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A Review of New Testudine Specimens from the Oligocene and Miocene of the Great Plains of
North America, Including Descriptions of Two New Taxa

By

Eric Michael Holt

A dissertation submitted in partial satisfaction of the
requirements for the degree of
Doctor of Philosophy
in
Integrative Biology
in the
Graduate Division
of the
University of California, Berkeley

Committee in charge:

Professor Emeritus Anthony D Barnosky, Chair

Professor Kevin Padian

Professor Jun Sunseri

Spring 2024

Abstract

A Review of New Testudine Specimens from the Oligocene and Miocene of the Great Plains of North America, Including Descriptions of Two New Taxa

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Doctor of Philosophy in Integrative Biology

University of California, Berkeley

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The fossil record of Testudines in North America is well known for some parts of the Tertiary period, but for many stages representing millions of years our knowledge of Testudine diversity is both poor and outdated. The gaps in knowledge are pronounced for the Oligocene and Miocene in North America, despite an abundant fossil record. This study begins to address the gap in our understanding of fossil turtles by utilizing existing museum specimens from the Great Plains and adjacent Rocky Mountain basins, the majority of which have not been previously identified beyond the ordinal level. Updated identifications based on fossil shells are provided and the morphological criteria for recognizing many taxa are clarified, despite there being a bias in museum collections towards subadult and juvenile testudine specimens. A previously unknown regional variant of *Gopherus edae* is described, and initial steps are taken toward documenting the range of intraspecific morphological variation found within various taxa of *Oligopherus*, *Gopherus*, *Stylemys*, and *Hesperotestudo*. Chapter One lays the groundwork for future studies on tortoise diversity through time and space, and the relationship between their evolution, distribution, and climate change.

In Chapter Two the largely complete shell of a new species of tortoise, *Hesperotestudo nicholsorum* n. sp., is described from Lemhi County, Idaho, USA. The tortoise genus *Hesperotestudo* Williams, 1950b, was widespread throughout North America from Canada to El Salvador from the earliest Miocene to the late Pleistocene but retains no extant members. The specimen was collected from Late Hemingfordian (~15-16.3 Ma) sediments in the Railroad Canyon Sequence of the Sixmile Creek Formation. Previous studies have established a late Eocene paleoelevation of 3.7 km for the area. Elevational decrease due to Basin and Range extension did not happen until the middle Miocene, indicating that the fossil locality was higher in the Hemingfordian than the roughly 2 km elevation it is today. This makes *H. nicholsorum* both the highest elevation specimen of *Hesperotestudo* currently described and one of the oldest members of its genus. The new taxon shares many morphological similarities with other *Hesperotestudo* but also exhibits characters more commonly found in *Gopherus*.

In Chapter Three I describe the shell of another new tortoise, *Hesperotestudo niobrarensis* n.

sp., from Cherry County, Nebraska, USA. The specimen was collected in 1933 from Clarendonian sediments in the Ash Hollow Formation of the Ogallala Group. An isolated left epiplastron from the Clarendonian Ash Hollow Formation near Merrit Reservoir in Cherry County, Nebraska is referred to the new species. This new taxon shares many morphological similarities with other *Hesperotestudo* but also exhibits a unique combination of characters not found in other members of the genus.

Dedicated

in memoriam of

Alonzo J. Holt

Diana E. Holt

Pamela J. North

and to my wife Katie Holt

without whom this would not have been possible

Table of Contents

Chapter 1: A review of new testudine specimens from the Oligocene and Miocene of the Great Plains region of North America.....	1
Chapter 2: Description of a new testudine species, <i>Hesperotestudo nicholsorum</i> sp. nov., from the Miocene of Lemhi County, Idaho, U.S.A.	67
Chapter 3: A new species of Testudines tortoise, <i>Hesperotestudo niobrarensis</i> sp. nov., from the Miocene of the Niobrara River region of Cherry County, Nebraska, U.S.A.	83
Bibliography	94
Appendix 1: Plates	102

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Chapter 1

A review of new testudine specimens from the Oligocene and Miocene of the Great Plains region of North America.

Introduction

Testudine fossils have been found throughout North America and are often among the most abundant vertebrate specimens found in Cenozoic strata (Franz, 2014; Petermann et al., 2022). The fossil lineage for turtles and tortoises extends to at least the Triassic and much research attention has been focused on turtle origins (Rieppel and Reisz, 1999; Reisz and Head, 2008; Pérez-García et al., 2015; Tong et al., 2015; Schoch & Sues, 2018; Lyson and Bever, 2020), turtle diversity and responses to a warming climate (Holroyd and Hutchison, 2000; Bourque, 2015; Cleary et al., 2020; Chiarenza et al., 2023), and the charismatic sea turtles (Kear and Lee, 2006; Chesi and Delfino, 2007; Parham and Pyenson, 2010; Gentry and Ebersole, 2019; Garza et al., 2021). While the fossil record of Testudines is well known for some parts of the Tertiary period, for many stages representing millions of years our knowledge of Testudine diversity is poor. The gaps in knowledge are particularly pronounced for the Oligocene and Miocene in North America, despite an abundant fossil record. In the last 15 years, only a handful of studies have dealt specifically with Oligo/Miocene Testudines in North America (Bourque, 2012; Joyce et al., 2012; Weems & George, 2013; among others), and have focused primarily on the description of a single specimen or locality.

The goal of this study was to address those gaps at least partially. Turtles and tortoises fossilize well, and their near ubiquity in fossiliferous Oligo/Miocene deposits has led to a very large number of specimens being housed in museum collections throughout North America. The sheer volume of specimens made it necessary to narrow the focus of this project to the Orellan, Hemingfordian, and Clarendonian North American Land Mammal Ages (NALMAS). This provides reasonable temporal coverage while helping to reduce the quantity of specimens to a manageable level. While the original aim of this study was to provide comprehensive geographic coverage of North America, it quickly became evident that focusing on primarily the Great Plains region was the most feasible approach, especially in view of shut-downs and reduced staffing in museums during the COVID pandemic.

Many researchers of testudines prefer to focus on cranial characteristics for identifications, and rightly so. Cranial characters are more reliable and less susceptible to individual variation than shell characters. However, it is rare to find a fossilized turtle skull. The vast majority of testudine specimens in museum collections are shells (carapace and plastron) and sometimes fragments of shells, many of which have never been identified beyond the ordinal level. By ignoring these specimens, we stand to lose a lot of information on the diversity

and abundance of this group of reptiles. A major goal of this study was to develop a method for reliably identifying fossil testudine shells and, in some cases, shell fragments.

Consideration of the vagaries of the fossil record and how the diversity of North American land turtles may have waxed and waned with climate change and other factors through the Tertiary are beyond the scope of the current study. The morphological descriptions and identifications provided in this work are a necessary preface, advancing the field to make such studies feasible in the future.

Methods

I scoured the literature for information on known testudine taxa from North America during the Oligocene and Miocene. Original descriptions were used whenever possible, and supplemented with more recent redescrptions, personal communications, personal experience, and character matrices previously used by other researchers (Hay, 1908; Auffenberg, 1964a; Crumly, 1984a and 1984b; Hutchison, 1996; Jasinski, 2013; Bourque & Schubert, 2014; Bramble & Hutchison, 2014; Franz, 2014; Vitek & Joyce, 2015; Joyce & Bourque, 2016; Valdes et al., 2017; Vlachos, 2018). I found that, while in some cases a single shell characteristic was sufficient to identify a specimen to the familial or even generic level, it was almost never sufficient by itself for specific designation; yet in conjunction with other shell characters identification to the species level was possible.

For this reason, I assembled a suite of morphological shell characters for each taxon. This also helps to mitigate the problems that arise with random individual variation in shell characters that often appear in testudines.

Testudine specimens from existing museum collections were photographed and identified to the finest taxonomic resolution possible based on the morphological characters visible. For each museum, all testudine specimens collected in North America from the Orellan, Hemingfordian and Clarendonian NALMAs were photographed. Marine turtles were later excluded. Specimens were prepared through use of an air-scribe and/or small picks when necessary and possible. Individual variation in the expression of shell characters is not uncommon within testudine species, so identifications are based primarily on suites of morphological characters rather than on a single character alone, where possible.

Systematic paleontology is organized in descending order, from higher taxonomic group rank to lower ranks and eventually to the specific level. Referred specimens are listed according to the following hierarchy: State (in alphabetical order), North American Land Mammal Age (NALMA) from oldest to youngest, Stratigraphic formation, County (alphabetical), Institution (alphabetical), Locality (listed alphanumerically), Specimen (listed alphanumerically).

Institutional Abbreviations – Seven museums across the United States were visited to examine specimens. Institutional abbreviations used in this publication for these museums are

as follows: **AMNH FARB**, American Museum of Natural History, “Fossil Amphibians Reptiles and Birds” Collection, New York City, New York; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **NHMLA**, Natural History Museum of Los Angeles County, Los Angeles, California; **RAM**, Raymond M. Alf Museum of Paleontology, Claremont, California; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **UNSM**, University of Nebraska State Museum, Lincoln, Nebraska; **USNM**, Department of Paleobiology, United States National Museum, Smithsonian National Museum of Natural History, Washington, D.C.

Anatomical Terms and Abbreviations (Fig. 1) – Scales: **M**, marginal; **PI**, pleural; **V**, vertebral; **Cv**, cervical; **G**, gular; **H**, humeral; **Pc**, pectoral; **Ab**, abdominal; **F**, femoral; **An**, anal. Bones: **nu**, nuchal; **n**, neural; **p**, peripheral; **c**, costal; **sp**, suprapygal; **py**, pygal; **ep**, epiplastron; **en**, entoplastron; **hyo**, hyoplastron; **hyp**, hypoplastron; **xp**, xiphiplastron.

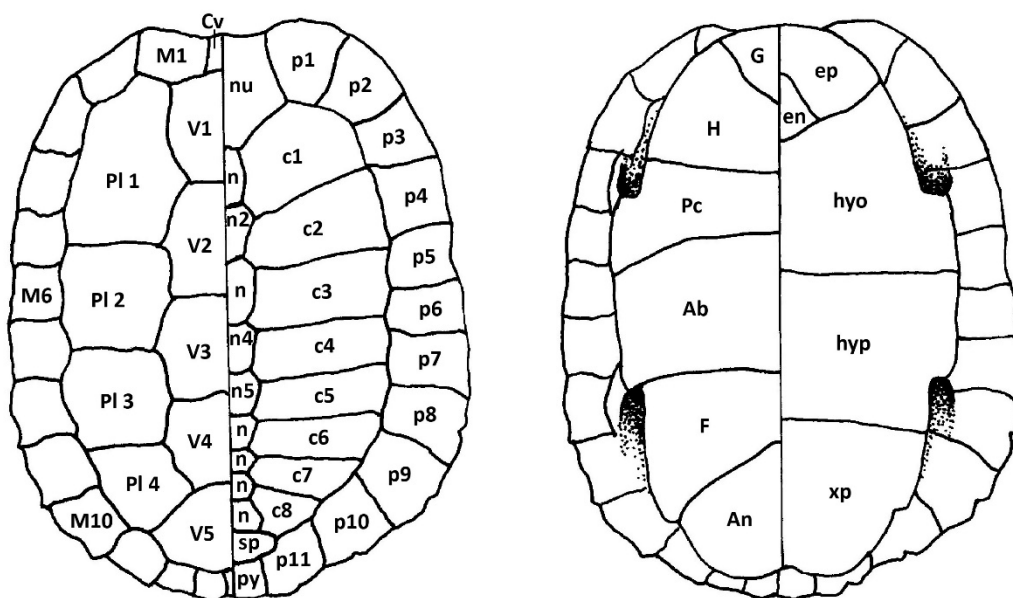


Figure 1. Anatomy of a typical turtle shell based on *Trachemys scripta*, showing carapace (left) and plastron (right). Each view is divided midline to show the pattern of scales on the left and bones on the right. Illustration by the author.

Neural patterns are provided for some taxa. The neurals are listed in order from first to last, numeric values indicate how many sides the neural in that position has, parentheses indicate whether the short sides are positioned anteriorly (“(” or posteriorly “)”). A straight bar | indicates a position of neural reversal, where the pattern of short side positioning is changing. A neural pattern of)6)6 | 4 (6 (6 (6 (6 (6 indicates that neurals 1 & 2 are hexagonal with short sides positioned posteriorly, neural 3 is rectangular and marks a point where the directionality of the short sides is changing, and neurals 4-8 are all hexagonal with short sides positioned anteriorly.

Throughout this work I use the term “scale” to refer to the keratinous plates that cover the bones of the turtle shell. These are often called “scutes”, but because that term is also used to describe the osteoderms of crocodilians I will avoid it.

Systematic Paleontology

Order TESTUDINES Batsch 1788

Suborder CRYPTODIRA

Unranked clade PAN-TRIONYCHIDAE Joyce et al. 2004

Diagnosis. Pan-trionychids can be distinguished from other testudines by their very reduced shells; a lack of peripherals (Vitek & Joyce, 2015); lack of pygals and suprapygals; the absence of carapacial and plastral scales and their corresponding sulci; the absence of ossified bridges (Ernst & Barbour, 1989); the presence of pitted sculpturing that covers all metaplastic surfaces of the shell bones (Bonin et al., 2006; Vitek & Joyce 2015).

Family TRIONYCHIDAE Gray 1825

Diagnosis. Trionychids may be identified as pan-trionychids by the suite of characters listed for that clade. They may be differentiated from other pan-trionychids by the presence of a chevron-shaped entoplastron (Meylan, 1987).

Subfamily TRIONYCHINAE Gray 1825

Tribe TRIONYCHINI Gray 1825

Genus *Trionyx* Geoffroy Saint-Hilaire 1809

Trionyx has historically been a wastebasket taxon for any New-World Paleogene soft-shelled turtle fossils (Vitek & Joyce, 2015). Although some progress has been made in recent years to establish greater taxonomic and phylogenetic clarity within the group (Meylan, 1987; Jasinski, 2013), this is complicated by a high degree of homoplasy in morphological character states. Here I follow the example of Vitek & Joyce in using the generic epithet of “*Trionyx*” to call attention to the uncertainty of phylogenetic relationships within the clade when referring to fossil pan-trionychid taxa.

“*Trionyx*” *miocaenus* (Matthew, 1924)

Synonymy. *Platypeltis miocaenus* Matthew, 1924; *Platypeltis miocaena* Hay, 1930.

Type material. AMNH 6298 (holotype), a carapace lacking the nuchal (Matthew, 1924, fig. 62).

Type locality. Trojan Quarry, *M. paniensis* zone, Sinclair Draw, Sioux County, Nebraska, Olcott Formation, Early Barstovian.

Referred material. Nebraska, Valentine Formation, Burge Member, Early Clarendonian: Cherry County – AMNH FARB Burge Quarry ½ mi. NW of Burge P.O., AMNH FARB 12533, the anterior 2/3 of a carapace.

Diagnosis. “*Trionyx*” *miocaenus* can be identified as a trionychid based on the characters for that group above. It can be distinguished from other trionychids by the following suite of characters: the presence of rounded suprascapular fontanelles; an elliptical carapace (Matthew, 1924); the absence of a preneural; a greatly reduced costal VIII; a reduction in the number of neurals to six (Vitek & Joyce, 2015).

Discussion. *Platypeltis miocaenus* was described as a new species by Matthew in 1924 based on a complete carapace, sans nuchal, from the Early Barstovian of Nebraska. Eight years later Hummel assigned it to the genus *Trionyx* (Hummel, 1932). Jasinski (2013) reported another Miocene trionychid, *Apalone* cf. *spinifera*, from the Hemphillian of Alabama.



Figure 2: Carapace of AMNH FARB 12533 from the Early Clarendonian of Nebraska, USA.

AMNH FARB 12533 (**Fig. 2**) is missing the posterior $\frac{1}{4}$ of the carapace, making distinction based on number of neurals and reduction of costal VIII impossible. The carapace has suprascapular fontanelles, although the lack of a sutured contact between costals I and the nuchal may indicate that this is a juvenile specimen and that the fontanelles may be closed in adults of the same species as in *Apalone* (Valdes et al., 2017). It is strikingly similar to AMNH FARB 6298 in this respect, as the same uncertainty surrounds the holotype (Vitek & Joyce, 2015). AMNH FARB 12533 bears an overall similarity to "*Trionyx*" *miocaenus*, and close geographic and temporal proximity to its type locality.

"Trionyx" sp.

Referred material. Nebraska, Ash Hollow Formation, Clarendonian: Brown County – AMNH FARB Pratt Quarry, AMNH FARB 9873, the left half of a nuchal.

Discussion. AMNH FARB 9873 is approximately 73 mm in width, leading to an estimate of roughly 140 mm for the complete nuchal with a maximum length of 32 mm. There is a clear sutural contact along the postero-lateral edge for attachment to costal I, and a non-sutured concavity in the posteromedial edge that would have formed the anterior part of a suprascapular fontanelle. The size of the specimen and the presence of a sutured contact with the first costal show that this was a mature individual. The presence of a suprascapular fontanelle in this mature specimen indicates that it is *Trionyx*. The temporal and geographic proximity of this specimen to those of both AMNH FARB 12533 and AMNH 6298 suggest that it may belong to a mature "*T.* *miocaenus*", but there is insufficient material and evidence to make this distinction without more complete mature specimens of "*T.* *miocaenus*" for comparison.

Trionychidae, genus indet.

Referred material. Nebraska, Sheep Creek Formation, Hemingfordian: Sioux County – UCMP V67121, UCMP 54333, two costal fragments; Ash Hollow Formation, Clarendonian: Brown County – AMNH FARB Alligator Loc., AMNH FARB 9085, a right hyoplastron fragment, neural, and four shell fragments; AMNH FARB Pratt Quarry on Plum Creek, AMNH FARB 9084, a humerus, right and left hypoplastron fragments, four proximal costal fragments, and 12 indeterminate fragments; AMNH FARB 9845, a plastral fragment; AMNH FARB 9846, a proximal costal fragment; AMNH FARB 9870, a collection of six costal fragments; AMNH FARB 9874, the distal end of a costal; AMNH FARB 9875, a costal; AMNH FARB 9876, left and right hypoplastron fragments, a left hyoplastron fragment, a small costal probably representing a second individual, the proximal end of a large costal, a partial limb element, and five indeterminate fragments; AMNH FARB 12560, a left hyoplastron; Cherry County – AMNH FARB Snake Rv., AMNH FARB 9878, a left hypoplastron fragment; AMNH FARB Gallup Gulch Quarry, AMNH FARB 9880, a right hypoplastron; AMNH FARB Hans Johnson Prosp. Loc., AMNH FARB 14260, a costal fragment; UCMP V3326, UCMP 63958, two costal fragments; Middle Clarendonian: Brown County – AMNH FARB Bone Creek, AMNH FARB 12569, a left hyoplastron; AMNH FARB 12570, a

right hypoplastron; AMNH FARB Pratt Quarry, AMNH FARB 12556, the posterior 1/3 of a carapace; AMNH FARB 12557, a neural and left 2nd costal; AMNH FARB 12558, a right hypoplastron; AMNH FARB 12559, a left hypoplastron fragment; AMNH FARB 12562, a right hypoplastron fragment; AMNH FARB 12564, two costals; Late Clarendonian: Brown County – AMNH FARB Eggers Q., AMNH FARB 12579, two costal fragments and a right hypoplastron fragment; AMNH FARB 14233, an entoplastron; AMNH FARB Pratt Place N. of Johnstown, AMNH FARB 12576, a left hypoplastron; AMNH FARB Pratt Quarry, AMNH FARB 12561, three costals and a plastral fragment; AMNH FARB 12565, a right hypoplastron; AMNH FARB 12566, a right 2nd costal and five costal fragments; AMNH FARB 12568, two right hypoplastron fragments and two costals; AMNH FARB 12573, a right hypoplastron and two plastral fragments; Cherry County – AMNH FARB Alligator Mefferdi Channel, AMNH FARB 12575, a left hypoplastron; Sheridan County – AMNH FARB Road-cut 10 ¾ mi W of Gordon, AMNH FARB Ains 837- Prosp. 495-63, a costal fragment; Snake Creek Formation, Clarendonian: Sioux County – AMNH FARB Kilpatrick Pasture – Quarry 7, AMNH FARB 6619, a costal and right hypoplastron fragment; Valentine Formation, Clarendonian: Cherry County – UCMP V3312, UCMP 36645, a costal; South Dakota, White Slim Buttes Formation, Early Oligocene (Orellan): Harding County – FMNH 2 mi. N. of E. Short Pine Hills, FMNH PR1407, a costal fragment; Ogallala Formation, Clarendonian: Todd County – AMNH FARB Sawmill Canyon, Little White R., AMNH FARB 14261, a costal; Valentine Formation, Early Clarendonian: Mellette County – AMNH FARB Thin Elk Gravel Pit, AMNH FARB Ains 805- Pros. 498-22, a costal fragment; AMNH FARB 12574, the left ½ of a nuchal.

Discussion. The specimens referred herein can be easily distinguished as softshell turtles by the characteristic pattern of sculpturing on the external surfaces of the shell bones. However, it is not currently possible to identify most fragments of fossil Trionychid shells beyond the familial level based on surface sculpture alone. Some promising progress has been made recently using topographic measuring techniques (see Pamfilie et al., 2022), but until such methods are applied to the above specimens, Trionychidae indet. will have to suffice.

Unranked clade PAN-CHELYDRIDAE Joyce et al. 2004

Diagnosis. Members of Pan-chelydridae can be distinguished from other testudines by the following suite of characters: lateral reduction of the costals; presence of a cruciform entoplastron; reduction of the abdominal scales to the bridge, not meeting medially (Joyce, 2016); presence of very fine vermiform texturing usually covering the external surfaces of all shell bones.

Family CHELYDRIDAE Swainson 1839

Diagnosis. Members of Chelydridae can be identified as pan-chelydrids by the suite of characters provided above. They may be distinguished from other pan-chelydrids by: costiform lateral processes present on the nuchal that extend below the peripherals (Hutchison, 2013);

the presence of a median plastral fontanelle and costal fontanelles even in mature individuals (Joyce, 2016).

Subfamily CHELYDRINAE

Genus *Macrochelys* Gray 1856

Synonymy. *Macrolemys* Troost in Harlan 1835; *Gypochelys* Agassiz 1857

Type species. *Macrochelys temminckii* Troost in Harlan 1835

Referred material. Nebraska, Ash Hollow Formation, Clarendonian: Brown County – AMNH FARB Rhino Horizon Quarry 3, Quinn Ranch, AMNH FARB 12511, associated right and left mandibles; Cherry County – AMNH FARB Gallup Gulch Quarry, AMNH FARB 9827, a pygal.

Diagnosis. Members of *Macrochelys* can be identified as chelydrids using the suite of characters provided for that group. They can be distinguished from other chelydrids by the following suite of shell characters. Carapace strongly tricarinate; vertebral 1 wider than long and wider than vertebrals 2 and 3; caudal notch completely contained by the pygal, not extending beyond its lateral borders; transverse division of the abdominal scale (Hutchison, 2008).

Discussion. AMNH FARB 9827 (**Fig. 3**) is narrower than would be anticipated in *Macrochelys*, but also has a deep caudal notch that is fully contained by the pygal and fine vermiform texturing on the bone surface.

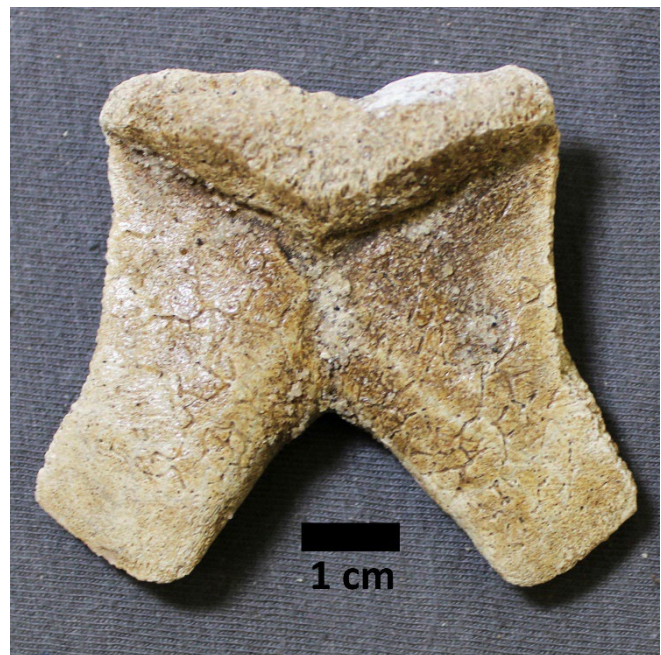


Figure 3: AMNH FARB 9827, a *Macrochelys* pygal from the Clarendonian of Nebraska, USA.

Chelydridae, genus indet.

Referred material. Nebraska, Runningwater Formation, Hemingfordian: Box Butte County – AMNH FARB Dry Creek Prosp. C, AMNH FARB 14464, an isolated third neural; Nebraska, Sheep Creek Formation, Hemingfordian: Sioux County – AMNH FARB Greenside Quarry, AMNH FARB 11602, a partial costal and left peripherals I – III; Nebraska, Late

Hemingfordian: Sioux County – AMNH FARB Green Side Quarry, Ranch House Draw, AMNH FARB 11391, associated right and left mandibles; Nebraska, Ash Hollow Formation, Clarendonian: Brown County – AMNH FARB Alligator Slide, AMNH FARB 9083, three shell fragments and a pelvic girdle fragment; Nebraska, Clarendonian: Todd County – AMNH FARB Mission Micro Loc., AMNH FARB 14469, a posterior peripheral fragment.

Discussion. AMNH FARB 14464 is 24.7 mm long, has a strong dorsal keel, and straight medial portions of both the anterior and posterior borders.

The external surfaces of the shell bones of AMNH FARB 11602 are covered with very fine vermiform texturing. The costal rib heads are flat and wide and emerge from the costal a substantial distance from the neuro-costal suture. The lateral portion of the costal is somewhat reduced.

The external surfaces of the shell bones of AMNH FARB 9083, AMNH FARB 14464, and AMNH FARB 14469 all have the very fine vermiform texturing commonly found in chelydrids.

Unranked clade PAN-TESTUDINOIDEA Joyce et al. 2004

Diagnosis. Members of pan-testudinoidea may be diagnosed relative to other turtles by: axillary and inguinal scales are present; presence of musk-duct foramina; axillary and inguinal buttresses are well-developed; plastral scales extensively overlap onto the visceral side of the plastron (Vlachos, 2018).

Superfamily TESTUDINOIDEA Gray 1825

Family EMYDIDAE Rafinesque 1815

Diagnosis. Members of emydidae can be identified as pan-testudinoids based on the characters for that clade provided above. They may be distinguished from other pan-testudinoids by: overlap of the pygal by the vertebral V scale; wide rib heads; musk-ducts and musk-duct foramina are absent; paired marginals XII (Vlachos, 2018)

Genus *Terrapene* Merrem 1820

Synonymy. *Cistudo* Dumeril and Bibron 1835; *Toxaspis* Cope 1889.

Type species. *Terrapene carolina* Linnaeus 1758.

Referred material. Nebraska, Ash Hollow Formation, Clarendonian: Cherry County – UCMP V3326, UCMP 118235, a right hypoplastron.

Diagnosis. Members of *Terrapene* can be identified as emydids based on the suite of characters provided for emydidae above. They may be distinguished from other emydids by the following suite of characters: presence of a ligamentous bridge connection and the absence of

buttresses (Vlachos, 2018); presence of a hinge between the hyoplastron and hypoplastron (Holman & Fritz, 2005); medial contact between the posterior costals; a single suprapygals present (Vlachos, 2018).

Discussion. UCMP 118235 (**Fig. 4**) measures 32 mm in length by 33.5 mm in width and is missing the anterolateral-most corner. The anterior border lacks a sutured contact and is instead relatively straight and smooth where the hinge with the hyoplastron would be.

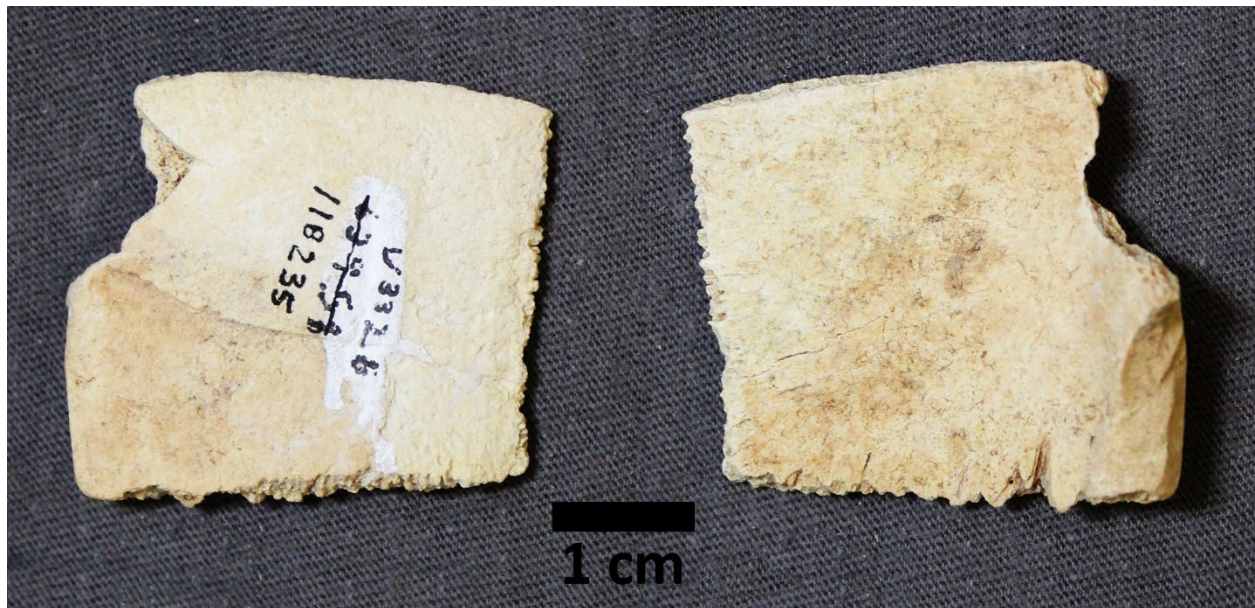


Figure 4: UCMP 118235, a terrapin right hypoplastron from the Clarendonian of Nebraska, USA.

Unranked clade PAN-TESTUDINIDAE Joyce et al. 2004

Diagnosis. Members of pan-testudinidae can be identified as pan-testudinoids based on the suite of characters for that clade provided above. They may be distinguished from other pan-testudinoids by: proximal rib heads are thin and narrow; two suprapygals present, with the first embracing the lenticular second; buttresses are long and barely contact the costals (Vlachos, 2018).

Monotypic genus *Oligopherus laticuneus* (Cope, 1873a)

Synonymy. *Testudo laticuneus* Cope, 1873a; *Testudo laticuneata* Loomis, 1909; See Hutchison (1996) for more.

Type material. AMNH FARB 1160 (holotype), shell and some appendicular elements (Hay, 1908, figs. 509-510).

Type locality. Head of Horsetail Creek, Weld County, Colorado; Horsetail Creek Member, White River Formation, Chadronian, Eocene.

Referred material. Colorado, White River Formation, Orellan: Logan County – UCMP V72243, UCMP 223092, a proximal fragment of the left 3rd costal, partial right epiplastron, plastron fragment and 3 peripherals; Weld County – UCMP V3743, UCMP 36443, a partial carapace and plastron, partial innominate, femur, both scapulae, coracoid; UCMP V71042, UCMP 94709, a complete carapace and plastron, innominate, partial femur, L/R scapulae, L/R coracoids, L/R humeri, L/R radii, L/R ulnae, and several carpals and phalanges; UCMP V93189, UCMP 299046, a relatively complete carapace and partial plastron consisting of both xiphiplastra and the hindmost portions of both hypoplastra; UCMP V71047, UCMP 299051, a somewhat worn right epiplastron; Nebraska, Brule Formation, Orellan: Dawes County – UCMP V6902, UCMP 86301, a complete carapace and partial plastron consisting of both epiplastra, anterior fragments of both hyoplastra, and most of the entoplastron; Sioux County – USNM 11 mi. S.W. of Crawford, Nebraska, USNM 11873, the relatively complete carapace and full plastron of a juvenile; USNM Everson Ranch 12 mi. N.W. of Crawford Neb., USNM 358083, the anterior lobe of a plastron consisting of both epiplastra, the anterior 2/3 of the entoplastron, and the anteriormost ¼ of the left hyoplastron; RAM V96219, RAM 27148, the partial anterior lobe of a plastron consisting of a complete entoplastron, parts of both epiplastra and the anteriormost portions of both hyoplastra, both scapulae and both coracoids; RAM V94150, RAM 27149, a partial carapace and plastron; Wyoming, Brule Formation, Orellan: Niobrara County – USNM South side of Indian Creek, USNM 15866, the complete carapace and plastron of a juvenile; USNM E. side of Little Indian Creek, USNM 15878, a carapace and plastron; USNM about 1 mi. N. of Whitmans post office, USNM 16728, a carapace and partial plastron; USNM 16737, an “epiplastral beak” consisting of most of both epiplastra and the anterior half of the entoplastron; USNM 358084, the partial carapace and plastron of a juvenile; USNM 1MI NW of Whitman post office, USNM 16731, a carapace and plastron; USNM 16733, a carapace and most of a plastron; USNM N side of Young Woman Creek, USNM 16732, a carapace and plastron.

Diagnosis. *Oligopherus laticuneus* can be identified as belonging to pan-testudinidae based on the suite of characters provided for that clade above. They may diagnosed by the following suite of characters: presence of a rectangular 3rd neural (Vlachos, 2018); typical neural pattern of)6)6 | 4 (6 (6 (6 (6 (6 or 4 8 4 (6 (6 (6 (6 (6 (Hutchison, 1996); a cervical scale that is as wide as it is long and often wedge shaped (Franz, 2014), a 1st pleural that does not intrude onto the nuchal (Vlachos, 2018); sulci that are strongly perched, especially in the anterior region of the carapace (Personal observation); vertebral scales that are rather narrow, with arcuate lateral borders; a 1st vertebral scale that is wider than the 2nd vertebral (Bramble & Hutchison, 2014); the presence of a pygal scale (Vlachos, 2018); shell bones that are somewhat thin (Franz, 2014); epiplastron with a very shallow excavation (Hutchison, 1996); presence of an elongated gular protrusion relative to other testudinoids; gular protrusion with toothed margins (Franz, 2014); inguinal scale not contacting the femoral (Bramble & Hutchison, 2014); posterior xiphiplastral border with toothed margins (Franz, 2014); gular scales covering the

anterior portion of the entoplastron; humero-pectoral sulcus positioned posterior to the entoplastron, medially perpendicular to the midline and anterolaterally concave (Pers. obs.).

Discussion. Reynoso and Montellano-Ballesteros (2004) were of the opinion that *Oligopherus* belongs to *Gopherus* and should be subsumed therein. Vlachos and Rabi (2017) conducted a total-evidence analysis that recovered *Oligopherus* outside Testudinidae proper as the most derived stem testudinid. Its flat epiplastral lip and (in many specimens) coincidence between the pleuro-marginal sulcus and the costo-peripheral suture are synapomorphies shared with members of Testudinidae. However, *Oligopherus* lacks the Testudinidae synapomorphies of having vertebral scales nearly equal to the pleurals in width and having no contact between the first pleural and the nuchal.

I follow Vlachos and Rabi here and retain *Oligopherus* as a valid genus, based on a suite of morphological differences between members of this genus and *Gopherus*. This includes the narrowness of the vertebral scale series relative to the width of the pleurals, the non-overlapping contact between the Pleural I scales and the postero-lateral corners of the nuchal, the shape and relative width of the cervical scale; presence of a prominent gular protrusion; depth of the posterior epiplastral excavation; lack of entoplastral sculpturing; degree of differentiation of the neural series; lack of a gular shelf; presence of toothed margins on the gular and xiphiplastron; degree to which the sulci on the anterior moiety of the carapace are perched; absence of contact between the inguinal and femoral scales; width of the vertebral I scale relative to vertebral II.

In most testudines the sulci that mark the junction between two shell scales are impressed into the bone surface. “Perched” sulci have a low ridge on either side of the sulcus that rises above the normal bone surface (Biewer et al., 2016).

The type specimen, AMNH 1160, has a neural formula of 6) 6) | 4 (6 (6 (6 (6 (6. Although the 5th neural appears more nearly trapezoidal than hexagonal, it is difficult to distinguish as the preservation is far from pristine. The cervical scale is wider than long, and wedge shaped. Pleural 1 nearly touches but does not overlap the nuchal and does not intrude onto the peripherals. The anterior sulci of the carapace are strongly perched. The lateral borders of the vertebrae are arcuate, and vertebral 1 is wider than vertebral 2. The costals are strongly wedge shaped, with the distal ends alternating wide and narrow down each side of the carapace. The posterior peripherals are strongly flared. The plastron has elongated gular protrusions with the saw-toothed anterior margins typical of *Oligopherus* and not seen in *Gopherus*. The posterior apices of the xiphiplastron are toothed, though less so than the gulars. The inguinal scale does not contact the femoral, and the gular scales overlap the anterior portion of the entoplastron. The humero-pectoral sulcus (HPS) is positioned posterior to the entoplastron, with a medial portion that is perpendicular to the axial plane and a lateral portion that is perpendicular to the axial plane and anterolaterally concave, being relatively straight throughout its length.

UCMP 223092 has a rectangular neural 3, strongly perched sulci on the peripherals, and a well-developed gular protrusion. Growth annuli are visible on the bone surfaces, and the pleuro-marginal sulcus coincides with the costo-peripheral suture. The posterior epiplastral excavation is shallow. The gularo-humeral sulcus forms an angle far greater than 90 degrees, and somewhat unusually for *Oligopherus*, the gulars appear to have met midline with their posterior edges coinciding with the anteriormost part of the ento-epiplastral suture. A plastral fragment including much of the right hyoplastron and hypoplastron is present, but the size difference of the specimens suggest that it should be regarded as belonging to a second, smaller individual. Visible on this fragment, the HPS is located posterior to the entoplastron and is not medially perpendicular to the axial plane but forms a wide shallow arc with an anterolaterally concave lateral portion.

The anterior and posterior borders of the carapace are missing in UCMP 36443 and the plastron is encased in plaster, but several distinguishing features are still visible. The sulci of the carapace are strongly perched and the vertebrals are narrower than the pleurals. Neurals 7 – 8 and the posterior half of neural 6 are missing, but the pattern for the first six neurals is 6 6 | 4 (6 (6 (6. The costals are strongly wedge-shaped, with alternating narrow and wide ends distally, and there is a close coincidence between the pleuro-marginal sulcus and the costo-peripheral suture. Vertebral 3 appears to be oddly elongated posteriorly and the sulcus between vertebrals 3 and 4 crosses the anterior edge of neural 6, rather than crossing neural 5.

UCMP 94709 has strongly perched anterior sulci and a neural pattern of 4 8 4 (6 (6 (6 (6. The costals are strongly cuneate, alternating narrow and wide ends distally. Two suprapyrgals are present, the first embracing the lenticular second. Pleural 1 intrudes onto the first two peripherals and contacts but does not overlap the nuchal. The cervical scale is wedge-shaped and wider than long. The vertebrals are narrower than the pleurals, and vertebral 1 is wider than vertebral 2 and widely separated from marginal 2. The posterior peripherals are strongly flared. The plastron has a well-developed gular protrusion with toothed anterior margins, as are the posterior margins of the xiphiplastra. The epiplastra have shallow posterior excavations, the gulars cover the anterior portion of the entoplastron, and the inguinal scales do not contact the femorals. The angle formed by the gularo-humeral sulcus is greater than 90 degrees, and the medial antero-posterior length of the gular scales is less than that of the humerals. The HPS is positioned well behind the entoplastron, being roughly perpendicular to the midline of the plastron throughout its length and having an anterolaterally concave lateral portion. The medial length of the anal scales is less than that of the femorals and there is a protuberance on the lateral border of the xiphiplastron where the femoral-anal sulcus crosses it. The anal notch is deep and angular.

UCMP 299046 is a very fragmented but relatively complete carapace with highly perched anterior sulci, a 1st pleural that does not contact the nuchal, and a neural formula of 4 8 4 8 (6 (6 (6 (6. The costals are strongly cuneate, with distal ends alternating wide and narrow.

The cervical scale is wider than long and wedge-shaped, the vertebrals are narrower than the pleurals, and vertebral 1 is wider than vertebral 2. The pleuro-marginal sulcus lies along the costo-peripheral suture. The specimen has two suprapygals, the lenticular second embraced anteriorly by the first. Only the posterior-most moiety of the plastron is preserved, but it is clear that the inguinal and femoral scales are not in contact. The medial antero-posterior length of the femorals is greater than that of the anal scales and the anal notch is deep and angular.

UCMP 299051 has perched sulci and a shallow posterior epiplastral excavation. Although the entoplastron is missing, the angle at which the gularo-humeral sulcus intersects the epiplastral-entoplastral suture indicates that the gulars covered the anterior portion of the entoplastron.

The anterior carapacial sulci of UCMP 86301 are highly perched and pleural 1 does not contact the nuchal. The specimen has a neural formula of 4 8 4 (6 (6 (6 (6 (6 and costals that are strongly wedge-shaped, alternating wide and narrow ends distally. The wedge-shaped cervical scale is wider than long. The vertebral scales are narrower than the pleurals, and vertebral 1 is wider than vertebral 2 and well-separated from marginal 2. The pleuro-marginal sulcus coincides with the costo-peripheral suture, the posterior peripherals are flared, and there are two suprapygals with the first embracing the lenticular second. The epiplastra have elongated gular protrusions that extend well beyond the anterior edge of the carapace and have toothed anterior margins. The gular scales overlap the anterior portion of the entoplastron, and the two sides of the gularo-humeral sulcus form an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, is roughly perpendicular to the axial plane throughout its length and is anterolaterally convex.

USNM 11873 is the shell of a juvenile measuring roughly 10 cm in length by 9 cm in width. The carapace is missing the right half of the nuchal, right peripheral 1, left peripherals 2-3, and the distal end of the left 1st costal. The cervical scale is wider than it is long, but the shape is indiscernible. The sulci are perched but not as strongly as in more mature specimens, pleural 1 does not contact the nuchal, and vertebral 1 is widely separated from marginal 2. The costals are strongly cuneate and the pleuro-marginal sulcus is aligned with the costo-peripheral suture. Uncommon for the species, the vertebrals here are wider than long and the width of vertebral 2 exceeds that of vertebral 1. The epiplastra have gular protrusions with slightly toothed anterior margins, and the gular scales cover the anterior portion of an entoplastron that is longer than wide. The HPS is located well posterior to the entoplastron and forms a wide shallow arc as it crosses the plastron. The inguinal scales do not contact the femorals, and the medial length of the femoral scales is greater than the medial length of the anals. The anal notch is angular, and there are notches in the lateral margins of the xiphiplastra coinciding with the femoral-anal sulci.

USNM 358083 has perched sulci and a very well-developed gular protrusion with a strongly toothed anterior margin. The gulars cover the anterior part of the entoplastron, the

posterior epiplastral excavation is shallow, and the angle formed by the gularo-humeral sulcus is slightly acute. The posterior part of the entoplastron and the medial portion of the HPS are absent, but the lateral portion of the HPS is anterolaterally concave.

RAM 27148 has well developed gular protrusions, although the anterior ends are absent, so it is impossible to say whether the margins were serially notched. The gular scales cover the anterior portion of the entoplastron, and the epiplastra have shallow posterior excavations. The HPS is positioned posterior to the entoplastron and is medially perpendicular to the axial plane.

Much of the left side of RAM 27149 is badly fragmented. The carapace is broad and low-domed, though this may be due in part to post-depositional diagenetic compression. The anterior sulci are well-perched, pleural 1 does not contact the edge of the nuchal, and the cervical scale is wider than long. The pleuro-marginal sulcus is closely coincident with the costo-peripheral suture. The epiplastra have well-developed gular protrusions with toothed anterior margins.

The anterior sulci of USNM 15866 are only very slightly perched, though as this specimen is of a juvenile it may be presumed that the perching might increase with maturity. Pleural 1 does not contact the nuchal, the costals are strongly cuneate, and the neural formula is)6)6 |4 (6 (6 (6 (6 (6. The cervical scale is wedge-shaped and the vertebrals have arcuate borders. The pleuro-marginal sulcus is coincident with the costo-peripheral suture, vertebral 1 is widely separated from marginal 2. The epiplastra have well-developed gular protrusions with slight serial notching along the anterior margins, and the gular scales intrude onto the anterior portion of the entoplastron. The HPS is located posterior to the entoplastron and is relatively straight throughout its length. It forms a wide angle medially and is slightly anterolaterally convex at the lateral ends. The inguinal scale does not contact the femoral, the anal notch is angular, and a lateral protuberance is present on the xiphiplastron at the femoral-anal sulcus. This specimen is unusual for *Oligopherus* in that the vertebral scales are wider than long and vertebral 1 is equal in width to vertebral 2. It was previously identified as "*Stylemys* sp.", but the presence of a well-developed gular protrusion with a notched anterior margin even at the juvenile stage invalidates that conclusion.

USNM 15878 is listed as a hypotype of *Gopherus praeextans* (Gilmore, 1946, pl.38, 40). Auffenberg (1974) considered *G. praeextans* as a possible "chronologic race of *G. laticuneus*", and it was synonymized with *G. laticuneus* by Bramble (1982). The carapace is low-domed, with highly perched anterior sulci. The nuchal is wider than it is long and is not contacted by pleural 1. The neural pattern is 4 8 4 (6 (6 (6 (6 (6, with neural 7 being subdivided into anterior and posterior hexagons. The costals are strongly cuneate, though there is little distal narrowing of costal 5. Two suprapygals are present, with the first embracing the lenticular second, and the posterior sulcus of vertebral 5 crosses suprapygal 2 transversely. Pleural 1 intrudes onto peripherals 1 and 2 but there is otherwise close coincidence between the pleuro-marginal

sulcus and the costo-peripheral suture. The posterior peripherals are flared, and there are protrusions on peripherals 1-2 and the posterior peripherals where the sulci cross the margins. The cervical scale is only slightly wedge-shaped and is wider than long. The marginal rim, including the cervical and marginal 1 scales, is quite broad in relation to the width of the nuchal. Vertebral 1 does not contact the peripherals and is widely separated from marginal 2, and the vertebral scales have arcuate borders. The epiplastra extend well beyond the leading edge of the carapace, with well-developed gular protrusions. The gulars cover the anterior part of the entoplastron, with a slightly obtuse angle being formed by the gularo-humeral sulcus. The medial anteroposterior length of the gular scales is equal to that of the humerals. The HPS is positioned posterior to the entoplastron and medially forms a very wide angle that is relatively straight throughout its width. The inguinal scale does not contact the femoral. The medial anteroposterior length of the anal scales is shorter than that of the femorals, the anal notch is deep and angular, and the xiphiplastra are flange-like with serially notched margins. It should be noted that in plate 38 of Gilmore (1946) the text claims that the right carapace is USNM 15878, when in fact it is the left.

USNM 16728 is also listed as a hypotype of *G. praeextans* (Gilmore, 1946, pl.39, 41). The plastron is fragmentary, but the carapace is nearly complete. The anterior sulci are highly perched, and the carapace is low-domed, with a neural formula of 6) 6) | 4 (6 (6 (6 (6 (6, though what little remains of neural 8 is highly obscured by plaster. The nuchal is not in contact with pleural 1, the costals are strongly wedge-shaped, and two suprapygals are present, the posterior margin of the first embraces the anterior margin of the lenticular second and the suture between them is nearly fused. Pleural 1 intrudes onto peripherals 1 and 2, but there is close coincidence elsewhere between the costo-peripheral suture and the pleuro-marginal sulcus. The posterior peripherals are strongly flared, and there are protrusions on peripherals 1-2 and the posterior peripherals where the sulci cross the margins. The cervical scale is equally wide as it is long, and wedge-shaped with gently curving borders. The marginal rim is broader than the width of the nuchal. The vertebrals have arcuate borders, and vertebral 1 contacts but does not overlap peripheral 1 and is widely separated from marginal 2. The posterior sulcus of vertebral 5 crosses the second suprapygal transversely, and the 12th marginal scales are fused. The epiplastra extend well beyond the leading edge of the carapace, with the well-developed gular protrusions having toothed anterior margins. The gulars meet midline just at the anterior border of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The entire medial portion of the HPS is missing, but the lateral portion is anterolaterally convex.

USNM 16737 ("*Testudo quadrata* Cope" of Gilmore, 1946, pl.44, f.1) has a well-developed gular protrusion and a shallow-to-moderate posterior epiplastral excavation. The gulars cover the anterior area of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle.

USNM 358084 is missing the carapace posterior to costal 6, and the plastron posterior to the midline junction of the femoral-anal sulci. The carapacial sulci are slightly perched and the first pleural contacts but does not overlap the nuchal. The visible neural series has a pattern of 6) | 8 4 (6 (6 (6. The sutures with neural 6 and the costal 6 pair indicate that neural 7 was likely hexagonal as well, with the short sides positioned anterolaterally, and the full neural series may be presumed to have been 6) | 8 4 (6 (6 (6 (6? (6? as a non-hexagonal neural 7 or 8 would have been extremely unlikely for a North American tortoise at this time. The costals are wedge-shaped and the pleuro-marginal sulcus is coincident with the unfused costo-peripheral suture. The cervical scale is wider than long and wedge-shaped. The vertebral scales have arcuate borders and are wider than long. Vertebral 1 is roughly equal in width to vertebral 2 and terminates anterolaterally well short of marginal 2. Expanding beyond the anterior border of the carapace, the epiplastra have well-developed gular protrusions with very slightly serrated anterior margins. The entoplastron is wider than long and the anterior part is covered by the posteromedial ends of the gulars. The medial anteroposterior length of the humerals is greater than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is located posterior to the entoplastron. It is medially straight and perpendicular to the axial plane, and laterally concave. The inguinal scale is not in contact with the femoral.

USNM 16731 ("*Testudo laticuneus* Cope" of Gilmore, 1946, pl.42) has a low-domed carapace with strongly perched anterior sulci. The first pleural does not contact the nuchal but does overlap the edges of peripherals 1 and 2, the pleuro-marginal sulcus is otherwise highly coincident with the costo-peripheral suture. The costals are strongly wedge-shaped, with alternating wide and narrow ends distally, and the neural series has a pattern of 4 8 4 (6 (6 (6 (6 (6 (6. The cervical scale is wedge-shaped and wider than long, and the marginal rim is broader than the width of the nuchal. Two suprapygals are

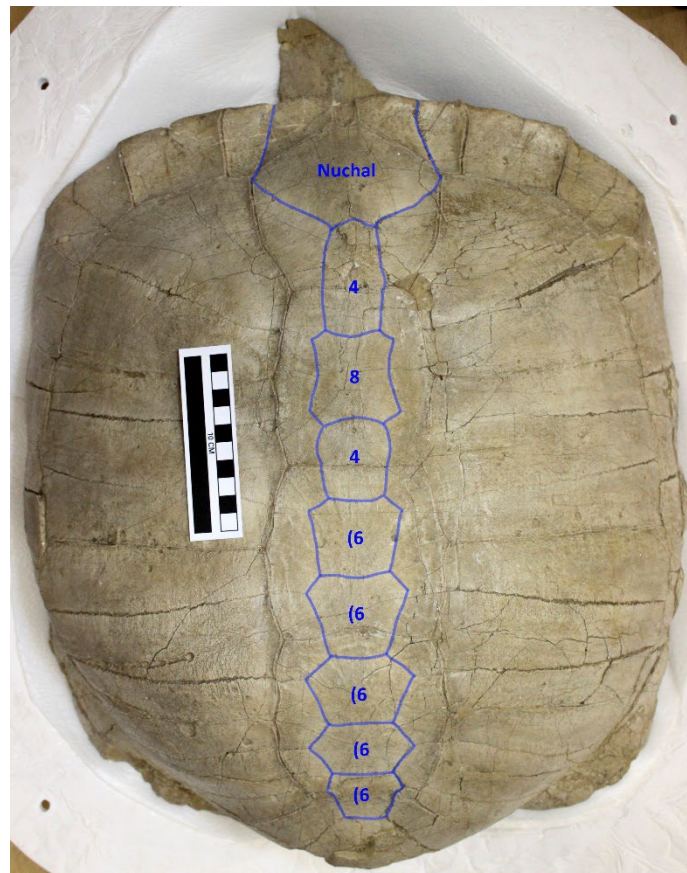


Figure 5: USNM 16732, a mature individual with the nuchal and neural series marked. Typical for *O. laticuneus* in most respects.

present, the first embracing the lenticular second, and the posterior sulcus of vertebral 5 crosses the second suprapygal transversely. The vertebrals are narrower than the pleurals, and vertebral 1 is well-separated from marginal 2 and wider than vertebral 2. The marginal scale 12 pair is fused in dorsal view. The epiplastra extend beyond the anterior border of the carapace, having elongated gular protrusions with toothed margins. The entoplastron is longer than wide. The gulars cover the anterior portion of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is posterior to the entoplastron and is medially perpendicular to the axial plane and laterally concave. The inguinal does not contact the femoral, and the anal notch is deep and angular.

USNM 16732 (**Fig. 5**) ("*Testudo praeextans* Lambe" of Gilmore, 1946, pl.39, 41) has a low-domed carapace and strongly perched anterior sulci. The first pleural contacts, but does not overlap the nuchal, which is wider than long. The neural pattern is 4 8 4 (6 (6 (6 (6 (6 and the costals are strongly cuneate. Pleural 1 overlaps peripherals 1-2 and the anteromedial corner of peripheral 3, but the pleuro-marginal sulcus is otherwise coincident with the costo-peripheral suture. The specimen has two suprapygals, the first embracing the lenticular second, and the posterior sulcus of vertebral 5 crosses the second suprapygal transversely. The cervical is rectangular, longer than it is wide, and somewhat short. The marginal rim is broad in relation to the width of the nuchal. Vertebral 1 is widely separated from marginal 2, does not overlap the peripherals, and is wider than vertebral 2. The vertebrals have arcuate borders, and are narrower than the pleurals, only vertebral 2 is narrower than it is long. The epiplastra have well-developed gular protrusions that extend beyond the leading edge of the carapace, and the entoplastron is wider than long. The gulars cover the anterior part of the entoplastron, and the

gularo-humeral sulcus forms an obtuse angle. Posterior to the entoplastron, the HPS is medially perpendicular to the axial plane and anterolaterally concave. The inguinal scale is small and not in contact with the femoral. The anal scales are medially shorter than the femorals, the anal notch is deep and angular, and the xiphiplastra have toothed apical margins.

USNM 16733 (**Fig. 6**) was collected by C.W. Gilmore from the same locality as USNM 16731. The carapace is low-domed, and the anterior sulci are highly perched. The nuchal is wider than long. The vertebral 1 scale is oddly truncated at the lateral corners, giving it an almost urn-like shape, and causing the anteromedial corners of the pleural 1 pair to overlap the lateral corners of the nuchal. Pleural 1 overlaps peripherals 1 and 2, but there is otherwise close coincidence between the costo-peripheral suture and the pleuro-marginal sulcus. The neural pattern of 4 8 4 8 4 (6 (6 4 deviates from the norm for *Oligopherus*. The costals are very strongly wedge-shaped, particularly the costal 5 pair, the left of which is reduced to a width of 3 mm at the lateral end and the right of the pair terminates well above the peripheral row into a suture between costals 4 and 6. A similar state is seen in UCMP 36443, though to a less dramatic degree. Two suprapyrgals are present, the first embracing the lenticular second, and the posterior sulcus of vertebral 5 crosses suprapygal 2 transversely. The cervical scale is wedge-shaped and over twice as wide as long, and the marginal rim is broad in relation to the width of the nuchal. The vertebrals are longer than wide and narrower than the pleurals. Vertebral 1 is substantially wider than vertebral 2, does not contact the peripherals, and is widely separated from marginal 2. The posterior peripherals are strongly flared, and the twelfth marginal scales are fused. The anterior parts of the epiplastra are missing. The anterior portion of the entoplastron is fragmentary, but the gulars appear to contact it. The HPS crosses just behind the entoplastron, forming a wide angle medially and being

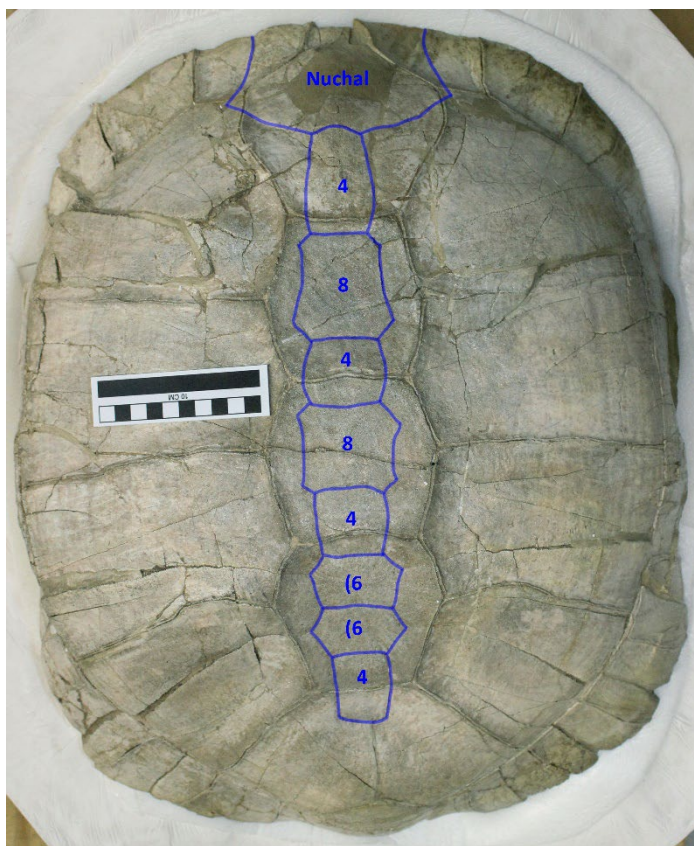


Figure 6: USNM 16733, a mature individual with the nuchal and neural series marked. Note the overlap of the nuchal by pleural 1, and the extreme distal narrowing of the costal 5 pair.

laterally concave. The inguinal scale is small and does not contact the femoral. The medial length of the femorals is greater than that of the anals, the anal notch is deep and angular.

USNM 16733 is perhaps the finest example of intraspecific variation one could hope for within *O. laticuneus*, possessing no fewer than five morphological characters that individually are unusual for the species. The extreme distal narrowing of costal 5 found in USNM 16733 is also present, to a lesser extent, in UCMP 86301, UCMP 36443, USNM 358084, and RAM 8327. The presence of a cervical scale that is over twice as wide as long can be seen in both USNM 16731 and USNM 16733. There are two main varieties of neural pattern within the species; the 6) 6) 4 (6 (6 (6 (6 (6 pattern found in the holotype and USNM 15866 and 16728, and the 4 8 4 (6 (6 (6 (6 (6 pattern found in UCMP specimens 86301, 94709 and 299046, and USNM specimens 15878, 16731 and 16732. Deviations from these typical patterns can be seen in USNM 358084 and USNM 16733, although the rectangular neural 8 in USNM 16733 appears to be somewhat unique. It is clear that intraspecific variation is not uncommon within *Oligopherus*, and some characters such as the overlap of pleural 1 onto peripherals 1-2 are highly variable.

Maturity in tortoise fossils can be determined by the fusion of the costo-peripheral suture. Juveniles will still have an open or unfused suture. Several specimens of juveniles exhibit unusual characters for *Oligopherus*, and it would serve the discipline well were someone to conduct both an ontogenetic study of the genus and a comprehensive quantification of the range of morphological variation possible within it.

Family TESTUDINIDAE Batsch 1788

Diagnosis. Members of Testudinidae can be identified as belonging to pan-testudinidae based on the suite of characters provided for that clade above. Testudinids may be distinguished from other pan-testudinidae by: neural differentiation into octagonal and quadrangular neurals; costo-peripheral suture coincides with the pleuro-marginal sulcus; short pectoral scales; well-developed epiplastral lip; humero-pectoral sulcus does not overlap the entoplastron (Vlachos, 2018).

Genus *Gopherus* Rafinesque 1832

Diagnosis. Members of *Gopherus* can be diagnosed as belonging to Testudinidae based on the suite of characters provided for that group above. *Gopherus* share the following suite of characters that help to distinguish them from other testudinids: presence of a rectangular cervical scale that is as wide or wider than long (Vlachos, 2018); costals that are strongly cuneate, alternating between wide and narrow laterally (Hutchison, 1996); sulci that are perched, especially on the carapace (Biewer et al., 2016); an adult shell than is usually low-domed (Hutchison, 1996); shell bones that are relatively thin (Franz, 2014); a 1st vertebral scale that is narrower than the 2nd vertebral (Bramble & Hutchison, 2014); an epiplastron that lacks a prominent gular protrusion (Vlachos, 2018); the presence of a deep posterior epiplastral

excavation; a rounded gular lacking a toothed anterior margin; the presence of an entoplastral sculpture (Franz, 2014); a humero-pectoral sulcus that is positioned posterior to the entoplastron and is medially rounded, forming a broad “U” shape (Vlachos, 2018); inguinal scale contacting the femoral (Hutchison, 1996); posterior xiphiplastral border tapered to rounded, but without distinct serial notching (Franz, 2014).

Gopherus edae (Hay, 1906b)

Synonymy. *Testudo edae* Hay, 1906b; *Testudo hollandi* Hay, 1906b; *Testudo pansa* Hay, 1908; *Testudo vaga* Hay, 1908.

Type material. CM1535, a carapace and plastron (Hay 1908, pl. 83: 1-2)

Type locality. Near Running Water Creek, Sioux County, Nebraska, Harrison Formation, Late Arikareean (Hay 1906b).

Referred material. Wyoming, Arikaree Formation, Hemingfordian: Fremont County – UCMP V69190, UCMP 124958, the somewhat fragmentary anterior half of a carapace; UCMP V69191, UCMP 125536, a partial carapace and plastron.

Diagnosis. *Gopherus edae* can be identified as belonging to *Gopherus* based on the suite of characters provided for that genus above. *G. edae* may be distinguished from other *Gopherus* by the following suite of characters: a neural series that is fully differentiated, with pattern 4 (8) 4 (8) 4 (6 (6 (6 (Hay, 1906b); a wide cervical scale, although narrower than that found in *Gopherus mohavensis*; wide vertebral scales; a pectoral scale that is medially shorter than that seen in *G. mohavensis*; gulars that cover the anterior part of the entoplastron; an inguinal scale that contacts the femoral; the presence of a well-developed anal notch (Vlachos, 2018).

Discussion. The type specimen, CM1535, is a carapace and plastron, from both of which about half of the right side is missing. The carapacial sulci are perched, the nuchal is notably wider than long and is not contacted by pleural 1. Only seven neurals are present in the type, with neural 5 apparently either subsumed by the somewhat misshapen neural 4 or entirely absent. This yields a neural pattern of 4 8 4 8 (6 (6 (6. The costals are strongly wedge-shaped and there are two suprapyrgals, with the first surrounding the anterior part of the lenticular second. The cervical scale is rectangular and longer than wide. The vertebrals are wider than the pleurals, and vertebrals 1 and 2 are equal in width. The epiplastra expand beyond the anterior edge of the carapace, with relatively short but well-developed gular protrusions with rounded apices. The gular scales overlap the anterior edge of the entoplastron, the gularo-humeral sulci form a slightly acute angle, and the medial anteroposterior length of the humerals and gulars is roughly equal. The HPS is positioned behind the entoplastron, medially

straight and perpendicular to the axial plane, and anterolaterally concave. The anal notch is deep and angular, the apices of the xiphiplastra are broken.

UCMP 125536 (**Fig. 7**) has mildly perched sulci and a neural formula of 6) 6) 4 8 4 (6 (6 (6, the hexagonal shape of neural 1 is quite exaggerated posteriorly into a shape described as “clavate” by Hay (1908). The costals are strongly wedge-shaped, there is close coincidence between the pleuro-marginal sulcus and the costo-peripheral suture, and two suprapygals are present, the first embracing the lenticular second. The vertebral scales are much wider than long, wider than the pleurals, vertebral 1 is narrower than vertebral 2, and the posterior sulcus of vertebral 5 crosses suprapygal 2 transversely. The anterior portion of the plastron is not

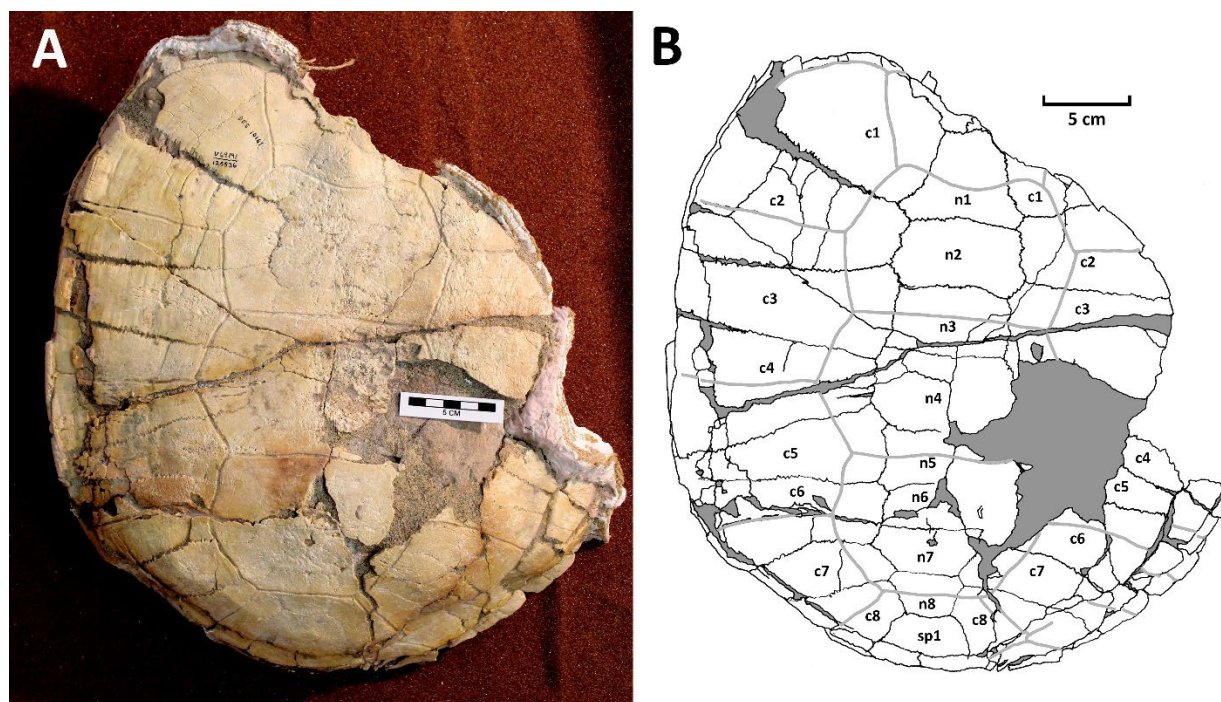


Figure 7: A) UCMP 125536, a *Gopherus edae* variant. **B)** Diagrammatic view showing the clavate first neural. Sulci in light gray.

preserved, but it is clear from what remains that the HPS is positioned posterior to the entoplastron and forms a wide angle medially. The inguinal scale is in contact with the femoral, and there is a substantial femoral-anal notch in the lateral border of the xiphiplastron. The medial length of the anals is shorter than the medial length of the femoral scales, the anal notch is angular, and the apices of the xiphiplastron are rounded.

A second specimen, UCMP 124958 (**Fig. 8**), was collected from a nearby locality at around the same time and bears striking resemblance to UCMP 125536, particularly in the exaggerated, clavate shape of the first neural. This specimen does not appear to have perched sulci, has a nuchal that is nearly rectangular in shape, and has a wedge-shaped cervical scale

that is equally wide as it is long. The vertebral scales are wider than the pleurals and vertebral 1 is narrower than vertebral 2. The costo-peripheral sutures are unfused, indicating that the individual was a juvenile.

The clavate first neural is an anomaly that I have not encountered in any other *Gopherus* specimens to-date. It is discussed by Hay (1908) in his description of AMNH 6027, a nearly complete shell of *Hadrianus corsoni* (pg. 377-8, Fig. 473, pl. 60), but is far from ubiquitous within that genus as well. It is unclear whether this may be a case of homoplasy or atavism.

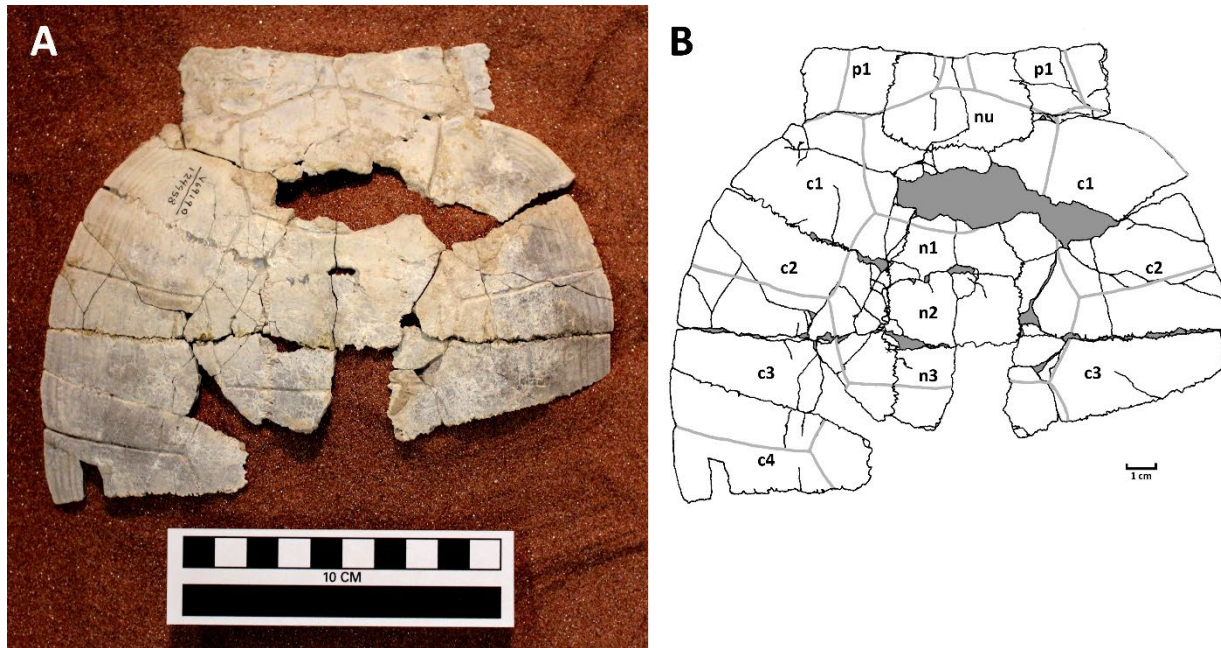


Figure 8: A) *Gopherus edae*, UCMP 124958. **B)** Diagrammatic view showing the clavate first neural. Sulci in light gray.

That this character occurs in two specimens of *G. edae* from the same NALMA and from localities in very close proximity to each other (within walking distance), and apparently nowhere else, may indicate that these specimens are from a distinct regional geographic variant of *G. edae*. It is entirely possible, however, that because there is such a small sample size this is simple random chance. Another juvenile specimen (UCMP 125535, see below), likely also *G. edae*, was collected from the same locality as UCMP 124958 at approximately the same time, but does not show evidence of having a clavate first neural.

Gopherus sp.

Referred material. Nebraska, Runningwater Formation, Hemingfordian: Dawes County – AMNH FARB Cottonwood Creek on Moody Ranch, AMNH FARB 9096, a plastron exposed in a

field jacket; Wyoming, Arikaree Formation, Hemingfordian: Fremont County – UCMP V69190, UCMP 125535, a partial carapace and plastron.

Discussion. The epiplastra of AMNH FARB 9096 have well-developed gular protrusions with rounded apices. The gular scales cover the anterior portion of the entoplastron, which is longer than wide, and the gularo-humeral sulcus forms an acute angle. The HPS is positioned posterior to the entoplastron, is medially rounded and laterally concave, and the pectoral scale is medially short, but not as short as seen in *Hesperotestudo*. The inguinal scale contacts the femoral, a lateral femoral-anal notch is present on the xiphiplastron, and the anal notch is angular.

UCMP 125535 has growth annuli visible on the bone surfaces. The nuchal and first neural are both missing, but there is no evidence on the connecting bones that N1 was once clavate. The second and fourth neurals are octagonal, the third and fifth are squared, the sixth is hexagonal. Neurals 7-8 and the suprapygal(s) are not preserved. The costals are strongly cuneate, with wide and narrow ends alternating distally. The pleuro-marginal sulcus coincides closely with the costo-peripheral suture. The vertebral scales are wider than the pleurals, and the vertebral 3-4 sulcus appears to coincide with the neural 5-6 suture. The HPS is located posterior to the entoplastron, and forms such a wide angle medially so as to be very nearly perpendicular to the midline. The lateral portion of the HPS is convex and terminates perpendicular to the axial plane. The inguinal scale contacts the femoral, the anal scales are shorter medially than the femorals, and the anal notch is angular. This specimen has previously been identified as *G. edae*, but I find insufficient morphological evidence to refer it to that taxon.

Genus *Hesperotestudo* Williams 1950b

Diagnosis. Members of *Hesperotestudo* can be diagnosed as belonging to Testudinidae based on the suite of characters provided for that group above. They share the following suite of characters that help to distinguish them from other testudinids: a cervical scale that is markedly longer than wide; a neural series that is fully differentiated, with pattern 4 (8) 4 (8) 4 (6) 6 (6) 6; costals that are moderately to strongly cuneate, alternating between wide and narrow laterally; moderate to deep posterior epiplastral excavation (Hutchison, 1996); entoplastron wider than long (Biewer et al., 2016); pectoral scales that are medially much shorter than those found in *Gopherus* or *Stylomys*; a humero-pectoral sulcus that is medially perpendicular to the axial plane and laterally concave; an inguinal scale that is enlarged and broadly contacts the femoral (Vlachos, 2018); the presence of varying degrees of dermal armor covering the limbs and tail (Hutchison, 1996).

Hesperotestudo orthopygia (Cope, 1878)

Synonymy. *Xerobates orthopygius* Cope, 1878; *Xerobates cyclopygius* Cope, 1878; *Testudo rexroadensis* Oelrich, 1952; *Geochelone nordensis* Holman, 1973b.

Type material. AMNH 3929, a carapace, plastron, skull, and appendicular elements (Hay 1908, figs. 579-590). See also AMNH 6108 (Hay, 1908)

Type locality. Decatur County, Kansas. Clarendonian (Barstovian to Blacuan).

Referred material. Nebraska, Sheep Creek Formation, Late Hemingfordian: Sioux County – AMNH FARB Greenside Quarry, AMNH FARB 12001, a partial carapace and most of a plastron; Valentine Formation, Burge Member, Early Clarendonian: Sheridan County – AMNH FARB Paleo-channel Quarry, AMNH FARB 12482, a plastron, exposed in a field jacket; Ash Hollow Formation, Cap Rock Member, Middle Clarendonian: Cherry County – AMNH FARB Tunnel Rock locality, AMNH FARB uncatalogued specimen with field number “Ains. Box 71.”, a large plastron, exposed in a field jacket; Ash Hollow Formation, Late Clarendonian: Cherry County – AMNH FARB Gallup Gulch Quarry, AMNH FARB 12488, the posterior right ¼ of a juvenile carapace and partial plastron; AMNH FARB 12494, a carapace and plastron.

Diagnosis. *Hesperotestudo orthopygia* can be identified as belonging to *Hesperotestudo* based on the above suite of characters for that genus. *H. orthopygia* may be distinguished from other *Hesperotestudo* by the following suite of characters: number of neurals usually reduced to seven; pectoral scales medially longer than in *Hesperotestudo osborniana* (Vlachos, 2018); entoplastron is rhomboidal in shape (Biewer et al., 2016); humero-pectoral sulcus lies just behind the entoplastron; anal scales are short (Vlachos, 2018; Pers. obs.).

Discussion. AMNH FARB 12001 has growth annuli visible on the bone surfaces. The nuchal is not contacted by pleural 1, and the anterior margin of the vertebral 1 scale is much wider than the posterior margin. The visible neural series is a fully differentiated 4 (8) 4 (8) 4 (6), but the carapace posterior to neural 7 is missing so it is not possible to conclusively state that the neural series ends at 7. The costals are strongly cuneate, alternating wide and narrow ends distally. The costal rib heads are thin and elongated, emerging from the costals close to the neuro-costal suture. The cervical scale is narrow and rectangular, and there is close coincidence between the pleuro-marginal sulcus and the costo-peripheral suture. The vertebral scales are wider than long, and vertebral 1 is wider at its greatest point than vertebral 2. The posterior epiplastral excavation is moderate, and the epiplastra have slightly serrated anterior margins but do not have elongated gulars. The entoplastron is wider than long, with the anterior portion being covered by the gular scales. The gularo-humeral sulcus forms an acute angle, and the medial length of the humerals is shorter than the medial length of the gulars. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally concave. The medial length of the pectoral scales is very short. The inguinal scale contacts the femoral, although it is impossible to determine how extensive the contact is because the specimen is missing much of the bridge region. A moderate femoral-anal notch is present on the lateral border of the xiphiplastron. The medial length of the femoral scales is greater than that of the anals, which are quite short. The anal notch is angular.

AMNH FARB 12482 has epiplastra with rounded gulars and no serial notching, and pectoral scales that are quite short medially. The gular scales intrude onto the anterior part of the rhomboidal entoplastron, and the gularo-humeral sulcus forms a slightly obtuse angle. The medial length of the humerals is longer than that of the gulars. The HPS is positioned behind the entoplastron, medially straight and perpendicular to the midline, and laterally concave. The inguinal scale is large and broadly contacts the femoral. The medial length of the femoral scales is greater than that of the anals, and the anal notch is angular and very shallow. The xiphiplastron is wider than long.

AMNH FARB uncatalogued specimen with field number "Ains. Box 71." has a rhomboidal entoplastron that is slightly wider than long and pectoral scales that are quite short medially. The gulars cover the anterior part of the entoplastron, the gularo-humeral sulcus forms an obtuse angle, and the medial length of the humerals is greater than that of the gulars. The HPS coincides medially with the posterior-most part of the ento-hyoplastral suture, is medially straight and perpendicular to the midline, and laterally concave. The inguinal scale contacts the femoral.

AMNH FARB 12488 has only neurals 3-5 present, with a pattern of 4 (8) 4. The costals are slightly wedge-shaped, and there is close coincidence between the pleuro-marginal sulcus and the unfused costo-peripheral suture. The vertebral scales are wider than long. A moderate posterior epiplastral excavation is present. The entoplastron is longer than wide, and rhomboidal in shape. The gulars cover the anterior of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned immediately posterior to the ento-hyoplastral suture, forms a wide arc medially, and is slightly concave and perpendicular to the midline laterally. The inguinal scale is large and in contact with the femoral. The anal scales are quite short, much shorter medially than the femorals. The anal notch is angular and somewhat shallow, the xiphiplastron is wider than long, and there is a femoral-anal notch on the lateral border of the xiphiplastron.

AMNH FARB 12494 (**Fig. 9**) has growth annuli visible on the bone surfaces. Pleural 1 does not contact the nuchal and there is close coincidence between the costo-peripheral suture and the pleuro-marginal sulcus. The neural series is a fully differentiated 4 (8) 4 (8) 4 (6) 6, and the costals are slightly wedge-shaped. The rectangular cervical scale is longer than wide, vertebral scales 1 and 3 are wider than long, and vertebral scales 2 and 4 are roughly equilateral. Vertebral 1 contacts but does not overlap peripheral 1 and is widely separated from marginal 2. A moderate posterior excavation is visible on the epiplastra. The rhomboidal entoplastron is wider than long and the gulars cover the anterior part of the entoplastron. The gularo-humeral sulcus forms an obtuse angle and the medial length of the humerals is greater than the medial length of the gulars. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally concave. The medial length of the pectoral scale is very short. The inguinal scale contacts the femoral, the medial length of

the anals is much shorter than that of the femorals, and the anal notch is angular. The xiphiplastron is broad and has a femoral-anal notch on the lateral border.

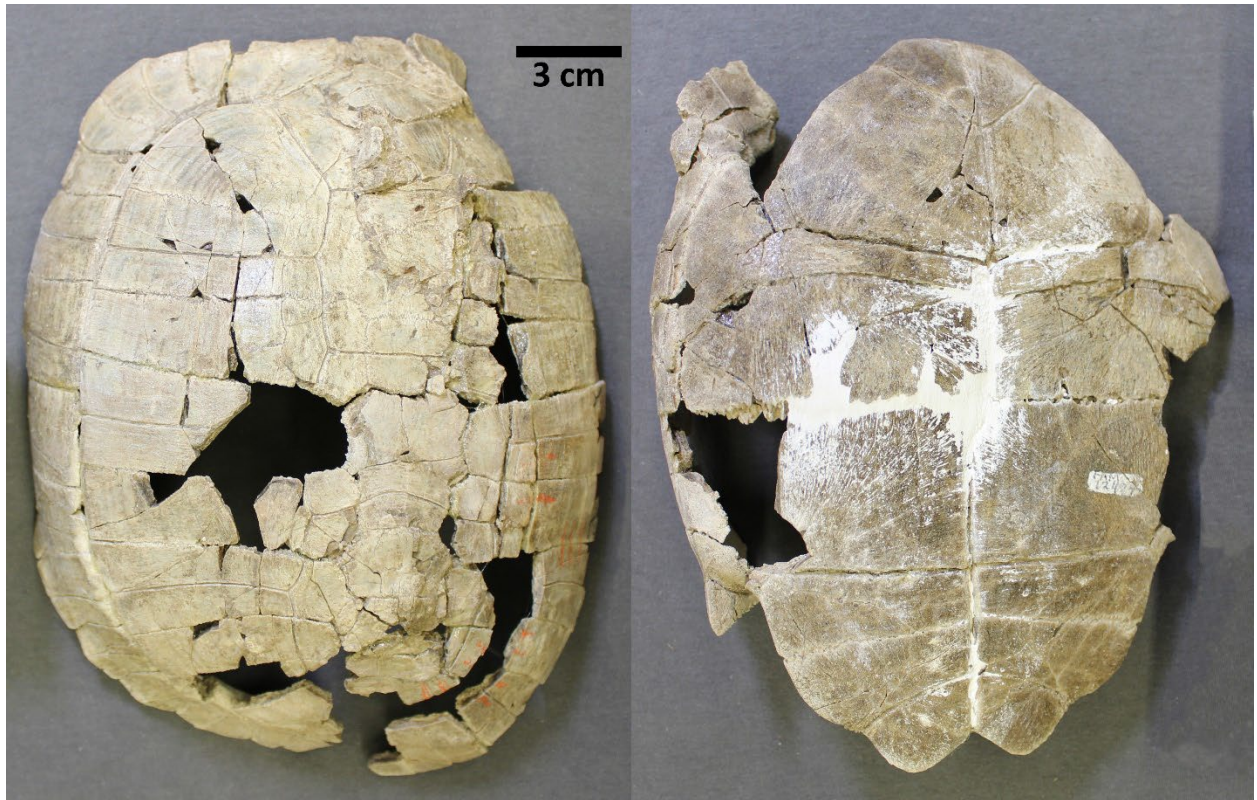


Figure 9: AMNH FARB 12494, a juvenile *Hesperotestudo orthopygia* from the Late Clarendonian of Nebraska, USA.

Hesperotestudo osborniana (Hay, 1904)

Synonymy. *Testudo osborniana* Hay, 1904; *Testudo farri* Hay, 1908; *Testudo arenivaga* Hay, 1906; *Testudo impensa* Hay, 1908.

Type material. AMNH 5668 (Hay 1908, figs. 552-560, pls. 72-73).

Type locality. Pawnee Creek, Logan Co., Colorado

Referred material. Nebraska, Sheep Creek Formation, Late Hemingfordian: Sioux County – AMNH FARB Greenside Quarry, AMNH FARB 11706, the partial anterior half of a carapace and most of a plastron; AMNH FARB 11811, a carapace and plastron; AMNH FARB 11991, most of a carapace and plastron; AMNH FARB 11998, the anterior 2/3 of a carapace and a plastron; AMNH FARB 12002, a fragmentary carapace and most of a plastron; AMNH FARB 12377, a carapace and plastron; AMNH FARB Long Quarry, AMNH FARB 11710, the carapace and plastron of a juvenile; AMNH FARB 11999, a carapace and plastron; AMNH FARB Stonehouse

Draw, AMNH FARB 11500, a carapace and plastron; Valentine Formation, Early Clarendonian: Sheridan County – AMNH FARB Extension Quarry, AMNH FARB 12480, the anterior half of a plastron and anteromedial fragments of a carapace; Sherman County – AMNH FARB Paleo-channel Q., AMNH FARB 14347, a plastron and the anterior half of a carapace; Ash Hollow Formation, Cap Rock Member, Middle Clarendonian: Cherry County – AMNH FARB Head of Pole Creek, AMNH FARB 12550, a plastron and the anterior 2/3 of a carapace; South Dakota, Basal Ash Hollow Formation, Middle Clarendonian: Todd County – AMNH FARB Hollow Horn Bear Quarry, AMNH FARB 12514, the anterior 2/3 of a juvenile carapace and plastron; Ogallala Group, Clarendonian: Bennett County – UCMP V3335, UCMP 36646, a partial carapace with fragments of a xiphiplastron, the right hyoplastron, and a xiphiplastron fragment from a second individual.

Diagnosis. *Hesperotestudo osborniana* can be identified as belonging to *Hesperotestudo* based on the above suite of characters for that genus. *H. osborniana* can be distinguished from other *Hesperotestudo* by the following suite of characters: hexagonal neural VIII (Vlachos, 2018); pectoral scales medially extremely short (Biewer et al., 2016; Vlachos, 2018); anal notch is shallow; heavy concentration of fused dermal ossicles on the tail forms a caudal buckler (Vlachos, 2018).

Discussion. AMNH FARB 11706 has growth annuli visible on the bone surfaces. Pleural 1 does not contact the nuchal, vertebral 1 contacts but does not overlap peripheral 1 and is widely separated from marginal 2. Only the first five neurals are preserved, giving a neural pattern of 4 (8) 4 (8) 4 X X X. The costals are slightly cuneate, the rib heads are thin and emerge from the costal close to the neural-costal suture. The cervical scale is rectangular, the pleuro-marginal sulcus coincides with the costo-peripheral suture, and the vertebral scales have arcuate borders. The gular region of the epiplastron protrudes slightly and has a mildly notched anterior margin, while the visceral surface of the epiplastron has a moderate posterior excavation. The entoplastron is longer than wide, has a well-curved posterior border, and has no sculpturing on the visceral surface. The gulars cover the anterior part of the entoplastron, the gularo-humeral sulcus forms an obtuse angle, and the medial length of the humeral scales is longer than that of the gulars. The HPS is located posterior to the entoplastron, the medial portion is straight and roughly perpendicular to the midline, and the lateral part is anterolaterally concave. The pectoral scale is medially very short, and the inguinal scale contacts the femoral. The medial length of the anal scales is shorter than that of the femorals, and the anal notch is angular. The xiphiplastron is wider than long and has a lateral femoral-anal notch.

AMNH FARB 11811 also has growth annuli visible. Pleural 1 contacts but does not overlap the nuchal, and the pleuro-marginal sulcus coincides with the costo-peripheral suture. The cervical scale is rectangular, the posterior border of vertebral 1 is narrower than the anterior border, and the vertebrae are wider than long. The neural pattern is 4 (8) 4 (8) 4 (6 (6 (6. Suprapygal 2 is lenticular and embraced by the posterior part of suprapygal 1. The epiplastra have a moderate posterior excavation and mildly protruding gulars due to constriction in the

lateral border where the gularo-humeral sulcus crosses, with a slight notch in the anterior margin of each gular. The entoplastron is wider than long, with the anterior portion covered by the gulars. The gularo-humeral sulcus forms an obtuse angle, and the medial length of the humerals is longer than the gulars. The HPS coincides medially with the posterior-most portion of the ento-hyoplastral suture, is medially straight and perpendicular to the axial plane, and laterally concave. The pectoral scale is very short, and the inguinal scale has a broad contact with the femoral. The medial length of the femoral scales is longer than that of the anals, and the anal notch is angular. A femoral-anal notch is present in the lateral border of the xiphiplastron.

Growth annuli are visible on the bone surfaces of AMNH FARB 11991. The nuchal is wider than long and is not in contact with pleural 1. The neural series is fully differentiated, but with an anomalous ninth neural appearing between neural 8 and suprapygal 1, giving a neural pattern of 4 (8) 4 (8) 4 (6 (6 (6 [*4]. The costal rib heads are thin and emerge from the costal close to the neural-costal suture. Two suprapygals are present, the first cradling the lenticular second. The rectangular cervical scale is long and narrow and has a median notch in the anterior border. The pleuro-marginal sulcus coincides with the costo-peripheral suture, and the vertebral scales are wider than the pleurals and have arcuate borders. Vertebral 1 is narrower than vertebral 2 and is widely separated from marginal 2. The epiplastra have weak gular protrusions with slightly notched anterior margins, and a moderate posterior epiplastral excavation. The gulars cover the anterior portion of the entoplastron, the gularo-humeral sulcus forms an obtuse angle, and the medial length of the humeral scales is longer than that of the gulars. The HPS coincides medially with the posterior contact between the entoplastron and hyoplastron, is medially straight and perpendicular to the midline, and laterally concave. The pectoral scale is very short medially, and the inguinal scale broadly contacts the femoral. The medial length of the anal scales is much shorter than that of the femorals, and the anal notch is angular. The xiphiplastron is wider than long and has a notch in the lateral border at the femoral-anal sulcus.

AMNH FARB 11998 has growth annuli visible on the bone surfaces. Pleural 1 does not contact the nuchal, and the costo-peripheral suture coincides with the pleuro-marginal sulcus. The neural series is fully differentiated, although the hindmost pair of neurals are missing, yielding a pattern of 4 (8) 4 (8) 4 (6 X X. The costal rib heads are thin and emerge from the wedge-shaped costals close to the neural-costal suture. The cervical scale is thin and rectangular, with a median notch in the anterior edge. The posterior border of vertebral 1 is much narrower than the anterior border, and the vertebrae are wider than long. The gular regions of the epiplastra protrude but a little and are overall rounded in shape along the anterior margins, with a small anterolateral protuberance occurring about halfway between the midline suture and the lateral edge of the gularo-humeral sulcus. The posterior epiplastral excavation is of moderate depth. The entoplastron is longer than wide and has a well-curved posterior border. The gular scales overlap the anterior part of the entoplastron, their medial length is less than that of the humerals, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally concave. The pectoral scale is very short medially, and the inguinal

scale contacts the femoral. The medial length of the femorals is greater than that of the anal scales and the anal notch is angular and relatively shallow. A femoral-anal notch is present on the lateral margin of the xiphiplastron.

AMNH FARB 12002 has growth annuli visible. Pleural 1 is not in contact with the nuchal, there is close coincidence between the pleuro-marginal sulcus and the costo-peripheral suture, and the anterior margin of vertebral 1 is much wider than the posterior margin. The carapacial midline is fragmented and the posterior pair of neurals are absent, but the discernible neural pattern is 4 (8) 4 (8) 4 (6 X X. The thin costal rib heads emerge from the slightly cuneate costals close to the neural-costal suture. The rectangular cervical scale is longer than wide but is still relatively short, making up only about 23% of the nuchal length. The gular regions of the epiplastra protrude slightly and are rounded along the anterior margins, with a small anterolateral protuberance, and there is a moderate posterior epiplastral excavation. The entoplastron has a curved posterior border. The gulars cover the anterior part of the entoplastron, and the gularo-humeral sulcus forms an acute angle. The HPS crosses just posterior to the entoplastron, the medial portion being straight and perpendicular to the axial plane and the lateral part being concave. The pectoral scale is quite short medially, and the inguinal contacts the femoral scale. The medial length of the anal scale is shorter than that of the femoral, and the anal notch is relatively shallow and angular. The lateral border of the xiphiplastron is indented by the femoral-anal notch.

AMNH FARB 12377 has growth annuli visible on the bone surfaces. Pleural 1 does not contact the nuchal, and there is close coincidence between the pleuro-marginal sulcus and the costo-peripheral suture. The neural pattern is 4 (8) 4 (8) 4 (6 (6 (6. The costals are mildly cuneate, and the rib heads are thin and emerge close to the neural-costal suture. The rectangular cervical scale is longer than wide and takes up approximately 29% of the nuchal length. The vertebral scales are wider than long and have arcuate borders. The lenticular suprapygal 2 is embraced anteriorly by suprapygal 1. The epiplastra have moderate posterior epiplastral excavations and short but distinct gular protrusions, caused by constriction at the gularo-humeral sulcus. The entoplastron is wider than long and has a curved posterior border. The gular scales cover the anterior part of the entoplastron and are shorter medially than the humerals. The angle formed by the gularo-humeral sulcus is obtuse. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally concave. The pectoral scale is medially short, and the inguinal scale broadly contacts the femoral. The anal notch is shallow and angular. The anal scales are shorter medially than the femorals, and a femoral-anal notch is present in the lateral border of the xiphiplastron.

AMNH FARB 11710 has growth annuli present on both the carapace and plastron. Pleural 1 does not contact the nuchal, the anterior margin of the vertebral 1 scale is wider than the posterior margin, and vertebral 1 is widely separated from marginal 2. The neural pattern is 4 (8) 4 (8) 4 (6 (6 (6. The costals are slightly cuneate, alternating wide and narrow ends distally. The cervical scale is also slightly wedge-shaped, and the costo-peripheral suture is unfused and coincides with the pleuro-marginal sulcus. The vertebrae are wider than long, wider even than the pleurals. The gular regions of the epiplastra protrude slightly due to constriction at the gularo-humeral sulcus and are rounded along the apices with a moderate anterolateral

protuberance. The entoplastron is pyriform and slightly wider than long. The gular scales cover the anterior portion of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle medially. The HPS is positioned behind the entoplastron, is medially straight and perpendicular to the midline, and laterally concave. The medial part of the pectoral scale is very short, and the large inguinal scale contacts the femoral broadly. The medial length of the anal scales is shorter than that of the femorals, and the anal notch is shallow and angular. The xiphiplastron is wider than long and has a distinct femoral-anal notch in the lateral border.

AMNH FARB 11999 also has growth annuli visible on the bone surfaces. The nuchal is notably wider than long and is contacted but not overlapped by pleural 1. The costo-peripheral suture coincides with the pleuro-marginal sulcus. The neurals are fully differentiated, with pattern 4 (8) 4 (8) 4 (6) (6) (6). The suprapyrgals are not preserved. The rib heads are thin and emerge from the slightly cuneate costals close to the neural-costal suture. The cervical scale is rectangular, and the vertebral scales are wider than the pleurals. Vertebral 1 is narrower than vertebral 2, does not contact the peripherals, and is widely separated from marginal 2. The epiplastra have moderate posterior excavations and short but well-developed gular protrusions with rounded apices. The entoplastron is longer than wide and has a rounded posterior border. The gulars cover the anterior area of the entoplastron and are medially roughly equal in length to the humerals, and the gularo-humeral sulcus forms an obtuse angle. The HPS coincides medially with the most posterior contact between the entoplastron and hyoplastra, is medially straight and perpendicular to the axial plane, and laterally concave. The pectoral scale is medially very short, and the large inguinal scale forms a broad contact with the femoral. The anal notch is shallow and angular. The femoral scales are medially longer than the anals, and the lateral border of the xiphiplastron has a femoral-anal notch.

AMNH FARB 11500 (**Fig. 10**) has growth annuli on the bone surfaces. Pleural 1 does not contact the nuchal, and the posterior border of vertebral 1 is much narrower than the anterior border. Suprapygal 1 embraces the lenticular suprapygal 2, the costals are strongly cuneate, and the neural pattern is 4 (8) 4 (8) 4 (6) (6) (6). The vertebral scales are wider than the pleurals and have arcuate borders. The epiplastra expand just beyond the anterior border of the carapace, their short but well-developed gular protrusions having rounded apices. The entoplastron is longer than wide and somewhat pyriform. The gulars cover the anterior portion of the entoplastron and are medially shorter than the humerals, and the gularo-humeral sulcus forms an obtuse angle. The HPS crosses posterior to the entoplastron, is medially straight and perpendicular to the midline, and laterally concave. The medial part of the pectoral scale is short, and the large inguinal scale broadly contacts the femoral. The anal scales are medially shorter than the femorals, the anal notch is shallow and angular, and a femoral-anal notch is present in the lateral border of the xiphiplastron.

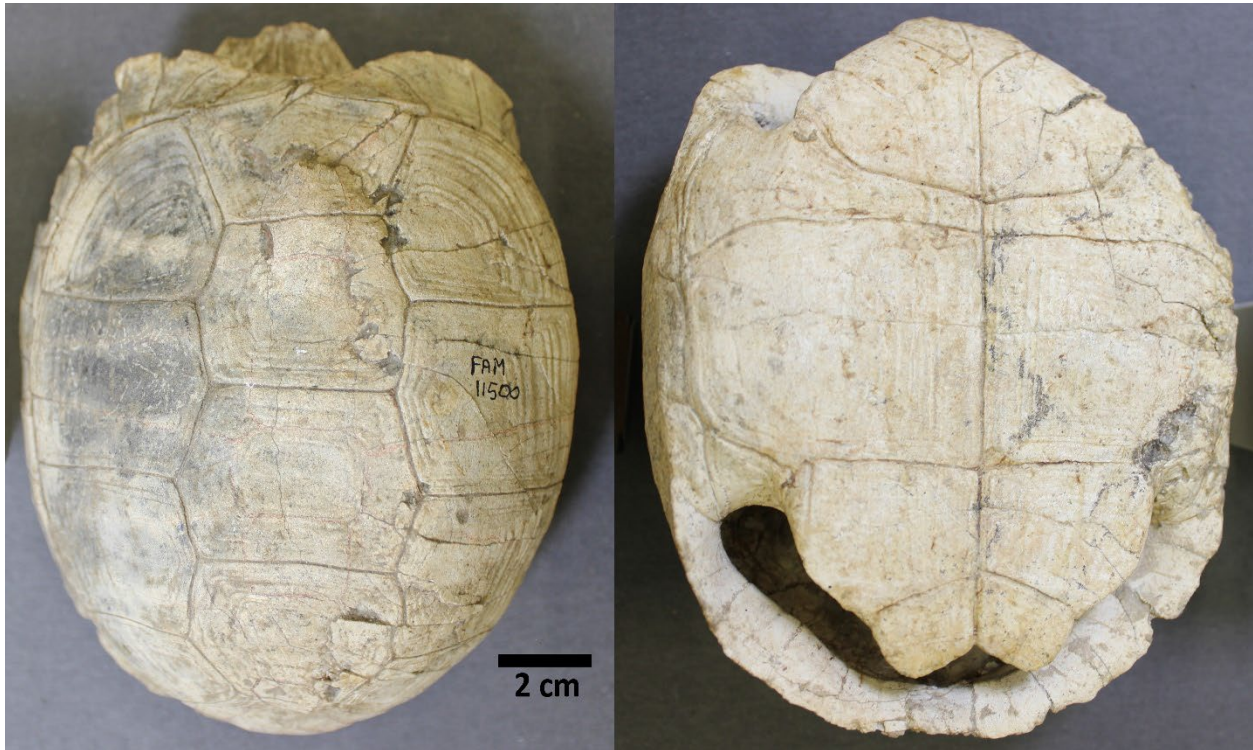


Figure 10: AMNH FARB 11500, a juvenile *Hesperotestudo osborniana* from the Late Hemingfordian of Nebraska, USA.

The nuchal of AMNH FARB 12480 is not contacted by pleural 1, and the posterior margin of vertebral 1 is narrower than the anterior margin. Only the first pair of neurals are preserved. Neural 1 is hexagonal with the short sides positioned posteriorly, and neural 2 is octagonal. The cervical scale is rectangular and longer than wide. The epiplastra have moderate posterior epiplastral excavations and short but well-developed gular protrusions with rounded margins. The entoplastron is wider than long and the anterior portion is covered by the gular scales. The medial length of the humeral scales is longer than that of the gulars, and the angle formed by the gularo-humeral sulcus is obtuse. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally concave. The pectoral scales are very short medially, and the large inguinal scale contacts the femoral.

AMNH FARB 14347 has a nuchal that is about 1/3 wider than it is long and is not contacted by pleural 1. The neural series is 4 (8) 4 (8) 4 (6) 6 (6), and two suprapygals are present, with the first embracing the lenticular second. The thin rib heads emerge from the strongly cuneate costals close to the neural-costal suture. The rectangular cervical scale is long and thin, covering approximately 30% of the overall length of the nuchal. There is close coincidence between the pleuro-marginal sulcus and the costo-peripheral suture, and the vertebral scales are wider than long. Vertebral 1 is wider than vertebral 2, is widely separated from marginal 2, and the posterior margin of vertebral 1 is markedly narrower than the anterior margin. The posterior epiplastral excavation is of moderate depth, and there is no constriction in the gularo-humeral sulcus along the lateral borders of the epiplastra. The gular scales are

marginally longer medially than the humerals, and the gularo-humeral sulcus forms a very slightly acute angle. The anterior area of the entoplastron is covered by the gulars, and the entoplastron is wider than long. The HPS is positioned immediately posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally concave. The pectoral scale is very short medially. The anal scales are medially shorter than the femorals, and the anal notch is shallow and angular. The xiphiplastron is wider than long and has only a very shallow indentation in the lateral border where the femoral-anal sulcus crosses.

AMNH FARB 12550 has a highly domed carapace with growth annuli visible on the lower portions of the costals. There is close coincidence between the costo-peripheral suture and the pleuro-marginal sulcus, and pleural 1 does not contact the nuchal. There is a slightly raised boss at the nuchal-neural 1 junction, and the posterior pair of neurals and both suprapyrgals are missing, giving a neural pattern of 4 (8) 4 (8) 4 (6 X X, though neural 7 is likely hexagonal. The thin rib heads emerge from the slightly cuneate costals close to the neural-costal suture. The cervical scale is rectangular and longer than wide. The vertebral scales are wider than long and have arcuate borders. Vertebral 1 is wider than vertebral 2 and is widely separated from marginal scale 2. The posterior epiplastral excavation is of moderate depth. The epiplastra have short gular protrusions with rounded margins, and a small protuberance is present on the anterolateral edges of the epiplastra about midway between the gularo-humeral sulcus and the midline suture. The entoplastron is wider than long and its anterior area is covered by the gulars. The median length of the humerals is greater than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS crosses posterior to the entoplastron, is medially straight forming such a wide angle as to be nearly perpendicular to the axial plane, and laterally concave. The pectoral scale is very short medially, and the inguinal scale forms a broad contact with the femoral. The femoral-anal sulcus is straight and nearly perpendicular to the midline, creating a femoral-anal notch where it crosses the lateral border of the xiphiplastron. The medial length of the anal scales is shorter than that of the femorals, and the anal notch is angular and quite shallow.

AMNH FARB 12514 has a highly domed carapace with growth annuli visible. Pleural 1 does not contact the nuchal, and the posterior margin of vertebral 1 is narrower than the anterior margin. The suprapyrgals and neurals 7 and 8 are missing, giving a visible neural pattern of 4 (8) 4 (8) 4 (6 X X, where neural 7 is likely hexagonal. The costals are slightly cuneate, and the pleuro-marginal sulcus coincides with the costo-peripheral suture. The rectangular cervical scale is longer than wide and covers more than 26% of the length of the nuchal. The vertebrae are wider than long, and vertebral 1 is widely separated from marginal 2. The gular regions of the epiplastra expand slightly past the anterior border of the carapace and are rounded along the anterior margins, with a small anterolateral protuberance. The entoplastron is wider than long and its anterior area is covered by the gular scales. The gularo-humeral sulcus forms an obtuse angle. The HPS coincides medially with the posterior contact between the entoplastron and hyoplastra, and is both medially and laterally straight and perpendicular to the midline. The pectoral scale is very short medially, and the inguinal scale is large and forms a broad contact with the femoral.

UCMP 36646 is a large specimen with growth annuli visible on the bone surfaces. The vertebrals are wider than long, the anterior border of vertebral 1 is markedly wider than the posterior border, and the neural pattern is 4 (8) 4 (8) 4 (6 (6 (6. The costals are slightly cuneate, and the costo-peripheral suture coincides with the pleuro-marginal sulcus. The rectangular cervical scale is long and thin, taking up approximately 35% of the overall length of the nuchal. The HPS is medially straight and perpendicular to the midline, and laterally concave. The anal notch is shallow and angular.

Hesperotestudo turgida (Cope, 1892a)

Synonymy. *Testudo turgida* Cope, 1892a; *Testudo incisa* Hay, 1916a; *Testudo riggsi* Hibbard, 1944; *Testudo wilsoni* Milstead, 1956; *Geochelone johnstoni* Auffenberg, 1962b; *Geochelone allenii* Auffenberg, 1966; *Geochelone mlynarskii* Auffenberg, 1988.

Type material. ANSP 14689

Type locality. Espuella, Dickens County, Texas, Blacan (Hemphillian to Pleistocene).

Referred material. Nebraska, Ash Hollow Formation, Middle to Late Clarendonian: Brown County – AMNH FARB Plum Creek, AMNH FARB 12505, a carapace and plastron.

Diagnosis. *Hesperotestudo turgida* can be identified as belonging to *Hesperotestudo* based on the suite of characters provided above for that genus. *H. turgida* can be distinguished by the following suite of characters: shell bones thickened relative to other *Hesperotestudo* (Vlachos, 2018); carapace more highly domed and shell size smaller on average (22-25 cm) than in other *Hesperotestudo* (Oelrich, 1957); presence of ventral keels on the epiplastra; epiplastra with substantial gular protrusions, expanding beyond the anterior edge of the carapace; presence of a caudal buckler that is disproportionately large relative to other *Hesperotestudo* (Vlachos, 2018).

Discussion. AMNH FARB 12505 (**Fig. 11**) is small for a *Hesperotestudo*, measuring roughly 20.5 cm in carapace length and 21.5 cm in plastron length. The costo-peripheral suture coincides with the pleuro-marginal sulcus, and is fully closed, indicating that the specimen is of a mature individual. The shell bones are somewhat thickened, the carapace is highly arched, and growth annuli are present on the bone surfaces. Pleural 1 is not in contact with the nuchal, and the neural pattern is 4 (8) 4 (8) 4 (6 (6 (6. The costals are slightly cuneate, and two suprapyrgals are present, the first embracing the lenticular second. The cervical scale is also cuneate, and the vertebral scales are wider than the pleurals. Vertebral 1 is narrower than vertebral 2 and is widely separated from marginal 2. The epiplastra extend beyond the anterior edge of the carapace and are bifurcate, with well-developed gular protrusions created by constriction in the gularo-humeral sulcus. The protrusions are thickened, somewhat conical in shape, and have rounded apices. Ventral keels are present on the epiplastra, extending from the anterolateral edge of the gular protrusions to the midline on the anterior surface of the entoplastron, just anterior to the gularo-humeral sulcus. The entoplastron is wider than long.

The gular scales cover the anterior part of the entoplastron, and the gularo-humeral sulcus medially forms an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally concave. The pectoral scale is very short medially, and the inguinal scale is large and broadly contacts the



Figure 11: Carapace and plastron of AMNH FARB 12505, an adult *Hesperotestudo turgida* from the Clarendonian of Nebraska, USA.

femoral. The medial length of the femoral scales is much greater than that of the anals, and the anal notch is wide and angular. The xiphiplastron is wider than long and has a well-developed femoral-anal notch in the lateral border.

This specimen is very close to the 22-25 cm range for *H. turgida* mentioned by Oelrich (1957) and is not a juvenile. Interestingly, this locality is within 40 miles of Valentine, Neb. and quite far from the type locality for *H. turgida*, some 696 miles to the south in Dickens County, TX.

Hesperotestudo sp.

Referred material. Kansas, Clarendonian: Decatur County – AMNH FARB Decatur Co., Kans., AMNH FARB 12929, a partial shell; Ogallala Formation, Clarendonian: Phillips County – AMNH FARB Loup Fork, AMNH FARB 4903, a left xiphiplastron with part of the left hypoplastron, and miscellaneous shell fragments; Nebraska, Ash Hollow Formation, Late Clarendonian: Cherry County – AMNH FARB Gallup Gulch Quarry, AMNH FARB 12492, a partial

carapace; Ash Hollow Formation, Merrit Reservoir Member, Late Clarendonian: Cherry County – AMNH FARB Wade Quarry, AMNH FARB 12515, fragments of a carapace and plastron, including most of both hyoplastra and the posterior 2/3 of the entoplastron; Ash Hollow Formation, Clarendonian: Brown County – AMNH FARB Channel Deposits, Pratt Place, AMNH FARB 12510, the partial carapace and complete plastron of a juvenile; Cherry County – AMNH FARB Gallup Gulch Quarry, AMNH FARB 8881, the anterior half of a plastron; UCMP V3325, UCMP 36521, shell fragments including a partial nuchal, right 1st costal, half of an octagonal neural, both hyoplastra, a partial left hypoplastron, and a right xiphiplastron; Keya Paha County – AMNH FARB Murphy's Gulch, AMNH FARB 23065, a carapace; Valentine Formation, Clarendonian: Cherry County – UCMP V3312, UCMP 36642, a partial carapace; UCMP 36643, a partial carapace; UCMP 36644, the anterior half of a plastron; Sheridan County – AMNH FARB "Niobrara River", Sec. 21, T. 29N., R. 46W., AMNH FARB 12484, a carapace; Upper Valentine Formation, Burge Member, Early Clarendonian: Brown County – AMNH FARB June Quarry, AMNH FARB 11320, a nuchal and the anterior half of a plastron; Sheep Creek Formation, Late Hemingfordian: Sioux County – AMNH FARB Greenside Quarry, AMNH FARB 11588, the carapace, plastron, scapula, coracoids, ilium, pubes and ischium of a juvenile; AMNH FARB 11593, a plastron and fragmentary carapace; AMNH FARB 11997, an anterior plastral fragment including both epiplastra and the anterior part of an entoplastron; AMNH FARB Long Quarry, AMNH FARB 11707, a plastron; AMNH FARB 11995, the anterior half of a plastron; AMNH FARB 11996, the posterior 2/3 of a plastron; Hemingfordian: Sioux County – AMNH FARB Stonehouse Draw, AMNH FARB 6293, a plastron and fragmentary carapace; AMNH FARB 6808, a plastron and fragmentary carapace; Lower Sheep Creek Formation, Late Hemingfordian: Sioux County – AMNH FARB Greenside Quarry, AMNH FARB 11599, a plastron and partial carapace; AMNH FARB 11600, carapace and plastron fragments including both epiplastra and a right hyoplastron; AMNH FARB Long Quarry, AMNH FARB 11596, the anterior half of a plastron; Box Butte Formation, Red Valley Member, Middle Hemingfordian: Box Butte County – AMNH FARB Dry Creek Pros. A, AMNH FARB 11325, the anterior 2/3 of a plastron; AMNH FARB Dry Creek Pros. D, AMNH FARB 12769, plastron fragments including a right hyoplastron and right xiphiplastron; AMNH FARB Foley Quarry, AMNH FARB 11326, a partial left hyoplastron; ~ Runningwater Formation, Early Hemingfordian: Cherry County – AMNH FARB 2 mi. W. of Pole Creek Loc., AMNH FARB 11368, a partial plastron.

Discussion. The above specimens are distinguishable to the genus *Hesperotestudo*, but lack sufficient morphological information to enable further identification.

Genus *Stylemys* Leidy 1851a

Type species. *S. nebrascensis*, Leidy 1851

Diagnosis. Members of *Stylemys* can be diagnosed as belonging to Testudinidae based on the suite of characters provided for that clade above. *Stylemys* share the following suite of characters that help to distinguish them from other testudinids: cervical scale is longer than wide (Hutchison, 1996); poorly differentiated to undifferentiated neural series, with pattern 4 (6/8 (6/4 (6 (6 (6 (6 (6 (6 (Vlachos, 2018); costals are not strongly wedge-shaped (Hutchison, 1996); no posterior epiplastral excavation; humero-pectoral sulcus that is medially straight and anterolaterally convex (Vlachos, 2018); inguinal scale relatively small, not contacting the femoral (Hutchison, 1996).

Discussion. *Stylemys* is perhaps the most common genus of fossil tortoise found in museum collections throughout North America; vast numbers of them are preserved in Oligocene deposits of the Great Plains region. The genus was created by Leidy while describing the type species and derives its name from his misinterpretation of the plastral buttresses as separate stylus-shaped bones. In the period from 1851–1852, Leidy described several tortoise taxa from the same region of the Nebraska Territory (present-day South Dakota). Hay (1908) synonymized many of these under the type species. The most recent revision of *Stylemys* was by Auffenberg (1964a), from which much of my current diagnosis is derived.

Stylemys capax (Hay, 1908)

Synonymy. *Stylemys conspecta* Hay, 1908.

Type material. AMNH 1357

Type locality. Near junction of North and South Forks of John Day River, Grant County, Oregon, Arikareean-2.

Referred material. No referred specimens.

Diagnosis. *Stylemys capax* can be diagnosed as belonging to *Stylemys* based on the suite of characters for that genus provided above. *S. capax* may be distinguished from other members of the genus by the following suite of characters: presence of an octagonal neural II; vertebral I and the pleural I pair overlap the peripherals; femoral scales medially longer than the anals (Vlachos, 2018).

Discussion. *S. capax* is only known from the John Day Fossil Beds in Oregon, USA.

The octagonal neural II (and rectangular neural III) are also characteristic of *Emys/Testudo culbertsonii* which was included within *S. nebrascensis* by Hay (1908) and upheld by Vlachos (2018). If the octagonal second neural is not distinctive to *S. capax*, then the species' identity hinges morphologically on the femoral/anal length difference and the overlap of the peripherals by the first neural and first pleurals; and on the spatial distinction of being the only known member of the genus from the Pacific Northwest of the USA.

Stylemys inusitata (Hay, 1906b)

Synonymy. *Testudo inusitata* Hay, 1906b; *Gopherus copei*/*Stylemys copei*/*Testudo copei* Koerner, 1940; *Gopherus inusitata* Williams, 1950b; *Geochelone* (*Hesperotestudo*) *inusitata* Auffenberg, 1974.

Type material. CM 311 (see Hay, 1908 pl. 68)

Type locality. Canyon Ferry Reservoir, Broadwater County, Montana, Hemingfordian.

Referred material. No referred specimens.

Diagnosis. *Stylemys inusitata* can be diagnosed as belonging to *Stylemys* based on the suite of characters for that genus provided above. *S. inusitata* can be distinguished from other *Stylemys* by the following suite of characters: epiplastral lip is more prominent than that found in *S. nebrascensis* (Vlachos, 2018); gulars are short and do not overlap the entoplastron (Hay, 1908; Vlachos, 2018); neural pattern of 4 (6 (6 (6 (6 (6 (6 (Hay, 1906b; Vlachos, 2018).

Discussion. In terms of shell morphology, *S. inusitata* differs from other members of the genus primarily in the length of the gular scales. In his description of the type specimen, Hay (1906b) states that “The gular scutes extend backward on the entoplastron”, but in 1908 he amended this to “barely reaching the entoplastron”. In the type specimen, the gulars contact but do not overlap the anterior border of the entoplastron. *S. inusitata* differs specifically from *S. capax* in having a hexagonal (rather than octagonal) second neural.

Although no specimens in the current study are referred to either *S. inusitata* or *S. capax*, both taxa are included here as a point of reference.

Stylemys nebrascensis (Leidy, 1851a; Leidy 1853, pl. 19 fig. 1))

Synonymy. *Emys hemispherica* Leidy, 1851b; *Emys oweni* Leidy, 1851c; *Testudo lata* Leidy, 1851b; *Emys culbertsonii* Leidy, 1852a; *Testudo culbertsonii* Leidy, 1852a; *Geochelone* (*Caudochelys*) *ligonia* Cope, 1873a; *Testudo amphithorax* Cope, 1873a; *Testudo ligonia* Cope, 1873a; *Testudo ligonius* Cope, 1873a; *Testudo emiliae* Hay, 1908; *Gopherus neglectus* Brattstrom, 1961; *Stylemys neglectus* Brattstrom, 1961.

Type material. USNM 97, the incomplete shell of a juvenile

Type locality. White River Badlands, South Dakota, Orellan (Orellan to Arikareean 2)

Referred material. Colorado, White River Formation, Orellan: Logan County – UCMP V72243, UCMP 223091, carapace and plastron fragments including parts of neurals 1-6, the right epiplastron and ¼ of the entoplastron, both xiphiplastra, and the hindmost parts of both hypoplastra; Weld County – AMNH FARB Head of Horsetail Creek, AMNH FARB 1139 (referred

material of *Styemys amphithorax* of Hutchison 1996)(Hay, 1908, p. 408), the anterior half of a plastron and fragments of a carapace including the nuchal; UCMP V3743, UCMP 36601, the partial carapace and plastron of a juvenile; UCMP V70106, UCMP 86314, a carapace and plastron, several cervical vertebrae, and the left half of a mandible; UCMP V71042, UCMP 95648 (referred material of Hutchison 1996), a carapace and plastron; Nebraska, White River Group, Brule Formation, Orella Member, Orellan: Dawes County – AMNH FARB H.C. Morris Ranch, AMNH FARB 12546, the partial carapace and plastron of a juvenile; White River Group, Brule Formation, Orellan: Dawes County – AMNH FARB 8 mi. N. of Crawford, AMNH FARB 3270, the carapace and plastron of a juvenile; AMNH FARB 6077, a carapace and plastron; AMNH FARB 6082, a carapace and plastron; Sioux County – AMNH FARB Schnurr Butte, AMNH FARB 8886, a carapace and the right half of a plastron; RAM V94157, RAM 7682, a carapace and plastron; RAM V94158, RAM 7683, a carapace and plastron; RAM V96229, RAM 16177, the carapace and plastron of a juvenile; RAM V96230, RAM 16187, a partial carapace and plastron; RAM V96226, RAM 16188, a carapace and plastron; UCMP RV5704, UCMP 314263, a carapace and plastron; USNM 10 mi. N. of Harrison, USNM 15609, the carapace and plastron of a juvenile; USNM 15871, the carapace and plastron of a juvenile; USNM 15872, the carapace and plastron of a juvenile; USNM 7 mi. N.E. of Harrison, USNM 15657, the carapace and plastron of a juvenile; USNM 15868, a carapace and plastron; USNM Munson Ranch, USNM 442573, a carapace and plastron; USNM 442647, a carapace and plastron; South Dakota, White River Group, Brule Formation, Orellan – AMNH FARB Cheyenne River, AMNH FARB 700, a carapace and plastron; RAM V96233, RAM 27150, the carapace and plastron of a juvenile; RAM V96233, RAM 27151, the carapace and plastron of a juvenile; USNM 94, a plastron and partial carapace (Leidy, 1854, p.104, pl. XIX); USNM 98, a carapace and plastron, (holotype of *Emys hemispherica* Leidy 1851, p173; Leidy, 1854, pl. XX); USNM 6671, a carapace and plastron; Pennington County – AMNH FARB Saddle Horse Pass, AMNH FARB 12410, the carapace and plastron of a juvenile; NHMLA LACM 5542, LACM 127917, a carapace and plastron; UCMP V80035, UCMP 124374 (referred material of Hutchison 1996), a carapace and the anterior ½ of a plastron; UCMP 299041, a carapace and plastron; UCMP 299042, a carapace and plastron; UCMP 299045, the anterior 2/3 of the carapace and plastron of a juvenile; UCMP RV3702, UCMP 314262, the carapace and plastron of a juvenile; Washington County – USNM Badlands of White River, USNM 102, a carapace and plastron; USNM 5261, a carapace and plastron; USNM 4 mi. S.E. of Scenic, USNM 15962, the carapace and plastron of a juvenile; Wyoming, Orellan: Converse County – AMNH FARB Reno Ranch East area, AMNH FARB 12401, carapace and plastron; AMNH FARB 12403, the partial carapace and plastron of a juvenile; AMNH FARB Reno Ranch S. of Tower, AMNH FARB 12405, the carapace and plastron of a juvenile; White River Group, Orellan – RAM V96215, RAM 8322, a plastron and the posterior ½ of a carapace; RAM 8324, the plastron and fragmentary carapace of a juvenile; Platte County – AMNH FARB E. of Laramie Peak, AMNH FARB 1163, a plastron and partial fragmentary carapace; White River Group, Brule Formation, Orellan: Niobrara County – USNM West side of Little Indian Creek, USNM 15859, a carapace and plastron; USNM South side of Indian Creek, USNM 15867, a carapace and

plastron; USNM Young Woman Creek, USNM 15869, a carapace and plastron; USNM 3 mi. E. of Walker Ranch, USNM 357944, a carapace and plastron; USNM 1 mi. N.W. Whitman P.O., USNM 357950, a carapace and plastron; USNM 357957, a carapace and plastron; USNM 1 mi. N. Whitman P.O., USNM 357962, a carapace and fragmentary plastron; USNM About 1.5 mi. East Walker Ranch House, USNM 357955, a carapace and plastron; USNM N. side Indian Creek about 3 mi. N.W. Walker Ranch, USNM 357958, a carapace and plastron; USNM 357961, the plastron and endocast of the carapace of a juvenile; Brule Formation, Orellan: Converse County – NHMLA Southeast of Douglas, LACM CIT 1451, the carapace and plastron of a juvenile; LACM CIT 1522, the carapace and partial plastron of a juvenile; LACM CIT 1661, the posterior 2/3 of the carapace and anterior 2/3 of the plastron of a juvenile; LACM 4890, the plastron and endocast of a hatchling; Niobrara County – RAM V96237, RAM 8316, a carapace and plastron; UCMP V7090, UCMP 86300, the plastron and anterior ½ of the carapace of a juvenile; Above Chadron Formation, Orellan/Whitneyan: Goshen County – AMNH FARB Nr. Horse Cr. N. of Hat Crk. Basin, AMNH FARB 7194, the carapace and plastron of a juvenile; Wyoming, Nebraska, South Dakota, White River Group, Orellan: RAM V96215, RAM 12520, the carapace and plastron of a juvenile; RAM 12521, the partial carapace and plastron of a juvenile; RAM 12523, the plastron and partial carapace of a juvenile; RAM 12526, the right side of the carapace and plastron of a juvenile; RAM 12529, the carapace and plastron of a juvenile; RAM 12530, a carapace and partial plastron; RAM 12534, the carapace and plastron of a juvenile; RAM 12535, a carapace and plastron; RAM 12546, a carapace; RAM 12549, a carapace and plastron; RAM 16551, the carapace and plastron of a juvenile; RAM 17841, a carapace and plastron with encased skull and humeri.

Diagnosis. *Stylemys nebrascensis* can be identified as belonging to *Stylemys* based on the suite of characters provided above for that genus. *S. nebrascensis* can be distinguished by the following suite of characters: cervical scale relatively short and broad (Hutchison, 1996); usually undifferentiated neural series with pattern 4 (6 (6 (6 (6 (6 (6 (6 (6; lip of epiplastron not strongly developed (Vlachos, 2018); posterior epiplastral excavation either very shallow or fully absent (Auffenberg, 1964a; Vlachos, 2018); humero-pectoral sulcus that is medially straight and anterolaterally convex; humero-pectoral sulcus located posterior to the entoplastron; gulars covering the anterior part of the entoplastron; vertebral I and pleural I scales do not intrude onto the peripherals (Vlachos, 2018); presence of a weak lateral notch on the xiphiplastron (Hutchison, 1996); anal scales medially as long as or longer than the femorals (Hay, 1908).

Discussion. USNM 97 (Holotype) (**Fig. 12**) is missing the nuchal, the anterior and posterior peripherals, part of the carapace posterior to the midline of the suprapygal, the anterior plastral lobe, and the posterior half of both xiphiplastrs. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6 and the costals are strongly cuneate. The costo-peripheral suture appears to coincide with the pleuro-marginal sulcus based on the morphology visible along the left peripherals 3-8, and is unfused, indicating that the specimen is of a juvenile. The vertebrae are wider than long, and the posterior margin of vertebral 1 seems to have been substantially narrower than the

anterior margin. The HPS coincides medially with the posterior border of the entoplastron, is medially straight and perpendicular to the axial plane, and laterally convex. It is notable that the lateral portion of the HPS is somewhat indistinct and old pencil marks on the left side mark a straight path for the lateral portion while simultaneously obscuring any underlying morphology that could confirm this course. The inguinal scale is small and does not contact the femoral.



Figure 12: The carapace and plastron of USNM 97, holotype of *S. nebrascensis*.

The neural fragments present in UCMP 223091 indicate the presence of at least two individuals of similar size. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6. The costals are moderately cuneate, and the thin rib heads emerge close to the neural-costal suture. The cervical scale is rectangular, and the vertebrals are wider than long and have arcuate borders. The epiplastron lacks a gular protrusion and has a very shallow posterior excavation. The gulars cover the anterior part of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The anal scales are longer medially than the femorals, and the anal notch is angular and quite shallow.

AMNH FARB 1139 is listed as one of two type specimens for *Testudo amphithorax* Cope, 1873a. This large, but fragmentary, specimen was figured in Hay, 1908 (pp. 407-410, figs. 526-530). Pleural 1 does not contact the nuchal, the costals are slightly cuneate, and there is close coincidence between the pleuro-marginal sulcus and the costo-peripheral suture. The rectangular cervical scale is longer than wide, and vertebral 1 is widely separated from marginal 2. Two suprapygals are present, with the first embracing the lenticular second, and the

marginal scale 12 pair are fused in posterior view. The posterior epiplastral excavation is shallow, and the gulars cover the anterior portion of the entoplastron. The gularo-humeral sulcus forms an obtuse angle. The HPS is coincides with the posterior entoplastral-hyoplastral contact, is medially straight and perpendicular to the midline, and laterally convex.

UCMP 36601 is a juvenile and missing the posterior part of the carapace, including neurals 7-8 and the suprapyrgals. The visible neural pattern is 4 (6 (6 (6 (6 X X. The costals are mildly cuneate, and the pleuro-marginal sulcus coincides with the unfused costo-peripheral suture. The vertebrals are wider than long, with arcuate borders. The entoplastron is longer than wide, and the anterior portion is covered by the gulars. The gularo-humeral sulcus forms an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, forms a wide, shallow curvature medially, and is laterally convex.

UCMP 86314 is a fossil of a mature individual. The neural pattern is an unusual 4 (6 (6 (6 (6 (8) 4 (6, and the left side of neural 2 is malformed into what would be expected for an octagonal neural. The costo-peripheral suture coincides with the pleuro-marginal sulcus and there are two suprapyrgals, with the lenticular second being cradled by the first. The cervical scale is rectangular, the vertebrals are wider than long, and vertebral 1 is slightly wider than vertebral 2.

UCMP 95648 was previously referred to *S. nebrascensis* by Hutchison (1996, p. 347). The specimen has growth annuli visible on the bone surfaces. Pleural 1 does not contact the nuchal, and the anterior border of vertebral 1 is much wider than the posterior border. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and the costals are slightly cuneate. Two suprapyrgals are present, with the lenticular second being cradled anteriorly by the first. The costo-peripheral suture coincides with the pleuro-marginal sulcus and is unfused, indicating that the individual was a juvenile. The cervical scale is longer than wide, and cuneate. The vertebral scales are wider than long and have arcuate borders. Vertebral 1 is wider than vertebral 2 and is widely separated from marginal 2. The entoplastron is wider than long, and the anterior part is covered by the gulars. The medial length of the humerals is greater than that of the gulars, and the gularo-humeral sulcus forms a slightly acute angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale is relatively small and does not contact the femoral. The anal notch is angular. A femoral-anal notch is present in the lateral border of the xiphiplastron, and the posterior apices of the xiphiplastron are slightly serrate.

AMNH FARB 12546 is a small specimen, 80 mm in length and 62 mm in width, and has growth annuli on the carapacial surfaces. The neural series is 4 (6 (6 (6 (6 (6 (6 (6, and the costals are slightly cuneate. The suprapyrgals are missing. The vertebral scales are wider than long and have arcuate borders. A small conical protuberance is present on the anterolateral border of each epiplastron. The gularo-humeral sulcus forms an obtuse angle, and the gulars cover the anterior portion of the entoplastron. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex.

AMNH FARB 3270 has a nuchal that is wider than long and not in contact with pleural 1. The anterior border of vertebral 1 is markedly wider than the posterior margin. The neural sequence is 4 (6 (6 (6 (6 (6 (6 (6, and the costals are slightly cuneate. The costo-peripheral suture is not yet fully fused and coincides with the pleuro-marginal sulcus. The cervical scale is rectangular and longer than wide. The vertebral scales are wider than long and have arcuate borders. Vertebral 1 is wider than vertebral 2 and widely separated from marginal 2. The entoplastron is longer than wide, and the anteriormost part is covered by the gulars. The medial length of the humeral scales is longer than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The medial portion of the HPS coincides with the posterior point of contact between the entoplastron and hyoplastron and is roughly straight and perpendicular to the midline, while the lateral portion is convex. The inguinal scale is relatively small and does not contact the femoral. The anal scales are medially equal in length to the femorals, and the anal notch is shallow and angular.

The carapace of AMNH FARB 6077 is quite fragmented and the details are heavily obscured by sediment. The first neural is rectangular and the second is hexagonal with the short sides positioned anterolaterally, but the remaining neurals are indistinct. The costals are slightly cuneate and there appears to be coincidence between the pleuro-marginal sulcus and the seemingly unfused costo-peripheral suture. The entoplastron is longer than wide, and the anterior part is covered by the gulars. The medial length of the humerals is greater than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale does not contact the femoral, and the femorals are medially longer than the anal scales. The anal notch is angular.

AMNH FARB 6082 has a relatively low-domed carapace with growth annuli visible on the surface. The anterior border of vertebral 1 is markedly wider than the posterior border, and pleural 1 does not contact the nuchal. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and suprapygal 1 embraces the lenticular suprapygal 2. The costals are slightly cuneate, and the unfused costo-peripheral suture is aligned with the pleuro-marginal sulcus. The cervical scale is longer than wide and rectangular, though with a somewhat ovoid bowing to the lateral margins that is reminiscent of the state often seen in *Oligopherus*. Vertebral 1 is wider than vertebral 2 and widely separated from marginal 2. The vertebrals have arcuate borders and are wider than long, excepting the unusually elongated vertebral 3. The vertebral 3-4 sulcus crosses neural 6 in this specimen, rather than neural 5. The plastron is poorly preserved, with details of the anterior and posterior parts being obscured. The HPS is located posterior to the entoplastron, is medially straight and perpendicular to the midline, and laterally convex. The inguinal scale is small and not in contact with the femoral. The anal notch is shallow and angular.

The details of the carapace of AMNH FARB 8886 are heavily obscured by sediment and the portion anterior to neural 2 is missing, including the nuchal and neural 1. The neural pattern is X (6 (6 (6 (6 (6 (6 (6. There appear to have been two suprapygals, as the shape of the first indicates that it would have cradled a lenticular second that is no longer present. The costals are slightly cuneate, and the vertebral scales are wider than long. The entoplastron is longer

than wide and the anteriormost part is covered by the gulars. The gulars are medially shorter than the humerals, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned just posterior to the entoplastron, medially perpendicular to the axial plane, and laterally convex. The inguinal scale is small and not in contact with the femoral. The medial length of the femorals is greater than that of the anal scales, and the anal notch is shallow and angular.

RAM 7682 has growth annuli visible on the bone surfaces. Pleural 1 does not contact the nuchal. Neural 1 is rectangular and neurals 2 and 3 are hexagonal, with the short sides positioned anterolaterally. The remainder of the neural sequence is indistinct. Suprapygals 1 and 2 embrace the lenticular suprapygals 3 and 4, and the costals are slightly cuneate. The unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The cervical scale is slightly cuneate and longer than wide. The vertebral scales are wider than the pleurals, and the anterior border of vertebral 1 is markedly wider than the posterior border. Vertebral 1 is wider than vertebral 2 and well-separated from marginal 2. The gulars cover the anterior part of the entoplastron. The HPS is positioned posterior to the entoplastron and is laterally convex. The anal notch is shallow and angular.

Pleural 1 of RAM 7683 does not contact the nuchal. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, and the costals are mildly cuneate. The cervical scale is rectangular and unusually long and thin for a *Stylemys*. The vertebrae are wider than the pleurals and have arcuate borders. Vertebral 1 is wider than vertebral 2, and the anterior border of vertebral 1 is markedly wider than the posterior border. A small protuberance is present on the anterolateral border of the epiplastron where the gularo-humeral sulcus crosses. The entoplastron is wider than long and the anterior portion of it is covered by the gular scales. The medial length of the humerals is greater than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially straight and perpendicular to the midline, and laterally convex. The inguinal scale is relatively small and does not contact the femoral. The anal scales are medially longer than the femorals, and the anal notch is reduced and angular.

RAM 16177 is a hatchling shell measuring 63 mm in length and 57 mm in width. The carapace posterior to neural 7 is missing. The visible neural pattern is 4 (6 (6 (6 (6 (6 (6 X, and the cervical scale is cuneate. The vertebral scales are wider than the pleurals, and vertebral 2 is wider than vertebral 1. The gulars overlap the anterior part of the entoplastron, and the entoplastron is longer than wide. The medial length of the humerals is roughly equal to that of the gulars, and the angle formed by the gularo-humeral sulcus is obtuse. The HPS forms a wide angle medially, is relatively straight laterally, and appears to coincide medially with the posterior ento-hyoplastral contact. The inguinal scale does not contact the femoral, and the anal notch is reduced and angular.

RAM 16187 has a neural pattern of 4 (6 (6 (6 (6 (6 (6 (6 (6. The costals are slightly cuneate, and the first suprapygals 1 and 2 embrace the lenticular second. The nuchal is not contacted by pleural 1, and the cervical scale is rectangular. The anterior margin of vertebral 1 is markedly wider than the posterior margin. The posterior epiplastral excavation is shallow, and the inguinal scale

does not contact the femoral. The anal notch is angular. The xiphiplastron has a femoral-anal notch in the lateral border.

RAM 16188 has a nuchal that is wider than long and not contacted by pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and the costals are slightly cuneate. Two suprapygals are present, the first embraces the lenticular second. The costo-peripheral suture is unfused and aligned with the pleuro-marginal sulcus. The cervical scale is small and rectangular. Vertebral scale 1 is wider than vertebral 2, and the posterior margin of vertebral 1 is markedly narrower than the anterior margin. The vertebrae are wider than long, with arcuate borders. The gulars intrude onto the anterior portion of the entoplastron, and the entoplastron is longer than wide. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale does not contact the femoral.

UCMP 314263 has growth annuli present on the bone surfaces. Pleural 1 contacts, but does not overlap, the nuchal. The anterior margin of vertebral 1 is substantially wider than the posterior margin. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and there are two suprapygals, the first cradles the lenticular second. The costals are slightly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The pygal is roughly quadrangular and the anterior border is slightly concave. The cervical scale is rectangular and longer than wide. The vertebrae are wider than long, with arcuate borders. Vertebral 1 is wider than vertebral 2 and well-separated from marginal 2. The marginal 12 scales are fused in dorsal view. The epiplastron has a small protuberance on the anterolateral border just anterior to the crossing of the gularo-humeral sulcus. The gulars cover the anterior area of the entoplastron, and the entoplastron is wider than long. The humeral scales are medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The small inguinal scale does not contact the femoral, and the femoral scales are medially longer than the anals.

The first pleural scale of USNM 15609 does not contact the nuchal. The anterior margin of vertebral 1 is markedly wider than the posterior margin. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and neurals 3-7 are wider than long. The costals are strongly cuneate, and the pleuro-marginal sulcus coincides closely with the unfused costo-peripheral suture. Two suprapygals are present, with the first embracing the lenticular second. The cervical scale is rectangular and longer than wide. The vertebrae are wider than long, and vertebral 1 is widely separated from marginal 2. The gulars overlap the anterior region of the entoplastron, and the entoplastron is longer than wide. The humerals are medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex. The anal scales are medially longer than the femorals, and the anal notch is angular. The xiphiplastron is wider than long and has a lateral femoral-anal notch.

USNM 15871 is a small specimen, 73 mm long by 69 mm wide, and has growth annuli visible on the bone surfaces. The nuchal is wider than long and not in contact with pleural 1.

The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, and the suprapyrgals are missing. The costals are slightly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The cervical scale is cuneate and wider than long. The vertebrals are wider than long and have arcuate borders. The gulars cover the anterior part of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, nearly perpendicular to the axial plane medially, and slightly convex laterally.

USNM 15872 is a small specimen, 93 mm long by 85 mm wide. Growth annuli are visible on the bone surfaces. Pleural 1 does not contact the nuchal, and the neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6. The costals are slightly cuneate, and the unfused costo-peripheral suture is aligned with the pleuro-marginal sulcus. The vertebrals are wider than long, with arcuate borders. Vertebral 1 is well-separated from marginal 2 and wider than vertebral 2. The plastron is approximately equal in length to the carapace. The gulars cover the anterior area of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is located posterior to the entoplastron, is medially straight and perpendicular to the midline, and laterally convex. The inguinal scale is small and not in contact with the femoral. The anal notch is reduced and angular. The xiphiplastron is wider than long and has a femoral-anal notch in the lateral border.

The nuchal of USNM 15657 is not contacted by pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, and the lenticular suprapyrgal 2 is embraced by suprapyrgal 1. The costals are strongly cuneate, and there is close coincidence between the pleuro-marginal sulcus and the unfused costo-peripheral suture. The cervical scale is rectangular and longer than wide. The vertebral scales are wider than long and have arcuate borders. Vertebral 1 appears to contact but does not overlap peripheral 1 and is widely separated from marginal 2. The gular scales cover the anterior area of the entoplastron, and the entoplastron is longer than wide. The gularo-humeral sulcus forms a right angle, and the medial length of the humerals is greater than that of the gulars. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially wavy and largely perpendicular to the axial plane, and laterally convex. The inguinal scale is relatively small and not in contact with the femoral. The anal scales are medially longer than the femorals, and the anal notch is angular. The xiphiplastron is wider than long and has a shallow femoral-anal notch in the lateral border.

USNM 15868 has growth annuli visible on the carapace, and a nuchal that is untouched by pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, and two suprapyrgals are present, the first cradles the lenticular second. The costals are slightly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The cervical scale is cuneate and longer than wide. The vertebrals are wider than long and have arcuate borders. Vertebral 1 is wider than vertebral 2 and well-separated from marginal 2. The gular scales overlap the anterior portion of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex. The inguinal scale does not contact the femoral. The posterior borders of the xiphiplastron are too worn to be informative, though no femoral-anal notch is evident in the lateral borders.

USNM 442573 shows no contact between the nuchal and pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, and neurals 3-7 are wider than they are long. Two suprapygals are present, the lenticular second cradled anteriorly by the first. The costals are strongly cuneate, and the pleuro-marginal sulcus is closely aligned with the unfused costo-peripheral suture. The cervical scale is rectangular and longer than wide. The vertebrae are wider than long and have arcuate borders. Vertebral 1 is wider than vertebral 2, and its anterior border is markedly wider than its posterior border. The entoplastron is longer than wide. The gulars cover the anterior area of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially perpendicular to the axial plane, and laterally convex. The femoral-anal sulcus is slightly omega-shaped, and the anal notch is angular.

USNM 442647 has a neural pattern of 4 (6 (6 (6 (6 (6 (6 (6 (6, and neurals 3-7 are wider than long. The cervical scale is cuneate, and pleural 1 does not contact the nuchal. The costals are slightly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The vertebral scales are wider than long and have arcuate borders. The anterior margin of vertebral 1 is wider than the posterior margin, and vertebral 1 is wider than vertebral 2. The gulars cover the anterior part of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex. The inguinal scale is small and does not contact the femoral. The anal scales are medially longer than the femorals, and the anal notch is shallow and angular. The xiphiplastron is wider than it is long.

AMNH FARB 700 has growth annuli present on the bone surfaces. Pleural 1 does not contact the nuchal, and the posterior margin of vertebral 1 is notably narrower than the anterior margin. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, and two suprapygals are present, the first embraces the lenticular second. The cervical scale is rectangular, and the costals are slightly cuneate. The costo-peripheral suture is not yet fully fused and coincides with the pleuro-marginal sulcus. The vertebrae are wider than long and possess arcuate borders, and vertebral 1 is wider than vertebral 2. The entoplastron is longer than wide. The gulars cover the anterior area of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale is small and does not contact the femoral.

RAM 27150 is a very small shell, 83 mm wide by 89 mm long. Pleural 1 is well-separated from the edge of the nuchal, and the anterior margin of the vertebral 1 scale is wider than the posterior margin. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, and the costals are slightly cuneate. The pleuro-marginal sulcus coincides with the unfused costo-peripheral suture. The cervical scale is unusually large, rectangular, and wider than long. The marginal rim is broad in relation to the width of the nuchal. The vertebral scales are wider than the pleurals and have arcuate borders. Vertebral 1 is markedly wider than long, only slightly wider than vertebral 2, well-separated from marginal 2, and does not contact the peripherals. The entoplastron is ovoid and markedly longer than wide. The gulars cover the anterior portion of the entoplastron, the gularo-humeral sulcus forms an obtuse angle, and the medial antero-posterior length of the

humeral is longer than that of the gulars. The HPS is positioned immediately posterior to the entoplastron, medially perpendicular to the midline, and laterally convex. The inguinal scale is small and does not contact the femoral.

RAM 27151 is another small shell, 87 mm wide by 92 mm long, though the live length would have been greater because the portion posterior to neural 6 is missing. The carapace is highly domed and the costals are strongly cuneate. The proximal ends of the costal 6 pair indicate that the missing neural 7 was hexagonal, but no trace remains of neural 8 and the suprapyrgals. The visible neural pattern is 4 (6 (6 (6 (6 (6 X. The vertebral scales are wider than long and have arcuate borders. The costo-peripheral suture is unfused and coincides with the pleuro-marginal sulcus. The posterior and anterior apices of the plastron are missing. The entoplastron is longer than wide, and the anterior area is covered by the gulars. The HPS is located just posterior to the entoplastron, is nearly perpendicular to the midline medially, forming a very wide angle, and only slightly convex laterally. The inguinal scale is not in contact with the femoral.

The plastron of USNM 94 is figured as a hypotype of *Testudo nebrascensis* in Leidy 1854 (p.104, pl.19, fig.3). Most of the carapace is missing, but a detailed endocast remains, from which some information may be gleaned. The neural pattern is 4 (6 (6 (6 (6 (6 (6, the costals are strongly cuneate, and the costo-peripheral suture is unfused. The gulars cover the anterior part of the pyriform entoplastron. The medial length of the humeral is greater than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale is of moderate size and does not contact the femoral.

The specimen tag associated with USNM 98 notes it as the holotype of "*Emys hemispherica*" Leidy 1851, but there may be some question about this because Leidy noted that the "specimen consists of four-fifths of the sternum and about one-third of the carapax". USNM 98 has a complete carapace, as figured in Leidy 1854 (pl. 20) where it is referred to "*Testudo hemispherica*". The lateral corners of the nuchal are contacted by pleural 1, but not overlapped by it. The neural pattern is 6 (6 (6 (6 (6 (6 (6, and two suprapyrgals are present, the first embraces the lenticular second. The costals are strongly cuneate, and the unfused costo-peripheral suture aligns closely with the pleuro-marginal sulcus. The anterior margin of vertebral 1 is markedly wider than the posterior margin, it does not appear to contact the peripherals, and is well-separated from marginal 2. The vertebrae are wider than long, and the posterior sulcus of vertebral 5 crosses suprapyrgal 2 transversely. The entoplastron is pyriform and wider than long. The gulars cover the anterior part of the entoplastron, the humeral is medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale is relatively small and does not contact the femoral. The anal scales are medially shorter than the femorals, and the anal notch is reduced and angular.

USNM 6671 has a neural pattern of 4 (6 (6 (6 (6 (6 (6 and two suprapyrgals, the first cradles the lenticular second. Pleural 1 contacts but does not overlap the nuchal. The costals

are strongly cuneate and the costo-peripheral suture coincides with the pleuro-marginal sulcus. The carapace is well-arched, and the posterior peripherals are flared. The cervical scale is rectangular and longer than wide, and the vertebrals are wider than long. The anterior margin of vertebral 1 is much wider than the posterior margin. Vertebral 1 is markedly wider than vertebral 2 and well-separated from marginal 2. The posterior sulcus of vertebral 5 crosses suprapygal 2. The entoplastron is pyriform. The gulars cover the anterior area of the entoplastron, the humeral scales are medially longer than the gulars, and the gularo-humeral sulcus forms a right angle. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially straight and perpendicular to the midline, and laterally convex. The inguinal scale does not contact the femoral, and the anal notch is angular.

AMNH FARB 12410 is a relatively small specimen, measuring 135 mm in length by 120 mm in width. Pleural 1 does not contact the nuchal, and the posterior margin of vertebral 1 is narrower than the anterior margin. Only the two anteriormost neurals are preserved; neural 1 is rectangular and neural 2 is hexagonal with the short sides positioned anterolaterally. The costals are cuneate, and there is close coincidence between the pleuro-marginal sulcus and the unfused costo-peripheral suture. The cervical scale is rectangular. The vertebrals are wider than long and have arcuate borders. The gulars cover the anterior part of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, is medially straight and perpendicular to the midline, and laterally convex. The inguinal scale is small and not in contact with the femoral.

LACM 127917 has been dorsoventrally compressed. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 and two suprapygals are present, the lenticular second is cradled anteriorly by the first. The costals are slightly cuneate, and the unfused costo-peripheral suture is aligned with the pleuro-marginal sulcus. The vertebrals are wider than long and have arcuate borders. The gulars cover the anterior portion of the entoplastron. The HPS crosses posterior to the entoplastron, is medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale is small and does not contact the femoral.

UCMP 124374 was referred to *S. nebrascensis* but not described by Hutchison (1996, p.348). Growth annuli are visible on the costals. Pleural 1 does not contact the nuchal, and the anterior border of vertebral 1 is wider than the posterior border. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, but the suprapygals are missing. The costals are slightly cuneate, and the unfused costo-peripheral suture aligns well with the pleuro-marginal sulcus. The cervical scale is rectangular and wider than long. The vertebrals are wider than long, with arcuate borders. Vertebral 1 is wider than vertebral 2. The plastron is in a poor state of preservation. The gulars cover the anterior area of the entoplastron. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex.

The nuchal of UCMP 299041 is not in contact with pleural 1. The anterior border of the vertebral 1 scale is markedly wider than the posterior border. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6 and neural 8 is anomalously subdivided anteriorly. The costals are slightly cuneate, and the pleuro-marginal sulcus coincides with the unfused costo-peripheral suture. Two suprapygals are present, with the first cradling the anterior border of the lenticular second, and the

posterior sulcus of vertebral 5 crosses suprapygal 2 transversely. The cervical scale is rectangular, thin, and abnormally long for *S. nebrascensis*, equal to 30.9% of the overall length of the nuchal. The vertebrae are wider than long, with arcuate borders. Vertebral 1 is much wider than vertebral 2 and is well-separated from marginal 2. The entoplastron is pyriform and wider than long. The gulars cover the anterior part of the entoplastron, and the gularo-humeral sulcus forms a mildly obtuse angle. The humeral scales are slightly longer medially than are the gulars. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale is small and does not contact the femoral. The medial length of the anal scales is greater than that of the femorals, and the anal notch is angular and somewhat reduced. A shallow femoral-anal notch is present in the lateral border of the xiphiplastron.

Growth annuli are visible on the carapace of UCMP 299042. The anterior margin of vertebral 1 is wider than the posterior margin, and pleural 1 does not contact the lateral corners of the nuchal. The neural pattern is 4 (6 (6 (6 (6 (6 (6, and the suprapygal region is incomplete. The costals are slightly cuneate, and the unfused costo-peripheral suture is closely aligned with the pleuro-marginal sulcus. The cervical scale is rectangular and longer than wide. The vertebral scales are wider than long and have arcuate margins. Vertebral 1 is wider than vertebral 2. The lateral borders of the epiplastra are slightly constricted at the crossing of the gularo-humeral sulcus. The entoplastron is pyriform and longer than wide, the anterior area is covered by the gular scales. The humeral scales are medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and nearly perpendicular to the midline, and laterally convex. The inguinal scale is not in contact with the femoral.

The posterior border of the vertebral 1 scale of UCMP 299045 is much narrower than the anterior border. Faint growth annuli are visible on the costals, and the nuchal is not contacted by pleural 1. The neurals posterior to neural 4 are missing, but the proximal end of the left costal 4 indicates that neural 5 would likely have been hexagonal, yielding a visible neural pattern of 4 (6 (6 (6 (6 X X X. The costals are strongly cuneate, and there is close coincidence between the pleuro-marginal sulcus and the unfused costo-peripheral suture. The cervical scale is rectangular, thin, and long, equal to about 30% of the nuchal length. The vertebrae are wider than long and have arcuate borders. Vertebral 1 is markedly wider than vertebral 2 and is well-separated from the marginal 2 scale. The gulars cover the anterior part of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, is medially straight and perpendicular to the midline, and laterally convex. The inguinal scale does not contact the femoral.

UCMP 314262 (**Fig. 13**) has growth annuli faintly visible on the carapace. Pleural 1 is well-separated from the lateral corners of the nuchal, and the anterior margin of vertebral 1 is much wider than the posterior margin. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and two suprapyghals are present, with the lenticular second being cradled anteriorly by the first. The costals are slightly cuneate, and the unfused costo-peripheral suture is aligned with the pleuro-marginal sulcus. The cervical scale is cuneate and longer than wide.

The vertebral scales are wider than long and have arcuate margins. Vertebral 1 is

substantially wider than vertebral 2 and well-separated from marginal 2. The entoplastron is pyriform and longer than wide. The gular scales cover the anterior region of the entoplastron and are medially shorter

than the humerals. The gularo-humeral sulcus forms a right angle. The HPS is positioned immediately posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale is relatively small and not in contact with the femoral scale. The anals are shorter medially than the femorals, and the anal notch is angular.

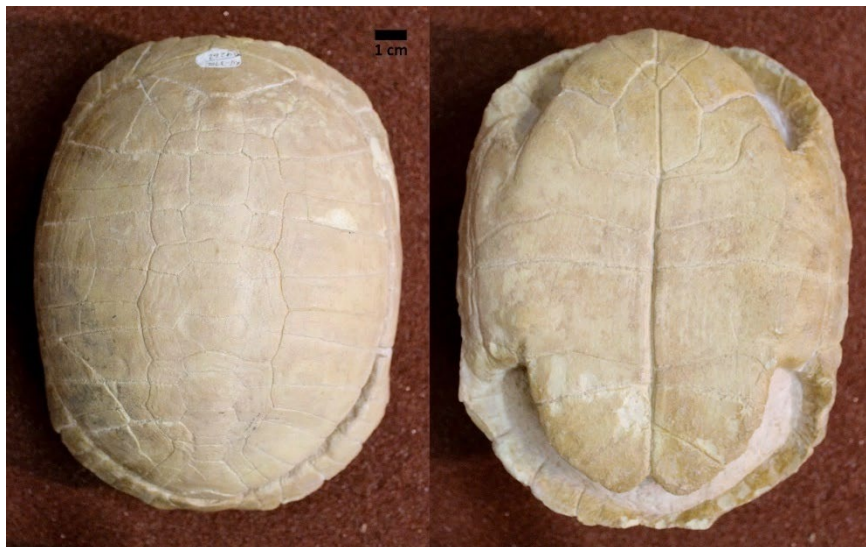


Figure 13: Carapace and plastron of UCMP 314262, a typical *S. nebrascensis* juvenile from the Orellan of South Dakota, USA.

The carapace of USNM 102 is highly arched. Pleural 1 does not contact the nuchal. Vertebral 1 is wider than vertebral 2, well-separated from marginal 2, and the anterior border of vertebral 1 is much wider than the posterior border. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, and neurals 2-8 are wider than long. The contact between the two suprapyghals is unusually straight and perpendicular to the axial plane. The costals are strongly cuneate, and the pleuro-marginal sulcus coincides with the unfused costo-peripheral suture. The cervical scale is rectangular and longer than wide. It is equal to 27% of the length of the nuchal and has a wide V-shaped indentation in the posterior margin. The vertebrals are wider than long and have arcuate borders. The posterior sulcus of vertebral 5 crosses suprapygal 2 transversely. The entoplastron is pyriform and wider than long. The gular scales are shorter medially than the humerals and overlap the anterior area of the entoplastron. The HPS coincides medially with the posterior ento-hyoplastral contact. It is medially wavy, developed mainly perpendicular to the axial plane, and laterally convex. The inguinal scale is small and does not contact the femoral. The anal scales are shorter medially than the femorals, and the anal notch is angular.

USNM 5261 has a highly arched carapace. Pleural 1 contacts the lateral corner of the nuchal but does not overlap it. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 and neurals 2-7 are wider than long. The costals are strongly cuneate, and the unfused costo-peripheral suture is closely aligned with the pleuro-marginal sulcus. The vertebral scales are wider than long and have arcuate margins. Vertebral 1 is markedly wider than vertebral 2. The entoplastron is pyriform and wider than long. The gulars cover the anterior part of the entoplastron. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially straight and perpendicular to the midline, and laterally convex. The inguinal scale is relatively small and not in contact with the femoral. The anal scales are medially longer than the femorals, and the anal notch is angular.

USNM 15962 is a small specimen, 97 mm long by 83 mm wide. The nuchal is wider than long and not in contact with the pleural 1 scale. Only seven neurals are present, and the posterior-most neural is rectangular. The neural pattern is 4 (6 (6 (6 (6 (6 4 and neurals 2-7 are wider than long. Two suprapygals are present, the first cradles the anterior border of the lenticular second. The posterior sulcus of vertebral 4 crosses neural 7, and the posterior sulcus of vertebral 5 crosses suprapygal 2 transversely. The costals are slightly cuneate, and the pleuro-marginal sulcus coincides with the unfused costo-peripheral suture. The leading edge of peripheral 1 extends beyond the anterior margin of the nuchal. The cervical scale is slightly cuneate and wider than long. The vertebrals are wider than long and have arcuate borders. Vertebral 1 is well-separated from marginal 2. A small protuberance is present on the lateral border of the epiplastron anterior to the gularo-humeral sulcus. The entoplastron is longer than wide, and the anterior area is covered by the gular scales. The medial length of the gulars is shorter than that of the humerals, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, forms a wide angle medially that is nearly perpendicular to the axial plane, and is only slightly convex laterally. The inguinal scale is quite small and well-removed from the femoral. The anal scales are shorter medially than the femorals, and the anal notch is angular. The xiphiplastron is wider than long, and the lateral border has a well-developed femoral-anal notch.

Growth annuli are visible on the costals of AMNH FARB 12401. Pleural 1 does not contact the nuchal, and the anterior border of vertebral 1 is wider than the posterior border. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and the lenticular suprapygals 1 and 2 are cradled anteriorly by suprapygals 1 and 2. The costals are not cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The vertebrals are wider than long and have arcuate borders, and vertebral 1 is wider than vertebral 2. The entoplastron is pyriform and wider than long. The gular scales cover the anterior portion of the entoplastron and are medially shorter than the humerals. The gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale does not contact the femoral. The anal scales are medially longer than the femorals, and the anal notch is angular. A shallow femoral-anal notch is present in the lateral border of the xiphiplastron.

AMNH FARB 12403 has growth annuli present on the bone surfaces. Pleural 1 does not contact the lateral corners of the nuchal. Neural 8 is indistinguishable, but the remaining neurals have a pattern of 4 (6 (6 (6 (6 (6 X. The costals are slightly cuneate, and there is close alignment between the unfused costo-peripheral suture and the pleuro-marginal sulcus. The vertebrae are wider than long, with arcuate borders. Vertebral 1 is wider than vertebral 2, and its anterior margin is markedly wider than its posterior margin. The sulcus between vertebrae 3 and 4 lies along the suture between neurals 5 and 6. The entoplastron is pyriform and longer than wide. The gulars cover the anterior part of the entoplastron. The medial length of the humerals is greater than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex. The inguinal scale does not contact the femoral.

The shell of AMNH FARB 12405 has been dorsoventrally compressed. The lateral corners of the nuchal are not contacted by pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6. The costals are slightly cuneate and the pleuro-marginal sulcus is aligned with the unfused costo-peripheral suture. The vertebrae have arcuate borders and are wider than they are long. The anterior border of vertebral 1 is wider than the posterior border, and vertebral 1 is wider than vertebral 2. The entoplastron is longer than wide, and its anterior region is covered by the gular scales. The humerals are medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS crosses posterior to the entoplastron, is medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale does not contact the femoral, and the anal notch is angular.

The carapace of RAM 8322 is well-domed. Only endocast traces of neurals 1 and 2 remain, but the neural pattern is 4 (6 (6 (6 (6 (6 (6. The costals are slightly cuneate, and there is coincidence between the unfused costo-peripheral suture and the pleuro-marginal sulcus. The cervical scale is cuneate and longer than wide, and the lateral corners of the nuchal are untouched by pleural 1. The vertebral scales are wider than long and have arcuate margins. The entoplastron is pyriform and wider than long. The gular scales overlap the anterior portion of the entoplastron. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex. There is no contact between the inguinal and femoral scales. The anal scales are longer than the femorals, and the anal notch is angular.

The carapace of RAM 8324 is highly arched and shows growth annuli. The nuchal is wider than long and not in contact with pleural 1. The neural series is incomplete, missing neurals 3, 7, 8, and the posterior half of neural 2. The remaining neurals yield a pattern of 4 X X (6 (6 (6 X X, and the lenticular suprapygal 2 is cradled anteriorly by suprapygal 1. The costals are strongly cuneate, and the rib heads are thin and emerge close to the neural-costal suture. The pleuro-marginal sulcus coincides with the unfused costo-peripheral suture. The cervical scale is cuneate and wider than long. Vertebral 1 is wider than long, the anterior margin is wider than the posterior margin, and it is well-separated from marginal 2. The posterior sulcus of vertebral 5 crosses suprapygal 2. The lateral borders of the epiplastra are mildly constricted at the gularo-humeral sulcus. The entoplastron is pyriform, longer than wide, and is overlapped anteriorly by the gulars. The humerals are medially longer than the gulars, and the gularo-humeral sulcus

forms an obtuse angle. The HPS is positioned posterior to the entoplastron, forms a wide angle medially, and is laterally convex. The inguinal scale does not contact the femoral. The medial length of the femoral scales is greater than that of the anals, and the anal notch is angular and shallow. The lateral margin of the xiphiplastron has a femoral-anal notch.

AMNH FARB 1163 is a larger specimen, with a plastron length of 363.5 mm. Neural 1 is missing, but the remaining neurals have the undifferentiated X (6 (6 (6 (6 (6 (6 pattern typical of *Styemys*. Two suprapyrgals are present, the first cradles the lenticular second. The costals are slightly cuneate and their thin rib heads emerge close to the neural-costal suture. The vertebrae have arcuate borders and are wider than long. The posterior sulcus of vertebral 5 crosses suprapyrgal 2 transversely. The epiplastron has shallow posterior excavations. The entoplastron is pyriform and wider than long. The gulars cover the anterior area of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex. There is no contact between the inguinal and femoral scales.

The nuchal of USNM 15859 does not contact pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and suprapyrgal 1 cradles the anterior margin of suprapyrgal 2. The costals are strongly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The cervical scale is cuneate and wider than long. The vertebrae are wider than long and have arcuate borders. Vertebral 1 is wider than vertebral 2, the anterior margin is wider than the posterior margin, and it is well-separated from marginal 2. The entoplastron is longer than wide and is overlapped anteriorly by the gulars. The medial length of the humeral scales is greater than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale is small and not in contact with the femoral. The anal scales are shorter medially than the femorals, and the anal notch is angular. The xiphiplastron is wider than long.

The first pleural scale of USNM 15867 does not contact the lateral corners of the nuchal. The anterior margin of vertebral 1 is wider than the posterior margin. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and neurals 2-8 are wider than long. The costals are strongly cuneate, and the pleuro-marginal sulcus coincides well with the unfused costo-peripheral suture. Two suprapyrgals are present, with the second cradled anteriorly by the first, and the posterior sulcus of vertebral 5 crosses suprapyrgal 2 transversely. The cervical scale is cuneate and wider than long and has a wide V-shaped indentation in the posterior margin with vertebral 1. The vertebral scales are wider than long and have arcuate borders. Vertebral 1 is widely separated from marginal 2. The entoplastron is pyriform, longer than wide, and the anterior area is covered by the gular scales. The humerals are longer medially than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex. The inguinal scale is of moderate size and not in contact with the femoral. The medial length of the anal scales is less than that of the femorals, and the anal notch is angular. The xiphiplastron is wider than it is long and has a shallow femoral-anal notch in the lateral border.

There is no contact between the pleural 1 scale of USNM 15869 and the lateral corner of the nuchal. The neural pattern is 4 (6 (6 (6 (6 (6 (6, and neurals 2-7 are wider than long. The costals are slightly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The cervical scale is rectangular. The vertebral scales have arcuate margins and are wider than long. Vertebral 1 is wider than vertebral 2, and its anterior border is markedly wider than its posterior border. The entoplastron is pyriform, longer than wide, and overlapped anteriorly by the gular scales. The humerals are much longer medially than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the midline, and laterally convex. The inguinal scale is quite small and does not contact the femoral. The anal scales are medially longer than the femorals, and the anal notch is angular. The xiphiplastron is wider than long and has a well-developed femoral-anal notch in the lateral border.

The normal vertebral scales 2-4 of USNM 357944 are misshapen and vertebrals 2-3 are subdivided to form a “sharks-tooth” pattern of interlocking opposed triangles running along the axial midline of the carapace. This results in a series of seven vertebrals and is most certainly an individual anomaly. Vertebral scale 1 appears to be largely normal, with an anterior margin that is markedly wider than the posterior margin. The cervical scale is cuneate, and the lateral corners of the nuchal are untouched by pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6, and two suprapygals are present, the lenticular second is embraced anteriorly by the first. The costals are slightly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The pyriform entoplastron is longer than wide and covered anteriorly by the gular scales. The medial length of the humerals is greater than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, forms a wide angle medially that is nearly perpendicular to the axial plane and is laterally convex. The inguinal scale is small and not in contact with the femoral. The femoral scales are longer medially than the anals, and the anal notch is reduced and angular. The xiphiplastron is wider than it is long and has a shallow femoral-anal notch in the lateral border.

Growth annuli are visible on the carapace of USNM 357950. The cervical scale is cuneate and longer than wide, there is no contact between pleural 1 and the nuchal, and the marginal rim is broad in comparison to the width of the nuchal. The neural pattern is 4 (6 (6 (6 (6 (6 (6, and neurals 2-8 are wider than long. Suprapygals 1 and 2 cradle the anterior margin of the lenticular suprapygals 2, and the posterior sulcus of vertebral 5 crosses suprapygals 2 transversely. The costals are slightly cuneate, and the pleuro-marginal sulcus is closely aligned with the unfused costo-peripheral suture. The vertebrals have arcuate margins and are wider than long. Vertebral 1 is wider than vertebral 2 and well-separated from marginal 2. The entoplastron is longer than wide and covered anteriorly by the gulars. The humeral scales are medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS crosses immediately posterior to the entoplastron, is medially straight and perpendicular to the axial plane, and mildly convex laterally. The inguinal scale is small and widely separated from the femoral. The anal scales are shorter medially than the femorals, and the anal notch is angular. The xiphiplastron is wider than long and has a well-developed femoral-anal notch in the lateral border.

The first pleural scale of USNM 357957 barely intrudes onto the lateral corner of the nuchal. The cervical scale is rectangular, and the anterior border of vertebral 1 is much wider than the posterior border. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and neurals 2-8 are wider than long. The costals are slightly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The vertebral scales are wider than long and have arcuate borders. Vertebral 1 is wider than vertebral 2 and well-separated from marginal 2. The pyriform entoplastron is wider than long and overlapped anteriorly by the gular scales. The humerals are medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is medially straight and perpendicular to the axial plane, positioned immediately posterior to the entoplastron, and laterally convex. The small inguinal scale has no contact with the femoral. The anal notch is angular. The xiphiplastron is wider than long and has a shallow femoral-anal notch in the lateral border.

USNM 357962 is missing the carapace posterior to neural 7 and much of the anterior rim. The visible neural pattern is 4 (6 (6 (6 (6 (6 (6 X, and neurals 2-7 are wider than long. The costals are slightly cuneate, and there appears to be close coincidence between the pleuro-marginal sulcus and the unfused costo-peripheral suture. The vertebral scales are wider than long and have arcuate borders. The plastron is heavily damaged. The entoplastron is pyriform and covered anteriorly by the gular scales. The inguinal scale is small and does not contact the femoral, and the anal notch is angular.

The nuchal of USNM 357955 is not contacted by the pleural 1 scale. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and neurals 2-8 are wider than long. The lenticular suprapygal 2 is cradled anteriorly by suprapygal 1. The costals are slightly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The cervical scale is cuneate and longer than wide. The vertebrals have arcuate margins and are wider than long. Vertebral 1 is wider than vertebral 2, well-separated from marginal 2, and has an anterior border that is much wider than the posterior border. A small protuberance is present on the lateral border of the epiplastron at the gularo-humeral sulcus. The pyriform entoplastron is longer than wide and overlapped anteriorly by the gular scales. The gulars are shorter medially than the humerals, and the gularo-humeral sulcus forms an obtuse angle. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially straight and perpendicular to the midline, and strongly convex laterally. The inguinal scale is small and widely separated from the femoral. The anal scales are medially longer than the femorals, and the anal notch is angular. The xiphiplastron is wider than long.

USNM 357958 has a neural pattern of 4 (6 (6 (6 (6 (6 (6 (6, and neurals 2-8 are wider than long. Two suprapygals are present, the first cradles the anterior border of the lenticular second, and the posterior sulcus of the vertebral 5 scale crosses suprapygal 2 transversely. The costals are slightly cuneate, and the pleuro-marginal sulcus coincides with the unfused costo-peripheral suture. The vertebrals are wider than long and have arcuate borders. The lateral border of the epiplastron is constricted at the gularo-humeral sulcus. The pyriform entoplastron is longer than wide and covered anteriorly by the gular scales. The humeral scales are shorter medially than the gulars, and the gularo-humeral sulcus forms a right angle. The HPS is

positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale is small and well removed from the femoral. The anal and femoral scales are equal length medially, and the anal notch is angular. The xiphiplastron is wider than long.

Most of the carapace of USNM 357961 is missing. From the endocast it appears that neural 1 was either hexagonal with the short sides positioned posterolaterally, or rectangular. Neurals 2-8 appear to have been hexagonal with the short sides positioned anterolaterally. The pleuro-marginal sulcus is coincident with the unfused costo-peripheral suture. The lateral border of the epiplastron is constricted at the gularo-humeral sulcus. The entoplastron is longer than wide and covered anteriorly by the gulars. The humeral scales are medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS crosses just posterior to the entoplastron, is medially straight and perpendicular to the midline, and slightly convex laterally. The inguinal scale is small and not in contact with the femoral.

The nuchal of LACM CIT 1451 is markedly wider than long, and the lateral corners are well removed from the anterolateral corners of the pleural 1 pair. The carapace posterior to neural 7 is missing. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and neurals 2-8 are wider than long. The costals are strongly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The cervical scale is cuneate and wider than long. The vertebrales have arcuate borders and are wider than long. Vertebral 1 is wider than long, wider than vertebral 2, and has a posterior margin that is much narrower than the anterior margin. The pyriform entoplastron is longer than wide and covered anteriorly by the gular scales. The gulars are medially shorter than the humerals, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, medially straight and perpendicular to the axial plane, and strongly convex laterally. The inguinal scale is of moderate size and widely separated from the femoral. The anal scales are longer medially than the femorals, and the anal notch is angular. A well-developed femoral-anal notch is present in the lateral border of the xiphiplastron.

LACM CIT 1522 is a small specimen measuring 83 mm in length by 81 mm in width. The anterior 1/3 of the nuchal is missing, and the lateral corners are untouched by pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and neurals 2-8 are wider than long. The costals are strongly cuneate, and there is close coincidence between the pleuro-marginal sulcus and the unfused costo-peripheral suture. Two suprapygals are present, the lenticular second is cradled anteriorly by the first. The vertebral scales are wider than the pleurals and have arcuate margins. Vertebral 1 is equal in width to vertebral 2 and has an anterior margin that is much wider than the posterior margin. The plastron is in a very poor state. The HPS is positioned posterior to the entoplastron, medially forming a very wide angle and nearly perpendicular to the midline, and laterally convex. The inguinal scale is not in contact with the femoral.

The carapace of LACM CIT 1661 has growth annuli visible and is missing the region anterior to the posterior-most 1/3 of neural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and neurals 2-8 are wider than they are long. Two suprapygals are present, the lenticular second being cradled anteriorly by the first, and the posterior sulcus of vertebral scale 5 crosses

suprapygals 2 transversely. The costals are slightly cuneate, the costo-peripheral suture unfused and coincident with the pleuro-marginal sulcus. Part of the posterior sulcus of vertebral 1 and the right vertebral 1/pleural 1 sulcus are preserved and demonstrate that the anterior margin of vertebral 1 would have been much wider than the posterior margin, and vertebral 1 was wider than vertebral 2. The vertebral scales are wider than long, and the marginal 12 pair is fused in dorsal view. A small protuberance is present along the lateral border of the epiplastron just anterior to the gularo-humeral sulcus. The entoplastron is longer than wide, and nearly pentagonal. The gulars intrude onto the anterior area of the entoplastron and are medially shorter than the humerals, and the gularo-humeral sulcus forms an obtuse angle. The HPS passes immediately posterior to the entoplastron, is medially straight and perpendicular to the midline, and laterally convex. The inguinal scale is well-separated from the femoral. The xiphiplastron are missing.

LACM 4890 is a very small specimen, 48 mm long by 49 mm wide. The neural pattern, interpreted from the endocast, is 4 (6 (6 (6 (6 (6 (6 (6, and the costals are slightly cuneate. The entoplastron is longer than wide and covered anteriorly by the gular scales. The humerals are longer medially than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, forms a wide angle medially, and is laterally convex. The inguinal scale is small and widely separated from the femoral.

RAM 8316 has a well-arched carapace. The nuchal is wider than long and not in contact with the first pleural. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and the costals are strongly cuneate. The posterior border of vertebral 1 is narrower than the anterior border, and the pleuro-marginal sulcus coincides with the unfused costo-peripheral suture. The cervical scale is cuneate, and the marginal rim is broad in relation to the width of the nuchal. Two suprapygals are present, with the lenticular second being cradled anteriorly by the first. Vertebral 1 is wider than long, wider than vertebral 2, and well-separated from marginal 2. Vertebrae 2-4 are wider than long and have arcuate margins. The entoplastron is longer than wide and covered anteriorly by the gular scales. The humerals are medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned immediately posterior to the entoplastron, medially perpendicular to the axial plane, and laterally concave. The inguinal scale is of moderate size and not in contact with the femoral. The anal scale is quite short and medially shorter than the femoral. The anal notch is angular, and a shallow femoral-anal notch is present in the lateral border of the xiphiplastron.

Growth annuli are visible on the carapacial bones of UCMP 86300. The lateral corners of the nuchal are well-separated from pleural 1. Neural 1 is rectangular, and neurals 2-5 are hexagonal with the short sides positioned anterolaterally. The posterior region of the carapace is missing, including neurals 6-8 and the suprapygals. The costals are cuneate, and the thin rib heads emerge close to the neural-costal suture. The costo-peripheral suture is unfused and coincides well with the pleuro-marginal sulcus. The vertebral scales are wider than long and have arcuate borders. The posterior margin of vertebral 1 is narrower than the anterior margin, and vertebral 1 is wider than vertebral 2. The entoplastron is somewhat pyriform, longer than wide, and covered anteriorly by the gulars. The medial length of the humeral scales is greater

than that of the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially very slightly wavy and perpendicular to the midline, and laterally convex. The inguinal scales are not in contact with the femorals. The femoral scales are medially shorter than the anals, and the anal notch is wide and angular.

The cervical scale of AMNH FARB 7194 is cuneate and longer than wide, and the pleural 1 scale is not in contact with the nuchal. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6. The costals are mildly cuneate, and the pleuro-marginal sulcus is closely aligned with the unfused costo-peripheral suture. The anterior border of vertebral 1 is wider than the posterior border, and vertebral 1 is wider than vertebral 2. The vertebrae have arcuate borders and are all wider than long. A small protuberance is present in the lateral border of the epiplastron just anterior to the gularo-humeral sulcus. The entoplastron is somewhat pyriform, longer than wide, and anteriorly overlapped by the gulars. The humerals are longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS coincides medially with the posterior ento-hyoplastral contact, is medially perpendicular to the axial plane, and laterally convex. The inguinal scale is small and well-removed from the femoral. The anals are medially longer than the femorals, and the anal notch is angular and reduced. The xiphiplastron has a shallow femoral-anal notch in the lateral border.

RAM 12520 measures 156 mm in length by 132 mm in width. The carapace is highly arched and has growth annuli visible on the bone surfaces. The anterior border of vertebral 1 is markedly wider than the posterior border, and pleural 1 does not contact the nuchal. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6. The costals are slightly cuneate, and the unfused costo-peripheral suture coincides with the pleuro-marginal sulcus. The vertebral scales are wider than long and have arcuate margins. Vertebral 1 is wider than vertebral 2 and well-separated from marginal 2. The entoplastron is pyriform and longer than wide. The gular scales cover the anterior region of the entoplastron, are medially shorter than the humerals, and the angle formed by the gularo-humeral sulcus is obtuse. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The femoral scale is medially shorter than the anal, and not in contact with the inguinal. The anal notch is angular, and a well-defined femoral-anal notch is present in the lateral margin of the xiphiplastron.

RAM 12521 is a small specimen with a well-domed carapace. It has slightly cuneate costals and a neural pattern of 4 (6 (6 (6 (6 (6 (6 (6 (6. The vertebrae are wider than long and have arcuate margins. The gulars cover the anterior area of the entoplastron. The HPS is positioned posterior to the entoplastron, medially perpendicular to the midline, and laterally convex. The inguinal scale does not contact the femoral.

Part of the anterior plastral lobe and much of the anterior portion of the carapace of RAM 12523 is missing, including the nuchal and neurals 1-3. The proximal ends of the left costals indicate that neurals 2 and 3 were hexagonal with short anterolateral sides, and neural 1 was likely rectangular. This gives us a neural pattern of 4 (6 (6 (6 (6 (6 (6 (6 (6. The costals are slightly cuneate, and the costo-peripheral suture unfused. The vertebrae are wider than long,

with arcuate borders. The gulars overlap the anterior part of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The anal scales are medially shorter than the femorals, and the anal notch is angular and of moderate depth.

Most of the left side of RAM 12526 is missing, and portions of the midline carapace are absent as well. The nuchal is intact, wider than long, and not contacted by pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6. The costals are slightly cuneate, and the pleuro-marginal sulcus coincides with the unfused costo-peripheral suture. The cervical scale is wider than long, cuneate, and has a small median notch in the anterior edge. The vertebral scales are wider than long and have arcuate margins. The anterior border of vertebral 1 is wider than its posterior border and exceeds the maximum width of vertebral 2. The entoplastron is longer than wide, pyriform, and covered anteriorly by the gulars. The gularo-humeral sulcus forms an obtuse angle medially. The HPS is positioned posterior to the entoplastron, medially straight and perpendicular to the axial plane, and laterally convex. The inguinal scale does not contact the femoral.

RAM 12529 has a highly arched carapace. The nuchal is wider than long, and not in contact with pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6. The costals are mildly cuneate, and the unfused costo-peripheral suture is coincident with the pleuro-marginal sulcus. The vertebral scales have arcuate borders and are wider than long. Vertebral 1 is wider than vertebral 2, and its anterior margin is wider than the posterior margin. A small protuberance is present on the anterolateral border of the epiplastron, just anterior to the gularo-humeral sulcus. The entoplastron is wider than long, pyriform, and anteriorly overlapped by the gulars. The gularo-humeral sulcus forms an obtuse angle. The HPS coincides medially with the posterior contact between the entoplastron and the hyoplastra, is medially straight and perpendicular to the midline, and laterally convex. The inguinal scale does not contact the femoral. The anal scales are medially longer than the femorals, and the anal notch is somewhat reduced and angular.

The carapace of RAM 12530 is highly arched and has the typical neural pattern of 4 (6 (6 (6 (6 (6 (6 (6 (6. The nuchal is notably wider than long and is not contacted laterally by pleural 1, and the cervical scale is rectangular. The costals are slightly cuneate, and there is close coincidence between the pleuro-marginal sulcus and the unfused costo-peripheral suture. The suprapyrgals and hindmost portion of neural 8 are missing. The vertebral scales are wider than long and have arcuate borders. Vertebral 1 is wider than vertebral 2, and well-separated from marginal 2. The plastron is fragmentary and most of the central and posterior regions are missing. The entoplastron is pyriform, wider than long, and overlapped anteriorly by the gular scales. The gularo-humeral sulcus forms an obtuse angle medially. The HPS is positioned posterior to the entoplastron, is medially straight and perpendicular to the axial plane, and anterolaterally convex. The inguinal scale does not contact the femoral.

RAM 12534 has a well-domed carapace and a nuchal that is wider than long and not contacted by the first pleural. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 (6, and the costals are

mildly cuneate. The pleuro-marginal sulcus coincides closely with the unfused costo-peripheral suture. The cervical scale is slightly cuneate. The vertebrals are wider than long and have arcuate borders. Vertebral 1 is wider than vertebral 2. The gular region is well-rounded and without protrusion. The gulars cover the anterior portion of the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is medially straight and perpendicular to the midline, laterally convex, and coincides medially with the posterior contact between the entoplastron and the hyoplastra. The femoral scale is not in contact with the inguinal and is medially shorter than the anal. The anal notch is angular and the xiphiplastron is wider than long.

The nuchal of RAM 12535 is wider than long and not in contact with pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6 and the costals are mildly cuneate. The costo-peripheral suture is unfused and coincident with the pleuro-marginal sulcus. The posterior border of the first suprapygal cradles the anterior border of the lenticular second suprapygal. The vertebrals are wider than long, with the first vertebral being wider than the second. The gulars intrude onto the entoplastron, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned posterior to the entoplastron, forms a wide, shallow angle medially, and is laterally convex. The inguinal scales do not contact the femorals.

RAM 12546 has a neural pattern of 4 (6 (6 (6 (6 (6 (6 (6 and two suprapygals, the first embraces the lenticular second. The costals are slightly cuneate, the costo-peripheral suture is unfused and coincides closely with the pleuro-marginal sulcus. The vertebrals are wider than long and have arcuate borders.

RAM 12549 has a nuchal that is wider than long and is not contacted by the first pleural. The cervical scale is rectangular, and the neural pattern is 4 (6 (6 (6 (6 (6 (6 (6. The costals are slightly cuneate, and two suprapygals are present, the lenticular second is cradled anteriorly by the first. The pleuro-marginal sulcus coincides well with the costo-peripheral suture. The vertebrals are wider than long and have arcuate margins. Vertebral 1 is much wider than long, wider than vertebral 2, and is well-separated from marginal 2. The anterior border of the gular region is rounded, and the angle formed by the gularo-humeral sulcus is obtuse. The entoplastron is wider than long, pyriform, and overlapped anteriorly by the gulars. The humeral scales are anteromedially longer than the gulars. The HPS is located posterior to the entoplastron, is medially straight and perpendicular to the axial plane, and anterolaterally convex. A lateral femoral-anal notch is present on the xiphiplastron, and the femorals are medially shorter than the anals. The inguinal scale is small and not in contact with the femoral. The anal notch is angular.

The shell of RAM 16551 is quite small, measuring 114 mm in length by 108 mm in width. The nuchal is not in contact with pleural 1. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and the costals are mildly cuneate. There is a close coincidence between the pleuro-marginal sulcus and the unfused costo-peripheral suture. Suprapygal 1 embraces the lenticular suprapygal 2. The

vertebrals are wider than long, and vertebral 1 is wider than vertebral 2 and well separated from marginal 2. A small protuberance is present on the corners of the anterior edge of the epiplastra, just anterior to the crossing of the gularo-humeral sulcus. The entoplastron is longer than wide and covered anteriorly by the gulars. The gularo-humeral sulcus forms a right angle, and the medial length of the humerals is equal to that of the gulars. The HPS is positioned posterior to the entoplastron, is medially straight and perpendicular to the midline, and anterolaterally convex. The inguinal scale is not in contact with the femoral, and the anal notch is angular and reduced.

Growth annuli are visible on the carapace of RAM 17841. Pleural 1 is well-separated from the lateral corners of the nuchal. The neural pattern is 4 (6 (6 (6 (6 (6 (6 (6, and the first suprapygal embraces the lenticular second. The costals are slightly cuneate, and the costo-peripheral suture coincides with the pleuro-marginal sulcus. The cervical scale is rectangular, and the posterior peripherals are strongly flared. The vertebrals are wider than long, with arcuate margins. Vertebral 1 is much wider than it is long, wider than vertebral 2. The anterior border of the gular region is rounded. The entoplastron is pyriform, longer than wide, and covered anteriorly by the gulars. The humerals are medially longer than the gulars, and the gularo-humeral sulcus forms an obtuse angle. The HPS is positioned just posterior to the entoplastron, is medially straight and perpendicular to the axial plane, and anterolaterally convex. The femoral scales are medially longer than the anals do not contact the inguinals. The anal notch is angular, and the xiphiplastron is wider than long.

The type specimen for this species is somewhat problematic for a couple of reasons. It is the shell of a juvenile. Any ontogenetic changes experienced by members of the species as they mature would not be in evidence with this specimen. As an “international standard of reference” (ICZN), this not only makes it a poor example, but may also be misleading and begs the question of whether members of several biological species of *Stylemys* have inadvertently been lumped under one banner. Best practices should dictate that the type specimen for a species would be of an individual that has reached the age of sexual maturity. USNM 97 is also missing the anterior part of the plastron and, critically, the epiplastra and entoplastron. It is not possible to tell, based on this specimen, whether or not the gulars cover the entoplastron, and how prominent the epiplastral lip was – the two important points of distinction between *S. nebrascensis* and *S. inusitata*.

Stylemys sp.

Referred material. Colorado, White River Formation, Orellan: Logan County – AMNH FARB Horse Tail – Lewis Cr., AMNH FARB 1252, the carapace of a juvenile; Weld County – AMNH FARB Head of Horsetail Creek, AMNH FARB 1145 the type specimen of *Stylemys*

amphithorax Cope 1873a, the anterior ¼ of a plastron and portions of the right hypoplastron and xiphiplastron; AMNH FARB Horse Tail Creek, AMNH FARB 1148 the type specimen of *Testudo ligonia* Cope 1873a, a partial nuchal and right 1st peripheral, fragment of the left hyoplastron, the left epiplastron, the posterior part of the left hypoplastron, and a right 9th peripheral; UCMP V71042, UCMP 299049, a left hyoplastron; Nebraska, White River Group, Brule Formation, Orella Member, Orellan: Dawes County – AMNH FARB H.C. Morris Ranch, 2.5 mi. NW of Chadron, AMNH FARB 12544, the carapace and partial plastron of a juvenile; AMNH FARB 12545, the plastron and partial carapace of a juvenile; White River Group, Brule Formation, Orellan: Sioux County – AMNH FARB Plunkett Ranch, Plunkett-Parsons Loc., AMNH FARB 12413, the carapace and plastron of a juvenile; RAM V94153, RAM 27153, a carapace and plastron; RAM V94158, RAM 27152, the posterior 2/3 of the carapace and plastron of a juvenile; South Dakota, White River Group, Orellan: AMNH FARB S. Dakota, AMNH FARB 698, the carapace and partial plastron of a juvenile; FMNH White River Badlands, FMNH UC320, the plastron and partial carapace of a juvenile; FMNH UC322, the anterior half of a plastron; White River Group, Orellan: Pennington County – FMNH Near Scenic, FMNH UR507, the carapace and plastron of a juvenile; RAM V96220, RAM 27154, the partial plastron and carapacial endocast of a juvenile; White River Group, Brule Formation, Orellan: AMNH FARB Badlands Area, AMNH FARB 1141, the partial carapace and plastron of a juvenile; UCMP V6523, UCMP 137567; Pennington County - NHMLA LACM 5542, LACM 127918, the anterior ¼ of a carapace and plastron; Wyoming, White River Group, Brule Formation, Orellan: Niobrara County -- USNM Near Anderson Ranch, Young Woman Creek, USNM 357959, a laterally compressed carapace and plastron.

Discussion. The referred specimens listed are diagnosable to *Stylemys* but lack sufficient morphological information for any further taxonomic identification.

Discussion

The tortoise taxa described herein share the synapomorphic presence of 2 suprapyrgals arranged such that the chevron-shaped first sends two arms back to embrace the lenticular second and in having (whenever visible) thin and narrow proximal rib heads, features which distinguish them as members of *Pan-Testudinidae*. *Gopherus*, *Hesperotestudo*, and *Stylemys* are united as members of *Testudinidae* by the coincidence of the pleuro-marginal sulcus with the underlying costo-peripheral suture, the shortening of the pectoral scales relative to most other testudines, and the lack of entoplastral overlap by the humero-pectoral sulcus (HPS).

Turtles have maintained the same *Bauplan* for 200 million years with usually only minor modifications. These modifications form the basis of the synapomorphies we use to help us understand the evolutionary relationships among testudinoid taxa. However, it has long been understood that there is a high degree of homoplasy and atavism within Testudinoidea (see

especially Crumly, 1984a; but also Auffenberg, 1974; May, 2019; Meylan, 1987; Feldman & Parham, 2002; Engstrom et al., 2004; Vlachos & Rabi, 2018; Adrian et al., 2021 among others) which complicate phylogenetic analyses. These morphological variations and reversals are found intraspecifically as well, complicating fossil specimen identification.

Among *Stylemys*, the lack of an overlap of the entoplastron by the gular scales is considered an autapomorphy of *S. inusitata*, but Hay (1908) included Leidy's *Emys oweni* in *Stylemys nebrascensis*. The type specimen for *E. oweni*, USNM 95, a nearly complete carapace and plastron from the type locality of *S. nebrascensis*, is distinctive in having a gularo-humeral sulcus that touches the anterior edge of the entoplastron but does not intrude onto it. While I concur with Hay's assessment that USNM 95 agrees with *S. nebrascensis* in all other respects, it's inclusion in *S. nebrascensis* and the *de facto* inclusion of this character within the range of individual morphological variation for *S. nebrascensis* appears to weaken the morphological definition of *S. inusitata*. The greater distinction between the two taxa becomes their spatiotemporal separation because *S. nebrascensis* comes from the Orellan-to-Arikareean of the White River deposits from South Dakota to eastern Colorado and Wyoming, and *S. inusitata* is from the Hemingfordian of Montana.

A similar situation occurs with *Stylemys capax*. Leidy (1852a) described a fossil tortoise from Nebraska as notable in having an octagonal second neural and named it *Emys culbertsoni*, later renaming it *Testudo culbertsoni* after he realized that it was terrestrial rather than aquatic. Hay (1908) also included this taxon in his redefinition of *S. nebrascensis*. Both Leidy's type specimen for *E. culbertsoni*, USNM 2348, and another specimen from the Oligocene of Nebraska, USNM 15870, have octagonal second neurals. The presence of an octagonal neural II is one of the few morphological characters that distinguish *S. capax* from *S. nebrascensis*, and its *de facto* inclusion in the range of individual variation for *S. nebrascensis* would seem to weaken the morphological definition of *S. capax*. The primary distinction of *S. capax* reflects spatiotemporal separation as well, because the taxon is restricted to the Arikareean John Day beds of Oregon. This partial reliance on spatiotemporal information allows for valid concerns about ghost lineages to be raised – concerns that can be best addressed with the collection and study of more specimens.

Because there is so much individual variation, homoplasy, and atavism in tortoises, it becomes important to look at the entire suite of morphological characters that define a species; to look at the morphological norm for a testudine population at a given time and place and compare it to the norm of another population, rather than comparing individuals. While I am of the opinion that only morphology should be used in the fossil record, morphological analyses must also include an understanding of the full range of variation in a population or group of populations. In the examples provided above, the norm for the *S. inusitata* population in the Hemingfordian of Texas was to have short gulars that did not intrude onto the entoplastron; the norm for the *S. capax* population from the Arikareean of Oregon was to have an octagonal second neural. These norms deviate from the norm of the *S. nebrascensis* population from the

Orellan-to-Arikareean of the South Dakota/Nebraska region, which was to have gular scales that overlap the entoplastron and a hexagonal second neural.

When viewed in this manner, specimens USNM 95, USNM 2348, and USNM 15870 can all be treated as cases of intraspecific variation within the well-defined *S. nebrascensis* population. Rather than weakening the morphological definitions of *S. capax* and *S. inusitata*, the presence of these variant characters within *S. nebrascensis* only serves to strengthen the relationship among the three taxa.

Although there are many testudine specimens in museum collections throughout the USA, they have often been in the collections for quite some time and were usually not collected by researchers with a particular interest in testudines. The tortoise fossils in most museum collections are juveniles, and often only complete shells have been collected. The reasons for this bias are many. Tortoise fossils are usually found in the same deposits as mammals, and it is often mammalian researchers that encounter them. With time, materials, transportation, and storage space all being at a premium both in the field and in museum collections, mammalian paleontologists usually bypass tortoise fossils in their dozens as they seek specimens more closely related to their research. When the odd tortoise has been collected, it is often a juvenile due to the ease of collection and transport/storage, and usually a complete specimen, a nice compact “showpiece” for the museum.

While perhaps understandable, this collection bias is harmful to the discipline. While the amount of ontogenetic change undergone by the fossil taxa in this study has yet to be quantified, Gerlach (2012) found that important morphological differences exist within the skeleton, cranium, and shell in an ontogenetic series of the extant Aldabra giant tortoises. With mostly juvenile fossil specimens available for study, errors in testudine taxonomy have historically been made. Leidy (1851a) originally named *Stylemys* for the stylus-shape of the plastral buttresses in his specimen, which he thought to be separate bones (he later realized his error). Hay (1908) noted that the extent of the plastral buttresses under the shell in *Stylemys* was greater than that found in *Gopherus*. Auffenberg (1964a) corrected these mistakes and showed that they were relics of studying juveniles, and that as the tortoise matures the relative extent of the plastral buttresses diminishes. At the same time he did away with another of Leidy’s misconceptions regarding the importance of peripheral pits being present in *Stylemys*, again an error born of studying juveniles.

Of the *Stylemys* specimens included in the current study, a staggering 94.6% are juveniles or sub-adults. I estimate the average carapace length of the *Stylemys* specimens in this paper to be approximately 25 cm, with some of the larger specimens I have encountered in collections measuring perhaps 61 cm; yet Hay (1908) claims to have heard from reliable collectors that uncollected specimens may exceed 91 cm. More of these large specimens of mature individuals need to be collected so that a proper examination of adult morphology and the range of ontogenetic variation in these fossil tortoises can be conducted.

It appears that there may be a trend in general body size distribution in North America toward two contemporaneous testudinid taxa, one large and one smaller, at a given time and place. For example, both *Stylemys* and *Oligopherus* lived in the Great Plains region during the Orellan. An adult size of 91 cm for *Stylemys* would well-exceed the roughly 50 cm carapace length average for the mature specimens of its conspecific, *Oligopherus*, housed in the USNM collections. If this trend holds true, it may have interesting implications toward a more complex understanding of these animals, how they utilized resources, and how they interacted with their environment and each other. This too will require the study of a greater number of fossils of mature individuals to resolve fully.

The morphological descriptions and identifications furnished in this study should provide a framework for fossil shell identifications going forward and a foundation on which future research into diversity changes in North American tortoises, the drivers of such changes, and discrepancies in the fossil record may be built.

Summary and Conclusions

- Abundant tortoise and turtle specimens reside in many museum collections and are severely understudied. They hold great potential for unlocking information about the relationship between evolution, biogeography, and climate change.
- This study has advanced the field by focusing primarily Oligo-Miocene specimens from the Great Plains and adjacent Rocky Mountain basins, by providing identifications for many previously unidentified specimens, and by clarifying the morphological criteria for recognizing the following taxa in particular: *Oligopherus laticuneus*, *Gopherus edae*, *Hesperotestudo orthopygia*, *Hesperotestudo osborniana*, *Hesperotestudo turgida*, *Stylemys nebrascensis*.
- Study of these taxa is complicated by the fact that most specimens in collections are juveniles.
- Even so, this study has found a previously unknown regional variant of *Gopherus edae* and taken initial steps toward documenting the range of intraspecific morphological variation within the several taxa of *Oligopherus*, *Hesperotestudo*, and *Stylemys* discussed herein.
- With these identifications now secure, it should be possible for these specimens/taxa to be used in future studies that focus on such topics as tortoise diversity through time and space, and the relationship between their evolution, distribution, climate change, and related phenomena.

Chapter 2

Description of a new testudine species, *Hesperotestudo nicholsorum* sp. nov., from the Miocene of Lemhi County, Idaho, U.S.A.

Introduction

The genus *Hesperotestudo* Williams, 1950b was created as a subgenus within Nearctic “Testudo” to encapsulate Eocene to Pleistocene tortoises of North America with reduced pectoral scales and heavy dermal ossicle armoring on the tail and limbs. Auffenberg (1963) further separated this group into two subgenera based on morphology: *Hesperotestudo* has a caudal buckler formed by the fusion of dermal ossicles, and *Caudochelys* Auffenberg, 1963 has dermal armoring on the posterior limbs and lacks the caudal buckler. Meylan and Sterrer (2000) included both of Auffenberg’s subgenera within the genus *Hesperotestudo*. This has subsequently been reinforced by phylogenetic analysis (Vlachos, 2018). *Hesperotestudo* has no extant members and is represented by 9 extinct species ranging through much of the continental United States and as far south as El Salvador, from the Early Miocene to Quaternary. The currently recognized members of the genus are *H. orthopygia* Cope, 1878, *H. bermudae* Meylan and Sterrer, 2000, *H. crassiscutata* Leidy, 1899, *H. ducатели* Collins and Lynn, 1936, *H. gilbertii* Hay, 1899, *H. harrisi* Lichtig and Lucas, 2022, *H. osborniana* Hay, 1904, *H. turgida* Cope, 1892a, and *H. williamsi* Auffenberg, 1964b.

This chapter will describe a new fossil of the genus *Hesperotestudo* from the Late Hemingfordian of Idaho. The specimen, UCMP 299039, is housed at the University of California Museum of Paleontology in Berkeley, California, USA. UCMP 299039 was discovered by Sara Nichols with her sister Rachel and her father Ralph while prospecting for fossils in the Railroad Canyon Sequence of Idaho with a UCMP field team led by Anthony Barnosky in 1993. The specimen was found at the West Railroad Cut locality (UCMP V99092, UM MV7328) in Lemhi Valley (Fig. 14).

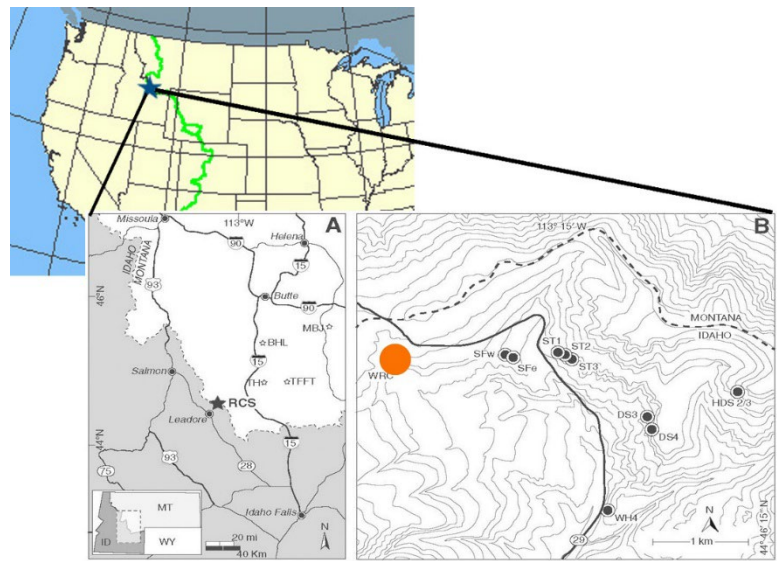


Figure 14. Map showing provenance of UCMP 299039, holotype of *Hesperotestudo nicholsorum* n. sp. **A.** Location of the Railroad Canyon Sequence (RCS) on the Idaho/Montana border. **B.** Map of the region showing location of the West Railroad Cut (WRC) locality. Inset from Harris et. al, 2017.

Railroad Canyon today is 2.28 km (7485 ft) above sea level on the Idaho-Montana border just west of the continental divide. A previous study found that $\delta^{18}\text{O}$ of soil carbonates in nearby southern Montana indicates the formation of a broad, high-elevation plateau across Idaho, Montana, and Nevada during the late Eocene to early Oligocene (Chamberlain et al., 2012). The $\delta^{18}\text{O}$ data combined with leaf physiognomic studies suggest that this plateau did not begin to collapse until approximately 17.5 Ma during the mid-Miocene with the beginning of Basin and Range extension (Atwater & Stock, 1998; Chamberlain et al., 2012). Isotopic data have established an estimated paleoelevation of 3.7 km (12,139 ft), and leaf physiognomy analysis estimates a 2 km (6562 ft) basinal paleoelevation for the Railroad Canyon region at 39 Ma (Wolfe et al., 1998; Kent-Corson et al., 2006; Mix et al., 2011). Thus, the region may have been even higher in elevation during the late Oligocene and early Miocene than its present elevation.

When discovered, the specimen was located at the base of a rocky knob close to where the team had measured the section and it had a sagebrush bush growing through it (**Fig. 15**). It was in a blocky B soil horizon within a massive to blocky tannish grey sandstone. The specimen was right side up, dipping into the hillside at 18° . It had been damaged by the formation of the blocky soil and had suffered somewhat severe root damage from the sagebrush. When excavated in 1993 it came out as several blocks within a single jacket along with several additional bags of bone. The shell was transported back to U.C. Berkeley, where it remained in storage at an off-site facility.

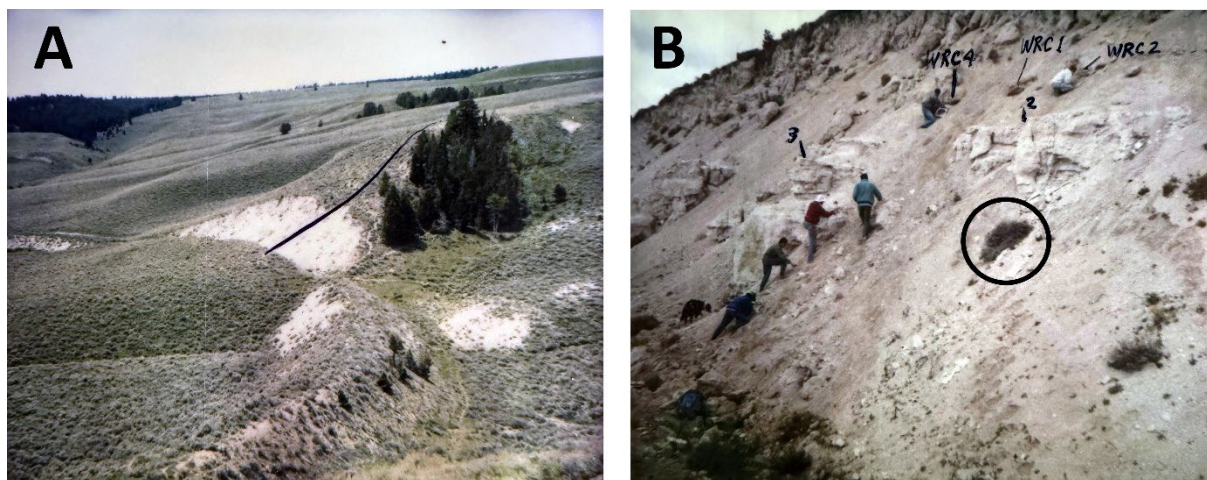


Figure 15. A) View of West Railroad Cut locality from the North-east in 1992. Dark line marks where the UCMP team measured the section. **B)** West Railroad Cut, approximate location of UCMP 299093 circled.

Age of the Railroad Canyon Sequence – Two contrasting age models have been proposed for the Railroad Canyon sequence. Barnosky et al. (2007), based on biostratigraphy and magnetostratigraphy, interpreted the part of the section above the mid-Tertiary Unconformity (also called mid-Miocene or Early Miocene Unconformity) to range from late Hemingfordian to

late Barstovian, or ~17 to 13 Ma, with the part of the section that yielded the turtle described here dating to late Hemingfordian. This interpretation would be consistent with previously recognized distinctive sedimentation patterns and ages of the Renova and Sixmile Creek Formations throughout the northern Rockies, and with the biostratigraphic distribution of taxa elsewhere throughout the Rockies and beyond.

Harris et al. (2017) provide an interpretation that would place sediments near the mid-Tertiary Unconformity (MTU, their EMU) in the late Arikareean, and those at the top in the early Barstovian, which would date the post-unconformity sediments to ~22-15 Ma. In this case the specimen described here would date to the late Arikareean. They base their interpretation on three U-Pb dates from zircon, one from just below the MTU (their EMU), one just above, and one near the top of the section. This model would require extending the biostratigraphic ranges of 13 taxa by up to 4 million years and does not take into account that the dated ashes are from distant sources and may well include reworked materials from older sediments, as is the case for detrital feldspars that were shown to yield unreasonably old Ar-Ar dates from the sequence (Barnosky et al., 2007). Whether or not the dated zircons, like the feldspars, may be reworked from older sediments is unknown.

Because the two age models yield different results, two alternative interpretations regarding age of the new species, and its age relationships to congeners, are presented in the discussion below.

Institutional Abbreviations – **AMNH FARB**, American Museum of Natural History, “Fossil Amphibians, Reptiles, and Birds” collection, New York City, New York; **FLMNH**, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **UCMP**, University of California Museum of Paleontology, University of California, Berkeley, California; **UM**, University of Montana; **USNM**, Department of Paleobiology, United States National Museum, Smithsonian National Museum of Natural History, Washington, D.C.

Anatomical Terms and Abbreviations (Fig. 1) – Scales: **M**, marginal; **Pl**, pleural; **V**, vertebral; **Cv**, cervical; **V**, vertebral; **G**, gular; **H**, humeral; **Pc**, pectoral; **Ab**, abdominal; **F**, femoral; **An**, anal. Bones: **nu**, nuchal; **n**, neural; **p**, peripheral; **c**, costal; **sp**, suprapygial; **py**, pygal; **ep**, epiplastron; **en**, entoplastron; **hyo**, hyoplastron; **hyp**, hypoplastron; **xp**, xiphoplastron; **HPS**, humero-pectoral sulcus.

Materials and Methods

Preparation – UCMP 299039 was collected in 1993 by then-graduate student Chris Bell, who noted that the specimen was in a very blocky soil, had a sagebrush bush growing up through it, and had suffered substantial root damage.

In the spring of 2018 I retrieved the specimen, then known as “Sara’s Turtle” and by its field number ADB 1077A, from storage in the UCMP offsite Regatta facility. It consisted of a large main half-jacket containing the bulk of the specimen along with 7 smaller blocks and 4 large Ziplock baggies containing the remainder. Several additional smaller jackets were also labeled

as “Sara’s Turtle”, but upon preparation turned out to be bones from a camel. It can be presumed that the jackets were simply mislabeled sometime between 1993 and 2018. I prepared Sara’s Turtle over the summer and fall of 2018, and additional work continued over several years. Preparation of the bone surfaces was done with a #4 air scribe and, in some cases, manually with dental tools. No preparation of the matrix within the shell cavity was done even though additional limb elements were visible embedded in cross-section. The carapacial bones are quite thin and would not support their own weight upon removal of the supporting internal matrix of the shell. The roots of the offending sagebrush proved impossible to remove without causing great damage to the specimen, and so were cut as close to the bone surface as possible and left in place. The damage caused by the roots and displacement of the blocks containing the specimen during soil development have led to some artificial separation and slight distortion between the shell fragments constituting the carapace. To ensure continued stability of the specimen it was necessary to fill gaps between some of the blocks in the shell cavity with an artificial matrix composed of 50% clay and 50% silica sand. Once prepared, assembled, and stabilized, the specimen was cataloged as UCMP 299039.

I examined the following fossils for comparative purposes: UCMP 36642, a large partial carapace, and UCMP 36644, a partial juvenile anterior carapace and plastron, both assigned to *Hesperotestudo orthopygia*; AMNH FARB 11500, a complete juvenile shell, UCMP 36646, a large partial carapace with plastron fragments, AMNH FARB 5871, a complete shell, and AMNH FARB 5868, a complete shell and the type of *Hesperotestudo osborniana*; AMNH FARB 12505, a complete shell of *Hesperotestudo turgida*; FMNH P12316, a complete juvenile shell of *Gopherus edae*; AMNH FARB 700, a complete juvenile shell, UCMP 314262, a complete juvenile shell, USNM 15868, a complete juvenile shell, and USNM 97, a juvenile shell and the holotype of *Stylomys nebrascensis*; FLMNH 2517, a complete plastron, FLMNH 3139, a complete juvenile shell, and FLMNH 3151, a complete shell of *Hesperotestudo crassiscutata*; USNM 13783, a complete plastron and carapace fragments of *Hesperotestudo ducateli*. The following taxa were compared only from published material: *Hesperotestudo williamsi* (Auffenberg, 1964b, Figs. 1-2); *Hesperotestudo bermudae* (Meylan & Sterrer, 2000, Fig. 1). *Hesperotestudo gilbertii* is only known from skull material, so no comparison with this taxon is currently possible. Similarly, *Hesperotestudo harrisi* is only known from skulls and an epiplastron, and no comparison with this taxon is possible. *Hesperotestudo angusticeps* may be considered a junior synonym of *H. osborniana*, *H. wilsoni* has been synonymized with *H. turgida*, *H. tedwhitei* may be considered nomen dubium (Vlachos, 2018), and all are treated as such here.

Systematic Paleontology

Order TESTUDINES Batsch, 1788

Suborder CRYPTODIRA Cope, 1868

Unranked clade PAN-TESTUDINOIDEA Joyce et al. 2004

Diagnosis. Members of pan-testudinoidea may be diagnosed relative to other turtles by: axillary and inguinal scales are present; presence of musk-duct foramina; axillary and inguinal buttresses are well-developed; plastral scales extensively overlap onto the visceral side of the plastron (Vlachos, 2018).

Superfamily TESTUDINOIDEA Gray, 1825

Unranked clade PAN-TESTUDINIDAE Joyce et al. 2004

Diagnosis. Members of pan-testudinidae can be identified as pan-testudinoids based on the suite of characters for that clade provided above. They may be distinguished from other pan-testudinoids by: proximal rib heads are thin and narrow; two suprapygals present, with the first embracing the lenticular second; buttresses are long and barely contact the costals (Vlachos, 2018).

Family TESTUDINIDAE Batsch 1788

Diagnosis. Members of Testudinidae can be identified as belonging to pan-testudinidae based on the suite of characters provided for that clade above. Testudinids may be distinguished from other pan-testudinidae by: neural differentiation into octagonal and quadrangular neurals; costo-peripheral suture coincides with the pleuro-marginal sulcus; short pectoral scales; well-developed epiplastral lip; humero-pectoral sulcus does not overlap the entoplastron (Vlachos, 2018).

Genus *HESPEROTESTUDO* Williams, 1950b

Diagnosis. Members of *Hesperotestudo* can be diagnosed as belonging to Testudinidae based on the suite of characters provided for that group above. They share the following suite of characters that help to distinguish them from other testudinids: a cervical scale that is markedly longer than wide; a neural series that is fully differentiated, with pattern 4 (8) 4 (8) 4 (6) 6 (6) 6; costals that are moderately to strongly cuneate, alternating between wide and narrow laterally; moderate to deep posterior epiplastral excavation (Hutchison, 1996); entoplastron wider than long (Biewer et al., 2016); pectoral scales that are medially much shorter than those found in *Gopherus* or *Stylomys*; a humero-pectoral sulcus that is medially perpendicular to the axial plane and laterally concave; an inguinal scale that is enlarged and broadly contacts the femoral (Vlachos, 2018); the presence of varying degrees of dermal armor covering the limbs and tail (Hutchison, 1996).

HESPEROTESTUDO NICHOLSORUM, sp. nov.

Holotype – UCMP 299039, a nearly complete adult carapace and plastron with caudal vertebrae and limb elements.

Type Locality and Horizon – UCMP V99092 (UM MV7328), West Railroad Cut, Lemhi County, Idaho, U.S.A.: Railroad Canyon Sequence, Sixmile Creek Formation (Barnosky et. al, 2007; Harris et. al, 2017).

Etymology – Specific epithet is in memoriam of Ralph Nichols and is also in reference to his daughter Sara Nichols who found the specimen. Ralph was a widely acclaimed rancher/paleontologist who introduced UCMP crews to the Railroad Canyon area, where he grew up and spent formative years riding over the outcrops when he was packing supplies into sheep herders in the high country. He subsequently earned his master’s degree in vertebrate paleontology at the University of Montana and published important papers on the mammalian paleontology of the northern Rocky Mountains. He always lent a helping hand and generously shared his knowledge of fossil localities with his many paleontology colleagues. In 1993 he was honored with the Morris Skinner Award by the Society of Vertebrate Paleontology. He passed away at the age of 98 in 2019.

Referred Material – No other specimens are referred at this time.

Diagnosis – *Hesperotestudo nicholsorum* may be identified as a member of *Hesperotestudo* by the suite of characters provided for that genus above. It may be distinguished from other members of *Hesperotestudo* by: the extreme thinness of the carapacial bones, especially near the apex; humero-pectoral sulcus crosses well posterior to the ento-hyoplastral suture and is ‘wavy’ throughout its medial 2/3 (as opposed to relatively straight in other members of the genus) and accompanying constriction of the pectoral scale; entoplastron medially shorter than in *H. orthopygia* and *H. osborniana*; the presence of “perched” sulci on the posterior peripherals similar to the condition found in both *Oligopherus* and *Gopherus*.

Description and Comparisons

Carapace

UCMP 299039 (**Fig. 16, Plate I**) has a shell length of 512 mm, width of 392 mm, and a shell height of 231 mm. The anteriormost part of the carapace is not present in this specimen, including: the nuchal; peripherals 1, 2, and all but the postero-medial corner of peripheral 3 on the right side; peripherals 1-4 and the anterolateral 1/3 of peripheral 5 on the left side; the anterior 1/2 - 2/3 of neural 1. Owing to the root and soil-formation damage to the specimen, several other pieces of the carapace are also missing, including: the left posterolateral corner of neural 3; the middle 1/3 of the left side of neural 4, including the left anterolateral corner; part of the middle left side of neural 5, including approximately 1/3 of the anterior border; the posterior border of neural 7; the entirety of a presumptive neural 8; the anterior border of suprapygal 1; the posterolateral 1/3 of left costal 2; much of the medial 1/4 of left costal 3; the posterolateral-most corner of left costal 4; small middle portions of left costals 6 and 7; the medial border of left costal 8; the anteromedial 1/5 of left peripheral 6; a small middle piece of right costal 2; 1/3 of the posterior border of right costal 7 with costal 8; a middle portion including part of the anterior border of right costal 8 with costal 7; part of the posterior border of right peripheral 7; a middle piece and part of the anterior border of right peripheral 8.

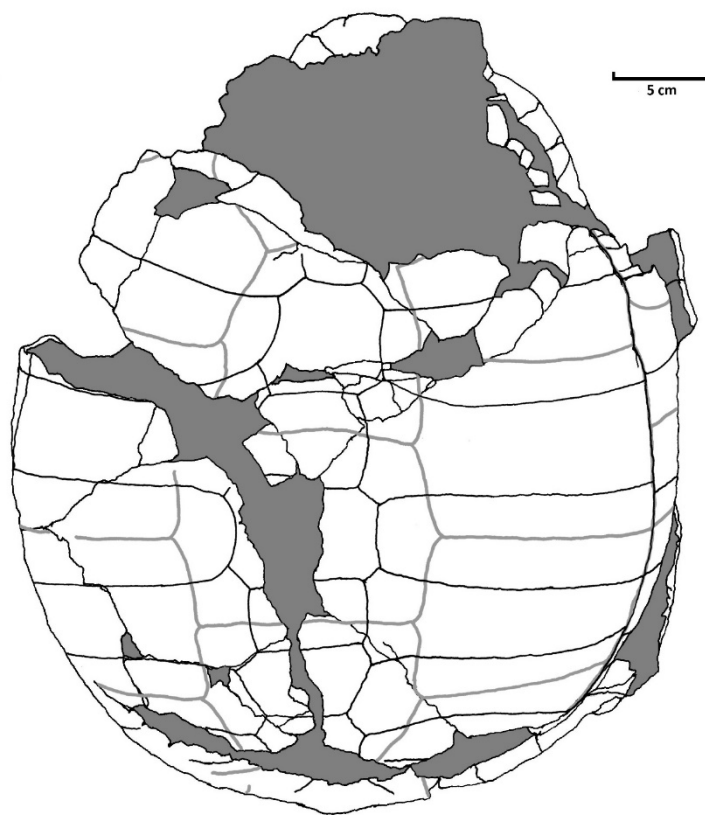
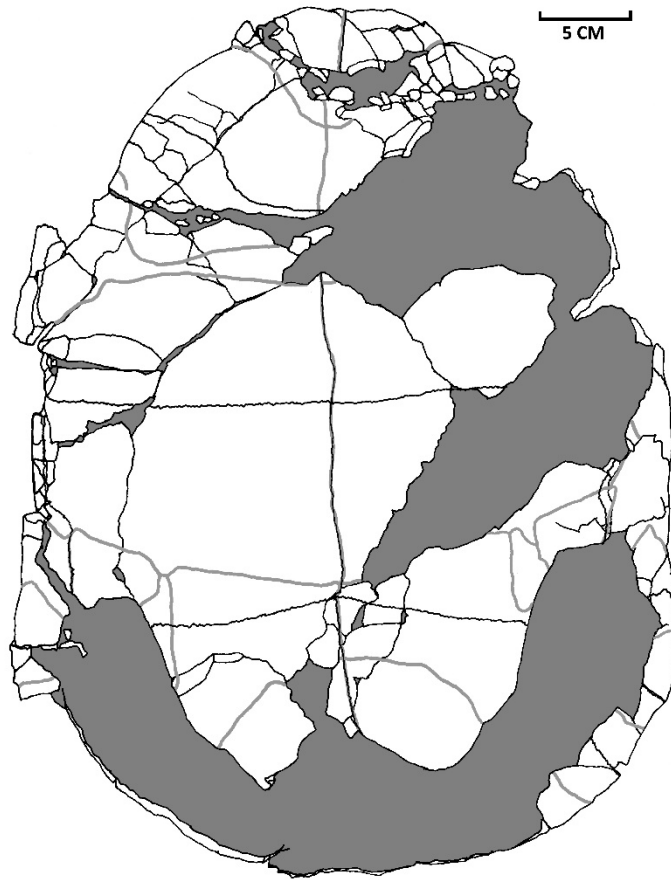


Figure 16. Illustrated view of the carapace of UCMP 299039. Sutures in black, sulci in light grey. Dark grey represents fill.

Hesperotestudo nicholsorum has 8 costals and 11 peripherals per side, two suprapygals of which the larger chevron-shaped first embraces the lenticular second, a single pygal, and a visible neural pattern of 4 8 4 8 4 (6 (6. The *in vivo* presence of an 8th neural is indicated by the shape and angle of the anterior end of suprapygal 1 and the shape and angles of the visible medial portions of costal 8 on both sides. It may be presumed that the 8th neural was hexagonal as is common for *Hesperotestudo*, but the evidence for this is absent at this time. This would yield a full neural pattern of 4 8 4 8 4 (6 (6 (6*. The costals of *Hesperotestudo nicholsorum* are moderately cuneate in shape, alternating narrow and wide ends laterally. Along the right side of UCMP 299039 costal 2 measures 37.18 mm wide medially and 66.55 mm wide laterally,

costal 3 is 65.11 mm medially and 48.69 mm laterally, costal 4 is 35.12 mm medially and 65.31 mm laterally, and costal 5 is 53.94 mm medially and 36.74 mm distally. The visible posterior end of neural 1 articulates with both first costals laterally and with neural 2 posteriorly. Traces of the crossing of neural 1 by the vertebral 1-2 sulcus are visible. Neural 2 is octagonal, sharing straight borders with neural 1 anteriorly and neural 3 posteriorly, and articulates on each side with the medial ends of costals 1-3. Neural 3 is rectangular in shape, shares straight borders with neural 2 anteriorly and neural 4 posteriorly, articulates with only costal 3 on each side, and is crossed transversely by the vertebral 2-3 sulcus. Neural 4 is octagonal, sharing straight borders with neural 3 anteriorly and neural 5 posteriorly, and articulates on each side with the medial ends of costals 3-5. Neural 5 is rectangular in shape, shares straight borders with neural 4 anteriorly and neural 6 posteriorly, articulates with only costal 5 on each side, and is crossed transversely by the vertebral 3-4 sulcus. Neural 6 is hexagonal with the short sides positioned anterolaterally, shares straight borders with neural 5 anteriorly and neural 7 posteriorly, and articulates with costals 5 and 6 on each side. Neural 7 is hexagonal with the short sides positioned anterolaterally, shares a straight border with neural 6 anteriorly (and presumably with neural 8 posteriorly), and articulates with costals 6 and 7 on each side. Suprapygal 1 is chevron-shaped with the narrow end positioned anteriorly and the angled arms extending posterolaterally. It articulates laterally with costal 8 on each side, shares a concave border with suprapygal 2 posteromedially, and articulates posterolaterally with peripheral 11 on each side. It may be presumed that it shared a straight border with an 8th neural anteriorly. Suprapygal 2 is lenticular in shape, shares a convex border with suprapygal 1 anteriorly, and articulates with both 11th peripherals and the pygal posteriorly. The bones of the carapace are unusually thin, particularly near the apex of the shell where minimum bone thickness achieves 3.79 mm. Although thin shells have previously been noted in *H. osborniana* and *H. orthopygia* (Auffenberg, 1963), a recent study consistently recorded greater shell thickness in *Hesperotestudo* than in *Gopherus*, and none of the measurements seem to approach the thickness observed in *H. nicholsorum*. For comparison, the minimum carapace thickness of an *H. osborniana* specimen (UCMP 36646) was 6.94 mm. UCMP 36646 is a larger specimen than UCMP 299039, but even when corrected for size based on the length of the V2 scale a minimum thickness approaching 4.11 mm would have been expected for UCMP 36646 if they were the same taxon.

The carapacial scales of *Hesperotestudo nicholsorum* are typical for the genus. There are 11 marginal scales and 4 pleural scales on each side, 5 vertebral scales, and the 12th marginal scales are fused into a single scale covering the pygal. The lateral borders of the vertebral scales are moderately arcuate, and the pleural scales are wider than the vertebrals. In UCMP 299093 the cervical scale, marginal scales 1-3 and the anterior half of M4 are missing on the right side, M1-5 are missing on the left side, and nearly all of vertebral scale 1 is missing, save the posterior-most edges. It appears V1 may have been wider than V2, but not enough of the first scale remains to state conclusively. The anterior border of vertebral 2 is 70.56 mm wide, the posterior border is an estimated 102.5 mm wide, and the scale is 96.73 mm in length. Vertebral 3 is 95.94 mm long, but due to separation between the underlying blocks of the carapace I can only measure the width of the posterior border of the scale and subtract the width of the visible gap in the blocks at that point, which yields an estimated posterior border width of 98.54 mm. Based on this the vertebral scales are only slightly wider at their widest points than they are long. The sulci between marginals 9-10, 10-11, and 11-12 are all perched above the normal bone surface, a condition typical of *Oligopherus* and *Gopherus*, not of *Hesperotestudo* where the sulci are impressed into the normal bone surface (Biewer et. al, 2016).



Plastron

Approximately 1/3 of the plastron of UCMP 299093 (**Fig. 17, Plate II**) is fragmentary or

missing, including: the anterior edge and left postero-lateral corner of the entoplastron; part of the medial border of the right hyoplastron; the anterior half and lateral border of the left hyoplastron; the posterior half and much of the medial edge of the left epiplastron;

Figure 17. Illustrated view of the plastron of UCMP 299093. Sutures in black, sulci in light grey. Dark grey represents matrix or fill. Modified for best fit and least fill.

approximately 1/3 of the middle part of the left hypoplastron; parts of the postero-medial portion of the right xiphiplastron, including the posterior-most apex.

The plastron is 450 mm in length and 290.33 mm in width. Width was measured between the postero-lateral borders of the hypoplastra and estimated based on a measured 335.5 mm with correction for a minimum 45.17 mm gap. There is a broad, shallow concavity in the ventral surface of the plastron extending from the anterior moiety of the xiphiplastron to the posterior border of the hyoplastron, indicating that this individual was a male. Of the epiplastra, the right is the most complete and measurements are of that side; 131.14 mm length measured at the lateral border (midline suture to epi-hyoplastral suture), and 45.87 mm width measured at the epi-hyoplastral suture. The epiplastron has a shallow notch in the lateral border where the gularo-humeral sulcus crosses and has a smooth and rounded anterior margin with no serial notching or gular protrusion. The visceral or dorsal side of the epiplastron has not been prepared, so the extent to which the epiplastron may be excavated posteriorly is unknown. The medial antero-posterior length of the entoplastron is shorter than that found in *H. orthopygia* and *H. osborniana*. It has a right-side width of 62.30 mm from the midline sulcus to the lateral corner; doubling that measurement gives an estimated total width of 124.60 mm. The midline length of the entoplastron I estimate to be 80.98 mm. The entoplastron is embraced on both antero-lateral sides by the epiplastra, posteriorly by the hyoplastral pair, is wider than long, and is overall shaped like a broad aspen (*Populus tremuloides*) leaf or acorn. The posterior border with the hyoplastra is nearly perpendicular to the axial plane, developing a moderate posterolaterally convex curvature as it passes laterally and anteriorly, and terminating in a short posterolaterally concave curvature at the lateral corner contact with the epi-hyoplastral suture. The anterior border rises from the epi-hyoplastral contact at a 45° angle anteromedially, is relatively straight throughout its length, and terminates in an antero-medial curvature that appears to bring it back nearly perpendicular to the axial plane at its anterior apex. The right hyoplastron is the more complete of the pair. It has a width of 171.13 mm, a lateral length of 173.47 mm, and an estimated medial length of 105.03 mm. The right hypoplastron has a medial length of 106.55 mm, a lateral length of 122.85 mm, and a width of 167.83 mm along the anterior suture with the hyoplastron. The right xiphiplastron has an anterior width of 105.36 mm, and the left xiphiplastron has a maximum length of 96.03 mm. A shallow notch is present along the lateral margin where the femoral-anal sulcus crosses. The posterior border of the xiphiplastron is smooth and curved with no tooth-like serrations. The anal notch between the xiphiplastra appears to be angular and moderately deep.

The right gular scale has an anterior width of 75.75 mm and an estimated medial length of 85.53 mm. The gular scales intrude onto the anterior portion of the entoplastron. The gularo-humeral sulcus forms an 85° angle with the axial plane medially, is shallowly sigmoid in shape, and forms a 48.5° angle with the axial plane overall. The right humeral scale has a maximum length of 132.48 mm and a maximum width of 114.75 mm. The short pectoral scale does not contact the entoplastron and has an estimated medial length of 21.68 mm. The scale constricts further as it passes laterally, to a minimum length of 7.81 mm, before flaring out into a length of 105.03 mm at the lateral margin of the hyoplastron. The humero-pectoral sulcus (**HPS**)

crosses the plastron posterior to the entoplastron. It is approximately perpendicular to the axial plane medially, forming a very wide, shallow curvature that is anteriorly convex along the medial 2/3 of its length. It is the postero-lateral terminus of this curve that causes the constriction seen in the pectoral scale. The lateral 1/3 of the HPS forms a pronounced antero-medially concave curvature, passing anteriorly approximately parallel to the axial plane before forming a short, slightly anterolaterally convex curve as it approaches the lateral border of the hyoplastron. The HPS crosses the hyoplastral border approximately midway between the gularo-hyoplastral suture and the anterior border of the bridge. The 'wavy' medial portion of the HPS is reminiscent of *Echmatemys* (see Hay, 1908 figs. 395, 403, 412, 421, and plates 51-53) and *Testudo brontops* (Hutchison, 1996, fig. 7; Vlachos, 2018), but the sigmoid lateral portion is distinctly different from those genera, more resembling the condition seen in *Stylemys* in this respect even though the postero-lateral curvature in that genus is often so abrupt as to form a 90° corner. It differs from *T. brontops* in having no contact between the pectoral scale and the entoplastron. The extremely short pectoral most resembles *H. osborniana*, but in *H. osborniana*, *H. bermudae*, *H. williamsi*, and *H. orthopygia* the medial portion of the HPS is straight and the pectoral scale is a uniform length throughout its medial 2/3 (Hay, 1908; Auffenberg, 1963 & 1964b; Meylan & Sterrer, 2000; Vlachos, 2018), not medially wider and laterally constricted as in *H. nicholsorum*. The short pectoral scale is a strong indication that UCMP 299039 is not a member of either *Gopherus* or *Stylemys* (Vlachos, 2018), and the specimen differs from *Gopherus* in not having a rounded HPS that forms a wide arc. The axillary scales are not preserved. The right abdominal scale has a medial length of 160 mm and covers the middle 1/3 of the plastron's length. The femoral scales of UCMP 299039 are unusual in that they are both subdivided laterally to form an accessory femoral 2 scale between the femoral proper and the inguinal scale. The medial length of the left femoral is 53.93 mm, the maximum lateral length measured from the lateral femoral-anal notch of the xiphiplastron to the femoral-abdominal sulcus is 99.91 mm, and the maximum lateral length of the right femoral is 102.85 mm. The right femoral scale has an anterior width of 100.35 mm measured along the femoral-abdominal sulcus from the midline suture to the lateral contact with the accessory femoral 2 scale. The right femoral 2 scale is 4.01 mm wide at the anterior border, 47.68 mm long at the medial border with the femoral, and 18.88 mm wide at its maximum where the lateral border crosses the lateral edge of the xiphiplastron. The left femoral 2 is 11.49 mm wide at its anterior end, 49.15 mm long at the medial sulcus with the femoral, and 23.79 mm wide at the point where the lateral border crosses the lateral edge of the xiphiplastron. Because the femoral 2 scales are asymmetrical in form and unequal in size, I suspect that the presence of the subdivided femoral is due to individual variation. The discovery of additional specimens of *H. nicholsorum* will help to determine if this is the case, or whether they are synapomorphic for the species. The inguinal scale is large as would be anticipated in *Hesperotestudo* but not in *Stylemys* (Hutchison, 1996). It has an extensive contact with the femoral (femoral 2) scale, very unlike *Stylemys* and to a much greater extent than seen in *Gopherus* (Hutchison, 1996; Vlachos, 2018). The right inguinal has an anterior width of 59.84 mm and a minimum visible 31.89 mm medial border with the femoral (femoral 2). The left inguinal has an anterior width of 56.90 mm, it is not prepared enough laterally to permit measurement of the medial border but the visible portion contacts the femoral (femoral 2) along its length. The left anal scale is the more

complete of the pair. It is 33.58 mm long at its medial sulcus with the right anal, 80.98 mm wide along its anterior contact with the femoral, and has a maximum length of 53.26 mm. The femoral-anal sulcus crosses the midline suture at a nearly perpendicular angle to the axial plane, curving postero-laterally to cross the lateral border of the xiphiplastron at the femoral-anal notch.

Vertebrae

A series of 4 articulated caudal vertebrae is preserved in UCMP 299039 (**Fig. 18**). Only the dorsal surfaces have been prepared, and a crack passes through the most anterior vertebra, splitting the right transverse process longitudinally. The tips of all 4 transverse processes on the right side are absent. The transverse processes on the left side appear somewhat expanded relative to the dorsal length of the vertebrae. To evaluate how expanded the processes are, 44 caudal vertebrae from 7 individuals of *Gopherus agassizii* from the UCMP Recent Elements collection were measured. The specimens used were UCMP 119060, UCMP 119061, UCMP 119063, UCMP 119066, UCMP 137993, UCMP 138018, and UCMP 140610. The length of the transverse process (centrum to tip) and the dorsal length of the vertebrae (tip of prezygapophysis to tip of postzygapophysis) were measured for all 44 caudal vertebrae, and for the 4 caudal vertebrae of UCMP299039. The ratio of transverse process length to dorsal vertebra length was calculated for each. The recent *Gopherus* specimens had a mean ratio of 0.693, a minimum ratio of 0.300, and a maximum ratio of 1.379. The 4 vertebrae from *H. nicholsorum* had a mean ratio of 1.176, a minimum ratio of 0.916, and a maximum ratio of 1.385. While the mean for *H. nicholsorum* is markedly higher than that for the *G. agassizii* sample set, the maximum ratio for *H. nicholsorum* is very close to the recorded *G. agassizii* maximum. There is some expansion of the transverse processes in *H. nicholsorum*, but these are not the terminal vertebrae in the caudal series. Despite the recovery of some of the caudal vertebrae and both femora, only 5 small dermal ossicles ranging in diameter from 4.78-8.47 mm were recovered during preparation. No trace of a heavily armored caudal buckler was found.



Figure 18. UCMP 299093 caudal vertebrae, dorsal view.

Appendicular Elements

Both femora of UCMP 299039 are preserved (**Fig. 19**), but neither of them has the epiphyses intact. The left femur has a minimum diaphysis width of 11.62 mm and the right has a minimum width of 12.13 mm. Although both femora were present, neither tibiae nor fibulae were found. Eight isolated and unidentified podial elements were also retrieved from the matrix.



Figure 19. The right and left femora of UCMP 299039 in **A)** dorsal view, and **B)** tibial view.

Discussion

Hesperotestudo nicholsorum can be identified as a member of pan-testudinidae and as a testudinid by the presence of 2 suprapygals, the differentiation of the neural series into rectangular and octagonal neurals, the coincidence of the pleuro-marginal sulcus with the costo-peripheral suture, the short pectoral scales, and in having an HPS that does not cross the entoplastron (Vlachos, 2018). The characters that unite it with *Hesperotestudo* are the full differentiation of the neural series into a pattern of 4 (8) 4 (8) 4 (6) 6 (6), costals that are moderately cuneate (Hutchison, 1996), the entoplastron that is wider than long (Biewer et al., 2016), and the enlarged inguinal scale that shares a broad contact with the femoral (Vlachos, 2018).

H. nicholsorum may be distinguished from *Gopherus* in having a pectoral scale that is medially much shorter than found in that genus (Vlachos, 2018). Other characters not shared with *Gopherus* include: a vertebral 1 scale that is not narrower than the vertebral 2 (Bramble & Hutchison, 2014); a HPS that is roughly perpendicular to the axial plane medially, rather than rounded and forming a wide arc; a larger inguinal scale that has a much more extensive contact with the femoral (Vlachos, 2018). *H.*

nicholsorum may be distinguished from *Stylemys* by the full differentiation of the neural series, particularly the 4th and 5th neurals which are octagonal and rectangular respectively here but are hexagonal in *Stylemys* (Vlachos, 2018). The enlarged inguinal scale and contact between the inguinal and femoral scales helps to further distinguish the new taxon from *Stylemys* (Hutchison, 1996).

H. nicholsorum differs from other members of *Hesperotestudo* in the presence of perched sulci between the marginals, the extreme thinness of the carapacial bones, and in having a medially “wavy” HPS. It differs from *H. orthopygia* by having 8 neurals opposed to only 7, having shorter pectorals (Vlachos, 2018), in showing no signs of extensive dermal armoring (Hutchison, 1996), and by having a shorter entoplastron. The new taxon differs from *H. osborniana* by having a deeper anal notch and showing no signs of a caudal buckler or extensive dermal armoring (Vlachos, 2018), and by having a shorter entoplastron. It differs from *H. turgida* in its much larger size (Oelrich, 1957), apparent lack of dermal armoring, and in the lack of ventral keels on the epiplastra (Vlachos, 2018). It differs from *H. crassiscutata* by its smaller size and thinner bones (Hay, 1908), and in the apparent lack of dermal armoring (Vlachos, 2018). *H. nicholsorum* differs from *H. ducatei* by not having a sharply pentagonal entoplastron (Collins & Lynn, 1936). It differs from *H. williamsi* by having a hexagonal neural 6 rather than octagonal, in having shorter pectoral scales (Auffenberg, 1964b), and by having a shorter entoplastron. It differs from *H. bermudae* by having shorter pectorals medially and in its much larger size, nearly double that reported for *H. bermudae* (Meylan & Sterrer, 2000).

The apparent dearth of dermal ossicles is highly unusual for *Hesperotestudo*. As reported above, prior to preparation the specimen consisted of 8 main blocks from which the fossil had to be extricated. Despite careful preparation of the substantial amount of surrounding matrix, only 5 very small dermal



Figure 20. Comparison of the sulci of **A)** typical *Hesperotestudo* (top) and typical *Gopherus* (bottom) from Biewer et al. 2016, and **B)** the marginal 10-11 sulcus of UCMP 299039.

ossicles were recovered; this despite recovering part of the caudal vertebrae sequence, both femora, and several tarsal elements. The paucity of dermal ossicles may further distinguish this specimen from *Hesperotestudo osborniana* in which the caudal buckler and expansive dermal armoring is present (Auffenberg, 1963; Auffenberg, 1974; Meylan & Sterrer, 2000; Vlachos, 2018). It is also possible that this may be a

difference between sexes. It is a difficult topic to address with only one specimen of one sex. UCMP 299039 is from a mature male as evidenced by the posterior concavity on the plastron and is ontogenetically mature based on the complete closure of the costo-peripheral sutures. Ultimately the questions of the presence/absence of a caudal buckler, the extent of dermal armoring, and what if any

morphological differences existed between males and females of *H. nicholsorum* (such as shell dome height and body size) will require the collection of more specimens to be resolved.

The presence of perched sulci is also very unusual. As reported by Biewer et al., 2016, like many testudines *Hesperotestudo* have sulci that are impressed into the bone, lying below the normal bone surface. In *Oligopherus* and *Gopherus* we find sulci that are ‘perched’, rising above the normal bone surface in a low ridge on either side of the sulcus (see **Fig. 20**). It should be noted that in UCMP 299039 the perched sulci only appear between the marginal scales and not higher up on the carapace, but the perching is present in both *Oligopherus* and *Gopherus* throughout the carapace.

Testudinids are known for their short pectoral scales (Vlachos, 2018). *Hesperotestudo* in particular exhibits a more medially shortened pectoral than *Gopherus* or *Stylemys* (**Fig. 21**). Yet even among *Hesperotestudo* the extreme constriction of the pectoral scale seen in *H. nicholsorum* is unusual. The closest resemblance may be found in *H. osborniana*, but the ‘wavy’ shape of the HPS, medially shorter entoplastron, and relatively greater separation between the HPS and ento-hyoplastral suture set

H. nicholsorum apart from the former taxon.

If we follow the age model set forth by Barnosky et al. (2007), *H. nicholsorum* would be Late Hemingfordian in age. This would potentially place it on the landscape at the same time as *H. osborniana* and *H. williamsi*; the latter is known only from Texas but the former has been recovered from Barstovian and Hemphillian deposits in nearby Montana. Under this model *H. nicholsorum* would predate its later Miocene congeners *H. orthopygia*, *H. harrisi*, *H. ducateli*, *H. gilberti*, and

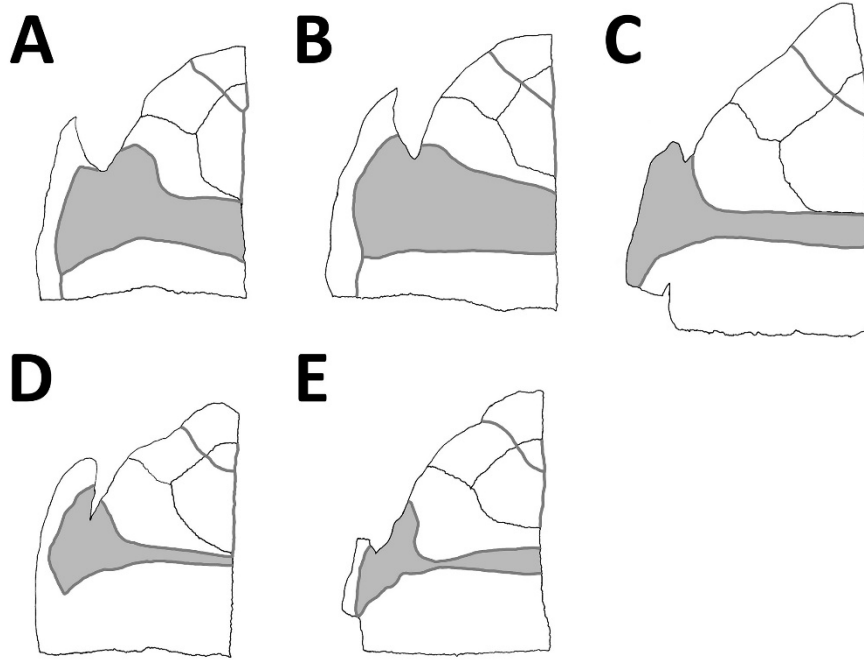


Figure 21. Shape comparison of the pectoral scales (grey) of **A)** *Stylemys nebrascensis* (UCMP 314262), **B)** *Gopherus edae* (FMNH P12316), **C)** *Hesperotestudo orthopygia* (UCMP 36644), **D)** *Hesperotestudo osborniana* (AMNH FARB 5871), and **E)** *Hesperotestudo nicholsorum* (UCMP 299039). Drawings are not to scale.

H. turgida, as well as the Pleistocene taxa *H. crassiscutata* and *H. bermudae*.

The age model proposed by Harris et al. (2017) would shift the age of the West Railroad Cut sediments and *Hesperotestudo nicholsorum* back to the Late Arikareean, in which case it would predate

all other currently accepted congeners. If valid, this may raise intriguing questions about whether the Railroad Canyon occurrence of *H. nicholsorum* may represent a point from which other members of the genus dispersed East and West.

Until the zircon dates of Harris et al. are replicated by other researchers though, I will err on the side of caution and follow the well-established biostratigraphic and magnetostratigraphic framework from Barnosky et al. in assigning a Late Hemingfordian age for the new taxon.

Chapter 3

A new species of Testudines tortoise, *Hesperotestudo niobrarensis* sp. nov., from the Miocene of the Niobrara River region of Cherry County, Nebraska, U.S.A.

Introduction

This chapter describes another new fossil of the genus *Hesperotestudo*, from the Clarendonian of Nebraska. The specimen is housed at the University of California Museum of Paleontology (UCMP) under catalog number UCMP 36522.

UCMP 36522 was collected in April of 1933 by Nathan Geer and Ruben A. Stirton at a site they named Big Beaver locality A during their “Nebraska Expedition” (**Fig. 22**). Stirton’s field notes describe the locality as an east facing slope about 8’ or 10’ (2.43-3.05 m) below the heavy sandstone cap rock of the high plain. The fossiliferous material was found in a 2.5’ (76.2 cm) thick layer of sandy clay. He noted that many fragments of tortoise and rhinoceros were visible on the surface. After Geer collected all of the tortoise fragments, Stirton assigned them the field number RAS#606. Other fauna recovered from this site include: *Aelurodon*, *Brachypsalis pristinus*, *Domninoidea*, *Hypolagus*, *Ischyrocyon gidleyi*, *Merycodus*, *Neohipparion*, *Pliohippus*, *Pseudhipparion*, *Teleoceras*, and *Ticholeptus compressidens*. The locality is part of the Fort Niobrara National Wildlife Refuge.

Institutional Abbreviations –
AMNH FARB, American Museum of Natural History, “Fossil Amphibians, Reptiles, and Birds” collection, New York City, New York; **FLMNH**, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **UCMP**, University of California Museum of Paleontology, University of California, Berkeley, California; **USNM**, Department of Paleobiology, United States National Museum, Smithsonian National Museum of Natural History, Washington, D.C.



Figure 22. Map of the United States with inset showing **A)** the type locality V3325, and **B)** the approximate location that the referred specimen was collected from.

Anatomical Terms and Abbreviations (Fig. 1) – Scales: **M**, marginal; **Pl**, pleural; **V**, vertebral; **Cv**, cervical; **V**, vertebral; **G**, gular; **H**, humeral; **Pc**, pectoral; **Ab**, abdominal; **F**, femoral; **An**, anal. Bones: **nu**, nuchal; **n**, neural; **p**, peripheral; **c**, costal; **sp**, suprapygial; **py**, pygal; **ep**, epiplastron; **en**, entoplastron; **hyo**, hyoplastron; **hyp**, hypoplastron; **xp**, xiphiplastron; **HPS**, humero-pectoral sulcus.

Neural patterns are provided for some taxa. The neurals are listed in order from first to last, numeric values indicate how many sides the neural in that position has, parentheses indicate whether the short sides are positioned anteriorly “(” or posteriorly “)”. A straight bar | indicates a position of neural reversal, where the pattern of short side positioning is changing. A neural pattern of “)6)6 |4 (6 (6 (6 (6 (6” indicates that neurals 1 & 2 are hexagonal with short sides positioned posteriorly, neural 3 is rectangular and marks a point where the directionality of the short sides is changing, and neurals 4-8 are all hexagonal with short sides positioned anteriorly.

Materials and Methods

I encountered the specimen in the collections of the University of California Museum of Paleontology (UCMP) in 2021 while taking photographs and notes on fossil tortoise specimens as part of my dissertation research. At that time, it was a collection of mostly separate carapace and plastron elements filling two museum drawers. A few of the elements had been joined in the past using a grey putty.

After the pandemic isolation, I reexamined the specimen in March and April of 2024 based on some unusual characteristics I had previously noticed. Most of the shell elements were from a single individual, but nine fragments could not be conclusively attributed to that individual, including three caudal vertebrae and a partial scapula. These elements have been left with the specimen but are not described as part of the type here. A further 23 tortoise elements and one crocodilian skull fragment were determined not to belong to the same specimen. The tortoise elements were recataloged under UCMP 297738, and the crocodilian fragment was recataloged under UCMP 297739.

I reassembled the remaining elements of UCMP 33642, which proved to form the mostly complete carapace and plastron of a single, large individual tortoise.

I examined the following fossils for comparative purposes: UCMP 36642, a large partial carapace, and UCMP 36644, a partial juvenile anterior carapace and plastron, both assigned to *Hesperotestudo orthopygia*; AMNH FARB 11500, a complete juvenile shell, UCMP 36646, a large partial carapace with plastron fragments, AMNH FARB 5871, a complete shell, and AMNH FARB 5868, a complete shell and the type of *Hesperotestudo osborniana*; AMNH FARB 12505, a complete shell of *Hesperotestudo turgida*; FMNH P12316, a complete juvenile shell of *Gopherus edae*; AMNH FARB 700, a complete juvenile shell, UCMP 314262, a complete juvenile shell, USNM 15868, a complete juvenile shell, and USNM 97, a juvenile shell and the holotype of *Stylomys nebrascensis*; FLMNH 2517, a complete plastron, FLMNH 3139, a complete juvenile shell, and FLMNH 3151, a complete shell of *Hesperotestudo crassiscutata*; USNM 13783, a

complete plastron and carapace fragments of *Hesperotestudo ducateli*. The following taxa were compared only from published material: *Hesperotestudo williamsi* (Auffenberg, 1964b, Figs. 1-2); *Hesperotestudo bermudae* (Meylan & Sterrer, 2000, Fig. 1), *Hesperotestudo harrisi* (Lichtig & Lucas, 2022, Fig. 3). *Hesperotestudo gilbertii* is only known from skull material, so no comparison with this taxon is currently possible. *Hesperotestudo angusticeps* may be considered a junior synonym of *H. osborniana*, *H. wilsoni* has been synonymized with *H. turgida*, *H. tedwhitei* may be considered *nomen dubium* (Vlachos, 2018), and all are treated as such here.

Systematic paleontology is organized in descending order, from higher taxonomic group rank to lower ranks and eventually to the specific level. Referred specimens are listed according to the following hierarchy: State (in alphabetical order), North American Land Mammal Age (NALMA) from oldest to youngest, Stratigraphic formation, County (alphabetical), Institution (alphabetical), Locality (listed alphanumerically), Specimen (listed alphanumerically).

Systematic Paleontology

Order TESTUDINES Batsch, 1788

Suborder CRYPTODIRA Cope, 1868

Unranked clade PAN-TESTUDINOIDEA Joyce et al. 2004

Diagnosis. Members of pan-testudinoidea may be diagnosed relative to other turtles by: axillary and inguinal scales are present; presence of musk-duct foramina; axillary and inguinal buttresses are well-developed; plastral scales extensively overlap onto the visceral side of the plastron (Vlachos, 2018).

Superfamily TESTUDINOIDEA Gray, 1825

Unranked clade PAN-TESTUDINIDAE Joyce et al. 2004

Diagnosis. Members of pan-testudinidae can be identified as pan-testudinoids based on the suite of characters for that clade provided above. They may be distinguished from other pan-testudinoids by: proximal rib heads are thin and narrow; two suprapygals present, with the first embracing the lenticular second; buttresses are long and barely contact the costals (Vlachos, 2018).

Family TESTUDINIDAE Batsch 1788

Diagnosis. Members of Testudinidae can be identified as belonging to pan-testudinidae based on the suite of characters provided above for that clade. Testudinids may be distinguished from other pan-testudinidae by: neural differentiation into octagonal and quadrangular neurals; costo-peripheral suture coincides with the pleuro-marginal sulcus; short pectoral scales; well-developed epiplastral lip; humero-pectoral sulcus does not overlap the entoplastron (Vlachos, 2018).

Genus *HESPEROTESTUDO* Williams, 1950b

Diagnosis. Members of *Hesperotestudo* can be diagnosed as belonging to Testudinidae based on the suite of characters provided above for that group. They share the following suite of characters that help to distinguish them from other testudinids: a cervical scale that is markedly longer than wide; a neural series that is fully differentiated, with pattern “4 (8) 4 (8) 4 (6 (6 (6””; costals that are moderately to strongly cuneate, alternating between wide and narrow laterally; moderate to deep posterior epiplastral excavation (Hutchison, 1996); entoplastron wider than long (Biewer et al., 2016); pectoral scales that are medially much shorter than those found in *Gopherus* or *Styemys*; a humero-pectoral sulcus that is medially perpendicular to the axial plane and laterally concave; an inguinal scale that is enlarged and broadly contacts the femoral (Vlachos, 2018); the presence of varying degrees of dermal armor covering the limbs and tail (Hutchison, 1996).

HESPEROTESTUDO NIOBRARENSIS sp. nov.

Holotype – UCMP 36522, a largely complete adult carapace and plastron.

Type Locality and Horizon – UCMP V3325, Big Beaver A, Cherry County, Nebraska, U.S.A.: Ash Hollow Formation, Ogallala Group.

Etymology – The specific epithet refers to the nearby Niobrara River.

Referred Material – Nebraska, Ash Hollow Formation, Clarendonian: Cherry County – AMNH FARB Merrit Reservoir, AMNH FARB 12518, a left epiplastron.

Diagnosis – *Hesperotestudo niobrarensis* can be diagnosed as belonging to *Hesperotestudo* based on the suite of characters provided for the genus above. It may be distinguished from all other *Hesperotestudo* except *Hesperotestudo turgida* by the presence of ventral keels on the epiplastra. It may be distinguished from *H. turgida* by having a carapace length over 3 times the adult size of *H. turgida*.

Description and Comparisons

The type specimen is incomplete, but the only shell elements for which no information is available are the nuchal, pygal, and both first peripherals. When describing elements and providing measurements I will use the most complete option available between the right and left sides. It may be assumed that the counterpart mirrors the element described.

Carapace

The carapace of UCMP36522 (**Fig. 23**) is missing the anteriormost portion, including: the neural; both the right and left first peripherals; left peripherals 2-7 and 9-11; right peripherals 5, 7 and 10; neurals 1-3 and 7-8; the right posterior arm of suprapygal 1; suprapygal 2; the pygal; the medial half of left costal 2 and right costal 3; most of left costal 4. Based on the shape of the medial borders of right costal 1-2 and left costal 3 we can deduce that the first neural was rectangular, the second neural was octagonal, and the third neural was rectangular. Neural 1 would have been crossed transversely by the sulcus between vertebral scales 1 and 2, and neural 3 would have been crossed transversely by the vertebral 2-3 sulcus. The fourth neural is octagonal and wider than long, and contacts costals 3-5 on each side. It is 101.85 mm long, 142.8 mm wide, and has a minimum thickness of 9.55 mm.

The fifth neural is quadrangular, contacting only the fifth costal on each side, and is crossed transversely by the sulcus between vertebral scales 3 and 4. It is 75.12 mm long, 106.17 mm wide, and has a minimum thickness of 9.39 mm near the right posterolateral border. The sixth neural is hexagonal with the short sides positioned anteriorly. It contacts costals 5-6 on each side, is 73.27 mm long, 127.97 mm maximum width, and has a minimum thickness of 7.62 mm near the anterolateral border. The missing neural 7 is hexagonal with the short sides positioned anteriorly. It contacts the costal 6-7 pair on each side and is 63.57 mm long and an estimated 117.18 mm in maximum width. The missing eighth neural is hexagonal with the short sides positioned anteriorly and contacts the costal 7-8 pair on each side and the anterior border of the first suprapygal posteriorly. It is crossed transversely by the vertebral 4-5 sulcus. It measures 70.42 mm in length and has an estimated maximum width of 76.5 mm. This gives a

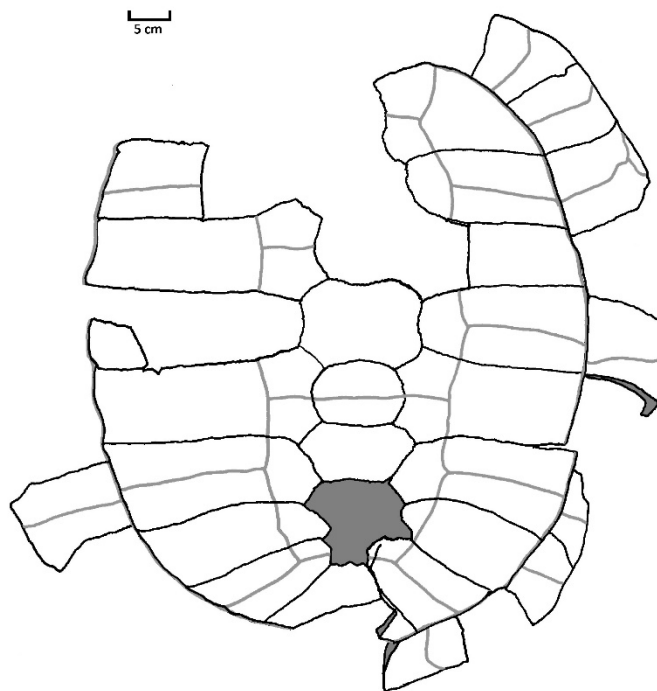


Figure 23. Illustration of the carapace of UCMP 36522. Black lines mark sutures, light grey lines mark sulci. Dark grey marks an enclosed gap in the carapace.

fully differentiated neural pattern of “4 (8) 4 (8) 4 (6 (6 (6”. Suprapygal 1 is missing part of the right posterior branch. It is 52.78 mm wide at the anterior border with the eighth neural, 210 mm wide across the posterior border measured between the right and left junctions of sp1 with costal 8 and peripheral 11, and has an “arm” length of 165 mm from the anterior border to the posterior suture with peripheral 11. The shape of the posterior branches indicate that they would have embraced a missing lenticular second suprapygal. The right first costal is crossed by the sulci between vertebrals 1 & 2 and the first pleural scale. It contacts the missing neurals 1 and 2 medially, the missing nuchal anteromedially, peripherals 1-3 anterolaterally, and costal 2 posteriorly. It is 260 mm wide and 164 mm long, and has a minimum thickness of 6.04 mm along the medial border and maximum thickness of 16.68 mm along the lateral border. Right costal 2 is crossed by the sulci between vertebral 2 and the pleural 1-2 pair. It contacts the second neural medially, first costal anteriorly, peripheral 4 laterally, and costal 3 posteriorly. It is 282 mm wide and 110 mm long. Left costal 3 is crossed by the sulci between vertebrals 2 & 3 and pleural 2. It contacts neural 4 and the missing neurals 2-3 medially, costal 2 anteriorly, peripherals 4 and 5 laterally, and costal 4 posteriorly. It is 328 mm wide, 118 mm in maximum length medially, and 79.4 mm long at the distal end. Right costal 4 is crossed by the sulci between pleurals 2 & 3 and vertebral 3. It contacts neural 4 medially, costal 3 anteriorly, peripherals 5-6 laterally, and costal 5 posteriorly. It is 322 mm in maximum width and 112 mm long at the distal border. Right costal 5 is crossed by the sulci between vertebrals 3 & 4 and pleural 3. It contacts neurals 4-6 medially, costal 4 anteriorly, peripheral 7 laterally, and costal 6 posteriorly. It is 340 mm wide, 91 mm long distally, and 110.5 mm in maximum length medially. Right costal 6 is crossed by the sulci between pleural scales 3 & 4 and the fourth vertebral scale. It contacts neural 6 and the missing neural 7 medially, costal 5 anteriorly, peripherals 7-9 laterally, and costal 7 posteriorly. It is 340 mm wide and 120 mm long distally. Right costal 7 is crossed by the vertebral 4 – pleural 4 sulcus. It contacts the missing neurals 7 & 8 medially, costal 6 anteriorly, peripherals 9-10 laterally, and costal 8 posteriorly. It is 91 mm long distally. The more complete left costal 7 is 264 mm wide. Right costal 8 is crossed by the sulci between vertebrals 4 & 5 and pleural 4. It contacts neural 8 medially, costal 7 anteriorly, peripherals 10-11 posterolaterally, and suprapygal 1 posteromedially. It is 198 mm wide and 112 mm long distally. The sulci throughout are impressed into the bone surface as is typical for the genus. The costals are slightly cuneate with alternating wide and narrow ends distally. The costal rib heads are thin and emerge close to the neural-costal suture. The pleuromarginal sulcus coincides closely with the costo-peripheral suture. Vertebral scales 2-4 are wider than long, and are wider than the pleural scales. Vertebral 2 is 242.58 mm wide and 149 mm long; vertebral 3 is 251.24 mm wide and 183.5 mm long; vertebral 4 is 222.51 mm wide and 200.12 mm long. The sulcus along the right side of vertebral 4 is slightly arcuate, but the other lateral sulci surrounding the vertebral scales do not seem to be. The carapace length is estimated to be 795.85 mm.

Plastron

The plastron of UCMP 36522 is missing several pieces, including: the right hyoplastron; the posterolateral 1/3 of the left hyoplastron; the posterolateral 1/5 of the right hypoplastron;

the posterolateral 4/5 of the left hypoplastron; the posterolateral ¾ of the left xiphiplastron. The specimen's overall plastron length is 810 mm, slightly longer than the carapace. The right epiplastron is 138 mm long, 223.5 mm wide from the midline suture to the posterolateral corner, 89.37 mm wide along the gularo-humeral sulcus, and has a midline suture length of 101.25 mm. It contacts the missing right hyoplastron posterolaterally, the entoplastron posteromedially, and the left epiplastron medially. It is crossed obliquely by the sulcus between the right gular and humeral scales. The anterior border is rounded and smooth with no serial notching or pointed projections. Joined with the left epiplastron, this produces a rounded apex to the plastron with a shallow midline depression (**Fig. 24**). The posterior epiplastral excavation is moderately deep. The most distinctive feature of the epiplastra is that each has a ventral keel that begins on the anterior border 40.51 mm from the midline suture, and courses posteriorly and medially to join with the keel from its partner just posterior to the anterior edge of the suture between the epiplastra and the entoplastron (**Fig. 25**). This is unlike any other *Hesperotestudo* except *H. turgida*. The lateral border is smooth with only a very gradual depression near the crossing of the gularo-humeral sulcus. The entoplastron is hexagonal with very short lateral sides and is wider than long. It is 195.72 mm long, 214.5 mm wide, and has a minimum thickness of 11.88 mm near the right posterolateral border. It contacts both epiplastra anteriorly, and both hyoplastra posteriorly. It is crossed by the sulci between the right and left gular scales and right and left humerals. There is no epiplastral sculpturing on the visceral (dorsal) surface. The left hyoplastron is 314 mm long, 214.5 mm wide, 182 mm in length along the midline suture in the axial plane, and has a minimum thickness of 10.31 mm. It contacts the left epiplastron anteriorly, the entoplastron anteromedially, the missing right hyoplastron medially, and the left hypoplastron posteriorly. It is crossed transversely in the anterior moiety by the HPS and the sulcus formed between the pectoral and abdominal scales. The right hypoplastron is crossed transversely near the posterior border by the sulcus between the

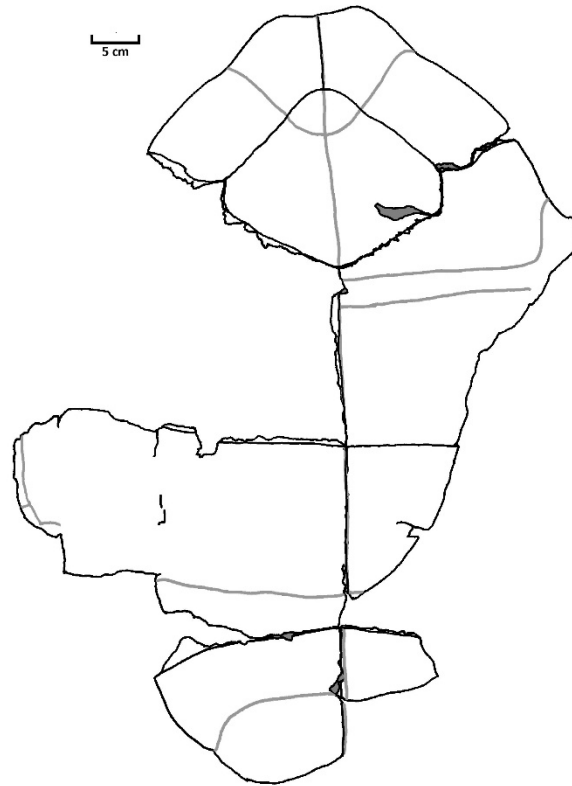


Figure 24. Illustration of the plastron of UCMP 36522. Black lines mark sutures, light grey lines mark sulci.

abdominal and femoral scales. It is 292 mm wide, 182 mm in length at the midline suture, and has a minimum thickness of 9.46 mm near the anteromedial corner. It contacts the missing right hyoplastron anteriorly, the left hypoplastron medially, and the right xiphiplastron posteriorly. The right xiphiplastron is crossed by the sulcus between the femoral and anal scales. It is 137.78 mm long at the midline suture, 155.54 mm in maximum length, 186 mm wide, and has a minimum thickness of 8.46 mm at the anteromedial border. It contacts the right hypoplastron anteriorly and the left xiphiplastron medially. The lateral and posterior borders are smooth with no serial notching or pointed projections. The notch along the lateral border where the femoral-anal sulcus crosses is shallow. The anal notch is angular and extremely shallow, and the posterior margin of the xiphiplastron forms a rounded apex. The gular scales overlap the anterior 68.51 mm of the entoplastron. The gularo-humeral sulcus forms a wide “U” medially at the junction of the gulars and humerals from both sides but forms an overall angle just slightly less than 90 degrees. The medial length of the humeral scales is slightly less than that of the gulars. The HPS crosses the plastron posterior to the entoplastron and is medially perpendicular to the axial plane. It is straight throughout most of its width, and laterally concave. The pectoral scale is quite short at only 27.32 mm along the midline suture. It’s anterior and posterior borders are straight and parallel along most of its width. The femoral scale is 92.83 mm long at the midline suture. The anal scale has a midline length of 82.22 mm.



Figure 25. The epiplastra of UCMP 36522. Arrows mark the left ventral keel.

Discussion

AMNH FARB 12518 (**Fig. 26**) is a large left epiplastron measuring approximately 8cm in width by 18cm in maximum length, although this is the isolated total length and not the true anteroposterior length of the epiplastron in situ as it lies obliquely along the anterolateral border of the anterior lobe of the plastron. It has a well-defined ventral keel and a moderate posterior epiplastral excavation. It is clear from the path of the gularo-humeral sulcus that the gulars covered the anterior part of the entoplastron. The specimen was collected by Morris Skinner in 1978 from Clarendonian deposits of the Ash Hollow Formation at the AMNH “Merritt Reservoir” locality in Cherry County, Nebraska. This locality is on the southern side of the Niobrara River some 38 miles to the southwest of UVMP V3325. Because it has a ventral keel, its overall size similarity to UCMP 36522, and its temporal and geographic proximity to the type, I refer this specimen to *H. niobrarensis*.



Figure 26. AMNH FARB 12518, an isolated epiplastron from the Clarendonian of Cherry Co., Nebraska

Hesperotestudo niobrarensis (**Fig. 27**) can be identified as a member of pan-testudinidae and as a testudinid by the presence of two suprapygals, the differentiation of the neural series into rectangular and octagonal neurals, the coincidence of the pleuro-marginal sulcus with the costo-peripheral suture, the short pectoral scales, and an HPS that does not cross the entoplastron (Vlachos, 2018). The characters that unite it with *Hesperotestudo* are



Figure 27. The carapace and plastron of UCMP 36522, type specimen of *Hesperotestudo niobrarensis*.

the full differentiation of the neural series into a pattern of “4 (8) 4 (8) 4 (6 (6 (6”, costals that are moderately cuneate (Hutchison, 1996), and the entoplastron that is wider than long (Biewer et al., 2016).

H. niobrarensis may be distinguished from *Gopherus* in having a pectoral scale that is medially much shorter than found in that genus (Vlachos, 2018), sulci that are impressed into the bone surface rather than perched above it as found in *Gopherus* (Biewer et al., 2016), and a HPS that is roughly perpendicular to the axial plane medially, rather than rounded and forming a wide arc (Vlachos, 2018). *H. niobrarensis* may be distinguished from *Stylemys* by the full differentiation of the neural series, particularly the 4th and 5th neurals that are octagonal and rectangular respectively here but are hexagonal in *Stylemys* (Vlachos, 2018).

H. niobrarensis differs from all other members of *Hesperotestudo* except *H. turgida* in the presence of ventral keels on the epiplastra. It also differs from *H. orthopygia* by having eight neurals instead of only seven (Vlachos, 2018). The new taxon differs from *H. ducatei* by lacking a sharply pentagonal entoplastron (Collins & Lynn, 1936). It differs from *H. williamsi* by having a hexagonal rather than octagonal neural six, and in having shorter pectoral scales (Auffenberg, 1964b). It differs from *H. bermudae* by having shorter pectorals medially and in its much larger size (Meylan & Sterrer, 2000).

Hesperotestudo turgida (Fig. 28) is the only other member of the genus reported as having ventral keels on the epiplastra (Cope, 1892a; Oelrich, 1957). *H. niobrarensis* differs from *H. turgida* in its much larger size, over 3 times the 22-25 cm carapace length reported for mature *H. turgida* (Oelrich, 1957), in having epiplastra without significant gular protrusions and not expanding well beyond the anterior edge of the carapace, and in lacking a highly vaulted shell (Vlachos, 2018).



Figure 28. *Hesperotestudo turgida* (AMNH FARB 12505) showing the gular protrusions, keeled epiplastra, and small size typical for that species.

The closure of the costo-peripheral sutures indicates that UCMP 36522 is from a mature individual. The posterior portion of the hypoplastron has a shallowly concave surface, indicating that this may have been a male. With such a small sample size, it is possible that the keeled epiplastra are a sexually dimorphic character and that females would lack them. Keeled epiplastra are not known in other large *Hesperotestudo*, though, so even if sexually dimorphic, this is a unique character for individuals of this size.

The new taxon would have been contemporary with *H. orthopygia* and *H. osborniana* because both have been found in Nebraska and have temporal ranges that encompass the Clarendonian. Although *H. turgida* is also known from Nebraska, it is younger with a temporal range extending from the Hemphillian to the Rancholabrean. *H. niobrarensis* also predates the Hemphillian taxon *H. gilberti* (Hay, 1899a), and the Pleistocene taxa *H. crassiscutata* and *H. bermudae* (Meylan & Sterrer, 2000), none of which has been found in Nebraska. *Hesperotestudo niobrarensis* is younger than both the Hemingfordian *H. williamsi* (Auffenberg, 1964b) and the Barstovian *H. harrisi* (Lichtig & Lucas, 2022), known only from Texas and New Mexico, respectively. *H. ducateli* is only known from Maryland (Collins & Lynn, 1936), so although it is possible that this middle Miocene tortoise shared temporal space with the new taxon, they almost certainly did not overlap geographically.

Conclusions

Hesperotestudo niobrarensis is a new tortoise species from the Clarendonian (middle-late Miocene) of Cherry County, Nebraska. It is distinct from contemporaneous members of *Hesperotestudo* in its large size and the presence of ventral keels on the epiplastra. The environmental or behavioral drivers behind these differences, if any, will require further study and the collection of more specimens.

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Appendix 1

List of Plates

PLATE I.

Hesperotestudo nicholsorum sp. nov.

Carapace of type.

No. UCMP 299039

PLATE II.

Hesperotestudo nicholsorum sp. nov.

Plastron of type.

No. UCMP 299039



Plate I. *Hesperotestudo nicholsorum* sp. nov. (UCMP 299039) from the late Arikareean/ early Hemingfordian of Idaho, U.S.A.



Plate II. *Hesperotestudo nicholsorum* sp. nov. (UCMP 299039) from the late Arikareean/ early Hemingfordian of Idaho, U.S.A.