TAPHONOMIC AND BIOSTRATIGRAPHIC ANALYSIS OF FOSSIL FRESHWATER TURTLES IN THE UPPER CRETACEOUS (CAMPANIAN) KAIPAROWITS FORMATION OF SOUTHERN UTAH, USA

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Earth Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

November 2012

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November 2012

DEDICATION

I dedicate this dissertation to my parents, who have supported me emotionally, and frequently financially, through my undergraduate and graduate education. They both encouraged me to follow my interests in the sciences ever since I became hooked on the subject in grade school. I would like to thank them for constantly pushing me to do my best and for being patient through, what seemed like, endless years of graduate school. Thanks to my Dad for making sure my bills were paid and my car was running smoothly. I also need to acknowledge the extraordinary efforts of my Mom, who always offered helpful advice when I needed it and frequently went above and beyond to ensure that I was healthy and well fed. If she hadn’t taken me on summer trip to Montana to look for dinosaur bones back in 1994, I’m not sure I would have followed the path that I did. Now, nearly 20 years later, I’m continuing to do what I love the most, and it all began with that first taste of paleontology. Thank you, Mom and Dad, for everything!

ACKNOWLEDGEMENTS

I would like to first acknowledge my primary advisor, David Varricchio, my dissertation committee, Jack Horner, Frankie Jackson, Jim Schmitt, and my graduate representative Jioanna Carjuzaa for their helpful suggestions, edits, and expertise. I must thank Alan Titus at the Bureau of Land Management, Grand Staircase-Escalante National Monument Field Office, for first introducing me to the fossils of the Kaiparowits Formation and for supporting my project, and also Scott Richardson for assistance with fieldwork and fossil preparation. Thanks to Eric Roberts for greatly assisting with my fieldwork questions, use of published figures, and helpful advice regarding my project. I must also thank his father, Steve Roberts, for allowing me to camp on his property while conducting fieldwork. Thanks to Mike Getty and field crew at the Natural History Museum of Utah for their support during fieldwork and also for assisting with collections visits to the museum. Thanks to Pat Holroyd at the University of California Museum of Paleontology and Rod Sheetz at Brigham Young University for access to their collections. Thanks to Howard Hutchison for sharing his wisdom during multiple conversations regarding the fossil turtles of the Kaiparowits. This project would not have been possible without donations of extant turtle specimens by Bill Belzer, George Phillips, and Bob Thomson. I owe a great amount of gratitude to my roommate, and fellow student, Tom Evans for his valuable advice and assistance with my project and preparation of my dissertation. Finally, I wouldn’t have survived without the support and friendship from my fellow Earth Science graduate students through the years, so I want to share my gratitude and wish you all the best in your future endeavors. Cheers!

VITA

Michael Jo Knell was born in Cedar Rapids, IA on November 14, 1979 to Randolph and Linda Knell. His hometown is Council Bluffs, IA where he graduated from Lewis Central Senior High School in 1998. He attended the University of Nebraska in Lincoln where he graduated with a B.S. in Geology in 2002. He subsequently attended South Dakota School of Mines & Technology where he earned his M.S. in Paleontology in 2004. Michael then attended Montana State University to earn his Ph.D. in Earth Sciences. He currently is teaching as an Assistant Professor in the Department of Earth Sciences at Southern Connecticut State University in New, Haven Connecticut.

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ABSTRACT

Freshwater turtles comprise a large percentage of many fossil vertebrate assemblages in western North America. The Upper Cretaceous (Campanian) Kaiparowits Formation, a thick sedimentary unit composed primarily of fluvial and floodplain deposits, is well-exposed within Grand Staircase-Escalante National Monument in southern Utah and is known for abundant fossil turtle remains. The abundance of fossil turtles may be attributed to a variety of factors including high preservation potential. The purpose if this project is to analyze the preservation potential of freshwater turtles, particularly in fluvial depositional environments, by examining the morphology of turtles in relation to transportability and the environment of deposition. It is hypothesized, for instance, that turtles with large, robust shells that were deposited in locations offering rapid burial had a greater preservation potential than those with more fragile shells and those that were exposed for longer periods of time prior to burial. Taphonomic data, including preservation quality, taxon identification, and sedimentary context, was collected for over 700 turtle specimens in both museum collections and in the field. Depositional environment was inferred for specimens with sedimentary context data. A comparison of taphonomic data shows a preservation preference towards turtles that were buried within channel deposits, but only for those with robust shells. Remains of larger turtles are common, but typically only as fragmentary remains. Small turtle taxa are all found as fragments, primarily in overbank, pond, and other floodplain deposits. An analysis of transport and deposition trends was conducted by comparing the orientation and alignment data from *in situ* fossil specimens to the results of a flume study using the shells from a variety of extant taxa. Results show that shells with a more highly domed carapace tend to be deposited in a carapace-up orientation. There is also a trend for oblong shells to align themselves lateral-to-flow in the channel prior to burial. Examination of alignment trends supports previous paleoflow direction estimates using sedimentary structures. An analysis of the biostratigraphic distribution of the various turtle taxa within the Kaiparowits Formation reveals no apparent change in turtle fauna during deposition of the formation.

CHAPTER ONE

INTRODUCTION

The overall theme of this dissertation is the taphonomy of freshwater turtles. In particular, focus was placed on the taphonomic processes of disarticulation, transport, and burial as applied to freshwater turtles in fluvial settings. Fieldwork for this project was centered on collecting taphonomic data from fossil turtles collected from the Cretaceous (Campanian) Kaiparowits Formation of southern Utah, which contains a wealth of fossil vertebrates, with turtles representing one of the largest components. These fossil deposits, which are located within the boundaries of Grand Staircase-Escalante National monument, have only recently become a “hotspot” for vertebrate paleontology research. This project is the first to focus on the taphonomy of fossil freshwater turtles in the Kaiparowits Formation and also includes examinations of turtle paleoecology and biostratigraphy.

Chapter 2 is comprised of a literature review, which is divided into two parts. The first part is a review of the Cretaceous freshwater and terrestrial turtles of western North America followed by a list of the major turtle families and known species. The second part of Chapter 2 includes a review of the fossil turtle-producing formations in western North America along with the primary turtle taxa found within them. Some useful summary tables and maps are included for reference.

A detailed analysis of turtle taphonomy in the Kaiparowits Formation is found within Chapter 3. This chapter begins with background information to assist the reader regarding Cretaceous fossil turtles and the geologic setting. The known families of freshwater turtles present in the Kaiparowits Formation along with descriptions of the most common genera are described. An introduction to the geology and stratigraphy of the Kaiparowits Formation based on previous work is also provided along with a brief geologic history of the region. Chapter 3 primarily focuses on data collected both in the field and in museum collections in order to assess relationships between the turtle taxa, their depositional environments, and preservation quality. These relationships and associated taphonomic trends are discussed for each of the major turtle families.

Chapter 4 specifically focuses on the taphonomy of freshwater turtles within fluvial channels. As discussed in Chapter 3, several fossil turtles occur in river channel deposits in the Kaiparowits Formation, some of which are in better condition than others. The size and shape of multiple turtle shells are analyzed to determine the relationship between morphology and preservation potential. The possibility of a common orientation trend was hypothesized for turtles from channel deposits. In order to better understand how turtle shells are transported in fluvial channels and to determine what factors affect the transportability of a turtle shell, a variety of modern turtle shells were placed in a demonstration flume to observe the processes of transport and deposition. The data collected from the flume observations was compared to multiple fossil turtle sites in the Kaiparowits Formation to see if the same trends were identifiable.

An analysis of Kaiparowits turtle biostratigraphy is presented in Chapter 5. A review of Kaiparowits Formation stratigraphy is provided along with an overview of the primary fossil turtle taxa. The locations of each fossil turtle locality are placed in stratigraphic sequence to identify changes in the turtle fauna during the deposition of the formation. Each turtle family is examined and discussed in terms of its presence or absence within various formation subdivisions to identify faunal turnover as depositional environments changed during the Campanian. Additional discussions are provided regarding taphonomic and geographic biases, as well as the utility of using turtles as index fossils.

Chapter 6 focuses on a unique fossil turtle specimen found in the Kaiparowits Formation. This fossil turtle, of the genus *Adocus*, contains a partial clutch of eggs within its carapace. This find was extremely rare as only two other gravid fossil turtles are known to exist, both of which were collected in Canada. Chapter 6 provides the first description of this gravid fossil turtle specimen, including a description of the eggs and an analysis of the egg shell structure. This chapter has already been published as an article in the journal Historical Biology.

An appendix follows a general conclusion statement in Chapter 7. Appendix A consists of a data spreadsheet containing all information pertaining to the fossil turtles of the Kaiparowits Formation used throughout the dissertation. Information regarding specimen numbers, taxon identification, amount of material, and stratigraphic data are included.

CHAPTER TWO

BIOGEOGRAPHIC ANALYSIS OF THE CRETACEOUS FRESHWATER AND TERRESTRIAL TURTLES OF WESTERN NORTH AMERICA

Introduction

Turtles are considered to be one of the most successful vertebrates that ever lived, surviving worldwide since the early Jurassic (Rieppel 2008). Their fossil remains are frequently recovered from fluvial, paludal, and floodplain deposits in which they lived. Freshwater turtles have been extremely useful in biostratigraphic research (Brinkman 2003; Hirayama et al. 2000; Hutchison 2000), paleoenvironmental reconstructions (Difley and Ekdale 2002; Eberth and Brinkman 1997; Fastovsky 1987; Fiorillo 1991; Ogunyomi and Hills 1977; Parrish et al. 1987; Rogers 2000), and biogeographic studies (Brinkman 2003; Hirayama et al. 2000; Hutchison 2000) because of their preservation potential. The majority of this research has focuses on freshwater turtles that lived during the Cretaceous, a time when turtle taxa were greatly diversified and widespread geographically (Hutchison 2000). From the Aptian through the Maastrichtian, the freshwater turtle fauna of North America experienced numerous changes because of faunal interchange with other continents and minor extinction events (Hutchison 2000). This chapter serves to identify and describe the major faunal turnover events in the North American freshwater turtle fauna during the Cretaceous by reviewing all known freshwater and terrestrial Cretaceous turtle taxa and the stratigraphic units that produced their fossilized remains. This compilation of data will also serve as a reference in which all known Cretaceous freshwater turtle taxa are listed in concordance with the major fossil turtle producing localities and their approximate ages.

The Turtle

Turtles belong to the Order Testudines (aka Testudinae or Chelonia) of the Class Sauropsida (Bonin et al. 2006). There are two suborders of turtles, Cryptodira and Pleurodira, which are divided by neck morphology and how the turtle retracts its head (Pritchard 1979). Cryptodire ("hidden-neck") turtles retract their heads straight back into their shell by vertically bending their cervical vertebrae in an S-shape. Pleurodire ("side-neck") turtles retract their head by bending their necks along a horizontal plane in either a left or right direction. Turtles are recognizable by their characteristic shell that is divided into the dorsal carapace and ventral plastron (Pritchard 1979). The carapace is comprised of the expanded ribs that fuse into the solid dorsal shell (Rieppel 2008). Another characteristic of turtles is that both the shoulder and pelvic girdles are encased within the ribs of the carapace (Bonin et al. 2006). Modern cryptodires and pleurodires can both withdraw their head and limbs inside their shell for defense at least some degree. Only marine turtles cannot retract their limbs and head (Bonin at al. 2006). Modern turtles live in a variety of environments including freshwater lakes and rivers, terrestrial deserts, and in the seas (Bonin et al. 2006). Evidence of desert dwelling turtles is lacking from the Cretaceous fossil record, but the majority of other habitat dwellers are moderately to well represented (Hay 1908; Williston 1914).

Freshwater Turtles

Freshwater turtles are the most diverse group of living chelonians and include both cryptodires and pleurodires (Bonin et al. 2006). Freshwater turtles are those turtles which spend the majority of their lives feeding in or occupying terrestrial freshwater environments including lakes, ponds, rivers, etc. Some may tolerate brackish marine water conditions, but only in limited exposure. These turtles rarely venture far from a source of fresh water and can suffer dehydration if removed from fresh water for an extended period of time (Pritchard 1979). Their swimming ability is generally very good, although some species prefer walking along riverbeds or lake bottoms (Bonin et al. 2006; Pritchard 1979). Their limbs, particularly the forelimbs, are characterized by long, thin digits, which support a web-like membrane. Sizes of adult modern freshwater turtles vary greatly from as small as 10 cm to over 150 cm in length (Bonin et al. 2006). The carapace of freshwater turtles generally has a low dome profile or is nearly flat in some instances. Many of the most colorful and unusually shaped turtles live in freshwater environments today. Their diets are quite variable but most are at least partially carnivorous and feed upon small fish, amphibians, insects, and aquatic invertebrates (Bonin at al. 2006; Pritchard 1979). Some larger species are also known to feed upon small mammals and birds. Nesting often occurs along the banks of rivers or ponds. The number, size, and shape of eggs are quite variable amongst modern freshwater turtle species (Bonin at al. 2006; Miller and Dinkelacker 2008; Pritchard 1979). This variance is primarily due to environment, predation rate, and size of the turtle (Dinkelacker 2008).

Terrestrial Turtles

Turtles that spend the majority of their time walking on dry land are often referred to as “tortoises”. Modern terrestrial turtles include all the turtles of the family Testudinidae and are all cryptodires (Bonin et al. 2006; Pritchard 1979). These turtles often live in drier environments and can go without fresh water for long periods of time. Most are excellent diggers with some actually living inside underground burrows (Pritchard 1979). Terrestrial “tortoises” are characterized by large, solid, highly-domed shells. They can support their own weight using strong limbs that are directed vertically beneath the body rather than to the sides, as with most freshwater species. Some have bony ossicles on their limbs embedded into the epidermis for extra protection (Hay 1908). Body sizes vary for terrestrial turtles but they include some of the largest living turtles today, at over 300 kg (Bonin et al. 2006). Terrestrial turtles have an herbivorous diet, which may consist of a variety of grasses, shrubs, fruits, and roots (Bonin et al. 2006; Pritchard 1979).

Cretaceous Freshwater Turtles of Western North America

During the Cretaceous Period turtle diversity increased substantially in many parts of the world, including North America (Hirayama et al. 2000) (Table 2.3; Fig. 2.1). Many new families of turtles appeared during this time and some survive today. The first appearance of both the pleurodires and cryptodires occurred during the Early Jurassic. The majority of Cretaceous turtles are assigned to Cryptodira, with only the Bothremydidae belonging to Pleurodira. The warm, tropical climate of North America during much of the Cretaceous promoted the spread of turtles from Europe and Asia and an increase in body size where food was plentiful (Hutchison 2000). Freshwater turtles were common to most Cretaceous lakes, ponds, or large rivers as seen in fossil assemblages found in these depositional environments. The humid climate may have limited the diversity of terrestrial "tortoises" because a single genus is recognized during the Cretaceous of North America. The following is a complete list of North American Cretaceous freshwater and terrestrial turtle taxa in familial alphabetical order. This data is also summarized in Table 2.1. A list of turtle producing formations with known taxa is provided in Table 2.2.

Adocidae (Cope 1870)

Adocids are a well-known family of large, aquatic turtles in the Late Cretaceous of both Asia and North America (Brinkman 2003; Hutchison 2000). The family is represented by a single genus, *Adocus*, in North America, which possesses a characteristic dimpled carapace texture. The carapace shape is an elongated oval, approximately 60 cm in length, with a flared posterior margin (Holroyd and Hutchison 2002). The precise number of *Adocus* species in North America during the Late Cretaceous is currently unknown, and a revision of the taxonomy of the Adocidae is sorely needed (Meylan and Gaffney 1989).

Cretaceous Species

Adocus bossi (Hunt 1993)
Adocus kirtlandicus (Hunt 1993)
Adocus vigoratus (Hunt 1993)

Baenidae (Cope 1882)

The Baenidae are primarily a North American family and represent some of the most primitive cryptodires (Brinkman 2003; Lyson and Joyce 2010). The family appears in the mid Cretaceous, reaches maximum diversity towards the end of the Cretaceous, and disappears by the mid Tertiary (Hutchison 2000). Two evolutionary grades are discernable within the family; a primitive grade and a more advanced grade known as the Baenodda (Gaffney and Meylan 1988). The primitive grade includes the genera *Thescelus* and *Neurankylus*. The more advanced Baenodda includes *Boremys* and *Plesiobaena*. Carapace ornamentation varies substantially amongst the baenids. *Denazinemys* is characterized by possessing scattered, parallel tubercles along its carapace while the carapace of *Neurankylus* is nearly smooth. Size ranges are also quite variable within the Baenidae. Most have carapace lengths around 30 cm, but *Neurankylus* is a large turtle with carapace lengths of over 50 cm (Holroyd and Hutchison 2002). It has been suggested that *Neurankylus* should be placed in its own subfamily because it differs from most other baenids (Holroyd and Hutchison 2002; Hutchison 2009). The posterior carapace margin of many smaller baenids is scalloped. Baenids were adapted for aquatic habitats and common in the Late Cretaceous of North America (Hutchison 2000). They most likely lived in rivers and were primarily carnivorous, based on comparisons to some living turtles of similar morphology (Holroyd and Hutchison 2002).

Cretaceous Species

"Baena" hatcheri (n. Hay 1901) (Holroyd and Hutchison 2002)
"Baena" hayi (n. Gilmore 1916) (Holroyd and Hutchison 2002)
Boremys grandis (Sullivan and Lucas 2006)

Boremys pulchra (n. Lambe 1906) (Brinkman 2003; Eaton et al. 1999; Hunt 1993)
Denazinemys nodosa (n. Lucas and Sullivan 2006) (formerly *"Baena" nodosa*; n. Gilmore 1916) (Eaton et al. 1999; Hunt 1993; Hutchison 2009)
Denazinmeys ornata (formerly *"Baena" ornata*) (Lyson and Joyce 2010)
Eubaena cephalica (n. Hay 1908) (Holroyd and Hutchison 2002; Hutchison and Archibald 1986) (possible synonymy with *"Baena" hatcheri*) (Lyson and Joyce 2010)
Gamerabaena sonsalla (possible synonymy with *Thescelus insiliens*) (Lyson and Joyce 2010)
Hayemys latifrons (possible synonymy with 'Baena" hayi) (Lyson and Joyce 2010)
Neurankylus eximius (n. Lambe 1902) (Brinkman 2003; Hunt 1993; Holroyd and Hutchison 2002; Hutchison and Archibald 1986)
Palatobaena cohen (Lyson and Joyce 2010)
Plesiobaena antiqua (n. Lambe 1902) (Brinkman 2003; Holroyd and Hutchison 2002; Hutchison and Archibald 1986)
Stygiochelys estesi (n. Gaffney 1972) (Holroyd and Hutchison 2002; Hutchison and Archibald 1986)
Thescelus insiliens (n. Hay 1908) (Hunt 1993; Holroyd and Hutchison 2002; Hutchison and Archibald 1986)

Bothremydidae (Baur)
(aka Pelomedusidae) (Cope 1868)

Bothremydids are a poorly studied family of turtles that arose during the Early Cretaceous and survived until the mid Tertiary. A single genus, *Bothremys*, has been described from the Cretaceous, representing the oldest and only known pleurodire in North America during this time (Hutchison 2009). They are thought to have inhabited brackish or near-shore freshwater environments based on morphological comparisons of the carapace and limbs to some living turtles and the interpreted depositional environments where their remains have been collected (Hutchison 2000).

Cretaceous Species

Bothremys sp. (n. Leidy 1865) (Eaton et al. 1999)

Chelydridae (Gray 1870)

Chelydrids (snapping turtles) were once thought to only be a Cenozoic family, but recently their remains have been identified in the Late Cretaceous of North America and may extend back even further (Brinkman 2003). Carapace elements of chelydrid turtles have distinctive impressed sulci with a visible change in elevation and plications extending away from these sulci. Chelydrids also exhibit a groove on the underside of the first two peripherals (Brinkman 2003). Chelydrid remains are generally rare and are sometimes confused with macrobaenid elements. A full description and comparison of Cretaceous chelydrids is lacking due to a limited number of specimens.

Cretaceous Species

Protochelydra sp. (referred to in Hutchison and Archibald 1986)

Kinosternidae (Agassiz 1857)

Kinosternids (mud turtles) first appeared in the Late Cretaceous and are one of a few Cretaceous families alive today. Generally small (< 20 cm in length), kinosternids lived in small ponds or lakes (Holroyd and Hutchison 2002). They are represented only by small, fragmentary material in North America and therefore, very little is known about their overall morphology or diversity in the Cretaceous. The carapace texture is smooth with a faint grainy appearance.

Cretaceous Species

Emarginochelys cretacea (n. Whetstone 1978) (Holroyd and Hutchison 2002)
Hoplochelys sp. (n. Hay 1908) (Brinkman 2003; Hunt 1993, Hutchison 2000, Sankey 2006)

Macrobaenidae (Sukhanov 1964)

The Macrobaenidae are well known from Asia, but not well documented in North America. Evidence of this clade consists of mostly sparse, undescribed fragmentary material (Brinkman 2003). *Borealochelys* and *Aurorachelys* are only known from the Canadian High Arctic and resemble Asian macrobeanids (Brinkman and Tarduno 2005; Vandermark et al. 2009). Based on the limb and carapace morphology of Asian varieties, the macrobaenids were large aquatic turtles, possibly inhabiting large lakes or even brackish estuaries (Hutchison 2000).

Cretaceous Species

Aurorachelys gaffneyi (n. Vandermark et al. 2009)
Borealochelys axelheibergensis (n. Brinkman and Tarduno 2005)
"Clemmys" backmani (n. Russell 1935) (Holroyd and Hutchison 2002; Hutchison and Archibald 1986)
Judithemys sukhanovi (Vandermark et al. 2009)

Nanhsiungchelyidae (Ye 1966)

A predominantly Asian family, the Nanhsiungchelyidae were large, terrestrial herbivores (Brinkman 2003). A single genus is known from the Late Cretaceous of North America. Characterized by a closely-spaced, deeply-pitted or triturating texture on both the carapace and plastron, the genus *Basilemys* may include as many as four species (Brinkman 2003). *Basilemys* is one of the largest Cretaceous turtles, with carapace lengths averaging 90 cm (Holroyd and Hutchison 2002). The high-domed morphology of *Basilemys* and the bony ossicles of its forelimbs suggest it may represent one of few "tortoises" in North America during the Late Cretaceous (Hutchison 2000).

Cretaceous Species

Basilemys nobilis (Hunt 1993)
Basilemys sinuosa (n. Riggs 1906) (Holroyd and Hutchison 2002; Hutchison and Archibald 1986)
Basilemys praeclara (n. Hay 1910) (Brinkman and Nicholls 1993)
Basilemys variolosa (n. Cope 1876) (Brinkman 2003)

Pleurosternidae (Cope 1868)

Multiple genera of the Pleurosternidae are recognized from the Early Cretaceous of North America (Brinkman 2003; Eaton et al. 1999). *Glyptops*, which was formerly within its own family of Glyptopsidae, and *Dinochelys* were particularly common between the Late Jurassic and Early Cretaceous. Hutchison (1987) suggested that the primitive cryptodire *Compsemys*, a small, easily recognizable turtle from the Late Cretaceous, is also a pleurosternid. It is characterized by low, sinuous ridges that resemble human fingerprints, and the presence of distinguishable sulci. This carapace texture is commonly shared in the Pleurosternidae, which can sometimes cause confusion if identification is based upon carapace fragments alone.

Cretaceous Species

Dinochelys sp. (Eaton et al. 1999) (most recent familial placement) (Joyce 2007)
Compsemys victa (n. Leidy 1856) (Eaton et al. 1999; Holroyd and Hutchison 2002; Hutchison and Archibald 1986)
Glyptops pervicax (n. Marsh 1890) (Forster 1984)

Solemydidae

Turtles of the Solemydidae are considered primitive cryptodires. They are recognizable by a distinctive carapace texture, which consists of hundreds of small, enamel-covered tubercles that are evenly spaced (Brinkman 2003). Solemydids are known from the Early Cretaceous of Europe, but do not appear in North America until at least the Aptian-Albian (Forster 1984; Nydam et al. 1997). A single genus, *Naomichelys*, is recognized in North America.

Cretaceous Species

Naomichelys speciosa (n. Hay 1908) (Forster 1984)

Trionychidae (Bell 1828)

The Trionychidae are perhaps the most well-known freshwater turtles from the Late Cretaceous of North America (Brinkman 2003). Trionychids (soft-shelled turtles) first appeared in the mid to Late Cretaceous and continue to survive today. A group of highly aquatic carnivores, living trionychids occupy ponds, lakes, and rivers (Holroyd and Hutchison 2002). Taxonomically challenging, the family has undergone extensive changes and re-organization. They are commonly recovered as portions of the carapace and/or plastron and there may be a great deal of variation within each genus (Gardner and Russell 1994). However, a distinct sculpture pattern characterizes most genera. The trionychids are divided into two groups in the Late Cretaceous; the primitive Trionychinae and the more advanced Plastomeninae. These two groups are differentiated based on plastron morphology. The Trionychinae have a loosely connected plastron at the midline, whereas the Plastomeninae have an extensively ossified plastron with a closed or reduced mid-plastral fontanelle. Numerous Trionychinae genera are recognized in North America during the Late Cretaceous including the common genus *Aspideretes* (aka

Aspideretoides or *Trionyx*), but only a single Plastomeninae genus is known, *Plastomenus* (Hunt 1993). Over-splitting of trionychid taxa has created a need for taxonomic revision of this family. Another problem is that the generic names of *Trionx* and *Aspideretes* were used frequently in the past as "basket" taxa (Hutchison pers. comm.).

Cretaceous Species

Apalone latus (Brinkman 2003)
Aspideretes alleni (Brinkman 2003)
Aspideretes austerus (Hunt 1993)
Aspideretes fontanus (Hunt 1993)
Aspideretes foveatus (n. Leidy 1856) (Brinkman 2003)
Aspideretes ovatus (Hunt 1993)
Aspideretes splendidus (Brinkman 2003)
Aspideretes vorax (Hunt 1993)
Helopanoplia distincta (n. Hay 1908) (Holroyd and Hutchison 2002; Hutchison and Archibald 1986)
Plastomenus robustus (Hunt 1993)
Platypeltis sternbergi (Hunt 1993)

Biogeography of Cretaceous Turtles in Western North America

Primary Cretaceous fossil turtle assemblages were mapped to show the known distribution of each fossil turtle family in western North America (Figs. 2.3 - 2.12). Examination of these maps reveals that some taxa were confined to certain latitudes while others were more widespread geographically. The Adocidae, Baenidae, Pleurosternidae, and Trionychidae are the most widespread Cretaceous turtle families (Figs. 2.3, 2.4, 2.10, and 2.12). These families contain characteristically medium-sized turtles (30 – 60 cm in length), and were probably good swimmers that occupied medium to large rivers or perhaps large ponds (Holroyd and Hutchison 2002). These taxa are also some of the easiest to identify, even if only small fragments of the carapace are recovered. It is possible that a collection bias has enhanced their wide geographic distribution. The Nanhsiungchelyidae, a family of terrestrial turtles, are also widely distributed during the Late Cretaceous (Fig. 2.9). Although a terrestrial lifestyle is suggested for this family (Hutchison 2000), their remains are primarily recovered in freshwater deposits. The subtropical environment of western North America, with numerous river systems during the Cretaceous, appears to have aided in the preservation of this terrestrial turtle family in addition to the others. The chelydrids and kinosternids also have a fairly wide distribution in western North America (Hutchison 2000; Brinkman 2003) (Figs. 2.6 and 2.7). These two families of turtles, which are both still present in North America today, were small in the Cretaceous and probably preferred small pond habitats based on extant kinosternids (Bonin et al. 2006). Their small size, restrictive habitat, and lower preservation potential may be reflected in their fewer fossil localities than those previously mentioned.

While several turtle families are widespread geographically during the Cretaceous, others have a more limited range. The macrobaenids were immigrants from Asia, which is evident in their fossil distribution in Alaska and primarily northern states and provinces (Holroyd and Hutchison 2002; Vandermark et al. 2009) (Fig. 2.8). This group of turtles may have preferred more temperate climates during the Cretaceous because no remains have been identified in central or southern states. It should be noted, however, that macrobaenids are one of the more difficult taxa to identify in the field, so their currently known range may be a factor of misidentification elsewhere. The range of the solemydids extends farther south than the macrobaenids, including localities in Utah, Nevada, and Oklahoma (Forster 1984) (Fig. 2.11). This family has a distinct, recognizable carapace texture, so the data for this range in well-supported. The final group, the Bothremydidae, has one of the most restrictive ranges (Fig. 2.5). It is only known from southern Utah and northern Mexico (Brinkman and Rodriguez de la Rosa 2006). This taxa remains poorly known as current specimens are incomplete and, therefore, difficult to identify in the field. Once this family has been further analyzed and described the range may be further extended.

Cretaceous Fossil Turtle Assemblages of Western North America

Fossil turtles of the Cretaceous have been recovered in many areas of western North America including as far south as Mexico (Brinkman 2003) and as far north as the high Arctic of Canada (Vandermark et al. 2009). Their remains are typically recovered from fluvial, lacustrine, and floodplain deposits. Very few Early Cretaceous localities are known, so turtle diversity during this time remains unclear. However, numerous Late Cretaceous localities indicate a high diversity of freshwater turtles near the end of the Mesozoic. The following is a list of all major fossil turtle producing geologic units of Western North America with known turtle taxa organized by Stage. This data is summarized in Table 2.2, and a generalized map of North American Cretaceous turtle localities is provided in Fig. 2.2.

Berriasian-Barremian

There are no reported fossil freshwater turtles for the earliest Cretaceous (145-125 Ma) in North America. There were undoubtedly turtles living in North America at this time since they were present in the Jurassic and are known through the remainder of the Cretaceous. Likely, the turtles lived in environments that did not preserve their remains, or the deposits were subsequently eroded or have yet to be exposed.

Aptian-Albian

Antlers Formation: A variety of vertebrate fossils have been identified in the Antlers Formation, which is dominated by thick mudstone exposures (Nydam et al. 1997). A few turtle taxa have been collected in Oklahoma and Texas, including *Naomichelys* sp. and *Glyptops* sp. (Nydam et al. 1997).

Cloverly Formation: The Cloverly Formation is divided into three members, a lower Pryor Conglomerate, the middle Little Sheep Mudstone, and upper Himes Member (Moberly 1960). Vertebrate fossils are only known from the top two members, and only the top portion of the Himes member contains turtle remains. Turtles from the Cloverly Formation of Wyoming and Montana include *Naomichelys speciosa*, *Glyptops pervicax*, and an unknown “tortoise” (Forster 1984; Horner 1989).

Albian

Glen Rose Formation: The Glen Rose Formation of Texas contains a few fossil turtles but the number of taxa has not been confirmed (Rogers 2000). However, elements of at least three types of baenid turtles have been identified (Vineyard 1999).

Paluxy Formation: Fossil turtle remains have been recovered from the Paluxy Formation of Texas, but the exact identification and number of taxa has not been clarified (Gallup and Langston 1975).

Willow Tank Formation: The Willow Tank Formation in Nevada has only recently produced identifiable vertebrate fossil remains. Deposits of both braided and anastomosing rivers comprise the formation, which has limited exposure in southern Nevada (Bonde et al. 2008). Identified turtle material includes *Naomichelys* sp., *Adocus* sp., a baenid, and a possible trionychid (Bonde et al. 2008). This early appearance of *Adocus* is questionable since there are no other adocids identified in North America until at least the Turonian-Coniacian (Eaton et al. 1999), but additional material could help validate this taxonomic assignment.

Albian-Cenomanian

Blackleaf Formation: The Blackleaf Formation is composed of predominantly fluvial and deltaic deposits of sandstone and siltstone (Dyman and Nichols 1988). Vertebrate remains have only recently been recovered from the Blackleaf Formation in Montana. A few turtle remains have been identified including *Glyptops* sp. and perhaps either a macrobaenid or chelydrid (Ullmann et al. 2011). If a chelydrid exists in the Blackleaf Formation it would represent the oldest occurrence of the family in the world.

Cedar Mountain Formation: The Cedar Mountain Formation of Utah is divided into five members, which are from oldest to youngest the Buckhorn Conglomerate, Yellow Cat Member, Poison Strip Sandstone, Ruby Ranch Member, and Mussentuchit Member (Kirkland et al. 1999). Fluvial sandstones and siltstones dominate the lithology of the formation, with interbedded paleosols and mudstones (Cifelli et al. 1999). Turtle remains have been identified in the Yellow Cat Member and Mussentuchit Member only. *Glyptops* sp. has been collected in both members, but the Mussentuchit Member also contains *Naomichelys* sp. and a trionychid (Cifelli et al. 1999).

Dakota Formation: The Dakota Formation has been identified over a large area of the southwestern U.S. including Arizona, Colorado, New Mexico, and Utah, and the turtle fauna is somewhat inconsistent over this large geographic area due to poorly preserved specimens and uncertain stratigraphic identification for some localities. The formation is composed of a variety of fluvial, paludal, and brackish water deposits (Eaton et al. 1999). The turtle fauna of the Dakota Formation in Utah includes *Glyptops* sp., *Dinochelys* sp., *Naomichelys* sp., a second baenid, and possibly another pleurosternid (Eaton et al. 1999). A bothremydid pleurodire has also been recovered from the Dakota Formation in Utah, which represents the oldest known pleurodire in North America (Hutchison 2009).

Wayan Formation: Deposits of the Wayan Formation in Idaho include conglomerates, sandstones, mudstones, and tuffs representing a semi-arid, meandering fluvial system (Krumenacker 2005). Only a few turtle fragments have been recovered from the Wayan Formation, but they have been identified as *Naomichelys* sp. and *Glyptops* sp. (Krumenacker 2005).

Cenomanian

Chandler Formation: Very little in terms of vertebrate fossils are known from the Chandler Formation of Alaska. The Niakogon Tongue within the Chandler Formation consists of channel sandstones, abundant coal, overbank mudstones, and small lenses of lacustrine sediments (Parrish et al. 1987). A single turtle was identified, which may be related to a Cretaceous Asian family of turtles or possibly the extant Dermatemydidae (Parrish et al. 1987).

Dunvegan Formation: The Dunvegan Formation of Alberta, Canada is composed of interbedded marine to nonmarine sandstones and shales (Bhattacharya and Walker 1991). There are only turtle fragments known from the Dunvegan Formation. The only family recognized is the Trionychidae, which may represent one of the first appearances of the trionychids in North America (Brinkman 2003).

Frontier Formation: A few fragments of turtle have been collected from the Frontier Formation, which consists of deltaic, fluvial, and estuarine deposits (Dyman and

Tysdal 1998). This fossil turtle material, collected from Wyoming and Montana, has yet to be identified to the family level.

Woodbine Formation: A few fossil turtles have been recovered in the Woodbine Formation of Texas, but specific taxa remain unidentified (Winkler and Jacobs 2002).

Turonian-Coniacian

Kaskapau Formation: The Kaskapau Formation of northern British Columbia, Canada consists of a variety of near-shore and lagoonal deposits (Rylaarsdam et al. 2006). Deposits of beach and deltaic sands, coal, and silty mudstones dominate the area. Invertebrate remains are abundant, but vertebrate fossils have been identified as well. Of turtles, only *Naomichelys* sp. has been recognized (Rylaarsdam et al. 2006).

Straight Cliffs Formation: Four members comprise the Straight Cliffs Formation in Utah including from oldest to youngest, the Tibbet Canyon Member, Smoky Hollow Member, John Henry Member, and Drip Tank Member (Peterson 1969). The Tibbet Canyon Member (Turonian) is marine in origin; although this member includes numerous fish and shark remains, no turtle fossils are reported. The overlying Smoky Hollow Member (Turonian) is composed of coal with brackish lacustrine and floodplain deposits (Eaton et al. 1999). Several turtle taxa are known, including *Bothremys* sp., *Compsemys* sp., *Neurankylus* sp., a baenid, an adocid, a trionychid, and a chelydrid (Eaton et al. 1999; Hutchison 2009). The trionychid and chelydrid in the Smoky Hollow Member are considered the first definitive appearances of each family in North America, and the chelydrid may be the first appearance documented in the world (Hutchison 2009). The adocid identification is based on poor material, so the first appearance of the Adocidae may not be until the Coniacian (Hutchison 2000).

The John Henry Member (Coniacian-Santonian) also contains a diverse turtle fauna. Fluctuations in sea level during this time are evident in brackish deposits that comprise the lithology (Eaton et al. 1999). The turtle taxa of the John Henry Member includes *Bothremys* sp., *Denazinemys nodosa*, *Adocus* sp., *Basilemys* sp., *Naomichelys* sp., *Compsemys* sp., *Neurankylus* sp., a trionychid, and a chelydrid (Hutchison 2009). The uppermost member, the Drip Tank (Santonian), is composed of braided and meandering stream deposits; only fragmentary turtle remains, possibly chelydrid, have been recovered (Eaton et al. 1999; Hutchison 2009).

Santonian

Menefee Formation: The Menefee Formation of New Mexico is composed of thick fluvial and paludal deposits, but vertebrate fossil material is scattered and poorly preserved (Hunt 1993). A few turtle fragments have been identified including a trionychid and a baenid (Hunt 1993).

Milk River Formation: The Milk River Formation of Alberta, Canada is divided into three members, which are in ascending order, the Telegraph Creek Member, Virgelle Sandstone Member, and the Deadhorse Coulee Member (Brinkman 2003). Only the Deadhorse Coulee Member is nonmarine and it contains numerous vertebrate fossils. A diverse assemblage of fossil freshwater turtles has been identified including *Neurankylus* sp., *Boremys* sp., *Plesiobaena* sp., *Basilemys* sp., *Compsemys* sp., *Adocus* sp., two types of trionychids, a solemydid, and a chelydrid (Brinkman 2003).

Campanian

Aguja Formation: A variety of depositional environments are identifiable within the Aguja Formation of Texas including marine and floodplain, with deposits of sandstone, shale, and lignite (Lehman 1985). Turtle fossils have been collected from marginal marine, brackish, and floodplain deposits and include *Basilemys* sp., *Adocus* sp., *Helopanoplia* sp., *Hoplochelys* sp., additional trionychids, and a baenid (Sankey 2006).

Cerro del Pueblo Formation: Numerous fossil vertebrate remains have been collected from the Cerro del Pueblo Formation of Coahuila State, Mexico including a variety of freshwater turtles (Brinkman and Rodriguez de la Rosa 2006). Identified turtle taxa include *Compsemys* sp., *Neurankylus* sp., *Adocus* sp., *Hoplochelys* sp., at least one bothremydid, a trionychid, and a chelydrid (Brinkman and Rodriguez de la Rosa 2006).

Fort Crittenden Formation: The Fort Crittenden Formation of southern Arizona is believed to be approximately Campanian in age and consists of shale and siltstone deposits (Ratkevich 1994). Fragments of trionychid turtles including *Plastomenus* sp. and *Aspideretes* sp. have been identified (Ratkevich 1994).

Fruitland Formation: Numerous vertebrate remains have been discovered in the Campanian Fruitland Formation of New Mexico. The formation is composed of interbedded sandstones, mudstones, and coal (Lucas et al. 2006). A diverse turtle fauna includes *“Baena” nodosa*, *Boremys pulchra*, *Compsemys* sp., *Neurankylus eximius*, *Adocus bossi*, *Adocus kirtlandicus*, *Basilemys* sp., *Aspideretes* sp., another adocid, and a second trionychid (Hunt 1993).

Judith River Group: The Judith River Group of Alberta and Saskatchewan, Canada is mid Campanian in age and includes three formations, which are in depositional order, the Foremost Formation, Oldman Formation, and Dinosaur Park Formation (Brinkman 2003). The Oldman and Dinosaur Park formations comprise Dinosaur Provincial Park in Alberta and contain a variety of vertebrate remains. The Foremost Formation has been interpreted as a sequence of near shore marine and nonmarine environments (Ogunyomi and Hills 1977). The Oldman Formation is divided into three informal units and consists of braided river deposits (Hamblin 1997). Meandering river deposits dominate the overlying Dinosaur Park Formation, which has been radiometrically dated to 79.14-74.5 Ma (Eberth and Brinkman 1997). Fossil turtle remains are quite abundant in the Judith River Group with over a hundred articulated specimens and many more isolated elements (Brinkman 2003). The Judith River Group turtle fauna, which is one of the most diverse in North America, includes *Boremys pulchra*, *Plesiobaena antiqua*, *Neurankylus eximius*, *Adocus* sp., *Basilemys variolosa*, *Aspideretoides foveatus*, *Aspideretoides splendidus*, *Aspideretoides alleni*, *Apalone latus*, a solemydid, a macrobaenid (*Judithemys sukhanovi*), an unknown trionychid, and a chelydrid (Brinkman 2003; Gardner et al. 1995). The solemydid was recovered from the Foremost Formation and represents the youngest occurrence of the family in western

North America (Hirayama et al. 2000). The first described fossil gravid turtle, an *Adocus* sp., was collected from the Dinosaur Park Formation (Zelenitsky et al. 2008).

Judith River Formation: The Judith River Formation of central Montana is composed of channel and floodplain deposits of a meandering river system (Fiorillo 1991). A variety of fossil turtles have been identified from the Judith River Formation including *Boremys pulchra*, *Plesiobaena antiqua*, *Baena hatcheri*, *Neurankylus* sp., *Adocus* sp., *Basilemys* sp., *Aspideretes* sp., *Naomichelys* sp., a chelydrid, and a macrobaenid known as '*Clemmys*" (Hutchison and Archibald 1986).

Kaiparowits Formation: Meandering river, floodplain, and to a lesser extent paludal deposits, comprise the late Campanian Kaiparowits Formation of Utah (Roberts 2007). The Kaiparowits contains numerous vertebrate fossils, particularly in the lower portions of the formation (Eaton et al. 1999). The fossils, including turtle remains, are often concentrated in channel sandstones and floodplain mudstones. Radiometric dating of bentonites horizons within the formation indicates a depositional age between 74.1 and 76 Ma (Roberts et al. 2005). The fossil turtle fauna of the Kaiparowits Formation is extremely diverse and includes *Adocus kirtlandicus*, *Compsemys victa*, *Neurankylus eximius*, *Denazinemys nodosa*, *Boremys pulchra*, *Basilemys variolosa*, *Helopanoplia* sp., *Aspideretoides* sp., a second adocid, two additional trionychids, a kinosternid, and a chelydrid (Hutchison 2009). Numerous well-preserved, articulated turtle skeletons have been recovered from the Kaiparowits Formation including a specimen of *Adocus* sp. containing fossilized eggs (Knell et al. 2011).

Mesaverde Formation: The depositional environment of the Mesaverde Formation has been interpreted as a meandering river complex with point bar and floodplain deposits (Demar and Breithaupt 2006). A variety of turtles have been identified from this formation in Colorado, Utah, and Wyoming including *Neurankylus* sp., *Aspideretes foveatus*, *Basilemys* sp., a chelydrid, two additional trionychids, and a solemydid (Demar and Breithaupt 2006).

Muerto Formation: The Muerto Formation of Coahuila State, Mexico shares a similar turtle fauna with the nearby Cerro del Pueblo Formation. The Muerto Formation turtles include *Compsemys* sp., *Adocus* sp., *Hoplochelys* sp., a trionychid, and a chelydrid (Brinkman and Rodriguez de la Rosa 2006).

San Carlos Formation: Outcrops of the San Carlos Formation have been explored in both Texas and Mexico for vertebrate fossils. The formation is comprised of mostly deltaic mudstones, in which a few turtle remains have been identified including *Aspideretes* sp. (Westgate et al. 2002).

Two Medicine Formation: The Two Medicine Formation of Alberta, Canada and Montana is composed of fluvial and floodplain deposits which are “upland” of the deposits of the Judith River Formation (Rogers 1998). Turtle remains including fragments of a chelydrid, *Compsemys* sp., *Aspideretes* sp., and *Basilemys* sp. have been collected in the Two Medicine Formation (Horner 1989; Varricchio 1995). The turtle taxa of this formation are somewhat comparable to the taxa of the Judith River Formation, which was deposited further to the east at about the same time.

Wahweap Formation: The Wahweap Formation (early Campanian) in Utah consists of meandering river deposits with most of the collected fossils recovered from stream lags (Eaton et al. 1999). The age of the Wahweap may extend down into the Santonian, which would be comparable to the Milk River Formation, as recent research on mollusks and pollen recovered from the Wahweap Formation seems to indicate (Leahy and Lerbekmo 1995). Turtles identified from the Wahweap Formation include *Compsemys victa*, *Neurankylus eximius*, *Denazinemys nodosa*, *Boremys pulchra*, *Naomichelys* sp., *Adocus* sp., *Basilemys* sp., and a trionychid (Hutchison 2009).

Campanian-Maastrichtian

Horseshoe Canyon Formation: The Horseshoe Canyon Formation is exposed in Alberta and consists of estuarine and fluvial beds with intervals of coal (McCabe at al. 1986). A lower Campanian unit is divided from and upper Maastrichtian unit by a brackish marine interval. Turtle fossils are common in the lower unit and rare above the marine interval. Turtle taxa identified include *Aspideretoides* sp., *Basilemys* sp., a macrobaenid, and a chelydrid (Brinkman 2003).

Kirtland Formation: The Kirtland Formation of New Mexico has three members. The lower two members are the Farmington and De-na-zin members, which contain numerous taxa of fossil turtles including *Denazinemys nodosa*, *Denazinemys ornata*, *Boremys grandis*, *Neurankylus eximius* (or *N. baueri*), *Thescelus insiliens* (or *T. hemispherica*), *Adocus bossi*, *Adocus kirtlandicus*, *Basilemys nobilis*, *Aspideretes ovatus*, *Aspideretes vorax*, *Plastomenus robustus*, and *Platypeltis sternbergi* (Hunt 1993;

Sullivan and Lucas 2006)). The upper member of the Kirtland Formation, the Naashoibito Member, includes similar turtle taxa such as *Denazinemys nodosa*, *Thescelus insiliens*, *Neurankylus eximius*, *Aspideretes vorax*, and *Basilemys nobilis*, but also a different group of turtles which includes *Compsemys* sp., *Aspideretes fontanus*, *Aspideretes austerus*, *Adocus vigoratus*, and *Hoplocheys* sp. (Hunt 1993). This apparent high number of turtle taxa in the Kirtland Formation may represent an exaggeration of taxa-splitting.

St. Mary's River Formation: Vertebrate material is rare in the St. Mary's River Formation, which is believed to be equivalent to the Horseshoe Canyon Formation (Brinkman 2003). Evidence of fossil turtles from Alberta, Canada and Montana included *Boremys* sp. and a trionychid (Langston 1975).

Maastrichtian

Arapahoe Formation: The Arapahoe Formation (the lowest part of the D1 sequence) overlies the Laramie Formation in the Denver Basin of Colorado and consists of lacustrine and fluvial deposits with some interbedded conglomerates (Johnson et al. 2003). In regards to turtle fossils, only a few remnants of the freshwater turtle *Adocus* sp. have been positively identified in the deposits of the Arapahoe Formation (Hutchison and Holroyd 2003).

Denver Formation: The Denver Formation, which is the upper portion of the D1 sequence in the Denver Basin of Colorado, is comprised of fluvial and lacustrine deposits (Johnson et al. 2003). A variety of freshwater turtles are known from the Cretaceous

Denver Formation including *Neurankylus eximius*, *Eubaenia* sp., *Adocus* sp., *Basilemys* sp., *Helopanoplia* sp., two additional baenids, and two trionychids (Hutchison and Holroyd 2003).

Ferris Formation: Deposits of the Ferris Formation are found within the Hanna Basin in Wyoming and are characterized by channel sandstones and conglomerates representing a fluvial system (Jones and Hajek 2007). A few freshwater turtles have been collected from the Ferris Formation and include *Compsemys victa*, *Neurankylus eximius*, *Adocus* sp., and *Basilemys sinuosa* (Holroyd and Hutchison 2002).

Fox Hills Formation: Deposition of the Fox Hills Formation in North and South Dakota and Colorado is considered to be the result of a prograding beach and coastal barrier island system and consists of mostly sandstone (Daly 1991). The only freshwater turtle fossils identified from the Fox Hills Formation belong to *Aspideretoides* sp. and *Basilemys* sp. (Hutchison and Holroyd 2003).

Frenchman Formation: The Frenchman Formation of Saskatchewan is composed of fluvial sandstones with interbedded thin lenses of mudstones and siltstones (McIver 2002). A few turtle specimens have been recovered from the Frenchman Formation including *Basilemys praeclara* (Brinkman and Nicholls 1993).

Hell Creek Formation: The Hell Creek Formation is well known for its abundant, well-preserved dinosaur remains in North and South Dakota and Montana. The formation consists of predominantly interbedded fluvial siltstones and sandstones (Fastovsky 1987).

In addition to the numerous dinosaur fossils, the Hell Creek Formation also contains one of the greatest diversity of fossil freshwater turtles in the world (Hutchison 2009). The Hell Creek turtles include *Plesiobaena antiqua*, *Eubaena cephalica*, *Stygiochelys estesi*, *Palatobaena cohen*, *Neurankylus* sp, *Thescelus insiliens*, *Gamerabaena sonsalla*, *Hayemys latifrons*, *Adocus* sp., *Basilemys* sp., *Aspideretes* sp., *Helopanoplia distincta*, *Emarginochelys cretacea*, *Compsemys victa*, the macrobaenid "*Clemmys*", a chelydrid, as many as three additional trionychids, and a kinosternid (Hutchison and Archibald 1986; Lyson and Joyce 2010). A thorough examination of the stratigraphic placement of these taxa within the Hell Creek Formation would prove extremely useful for biostratigraphic and biogeographic studies of Maastrichtian turtles.

Javelina Formation: The Javelina Formation of Texas is primarily composed of fluvial channel and floodplain deposits (Tomlinson 1995). The fossil turtle assemblage of the Javelina Formation includes *Aspideretes* sp., *Baena* sp., *Neurankylus* sp., *Adocus* sp., and *Basilemys* sp. (Tomlinson 1995).

Lance Formation: The Lance Formation consists of mostly sandstone and siltstone deposited in a fluvial system not far upstream from a delta coast (Carvajal and Steel 2009). The Lance Formation in South Dakota and Wyoming contains a variety of vertebrate fossils including dinosaurs and turtles. Several species of Late Cretaceous turtles have been indentified and include *Compsemys victa*, *Plesiobaena antiqua*, *Eubaena cephalica*, *Thescelus insiliens*, *Baena hatcheri*, *Baena hayi*, *Adocus* sp., *Basilemys sinuosa*, *Helopanoplia distincta*, *Aspideretes* sp., "*Clemmys*" *backmani*, *Protochelydra* sp., and another trionychid (Holroyd and Hutchison 2002).

Laramie Formation: The Laramie Formation within the Denver Basin of Colorado is composed primarily of coal deposits with interbedded sandstones and siltstones of a coastal plain (Johnson et al. 2003). Some turtle fossils have been identified in the Laramie Formation including *Compsemys victa*, *Plesiobaena antiqua*, *Adocus* sp., *Basilemys* sp., *Helopanoplia* sp., and two different trionychids (Hutchison and Holroyd 2003).

North Horn Formation: The North Horn Formation of Utah has a Maastrichtian base but extends across the K/T Boundary. The Cretaceous portion of the formation consists of variegated mudstones and thin sandstones becoming more carbonaceous near the K/T Boundary (Difley and Ekdale 2002). A large variety of vertebrate fauna has been identified in the North Horn Formation but surprisingly only a few turtle taxa. The known freshwater turtles from the formation are *Basilemys* sp., *Adocus* sp., *Compsemys* sp., and *Aspideretes* sp. (Cifelli et al. 1999b).

Scollard Formation: The Maastrichtian Scollard Formation of Alberta, Canada is divided into two informal units, which only the lower unit is considered to be Late Cretaceous (Brinkman 2003). The upper unit is divided from the lower unit by a coal bed which marks the K-P boundary. Several fossil turtles have been collected and identified from the Scollard Formation and include *Compsemys* sp., *Plastomenus* sp., *Basilemys* sp., a macrobaenid, an unknown trionychid, and a chelydrid (Brinkman 2003).

Discussion

Changes in Diversity and Faunal Turnover

The diversity of turtles in North America appears to increase during the Cretaceous reaching a peak in the Campanian-Maastrichtian (Fig. 2.1). A similar diversity trend is apparent at both the family and genera levels. The lack of any turtle remains during the earliest Cretaceous of western North America is likely a consequence of little to no terrestrial outcrops, rather than a complete lack of turtle taxa during this time. The turtle fauna of the Aptian-Albian consists of a Jurassic holdover (*Glyptops* sp), and mostly *Naomichelys* sp. and baenids, which are considered primitive cryptodires. It is believed that both the trionychids and adocids first originated in Asia and seem to arrive in North America around the Cenomanian-Turonian (Hutchison 2000). By the Turonian, *Glyptops* has disappeared, and is possibly replaced by the smaller *Compsemys*, based upon similar familial morphology. *Naomichelys*, however, survives until as late as the Campanian in North America before disappearing, probably due to increased competition from immigrant taxa. The baenids had greatly diversified by the Turonian-Coniacian with the appearance of *Neurankylus* sp., *Baena* sp., and *Denazinemys* sp. The arrival of *Basilemys* from Asia occurred during the Coniacian, representing the only known terrestrial “tortoise” of the Cretaceous in North America (Hutchison 2000). Evidence of the bothremydids is sparse during the mid Cretaceous, but are identified in the Coniacian and reappear sporadically through the end of the Cretaceous. The first definitive chelydrid also appears during the Coniacian in North America and the family survives today.

By the Santonian, the baenids were a diverse group of freshwater turtles that included *Boremys* sp. and the large *Neurankylus* sp. among others. *Adocus* and *Basilemys* had established themselves widely in western North America in addition to the trionychids, which were just beginning to greatly diversify. The first appearance of the kinosternids (small mud turtles) (represented by *Hoplochelys* sp.) occurred around Campanian time. Freshwater turtle diversity was high during the Campanian with as many as seven different turtle families comprised of nearly twenty genera living in multiple regions of North America. The number of trionychid species during the Campanian may have exceeded a dozen, but further taxonomic descriptions are required. The arrival of the macrobaenids from Asia also occurred during the Campanian, which only added to the previous diversity (Hutchison 2000). This diversity dropped only slightly between the Campanian and Maastrichtian in North America, as evident in the Hell Creek Formation, which may have as many as twenty different fossil freshwater turtles. At the termination of the Cretaceous, turtle diversity across the world was quite high (Hutchison 2000). Of the Late Cretaceous turtle families only the Nanhsiungchelyidae fails to survive into the Paleocene. It is of note that the diversity of dinosaurs also appears to follow a similar pattern to turtles during the Late Cretaceous (Weishampel 1990). Undoubtedly, many turtle and dinosaur taxa immigrated and mixed with North American taxa along similar routes. But following the K/T extinction in which dinosaurs disappeared, turtle diversity continues to increase, reaching its maximum in the Paleocene (Holroyd and Hutchison 2002).

Phylogenetics and Diversity

The phylogenetic relationships of the Cretaceous North American turtles are primarily based on examinations of both ancient and living turtle morphology. This information has been used to create a phylogenetic tree for both extinct and living turtles (Joyce 2007). The known Cretaceous fossil turtles from North America were extracted and placed together in a smaller format with Cretaceous subdivisions and approximate branches of separation (Fig. 2.13). This figure also shows the change in diversity of these families through the Cretaceous. Only the Bothremydidae belongs to the Pleurodira with the other nine families belonging to the Cryptodira. The more primitive cryptodires, including the solemydids and pleurosternids, are the first to thrive in North America, although they never fully diversify. Only one, and in a single instance two, genera of each clade is present at any one time during the Cretaceous. The other primitive cryptodire family, the Baenidae, is far more successful. Appearing between the Albian and Turonian, the baenids explode in diversity towards the end of the Cretaceous. Why these primitive cryptodires were successful and the others were not may be related to dietary preferences or habitat.

The macrobaenid origin lies somewhere in the Early to mid Cretaceous in Asia representing a split from a primitive cryptodiran family. During the Turonian this family crossed into North America, but never greatly diversified. The chelydrids and kinosternids, both small turtles in the Cretaceous, also fail to diversify beyond a single genus for any one time (Hutchison 2000). The poor preservation of these smaller turtles limits understanding of their origins and diversity. The Adocidae and

Nanhsiungchelyidae are sister families which both originated in Asia, with the adocids emigrating first during the Turonian. Only a single genus is known in the Late Cretaceous of North America, but multiple species are recognized in the Campanian. Their sister taxa, the nanhsiungchelyids, arrive from Asia during the Coniacian, probably along a similar route. These large terrestrial turtles share some similarities with their adocid relatives (Hutchison 2000). Again, only a single genus of nanhsiungchelyids is known in North America, and species level diversification occurs in the Campanian-Maastrichtian. The trionychids are the most derived cryptodires of the Cretaceous. They also stem from Asian relatives and arrive in North America during the Cenomanian. They remain poorly diversified until the Campanian when the number of genera increases sharply.

The phylogenetic tree of these Cretaceous turtles does not seem to show any specific patterns or trends, but in general the turtle families, whether endemic or immigrant, start off slow, taking long periods of time for diversification at the genera or species level. Only the baenids and trionychids are considered successfully diverse by the end of the Cretaceous, with trionychids remaining diverse today. The chelydrids and kinosternids, although lacking diversity, survive through the K/T boundary and the climate changes of the Cenozoic (Holroyd and Hutchison 2002).

Spatial Trends

As described previously, many freshwater turtles had widespread geographical distributions during the Cretaceous while others were more confined. The distribution of known fossil freshwater turtles was mapped to show the ages of the deposits in which each fossil turtle family has been recovered (Figs. 2.3 - 2.12). These maps reveal that some turtle families may have preferred specific environments or climates, as shown by their distribution relative to the changing geography of North America through the Cretaceous.

During much of the Cretaceous central North America was covered by a vast epicontinental sea, known as the Western Interior Cretaceous Seaway, which stretched from the modern Arctic Ocean to the Gulf of Mexico (Fig. 2.14). This sea was at its widest during the mid Cretaceous and then began to recede towards the Maastrichtian (Levorsen 1960). The fossil distribution of many of the turtle families, including the Adocidae, Baenidae, Chelydridae, Nanhsiungchelyidae, and Trionychidae, follows the recession of this seaway from west to east as lowland sedimentary deposits move eastward becoming younger with age. The majority of these deposits are fluvial and floodplain in nature, which is common near a passive coastal margin. Fossil vertebrates are primarily preserved in subsiding foreland basins where sediment is deposited in abundance and in high frequency. Turtles that occupy habitats within these foreland basins, including rivers, floodplains, and ponds, are undoubtedly more abundant in the fossil record than those taxa that inhabited upland environments where deposition is limited. In other words, accurately estimating the ranges of turtles in the Cretaceous is a difficult task with the little information that is available.

Table 2.1. Cretaceous turtle taxa of western North America.

	APTIAN	ALBIAN	CENOMANIAN	TURONIAN	CONIACIAN	SANTONIAN	CAMPANIAN	MAASTRICHTIAN
ADOCIDAE								
Adocus bossi							X	
Adocus kirtlandicus							X	
Adocus vigoratus							X	
Adocus sp.		X?		X	X	X	X	X
BAENIDAE								
Baena hatcheri							X	X
Baena hayi								X
Baena sp.								X
Boremys grandis							X	
Boremys pulchra							X	
Boremys sp.						X	X	
Denazinemys nodosa					X		X	
Denazinemys ornata							X	
Eubaena cephalica								X
Eubaena sp.								X
Gamerabaena sonsalla								X
Hayemys latifrons								X
Neurankylus eximius							X	X
Neurankylus sp.				X	X	X	X	X
Palatobaena cohen								X
Plesiobaena antiqua							X	X
Plesiobaena sp.						X		
Stygiochelys estesi								X
Thescelus insiliens							X	X
Baenidae indet.		X		X		X	X	X

Table 2.1 Continued. Cretaceous turtle taxa of western North America.

	APTIAN	ALBIAN	CENOMANIAN	TURONIAN	CONIACIAN	SANTONIAN	CAMPANIAN	MAASTRICHTIAN
BOTHREMYDIDAE								
Bothremys sp.				X	X			
Bothremydidae indet.		X					X	
CHELYDRIDAE								
Protochelydra sp.								X
Chelydridae indet.		X?		X	X	X	X	X
KINOSTERNIDAE								
Emarginochelys cretacea								X
Hoplochelys sp.							X	
Kinosternidae indet.							X	X
MACROBAENIDAE								
Aurorachelys gaffneyi				X				
Borealochelys axelheibergensis				X				
"Clemmys" backmani								X
"Clemmys" sp.							X	X
Judithemys sukhanovi							X	
Macrobaenidae indet.		X?					X	X
NANHSIUNGCHELYIDAE								
Basilemys nobilis							X	
Basilemys sinuosa								X
Basilemys praeclara								X
Basilemys variolosa							X	
Basilemys sp.					X	X	X	X

Table 2.1 Continued. Cretaceous turtle taxa of western North America.

	APTIAN	ALBIAN	CENOMANIAN	TURONIAN	CONIACIAN	SANTONIAN	CAMPANIAN	MAASTRICHTIAN
PLEUROSTERNIDAE								
Compsemys victa							X	X
Compsemys sp.				X	X	X	X	X
Dinochelys sp.		X						
Glyptops pervicax	X							
Glyptops sp.	X	X						
SOLEMYDIDAE								
Naomichelys speciosa	X							
Naomichelys sp.	X	X	X	X	X		X	
Solemydidae indet.						X	X	
TRIONYCHIDAE								
Apalone latus							X	
Aspideretes alleni							X	
Aspideretes austerus							X	
Aspideretes fontanus							X	
Aspideretes foveatus							X	
Aspideretes ovatus							X	
Aspideretes splendidus							X	
Aspideretes vorax							X	
Aspideretes sp.							X	X
Helopanoplia distincta								X
Helopanoplia sp.							X	X
Plastomenus robustus							X	
Plastomenus sp.							X	X
Platypeltis sternbergi							X	
Trionychidae indet.			X	X	X	X	X	X

Table 2.2. Cretaceous turtle assemblages of western North America.

	KNOWN TURTLE TAXA	DEPOSITIONAL ENVIRONMENT
APTIAN-ALBIAN		
Antlers Formation	*Naomichelys* sp., *Glyptops* sp.	overbank, floodplain
Cloverly Formation - Himes Member	*Naomichelys speciosa* , *Glyptops pervicax*	fluvial
ALBIAN		
Glen Rose Formation	Baenidae	fluvial
Paluxy Formation	unknown	fluvial
Willow Tank Formation	*Naomichelys* sp., *Adocus* sp.?, Baenidae, Trionychidae	fluvial
ALBIAN-CENOMANIAN		
Blackleaf Formation	*Glyptops* sp., Macrobaenidae?, Chelydridae?	fluvial, deltaic
Cedar Mountain Formation - Yellow Cat Member	*Glyptops* sp.	fluvial
Cedar Mountain Formation - Mussentuchit Member	*Glyptops* sp., *Naomichelys* sp., Trionychidae	fluvial
Dakota	*Glyptops* sp., *Dinochelys* sp., *Naomichelys* sp., Pleurosternidae?, Bothremydidae	fluvial, paludal, brackish marine
Wayan	*Glyptops* sp., *Naomichelys* sp.	fluvial
CENOMANIAN		
Chandler Formation	Dermatemydidae?	fluvial, overbank, lacustrine
Dunvegan Formation	Trionychidae	fluvial, brackish marine
Frontier Formation	unknown	deltaic, fluvial, estuarine
Woodbine Formation	unknown	fluvial
TURONIAN-CONIACIAN		
Kaskapau Formation	*Naomichelys* sp.	deltaic
Straight Cliffs Formation - Smoky Hollow Member	*Bothremys* sp., *Compsemys* sp., *Neurankylus* sp., Adocidae, Baenidae, Trionychidae, Chelydridae	floodpain, lacustrine
Straight Cliffs Formation - John Henry Member	*Bothremys* sp., *Naomichelys* sp., *Compsemys* sp., *Neurankylus* sp., *Adocus* sp., *Denazinemys nodosa* , *Basilemys* sp., Trionychidae, Chelydridae	brackish marine, deltaic

Table 2.2 Continued. Cretaceous turtle assemblages of western North America.

	KNOWN TURTLE TAXA	DEPOSITIONAL ENVIRONMENT
SANTONIAN		
Menefee Formation	Trionychidae, Baenidae	fluvial, paludal
Milk River Formation - Deadhorse Coulee Member	*Neurankylus* sp., *Boremys* sp., *Plesiobaena* sp., *Basilemys* sp., *Compsemys* sp., *Adocus* sp., Trionychidae, Solemydidae, Chelydridae	fluvial, overbank
Straight Cliffs Formation - Drip Tank Member	Chelydridae	fluvial
CAMPANIAN		
Aguja Formation	*Basilemys* sp., *Adocus* sp., *Helopanoplia* sp., *Hoplochelys* sp., Baenidae	brackish marine, floodplain
Cerro del Pueblo Formation	*Compsemys* sp., *Neurankylus* sp., *Adocus* sp., *Hoplochelys* sp., Bothremydidae, Trionychidae, Chelydridae	fluvial
Fort Crittenden Formation	*Plastomenus* sp., *Aspideretes* sp.	overbank, floodplain
Fruitland Formation	*"Baena" nodosa*, *Boremys pulchra*, *Compsemys* sp., *Neurankylus eximius*, *Adocus bossi*, *Adocus kirtlandicus*, *Basilemys* sp., *Aspideretes* sp.	fluvial, overbank
Judith River Group - undifferentiated Oldman, Foremost, and Dinosaur Park Formations	*Boremys pulchra*, *Plesiobaena antiqua*, *Neurankylus eximius*, *Adocus* sp., *Basilemys variolosa*, *Aspideretoides foveatus*, *Aspideretoides splendidus*, *Aspideretoides alleni*, *Apalone latus*, Solemydidae, *Judithemys sukhanovi*, Chelydridae	brackish marine, fluvial
Judith River Formation	*Boremys pulchra*, *Plesiobaena antiqua*, *Baena hatcheri*, *Neurankylus* sp., *Adocus* sp., *Basilemys* sp., *Aspideretes* sp., *Naomichelys* sp., Chelydridae, "*Clemmys*" sp.	fluvial, floodplain
Kaiparowits Formation	*Adocus kirtlandicus*, *Compsemys victa*, *Neurankylus eximius*, *Denazinemys nodosa*, *Boremys pulchra*, *Basilemys variolosa*, *Helopanoplia* sp., *Aspideretoides* sp., Kinosternidae, Chelydridae	fluvial, floodplain, paludal
Mesaverde Formation	*Neurankylus* sp., *Aspideretes foveatus*, *Basilemys* sp., Chelydridae, Solemydidae	fluvial, floodplain
Muerto Formation	*Compsemys* sp., *Adocus* sp., *Hoplochelys* sp., Trionychidae, Chelydridae	fluvial
San Carlos Formation	*Aspideretes* sp.	deltaic
Two Medicine Formation	*Compsemys* sp., *Aspideretes* sp., *Basilemys* sp., Chelydridae	fluvial, floodplain
Wahweap Formation	*Compsemys victa*, *Neurankylus eximius*, *Denazinemys nodosa*, *Boremys pulchra*, *Naomichelys* sp., *Adocus* sp., *Basilemys* sp., Trionychidae	fluvial

Table 2.2 Continued. Cretaceous turtle assemblages of western North America.

	KNOWN TURTLE TAXA	**DEPOSITIONAL ENVIRONMENT**
CAMPANIAN-MAASTRICHTIAN		
Horseshoe Canyon Formation	*Aspideretoides* sp., *Basilemys* sp., Macrobaenidae, Chelydridae	brackish marine, fluvial
Kirtland Formation - Farmington/De-na-zin Members	*Denazinemys nodosa*, *Denazinemys ornata*, *Boremys grandis*, *Neurankylus eximius*, *Thescelus insiliens*, *Adocus bossi*, *Adocus kirtlandicus*, *Basilemys nobilis*, *Aspideretes ovatus*, *Aspideretes vorax*, *Plastomenus robustus*, *Platypeltis sternbergi*	fluvial, floodplain
Kirtland Formation - Naashoibito Member	*Denazinemys nodosa*, *Neurankylus eximius*, *Thescelus insiliens*, *Adocus vigoratus*, *Basilemys nobilis, Aspideretes fontanus, Aspideretes austerus*, *Aspideretes vorax*, *Compsemys sp.*, *Hoplocheys sp.*	fluvial, floodplain
St. Mary's River Formation	*Boremys* sp., Trionychidae	fluvial
MAASTRICHTIAN		
Arapahoe Formation	*Adocus* sp.	lacustrine, fluvial
Denver Formation	*Neurankylus eximius*, *Eubaenia* sp., *Adocus* sp., *Basilemys* sp., *Helopanoplia* sp.	lacustrine, fluvial
Ferris Formation	*Compsemys victa*, *Neurankylus eximius*, *Adocus* sp., *Basilemys sinuosa*	fluvial
Fox Hills Formation	*Aspideretoides* sp., *Basilemys* sp.	brackish marine, coastal
Frenchman Formation	*Basilemys praeclara*	fluvial, overbank
Hell Creek Formation	*Plesiobaena antiqua*, *Eubaena cephalica*, *Stygiochelys estesi*, *Palatobaena cohen*, *Neurankylus* sp, *Thescelus insiliens*, *Gamerabaena sonsalla*, *Hayemys latifrons*, *Adocus* sp., *Basilemys* sp., *Aspideretes* sp., *Helopanoplia distincta*, *Emarginochelys cretacea*, *Compsemys victa*, *"Clemmys"* sp., Chelydridae, Kinosternidae	fluvial, floodplain
Javelina Formation	*Aspideretes* sp., *Baena* sp., *Neurankylus* sp., *Adocus* sp., *Basilemys* sp.	fluvial, floodplain
Lance Formation	*Compsemys victa*, *Plesiobaena antiqua*, *Eubaena cephalica*, *Thescelus insiliens*, *Baena hatcheri*, *Baena hayi*, *Adocus* sp., *Basilemys sinuosa*, *Helopanoplia distincta*, *Aspideretes* sp., *"Clemmys" backmani*, *Protochelydra* sp.	fluvial
Laramie Formation	*Compsemys victa*, *Plesiobaena antiqua*, *Adocus* sp., *Basilemys* sp., *Helopanoplia* sp.	coastal plain
North Horn Formation	*Basilemys* sp., *Adocus* sp., *Compsemys* sp., *Aspideretes* sp.	floodplain
Scollard Formation	*Compsemys* sp., *Plastomenus* sp., *Basilemys* sp., Macrobaenidae, Chelydridae	floodplain

Table 2.3. Mid to Late Cretaceous turtle diversity of western North America by family and genus.

	Number of Turtle Genera	**Number of Turtle Families**
Aptian	2	2
Albian	3	4
Cenomanian	1	2
Turonian	7	8
Coniacian	7	8
Santonian	7	7
Campanian	18	10
Maastrichtian	15	8

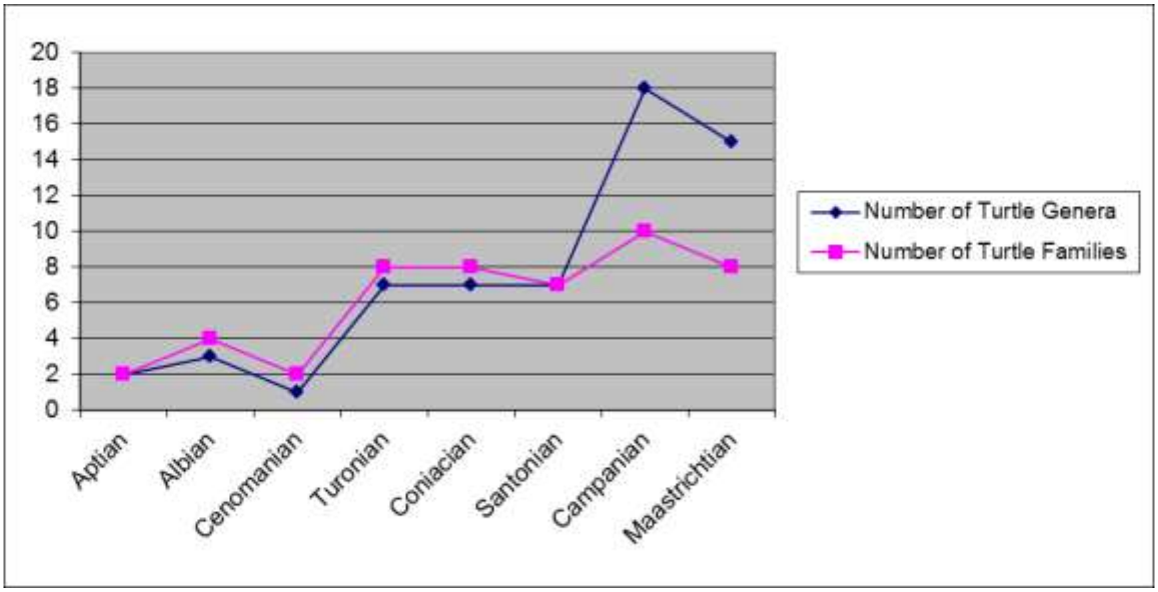

Figure 2.1. Graph of Mid to Late Cretaceous turtle diversity of western North America.

Figure 2.2. Map of western North American Cretaceous fossil turtle localities.

Figure 2.3. Map of Cretaceous Adocidae localities in western North America.

Figure 2.4. Map of Cretaceous Baenidae localities in western North America.

Figure 2.5. Map of Cretaceous Bothremydidae localities in western North America.

Figure 2.6. Map of Cretaceous Chelydridae localities in western North America.

Figure 2.7. Map of Cretaceous Kinosternidae localities in western North America.

Figure 2.8. Map of Cretaceous Macrobaenidae localities in western North America.

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Figure 2.9. Map of Cretaceous Nanhsiungchelyidae localities in western North America

Figure 2.10. Map of Cretaceous Pleurosternidae localities in western North America.

Figure 2.11. Map of Cretaceous Solemydidae localities in western North America.

Figure 2.12. Map of Cretaceous Trionychidae localities in western North America.

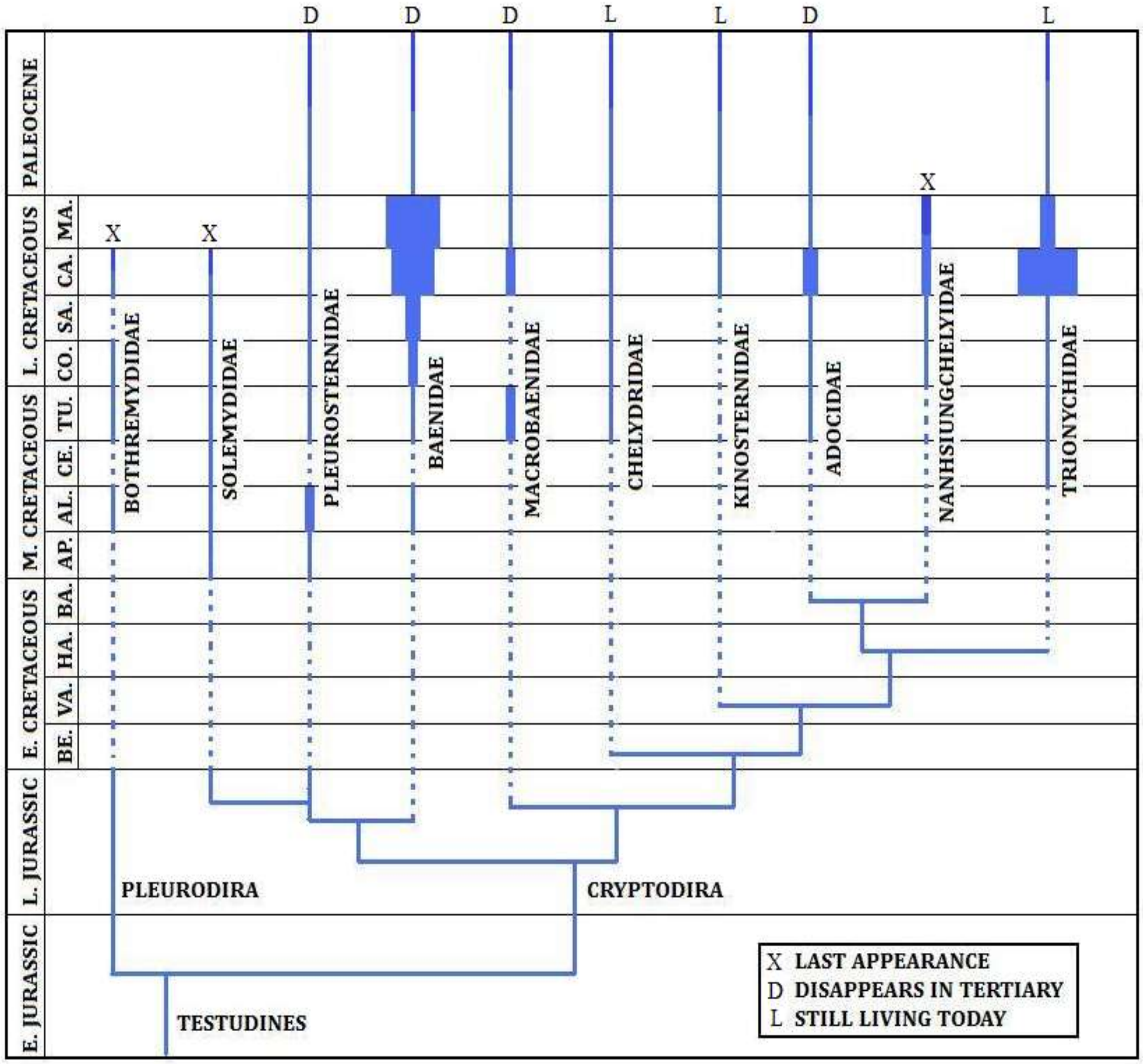
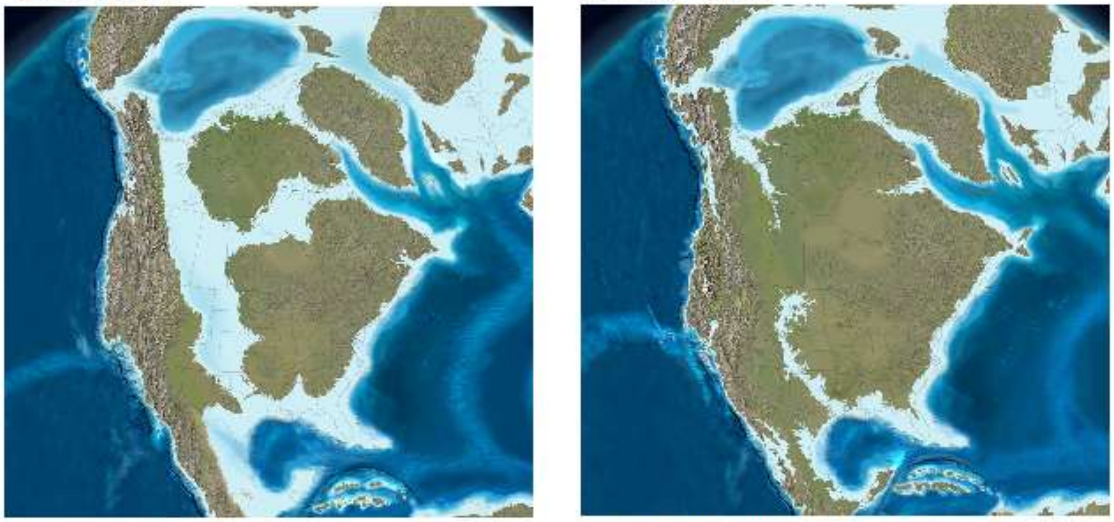


Figure 2.13. Cretaceous turtle diversity and general phylogeny. Timing for branching events is estimated. Width of lines represents the relative abundance of genera known for that time period. Phylogenetic tree based on Joyce (2007).

Aptian - 115 Ma

Coniacian - 85 Ma



Campanian - 75 Ma

Maastrichtian/Paleocene - 65 Ma

Figure 2.14. Paleogeography of North America during the Cretaceous. Images by R. Blakey of Northern Arizona University.

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CHAPTER THREE

TRANSPORT AND DEPOSITION OF FOSSIL FRESHWATER TURTLES IN FLUVIAL DEPOSITIONAL ENVIRONMENTS INTEGRATING FLUME EXPERIMENTATION

Contribution of Authors and Co-authors

Manuscript in Chapters 3, 4, and 6

Author: Michael J. Knell

Contributions: All work relating to completion and preparation of manuscript.

Manuscript Information Page

Michael J. Knell
PALAIOS
Status of Manuscript:
_X_Prepared for submission to a peer-reviewed journal
____Officially submitted to a peer-reviewed journal
____Accepted by a peer-reviewed journal
____Published in a peer-reviewed journal

Published by SEPM Society for Sedimentary Geology

TAPHONOMIC ANALYSIS OF FOSSIL FRESHWATER TURTLES IN THE UPPER CRETACEOUS (CAMPANIAN) KAIPAROWITS FORMATION OF SOUTHERN UTAH WITH EMPHASIS ON TRANSPORT AND DEPOSITION

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RRH: KAIPAROWITS TURTLE TAPHONOMY
LRH: KNELL
Keywords: Chelonia, morphology, depositional environments, preservation, Grand Staircase-Escalante National Monument

ABSTRACT

A diverse assemblage of fossil freshwater turtles occurs within the fluvial and floodplain deposits of the Kaiparowits Formation of southern Utah. A taphonomic analysis of these fossil turtles examines the links between the morphology of each turtle taxon, the depositional environment in which it was buried, and the quality of preservation. A total of 700 turtle specimens were examined in both museum collections and in the field in order to collect taphonomic data. The results of this analysis showed a preservation preference towards turtles that were buried within channel deposits, but only for those with robust shells. Remains of large turtles were common, and typically represented by fragmentary remains. Specimens of baenids and adocids were more likely found as intact shells in channel deposits due to their robust shell morphology. Fragments of small turtle taxa occurred primarily in crevasse splay, pond, and other floodplain deposits. The abundance of taxa within each depositional environment supports habitat preferences inferred from extant turtle taxa. *Adocus*, *Neurankylus*, and *Denazinemys* likely preferred riparian habitats as they are commonly found in channel deposits, whereas those taxa preserved more commonly in floodplain deposits, such as

Compsemys, chelydrids, and kinosternids, probably preferred ponds or other quieter water environments on the floodplain.

INTRODUCTION

Taphonomy has been an important and valuable component of vertebrate paleontology field research over the past few decades. Understanding taphonomic processes, which includes the decay of an organism, transport and deposition of the organism's remains, and modification of bones before and after burial, allows us to form hypotheses regarding the organism's behavior while alive as well as reconstruct the events that occurred from the moment of death until its discovery millions of years later by paleontologists (e.g. Dodson, 1971; Dodson et al., 1980; Fiorillo, 1991; Rogers, 1990; Varricchio, 1995). A large portion of taphonomy involves understanding transport of an organism's remains and the environment in which they were subsequently buried. This relationship can be used to help reconstruct the paleoenvironment of a region during a moment in geologic time and also the paleoecology of fauna that lived there. For this study, the paleoecology of a group of freshwater turtles will be interpreted based upon taphonomic relationships between the various turtle taxa, their depositional environments, and the quality of their preservation.

Typically, taphonomic studies consider all vertebrate taxa within an assemblage, however in this case only the fossil freshwater turtles are examined. There are multiple reasons for this. First, turtles possess unique morphology. There are very few other vertebrates with a skeletal structure like that of turtles, which is characterized by the enclosure of both the pectoral and pelvic girdles within a bony shell comprised of a dorsal carapace and ventral plastron. Because of their anatomy, turtle carcasses decompose and disarticulate differently from other tetrapods, therefore turtles should not be combined with other vertebrates in taphonomic studies (Brand et al., 2003; Knell, 2004; Fielding, 2006). A second reason to use freshwater turtles is that they are typically very abundant in terrestrial sedimentary deposits, especially in fluvial and lacustrine depositional environments (e.g. Brand et al., 2000; Brinkman, 2003). A greater number of specimens increase the probability that observed trends are real, and will also increase the accuracy of subsequent interpretations. A third reason is that turtles are a valuable tool for understanding the paleoecology of a particular region. Because many turtle families still exist today, it is possible to make well-educated inferences regarding the likely habitats and behaviors of ancient turtles by observing their living relatives. Observing the decay of extant turtles also allows for comparison and better understanding of Cretaceous turtle taphonomy, which is not possible for extinct vertebrates like dinosaurs whose extant relatives are too highly modified from their typical Cretaceous forms. Turtles are among a small number of living vertebrates that possess a lineage extending back into the early Mesozoic; in addition, they are also easily observed today in great numbers and high diversity, thus allowing for reliable comparisons between living and extinct taxa.

In the past few decades the Upper Cretaceous (Campanian) Kaiparowits Formation in southern Utah has been a “hot spot” for vertebrate paleontology research (Fig. 3.1). Several new species of dinosaur are described from the Kaiparowits Formation, including some that are unique to the Grand Staircase region (e.g. Smith et al., 2004; Zanno et al., 2005; Zanno et al., 2011). Additional discoveries include the remains numerous crocodiles, birds, mammals, and turtles (Hutchison et al., 1998; Eaton et al., 1999). These discoveries greatly aid in understanding the biodiversity of this region during the late Campanian. Of all non-dinosaurian fossil vertebrate groups recovered from the Kaiparowits Formation, none are more diverse than the freshwater turtles. The preservation quality of these freshwater turtles is quite variable. Some turtles are collected in excellent condition with fully articulated shells and associated skeletal material; in other cases, only fragmentary remains are recovered. These differences in preservation are noticeable when comparing of the depositional environments in which the turtle fossils were discovered. There are also differences in preservation among turtle families, which may indicate a bias that preferentially selects the preservation of certain turtle taxa over others.

This paper examines the variation in preservation in the Kaiparowits freshwater turtles and the taphonomic processes responsible for this variation by linking three components: (1) the depositional environment in which the turtle remains occurred, (2) the turtle taxon, and (3) the turtle's skeletal completeness. The purpose of examining these specific attributes is to identify a link between the morphology of a turtle, the environment of deposition, and the preservation potential of that turtle. This in turn aids in explaining observable taphonomic patterns in order to address a number of hypotheses regarding turtle taphonomy and paleoecology. These hypotheses are provided in further detail at the end of the introduction below. This taphonomic approach allows identification of potential morphologic or environmental biases that may affect the preservation of each turtle taxon in their respective depositional environments. Understanding the link between morphology, environment of deposition, and preservation will prove valuable to paleontologists seeking explanations for taphonomic patterns in the vertebrate fossil record. It will also serve to increase our understanding of Campanian freshwater turtle paleoecology.

PREVIOUS WORK

The following two sections will provide an overview of what we know about the Kaiparowits fossil turtle taxa as well as the geologic setting prior to an explanation of the methods used in this project. A review of the Kaiparowits fossil turtle taxa is provided to give the reader an understanding of the variety of turtles that existed in this region during the Cretaceous, as well as to describe the morphologic differences between the major turtle families. An introduction of the geologic setting, based on the work of Roberts (2007), will serve to give the Kaiparowits Formation context as an active fluvial system during the late Campanian by describing the primary lithofacies associations and their interpreted depositional environments. The methods section that follows will describe how taphonomic data was collected from museum and field specimens.

Freshwater Turtles of the Kaiparowits Formation

A diverse assemblage of fossil freshwater turtles has been collected from the Kaiparowits Formation. As many as seven families (four extinct and three extant) are represented, including at least ten named genera. This designates the Kaiparowits Formation as one of the most diverse turtle-bearing units in the Cretaceous, second only to the Hell Creek Formation (Hutchison and Archibald, 1986; Hutchison et al., in press). A wide variety of turtle taxa can be found in the Kaiparowits Formation, with sizes ranging from 10 cm to nearly 100 cm in length along with a variety of shell morphologies.

Adocidae.— *Adocus*, the only genus of this family recognized in North America, is a medium-sized turtle (carapace lengths between 45 and 60 cm) recognized by a faint, dimpled texture on both the carapace and plastron (Fig. 3.2). The carapace is longer than wide with a flared posterior margin. Currently, the *Adocus* remains reported from the Kaiparowits Formation are not assigned to any known species, but future taxonomic studies of this family will provide clarity. Perhaps the best-preserved freshwater turtle from the Kaiparowits Formation is an *Adocus* that contains a partial skeleton with a skull, in addition to several fossilized partial eggs within the shell (Knell et al., 2011). The shell and limb morphology of *Adocus* is very similar to that of the extant river turtle *Dermatemys mawii* of Central America (Bonin et al., 2006), so it seems probable that *Adocus* also preferred a riparian habitat.

Baenidae.— Several members of the baenid family are described from the Kaiparowits Formation. The limb morphology of the Baenidae is similar to Adocidae, and therefore this family presumably consists of primarily aquatic turtles that spend most of their time in and around large fluvial channels (Hutchison, 2000). *Neurankylus* represents one of the largest turtles in the Kaiparowits Formation and the broad, smooth, sub-rectangular carapace can measure nearly a meter in length (Hutchison et al., in press) (Fig. 3.2). Perhaps as many as two new *Neurankylus* species may occur in the

Kaiparowits Formation; however, diagnostic material is currently sparse (Hutchison et al., in press). *Boremys*, another baenid from the Kaiparowits Formation, is less than half the size of *Neurankylus*. The carapace exhibits multiple low, elongate nodules extending along the neurals. Two species of *Boremys* occur in North America, *B. pulchra* and *B. grandis*, from northern and southern latitudes respectively. The Kaiparowits Formation specimens are referable to *B. grandis*; however, like *Neurankylus*, diagnostic material is sparse (Hutchison et al., in press). *Denazinemys* represents a third, easily-recognizable baenid from the formation (Fig. 3.2). Formerly known as "*Baena*", *Denazinemys* is a medium-sized freshwater turtle similar in size to *Boremys*. Carapace fragments are recognized by numerous, densely-packed, rounded, elongate nodules that extend parallel in an anterio-posterior orientation, centralized along the neurals (the bones of the carapace that extend along the vertebral midline). The posterior margin of the carapace is also scalloped as opposed to rounded, as with *Boremys*. The *Denazinemys* material in the Kaiparowits Formation has all been assigned to *D. nodosa* (Hutchison et al., in press). A fourth baenid, *Plesiobaena*, is also currently recognized from the Kaiparowits Formation (Fig. 3.2). It differs from *Denazinemys* and *Boremys* by having a smooth carapace with no discernible ornamentation; however the posterior margin is scalloped like that of *Denazinemys*. Morphologically, all adult baenids share a well-fused shell that has a solid construction, though *Denazinemys* has a more pronounced arching of the carapace than other members of the family.

Chelydridae.— Remains of chelydrids, or snapping turtles, are also known from the Kaiparowits Formation. These turtles are small in size (estimated < 20 cm in length), and their carapaces are characterized by a raised edge along peripherals with a plication texture (Brinkman, 2003). Specimens are typically more ornate than pleurosternids or kinosternids. To date, the collected material belonging to this turtle has proven to be non-diagnostic, and thus unsuitable for assigning the taxa to any known genus. Living members of this family are carnivorous and typically inhabit large ponds and lakes (Bonin et al., 2006).

Kinosternidae.— Kinosternids, also known as mud turtles, are characterized by rounded, highly-domed shells and small body size (estimated < 15 cm in length) (Hutchison et al., in press). In the Kaiparowits Formation, kinosternid fragments are possibly assignable to the genus *Hoplochelys* or another closely related kinosternid. Carapace fragments are very small with a smooth surface, and they frequently possess sulci (grooves) where the keratin scutes once fitted together. Living members of the Kinosternidae frequently inhabit quiet waters of small ponds (Bonin et al, 2006). The carapace of kinosternids is highly arched, with poorly fused shell elements, even in adults.

Nanhsiungchelyidae.— Nanhsiungchelyids, a family first recognized in eastern Asia, are represented in the Kaiparowits Formation by the genus *Basilemys* (Fig. 3.2). Believed to be more terrestrial than semi-aquatic, *Basilemys* is one of the largest Cretaceous non-marine turtles, measuring over 80 cm in length (Hutchison, 2000). This genus possesses several “tortoise-like” features including a large, thick, moderately-domed carapace as well as stout limbs covered with ossicles that form a bony protective armor. The surface texture is characterized by closely-spaced, deep pits that form small peaks between them. The collected material of *Basilemys* from the Kaiparowits Formation most closely resembles that of *B. nobilis*, a species of *Basilemys* commonly found in other Campanian localities in New Mexico and Texas (Hutchison et al., in press).

Pleurosternidae.— Pleurosternids are represented in the Kaiparowits Formation by the genus *Compsemys*, more specifically *Compsemys victa*, which is small in size (estimated < 20 cm in length) (Hutchison et al., in press). A texture comprised of numerous, closely spaced, faint, wavy ridges, similar to a human fingerprint pattern, distinguishes *Compsemys* from other taxa. The shell of *Compsemys* is fairly thin with a low to moderate curvature, and sulci are frequently recognizable on carapace fragments. A few researchers have previously noted that *Compsemys* remains are typically found in mudstone in other formations and have interpreted this as taphonomic evidence supporting a quiet water habitat for this turtle (Hutchison and Holroyd, 2003; Lyson and Joyce, 2011).

Trionychidae.— The trionychids, or soft-shelled turtles, are common in many Cretaceous terrestrial deposits and the Kaiparowits Formation is no exception (Brinkman, 2003; Hutchison et al., in press). Trionychids, unlike the other turtle families, typically possess a flat, circular carapace that is not fused to the plastron and lacks peripherals. The plastron consists of multiple separate elements that frequently disarticulate during decomposition, the largest of which are the hyoplastron and hypoplastron. At least four different trionychids are currently recognized from the formation, with *Aspideretoides* and *Helopanoplia* representing the largest. *Aspideretoides* is recognized by a closely packed, circular, pitting texture of the carapace, which can be quite large in diameter (> 50 cm) (Fig. 3.2). *Helopanoplia*, which is slightly smaller than *Aspideretoides*, possesses a more ornate carapace texture composed of closely spaced, thinly walled pits of irregular shape. Remnants of the small plastomenid trionychid *Plastomenoides* also occur in the Kaiparowits Formation. Only plastron elements, which are identified as smooth and lacking in ornamentation, have been identified to date. A fourth trionychid of unknown genus also occurs in the Kaiparowits Formation. Carapace fragments are recognized by a dimpled texture in addition to isolated thin, wavy ridges extending anterio-posteriorly. Species-level designations have yet to be assigned to the known Kaiparowits trionychid genera due to slight differences in skeletal features that distinguish them from one another and from other trionychid species elsewhere in Campanian deposits (Hutchison et al., in press). Living members of the Trionychidae are known to occupy a variety of habitats, including ponds and large streams. Trionychids are known to wallow in the sandy sediments of the riverbed or muddy sediments of the lake bottom for camouflage while feeding (Bonin et al., 2006).

Geologic Setting

The Kaiparowits Formation, which is exposed within the boundaries of Grand Staircase-Escalante National Monument in southern Utah, was first named and partially described by Gregory and Moore (1931). However, Lohrengel (1969) was the first to fully measure and describe the formation in detail. Gregory and Moore (1931) labeled the Kaiparowits Formation as Tertiary in age, whereas palynological work by Lohrengel (1969) and later biostratigraphic work by Eaton (1991) firmly placed the Kaiparowits

Formation in the Late Cretaceous, more specifically the late Campanian. Roberts et al. (2005) reported a more precise age determination using 40Ar/39Ar dating of bentonite horizons within the Kaiparowits Formation indicating an age range of 76.1 – 74.0 Ma. Very recently, an analysis of Kaiparowits Formation facies architecture and depositional environments was conducted by Roberts (2007) to further understand the tectonic and depositional history of the region during the Late Cretaceous.

The Kaiparowits Formation has been thoroughly measured and described multiple times (Gregory and Moore, 1931; Eaton, 1987; Roberts, 2005, 2007). Approximately 860 m thick, the Kaiparowits Formation conformably overlies the Upper Cretaceous Wahweap Formation. An erosional, unconformable contact separates the formation from the overlying Maastrichtian-Tertiary Canaan Peak Formation. One of the thickest units in the Kaiparowits Plateau (Eaton, 1987; Roberts, 2007), the Kaiparowits Formation consists predominantly of fluvial channel and floodplain deposits represented by a variety of lithofacies associations (Roberts, 2007). The clastic material was transported northward from the Mogollon Highlands of southwestern Arizona and eastward from the Sevier orogenic belt of southeastern Nevada and southern California and deposited in a subsiding foreland basin in south-central Utah (Goldstrand, 1992; Lawton et al., 2003). Today, these deposits are seen as impressive grayish-blue badlands exposed within the Kaiparowits Plateau region of Grand Staircase-Escalante National Monument.

Roberts (2007) measured and described several sections of Kaiparowits exposures in Grand Staircase-Escalante National Monument. He subsequently divided the Kaiparowits Formation informally into lower, middle, and upper units based on subtle changes in sandstone-mudstone ratios. Based on his lithofacies identifications, he named nine distinct lithofacies associations (FAs, as used by Roberts, 2007) that comprise the Kaiparowits Formation (Roberts, 2007) (Table 3.1). Each lithofacies association was assigned to a depositional environment along with common fossil inclusions. The distribution of the nine lithofacies varies throughout the Kaiparowits Formation. The approximate abundance of each lithofacies association is estimated on the basis of stratigraphic section KBC (Kaiparowits Blues Ceratopsian) measured and described by Roberts (2007) through the entire thickness of the formation. Of the nine lithofacies associations, five of these contain fossil turtle remains. These five lithofacies associations represent the framework for identifying and distinguishing the dominant fossil turtle-bearing taphofacies in the Kaiparowits Formation. Nevertheless, for the sake of completeness, all nine lithofacies associations (FA 1 – 9) are described below.

FA1 - Intraformational Conglomerate.— Conglomerates, in the form of fluvial channel lag deposits, are uncommon in the Kaiparowits Formation. Both clast-supported and matrix-supported conglomerates are associated with planar and trough cross-stratified sandstones. The matrix-supported conglomerates typically consist of poorly sorted, sub-angular to rounded, granule to pebble-sized clasts of intraformational mudstone or siltstone with a matrix of medium to coarse sand (Roberts, 2007). The clast-supported conglomerates contain a matrix, if present, comprised of coarse sand with granule to boulder-size clasts that are poorly sorted and sub-angular to rounded, consisting of predominantly intraformational mudstone and sandstone (Roberts, 2007).

Fossils within the Intraformational Conglomerate are typically isolated bones, bone fragments, teeth, or invertebrate shell fragments (Fig. 3.3).

Channel lag deposits often consist of pebbles and debris that can damage or destroy fragile bones and modify larger ones (Behrensmeyer, 1988). It is predicted that turtle remains present in these lag deposits should be moderately to heavily abraded, exhibiting rounding of edges and occasional pitting. Burial in channel lags is usually slow, and material can often be re-worked (Behrensmeyer, 1988). Based upon these characteristics, it is predicted that channel lag deposits represent a poor environment for quality preservation of vertebrate skeletal material including that of turtles.

FA2 - Mollusc-shell Conglomerate.— The Mollusc-shell Conglomerate lithofacies association is one of the rarest lithofacies associations identified in the Kaiparowits Formation. It appears as a wedge-shaped or lenticular body of 1 to 3 meters in thickness. Tightly-packed unionid bivalve shells form a clast-supported conglomerate with a matrix of fine to medium sand (Roberts, 2007). Stratification, if present, can sometimes be trough cross-bedded or horizontally-bedded; however, these are often difficult to distinguish. Roberts (2007) interpreted this lithofacies association as a storm-generated, mass mortality event in which a storm surge swept up and deposited thousands of bivalves as large accumulations, thus resulting in suffocation. Although a few bone fragments have been observed in this facies association, no turtle remains have been identified to date.

FA3 - Major Tabular Sandstone.— Meandering fluvial channel deposits are abundant and are the primary depositional environment for major tabular sandstones in the Kaiparowits Formation. Identified by thick sequences of sandstone (typically over 5 meters) the Major Tabular Sandstone lithofacies association is frequently composed of trough cross-bedded or planar cross-bedded deposits of fine to medium-grained sand (Roberts, 2007). It is less commonly composed of massive sandstone, horizontally stratified sandstone, or ripple cross-laminated sandstone. These, however, do occur sporadically (Roberts, 2007). In some instances the Major Tabular Sandstone will contain isolated lenses of intraformational conglomerate. Frequently, thick major tabular sandstones form steep vertical ledges and cliffs in Kaiparowits Formation exposures. Isolated, frequently partially articulated, skeletal remains of several types of vertebrates occur in these deposits, along with fossilized wood and invertebrates (Fig. 3.3).

The fine to medium sands that are deposited in meandering channels are excellent for resisting compaction, which provides protection for skeletal remains (Behrensmeyer, 1988). Burial time can be rapid with high sediment influx and reworking of previously deposited sediment can occur due to the shifting nature of meandering channels (Behrensmeyer, 1988). This movement of the channel also means that turtle remains deposited on the floodplain would occasionally have been swept into the channel as the river cut into floodplain deposits. However, it is predicted that turtle taxa that spent a great deal of time in the river and along the riverbank would have been more commonly deposited in the channels of meandering rivers, and therefore, should be more abundant. Turtles that were entrained and buried quickly had a greater potential for preservation, whereas turtles that were transported for longer periods of time or frequently reworked would have been more susceptible to breakage (Behrensmeyer, 1988).

FA4 - Major Lenticular Sandstone.— The Major Lenticular Sandstone lithofacies association is similar in many aspects to the Major Tabular Sandstone lithofacies association but typically contains less massive sandstone deposits and more frequent intraformational conglomerate lenses, particularly near the base (Roberts, 2007). Trough cross-bedding and planar cross-bedding of fine to medium sand comprises the majority of these deposits. Estimates of channel size range from 3 to 10 meters in bankful depth and 19.5 to 81 meters in bankful width, which is within parameters for measurements of both modern meandering and anastomosing channels (Miall, 1984; Roberts, 2007). Isolated, partially articulated vertebrate remains are frequently discovered in these deposits (Fig. 3.3).

Anastomosing channel deposits share several characteristics with the meandering channel deposits in terms of turtle preservation potential. As with meandering channels, it is predicted that turtles that spent most of their time in and near the anastomosing channels would be represented in greater numbers than those that lived farther away. The distance of transport in anastomosing channels would also affect preservation potential since damage typically increases with exposure duration, as with meandering channels.

FA5 - Minor Tabular or Lenticular Sandstone.— Minor sandstone bodies between 0.2 and 2 meters in thickness are interpreted in the Kaiparowits Formation as crevasse splay and crevasse channels deposited during flood events (Roberts, 2007). Minor tabular sandstones are more extensive and more abundant than minor lenticular sandstones, particularly in the middle unit of the formation. Trough cross-bedded, ripple cross-laminated, and horizontally stratified deposits of fine to medium sand comprise this lithofacies association (Roberts, 2007). Some weakly developed soil horizons are evident as well by the presence of root, burrow, and insect traces. Vertebrate fossil localities in the Minor Tabular or Lenticular Sandstone lithofacies association frequently contain isolated bones and bone fragments along with fossilized wood and leaves (Fig. 3.3).

The crevasse splay and crevasse channel deposits represent an overbank setting where channel sediments are deposited on the floodplain (Miall, 1984). In this setting sedimentation rates can be high for very short periods of time during flooding, whereas individual deposition events are sporadic (Miall, 1984). Within these deposits it is predicted that we should find a mix of river and floodplain turtle taxa. It is predicted that many of the floodplain taxa will show evidence of weathering due to exposure, while many river taxa will exhibit abrasion due to transport (Behrensmeyer, 1988).

FA6 - Finely Laminated, Calcareous Siltstone.— Tabular calcareous siltstone beds range from 10 to 250 cm in thickness in the formation and can be laterally extensive (Roberts, 2007). These finely laminated beds are interpreted as shallow lake or pond deposits with some noticeable bioturbation (Roberts, 2007). Plant fossils are not uncommon, but invertebrate and vertebrate fossils are typically absent. Turtle remains have yet to be recovered from these units.

FA7 - Inclined Heterolithic Sandstone and Mudstone.— Rare in the Kaiparowits Formation, the Inclined Heterolithic Sandstone and Mudstone lithofacies association consists of interbedded sandstone and mudstone beds which are gently dipping and between 7 and 9 meters in total thickness (Roberts, 2007). Fine-grained beds are typically laminated and composed of fine sandy mudstone, whereas coarse-grained beds are often a planar or cross-bedded fine to medium-grained sandstone (Roberts, 2007). Inclined heterolithic stratification is typically associated with tidally influenced rivers in which current energy fluctuates (Shanley et al., 1992). Evidence of lenticular and flaser bedding, draped foresets, and the presence of the marine trace fossil *Teredolites* in pieces of fossilized wood, have been used as evidence to support the interpretation of a tidally influenced channel deposit (Roberts, 2007). No vertebrate fossil remains have been recovered from the Inclined Heterolithic Sandstone and Mudstone, which is only identifiable in the lower parts of the formation.

FA8 - Sandy Mudstone.— Sandy mudstone is one of the most common lithofacies associations in the Kaiparowits Formation and represents overbank floodplain deposits associated small ponds and lakes. Massive siltstone and claystone along with laminated sandstone, siltstone, and claystone comprise the majority of this lithofacies association (Roberts, 2007). Bentonite-rich claystones are also common, and identifiable by a popcorn-like erosional surface texture. Other features, including occasional calcium carbonate nodules, concretions of siderite and pyrite, root traces, and burrows, are indicative of soil development, though the horizons are weakly preserved (Roberts, 2007). A variety of fossil remains can be found in the sandy mudstone including several types of isolated, partial vertebrate skeletons, invertebrates, and carbonized plant fragments.

In floodplain and pond deposits, it is predicted that river turtle taxa would be absent and terrestrial and pond taxa would be in greater abundance (Badgley et al., 1995). Preservation potential is predicted to be lower due to reduced sedimentation rates and higher potential for weathering of exposed skeletal materials, especially for larger taxa that require greater time for burial (Badgley et al., 1995). It is also predicted that abrasion should be absent from floodplain turtle specimens due to a lack of transport opportunity. The muddy sediments comprising these deposits would offer little protection from post-depositional compaction, so complete, intact turtle shells in these deposits would be rare.

FA9 - Carbonaceous Mudstone.— The Carbonaceous Mudstone lithofacies association is rare in the Kaiparowits Formation, but where it occurs, it is usually lenticular and overlying the Sandy Mudstone lithofacies association (Roberts, 2007). Bentonites and dark, organic-rich beds are not uncommon in this lithofacies association, but fossil content is highly variable, with carbonized plant fragments, freshwater molluscs, teeth, and fish scales comprising the majority of fossil material in the Carbonaceous Mudstone. Turtle remains are notably absent from this lithofacies association, likely due to slow sedimentation rates in this environment. The carbonate mudstone association has been interpreted as representing a swamp-like pond environment on the floodplain, perhaps formed in abandoned channels (Roberts, 2007).

Turtle Taphonomy Hypotheses

Based upon previous knowledge of Kaiparowits turtle morphology and the nature of Kaiparowits Formation sedimentology, several hypotheses (H) regarding turtle taphonomy were developed. These hypotheses are divided into three groups; 1) based on turtle anatomy or morphology, 2) depositional environment, and 3) turtle ecology. Hypotheses based on turtle anatomy and morphology include: (H1) larger turtle shells (i.e. *Neurankylus*, *Basilemys*, and *Adocus*) will be more abundant and better preserved than smaller shells (i.e. *Compsemys*, kinosternids, and chelydrids) due to greater shell thickness; and (H2) turtle shells that have a strong, durable construction (i.e. baenids) will be preserved intact more often than shells that have a weak construction (i.e. *Compsemys*, kinosternids, chelydrids). Hypotheses based on depositional environment include: (H3) preservation quality will be poor (higher fragmentation) in environments with slow deposition rates (i.e. FA8) due to longer exposure prior to burial, and preservation quality will be better (more intact shells) where deposition rates are higher (i.e. FA3, FA4, and FA5); (H4) evidence of abrasion should be more prevalent on turtle specimens found in channel deposits (i.e. baenids, adocids, and trionychids), whereas evidence of weathering should be prevalent on specimens collected from floodplain deposits (i.e. *Basilemys* and *Compsemys*); and (H5) small turtles (i.e. *Compsemys*, kinosternids, and chelydrids) will be rare in channel deposits due to increased potential of shell destruction due to abrasion, and remains of larger turtles (i.e. baenids and adocids) will be common. Finally, hypotheses based on turtle ecology include: (H6) a turtle taxon will occur in greater abundance and in better condition in depositional environments that represent the preferred habitat of that taxon when alive; and (H7) abundance of a turtle taxon should decrease in depositional environments as you move away from the preferred habitat. In other words, turtles that are assumed to prefer riparian habitats (i.e. baenids and adocids) should be well-preserved and abundant in river channel deposits (i.e. FA3, FA4, and FA5) and decrease in abundance in more distal portions of the floodplain (i.e. FA8). Conversely, turtles that are presumed to inhabit the floodplain (i.e. *Compsemys*, kinosternids, chelydrids, and *Basilemys*) should be well-preserved and abundant in floodplain deposits (i.e. FA8) (relative to the channel deposits) and be less uncommon in channel deposits (i.e. FA3, FA4, and FA8) (relative to floodplain deposits).

METHODS

This project includes the collection of taphonomic data from both museum curated specimens as well as specimens studied *in situ* in the Kaiparowits Formation. All information was assembled in order to generate a comprehensive list of Kaiparowits Formation turtle specimens and associated taxonomic, taphonomic, and lithologic data. The methods for collecting this information are described below.

Museum Collection Data

The majority of previously collected fossil freshwater turtles from the Kaiparowits Formation are housed in the collections of the Natural History Museum of Utah (formerly Utah Museum of Natural History - UMNH), Brigham Young University (BYU), and the University of California Museum of Paleontology (UCMP). Each of these institutions was visited in order to record taxonomic and taphonomic information. Information recorded for each catalogued specimen includes taxonomic identification, specimen completeness, original specimen locality information, notes regarding observable abrasion and weathering, as well as any information regarding associated fossils or original sedimentary matrix.

Taxonomic identification for each turtle specimen, both in the museum and in the field, was recorded at the genus level or higher due to a lack of detailed taxonomic analysis for many Cretaceous turtle families and diagnostic material which permits further identification. For this analysis, the turtle taxa were predominantly grouped together in order to reduce complexity in the dataset. The groups are comprised of common family members, or at least commonly shared morphological characteristics. The Baenid Group included *Boremys*, *Denazinemys*, *Neurankylus*, *Plesiobaena*, and other unknown baenids. The Trionychid Group included *Aspideretoides*, *Helopanoplia*, *Plastomenoides*, and other trionychids. *Adocus* and *Basilemys* were placed in their own individual groups as they are morphologically unique and the only representatives of their respected families. The remaining turtles (kinosternids, chelydrids, and *Compsemys*) were placed into the Small Turtle group because of their similar size and also because living members of these families are frequently found in association (Bonin et al., 2006).

For each specimen in collections, an assessment of preservation quality was given based primarily on skeletal completion (primarily the turtle shell). For specimen completeness, each turtle specimen examined was categorized into four groups. The Complete Shell Group includes the best-preserved specimens and includes complete turtle skeletons, those with an entire shell plus a partial skeleton, and those that possess only a complete shell without other skeletal elements. The Partial Shell Group includes specimens with at least a partially intact carapace and/or plastron (between 99% and 50% of the shell). The Shell Portions Group includes turtle specimens comprised of large pieces of the carapace or plastron and/or isolated, complete skeletal material that makes up less than half of the complete turtle. Finally, the Shell Fragments Group is comprised of fragmentary turtle specimens, typically comprising pieces of the carapace and/or plastron.

A quantitative assessment of abrasion and weathering was not attempted at this time due to the high amount of variation for each specimen, the possibility that specimens may have experienced additional modification after exposure prior to collection, as well as to avoid any observational bias in determining amounts of modification, however general notes were recorded on preliminary observations. Abrasion was recognized as rounding of edges and corners of turtle elements. Weathering was recognized by a reduction in surface texture of shell elements and/or absence of the cortical layer. A quantitative assessment of abrasion and weathering of turtle elements with well-defined abrasion and weathering stages would likely prove valuable in future taphonomic studies.

Lithofacies association data was mostly absent from museum specimens. Unfortunately, most specimens even lacked any information regarding the original sedimentary matrix; however several turtles were examined prior to complete matrix removal and preparation for storage with limited information recorded. In many instances, specimens collected within the past 20 years included locality information and GPS coordinates. For most of these turtle specimens, an attempt was made to re-locate their original sites of collection to identify the original lithofacies in which they were recovered. Most handheld GPS devices are accurate to only within about 5 meters with good satellite reception. This was taken into account and unless evidence of collection could be identified in the field, many specimens were recorded in the dataset without lithofacies association data.

Field Collection Data

Four field seasons permitted collection of new fossil turtle specimens and *in situ* taphonomic data. This fieldwork proved extremely useful for obtaining greater familiarity of various lithofacies associations of the Kaiparowits Formation. Indeed, several new fossil turtle specimens were discovered and collected by myself, in addition to field crews from the Bureau of Land Management (BLM), Natural History Museum of Utah, and Raymond Alf Museum. For each new fossil turtle specimen that was viewed *in situ*, information regarding the taxonomic identification and specimen completeness was recorded. Of additional importance, however, was the documentation of the *in situ* specimen orientation for those specimens that possessed a shell, along with a detailed description of the surrounding lithofacies. Orientation data, measured with a Brunton compass, included strike and dip of the turtle shell using the plastron as a plane of reference. This data was used for a separate study on turtle shell transport and deposition trends (Knell, in preparation).

The lithofacies association for each turtle locality observed in the field was based upon the primary lithofacies from which the turtle specimen originated. A single lithofacies can be matched to multiple lithofacies associations, so the placement of the lithofacies had to be examined in a larger context with the surrounding deposits. Only by identifying the surrounding lithofacies and associated sedimentary structures could the lithofacies association be matched with those identified by Roberts (2007). Identifying the lithofacies association of each turtle locality was important for establishing the environment of deposition; therefore this was recorded for as many turtle specimens as possible.

RESULTS

In total (collections data and field data), taxonomic and taphonomic information was collected for 465 Kaiparowits turtle localities comprising 700 fossil turtle specimens. Some localities consisted of a single specimen while others were comprised of a mix of multiple turtle taxa. All of the available information for each turtle locality with associated specimens was compiled into a spreadsheet for analysis (Appendix A). Of the 465 Kaiparowits turtle localities recorded, 182 with *in situ* turtle remains were examined or were re-located using GPS data and assigned to lithofacies associations based on Roberts (2007).

Turtle Taxa - Preservation Relationships

Comparisons of Kaiparowits turtle specimens revealed patterns of similar preservation condition within taxonomic groups (Table 3.2). For the Small Turtles and *Basilemys*, nearly all specimens collected are fragmentary. There are currently no complete shells collected from the Kaiparowits Formation for kinosternids, chelydrids, *Compsemys*, or *Basilemys*. Fragmentary specimens are also common for baenids, adocids, and trionychids. Trionychids and *Adocus* follow a similar trend with several specimens identified as having shell portions, fewer having partial shells, and only a handful with complete shells. Complete *Adocus* shells from the Kaiparowits Formation can be remarkably well-preserved, with high retention of morphologic detail. One specimen in particular includes a partial skeleton and skull within the shell, along with a few fossilized eggs, representing one of only a three known fossil gravid turtles in existence (Knell et al., 2011). Well preserved trionychid shells may include the complete carapace and associated plastron, which is unfused to the carapace in this family. It is rare to find the plastron in complete articulation, but multiple Kaiparowits trionychid specimens that have complete shells or partial shells possess associated intact plastron elements. Among all of the Kaiparowits turtle families, baenids have the most unusual preservation pattern. It would be expected that the majority of baenid specimens would be found as fragments and the number of more complete specimens would decrease in a similar pattern as seen with *Adocus* and the trionychids. However, only half of all baenids in this study are represented as fragmentary specimens, and nearly a third are partial or complete shells. According to the data, baenids occur intact more often than representatives of other turtle families.

Bone modification (abrasion and weathering) patterns are not evident among the various turtle taxonomic groups. There are, however, a few trends that were noted after examining 700 turtle specimens. The shell fragments of the Small Turtle Group often retain much of their original morphology and rarely exhibit signs of weathering or abrasion. *Basilemys* specimens frequently include pieces of the bridge, which connects the plastron to the carapace, and many of these pieces exhibit worn, textured surfaces or rounding. Larger shell fragments (usually belonging to *Neurankylus*) often show evidence of rounding and sometime surface cracking, which may be caused by exposure prior to burial. Interestingly, the smaller the turtle size, the least likely the fragments were to exhibit weathering or abrasion, whereas larger-sized fragments were more often modified.

Lithofacies Association - Preservation Relationships

The specimen completeness, or average specimen completeness if multiple taxa were present, for 182 fossil turtle localities in the Kaiparowits Formation was compared to the lithofacies association in which they occurred (Table 3.3). Distinct differences in skeletal completeness characterize different lithofacies associations. In the FA1 - Intraformational Conglomerate, FA5 - Minor Tabular or Lenticular Sandstone, and FA8 - Sandy Mudstone fragmentary remains are by far the most commonly representative turtle fossils. Only fragments are present in FA1 - Intraformational Conglomerate, whereas some larger pieces of turtle shell and perhaps even partial to full shells occur in the FA8 - Sandy Mudstone, but not typically. Partial shells (i.e. 50 and 99% complete) are commonly present in the FA3 - Major Tabular Sandstone and FA4 - Major Lenticular Sandstone, with some occurring in the FA8 - Sandy Mudstone as well. Complete turtle shells and those specimens with additional, articulated skeletal elements are more commonly present in the FA3 - Major Tabular Sandstone and occasionally in the FA8 - Sandy Mudstone.

Bone modification, including weathering and abrasion, was more prevalent on turtle specimens from certain lithofacies associations than others. All specimens collected from the FA1 - Intraformational Conglomerate had at least some rounding. In contrast, complete turtle shells collected from the FA3 - Major Tabular Sandstone and FA4 - Major Lenticular Sandstone typically displayed very little rounding; however, several fragmentary specimens possessed rounded edges. Specimens collected in FA8 - Sandy Mudstone usually exhibited no evidence for rounded edges, often retaining original morphology and texture. Evidence of weathering was not commonly observed in the Kaiparowits turtle specimens overall. Some shell fragments from the FA5 - Minor Tabular or Lenticular Sandstone and a few larger specimens from the FA8 - Sandy Mudstone exhibited surficial cracking, which could indicate exposure to weathering prior to burial. However, this was not prevalent for all specimens in those lithofacies associations.

Turtle Taxa – Lithofacies Association Relationships

Of the approximately 700 turtle specimens examined for this study, nearly half (315) have lithofacies information useful for interpretation of depositional environment (Table 3.4). Of the five lithofacies associations that are known to contain turtle remains, just over half of Kaiparowits fossil turtles are recovered from FA5 - Minor Tabular or Lenticular Sandstone. Interestingly, this lithofacies association encompasses only about 10% of the entire Kaiparowits Formation. The FA1 - Intraformational Conglomerate comprises only about 5% of the Kaiparowits Formation, and only two turtle specimens have been collected directly from these conglomerates. Turtle specimens from FA3 - Major Tabular Sandstone, FA4 - Major Lenticular Sandstone, and FA8 - Sandy Mudstone are not uncommon, and they are nearly equally abundant among these lithofacies associations.

A chi square test was performed using 312 turtle specimens and their associated lithofacies associations to determine if there was a statistical link between the turtle families and their depositional environments. Three specimens (of the original 315) of unknown family designation were omitted from this test. A 7x5 grid was constructed using the seven turtle families represented in the Kaiparowits Formation and the five lithofacies associations that are known to contain turtle remains (Table 3.5a). The number of degrees of freedom is 24 [(7 rows – 1) x (5 columns – 1)]. Based on the number of turtle family occurrences for each lithofacies association from Table 3.4, the number of expected occurrences is determined based on the percentage of each lithofacies association in the Kaiparowits Formation (Table 3.5b). The chi square number for this set of data is calculated to be 75.12 (Table 3.5c). Using chi square probability charts for 24 degrees of freedom and a chi square number of 75.12 the p value is basically 0. This means that there is nearly zero probability that the turtle families are independent of their depositional environment. Therefore, a direct link exists between each turtle family and the lithofacies association in which they are recovered; the nature of this link requires further analysis.

Comparison of each lithofacies association containing turtle taxa reveals some interesting patterns. Only one small turtle (*Compsemys*) occurs in the FA3 - Major

Tabular Sandstone, with no kinosternids or chelydrids. *Basilemys* has a single appearance in FA3 - Major Tabular Sandstone as well. Only a few trionychids occur in contrast to all known genera of baenids and several *Adocus*. Comparison of these taxa abundances with those from the FA8 - Sandy Mudstone shows nearly the opposite trend. In the FA8 - Sandy Mudstone baenids are rare; fewer numbers of *Adocus*, and the trionychids and *Basilemys* are in slightly greater numbers in comparison to the FA3 - Major Tabular Sandstone. The smaller turtles (*Compsemys*, kinosternids, and chelydrids) appear to be a major component of the FA8 - Sandy Mudstone taxa. In the FA4 - Major Lenticular Sandstone there is some similarity in turtle taxa abundance to the FA3 - Major Tabular Sandstone; however more taxa are more abundantly represented. Very few specimens of small turtles and *Basilemys* characterize the FA4 - Major Lenticular Sandstone, whereas there are slightly more trionychids and *Adocus* than in the FA3 - Major Tabular Sandstone. FA4 - Major Lenticular Sandstone shows a slight drop in diversity and total numbers of baenids compared to the FA3 - Major Tabular Sandstone, but baenids are not rare.

As stated earlier, the FA5 - Minor Tabular or Lenticular Sandstone contains the majority of the Kaiparowits turtle specimens, which are characterized by high diversity. *Adocus*, *Basilemys*, and some trionychids are present in relatively high abundance. Baenids are not uncommon as a family, whereas *Denazinemys* and *Neurankylus* represent more common genera. Remains of smaller turtles are not rare, with several specimens of kinosternids and chelydrids having been collected from this lithofacies association. A discernible pattern is evident which links turtle taxa and common lithofacies association.

Baenids and *Adocus* are more frequently recovered in the FA3 - Major Tabular Sandstone, FA4 - Major Lenticular Sandstone, and FA8 - Sandy Mudstone lithofacies associations. The smaller turtles and *Basilemys* are more commonly collected in the FA8 - Sandy Mudstone lithofacies association. Trionychids, as a family, are more dispersed among the different lithofacies associations, but some genera more commonly occur in FA8 - Sandy Mudstone while others are more common in FA3 - Major Tabular Sandstone or FA4 - Major Lenticular Sandstone.

Turtle Fossil Associations

Out of 465 Kaiparowits turtle localities, 179 consist of an association of multiple turtle taxa. Of these 179 localities, 67 include lithofacies association data. The majority of these localities (64 of 67) consist of fragmented specimens, which are more common in the FA5 - Minor Tabular or Lenticular Sandstone (N = 41) and FA8 - Sandy Mudstone (N = 13) lithofacies associations. Some turtle taxa in particular occur in association with other taxa on a regular basis. For instance, all three small turtles (*Compsemys*, kinosternids, and chelydrids) were recovered in association in 11 localities (1 in FA4 - Major Lenticular Sandstone, 4 in FA5 - Minor Tabular or Lenticular Sandstone, 1 in FA8 - Sandy Mudstone, and 5 unknown), and any two of the three taxa were associated in 46 localities (9 in FA5 - Minor Tabular or Lenticular Sandstone, 5 in FA8 - Sandy Mudstone, and 32 unknown). For the baenids and trionychids, multiple genera from the same family were often recovered from the same locality. In the meandering channel and anastomosing channel lithofacies associations, partial and complete turtle shells almost always occur in isolation. There are at least four localities in the Kaiparowits Formation where a complete turtle shell was discovered with articulated dinosaur remains; however, there were only one or two instances where a turtle was found in association with other intact turtles. There are also multiple instances (N = 8) of turtle shells identified in close association with large pieces of fossilized wood, and these occurred in FA3 - Major Tubular Sandstone, FA4 - Major Lenticular Sandstone, and in FA5 - Minor Tabular or Lenticular Sandstone.

DISCUSSION

Preservation Trends of Kaiparowits Turtles

The comparison of turtle taxa with preservation quality shows a taphonomic bias that affects certain taxa over others, based on the size and shape of the turtle. Some turtle taxa are frequently collected in good condition, while others are almost always fragmentary. Examination of the five turtle groups (baenids, adocids, trionychids, *Basilemys*, and small turtles) reveals that size and morphology are important controls on preservation potential.

Baenids.—Baenids are some of the most commonly found fossil freshwater turtles in the Kaiparowits Formation. This is not necessarily because they were more abundant in the Campanian (even though they were diverse), but more likely this abundance reflects taphonomic bias that has aided their preservation. The baenid shell is particularly robust and would have been particularly resistant to breakage during transport in fluvial channels after death, thus increasing the potential for preservation of an intact shell when buried in a short amount of time.

Neurankylus is one of the two largest turtles known from the Kaiparowits Formation. Complete and nearly complete shells of *Neurankylus* are known from the Kaiparowits, whereas cranial and appendicular remains are sparse. Due to the size of this baenid and its lack of carapace surface texture, nearly all smooth, large or thick fragments of turtle shell collected from the Kaiparowits are assigned to *Neurankylus*. There are at least two species of *Neurankylus* that are recognized in the formation; however identification of these species requires the preservation of specific, complete elements and these are uncommon. It may be possible that these two species of *Neurankylus* represent the sexually dimorphic forms of the same species, thus requiring additional specimens and analysis. Large pieces of *Neurankylus* shell exhibit signs of abrasion and weathering more often than those from other baenid genera. This is probably due to the durability of shell fragments that survive re-working and long exposure time without complete destruction prior to final burial.

Adocids.— Although adocid turtles, represented by the genus *Adocus* in the Kaiparowits Formation, are not as common as the baenid turtles, they are still rather abundant. Multiple complete and partial *Adocus* shells have been collected, including a few that are particularly well-preserved. However, the majority of *Adocus* specimens are recovered as fragments or shell portions. The shell of *Adocus* is not as strongly constructed as that of most baenids, increasing vulnerability to breakage during transport. The shell of an adult is fairly large, although the thickness is not great, with weaker bridges between the carapace and plastron. The texture of the carapace is fairly distinguishable in the field from other taxa, therefore many *Adocus* fragments can be found in museum collections. Evidence of abrasion and weathering is present on many *Adocus* fragments indicating that several specimens were exposed and/or transported for long periods prior to burial.

Trionychids.— Trionychids are the most commonly collected turtle specimens in the Kaiparowits Formation. Within the family, *Aspideretoides* specimens greatly outnumber *Helopanoplia* and plastomenid trionychids. The vast majority of trionychid specimens are fragments, typically pieces of the carapace. The texture on these carapace fragments is diagnostic for differentiating the different trionychid genera. However, some ontogenetic changes in carapace texture may be overlooked resulting in misidentifications, thus warranting further taxonomic investigation. Only a few complete *Aspideretoides* and *Helopanoplia* carapaces have been recovered to date. The large, flat morphology of trionychid shells facilitates burial under the right conditions, thus increasing preservation potential. But the lack of structural support provided by a bridge and fused plastron, increases the breakage potential of the carapace. Only rapid burial would prevent a trionychid carapace from breaking, which may explain why intact specimens are so uncommon. Very few partial trionychid plastrons occur in association with the carapace because they were never directly fused, therefore hyo- or hypoplastron elements are more commonly recovered in isolation. Even though the trionychid shells are susceptible to separation and breakage, their pieces and fragments are typically recovered with only moderate to light amounts of abrasion or weathering.

Basilemys.— The “tortoise-like” *Basilemys* (Hutchison, 2000) is one of the most uncommon turtles in the Kaiparowits Formation. Complete shells are absent and only a few partial shells are known. Although one of the largest turtles known in the Kaiparowits Formation, the majority of *Basilemys* remains are fragments, some quite large. *Basilemys* has a very distinctive and pronounced texture on the carapace and plastron that is easily recognized and distinguishable from *Neurankylus*. Though the shell of *Basilemys* is large, it is not as well constructed as some baenid shells, which suggests that it may have broken apart rather easily during fluvial transport. Many *Basilemys* fragments consist of pieces of the bridge between the carapace and plastron, which is the thickest part of the entire shell and the most resistant to breakage. However, nearly all of these fragments exhibit signs of weathering and abrasion indicating prolonged exposure.

Small Turtles.— The small turtles of the Kaiparowits Formation are uncommon when compared to the number of specimens of baenids, adocids, and trionychids. Of the small turtles, *Compsemys* is the most common and also estimated to be the largest. *Compsemys* is also the only Kaiparowits small turtle for which a partial shell has been recovered. Kinosternids and chelydrids are only represented by fragmentary remains. Although a few limb elements from small turtles have been collected, most remain unassigned to a particular genus. Nearly all of the fossil remains of the small turtle group consist of carapace and plastron fragments. The three taxa of small turtles are easily distinguished by differences in carapace texture, which is usually well-preserved. Costal fragments are the most commonly collected elements for *Compsemys* and kinosternids. For the chelydrids, carapace peripherals are easily recognizable in the field. Plastron fragments of each taxon are a bit more difficult to discern due to similarity in size. Unlike the other turtle groups, the fragments of small turtles in the Kaiparowits Formation are frequently recovered in excellent condition with little to no abrasion or weathering.

Summary of Turtle Preservation Trends

A correlation between turtle size and preservation potential is evident from the taphonomic data available for Kaiparowits turtles. Large turtles, like *Neurankylus* and *Basilemys*, frequently occur as fragments, but some intact shells are recovered within channel deposits. The durability of these large turtle shell fragments ensures that they survive re-working and exposure without complete destruction; however, they frequently exhibit signs of abrasion and weathering. Baenids and adocids, though not the largest turtles, have well-constructed shells, which allows them to survive intact within channels until final burial and explains why complete shells of these taxa are relatively common in the Kaiparowits Formation. Trionychid carapaces frequently occur as fragments, suggesting that they are easily broken if transported or exposed. Small turtles only occur as fragments due to weak shell construction, but individual fragments are frequently well-preserved, indicating very little transport and/or exposure prior to deposition.

Kaiparowits Turtle Paleoecology

The environment of deposition has a large impact on turtle preservation; and how that turtle comes to rest in that depositional environment is largely controlled by the turtle’s habitat preferences and behavior. For extant turtle families it is possible to infer the paleoecology of their extinct relatives based on observing living members. For families that are extinct it becomes necessary to infer their paleoecology based upon depositional environments. Based upon the taphonomic evidence, the Kaiparowits turtles can now be grouped by inferred habitats (Table 3.6).

River Turtles.— River turtles of the Kaiparowits Formation include all of the baenids, *Adocus*, and the larger trionychids. Of these taxa, only the trionychids have living relatives, which are known to occupy river environments. However, based on comparative morphology of baenids and *Adocus* to living relatives, these turtles likely preferred a riparian habitat. Taphonomic evidence supports the morphologic evidence by revealing that these turtles are frequently found within channel and overbank deposits. Baenids and adocids likely inhabited these riparian environments. The number of baenid and *Adocus* occurrences in meandering and anastomosing channel deposits is higher compared to floodplain deposits. This would suggest that there were greater numbers of baenid and *Adocus* turtles near the channels than farther away on the distal floodplain or in ponds. The greater number of well-preserved baenid and *Adocus* specimens in the meandering stream deposits, some with articulated skeletal elements, suggests that several of these turtles were deposited and buried quickly after death. This required them to be either in the channel or in close proximity to the channel at the time of death. The *Denazinemys* carapace has is more arched than other baenids, which is atypical for riparian turtles; however, the large number of specimens recovered from fluvial deposits suggests that it spent much of its time in rivers. The lower carapace profile of *Neurankylus*, *Boremys*, *Plesiobaena*, and the trionychids, would allow them to sit on the bottom of the river channel and be less affected by river current. The trionychids in particular probably wallowed in the river channel bottom as extant trionychids do for camouflage (Bonin et al., 2006). If all of these river taxa existed together at the same time, they must have avoided competition in the ecosystem. There was likely some overlap in dietary preferences among these river turtle taxa, but the exact nature of those preferences remain unknown. All were likely omnivorous or dominantly carnivorous, based upon their skull morphology. In any case, food resources must have been plentiful in order to allow so many river turtles to live in such close quarters, assuming they did.

Pond Turtles.— Compsemys, kinosternids, chelydrids, and the smaller trionychids are found more commonly in overbank, floodplain, and pond deposits, supporting a pond and/or lacustrine habitat for these taxa. Preservation in floodplain deposits is typically poor. These taxa are more frequently recovered as fragments in the floodplain and pond deposits, rather than the channel deposits, thus indicating greater numbers in these environments. Living chelydrids and kinosternids are known to inhabit small lakes and ponds (Bonin et al., 2006), so it is likely that their ancient relatives also preferred quiet water environments. All of these turtles were small in size and were probably proficient swimmers. Since *Compsemys* is typically found in association with kinosternids and chelydrids, it is likely that they also spent much of their time in similar habitats. Although these turtles may have been good swimmers based on their limb morphology, it is unlikely that they spent much time in river channels, where the current was stronger and there was more competition for food, due to their small size. The smaller trionychids, such as *Plastomenoides*, were likely more at home in ponds than river channels, though larger trionychids likely spent time in these ponds as well based on the habitats of extant species (Bonin at al., 2006). In terms of diet, living chelydrids are carnivorous while kinosternids are more omnivorous (Bonin at al., 2006). It is possible that their Kaiparowits relatives had similar diets; however, skull material from these taxa is inadequate to postulate about dietary preferences.

The lack of turtle remains in shallow lake and oxbow lake depositional environments in the Kaiparowits Formation is peculiar because these environments would likely be well suited for freshwater turtles. However, shallow lakes and oxbow lakes comprise 2% and 6% of the formation respectively, so a lack of turtle specimens may be due to an absence of abundant deposits representing these environments. Another possibility is that these deposits were frequently re-worked and many vertebrate remains were subsequently destroyed. It would not be surprising, however, if future concentrated examinations of these deposits revealed an increased presence of vertebrate remains, including turtles, in these environments.

Terrestrial Turtles.— The only turtle that seems to fit with a terrestrial habitat is the “tortoise-like” *Basilemys* (Hutchison, 2000). The robust limb morphology of *Basilemys* suggests it was not a great swimmer; therefore it is not surprising that channel specimens are rare. It would be expected that if *Basilemys* lived on the floodplain or near ponds there would be a greater number of specimens recovered from floodplain deposits, but this is not the case. The actual habitat of this turtle (possibly an upland habitat) may be an environment that is not well preserved in the Kaiparowits Formation. The *Basilemys* remains that occur in the Kaiparowits Formation are typically fragmented, weathered, and abraded, suggesting that elements were often exposed and transported prior to final burial. Many of these remains were likely swept into river channels from the floodplain and often re-deposited in the form of crevasse splays.

CONCLUSIONS

1. The freshwater turtles of the Kaiparowits Formation are abundant and diverse, representing a variety of morphologies and preferred habitats.
2. The preservation potential of freshwater turtles is dependent on the morphology of the turtle, the environment of deposition, and the habitat preference of the turtle, and these factors can often work together to increase or reduce preservation potential.
3. The preferred habitats of the Kaiparowits turtles have been inferred based on the greatest number of skeletal occurrences in a designated depositional environment and a decrease in abundance of skeletal material in depositional environments representing habitats that are less preferable.
4. Turtles found within channel lag deposits are rare, typically fragmented, highly abraded, and often represent larger taxa.
5. In meandering river channel deposits, many well-preserved turtles can be recovered due to high sedimentation rates, and these taxa are often from riparian habitats.
6. Overbank crevasse splay and crevasse channel deposits contain a diverse assemblage of both river and floodplain turtle taxa. Although well-preserved specimens do occur, many of these specimens are poorly preserved due to abrasion caused by transport or prolonged exposure prior to burial.

7. Floodplain and pond deposits are dominated by turtle taxa that prefer these habitats; however, slow sedimentation rates reduce the potential for well-preserved specimens.

8. All baenid and *Adocus* turtles occur more frequently in channel deposits than floodplain deposits indicating a preference for riparian habitats, and they are also more often recovered in better condition than smaller turtles due to their larger size and solid shell construction.

9. Trionychid turtles occur frequently in both channel and floodplain deposits, indicating no preference for either habitat; however larger trionychid taxa more often occur in channels while smaller taxa are more frequently recovered in floodplain deposits.

10. The smallest turtles in the Kaiparowits Formation are typically recovered together in floodplain and pond deposits indicating a preference for quiet water habitats. Preservation of these taxa is poor due to their small size and weakly constructed shells.

11. The “tortoise-like” *Basilemys* has many terrestrial turtle characteristics and is rare in channel and floodplain deposits, possibly indicating that this turtle preferred other habitats.

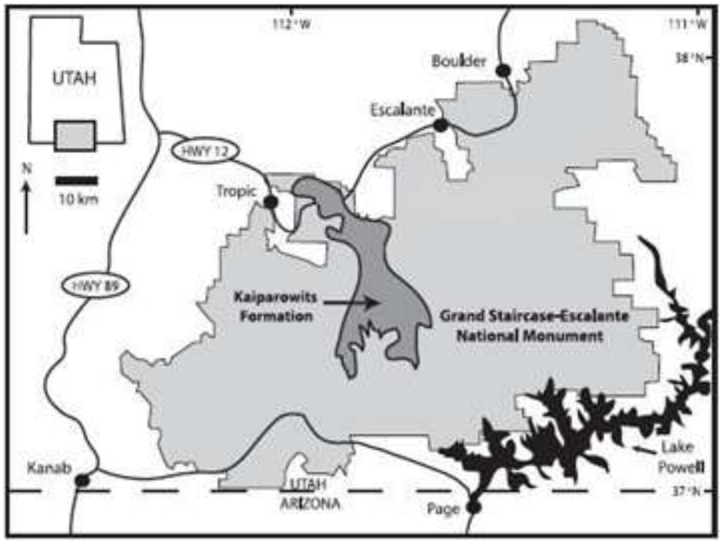


FIGURE 3.1—Map of Kaiparowits Formation outcrops within Grand Staircase-Escalante National Monument in southern Utah. (Modified from Roberts et al., 2005)

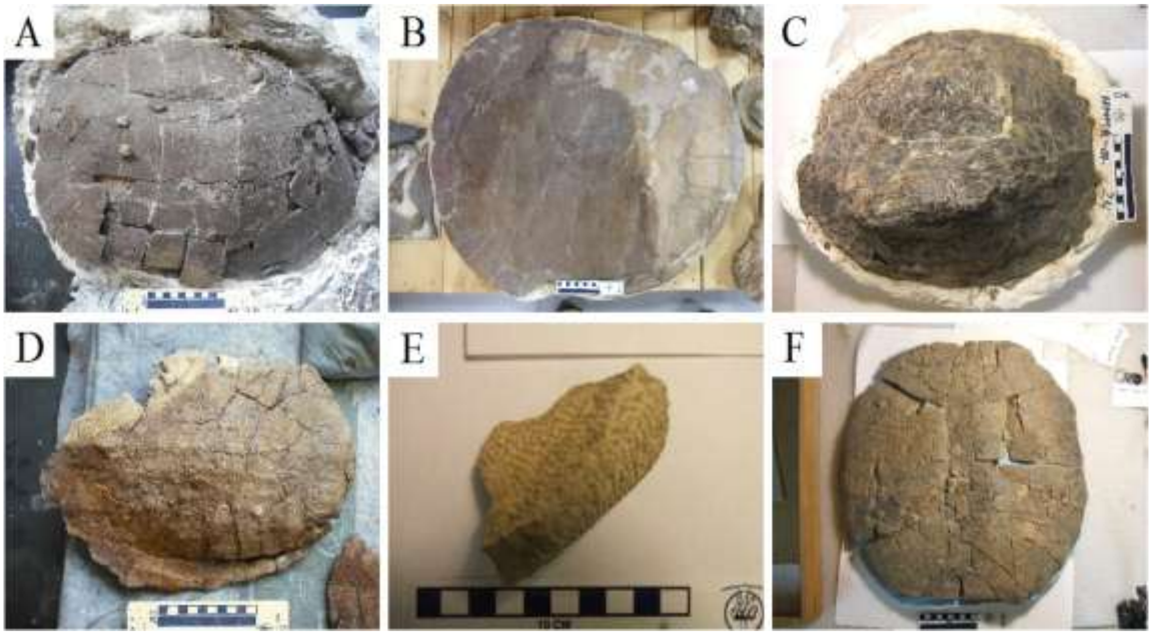


FIGURE 3.2—Photos of common Kaiparowits fossil turtles. (A) *Adocus* (UMNHVP 20452); (B) *Neurankylus* (BYU 12001); (C) *Denazinemys* (Field# HMMA-09-24); (D) *Plesiobaena* (UMNHVP 20451); (E) *Basilemys* bridge fragment (UMNHVP 11798); (F) *Aspideretoides* (UMNHVP 17026).

TABLE 3.1—Roberts (2007) Kaiparowits Formation lithofacies associations and interpreted environments. Lithofacies association abundance is estimated from KBC section measurements and descriptions by Roberts (2007).

LA	DESIGNATION	INTERPRETED DEPOSITIONAL ENVIRONMENT	LITHOFACIES ASSOCIATION ABUNDANCE (% OF KAIPAROWITS FM)	FOSSIL TURTLES PRESENT?
FA1	INTRAFORMATIONAL CONGLOMERATE	FLUVIAL CHANNEL LAGS	5%	YES
FA2	MOLLUSC-SHELL CONGLOMERATE	STORM-GENERATED MASS MORTALITY SHELL BEDS	2%	NO
FA3	MAJOR TABULAR SANDSTONE	DOMINANTLY MEANDERING FLUVIAL CHANNELS	28%	YES
FA4	MAJOR LENTICULAR SANDSTONE	DOMINANTLY ANASTOMOSING FLUVIAL CHANNELS	15%	YES
FA5	MINOR TABULAR OR LENTICULAR SANDSTONE	CREVASSE SPLAYS AND CREVASSE CHANNELS	10%	YES
FA6	FINELY LAMINATED, CALCAREOUS SILTSTONE	SHALLOW LAKES	2%	NO
FA7	INCLINED HETEROLITHIC SANDSTONE AND MUDSTONE	TIDALLY INFLUENCED FLUVIAL CHANNELS	1%	NO
FA8	SANDY MUDSTONE	FLOODBASIN PONDS, LAKES, AND WEAKLY DEVELOPED PALEOSOLS	31%	YES
FA9	CARBONACEOUS MUDSTONE	BACKSWAMPS AND OXBOW LAKES	6%	NO

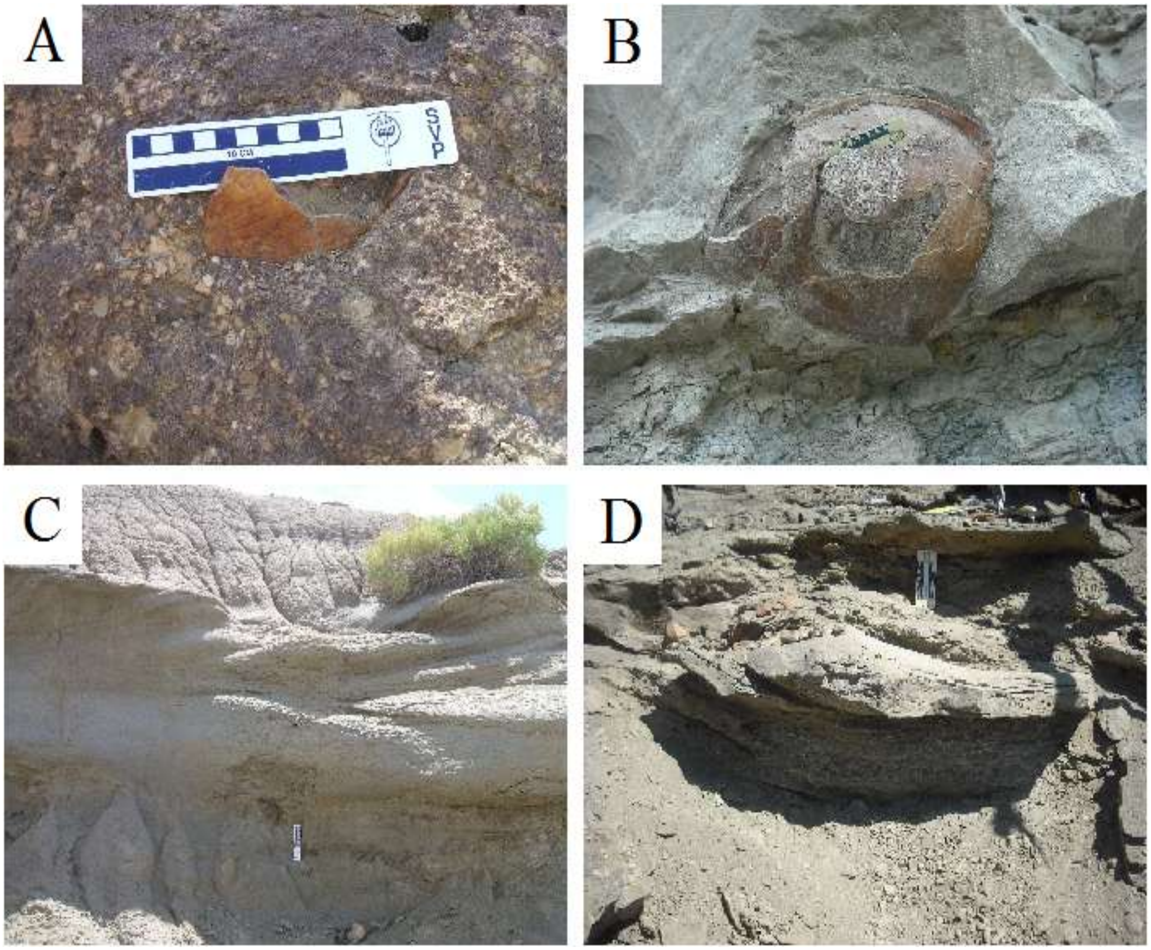
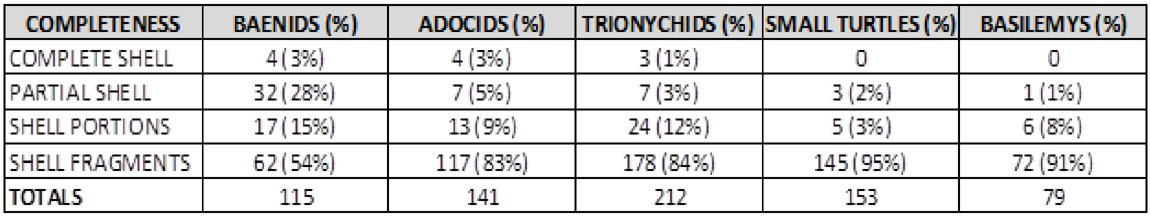


FIGURE 3.3—Examples of some lithofacies associations with in situ fossil turtle remains. (A) Intraformational Conglomerate (FA1) with a turtle plastron fragment. (B) Major Tabular Sandstone with a *Neurankylus* shell. (C) Major Lenticular Sandstone with a *Denazinemys* shell (dark object in center, scale bar = 10 cm). (D) Minor Tabular or Lenticular Sandstone with a partial *Denazinemys* shell and other bone fragments (shell is left of center).

TABLE 3.2—Table of turtle specimen completeness and taxa grouping. Turtle taxa are grouped by family (common shell morphology) or size of shell. Number of specimens for each completeness assessment is given along with percentage of specimens per each assessment. Total number of turtle specimens is 700.



COMPLETENESS	BAENIDS (%)	ADOCIDS (%)	TRIONYCHIDS (%)	SMALL TURTLES (%)	BASILEMYS (%)
COMPLETE SHELL	4 (3%)	4 (3%)	3 (1%)	0	0
PARTIAL SHELL	32 (28%)	7 (5%)	7 (3%)	3 (2%)	1 (1%)
SHELL PORTIONS	17 (15%)	13 (9%)	24 (12%)	5 (3%)	6 (8%)
SHELL FRAGMENTS	62 (54%)	117 (83%)	178 (84%)	145 (95%)	72 (91%)
TOTALS	115	141	212	153	79

TABLE 3.3—Table of specimen completeness and lithofacies association. Number of localities within each lithofacies association that have the specified completeness assessment are given along with percentage of occurrence in each lithofacies association. Total number of localities assessed is 182.

COMPLETENESS	FA1 (%)	FA3 (%)	FA4 (%)	FA5 (%)	FA8 (%)
COMPLETE SHELL	0	7 (19%)	0	3 (4%)	0
PARTIAL SHELL	0	16 (43%)	13 (35%)	7 (8%)	1 (5%)
SHELL PORTIONS	0	6 (16%)	5 (14%)	6 (7%)	2 (8%)
SHELL FRAGMENTS	2 (100%)	8 (22%)	19 (51%)	68 (81%)	19 (86%)
TOTALS	2	37	37	84	22

TABLE 3.4—Kaiparowits Formation turtles by family, taxon group, and genus with known lithofacies associations. Numbers and percentages of each taxon per lithofacies association is provided. Total number of specimens examined with lithofacies association data is 315, some of which were found within the same locality.

FAMILY	% OF TAXA	TAXON GROUP	GENUS	FA 1	FA 3	FA 4	FA 5	FA 8	TOTALS
ADOCIDAE	17.80%	ADOCIDS	*ADOCUS*	0	8	10	32	6	56
BAENIDAE	21%	BAENIDS	*BOREMYS*	0	1	0	0	0	1
			DENAZINEMYS	1	11	5	6	0	23
			NEURANKYLUS - A	0	2	1	1	0	4
			NEURANKYLUS - B	0	1	0	0	0	1
			NEURANKYLUS - UNK.	0	4	6	9	0	19
			PLESIOBAENA	0	1	1	0	0	2
			UNKNOWN BAENID	0	4	5	5	2	16
CHELYDRIDAE	4.40%	SMALL TURTLES	UNKNOWN CHELYDRID	0	0	1	8	5	14
KINOSTERNIDAE	6.30%		UNKNOWN KINOSTERNID	0	0	1	13	6	20
PLEUROSTERNIDAE	14%		*COMPSEMYS*	0	1	6	26	11	44
NANHSIUNGCHELYIDAE	9.50%	"TORTOISES"	*BASILEMYS*	0	1	3	22	4	30
TRIONYCHIDAE	26%	TRIONYCHIDS	*ASPIDERETOIDES*	1	3	4	10	2	20
			HELOPANOPLIA	0	0	3	6	2	11
			PLASTOMENOIDES	0	0	1	0	0	1
			UNKNOWN TRIONYCHID	0	4	9	28	9	50
UNKNOWN FAMILY	1%	NONE	UNKNOWN GENUS	0	1	1	1	0	3
TOTALS				2	42	57	167	47	315
% OF TAXA				0.60%	13.30%	18.10%	53.00%	15.00%	

TABLE 3.5a—Chi Square Test data using all seven Kaiparowits turtle families and the five lithofacies associations with fossil turtle remains. Degrees of freedom = 24.

	FA1	**FA3**	**FA4**	**FA5**	**FA8**	**TOTALS**
ADOCIDAE	0	8	10	32	6	56
BAENIDAE	1	24	18	21	2	66
CHELYDRIDAE	0	0	1	8	5	14
KINOSTERNIDAE	0	0	1	13	6	20
NANHSIUNGCHELYIDAE	0	1	3	22	4	30
PLEUROSTERNIDAE	0	1	6	26	11	44
TRIONYCHIDAE	1	7	17	44	13	82
TOTALS	2	41	56	166	47	312

TABLE 3.5b—Data table for Chi Square Test with numbers of observed specimens and expected specimens for each lithofacies association in Kaiparowits Formation.

		LITHOFACIES ASSOCIATION	FA1	FA2	FA3	FA4	FA5	FA6	FA7	FA8	FA9	
		PERCENT OF KAIPAROWITS	0.05	0.02	0.28	0.15	0.1	0.02	0.01	0.31	0.06	
TAXA	**SPECIMENS**	**CHI SQUARE TEST**										**TOTALS**
ADOCIDAE	56	EXPECTED	2.8	1.12	15.68	8.4	5.6	1.12	0.56	17.36	3.36	56
		OBSERVED	0	0	8	10	32	0	0	6	0	56
		CHI SQUARE	2.8	1.12	3.761632653	0.304761905	124.4571429	1.12	0.56	7.433732719	3.36	
BAENIDAE	66	EXPECTED	3.3	1.32	18.48	9.9	6.6	1.32	0.66	20.46	3.96	66
		OBSERVED	1	0	24	18	21	0	0	2	0	66
		CHI SQUARE	1.603030303	1.32	1.648831169	6.627272727	31.41818182	1.32	0.66	16.65550342	3.96	
CHELYDRIDAE	14	EXPECTED	0.7	0.28	3.92	2.1	1.4	0.28	0.14	4.34	0.84	14
		OBSERVED	0	0	0	1	8	0	0	5	0	14
		CHI SQUARE	0.7	0.28	3.92	0.576190476	31.11428571	0.28	0.14	0.100368664	0.84	
KINOSTERNIDAE	20	EXPECTED	1	0.4	5.6	3	2	0.4	0.2	6.2	1.2	20
		OBSERVED	0	0	0	1	13	0	0	6	0	20
		CHI SQUARE	1	0.4	5.6	1.333333333	60.5	0.4	0.2	0.006451613	1.2	
NANHSIUNGCHELYIDAE	30	EXPECTED	1.5	0.6	8.4	4.5	3	0.6	0.3	9.3	1.8	30
		OBSERVED	0	0	1	3	22	0	0	4	0	30
		CHI SQUARE	1.5	0.6	6.519047619	0.5	120.3333333	0.6	0.3	3.020430108	1.8	
PLEUROSTERNIDAE	44	EXPECTED	2.2	0.88	12.32	6.6	4.4	0.88	0.44	13.64	2.64	44
		OBSERVED	0	0	1	6	26	0	0	11	0	44
		CHI SQUARE	2.2	0.88	10.40116883	0.054545455	106.0363636	0.88	0.44	0.510967742	2.64	
TRIONYCHIDAE	82	EXPECTED	4.1	1.64	22.96	12.3	8.2	1.64	0.82	25.42	4.92	82
		OBSERVED	1	0	7	17	44	0	0	13	0	82
		CHI SQUARE	2.343902439	1.64	11.09414634	1.795934959	156.297561	1.64	0.82	6.068308419	4.92	

TABLE 3.5c—Calculation table for Chi Square Test based on Table 3.5b. The resulting chi square value is 75.12.

OBSERVED	EXPECTED	O - E	(O-E)^2	((O-E)^2)/E
0	0.36	-0.36	0.13	0.358974359
1	0.42	0.58	0.33	0.786713287
0	0.09	-0.09	0.01	0.08974359
0	0.13	-0.13	0.02	0.128205128
0	0.19	-0.19	0.04	0.192307692
0	0.28	-0.28	0.08	0.282051282
1	0.53	0.47	0.23	0.42808005
8	7.36	0.64	0.41	0.05583847
24	8.67	15.33	234.91	27.08549377
0	1.84	-1.84	3.38	1.83974359
0	2.63	-2.63	6.91	2.628205128
1	3.94	-2.94	8.66	2.195966229
1	5.78	-4.78	22.87	3.955000284
7	10.78	-3.78	14.26	1.322934303
10	10.05	-0.05	0.00	0.000261643
18	11.85	6.15	37.87	3.196803197
1	2.51	-1.51	2.29	0.910779696
1	3.59	-2.59	6.71	1.868315018
3	5.38	-2.38	5.69	1.056043956
6	7.90	-1.90	3.60	0.455877456
17	14.72	2.28	5.21	0.35383722
32	29.79	2.21	4.86	0.16320226
21	35.12	-14.12	199.24	5.673982644
8	7.45	0.55	0.30	0.040800565
13	10.64	2.36	5.56	0.522953352
22	15.96	6.04	36.46	2.284430028
26	23.41	2.59	6.71	0.286488612
44	43.63	0.37	0.14	0.003168396
6	8.44	-2.44	5.93	0.70337464
2	9.94	-7.94	63.08	6.344628775
5	2.11	2.89	8.36	3.963077702
6	3.01	2.99	8.92	2.961756683
4	4.52	-0.52	0.27	0.059656301
11	6.63	4.37	19.11	2.883524277
13	12.35	0.65	0.42	0.033934108
				75.1161537

TABLE 3.6—Inferred habitats of Kaiparowits turtles based on extant relatives and/or morphologic and taphonomic evidence.

TURTLE TAXON	GENERAL SIZE	SHELL SHAPE	SHELL ROBUSTNESS	HABITAT
ADOCUS	large	oblong	strong	river
BOREMYS	moderate	oblong	strong	river
DENAZINEMYS	moderate	oblong	strong	river
PLESIOBAENA	moderate	oblong	strong	river
NEURANKYLUS	very large	rectangular	strong	river
CHELYDRIDAE	small	round	weak	pond
KINOSTERNIDAE	small	round	weak	pond
COMPSEMYS	small	round	weak	pond
BASILEMYS	very large	rectangular	strong	terrestrial
ASPIDERETOIDES	large	round	weak	river and pond
HELOPANOPLIA	moderate	round	weak	pond
PLASTOMENOIDES	small	round	weak	pond

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CHAPTER FOUR

TRANSPORT AND DEPOSITION OF FOSSIL FRESHWATER TURTLES IN FLUVIAL DEPOSITIONAL ENVIRONMENTS INTEGRATING FLUME EXPERIMENTATION

Contribution of Authors and Co-authors

Manuscript in Chapters 3, 4, and 6

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Contributions: All work relating to completion and preparation of manuscript.

Manuscript Information Page

Michael J. Knell
Journal of Sedimentary Research
Status of Manuscript:
_X_ Prepared for submission to a peer-reviewed journal
____Officially submitted to a peer-reviewed journal
____Accepted by a peer-reviewed journal
____Published in a peer-reviewed journal

Published by SEPM Society for Sedimentary Geology

Journal: Journal of Sedimentary Research

Running Head: Turtle Taphonomy in Fluvial Systems

Title: TRANSPORT AND DEPOSITION OF FOSSIL FRESHWATER TURTLES IN FLUVIAL DEPOSITIONAL ENVIRONMENTS INTEGRATING FLUME EXPERIMENTATION

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Keywords: Taphonomy, Cretaceous, Campanian, Kaiparowits Formation, Chelonia

ABSTRACT

Fossil freshwater turtles are a common occurrence in terrestrial fluvial deposits. However, the taphonomy of these turtles is rarely analyzed for depositional patterns. A comparison of transport and deposition trends was conducted using a variety of modern turtle taxa and fossil turtles collected in the Upper Cretaceous (Campanian) Kaiparowits Formation of southern Utah. A flume was used in conjunction with extant turtle shells to observe trends in transport and deposition based on the size and morphology of the shells. The resulting data was compared to taphonomic data collected from *in situ* fossil turtles to reveal patterns in the orientation and alignment of turtle shells in fluvial systems. An analysis of the results indicates a preference for the preservation of larger, more robust turtle shells over smaller, poorly-constructed shells. Shells with a more highly domed carapace tend to be deposited in a carapace-up orientation. There is also a trend for oblong shells to align themselves lateral-to-flow in the channel prior to burial. Alignment trends recorded for multiple fossil turtle shells from the Kaiparowits Formation supports previous paleoflow direction estimates using sedimentary structures.

INTRODUCTION

Taphonomy can be divided into pre-burial and post-burial processes, which are collectively known as biostratinomy and diagenesis respectively (Cadée 1990; Lawrence 1979). The processes of diagenesis, particularly fossilization, is difficult to assess and discern due to long time periods and often extreme conditions required for diagenesis to occur. Biostratinomy, which includes decomposition, transport, deposition, and burial of biologic remains, can be modeled or observed in controlled conditions within a laboratory. These observation-based experiments, sometimes referred to as actualistic experiments, are becoming more common in taphonomic studies because they allow researchers to observe the processes of decomposition, transport, deposition, and burial as a proxy for understanding the taphonomy of fossil organisms (Blob 1997; Fielding 2006; Knell 2004).

The Upper Cretaceous (Campanian) Kaiparowits Formation in southern Utah is well-known for fossil vertebrates including a variety of freshwater turtles (Eaton et al. 1999). Fluvial deposits, in the form of tabular and lenticular channel sandstone bodies, comprise a large portion of the Kaiparowits Formation, which is exposed entirely within the boundaries of Grand Staircase-Escalante National Monument (Roberts 2007). Several fossil freshwater turtle specimens with complete shells have been collected from these fluvial deposits (Fig. 4.1), some with partial or nearly complete appendicular skeletons (Knell et al. 2011). In contrast, other taxa are absent or poorly preserved in the same deposits. For example, baenid and adocid turtles are more abundant and more frequently found with intact shells in Kaiparowits channel deposits than kinosternid or chelydrid turtles (Knell, in prep). Thus, a taphonomic bias may have operated during the transport and deposition of turtle shells that favored the preservation of some taxa over others. A similar taphonomic bias based on skeletal morphology has been previously described for mammal remains in the terrestrial realm (Aslan and Behrensmeyer 1996; Voorhies 1969). The size and shape of the turtle shell may be a primary control in determining preservation quality in fluvial channel deposits. It is predicted that (1) turtle shells with a more highly domed carapace will be transported more easily and farther than shells with a low profile, (2) that highly domed shells will have a preferred orientation when deposited and low profile shells will not, and that (3) oblong shells will be deposited with a preferred alignment whereas more circular shells will show no alignment trend. To test these hypotheses, several experimental trials were conducted to observe the transport and deposition of five modern turtle shells within a model river channel (flume) to determine the effect shell morphology has on biostratinomic processes and to identify patterns in deposition, orientation, and alignment. The morphological similarity between extant and Cretaceous turtles allows the use of modern turtle shells as a proxy for understanding taphonomic processes which helps to explain the abundances or absences of particular taxa in the fossil record.

PREVIOUS WORK

Observations of modern freshwater turtle decomposition and decay were recorded by the German taphonomist Johannes Weigelt as early as the 1920s (Weigelt 1989, pp. 147-148). Many taphonomists (e.g. Rogers 1990, Sander 1989, Smith 1993, Varricchio 1995) reference Weigelt's research on large terrestrial mammal taphonomy but few (Brand et al. 2003) mention his taphonomic observations of various other vertebrates, including turtles. Weigelt (1989) noticed some common features among freshwater turtle carcasses, particularly that the limbs and head of turtles are often observed in a relaxed, extended position after death, and also that turtle shells are frequently deposited in a natural carapace-up orientation. He subsequently found similar trends with fossil turtles in the famous Jurassic fossil beds of Solnhofen, Solothurn, and Hanover in Germany

(Weigelt 1989). Since Weigelt's published observations in 1925, very little additional research on turtle taphonomy has been published until recently.

Blob (1997) directly compared the taphonomy of an *in situ* fossil turtle (*Aspideretoides*) specimen with flume observations using the skeleton of a similar extant turtle. Blob intended to identify the dispersal potential of turtle skeletal elements in a flume to aid in interpreting the dispersal pattern of fossil turtle elements discovered in Cretaceous fluvial deposits in Alberta, Canada (Blob 1997). Blob understood that mammal bones and non-mammalian bones are transported and deposited differently under the same flow conditions. The results presented in Voorhies (1969, pp. 66-69) and others (e.g. Aslan and Behrensmeyer 1996, Behrensmeyer et al. 1979) using modern mammal remains are not applicable to non-mammalian fossil assemblages because the shape and density differences between mammal and non-mammalian skeletal elements are too great for comparison. Blob (1997) placed the disarticulated skeleton of an extant soft-shelled turtle (trionychid) into a small flume (126.5 cm x 50.3 cm) and observed the movement of elements exposed to a flow. The dispersal potential of the turtle bones did not correlate to corresponding mammal bones of the same type and size. Importantly, Blob (1997) verified a link between bone shape and transport potential for trionychid turtle elements.

Other turtle taphonomic research has focused on disarticulation and decay in laboratory settings. Brand et al. (2003) conducted several experiments using red-eared sliders (*Trachemys scripta*) to observe the disarticulation and decay of turtle carcasses in controlled settings. Their results indicate that turtles in water-filled aquariums decay more rapidly than those in dry, terrestrial settings (Brand et al. 2003). They also established a common disarticulation sequence for turtle carcasses in aquatic settings. The head, tail, and limbs of turtles typically detach from the carcass early during decomposition, and then subsequently break apart into individual elements given additional time (Brand et al. 2003). The shell is often the last to disarticulate, with the carapace commonly separating into individual components prior to the plastron (Brand et al. 2003). Numerous observations of natural turtle disarticulation suggest that skeletal separation begins distally at the weakest exposed joints and proceeds proximally (Fielding 2006; Knell 2004). When only the shell and girdle elements remain there is a temporary pause in disarticulation until the shell itself begins to separate (Fig. 4.2). This disarticulation pattern is unique to turtles because of the solid construction of the turtle shell, which no other vertebrate group possesses.

Similar experiments were conducted by Fielding (2006) who used a variety of freshwater turtle taxa to identify patterns in decomposition and decay for comparison to the same fossil marine turtle localities studied by Weigelt in Germany. The results of Fielding's experiments were not substantially different from those conducted by Brand et al. (2003). Importantly, Fielding (2006) reports that intact turtle carcasses in water will bloat and float for a period of a few days prior to deposition. Some turtle carcasses may sink immediately when placed in water, float after a few days as gases build within, and then sink once more when the gases escape. Fielding's (2006) experiments also included collecting data on invertebrate scavenger activities, in addition to using multiple tanks with recycled flowing water, which permits continued observation without disturbing the specimens. This was a problem for Brand et al. (2003) as bodily fluids clouded the aquariums making observation difficult. My own observations (Knell 2004) confirm the results of both Brand et al. (2003) and Fielding (2006). Turtles, both marine and freshwater, appear to decompose and disarticulate in a similar pattern (Knell 2004, 2009). One primary difference between decomposition and disarticulation in freshwater versus seawater in natural settings is the difference in the number and variety of scavengers, which when present, can greatly speed up these processes (Knell 2004; Fielding 2006).

Because turtles have changed little morphologically over the past 100 million years, extant turtle carcasses are useful proxies for understanding the taphonomic processes of extinct turtles. Previous research has presented a timeline for turtle decomposition in both aquatic and terrestrial environments (Brand et al. 2000), an order for turtle disarticulation (Fielding 2006; Knell 2004), and an order of turtle skeletal transport (Blob 1997). However, multiple aspects of fluvial transport of turtles remain unaddressed. For example, relationships between shell morphology, transport potential, and shell deposition trends have not yet been considered. A taphonomic comparison of ancient and extant turtle taxa, other than trionychids (Blob 1997), has not been presented.

METHODS

Flume Trials

For this paper, flume trials consisted of placing the shells of a variety of extant turtle taxa within a demonstration flume using different orientations and alignments to observe the biostratinomic processes of transport and deposition. The results were then compared to taphonomic data collected from multiple fossil turtle localities in the Upper Cretaceous (Campanian) Kaiparowits Formation to explain local taphonomic phenomena. A series of experimental trials were performed using a flume in the Engineering Department at Montana State University (Fig. 4.3). The flume dimensions are 9 m x 0.45 m x 0.30 m with sides composed of clear Plexiglas to permit observation, The discharge, bed tilt, and bed composition can be modified, which allows the experimenter to produce a variety of flow conditions. Because of its flexibility and larger dimensions, this flume can more accurately model fluvial conditions than smaller flumes, which limit the distance of observable transport. Because many well-preserved turtles from the Kaiparowits Formation are collected from sand-dominated channel deposits, the flume was set up to resemble the conditions of a sand-dominated river. To simulate these conditions, 4 to 8 cm of medium-grain sand was added to the flume bed, which is more comparable to an actual fluvial channel than using a smooth, unnatural surface. Lining the flume bed with sand also increased the complexity of the bed with the development of rippled bedforms. The flume trials in this study, however, were only intended for qualitative observational data collection, so no measurements of transport potential or shear stress were recorded. This, however, may be considered in future work.

Flume trials consisted of multiple runs in which each extant turtle shell was observed during transport and deposition. Each of the flume trials used a specific flume setting, which controlled the flow velocity. Each observation within each trial group used the same flume settings. The flow velocity within the flume was manipulated by changing the amount of water discharge and the tilt of the bed. Six different flume settings were used, each of which was kept within a comparable range for modern braided and meandering rivers with sand-dominated beds (Schulze et al. 2005). Flow velocity was calculated using the equation $Q = VA$, where Q equals discharge, V equals flow velocity, and A equals the cross-sectional area of the water in the flume. The calculated values for flow velocity for each flume setting are provided in Table 4.1. Each of the five shells was used with each of the six flume settings for a total of 30 different flume setting-shell combinations. The water depth varied slightly from the upper end of the flume to the lower end of the flume due to flume tilt; however, the shells were constantly submerged during each trial. Water depth was measured at the same location for each set of trials, namely two meters from the upper end of the flume, which represents the starting point for each turtle shell.

Shells (carapace and plastron) or just carapaces from five freshwater turtles representing four extant species were used for flume trials: the low-profile carapace of a Chinese soft-shell turtle (*Pelodiscus sinensis*), the moderate-profile carapace of the common snapping turtle (*Chelydra serpentina*), the moderate-profile shell of both an adult and juvenile red-eared slider (*Trachemys scripta*), and the high-profile shell of a geometric tortoise (*Psammobates geometricus*) (Fig. 4.4). These shells, which range in size between 10 and 26 cm in length, encompass a range of common turtle shell morphologies and were obtained via donations by museums and private collectors. Only the carapace was used in flume trials for the soft-shell and snapping turtles due to the lack of fusion between the carapace and plastron in these taxa. Due to size limitations of the flume, no carapace or shell larger than the snapping turtle was used. A flume with greater dimensions would permit flume trials with larger turtle shells in the future.

Each run within a flume trial consisted of placing a turtle shell in the flume at a point two meters from the upstream end and observing its transport in the flow, if it occurred. The shells were each placed into the flume in four different configurations combining: 1) carapace-up and 2) carapace-down (orientation), 3) anterio-posteriorly to flow and 4) lateral-to-flow (alignment) for each flume setting. With six different flume settings and four different alignment and orientation combinations, each turtle shell was observed in 24 different configurations and each configuration was run 10 times to ensure accurate records. Notes were recorded on the ease and method of movement for each turtle shell in each configuration over five minutes, in which time the shell either ceased movement (deposition) or the shell reached the lower end of the flume. These flume trials served to gather empirical observations of the variability in transport and deposition behaviors of different turtle shell sizes and shapes under the same conditions, starting orientations and alignments.

In addition to the flume trials described above, a piece of wood (5 cm x 10 cm) was wedged perpendicular-to-flow to model a log jam or an accumulation of woody debris in the channel. This seventh flume trial, which will be referred to as the “log jam trial”, used the same flume setting as Trial 4. Each of the turtle shells was also used in the log jam trial (10 runs each) and observed as they were transported into the wood obstruction and notes were taken on its effect on shell deposition.

Field and Laboratory

Fossil freshwater turtles from the Kaiparowits Formation were used for comparison to the flume studies because (1) dozens of fossil turtle specimens were available in museum collections, (2) the field area where they were collected was easily accessible, (3) the Kaiparowits Formation contains a variety of turtle taxa of varying morphology in the same deposit, and (4) the author was already collecting taphonomic data on Kaiparowits Formation turtles for another paper. Fieldwork in the Kaiparowits Formation was conducted between 2008 and 2011 to collect taphonomic data and record the lithofacies for *in situ* turtle specimens. For each fossil freshwater specimen examined *in situ*, field data was recorded regarding taxonomic identification, specimen completeness, specimen orientation and alignment, fossil associations, and specific site lithology. Specimen orientation and alignment data was only discernible for those *in situ* specimens that possessed most or all of the carapace and plastron. A Brunton compass was used to measure the alignment direction of the long axis of the shell (anterior-posterior). The direction and amount of shell tilt was also measured using a Brunton compass based on the angle of the nearly flat plastron above or below the horizontal bedding plane. For those specimens not examined while *in situ*, the site of extraction was examined to collect lithology data and the fossil turtle itself was examined in the preparation laboratory or museum collections to record the taxonomy and specimen completeness. The fossil turtle collections of the University of California Museum of Paleontology (UCMP), the Natural History Museum of Utah (UMNH), and Brigham Young University (BYU) were examined for taxonomic reference. Unfortunately, some turtle specimens were collected in the field by other researchers prior to gathering shell orientation and alignment data. For these specimens only general lithology data and carapace position could be recorded from the collector's field notes.

FLUME TRIAL RESULTS

Pelodiscus sinensis

As mentioned earlier, only the carapace of the *Pelodiscus* was used in flume trials. This carapace had a small gap between two of the central costals, which formed during drying after skeletonization. I assumed that this feature did not affect performance in the flume. The small, light *Pelodiscus* carapace had the lowest profile among the five shells and was also more circular than oblong, so there was little difference between placing the shell anterior or posterior-to-flow versus lateral-to-flow (Table 4.2). Very little movement occurred when the carapace was placed concave-down in lower flow velocities (settings 1-4). Even in higher flow velocities (settings 5-6) the carapace resisted transport, and occasionally flipped over to a concave-up orientation. When placed concave-up in lower flow velocities, the carapace tilted slightly away from the direction of flow and pushed along the bed as flow velocity increased. In higher flow velocities the *Pelodiscus* carapace frequently flipped to a concave-down position. At the highest flow velocity the final resting position of the carapace was frequently carapace-up (70%), although carapace-down deposition (30%) did occur.

Chelydra serpentina

The large, round and moderately-arched carapace of the *Chelydra* was stable in a concave-down position when anterior, posterior, or lateral-to-flow in lower flow velocities. As flow velocity increased the lateral-to-flow carapace slid more easily and sometimes turned anterior or posterior-to-flow or flipped over (carapace down). The concave-up carapace slid along the bed in moderate to higher flow velocities, often for long distances; however, it also flipped carapace-up if an edge of the carapace was caught along the bed. The *Chelydra* carapace was never observed to roll continuously along the bed, but it flipped and turned many times in higher flow velocities. Of all the extant specimens studied, the *Chelydra* carapace was the only shell that exhibited cracking and breakage during repeated flume trials. As seen with the *Pelodiscus* carapace, the carapace of the *Chelydra* was deposited more frequently (90%) as carapace-up in the highest flow velocity.

Trachemys scripta (adult)

The adult, moderately-arched *Trachemys* shell was more stable in the carapace-up position than carapace-down. When the shell was placed anterior or posterior to flow, carapace-up or carapace-down, the water easily passed through and around the shell in lower flow velocities, resulting in no movement. In higher flow velocities the shell was turned to a lateral-to-flow position. While carapace-up and lateral-to-flow the shell was pushed along the bed, but never completely overturned. When lateral-to-flow during higher flow velocities, occasionally the shell would roll over onto the carapace and continue rolling onto the plastron if a scour occurred beneath the upstream or downstream side of the shell. When placed carapace-down the shell would barely move during lower flow velocities, but easily rolled over onto the plastron in moderate to higher flow velocities. The adult *Trachemys* was always deposited in a carapace-up position and always lateral-to-flow.

Trachemys scripta (juvenile)

The smallest complete shell used during flume trials was the juvenile *Trachemys*, which had a similar morphology to the adult *Trachemys* but with less weight. In lower flow velocities the juvenile shell moved very little when carapace-up, but tilted away from the current when carapace-down and lateral-to-flow. As flow velocity was increased the juvenile shell began to roll more easily when carapace-down, as well as in carapace-up position. This rolling was initially slow, but became more rapid as flow velocity was increased. In higher flow velocities the shell began to roll continuously, and sometimes was entrained and tumbled in the flow, bouncing along the bed. Deposition of the juvenile *Trachemys* was always in the carapace-up position and always lateral-to-flow.

Psammobates geometricus

The *Psammobates* shell was one of the heaviest shells used and it had the highest shell profile. When placed in the flume in a carapace-up, anterior or posterior-to-flow position, movement only occurred in the highest flow velocity. Even when placed in a lateral-to-flow position, the shell resisted movement until the higher flow velocities, indicating a particularly high stability in the carapace-up position. Sliding of the shell was more common than rolling when oriented carapace-up and aligned lateral-to-flow in higher flow velocities. If the *Psammobates* shell was placed carapace-down, the shell rolled rather easily onto the plastron when placed lateral-to-flow. In lower flow velocities the shell sometimes rolled only onto its side, however, as flow velocity increased the shell rolled more easily onto the plastron, and even rolled multiple times in the highest flow velocity. The deposition of the *Psammobates* was always carapace-up and lateral-to-flow.

The "Log Jam"

The results of the "log jam trial" were consistent between the various turtle taxa. During most of the flume runs the shells simply stopped in carapace-up position against the wood. However, for those shells that were prone to rolling (i.e. *Trachemys* and *Psammobates*), frequently the shells would run into the wood midway through a roll so that they would stop in some form of carapace-down orientation (Fig. 4.5). The wood appeared to prevent the shell from completing its typical revolution.

FIELD RESULTS

Six different fossil freshwater turtle taxa from the Kaiparowits Formation are represented in this taphonomic data analysis, five of which are commonly found in fluvial deposits (Table 4.3). The most abundant are the Baenidae, which includes the genera *Denazinemys*, *Plesiobaena*, and *Neurankylus*. Other taxa examined include *Adocus*, *Basilemys*, and the trionychid *Aspideretoides*. All of these turtles, except *Basilemys*, have been previously described as preferring riparian habitats based on comparisons of their morphology to living turtles (Hutchison 2000), therefore, it is not surprising that their remains are found within channel deposits of the Kaiparowits Formation. The morphology of *Basilemys*, on the other hand, more closely resembles that of living tortoises (Hutchison 2000). The size and morphology of these extinct turtles differs greatly. *Denazinemys* and *Plesiobaena* are the smallest of these taxa, with average carapace lengths of 40-50 cm. On the larger end of the size scale is *Neurankylus* and *Basilemys*, some of the largest Cretaceous turtles known, with average carapace lengths of 80-90 cm. *Adocus* and *Aspideretoides* are of intermediate size in this collection of turtle taxa. All but *Aspideretoides* possess an oblong carapace (longer anterior-dorsally than laterally). *Aspideretoides* has a more circular carapace and also has the lowest shell profile, which is typical of trionychids. The amount of carapace arch is slightly reduced on *Adocus*, *Plesiobaena*, *Neurankylus*, and *Basilemys* so that the top of the shell has a flattened appearance. The carapace of *Denazinemys* is more highly arched in comparison to the others.

Taphonomic data was collected on 18 nearly complete fossil freshwater turtle specimens in the Kaiparowits Formation (Table 4.3). The channel deposits in which they were found are composed of fine to medium-grain sandstone, frequently exhibiting trough cross-bedding (Roberts 2007). These deposits are seen as tabular or lenticular sandstone bodies representing meandering and braided stream depositional environments, respectively (Roberts 2007). Some of the turtles were discovered within channel lag deposits consisting of pebble-sized rip-up clasts and some fragmentary fossil debris of vertebrates and invertebrates in addition to fossilized wood. Of the 18 turtle specimens analyzed, 7 were examined while *in situ* and 11 were examined post-collection.

Two-thirds of the turtle specimens (12 of 18) examined were discovered in a natural carapace-up position. Of the remaining six turtles, four specimens were found carapace-down and two were observed resting on the lateral margin of the shell. Three of the four carapace-down turtles were found with associated fossilized wood or bone fragments. Half of the carapace-up turtles were found in association with other bone material. No carapace-up turtles were found in association with wood. Alignment data was collected for the seven *in situ* turtle shells using a Brunton compass. Of these seven turtle shells, five were found to have an anterio-posterior alignment within 10º of due N-S, one was aligned to NW-SE, and one was aligned NE-SW.

DISCUSSION

The sample of turtle shells available for analysis provides an opportunity to examine three primary factors influencing transport of turtle shells in fluvial settings; size, shape, and initial position (orientation and alignment). Each of these factors will be discussed individually below.

Size

The mass and dimensions of a turtle shell can affect its transportability. The turtle shells with the largest dimensions and mass were more resistant to transport than the smaller, lighter shells under the same settings. The adult *Trachemys* and the *Psammobates* had the greatest mass of the turtle shells placed in the flume, and as one would expect, it required a higher flow velocity and greater force to move them. Comparison of the adult *Trachemys* with the juvenile *Trachemys* allows direct observation of how weight affects transport because both shells have similar morphology. The smaller, lighter juvenile shell was transported more easily under the same conditions. However, having a small mass does not always indicate high transport potential. The *Pelodiscus* carapace was the lightest of the group, so we would hypothesize that it would transport easily, however, except at higher flow velocities, it resisted transport. In this instance size did not have a control on transportability.

Shape

Shape is particularly important in a moving fluid (e.g. an airplane wing). In the flume, the shells and carapaces with the lowest profiles resisted transport until the highest flow velocities were obtained. As for the *Pelodiscus* carapace, the low-profile provides very little surface area for the force of the water to act upon even in moderate flow velocity. The *Chelydra* carapace provides another example, exhibiting a large mass and a large surface area. When placed in the flume the weight of the carapace was overcome by the force of the water, which was able to act upon the large surface area. Thus, the *Chelydra* carapace moved at lower flow velocities even though it weighed more than other shells. Shape rather than size, is a primary control of transport potential in fluvial channels for turtle shells. The more arched a turtle shell, the greater the surface area exposed to the current and thus more force is acting upon it, which results in shell movement. The arched, high-profile turtle shell prefers a carapace-up position in the flume. With the flat (plastron) side of the shell against the bed there are no surfaces or edges on the rounded carapace for the flow to act upon. Instead, the water flows over and around the shell, holding the shell in a carapace-up position. This observation may be explained by the Bernuli Principle.

Initial Shell Orientation and Alignment

Original post-mortem shell orientation determines if and how a shell will move in a flow. At low flow velocities the turtle shell resists movement in a carapace-up position. If the shell is anterior or posterior to flow the water passes through and around the shell (Fig. 4.6). In this orientation shells have a small hydrodynamic area, thus they experience minimal force from the surrounding water. Turning lateral-to-flow exposes more surface area to the current (Fig. 4.6). In low flow velocity insufficient force exists to move the shell, even with a greater surface area against the flow, due to friction with the bed. But as the flow velocity is increased the force of the flow overcomes friction with the bed, resulting in the shell being pushed. This was less obvious for the *Pelodiscus* and *Chelydra* due to their lower lateral shell profiles, but more prevalent in the moderate to high profile shells, as demonstrated by *Trachemys* and *Psammobates*.

When shells are placed carapace-down, flow dynamics change considerably. Shells with moderate to high profiles resemble inverted bowls and little contact occurs between the carapace surface and the bed (Fig. 4.7). When a shell lies anterior or posterior-to-flow and carapace-down, the point of contact between the shell and bed acts like a pivot point, allowing the shell to turn and tilt. Turbulence that develops as water passes through the shell turns the shell from anterior or posterior-to-flow to lateral-to-flow at higher flow velocities. Once the shell is lateral-to-flow it tilts away from the flow as the water pushes against the lateral side (Fig. 4.7). As the force increases with increased flow velocity, the shell can roll over onto the opposite lateral side and eventually onto the plastron, which results in a carapace-up shell orientation (Fig. 4.8). If the shell has enough momentum while rolling, it will continue to roll from the carapace-up to carapace-down position, thus repeating the roll. This shell rolling is more evident for turtle shells with a moderate to high shell profile with an attached, flat plastron.

Final Shell Orientation and Alignment

Turtle shells display a pattern in deposition, evident by the flume trials. Because of the shape difference between the carapace and plastron of most turtles, a bias exists towards carapace-up deposition, i.e. life position. The results show that turtles with a moderate to high-profile carapace will preferably come to rest carapace-up 100% of the time if there is no interference from the side of the flume. A carapace-up orientation was more commonly observed (about 60% of the time) with the *Chelydra* and *Pelodiscus* also, but there were many instances when the opposite was true. With flat shells it seems that the odds of being deposited carapace-up or carapace-down are practically equal (probably closer to 50-50).

For circular-shaped shells there is no alignment preference for anterior, posterior, or lateral-to-flow. However, for arched, oblong shells, there appears to be a trend towards a carapace-up orientation and a lateral-to-flow alignment, which occurred in nearly every flume trial in which the shells were transported. This combination of arched and oblong shape appears to be the most stable as witnessed in the flume trials, thus facilitating burial more commonly in this position.

Kaiparowits Fossil Turtle Analysis

Based on the results of the flume trials, there are multiple predictions regarding the orientations and alignments of fossil freshwater turtle shells in fluvial channel environments. Those taxa with low-profile shells, e.g. *Aspideretoides*, should occur equally in carapace-up or carapace-down orientations and show no preferred alignment to paleoflow direction. Turtle taxa with moderate to high-profiles, e.g. the baenids and adocids, should be recovered more often in carapace-up orientation and show an alignment preference lateral-to-paleoflow. If turtle shells occur adjacent to fossil wood or other debris, a carapace-down orientation likely would prevail.

An analysis of *in situ* fossil turtles in the Kaiparowits Formation corresponds well with predictions based on flume trials using shells of extant turtles. Although dissimilar in size, the carapace of the Cretaceous *Aspideretoides* and extant *Pelodiscus* share similar morphology as trionychids. As demonstrated in the flume, the low profile of the *Pelodiscus* carapace resists transport in low and moderate flow conditions. This suggests that the *Aspideretoides* carapace would have been resistant to transport, thus permitting rapid burial. However, the greater surface area of the larger fossil trionychid carapace suggests it would have easily been broken if tumbled at higher flow velocities. A depositional trend is less noticeable with trionychids as demonstrated in the flume due to a similarity in stability between carapace-up or carapace-down orientations. A similar carapace-up or carapace-down probability of nearly equal is possible with Kaiparowits trionychid specimens, with one specimen occurring carapace down and the other carapace up, but a larger sample size is needed in order to reach a similar conclusion.

The baenids (*Denazinemys*, *Plesiobaena*, and *Neurankylus*) along with *Adocus*, most closely resemble the extant turtle *Trachemys* used in the flume trials. These turtles all have oblong shells and a moderate to high shell profile. The fossil baenids are predominantly deposited in a carapace-up position (69%). This is somewhat lower than expected based on the flume data for *Trachemys* (100%). However, this is not surprising since the flume was operated under ideal conditions without natural hindrances to transport. The similar size and morphology of *Plesiobaena* to *Trachemys* is evident in the data, which shows that these turtles would be transported and deposited in a similar manner. *Denazinemys* has a similar size, but slightly higher profile than *Plesiobaena*. Therefore, it is not surprising that *Denazinemys* often occurs in a carapace-up position, similar to the higher profile *Psammobates* in the flume studies. *Neurankylus* is much larger than *Trachemys*, but of similar shape. The greater mass of *Neurankylus* would prevent the shell from moving in lower flow regimes and may explain why it is often found carapace-up. *Adocus* is more oblong in shape, with a heavier posterior margin than the baenids. Its profile is intermediate between *Plesiobaena* and *Denazinemys*. The shape of baenid and adocid shells explains their frequent carapace-up and lateral-to-flow orientation, similar to *Trachemys* and *Psammobates* in the flume studies.

The less arched and rounded shell profile of *Basilemys* differs from those of modern tortoises. A shell profile intermediate between *Trachemys* and *Psammobates* would provide a better analog for *Basilemys*. However, *Psammobates* has the strongest, heaviest shell of the extant group used in the flume, which is also true for *Basilemys* among the fossil taxa, and therefore some comparisons can be made. Like the *Psammobates* shell in the flume, the shell of *Basilemys* would be very resistant to transport at most flow velocities due to its weight, but it still shows preferred carapace-up orientation. In a higher flow a *Basilemys* shell would likely roll numerous times, similar to the *Psammobates* shell in the flume study. Unfortunately, as with the fossil trionychids, a small sample size prohibits recognition of a deposition pattern for *Basilemys* in the Kaiparowits Formation. However, based on the near-oblong shape of the *Basilemys* shell, a preferred alignment to paleoflow would be predicted.

The juvenile *Trachemys* shell transported easily and tumbled in the flume at higher flow velocities. This suggests that the shells of juveniles and small adults would have responded similarly under similar flow conditions in the Cretaceous. Extensive transport in rivers likely caused shells to crack and disarticulate over time. This was also observed in the flume (especially with *Chelydra*) when shells were repeatedly tumbled. This suggests that larger, well-constructed turtle shells would survive longer intact under transport conditions and be found well-preserved more frequently than smaller, poorly-constructed shells. An examination of nearly 500 Kaiparowits turtles in museum collections confirms this hypothesis. Only a single intact juvenile turtle shell (UMNHVP 21333) is known from the entire Kaiparowits Formation, and small turtle taxa (< 15 cm in length) are represented only by fragmentary material. Fluvial deposits appear to favor the preservation of larger, more robust turtle shells over small, fragile shells.

Most of the fossil turtle shells examined *in situ* in the Kaiparowits Formation and used for this analysis occurred in a carapace-up position (N = 11 of 16 for moderate to high profile), as expected from flume trials. However, four (4) were found carapace-down. This may be explained by the log jam flume trial, which used pieces of wood to simulate river channel debris. Shells observed in the flume sometimes stopped mid-roll in a carapace-down orientation as they came into contact with wood. Three out of the four carapace-down shells observed in the Kaiparowits Formation were found either in direct contact or within a few centimeters of fossil wood or large bone fragments. It is likely that these carapace-down shells became trapped in a log jam or debris which interrupted their transport and were subsequently buried in these orientations.

Fossil Freshwater Turtle Shells and Paleoflow Analyses

Some turtle taxa are deposited in specific orientations and alignments in fluvial systems, as demonstrated by flume trials and observed in Kaiparowits Formation deposits. This is particularly evident in the baenids and possibly in the adocids. These are the only turtles that have an oblong shell shape and appear to follow the trend of carapace-up and perpendicular-to-flow deposition, assuming no bed interference.

Because the final orientation of turtle shells is dependent on flow direction, it may be possible to use shell alignment to determine local channel paleoflow direction.

The alignment data collected for seven *in situ* baenid turtles in the Kaiparowits Formation (Table 4.3) showed the average long-axis (anterior-posterior) trend was approximately N-S. Four of these turtles occurred carapace-up, two were tilted on their side, and one was carapace-down. The carapace-down shell was discovered adjacent to fossil wood indicating its final deposition was likely disrupted, thus this specimen was excluded from the analysis. Of the six remaining shells, four were aligned nearly due N-S, one was aligned NE-SW, and one was aligned NW-SE. These alignments suggest a possible local paleoflow direction of east to west or west to east, if flow direction is lateral to anterio-posterior alignment as observed with the flume. Roberts (2007) conducted an extensive study of the lithology and alluvial architecture of the Kaiparowits Formation. As part of this study he collected local paleoflow data at hundreds of localities based on cross-bedding structures within channel sandstone bodies using a Brunton compass. The seven baenid turtles came from the middle unit of the Kaiparowits Formation, as defined by Roberts (2007). The dominant paleoflow direction is to the east (mean vector of 87º), towards the ancient Western Interior Cretaceous Seaway. This easterly flow direction is consistent with paleogeographic reconstructions of southern Utah during the Campanian (Goldstrand 1992). Therefore, the six carapace-up fossil turtle shells examined in the Kaiparowits Formation support the paleoflow analysis by Roberts (2007). The future validation and application of this technique requires a much larger dataset to counter any effects of false alignments in a sinuous meandering river channel.

CONCLUSIONS

Observations of transport and deposition of several extant turtle shells in flume studies provided useful information for understanding the depositional pattern of fossil turtles in the Kaiparowits Formation. In fluvial systems, turtle shell morphology represents the primary control on transport potential. Larger and more massive turtle shells are more resistant to transport. However, resistance to transport decreases as the shell profile height increases. Lower profile shells resist transport longer than those of higher profile, even if they have less mass. The longer a shell is transported the more damage the shell incurs; therefore, well-constructed shells (e.g. baenids) and those that are buried quickly (e.g. trionychids) have the greatest preservation potential.

Shells with higher profiles (flat plastron and domed carapace) are always deposited in a carapace-up orientation if unhindered. Oblong shaped shells (e.g. baenids) are frequently deposited in a position that is lateral to flow direction, whereas rounded shells or carapaces (e.g. trionychids) show no alignment trend. The tendency to align lateral-to-flow may be useful for estimating local paleoflow direction for channels in which the turtles were deposited. However, this would require a large sample-size of turtle shell alignments over a large area. Understanding how size and morphology of turtle shells affects their deposition, orientation, and alignment should prove valuable for interpreting the taphonomy of any assemblage of fossil turtles, or any assemblage with a fossil turtle component, in fluvial deposits.

ACKNOWLEDGEMENTS

This project was completed as part of a Ph.D. dissertation at Montana State University. The author would like to thank his primary advisor, David Varricchio, and committee members Jack Horner, Frankie Jackson, and Jim Schmitt for helpful edits and feedback. Additional thanks are given to the Department of Engineering at Montana State University for use of their flume and Tom Evans for flume assistance and suggestions. This project would not have been possible without donations of extant turtle specimens by Bill Belzer, George Phillips, and Bob Thomson. I would also like to thank the members of the Center for North American Herpetology for their assistance in providing me with contacts and useful references.

FIGURES AND TABLES

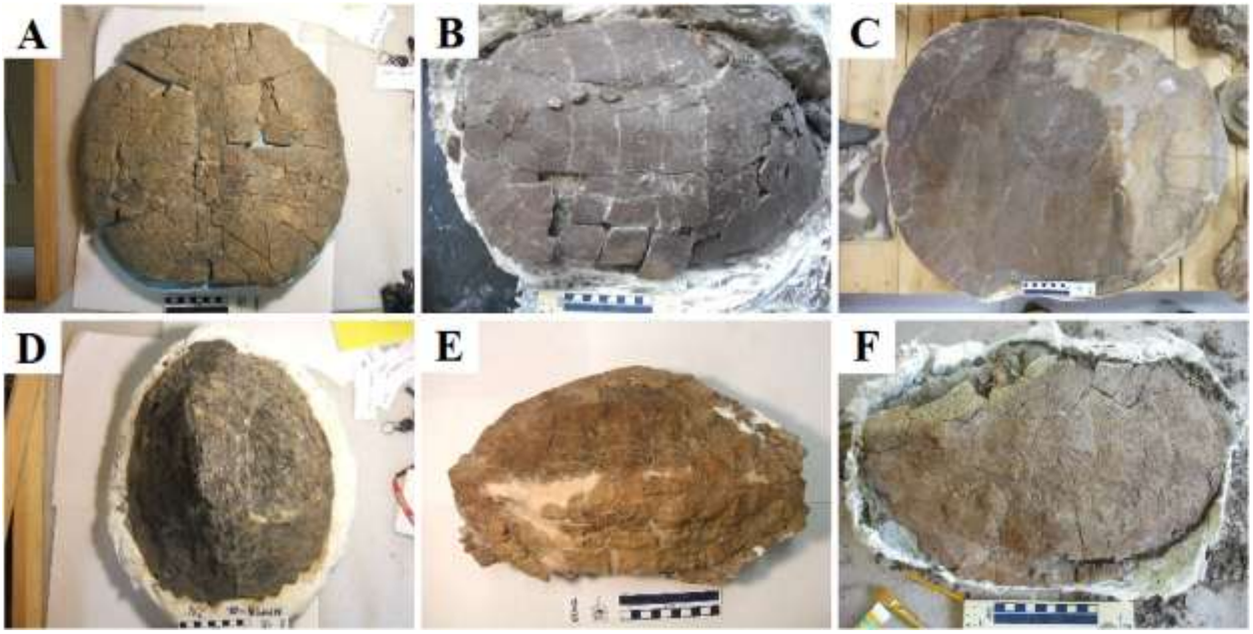

Figure 4.1. Fossil turtle shells from the Kaiparowits Formation. (A) *Aspideretoides*; (B) *Adocus*; (C) *Neurankylus*; (D) *Denazinemys*; (E) *Denazinemys*; (F) *Plesiobaena*.

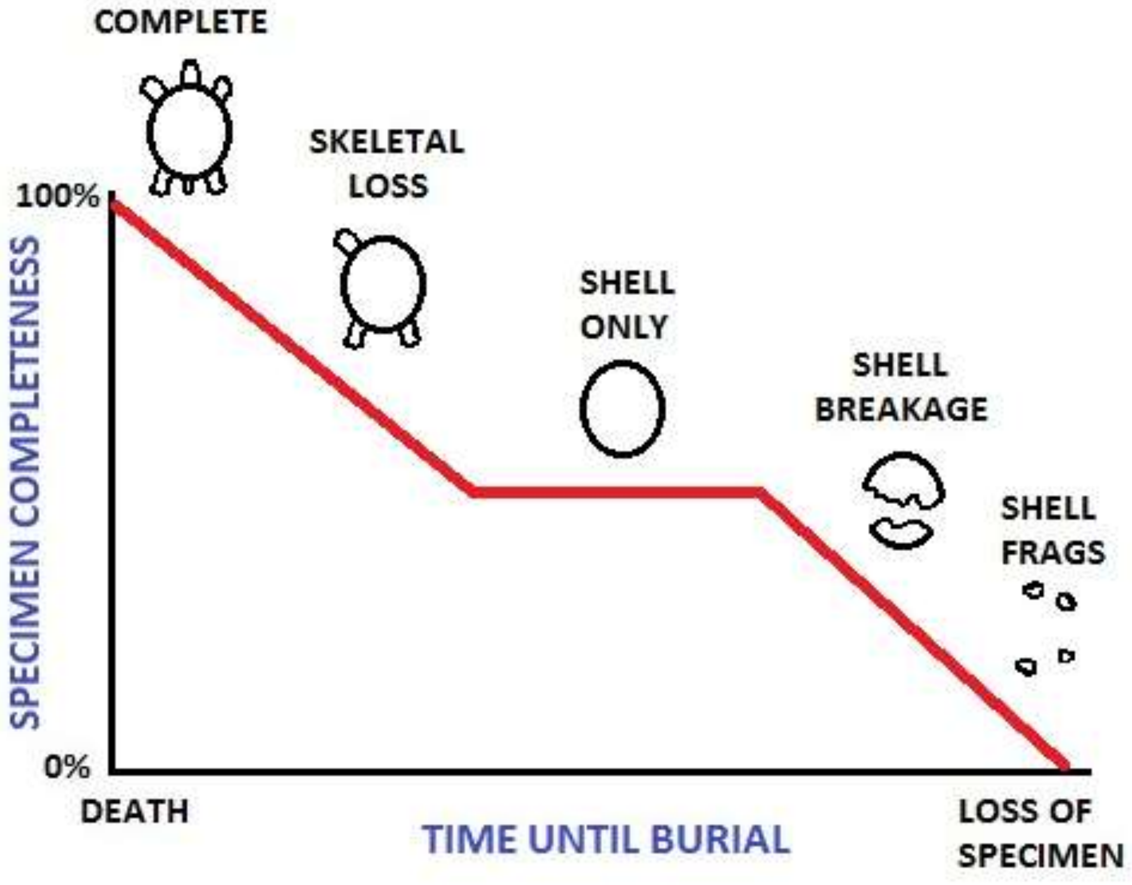

Figure 4.2. The common disarticulation trend for freshwater and marine turtles as observed in field and laboratory studies.

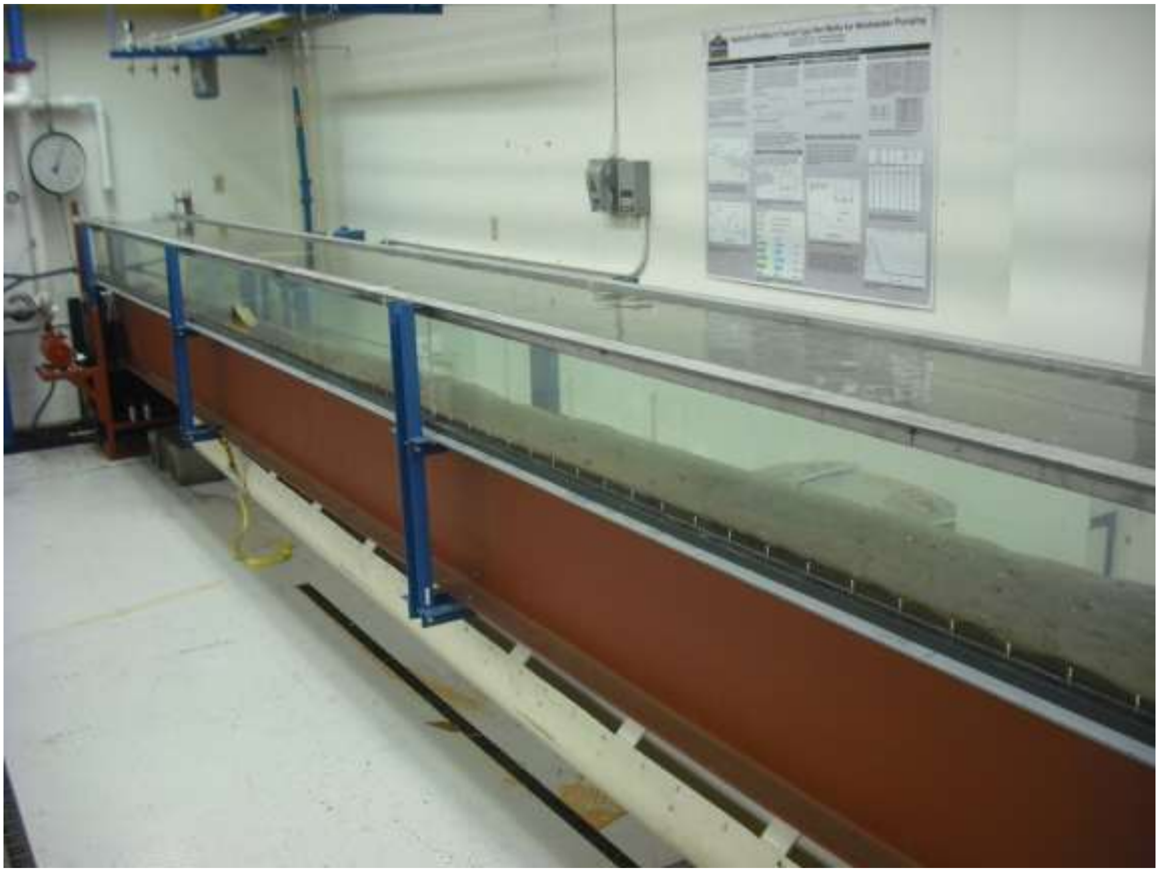

Figure 4.3. The flume in the Engineering Department at Montana State University which was used for observing the transport of extant turtle shells.

Table 4.1. Flume settings for each trial and calculations of flow velocity in meters/sec.

Trial	Depth (cm)	Width (cm)	Area (A) (cm^2)	Discharge (Q) (gpm)	Q (L/min)	V (cm/min)	V (m/sec)
1	26.5	45.72	1211.58	315	1192.404712	984.1733208	0.164028887
2	26	45.72	1188.72	390	1476.310596	1241.933	0.206988833
3	24	45.72	1097.28	385	1457.383537	1328.178347	0.221363058
4	22	45.72	1005.84	387	1464.95436	1456.4487	0.24274145
5	20	45.72	914.4	387	1464.95436	1602.09357	0.267015595
6	18	45.72	822.96	440	1665.581185	2023.890815	0.337315136

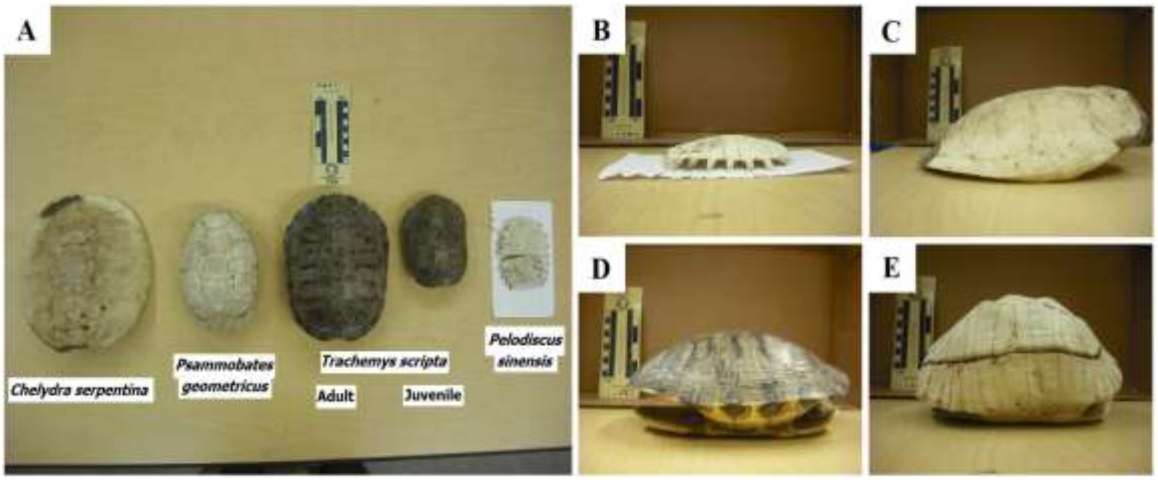

Figure 4.4. (A) Five extant freshwater turtle taxa shells used in flume trials; (B) *Pelodiscus sinensis*; (C) *Chelydra serpentina*; (D) *Trachemys scripta* (adult); (E) *Psammobates geometricus*.

Table 4.2. Observation data from flume trials using shells of extant freshwater turtles with initial and final orientation and alignment. CU = Carapace Up; CD = Carapace Down.

TAXA	TURTLE DESCRIPTION	INITIAL ORIENTATION AND ALIGNMENT	TRIAL 1 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 2 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 3 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 4 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 5 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 6 - FINAL ORIENTATION AND ALIGNMENT
Pelodiscus sinensis	LOW-PROFILE CARAPACE	CU - PARALLEL TO FLOW	No change	No change	No change	No change	Can be pushed or flipped, 60% to CU, 40% to CD, alignment is random	Can be pushed or flipped, 70% to CU, 30% to CD, alignment is random
	CARAPACE SHAPE: OVAL	CU - PERPENDICULAR TO FLOW	No change	No change	No change	No change	Can be pushed or flipped, 60% to CU, 40% to CD, alignment is random	Can be pushed or flipped, 70% to CU, 30% to CD, alignment is random
	DRY MASS: 20.6 g	CD - PARALLEL TO FLOW	No change	No change	No change	Easily flipped, 50% to CU, 50% to CD, final alignment is random	Easily flipped, 60% to CU, 40% to CD, final alignment is random	Easily flipped, 70% to CU, 30% to CD, final alignment is random
	CARAPACE LENGTH: 10.4 cm	CD - PERPENDICULAR TO FLOW	Tilted away from flow	Pushed, but always remains in same orientation and alignment	Pushed, but always remains in same orientation and alignment	Easily flipped, 50% to CU, 50% to CD, final alignment is random	Easily flipped, 60% to CU, 40% to CD, final alignment is random	Easily flipped, 70% to CU, 30% to CD, final alignment is random
Chelydra serpentina	MODERATE-PROFILE CARAPACE	CU - PARALLEL TO FLOW	No change	No change	Can flip to CD, parallel to flow	Can flip to CD, final alignment is random	Pushed, flipped easily, always deposited CU, 80 % perpendicular to flow, 20% parallel to flow	Pushed, flipped easily, always deposited CU, 90 % perpendicular to flow, 10% parallel to flow
	CARAPACE SHAPE: ROUND	CU - PERPENDICULAR TO FLOW	No change	Pushed, but remains in same orientation and alignment	Pushed, can turn to parallel to flow or flipped to CD	Pushed, can turn to parallel to flow or be flipped to CD	Pushed, flipped easily, always deposited CU, 80 % perpendicular to flow, 20% parallel to flow	Pushed, flipped easily, always deposited CU, 90 % perpendicular to flow, 10% parallel to flow
	DRY MASS: 179.2 g	CD - PARALLEL TO FLOW	No change	No change	No change	Can be turned to perpendicular to flow	Pushed, flipped easily, always deposited CU, 80 % perpendicular to flow, 20% parallel to flow	Pushed, flipped easily, always deposited CU, 90 % perpendicular to flow, 10% parallel to flow
	CARAPACE LENGTH: 26 cm	CD - PERPENDICULAR TO FLOW	Pushed, but always remains in same orientation and alignment	Pushed, but always remains in same orientation and alignment	Pushed, but always remains in same orientation and alignment	Pushed, but always remains in same orientation and alignment	Pushed, flipped easily, always deposited CU, 80 % perpendicular to flow, 20% parallel to flow	Pushed, flipped easily, always deposited CU, 90 % perpendicular to flow, 10% parallel to flow
***Trachemys scripta* (adult)**	MODERATE-PROFILE SHELL	CU - PARALLEL TO FLOW	No change	No change	No change	No change	No change	Turned to perpendicular to flow then pushed, always remains perpendicular to flow
	SHELL SHAPE: OBLONG	CU - PERPENDICULAR TO FLOW	No change	No change	No change	Pushed, but always remains in same orientation and alignment	Pushed, but always remains in same orientation and alignment	Pushed, but always remains in same orientation and alignment
	DRY MASS: 394.3 g	CD - PARALLEL TO FLOW	No change	No change	No change	No change	No change	Turns to perpendicular to flow, then rolls several times to CU, always remains perpendicular to flow
	CARAPACE LENGTH: 23.6 cm	CD - PERPENDICULAR TO FLOW	No change	Tilted away from flow	Can roll to CU, but always remains perpendicular to flow	Rolls to CU, but always remains perpendicular to flow	Rolls to CU, but always remains perpendicular to flow	Rolls several times to CU, but always remains perpendicular to flow

Table 4.2 Continued.

TAXA	TURTLE DESCRIPTION	INITIAL ORIENTATION AND ALIGNMENT	TRIAL 1 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 2 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 3 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 4 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 5 - FINAL ORIENTATION AND ALIGNMENT	TRIAL 6 - FINAL ORIENTATION AND ALIGNMENT
***Trachemys scripta* (juvenile)**	MODERATE-PROFILE SHELL	CU - PARALLEL TO FLOW	No change	No change	No change	No change	Turns to perpendicular to flow, then rolls several times to CU, always remains perpendicular to flow	Tumbled within flow, rolling several times, always deposited CU, perpendicular to flow
	SHELL SHAPE: OVAL	CU - PERPENDICULAR TO FLOW	No change	No change	Pushed, but always remains in same orientation and alignment	Slight push, but can roll to CU again, always remains perpendicular to flow	Rolls several times to CU, but always remains perpendicular to flow	Tumbled within flow, rolling several times, always deposited CU, perpendicular to flow
	DRY MASS: 95 g	CD - PARALLEL TO FLOW	No change	No change	No change	No change	Turns to perpendicular to flow, then rolls several times to CU, always remains perpendicular to flow	Tumbled within flow, rolling several times, always deposited CU, perpendicular to flow
	CARAPACE LENGTH: 15.1 cm	CD - PERPENDICULAR TO FLOW	Tilted away from flow	Can roll to CU, but always remains perpendicular to flow	Rolls to CU, but always remains perpendicular to flow	Rolls to CU, but always remains perpendicular to flow	Rolls several times to CU, but always remains perpendicular to flow	Tumbled within flow, rolling several times, always deposited CU, perpendicular to flow
Psammobates geometricus	HIGH-PROFILE SHELL	CU - PARALLEL TO FLOW	No change	No change	No change	No change	No change	Turned to perpendicular to flow then pushed, always remains perpendicular to flow
	SHELL SHAPE: OBLONG	CU - PERPENDICULAR TO FLOW	No change	No change	No change	No change	Pushed, but always remains in same orientation and alignment	Turned to perpendicular to flow then pushed, always remains perpendicular to flow
	DRY MASS: 293.9 g	CD - PARALLEL TO FLOW	No change	No change	No change	Turns to perpendicular to flow, then rolls to CU, always remains perpendicular to flow	Turns to perpendicular to flow, then rolls to CU, always remains perpendicular to flow	Turns to perpendicular to flow, then rolls several times to CU, always remains perpendicular to flow
	CARAPACE LENGTH: 24.3 cm	CD - PERPENDICULAR TO FLOW	No change	Tilt and roll onto side, remains perpendicular to flow	Rolls to CU, but always remains perpendicular to flow	Rolls to CU, but always remains perpendicular to flow	Rolls to CU, but always remains perpendicular to flow	Rolls several times to CU, but always remains perpendicular to flow

Figure 4.5. The “log jam trial”. A piece of wood (5 cm x 10 cm) is used to model a log jam in the channel. The shell would have continued rolling over onto the plastron if not obstructed. Flow direction is towards the left.

Table 4.3. Taphonomic data for 18 in situ fossil turtles from the Kaiparowits Formation.

SPECIMEN ID	TAXA	MORPHOLOGY	LITHOLOGY	COMPLETENESS	ORIENTATION	ALIGNMENT	PALEOFLOW	DIP	ASSOCIATED FOSSILS
UMNHVP 20449	*Aspideretoides*	round, low-profile	channel lag in lenticular sandstone	partial carapace with skeletal elements	up	unavailable	unavailable	unavailable	other bone material
UMNHVP 20453	*Aspideretoides*	round, low-profile	lenticular sandstone	partial carapace and partial plastron	down	unavailable	unavailable	unavailable	fossil wood
08UTKA-16	*Neuronkylus*	square, moderate-profile	channel lag in lenticular sandstone	partial carapace and partial plastron	up	N - S (due N)	90° to E	no dip	none
HSR 10-1	*Neuronkylus*	square, moderate-profile	lenticular sandstone	complete shell	up	NW - SE (N40W)	50° to E	15° to W	clams and bone material
MJK060908-2	*Neuronkylus*	square, moderate-profile	tabular sandstone	full carapace and partial plastron	up	N - S (due N)	90° to E	38° to E	none
MJK060909-5	*Neuronkylus*	square, moderate-profile	tabular sandstone	complete shell	down	NE - SW (N40E)	130° to E	5° to E	fossil wood
UMNHVP 20950	*Neuronkylus*	square, moderate-profile	channel lag in lenticular sandstone	partial carapace and partial plastron	up	unavailable	unavailable	unavailable	none
MJK061008-3	*Plesiobaena*	oblong, moderate-profile	channel lag in lenticular sandstone	partial carapace and partial plastron	side	N - S (due N)	90° to E	50° to E	none
UMNHVP 20451	*Plesiobaena*	oblong, moderate-profile	tabular sandstone	partial carapace and partial plastron	down	unavailable	unavailable	unavailable	none
MJK062508-2	*Adocus*	oblong, moderate-profile	lenticular sandstone	partial carapace and partial plastron	down	unavailable	unavailable	unavailable	other bone material
RAMV2008-9	*Adocus*	oblong, moderate-profile	tabular sandstone	partial carapace and partial plastron	up	unavailable	unavailable	unavailable	none
UMNHVP 16868	*Adocus*	oblong, moderate-profile	tabular sandstone	complete shell with partial skeleton	up	unavailable	unavailable	unavailable	none
UMNHVP 20452	*Adocus*	oblong, moderate-profile	tabular sandstone	complete shell	up	unavailable	unavailable	unavailable	other bone material
HSR-11-14	*Basilemys*	oblong, moderate-profile	tabular sandstone	partial carapace and partial plastron	up	unavailable	unavailable	unavailable	none
HSR-10-43	unknown baenid	oblong, moderate-profile	lenticular sandstone	partial carapace and partial plastron	up	unavailable	unavailable	unavailable	other bone material
MJK081511-1	unknown baenid	oblong, moderate-profile	lenticular sandstone	partial carapace and partial plastron	side	N - S (due N)	90° to E	85° to W	none
HSR-09-56	*Denazinemys*	oblong, high-profile	tabular sandstone	partial carapace and partial plastron	up	N - S (N10W)	80° to E	48° to W	other bone material
UMNHVP 20446	*Denazinemys*	oblong, high-profile	tabular sandstone	complete shell	up	unavailable	unavailable	unavailable	other bone material

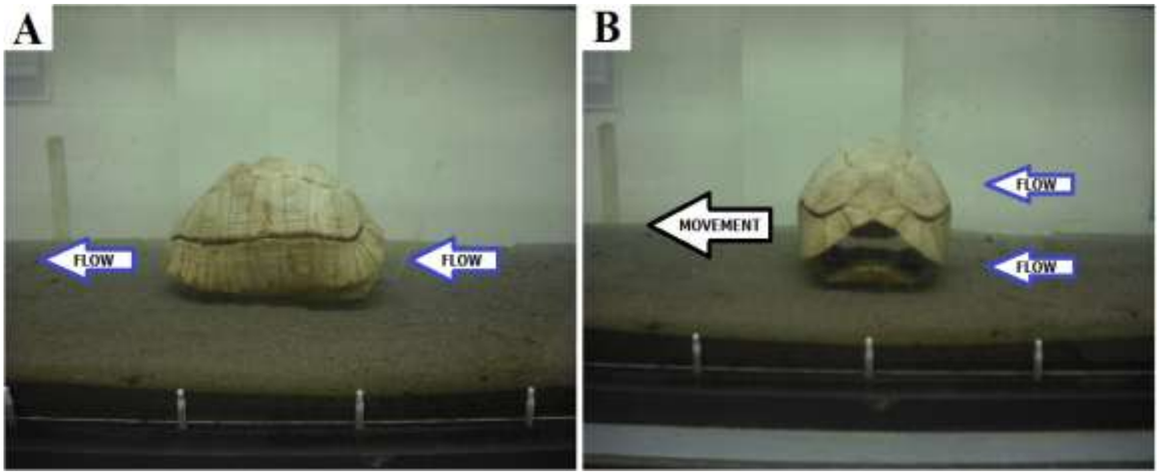

Figure 4.6. Turtle shell alignment and flow characteristics. (A) Water passing through the turtle shell in an anterior-to-flow position without causing movement in moderate flow conditions. (B) If the shell is placed lateral-to-flow there is a larger surface area for the water flow to act upon resulting in the shell being pushed laterally downstream along the bed.

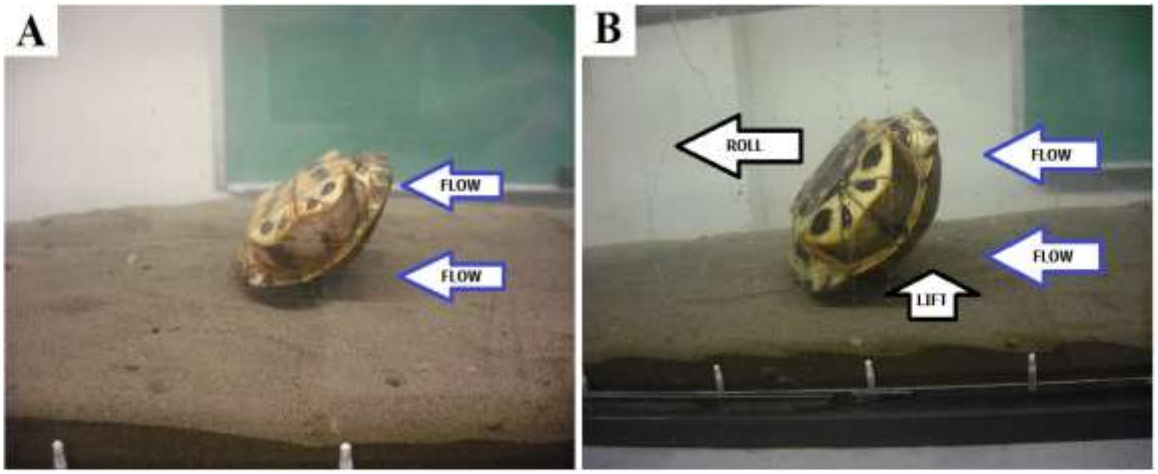

Figure 4.7. Tilting of carapace-down turtle shells. (A) A shell placed in carapace-down position has little contact with the bed, thus allowing for tilt and easy movement in high flow conditions. (B) Lift is generated under the carapace as water flows against the curved surface resulting in a rolling motion.

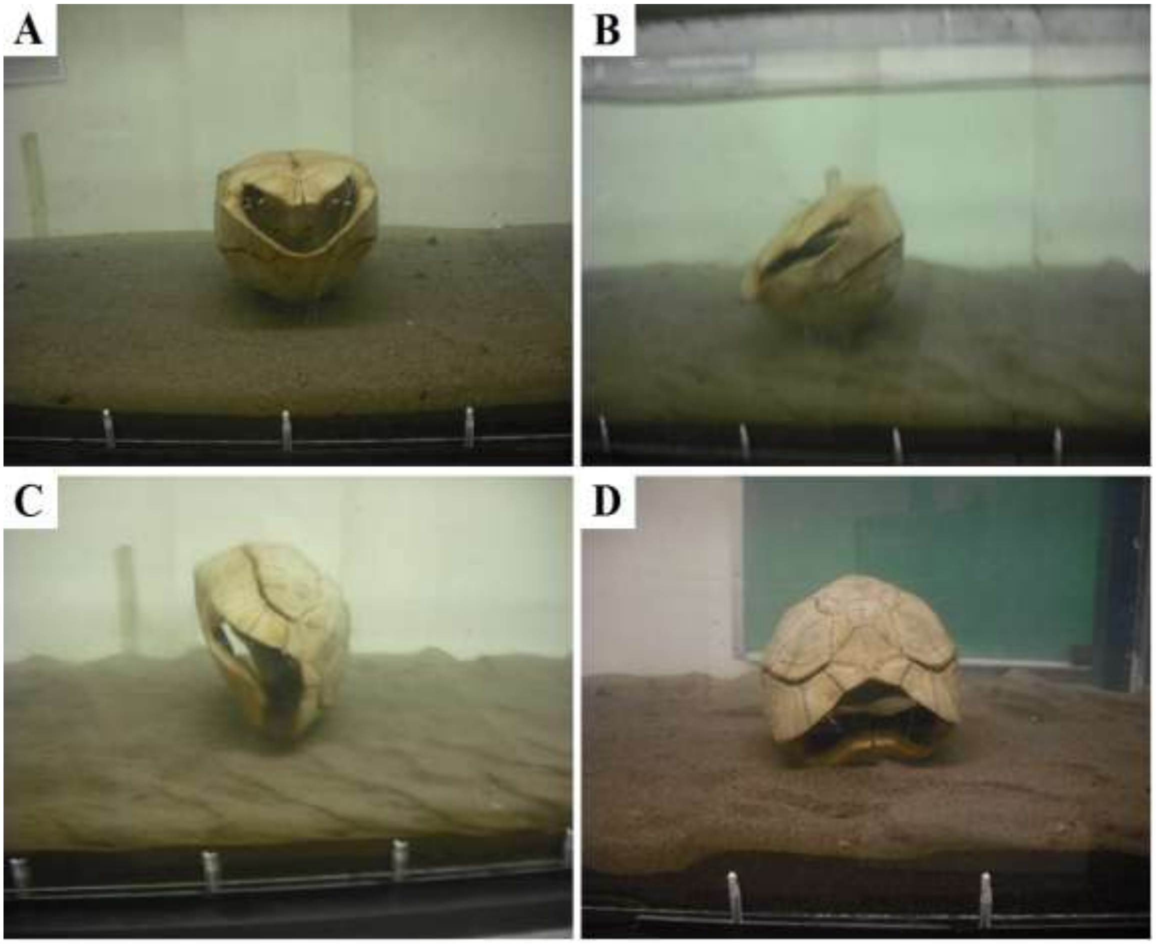

Figure 4.8. A shell rolling sequence from an unstable carapace-down position to a stable carapace-up position. Note: photos are from separate events.

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CHAPTER FIVE

BIOSTRATIGRAPHIC ANALYSIS OF FRESHWATER TURTLES IN THE UPPER CRETACEOUS KAIPAROWITS FORMATION OF SOUTHERN UTAH

Abstract

Hundreds of fossil freshwater turtle specimens have been collected from the Upper Cretaceous (Campanian) Kaiparowits Formation of southern Utah. The localities for these turtle specimens occur throughout the formation, which is informally divided into smaller units based primarily on sandstone/mudstone ratios. Each of these units has been interpreted as representing a specific depositional environment that changed over time with fluctuations in eustatic sea level. Using these interpretations, the types and abundances of a variety of turtle taxa were analyzed within each informal unit to determine if changes in the local ecosystem caused any faunal turnover during the deposition of the Kaiparowits Formation. The results indicate that river taxa experienced little to no faunal turnover between the base and top of the formation. There is, however, a stronger signal to suggest a change in smaller turtle taxa that inhabited small ponds on the floodplain. However, any apparent change in turtle fauna can be explained by taphonomic biases that favor the preservation of larger turtles, or other biases that have resulted in greater preservation and exposure of the upper middle unit than other parts of the formation. It is concluded that no apparent change in turtle fauna occurred during deposition of the Kaiparowits Formation.

Introduction

Freshwater turtles are a common component of fossil assemblages in Late Cretaceous terrestrial deposits of southern Utah (Eaton, 1991; Hutchison et al., 1997; Hutchison et al., in press). The Upper Cretaceous (Campanian) Kaiparowits Formation, exposed within Grand Staircase-Escalante National Monument, was deposited during a two million year time span and consists of dominantly fluvial and floodplain deposits (Roberts et al., 2005; Roberts, 2007). Roberts (2007) described lithologic changes throughout the Kaiparowits Formation and interpreted these changes as corresponding to fluctuations in eustatic sea level, which influenced local depositional environments. Roberts (2007) also noted an uneven distribution of vertebrate fossil localities through the formation, with some parts of the formation containing more fossil remains than others. In addition to abundant dinosaur remains, the Kaiparowits Formation contains a diverse assemblage of fossil freshwater turtles with as many as ten different known genera comprising seven different families (Hutchison et al., in press). This high diversity of turtle taxa is rare in the fossil record and may indicate prime ecological conditions during the late Campanian for the diversification of turtles in this region. Based upon these previous observations and interpretations, it is proposed that the biostratigraphic distribution of fossil turtles in the Kaiparowits Formation corresponds to (1) changes in the environmental conditions at the time of deposition and (2) the preservation potential of a turtle in each depositional environment. It is hypothesized that the number and diversity of those turtles that prefer only freshwater habitats will be reduced during times of higher regional sea level and more abundant when sea level is lower and the effects of brackish waters on freshwater fauna are minimal. Over 200 Kaiparowits turtles were placed within a stratigraphic context using informal divisions of the formation, bentonite horizons, and distinctive marker beds (Roberts, 2007). Changes in turtle taxa abundances in each division were analyzed from both a taphonomic and paleoecologic perspective to identify changes in the diversity of freshwater turtles. In addition to analyzing freshwater turtle diversity, the discussion includes the utility of freshwater turtles as index fossils.

Previous Work

Roberts (2005; 2007) provides a thorough description and sedimentologic analysis of the Kaiparowits Formation. His work, along with other geologists (e.g. Gregory and Moore, 1931; Lohrengel, 1969; Eaton, 1987), provide a nearly complete geologic history of the Kaiparowits Formation, including its tectonic history and sedimentary provenance. Paleontologists have also worked extensively in the Kaiparowits Formation during the past decade, recovering a variety of vertebrate fossils including mammals, crocodiles, dinosaurs, and turtles (Eaton, 1991; Hutchison et al., 1997). The following sections summarize current knowledge about the stratigraphy, depositional history, and fossil turtles of the Kaiparowits Formation.

Geologic Setting

The Kaiparowits Formation was first named and partially described by Gregory and Moore (1931); however, Lohrengel (1969) was first to fully measure and describe the formation in detail. Gregory and Moore (1931) first interpreted the Kaiparowits Formation as Tertiary in age, but palynological work by Lohrengel (1969) and later biostratigraphic work by Eaton (1991) firmly placed the Kaiparowits Formation into the Upper Cretaceous, more specifically the late Campanian. Roberts et al. (2005) obtained more precise age determinations using 40Ar/39Ar dating of bentonite horizons in the formation and the results indicate an age range of 76.1 – 74.0 Ma. Roberts (2007) also analyzed facies architecture and depositional environments to further understand the tectonic and depositional history of the region during the Late Cretaceous (Fig. 5.1).

The stratigraphy of the Kaiparowits Formation has been thoroughly measured and described multiple times (Gregory and Moore, 1931; Eaton, 1987; Roberts, 2005, 2007). At approximately 860 m from its base above the Upper Cretaceous Wahweap Formation to its erosional, unconformable contact with the overlying Maastrichtian-Tertiary Canaan Peak Formation, it is one of the thickest units in the Kaiparowits Plateau (Eaton, 1987; Roberts, 2007). The Kaiparowits Formation consists dominantly of fluvial channel and floodplain deposits represented by a variety of lithofacies associations (Roberts, 2007). The clastic material of the Kaiparowits Formation was transported northward from the Mogollon Highlands of southwestern Arizona and eastward from the Sevier orogenic belt of southeastern Nevada and southern California and deposited in a subsiding foreland basin in south-central Utah (Goldstrand, 1992; Lawton et al., 2003). Today, these deposits are seen as impressive grayish-blue badlands exposed within the Kaiparowits Plateau region of Grand Staircase-Escalante National Monument. Roberts (2007) measured and described several sections of Kaiparowits exposures in Grand Staircase-Escalante National Monument. He subsequently divided the Kaiparowits Formation informally into lower, middle, and upper units based on subtle changes in sandstone-mudstone ratios (Fig. 5.1). These informal subdivisions will serve as a reference for examining the intraformational biostratigraphy of freshwater turtles in the Kaiparowits Formation.

Lower Unit- The lower unit of the Kaiparowits Formation (Unit A) lies conformably over the early Campanian Wahweap Formation and is distinguished by a change to widespread overbank deposits from channel-dominated facies (Roberts, 2007). Unit A is approximately 90 to 110 m in thickness and is dominated by major tabular sandstones (Roberts, 2007). Roberts (2007) estimates the sandstone/mudstone ratio of Unit A as approximately 75:25, distinguishing it from the middle unit, that contains a higher concentration of mudstone. Unit A has been interpreted as consisting of predominantly meandering channel deposits in an increasingly wet environment (Roberts, 2007). Vertebrate fossil remains in Unit A are sparse, but partially articulated skeletons have been recovered from isolated channel deposits.

Middle Unit- The middle unit is the thickest informal division of the Kaiparowits Formation, ranging between 440 and 510 m in total thickness (Roberts, 20007). The middle unit contains the highest concentration of mudstone in the formation with a ratio of sandstone/mudstone around 45:55 (Roberts, 2007). Roberts (2007) established the lower boundary of the middle unit at the base of a ~10 m thick sequence of overbank deposits, around 90 to 110 m from the base of the formation. The top of the middle unit occurs at the base of a multistory channel sandstone complex, about 550 m above the base of the section. Based upon changes in depositional environment, the middle unit is, herein, further sub-divided into a lower middle (Unit B) and upper middle unit (Unit C). Unit B (about 190 m in thickness) contains an inclined heterolithic mudstone and sandstone sequence between 110 and 300 m above the base of the section that has been interpreted to represent tidally-influenced channel deposits (Roberts, 2007). The marine trace fossil *Teredolites* has also been identified in Unit B, which may indicate a near-coastal depositional environment and maximum marine transgression of the Western Interior Cretaceous Seaway (Roberts, 2007). Unit C (about 250 m in thickness) has been interpreted to comprise both meandering and anastomosing channel deposits with frequent intervals of overbank deposition (Roberts, 2007). Unit C is by far the most fossiliferous of the Kaiparowits informal subdivisions with several hundred vertebrate fossil localities recognized (Eaton, 1991; Hutchison et al., 1997; Knell, in preparation).

Upper Unit- The upper unit (Unit D) (about 310 m in thickness) as defined by Roberts (2007) includes the base of the multistory channel complex, around 550 m from the base of the section to the top of the formation, which is marked by an erosional unconformity with the overlying Maastrichtian-Tertiary Canaan Peak Formation at around 860 m. The sandstone/mudstone ratio in Unit D is estimated at around 60:40, similar to that of Unit A (Roberts, 2007). This has been interpreted by Roberts (2007) as a return to dominance of meandering channel deposition in association with a decrease in regional base level in a humid to sub-humid climate. Fossil content is the poorest in Unit D, compared to Units A, B, and C (pers. observ.).

Kaiparowits Turtles

The diverse assemblage of fossil freshwater turtles collected from the Kaiparowits Formation includes as many as seven families with at least ten named genera. This designates the Kaiparowits Formation as one of the most diverse turtle-bearing units in the Cretaceous, second only to the Hell Creek Formation (Hutchison and Archibald, 1986; Hutchison, 2009; Hutchison et al., in press). A wide variety of turtle morphologies can be found in the Kaiparowits Formation, with sizes ranging from 10 cm to nearly 100 cm in length along with a variety of shell morphologies. Table 5.1 summarizes Kaiparowits turtle specimens, including taxon description, probable habitat, and additional occurrences in other formations.

Predictions

Based upon previous research on fossil turtle biostratigraphy (Hutchison, 2000; Hutchison and Archibald, 1986), taphonomy (Knell, in preparation), and Campanian depositional environments in southern Utah (Roberts, 2007), some predictions can be made regarding the expected distribution of fossil turtles in the Kaiparowits Formation. The ecology of living turtles has allowed paleontologists to infer similar habitat preferences for turtles of the same family or of similar morphology (Blob, 1997; Lyson and Joyce, 2011). Cretaceous baenids, adocids, and trionychids likely occupied rivers and small streams based on their morphological similarities to modern river turtles (Hutchison, 2000). Their taphonomic context indicates they are frequently well-preserved and in higher abundance in river channel deposits (Knell, in preparation). River deposits, which are characterized by either massive or lenticular sandstone bodies, occur in many exposures of the Kaiparowits Formation (Roberts, 2007). It is expected that river turtle taxa will be more abundant in parts of the formation with higher percentage of sandstone representing these river deposits, namely Units A and D. It is unknown how tolerant these, presumably freshwater, turtle taxa are to brackish waters, and absence of these turtle taxa in Unit B may indicate brackish water intolerance and a period of locally high sea level.

The smaller turtle taxa (*Compsemys*, kinosternids, and chelydrids) probably preferred freshwater bodies in the form of lakes and ponds (Lyson and Joyce, 2011; Knell, in preparation). As with the river turtles, the habitat preferences of these small turtles is based on known preferred habitats of living family members or close relatives. Additionally, the majority of small turtle fossils are recovered from pond and floodplain deposits, which may indicate greater abundance in these habitats than in rivers (Knell, in preparation). Most living pond turtles prefer only freshwater environments (Bonin et al., 2006), so it would be expected that these smaller turtle taxa should be absent during periods of higher regional sea level and increased brackish conditions during Kaiparowits deposition. Unit C in the Kaiparowits Formation contains more floodplain deposits in the form of mudstone and siltstone than Units A or D, thus the smaller turtle taxa should be more abundant in this unit.

Methods

Stratigraphic data was collected for 209 Kaiparowits fossil turtle localities comprising 286 turtle specimens (Table 5.2). Some of these localities were identified while the fossil turtle remains were still *in situ*, while other localities were relocated based upon previously recorded GPS coordinates for curated museum specimens. Each locality was placed stratigraphically into Unit A, B, C, or D in the Kaiparowits Formation based upon measured distance above or below identifiable marker beds. These marker beds included contacts with the underlying Wahweap Formation and overlying Canaan Peak Formation, as well as prominent bentonite horizons and distinctive sedimentary marker beds based on Roberts et al. (2005) and Roberts (2007). The turtle taxa from each locality were identified to the family and genus level and recorded. A biostratigraphic range for each turtle taxa was generated by plotting taxa occurrences within each stratigraphic subdivision (Fig. 5.2). The resulting range chart was analyzed to identify any disruptions in the biostratigraphic lineage of each turtle genus through the deposition of the Kaiparowits Formation.

Results

The stratigraphic distribution of turtle localities and taxa in the Kaiparowits Formation is far from equal. Unit A is very poor in turtle remains, with only 13 specimens comprising six different taxa (*Adocus*, *Aspideretoides*, *Basilemys*, *Compsemys*, a kinosternid, and *Neurankylus*). Unit B also lacks abundant turtles with only 15 reported specimens. Diversity slightly increases from Unit A to Unit B with the addition of

Denazinemys and a chelydrid, whereas *Aspideretoides* is now absent. Together, Units A and B comprise approximately 10% of turtle specimens and yet account for about 35% of the formation thickness (0 to 300 m).

Unit C in the Kaiparowits Formation contains the highest number of turtle specimens, as well as the highest represented turtle diversity. Approximately 87% of all freshwater turtle specimens come from Unit C, which accounts for about 30% of the formation thickness (300 to 550 m). All 12 turtle taxa occur in this unit, and all but *Plesiobaena*, *Boremys*, and *Plastomenoides* are represented by more than a dozen specimens.

Unit D in the Kaiparowits Formation is again poor in turtle remains with only nine specimens collected, or about 3% of the specimens from the entire formation. However, this unit contains approximately 36% of the formation thickness (550 to 860 m). Only five taxa (*Adocus*, a chelydrid, *Compsemys*, *Helopanoplia*, and *Neurankylus*) occur within Unit D.

Of the twelve taxa included in this study, three are present in every informal unit (*Adocus*, *Compsemys*, and *Neurankylus*). Interestingly, there is very little morphological similarity in these three taxa and each represents a different family. *Aspideretoides* is the only taxa that disappears (Unit B) and then reappears (Unit C) within the formation, only to disappear again (Unit D). *Basilemys* and the kinosternid are the only taxa that are present at the base of the formation but disappear by Unit D. The chelydrid (Unit B) and *Helopanoplia* (Unit C) are the only two taxa that first appear in the middle of the

Kaiparowits Formation and continue through to Unit D. *Denazinemys* is present only in Units B and C of the formation and is absent from Units A and D.

Discussion

The results of the biostratigraphic analysis clearly show that Unit C in the Kaiparowits Formation is by far the most fossiliferous for turtle remains; this is also true for other fossil vertebrates (pers. observ.). Turtle diversity in the Kaiparowits Formation is also the greatest in Unit C. Based on this information alone it is assumed that there were larger numbers of turtles during deposition of Unit C and that diversity had reached its peak during this period as well. In terms of predictions regarding turtle taxa, probable habitats, and their stratigraphic occurrences, there does not seem to be a strong correlation. The low numbers of specimens in Units A, B, and D are probably masking any trends. The river turtle taxa appear in the sandstone dominated units, in limited numbers; as predicted they occur in abundance in the mudstone-dominated Unit C. In terms of the smaller turtle taxa, they were predicted to be more abundant in Unit C, which is dominated by floodplain deposits, and the resulting data supports this. However, this result may reflect a taphonomic bias rather than an ecologic signal because smaller turtles would be poorly preserved in higher energy river deposits.

The resulting data does not refute the possibility that changes in sea level during deposition of the Kaiparowits Formation may have affected some of the local turtle fauna in southern Utah during the Campanian. The chelydrid and *Helopanoplia*, for example, both appear in Unit B and continue into Unit D. It is possible that these taxa were absent from the area during deposition of Unit A, but it is more likely that they simply have yet to be collected there. Chelydrids are known from Turonian deposits in the vicinity, but the origins of *Helopanoplia* are unclear (Hutchison, pers. comm.). *Basilemys* and the kinosternid occur in Unit A but disappear prior to Unit D. Again, this may be an instance where specimens of these taxa have yet to be discovered in Unit D, or they emigrated from the area in the late Campanian. However, because these taxa occur together in younger Maastrichtian deposits to the north in the Hell Creek Formation (Hutchison and Archibald, 1986) and south in the Kirtland Formation (Hunt, 1993), it seems more likely that *Basilemys* and the kinosternid will eventually be recovered from Unit D as well. The same can be stated for *Denazinemys* and *Aspideretoides*, which occur in some, but not all of the Kaiparowits subdivisions, and should be collected in all of them given time. *Adocus*, *Compsemys*, and *Neurankylus*, having been recovered in all of the Kaiparowits subdivisions, show no evidence for faunal turnover during Kaiparowits deposition. This set of conclusions assumes all taxa have an equal chance of preservation in the fossil record and that the amount of exposure is equal amongst all Kaiparowits subdivisions, but this assumption represents an oversimplification.

Taphonomic and Geographic Biases

A taphonomic analysis of the Kaiparowits fossil turtles indicates a preference towards the preservation of larger taxa and those with more robust shells, which resists destruction during transport and burial (Knell, in preparation). This taphonomic bias increases the potential for taxa like *Neurankylus*, *Adocus*, and *Denazinemys* to be successfully fossilized and subsequently discovered in the field. Smaller taxa (e.g. *Compsemys*, kinosternids, and chelydrids) likely show a reduced potential for preservation. Therefore, absence of these taxa in certain subdivisions of the Kaiparowits may not be a result of absence in the Campanian ecosystem. Instead, absence may result from taphonomic bias working against their preservation and subsequent appearance in the fossil record.

Geologists or paleontologists conducting fieldwork in the Kaiparowits Formation soon discover that exposure of the formation is not equal for Units A, B, C, and D within Grand Staircase-Escalante National Monument. The amount of erosional exposure appears to be much more extensive for Unit C than the other subdivisions. This factor is probably why the number of turtle localities is substantially greater in Unit C. Accessibility to outcrops is also much easier in Unit C. Exposures of Unit D, in particular, are frequently covered in vegetation or include treacherous cliff faces that make access extremely difficult and hazardous. Unit A exposures are also often vegetated or covered in alluvium, contributing to the difficulty of collection. These geographic biases are purely personal observations at this point, with no quantitative data to support them. However, a future application of geologic maps and GIS software would provide this data.

Biostratigraphic and Paleobiogeographic Implications

Roberts (2007) has interpreted a marine incursion during Unit B. However, there does not appear to be a strong signal that indicates that any turtle taxa were strongly affected by this change. Further, those taxa that appear to be affected on a minor scale can be largely ignored based on taphonomic and geographic biases. All 12 turtle taxa included in this biostratigraphic analysis are present in older, younger, or equivalent deposits in Utah and elsewhere (Table 5.2); therefore, there does not appear to be any significant first appearances or last appearances of turtle taxa in southern Utah during the deposition of the Kaiparowits Formation.

In terms of paleogeography, the Kaiparowits Formation represents a central location along the eastern shore of Laramidia, between the northern Judith River/Dinosaur Park Formations of Montana/Alberta and the southern Fruitland/Kirtland/Aguja Formations of New Mexico/Texas. Regional endemism (a northern fauna and southern fauna) has been described before in terms of dinosaur diversity in the Late Cretaceous (Farke et al., 2011; Loewen at al., 2011). As seen above, the Kaiparowits Formation contains a diverse assemblage of turtle taxa, possibly the most diverse assemblage in the Campanian. Many of these same taxa occur in Campanian localities to the north and south. It is likely that many southern turtle taxa spread northward and many northern turtle taxa spread southward through this region of southern Utah either prior to or during this isolation of northern, central, and southern vertebrate faunas of Laramidia. Currently, however, the taxonomy of many Cretaceous turtle families remains too poorly resolved to accurately determine the origin and emigration of turtle taxa during this time. With continued taxonomic work these questions of Cretaceous turtle paleobiogeography can be addressed.

Fossil Turtles as Index Fossils

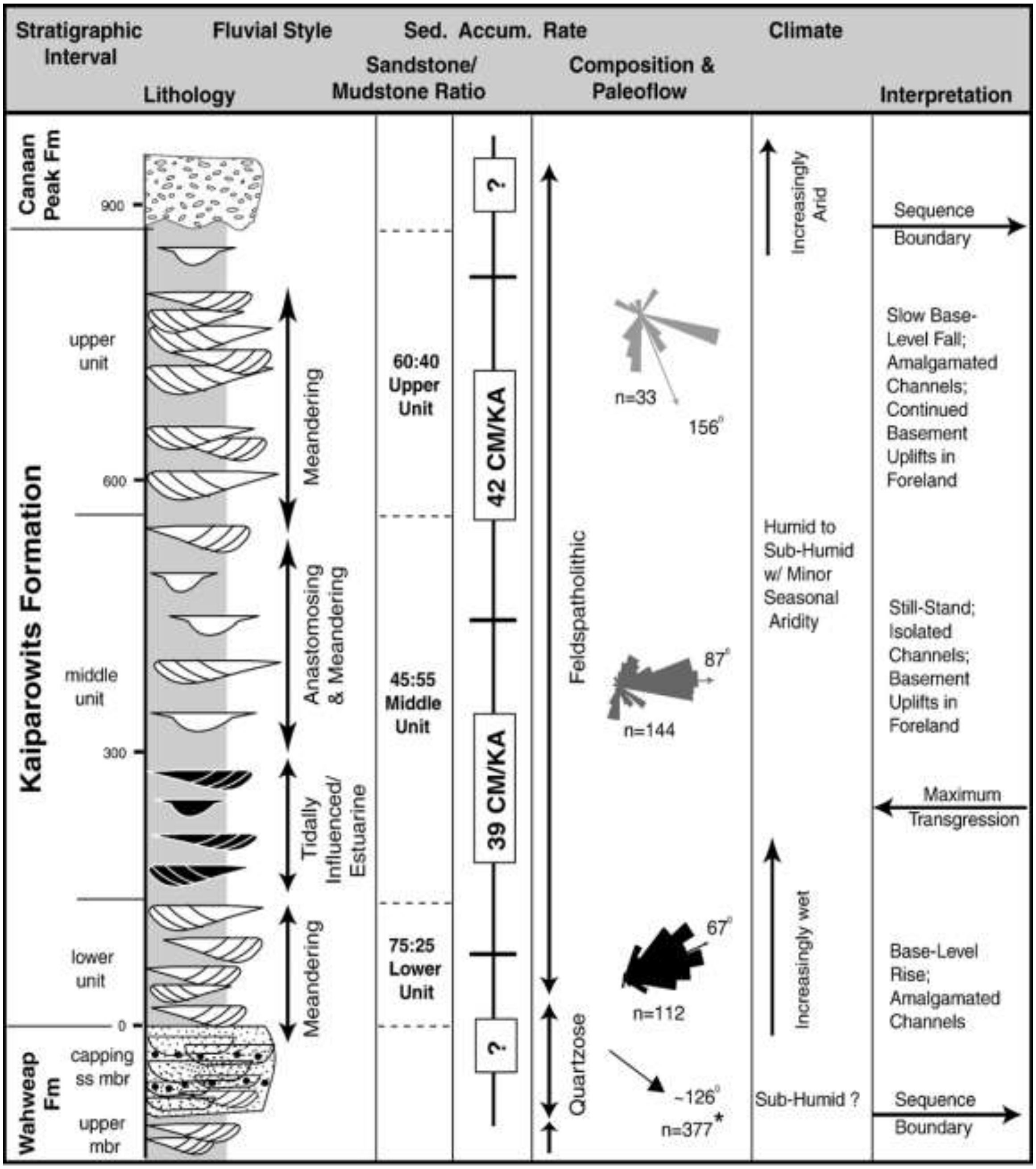
Of any vertebrate group, freshwater fossil turtles likely have the greatest potential to serve as terrestrial index fossils based on their abundance in many fossil bearing units. In order to be a useful index fossil, a taxa needs to (1) be very abundant and easily recognized in the fossil record, (2) have a large geographic range, and (3) only exist for a short length of time in the geologic record. Turtles are very abundant in some terrestrial vertebrate assemblages and many have a large geographic range; however, turtles remain poor candidates for index fossils. There are multiple reasons for this, but most involve fossil turtle taxonomic issues. The taxonomy of many fossil turtle families is either too complex or in desperate need of revision with the addition of new specimens. Several paleontologists are currently working to resolve this problem, although it may be some time before a thorough understanding of the primary turtle families and their relationships is established. The skull offers the most diagnostic elements for distinguishing the genus or species of a fossil turtle. Unfortunately, turtle skulls are extremely uncommon due to their often delicate construction and subsequent poor preservation potential. The vast majority of turtle elements found in collections are pieces of turtle shell or limb elements. These fragments often only permit identification to the family or sometimes genus level. Index fossils are often designated at the species level, and this remains impractical for turtle specimens. Another problem for using turtles as index fossils is that several genera, and even species, are known for their extensive biostratigraphic ranges. This factor, in combination with a poor taxonomic understanding, renders most fossil turtles useless as proper index fossils. However, there are some fossil turtles that currently meet, or approximate, the criteria required for utility as index fossils. With further taxonomic clarification, some Campanian freshwater turtle taxa that might be considered as index fossils in the future may include the genera *Aspideretoides* and *Denazinemys*.

Conclusions

An intraformational biostratigraphic analysis of the freshwater turtles in the Upper Cretaceous (Campanian) Kaiparowits Formation has shown that there was no evident change in turtle taxa through the two million years of formation deposition. Geographic and taphonomic biases have masked any apparent emigrations or immigrations of turtle taxa during deposition of each informal unit subdivision where a taxon is missing. A marine incursion during deposition of Unit B apparently had no effect on turtle taxa in the late Campanian of southern Utah.

Unit C of the Kaiparowits Formation contains abundant fossil turtle specimens, but this unit is highly exposed in Grand Staircase-Escalante National Monument and these outcrops are easily accessible to paleontologists. Given time, additional prospecting in Units A and D may uncover additional turtle specimens. Further taxonomic study of Campanian turtles is recommended for further detailed analysis of Cretaceous turtle biostratigraphy and paleobiogeography. And although fossil turtles currently do not appear to be useful as index fossils in correlation studies, they should continue to provide depositional environment information for reconstructing local paleoenvironments.

FIGURES AND TABLES



* from Lawton et al., 2003

Figure 5.1. Summary and interpretation of Kaiparowits Formation depositional history. (cm/ka = estimated amount of deposition in cm per thousand years). Created by Lawton et al. (2003) and modified by Roberts (2007). Used with permission.

Table 5.1. Summary of Kaiparowits fossil turtles including general descriptions, probable habitat, and occurrences in other Cretaceous formations in North America.

TURTLE FAMILY	TURTLE GENUS	AVERAGE SIZE	SHELL MORPHOLOGY	PROBABLE HABITAT	OLDER OCCURENCES	EQUIVALENT OCCURENCES	YOUNGER OCCURENCES
Adocidae	*Adocus*	40 to 50 cm	Oblong, moderate carapace arch	fluvial	Straight Cliffs Fm, Wahweap Fm (Hutchison 2009), Milk River Fm (Brinkman 2003)	Judith River Group (Brinkman 2003), Aguja Fm (Sankey 2006), Fruitland Fm (Hunt 1993)	Kirtland Fm (Hunt 1993), Hell Creek Fm (Hutchison and Archibald, 1986), North Horn Fm (Cifelli et al. 1999)
Baenidae	*Boremys*	30 to 40 cm	Oblong, moderate carapace arch	fluvial	Wahweap Fm (Hutchison 2009), Milk River Fm (Brinkman 2003)	Judith River Group (Brinkman 2003), Fruitland Fm (Hunt 1993)	Kirtland Fm (Hunt 1993)
	Denazinemys	30 to 40 cm	Oblong, high carapace arch	fluvial	Straight Cliffs Fm, Wahweap Fm (Hutchison 2009)	Fruitland Fm (Hunt 1993)	Kirtland Fm (Hunt 1993)
	Neurankylus	80 to 100 cm	Circular, moderate carapace arch	fluvial	Straight Cliffs Fm, Wahweap Fm (Hutchison 2009), Milk River Fm (Brinkman 2003)	Judith River Group (Brinkman 2003), Fruitland Fm (Hunt 1993)	Kirtland Fm (Hunt 1993), Hell Creek Fm (Hutchison and Archibald, 1986)
	Plesiobaena	30 to 40 cm	Oblong, moderate carapace arch	fluvial	Milk River Fm (Brinkman 2003)	Judith River Group (Brinkman 2003)	Kirtland Fm (Hunt 1993), Hell Creek Fm (Hutchison and Archibald, 1986)
Chelydridae	Unknown	15 to 20 cm (estimated)	Circular, moderate carapace arch	pond, floodplain	Straight Cliffs Fm (Hutchison 1999), Milk River Fm (Brinkman 2003)	Judith River Group (Brinkman 2003)	Hell Creek Fm (Hutchison and Archibald 1986)
Kinosternidae	Unknown	15 to 20 cm (estimated)	Circular, high carapace arch	pond, floodplain	None	Aguja Fm (Sankey 2006)	Kirtland Fm (Hunt 1993)
Nanhsiungchelyidae	*Basilemys*	70 to 90 cm	Rectangular, high carapace arch	floodplain, terrestrial	Straight Cliffs Fm, Wahweap Fm (Hutchison 2009), Milk River Fm (Brinkman 2003)	Judith River Group (Brinkman 2003), Aguja Fm (Sankey 2006), Fruitland Fm (Hunt 1993)	Kirtland Fm (Hunt 1993), North Horn Fm (Cifelli et al. 1999)
Pleurosternidae	*Compsemys*	15 to 20 cm	Circular, moderate carapace arch	pond, floodplain	Straight Cliffs Fm, Wahweap Fm (Hutchison 2009), Milk River Fm (Brinkman 2003)	Judith River Group (Brinkman 2003), Fruitland Fm (Hunt 1993)	Kirtland Fm (Hunt 1993), Hell Creek Fm (Hutchison and Archibald, 1986), North Horn Fm (Cifelli et al. 1999)
Trionychidae	*Aspideretoides*	50 to 60 cm	Circular, flat carapace	fluvial, pond	None	Judith River Group (Brinkman 2003), Fruitland Fm (Hunt 1993), Fort Crittenden Fm (Ratkevich 1994)	Kirtland Fm (Hunt 1993), Hell Creek Fm (Hutchison and Archibald, 1986), North Horn Fm (Cifelli et al. 1999)
	Helopanoplia	40 to 50 cm	Circular, flat carapace	fluvial, pond	None	Aguja Fm (Sankey 2006)	Hell Creek Fm (Hutchison and Archibald 1986)
	Plastomenoides	20 to 30 cm	Circular, flat carapace	fluvial, pond	None	Fort Crittenden Fm (Ratkevich 1994)	Kirtland Fm (Hunt 1993)

Table 5.2. The biostratigraphic distribution of the Kaiparowits fossil turtles by family and genus.

TURTLE FAMILY	TURTLE GENUS	Lower Unit	Lower Middle Unit	Upper Middle Unit	Upper Unit	Total Specimens	Percent of Taxa
Adocidae	*Adocus*	3	2	59	3	67	23.40%
Baenidae	*Boremys*	0	0	1	0	1	0.35%
	Denazinemys	0	1	24	0	25	8.70%
	Neurankylus	1	5	19	1	26	9.10%
	Plesiobaena	0	0	2	0	2	0.70%
Chelydridae	Unknown	0	1	13	2	16	5.60%
Kinosternidae	Unknown	1	2	19	0	22	7.70%
Nanhsiungchelyidae	*Basilemys*	3	2	33	0	38	13.30%
Pleurosternidae	*Compsemys*	3	2	43	2	50	17.50%
Trionychidae	*Aspideretoides*	2	0	22	0	24	8.40%
	Helopanoplia	0	0	13	1	14	4.90%
	Plastomenoides	0	0	1	0	1	0.35%
	Total Occurrences	**13**	**15**	**249**	**9**	**286**	
	Percent of Specimens	**5%**	**5%**	**87%**	**3%**		

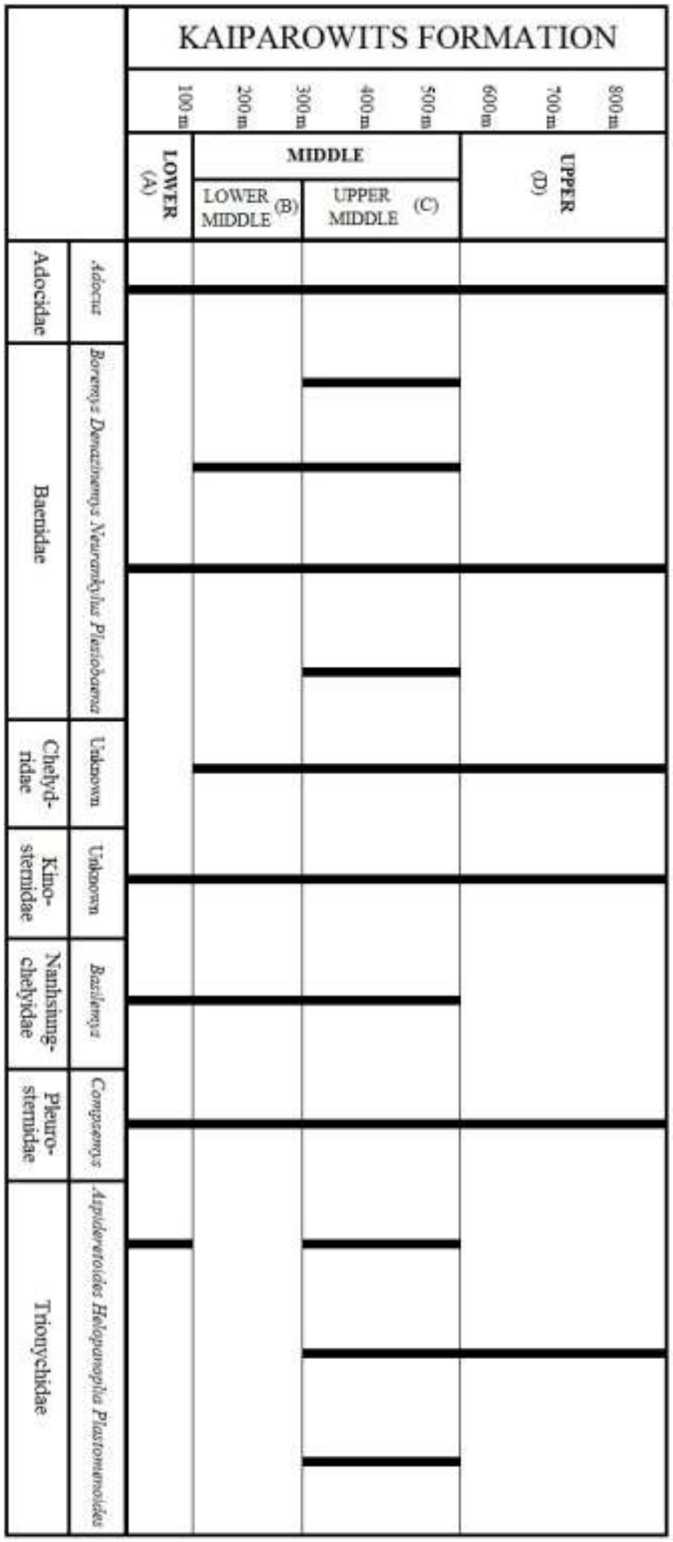


Figure 5.2. The biostratigraphic ranges of fossil turtle taxa within the Kaiparowits Formation based on known stratigraphic occurrence.

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CHAPTER SIX

A GRAVID FOSSIL TURTLE FROM THE UPPER CRETACEOUS (CAMPANIAN) KAIPAROWITS FORMATION, SOUTHERN UTAH

Contribution of Authors and Co-authors

Manuscript in Chapters 3, 4, and 6

Author: Michael J. Knell

Contributions: Assisted with preparation of the fossil turtle after discovery of turtle eggs within. Contributed geology and turtle description portions of the manuscript. Provided specimen photos and location map for the manuscript. Contributed to the introduction, discussion, and conclusions sections of the manuscript. Presented findings relating to the specimen at the Dinosaur Eggs & Babies Symposium in Bozeman, Montana in 2009.

Co-Author: Dr. Frankie Jackson

Contributions: Completed the fossil egg description and analysis portions of the manuscript. Provided valuable SEM images of turtle eggs, a table of known turtle egg research, and useful references. Also contributed to the introduction, methods, discussion, and conclusion sections of manuscript.

Co-Author: Dr. Alan Titus

Contributions: Helped with identification and collection of turtle specimen in the field. Assisted with fossil preparation of specimen. First identified the presence of eggs within the turtle. Provided field data for manuscript in addition to helpful feedback and edits during preparation.

Co-Author: Dr. L. Barry Albright, III

Contributions: First discovered turtle specimen in the field. Assisted with editing during preparation of manuscript.

Manuscript Information Page

Michael J. Knell, Frankie Jackson, Alan Titus, L. Barry Albright, III
Historical Biology
Status of Manuscript:
____Prepared for submission to a peer-reviewed journal
____Officially submitted to a peer-reviewed journal
____Accepted by a peer-reviewed journal
_X_Published in a peer-reviewed journal

Published by Taylor & Francis
Volume 23, Number 1 (March 2011)

A gravid fossil turtle from the Upper Cretaceous (Campanian) Kaiparowits Formation, southern Utah

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(Received xx July 2009; final version received xx August 2010).

An *Adocus* turtle collected from the Upper Cretaceous (late Campanian) Kaiparowits Formation in southern Utah contains partial eggs and numerous well-preserved bones beneath the carapace. The bones include the closely associated/articulated elements of the right pectoral girdle, skull, and cervical vertebrae. The eggs are about 35 mm in diameter, and the rigid 250–280 µm-thick eggshell exhibits needle-like aragonitic crystals that form the narrow, straight shell units. The eggs appear smaller than those within a gravid *Adocus* from Alberta, and the eggshell is thinner and lacks the feathered structure reported in the Alberta eggs. Differences in the Utah and Alberta *Adocus* eggs may result from differences in the stage of egg formation or the specimens may represent different *Adocus* species.

Keywords: gravid turtle; *Adocus*; eggs, *Testudoolithus*; Kaiparowits Formation

Introduction

Fossil turtle eggs are relatively rare in the fossil record and seldom assigned to a specific taxon. Although some fossil turtle eggs contain embryonic remains (Mikhailov 1991, 1997; Mikhailov et al. 1994; Jackson et al. 2002; Jackson and Schmitt 2008; Jackson et al. 2008), these eggs remain taxonomically unidentified. The only fossil turtle eggs definitively assigned to an extinct taxon are those discovered within a female *Adocus* (Cryptodira: Adocidae) from the Upper Cretaceous (late Campanian) Dinosaur Park Formation, Alberta, Canada (Zelenitsky et al. 2008). Here we describe a second fossil *Adocus* that contains eggs and skeletal elements within its body cavity, from the Upper Cretaceous (late Campanian) Kaiparowits Formation of Utah. We compare the eggs from this specimen to previously described turtle eggs, and assess the stage of eggshell formation relative to the gravid *Adocus* from Alberta.

Geology

Exposures of the Upper Cretaceous (late Campanian) Kaiparowits Formation occur in the Kaiparowits and Table Cliffs plateaus in Grand Staircase-Escalante National Monument (GSENM) of southern Utah (Figure 6.1). The sediments comprising the formation were deposited in the rapidly subsiding Cordilleran foreland basin, sourced from thrust sheets of the Sevier orogenic belt in southeastern Nevada and southern California and the Mogollon Highlands of southern Arizona (Goldstrand 1992; Lawton et al. 2003). The sedimentary record of the formation includes pond deposits, suspended-load channels, and poorly-developed hydromorphic paleosols, indicative of a relatively wet, sub-humid alluvial system (Roberts 2007). The Kaiparowits Formation rests conformably on the middle Campanian Wahweap Formation, whereas a subtle angular unconformity separates the Kaiparowits from the overlying Canaan Peak Formation. Roberts et al. (2005) dated multiple bentonite horizons within the formation, obtaining ^{40}Ar/^{39}Ar dates that range from 76.1–74.0 Ma. In addition, Roberts (2007) informally subdivided the Kaiparowits Formation into lower, middle, and upper units, based on changes in alluvial architecture, sandstone to mudstone ratios, and interpreted channel morphology. The *Adocus* specimen described here was collected from Blue Wash in the center of Grand Staircase-Escalante National Monument near Horse Mountain. Stratigraphically, the *Adocus* site is sandwiched approximately equal distance between two dated ash beds (75.97 Ma and 75.51 Ma respectively) within the middle portion of the middle unit (E. Roberts personal communication).

Methods

Preparation of the fossil turtle (LBA-06-7) consisted of removing the sandstone matrix with small hand tools and an air scribe. Eggshell fragments were removed from an egg from within the body cavity and broken in half. Half of each fragment was prepared as a standard petrographic thin section (30 μm thick) and studied with a transmitted and polarized light microscope. The other half of each eggshell was coated with gold (10 nm), mounted on an aluminum stub, and imaged at 15 kV with a JEOL 6100 scanning electron microscope (SEM). Structural attributes (shell thickness, shell unit width) were measured with *Scion* image analysis software. A Philips Brilliance CT scanner at Bozeman

Deaconess Hospital Radiology Department, Bozeman, Montana was used for Computerized Tomography (CT) imaging.

Results

Osteological remains

The fossil turtle occurred in a carapace-up position in a medium to fine-grained, well-cemented sandstone, interpreted as a channel-fill deposit. Approximately 75–80% complete, the specimen measures approximately 33 cm long and 26 cm wide (Figure 6.2(A)). Portions of the left, anterior, and posterior margins of the carapace and plastron are missing. The carapace surface often exhibits a dimpled texture, and the right rear quadrant shows substantial dorso-ventral crushing. We estimate the original carapace length and width as 50-55 cm and 40-45 cm, respectively.

Although not complete, laboratory preparation exposed several bones under the right marginal portion of the carapace, including two cervical vertebrae, two bones tentatively identified as parts of the hyoid, and several unidentified bone fragments (Figure 6.2(B,C)). Removal of a few costal portions of the carapace in this region revealed the superior surface of the disarticulated skull which faces toward the left side of the specimen (Figure 6.2(B)). Elements include the parietals, supraoccipital, and frontals which appear intact, in addition to a partial right squamosal. Several skeletal elements are also present along the right central margin of the carapace (Figure 6.2(A,C)). The right pectoral girdle includes the humerus, scapula, and coracoid, with the scapula and coracoid nearly articulated and approximately in life position. The right humerus, however, was moved a short distance posteriorly relative to the scapula and coracoid, and the in-filling sandstone matrix conceals the distal portion of this element. In the left rear quadrant the distal end of the left femur lies within a sediment-filled gap between the carapace and plastron. All bones show minimal post-mortem modification such as abrasion, weathering, or evidence of scavenging or predation. Surface collection included a nearly complete set of hind limb metapodials.

Taxonomic identification

The genus *Adocus* represents an extinct basal cryptodiran, diagnosed primarily on the distinctive texture on the carapace that consists of small irregular pits or dimples and the overlapping of the marginal scales onto the costals in the middle and posterior parts of the shell (Syromyatnikova and Danilov 2009**)**. *Adocus* is the only known member of the Adocidae in western North America during the Campanian (Brinkman 2003), and we assign the fossil turtle from Utah to this genus on the basis of these characters.

Egg description

In addition to skeletal elements, portions of at least two eggs occur within the carapace (Figure 6.2(C)). The pale, cream-colored eggs are incompletely preserved, with some distortion and fragmentation of the eggshell that likely resulted from fluvial transport and lithostatic compression. Although the eggs appear to be spherical in shape and about 35 mm in diameter, their fragmented condition leaves some doubt about these attributes. Computed tomography scans failed to detect additional eggs within the body cavity, although this may result from inadequate density difference between the eggshell and surrounding sandstone.

The needle-like structure of the eggshell suggests it consists of aragonite or possibly a pseudomorph of this mineral. Relatively straight, narrow, and interlocking shell units comprise the 250–280 μm-thick eggshell (Figure 6.2(D)). The shell unit heights are approximately 2.5 times their widths and flare slightly toward the outer portion of eggshell, terminating in a relatively smooth, flat surface. The absence of nucleation sites at the inner shell surface likely results from physical or chemical weathering. Due to diagenetic alteration, eggshell structural features are less apparent when examined under SEM.

Egg and eggshell comparisons

The eggs are referable to the oogenus *Testudoolithus* Hirsch 1996, within the oofamily Testudoolithidae Hirsch 1996 {as emended by Jackson et al. (2008)} on the basis of their aragonitic composition, interlocking shell units that form the rigid eggshell, and the shell unit height and width ratio. The eggshell is substantially thinner than *T. rigidus* and *T. jiangi*, as well as unassigned eggs containing embryonic remains from the Upper Cretaceous (Campanian) Judith River Formation in Montana (Table 6.1). In addition, the external surface of the shell units of the Montana turtle eggs are domed, whereas the *Adocus* eggs from Utah display a relatively flat surface except for irregularities that resulted from weathering.

The *Adocus* eggshells from Utah are thinner than eggshells from the elliptical eggs reported by Winkler and Sánchez-Villagra (2006) from Venezuela and purported turtle eggs from India (Table 6.1). Mohabey (1998) described these eggs from India as *Testudoolithus*; however, the 800 μm-thick eggshell exhibits a shell unit height-to-width ratio of 3.5:1, which exceeds that of the eggs from Utah (Table 6.1). In addition, Mohabey (1998) identified a mammillary layer at the inner portion of the shell, a feature characteristic of avian and non-avian theropod eggs. Extensive diagenetic alteration of the Indian eggshell obscures evidence of the original aragonitic structure and, therefore, we agree with Kohring (1999) that the identification of these eggs as testudine remains questionable.

Mikhailov et al. (1994) report an egg containing a turtle embryo, with an eggshell thickness of 300– 400 µm (Table 6.1). Mikhailov (1997) referred to this specimen as "*Testudinovum* oosp", but this may represent a misspelling of *Testudinarum*, a name previously established by Schleich et al. (1988). Published thin sections of the Mongolian egg show significant diagenetic alteration that prohibits comparison to the *Adocus* egg described here.

The size of the Utah eggs (~35 mm) is likely smaller than eggs from inside an *Adocus* female and those of a separate, isolated *Adocus* clutch from Alberta (Zelenitsky et al. 2008). The eggshell of the Utah specimens is also thinner and lacks the feathered structures and slightly domed shell units reported in the Alberta eggs.

Discussion

The gravid *Adocus* from Utah is exceptionally well preserved and represents only the second published occurrence of fossilized eggs within a turtle. The absence of significant bone modification, presence of eggs within the body cavity, and partial articulation of the pectoral girdle all suggest rapid burial of the turtle within a fluvial channel (Aslan and Behrensmeyer 1996; Voorhies 1969). Interestingly, this specimen includes the skull, an unusual occurrence for fluvially transported fossil turtles (Blob 1997). The skull lies within the central part of the carapace, along with several cervical vertebrae. This may reflect the normal retracted head position when the animal died or may result from rigor mortis. Alternatively, stream flow may have pushed the head into the carapace during decomposition of the turtle in the channel. Although the length of time between death and burial remains speculative, the absence of significant bone weathering and partial articulation of the scapula and coracoid suggest little or no subaerial exposure (Behrensmeyer 1978).

The presence of eggs in the body cavity indicates the *Adocus* specimen is a female. Dorso-ventral crushing in the right rear quadrant likely displaced the skeletal elements and forced the eggs forward into the region of the pectoral girdle. The eggs preserved in the *Adocus* from Alberta also occupy the anterior half of body cavity (Zelenitsky et al. 2008: fig. 1(a)). Remnants of the reproductive tract, as well as the carapace and plastron, likely helped retain the eggs in this position, prohibiting dispersal by water currents.

The original number of eggs within the body cavity remains uncertain. However, using the estimated carapace size (50–55cm long x 40–45cm wide) of the *Adocus* from Utah and the regression formula from Zelenitsky et al. (2008: supplementary material Fig. 1(b)) for carapace length to clutch size in extant turtles, we estimate the clutch contained 25 to 30 eggs. This is somewhat larger than the 19-egg clutch that Zelenitsky et al. (2008) estimated for the female *Adocus* from Alberta, whose carapace length measured 40.5 cm.

Mineral deposition in turtle eggs occurs over a protracted length of time. The relatively thick mineralized eggshells of the Utah eggs suggest that the female *Adocus* died during the latter stages of egg formation. Embryonic development occurs in the weeks subsequent to oviposition (Miller and Dinkelacker 2008), and therefore the presence of embryonic bones within these partial eggs seems unlikely.

The Utah eggs are somewhat smaller than those preserved in the *Adocus* from Alberta and exhibit substantially thinner eggshell (Table 6.1). The shell unit height to width ratio overlaps the lower range reported from the *Adocus* eggs from Alberta, and they lack the "feathered" structures described by Zelenitsky et al. (2008). The relatively smooth, flat egg surface also differs from the slightly domed shape of shell units in the Alberta eggs.

Zelenitsky et al. (2008) considered the eggs from the Alberta specimen to be within days of oviposition because of their 1) similar size to eggs in a separately collected clutch, and 2) the feathered structures of the shell units. Zelenitsky et al. (2008) also noted that eggs discovered within the *Adocus* were thinner than those from the isolated clutch. They suggested that eggshell formation was not as complete in the gravid female. The differences in eggshell attributes (i.e., shell thickness, shell unit height to width ratio, exterior morphology, and absence of feathered structures) suggest that the gravid *Adocus* from Utah died at an earlier stage of egg formation than the Alberta specimen. Alternatively, the Utah and Alberta specimens may represent different species of *Adocus*.

Conclusions

The *Adocus* specimen from the Upper Cretaceous (late Campanian) of Grand Staircase-Escalante National Monument contains well-preserved osteological remains, including a closely associated right pectoral girdle, skull, cervical vertebrae, and associated elements of the hind limbs. At least two partial eggs are preserved within the body cavity of the female *Adocus*. Based on eggshell microstructure, these eggs are referable to the oogenus *Testudoolithus*. Comparison of the eggs described here to those preserved in a gravid *Adocus* from Alberta reveals thinner eggshell, lower shell unit height to width ratio, and a lack of feathered structures in the outer portion of the shell. These features may result from preservation of the Utah eggs at an earlier stage of eggshell formation than those within the gravid *Adocus* from Alberta or the specimen may represent a different species.

Acknowledgements

We thank S. Richardson for fossil preparation, D. Majerus and T. Spence at Bozeman Deaconess Hospital Department of Radiology for CT scans. R. Jackson, D. Zelenitsky, and D. Brinkman provided helpful editorial comments and suggestions that improved the manuscript. Finally, we thank the staff at the Utah Bureau of Land Management and Grand Staircase-Escalante Partners for support and access to the Monument for this research.

FIGURES AND TABLES

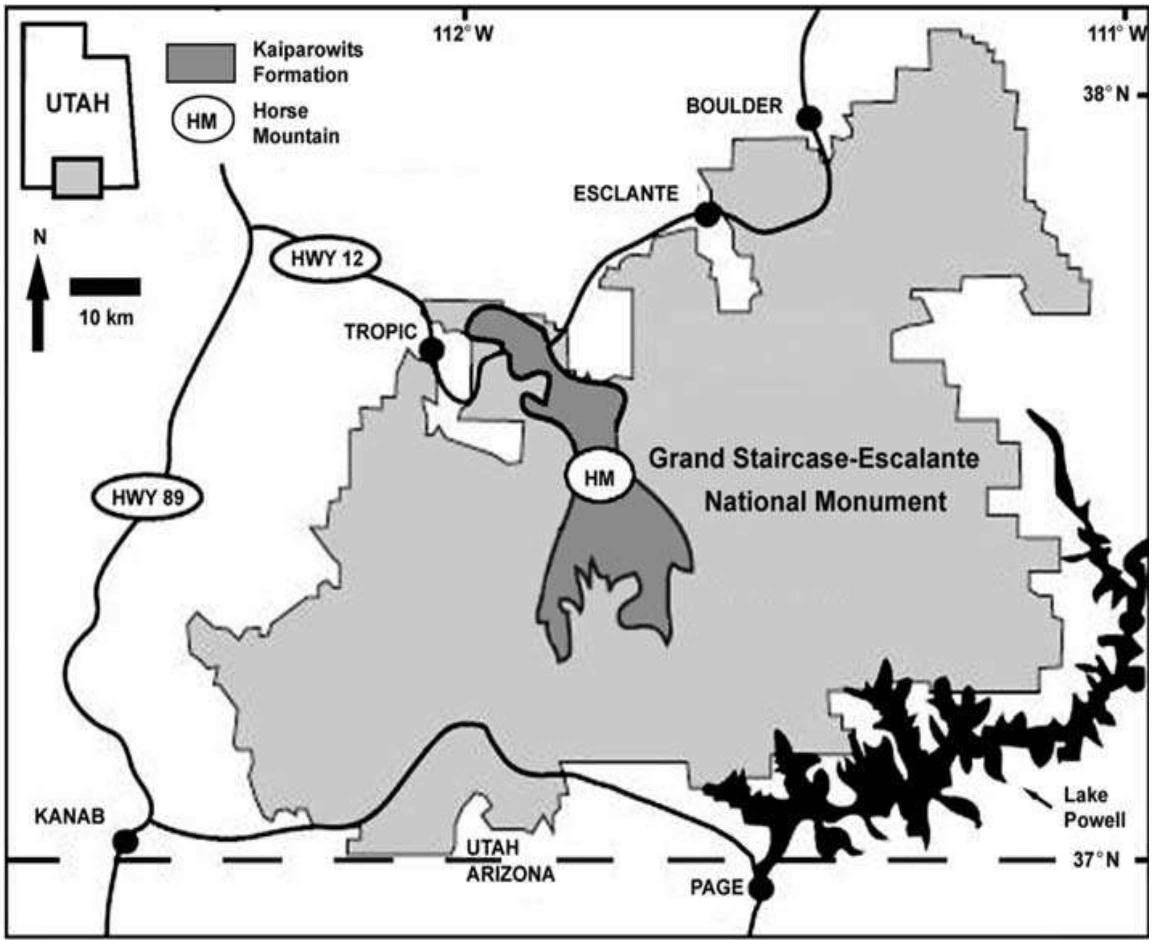

Figure 6.1. Map of Kaiparowits Formation within Grand Staircase-Escalante National Monument. (Modified from Roberts et al. 2005).

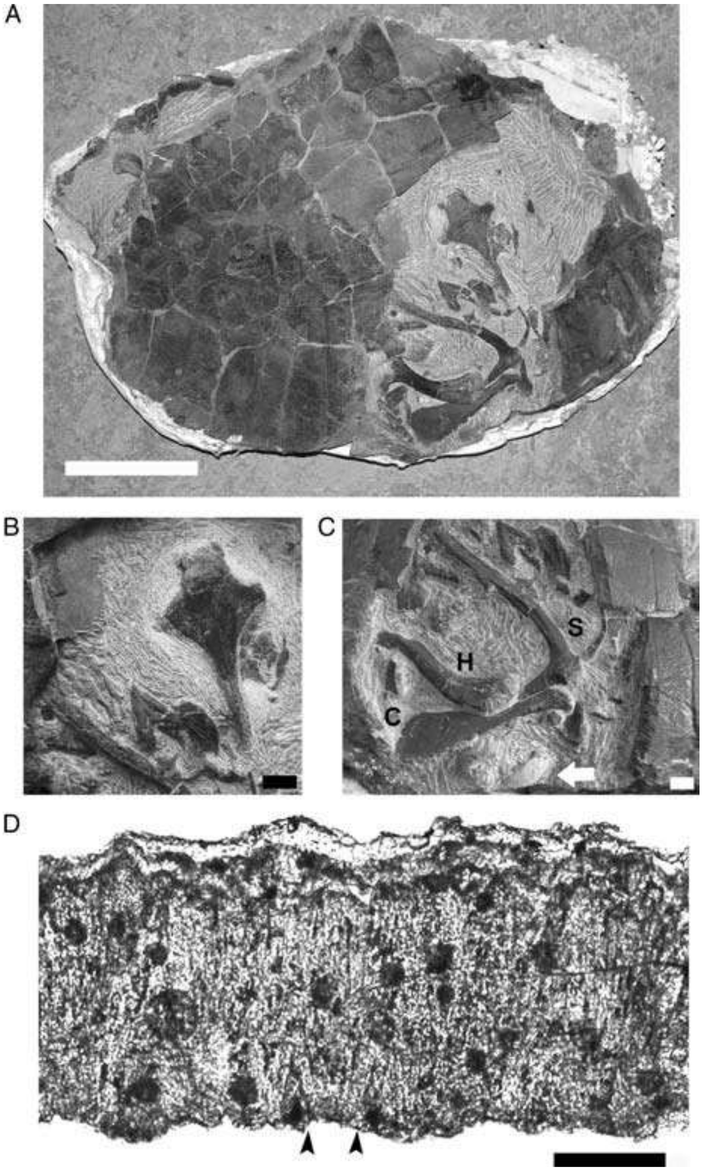

Figure 6.2. Adocus cf. (LBA-06-7) and partial eggs: (A) Dorsal view of the carapace. The right pectoral girdle elements and two cervical vertebrae are clustered in the opening along the right margin of the carapace. Scale bar equals 5 cm; (B) skeletal elements in A at higher magnification. Arrow points to partial eggs at the bottom of the image; scale bar equals 1 cm; H, humerus; C, coracoid, S, scapula; (C) partially exposed skull and cervical vertebrae. The frontals, parietals, supraoccipital, and right squamosal are not visible at this stage of preparation. Scale bar equals 1 cm; (D) thin section of eggshell showing needle-like aragonite crystals. Outer eggshell surface at top of the image; triangles indicate width of individual shell unit. Scale bar equals 100 µm.Table 6.1

(See next page)

Table 6.1. Comparison of Adocus eggs described here and other rigid-shell fossil turtle eggs and ootaxa, arranged in chronological order.

1. Table omits Testudoolithus from India (Mohabey, 1998) due to alteration or inadequate information. Testudinovum (Mikhailov, 1997) may be a misspelling of Testudinarum, an oogenus erected by Schleich et al. (1988). Reference: 1) Kohring, 1999;2) Fang et al. 2003; 3) Jackson et al., 2008; 4) Mikhailov, 1991; 5) Mikhailov, 1997; 6) Mikhailov et al., 1994; 7) Jackson et al., 2008; 8) Schleich et al., 1988; 9) Schleich and Kästle, 1988;10) Hay, 1908; 11) Hirsch and Bray, 1988; 12) Hirsch 1996; 13) Winkler and Sanchez-Villagra, 2006; 14) Zelenitsky et al., 2009.

Table 1. Comparison of *Adocus* eggs described here and other rigid-shell fossil turtle eggs and ootaxa, arranged in chronological order.

Ootaxon	Age	Location	Shell/Egg shape	Number of eggs	Egg size (mm)	Shell unit height-to-width ratio	Shell thickness (μm)	References
Testudoolithus hirschi	Jurassic	Portugal	Rigid	Egg shell	?	1:3	150	1
Testudoolithus jiangi	Cretaceous	China	Rigid/round	27	42 × 45	2:1–2.5:1	500–700	2, 3
Testudinovum/egg containing embryo	Cretaceous	Mongolia	Rigid/round	?	30 × 40	?	180 (1991) 300–400 (1994)	4, 5, 6
Unnamed, gravid *Adocus*	Cretaceous	Alberta, Canada	Rigid/round	5	40 × 42–40 × 43	2.5–3.5:1	500–650	14
Testudoolithus sp.	Cretaceous	Utah, USA	Rigid/round	1–2	?35	2.5:1	240–280	This paper
Unnamed (egg containing embryo)	Cretaceous	Montana, USA	Rigid/round to slightly elliptical	13	30 × 40	2:1	676	7
Haininchelys curiosa	Paleocene	Belgium	Rigid/round	?	?	2:1	110–240	8
Testudinarum ovum	Paleocene, Miocene	Belgium, Germany	Rigid/round	?	?	2:1	50–130	9, 8
Unnamed	Oligocene	S.Dak./Nebr USA	Rigid	?	43 × 47	?	?	10, 11, 12
Unnamed	Miocene	Venezuela	Rigid/elliptical	<1	43.5 × 56.5	1:0.6	565–730	13
Testudoolithus rigidus	Cretaceous-Pliocene	Various localities	Rigid/round	6	42 × 47	2:1	220–250	11

Notes: Table omits *Testudoolithus* from India (Mohabey 1998) due to alteration or inadequate information. *Testudinovum* (Mikhailov 1997) may be a misspelling of *Testudinarum*, an oogenus erected by Schleich et al. (1988). References: 1) Kohring 1999; 2) Fang et al. 2003; 3) Jackson et al. 2008; 4)Mikhailov 1991; 5) Mikhailov 1997; 6) Mikhailov et al. 1994; 7) Jackson et al. 2008; 8) Schleich et al. 1988; 9) Schleich and Kästle 1988; 10) Hay 1908; 11) Hirsch and Bray 1988; 12) Hirsch 1996; 13) Winkler and Sanchez-Villagra 2006; 14) Zelenitsky et al. 2008.

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CHAPTER SEVEN

CONCLUSION

The abundant, diverse assemblage of fossil turtle morphologies in the Campanian Kaiparowits Formation of southern Utah has permitted a thorough taphonomic study linking turtle taxa, preservation quality, and depositional environment. Examination of fossil turtles found in fluvial deposits permits an estimate of transport and exposure prior to burial with greater confidence, based on the preservation quality. The preservation potential of freshwater turtles is dependent on the morphology of the turtle, the environment of deposition, and the habitat preference of the turtle, and these factors can often work together to increase or reduce potential. Turtle taxa with medium-sized, robust shells (e.g. baenids) are more commonly well-preserved in fluvial channel deposits than other taxa suggesting that this morphology/habitat combination provides the best preservation potential, but rapid burial is of key importance. Smaller turtles and turtles with large, well-rounded shells are rare and poorly preserved in channel deposits due to high transportability, which reduces preservation potential. Taphonomic biases aside, turtle taxa that inhabited fluvial channels when alive are found in greater numbers within fluvial deposits, while taxa that preferred low-energy environments are more commonly recovered in floodplain deposits. Most turtle fossils in the Kaiparowits Formation are recovered from crevasse splay and crevasse channels deposits, probably formed during flood events, but preservation quality in these deposits is poor due to a combination of high energy and prolonged exposure prior to final burial. By combining known habitat preferences for extant turtles with morphologic evidence and the depositional environment data collected for fossil turtles, the fossil Kaiparowits turtles can be confidently assigned to preferred habitats.

Turtle shells with an oblong, medium to high profile carapace will frequently be deposited in a preferred orientation of carapace up with a preferred alignment of lateral-to-flow in fluvial channels. The use of fossil turtle shells in estimating paleoflow direction is not recommended without a very large sample size of turtle specimens with alignment data spread out over a large area and supporting evidence in the form of sedimentary paleoflow indicators. Data collected from hundreds of museum specimens, combined with flume observations using multiple extant taxa, provides a better understanding of the effects of morphology on transportability on subsequent preservation potential. Whenever possible, the use of extant taxa for taphonomic observations of decay, disarticulation, and transport is highly recommended for better understanding taphonomic patterns in the fossil record.

There is much paleontological work yet to be completed in the Kaiparowits Formation as new discoveries are made year-round. Even though a great amount of research has been completed on the fossil turtles to this point, there are still several questions to be answered regarding fossil turtle taxonomy and paleobiogeography. It is hoped that paleontologists will continue to conduct research on the fossils vertebrates of the Kaiparowits Formation in order to better understand the paleoecology of North America during the Late Cretaceous.

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APPENDIX A

KAIPAROWITS FOSSIL TURTLE FIELD AND COLLECTION DATA

Specimen #	Collection #	Field # or Name	Locality ID	Taxa
1	BYU			Basilemys
2	BYU			Adocus
3	BYU			trionychid
4	BYU 11338		No. 1071	Adocus
5	BYU 12001	Jim Smith Turtle	No. 1030	Neurankylus Type A
6	BYU 1441			Denazinemys
7	BYU unknown A			Adocus
8	BYU unknown B			Aspideretoides
9	In Field	MJK060908-2		Neuranklyus
10	In Field	08UTKA-16		Neurankylus
11	Not Collected	MJK072309-3		Denazinemys
12	Not Collected	MJK060909-2		Aspideretoides
13	Not Collected	MJK070809-1		Aspideretoides
14	Not Collected	MJK060209-1		Aspideretoides, Adocus, Comps., Helo.
15	Not Collected	MJK052510-1		Helopanoplia
16	Not Collected	MJK051908-1		baenid
17	Not Collected	MJK071309-1		trionychid
18	Not Collected	MJK052208-1		Denazinemys
19	Not Collected	MJK060409-2		Aspideretoides
20	Not Collected	MJK062509-1		Neurankylus
21	Not Collected	MJK060309-1		Adocus, trionychid, kinosternid
22	Not Collected	MJK051408-1		Basilemys
23	Not Collected	MJK052008-4and5		Basilemys, trionychid
24	Not Collected	MJK052708-1		Basilemys, trionychid, Compsemys
25	Not Collected	MJK052008-2		trionychid
26	Not Collected	MJK052008-3B		Basilemys
27	Not Collected	MJK071309-2		Adocus, Compsemys, trionychid
28	Not Collected	MJK072309-1		kinosternid, Helopanoplia
29	Not Collected	MJK062608-2		Adocus, Denazinemys
30	Not Collected	MJK062810-1		Basilemys, Aspideretoides
31	Not Collected	MJK062910-1		Adocus
32	Not Collected	HSR-06-33		Neurankylus
33	Not Collected	MJK061208-1		trionychid, kinosternid
34	Not Collected	MJK061008-5		Adocus, Denazinemys
35	Not Collected	11UTKA-33		Adocus, Aspideretoides, Helopanoplia
36	Not Collected	11UTKA-23		Basilemys
37	Not Collected	MJK081511-1		baenid
38	Not Collected	MJK081711-1		Neurankylus
39	Not Collected	MJK051408-3A		Basilemys, trion., Compsemys
40	Not Collected	MJK081908-1		Adocus, Aspid., Compsemys, kino.
41	Not Collected	MJK051608-1		Basilemys, trionychid
42	Not Collected	MJK061909-1		Compsemys, kinosternid
43	Not Collected	MJK072309-2		Compsemys, kinosternid
44	Not Collected	MJK072108-1		Basilemys, Adocus, Compsemys
45	Not Collected	MJK061208-2		Compsemys
46	Not Collected	MJK070809-2		Compsemys, Adocus, trionychid
47	Not Collected	MJK061308-3		Neurankylus
48	Not Collected	MJK052208-4		trionychid
49	Not Collected	HSR-06-41		Adocus
50	RAMV2008-09	RAM2008-02	Raymond Alf Museum, Franklin Site	Adocus
51	RAMV2008-20	RAM2008-29	Raymond Alf Museum, Big Turtle Site	unknown
52	UCMP	95H6-22-1	V95083	trionychid, Adocus
53	UCMP	95H8-19-1b	V95082	Aspideretoides
54	UCMP	93H7-14-7	V97096	Basilemys, Adocus, Compsemys
55	UCMP	95H6-22-1b	V95083	trionychid, Adocus
56	UCMP	97H11-3-1	V97097	baenid
57	UCMP	92H7-10-1	V93070	Denazinemys
58	UCMP	92H7-10-4b	V93073	Neurankylus
59	UCMP	92H7-10-6	V93075	Aspideretoides, Compsemys
60	UCMP	92H7-10-2	V93071	trionychid, Compsemys

Specimen #	Collection #	Field # or Name	Locality ID	Taxa
61	UCMP	92H7-10-4	V93073	Neurankylus
62	UCMP	92H7-10-7	V93076	Comps., Basil., trion., chelyd., Helo.
63	UCMP	92H7-10-3	V93072	trionychid, Compsemys
64	UCMP	92H7-10-5	V93074	trionychid, Compsemys
65	UCMP	92H7-10-6	V93075	trionychid
66	UCMP	92H7-10-8	V93077	Helopanoplia
67	UCMP	92H10-18-5	V93078	Compsemys, Basilemys, Helo.
68	UCMP	92H10-19-4	V93086	Aspideretoides
69	UCMP	92H10-19-4	V93086	trionychid
70	UCMP	92H10-17-6	V93085	Compsemys
71	UCMP	92H10-17-7	V93084	Aspideretoides, Denaz., Adocus
72	UCMP	92H10-17-5	V93083	Aspideretoides, Denaz., Adocus
73	UCMP	92H10-17-5	V93083	Adocus
74	UCMP	92H10-18-4	V93081	trionychid, chelydrid
75	UCMP	92H10-18-3	V93080	trionychid, Compsemys
76	UCMP	92H10-18-2	V93079	trionychid, Adocus, Compsemys
77	UCMP	92H7-5-3	V93096	trionychid
78	UCMP	92H7-5-2	V93096	Denazinemys
79	UCMP	92H7-3-1	V93095	Adocus
80	UCMP	92H7-2-2	V93094	trionychid
81	UCMP	92H7-6-1	V93092	Helopanoplia
82	UCMP	92H10-19-1	V93090	Compsemys, trionychid
83	UCMP	92H10-19-2	V93088	Aspid., Helo., Comps., Adocus
84	UCMP	92H7-5-4	V93100	trionychid, Adocus
85	UCMP	92H7-21-1	V93099	trionychid
86	UCMP	92H7-4-3	V93098	Aspid., Helo., kinosternid
87	UCMP	92H7-4-3	V93093	kinosternid
88	UCMP	93H7-12-3	V93098	trionychid, kinosternid, chelydrid
89	UCMP	92H7-4-2	V93097	trionychid, Compsemys
90	UCMP	92H7-5-2	V93096	unknown
91	UCMP	92H7-5-1	V93096	trionychid, Adocus
92	UCMP	92H7-5-4	V93100	Adocus
93	UCMP	92H10-16-1	V93104	Adocus, trionychid
94	UCMP	92H10-16-1	V93103	Adocus, Helo., Compsemys, kino.
95	UCMP	90H7-21-2	V93116	Basilemys, Adocus
96	UCMP	90H7-20-4	V93113	Compsemys
97	UCMP	92H10-14-1	V93110	trionychid
98	UCMP	92H7-9-1	V93111	Compsemys, kino., trion., chelyd.
99	UCMP	92H7-14-2	V93108	Compsemys, chelyd.
100	UCMP	92H10-15-2	V93106	Comps., Adocus, trion., Basilemys
101	UCMP	90H7-18-2	V93120	Adocus, trionychid
102	UCMP	90H7-18-1	V93119	Compsemys, trionychid
103	UCMP	93H7-14-5	V94008	Denazinemys
104	UCMP	93H7-14-4	V94008	Adocus
105	UCMP	93H7-12-1	V94004	Adocus
106	UCMP	93H7-16-1	V94010	trionychid, Denazinemys
107	UCMP	94H8-12-2	V94026	Compsemys, kinosternid
108	UCMP	94H8-16-1	V94028	Denazinemys
109	UCMP	94H8-16-3	V94030	Adocus
110	UCMP	94H8-16-2	V94029	Compsemys, Basilemys, trion.
111	UCMP	94H8-28-1	V94038	Basilemys, kinosternid, trionychid
112	UCMP	94H8-28-4	V94041	Helopanoplia
113	UCMP	94H8-28-2	V94039	Denazinemys
114	UCMP	94H8-28-3	V94040	Basilemys, Adocus, trion., kino.
115	UCMP	94H8-16-4	V94031	Basilemys
116	UCMP	94H10-9-4	V94052	Aspideretoides
117	UCMP	94H10-10-1	V94056	kinosternid, Compsemys
118	UCMP	94H10-9-7	V94055	Basilemys
119	UCMP	94H10-9-2	V94050	Adocus, trion., Compsemys, kino.
120	UCMP	95H9-13-4	V94053	trionychid

Specimen #	Collection #	Field # or Name	Locality ID	Taxa
121	UCMP	94H10-9-5	V94053	Basilemys
122	UCMP	94H10-9-3	V94051	Basilemys, Adocus, trionychid
123	UCMP	94H8-16-7	V94034	trionychid, Adocus, Compsemys
124	UCMP	94H9-21-5	V94048	Basilemys, Adocus
125	UCMP	94H9-23-2	V94046	Adocus
126	UCMP	94H9-22-1	V94064	trionychid, Adocus, Compsemys
127	UCMP	94H5-10-2	V94062	trionychid, Compsemys
128	UCMP	94H10-10-10	V94059	trionychid, Adocus, Denaz., Helo.
129	UCMP	94H5-10-3	V94063	trionychid, Adocus, chelyd., Comps.
130	UCMP	94H5-10-1	V94061	Aspid., Helo., kino., Comps.
131	UCMP	94H10-10-9	V94058	trionychid
132	UCMP	94H10-10-2	V94057	Adocus
133	UCMP	95H6-22-3	V95083	trionychid, Denazinemys
134	UCMP	95H7-5-2	V95083	trionychid, Adocus
135	UCMP	95H6-22-1c	V95083	Basilemys, trionychid, kinosternid
136	UCMP	95H8-19-1	V95082	Denazinemys
137	UCMP	95H7-5-2b	V95083	kinosternid
138	UCMP	95H6-22-5	V95087	trionychid, Neurankylus
139	UCMP	95H6-22-2	V95086	Adocus, trion., Basilemys, Comps.
140	UCMP	95H8-17-1	V95085	trionychid
141	UCMP	95H6-22-1a	V95085	Denazinemys
142	UCMP	95H8-17-3	V95089	trionychid, Compsemys, Adocus
143	UCMP	95H6-22-6a	V95088	trionychid
144	UCMP	95H6-22-6b	V95088	trionychid
145	UCMP	95H7-5-5	V95088	Adocus
146	UCMP	95H6-22-6c	V95088	Adocus, trionychid
147	UCMP	95H9-13-3	V95090	trionychid, Compsemys
148	UCMP	95H6-20-1	V95090	trionychid
149	UCMP	95H6-20-1b	V95050	kinosternid
150	UCMP	95H8-17-2	V95089	Neurankylus
151	UCMP	95H9-13-1	V95095	Basilemys, Compsemys, trionychid
152	UCMP	95H9-13-2	V95094	trionychid, kinosternid
153	UCMP	95H6-20-3	V95092	trionychid, Adocus
154	UCMP	95H6-20-2	V95091	Neurankylus
155	UCMP	92H7-4-1	V97095	trion., Adocus, kino., Comps., chelyd.
156	UCMP	90H7-22-4	V97093	Compsemys, trionychid, Adocus
157	UCMP	90H7-22-4b	V97093	chelydrid
158	UCMP	92H10-17-4	V97094	Basilemys
159	UCMP	90H7-22-2	V98054	Compsemys
160	UCMP	90H7-22-2b	V98054	Compsemys, trionychid, kinosternid
161	UCMP	90H7-19-3	V98053	Compsemys, Basilemys, trion., kino.
162	UCMP	90H7-19-4	V98051	Compsemys, Neurankylus
163	UCMP	90H7-19-2	V98051	trionychid, Compsemys, Adocus
164	UCMP	90H7-19-1	V98050	trionychid, kinosternid
165	UCMP	90H7-22-1		Neurankylus
166	UCMP	92H7-13-4	V98157	Adocus, trionychid
167	UCMP	92H7-2-3	V98055	Compsemys, trionychid
168	UCMP	20H8-29-1		Neurankylus
169	UCMP	03H8-29-2		Adocus
170	UCMP	03H8-29-3		Compsemys, Adocus, Basilemys
171	UCMP	99H9-20-5		trionychid
172	UCMP	95H6-21-3		trion., Adocus, kino., Comps., chelyd.
173	UCMP	90H7-18-4		unknown
174	UCMP	95H6-21-1		Neurankylus
175	UCMP	94H10-10-7		Neurankylus
176	UCMP	95H6-21-1		trionychid, kinosternid, Basilemys
177	UCMP	95H6-21-1b		Compsemys
178	UCMP	95H6-21-1c		Adocus
179	UCMP	95H6-21-1d		Helopanoplia, Aspideretoides
180	UCMP	92H7-2-1		Adocus

Specimen #	Collection #	Field # or Name	Locality ID	Taxa
181	UCMP	92H7-13-1		trionychid, Adocus
182	UCMP	94H10-10-7		Adocus
183	UCMP	90H7-18-4		trionychid, Compsemys
184	UCMP	95H6-21-2		Basilemys
185	UCMP	JGE 9209		Adocus
186	UCMP	BEC 9208		trionychid
187	UCMP	JGE 9210		Adocus
188	UCMP	03H5-3-2		Compsemys, trionychid, Adocus
189	UCMP	unknown A		trionychid
190	UCMP	unknown B		trionychid
191	UCMP		V159399	Denazinemys
192	UCMP		V149173	Adocus
193	UCMP		V194262-265	trionychid, Adocus, Compsemys
194	UCMP		V194298-299	trionychid, Adocus
195	UCMP		V194260-261	Helopanoplia
196	UCMP		V194100-101	trionychid, Compsemys
197	UCMP		V158864, V194165-169	kinosternid, Adocus, chelydrid, Comps., trion.
198	UCMP		V154450	Neurankylus
199	UCMP		V194107-111	trionychid, Adocus, Compsemys, Basilemys
200	UCMP		V194271-275	Denazinemys, Adocus, baenid, trionychid
201	UCMP		V194243-245	Denazinemys, Adocus, trionychid
202	UCMP		V194285-286	Adocus
203	UCMP		V194300-301	Adocus, trionychid
204	UCMP		V194354	baenid
205	UCMP		V158851-854 and V194321-324, 327	kino., Adocus, Denaz., Helopanoplia
206	UCMP		V194325-326	Compsemys, trionychid
207	UCMP		V194142-143	Adocus
208	UCMP		V194160-164	trionychid, Compsemys, Basilemys, Adocus
209	UCMP		V194066	Adocus
210	UCMP		V194355-356	Adocus, baenid
211	UCMP		V194148-151	Helopanoplia, Adocus, Compsemys
212	UCMP		V159500, V194204	Basilemys, baenid
213	UCMP		V194266-270	Adocus, baenid, trionychid
214	UCMP		V194202-203	Compsemys, trionychid
215	UCMP		V194195-201	Comps., chelydrid, Adocus, trion., Neurankylus
216	UCMP		V194190-194	Neurankylus, chelydrid, trion., Compsemys
217	UCMP	JGE 8659	V158861-863	kinosternid
218	UCMP		V194096-099	trionychid, Adocus
219	UCMP		V194102-106	Compsemys, chelydrid, Adocus, trionychid
220	UCMP		V194284	trionychid
221	UCMP		V194257-258	Compsemys, trionychid
222	UCMP		V194250	Aspideretoides
223	UCMP		V194252-256	Aspideretoides, Helopanoplia, Adocus
224	UCMP		V194331	Basilemys
225	UCMP		V194170-173	Adocus, Basilemys, Compsemys
226	UCMP		V194174-177	Compsemys, Adocus, trionychid
227	UCMP		V158878, V194276-283	kinosternid, trionychid, Adocus, Compsemys
228	UCMP		V158880-884, V194234-240	kino., chelydrid, Comps.,trion., Adocus, Basil.
229	UCMP		V158865, V194302-305	kinosternid, trionychid, Adocus, Basil., Comps.
230	UCMP		V194306-308	Compsemys, trionychid
231	UCMP		V158855-860, V194287-289	kinosternid, Compsemys, Basilemys
232	UCMP		V194241-242	trionychid
233	UCMP		V194228-233	trionychid, Adocus, Basil., Comps., Neurankylus
234	UCMP		V194246-248	trionychid, Adocus, Denazinemys
235	UCMP		V194249	Compsemys
236	UCMP		V194086	Basilemys
237	UCMP		V194357-366	Comps., Adocus, Basil., chelyd., baenid, Helo.
238	UCMP		V191480	trionychid
239	UCMP		V158847-850	kinosternid
240	UCMP		V194319-320	Adocus

Specimen #	Collection #	Field # or Name	Locality ID	Taxa
241	UCMP	JGE 8660	V194183-189	trionychid, baenid, chelydrid, Compsemys
242	UCMP	JGE 8653	V194179-182	trionychid, Compsemys, chelydrid
243	UCMP		V194367-372	Basilemys, Adocus, trionychid, chelydrid
244	UCMP		V194207	Denazinemys
245	UCMP		V194208-211	Basilemys, Aspid., Compsemys
246	UCMP		V194212-215	chelydrid, Adocus, trionychid
247	UCMP		V194216-217	Aspideretoides
248	UCMP		V194218-220	Basilemys, Adocus, trionychid
249	UCMP		V194221-222	Adocus, trionychid
250	UCMP		V194223-226	Comps., Basilemys, chelydrid, trion.
251	UCMP		V194227	Helopanoplia
252	UCMP		V194341, 343-346	Comps., Basilemys, Adocus, Aspid.
253	UCMP		V194342	Denazinemys, Aspideretoides
254	UCMP		V194347-350	Basilemys, trionychid, Adocus
255	UCMP		V194351-353	Adocus, trionychid
256	UCMP		V159702-703, V194113-123, 125, 127-129	Adocus, Bor., Basil., Helo., Denaz., Neur., Aspid.
257	UCMP		V194130-133	Denaz., Adocus, trionychid
258	UCMP		V178394, V194158-159	trionychid
259	UCMP		V194205-206	Adocus, trionychid
260	UCMP		V194259	Neuranklyus
261	UCMP		V191481	Denazinemys
262	UCMP		V194316-318	Compsemys, Adocus, trionychid
263	UCMP		V194332-333	Denazinemys, trionychid
264	UCMP		V194329-330	Denazinemys, Adocus, Helopanoplia
265	UCMP		V194309-310	baenid, trionychid
266	UCMP		V194328	Adocus
267	UCMP		V194311-315	trionychid, Adocus, chelyd., Comps.
268	UCMP		V194090-091	Basilemys, Adocus
269	UCMP		V194112, V194152	Denazinemys, Neurankylus
270	UCMP		V194153-157	Basilemys, Adocus, Comps., trion., kinosternid
271	UCMP		V194144-147	Neurankylus, trionychid, Basilemys
272	UCMP		V194092-095	Adocus, Comps., Denazinemys, Helopanoplia
273	UCMP		V194087-088	trionychid
274	UCMP		V194089	Adocus
275	UCMP		V194082-083	Aspideretoides, Compsemys
276	UCMP		V194067-070	Adocus, Basilemys, trionychid
277	UCMP		V194078-081	Compsemys, Adocus, trionychid
278	UCMP		V194084-085	trionychid
279	UCMP		V194340	Basilemys
280	UCMP		V194076-077	Basilemys, trionychid
281	UCMP		V194339	Adocus
282	UCMP		V157456	"Echmatemys"
283	UCMP		V194071-075	trionychid, Denaz., Comps., Adocus, Basilemys
284	UCMP		V194335	Denazinemys
285	UCMP		V194336-338	Compsemys, Basilemys, trionychid
286	UCMP		V194334	Compsemys
287	UCMP		V194290	Helopanoplia, Adocus, Compsemys
288	UCMP 150284	HSR-2003-6	V99463	Neurankylus
289	UCMP 150818	94H10-9-1	V94049	Adocus
290	UCMP 150820	92H10-17-4	V97094	Compsemys
291	UCMP 150821	92H10-17-4	V97094	trionychid
292	UCMP 150822	92H10-17-4	V97094	Adocus
293	UCMP 151773	93H7-14-6	V94004	Boremys
294	UCMP 154450	90H7-21-3	V93118	Neurankylus Type B
295	UCMP 156996	97H11-3-2	V97098	baenid
296	UCMP 156997	97H11-3-1	V97098	Boremys
297	UCMP 159399	01UT6A-1	V99441	Denazinemys
298	UCMP 159500	92H7-13-3	V98156	Basilemys
299	UCMP 159702	95H7-5-1	V95084	Adocus
300	UCMP 159703	95H7-5-4	V95087	Denazinemys

Specimen #	Collection #	Field # or Name	Locality ID	Taxa
301	UCMP 178394	95H9-13-2	V95094	trionychid
302	UCMP 191479			Helopanoplia
303	UMNH	Alan Titus		Denazinemys
304	UMNH	UMNH-HMG-10		unknown
305	UMNH	HMMA-09-24		Denazinemys
306	UMNH	95DLL9-30-1		baenid
307	UMNH	HSR-07-39		Adocus
308	UMNH	HSR-05-19		Neurankylus
309	UMNH	HSR-09-56		Denazinemys
310	UMNH	HSR-11-14		Basilemys
311	UMNH	HSR-10-17		Neurankylus
312	UMNH	HSR-09-26		Neurankylus
313	UMNH	MJK061008-3		Plesiobaena
314	UMNH	HSR-10-43		baenid
315	UMNH	HSR-08-21		Denazinemys
316	UMNH	MJK062508-2		Adocus
317	UMNH	HSR-10-1		Neurankylus
318	UMNH unknown A			Denazinemys
319	UMNHVP 09519		No. 137	Compsemys
320	UMNHVP 09521		No. 138	Neurankylus
321	UMNHVP 09524		No. 138	kinosternid
322	UMNHVP 09543		No. 142	kinosternid
323	UMNHVP 09545		No. 143	Denazinemys
324	UMNHVP 09556		No. 152	Basilemys
325	UMNHVP 11787		No. 179	baenid
326	UMNHVP 11789		No. 199	Compsemys
327	UMNHVP 11790		No. 245	Basilemys
328	UMNHVP 11793		No. 257	Adocus
329	UMNHVP 11794		No. 220	Basilemys
330	UMNHVP 11795		No. 173	Basilemys
331	UMNHVP 11796		No. 188	kinosternid
332	UMNHVP 11797		No. 195	Compsemys
333	UMNHVP 11798		No. 174	Adocus, Basilemys
334	UMNHVP 11799	KB01-46	No. 218	Helopanoplia
335	UMNHVP 11812		No. 215	Adocus
336	UMNHVP 11916		No. 205	Compsemys
337	UMNHVP 11921		No. 168	Compsemys, kinosternid
338	UMNHVP 12219		No. 291	Aspideretoides
339	UMNHVP 12496		No. 186	Denazinemys
340	UMNHVP 12497		No. 179	Neurankylus
341	UMNHVP 12501		No. 279	Denazinemys
342	UMNHVP 12502		No. 283	Compsemys, kinosternid
343	UMNHVP 12530		No. 277	Aspideretoides
344	UMNHVP 12542		No. 372	Compsemys, chelydrid, kinosternid
345	UMNHVP 12543		No. 361	kinosternid
346	UMNHVP 12544		No. 340	Compsemys, kinosternid
347	UMNHVP 12548		No. 362	Basilemys
348	UMNHVP 12564		No. 308	Aspideretoides
349	UMNHVP 12566		No. 306	kinosternid, trionychid
350	UMNHVP 12567		No. 341	Aspideretoides
351	UMNHVP 12568		No. 338	Aspideretoides
352	UMNHVP 12591	KHM-11-04		Aspideretoides
353	UMNHVP 12594		No. 343	Aspideretoides
354	UMNHVP 12595		No. 343	Basilemys
355	UMNHVP 12598		No. 343	Basilemys
356	UMNHVP 12631		No. 337	trionychid, Compsemys, kinosternid
357	UMNHVP 12645		No. 330	baenid
358	UMNHVP 12647		No. 179	Denazinemys
359	UMNHVP 12655	KDR-02-02	No. 326	trionychid, Compsemys
360	UMNHVP 12660		No. 317	Compsemys, kinosternid

Specimen #	Collection #	Field # or Name	Locality ID	Taxa
361	UMNHVP 12674		No. 345	Adocus
362	UMNHVP 12678			Adocus
363	UMNHVP 12682		No. 375	Compsemys
364	UMNHVP 12755		No. 193	baenid
365	UMNHVP 12951		No. 290	Aspideretoides
366	UMNHVP 13897		No. 508	Aspideretoides
367	UMNHVP 13898	KHM-03-01	No. 498	Aspideretoides
368	UMNHVP 13900		No. 469	baenid
369	UMNHVP 13901		No. 499	Adocus
370	UMNHVP 13902		No. 565	trionychid
371	UMNHVP 13903		No. 500	Basilemys
372	UMNHVP 13906		No. 179	baenid
373	UMNHVP 13907		No. 504	Adocus, trionychid
374	UMNHVP 13908	KSC-03-20	No. 484	Basilemys
375	UMNHVP 13945		No. 533	baenid
376	UMNHVP 13946		No. 300	Adocus, Neurankylus
377	UMNHVP 13966	KSC-03-03	No. 467	Compsemys
378	UMNHVP 13968	KSC-03-02	No. 466	Compsemys
379	UMNHVP 13978		No. 489	Basilemys
380	UMNHVP 13979		No. 452	Neurankylus Type A
381	UMNHVP 14020	KHM-03-11	No. 508	Aspideretoides
382	UMNHVP 16040		No. 538	Plastomenoides
383	UMNHVP 16046	KSC-03-15	No. 479	Compsemys, chelydrid, kino., trion.
384	UMNHVP 16049	KSC-03-16	No. 480	trionychid Type B
385	UMNHVP 16056		No. 468	unknown
386	UMNHVP 16062	KSC-03-32	No. 496	Compsemys, kinosternid
387	UMNHVP 16068		No. 495	Compsemys, chelydrid, kinosternid
388	UMNHVP 16074	KSC-03-19	No. 483	Compsemys, kinosternid
389	UMNHVP 16078		No. 504	trionychid
390	UMNHVP 16092		No. 473	Compsemys, kinosternid
391	UMNHVP 16104		No. 476	Compsemys, chelydrid, kinosternid
392	UMNHVP 16109		No. 505	Basilemys
393	UMNHVP 16113		No. 288	Denazinemys
394	UMNHVP 16115		No. 249	Adocus
395	UMNHVP 16126		No. 655	Denazinemys
396	UMNHVP 16136		No. 604	Compsemys
397	UMNHVP 16137		No. 611	Compsemys, Adocus
398	UMNHVP 16143		No. 607	unknown
399	UMNHVP 16147		No. 594	trionychid
400	UMNHVP 16154		No. 615	unknown
401	UMNHVP 16157		No. 577	Basilemys
402	UMNHVP 16159		No. 592	Neurankylus Type A
403	UMNHVP 16173		No. 617	baenid
404	UMNHVP 16180		No. 614	Basilemys
405	UMNHVP 16182		No. 486	unknown
406	UMNHVP 16198		No. 685	unknown
407	UMNHVP 16199		No. 740	Compsemys
408	UMNHVP 16248		No. 698	Chelyd., Comps., kino., Basilemys, trionychid
409	UMNHVP 16272		No. 716	unknown
410	UMNHVP 16279		No. 728	chelydrid, kinosternid, Compsemys
411	UMNHVP 16284		No. 584	Helopanoplia
412	UMNHVP 16318		No. 969	Compsemys, kinosternid
413	UMNHVP 16379		No. 249	unknown
414	UMNHVP 16386		No. 744	Basilemys
415	UMNHVP 16387		No. 744	Compsemys, kinosternid, trionychid
416	UMNHVP 16706		No. 893	kinosternid
417	UMNHVP 16712		No. 426	Compsemys
418	UMNHVP 16718		No. 897	kinosternid
419	UMNHVP 16725		No. 874	Adocus
420	UMNHVP 16726		No. 885	trionychid

Specimen #	Collection #	Field # or Name	Locality ID	Taxa
421	UMNHVP 16727		No. 889	Basilemys, Adocus
422	UMNHVP 16729		No. 930	Aspideretoides
423	UMNHVP 16747		No. 883	unknown
424	UMNHVP 16858	KBW-06-21		Basilemys
425	UMNHVP 16868	LBA-06-7		Adocus
426	UMNHVP 16872	HSR-03-11		Denazinemys
427	UMNHVP 16981	KHM-07-56		unknown
428	UMNHVP 16982	KFR-07-21		Compsemys
429	UMNHVP 17025		Joe's Turtle 2006	Helopanoplia
430	UMNHVP 17026			Aspideretoides
431	UMNHVP 17027	KHM-07-1		Basilemys
432	UMNHVP 18595	KFMB-07-1		trionychid, baenid
433	UMNHVP 18598	KFR-07-10		Basilemys
434	UMNHVP 18600	KFMB-07-3		trionychid
435	UMNHVP 18628	KFR-07-3		Denazinemys
436	UMNHVP 18663	KBLO-07-11		Compsemys, kinosternid
437	UMNHVP 18741	KHM-07-45		plastomenid trionychid
438	UMNHVP 19303	KHM-08-5		Compsemys, trionychid, chelydrid
439	UMNHVP 19646	KDR-08-1		Adocus
440	UMNHVP 20183			baenid
441	UMNHVP 20443			Neurankylus Type A
442	UMNHVP 20446			Denazinemys
443	UMNHVP 20448			baenid
444	UMNHVP 20449	HSR-07-63		Aspideretoides
445	UMNHVP 20451	HSR-09-18		Plesiobaena
446	UMNHVP 20452	07UTKA-68		Adocus
447	UMNHVP 20453	08UTKA-31		Aspideretoides
448	UMNHVP 20534	KFR-05-16		unknown
449	UMNHVP 20540	KFR-05-16		Aspideretoides
450	UMNHVP 20552	KB-05-3	No. 741	chelydrid
451	UMNHVP 20565	KHM-09-14	No. 1245	Aspideretoides
452	UMNHVP 20612	KHM-09-15	No. 1246	Neurankylus
453	UMNHVP 20621		No. 1264	trionychid
454	UMNHVP 20674	KFMB-04-5	No. 616	unknown
455	UMNHVP 20755	HSR-10-4		Neurankylus
456	UMNHVP 20908	MJK060909-5	still in field partially	Neurankylus
457	UMNHVP 20941	EMR-06-10		Denazinemys
458	UMNHVP 20950	HSR-07-28		Neurankylus
459	UMNHVP 20987			Adocus
460	UMNHVP 20999	KSC-02-18		baenid
461	UMNHVP 21243	KB-10-3		Neurankylus
462	UMNHVP 21245	KB-10-5		Adocus
463	UMNHVP 21261	KHM-10-24		baenid
464	UMNHVP 21333			Juvenile baenid
465	UMNHVP 21740			Aspideretoides
466	UMNHVP 21764			Aspideretoides

Specimen #	General Locality	Kaiparowits Unit	Lithology	Roberts (2005) FA	In Situ?
1					
2					
3					
4					
5			ss w/ mud	5	
6			ss	3	
7			ss w/ mud	5	
8					
9	Dog Flat	Lower Middle	channel ss, trough x-beds	3	Y
10	Horse Mtn	Middle	ss/congl channel lag deposit	4	Y
11	The Blues	Middle	lag congl.	1	
12	Horse Mtn	Middle	lag congl.	1	
13	Death Ridge	Lower	ss	3	
14	Tommy Water	Middle	channel lens	4	
15	Tommy Water	Middle	tabular ss float	4	
16	Horse Mtn	Middle	ss, conglomerate lag	4	Y
17	The Blues	Middle	ss channel float	4	
18	Horse Mtn	Middle	channel ss lenses	4	
19	Tommy Water	Middle	ss float	4	
20	Four Mile Bench	Lower	ms/sltst/ss	5	Y
21	Tommy Water	Middle	float, ms/ss mix	5	
22	Horse Mtn	Middle	ms/ss/sltst lens	5	Y
23	Horse Mtn	Middle	ms, sltst dominates	5	
24	Horse Mtn	Middle	ms/sltst/congl	5	
25	Horse Mtn	Middle	ms/sltst/congl	5	
26	Horse Mtn	Middle	channel ss, interbedded ms/sltst	5	
27	The Blues	Middle	sltst/ms/ss lenses	5	
28	The Blues	Middle	sltst/ms	5	
29	The Blues	Middle	sltst/ss	5	
30	Horse Mtn	Middle	ms/ss channels	5	
31	Blue Wash	Lower Middle	sltst/ms/ss lenses	5	
32	Four Mile Bench	Lower Middle	ms/ss float	5	
33	Tommy Water	Middle	sltst/ms	5	
34	Tommy Water	Middle	sltst/ss	5	
35	Fossil Ridge	Middle	ms/sltst lenses	5	
36	Fossil Ridge	Middle	ms/sltst lenses	5	
37	Tommy Water	Upper Lower	ss, congl. lag	5	
38	The Blues	Middle	sltst/ss lenses	5	
39	Horse Mtn	Middle	ms/sltst with caliche	8	
40	Horse Mtn	Middle	ms/sltst with caliche	8	
41	The Blues	Middle	sltst/ms with caliche	8	
42	The Blues	Middle	sltst/ms with caliche	8	
43	The Blues	Middle	sltst/ms with caliche	8	
44	The Blues	Middle	sltst/ms with caliche	8	
45	Tommy Water	Middle	sltst/ms with caliche	8	
46	Death Ridge	Lower	ss/ms with caliche	8	
47	Tommy Water	Middle	float		
48	Horse Mtn	Middle	unknown		
49					
50	Canaan Peak	Upper	channel ss	3	
51	Canaan Peak	Upper	channel ss with congl.	4	
52			"lower ss"	3	
53			ss-congl	4	
54			ss-congl	4	
55			mud abv prev	8	
56			ms	8	
57					
58					
59					
60					

Specimen #	General Locality	Kaiparowits Unit	Lithology	Roberts (2005) FA	In Situ?
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Specimen #	General Locality	Kaiparowits Unit	Lithology	Roberts (2005) FA	In Situ?
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Specimen #	General Locality	Kaiparowits Unit	Lithology	Roberts (2005) FA	In Situ?
181					
182					
183					
184					
185	Henrieville Creek	Middle			
186	The Blues	Middle			
187	The Blues	Middle			
188					
189					
190					
191	The Blues	Middle	channel ss	3	
192	The Blues	Middle	channel ss	3	
193	Henrieville Creek	Middle	channel ss	3	
194	The Blues	Middle	channel ss	3	
195	The Blues	Upper Middle	ss float	4	
196	The Blues	Upper Middle	channel ss lenses	4	
197	The Blues	Middle	ss, conglomerate lag	4	
198	The Blues	Middle	ss, conglomerate lag	4	
199	The Blues	Middle	ss float	4	
200	The Blues	Middle	ss channel lenses	4	
201	The Blues	Middle	ss channel lenses	4	
202	The Blues	Middle	ss channel lenses	4	
203	The Blues	Middle	ss channel lenses	4	
204	R.H. Collet Canyon	Lower	ss with congl.	4	
205	Horse Mtn	Middle	ms/sltst/ss mix	5	
206	Horse Mtn	Middle	sltst/ms/ss lenses	5	
207	Fossil Gulch	Middle	ms/sltst	5	
208	Blue Bone Pocket	Middle	ms/sltst	5	
209	Blue Wash Head	Middle	ms/sltst	5	
210	Blue Wash Head	Middle	ms/sltst	5	
211	Horse Mtn	Middle	sltst/ss lenses	5	
212	The Blues	Middle	sltst/ss lenses	5	
213	Henrieville Creek	Middle	sltst/ss with congl.	5	
214	The Blues	Upper Middle	sltst/ms/ss lenses	5	
215	The Blues	Middle	sltst/ms	5	
216	The Blues	Middle	sltst/ms/ss lenses	5	
217	The Blues	Middle	sltst/ms/ss lenses	5	
218	The Blues	Upper Middle	sltst/ms/ss lenses	5	
219	The Blues	Upper	sltst/ms/ss lenses	5	
220	The Blues	Middle	sltst/ss/congl	5	
221	The Blues	Middle	sltst/ms	5	
222	The Blues	Middle	sltst/ss	5	
223	The Blues	Middle	sltst/ms/ss lenses	5	
224	The Blues	Middle	sltst/ss/congl	5	
225	The Blues	Middle	sltst/ms/ss lenses	5	
226	The Blues	Middle	sltst/channel ss	5	
227	The Blues	Middle	ms/channel ss	5	
228	The Blues	Middle	tabular ss with ms lenses	5	
229	The Blues	Middle	channel ss w/ interbedded ms	5	
230	The Blues	Middle	channel ss w/ interbedded ms/sltst	5	
231	The Blues	Middle	sltst/ms/ss lenses	5	
232	The Blues	Middle	channel ss with interbedded ms	5	
233	The Blues	Middle	channel ss with interbedded ms	5	
234	The Blues	Middle	channel ss with interbedded ms	5	
235	The Blues	Middle	ms lenses within channel ss	5	
236	Paradise Canyon	Lower	sltst/ms/ss lenses	5	
237	Fossil Ridge	Middle	sltst/ms lenses	5	
238	The Blues	Middle	channel ss/sltst/congl	5	
239	Fossil Gulch	Middle	float with caliche	8	
240	The Blues	Middle	sltst/ms with caliche	8	

Specimen #	General Locality	Kaiparowits Unit	Lithology	Roberts (2005) FA	In Situ?
241	The Blues	Middle	sltst/ms with caliche	8	
242	The Blues	Middle	sltst/ms with caliche	8	
243	Fossil Ridge	Middle	sltst/ms with caliche	8	
244	Blue Wash	Middle	float		
245	Blue Wash	Middle	float		
246	Blue Wash	Middle	float		
247	Blue Wash	Middle	float		
248	Blue Wash	Middle	float		
249	Blue Wash	Middle	float		
250	Blue Wash	Middle	float		
251	Blue Wash	Middle	float		
252	Blue Wash	Middle	float		
253	Blue Wash	Middle	float		
254	Blue Wash	Middle	float		
255	Blue Wash	Middle	float		
256	Fossil Gulch	Middle	float		
257	Fossil Gulch	Middle	float		
258	Blue Wash Head	Middle	float		
259	The Blues	Middle	float		
260	The Blues	Upper Middle	float		
261	The Blues	Middle	unknown		
262	The Blues	Middle	unknown		
263	The Blues	Middle	unknown		
264	The Blues	Middle	unknown		
265	The Blues	Lower Middle	unknown		
266	The Blues	Middle	unknown		
267	South Hollow	Upper	unknown		
268	Blue Wash Head				
269	Blue Wash Head				
270	Blue Wash Head				
271	Blue Wash Head				
272	Blue Wash Head				
273	Blue Wash Head				
274	Blue Wash Head				
275	Blue Wash Head				
276	Blue Wash Head				
277	Blue Wash Head				
278	Blue Wash Head				
279	Wahweap Ck Head				
280	Death Ridge				
281	Wahweap Ck Head				
282	Wahweap Ck Head				
283	Wahweap Ck Head				
284	Wahweap Ck Head				
285	Wahweap Ck Head				
286	Canaan Peak				
287	The Blues				
288		Lower to Middle	channel ss lenses, congl.	4	
289					
290					
291					
292					
293			ss	3	
294			ss	3	
295			ss	3	
296					
297	Titus		ss	3	
298					
299					
300			ss	3	

Specimen #	General Locality	Kaiparowits Unit	Lithology	Roberts (2005) FA	In Situ?
301					
302			ms	8	
303	Wahweap Creek	Middle	ss	3	
304	Horse Mtn	Middle	ss channel	3	late
305					
306			ss	3	
307	Horse Mtn	Middle	channel ss	3	
308	Horse Mtn	Middle	ss	3	
309	Four Mile Bench	Lower Middle	channel ss	3	Y
310			channel ss	3	
311	Blue Wash	Lower Middle	x-bedded, channel ss	3	
312	Tommy Water	Middle	ss channel lens	4	Y
313	Tommy Water	Middle	ss channel with conglomerate lag	4	Y
314	Blue Wash	Lower Middle	channel ss lens	4	
315	Tommy Water	Middle	tabular ss, sltst/ss talus	5	
316	The Blues	Middle	sltst/ms	5	Y
317	South Horse Mtn	Middle	ss/sltst	5	
318			ss	3	
319					
320	The Blues	Middle	sltst/ss lenses	5	
321					
322					
323	The Blues	Middle	x-bedded channel ss	3	
324	Death Ridge	Lower	ss channel lenses	4	
325	The Blues	Middle			
326					
327					
328	Horse Mtn	Middle	ms/sltst	5	
329	The Blues	Middle	ms/sltst/ss/congl	5	
330	The Blues	Middle			
331	The Blues	Middle			
332					
333					
334	The Blues				
335					
336	The Blues				
337					
338					
339					
340	Pine Lake				
341	Blue Wash Head	Middle	"loose on ss", channel ss	3	
342					
343	Blue Wash Head	Middle	ms/sltst/ss	5	
344					
345	Death Ridge				
346	Death Ridge	Lower Middle	sltst/ss/ms	5	
347	Death Ridge				
348	The Blues	Middle	sltst/ss/ms	5	
349	The Blues	Middle	sltst/ms with caliche	8	
350	Death Ridge				
351					
352					
353					
354	The Blues	Middle	ms/ss channels	5	
355					
356					
357					
358	The Blues				
359					
360					

Specimen #	General Locality	Kaiparowits Unit	Lithology	Roberts (2005) FA	In Situ?
361	Death Ridge	Lower	channel ss lens	4	
362	Death Ridge	Lower Middle	sltst/ms/ss channel	5	
363	Death Ridge				
364	The Blues	Middle			
365	Blue Wash Head		ss	3	
366	Horse Mtn	Middle	slope below tabular ss/sltst	5	
367	Blue Wash Head	Middle	sltst/ms	8	
368	Death Ridge				
369					
370	Fossil Ridge				
371	Horse Mtn	Middle	sltst/ss channels with congl lag	5	
372	The Blues				
373	Death Ridge	Lower	ss float	4	
374	Death Ridge				
375	The Blues	Middle	"massive ss"	3	
376	Fossil Gulch	Middle	slope of sltst/ms	5	
377	Death Ridge				
378	Death Ridge				
379	Death Ridge				
380	Dog Flat - Camp K	Lower to Middle	channel ss lenses	4	
381	Horse Mtn	Middle	slope below tabular ss/sltst	5	
382					
383	Death Ridge		"on coal bed"	8	
384	Death Ridge				
385					
386	Horse Mtn	Middle			
387	Death Ridge				
388	Death Ridge				
389	Death Ridge	Lower	ss float	4	
390	Death Ridge				
391					
392	Horse Mtn	Middle	ss channel with sltst/congl beds	5	
393	Fossil Ridge				
394					
395	The Blues	Middle	sltst/ss	5	
396	Horse Mtn	Middle	then ss lens, with congl.	4	
397	Horse Mtn	Middle	ms/sltst	5	
398					
399	The Blues	Middle	ss channels/slst	5	
400					
401					
402	The Blues	Middle	channel ss	3	
403	Four Mile Bench	Lower Middle	unknown		
404	Horse Mtn	Lower to Middle	ss/sltst	5	
405					
406	Horse Mtn	Middle			
407	The Blues	Middle	sltst/ms with caliche	8	
408	Horse Mtn	Lower Middle	ss/sltst	5	
409	Horse Mtn	Middle	ms, sltst	5	
410	Horse Mtn	Middle	some sltst/ms, float	5	
411	The Blues	Middle	sltst/ms with caliche	8	
412	Horse Mtn	Middle	ms/sltst/ss bodies	5	
413					
414	Death Ridge	Lower	unknown		
415	Death Ridge	Lower	unknown		
416					
417					
418					
419					
420					

Specimen #	General Locality	Kaiparowits Unit	Lithology	Roberts (2005) FA	In Situ?
421					
422	Blue Wash	Middle			
423	Horse Mtn	Middle			
424	Blue Wash	Middle			
425	Horse Mtn	Middle	channel ss	3	
426			ss-congl	4	
427	Horse Mtn	Middle			
428	Fossil Ridge	Lower			
429	Horse Mtn	Middle	unknown		
430	Death Ridge	Lower	channel ss	3	
431	Horse Mtn	Middle	unknown		
432	Four Mile Bench	Lower	channel ss	3	
433	Fossil Ridge				
434	Four Mile Bench	Lower Middle	unknown		
435	Fossil Ridge				
436	Blue Wash				
437	Horse Mtn	Middle	channel ss lenses	4	
438	Horse Mtn	Middle	ms/ss channels	5	
439	Death Ridge				
440			ss-congl	4	
441			ss channel	3	
442	Horse Mtn	Middle	channel ss	3	Y
443					
444	Horse Mtn	Middle	x-bedded ss, with congl.	4	
445	Horse Mtn	Middle	channel ss	3	
446	Horse Mtn	Middle	channel ss	3	Y
447	Tommy Water	Middle	ss channel lens, with sltst	5	Y
448	Fossil Ridge				
449	Fossil Ridge				
450	The Blues	Middle	ms	8	
451	Horse Mtn	Middle			
452	Horse Mtn	Middle			
453					
454	Four Mile Bench	Lower			
455	Tommy Water	Middle	channel ss lens	4	
456	Horse Mtn	Middle	ss channel	3	Y
457	The Blues	Middle	x-bedded channel ss with lags	4	
458	Horse Mtn	Middle	ss/congl channel lag deposit	4	late
459					
460					
461	The Blues	Middle			
462	The Blues	Middle			
463	Horse Mtn	Middle			
464	Blue Wash	Middle	channel ss	3	
465					
466			ms, sltst	5	

Specimen #	Material	Shell Orientation	Carapace Up/Down	Fossil Associations
1	carapace frags	N/A	N/A	
2	carapace frags	N/A	N/A	
3	carapace frags	N/A	N/A	
4	carapace and plastron portions	N/A	N/A	
5	complete carapace and plastron and skeletal	N/A	N/A	
6	complete carapace, plastron, skull, and limb	N/A	N/A	
7	complete carapace and plastron	N/A	N/A	
8	partial carapace	N/A	N/A	
9	carapace with partial plastron	N-S, dip 38 to E	up	
10	partial shell	N-S, no dip	up	
11	shell fragments	N/A	N/A	other bone frags
12	shell fragments	N/A	N/A	wood, other bone frags
13	shell fragments	N/A	N/A	
14	numerous carapace frags	N/A	N/A	with eggshell and croc scutes
15	shell fragments	N/A	N/A	
16	plastron fragment	N/A	N/A	
17	shell fragments	N/A	N/A	other bone frags
18	shell fragments	N/A	N/A	other bone frags
19	plastron fragments	N/A	N/A	other bone frags
20	partial carapace and plastron portions	N/A	N/A	multiple Neurankylus together
21	shell fragments	N/A	N/A	
22	shell fragments	N/A	N/A	associated dino material
23	shell fragments	N/A	N/A	
24	shell fragments	N/A	N/A	
25	shell fragments	N/A	N/A	
26	shell fragments	N/A	N/A	fossil wood, bone frags around
27	shell fragments	N/A	N/A	
28	shell fragments	N/A	N/A	
29	shell and limb fragments	N/A	N/A	other bone frags
30	shell fragments	N/A	N/A	other bone frags
31	bridge, shell fragments	N/A	N/A	other bone frags
32	shell fragments	N/A	N/A	other bone frags
33	shell fragments	N/A	N/A	other bone frags
34	shell fragments	N/A	N/A	other bone frags
35	shell fragments	N/A	N/A	
36	shell fragments	N/A	N/A	
37	partial carapace/plastron	N/A	side	
38	plastron and skeletal frags	N/A	N/A	
39	shell fragments	N/A	N/A	other bone and eggshell
40	shell fragments	N/A	N/A	
41	shell fragments	N/A	N/A	other bone frags
42	shell fragments	N/A	N/A	
43	shell fragments	N/A	N/A	
44	shell fragments	N/A	N/A	other bone frags
45	shell fragments	N/A	N/A	other bone frags
46	shell fragments	N/A	N/A	
47	carapace fragments	N/A	N/A	
48	shell fragments	N/A	N/A	other bone frags
49	shell fragments	N/A	N/A	
50	partial carapace and plastron	N/A	up	
51	carapace and plastron	N/A	N/A	
52	carapace and plastron chunks	N/A	N/A	
53	partial carapace	N/A	N/A	
54	carapace and plastron chunks and frags,bridge	N/A	N/A	
55	carapace and plastron portions	N/A	N/A	
56	carapace frags	N/A	N/A	
57	carapace portion	N/A	N/A	
58	carapace and plastron frags	N/A	N/A	
59	carapace frags	N/A	N/A	
60	carapace frags	N/A	N/A	

Specimen #	Material	Shell Orientation	Carapace Up/Down	Fossil Associations
61	carapace frags	N/A	N/A	
62	carapace frags	N/A	N/A	
63	carapace and plastron frags	N/A	N/A	
64	carapace frags	N/A	N/A	
65	carapace and plastron frags and phalanx?	N/A	N/A	
66	carapace and plastron portions	N/A	N/A	
67	carapace and plastron frags	N/A	N/A	
68	carapace and plastron and limb frags, phalanx	N/A	N/A	
69	carapace frags	N/A	N/A	
70	carapace portions and frags	N/A	N/A	
71	carapace and plastron frags	N/A	N/A	
72	carapace frags	N/A	N/A	
73	carapace frags and bridge	N/A	N/A	
74	carapace frags	N/A	N/A	
75	carapace frags	N/A	N/A	
76	carapace and limb frags	N/A	N/A	
77	plastron portion	N/A	N/A	
78	carapace portion and frags	N/A	N/A	
79	carapace and limb frags	N/A	N/A	
80	carapace and plastron and limb frags	N/A	N/A	
81	carapace portions and frags	N/A	N/A	
82	carapace frags and bridge	N/A	N/A	
83	carapace and plastron frags	N/A	N/A	
84	carapace frags	N/A	N/A	
85	carapace frags	N/A	N/A	
86	carapace and plastron and limb frags	N/A	N/A	
87	carapace frags	N/A	N/A	
88	carapace frags	N/A	N/A	
89	carapace frags	N/A	N/A	
90	carapace frags	N/A	N/A	
91	carapace and plastron frags	N/A	N/A	
92	carapace and plastron frags	N/A	N/A	
93	carapace frags and bridge	N/A	N/A	
94	carapace and plastron portions and frags, limb	N/A	N/A	
95	carapace frags	N/A	N/A	
96	carapace frags	N/A	N/A	
97	carapace frags	N/A	N/A	
98	carapace frags	N/A	N/A	
99	carapace frags	N/A	N/A	
100	carapace and plastron frags	N/A	N/A	
101	carapace and plastron frags, vert?	N/A	N/A	
102	carapace frags	N/A	N/A	
103	carapace and plastron frags	N/A	N/A	
104	carapace frags	N/A	N/A	
105	carapace and limb frags	N/A	N/A	
106	carapace and limb frags	N/A	N/A	
107	carapace and plastron frags	N/A	N/A	
108	carapace and plastron portions and frags	N/A	N/A	
109	carapace frags	N/A	N/A	
110	carapace frags	N/A	N/A	
111	carapace frags	N/A	N/A	
112	carapace frags	N/A	N/A	
113	carapace and plastron portions and frags	N/A	N/A	
114	carapace frags	N/A	N/A	
115	carapace frags	N/A	N/A	
116	carapace frags	N/A	N/A	
117	carapace frags	N/A	N/A	
118	carapace frags and bridge	N/A	N/A	
119	carapace frags	N/A	N/A	
120	carapace	N/A	N/A	

Specimen #	Material	Shell Orientation	Carapace Up/Down	Fossil Associations
121	carapace frags	N/A	N/A	
122	carapace and plastron frags	N/A	N/A	
123	carapace frags	N/A	N/A	
124	carapace frags	N/A	N/A	
125	carapace portions and frags	N/A	N/A	
126	carapace frags	N/A	N/A	
127	carapace frags	N/A	N/A	
128	carapace frags and plastron portions	N/A	N/A	
129	carapace frags	N/A	N/A	
130	carapace and plastron frags	N/A	N/A	
131	carapace chunks	N/A	N/A	
132	carapace and plastron frags	N/A	N/A	
133	carapace chunks	N/A	N/A	
134	carapace frags	N/A	N/A	
135	carapace and bridge frags	N/A	N/A	
136	carapace frags	N/A	N/A	
137	hypoplastron	N/A	N/A	
138	carapace and plastron chunks	N/A	N/A	
139	carapace frags	N/A	N/A	
140	carapace and plastron chunks	N/A	N/A	
141	carapace frags	N/A	N/A	
142	carapace and plastron frags	N/A	N/A	
143	carapace and plastron chunks	N/A	N/A	
144	carapace and plastron frags	N/A	N/A	
145	carapace frags	N/A	N/A	
146	carapace and plastron frags	N/A	N/A	
147	carapace and plastron frags	N/A	N/A	
148	carapace frags	N/A	N/A	
149	hypoplastron frag	N/A	N/A	
150	carapace and plastron portions and frags	N/A	N/A	
151	carapace and plastron frags and bridge	N/A	N/A	
152	carapace frags	N/A	N/A	
153	carapace and plastron frags	N/A	N/A	
154	carapace and plastron chunks and frags	N/A	N/A	
155	carapace frags	N/A	N/A	
156	carapace and plastron frags	N/A	N/A	
157	carapace frags	N/A	N/A	
158	carapace frags and bridge	N/A	N/A	
159	partial carapace or plastron	N/A	N/A	
160	carapace and plastron frags	N/A	N/A	
161	carapace and plastron frags	N/A	N/A	
162	carapace and plastron frags	N/A	N/A	
163	carapace frags	N/A	N/A	
164	carapace frags	N/A	N/A	
165	partial carapace and plastron	N/A	N/A	
166	carapace frags	N/A	N/A	
167	carapace frags	N/A	N/A	
168	carapace and plastron portions, chunks, frags	N/A	N/A	
169	carapace and plastron portions and frags	N/A	N/A	
170	carapace frags	N/A	N/A	
171	carapace chunk and frags	N/A	N/A	
172	carapace and plastron frags	N/A	N/A	
173	carapace frags	N/A	N/A	
174	carapace and plastron chunks and frags	N/A	N/A	
175	plastron chunk	N/A	N/A	
176	carapace frags	N/A	N/A	
177	carapace frags	N/A	N/A	
178	carapace frags	N/A	N/A	
179	carapace frags	N/A	N/A	
180	carapace frags	N/A	N/A	

Specimen #	Material	Shell Orientation	Carapace Up/Down	Fossil Associations
181	carapace frags	N/A	N/A	
182	plastron portion and carapace frags	N/A	N/A	
183	carapace frags	N/A	N/A	
184	carapace and plastron chunks and frags	N/A	N/A	
185	carapace and plastron frags	N/A	N/A	
186	carapace chunk and frags	N/A	N/A	
187	carapace and plastron chunks and frags	N/A	N/A	
188	carapace and plastron frags	N/A	N/A	
189	carapace portion	N/A	N/A	
190	carapace chunks and frags, limb frags?	N/A	N/A	
191	partial carapace	N/A	N/A	
192	partial carapace and plastron	N/A	N/A	other bone frags
193	shell fragments	N/A	N/A	
194	shell fragments	N/A	N/A	
195	shell fragments	N/A	N/A	
196	shell fragments	N/A	N/A	
197	shell fragments	N/A	N/A	
198	partial shell, limb bones	N/A	N/A	
199	Compsemys dentary, shell fragments	N/A	N/A	
200	Denazinimys partial carapace, shell fragments	N/A	N/A	
201	shell fragments	N/A	N/A	
202	shell fragments	N/A	N/A	other bone frags
203	shell fragments	N/A	N/A	
204	plastron fragments	N/A	N/A	
205	shell fragments	N/A	N/A	
206	shell fragments	N/A	N/A	
207	shell fragments	N/A	N/A	other bone frags
208	shell fragments	N/A	N/A	other bone frags
209	shell fragments	N/A	N/A	other bone frags
210	shell fragments	N/A	N/A	
211	shell fragments	N/A	N/A	other bone frags
212	shell fragments	N/A	N/A	
213	shell fragments	N/A	N/A	clams and gastropods, bone
214	shell fragments	N/A	N/A	
215	shell fragments	N/A	N/A	
216	shell fragments	N/A	N/A	
217	shell fragments	N/A	N/A	
218	shell fragments	N/A	N/A	
219	shell fragments	N/A	N/A	
220	shell fragments	N/A	N/A	
221	shell fragments	N/A	N/A	other bone frags
222	shell fragments	N/A	N/A	
223	shell fragments	N/A	N/A	other bone frags
224	shell fragments	N/A	N/A	
225	shell fragments	N/A	N/A	some gastropods
226	shell fragments	N/A	N/A	
227	shell fragments	N/A	N/A	other bone frags
228	shell fragments	N/A	N/A	
229	shell fragments	N/A	N/A	
230	shell fragments	N/A	N/A	
231	shell fragments	N/A	N/A	
232	shell fragments	N/A	N/A	
233	Neurankylus dentary, shell fragments	N/A	N/A	other bone frags
234	shell fragments	N/A	N/A	
235	partial shell	N/A	N/A	
236	plastron fragments	N/A	N/A	other bone frags
237	dentary and shell fragments	N/A	N/A	other bone frags
238	dentary	N/A	N/A	
239	shell fragments	N/A	N/A	
240	shell fragments	N/A	N/A	other bone frags

Specimen #	Material	Shell Orientation	Carapace Up/Down	Fossil Associations
241	shell fragments	N/A	N/A	other bone frags
242	shell fragments	N/A	N/A	
243	shell fragments	N/A	N/A	other bone frags
244	partial carapace	N/A	N/A	
245	shell fragments	N/A	N/A	
246	shell fragments	N/A	N/A	
247	shell fragments	N/A	N/A	
248	shell fragments	N/A	N/A	
249	shell fragments	N/A	N/A	
250	shell fragments	N/A	N/A	
251	shell fragments	N/A	N/A	
252	shell fragments	N/A	N/A	
253	shell fragments	N/A	N/A	
254	shell fragments	N/A	N/A	
255	shell fragments	N/A	N/A	
256	shell fragments	N/A	N/A	other bone frags
257	shell fragments	N/A	N/A	some fossil wood
258	shell fragments	N/A	N/A	
259	shell fragments	N/A	N/A	
260	shell fragments	N/A	N/A	
261	partial shell	N/A	N/A	
262	shell fragments	N/A	N/A	some fossil wood
263	shell fragments	N/A	N/A	
264	Helopanoplia partial shell, shell fragments	N/A	N/A	
265	shell fragments	N/A	N/A	
266	shell fragments	N/A	N/A	
267	shell fragments	N/A	N/A	
268	shell fragments	N/A	N/A	
269	shell fragments	N/A	N/A	
270	shell fragments	N/A	N/A	
271	shell fragments	N/A	N/A	
272	shell fragments	N/A	N/A	
273	shell fragments	N/A	N/A	
274	shell fragments	N/A	N/A	
275	shell fragments	N/A	N/A	
276	bridge, shell fragments	N/A	N/A	
277	shell fragments	N/A	N/A	
278	shell fragments	N/A	N/A	
279	shell fragments	N/A	N/A	
280	shell fragments	N/A	N/A	
281	shell fragments	N/A	N/A	
282	partial shell	N/A	N/A	
283	Basilemys phalanx, shell fragments	N/A	N/A	
284	shell fragments	N/A	N/A	
285	shell fragments	N/A	N/A	
286	shell fragments	N/A	N/A	
287	shell fragments	N/A	N/A	
288	partial plastron	N/A	N/A	turtle fragments: Aspid., Denaz.
289	carapace portion	N/A	N/A	
290	carapace frags	N/A	N/A	
291	carapace and plastron frags	N/A	N/A	
292	carapace frags	N/A	N/A	
293	partial carapace and plastron	N/A	N/A	
294	partial carapace, plastron, pelvis, and limbs	N/A	N/A	
295	partial carapace (plastron?)	N/A	N/A	
296	carapace portion and frags	N/A	N/A	
297	partial carapace and plastron	N/A	N/A	
298	left P11 & pygal	N/A	N/A	
299	complete plastron and carapace frags	N/A	N/A	
300	carapace portion	N/A	N/A	

Specimen #	Material	Shell Orientation	Carapace Up/Down	Fossil Associations
301	carapace and plastron frags	N/A	N/A	
302	partial carapace and plastron	N/A	N/A	
303	complete carapace	N/A	N/A	
304	unknown	N/A	N/A	associated plant/dino material
305	carapace and plastron	N/A	N/A	
306	unknown	N/A	N/A	
307	partial shell	N/A	N/A	other bone frags
308	partial carapace and plastron	N/A	N/A	
309	partial carapace and plastron	S 10 E, dip 20 W	up	dino bone frags
310	partial carapace/plastron	N/A	up	
311	shell fragments	N/A	N/A	
312	carapace portion, partial plastron	chunk tilted 36 to N	down	
313	partial carapace and plastron	N-S, dip 50 to E	on edge	
314	partial carapace	N/A	up	other bone frags
315	partial carapace and plastron	N/A	N/A	
316	partial shell	N/A	down	other bone frags
317	carapace and plastron	NW-SE, dip 15 to W	up	assoc. clams, near hadrosaur
318	carapace, plastron	N/A	N/A	
319	carapace frags and bridge	N/A	N/A	
320	plastron frag	N/A	N/A	
321	carapace and bridge frag	N/A	N/A	
322	carapace frag	N/A	N/A	
323	carapace and plastron? frags, 1 neural	N/A	N/A	other bone frags
324	femur and tibia frags	N/A	N/A	
325	carapace and plastron portions	N/A	N/A	
326	carapace frags	N/A	N/A	
327	carapace frag	N/A	N/A	
328	first neural	N/A	N/A	some trionychid frags also
329	plastron frag, bridge	N/A	N/A	clam fossils
330	carapace frags	N/A	N/A	
331	carapace portion	N/A	N/A	
332	carapace frags	N/A	N/A	
333	carapace frags, bridge, skeletal frags	N/A	N/A	
334	plastron portions	N/A	N/A	
335	carapace frags	N/A	N/A	
336	plastron frag, bridge	N/A	N/A	
337	carapace and bridge frags	N/A	N/A	
338	scapula	N/A	N/A	
339	carapace and skeletal frags	N/A	N/A	
340	plastron portion	N/A	N/A	
341	carapace and plastron frags, bridge	N/A	N/A	associated dino bones
342	carapace frags	N/A	N/A	
343	carapace costal	N/A	N/A	
344	carapace and limb frags	N/A	N/A	
345	carapace frags	N/A	N/A	
346	carapace frags, bridge	N/A	N/A	
347	carapace and limb frags	N/A	N/A	
348	carapace portions and frags	N/A	N/A	
349	carapace frags	N/A	N/A	other bone frags
350	carapace and postcrania frags	N/A	N/A	
351	carapace and plastron frags	N/A	N/A	
352	partial carapace	N/A	N/A	
353	partial scapula	N/A	N/A	
354	carapace and bridge frags	N/A	N/A	
355	carapace and limb frags	N/A	N/A	
356	carapace frags, 1 neural	N/A	N/A	
357	carapace and limb frags	N/A	N/A	
358	numerous carapace frags	N/A	N/A	
359	carapace frags	N/A	N/A	
360	carapace frags	N/A	N/A	

Specimen #	Material	Shell Orientation	Carapace Up/Down	Fossil Associations
361	numerous carapace frags	N/A	N/A	
362	many carapace frags, limb pieces	N/A	N/A	
363	carapace and bridge frags	N/A	N/A	
364	many carapace frags, limb pieces	N/A	N/A	
365	carapace portions	N/A	N/A	
366	carapace frags	N/A	N/A	
367	carapace frags	N/A	N/A	
368	carapace or plastron frag	N/A	N/A	
369	carapace or plastron frag	N/A	N/A	
370	limb, skeletal frags	N/A	N/A	
371	carapace frags	N/A	N/A	some fossil wood
372	plastron frags	N/A	N/A	
373	carapace frags	N/A	N/A	
374	carapace frags	N/A	N/A	
375	plastron portion	N/A	N/A	other bone frags
376	carapace portions, frags	N/A	N/A	other bone frags
377	carapace frags	N/A	N/A	
378	carapace and plastron portions	N/A	N/A	
379	carapace and bridge and limb frags	N/A	N/A	
380	plastron portion	N/A	N/A	
381	carapace pieces	N/A	N/A	
382	carapace frags	N/A	N/A	
383	carapace frags	N/A	N/A	
384	carapace costals	N/A	N/A	
385	humerus frag	N/A	N/A	
386	carapace frags	N/A	N/A	
387	carapace frags	N/A	N/A	
388	carapace frags	N/A	N/A	
389	plastron portion	N/A	N/A	
390	carapace frags, phalanx	N/A	N/A	
391	carapace frags	N/A	N/A	
392	"scute"	N/A	N/A	
393	carapace frag	N/A	N/A	
394	partial carapace with bridge	N/A	N/A	
395	carapace frags	N/A	N/A	
396	plastron portion	N/A	N/A	also Aspideretoides frags
397	carapace frags	N/A	N/A	
398	plastron portions	N/A	N/A	
399	carapace frag	N/A	N/A	
400	vert	N/A	N/A	
401	carapace pieces	N/A	N/A	
402	carapace frags	N/A	N/A	
403	carapace frags	N/A	N/A	
404	carapace and bridge frags	N/A	N/A	
405	plastron portions	N/A	N/A	
406	coracoid	N/A	N/A	
407	carapace and plastron frags	N/A	N/A	
408	carapace frags	N/A	N/A	
409	limb elements	N/A	N/A	
410	carapace frags	N/A	N/A	
411	carapace pieces	N/A	N/A	
412	carapace frags	N/A	N/A	
413	carapace and skeletal frags	N/A	N/A	
414	carapace frags	N/A	N/A	
415	carapace frags, limb frags	N/A	N/A	
416	neural	N/A	N/A	
417	carapace frags, bridge	N/A	N/A	
418	carapace frag	N/A	N/A	
419	carapace element (nuchal plate?)	N/A	N/A	
420	carapace and plastron frags (skull?)	N/A	N/A	

Specimen #	Material	Shell Orientation	Carapace Up/Down	Fossil Associations
421	carapace and bridge frags	N/A	N/A	
422	carapace portion and frags	N/A	N/A	
423	isolated limb end	N/A	N/A	
424	carapace and plastron portions	N/A	N/A	
425	complete carapace/plaston w/ skull and eggs	N/A	N/A	
426	partial carapace and plastron	N/A	N/A	
427	pelvic element	N/A	N/A	
428	partial carapace and plastron	N/A	N/A	
429	carapace, plastron, skull elements, postcrania	N/A	N/A	
430	complete carapace	N/A	N/A	
431	shell fragments	N/A	N/A	
432	shell fragments	N/A	N/A	
433	shell fragments	N/A	N/A	
434	partial skull	N/A	N/A	
435	shell fragments	N/A	N/A	
436	shell fragments	N/A	N/A	
437	shell fragments	N/A	N/A	other bone frags
438	shell fragments	N/A	N/A	other bone frags
439	shell fragments	N/A	N/A	
440	partial carapace and plastron	N/A	N/A	
441	skeletal elements (pelvis, scapula, coracoid)	N/A	N/A	
442	complete shell	late	up	other bone frags
443	partial carapace and plastron	N/A	N/A	
444	partial carapace with skeletal bits	N/A	up	also other Aspid and Basil.
445	partial carapace and plastron	N/A	down	
446	complete shell	late	up	associated theropod
447	partial carapace and plastron	N/A	down?	some woody material nearby
448	pelvic element	N/A	N/A	
449	plastron fragment	N/A	N/A	
450	peripheral	N/A	N/A	
451	shell fragments	N/A	N/A	
452	shell fragments	N/A	N/A	
453	shell fragments	N/A	N/A	
454	shell fragments	N/A	N/A	
455	plastron fragments	N/A	N/A	
456	complete shell	E-W, dip 5 to the E	down	fossil wood associated
457	partial shell with vertebrae	N/A	N/A	other bone frags
458	partial carapace and plastron	unk	up	
459	shell fragments	N/A	N/A	
460	shell fragments	N/A	N/A	
461	shell fragments	N/A	N/A	
462	shell fragments	N/A	N/A	
463	shell fragments	N/A	N/A	
464	carapace and plastron	N/A	N/A	
465	shell fragments	N/A	N/A	
466	complete carapace	N/A	N/A	