analysis should be: (1) common in a given lithostratigraphic unit; (2) diagnostic at the species level; and (3) unique in the skeleton and not replaced through ontogeny such that one and only one individual is represented (e.g., atlas, cranial element). Teeth present complications with respect to tooth replacement patterns and variation along the tooth row; however, because a modern analog is available for fossil crocodyliforms, and because sample size is large, it is possible to assess paleocommunity structure.

MATERIALS AND METHODS

Institutional abbreviations: **AMNH** – American Museum of Natural History, New York; **SMP** – State Museum of Pennsylvania, Harrisburg, Pennsylvania; **SVDM** – Shenandoah Valley Discovery Museum, Winchester, Virginia; **USNM** – United States National Museum of Natural History, Washington, D.C.

Whereas Taylor and Neal's (1984) model is advantageous in envisioning the size class structure of an ideal population of extant crocodyliforms by filtering out the effects of short-term environmental disturbances and data collection biases, the fossil record requires only that specimens be gathered without collection bias and from multiple localities. Although time averaging is most often a problematic source of bias (Kidwell and Behrensmeyer, 1993), in this model it is a prerequisite to assessing paleocommunity structure.

Shed crocodyliform teeth were collected by a program of microvertebrate screen washing in the upper Hell Creek Formation, Garfield County, eastern Montana, during the 2002-2003 field seasons, and are housed at the Shenandoah Valley Discovery Museum. The seven collection localities are all within 4 km of each other, and are located within the badland areas of Cottonwood Creek and Dry Fork Coulee, which are both contained within the drainage of Hell Creek. Five localities consist of grey, purple and brown mudstones representing floodplain deposits and two localities are buff, cross bedded channel sands (Table 1). The coarse grained sediments tend to contain relatively fewer and/or more poorly preserved fossils. Collection localities cannot all be directly correlated to one another, but all are within the upper third of the Hell Creek

Formation, and are stratigraphically constrained to 14 m (Table 1), with the highest locality (L-31) within 40 m of the overlying Hell Creek-Tullock formational contact which lies at 875 m (Goodwin et al., 2006). The teeth can be thought of as representing a series of populations through time that collectively represent an idealized paleopopulation.

Over 520 kg of sediment was screened through a 1000 µm mesh screen and the resulting concentrate was sorted under a binocular microscope. The two species of crocodyliforms from the Hell Creek Formation, the basal eusuchian *Borealosuchus sternbergii* and the basal alligatoroid *Brachychampsa montana*, possess indistinguishable anterior teeth (Brinkman, 2008, personal communication), and are combined in this study. The dataset does not represent a discreet population; nevertheless it can be used as a proxy for the numbers of individuals, irrespective of taxon, in each size category.

In order to address the problem of variable tooth size along the jaw line, the relatively larger caniniform teeth were removed from the dataset using relative dimensions as a criterion. Based on *A. mississippiensis*, the larger caniniform teeth possess relatively more rounded bases while the posterior and remaining anterior teeth possess slightly laterally compressed bases (unpublished data). Eliminating the teeth with a fore-aft basal length to basal width ratio of 1.1 or less preferentially removes most of the relatively large teeth from the tooth row of *A. mississippiensis* and is employed in the Hell Creek dataset to reduce the influence of variable tooth size on the results. Because of their different relative dimensions, the low-crowned, posterior molariform teeth of *Brachychampsa* were analyzed separately and not included in this data set. Surface collected teeth were also disregarded because of the collection bias toward larger, more visible teeth. Unshed, rooted teeth which were presumably a result of disarticulation and breakage, and not shed by living individuals were excluded from the sample. Using these criteria, the original dataset was reduced by more than 50 percent to 95 teeth. The rare marine gavialoid *Thoracosaurus* is known from the Hell Creek Formation (Estes and Berberian, 1970), but its distinctive thin, pointed teeth with fine striations and well developed carinae (Erickson, 1998) were not found in the study area.

Teeth were measured in three dimensions: crown height (CH), fore-aft basal length (FABL), and basal width (BW) (Figure 2). Dimensions on some teeth could not be measured due to breakage; however, the remaining measurements on such teeth

Table 1. Summary of tooth producing localities, upper Hell Creek Formation, Garfield County, Montana. The Hell Creek-Tullock formational contact is 875 m (Goodwin et al., 2006). Detailed locality information on file at the Shenandoah Valley Discovery Museum.

SVDM Locality Number	No. of Teeth	Lithology	Facies	Screen Washed Sediment (kg)	Elevation (m)	Teeth Recovered/ 100 kg Sediment
L-01	36	grey mudstone	floodplain	48.0	832	83.3
L-27	36	grey, purple, brown mudstone	floodplain	64.7	824	74.2
L-31	1	grey mudstone	floodplain	29.0	836	3.4
L-42	13	buff, brown x-bedded sandstone	channel	214.3	823	14.9
L-50	5	buff mudstone	floodplain	91.1	827	11.0
L-51	1	purple, grey mudstone	floodplain	17.7	822	5.6
L-75	3	buff, brown x-bedded sandstone	channel	57.1	822	10.5
Total	95	—	—	521.9	—	—

were included. Crown heights ranged from 1.5 mm to 10.2 mm (Appendix 1). Within each dimension, teeth were segregated into groups based on equal size categories (Table 2). The resulting histogram incorporating all three tooth measurements and yielding a size distribution is presented in Figure 3.

As in most crocodyliforms, tooth size along the jaw line in *Brachychampsa* and *Borealosuchus* is variable; however when eliminating molariform and caniniform teeth it is less than that seen in *Alligator*. In Figure 4 (see appendix 2 for supporting data), the fore-aft basal length to crown height ratio is compared in four individuals representing three taxa. These specimens consist of complete or partial skulls with the teeth intact and in place in the alveoli. A modern *A. mississippiensis* skull (uncataloged SVDM specimen; skull length 256 mm [premaxilla to end of parietal table]; estimated body length 2 m) with most teeth present was used as the standard for comparison. The right maxilla of the type specimen of *Brachychampsa montana* (AMNH 5032) contains seven non-molariform teeth (Gilmore, 1911) and has an estimated skull length of 230 mm based on comparison with UCMP 133901 (Norell et al., 1994). SMP VP-1312 consists of both maxillae and premaxillae, and the left dentary (Sullivan

Figure 2. Measurements taken on each tooth. **A**, lingual view; **B**, basal view; and **C**, mesial views. Scale bar equals 5 mm. **Abbreviations: BW**, basal width; **CH**, crown height; **FABL**, fore-aft basal width.

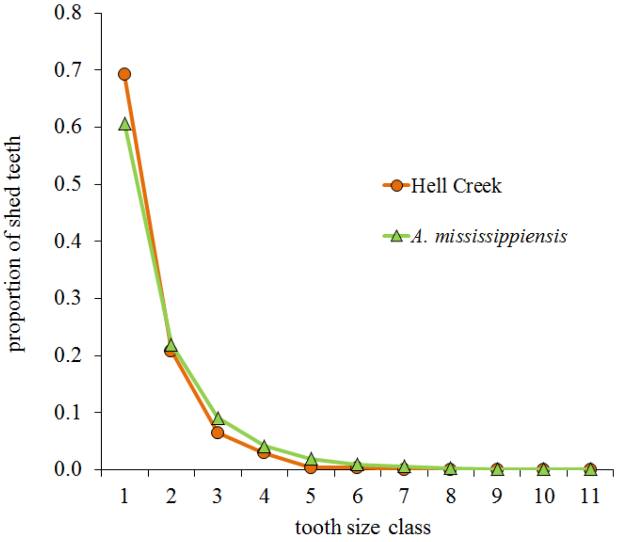

Figure 3. Size-frequency distribution of shed teeth in *A. mississippiensis* and Hell Creek crocodilians. High rate of tooth replacement and high infant mortality is reflected in the dramatic decline from size-class 1 to size-class 2. For measurement ranges of tooth size-classes, see Table 2.

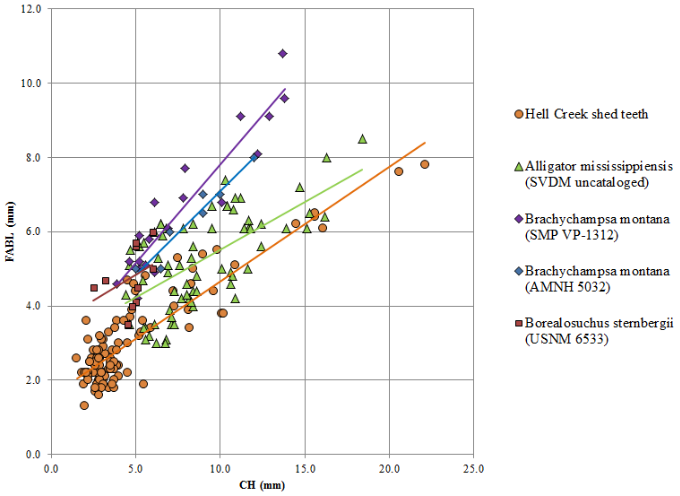

Figure 4. Relative dimensions of crocodyliform teeth. Hell Creek teeth are isolated shed teeth (SVDM various catalog numbers). *A. mississippiensis* teeth were measured from a single intact modern skull with a premaxilla-supraoccipital length of 265 mm. *B. montana* and *B. sternbergii* teeth are contained within partial skulls. Measurements for UNSM 6533 and AMNH 5032 are from Gilmore (1910) and Gilmore (1911), respectively. Body lengths are unknown, but SMP VP-1312 (Sullivan & Lucas, 2003) is approximately 20% larger than AMNH 5032. Molariform teeth are excluded. For tooth measurements see appendix 2. Abbreviations as in Figure 2.

& Lucas, 2003), including nineteen intact, non-molariform teeth. The right and left dentaries of the type specimen of *Borealosuchus* (=*Leidyosuchus*) *sternbergii* (USNM 6533) contain three and seven teeth, respectively, and has a skull length of 303 mm (Gilmore, 1910). The relative tooth dimensions of each of these taxa fall along the range observed in *A. mississippiensis*. Of the three fossil specimens, SMP VP-1312 contains the most teeth on which to base a comparison with *A. mississippiensis*. The crown height of teeth contained in SMP VP-1312 range from 3.9 to 13.8 mm (9.9 mm range) and the teeth in *A. mississippiensis* range from 4.4 to 18.4 mm (14.0 mm range) (Figure 4). Thus, tooth size variation in *B. montana* is even more constrained than *A. mississippiensis*.

In order to avoid a potentially misleading comparison between the size distribution of fossil teeth and that of modern body size, the proportionate number of teeth shed by the population of *Alligator mississippiensis* in Taylor and Neal's (1984) model is calculated (Table 3). Tooth replacement rate through ontogeny will affect the number of teeth in each size-class shed by a population. Erickson (1996b) measured the tooth replacement rate in various stages of growth of *A. mississippiensis* by observing the incremental lines formed daily in the teeth. This work supports the hypothesis that tooth replacement rate decreases with age and determines a linear regression defining this relationship as $y = 10.68 + 92.73x$ (Erickson, 1996b), which is herein used to calculate the number of teeth shed per year per alveolus (Table 3). The product of the number of individuals, the number of alveoli (which does not change through ontogeny), and the number of teeth lost per year per alveolus yields the total number of teeth shed annually by each size-class for an ideal population of *A. mississippiensis*.

RESULTS AND DISCUSSION

A strong relationship between the size distribution of shed teeth of both a modeled *A. mississippiensis* population and Hell Creek crocodyliforms suggests that both groups shed teeth at a similar rate, exhibit similar body size distributions, and that the microvertebrate fossil record preserves these biological signals despite potential preservational biases. A goodness of fit chi-square test was performed that confirms a statistical similarity between the two distributions (chi-square = 4.31; df = 2; $P > 0.05$). Like Taylor and Neal's (1984) model (Figure 1), the size distribution of shed teeth for both extant and extinct populations decreases logarithmically, but the latter reveals a more substantial decline between the first and second size classes (Figure 3). The smallest

Table 2. Distribution of Hell Creek tooth measurements in each of three dimensions. Abbreviations as in Figure 2.

Size Class	CH (mm)	n	FABL (mm)	n	BW (mm)	n	Total n
1	< 4.0	66	< 3.0	65	< 2.0	62	193
2	4.0 to 6.4	16	3.0 to 3.9	20	2.0 to 2.9	22	58
3	6.5 to 8.9	5	4.0 to 4.9	6	3.0 to 3.9	7	18
4	9.0 to 11.4	2	5.0 to 5.9	3	4.0 to 4.9	3	8
5	11.5 to 13.9	0	6.0 to 6.9	0	5.0 to 5.9	1	1
6	14.0 to 16.4	0	7.0 to 7.9	1	6.0 to 6.9	0	1
7	16.5 to 18.9	0	8.0 to 8.9	0	7.0 to 7.9	0	0
8	19.0 to 21.4	0	9.0 to 9.9	0	8.0 to 8.9	0	0
9	21.5 +	0	10.0 +	0	9.0 +	0	0
Total	—	89	—	95	—	95	279

teeth make up about sixty percent of both datasets, approximately tripling the next largest size-class. This is explained by the presence of more juveniles in the population replacing their teeth at a much higher rate than the adults. It has been suggested that crocodilians replace anterior teeth more rapidly than posterior teeth (Edmund, 1962); however, because tooth size does not trend along the jawline, this should not affect tooth size distribution. In both datasets the largest size-class of teeth contained less than 1% of the total sample. In a separate analysis of the posterior molariform teeth of *Brachychampsa* (n=45), a similar, but not statistically significant, pattern was observed in which over 81% of teeth fell within the first two size categories (Figure 5).

Taylor and Neal's (1984) population model of *A. mississippiensis* overcomes the difficulty of determining an accurate overall population structure of crocodilians based on field measurements (e.g., Campos et al., 1995; Lutterschmidt and Wasko, 2006). In this manner, localized or short-term population changes are muted, and the health of modern populations based on field-gathered data can be assessed in terms of an ideal population. The ability to collect unbiased samples by screen washing sediment from localities over time and space has similar advantages, and is a key factor in being able to attribute the observed size-frequency distribution of Hell Creek crocodyliforms to a true community structure. Teeth gathered by means of surface collection present an inaccurate size distribution biased toward larger, more easily spotted specimens.

Dental counts in extant crocodyliforms vary widely among taxa (68 to 86 in alligatorids, 60 to 84 in crocodylids, and 106 to 110 in *Gavialis gangeticus*, according to Brazaitis, 1973); however, species generally exhibit constant alveolar counts through ontogeny (Rauhut and Fechner, 2005). Determining ontogenetic changes in dental counts of fossil taxa, which would affect tooth size distributions, is problematic because it requires the recovery of an ontogenetic series. Two relatively complete adult *Brachychampsa montana* skulls possess 14 (AMNH 5032; Gilmore, 1911) and 15 (SMP VP-1312; contra Sullivan and Lucas, 2003)

Table 3. Number of teeth shed annually in a population (n = 2002) of *A. mississippiensis*. Body length in the second column and number of individuals in each size class is from Taylor and Neal (1984). The number of alveoli is constant through ontogeny. Body lengths in the fifth column are in 0.3 m increments beginning at an arbitrarily selected value near the upper limit of size class 1, i.e., 0.25 m. Tooth replacement rates were calculated from the linear equation (y = 10.68 + 92.73x) of Erickson (1996), and represent replacement in a single alveolus. The number of teeth lost per year in each alveoli was determined by dividing the number of days per year by the tooth replacement rate. The total teeth shed for each size class is the product of the number of individuals, number of alveoli, and the number of teeth lost per year per alveolus.

size class	body length (m)	individuals per size class	number of alveoli	body length (m)	tooth replacement rate (days)	teeth lost per year per alveoli	total teeth shed	proportion of all shed teeth
1	<0.3	758	78	0.25	33.9	10.8	637,310	0.6069
2	0.3	500	78	0.55	61.7	5.9	230,786	0.2198
3	0.6	300	78	0.85	89.5	4.1	95,431	0.0909
4	0.9	180	78	1.15	117.3	3.1	43,681	0.0416
5	1.2	103	78	1.45	145.1	2.5	20,204	0.0192
6	1.5	61	78	1.75	173.0	2.1	10,041	0.0096
7	1.8	45	78	2.05	200.8	1.8	6,381	0.0061
8	2.1	25	78	2.35	228.6	1.6	3,114	0.0030
9	2.4	13	78	2.65	256.4	1.4	1,443	0.0014
10	2.7	9	78	2.95	284.2	1.3	901	0.0009
11	>3.0	8	78	3.25	312.1	1.2	730	0.0007

maxillary tooth sockets, yet a possible juvenile skull half the size of the adult skulls possesses 15 maxillary teeth (Williamson, 1996; Sullivan and Lucas, 2003), suggesting individual variation, and not ontogenetic change in this taxon. The tooth count of an adult *Borealosuchus sternbergii* is 90 (Gilmore, 1910), although an ontogenetic series is not currently known. Erickson (1976) describes a growth series from the sister taxon *Leidyosuchus* (=*Borealosuchus*) *formidabilis* from Wannagan Creek, western North Dakota, in which the number of maxillary tooth sockets increases with age. The smallest skull (yearling) contains 15 or 16 maxillary teeth, while the largest adult maxillae contain 18 to 20 teeth. An ontogenetic increase in the number of tooth sockets of a cogener raises the possibility that the Hell Creek dataset may be skewed toward larger teeth, but the presence of relatively few large teeth in the sample does not bear this out.

Taphonomically, the floodplain deposits yield a much more accurate and unbiased record of shed teeth than do the channel deposits. Although the size distribution of teeth recovered from floodplain localities is not statistically similar to *A. mississippiensis* at the $P = 0.05$ level (chi-square $= 8.19$; $df = 1$; $P < 0.05$), its logarithmic curve is nevertheless visually similar to the expected distribution of shed teeth (Figure 6). As the crocodyliform teeth in the dataset are consistently conical, the possibility of fluvial shape sorting can be eliminated, but size sorting has affected the channel deposited teeth by concentrating larger teeth and removing smaller teeth. This suggests that some paleoecological studies may require the exclusion of fluvially deposited microvertebrate fossils in order to maintain an unbiased sample. However, it is of interest to note that the best agreement between the modern and ancient tooth datasets occurs when both channel and floodplain localities are combined.

The presence of two crocodyliform taxa in the Hell Creek Formation implies some measure of resource or habitat partitioning. Both *Brachychampsa* and *Borealosuchus* possess indistinguishable conical anterior teeth. The low-crowned, blunt posterior teeth of *Brachychampsa* were used for crushing hard-shelled food items such as turtles (Carpenter and Lindsey, 1980) or potentially, as in the extant *Alligator sinensis*, bivalves (Ross and Magnusson, 1989). It has been suggested that *Borealosuchus*

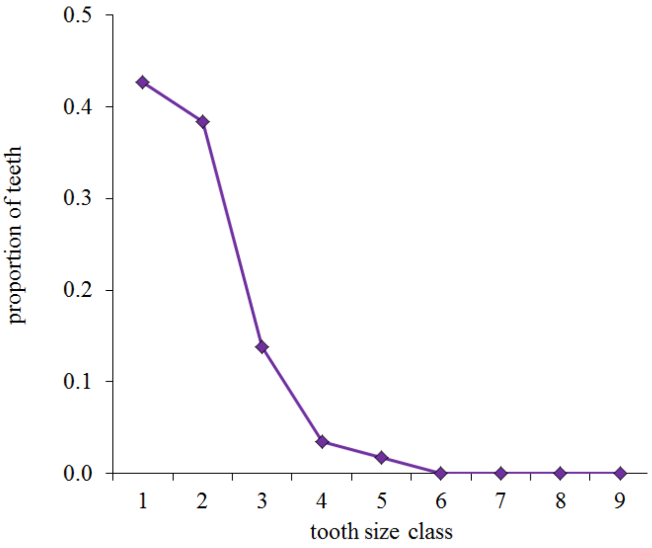

Figure 5. Size distribution of posterior molariform teeth (n=45) of *Brachychampsa montana*. Due to the low, wide crowns, these teeth were analyzed separately from the main data set, and show a similar, but not statistically significant, distribution to the conical Hell Creek teeth.

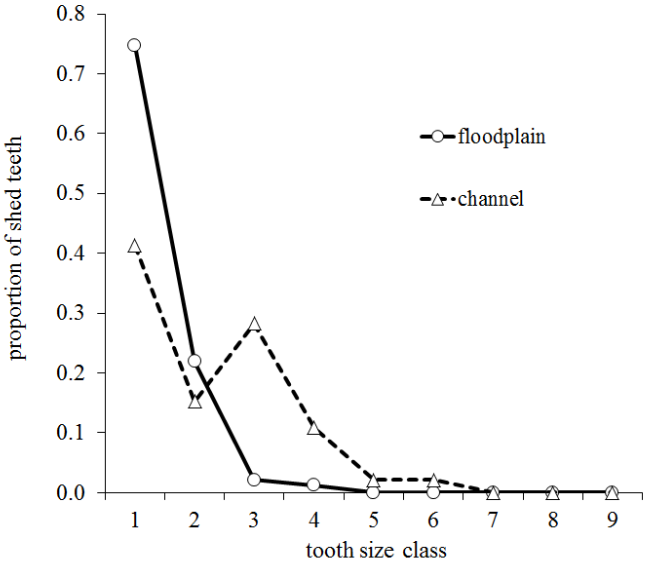

Figure 6. Size distribution of shed teeth of Hell Creek crocodyliforms recovered from flood plain and channel facies. Flood plain deposited teeth closely match the known population structure of *A. mississippiensis*.

also consumed turtles, although it lacked specialized posterior crushing teeth (Erickson, 1984); partitioning of food resources cannot be presently demonstrated. The posterior teeth of *Borealosuchus* are generally blunter than, but cannot be confidently distinguished from, the anterior teeth. If this were possible, the relative abundances of *Borealosuchus* and *Brachychampsa* posterior teeth in different facies might provide evidence of habitat partitioning.

Crocodyliforms were used in this study specifically because a population model of extant representatives was available for comparison. However, teeth are not necessarily an ideal element for size distribution studies because of variation in tooth size along the jaw and the necessity of quantifying tooth replacement rate in extinct animals. Considering the Hell Creek study area, tooth replacement rates for some dinosaur taxa are known; both tyrannosaurs and hadrosaurs form and replace their teeth more slowly with age (Erickson, 1996a) and would be suitable for further investigation. Although little is known about champsosaur tooth replacement, they have the advantage of near constant tooth size along the tooth row. Mammal teeth would not produce an accurate size distribution of the population because the teeth are not polyphyodont and do not increase in size through ontogeny; however, a survey of adult teeth would clarify the variability in relative adult size within a population.

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APPENDIX 1.

Measurements of shed conical crocodyliform teeth (n=95) from the Hell Creek Formation examined in this study. Abbreviations as in Figure 2.

specimen number	SVDM locality number	CH (mm)	FABL (mm)	BW (mm)
SVDM VP-414	L-27	5.3	3.3	2.2
SVDM VP-416	L-27	8.2	3.4	2.9
SVDM VP-615	L-42	4.9	4.6	3.3
SVDM VP-702	L-27	4.5	2.2	1.9
SVDM VP-703	L-27	4.0	2.1	1.8
SVDM VP-832	L-51	2.9	3.2	1.8
SVDM VP-903	L-75	3.0	2.2	1.3
SVDM VP-904	L-75	2.9	2.0	1.4
SVDM VP-951	L-42	3.1	3.1	1.9
SVDM VP-971	L-50	7.5	5.3	4.5
SVDM VP-1016	L-42	—	7.0	5.8
SVDM VP-1123	L-01	3.9	2.8	1.9
SVDM VP-1125	L-01	2.7	1.9	1.4
SVDM VP-1126	L-01	3.9	3.6	2.7
SVDM VP-1183	L-01	4.0	2.4	1.8
SVDM VP-1185	L-01	3.6	2.8	2.1
SVDM VP-1186	L-01	2.5	2.8	1.7
SVDM VP-1222	L-50	10.2	3.8	3.0
SVDM VP-1240	L-27	3.7	2.0	1.6
SVDM VP-1243	L-42	8.4	5.0	4.1
SVDM VP-1245	L-42	7.3	4.0	3.4
SVDM VP-1246	L-42	—	2.6	2.0
SVDM VP-1247	L-01	3.6	1.9	1.4
SVDM VP-1250	L-50	3.5	2.6	2.2
SVDM VP-1251	L-50	3.5	2.5	1.8
SVDM VP-1252	L-50	5.4	3.6	2.7
SVDM VP-1257	L-42	7.2	4.4	3.7
SVDM VP-1258	L-42	9.8	5.5	4.6
SVDM VP-1259	L-42	3.5	2.3	1.5
SVDM VP-1260	L-42	5.0	4.4	3.2
SVDM VP-1261	L-42	3.8	3.4	2.2
SVDM VP-1262	L-42	5.6	4.8	3.2
SVDM VP-1275	L-27	3.2	2.7	2.0
SVDM VP-1276	L-27	5.2	3.2	2.6
SVDM VP-1277	L-27	2.9	2.4	1.7
SVDM VP-1278	L-27	3.0	2.2	1.5
SVDM VP-1279	L-27	3.1	2.9	2.0
SVDM VP-1280	L-27	3.7	2.5	1.6
SVDM VP-1281	L-27	3.4	3.3	2.4
SVDM VP-1283	L-27	—	2.6	1.8
SVDM VP-1284	L-27	3.7	2.3	1.5
SVDM VP-1285	L-27	5.9	3.4	2.5
SVDM VP-1286	L-27	2.9	2.6	1.5
SVDM VP-1287	L-27	2.5	2.2	1.5
SVDM VP-1288	L-27	2.8	2.0	1.5

specimen number	SVDM locality number	CH (mm)	FABL (mm)	BW (mm)
SVDM VP-1289	L-27	4.3	3.6	2.3
SVDM VP-1291	L-27	4.7	3.7	2.8
SVDM VP-1292	L-27	—	1.9	1.1
SVDM VP-1293	L-27	—	2.5	1.5
SVDM VP-1296	L-27	—	3.3	2.8
SVDM VP-1298	L-27	2.4	2.6	1.7
SVDM VP-1299	L-27	2.8	2.6	1.5
SVDM VP-1300	L-27	2.2	2.2	1.5
SVDM VP-1301	L-27	2.8	2.8	1.7
SVDM VP-1302	L-27	3.0	3.1	1.9
SVDM VP-1304	L-27	2.3	2.5	1.8
SVDM VP-1305	L-27	2.0	2.2	1.2
SVDM VP-1306	L-27	2.2	3.1	2.1
SVDM VP-1310	L-27	2.7	1.9	1.4
SVDM VP-1311	L-27	3.0	1.9	1.5
SVDM VP-1312	L-27	4.0	3.0	2.1
SVDM VP-1313	L-27	3.5	2.4	1.5
SVDM VP-1315	L-27	4.5	4.7	3.4
SVDM VP-1329	L-01	2.6	1.7	1.1
SVDM VP-1330	L-01	3.5	2.3	1.6
SVDM VP-1331	L-01	3.0	1.8	1.2
SVDM VP-1332	L-01	2.6	2.4	1.5
SVDM VP-1333	L-01	3.4	2.3	1.7
SVDM VP-1334	L-01	2.7	2.2	1.6
SVDM VP-1335	L-01	3.5	2.4	1.8
SVDM VP-1336	L-01	2.0	1.3	0.8
SVDM VP-1337	L-01	2.7	1.7	1.4
SVDM VP-1338	L-01	2.9	1.9	1.5
SVDM VP-1339	L-01	1.8	2.2	1.4
SVDM VP-1340	L-01	2.2	2.1	1.4
SVDM VP-1341	L-01	2.3	2.5	1.5
SVDM VP-1342	L-01	2.7	2.6	1.6
SVDM VP-1343	L-01	2.2	2.0	1.1
SVDM VP-1344	L-01	2.1	2.2	1.1
SVDM VP-1345	L-01	2.6	2.5	1.5
SVDM VP-1346	L-01	1.9	1.9	1.1
SVDM VP-1347	L-01	3.1	2.2	1.8
SVDM VP-1348	L-01	3.1	1.9	1.3
SVDM VP-1349	L-01	4.5	3.0	2.4
SVDM VP-1350	L-01	3.9	2.4	1.7
SVDM VP-1351	L-01	2.6	2.4	2.0
SVDM VP-1352	L-01	3.0	2.0	1.5
SVDM VP-1353	L-01	3.1	2.0	1.6
SVDM VP-1354	L-01	2.8	1.6	1.0
SVDM VP-1355	L-01	2.7	2.8	1.6
SVDM VP-1356	L-01	1.5	2.6	1.7
SVDM VP-1357	L-01	2.1	3.6	2.2
SVDM VP-1367	L-75	3.2	2.1	1.5
SVDM VP-1369	L-42	2.6	1.8	1.1
SVDM VP-1572	L-31	4.8	3.9	2.5

APPENDIX 2.

Tooth measurements from complete and partial crocodyliform skulls. Measurements for USNM 6533 and AMNH 5032 are from Gilmore (1910) and Gilmore (1911), respectively. The tooth count of USNM 6533 is 90, although the remaining posterior-most teeth are not preserved. Abbreviations: **d**, dentary; **m**, maxilla; **p**, premaxilla, **CH**, crown height; **FABL**, fore-aft basal width. Asterisk (*) indicates alveolus not present in this taxon or individual. Dash (-) indicates tooth is missing, broken, or otherwise unmeasurable.

				Alligator mississippiensis **(SVDM uncataloged)**		***Brachychampsa montana*** **(SMP VP-1312)**		***Brachychampsa montana*** **(AMNH 5032)**		***Borealosuchus sternbergii*** **(USNM 6533)**	
	Element	**Side**	**Alveolus**	**CH**	**FABL**	**CH**	**FABL**	**CH**	**FABL**	**CH**	**FABL**
1	p	right	1	-	3.2	11.2	9.1	-	-	-	-
2	p	right	2	6.8	3.1	12.2	8.1	-	-	-	-
3	p	right	3	10.6	4.9	-	7.8	-	-	-	-
4	p	right	4	15.1	6.1	-	6.1	-	-	-	-
5	p	right	5	8.3	-	-	5.8	-	-	-	-
6	m	right	1	8.4	4.0	5.2	5	-	-	-	-
7	m	right	2	10.1	5.0	4.6	5.2	-	-	-	-
8	m	right	3	14.7	7.2	10.1	6.8	9.0	6.5	-	-
9	m	right	4	16.3	8.0	-	9.7	10.0	7.0	-	-
10	m	right	5	12.4	6.2	-	12.6	12.0	8.0	-	-
11	m	right	6	8.4	4.4	-	7	9.0	7.0	-	-
12	m	right	7	6.9	4.9	-	6.3	7.0	6.0	-	-
13	m	right	8	8.4	5.6	-	4.9	-	-	-	-
14	m	right	9	9.5	6.7	-	5.4	5.0	5.0	-	-
15	m	right	10	11.2	6.9	-	4.9	6.5	5.0	-	-
16	m	right	11	7.4	7.2	7.8	6.9	12.0	12.0	-	-
17	m	right	12	-	-	-	11.3	11.0	12.0	-	-
18	m	right	13	6.8	6.1	10.9	14.2	-	-	-	-
19	m	right	14	6.3	5.3	-	10.4	-	-	-	-
20	m	right	15	*	*	-	-	*	*	-	-
21	p	left	1	-	3.2	-	8.5	-	-	-	-
22	p	left	2	7.1	3.5	-	8.7	-	-	-	-
23	p	left	3	11.6	5.0	-	7.4	-	-	-	-
24	p	left	4	15.3	6.5	-	10.2	-	-	-	-
25	p	left	5	-	-	-	5.9	-	-	-	-
26	m	left	1	7.0	3.9	-	6.1	-	-	-	-
27	m	left	2	8.6	4.8	-	6.8	-	-	-	-
28	m	left	3	11.7	6.3	6.1	6.8	-	-	-	-
29	m	left	4	18.4	8.5	13.7	10.8	-	-	-	-
30	m	left	5	11.7	6.1	5.2	5.2	-	-	-	-
31	m	left	6	8.6	4.4	-	4.7	-	-	-	-
32	m	left	7	7.3	4.4	-	5.4	-	-	-	-
33	m	left	8	7.6	5.1	-	4.6	-	-	-	-
34	m	left	9	9.5	6.1	-	5.0	-	-	-	-
35	m	left	10	10.4	6.7	7.9	7.7	-	-	-	-
36	m	left	11	10.3	7.4	10.3	12.3	-	-	-	-

				***Alligator mississippiensis* (SVDM uncataloged)**		***Brachychampsa montana* (SMP VP-1312)**		***Brachychampsa montana* (AMNH 5032)**		***Borealosuchus sternbergii* (USNM 6533)**	
	Element	**Side**	**Alveolus**	**CH**	**FABL**	**CH**	**FABL**	**CH**	**FABL**	**CH**	**FABL**
37	m	left	12	6.5	6.2	12.0	14.2	-	-	-	-
38	m	left	13	6.6	5.9	10.7	13.3	-	-	-	-
39	m	left	14	5.4	4.7	-	9.2	-	-	-	-
40	m	left	15	*	*	-	7.0	*	*	-	-
41	d	right	1	11.4	6.1	-	-	-	-	-	-
42	d	right	2	10.7	4.8	-	-	-	-	-	-
43	d	right	3	10.6	4.6	-	-	-	-	-	-
44	d	right	4	16.2	6.4	-	-	-	-	-	-
45	d	right	5	10.9	4.2	-	-	-	-	-	-
46	d	right	6	-	-	-	-	-	-	-	-
47	d	right	7	6.2	3.0	-	-	-	-	5.0	4.1
48	d	right	8	5.8	3.2	-	-	-	-	5.1	4.5
49	d	right	9	4.6	3.5	-	-	-	-	5.0	5.6
50	d	right	10	5.6	3.4	-	-	-	-	-	-
51	d	right	11	7.3	3.5	-	-	-	-	-	-
52	d	right	12	7.7	4.2	-	-	-	-	-	-
53	d	right	13	11.8	6.1	-	-	-	-	-	-
54	d	right	14	10.4	6.7	-	-	-	-	-	-
55	d	right	15	8.4	6.2	-	-	-	-	-	-
56	d	right	16	8.3	5.3	-	-	-	-	-	-
57	d	right	17	6.9	5.1	-	-	-	-	-	-
58	d	right	18	6.5	6.2	-	-	-	-	-	-
59	d	right	19	4.7	5.5	-	-	-	-	-	-
60	d	right	20	5.2	5.6	-	-	-	-	-	-
61	d	left	1	12.4	5.6	6.9	6.1	-	-	4.5	3.5
62	d	left	2	8.2	4.2	5.2	5.9	-	-	-	-
63	d	left	3	8.0	4.3	5.6	5.1	-	-	-	-
64	d	left	4	13.9	6.1	12.9	9.1	-	-	-	7.5
65	d	left	5	8.3	4.1	-	5.3	-	-	-	-
66	d	left	6	7.1	3.7	-	5.2	-	-	6.0	5.0
67	d	left	7	-	-	6.1	4.9	-	-	-	-
68	d	left	8	5.6	3.1	-	4.6	-	-	4.8	4.0
69	d	left	9	6.8	3.0	-	2.5	-	-	-	-
70	d	left	10	5.5	3.4	-	4.0	-	-	-	-
71	d	left	11	6.1	3.5	3.9	4.6	-	-	-	-
72	d	left	12	8.0	4.6	5.1	4.2	-	-	6.0	6.0
73	d	left	13	10.8	6.6	5.8	5.8	-	-	5.0	5.7
74	d	left	14	10.9	6.9	13.8	9.6	-	-	-	-
75	d	left	15	7.8	6.1	6.2	6.4	-	-	-	-
76	d	left	16	6.1	6.0	7	7.0	-	-	-	-
77	d	left	17	5.5	5.7	7.9	7.9	-	-	3.2	4.7
78	d	left	18	5.1	5.7	8.1	13.3	-	-	2.5	4.5
79	d	left	19	4.6	5.1	9.3	16.4	-	-	-	-
80	d	left	20	4.4	4.3	-	15.2	-	-	-	-

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