

FAUNAL DIVERSITY IN PALEOECOSYSTEMS: A MODEL FOR USING THE SPECIES-
AREA RELATIONSHIP TO ANALYZE PALEOENVIRONMENTS

by

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A Thesis
Submitted to the
Graduate Faculty
of
George Mason University
in Partial Fulfillment of
The Requirements for the Degree
of
Master of Arts
Interdisciplinary Studies

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Spring Semester 2008
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Faunal diversity in paleoecosystems: A model for using the species-area relationship to
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Arts at George Mason University

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DEDICATION

This is dedicated to my parents, George and Linda, who have always encouraged me to do what I love.

ACKNOWLEDGEMENTS

Without the support of my wife Meg, this work would never have been completed. I can't tell her how much I appreciate all the slack she took up over the past four years! She also spent a great deal of time at the microscope putting her artistic skills to good use illustrating fossil fish bones.

I thank my committee members Drs. Richard J. Diecchio, Larry L. Rockwood, and George E. Taylor for agreeing to take on this unorthodox project and for keeping me on track. It was through Larry and George's classes that I originally stumbled on the idea that became the foundation of this work, and they helped with its development from the beginning. I thank Rick for his encouragement and friendship throughout my time at Mason, and for his willingness to always make time for me and for paleontology.

Even before arriving at George Mason, the paleontological field work that was eventually incorporated into this thesis was underway through my position at the Shenandoah Valley Discovery Museum. The original encouragement to go back to graduate school after many years as a paleontological technician came from the director of the Museum, Peggy McKee. I sincerely appreciate her understanding in allowing me to combine my work and school research into a single project. Hearty thanks to my fellow 'Pastafarian,' Mark Lawson for creating the fantastic, made-to-order digital artwork and assistance with images.

While working in the field in eastern Montana many people made my work both possible and enjoyable. Dr. John W. Happ originally introduced me to the town of Jordan and the exposures of the Hell Creek Formation where I've worked since 2001. Our discussions of dinosaurs and the lesser known animals of our shared field area have been a constant source of pleasure. Thanks to John and Silvia Trumbo for their hospitality while working on their ranch over the years, and to Lon Bolick, whose common sense and 'helpful hints' kept me ahead of the game on several occasions. Plus, he's just as good at finding fossils as most of my actual field assistants! I could not have completed my work without a great volunteer core, though, and I thank everyone who ever lugged a sack of sediment up a gully or broke their back leaning over a cattle trough: Scott Bailey, George Bennett, Jr., Rachel Harden, Derek Main, Ryan Ridgely, Velma Urbana-Garza, and Marissa Westerfield.

Back in the lab I had another group of dedicated folks who spent many long hours hunched over a microscope looking for little gems of the past: Scott Bailey, Melissa Beck, Dorothy Davis, Rachel Harden, Derek Main, Ryan Ridgely, Steve Ritter and Neil Tedrow. In particular, Dorothy Davis has been a reliable presence at the Museum for the past six years, showing remarkable dedication to projects that would send many people running for cover! The learning curve for microvertebrate osteology has been steep, and

I also thank the many colleagues who have helped me with identifications of Hell Creek microfossils: Dr. William A. Clemens, Robert Denton, Dr. Lance Grande, Dr. John R. Horner, Dr. Louis L. Jacobs, Dr. Yoshitsugu Kobayashi, Dr. Michael G. Newbrey, Dr. Randall L. Nydam, Dr. Julia T. Sankey, Dr. Dale A. Winkler, and Dr. Richard J. Zakrzewski. Dr. Michael G. Newbrey and Dr. Donald B. Brinkman were also kind enough to review the section on newly recognized taxa which greatly improved the final draft.

Fossils used in this study were collected under Bureau of Land Management permit M89972. Funding provided by the George Ohrstrom Foundation and the Friends of Hell Creek with assistance from Niki Wilson. Early research related to this thesis was presented at the Society of Vertebrate Paleontology annual meeting with funding assistance from the George Mason University Graduate Student Travel Fund.

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LIST OF ABBREVIATIONS/SYMBOLS

INSTITUTIONAL ABBREVIATIONS:

SVDM VP, Shenandoah Valley Discovery Museum, Winchester, Virginia. Specimens cataloged in the Vertebrate Paleontology Collection.

ANATOMICAL ABBREVIATIONS:

BOF, basioccipital facet
EXOF, exoccipital facet
HA, haemal arch base
MDP, mid-dorsal pit
MDR, mid-dorsal ridge
MVP, mid-ventral pit
NAP, neural arch articular pit
POZ, postzygapophysis
PRZ, prezygapophysis

COLLECTING LOCALITY ABBREVIATIONS:

FH, Fang Hill, SVDM locality L-27
FS, Fish Sticks, SVDM locality L-50
L-000, locality number (exact locality data on file at the Shenandoah Valley Discovery Museum).
LTH, Lone Tooth Hill, SVDM locality L-42
RR, Rancher Ridge, SVDM locality L-01
ZVP-000, locality number lacking specific GPS coordinates.

OTHER:

A, land area (km²)
BP, before present
c, constant
C.I., completeness index
K/T, Cretaceous/Tertiary boundary
Ma, million years ago
S_e, expected species richness
S_o, observed species richness

t , time in years

z , slope of regression representing species-area curve

ABSTRACT

FAUNAL DIVERSITY IN PALEOECOSYSTEMS: A MODEL FOR USING THE SPECIES-AREA RELATIONSHIP TO ANALYZE PALEOENVIRONMENTS

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George Mason University, 2008

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Preservational bias in the fossil record presents difficulties when knowledge of biodiversity in paleoecosystems is needed. In such cases paleobiodiversity must be assessed without having direct knowledge of undiscovered taxa. This study presents a new method to estimate paleobiodiversity (= species richness) in paleoecosystems, allowing 1) a reassessment of previous studies in which diversity affects conclusions; 2) future studies to be placed in the context of estimated paleobiodiversity figures; 3) fossil record completeness to be calculated; and 4) fossil collecting efforts to be tailored appropriately when known paleobiodiversity approaches projected figures.

The species-area curve expresses the observation that taxonomic diversity generally increases with geographic area. When anthropogenically introduced species are removed from consideration, the insular nature of islands and other refugia offer an uncontaminated picture of faunal richness within discrete boundaries. Log-log plots of

species richness against land area of islands with similar climatic regimes yield regressions with slopes of approximately 0.30.

The reptile and amphibian faunas from nearly one hundred modern islands with tropical, seasonal climatic regimes were compiled to create a species-area curve with a slope of 0.28. A second set of twenty-eight paleoisland faunas from analogous climates was compiled which ranged in age from 65 million years (Ma) to 500 years before present (BP). The species-area equation was applied by using the slope of the analogous modern island species-area curve, and the resulting expected species richness ranged from seven species on the smallest paleoisland to more than one hundred species on the largest.

Completeness indices (C.I.) for each paleoisland were calculated as a ratio of the diversity of known fossil taxa to expected diversity based on the species-area relationship. The completeness of the paleofaunal record on the selected paleoislands was found to decrease with island age, thereby quantifying a general paleontological and geologic trend of poorer data with age. Additionally, the C.I. is inversely correlated to island size, likely indicating a collecting bias caused by the prohibitive nature of exhaustive collecting over large areas, *i.e.* the fossil record is generally poorer with age and island size.

This technique is also applied to geographic or political subdivisions of continents, termed provinces. A dataset of species richness on modern provinces was compiled as a baseline by which to assess diversity in a paleoprovince. The definition of a modern province implies that it does not represent a significant (*i.e.* geologic) span of

time. In the absence of such “true” provinces in the geologic record, a lithostratigraphic unit which contains an areal as well as a temporal component, was used. The Upper Cretaceous Hell Creek Formation of the northern Great Plains was surveyed, both in the literature and through the active collection of fossil material. Three previously unrecognized taxa - at least two teleost fish and one solemydid turtle - were recovered and are described herein, for a total of 132 recovered taxa in the Hell Creek Formation. In order to test the accuracy and applicability of the species-area method, faunal paleobiodiversity was assessed by several other means, including the discovery curve, rarefaction, and jackknifing. These other methods are not able to predict undiscovered paleobiodiversity over a wide geographic area. In this study the Hell Creek Formation is estimated to have had 63 species of freshwater fish and 136 species of reptiles and amphibians, with C.I.s of 0.40 and 0.32, respectively. Although most of the species in these groups remain undiscovered, the law of diminishing returns will be invoked, and the effort required to find them will increase dramatically in the future.

CHAPTER 1

INTRODUCTION

1.1 Bias in the fossil record

While modern biodiversity is difficult to estimate, with hundreds of new species being discovered each year, assessing species richness in the past is significantly more problematic. The fossil record, our most important source of information about the vast range of extinct organisms, is far from complete. In fact, given even ideal geologic conditions, the fossil record would still be imperfect as a result of preservational bias.

A series of events preclude an organism from being found as a fossil, the most obvious being a lack of hard parts, such as bones or shells, that can be readily preserved. Other processes, like erosion, diagenesis, subduction, and metamorphism destroy fossils or eliminate the possibility of discovery. Still other factors prevent organisms from being incorporated into the geologic record, a requisite first step toward fossilization. If an animal inhabits upland regions, where erosion and not deposition of sediments occurs, burial is unlikely. Less common members of the fauna may be correspondingly rare as fossils. Small and/or fragile skeletons are often less well-preserved or more difficult to find and identify than large ones. It is also difficult to sample a representative portion of a three-dimensional rock record with all of its sub-environments when typically only a handful of outcrops are exposed. These factors oblige the fossil record to present a lop-

sided view of paleobiodiversity and community structure, with taxa either over or underrepresented. As a result, paleoecological studies can present an incomplete or inaccurate picture of past ecosystems.

1.2 Previous work

1.2a Island biogeography

Because of their restricted nature, modern islands have long been utilized as evolutionary testing grounds. Similar in character to oceanic islands are refugia such as lakes, mountaintops, and other environmentally isolated communities. Early studies of plants (Arrhenius, 1921) revealed a pattern of increasing species richness (= diversity or number of species) with land area, which was quantified by a linear regression in log-log space. This trend applies to a wide variety of climatic regimes and taxonomic groups including land plants (Preston, 1962), insects (Darlington, 1943), fish (Kodric-Brown and Brown, 1993), amphibians and reptiles (Dunn, 1934), birds (Hamilton *et al.*, 1964), and mammals (Brown, 1971).

The first cohesive theory of island biogeography was produced by MacArthur and Wilson (1963; 1967), who refined the species-area relationship to describe the species diversity of geographically localized island groups with similar climates (Figure 1). The relationship between island area and species richness is expressed by the species-area curve equation:

$$(1) \quad S_e = cA^z$$

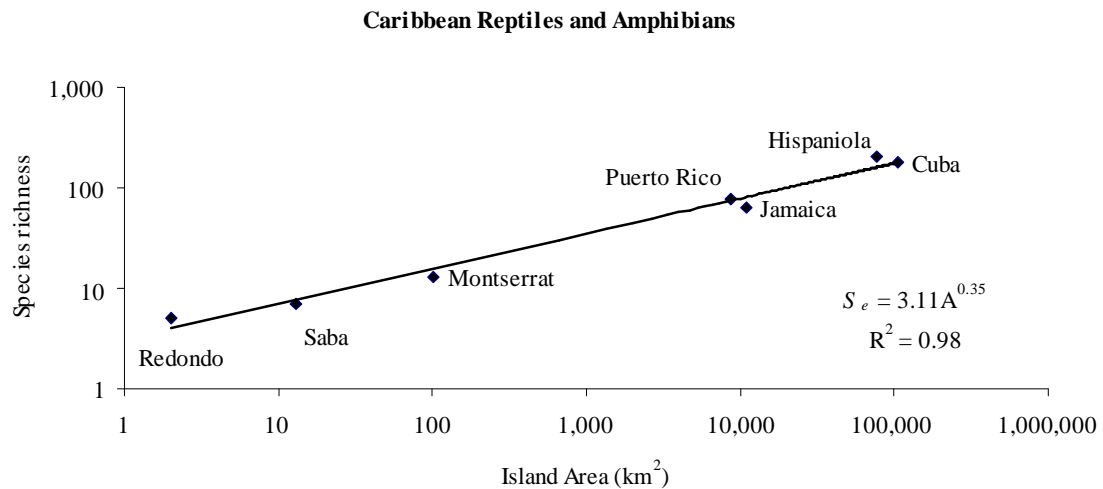


Figure 1. Species-area curve for reptiles and amphibians on selected islands of the Caribbean. Adapted from MacArthur and Wilson (1967).

where S_e is the number of species; c is a constant; and A is land area. The z value is the slope of the regression which is fairly consistent within island types or taxonomic group (Rockwood, 2006). The z values for oceanic islands fall within the range of approximately 0.20 to 0.40 (MacArthur and Wilson, 1967). Conversely, z values for areas within continental land masses are significantly lower, *e.g.* 0.17 for North American land birds (MacDonald, 2003), reflecting an inverse relationship between z values and land area when very small and very large land masses are compared. The larger the z value the greater the increase in diversity per unit area.

Studies by Simberloff and Wilson (1969; 1970) suggested that species diversity increases with island size alone and is not related to habitat diversity, a conclusion echoed by Rockwood (2006). Yet topographic variability has a positive effect on habitat diversity when incorporated into species-area curves resulting in better fit regressions (Lazell, 1983). Topographic variation by itself however is significantly, albeit more

weakly, correlated to species diversity than is land area, likely because there is a general worldwide trend toward decreasing species richness with elevation (MacDonald, 2003).

1.2b Paleobiodiversity and the completeness of the fossil record

It has long been acknowledged that the fossil record is incomplete; however the nature of its bias is often difficult to ascertain. Nicol (1977) exploited the fact that animals with mineralized skeletons were far more likely to be fossilized than those without. Using a ratio of all extant organisms to extant organisms with skeletons, he arrived at a fossil record completeness of 8%. Expressed in the form of the completeness index (C.I.), or the ratio of known to expected total diversity (Meehl, 1983), this yields a value of 0.08, where 1.00 is a perfect fossil record. Similar indices (ranging from 0.05 to 0.14) of organisms with mineralized hard parts versus those without were determined for the Burgess Shale invertebrate fauna by Conway Morris (1986) and Paul (1998). In this *Lagerstätten* both soft-bodied and shelled organisms are preserved and a relatively accurate ratio can be calculated by a simple tally. In this case exceptional fossil preservation can substantiate a theoretical estimate.

Numerous quantitative and theoretical methods exist to estimate fossil record completeness on relatively wide geologic or geographic scales (for a summary see Paul, 1998). The study presented here is an attempt to model paleofaunal diversity and quantify the completeness of the fossil record over a narrow time range and within a variety of discrete geographic areas (Bennett, 2004). Future paleoecological studies concerning will benefit from knowing how many species are absent from the fauna.

1.3 Purpose of study

The purpose of this work is to create an approach to estimate the diversity of paleofaunas from localities variable in space and time using the species-area relationship. First, the model will use the areas of paleoislands as the basis for determining paleobiodiversity. Second, the model will estimate the paleodiversity of an ancient continental area using a lithostratigraphic unit as a surrogate for a paleoprovince. (A lithostratigraphic unit is defined as a volume of rock composed of beds of similar lithology and which includes a geographic component of area as well as a vertical thickness representing a length of geologic time.) The utility of other methods of estimating paleobiodiversity will be assessed, and new taxa recovered during the course of fieldwork in eastern Montana, within the Hell Creek Formation paleoprovince, will be described and illustrated.

Determining paleobiodiversity is typically done in broad terms, *e.g.* worldwide diversity of known tetrapod families, because of the inherent incompleteness of the fossil record. Measuring total paleobiodiversity requires theoretical constructs such as a discovery curve (Benton, 1998) which do not lend themselves to estimating undiscovered diversity. If the present method is successful, and the paleobiodiversity of spatially restricted regions can be measured, it will allow for more accurate research in paleoecology by allowing ideas about faunal structure and predator-prey relationships to be viewed in light of the number and types of taxa that have not yet been, or in fact may never be, recovered from the fossil record. Specifically, applying this model in the future will allow 1) a reassessment of paleoecological studies in which diversity affects the

conclusions; 2) future studies to be placed in the context of estimated paleobiodiversity figures; 3) fossil record completeness to be calculated; and 4) fossil collecting efforts to be tailored appropriately when known species diversity approaches projected figures.

CHAPTER 2

ISLAND PALEOBIODIVERSITY

2.1 Methods

The model created herein is based on Arrhenius' (1921) species-area relationship for modern organisms, but will be used to predict species diversity on paleoislands and paleoprovinces (subdivisions of ancient continents). The model will be explored using a species-area curve constructed from modern faunal diversity data as a benchmark by which to estimate the biodiversity of extinct communities. A methodological approach is also employed, inasmuch as a new method for estimating paleobiodiversity will be devised and compared to previous methods.

Land area, climatic regime, and reptile and amphibian diversity data was gathered from a series of both modern and paleoislands. (Paleoislands are those known to have been islands in the geologic past, whether or not they are currently islands.) The model to be developed makes the following assumptions: 1) Islands of volcanic origin are of comparable topography. Most paleoisland elevations cannot be specifically estimated and will not be considered further. 2) The effects of relative island isolation are negligible. Although species richness can be influenced by an island's remoteness, and the proximity of the mainland to geologically recent islands can be estimated with some accuracy, this accuracy diminishes rapidly with age and increased tectonic activity.

Therefore, the effects of remoteness will be held constant in this model. However, in an effort to reduce these possible effects, volcanic hot spot islands (*e.g.* Hawai'i) that tend to be remote, were not used. 3) Modern tropical islands for which paleoclimate data are unavailable have been tropical throughout the Holocene. The transition from the Pleistocene to the Holocene is marked in the Caribbean by a change from xeric to more mesic conditions which were relatively constant until the present (Pregill and Crother, 1999). 4) Species turnover is zero, *i.e.* the paleoisland faunas are a snapshot in time and there were no faunal changes due to immigration, extinction, or evolution within that time. This likelihood was advocated by Pregill and Olson (1981), and has the benefit of not overestimating diversity. 5) The biodiversity of modern and paleofaunas is similar.

2.1a Modern island selection

The area and species richness of reptiles and amphibians was compiled from nearly one hundred modern islands and island groups (Appendix A). Due to their prevalence and taxonomic diversity, tropical islands with seasonal climates were selected. The Caribbean Islands in particular possess both well studied herpetofaunas (Crother, 1999) and great variability in island size, although islands from around the world (*e.g.* Indonesia, Oceania) are included for a more robust dataset. Islands under 1 km² were not considered because the species-area relationship breaks down for land masses of this small size (Barrett *et al.*, 2003). Taxonomic diversity on these islands provides the baseline to which paleoisland faunas are compared.

Although incorporating topographic variation into species-area curves can increase the accuracy of the regression (Lazell, 1983), it is unrealistic to estimate the elevation of most paleoislands. For the purposes of this study it is sufficient to limit comparisons of modern and paleoislands to those of similar origin (*i.e.* volcanic) under the assumption that they exhibit comparable topographic variation. Modern oceanic islands (*i.e.* derived from hot spots and sitting on oceanic crust) were not included. Continental islands (*i.e.* those on continental crust that are generally close to shore) were included so long as either: 1) the island is primarily volcanic in origin, or 2) the island elevation is not an outlier on a log-log plot of area against elevation for tropical seasonal islands. Hence, Anegada in the Caribbean is included because of its volcanic origin even though its elevation is far lower than would be expected, and the non-volcanic islands of New Caledonia are included as their topography is comparable to volcanic islands. Like elevation, the distance of islands from other land masses, which affects dispersal rates of species, is difficult to assess in paleoislands, a problem that increases with age. Thus, in an attempt to minimize the effects of isolation, oceanic islands formed from hot spot activity were not included.

2.1b Herpetofaunal data collection

Any meaningful comparison between modern and fossil faunas using the species-area relationship must be conducted with groups similar in size, metabolism, and ecological niche, which can often be approximated by using phylogenetically related groups (MacDonald, 2003). Modern reptiles and amphibians offer an opportunity to

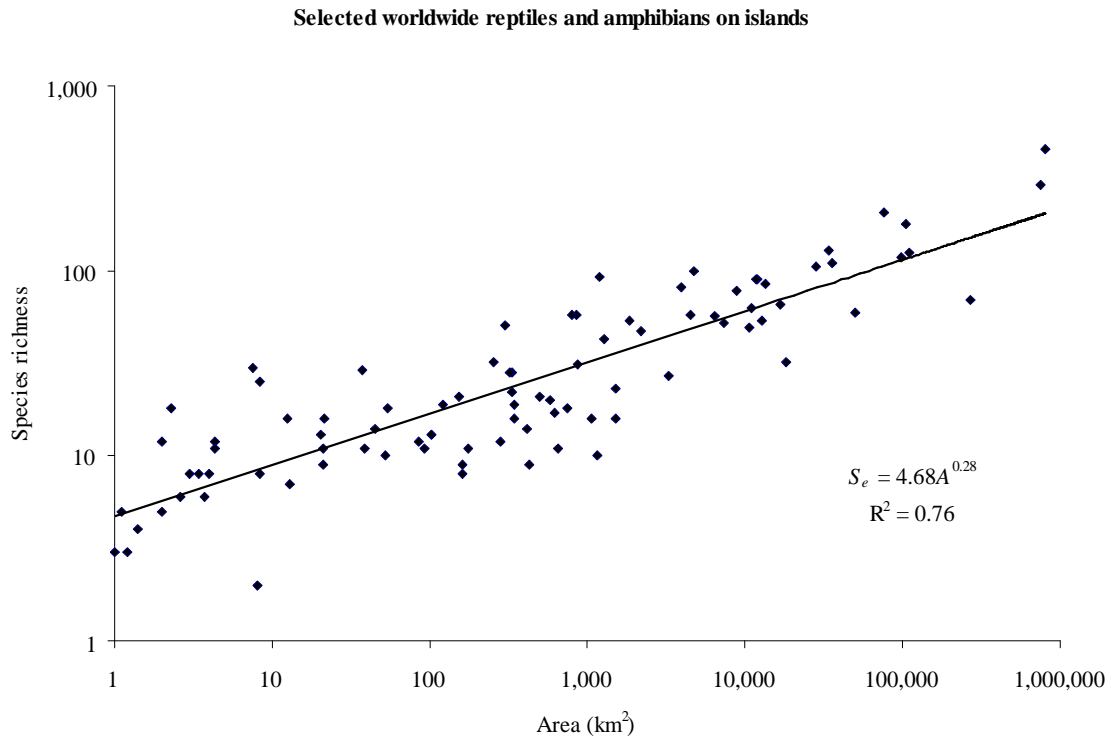


Figure 2. Species-area curve for reptiles and amphibians on modern tropical islands with seasonal climate. Regression is significant at the $P \ll .001$ level. See Appendix A for source data.

compare modern taxa of high species richness and similar metabolic rate and ecological roles with their ancient counterparts.

The species diversity of each modern island was plotted against island area on a log-log scale to present a species-area curve in the form of a linear regression (Figure 2). Frogs, salamanders, caecilians, turtles, lizards, snakes, amphisbaenians, and crocodilians are included. Only fully or partially terrestrial species are included; sea turtles, sea snakes, and records of vagrant individuals are excluded. Anthropogenically introduced species are also excluded.

The paleoisland herpetofaunas evaluated, including the case from the Late Cretaceous (Archibald, 1996) are modern in character in that all species fall within the above eight extant taxonomic groups and represent no additional extinct higher level reptile or amphibian groups. An exception was made for salamanders. The albanerpetontids are a family of extinct lissamphibians distinct from true caudates, but were morphologically and ecologically similar (Gardner, 2002). The proposed Late Cretaceous island in present-day Romania, “Hațeg” island, has produced the remains of at least two albanerpetontids which are herein grouped with true salamanders.

2.1c Paleoislands

Paleoislands were selected using criteria similar to those of modern islands; a relatively well-known reptile and amphibian paleofauna and a warm, seasonal climate were required. For paleoislands without published climatic regimes it was assumed that all islands that are currently tropical have had a similar climate since the beginning of the Holocene. Most of the islands in this category have faunas dating from <4000 years BP. Included paleoislands range in age from 500 years BP to 65 Ma. The oldest island is from the latest Cretaceous (Maastrichtian) of south-central Europe which at the time consisted of a series of large and small island land masses due to a combination of high sea level and tectonic activity. An island-arc system whose northern portion centered on modern-day Romania created an archipelago on its leading edge (Weishampel *et al.*, 1991). Among these volcanic land masses was “Hațeg” island, estimated at approximately 75,000 km² (Weishampel, 2004, personal communication). Originally

proposed by Nopcsa (1923) as an island when dwarf dinosaurs were uncovered in the early nineteenth century, more recent interpretations suggest “Hațeg” may be the tip of a narrow peninsula (Therrien, 2004; Willingshofer, 2000). However, based on the “peninsula effect” (Simpson, 1964), Means and Simberloff (1987) suggested that peninsulas display patterns of diversity similar enough to true islands to be analyzed using traditional island biogeography theory. Indeed, due to fluctuating sea levels, either an island or peninsula may have been present at any given time. The paleofauna recovered from present-day Hațeg Basin is thus envisioned as inhabiting an island system which experienced a warm and humid climate with seasonal rainfall (Grigorescu, 1983).

Land areas for paleoislands were gathered from published accounts and also estimated using digital topographic and bathymetric maps in conjunction with ImageJ area calculator software (Rasband, 2004). Sea level at the time of the paleofauna in question was matched to the nearest contour line to allow the software to calculate the number of pixels within both the modern and paleoshorelines. A ratio of pixels to true modern island area yields an estimate of paleoisland area.

2.1d Calculating paleobiodiversity and the completeness index

The species-area curve for modern tropical island reptiles and amphibians (Figure 2) was used to calculate the number of species expected on paleoislands of given sizes. The constants $c = 4.68$ and $z = 0.28$ from the species-area curve in Figure 2 are applied to the area of the pertinent island in the species-area equation to calculate the expected species richness, S_e , for that island. Thus, for a theoretical island of 1,000 km²:

$$(2) \quad S_e = cA^z = (4.68) (1000^{0.28}) = 32.4$$

or about thirty-two expected species. On this island the C.I. for a theoretical known fossil herpetofauna, S_o , of five species would be:

$$(3) \quad \text{C.I.} = S_o/S_e = 5/32.4 = 0.15$$

and the fossil record would be 85% incomplete.

2.2 Paleoisland faunas

The reptile and amphibian fauna for nearly one hundred modern islands from the Caribbean, the south Pacific (Oceania), and southeast Asia were compiled (Appendix A) to construct a species-area curve with a z value of 0.28 (Figure 2). Six species of salamander inhabit the relatively near-shore continental islands off the coast of China, a pattern consistent with salt water intolerance. A few species of caecilians and amphisbaenians are present on islands in the Philippines and the Caribbean, respectively. Turtles and crocodylians form a minor portion of the fauna while frogs, lizards, and snakes make up the majority of species on all of these modern islands.

The faunal and area data compiled from twenty-eight paleoislands are shown in Appendix B. As on modern islands, salamanders are rare with the exception of two species of albanerpetontid, a salamander sister taxon. Caecilians are absent from the paleoislands and amphisbaenians are present on a single island, which is unsurprising considering the limited diversity and range of these groups in the modern world. Turtles and crocodylians are also rare, representing no more than 7% and 3% of the total recorded

paleoisland fauna, respectively. Lizards are by far the most common fossil taxon, making up well over half of the recorded species.

2.3 Completeness index

The relationship of paleoisland area to the C.I. of their respective reptile and amphibian fossil records is displayed in Figure 3. The largest island (*i.e.* “Hațeg”) has a relatively low C.I. of 0.13, whereas some of the minute islands show very high indices of 0.90. Thus, a negative relationship exists such that, the larger the island, the more incomplete the fossil record. The majority of the fossils from cited studies were recovered by the wet or dry screening of sediment, producing isolated skeletal elements. Comprehensive screen washing efforts require a significant input of time and manpower, and few stratigraphic units have been successfully searched in this manner. No large paleoislands have thus far received this kind of treatment. In fact, this thoroughness may be unachievable in many cases due to a lack of source sediment. Most of the fossil reptiles and amphibians cited herein were recovered from cave sediments and fissures (Pregill, 1981; 1982; 1993; Pregill and Steadman, 2000; Pregill *et al.*, 1988; 1994) which, although crucial for their concentrations of bones within bird pellets and animal middens, ultimately represent a limited source of material.

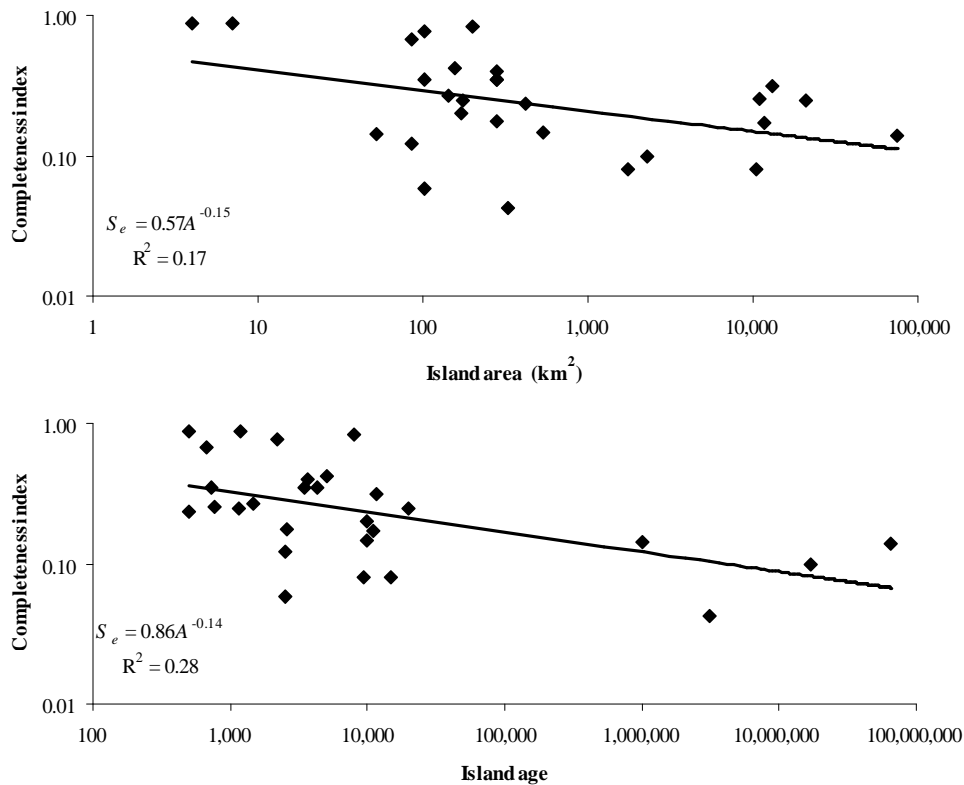


Figure 3. Relationship of the completeness indices of paleoisland reptile and amphibian faunas to island area and age. Data is from Appendix B. Both regressions are significant at the $P < .05$ level.

The C.I. of fossil island reptiles and amphibians also shows a linear relationship when plotted against island age (Figure 3; data from Appendix B). The older islands of Grenada, Isle de Mona, and “Haçeg” have completeness indices of no more than 0.14, while late Holocene islands can range from 0.24 to 0.90. By this standard of measure the fossil record is poorer with age. There can be little doubt that the more ancient portions of the stratigraphic record and the fossils contained therein are more poorly known than more recent deposits (Benton *et al.*, 2000).

In addition to burial, the destructive effects of subduction, erosion, and metamorphism tend to reduce the condition and availability of appropriate rocks. However, it has been suggested that although fewer fossil-producing units may be available, the quality of fossil material at any given locality may be excellent regardless of age (Benton *et al.*, 2000). This idea is consistent with the fact that the microvertebrate fossils (very small [typically <1cm] isolated bones, scales and teeth of small vertebrates) recovered on even the oldest paleoislands in this study can be preserved well enough to be taxonomically diagnostic. Vertebrate remains are aided by their composition: phosphatic bones are diagenetically resistant (*i.e.* not altered after burial) while calcareous invertebrate shells are preferentially broken down in most sedimentary environments (Lyman, 1994). The result is that vertebrate fossils can be well preserved and even, in the case of disarticulated microvertebrates, concentrated by fluvial or biotic actions within depositional environments that preserve little or no invertebrate remains.

2.4 Discussion

Modern island faunal composition varies widely, yet the species diversity of the islands surveyed is universally dominated by frogs, lizards, and snakes (Appendix C). On average, each island surveyed shows frog diversity at about 20% of the total reptile and amphibian fauna. Frogs make up only about 12% and 8% of the species on islands of the Caribbean and Oceania, respectively, but account for almost half of the species on Philippine islands. Paleoisland faunas of the Caribbean show frog diversity at 7%, suggesting that either: 1) frogs comprised an even smaller part of ancient Caribbean

faunas than they do today or; 2) that they are underrepresented in the fossil record. A bias against frogs in some cases is supported by the fact that several Caribbean islands (*e.g.* Antigua, Puerto Rico) record current frog richness at between 10% and 15% of the total herpetofauna, or even higher, while some islands record no frog taxa whatever. Modern frogs are rarely present on islands smaller than $\sim 10 \text{ km}^2$. Above this threshold 90% of the modern islands in this study possess frogs while only 50% of paleoislands have produced frog fossils, strongly implying that a significant portion of the frog fauna remains unknown.

Snakes are currently present on all but the smallest islands; below about 10 km^2 snakes are absent as often as present. (Frogs are even more conspicuously depauperate or absent from small islands.) A few notable exceptions are on islands of New Caledonia which range in area from 152 to $16,648 \text{ km}^2$, and possess either one or no species of snakes (Bauer, 1999; Sadlier and Bauer, 1997). Montserrat (Censky and Kaiser, 1999) and a handful of sizeable islands in the Philippines (Uetz *et al.*, 2005) also have no recorded snakes. Of paleoislands over 10 km^2 , 81% have produced at least one snake species (Appendix B), while for modern islands surveyed, 90% have snakes (Appendix C). This, in addition to the fact that the average portion of snake species is 17% and 19% for modern and paleoislands respectively suggests that, unlike frogs, there is no significant evidence of bias in the fossil record of snakes.

On the vast majority of islands, both modern and ancient, lizards are the most diverse taxon by a wide margin. In fact, published accounts exist for lizards on all paleoislands and all but one modern island in the study (Appendix B; C). Caribbean

islands of <3 km² that possessed no other reptiles or amphibians nevertheless are the home of up to six lizard species (Censky and Kaiser, 1999; Lazell, 1983). Lizard diversity may be marginally overrepresented in the fossil record, as the average proportion of lizards reaches 65% of the paleoherpetofauna, whereas the modern average percentage is just over 55%. Determining specific biases for recovery of fossil taxa is beyond the scope of this paper, but the larger size of many lizards and the occurrence of more skeletal elements that are diagnostic at the species level may be significant factors. The remaining reptile and amphibian groups make up a small portion of the total fauna; salamanders, caecilians, turtles, amphisbaenians and crocodilians comprise an average of only <9% and <6% of the respective ancient and modern island faunas. Salt-water intolerant salamanders are typically only present on continental islands that have been bridged to the mainland at some point in their geologic histories to allow safe migration. The presence of salamanders in prehistoric faunas may therefore suggest proximity to a continental body. This may be the case for ancient “Hațeg” island, although the environmental requirements of albanerpetontids remain unclear.

Turtles (exclusive of sea turtles) are also depauperate on truly oceanic islands, while near shore islands such as Taiwan, Hainan Dao (Lazell, 1999), and those on Africa’s east coast periphery (Downs and Wirminghaus, 1997) show greater turtle diversity. Many crocodilians are salt water tolerant and can reach distant islands, but do not show great species richness on modern islands. The fact that crocodile remains have not yet been found on many of the larger Caribbean islands may be the result of a collecting bias against larger animals due to screen washing sediment from caves, where

many of the bones accumulated from wash-in or predator droppings. Amphisbaenians are somewhat diverse in the modern Caribbean with a maximum of five species on any one island (Hedges, 1999a; Powell et al., 1999), although only one species has been found in the early Holocene of Puerto Rico; one might expect to recover several more taxa closely related or identical to extant species given more extensive field work on this island. No published accounts of fossil caecilians were noted, however future finds in the Philippine islands, which are inhabited by a handful of modern caecilians, would be consistent with the fact that these islands were either connected or immediately adjacent to mainland Asia at various times during the Pleistocene (Voris, 2000).

Two important biases affect the type and number of fossil taxa recovered. First, the environment of deposition will selectively preserve the animals that inhabited that particular environment. In most of the Holocene islands, fossil entombing sediments were washed into caves and fissures, and skeletal elements accumulated as a result of regurgitated pellets from birds of prey or fecal material from other predators. Thus the preferred prey of the predators that occupied these caves would be more likely to be preserved than non-prey species. Some island fossil sites, such as the Hațeg Basin localities, represent primarily fluvio-lacustrine environments in lowland areas of the paleoisland. Consequently many types of environments, particularly upland areas, are unsampled by fossil collecting efforts. As commonly occurs, the taxa recovered are biased toward lowland species with a predilection for water. Indeed, many upland taxa may be unrecoverable except in cases of fluvial transport to zones of deposition, and

these upland forms may constitute the bulk of the undiscovered forms in terrestrial habitats regardless of land mass area.

Second, the fossil collecting localities are often few in number and not spread evenly over the island. For instance, the modern extent of the Hațeg Basin is only ~600 km², far smaller than the land area of the original island (~75,000 km²). Thus, the modern collecting area severely limits the potential for completely sampling the entire paleoisland environment. However, the undiscovered fauna of “Hațeg” island may not be absent merely because the full array of paleohabitats has not been sampled; species diversity does not necessarily increase with habitat diversity according to theory and field data (Rockwood, 2006).

CHAPTER 3

PROVINCIAL PALEOBIODIVERSITY

The species-area relationship is valid for provinces as well as islands, although species diversity on larger land masses increases at a slower rate relative to area (Preston, 1960). If coeval deposits can be identified for an entire stratigraphic unit in order to estimate its geographic extent at a specific time, the species-area relationship can also be applied to determine the fossil record completeness of the continental rock record. Modern faunal and environmental analogs could provide additional insight into the paleoecology of such areas.

3.1 Methods

Like those created for islands, species area curves generated from continental land areas display a linear relationship in log-log space (Rosenzweig, 1998). In fact, Watson (1835) recognized this relationship within the English flora in the early nineteenth century, making it one of the earliest known ecological patterns.

Modern provinces with the appropriate climatic regime were selected to act as an analogue for extinct faunas in a similar manner to gathering data for modern islands. The provinces were based on both geographic and political boundaries according to the availability of data. Although political boundaries may not appear ideal as provinces

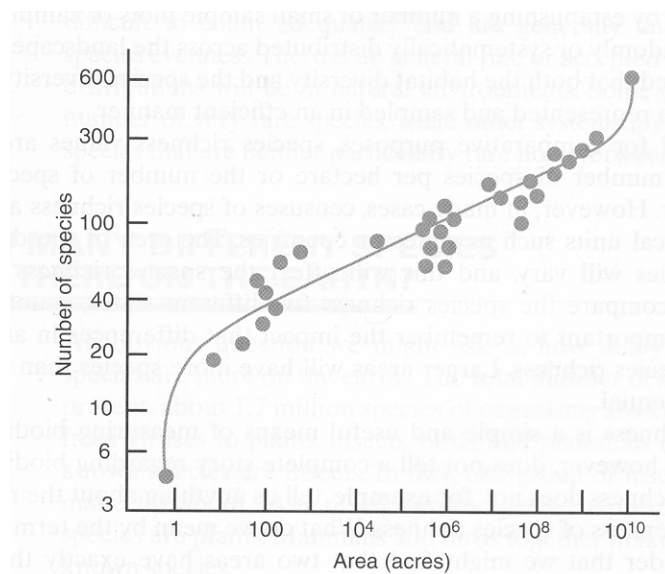


Figure 4. A typical species-area relationship (in this case birds of the world) using various continental sampling areas. Notice that in very large and small land areas the relationship breaks down, therefore, only the mid-size provinces are used to create a baseline in this study. From MacDonald (2003) adapted from Preston (1960).

because of their incongruence with natural boundaries, the tightness of fit of the regression in Figures 5 suggests they are a reasonable substitute. Selected reptile and amphibian diversity figures and land areas for modern provinces were compiled from various sources (Appendix D).

Applying the species area relationship to very large or very small provinces is inappropriate because the relationship is no longer linear on a log-log plot (Figure 4). Small areas within continents tend to be more or less diverse than expected (Barrett *et al.*, 2003). Instead of being completely isolated, as are islands, provinces can be infused with more species from adjacent territories. On the other hand, as found by Preston (1960; Figure 4), some taxa exhibit lower diversity than expected. Likewise, very large land areas, such as the Palearctic zoogeographic range (most of Eurasia and North Africa) or

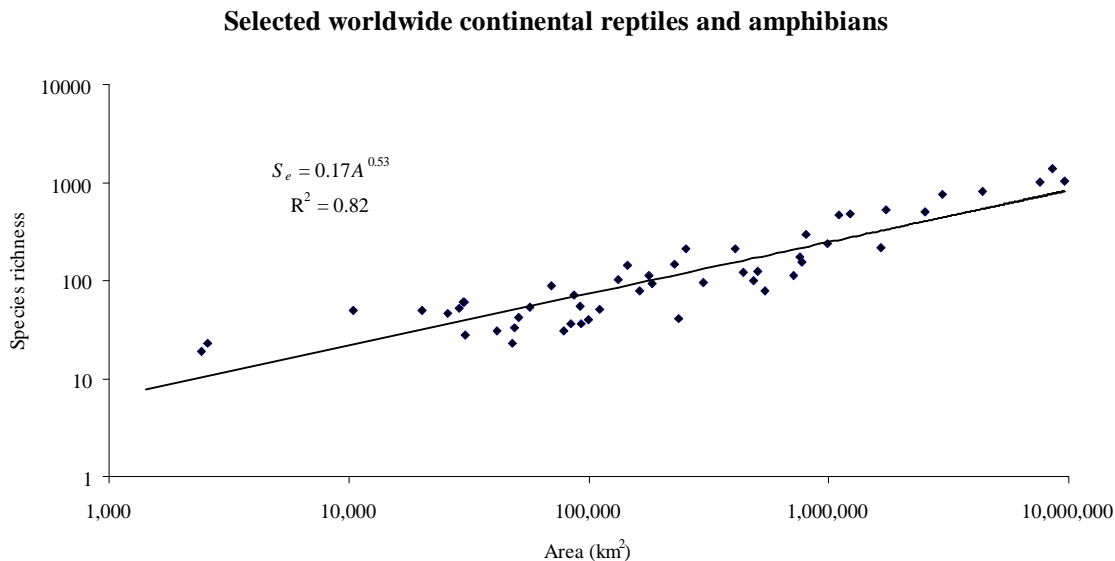


Figure 5. Species-area curve for reptiles and amphibians on modern continental areas with mild climates. Tightness of fit suggests that provinces based on political boundaries are appropriate proxies for natural or random boundaries. Regression is significant at the $P \ll .001$ level.

the entire world, are too diverse to be useful in this regression. Thus, the provinces used in this study are between approximately one thousand and ten million square kilometers in area.

Figure 5 presents a linear regression created using the reptile and amphibian diversity of fifty-one modern provinces from mild or moderate climatic conditions. This is the modern analog with which a paleogeographic province of like climate can be compared. A single paleocontinental area was selected as a case study: the Upper Cretaceous Hell Creek Formation of eastern Montana and western North and South Dakota. The Hell Creek Formation has a one hundred year history of paleontological and geological field work, and the fauna, flora, climate, and lateral extent are well known, making it an ideal model.

3.2 The Hell Creek Formation

3.2a Introduction

The Hell Creek Formation was first described by Brown (1907) as a vertebrate rich, fresh water sedimentary unit overlying the Fox Hills Sandstone in the Fort Peck region of eastern Montana. These fluvially dominated strata form an extensive meandering channel system and are also exposed in western North and South Dakota. Most of the formation consists of siltstones and claystones representing floodplain and swamp deposits with abundant paleosol horizons, and the remainder is channel sand (Fastovsky, 1987). Figure 6 shows the surface exposures of the Hell Creek Formation along with its implied subsurface extent beneath the overlying Fort Union Formation. Its total paleogeographic surface area, calculated using the ImageJ software of Rasband (2004) covers about 300,000 km². The Hell Creek Formation is late Cretaceous (Maastrichtian) in age and the upper boundary of the formation is regionally isochronous with the Cretaceous-Tertiary (K/T) boundary which dates to 65 Ma, although locally the boundary with the overlying Fort Union Formation can be just above or just below the K/T boundary (Johnson *et al.*, 2002).

As a lithostratigraphic unit, the Hell Creek Formation encompasses a span of time as well as a geographic range. The assumption that must be made is that the Hell Creek Formation is equivalent to a paleoprovince. So although the temporal duration of the Hell Creek Formation has been variously estimated at 1.36 Ma and 2.5 Ma by Hicks *et al.* (2002) and Lund *et al.* (2002), respectively, for our purposes it is assumed to have no

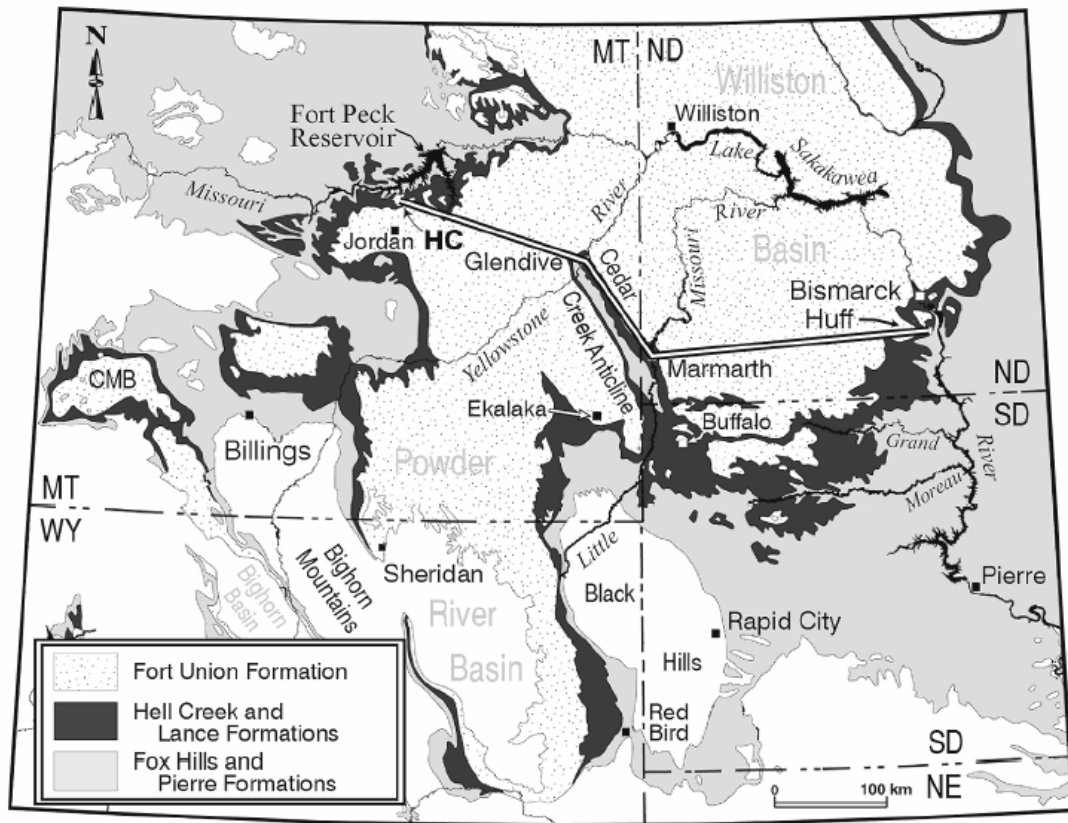


Figure 6. The surficial extent of the Upper Cretaceous Hell Creek Formation across the northern Great Plains. Calculated area of 300,000 km² includes subsurface portion of Hell Creek Formation not visible here. Field area indicated by “HC.” The stratigraphically equivalent beds of Wyoming are traditionally known as the Lance Formation. From Johnson et al. (2002).

temporal component. As with the above island scenario, this eliminates the possibility of species turnover which might overestimate diversity.

Late Cretaceous climate has been described as “green house” by Skelton (2003) and Hell Creek conditions were warm and subtropical based on paleobotanical studies (Johnson, 2002). Humid subtropical conditions are categorized as “mild” or “moderate” by the Köppen system of climate classification. The Hell Creek Formation is

paleontologically important due to the discovery of large dinosaur skeletons, mammal teeth and other small vertebrates, and its faunal diversity is now well known (Archibald, 1996). In addition to the well-publicized dinosaurs, the Hell Creek Formation contains one of the first essentially modern terrestrial faunas in the geologic record. Extant lineages comprised a significant portion of the fauna, and included crocodylians, turtles, lizards, snakes, frogs, salamanders, birds, mammals, and modern groups of freshwater fish.

Hell Creek vertebrate fauna has been recovered using two methods. Beginning at the turn of the twentieth century, large dinosaur skeletons and other reptiles were recovered using traditional prospecting and quarrying techniques (*e.g.* Brown, 1905; 1908; Case, 1939; Colbert and Bump, 1947; Osborn, 1905). However a new technique of soaking and sieving partially consolidated sediment was devised by Hibbard (1949) for use at a Cenozoic microvertebrate locality (site where the isolated remains of small vertebrates are concentrated by fluvial or biotic action) in Kansas, allowing the recovery of thousands of tiny bones and teeth. Screen washing was soon applied to the Hell Creek Formation (*e.g.* Archibald, 1982; Bryant, 1989; Estes *et al.*, 1969; Sloan and Van Valen, 1965) which resulted in the discovery of 63% of the known diversity (Appendix E). Currently 132 vertebrate taxa are known from the Hell Creek Formation of Montana, North Dakota and South Dakota, including new taxa described in this study (Appendix E).

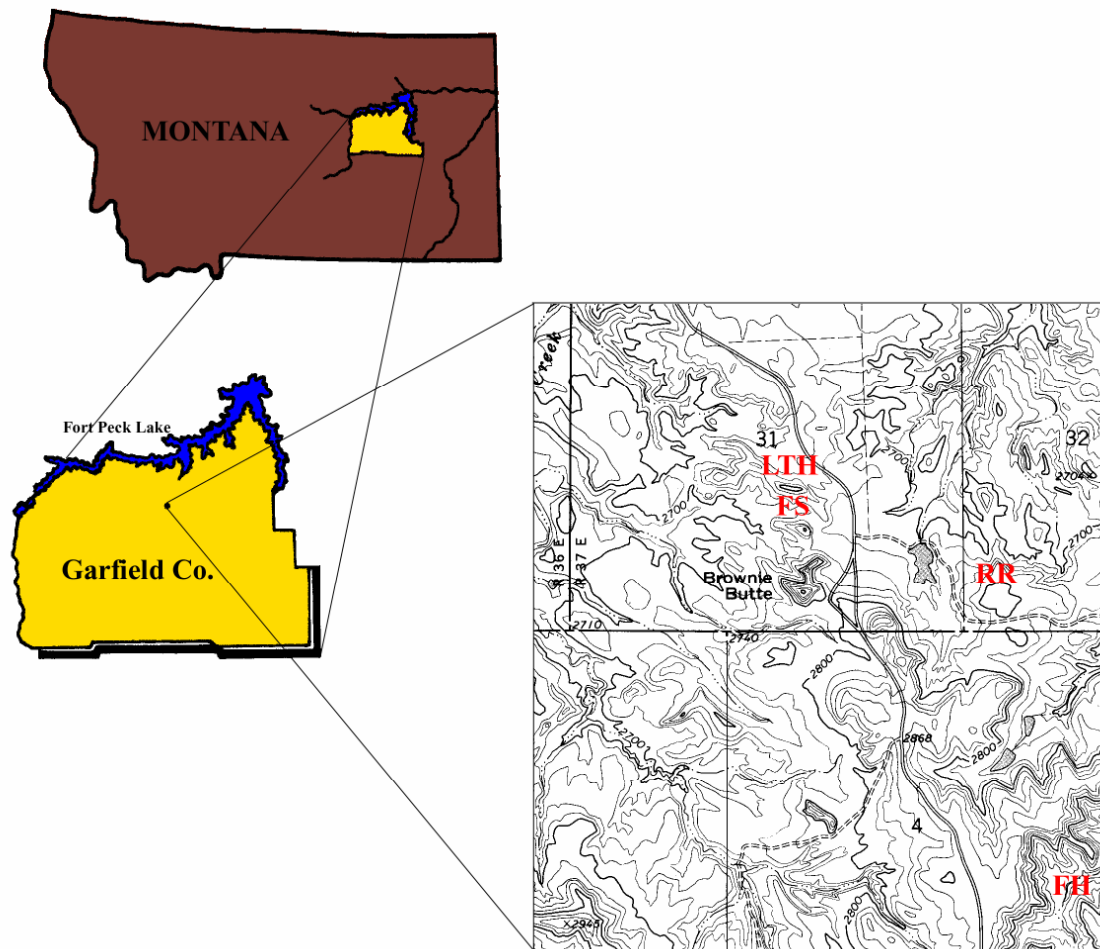


Figure 7. Location of field area in Garfield County, Montana. Topographic map section shows major collecting localities on Hell Creek Ranch. Locality abbreviations: FH, Fang Hill; FS, Fish Sticks; LTH, Lone Tooth Hill; RR, Rancher Ridge. Width of topographic map is approximately 2.5 km. Adapted from Fastovsky and McSweeney (1987).

3.3b Field methods

Field work was conducted on Hell Creek Ranch, Garfield County, eastern Montana during the 2002, 2003, and 2006 summer field seasons (Figure 7). The ranch, which has produced four new species of mammals (Sloan and Van Valen, 1965), was



Figure 8. Exposures of the Hell Creek Formation in the badlands of northern Garfield County, eastern Montana.

until 2007 managed by John and Sylvia Trumbo, who have hosted two generations of paleontologists on their land. The badlands terrain is a series of gullies, coulees, hoodoos, and intermittent streams: a highly erosional landscape which allows the continuous natural exposure and recovery of fossils (Figure 8).

Common fossil deposits within the Hell Creek Formation are in the form of microvertebrate localities: locally concentrated accumulations of isolated skeletal elements (Figure 9). In most cases disarticulated vertebrate material covers the surface of

the ground as a result of being eroded from an adjacent outcrop. Inference can be made as to the source bed of the fossils by observing the immediate topography and drainage rivulets. More rarely the source of the material can be pinpointed as coming from a specific bed, and can be “mined” from the stratum. At such localities judged by visual inspection to be potentially rich, sediment was shoveled into sacks, hand carried to a field vehicle and transported to a cattle trough. There the sediment was poured into wooden screen-bottom boxes, lowered into the trough, and soaked to disaggregate the sediment (Figure 10). Hours later, the boxes were agitated in the water by hand until the sediment passed through the screen leaving behind rock fragments and fossils. The boxes were then set out in the sun to dry, and the remaining concentrate was bagged for transport to the lab, where the fossil material was separated from the rock debris under a binocular microscope.

3.2c Localities sampled

Over 1200 kg of sediment were screenwashed from fifteen microvertebrate localities (Table 1). More than 1600 taxonomically useful (*i.e.* able to be identified to the family level or lower) microfossils were recovered, and are repositied at the Shenandoah Valley Discovery Museum (SVDM).

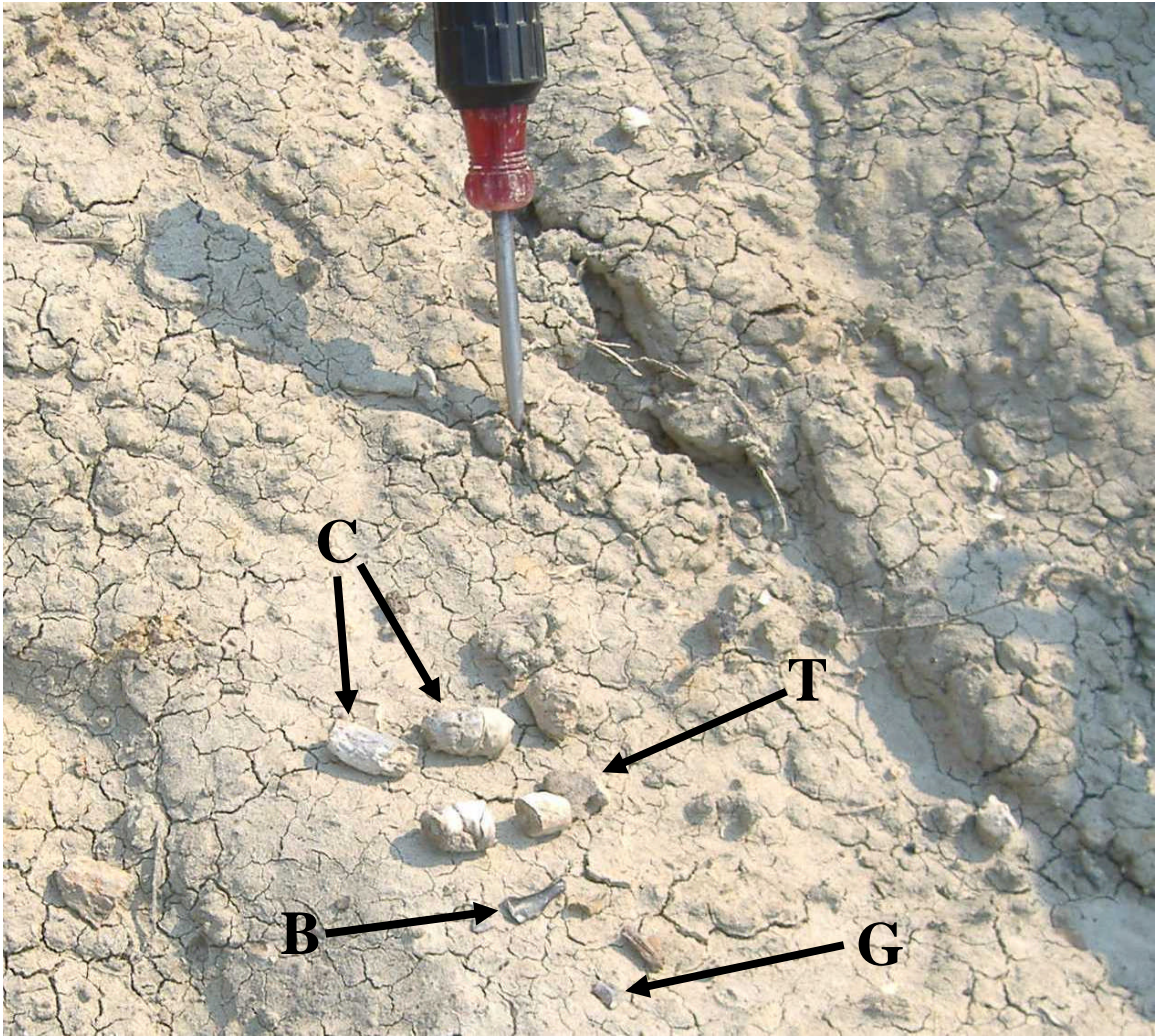


Figure 9. Typical microvertebrate locality in the Hell Creek Formation. This locality (L-28) consists of grey and buff banded mudstone mixed with fine to very fine sand. The surface shows polygonal mudcracks typical of the repeated wetting and drying of sediments with high clay content. Fossils shown include coprolites (**C**), a bird coracoid (**B**), turtle shell fragments (**T**), and a gar fish scale (**G**).



Figure 10. The screen washing process: A) sediment soaking in screen-bottom boxes in cattle trough; B) partially broken down clay and mud matrix; C) concentrate drying in the sun; D) dried concentrate ready to be bagged.

Table 1. All microvertebrate localities screenwashed during the 2002, 2003, and 2006 field seasons. Duplicate locality names indicate the site was collected on multiple occasions, as distinguished by unique field number. Concentrate weight represents rocks and pebbles remaining after sediment is removed. Detailed locality and field data are on file at the Shenandoah Valley Discovery Museum.

LOCALITY NUMBER	LOCALITY NAME	FIELD NUMBER	SEDIMENT WEIGHT (kg)	CONCENTRATE WEIGHT (g)
L-01	Rancher Ridge	03GB07-20-06	48.0	8,377
L-01	Rancher Ridge	06GB07-25-28	27.6	16
L-01	Rancher Ridge	06GB08-3-48	6.8	2,066
L-27	Fang Hill	01CC06-28-01	48.9	3,573
L-27	Fang Hill	03GB07-22-11	8.6	10
L-27	Fang Hill	03GB07-22-10b	7.2	416
L-27	Fang Hill	06GB07-17-05	24.9	171
L-27	Fang Hill	06GB08-3-47	6.8	298
L-28	L-28	06GB07-18-12	24.9	208
L-31	Gar Site	03GB07-19-xx	29.0	3,171
L-31	Gar Site	06GB07-28-38	5.4	498
L-42	Lone Tooth Hill	02DM06-17-01	140.9	33,601
L-42	Lone Tooth Hill	03GB07-16-03a	73.4	12,329
L-42	Lone Tooth Hill	06GB07-26-30	53.5	429
L-42	Lone Tooth Hill	06GB08-1-42	70.2	6,898
L-50	Fish Sticks	02RR07-03-09	63.0	3,047
L-50	Fish Sticks	03GB07-18-xx	28.1	1,359
L-51	L-51	03GB07-21-07	17.7	85
L-53	L-53	06GB07-28-39	57.1	2,271
L-65	Lone Tooth Hill East	03GB07-18-03b	37.1	1,812
L-65	Lone Tooth Hill East	06GB07-17-07	29.9	619
L-65	Lone Tooth Hill East	06GB07-31-40	82.0	726
L-75	L-75	03GB07-19-04	28.1	2,265
L-75	L-75	06GB07-27-32	100.6	3,580
L-91	Double Pine	06GB07-19-14	26.3	238
L-91	Double Pine	06GB07-20-15	57.5	1,281
L-92	Piney Butte	06GB07-18-10	40.8	414
L-98	L-98	06GB07-28-35	48.9	1,071
L-102	Micro Frill	06GB08-3-46	28.5	3,820
L-104	Crocodile Gumbo	06GB08-2-45	29.0	2,496
TOTAL:			1175.1	88,752

The microvertebrate localities sampled are within about five kilometers and twenty-five vertical meters of each other. They are attributed to several specific depositional environments, or facies ("architectural elements" of White et al., 1998), within the Hell Creek fluvial system (Table 2). Nine sites were once floodplains, most of which were paleosols (ancient soil horizons) or possibly ponds, as indicated by color-banded fine grained clays and silts and an absence of sand (Figure 11). The presence of fluvial sands and associated large-scale point bar deposits (Figure 12) and small-scale cross-bedding shows that four other sites were deposited in river or stream channels. Finally, two other sites show evidence of deposition within the natural levees of a river by the presence of banded mudstone and siltstone and very fine sandstone.

Coarse grained channel deposits are deposited under high energy current conditions which produce greater abrasion and breakage of the sediment grains and fossils contained therein. By contrast, fossils deposited within floodplain paleosols are typically more numerous and better preserved. Thus, it is often visually apparent whether a sample of fossils was buried under high or low energy conditions.

Table 2. Summary of depositional environments represented by Hell Creek screenwashed localities. Fluvial architectural elements follow the scheme of White *et al.* (1998).

LOCALITY NAME	DESCRIPTION OF LITHOLOGY	SUBFACIES	FACIES
Crocodile Gumbo	buff, purple and grey silty banded mudstone	floodplain paleosol or pond	floodplain
Double Pine	buff, purple and grey banded mudstone	floodplain paleosol	floodplain
Fang Hill	alternating grey, purple and brown banded mudstone	floodplain paleosol	floodplain
Fish Sticks	alternating buff and brown banded mudstone	floodplain paleosol	floodplain
Gar Site	grey, purple and buff banded mudstone	floodplain paleosol	floodplain
L-28	buff and grey banded mudstone mixed with subangular to subrounded, fine to very fine sandstone	floodplain paleosol or pond	floodplain
L-51	purple and grey banded mudstone	floodplain paleosol	floodplain
L-53	buff, cross-stratified, subangular, well-sorted, medium grained sandstone	thalweg	channel
L-75	buff, cross-stratified, subangular, well-sorted, medium grained sandstone	thalweg	channel
L-98	grey, purple and buff banded mudstone	floodplain paleosol	floodplain
Lone Tooth Hill	inclined strata of buff siltstone and brown, cross-stratified, very fine sandstone	toe-of-point bar	channel
Lone Tooth Hill East	inclined strata of buff, poorly sorted, sub-rounded, trough cross-stratified, very fine to medium grained sandstone	toe-of-point bar	channel
Micro Frill	brown and buff banded mudstone and brown silty fine sandstone	?distal levee	?distal levee
Piney Butte	buff and grey banded mudstone and silty mudstone	distal levee	distal levee
Rancher Ridge	grey, purple and brown banded mudstone, lesser amounts of subrounded very fine sand	floodplain paleosol or pond	floodplain



Figure 11. Buff, grey, and brown banded mudstones in the Hell Creek Formation (within dark lines). This lithology is indicative of floodplain pond or paleosol (ancient soil horizon) deposits. Bluff in foreground is about two meters high. Photo taken at L-27 (Fang Hill).



Figure 12. The gently inclined sandy strata of a point bar sequence dip to the left across the entire photograph. Channel sands are common in the field area along with associated trough cross-bedding indicating unidirectional current. Large boulders throughout bottom of outcrop are iron concreted sandstone blocks formed diagenetically (after deposition). Author for scale. Photo taken at Lone Tooth Hill East locality facing south.

3.2d Newly recognized taxa

Previous to this work, 129 vertebrate taxa had been discovered in the Hell Creek Formation. The fauna includes seven cartilaginous fish, sixteen bony fish, eight salamanders, three frogs, twenty turtles, ten lizards, two snakes, three crocodiles, one champsosaur, twenty-three dinosaurs, one bird, one pterosaur, and thirty-four mammals (Appendix E). Screen washing performed during this study establishes the first occurrence of three additional taxa: two spiny ray-finned (teleost) fishes (Bennett and Main, 2003), and a solemydid turtle. Fossil material listed below is noted first by the element, then by specimen number, and finally by the locality in brackets.

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII (Cope, 1887)
Infraclass TELEOSTEI Müller, 1846

Comments. Identification of teleosts (Figure 13) follows the nomenclature of Brinkman and Neuman (2002), who used characters of vertebral morphology to organize fish centra of the Dinosaur Park Formation in Alberta into parataxonomic groups called morphoserries based on fossil and extant taxa. Some of these morphoserries corresponded to specific taxonomic groups, while some were indeterminate.

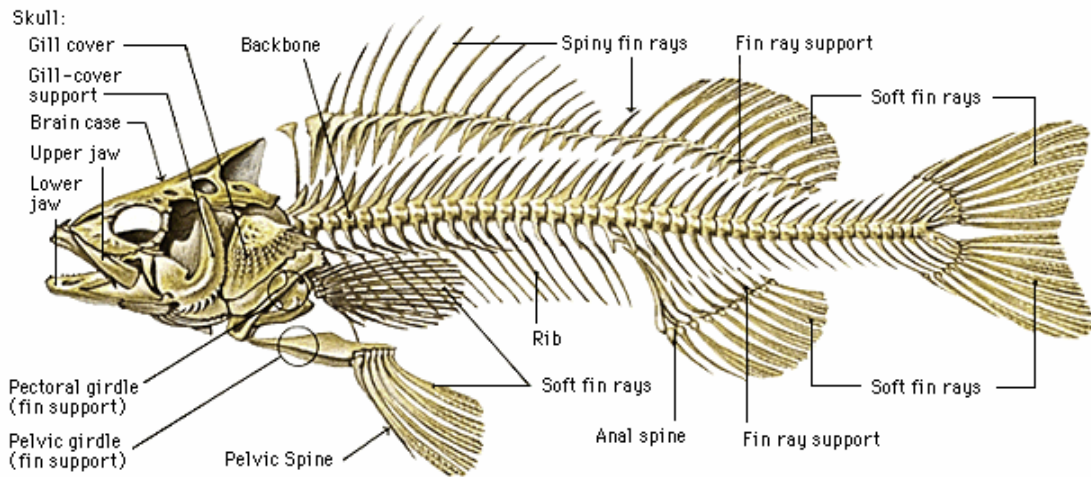


Figure 13. Generalized teleost skeleton. Note the vertebral centra of the backbone and the dorsal fin spines which are further described in the text. From *World Book Online Americas Edition*.

Anatomical terms. An individual vertebra consists of the main body, the centrum, and the adjacent bones or cartilaginous structures above and below the centrum. In this study, none of the adjacent bones were identified, with the exception of small fragments that were fused to the centra. Teleost vertebral centra are cylindrical in shape, sometimes antero-posteriorly flattened into a disc. Typically both anterior and posterior surfaces are concave (amphicoelous condition; Figure 14) in the shape of an inverted cone and are often connected by a central foramen, a remnant of the notochord. The atlas (plural: atlantes) of some teleosts differs from this pattern in that the anterior surface is platycoelous, or flat, instead of concave. The neural arch consists of two osseous processes on the dorsal surface of the centrum that meet to form an arch, through which

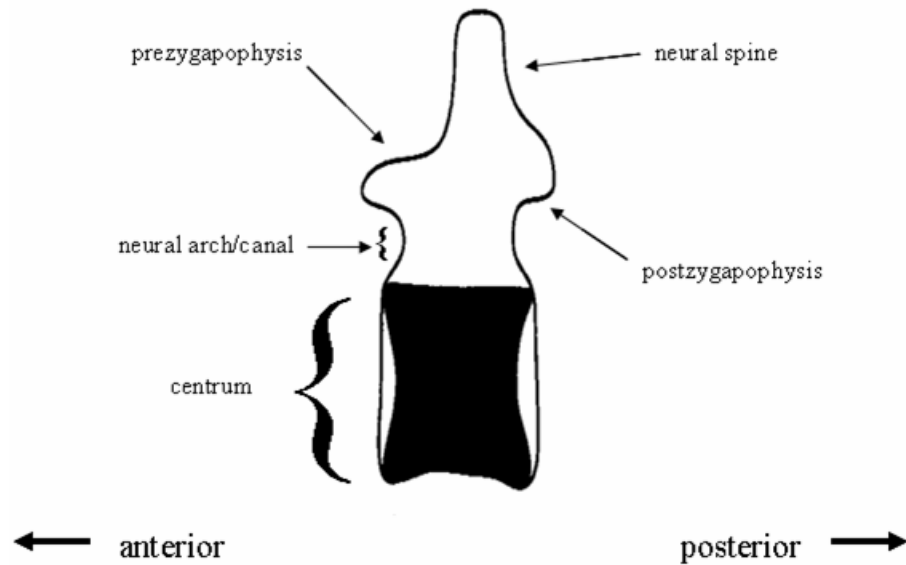


Figure 14. Generalized vertebra. Centrum is amphicoelous (concave on both ends).

the spinal cord penetrates. In lower teleosts the neural arch is separate from the centrum and can be inferred in fossils by the presence of a pair of neural arch articular pits on the centrum. Higher teleosts possess neural arches fused to the centrum. These processes are often broken away in isolated microfossils. Pleural ribs articulate with the centrum on the lateral surface by way of a parapophysis. In lower teleosts the parapophysis fits into a parapophyseal pit on the centrum. In advanced teleosts, the parapophysis is fused to the centrum. The autogenous condition results when the parapophyses are separate from the neural arch.

Zygapophyses are processes that extend anteriorly (prezygapophyses) and posteriorly (postzygapophysis) from the dorsal surface of the centrum. The two

prezygapophyses of one centrum articulate with the two postzygapophyses of the adjacent centrum (Figure 14). Their purpose is to simultaneously reduce the range of motion and increase stability in the spinal cord.

Caudal centra, in addition to neural arch pits or bases, possess ventrally directed haemal arches which enclose the major blood vessels of the tail.

Order HIODONTIFORMES McAllister 1968
Family HIODONTIDAE Valenciennes 1846
Genus and species indeterminate

(Figure 15-16)

Material examined. 1 atlas SVDM VP-337 (L-27 Fang Hill).

Description. Atlas with anterior articular surface that is tripartite, *i.e.* is divided into three facets that articulate with the base of the skull (Figure 15A, B); lower basioccipital facet is partially subdivided by a central pit (Figure 15A, B); two upper exoccipital facets are offset from basioccipital facet by about 60 degrees; all three anterior articular surfaces platycoelous (Figure 15A, B); neural arch pits present on the posterior dorsal surface (Figure 15C-D); mid-dorsal pit present (Figure 15C, D); mid-ventral pit absent (Figure 15E); interwoven, randomly oriented bone fibers on ventral surface (Figure 15E); posterior articular surface circular and concave (Figure 15F).

Discussion. The presence of hiodontids (Figure 16) in the Hell Creek Formation is shown for the first time with the recovery of a single distinctive atlas. The first vertebra of the extant genus *Hiodon* possesses several characters previously noted by Brinkman and Neuman (2002; Table 3) in common with SVDM VP-337 allowing confident

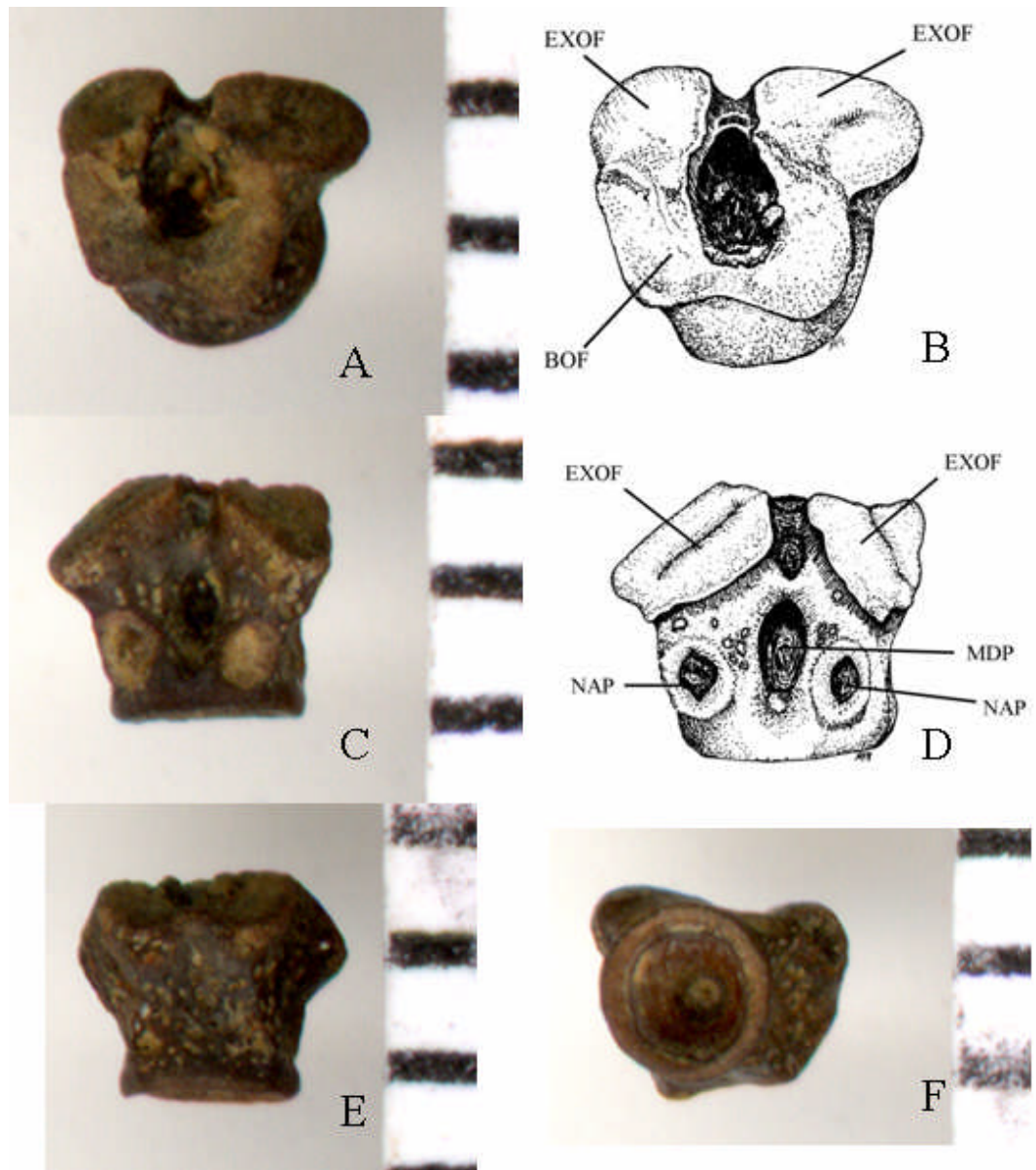


Figure 15. Hiodontidae indeterminate atlas (SVDM VP-337) in A-B) anterior; C-D) dorsal; E) ventral; and F) posterior views. Note presence of interwoven bone fibers and absence of mid-ventral pit in ventral view. Abbreviations: **BOF**, basioccipital; **EXOF**, exoccipital facet; **MDP**, mid-dorsal pit; **NAP**, neural arch pit. Scale in mm.

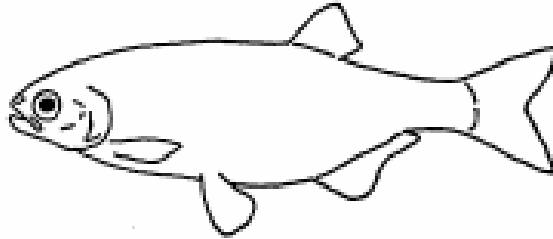


Figure 16. Typical modern hiodontid. Length about 40 cm. From Greenwood *et al.* (1966).

identification. Although hiodontids and acanthomorphs both have tripartite atlantes, the articular surfaces of the latter are amphicoelous. Several other characters in Table 3 distinguish these two lineages.

Until their recognition in the Campanian of Alberta, Cretaceous hiodontids were unknown from North America (Brinkman and Neuman, 2002). It is perhaps not surprising that hiodontids were present in the Maastrichtian Hell Creek Formation of Montana given that they are known from Alberta in the older rocks of the Dinosaur Park Formation and the younger Paleocene rocks of the Paskapoo Formation (Wilson, 1980). Hiodontids are known from the Early Cretaceous to Early Tertiary of Asia and were widespread, although not abundant, in northern North America in the middle Tertiary (Li *et al.*, 1997). Today they have a relatively reduced range in central and eastern Canada and the central and eastern United States. It appears that today's hiodontids occupy a remnant of a formerly wide distribution in the northern hemisphere (Wilson and Williams, 1993).

?HIODONTIDAE

Material examined. 1 precaudal centrum SVDM VP-1093 (L-01 Rancher Ridge).

Description and Discussion. SVDM VP-1093 is a partial precaudal centrum tentatively attributed to the Hiodontidae based on the presence of a rib articular pit and randomly oriented bone fibers.

Table 3. Osteological characters distinguishing the centra of Hiodontidae and Acanthomorpha.

	HIODONTIDAE	ACANTHOMORPHA
Atlas	platycoelous (flat) tripartite anterior articular surface on atlas anterior surface platycoelous, posterior surface concave parasagittal ridges present on anterior ventral surface postzygapophysis absent neural arch articular pits present	amphicoelous (concave) tripartite anterior articular surface on atlas anterior and posterior surfaces concave (amphicoelous condition) parasagittal ridges absent on ventral surface postzygapophysis present neural arch articular pits absent
Precaudal centra	pre- and postzygapophysis absent bone fibers on ventral surface have no preferred orientation mid-ventral pit absent neural arch articular pits oval in shape amphicoelous	pre- and postzygapophysis present bone fibers on ventral surface antero-posteriorly oriented mid-ventral pit present neural arch articular pits absent amphicoelous

Order ACANTHOMORPHA Rosen 1973
Genus and species indeterminate

(Figures 17-21)

Material examined. 1 caudal centrum SVDM VP-302 (L-50 Fish Sticks); 4 fin spines SVDM VP-336 (L-01 Rancher Ridge); 3 atlantes SVDM VP-338 (L-27 Fang Hill); 1 atlas SVDM VP-339 (L-27 Fang Hill); 1 fin spine SVDM VP-380 (L-42 Lone Tooth Hill); 1 fin spine SVDM VP-518 (L-01 Rancher Ridge); 1 caudal centrum SVDM VP-526 (L-01 Rancher Ridge); 1 anterior precaudal centrum SVDM VP-529 (L-01 Rancher Ridge); 1 precaudal centrum SVDM VP-917 (L-75); 1 anterior precaudal centrum SVDM VP-982 (L-50 Fish Sticks); 3 fin spines SVDM VP-1073 (L-01 Rancher Ridge); 1 precaudal centrum SVDM VP-1091 (L-01 Rancher Ridge); 1 precaudal centrum SVDM VP-1092 (L-01 Rancher Ridge); 1 caudal centrum SVDM VP-1094 (L-01 Rancher Ridge); 2 fin spines SVDM VP-1172 (L-01 Rancher Ridge); 1 atlas SVDM VP-2112 (L-27 Fang Hill); 1 anterior precaudal centrum SVDM VP-2113 (L-27 Fang Hill); 1 anterior precaudal centrum SVDM VP-2114 (L-50 Fish Sticks); 1 precaudal centrum SVDM VP-2115 (L-50 Fish Sticks).

Description. Atlas with tripartite anterior articular surface; parapophysis and parapophyseal articular pit absent; autogenous neural arch; antero-posteriorly directed bony fibers on ventral surface; anterior and posterior ends circular and amphicoelous. Atlas from morphoserries IIIB-1 with mid-ventral pit; wedge shaped in lateral view with the ventral edge narrow (Figure 17). Atlas from morphoserries IIIB-2 with ventral pit absent; centrum elongate and sub-rectangular in lateral view (Figure 18).

Precaudal centra with pre- and postzygapophyses; neural arches fused to centrum; amphicoelous; mid-ventral pits present; antero-posteriorly directed bony fibers on ventral and lateral surfaces. Morphoserries IIIB-1 and 2 with mid-dorsal ridge absent.

Morphoserries IIIB-3 with mid-dorsal ridge present (Figure 19).

Caudal centra (Figure 20) are amphicoelous; antero-posteriorly oriented bone fibers present; mid-dorsal pit present; zygapophyses absent; mid-ventral pit present; ventrally directed haemal arch bases present.

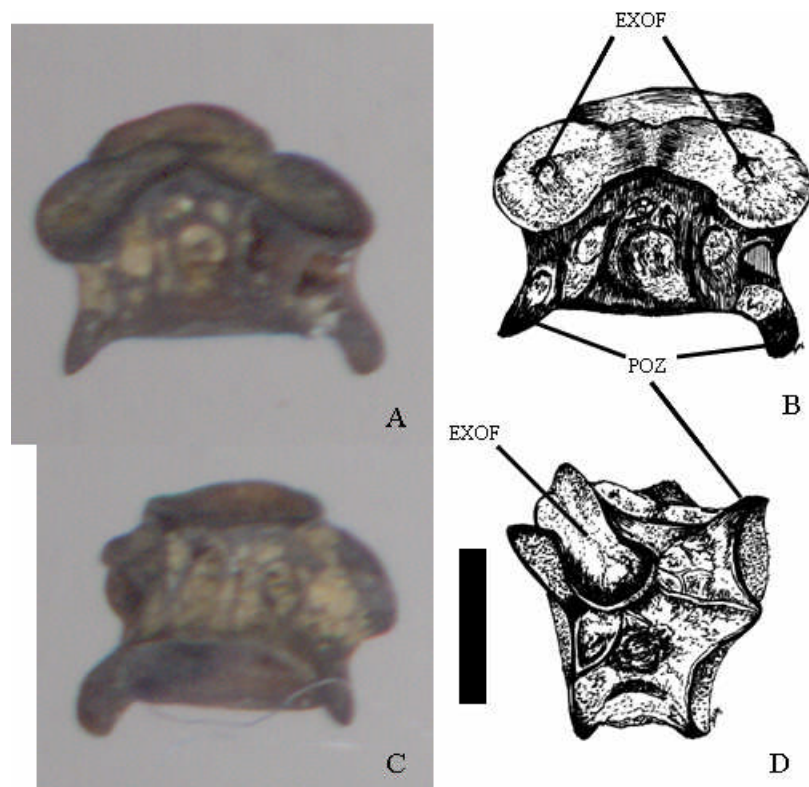


Figure 17. Acanthomorpha indeterminate atlas from morphoserries IIIB-1 (SVDM VP-2112) in A, B) dorsal; C) ventral; and D) left lateral views. Exoccipital facets combine with anterior surface of centrum to form characteristic acanthomorph tripartite articular surface. Note wedge-shape in lateral view (D), a character of morphoserries IIIB-1. Abbreviations: **EXOF**, exoccipital facet; **POZ**, postzygapophysis. Scale bar = 1 mm.

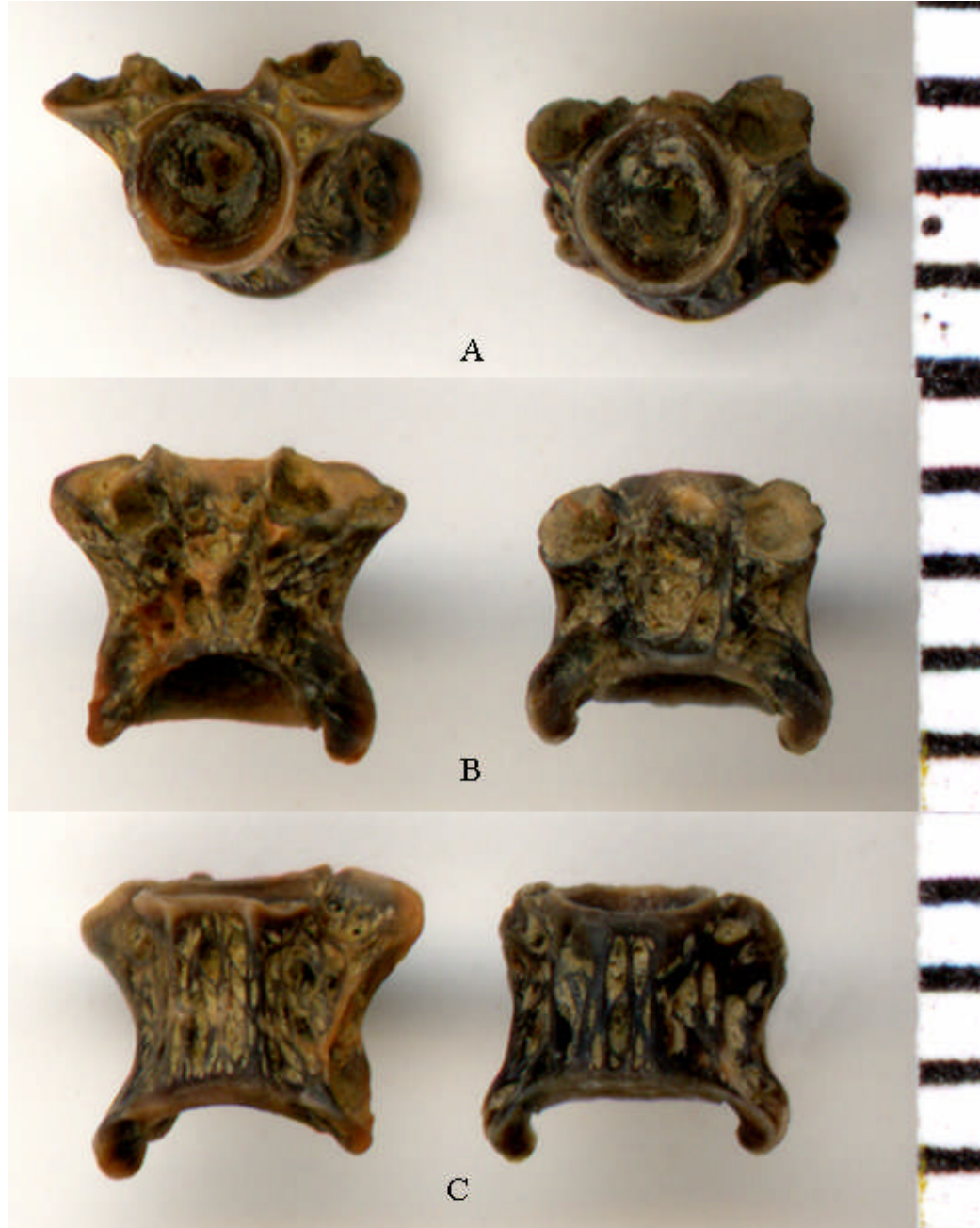


Figure 18. Acanthomorpha indeterminate atlantes from morphoserries IIIB-2 (SVDM VP-338) in A) anterior; B) dorsal; and C) ventral views. The tripartite articular surfaces are visible in anterior view. Scale in mm.

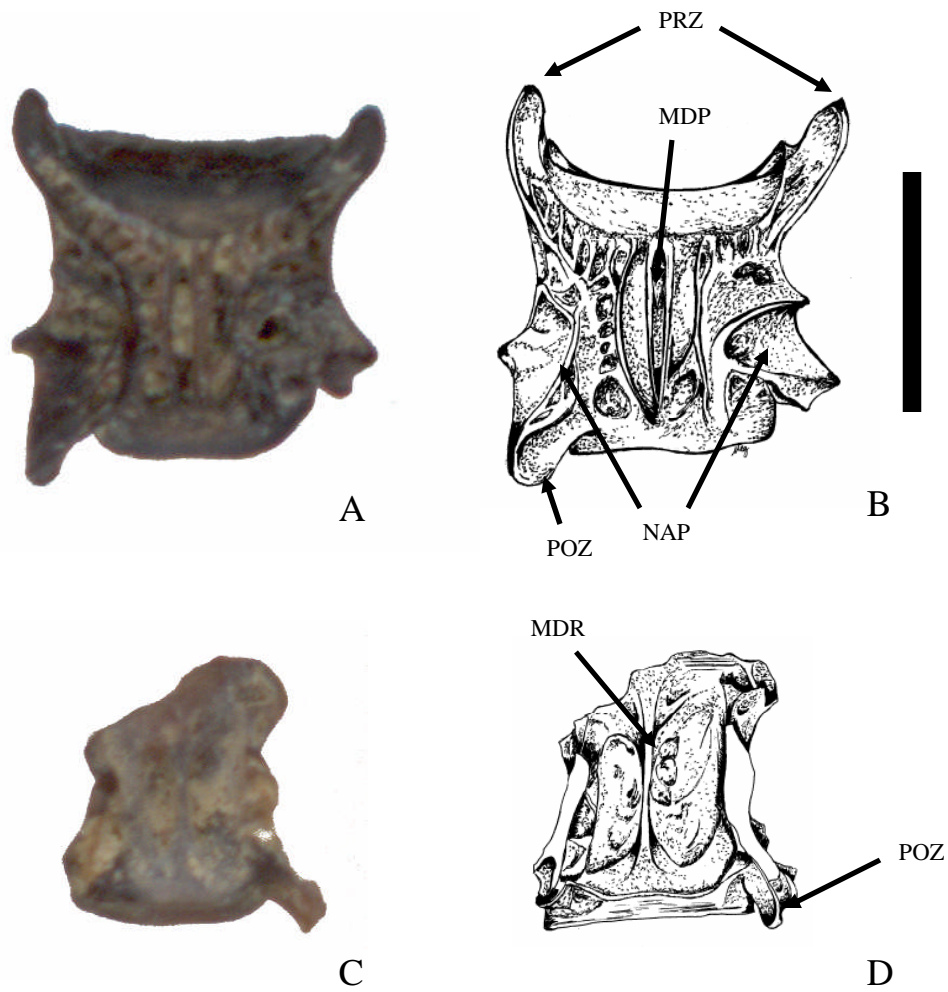


Figure 19. Acanthomorph precaudal centra from morphoserries IIIB. SVDM VP-2113 from morphoserries IIIB-1 or 2 in dorsal view (A, B). SVDM VP-1091 from new morphoserries IIIB-3 in dorsal view (C, D). Note zygapophyses that are synapomorphies of the Acanthomorpha. Mid-dorsal pit and mid-dorsal ridge distinguish morphoserries IIIB-1 and 2 from IIIB-3. Abbreviations: **MDP**, mid-dorsal pit; **MDR**, mid-dorsal ridge; **NAP**, neural arch pit; **POZ**, postzygapophysis; **PRZ**, prezygapophysis. Scale bar = 2

Median dorsal fin spines with two basal locking processes; distal end tapers to point; postero-ventral surface with channel running the length of the spine; spine slightly asymmetrical (Figure 21).

Discussion. The acanthomorphs are the most numerous group of modern fish with about 16,000 species, and make up about one-third of all living vertebrates. They include many well-known groups of fish (*e.g.* cods, tunas, flounders, basses, perches, etc.) and exhibit significant diversity of morphology and habitat (Johnson and Wiley, 2007).

Three different morphoserries can be distinguished within group IIIB, two (morphoserries IIIB-1 and 2) that were previously identified by Brinkman and Neuman (2002), and one new group (morphoserries IIIB-3) identified by a unique precaudal centrum.

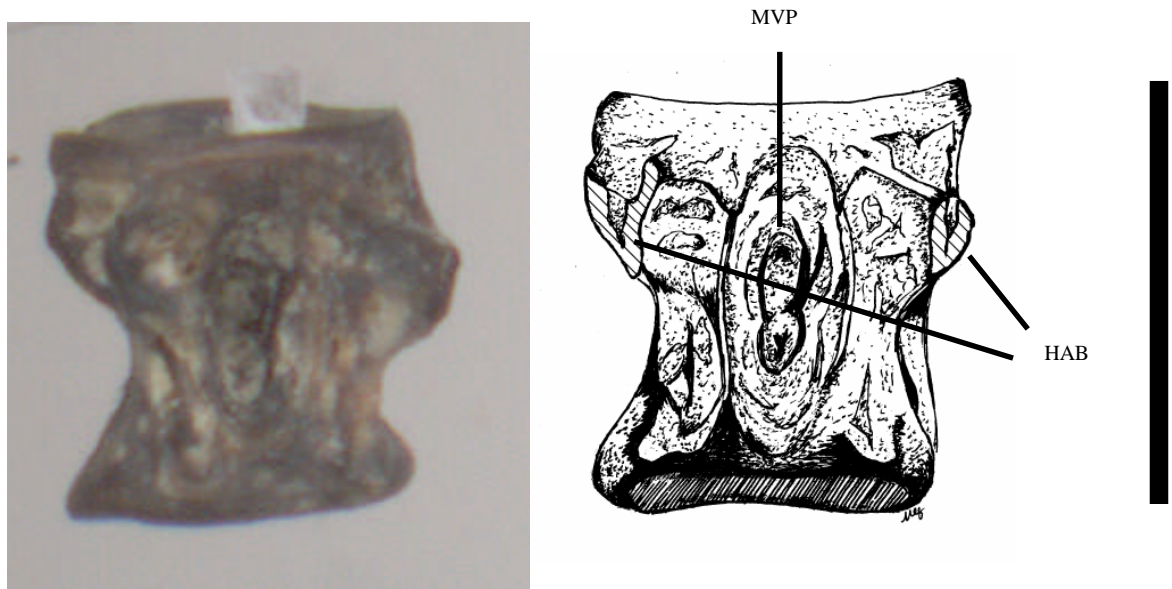


Figure 20. Acanthomorph caudal centrum SVDM VP-526 from morphoserries IIIB in ventral view. Wide parallel lines represent broken surfaces of haemal arches. Abbreviations: **HAB**, haemal arch base; **MVP**, mid-ventral pit. Scale bar = 2 mm.



Figure 21. Acanthomorpha indeterminate median dorsal fin spine (SVDM VP-336) in A) posterior and B) oblique views. Scale in mm.

Five atlantes were attributable to group IIIB based on a “tripartite anterior articular surface and with autogenous neural arch; parapophysis and parapophyseal articular pit absent” (Brinkman and Neuman, 2002, p. 151). Rosen (1985) notes the presence of distinct facets that articulate with the exoccipital condyles is a synapomorphy

of the Acanthomorpha. The three anterior articular surfaces (Figure 17A, B and 18A) represent the connection to the base of the skull. Atlas SVDM VP-2112 represents morphoseries IIIB-1 due to the presence of a mid-ventral pit, and its wedge shape in lateral view with the ventral part of the centrum being the narrowest (Figure 17D). Atlantes SVDM VP-338 and 339 represent morphoseries IIIB-2 and are distinguished from morphoseries IIIB-1 by the lack of a mid-ventral pit and a relatively more elongate centrum which is sub-rectangular in lateral view. Both morphoseries possess antero-posteriorly oriented bony struts on the ventral surface (Figure 17C and 18C).

Precaudal centra possess zygapophyseal articulations (Figure 19) which link one centrum to the next in order to reduce the range of motion and increase stability in the vertebral column. Although this feature also occurs in most tetrapods, it has been identified as a derived uniting character of the Acanthomorpha by Rosen (1985). Brinkman and Neuman (2002) characterize their group IIIB centra as lacking a mid-dorsal ridge between the neural arch bases, however only three of the specimens in this study, an anterior precaudal centrum (SVDM VP-2114) and two centra of undesignated location along the spine (SVDM VP-917 and 1092), display this character (Figure 19). Three other anterior precaudal centra (SVDM VP-529, 982, and 2113) and two other precaudal centra (SVDM VP-1091 and 2115) possess a mid-dorsal ridge (Figure 19). These five centra are designated as acanthomorph because of the presence of zygapophyseal articulations, mid-ventral pits, and antero-posteriorly oriented bone fibers (Table 4). This implies the presence of at least three species of acanthomorph in the Hell Creek Formation, two that are similar to those described by Brinkman and Neuman

(2002) from the Dinosaur Park Formation of Alberta, and an additional form designated herein as morphoserries IIIB-3.

Two caudal centra (SVDM VP-302 and 526) have been identified as acanthomorph based on the presence of antero-posteriorly oriented bone fibers and the lack of a mid-dorsal ridge. However, they lack zygapophyses but do possess ventrally directed haemal arch bases indicating centra from the tail (Figure 20). Caudal centrum SVDM VP-1094 has no bone fibers, but has both a mid-dorsal and a mid-ventral pit, and broken neural and haemal arches.

Eleven median dorsal fin spines belonging to acanthomorphs were recovered. Dorsal fin spines support the anterior and posterior dorsal fins and their presence is a synapomorphy of the Acanthomorpha (Filleul and Dutheil, 2001). The proximal end has two locking processes which articulate with the interneurals and the distal end tapers to a point. Most specimens in this study are incomplete and lack the distal portion of the spine. The only complete spine (SVDM VP-336; Figure 21) is 9.2 mm long and 1.8 mm wide at the base, although some incomplete spines approach twice that width.

?ACANTHOMORPHA

Material examined. 1 partial atlas SVDM VP-849 (L-51).

Description and Discussion. One centrum is questionably attributed to the Acanthomorpha. SVP VP-849 is a partial atlas with only a portion of the tripartite anterior articular surface preserved. Bone fibers and possibly a mid-ventral pit are also present.

Table 4. Characters distinguishing the three Hell Creek acanthomorph morphoserries of group IIIB. IIIB-1 and 2 are also found in the Campanian Dinosaur Park Formation of Alberta.

	Morphoserries IIIB-1	Morphoserries IIIB-2	Morphoserries IIIB-3
Atlas	wedge-shaped in cross section	sub-rectangular in lateral view	unknown
	mid-ventral pit present or absent	mid-ventral pit absent	unknown
	antero-posteriorly directed fibers on ventral surface	antero-posteriorly directed fibers on ventral surface	unknown
	amphicoelous	amphicoelous	unknown
Precaudal centra	antero-posteriorly directed fibers on ventral surface	antero-posteriorly directed fibers on ventral surface	antero-posteriorly directed fibers on ventral surface
	mid-ventral pit present?	mid-ventral pit present	mid-ventral pit present
	zygapophyses present	zygapophyses present	zygapophyses present
	mid-dorsal ridge absent	mid-dorsal ridge absent	mid-dorsal ridge present

Class REPTILIA Laurenti 1768
Order TESTUDINES Batsch 1788
Suborder CRYPTODIRA Cope 1868
Family SOLEMYDIDAE de Lapparent de Broin et Murelaga 1996
Genus and species indeterminate

(Figures 22-23)

Material examined. Shell fragments SVDM VP-1698 (ZVP-01).

Description and Discussion. Solemydids are a poorly known family of fresh water turtles described from the Upper Cretaceous of North America and the Iberian Peninsula and the Lower Cretaceous of Great Britain and Texas (Brinkman, 2003). Solemydids are diagnosed by the presence of distinctive enamel-covered tubercles on the external shell surface. These tubercles are pedicilate and often break off leaving distinctive scars rimmed by a subtle ridge (Brinkman, 2008, personal communication). Remains of this family from the late Cretaceous of North America, including the Campanian of Alberta (Peng *et al.*, 2001) and Wyoming (DeMar and Breithaupt, 2006) have been tentatively referred to *Naomichelys* (Brinkman, 2003), however the single shell fragment (Figure 22) recovered in this study allows confident assignment only to the family level. This is the first recorded solemydid from the Hell Creek Formation, and the first from the Maastrichtian of North America.

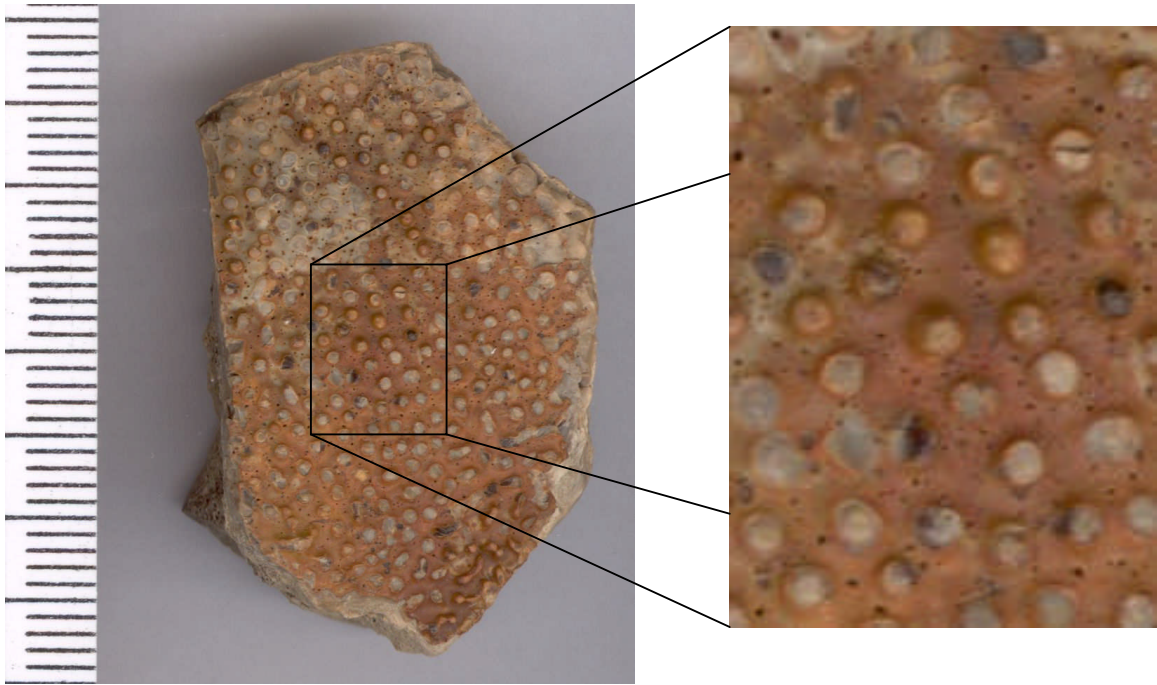


Figure 22. Solemydidae indeterminate. Isolated shell fragment (SVDM VP-1698) in external view. Most of the tubercles have broken off leaving circular scars. Scale in mm.

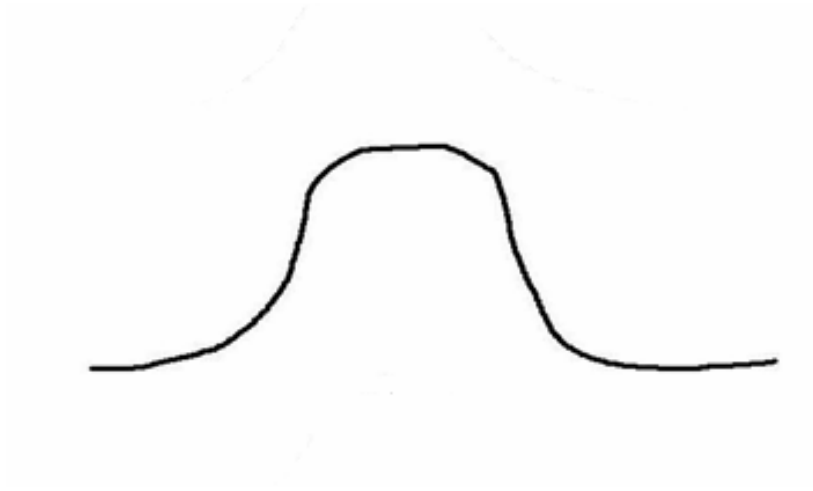


Figure 23. Solemydidae indeterminate. Cross-section of pediculate tubercle of SVDM VP-1698. The nearly vertical walls and the height of the tubercle encourage breakage. Tubercle is about 1 mm wide.

Tubercle morphology in the Hell Creek specimen is similar to those in the Campanian of Wyoming described by DeMar and Breithaupt (2006) in that they have restricted bases, nearly vertical walls, and relatively flat tops (Figure 23). SVDM VP-1698 is not diagnostic to element, however it does possess the pattern in the European genus *Helochelydra* described by Milner (2004) of having “thin pustules about 1 mm in diameter forming vermiculate ridges [formed by two or three tubercles] toward the medial parts of the pleurals,” and thus may be from the midline of the shell.

3.3 Paleobiodiversity and the Hell Creek fossil record

Assessing paleobiodiversity is a prerequisite to determining the completeness of the fossil record. In the following sections, Hell Creek data will be analyzed using four methods (*i.e.* discovery curve, rarefaction, jackknifing, and the species-area relationship) to determine their usefulness in predicting provincial paleobiodiversity and the completeness of the fossil record.

3.3a Discovery curve

One simple method of assessing paleobiodiversity is the discovery curve, which plots cumulative taxa formally described in the literature against the date of publication (Benton, 1998). In theory, initial finds will be made in rapid succession, followed by the more difficult to find rare species. In graphic form this appears as a logistic curve which levels out once most of the taxa have been discovered.

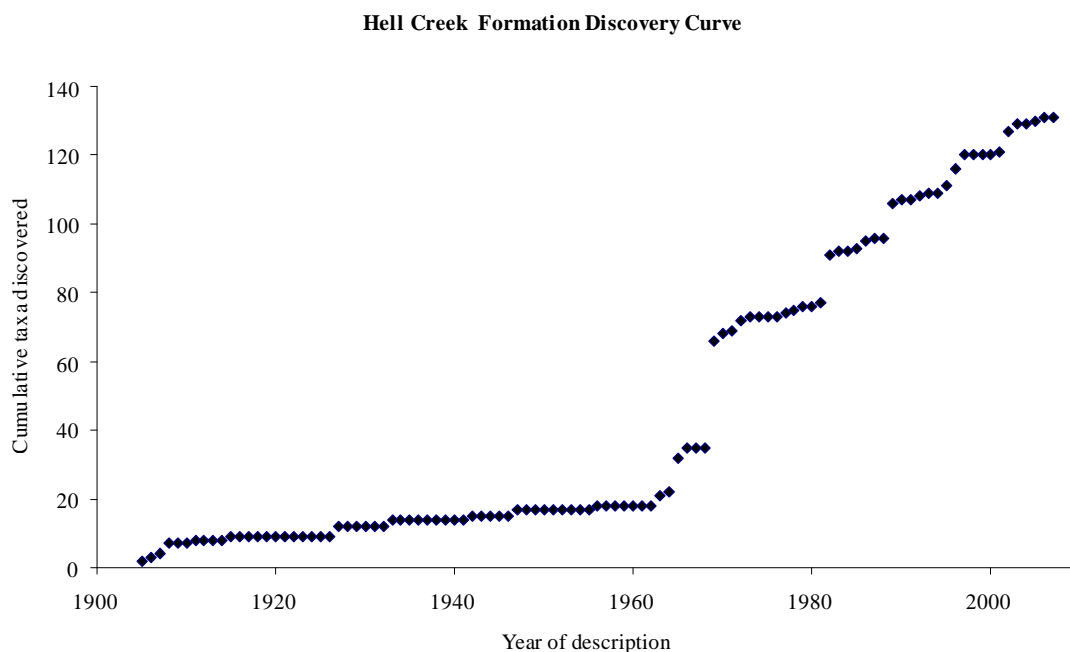


Figure 24. Hell Creek vertebrate discovery curve plotting the cumulative discovery of taxa as published in the literature. Discovery proceeded slowly for the first sixty years when primarily large animals were named, followed by the publication by Estes *et al.* (1969) of numerous new species of microvertebrates as a result of screen washing efforts. Data compiled from sources in Appendix D.

Over the past century and including this study, 132 taxa of Hell Creek vertebrates have been named in the literature (Appendix E). Beginning in 1905 with the first reptile (Brown, 1905), the first sixty years of collecting resulted mainly in large, easily spotted fossils, including many dinosaurs (Figure 24). Then in the late 1960s, the first publications resulting from an extensive program of screen washing began to appear (Estes *et al.*, 1969). This new technique illuminated a large, previously unnoticed,

portion of the fauna. In most ecosystems these microvertebrates are more numerous and diverse than large animals, but cannot be found using time-honored prospecting and quarrying techniques. Over the past four decades, as screen washing efforts have continued, discovery rates have remained high. It appears from Figure 24 that much diversity remains undiscovered, however quantifying this unknown diversity lies beyond the ability of a discovery curve to predict.

3.3b Rarefaction

Another method of assessing paleobiodiversity was originally devised by ecologists to analyze modern species richness. Rarefaction allows diversity at multiple localities to be compared by standardizing the number of samples. It is similar to the discovery curve in that it plots the number of taxa against some measure of accumulating data. In the discovery curve the x-axis is time, while in rarefaction it is the number of specimens collected. In both methods the result is a logistic curve which flattens out once maximum diversity is approached.

Rarefaction allows the analysis of individual microvertebrate localities sampled during this study, as well as an assessment of the Hell Creek as a whole based on all localities. Isolated identifiable fossil elements were counted individually and generally only included if they were recovered during screen washing (Appendix F). Exceptions made in an attempt to reduce preservational and/or collecting bias are as follows: 1) scales of the gar (*Lepisosteus*) were excluded because they are easily preserved, extremely common, and would over-represent the taxon; 2) multiple gar skull plates and

Rarefaction curves for Hell Creek fauna

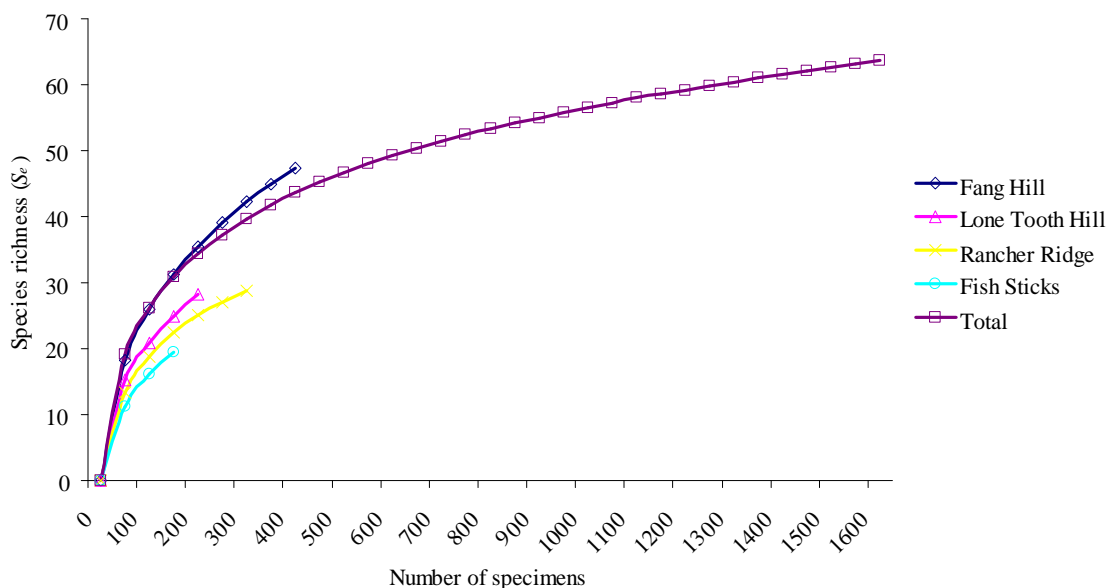


Figure 25. Rarefaction analysis of the entire fauna at the four most productive microvertebrate localities and the total for all microvertebrate localities collected in this study. Fang Hill is currently the most diverse single locality, and is also predicted to be the most diverse when samples are rarefied. Curves generated using the software program PAST (Hammer *et al.*, 2001).

bowfin (*Amia*) tooth plates are counted a single time because numerous broken fragments over-represent these taxa; 3) because larger taxa, such as turtles and champsosaurs, are underrepresented at microvertebrate localities, surface collected specimens are included in the tally; 4) taxa that are only represented by surface collected material are included to signify their presence in the fauna; 5) broken elements were only counted if they were at least half complete to avoid counting the same element twice.

Rarefaction analysis performed on the four most productive localities (Figure 25; Table 5) shows a range of species richness. Fang Hill is the most diverse site with a

Table 5. Abridged numerical representation of rarefied microvertebrate diversity data. Site diversity decreases from right to left. Missing values represent localities at which 400 identifiable specimens have not yet been recovered. Figures generated using the software program PAST (Hammer *et al.*, 2001).

Number of specimens	Rarefied Species Richness			
	Fang Hill	Lone Tooth Hill	Rancher Ridge	Fish Sticks
50	18.2	15.3	13.3	11.3
100	25.9	20.9	18.8	16.1
150	31.3	24.9	22.4	19.5
200	35.5	28.3	25.1	-
250	39.1	-	27.1	-
300	42.2	-	28.8	-
350	45.0	-	-	-
400	47.4	-	-	-

rarefaction curve steeper than the others, even steeper than the total for the entire study area. This may seem impossible, however, it should be remembered that the individual rarefaction curves represent an average of the total study area, and any single curve cannot be more diverse than the overall Hell Creek curve, given a large enough sample size. At a sample size of 150 specimens (the greatest sample size for which all four sites have a record), Fang Hill records an estimated 31.3 species (Table 5), while the least diverse site, Fish Sticks, yields only 19.5 species.

Given that high energy, coarse grained channel deposits have been responsible for abrading and fracturing fossils, one might expect Lone Tooth Hill to yield lower diversity, yet it is second in species richness. In order to recover comparable numbers of complete specimens, more than three times as much sediment had to be screened at Lone Tooth Hill than at any other site. It is necessary to use only identifiable fossil elements to

Rarefaction curves for reptiles and amphibians

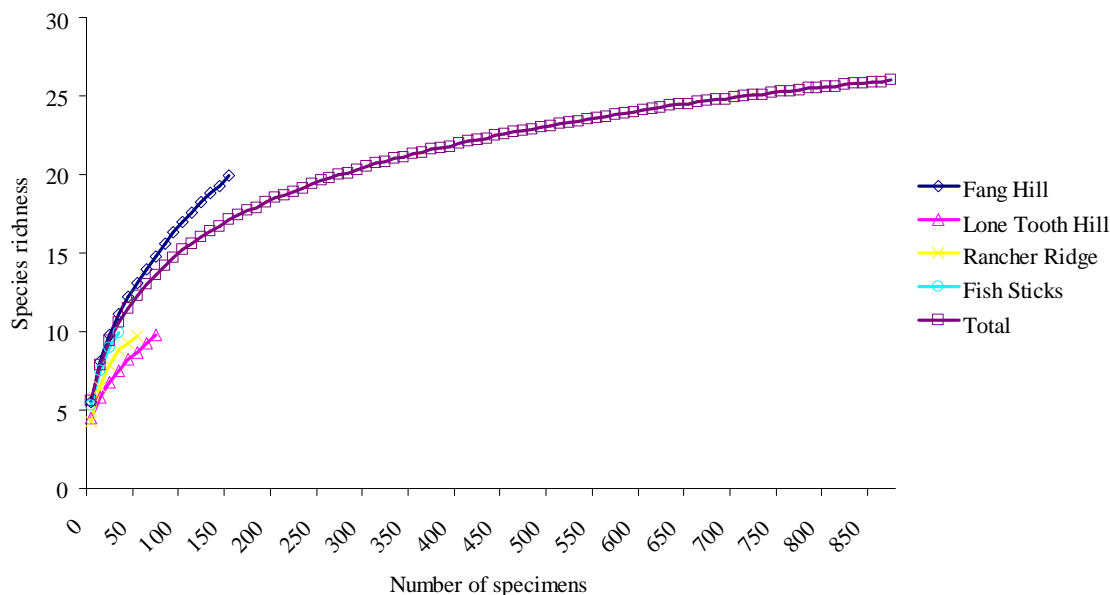


Figure 26. Rarefaction analysis of the reptiles and amphibians at the four most productive microvertebrate localities and the total reptile and amphibian fauna at all localities collected in this study. As with the entire fauna, Fang Hill is the most diverse single locality, however Lone Tooth Hill now has the lowest diversity. Rarefaction curve for the total fauna is $S_e = 4.67\text{Ln}(n) + 3.6$ where S_e is the expected number of species and n is the number of specimens. Curves generated using the software program PAST (Hammer *et al.*, 2001).

eliminate preservational bias, and allow accurate comparison across different depositional environments.

For the purposes of this study, we are interested specifically in the reptile and amphibian fauna to use as a basis for comparison to biogeographical methods. This is because the modern and ancient faunal data need to be of compatible taxonomic groups. Figure 26 and Table 6 eliminate all of the vertebrates except amphibians, turtles, lizards, snakes, champsosaurs, and crocodylians in order to evaluate reptile and amphibian species paleodiversity among several localities using rarefaction. As in the total faunal analysis

Table 6. Abridged numerical representation of rarefied reptile and amphibian diversity data. Missing values represent localities at which 160 identifiable specimens have not yet been recovered. Figures generated using the software program PAST (Hammer *et al.*, 2001).

Number of specimens	Estimated reptile and amphibian species richness			
	Fang Hill	Lone Tooth Hill	Rancher Ridge	Fish Sticks
10	5.5	4.5	4.3	5.3
20	8.1	5.8	6.5	7.5
30	9.8	6.8	7.9	9.0
40	11.1	7.5	8.8	9.9
50	12.2	8.2	9.3	-
60	13.1	8.7	9.7	-
70	14.0	9.3	-	-
80	14.8	9.8	-	-
90	15.6	-	-	-
100	16.3	-	-	-
110	17.0	-	-	-
120	17.6	-	-	-
130	18.2	-	-	-
140	18.8	-	-	-
150	19.3	-	-	-
160	19.9	-	-	-

(Figure 25), Fang Hill demonstrates the greatest diversity with the steepest curve. The channel deposits of Lone Tooth Hill yield the lowest relative diversity and correspondingly the shallowest curve because small fossils are more readily destroyed in a high energy channel environment with coarse, abrasive sand, than in the fine grained deposits of a low energy floodplain. The refraction curve for the total reptile and amphibian fauna includes all localities in the study area and will always have a greater species richness than any other single locality, regardless of the steepness of the initial curve.

Twenty-six reptile and amphibian taxa have been recovered in this study (Appendix F) out of a total of forty-eight published in the literature (Appendix E). Although there are many taxa that have not been recovered in the study area, the rarefaction curve in Figure 26 is flattening out, and new taxa will be found at an increasingly low rate. This diminishing return reflects the vast collecting efforts that have transpired over the past century.

Rarefaction is limited by its inability to extrapolate the diversity curve beyond the known diversity, and therefore cannot predict total expected species. It also predicts only relative diversities by visual comparison of the steepness of the curves.

3.3c Jackknifing

Capture-recapture techniques have long been used by ecologists to estimate diversity in modern ecosystems, and were adapted to assess the fossil record in 1980 by Rosenzweig and Taylor. This method is meant to allow for the fact that all species are not equally “catchable.” The authors resampled diversity in 232 successive fossil-bearing strata, and through a set of simple calculations (for a summary see Rosenzweig, 1995, p. 53) produced a series of diversity estimates over the entire stratigraphic section. The accuracy of this “jackknifing” method is reduced when the number of strata are reduced (Rosenzweig and Taylor, 1980), and as the Hell Creek study area has produced only four significant localities at different stratigraphic levels, the resulting diversity estimate of thirty-one reptile and amphibian species is suspect. This technique would only be useful at localities with a remarkably complete series of fossil-bearing strata, and as such, would

be inappropriate for use on a large geographic scale like the area circumscribed by the Hell Creek Formation.

3.3d Species-area relationship

As in the island example in Chapter 2, the first step in measuring continental paleobiodiversity using the species-area relationship is to create a species-area curve using an analogous modern fauna from the appropriate climatic regime. Figure 5 displays the species-area curve of modern provincial reptiles and amphibians in a mild climate, such as would have been present in the Hell Creek Formation (Johnson, 2002). Although the slope of the regression, z , is quite steep (*i.e.* 0.53), Rosenzweig (1998) points out that species-area curves “from areas with nearly independent evolutionary histories,” such as the disparate provinces cited herein, almost always have z values greater than 0.6. Using the Hell Creek Formation geographic area estimate of 300,000 km² and the species-area curve equation from Figure 5:

$$(4) \quad S_e = 0.17A^{0.53}$$

we can calculate the expected paleobiodiversity of reptiles and amphibians as follows:

$$(5) \quad S_e = (0.17)(300,000^{0.53}) = 135.9$$

To determine the Completeness Index:

$$(6) \quad \text{C.I.} = S_o/S_e = 44/136 = 0.32$$

or, put another way, the fossil record is 32% complete, or has yet to reveal ninety-two species of reptiles and amphibians that lived in the Hell Creek Formation.

Additionally, the diversity of North American freshwater fish can be used to estimate the paleobiodiversity of Hell Creek fish. Benke and Cushing (2005) and Patrick (1996; 1998) present species-area data appropriate as a baseline (Figure 27), such that using the species-area equation yields:

$$(7) \quad S_e = (6.49)(300,000^{0.18}) = 62.8$$

And the completeness index when the observed number of Hell Creek freshwater fish ($S_o = 25$ from Appendix E) would be:

$$(8) \quad \text{C.I.} = S_o/S_e = 25/62.8 = 0.40$$

Indeed, it is reasonable to expect similar Completeness Indices in fish (0.40) and reptiles and amphibians (0.32) because of their similar preservational and taphonomic qualities. The bones, scales, and teeth of both groups are small and fragile making their potential for recovery comparable (however, see discussion on identification bias below).

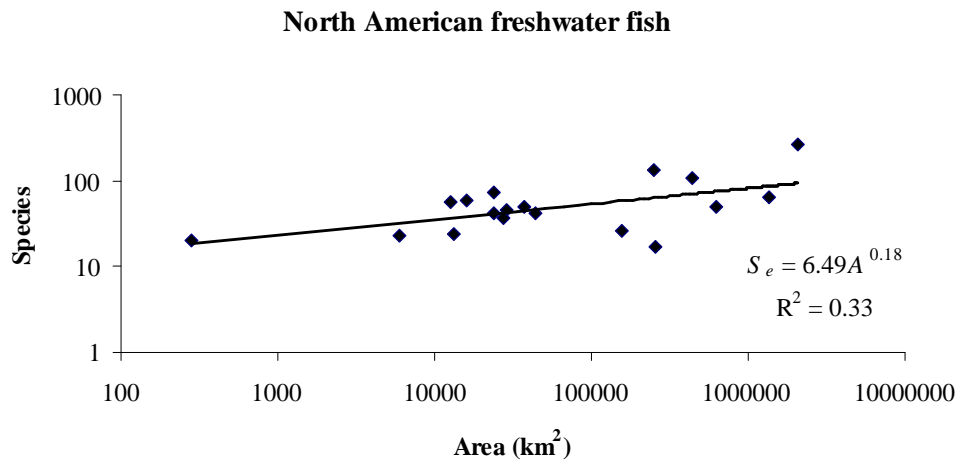


Figure 27. Species-area curve for freshwater fish in North American drainage basins. Data from Benke and Cushing (2005) and Patrick (1996; 1998). Regression is significant at the $P < .05$ level.

3.4 Discussion

Of the four methods presented here to assess paleobiodiversity, only the species-area curve has the potential to estimate the species richness of a paleoisland or province in the absence of a complete fossil record (Table 7). The three previously published diversity evaluation techniques are suitable for other research questions.

The discovery curve, while able to qualitatively estimate the likelihood of continued discoveries, cannot provide quantitative predictions of future finds. Therefore, S_e of Hell Creek reptiles and amphibians can only be predicted to be greater than the forty-eight species already discovered.

Rarefaction has the versatility to be used over great stratigraphic and geographic ranges, however because it is based on individual fossil specimens, data gathering is time consuming and cumbersome on these large scales. While quantitative in nature, rarefaction curves can only extend up to the maximum observed diversity (S_o) at any one locality, and cannot be extrapolated forward to estimate total expected diversity (S_e). Rarefaction is more useful in spotting diversity trends among individual localities.

Likewise, the capture-recapture method of jackknifing can also be enlightening in assessing trends in diversity over time, but requires rare examples of fossil preservation in numerous successive strata. Jackknifing yields a total of thirty-one expected reptile and amphibian taxa in the study area, but because it uses highly geographically localized source data, it is inappropriate to apply this technique to the large scale provinces that are being evaluated herein. In fact, $S_e = 31$ is fewer than the total number of taxa already recorded from the Hell Creek ($S_o = 48$).

The species-area relationship provides the only method that meets all of the required criteria: 1) covers a wide geographic area but can be restricted stratigraphically; 2) is quantitative; 3) can estimate diversity beyond what is actually observed; 4) can produce a Completeness Index indicating how many taxa are missing from the fossil record (Table 7).

Table 7. Comparison of the different methods of assessing paleobiodiversity discussed in the text. S_e and C.I. figures refer to the reptile and amphibian fauna of the Hell Creek Formation.

	DISCOVERY CURVE	RAREFACTION	JACKKNIFING	SPECIES-AREA CURVE
how it works	when log curve flattens, most species have been found	compares relative diversity at sites by equating collecting efforts	resamples successive strata to estimate diversity	uses modern faunal analogs to estimate diversity
drawbacks	expected diversity not easily quantified	unable to extrapolate forward to predict maximum expected diversity; will not work for an entire province	requires significant number of successive fossil-bearing strata; will not work for an entire province	must find accurate faunal and climatic analog
S_e	48+	n/a	31	136
C.I.	n/a	n/a	n/a (S_e is less than S_o)	0.32

3.4a Fish paleobiodiversity

Although it is impossible to assess the diversity of many of the taxonomic groups in the Hell Creek using the species-area relationship due to a lack of modern analogues, it is the author's contention that most of the taxa yet to be described will be among the teleost fishes. This is due to both taphonomic bias and a lack of study up to this point. Taphonomically, teleosts from the Upper Cretaceous are small, have fragile skeletons, and the most abundant identifiable skeletal elements are the tiny (<5mm) vertebrae (Brinkman and Neuman, 2002). Identifying taxa by vertebral morphology has not even been performed for most modern fishes, and studies have just begun on extinct forms. Fish microfossils have been overlooked for many years. For example, although J. Keith

Rigby, Jr., (personal communication, 2003) has collected several hundred thousand microfossils from Hell Creek Formation sites in McCone County during the 1980s and 1990s, no one has yet studied the fish portion of the collection. Likewise, much work has been done by the University of California, Berkeley, on Hell Creek microfossils but lacks any detailed study of teleost fishes.

The first significant report on isolated fish vertebrae recovered from microvertebrate localities was published by Brinkman and Neuman (2002), who studied material from the Upper Cretaceous Judith River Group of Alberta. These authors distinguished vertebral morphotypes corresponding to taxonomic groups, but generally did not apply genus or species epithets. Following their lead, Bennett and Main (2003) recently recognized teleost remains in the Hell Creek Formation. Two of these taxa are described above, and many other morphotypes are present in the sample set but require greater numbers of specimens to allow their segregation into specific groups. If distinguishing characters can be identified then many more new taxa will likely be recognized.

3.4b Reptile and amphibian paleobiodiversity

Known reptile and amphibian diversity in the Hell Creek Formation ($S_o = 48$), with a C.I. of 0.32, is comparable to that of fishes (C.I. = 0.38). It was not until screen washing began in the early 1960s that taxa smaller than crocodiles and turtles were found. Since that time lizards, snakes, frogs, and salamanders have been named on a regular basis, along with many more turtles. Given the generally small size of some of

these animals and the effort required to recover and identify the microscopic elements, it is reasonable to suggest that much of the missing Hell Creek diversity will be found among these taxa, particularly the frogs and snakes, which are depauperate relative to modern faunas. However, this may also be an artifact of their more recent evolutionary development: frogs and snakes may not have become as large a component of the fauna by the late Cretaceous as they have today.

Turtles (Figure 28) are surprisingly enriched in the Hell Creek, with some twenty-one taxa recognized (Holroyd and Hutchison, 2002), as opposed to only twenty-five for the entire modern Mississippi River basin (Bonin *et al.*, 2006), an area nearly seven times larger. If this diversity is not inflated by taxonomic “oversplitting,” it is possible that an unusually large number of turtle species were able to coexist due to extensive resource partitioning.

By using the diversity estimate of $S_e = 136$ (from equation 5), we can also speculate on the amount of work required to recover all of the reptile and amphibian taxa in the entire formation, operating under the assumption that all species are equally recoverable. Using the log-log transformed equation of the reptile and amphibian discovery curve in Figure 29, we have:

$$(9) \quad 136 = 0.68t^{0.78}$$

and solving for t , we can estimate that it would take 891 years of collecting to approach the total reptile and amphibian diversity for the Hell Creek Formation.



Figure 28. At twenty-one taxa, the diversity of turtles is comparable to dinosaurs in the Hell Creek Formation. This tortoise-like species dodges a herd of Triceratops. Original digital artwork by Mark Lawson.

By using rarefaction we can also estimate the number of identifiable skeletal elements needed before expected diversity would be reached in the study area, once again assuming all taxa are equally recoverable. The logarithmic curve for the total of all sites in the study area has been defined in Figure 26 by the equation:

$$(10) \quad S_e = 4.93\text{Ln}(n) + 3.7$$

where n is the number of elements. To recover the expected diversity of 136 taxa, we would have to find roughly 427 billion identifiable specimens!

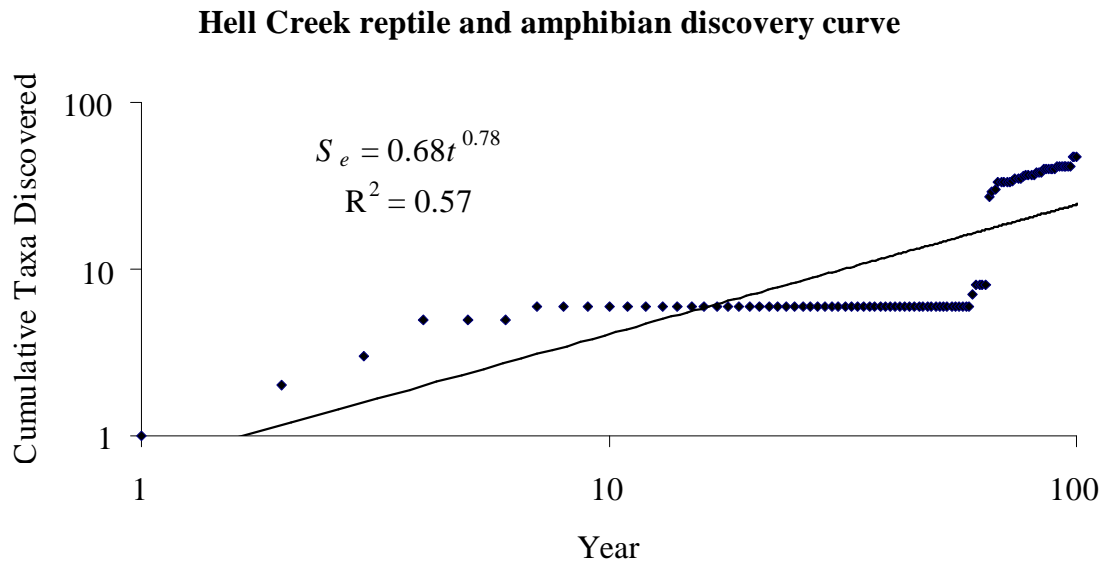


Figure 29. Discovery curve for reptiles and amphibians of the Hell Creek Formation over the past one hundred years. Abbreviations: S_e , expected diversity; t , time in years. $P \ll .001$.

CHAPTER 4

SUMMARY AND CONCLUSIONS

Numerous avenues of research demand an assessment of paleobiodiversity in order to yield valid conclusions. This is complicated by bias in the fossil record with respect to anatomy (lack of hard parts, small size), preservation (erosion, subduction, metamorphism), and collecting (research interests, inaccessibility). Theoretical models offer greater flexibility to assess paleobiodiversity without requiring an exhaustive search of the rock record.

The species-area relationship allows the opportunity to quantify total paleobiodiversity; other methods offer relative comparisons between sites (rarefaction), require rare examples of preservation (jackknifing), or are not readily quantifiable (discovery curve). With a series of fauna- and climate-appropriate modern islands or provinces to use as an analogue, a paleoecosystem's approximate diversity can be calculated through the use of a species-area curve. When compared to the paleofauna already discovered, the completeness of the fossil record (C.I.) can be determined. The mean C.I. of the paleoislands in the study set is 0.32, indicating a fairly poor, but in many cases "adequate," fossil record (Benton, 1998). There is a general decrease in the C.I. with age and size of the island (Figure 3), the former of which is in agreement with traditional thinking, *i.e.* that the fossil record is poorer with age (Benton *et al.*, 2000).

The latter finding likely reflects the fact that larger islands have not received a comparable increase in collecting effort. Differing relative abundance of extinct and extant members of certain taxonomic groups (*i.e.* frogs) may imply fossil record bias, however ecological or evolutionary factors may also be responsible.

Modern continental land areas (provinces) also demonstrate the species-area relationship, albeit with a greater z value. This fact allows a diversity analysis of a selected lithostratigraphic unit, the Upper Cretaceous Hell Creek Formation of eastern Montana and western South and North Dakota. This conservatively assumes zero species turnover over the geologic time represented by the formation. Fossils collected during this study in eastern Montana represent the established fauna and add to it two new taxa of fish and one turtle. A hiodontid fish is represented by vertebral centra and at least one acanthomorph fish is represented by centra and mid-dorsal fin spines. The solemydid turtle is represented by shell fragments with a distinctive sculpture pattern, and is the first recorded representative of the family from the Maastrichtian of North America.

Analysis of the published fauna and newly recovered fossils shows that only the species-area method allows the calculation of unknown paleobiodiversity. The discovery curve plots species discovered against time, but only encourages a rough visual estimate of the number of species left to discover, and is not quantifiable. Rarefaction compares the relative diversity of different localities (*i.e.* specific microvertebrate localities), but cannot make predictions about theoretical total paleobiodiversity. Jackknifing, while able to evaluate diversity through time, does not deal with diversity over a wide geographic

range, such as the Hell Creek Formation, and requires a series of localized fossil producing beds.

This new application of the species-area method predicts a total of 136 species of reptiles and amphibians in the Hell Creek Formation, of which forty-eight are known; the C.I. is 0.32. Hell Creek fish diversity is predicted to be 63 species, of which twenty-four are known; the C.I. is 0.38. Thus, only about one third of the taxa in these groups have been found, and there will likely be numerous future finds, although the effort required to do so will increase with time. Fish diversity is probably underrepresented in the literature because of a lack of research and the nature of distinguishing taxa, *i.e.* specific characteristics on microscopic vertebrae.

The species-area technique can only be applied if certain criteria are met. A modern faunal analogue must be available. For example, because dinosaurs are extinct and their metabolism is unknown (and likely varies between species), it is inappropriate to use this method. Similarly, comparable climates must be used in both the modern and ancient ecosystems being considered. Additionally, the early evolutionary history of the group must be considered. For example, if birds did not diversify until the Upper Cretaceous, then pre-Cretaceous avifaunas are not an appropriate comparison for modern avifaunas. If the aforementioned conditions are met the species-area curve can be a powerful tool to evaluate paleoecological diversity in order to facilitate 1) a reassessment of past studies in which diversity affects conclusions; 2) future studies to be placed in the context of estimated biodiversity figures; 3) fossil record completeness to be calculated;

and 4) fossil collecting efforts to be tailored appropriately when known diversity approaches projected figures.

APPENDIX A

AREA AND REPTILE AND AMPHIBIAN DIVERSITY FOR SELECTED MODERN TROPICAL ISLANDS

Source literature on species richness and itemized taxonomic information can be found in APPENDIX C. Unpublished land areas were calculated using ImageJ software (Rasband, 2004).

ISLAND or ARCHIPELAGO	REGION	AREA (km ²)	SPECIES RICHNESS
New Guinea	Oceania	800,000	456
Borneo	SE Asia	751,929	293
New Zealand	Oceania	268,670	70
Luzon	SE Asia	109,965	126
Cuba	Caribbean	105,007	179
Mindanao	SE Asia	97,530	118
Hispaniola	Caribbean	76,470	207
Bismarck Archipelago	Oceania	49,700	59
Taiwan	SE Asia	36,000	110
Hainan Dao	SE Asia	34,000	129
Solomon Islands	Oceania	28,446	106
Fiji Islands	Oceania	18,272	32
New Caledonia	Oceania	16,648	66
Negros	SE Asia	13,535	85
Samar	SE Asia	12,849	54
Panay	SE Asia	12,011	90
Palawan	SE Asia	11,750	90
Jamaica	Caribbean	10,992	63
Mindoro	SE Asia	10,572	49
Puerto Rico	Caribbean	8,768	78
Leyte	SE Asia	7,368	52
Andamans	SE Asia	6,408	57
Trinidad	Caribbean	4,769	100
Cebu	SE Asia	4,542	58
Bohol	SE Asia	3,970	82
Masbate	SE Asia	3,269	27
Isla de Juventud	Caribbean	2,200	47
Nicobars	SE Asia	1,841	54
Catanduanes	SE Asia	1,522	23
Guadeloupe	Caribbean	1,510	16
Basilan	SE Asia	1,266	43
Hong Kong	SE Asia	1,200	92
Lifou	Oceania	1,150	10
Martinique	Caribbean	1,060	16
Jolo	SE Asia	869	31
Polillo	SE Asia	853	58
Dinagat	SE Asia	803	58

Dominica	Caribbean	750	18
Mare	Oceania	650	11
St. Lucia	Caribbean	616	17
Tawitawi	SE Asia	581	20
Biliran	SE Asia	501	21
Barbados	Caribbean	430	9
Siargao	SE Asia	416	14
Grenada	Caribbean	344	19
St. Vincent	Caribbean	344	16
Siquijor	SE Asia	334	22
Babeldaob	Oceania	333	28
Balabac	SE Asia	319	28
Tobago	Caribbean	300	51
Antigua	Caribbean	280	12
Camiguin	SE Asia	255	32
St Christophers (Kitts)	Caribbean	176	11
Barbuda	Caribbean	161	8
Ouvea	Oceania	160	9
Ile des Pins	Oceania	152	21
Nan Ao	SE Asia	120	19
Anguilla	Caribbean	102	13
Montserrat	Caribbean	102	13
Nevis	Caribbean	93	11
St. Martin	Caribbean	85	12
Tortola	Caribbean	54	18
Isle de Mona	Caribbean	52	10
Grenadines	Caribbean	45	14
Anegada	Caribbean	39	11
Caluit	SE Asia	37	29
Virgin Gorda	Caribbean	21	16
St. Eustatius	Caribbean	21	11
St. Barthelemy	Caribbean	21	9
Ngeruktabel	Oceania	20	13
Saba	Caribbean	13	7
Belilou	Oceania	12	16
Jost Van Dyke	Caribbean	8	8
Ngeaur	Oceania	8	25
Mecherchar	Oceania	8	2
Oreor	Oceania	8	30
Ulebsechel	Oceania	4	12
Peter	Caribbean	4	11
Navassa	Caribbean	4	8
Beef	Caribbean	4	6
Great Camanoe	Caribbean	3	8
Guana	Caribbean	3	8
Norman	Caribbean	3	6
Ngerekebesang	Oceania	2	18
Kuia	Oceania	2	12
Redonda	Caribbean	2	5
Cooper	Caribbean	1	4

Great Thatch	Caribbean	1	3
Ginger	Caribbean	1	5
Scrub	Caribbean	1	3

APPENDIX B

REPTILE AND AMPHIBIAN FAUNAS FROM SELECTED PALEOISLANDS WITH MILD TO TROPICAL CLIMATES

Duplicate islands represent sites of different ages. For each group the number of fossil species (**N**) and proportion of overall fauna (%) is given. Abbreviations: **fro**, frogs; **sal**, salamanders; **cae**, caecilians; **tur**, turtles; **liz**, lizards; **sna**, snakes; **amp**, amphisbaenians; **cro**, crocodylians; **S_O**, observed species diversity as determined from the fossil record; **S_E**, expected species diversity as determined by species area curve; **C.I.**, completeness index for each island. Data from Anderson *et al.* (2001); Castillo *et al.* (2001); Crombie & Pregill (1999); Davis and Fitzgerald (2004); Frank and Benson (1998); Hedges (1999b); MacPhee and Wyss (1990); MacPhee *et al.* (2000); Molnar *et al.* (2002); Olson *et al.* (1990); Powell *et al.* (1999); Pregill, (1981; 1982; 1993); Pregill and Crother (1999); Pregill and Steadman (2000); Pregill and Worthy (2003); Pregill *et al.* (1991; 1988; 1994); Ries and Garong (2001); Schweitzer and Thompson (1996); Steadman (1986; 1999); Steadman and Pregill (2004); Thomas (1999); and Williams (1952).

Paleo island	Estimated age	Area (km ²)	fro		sal		cae		tur	
			N	%	N	%	N	%	N	%
Hateg, Romania	65,000,000	75,000	5	0.33	2	0.13	0	0.00	1	0.07
Puerto Rico Bank	20,000	21,000	4	0.21	0	0.00	0	0.00	0	0.00
Puerto Rico Bank	11,500	13,000	3	0.14	0	0.00	0	0.00	1	0.05
Palawan, Philippines	11,000	11,750	3	0.27	0	0.00	0	0.00	0	0.00
Jamaica	770	10,992	3	0.19	0	0.00	0	0.00	0	0.00
Viti Levu, Fiji	15,000	10,400	1	0.20	0	0.00	0	0.00	1	0.20
Puerto Rico	17,000,000	2,273	0	0.00	0	0.00	0	0.00	1	0.25
Fuerteventura, Canary Islands	9,300	1,730	0	0.00	0	0.00	0	0.00	0	0.00
Barbados	10,000	530	0	0.00	0	0.00	0	0.00	1	0.25
Palau	500	420	1	0.17	0	0.00	0	0.00	0	0.00
Grenada	3,150,000	325	0	0.00	0	0.00	0	0.00	0	0.00
Antigua	4,300	280	0	0.00	0	0.00	0	0.00	0	0.00
Antigua	3,695	280	1	0.11	0	0.00	0	0.00	0	0.00
Antigua	3,430	280	1	0.13	0	0.00	0	0.00	0	0.00
Antigua	2,560	280	0	0.00	0	0.00	0	0.00	0	0.00
New Providence	8,000	200	2	0.12	0	0.00	0	0.00	1	0.06
St. Kitts	1,150	176	0	0.00	0	0.00	0	0.00	0	0.00
Floreana	10,000	171	0	0.00	0	0.00	0	0.00	1	0.25
San Salvador	5,000	156	1	0.13	0	0.00	0	0.00	2	0.25
Tutuila, American Samoa	1,460	142	0	0.00	0	0.00	0	0.00	0	0.00
Montserrat	2,500	102	0	0.00	0	0.00	0	0.00	0	0.00
Anguilla	730	102	0	0.00	0	0.00	0	0.00	0	0.00
Tinian, Marianas	2,175	102	0	0.00	0	0.00	0	0.00	0	0.00
St. Martin	2,500	85	0	0.00	0	0.00	0	0.00	0	0.00
Rota, Marianas	675	85	0	0.00	0	0.00	0	0.00	0	0.00
Isle de Mona, Puerto Rico	1,000,000	52	0	0.00	0	0.00	0	0.00	1	0.50
Aguiguan, Marianas	1,175	7	0	0.00	0	0.00	0	0.00	0	0.00
Ulebsechel, Palau	500	4	1	0.17	0	0.00	0	0.00	0	0.00
			0.08		0.00		0.00		0.07	

liz		sna		amp		cro		S _o	S _e	C.I.
N	%	N	%	N	%	N	%			
4	0.27	1	0.07	0	0.00	2	0.13	15	108	0.14
10	0.53	4	0.21	1	0.05	0	0.00	19	76	0.25
12	0.57	4	0.19	1	0.05	0	0.00	21	66	0.32
5	0.45	3	0.27	0	0.00	0	0.00	11	65	0.17
10	0.63	3	0.19	0	0.00	0	0.00	16	63	0.25
1	0.20	1	0.20	0	0.00	1	0.20	5	62	0.08
1	0.25	1	0.25	0	0.00	1	0.25	4	41	0.10
3	1.00	0	0.00	0	0.00	0	0.00	3	38	0.08
2	0.50	1	0.25	0	0.00	0	0.00	4	27	0.15
3	0.50	2	0.33	0	0.00	0	0.00	6	25	0.24
1	1.00	0	0.00	0	0.00	0	0.00	1	24	0.04
5	0.63	3	0.38	0	0.00	0	0.00	8	23	0.35
5	0.56	3	0.33	0	0.00	0	0.00	9	23	0.40
5	0.63	2	0.25	0	0.00	0	0.00	8	23	0.35
3	0.75	1	0.25	0	0.00	0	0.00	4	23	0.18
9	0.53	4	0.24	0	0.00	1	0.06	17	21	0.82
4	0.80	1	0.20	0	0.00	0	0.00	5	20	0.25
2	0.50	1	0.25	0	0.00	0	0.00	4	20	0.20
4	0.50	0	0.00	0	0.00	1	0.13	8	19	0.42
4	0.80	1	0.20	0	0.00	0	0.00	5	19	0.27
1	1.00	0	0.00	0	0.00	0	0.00	1	17	0.06
5	0.83	1	0.17	0	0.00	0	0.00	6	17	0.35
12	0.92	1	0.08	0	0.00	0	0.00	13	17	0.76
1	0.50	1	0.50	0	0.00	0	0.00	2	16	0.12
10	0.91	1	0.09	0	0.00	0	0.00	11	16	0.68
1	0.50	0	0.00	0	0.00	0	0.00	2	14	0.14
6	0.86	1	0.14	0	0.00	0	0.00	7	8	0.87
3	0.50	2	0.33	0	0.00	0	0.00	6	7	0.87
0.63		0.19		0.00		0.03				

APPENDIX C

FAUNAL STRUCTURE OF REPTILES AND AMPHIBIANS ON SELECTED MODERN TROPICAL ISLANDS

Number of species (**N**) and relative abundances (%) of different groups of reptiles and amphibians on selected modern islands. Abbreviations: **fro**, frogs; **sal**, salamanders; **cae**, caecilians; **tur**, turtles; **liz**, lizards; **sna**, snakes; **amp**, amphisbaenians; **cro**, crocodylians; **n/a**, published diversity figures are only available for the fauna as a whole and not broken down into taxonomic groups. Data from Alviola *et al.* (1999), Bauer (1999), Brown and Alcala (1986), Censky and Kaiser (1999), Crombie (1999), Crombie and Pregill (1999), Das (1999), Estrada and Ruibal (1999), Ferner *et al.* (2001), Frank and Benson (1998), Gaulke (1999), Gaulke *et al.* (2003), Heatwole (1975), Hedges (1999a; 1999b), King and Burke (1997), Lazell (1983; 1999), Murphy (1997), Powell *et al.* (1999), Ross and Magnussen (1989), Sadlier and Bauer (1997), Tyler (1999), Uetz *et al.* (2005), and Worthy and Holdaway (2002).

Island	fro		sal		cae		tur		liz		sna		amp		cro		total
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	
New Guinea	203	0.45	0	-	0	-	11	0.02	181	0.40	59	0.13	0	-	2	0.00	456
Hispaniola	63	0.30	0	-	0	-	2	0.01	108	0.52	28	0.14	5	0.02	1	0.00	207
Cuba	57	0.32	0	-	0	-	1	0.01	90	0.50	26	0.15	3	0.02	2	0.01	179
Hainan Dao	32	0.25	1	0.01	0	-	15	0.12	25	0.19	56	0.43	0	-	0	-	129
Luzon	39	0.31	0	-	0	-	1	0.01	42	0.33	42	0.33	0	-	2	0.02	126
Mindanao	37	0.31	0	-	2	0.02	1	0.01	47	0.40	29	0.25	0	-	2	0.02	118
Taiwan	29	0.26	3	0.03	0	-	6	0.05	29	0.26	43	0.39	0	-	0	-	110
Solomon Islands	26	0.25	0	-	0	-	0	-	62	0.58	17	0.16	0	-	1	0.01	106
Trinidad	32	0.32	0	-	0	-	5	0.05	20	0.20	40	0.40	2	0.02	1	0.01	100
Hong Kong	19	0.21	1	0.01	0	-	9	0.10	21	0.23	42	0.46	0	-	0	-	92
Panay	22	0.24	0	-	1	0.01	1	0.01	34	0.38	31	0.34	0	-	1	0.01	90
Palawan	30	0.33	0	-	0	-	2	0.02	22	0.24	35	0.39	0	-	1	0.01	90
Negros	n/a	n/a	0	-	0	-	n/a	n/a	n/a	n/a	n/a	n/a	0	-	2	0.02	85
Bohol	n/a	n/a	0	-	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	0	-	1	0.01	82
Puerto Rico	19	0.24	0	-	0	-	2	0.03	39	0.50	13	0.17	5	0.06	0	-	78
New Caledonia	0	-	0	-	0	-	0	-	65	0.98	1	0.02	0	-	0	-	66
Jamaica	31	0.49	0	-	0	-	1	0.02	21	0.33	9	0.14	0	-	1	0.02	63
Bismarck Arch.	15	0.25	0	-	0	-	0	-	33	0.56	10	0.17	0	-	1	0.02	59
Cebu	n/a	n/a	0	-	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	0	-	n/a	n/a	58
Dinagat	11	0.19	0	-	0	-	1	0.02	26	0.45	19	0.33	0	-	1	0.02	58
Samar	18	0.33	0	-	0	-	1	0.02	15	0.28	18	0.33	0	-	2	0.04	54

Leyte	21	0.40	0	-	0	-	2	0.04	16	0.31	12	0.23	0	-	1	0.02	52
Tobago	14	0.27	0	-	0	-	0	-	15	0.29	21	0.41	0	-	1	0.02	51
Mindoro	19	0.39	0	-	0	-	1	0.02	13	0.27	14	0.29	0	-	2	0.04	49
Isla de Juventud	12	0.26	0	-	0	-	2	0.04	21	0.45	8	0.17	2	0.04	2	0.04	47
Basilan	21	0.49	0	-	1	0.02	1	0.02	6	0.14	13	0.30	0	-	1	0.02	43
Camiguin	18	0.56	0	-	0	-	1	0.03	9	0.28	3	0.09	0	-	1	0.03	32
Jolo	17	0.55	0	-	0	-	1	0.03	5	0.16	6	0.19	0	-	2	0.06	31
Oreor	1	0.03	0	-	0	-	1	0.03	21	0.70	6	0.20	0	-	1	0.03	30
Caluit	5	0.17	0	-	0	-	1	0.03	11	0.38	11	0.38	0	-	1	0.03	29
Babeldaob	1	0.04	0	-	0	-	0	-	20	0.71	6	0.21	0	-	1	0.04	28
Balabac	17	0.61	0	-	0	-	1	0.04	0	-	9	0.32	0	-	1	0.04	28
Ngeaur	1	0.04	0	-	0	-	0	-	18	0.72	5	0.20	0	-	1	0.04	25
Catanduanes	18	0.78	0	-	0	-	1	0.04	2	0.09	1	0.04	0	-	1	0.04	23
Siquijor	17	0.77	0	-	0	-	1	0.05	3	0.14	0	-	0	-	1	0.05	22
Ile des Pins	0	-	0	-	0	-	0	-	20	0.95	0	-	0	-	1	0.05	21
Biliran	19	0.90	0	-	0	-	1	0.05	0	-	0	-	0	-	1	0.05	21
Tawitawi	16	0.80	0	-	0	-	1	0.05	2	0.10	0	-	0	-	1	0.05	20
Grenada	3	0.16	0	-	0	-	1	0.05	9	0.47	6	0.32	0	-	0	-	19
Nan Ao	7	0.37	1	0.05	0	-	1	0.05	4	0.21	6	0.32	0	-	0	-	19
Dominica	3	0.17	0	-	0	-	1	0.06	9	0.50	5	0.28	0	-	0	-	18
Tortola	4	0.22	0	-	0	-	1	0.06	8	0.44	4	0.22	1	0.06	0	-	18
Ngerekebesang	1	0.06	0	-	0	-	0	-	13	0.72	3	0.17	0	-	1	0.06	18
St. Lucia	1	0.06	0	-	0	-	1	0.06	10	0.59	5	0.29	0	-	0	-	17
Guadeloupe	3	0.19	0	-	0	-	0	-	9	0.56	4	0.25	0	-	0	-	16
Martinique	3	0.19	0	-	0	-	0	-	10	0.63	3	0.19	0	-	0	-	16
St. Vincent	3	0.19	0	-	0	-	1	0.06	9	0.56	3	0.19	0	-	0	-	16
Virgin Gorda	3	0.19	0	-	0	-	0	-	9	0.56	3	0.19	1	0.06	0	-	16
Belilou	1	0.06	0	-	0	-	0	-	11	0.69	3	0.19	0	-	1	0.06	16
Grenadines	1	0.07	0	-	0	-	1	0.07	10	0.71	2	0.14	0	-	0	-	14
Siargao	2	0.14	0	-	0	-	0	-	7	0.50	4	0.29	0	-	1	0.07	14
Montserrat	2	0.15	0	-	0	-	1	0.08	8	0.62	0	-	2	0.15	0	-	13
Anguilla	0	-	0	-	0	-	1	0.08	11	0.85	1	0.08	0	-	0	-	13
Ngeruktabel	1	0.08	0	-	0	-	0	-	9	0.69	2	0.15	0	-	1	0.08	13
Antigua	2	0.17	0	-	0	-	1	0.08	7	0.58	2	0.17	0	-	0	-	12
St. Martin	1	0.08	0	-	0	-	1	0.08	9	0.75	1	0.08	0	-	0	-	12
Ulebsechel	1	0.08	0	-	0	-	0	-	9	0.75	1	0.08	0	-	1	0.08	12
St Christophers	1	0.09	0	-	0	-	1	0.09	7	0.64	2	0.18	0	-	0	-	11
Nevis	1	0.09	0	-	0	-	0	-	8	0.73	2	0.18	0	-	0	-	11

Anegada	1	0.09	0	-	0	-	0	-	8	0.73	2	0.18	0	-	0	-	11
St. Eustatius	1	0.09	0	-	0	-	1	0.09	8	0.73	1	0.09	0	-	0	-	11
Peter	0	-	0	-	0	-	1	0.09	8	0.73	2	0.18	0	-	0	-	11
Mare	0	-	0	-	0	-	0	-	11	1.00	0	-	0	-	0	-	11
Isle de Mona	1	0.10	0	-	0	-	0	-	6	0.60	3	0.30	0	-	0	-	10
Lifou	0	-	0	-	0	-	0	-	10	1.00	0	-	0	-	0	-	10
Barbados	1	0.11	0	-	0	-	0	-	6	0.67	2	0.22	0	-	0	-	9
St. Barthelemy	0	-	0	-	0	-	1	0.11	7	0.78	1	0.11	0	-	0	-	9
Ouvea	0	-	0	-	0	-	0	-	8	0.89	1	0.11	0	-	0	-	9
Barbuda	1	0.13	0	-	0	-	1	0.13	5	0.63	1	0.13	0	-	0	-	8
Jost Van Dyke	1	0.13	0	-	0	-	0	-	6	0.75	0	-	1	0.13	0	-	8
Navassa	0	-	0	-	0	-	0	-	6	0.75	2	0.25	0	-	0	-	8
Great Camanoe	0	-	0	-	0	-	0	-	6	0.75	1	0.13	1	0.13	0	-	8
Guana	0	-	0	-	0	-	0	-	7	0.88	1	0.13	0	-	0	-	8
Saba	1	0.14	0	-	0	-	0	-	5	0.71	1	0.14	0	-	0	-	7
Beef	0	-	0	-	0	-	0	-	5	0.83	1	0.17	0	-	0	-	6
Norman	0	-	0	-	0	-	0	-	6	1.00	0	-	0	-	0	-	6
Redonda	0	-	0	-	0	-	0	-	5	1.00	0	-	0	-	0	-	5
Ginger	0	-	0	-	0	-	0	-	5	1.00	0	-	0	-	0	-	5
Cooper	0	-	0	-	0	-	0	-	4	1.00	0	-	0	-	0	-	4
Great Thatch	0	-	0	-	0	-	0	-	3	1.00	0	-	0	-	0	-	3
Scrub	0	-	0	-	0	-	0	-	3	1.00	0	-	0	-	0	-	3
Mecherchar	0	-	0	-	0	-	0	-	1	0.50	0	-	0	-	1	0.50	2
AVERAGE:		0.19		0.00		0.00		0.03		0.55		0.17		0.01		0.02	

APPENDIX D

AREA AND FAUNAL STRUCTURE OF REPTILES AND AMPHIBIANS ON SELECTED MODERN PROVINCES OF MILD CLIMATE

Number of species (N) and relative abundances (%) of different groups of reptiles and amphibians on selected modern provinces in mild climatic zones. Taxon abbreviations as in Appendix C; x, published diversity figures are not broken down into finer taxonomic groups. ¹As defined by Das (1996) including Indian, Pakistan, Sri Lanka, Nepal, Bhutan and Maldives; ²Northeast physiographic region of Das (1996) including India and Bangladesh. Data from Anderson (1963; 1968; 1999); Arnold (2002); Bonin *et al.* (2006); Borkin (1999); Das (1996); Frost (2007); IUCN (2006); Macey *et al.* (2004); Ross and Magnussen (1989); Wilson and Swan (2003); and Zhao (1999).

Area	Area (km ²)	fro		sal		cae		tur		liz		sna		amp		cro		tot
		N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	
Brazil	8,547,400	725	0.52	1	0.00	26	0.02	31	0.02	x	x	x	x	x	x	6	0.00	1400
China	9,572,900	238	0.23	35	0.03	1	0.00	25	0.02	x	x	x	x	0	0.00	2	0.00	1038
Australia	7,623,622	211	0.21	0	0.00	0	0.00	25	0.02	622	0.61	156	0.15	0	0.00	2	0.00	1016
South Asia ¹	4,360,000	164	0.20	1	0.00	19	0.02	29	0.04	295	0.37	297	0.37	0	0.00	3	0.00	808
India	2,973,190	214	0.28	1	0.00	25	0.03	27	0.04	x	x	x	x	0	0.00	3	0.00	761
Queensland	1,730,650	122	0.23	0	0.00	0	0.00	15	0.03	298	0.57	86	0.16	0	0.00	2	0.00	523
Western Australia	2,529,880	77	0.15	0	0.00	0	0.00	7	0.01	323	0.65	88	0.18	0	0.00	2	0.00	497
South Africa	1,221,040	115	0.24	0	0.00	0	0.00	15	0.03	x	x	x	x	0	0.00	1	0.00	479
Bolivia	1,098,580	205	0.44	1	0.00	3	0.01	9	0.02	x	x	x	x	x	x	5	0.01	466
New South Wales	800,640	83	0.28	0	0.00	0	0.00	7	0.02	156	0.52	52	0.17	0	0.00	0	0.00	298
South Australia	983,470	28	0.12	0	0.00	0	0.00	3	0.01	172	0.72	37	0.15	0	0.00	0	0.00	240
Iran	1,648,000	11	0.05	7	0.03	0	0.00	7	0.03	125	0.58	65	0.30	1	0.00	0	0.00	216
South Asia ²	253,637	60	0.28	1	0.00	3	0.01	19	0.09	32	0.15	95	0.45	0	0.00	2	0.01	212
Paraguay	406,750	71	0.34	0	0.00	3	0.01	8	0.04	x	x	x	x	x	x	3	0.01	210
Chile	756,630	55	0.32	0	0.00	0	0.00	0	0.00	x	x	x	x	0	0.00	0	0.00	174
Turkey	774,820	14	0.09	9	0.06	0	0.00	11	0.07	x	x	x	x	x	x	0	0.00	156
Victoria	227,420	36	0.25	0	0.00	0	0.00	3	0.02	83	0.57	24	0.16	0	0.00	0	0.00	146
Bangladesh	144,000	32	0.22	0	0.00	0	0.00	23	0.16	x	x	x	x	0	0.00	3	0.02	144
Spain	504,782	18	0.14	8	0.06	0	0.00	3	0.02	x	x	x	x	0	0.00	0	0.00	125
Iraq	438,317	6	0.05	4	0.03	0	0.00	4	0.03	x	x	x	x	0	0.00	0	0.00	120
Morocco	712,550	9	0.08	2	0.02	0	0.00	2	0.02	x	x	x	x	x	x	0	0.00	114
Uruguay	177,410	42	0.38	0	0.00	1	0.01	5	0.04	x	x	x	x	x	x	1	0.01	112
Greece	131,990	12	0.12	6	0.06	0	0.00	6	0.06	x	x	x	x	0	0.00	0	0.00	102
Turkmeni- stan	488,000	4	0.04	0	0.00	0	0.00	2	0.02	x	x	x	x	0	0.00	0	0.00	101
Italy	301,277	22	0.23	18	0.19	0	0.00	3	0.03	x	x	x	x	0	0.00	0	0.00	95
Syria	184,004	5	0.05	2	0.02	0	0.00	6	0.06	x	x	x	x	x	x	0	0.00	94
Georgia	70,000	8	0.09	4	0.05	0	0.00	3	0.03	x	x	x	x	0	0.00	0	0.00	88
France	543,965	22	0.28	10	0.13	0	0.00	3	0.04	x	x	x	x	0	0.00	0	0.00	78

Tunisia	163,610	6	0.08	2	0.03	0	0.00	2	0.03	x	x	x	x	x	x	1	0.01	78
Azerbaijan	87,000	8	0.11	2	0.03	0	0.00	4	0.06	x	x	x	x	0	0.00	0	0.00	71
Lesotho	30,350	19	0.32	0	0.00	0	0.00	0	0.00	x	x	x	x	x	x	0	0.00	60
Armenia	30,000	6	0.10	1	0.02	0	0.00	3	0.05	x	x	x	x	0	0.00	0	0.00	60
Portugal	92,389	11	0.20	6	0.11	0	0.00	2	0.04	x	x	x	x	0	0.00	0	0.00	55
Croatia	56,538	13	0.24	7	0.13	0	0.00	4	0.07	x	x	x	x	0	0.00	0	0.00	54
Albania	28,748	10	0.19	5	0.10	0	0.00	4	0.08	x	x	x	x	0	0.00	0	0.00	52
Bulgaria	110,912	13	0.25	5	0.10	0	0.00	4	0.08	x	x	x	x	0	0.00	0	0.00	51
Slovenia	20,251	14	0.28	6	0.12	0	0.00	1	0.02	x	x	x	x	0	0.00	0	0.00	50
Lebanon	10,400	4	0.08	2	0.04	0	0.00	5	0.10	x	x	x	x	0	0.00	0	0.00	50
Macedonia	25,713	10	0.22	5	0.11	0	0.00	2	0.04	x	x	x	x	0	0.00	0	0.00	46
Bosnia and Herzegovina	51,129	12	0.29	7	0.17	0	0.00	4	0.10	x	x	x	x	0	0.00	0	0.00	42
Romania	237,500	13	0.32	6	0.15	0	0.00	1	0.02	x	x	x	x	0	0.00	0	0.00	41
South Korea	99,260	12	0.30	4	0.10	0	0.00	1	0.03	x	x	x	x	0	0.00	0	0.00	40
Hungary	93,030	12	0.33	6	0.17	0	0.00	1	0.03	x	x	x	x	0	0.00	0	0.00	36
Austria	83,865	13	0.36	7	0.19	0	0.00	1	0.03	x	x	x	x	0	0.00	0	0.00	36
Slovakia	49,006	12	0.36	6	0.18	0	0.00	1	0.03	x	x	x	x	0	0.00	0	0.00	33
Czech Republic	78,864	13	0.42	7	0.23	0	0.00	1	0.03	x	x	x	x	0	0.00	0	0.00	31
Netherlands	41,500	12	0.39	5	0.16	0	0.00	1	0.03	x	x	x	x	0	0.00	0	0.00	31
Belgium	30,518	11	0.39	5	0.18	0	0.00	1	0.04	x	x	x	x	0	0.00	0	0.00	28
Denmark	48,092	11	0.48	3	0.13	0	0.00	0	0.00	x	x	x	x	0	0.00	0	0.00	23
Luxembourg	2,586	8	0.35	5	0.22	0	0.00	1	0.04	x	x	x	x	0	0.00	0	0.00	23
Cap. Terr., Australia	2,432	2	0.11	0	0.00	0	0.00	2	0.11	7	0.37	8	0.42	0	0.00	0	0.00	19

APPENDIX E

VERTEBRATE DIVERSITY IN THE HELL CREEK FORMATION

All distinct fossil taxa from the Hell Creek Formation as of 2007 are listed below. First published references to Hell Creek taxa may have been preceded by published accounts from other strata. Species lists for turtles, dinosaurs and mammals were based on primarily on Holroyd and Hutchison (2002), Russell and Manabe (2002), and Archibald (1996), respectively. Abbreviations in the final column: **x**, taxon recovered; **cf.**, tentative identification; **?**, possible presence.

TAXON	GROUP (D=dinosaur; M=mammal)	FIRST PUBLISHED REFERENCE FROM HELL CREEK FORMATION	FIRST DIS- COVERED BY SCREEN WASHING	RECOVERED DURING THIS STUDY
<i>Lissodus selachos</i>	hybodont shark	Bryant, 1989	x	x
<i>Squatirhina americana</i>	orectolobid shark	Bryant, 1989	x	cf.
<i>Brachaelurus estesi</i>	orectolobid shark	Bryant, 1989	x	
<i>Myledaphus bipartitus</i>	ray	Estes, Berberian and Meszoely, 1969	x	x
" <i>Dasyatis</i> " sp.	ray	Bryant, 1989	x	cf.
<i>Ischyodus rayhaasi</i>	chimaera	Hoganson and Erickson, 2005		
<i>Ischyrhiza avonicola</i>	sawfish	Estes, Berberian and Meszoely, 1969	x	
" <i>Acipenser</i> " <i>eruciferus</i>	sturgeon	Estes, Berberian and Meszoely, 1969, p. 6	x	
" <i>Acipenser</i> " <i>albertensis</i>	sturgeon	Bryant, 1989	x	
<i>Protoscaphirhynchus squamosus</i>	sturgeon	Wilmovsky, 1956		
<i>Paleopsephurus wilsoni</i>	paddlefish	McAlpin, 1947		
<i>Belonostomus longirostris</i>	aspidorhynchid fish	Estes, Berberian and Meszoely, 1969	x	x
<i>Kindleia fragosa</i>	bowfin	Estes, Berberian and Meszoely, 1969	x	x
<i>Melvius thomasi</i>	bowfin	Bryant, 1987		x
<i>Lepisosteus occidentalis</i>	gar fish	Estes, Berberian and Meszoely, 1969	x	x
<i>Coriops amnicolus</i>	albulid fish	Estes, 1969 two new fishes..	x	cf.
<i>Paralbula casei</i>	phyllodontid fish	Estes, 1969, p. 323	x	
<i>Phyllodus paulkatoi</i>	phyllodontid fish	Bryant, 1989	x	
<i>Palaeolabrus montanensis</i>	paleolabrid fish	Estes, 1969, p. 14	x	
<i>Platacodon nanus</i>	sciaenid fish	Bryant, 1989	x	
Pachyrhizodontoidei indet.	ichthyodectiform fish	Bryant, 1989	x	

<i>Estesesox foxi</i>	pike	Wilson, Brinkman and Neuman, 1992	x	x
Hiodontidae indet.	hiodontid fish	Bennett and Main, 2003	x	x
Acanthomorpha indet.	acanthomorph fish	Bennett and Main, 2003	x	x
<i>Albanerpeton nexuosus</i>	amphibian	Estes, 1981	x	x
<i>Opisthotriton kayi</i>	salamander	Estes, 1969, "The Batrach..."	x	x
<i>Prodesmodon copei</i>	salamander	Estes, Berberian and Meszoely, 1969	x	
<i>Lisserpeton bairdi</i>	salamander	Estes, 1965	x	
<i>Piceoerpeton</i> sp.	salamander	Bryant, 1989	x	
<i>Scapherpeton tectum</i>	salamander	Estes, Berberian and Meszoely, 1969	x	x
<i>Habrosaurus dilatus</i>	salamander	Estes, Berberian and Meszoely, 1969	x	x
<i>Proamphiuma cretacea</i>	salamander	Estes, 1969, "The fossil record of..."	x	
<i>Scotiophryne pustulosa</i>	frog	Estes, 1969, "A new fossil discoglossid..."	x	x
<i>Eopelobates?</i> sp.	frog	Estes, Berberian and Meszoely, 1969	x	
<i>Palaeobatrachus occidentalis</i>	frog	Estes and Sanchez, 1982	x	
<i>Compsemys victa</i>	pleurosternid turtle	Estes, Berberian and Meszoely, 1969	x	x
<i>Hayemys latifrons</i>	baenid turtle	Gaffney, 1972		
<i>Neurankylus eximius</i>	baenid turtle	Hay, 1908		
<i>Plesiobaena antiqua</i>	baenid turtle	Gaffney, 1972		cf.
<i>Stygiochelys estesi</i>	baenid turtle	Gaffney and Hyatt, 1971		
<i>Eubaena cephalica</i>	baenid turtle	Hay, 1908		
<i>Palatobaena bairdi</i>	baenid turtle	Gaffney, 1972		
<i>Thescelus insiliens</i>	baenid turtle	Archibald, 1977 (see Bryant, 1989)	x	
<i>Emarginochelys cretacea</i>	kinosternoid turtle	Whetstone, 1978		
Kinosternia (<i>Hoplochelys</i> - <i>Agomphus</i> morph)	kinosternoid turtle	Holroyd and Hutchison, 2002		
Kinosternia (Kinosternid morph)	kinosternoid turtle	Holroyd and Hutchison, 2002		
<i>Adocus</i> sp.	adocid turtle	Brown, 1907		cf.
<i>Basilemys sinuosa</i>	nansuingchelyd turtle	Riggs, 1906		x
<i>Apalone</i> sp.	trionychid turtle	Gardner, Russell and Brinkman, 1995		
<i>Aspideretes</i> (= <i>Aspideretoides</i>) sp.	trionychid turtle	Hutchison and Archibald, 1986		x
<i>Helopanoplia distincta</i>	trionychid turtle	Bryant, 1989	x	
Plastominine A	trionychid turtle	Holroyd and Hutchison, 2002		?

Plastominine C	trionychid turtle	Holroyd and Hutchison, 2002		?
<i>"Clemmys" backmani</i>	macrobaenid turtle	Holroyd and Hutchison, 2002		
<i>Protochelydra</i> sp.	chelydrid turtle	Holroyd and Hutchison, 2002		cf.
Solemydidae indet.	solemydid turtle	Bennett, 2006, unpublished		x
<i>Chamops segnis</i>	teiid lizard	Estes, 1964	x	x
<i>Leptochamops denticulatus</i>	teiid lizard	Estes, Berberian and Meszoely, 1969	x	
<i>Haptosphenus placodon</i>	teiid lizard	Estes, Berberian and Meszoely, 1969	x	
<i>Peneteius aquilonius</i>	teiid lizard	Estes, 1969, "Relationships of two..."	x	
<i>Contogenys sloani</i>	skink	Estes, 1969, "A scincoid lizard..."	x	
<i>Exostinus lancensis</i>	crocodile lizard	Estes, Berberian and Meszoely, 1969	x	x
<i>Odaxosaurus piger</i>	anguid lizard	Meszoely, 1970	x	x
<i>Parasaniwa wyomingensis</i>	necrosaur lizard	Estes, Berberian and Meszoely, 1969	x	cf.
<i>Paraderma bogarti</i>	helodermatid lizard	Estes, Berberian and Meszoely, 1969	x	cf.
<i>Palaeosaniwa canadensis</i>	varanid lizard	Estes, Berberian and Meszoely, 1969	x	cf.
<i>Coniophis precedens</i>	aniliid snake	Estes, Berberian and Meszoely, 1969	x	x
Boidae indet.	boid snake	Estes, Berberian and Meszoely, 1969	x	x
<i>Champsosaurus</i> sp.	champsosaur	Brown, 1905		x
<i>Borealosuchus sternbergi</i>	crocodile	Estes, Berberian and Meszoely, 1969	x	x
<i>Brachychampsia montana</i>	crocodile	Gilmore, 1911		x
<i>Thoracosuchus neocensariensis</i>	crocodile	Estes and Berberian, 1970	x	
<i>Tyrannosaurus rex</i>	theropod (D)	Osborn, 1905		x
<i>Ornithomimus</i> sp.	theropod (D)	Archibald, 1996		?
<i>Struthiomimus</i> sp.	theropod (D)	Triebold, 1997		
<i>Dromaeosaurus albertensis</i>	theropod (D)	Baszio, 1997		
<i>Saurornitholestes langstoni</i>	theropod (D)	Baszio, 1997		x
<i>Chirolestes</i> (= <i>Caenagnathus</i>) sp.	theropod (D)	Currie <i>et al.</i> , 1993		
<i>Troodon formosus</i>	theropod (D)	Estes, Berberian and Meszoely, 1969	x	x
<i>Richardoestesia gilmorei</i>	theropod (D)	Estes, Berberian and Meszoely, 1969	x	x

<i>Richardoestesia</i> undescr. spec. (=R. isosceles?)	theropod (D)	Baszio, 1997	x	?
<i>Paronychodon lacustris</i>	theropod (D)	Estes, Berberian and Meszoely, 1969	x	x
<i>Edmontonia</i> sp.	ankylosaur (D)	Archibald, 1996		?
<i>Ankylosaurus magnaventr</i>	ankylosaur (D)	Brown, 1908		?
<i>Bugenasaura infernalis</i> (=The scelosaurus garbanii)	ornithopod (D)	Galton, 1995		
<i>The scelosaurus neglectus</i>	ornithopod (D)	Gilmore, 1915		
<i>Anatotitan copei</i>	ornithopod (D)	Brett-Surman, 1990		
<i>Edmontosaurus annectens</i>	ornithopod (D)	Lull and Wright, 1942		?
cf. Homalocephalinae	pachycephalosaur (D)	Galiano, 2001, unpubl. (in Russell and Manabe, 2002)		
<i>Pachycephalosaur</i> wyomingensis	pachycephalosaur (D)	Baird, 1979		
<i>Stegoceras validus</i>	pachycephalosaur (D)	Archibald, 1996		?
<i>Stygomoloch spinifer</i>	pachycephalosaur (D)	Galton and Sues, 1983		
<i>Torosaurus latus</i>	ceratopsian (D)	Colbert and Bump, 1947		
<i>Triceratops horridus</i>	ceratopsian (D)	Osborn, 1933		?
<i>Triceratops prorsus</i>	ceratopsian (D)	Osborn, 1933		?
<i>Avisaurus archibaldi</i>	bird	Brett-Surman and Paul, 1985		
cf. <i>Quetzalcoatlus</i> sp.	pterosaur	Henderson and Peterson, 2006		
<i>Cimexomys minor</i>	multituberculate (M)	Sloan et Van Valen, 1965	x	
<i>Mesodma formosa</i>	multituberculate (M)	Sloan et Van Valen, 1965	x	?
<i>Mesodma thompsoni</i>	multituberculate (M)	Clemens, 1963	x	?
<i>Mesodma hensleighi</i>	multituberculate (M)	Archibald, 1982	x	?
<i>Neoplagiaulax burgessi</i>	multituberculate (M)	Archibald, 1982	x	
<i>Paracimexomys priscus</i>	multituberculate (M)	Archibald, 1982	x	
<i>Cimolodon nitidus</i>	multituberculate (M)	Clemens, 1963	x	x
<i>Essonodon browni</i>	multituberculate (M)	Simpson, 1927		cf.
<i>Cimolomys gracilis</i>	multituberculate (M)	Clemens, 1963	x	
<i>Meniscoessus robustus</i>	multituberculate (M)	Archibald, 1982	x	cf.
<i>Stygimys kuszmauli</i>	multituberculate (M)	Sloan et Van Valen, 1965	x	
<i>Catopsalis joyneri</i>	multituberculate (M)	Sloan et Van Valen, 1965	x	
<i>Alphadon jasoni</i>	marsupial (M)	Johanson, 1996	x	?
<i>Alphadon marshi</i> (=A. wilsoni)	marsupial (M)	Simpson, 1927		?
<i>Didelphodon vorax</i>	marsupial (M)	Clemens, 1966	x	cf.
<i>Glasbius twitchelli</i>	marsupial (M)	Archibald, 1982	x	cf.

<i>Pedimys cooki</i>	marsupial (M)	Clemens, 1966	x	?
<i>Pedimys elegans</i>	marsupial (M)	Sloan et Van Valen, 1965	x	?
<i>Pedimys florencae</i>	marsupial (M)	Clemens, 1966	x	?
<i>Pedimys hatcheri</i>	marsupial (M)	Sloan et Van Valen, 1965	x	?
<i>Pedimys krejci</i>	marsupial (M)	Archibald, 1982	x	?
<i>Protalphadon foxi</i> (= <i>Alphadon lulli</i>)	marsupial (M)	Johanson, 1996	x	
<i>Turgidodon rhaister</i> (= <i>Alphadon rhaister</i>)	marsupial (M)	Archibald, 1982	x	
<i>Batodon tenuis</i>	deltatheridian (M)	Archibald, 1982	x	
<i>Cimolestes incisus</i>	deltatheridian (M)	Sloan et Van Valen, 1965	x	
<i>Cimolestes magnus</i>	deltatheridian (M)	Clemens, 1973	x	
<i>Cimolestes propalaeoryctes</i>	deltatheridian (M)	Archibald, 1982	x	
<i>Cimolestes stirtoni</i>	deltatheridian (M)	Archibald, 1982	x	
<i>Cimolestes cf. cerberoides</i>	deltatheridian (M)	Archibald, 1982	x	
<i>Procerberus formicarum</i>	deltatheridian (M)	Sloan et Van Valen, 1965	x	
<i>Gypsonictops hypoconus</i>	insectivore (M)	Simpson, 1927		?
<i>Gypsonictops illuminatus</i>	insectivore (M)	Archibald, 1982	x	?
<i>Protungulatum donnae</i>	condylarth (M)	Sloan et Van Valen, 1965	x	
<i>Mimatuta morgoth</i>	condylarth (M)	Archibald, 1982	x	

APPENDIX F

TAXONOMIC ABUNDANCE AT HELL CREEK MICROVERTEBRATE LOCALITIES

Numbers represent complete fossil elements (bones and teeth) recovered during this study, and were primarily recovered by screen washing except as noted in text. The four most productive localities are listed individually, followed by the total elements from remaining localities, and all localities combined. Abbreviations: **FH**, Fang Hill; **FS**, Fish Sticks; **LTH**, Lone Tooth Hill; **RR**, Rancher Ridge; *indicates herp (amphibian, turtle, lizard, snake, champsosaur, or crocodile.)

TAXON	FH	FS	LTH	RR	Other localities	Total
Trionychidae*	1	13	1	1	233	249
<i>Amia</i>	45	100	5	24	31	205
<i>Lepisosteus</i>	40	20	34	45	35	174
<i>Brachychampsia</i> *	66	11	23	41	13	154
<i>Champsosaurus</i> *	29	0	22	3	41	95
<i>Compsemys</i> *	2	0	0	2	72	76
<i>Borealosuchus</i> *	8	2	24	5	35	74
<i>Melvius</i>	5	5	2	43	10	65
Ceratopsidae indet.	2	1	41	0	11	55
<i>Myledaphus</i>	17	0	14	17	6	54
Acanthomorpha	11	4	3	10	11	39
Hadrosauridae indet.	2	0	9	2	22	35
<i>Scapherpeton</i> *	17	2	6	3	6	34
cf. <i>Adocus</i> *	1	0	0	3	29	33
<i>Richardoestesia</i>	15	0	4	5	6	30
<i>Opisthotriton</i> *	19	4	2	5	0	30
<i>Sauromitholestes</i> /Dromaeosauridae	7	2	4	4	10	27
<i>Odaxosaurus</i> /Anguimorpha*	11	3	1	0	0	15
Anura indet.*	0	2	1	0	11	14
<i>Paleosaniwa</i> /Varanidae*	8	1	0	4	1	14
Elopomorpha	2	1	0	1	7	11
<i>Paronychodon</i>	4	0	1	2	4	11
<i>Habrosaurus</i> *	2	1	0	0	5	8
Hiodontidae/Salmoniformes	7	0	0	1	0	8
cf. <i>Lissodus</i>	1	0	0	7	0	8
<i>Meniscoessus</i>	7	0	1	0	0	8
<i>Mesodma</i>	3	1	1	0	3	8
Ornithomimidae indet.	3	0	1	0	4	8
Chelydridae indet.*	0	0	1	1	5	7
?Osteoglossomorpha	1	3	0	3	0	7
<i>Basilemys</i> *	0	0	0	0	6	6
cf. <i>Plesiobaena</i> *	0	0	0	0	6	6
?Tyrannosauridae	2	0	1	0	3	6
<i>Estesesox</i> /Esocidae	3	0	0	1	1	5
<i>Belonostomus</i>	0	0	0	4	0	4

<i>Cimolodon</i>	1	0	1	0	2	4
?Pachycephalosauridae	2	1	0	0	1	4
Solemydidae indet.*	1	0	0	0	3	4
<i>Coniophis</i> *	4	0	0	0	0	4
<i>Gypsonictops</i>	2	0	0	0	1	3
<i>Paraderma</i> /Helodermatidae*	2	0	0	0	1	3
<i>Troodon</i>	1	0	1	0	1	3
<i>Exostinus</i> /Xenosauridae*	2	0	0	0	1	3
<i>Albanerpeton</i> *	2	1	0	0	0	3
Albuloidea	0	0	2	1	0	3
<i>Alphadon</i>	1	0	1	0	0	2
Aves indet.	0	0	0	0	2	2
<i>Chamops</i> /Teiidae*	1	0	0	0	1	2
cf. <i>Coriops</i>	0	0	0	2	0	2
<i>Scotiophryne</i> *	1	0	0	0	1	2
?Ankylosauria	1	0	0	0	0	1
Boidae indet.*	1	0	0	0	0	1
<i>Dasyatis</i>	0	0	0	1	0	1
cf. <i>Didelphodon</i>	0	0	0	1	0	1
cf. <i>Essonodon</i>	1	0	0	0	0	1
cf. <i>Gerrhonotus</i> *	1	0	0	0	0	1
<i>Glasbius</i>	1	0	0	0	0	1
?Hypsilophodontidae	1	0	0	0	0	1
?Ichthyodectidae	1	0	0	0	0	1
? <i>Lonchidon</i>	0	1	0	0	0	1
cf. <i>Lophochelys</i> *	0	0	0	0	1	1
<i>Parasaniwa</i> /Necrosauridae*	0	0	0	0	1	1
<i>Pedionmys</i>	0	0	1	0	0	1
cf. <i>Squatirhina</i>	0	0	0	1	0	1
Total:	368	179	208	243	643	1641

REFERENCES

REFERENCES

- IUCN, Conservation International, and NatureServe. 2006. Global Amphibian Assessment. <www.globalamphibians.org> Downloaded on 4 May, 2006.
- Alviola, P.A., Gonzales, J.C.T., Dans, A.T.L., Afuang, L.E. and Dimapilis, A.B., 1999. Herpetofauna of Puerto Galera, Mindoro Island, Philippines. *Sylvatrop*, 8: 86-93.
- Anderson, A.J. et al., 2001. The terminal age of the Fijian megafauna. In: A.J. Anderson, I. Lilley and S. O'Connor (Editors), *Histories of Old Ages: Essays in Honor of Rhys Jones*. Pandanus Book, Australian National University, Canberra, pp. 251-264.
- Anderson, S.C., 1963. Amphibians and reptiles from Iran. *Proceedings of the California Academy of Sciences*, 31(16): 417-498.
- Anderson, S.C., 1968. Zoogeographic analysis of the lizard fauna of Iran. In: W.B. Fisher (Editor), *The Cambridge History of Iran Volume I: The Land of Iran*. Cambridge University Press, Cambridge, pp. 305-371.
- Anderson, S.C., 1999. Lizards of Iran. *Contributions to Herpetology*. Society for the Study of Amphibians and Reptiles, 450 pp.
- Archibald, J.D., 1982. A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana. *University of California Publications in the Geological Sciences*, 122: 1-286.
- Archibald, J.D., 1996. *Dinosaur extinction and the end of an era*. Columbia University Press New York, 237 pp.
- Arnold, E.N., 2002. *Reptiles and Amphibians of Europe*. Princeton University Press, Princeton, 288 pp.
- Arrhenius, O., 1921. Species and area. *The Journal of Ecology*, 9(1): 95-99.
- Baird, D., 1979. The dome-headed dinosaur *Tylosteus ornatus* Leidy 1872 (Reptilia: Ornithischia: Pachycephalosauridae). *Notulae Naturae* 456: 1-11.

- Barrett, K., Wait, D.A. and Anderson, W.B., 2003. Small island biogeography in the Gulf of California: lizards, the subsidized island biogeography hypothesis, and the small island effect. *Journal of Biogeography*, 30(10): 1575-1581.
- Baszio, S., 1997. Investigations on Canadian dinosaurs. Courier Forschungsinstitut Senckenberg, 196: 1-77.
- Batsch, A.J.G.C., 1788. Versuch einer Anleitung zur Kenntniss und Geschichteder Thiere und Mineralien. Vol. 1. Akademische Buchhandlung, Jena.
- Bauer, A.M., 1999. The terrestrial reptiles of New Caledonia: the origin and evolution of a highly endemic herpetofauna. In: H. Ota (Editor), *Tropical Island Herpetofauna: Origin, Current Diversity, and Conservation. Developments in Animal and Veterinary Sciences 29*. Elsevier, Amsterdam, pp. 3–25.
- Benke, A.C. and Cushing, C.E. (Editors), 2005. *Rivers of North America*. Academic Press, San Diego, 1168 pp.
- Bennett, G.E., III, 2004. Ancient islands and the species-area curve: a new method for estimating the incompleteness of the fossil record. *Journal of Vertebrate Paleontology* 24(Supplement to number 3): 38A.
- Bennett, G.E., III and Main, D.J., 2003. Fish fauna of the Hell Creek Formation, Garfield County, Montana: New data from microvertebrate localities. *Journal of Vertebrate Paleontology* 23(Supplement to number 3): 33A.
- Benton, M.J., 1998. The quality of the fossil record of the vertebrates. In: S.K. Donovan and C.R.C. Paul (Editors), *The Adequacy of the Fossil Record*. John Wiley & Sons, New York, pp. 269–303.
- Benton, M.J., Wills, M.A. and Hitchin, R., 2000. Quality of the fossil record through time. *Nature*, 403(6769): 534-537.
- Bonin, F., Devaux, B. and Dupré, A., 2006. *Turtles of the World*. The Johns Hopkins University Press, Baltimore, 416 pp.
- Borkin, L.J., 1999. Distribution of amphibians in North Africa, Europe, western Asia, and the former Soviet Union. In: W.E. Duellman (Editor), *Patterns of Distribution of Amphibians: A Global Perspective*. The Johns Hopkins University Press, Baltimore, pp. 329-420.
- Brett-Surman, M.K. and Paul, G.S., 1985. A new family of bird-like dinosaurs linking Laurasia and Gondwanaland. *Journal of Vertebrate Paleontology*, 5(2): 133-138.

- Brinkman, D.B., 2003. A review of the nonmarine turtles from the late Cretaceous of Alberta. *Canadian Journal of Earth Sciences*, 40(4): 557-571.
- Brinkman, D.B. and Neuman, A.G., 2002. Teleost centra from uppermost Judith River Group (Dinosaur Park Formation, Campanian) of Alberta, Canada. *Journal of Paleontology*, 76(1): 138-155.
- Brown, B., 1905. The osteology of *Champsosaurus* Cope. *Memoirs of the American Museum of Natural History*, 9(Part 1): 1-26.
- Brown, B., 1907. The Hell Creek beds of upper Cretaceous of Montana. *Bulletin of the American Museum of Natural History*, 23: 823-845.
- Brown, B., 1908. The Ankylosauridae, a new family of armored dinosaurs from the Upper Cretaceous. *Bulletin of the American Museum of Natural History*, 24(Article 12): 187-201.
- Brown, J.H., 1971. Mammals on mountaintops: nonequilibrium insular biogeography. *The American Naturalist*, 105(945): 467-478.
- Brown, W.C. and Alcala, A.C., 1986. Comparison of the herpetofaunal species richness of Negros and Cebu Islands, Philippines. *Silliman Journal*, 33: 74-86.
- Bryant, L.J., 1987. A new genus and species of Amiidae (Holostei: Osteichthyes) from the late Cretaceous of North America with comments on the phylogeny of the Amiidae. *Journal of Vertebrate Paleontology*, 7(4): 349-361.
- Bryant, L.J., 1989. Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary boundary in northeastern Montana. *University of California Publications in the Geological Sciences*, 134: 1-107.
- Case, E.C., 1939. A nearly complete turtle skeleton from the Upper Cretaceous of Montana. *Contributions to the Museum of Paleontology University of Michigan*, 6(1): 1-19.
- Castillo, C., Martin-Gonzalez, E. and Coello, J.J., 2001. Small vertebrate taphonomy of La Cueva del Llano, a volcanic cave on Fuerteventura (Canary Islands, Spain). Palaeoecological implications. *Palaeogeography Palaeoclimatology Palaeoecology*, 166(3): 277-291.
- Censky, E.J. and Kaiser, H., 1999. The Lesser Antillean fauna. In: B.I. Crother (Editor), *Caribbean Amphibians and Reptiles*. Academic Press, San Diego, pp. 181-222.

- Clemens, W.A., 1963. Fossil mammals of the type Lance Formation, Wyoming: Part I. Introduction and Multituberculata. University of California Publications in the Geological Sciences, 48: 1-105.
- Clemens, W.A., 1973. Fossil mammals of the type Lance Formation, Wyoming: Part III. Eutheria and Summary. University of California Publications in the Geological Sciences, 94: 1-102.
- Colbert, E.H. and Bump, J., 1947. A skull of *Torosaurus* from South Dakota and a revision of the genus. Proceedings of the National Academy of Sciences, Philadelphia, 99: 93-106.
- Conway Morris, S., 1986. The community structure of the Middle Cambrian Phyllopod Bed (Burgess Shale). *Palaeontology*, 29(3): 423-467.
- Cope, E.D., 1868. On the origin of genera. Proceedings of the Academy of Natural Sciences of Philadelphia, 1868: 242-300.
- Cope, E.D., 1887. Zittel's Manual of Paleontology. *The American Naturalist*, 21: 1014-1019.
- Crombie, R.I., 1999. Jamaica. In: B.I. Crother (Editor), *Caribbean Amphibians and Reptiles*. Academic Press, San Diego, pp. 63-92.
- Crombie, R.I. and Pregill, G.K., 1999. A checklist of the herpetofauna of the Palau Islands (Republic of Belau), Oceania. *Herpetological Monographs*, 13: 29-80.
- Crother, B.I. (Editor), 1999. *Caribbean Reptiles and Amphibians*. Academic Press, San Diego.
- Currie, P.J., Godfrey, S.J. and Nessov, L., 1993. New caenagnathid (Dinosauria: Theropoda) specimens from the Upper Cretaceous of North America and Asia. *Canadian Journal of Earth Sciences*, 30: 2255-2272.
- Darlington, P.J., Jr., 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecological Monographs*, 13(1): 37-61.
- Das, I., 1996. *Biogeography of the Reptiles of South Asia*. Kreiger Publishing Co., Malabar, Florida, 87 pp.
- Das, I., 1999. Biogeography of the amphibians and reptiles of the Andaman and Nicobar Islands, India. In: H. Ota (Editor), *Tropical Island Herpetofauna: Origin, Current Diversity, and Conservation*. Developments in Animal and Veterinary Sciences 29. Elsevier, Amsterdam, pp. 43-77.

- Davis, R.A. and Fitzgerald, D.M., 2004. *Beaches and Coasts*. Blackwell Publishing, Malden, Massachusetts, 419 pp.
- DeMar, D.G., Jr. and Breithaupt, B.H., 2006. The non-mammalian vertebrate microfossil assemblages of the Mesaverde Formation (Upper Cretaceous, Campanian) of the Wind River and Bighorn Basins, Wyoming. *New Mexico Museum of Natural History and Science Bulletin*, 35: 33-53.
- Downs, C.T. and Wirminghaus, J.O., 1997. The terrestrial vertebrates of the Bazaruto Archipelago, Mozambique: a biogeographical perspective. *Journal of Biogeography*, 24(5): 591-602.
- Dunn, E.R., 1934. Physiography and herpetology in the Lesser Antilles. *Copeia*, 1934(3): 105-111.
- Estes, R., 1965. A new fossil salamander from Montana and Wyoming. *Copeia*, 1965(1): 90-95.
- Estes, R., 1969a. The Batrachosauroididea and Scapherpetontidae, late Cretaceous and early Cenozoic salamanders. *Copeia*, 1969(2): 225-234.
- Estes, R., 1969b. The fossil record of amphiumid salamanders. *Breviora*, 322: 1-11.
- Estes, R., 1969c. A new fossil discoglossid frog from Montana and Wyoming. *Breviora*, 328: 1-7.
- Estes, R., 1969d. Relationships of two Cretaceous lizards (Sauria, Teiidae). *Breviora*, 317: 1-8.
- Estes, R., 1969e. A scincoid lizard from the Cretaceous and Paleocene of Montana. *Breviora*, 331: 1-9.
- Estes, R., 1969f. Studies on fossil phyllodont fishes: Interrelationships and evolution in the Phyllodontidae (Albuloidei). *Copeia*, 1969(2): 317-331.
- Estes, R., 1969g. Two new late Cretaceous fishes from Montana and Wyoming. *Breviora*, 335: 1-15.
- Estes, R., 1981. *Gymnophiona, Caudata*. *Handbuch der Paleoherpetologie, Teil 2, 2*. Gustav Fischer Verlag, Stuttgart, 115 pp.
- Estes, R. and Berberian, P., 1970. Paleocology of a late Cretaceous vertebrate community from Montana. *Breviora*, 343: 1-35.

- Estes, R., Berberian, P. and Mesozoely, C.A.M., 1969. Lower vertebrates from the Late Cretaceous Hell Creek Formation, McCone County Montana. *Breviora*, 337: 1-33.
- Estes, R. and Sanchíz, B., 1982. New discoglossid and palaeobatrachid frogs from the Late Cretaceous of Wyoming and Montana, and a review of other frogs from the Lance and Hell Creek formations. *Journal of Vertebrate Paleontology*, 2(1): 9-20.
- Estrada, A.R. and Ruibal, R., 1999. A review of Cuban herpetology. In: B.I. Crother (Editor), *Caribbean Amphibians and Reptiles*. Academic Press, San Diego, pp. 31-62.
- Fastovsky, D.E., 1987. Paleoenvironments of vertebrate-bearing strata during the Cretaceous-Paleogene transition, eastern Montana and western North Dakota. *PALAIOS*, 2(3): 282-295.
- Fastovsky, D.E. and McSweeney, K., 1987. Paleosols spanning the Cretaceous-Paleogene transition, eastern Montana and western North Dakota. *Geological Society of America Bulletin*, 99(1): 66-77.
- Ferner, J.W., Brown, R.M., Sison, R.V. and Kennedy, R.S., 2001. The amphibians and reptiles of Panay island, Philippines. *Asiatic Herpetological Research*, 9: 34-70.
- Filleul, A. and Dutheil, D.B., 2001. *Spinocaudichthys oumtkoutensis*, a freshwater acanthomorph from the Cenomanian of Morocco. *Journal of Vertebrate Paleontology*, 21(4): 774-780.
- Frank, E.F. and Benson, R., 1998. Vertebrate paleontology of Isle de Mona, Puerto Rico. *Journal of Cave and Karst Studies*, 60(2): 103-106.
- Frost, D.R., 2007. *Amphibian Species of the World: an Online Reference*. Version 5.1. Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.php>. American Museum of Natural History, New York, USA.
- Gaffney, E.S., 1972. The systematics of North American family Baenidae (Reptilia, Cryptodira). *Bulletin of the American Museum of Natural History*, 147(Article 5): 243-319.
- Gaffney, E.S. and Hyatt, R., 1971. A new baenid turtle from the Upper Cretaceous of Montana. *American Museum Novitates*, 2443: 1-9.
- Galton, P.M., 1995. The species of the basal hypsilophodontid dinosaur *Thescelosaurus* Gilmore (Ornithischia: Ornithopoda) from the Late Cretaceous of North America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 198: 297-311.

- Galton, P.M. and Sues, H.-D., 1983. New data on pachycephalosaurid dinosaurs. *Canadian Journal of Earth Sciences*, 20: 462-473.
- Gardner, J.D., 2002. Monophyly and intra-generic relationships of *Albanerpeton* (Lissamphibia; Albanerpetontidae). *Journal of Vertebrate Paleontology*, 22(1): 12-22.
- Gardner, J.D., Russell, A.P. and Brinkman, D.B., 1995. Systematics and taxonomy of the soft-shelled turtles (Family Trionychidae) from the Judith River Group (mid-Campanian) of North America. *Canadian Journal of Earth Sciences*, 32.
- Gaulke, M., 1999. Die Herpetofauna von Calauit Island (Calamianes-Inseln, Provinz Palawan, Philippinen) (Amphibia et Reptilia). *Faunistische Abhandlungen Staatliches Museum für Tierkunde Dresden* 21: 273-282.
- Gaulke, M., Demegillo, A., Reiter, J. and Tacud, B., 2003. Additions to the herpetofauna of Panay Island, Philippines. *Salamandra*, 39: 111-122.
- Gilmore, C.W., 1911. A new fossil alligator from the Hell Creek beds of Montana. *Proceedings of the United States National Museum*, 41(1860): 297-302.
- Gilmore, C.W., 1915. Osteology of *Thescelosaurus*, an orthopodus dinosaur from the Lance Formation of Wyoming. *Proceedings of the United States National Museum*, 49(2127): 591-616.
- Greenwood, P.H., Rosen, D.E., Weitzman, S.H. and Myers, G.S., 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History*, 131: 339-456.
- Grigorescu, D., 1983. A stratigraphic, taphonomic and paleoecologic approach to a "forgotten land": the dinosaur-bearing deposits from the Hațeg Basin (Transylvania – Romania). *Acta Paleontologica Polonica*, 28(1-2): 103-121.
- Hamilton, T.H., Barth, R.H., Jr. and Rubinoff, I., 1964. The environmental control of insular variation in bird species abundance. *Proceedings of the National Academy of Sciences, Philadelphia*, 52(1): 132–140.
- Hammer, Ø., Harper, D.A.T. and Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1): 1-9.
- Hay, O.P., 1908. *The Fossil Turtles of North America*. Carnegie Institution of Washington Publication, 75, Washington, iv + 568 pp.

- Heatwole, H., 1975. Biogeography of reptiles on some of the islands and cays of eastern Papua-New Guinea. *Atoll Research Bulletin*, 180: 1-39.
- Hedges, S.B., 1999a. *Caribherp: database of West Indian amphibians and reptiles*. Pennsylvania State University, University Park, Pennsylvania.
- Hedges, S.B., 1999b. Distribution patterns of amphibians in the West Indies. In: W.E. Duellman (Editor), *Patterns of Distribution of Amphibians: A Global Perspective*. The Johns Hopkins University Press, Baltimore, pp. 211-254.
- Henderson, M.D. and Peterson, J.E., 2006. An azhdarchid pterosaur cervical vertebra from the Hell Creek Formation (Maastrichtian) of southeastern Montana. *Journal of Vertebrate Paleontology*, 26(1): 192-195.
- Hibbard, C.W., 1949. Techniques of collecting microvertebrate fossils. *Contributions to the Museum of Paleontology University of Michigan*, 8(2): 7-19.
- Hicks, J.F., Johnson, K.R., Obradovich, J.D., Tauxe, L. and Clark, D., 2002. Magnetostratigraphy and geochronology of the Hell Creek and basal Fort Union Formations of southwestern North Dakota and a recalibration of the age of the Cretaceous-Tertiary boundary. In: J.H. Hartman, K.R. Johnson and D.J. Nichols (Editors), *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the northern Great Plains: Geological Society of America Special Paper 361*. Geological Society of America, Boulder, Colorado, pp. 35-55.
- Hoganson, J.W. and Erickson, J.M., 2005. A new species of *Ischyodus* (Chondrichthyes: Holocephali: Callorhynchidae) from Upper Maastrichtian shallow marine facies of the Fox Hills and Hell Creek Formations, Williston Basin, North Dakota, USA. *Palaeontology*, 48(4): 709-721.
- Holroyd, P.A. and Hutchison, J.H., 2002. Patterns of geographic variation in latest Cretaceous vertebrates: Evidence from the turtle component. In: J.H. Hartman, K.R. Johnson and D.J. Nichols (Editors), *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains. Geological Society of America Special Paper 361*, Boulder, pp. 177-190.
- Huxley, T.H., 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*, 1880: 649-662.
- Johanson, Z., 1996. Revision of the Late Cretaceous North American marsupial genus *Alphadon*. *Palaeontographica Abteilung A*, 242: 127-184.

- Johnson, G.D. and Wiley, E.O., 2007. Acanthomorpha. Version 09 January 2007 (under construction). <http://tolweb.org/Acanthomorpha/15088/2007.01.09> in The Tree of Life Web Project, <http://tolweb.org/> Tree of Life Web Project.
- Johnson, K.R., 2002. Megaflora of the Hell Creek and lower Fort Union Formations in the western Dakotas: Vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression. In: J.H. Hartman, K.R. Johnson and D.J. Nichols (Editors), The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the northern Great Plains: Geological Society of America Special Paper 361. Geological Society of America, Boulder, Colorado, pp. 329-392.
- Johnson, K.R., Nichols, D.J. and Hartman, J.H., 2002. Hell Creek Formation: A 2001 Synthesis. In: J.H. Hartman, K.R. Johnson and D.J. Nichols (Editors), The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the northern Great Plains: Geological Society of America Special Paper 361. Geological Society of America, Boulder, Colorado, pp. 503-510.
- King, F.W. and Burke, R.L., 1997. Crocodylian, tuatara, and turtle species of the world: An online taxonomic and geographic reference. Association of Systematics Collections, Washington, D.C. .
- Kodric-Brown, A. and Brown, J.H., 1993. Highly structured fish communities in Australian desert springs. *Ecology*, 74(6): 1847-1855.
- Lapparent de Broin, F.d. and Murelaga, X., 1996. Une nouvelle faune de chéloniens dans le Crétacé supérieur européen (A new turtle fauna in the Late Cretaceous of Europe). *Comptes Rendus de l'Académie des Sciences. Série 2*, 323(8): 729-735.
- Laurenti, J.N., 1768. Specimen medicum, exhibens synopsis reptilium emendatam cum experimentiscirca venena et antidota reptilium austracorum, quod autoritate et consensu. Joan Thomae, Vienna.
- Lazell, J.D., Jr., 1983. Biogeography of the herpetofauna of the British Virgin Islands, with description of a new anole (Sauria: Iguanidae). In: A.G.J. Rhodin, Miyata, K. (Editor), *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams*. Museum of Comparative Zoology, Harvard University Press, Cambridge, pp. 99-117.
- Lazell, J.D., Jr., 1999. The origins and evolution of the herpetofaunas of the islands on the continental shelf of South China. In: H. Ota (Editor), *Tropical Island Herpetofauna: Origin, Current Diversity, and Conservation*. *Developments in Animal and Veterinary Sciences* 29. Elsevier, Amsterdam, pp. 79-96.

- Li, G.-Q., Wilson, M.V.H. and Grande, L., 1997. Review of Eohiodon (Teleostei: Osteoglossomorpha) from Western North America, with a Phylogenetic Reassessment of Hiodontidae. *Journal of Paleontology*, 71(6): 1109-1124.
- Lull, R.S. and Wright, N.E., 1942. The hadrosaurian dinosaurs of North America. *Geological Society of America Special Paper*, 40: 1-242.
- Lund, S.P., Hartman, J.H. and Banerjee, S.K., 2002. Magnetostratigraphy of interfingering upper Cretaceous-Paleocene marine and continental strata of the Williston Basin, North Dakota and Montana. In: J.H. Hartman, K.R. Johnson and D.J. Nichols (Editors), *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the northern Great Plains: Geological Society of America Special Paper 361*. Geological Society of America, Boulder, Colorado, pp. 57-74.
- Lyman, R.L., 1994. *Vertebrate Taphonomy*. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge, 524 pp.
- MacArthur, R.H. and Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. *Evolution*, 17(4): 373-387.
- MacArthur, R.H. and Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, 203 pp.
- MacDonald, G.M., 2003. *Biogeography: Introduction to Space, Time and Life*. John Wiley and Sons, Inc., New York, 512 pp.
- Macey, R.J., Papenfuss, T.J., Kuehl, J.V., Fourcade, H.M. and Boore, J.L., 2004. Phylogenetic relationships among amphisbaenian reptiles based on complete mitochondrial genomic sequences. *Molecular Phylogenetics and Evolution*, 33(2004): 22-31.
- MacPhee, R.D.E., Singer, R. and Diamond, M., 2000. Late Cenozoic land mammals from Grenada, Lesser Antilles island-arc. *American Museum Novitates*, 3302: 1-20.
- MacPhee, R.D.E. and Wyss, A.R., 1990. Oligo-Miocene vertebrates from Puerto Rico, with a catalog of localities. *American Museum Novitates*, 2965: 1-45.
- McAllister, D.E., 1968. Evolution of branchiostegals and classification of teleostome fishes. *Bulletin of the National Museum of Canada*, 221: 1-239.
- McAlpin, A., 1947. *Paleopseuphurus wilsoni*, a new polyodontid fish from the Upper Cretaceous of Montana, with a discussion of allied fish, living and fossil. *Contributions to the Museum of Paleontology University of Michigan*, 6(8): 167-234.

- Means, D.B. and Simberloff, D.S., 1987. The peninsula effect: habitat-correlated species decline in Florida's herpetofauna. *Journal of Biogeography*, 14(6): 551-568.
- Meehl, P.E., 1983. Consistency tests in estimating the completeness of the fossil record: a neo-Popperian approach to statistical paleontology. *Minnesota Studies in the Philosophy of Science*, 10: 413-473.
- Milner, A.R., 2004. Turtles of the Purbeck Limestone Group of Dorset, southern England. *Palaeontology*, 47(6): 1441-1467.
- Molnar, R.E., Worthy, T. and Willis, T.M.A., 2002. An extinct Pleistocene endemic mekosuchine crocodylian from Fiji. *Journal of Vertebrate Paleontology* 22(3): 612-628.
- Müller, J., 1846. Über den bau und die grenzen der ganoiden und über des natürliche system der fische. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, 1846: 117-216.
- Murphy, J.C., 1997. *Amphibians and Reptiles of Trinidad and Tobago*. Krieger Publishing Company, Malabar, 245 pp.
- Nicol, D., 1977. The number of living animal species likely to be fossilized. *Florida Scientist*, 40: 135-139.
- Nopcsa, F., 1923. On the geological importance of the primitive reptilian fauna in the uppermost Cretaceous of Hungary. *Quarterly Journal of the Geological Society of London*, 74: 100-116.
- Olson, S.L., Pregill, G.K. and Hilgartner, W.B., 1990. Studies on fossil and extant vertebrates from San Salvador (Watling's) Island, Bahamas. *Smithsonian Contributions to Zoology*, 508: 1-15.
- Osborn, H.F., 1905. *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of the American Museum of Natural History*, 21(Article 14): 259-265.
- Osborn, H.F., 1933. Mounted skeleton of *Triceratops elatus*. *American Museum Novitates*, 654: 1-14.
- Patrick, R., 1996. *Rivers of the United States, Volume III: The Eastern and Southeastern States*. John Wiley & Sons, Inc, New York, 848 pp.
- Patrick, R., 1998. *Rivers of the United States, Volume IV: The Mississippi River*. John Wiley & Sons, New York, 896 pp.

- Paul, C.R.C., 1998. Adequacy, completeness and the fossil record. In: S.K. Donovan and C.R.C. Paul (Editors), *The Adequacy of the Fossil Record*. John Wiley & Sons, New York, pp. 1-22.
- Peng, J., Russell, A.P. and Brinkman, D.B., 2001. Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman Formations of the Judith River Group (Campanian) of southeastern Alberta: an illustrated guide. *Provincial Museum of Alberta, Natural History Occasional Paper*, 25: 1-54.
- Powell, R., Ottenwalder, J.A. and Incháustegui, S.J., 1999. The Hispaniolan herpetofauna: diversity, endemism, and historical perspectives, with comments on Navassa Island. In: B.I. Crother (Editor), *Caribbean Amphibians and Reptiles*. Academic Press, San Diego, pp. 93-168.
- Pregill, G.K., 1981. Late Pleistocene herpetofaunas from Puerto Rico. *University of Kansas Museum of Natural History Miscellaneous Publications*, 71: 1-72.
- Pregill, G.K., 1982. Fossil reptiles and amphibians from New Providence Island, Bahamas. *Smithsonian Contributions to Paleobiology*, 48: 8-21.
- Pregill, G.K., 1993. Fossil lizards from the Late Quaternary of 'Eua, Tonga. *Pacific Science*, 47(2): 101-114.
- Pregill, G.K. et al., 1991. Living and Late Holocene fossil vertebrates, and the vegetation of the Cockpit Country, Jamaica. *Atoll Research Bulletin*, 353: 1-19.
- Pregill, G.K. and Crother, B.I., 1999. Ecological and historical biogeography. In: B.I. Crother (Editor), *Caribbean Amphibians and Reptiles*. Academic Press, San Diego, pp. 335-356.
- Pregill, G.K. and Olson, S.L., 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. *Annual Review of Ecology and Systematics*, 12(1981): 75-98.
- Pregill, G.K. and Steadman, D.W., 2000. Fossil vertebrates from Palau, Micronesia: a resource assessment. *Micronesia*, 33(1/2): 137-152.
- Pregill, G.K., Steadman, D.W., Olson, S.L. and Grady, F.V., 1988. Late Holocene fossil vertebrates from Burma, Antigua, Lesser Antilles. *Smithsonian Contributions to Zoology*, 463: 1-27.
- Pregill, G.K., Steadman, D.W. and Watters, D.R., 1994. Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. *Bulletin of the Carnegie Museum Natural History*, 30: 1-51.

- Pregill, G.K. and Worthy, T.H., 2003. A new iguanid lizard (Squamata, Iguanidae) from the Late Quaternary of Fiji, southwest Pacific. *Herpetologica*, 59(1): 57-67.
- Preston, F.W., 1960. Time and space and the variation in species. *Ecology*, 41(4): 611-627.
- Preston, F.W., 1962. The canonical distribution of commonness and rarity, part I. *Ecology*, 43(2): 185-215.
- Rasband, W., 2004. ImageJ. National Institutes of Health, USA.
- Ries, K.R. and Garong, A.M., 2001. Late Quaternary terrestrial vertebrates from Palawan Island, Philippines. *Palaeogeography Palaeoclimatology Palaeoecology*, 171: 409-421.
- Riggs, E.S., 1906. The carapace and plastron of *Basilemys sinuosus*: A new fossil tortoise from the Laramie Beds of Montana. *Field Columbian Museum of Natural History*, 2(7): 249-256.
- Rockwood, L.L., 2006. *An Introduction to Population Ecology*. Blackwell, Malden.
- Rosen, D.E., 1973. Interrelationships of higher teleostean fishes. In: P.H. Greenwood, R.S. Miles and C. Patterson (Editors), *Interrelationships of fishes* Academic Press, London pp. 397-513.
- Rosen, D.E., 1985. An essay on euteleostean classification. *American Museum Novitates*, 2827: 1-57.
- Rosenzweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, 436 pp.
- Rosenzweig, M.L., 1998. Preston's ergodic conjecture: the accumulation of species in space and time. In: M.L. McKinney and J.A. Drake (Editors), *Biodiversity Dynamics*. Columbia University Press, New York, pp. 311-348.
- Rosenzweig, M.L. and Taylor, J.A., 1980. Speciation and diversity in Ordovician invertebrates: filling niches quickly and carefully. *Oikos*, 35(2): 236-243.
- Ross, C.A. and Magnusson, W.E., 1989. Living crocodylians. In: C.A. Ross (Editor), *Crocodyles and Alligators*. Facts on File, Inc., New York.
- Russell, D.A. and Manabe, M., 2002. Synopsis of the Hell Creek (uppermost Cretaceous) dinosaur assemblage. In: J.H. Hartman, K.R. Johnson and D.J. Nichols (Editors), *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains*. Geological Society of America Special Paper 361, Boulder, pp. 169-176.

- Sadler, R.A. and Bauer, A.M., 1997. The terrestrial herpetofauna of the Loyalty Islands. *Pacific Science* 51(1): 76-90.
- Schweitzer, P.N. and Thompson, R.S., 1996. Global gridded Pliocene and Late Quaternary sea level, U. S. Geological Survey Open File Report 96-000.
- Simberloff, D.S. and Wilson, E.O., 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, 50(2): 278-296.
- Simberloff, D.S. and Wilson, E.O., 1970. Experimental zoogeography of islands: a two year record of recolonization. *Ecology*, 51(5): 934-937.
- Simpson, G.G., 1927. Mammalian fauna of the Hell Creek Formation of Montana. *American Museum Novitates*, 267: 1-7.
- Simpson, G.G., 1964. Species density of North American recent mammals. *Systematic Zoology*, 13(2): 57-73.
- Skelton, P.W., 2003. Introduction to the Cretaceous. In: P.W. Skelton (Editor), *The Cretaceous World*. Cambridge University Press, New York, pp. 9-41.
- Sloan, R.E. and Van Valen, L., 1965. Cretaceous mammals from Montana. *Science*, 148: 220-227.
- Steadman, D.W., 1986. Holocene vertebrate fossils from Isla Floreana, Galapagos. *Smithsonian Contributions to Zoology*, 413: 1-103.
- Steadman, D.W., 1999. The prehistory of vertebrates, especially birds, on Tinian, Aguiñan, and Rota, northern Mariana Islands. *Micronesia*, 31(2): 319-345.
- Steadman, D.W. and Pregill, G.K., 2004. A prehistoric, noncultural vertebrate assemblage from Tutuila, American Samoa. *Pacific Science* 58: 615-624.
- Therrien, F., 2004. Paleoenvironmental reconstruction of Late Cretaceous (Maastrichtian) dinosaur-bearing formations of Romania. Unpublished Ph.D. dissertation Thesis, Johns Hopkins University, Baltimore.
- Thomas, R., 1999. The Puerto Rico area. In: B.I. Crother (Editor), *Caribbean Amphibians and Reptiles*. Academic Press, San Diego, pp. 169-179.
- Triebold, M., 1997. The Sandy Site: Small dinosaurs from the Hell Creek Formation of South Dakota. In: D.L. Wolberg (Editor), *Dinofest International*. Philadelphia Academy of Natural Sciences, Philadelphia, pp. 245-248.

- Tyler, M.J., 1999. Distribution patterns of amphibians in the Australo-Papuan region. In: W.E. Duellman (Editor), *Patterns of Distribution of Amphibians: A Global Perspective*. The Johns Hopkins University Press, Baltimore, pp. 541-563.
- Uetz, P., Chenna, R., Etzold, T. and Hallermann, J., 2005. *The EMBL Reptile Database*. Research Center Karlsruhe.
- Valenciennes, M.A., 1846. *Histoire naturelle des poissons*. P. Bertrand, Paris, 534 pp.
- Voris, H.K., 2000. Maps of Pleistocene sea levels in southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, 27(5): 1153-1167.
- Watson, H.C., 1835. *Remarks on the geographical distribution of British plants*, London.
- Weishampel, D.B., Grigorescu, D. and Norman, D.B., 1991. The dinosaurs of Transylvania. *National Geographic Research* 7: 196-215.
- Whetstone, K.N., 1978. A new genus of cryptodiran turtles (Testudinoidea, Chelydridae) from the Upper Cretaceous Hell Creek Formation of Montana. *University of Kansas Science Bulletin*, 51(17): 539-563.
- White, P.D., Fastovsky, D.E. and Sheehan, P.M., 1998. Taphonomy and suggested structure of the dinosaurian assemblage of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota. *PALAIOS*, 13(1): 41-51.
- Williams, E.E., 1952. A new fossil tortoise from Mona Island, West Indies, and a tentative arrangement of the tortoises of the world. *Bulletin of the American Museum of Natural History*, 99: 547-561.
- Willingshofer, E., 2000. *Extension in collisional orogenic belts: the Late Cretaceous evolution of the Alps and Carpathians*. Unpublished Ph.D. dissertation Thesis, Research School of Sedimentary Geology, Amsterdam, Netherlands.
- Wilmovsky, N.J., 1956. *Protoscaphirhynchus squamosus*, a new sturgeon from the Upper Cretaceous of Montana. *Journal of Paleontology*, 30(5): 1205-1208.
- Wilson, M.V.H., 1980. Oldest known *Esox* (Pisces: Esocidae), part of a new Paleocene teleost fauna from western Canada. *Canadian Journal of Earth Sciences*, 17(3): 307-312.
- Wilson, M.V.H., Brinkman, D.B. and Neuman, A.G., 1992. Cretaceous Esocoidei (Teleostei): early radiation of the pikes in North American fresh waters. *Journal of Paleontology*, 66(5): 839-846.

- Wilson, M.V.H. and Williams, R.R.G., 1993. Phylogenetic, biogeographic, and ecological significance of early fossil records of North American freshwater teleostean fishes. In: R.L. Mayden (Editor), *Systematics, Historical Ecology, and North American Freshwater Fishes* Stanford University Press, Stanford, pp. 224-244.
- Wilson, S. and Swan, G., 2003. *Reptiles of Australia*. Princeton University Press, Princeton, 480 pp.
- Worthy, T.H. and Holdaway, R.N., 2002. *The Lost World of the Moa: Prehistoric Life of New Zealand*. Indiana University Press, Bloomington, 718 pp.
- Zhao, E.-M., 1999. Distribution patterns of amphibians in temperate eastern Asia. In: W.E. Duellman (Editor), *Patterns of Distribution of Amphibians: A Global Perspective*. The Johns Hopkins University Press, Baltimore, pp. 421-444.

CURRICULUM VITAE

George “Geb” Bennett was born in Oklahoma City on September 15, 1970. After graduating from Tabb High School in Grafton, Virginia, he attended Mary Washington College, receiving a B.S. in Geology in 1992. Geb began working in vertebrate paleontology by assisting in field work in Virginia (College of William and Mary, 1985-1988) and Montana (University of Notre Dame, 1990; Museum of the Rockies, 1993-1994), and as a lab technician at the Smithsonian’s Museum of Natural History (1991) working on Texas Permian microvertebrates. Geb spent a year at a molding and casting studio in Bozeman, Montana, creating skeletal displays for museums before accepting a position working for Dr. John “Jack” Horner at the Museum of the Rockies, also in Bozeman, working in a lab open to the public. While there, Geb developed his fossil preparation skills on material from the Egg Mountain site in Montana. In 1996, Geb transferred to the Dallas Museum of Natural History (now the Dallas Museum of Nature and Science) in order to prepare and mount an articulated skeleton of a new species of dinosaur for display, working under Dr. Anthony Fiorillo. This project yielded Geb’s first publication, a description of the skeletal mounting process in the journal *Curator*. While in Texas he also supervised the long term excavation and preparation of the large sauropod dinosaur *Alamosaurus* from Big Bend National Park. After a short stint as Assistant Curator at the State Museum of Pennsylvania in Harrisburg under Dr. Robert Sullivan, and associated field work in the Cretaceous of New Mexico, Geb moved to Winchester, Virginia, where he has worked at the Shenandoah Valley Discovery Museum since 2001. As Collection Manager and Fossil Preparator, Geb has initiated a field program in the badlands of eastern Montana, collecting primarily microvertebrates that became integral to this study. Geb’s current research hopes to use these microfossils to reveal the population structure of extinct taxa. Geb has been teaching introductory geology labs at George Mason University since 2006. Geb is presently involved in the design of a new LEED certified platinum green building for the Shenandoah Valley Discovery Museum, particularly the new paleontology exhibits, laboratory and collection storage facility.