

ABSTRACT

HERZOG, LISA L. Morphologic Characteristics and Variability of Helochelydrid Turtles in North America: Evidence for A New Species. (Under the direction of Dr. Lindsay E. Zanno.)

The Cretaceous Period was a key time for the ecological radiation of turtles and their fossil remains are commonly found in beds of this age. Turtle clades can often be diagnosed by shell patterning, especially when the pattern is distinct and diagnostic. One such group is Helochelydridae, restricted to, but widely reported in North America and Western Europe, and spanning a temporal range from the Late Jurassic to the Late Cretaceous. The shell texture of helochelydrid turtles is described as a series of small raised tubercles, vermiculations or pustules covering both the carapace and plastron. To date, there are eight identified species in this group; however, only one species has been named from North America, the taxon '*Naomichelys*'. This research summarizes the geographic distribution and chronostratigraphy of reported *Naomichelys* in North America and identifies morphologic variability in specimens recently collected from the Mussentuchit Member of the Cedar Mountain Formation of Utah. Three such specimens are included, with particular diagnostic autapomorphies illustrated and described. I argue that these specimens provide enough evidence to designate a new species of helochelydrid from North America.

The three specimens described are: an isolated entoplastron (NCSM 33526) dubbed "Kate's Ridge Taxon" to represent the holotype; a referred specimen consisting of a poorly-preserved, fragmented and disarticulated shell and skeleton (NCSM 33431); and a disarticulated partial carapace, plastron and several skeletal elements that are well preserved (FMNH PR 3895). Supporting evidence for this determination is detailed through comparative analysis of collected North American helochelydrid material held in museum collections.

An historical account of helochelydrid literature, dating back to 1827, is provided showing the complex taxonomic history of European species, as well as the temporal and geographic range.

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Morphological Characteristics and Variability of Helochelydrid Turtles in North America:
Evidence for A New Species

by
Lisa L Herzog

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APPROVED BY:

Lindsay E. Zanno
Committee Chair

Dr. Brian M. Wiegmann

Dr. Bryan Stuart

DEDICATION

I dedicate this thesis to my three boys (Niko, Milan, and Viktor) who are always there with a smile and a hug no matter what time I come home.

BIOGRAPHY

Lisa L. Herzog was born and raised in Country Club Hills, a suburb of Chicago, Illinois. She spent most of her formative years locally, and family vacations in northern Wisconsin. She graduated from high school in 1990 and received her bachelor's degree in 1994 from Western Illinois University, majoring in Geology with a minor in Geography. She then went on to train as a Fossil Preparator at The Field Museum of Natural History in Chicago Illinois, where she worked from 1996 to 2012. During her tenure there, she specialized in micropreparation, x-ray processing, histological sectioning, molding, casting, and became an active participant in the fossil preparation community. She also studied and received a master's degree in Sociology from DePaul University of Chicago in 2011. Her thesis was titled Institutional Analysis of a Natural History Museum: Formation and dissemination of scientific knowledge. In 2012 she took a position at the newly opened Nature Research Center of the North Carolina Museum of Natural Sciences in Raleigh North Carolina in the Paleontology Research Lab. She moved with her husband and two young sons.

Her foray into the study of helochelydrid turtles started in 2012 after an expedition where "Dory" was discovered by P.I. Lindsay Zanno. This enigmatic group sparked her interest due to the ubiquitous nature of shell material reported from the Cretaceous of North America, in unison with the paucity of clarification on this species. In 2013 she began part-time studies for this thesis while continuing to work full time.

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I would like to acknowledge all those who assisted me in the completion of this thesis, there are too many to name. It is with great difficulty that an undertaking such as this has been completed. Fellow students and researchers who work with me at the North Carolina Museum of Natural History encouraged me and provided insight to my hypothesis including Haviv Avrahami, Khai Button, Aurore Canoville, David Button, and Christian Kammerer. Additionally, the support of Peter Makovicky at The Field Museum by way of providing me with one of the key specimens for this work, and Akiko Shinya and William Simpson for providing me with associated data and collections access.

Special thanks to institutions who housed me in their collections to view helochelydrid materials. Collection visit to the Oklahoma Museum of Natural History was made smooth and available by Curator Rich Cifelli, preparator Kyle Davies, and Collection Manager Jennifer Larsen. I also visited the Texas Memorial Museum of the University of Texas at Austin and received valuable assistance from Chris Sagabiel, Joshua Lively, and Matthew Brown. The American Museum of Natural History visit was arranged and facilitated by Collection Manager Carl Mehling, and Preparator Amy Davidson. Amanda Millhouse and Matthew Miller hosted me while at the Smithsonian Institution and ensured I had the resources needed. The Yale Peabody museum was not visited thanks to the work of Marilyn Fox who provided photos of specimens and facilitated important specimen loans.

This thesis would not have been possible without the ongoing support of my committee chair, Lindsay Zanno. I am indebted to her for her generosity and time. Also, to all my friends and family who supported me through this six year long journey.

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LIST OF ABBREVIATIONS

Institutional Abbreviations

AMNH	American Museum of Natural History
BMNH	British Museum of Natural History
FMNH	Field Museum of Natural History
OMNH	Oklahoma Museum of Natural History
NCSM	North Carolina Museum of Natural Sciences
TMM	Texas Memorial Museum at University of Texas at Austin
UCMP	University of California Museum of Paleontology
USNM	United States Natural History Museum
YPM	Yale Peabody Museum

Anatomical Abbreviations

Carapace

co = costal
M = marginal scute
ne = neural
nu = nuchal
per = peripheral

Plastron

Ab = abdominal scute
An = anal scute
ento = entoplastron
Fe = femoral scute
Gu = Gular scute
H = humeral scute
hyo = hyoplastron
hypo = hypoplastron
Ig = intergular scute
Im = inframarginal scute
meso = mesoplastron
Pe = pectoral scute
per = peripheral
xi = xiphoplastron

Humerus

Lateral process
Shoulder
Ect. Foramen
Ectepicondyle
Entepicondyle
Medial process
Secondary intertubercular fossa
Medial process

INTRODUCTION

Stem turtles are recognized in the fossil record from the Upper Triassic (Gaffney 1975; Sterli, 2008) and by the end of the Jurassic, were well established on a global scale, inhabiting aquatic, semi-aquatic, and terrestrial biomes. During the Cretaceous, the turtle bauplan proved a successful evolutionary strategy for survival, helping turtles remain an important part of ecosystems to this day. Whereas, the phylogenetic history of fossil turtles continues to be updated as additional specimens and characters are added to the base of knowledge, the phylogenetic pathway of the turtle lineage remains unresolved. A paucity of fossil records of the earliest species has been a key factor effecting early turtle ambiguity among paleontologists. However, over the past decade the addition of a few key transitional fossil representatives allowed for a more robust morphologic dataset (Schoch and Seus 2015, Li et al 2008; 2018). These significant new fossils, along with extensive molecular phylogenetic studies of extant turtles, are challenging the existing classification and focusing attention on the key clades that remain uncertain.

Early turtle classification prioritized the anapsid state (vertebrates lacking caudal skull fenestrae), placing them among pareiasaurs, captorhinids, and procolophonomorphs, based on this shared condition of the skull (Williston 1917; Romer 1966; Gauthier 1984, et al. 1988). However, later analyses incorporating morphologic characters of the postcranial skeleton did not support an anapsid origin. Rather, these studies proposed that turtles be classified as “Parareptilia” (Lauren and Reisz 1995). Finally, Rieppel and de Braga (1996) argued against the practice of classifying turtles based on the absence of supratemporal and infratemporal fenestrae alone, positing a diapsid origin. Genome-scale molecular analysis of recent turtle groups has provided additional support for a diapsid classification (Crawford et al. 2011, 2015). With the

publication of *Pappochelys*, Schoch & Seus (2015) added significant morphological evidence that turtles were diapsids, corroborating the molecular findings. Acknowledging the anapsid state as an apomorphy in turtles heightened the importance of multiple post-cranial plesiomorphic diapsid characters (Li et al. 2018) and further favored inclusion within crown Diapsida (Bever et al. 2015; Schoch & Sues 2018), a classification that is now generally accepted.

Despite acceptance that turtles are diapsids, their relationships with other diapsid clades, specifically their phylogenetic proximity to either archosaurs or lepidosaurs, remains unresolved (Zardoya & Meyer 1998, 2001; Kumazawa & Nishida 1999; Iwabe et al. 2004; Caspers et al. 2012; Crawford et al. 2012; Field et al. 2014). Molecular, morphological, and total evidence analyses has not yielded consistent results. One genome-scale analysis produced a well resolved phylogenetic hypothesis that testudines are the sister group to archosaurs, and have no relationship to lepidosaurs (Crawford et al. 2015, 2012). Conversely, a MicroRNA analysis yielded a hypothesis of a turtle-lizard clade (Lyson et al. 2011). However, consensus is leaning towards a turtle – archosaur relationship with a clade termed Archelosauria (Crawford 2015) designated to include both. Turtle anatomy is highly derived and unique among diapsids, confounding morphological studies. Evidence shows the carapace and plastron evolved independently with a complex pattern of ossifications and keratinous scutes. Continued evolution seems to have resulted in a pattern of shell simplification (Szczygielski & Sulej 2019). Conversely, digital cranial analysis reveals a trend towards increase in brain size, regionalization and complexity as turtles diversified and evolved (Lautenschlager et al. 2018) into specific partitioned ecosystems.

In contrast to the contention over the phylogenetic relationships of all turtles, major phylogenetic divisions among turtles have been long established. Two major clades of turtles

Cryptodira and Pleurodira have been recognized for well over a century (Cope 1868). In the first published phylogenetic diagram of turtle evolution Gaffney(1975) produced a ‘speculative history’ diagram of turtle evolution placing the cryptodire/pleurodire split of all non-Proganochelydia at some point in the Late Triassic. His analysis was largely based on traits associated with skull and jaw functional morphology. Since then, there have been numerous hypotheses of the phylogenetic relationships of extinct and extant turtles that provide a nuanced understanding of turtle inter-relationships, yet the phylogenetic position of some turtle clades remained contentious for a long time. One such example is Helochelydridae (Nopcsa 1928) – an enigmatic clade of stem turtles diagnosed by its distinct shell pattern and the focus of this thesis. This phylogenetically contentious clade first appears in the fossil record in the Late Jurassic (Tithonian) of Western Europe (Joyce et al. 2011), and survived until the end of the Cretaceous (Joyce 2017). For nearly two centuries, scientists have debated the phylogenetic placement of Helochelydridae and its relationship among basal cryptodires. Only recently has the diversity and phylogenetic relationships of the helochelydrid lineage been more clearly understood.

Phylogenetic Relationships of Helochelydrid Turtles

Based on their geochronographic age and primitive characters present, helochelydrids are posited within stem testudines but do not belong to the crown Pancrypodira or Panpleurodira (Scheyer 2014) and therefore outside crown Testudinata (Joyce *et al.* 2011). The first phylogenetic analyses that hypothesized their relative taxonomic position was not published until 2000. In an analysis of non-marine Cretaceous turtles Hirayama *et al.* (2000; Figure 1A) included *Naomichelys speciosa* (Hay 1908) FMNH PR 273, the only complete helochelydrid specimen. However, Hirayama considered *Tretosternon* (Owen 1841) a senior synonym and

classified it as such. Results from this analysis placed *Tretosternon* within Cryptodira and the enigmatic clade Kallokibotionidae (Gaffney and Meylan 1992). In this arrangement *N. speciosa* is a sister taxon to *Kallokibotion* (Nopcsa 1923) and more advanced than Meiolaniidae, Sinochelyidae, *Otwayemys*, and *Mongolochelys*. The phylogenetic analysis of Joyce *et al.* (2011) (Figure 1B) found the European helochelydrid *Helochelydra nopcsai* to belong to a clade including these, however, classifying *H. nopcsai* as basal to Meiolaniidae, and *Kallokibotion* not as a sister taxon. Additionally, the interpretation places them along the phylogenetic stem of crown Testudines rather than as stem cryptodires as in Hirayama *et al.* (2000).

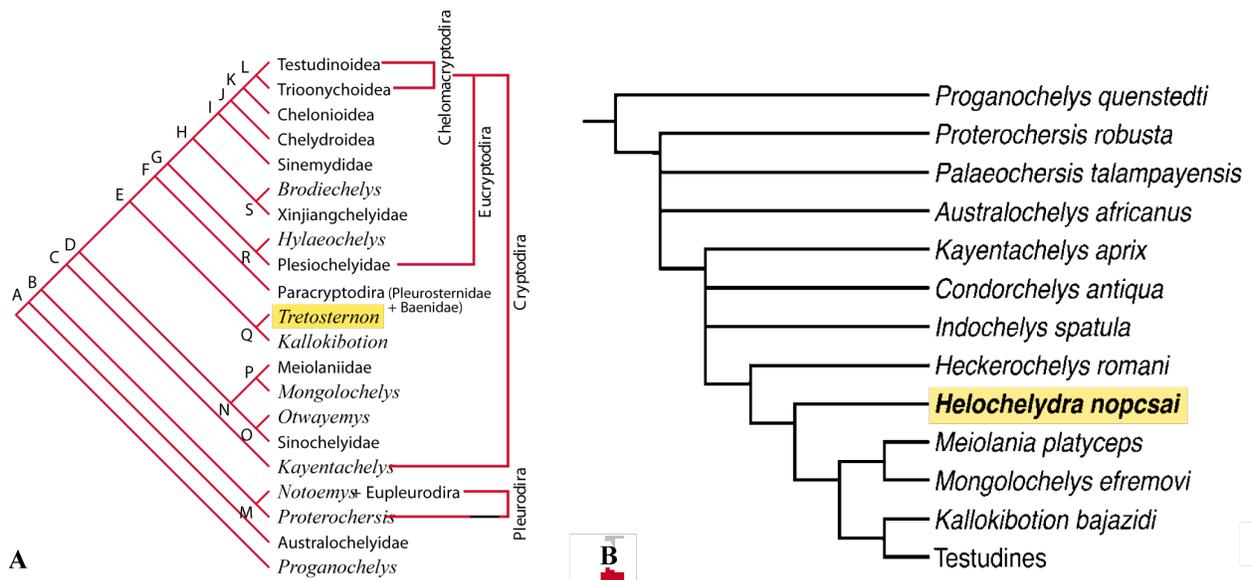


Figure 1: Phylogenetic hypotheses including Helochelydrids. Stem lineage of Testudines: **A**, Cladogram showing relationship among turtles produced by PAUP ver. 4.0b3a, reproduced from Hirayama *et al.* (2000); **B**, strict consensus (reproduced from Joyce *et al.* 2011).

Additionally, Joyce *et al.* (2011) placed *Kallokibotion* in a clade including *Meiolania*, *Mongolochelys* with *Naomichelys sp.* closely related but more basal than in Hirayama's analysis. Following Hirayama *et al.* and Joyce *et al.* Anquetin (2012) united meiolaniids, *Mongolochelys efremovi*, *Otwayemys cunicularius* and *Naomichelys speciosa* into a single clade. This

designation provides support for the ecological importance of these basal Cretaceous turtles that, taken together, have a global presence.

Most recently, Joyce (2017) analyzed Mesozoic stem testudines to highlight the most important clades and their respective diagnostic characters (Figure 2). This is the most accurate and up-to date taxonomic assessment of Helochelydridae and is followed here. Joyce has designated a new group termed *Perichelydia* to include both the Helochelydridae and Sichuancheyidae as well as the testudines lineage. This is an important designation that provides clarity to the stem lineages of Mesozoic turtles. Helochelydrids themselves are posited within stem testudines but do not belong to the crown Pancrypodira or Panpleurodira (Scheyer 2014) and therefore outside crown Testudinata (Joyce *et al.* 2011).

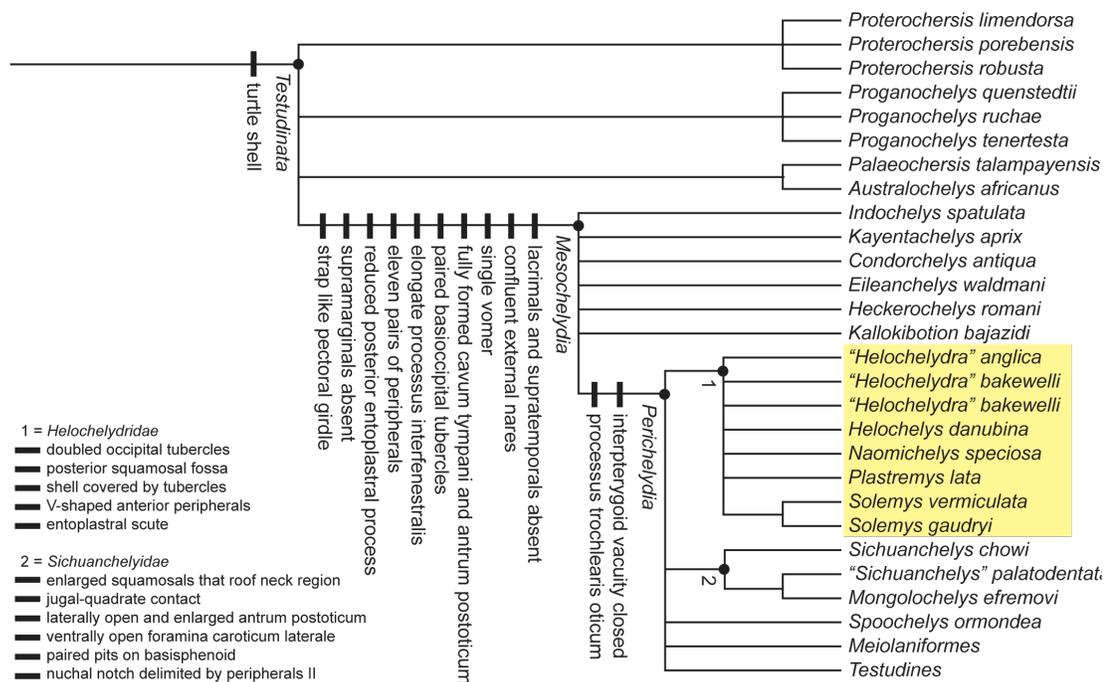


Figure 2: A phylogenetic hypothesis of Mesozoic stem testudines, with select diagnostic characters for the most important clades (reproduced from Joyce 2017). Helochelydrid clade highlighted in yellow.

Helochelyridae is primarily diagnosed by a histologically unique and easily recognizable shell surface texture characterized by a series of raised tubercles (Figure 3). This striking texture has been described using a multitude of expressive adjectives such as ‘small shot’ (Hay 1908), ‘warts’, ‘studded with buttons or high-headed nails’ (Meyer 1854), ‘tubercles’ (Nopcsa 1928) ‘pustules’ (Hirayama et al 2000), but remains conspicuous by the structure rising above the external carapace and plastral bony surfaces. This idiosyncratic texture allows for small fragments of carapace and plastron to be referred to the group with relative certainty. Although there are several species assigned to Helochelyridae in Western Europe (see Table 1), only one species has been named from North America: *Naomichelys speciosa* (Hay, 1908). Within North America, helochelyrid shell fragments have been reported from a multitude of sites with many referred to *Naomichelys sp.*(Hay 1908) and the rest assigned to the larger group Solemydidae, sp. indet. (Lapparent de Broin & Murelaga 1996) a junior subjective synonym to Helochelyridae (Nopcsa 1928).

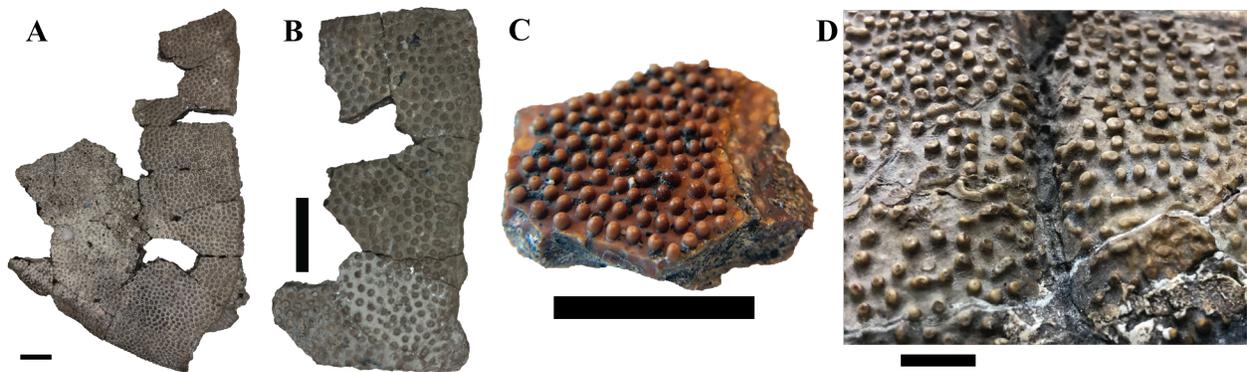


Figure 3: Shell patterning of helochelyrid turtles: A, USNM PAL 546760 left epiplastron from Cloverly Formation of Wyoming; B, USNM PAL 546454 indet. Plastron element from Cloverly Formation of Wyoming; C, AMNH VP 14588 indet. Shell fragment from Bollinger County Missouri (no Formation listed); D, Closeup of carapace, FMNH PR 273, Trinity Sandstone of Texas. Black bars represent 1cm.

Taxonomic History of Helochelydridae

The first published records of specimens now recognized as Helochelydridae appeared early in the 19th century. An illustrated costal from the Tilgate Forest of England was hesitantly diagnosed as the soft-shelled genus *Trionyx* (Mantell 1827) based on shell patterning alone. Publication on the same specimen was produced with two varying identifications each with a different illustration (Figure 4; Mantell 1827, 1833, 1851). However, the varying identifications of this enigmatic element stem more from nomenclatural partiality rather than scientific analysis.

Mantell, after assigning the specimen to genus *Trionyx* desired to honor his mentor and assigned the name *T. Bakewelli* without addressing the problematic soft-shell designation. An attempt was made by Owen in 1841 to address the clear presence of a sulcus, and suture to the peripheral – traits disbaring diagnosis to Trionichidae – and renamed the species *Tretosternon punctatum*. The correction was acknowledged by Mantell (1851), but he was piqued by the loss of homage to his mentor and amended the designation to *Tretosternum bakewelli*. The genus designation has subsequently been hypothesized as *Peltochelys* (Lydekker and Boulenger 1887), *Compsemys* (Joyce 2011) and finally *Helochelydra* (Milner 2004, Joyce 2017).

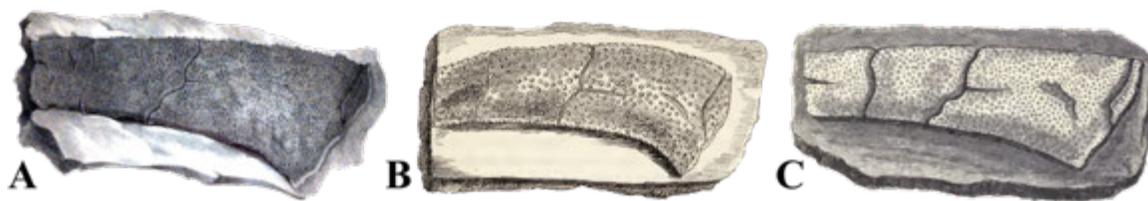


Figure 4: First published figures of a helochelydrid costal, identified as: **A** *Trionyx* (Mantell, 1827 p.87 plate VI); **B** *Trionyx Bakewelli* (Mantell 1833, p.255); and **C** *Tretosternum bakewelli* (Mantell 1851, p157).

Additional species continued to be added to the literature into the 20th century (Meyer 1855; Hutchinson and Bramble 1856; Matheron 1856, 1869; Owen 1881; Lydekker 1889; 1908 Hay), but continued to prove taxonomically enigmatic.

Since the diagnostic shell texture has been the defining character of helochelydrid taxonomy, it is important to clarify the morphology and appearance of the structure. The patterning has been uniquely identified as a small, raised, rounded structure that is 0.5-2mm wide at the base and 0.5-2mm high that covers the entire surface of both the plastron and carapace. Within Helochelydridae the pustules vary by species in height and width measurements as well as whether or not they coalesce. By 1928 several species had been described exhibiting the ‘very small, comparatively high, cylindrical bony bodies’ and were united into the group *Helochelydrinae* by Nopcsa (1928) but without a type specimen designated (Figure 5). Lapparent de Broin and Murelaga (1996) provided a diagnosis, but designated a new ‘family’ *Solemydidae*. This important designation has been reflected in subsequent analyses and referred specimens. However, most recently, Joyce (2017) has united eight species into this clade under the umbrella of *Helochelydridae* citing the International Code of Zoological Nomenclature (ICZN; Ride et al. 1999) validity of genus names without a designated type specimen and regardless of the rank assigned. Comprehensive analysis by Joyce not only clarified the group designation, he also provided diagnoses (with caveats) and taxonomic review of the complete fossil record of all helochelydrids that is used here.

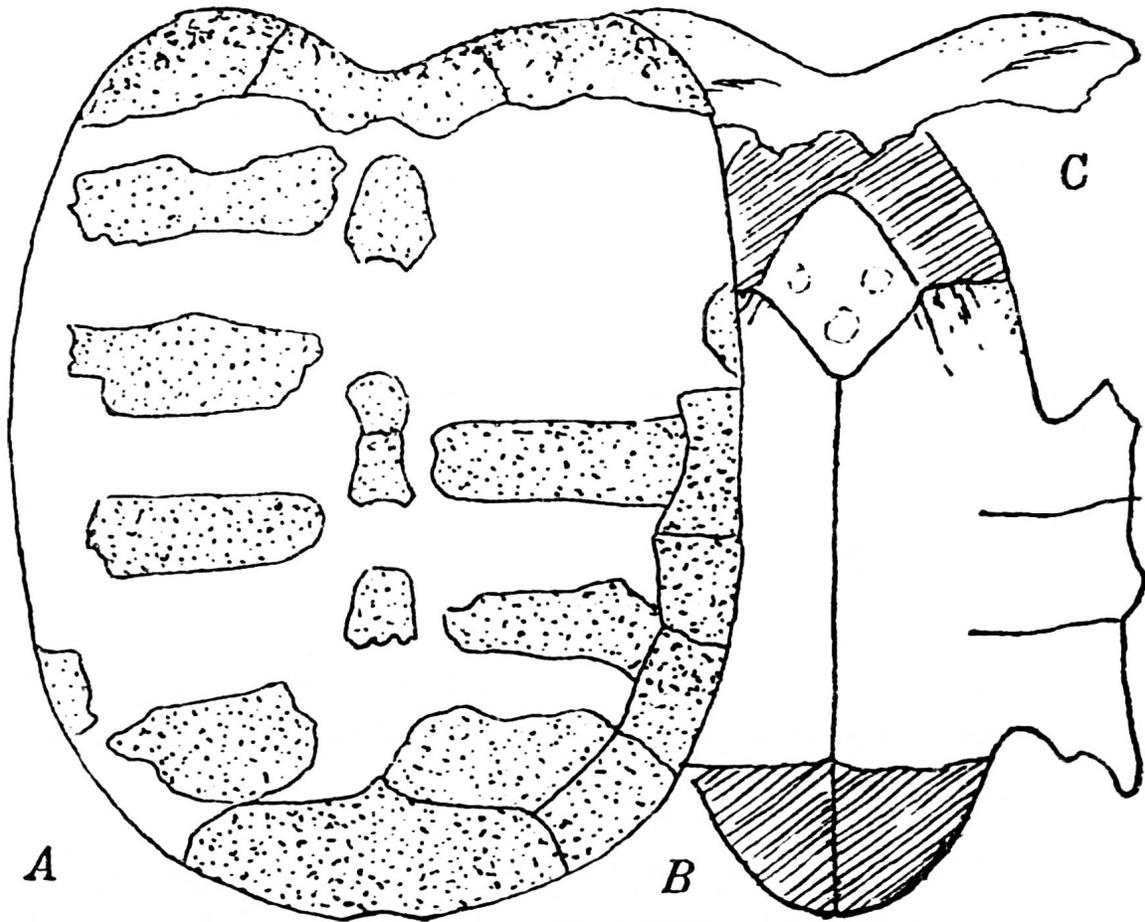


Fig. 7. Carapace and Plastron of *Helochelydra*. A) Carapace from above; B) Plastron; C) Nuchal from inside.

Figure 5: Illustration of key features of “Helochelydrinae” shell diagnosed by Nopcsa. Pustulation represented by dots. Reproduced from Nopcsa 1928. Generic shell shape indicates a nuchal embayment, and the presence of an entoplastron for all species in this group.

Table 1: Species assigned to Helochelydridae as summarized by Joyce 2017 with published historical species designations through time

Species	Synonyms
<i>Helochelydra anglica</i>	<i>Platycheilus (?) anglica</i> : Lydekker, 1889 <i>Helochelydra anglica</i> : Milner, 2004 <i>Compsemys anglica</i> : Joyce et al, 2011 <i>Helochelydra anglica</i> : Joyce, 2017
<i>Helochelydra bakewelli</i>	<i>Trionyx</i> : Mantell, 1827 <i>Trionyx bakewelli</i> : Mantell 1833 <i>Tretosternon punctatum</i> : Owen 1841 <i>Tretosternum bakewelli</i> : Mantell, 1851 <i>Peltochelys duchastelli</i> : Lydekker and Boulenger, 1887 <i>Tretosternum punctatum</i> : Lydekker, 1889 <i>Helochelydra bakewelli</i> : Milner, 2004 <i>Compsemys bakewelli</i> : Joyce, 2011 <i>Helochelydra bakewelli</i> : Joyce, 2017
<i>Helochelydra nopcsai</i>	<i>Helochelydra nopcsai</i> : Lapparent de Broin and Murelaga, 1999
<i>Naomichelys speciosa</i>	<i>Naomichelys speciosa</i> : Hay, 1908 <i>Tretosternon</i> : Hirayama, 2000
<i>Helochelys danubina</i>	<i>Helochelys danubina</i> : Meyer, 1854
<i>Plastremys lata</i>	<i>Plastremys lata</i> : Owen in Parkinson, 1881 <i>Trachydermochelys lata</i> : Andrews, 1920 <i>Trachyaspidis turbulensis</i> : Bergounioux, 1957 <i>Trachydermochelys rutteri</i> : Joyce et al, 2011 <i>Plastremys lata</i> : Joyce, 2017
<i>Solemys vermiculata</i>	<i>Solemys vermiculata</i> : Lapparent de Broin & Murelaga, 1996
<i>Solemys gaudryi</i>	<i>Apholidemys gaudryi</i> : Matheron, 1869 <i>Anosteira gaudryi</i> : Hummel 1929 <i>Solemys gaudryi</i> : Lapparent de Broin & Murelaga, 1996

Temporal and Geographic Distribution of Helochelyridae

The earliest reported Helochelyridae consists of two small fragments (2-3mm each) identified as *Helochelydra* indet. From the upper Chicks Grove Quarry, Wiltshire England. This specimen represents the only helochelydrid known from the Jurassic (Tithonian). Although these fragments are small, they exhibit the autapomorphic shell pattern diagnostic to Helochelyridae (Joyce et al. 2011). Cretaceous specimens from Europe have been recovered in England, Spain, France and Germany and span from the Berriasian to the Maastrichtian. Taxonomic resolution of European specimens is greater than the problematic North American record, and includes seven diagnosed species (Figure 6 and Table 2; Joyce 2017). In some instances, species diagnosis is generalized and includes character states defined as high or low tubercles, tubercles that easily dislocate or do not, and coalescing or non-coalescing tubercles. In conjunction with a midline keel and nuchal notch shape, these characters help to distinguish among species. Additionally, *H. anglica* and *H. bakewelli* are primarily distinguished by temporal variation as are *H. nopcsai* and *H. danubina*. European species distribution is detailed in Table 2.

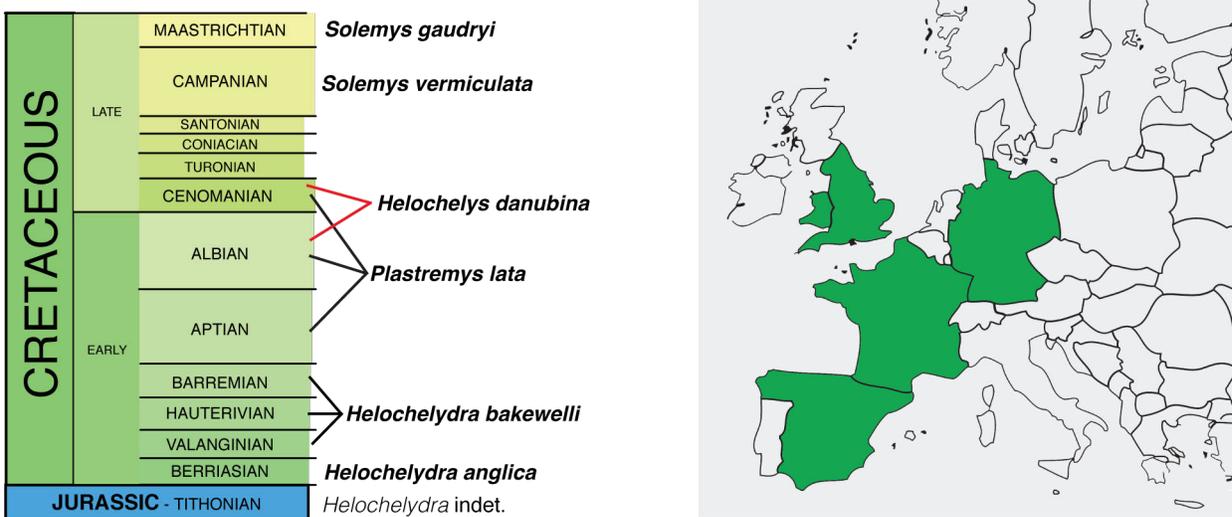


Figure 6: Geochronologic and geographic distribution of European Helochelyrids.

Table 2 European species distribution by stratigraphic identification and Location

Species	Formation and Location
<i>Helochelydra anglica</i>	Purbeck Limestone Group
<i>Helochelydra bakewelli</i>	Cuckfield Stone, Grinstead Clay Member, Tunbridge Wells Sand Formation, Wealden Group (West Susses, UK) Hastings Subgroup (East and West Sussex, UK)
<i>Helochelydra nopcsai</i>	Wessex Formation, Wealden Group (Isle of Wight, UK)
<i>Helochelys danubina</i>	Regensburger Grünsandstein Formation (Kelheim, Germany) Cambridge Greensand, Cambridge, UK Nouvelle-Aquitaine, France Castilla-La Mancha, Spain
<i>Plastremys lata</i>	Upper Greensand Formation (Isle of Wight, UK) Cambridge, UK Dorset, UK Aragon, Spain Nouvelle-Aquitaine, France
<i>Solemys vermiculata</i>	Laño locality, Condado de Treviño, Castile and León, Spain
<i>Solemys gaudryi</i>	Rognac, Bouches-du-Rhône, France

In contrast to the advancements recently made in refining the taxonomy of European helochelydrids, the taxonomy of North American helochelydrid materials is understudied and, given the proposed temporal and geographic scope of the single North American species: *Naomichelys speciosa*, undoubtedly incorrect (Joyce 2017). One abstract published from the Proceedings of the 2010 Annual Meeting of the Society for Vertebrate Paleontology indicates a new genus and species has been identified from the Santonian Haslam Formation of Vancouver Island (Larson et al. 2010). However, an official publication describing and naming this specimen is yet to be published.

Described material for North American Helochelydridae includes the type specimen of *Naomichelys speciosa* consisting of an isolated entoplastron (AMNH 6136, Hay 1908) and a nearly complete specimen cf. *Naomichelys speciosa* (FMNH PR 273) sensu Joyce et al (2014).

A variety of publications make note of specimens referred to Helochelydridae only to acknowledge the presence of this group in a particular formation. For example, Kranz (1998) published on turtles from the Aptian Arundel FM of Maryland with an illustration cf. *Naomichelys sp.* based on papillated shell texture alone. Published literature provides evidence of helochelydrids (solemydid, or *N. Speciosa*) in twenty-one formations in North America and are summarized in Table 3.

Currently there are no reported specimens from the Jurassic in North America. The type specimen of *N. speciosa* was collected by Barnum Brown in 1904 at a site “25 miles east of Pryor Mountain Montana” and was reported to be within the Jurassic Morrison Formation at the time. However, a reassessment of the locality (Figure 7) places it within the Early Cretaceous (Aptian) Kootenai Formation (Joyce et al 2011). With this determination, the geologic record in North America currently dates back to the Aptian and continues to the end of the Campanian, and possibly into the Maastrichtian. This is a significant delay from European helochelydrids, indicating a European origin, and supports the hypothesis of Brikiatis (2016) that a land bridge during the Hauterivian/Barremian existed connecting Northwestern Europe and North America.



Figure 7: Cropped image of Google earth map with Kootenai outcrop overlay in blue. Pink line represents 25 miles east of Pryor Montana along existing road.

Once helochelydrids radiated into North America, their distribution follows fossiliferous formations of the Western Interior Basin (Figure 8) with most records recovered from formations that would have been along the western shore of the Western Interior Seaway. The oldest recovered North American helochelydrid is from the Aptian Arundel Formation of Maryland.

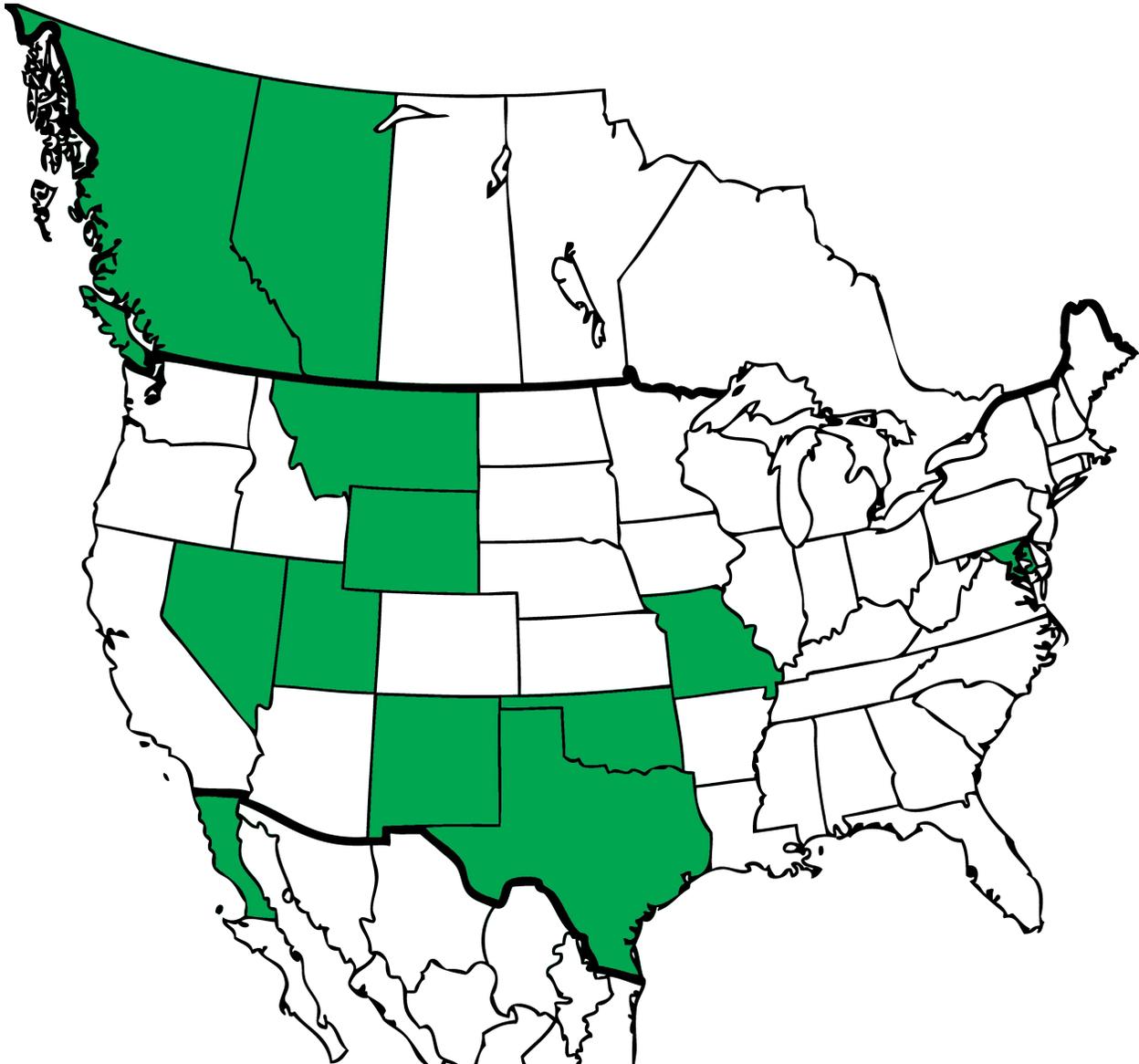


Figure 8: North American States and provinces where *Naomichelys* has been reported highlighted in green. In Canada – British Columbia (BC), Alberta (AB); In the United States – Montana (MT), Wyoming (WY), Utah (UT), Nevada (NV), New Mexico (NM), Texas (TX), Oklahoma (OK), Missouri (MO), Maryland (MD); In Mexico – Baja (BA).

Table 3 Summary of North American distribution of published occurrences of helochelydrid turtles by geologic age and formation.

Geologic Age Range	Formation and Location
Maastrichtian 72.1-66 Ma	<i>Missouri</i> (Fix and Darrough 2004), actual formation unclear
Campanian 83.6 – 72.1 Ma	<i>Foremost Formation of Alberta</i> (Peng et al. 2001; Scheyer and Anquetin 2008; Joyce et al. 2011; Scheyer et al. 2015),
	<i>Wahweap Formation of Utah</i> (Joyce et al. 2011),
	<i>Mesaverde Formation of Wyoming</i> (Demar and Breithaupt 2006),
	<i>Menefee Formation of New Mexico</i> (Joyce et al. 2011; Lichtig and Lucas 2015),
	<i>Two Medicine Formation of Montana</i> (Joyce et al. 2011). <i>El Gallo Formation of Baja California</i> (Lopez 2018)
Santonian–Campanian 86.3 – 72.1 Ma	<i>Milk River Formation of Alberta</i> (Brinkman 2003; Joyce et al. 2011)
Santonian 86.3 – 83.6 Ma	<i>Haslam Formation of British Columbia</i> (Larson et al. 2010)
Turonian–Santonian 93.9 – 83.6 Ma	<i>Straight Cliffs Formation of Utah</i> (Joyce et al. 2011)
	<i>Tropic Shale of Utah</i> (Albright et al. 2013)
Turonian 93.9 – 89.8 Ma	<i>Kaskapau Formation of British Columbia</i> (Rylaarsdam et al. 2006)
	<i>Iron Spring Formation of Utah</i> (Eaton et al. 2001), the
Cenomanian 100 – 93.9 Ma	<i>Dunvegan Formation of Alberta</i> (Larson et al. 2010),
Albian–Cenomanian 113 – 93.9 Ma	<i>Cedar Mountain Formation of Utah</i> (Joyce et al. 2011).
Albian 113 – 100 Ma	<i>Willow Tank Formation of Nevada</i> (Bonde et al. 2008);
Aptian-Albian 126 – 100 Ma	<i>Antlers Formation of Oklahoma</i> (Cifelli et al. 1997),
	<i>Trinity Group (Paluxy Formation)</i> of Texas (Jacobs et al. 1991; Scheyer and Anquetin 2008; Joyce et al. 2014; Scheyer et al. 2015)
Aptian 126 – 113 Ma	<i>Arundel Formation of Maryland</i> (Kranz 1998)
	<i>Kootenai Formation of Montana</i> (Joyce et al 2011)
	<i>Cloverly Formation of Montana</i> (Hay 1908; Ostrom 1970; Oreska et al. 2013) and <i>Wyoming</i> (Oreska et al. 2013)

New Helochelydrid Specimens

Recently, three new specimens were discovered in the Cedar Mountain Formation, Mussentuchit Member (NCSM 33431, NCSM 33526, FMNH PR 3895). These three specimens were discovered at separate localities no greater than three miles apart in Emery County Utah (Figure 9). Additional fragmentary helochelydrid material has been collected from multiple localities in the Mussentuchit without diagnostic material other than shell pattern.

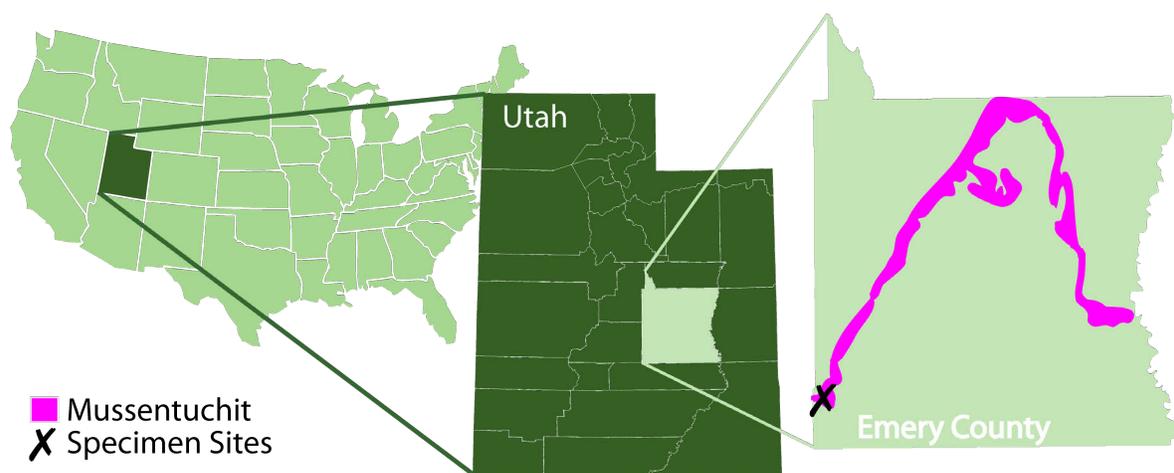


Figure 9: General locality of Mussentuchit specimens, and illustration of Mussentuchit outcrop in Utah.

The Mussentuchit is the uppermost member of the Cedar Mountain Formation and is identified by characteristic light grey to grey mudstones to silty or sandy mudstones. The lower portions of the Mussentuchit are interbedded fluvial deposits grading finer upward, with more massive mudstones predominant at the uppermost deposits (Garrison et al. 2007). Capping these sediments are the tan and brown to reddish sandstone blocks of the Naturita Formation. The separation between the two represents an unconformity of missing time (Figure 10). The Mussentuchit is underlain by the Ruby Ranch Member of the Cedar Mountain Formation and is easily diagnosed by abundant jagged carbonate clasts in grey to reddish/purple muddy-

silty sandstone sediments. The sediments are such that most flora is unable to take root, leaving a somewhat barren landscape to prospect for eroding fossils (Figure 10). Erosional surfaces are medium to steep sloped, and capped by the Naturita Sandstone that often erodes in blocks. Two of the three sites sit on land managed by the United States Department of the Interior, Bureau of Land Management (BLM) Utah State Office (NCSM 33431, and FMNH PR 3895). The third locality sits on land administered by the State of Utah, Trust Lands Administration (NCSM 33526). Collection at each of these sites was approved by permit through the associated managing authority.

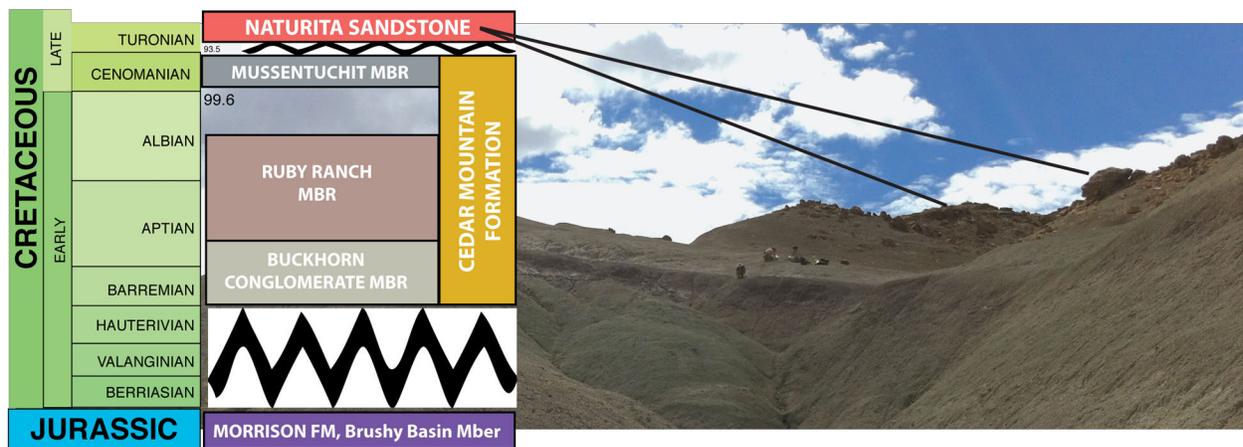


Figure 10: Geochronostratigraphic column showing placement of Mussentuchit Member of Cedar Mountain Formation within the Cretaceous. Right side: image of typical Mussentuchit outcrop and capping Naturita Sandstone Formation boulders.

During a prospecting expedition in 2012 a microsite, dubbed “Kate’s Ridge” after the discoverer Kate Dzikiewicz, was discovered along high narrow ridge very typical of the Mussentuchit lithology. Specimens collected at the site include dinosaurian eggshell fragments, gar scales, crocodylomorph teeth and osteoderm, and helochelydrid shell fragments, in conjunction with other fragmentary material typical of the Mussentuchit fauna (Cifelli et al, 1999). This site sits adjacent to, but up section from the recently described diminutive

tyrannosauroid *Moros intrepidus* (Zanno et al. 2019) also discovered in 2012. Upon further survey of Kate's Ridge, an isolated helochelydrid entoplastron was located by L. Zanno eroding from the bedrock and partially disarticulated (Figure 11).

After reassembly and preparation the specimen proved to be remarkably complete, with only small portions missing on the upper right and left edges. Most importantly, it permits detailed comparison with the holotype specimen of *N. speciosa*, itself an isolated entoplastron, unlike many fragmentary helochelydrid specimens from the continent.



Figure 11: Helochelydrid entoplastron, NCSM 33526, as discovered in the field (left) and reassembled (right).

The collection of the Kate's Ridge specimen coincided with two additional significant Mussentuchit discoveries. These three specimens are described herein and provide adequate morphologic evidence to support the presence of a unique species of helochelydrid in the Mussentuchit Member of the Cedar Mountain Formation. Here I describe and illustrate these new specimens as well as provide comparative material to support this hypothesis. Both FMNH PR 3895 and NCSM 33431 have undergone extensive and time-consuming preparation to reveal

morphologic disparities between localities and published specimens. Preparation of FMNH PR273 is complete, and NCSM 33431 requires further preparation for final description and diagnosis. Comparative material is provided by way of onsite visits to collections, specimens taken on loan, and a review of literature. None of the European specimens were viewed in person.

MATERIALS AND METHODS

New Mussentuchit Specimens

“Kate’s Ridge Taxon” NCSM 33526

Elements: Consists of an isolated entoplastron and one small fragment of shell with diagnostic helochelydrid patterning.

Collection History: This specimen was discovered by Lindsay Zanno in 2012 as a fragmented element eroding on the surface but only slightly scattered. It was collected from the erosional surface and subsurface and brought back to the lab for reassembly (see Figure 1).

Preparation History: NCSM 33526 was prepared by the author, Lisa Herzog. The preparation process largely consisted of cleaning the joining surfaces of sediment and adhering the broken elements together using archival materials. Some minor preparation was done on surfaces to remove any remaining sediment and exposing the granulated surface.

“Dory” – NCSM 33431

Elements: This specimen consists of large portions of shell and plastron, tibia, fibula, femur, osteoderms, carpals/tarsals and skull elements.

Collection History: Lindsay Zanno discovered this specimen within the Mussentuchit Member of the Cedar Mountain Formation in 2012. A significant number of fragments were exposed near the crest of a long sloping barren bluff and concentrated in erosional rivulets. Surface material was collected in an informal grid pattern by excavation participants Paul Brinkman, Kate Dzikiewicz, and Nathan Schiff, and brought back to the museum for any possible reassembly. The site was fully excavated in the summer of 2013 by Zanno expedition participants Lisa Herzog, Ashley Biscoe, and Erin Avery. Excavation of the site proceeded with successful

trenching of the perimeter of present bone. One field jacket was planned; however, a second smaller jacket was required to capture elements deep to the main jacket. The quarry consisted of one helochelydrid individual and all materials were collected. The Specimen is preserved in one large mass and did not require element mapping, however rough drawings and photos of the site were taken.

Preparation History: This specimen has been in the process of preparation since its arrival at the Paleontology Research Lab of the North Carolina Museum of Natural Sciences in 2013. It has undergone many hundreds of hours of preparation to identify diagnostic elements of both the shell and axial skeleton. Key components are described here. Volunteers Nancy Webb, Dick Webb and Kaitlyn Whittaker assisted in the frustrating process of attempting to find matching pieces among the hundreds of surface fragments collected. Volunteers Erin Avery, Ashley Biscoe, and Kaitlyn Whittaker assisted in early preparation and the author, Lisa Herzog, performed the majority of the ongoing preparation. At the time of writing, this specimen is still undergoing preparation. Fragmentary skull elements have been discovered that are still embedded in the mashed up shell; however, preparation cannot be completed in time to include complete data in this thesis.

FMNH PR 3895

Elements: Specimen is comprised of a disarticulated shell, plastron and several axial elements that include the following: complete nuchal; left costals I and II; right costals I, II, III, IV, and V; neural III; multiple fragmentary indet. Peripherals; right and left humerus; left hyoplastron and mesoplastron; right hyoplastron, hypoplastron, and xiphoplastron; left and right humerus; phalanx; and left pubis (Figure 12 and 13).

Collecting History: This specimen was collected from a multitaxon bone bed consisting of both highly fragmented and semi-complete skeletal elements of turtle, crocodile, and dinosaur. The site was discovered and excavated by Peter Makovicky of The Field Museum, Chief Preparator and field assistant Akiko Shinya, and crew. The site is expansive, with a bone-bearing horizon at least 20 feet long. Collection from the quarry was done in reference to a meter grid. Material removed was mapped either individually or by field jacket. Isolated turtle elements and field jackets containing significant turtle material was taken on loan from The Field Museum to the North Carolina Museum of Natural Sciences for preparation and research as a part of this thesis.

Preparation History: This specimen was prepared in the Paleontology Research Lab at the North Carolina Museum of Natural Sciences by L. Herzog. Preparation procedure included the use of carbide needle, air scribe, and micro abrasion with sodium bicarbonate. Paraloid B-72 dissolved in acetone was used as both consolidant and adhesive and is reversible. Preparation was done with the aid of a microscope. This specimen is fairly well preserved; however, it required significant reassembly of clean breaks.

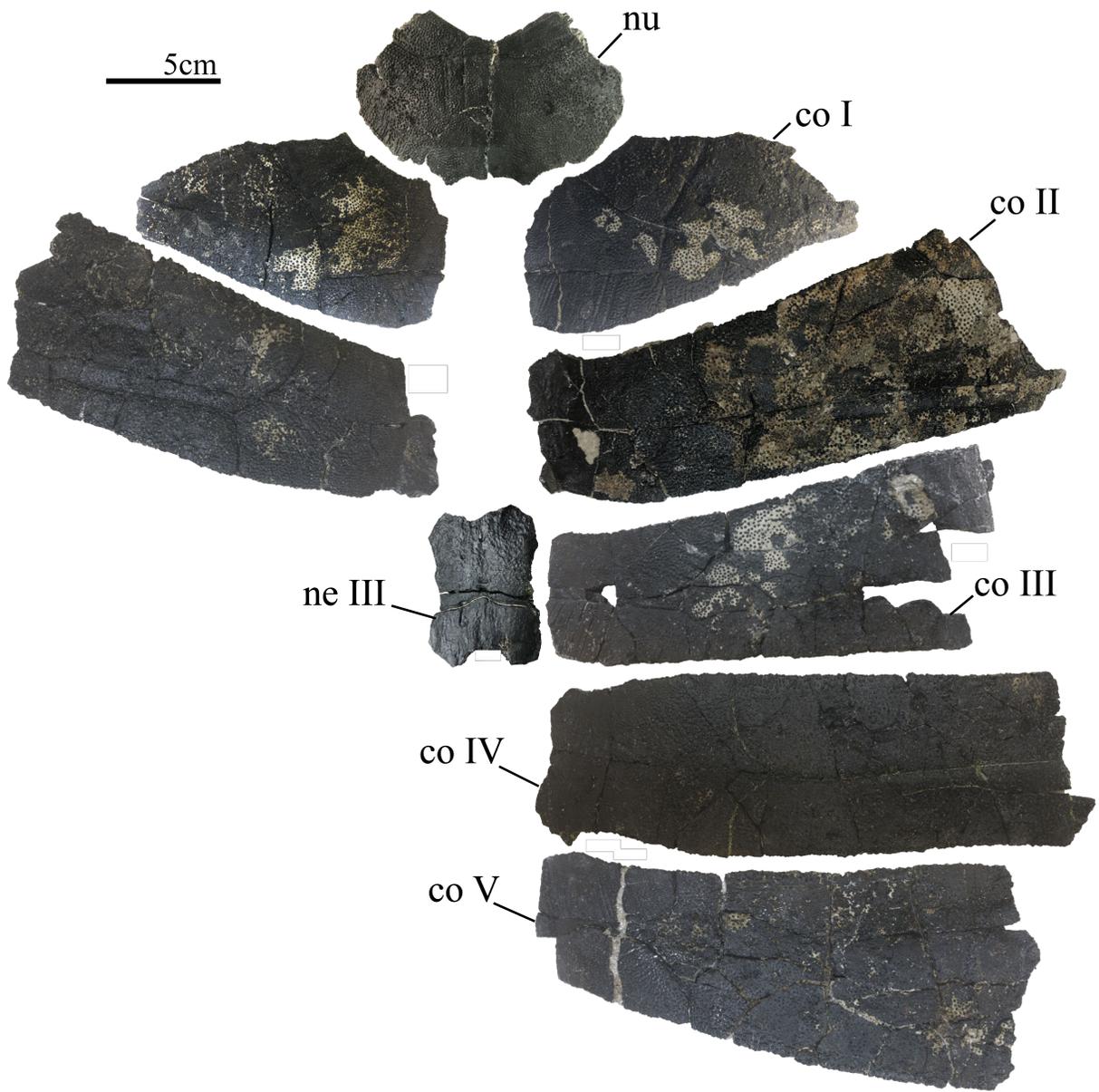


Figure 12: Composite illustration of FMNH PR 3895 carapace dorsal view. Abbreviation co=costal, ne=neural, nu=nuchal.

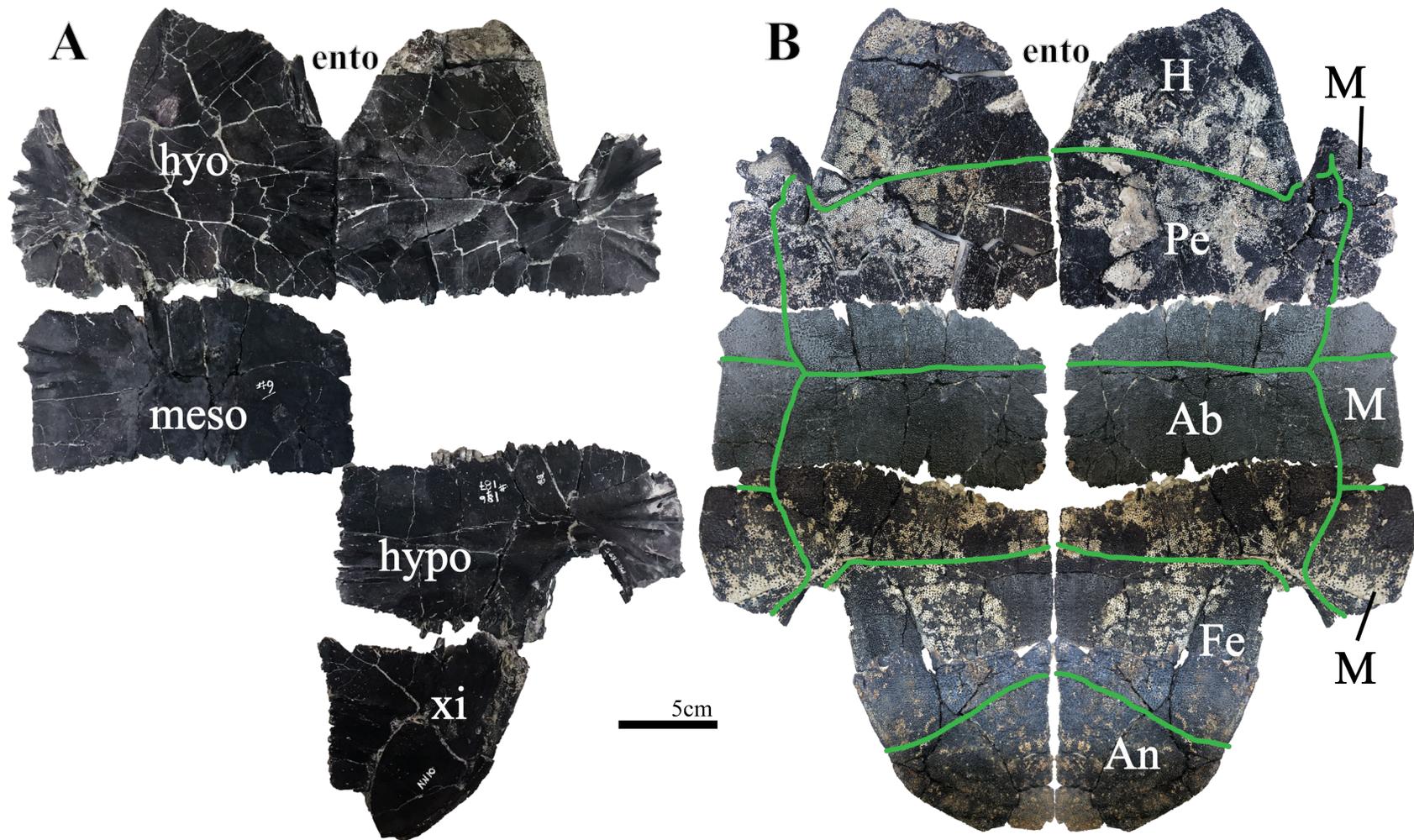


Figure 13: Plastron of FMNH PR 3895 in A, dorsal and B, ventral view. In ventral view the left hyoplastron, left mesoplastron, right hypoplastron and right xiphiplastron are mirrored to illustrate scute margins. Green lines represent scute margins. Abbreviations: ento=entoplastron, hyo=hyoplastron, me=mesoplastron, hypo=hypoplastron, xi=xiphiplastron, H=humeral, Pe=pectoral, Ab=abdominal, Fe=femoral, M=marginal.

NCSM 33380

Element: Shell fragment with diagnostic helochelydrid pattern.

Collection history: Collected from Microsite “Cliffs of Insanity”

Preparation history: This specimen was isolated from materials collected in bulk from microsite, screenwashed and sorted. A histological sample was prepared by Haviv Avrahami for a separate project with the methodology described in detail in Avrahami 2019.

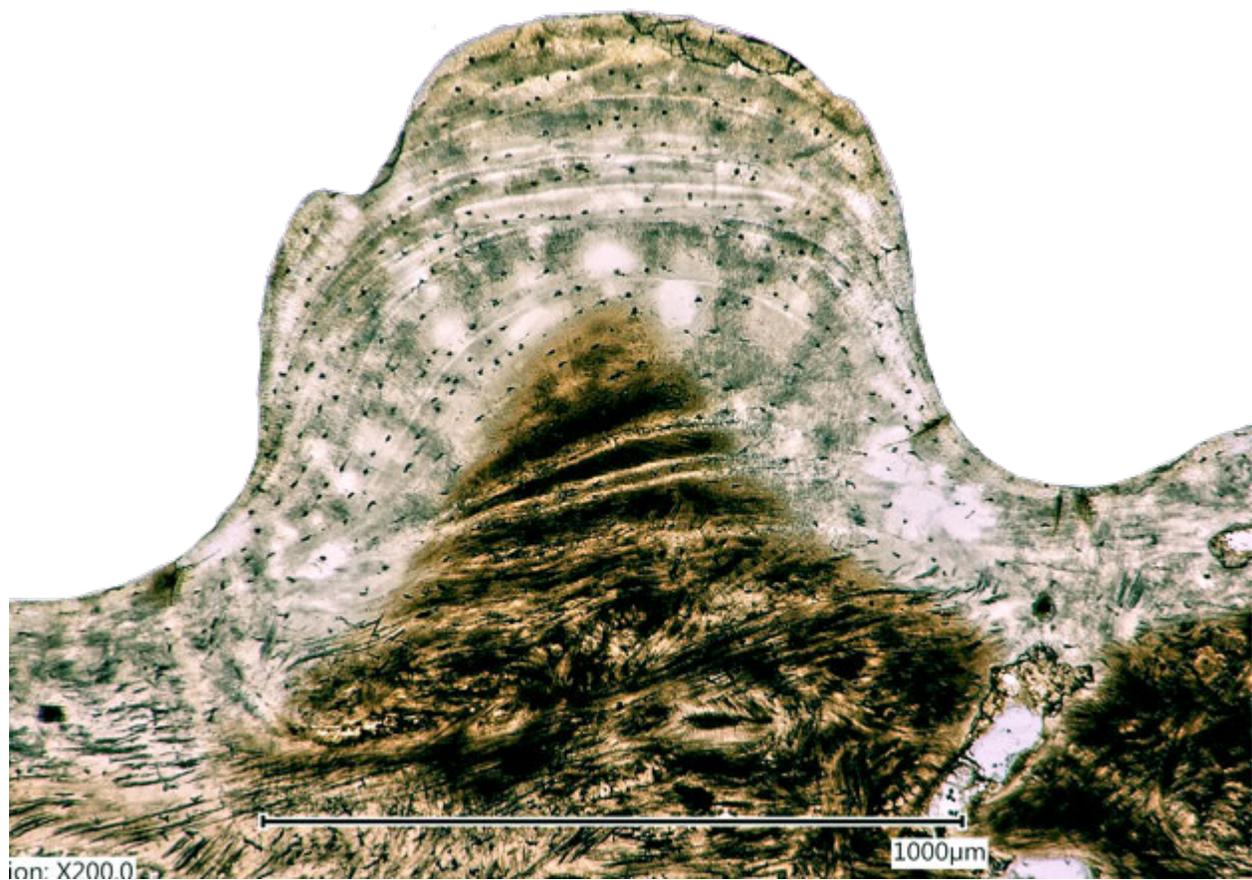


Figure 14: Highly magnified helochelydrid histological slide of a single pustule from a Mussentuchit microsite. Specimen NCSM 33380.

Comparative material and data collection

The North American occurrences of Helochelydrid specimens were identified and studied through review of published literature, online databases searches, and collection visits. Online resources for specimen data include the Paleobiology Database (paleobiologydb.org), Fossilworks (fossilworks.org), and institutional repositories with searchable database portals.

For visual comparative analysis and measurement, the collections of the American Museum of Natural History (AMNH), National Museum of Natural History (NMNH), Oklahoma Museum of Natural History (OMNH), University of California Museum of Paleontology (UCMP), Texas Memorial Museum at University of Texas at Austin (TMM), and Field Museum of Natural History (FMNH) were visited. All specimens catalogued as *Naomichelys*, solemydid or helochelydrid were reviewed. Additionally, Yale Peabody Museum specimens (YPM) were graciously photographed by Marilyn Fox and reviewed. Two specimens were selected as promising and received via mail on loan for use in this study.

Field Museum of Natural History

FMNH PR 273

cf. *Naomichelys speciosa*

Montague County, Texas USA

Collected in 1952 from the Trinity Group, Antlers Formation

Elements: Nearly complete specimen including skull, jaws, carapace, plastron, limb bones, several osteoderms

Description: The skull and jaws are partially complete, with plaster reconstruction in missing areas. The carapace is on view in the “Evolving Planet” exhibit at The Field Museum, but was

removed for study. Plaster reconstruction on the carapace and plastron was painted, presumably for display purposes, making some of the morphology difficult to discern. Additionally, lines have been drawn on the carapace and plastron to indicate sutures and sulci. Some preparation was undertaken of the nuchal notch area to remove plaster obscuring morphology important for comparative analysis. Likewise, the plastron had been prepared and partially reconstructed with plaster and painted, obscuring important morphological characters of the entoplastron. Removal of additive plaster was conducted for comparative analysis. Additional preparation is needed to fully reveal the entoplastral sutural margins, however, Adrienne Stroup of FMNH kindly took digital x-rays of the plastron that provide additional clarity. The axial skeleton has been completely prepared without reconstruction. All elements were examined, photographed and measured for comparison with elements of FMNH PR 3895.

FMNH PR 2360

cf. *Naomichelys speciosa*

Park County, Wyoming, USA

Collected in 2004 from the Hines Member of the Cloverly Formation

Elements: Costal

Description: This specimen consists of an isolated costal exhibiting the diagnostic shell pattern of helochelydrid turtles (Figure 15). It shares gross morphology with AMNH 3039, also from the Cloverly Formation (see Figure 17). It was taken on loan from The Field Museum and prepared by me. The specimen measures 24.5cm wide, 4.7cm tall proximally and 6.2cm tall distally.



Figure 15: FMNH PR 2360 isolated costal from the Cloverly Formation of Wyoming. Black bar represents 1cm.

American Museum of Natural History (AMNH)

AMNH 6136

Naomichelys speciosa Type

25 miles east of Pryor, Montana USA

Collected by Barnum Brown 1904, who reported it to be from the Jurassic Morrison Formation

Elements: Entoplastron

Description: The type specimen of *N. speciosa* consists of an isolated entoplastron that is well preserved. It is missing the uppermost point that restricts the ability to make a complete length measurement, however it can be estimated by projecting the angled lines to a common junction, based on the structure shared by other stem testudines. The left and right lateral points also exhibit a broken edge that implies missing data. Given the overall structure this likely represents only a small fraction of the total. The dorsal surface exhibits typical structure for the entoplastron in other stem testudines with lateral ridges close to the midline and trending posteriorly to join near the posterior most point. Ridge line angles gradually without forming an extensive horizontal line. The dorsal surface exhibits elongate striations starting near the apex and radiating out towards the lateral ridge. The ventral surface exhibits well-developed tubercles across the entire area with a ~1mm smooth margin around the edge. Pustules are dislocated near the top within the boundaries of the intergular (entoplastral) scute. Portions of five scutes are represented: left and right humeral, left and right gular and left and right intergular. Sulcus creating intergular beginning slightly off center of the lowermost point (right side of image, left site anatomically). The intergular is incomplete anteriorly, however, it appears that the intergular would be entirely contained on the entoplastron.

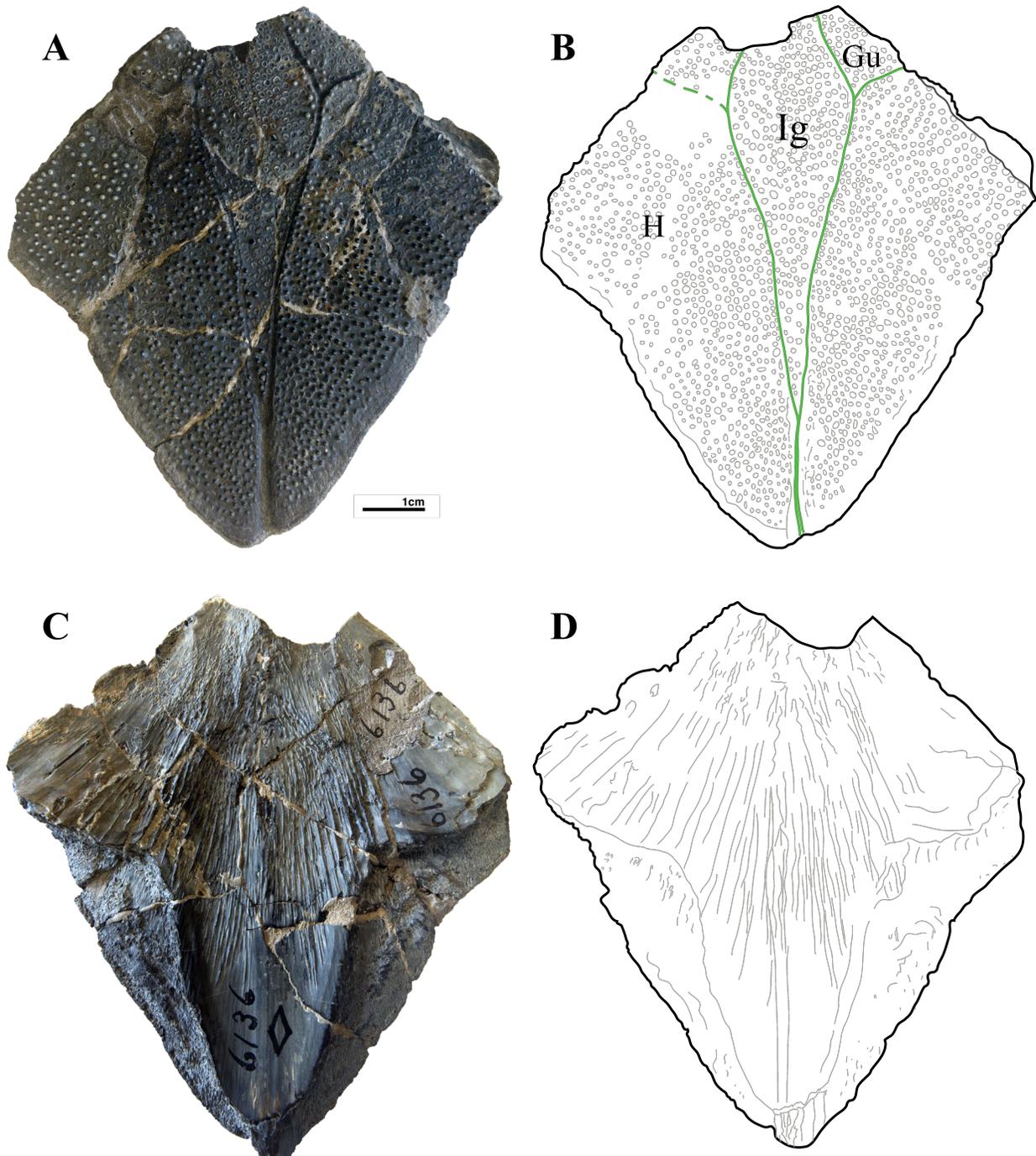


Figure 16: AMNH 6136 *Naomichelys speciosa* (Hay 1908) type specimen in ventral (A-B) and dorsal (C-D) views with line drawings detailing structural morphology. Green lines represent scute sulci. Gu=gular, H=humeral, and Ig=intergular.

AMNH 3039

Helopanoplia sp. (Original, B. Brown 1932)

Naomichelys (J.H.H. 1979); *Naomichelys* (= *Tretosternon*) Hirayama 1997

Cloverly Formation, Albian, Montana USA

Elements: Right fourth costal (per Hirayama 1997), plus one small fragment

Description: The costal is 24 cm wide at the center, 5.1 cm tall at medial end, and 6.3 cm tall at the distal end. The specimen is broken into five pieces with a natural fit. The specimen is clearly a helochelydrid based the vermiculated surface texture. It is comparable to FMNH PR 273 but some of the sulcus is obscured by remaining Cloverly clay sediment and surface consolidant. Along the longitudinal sulcus the specimen bears a raised ridge running the transverse width of the costal. The dorsal surface is textured and undulating. This morphology is more characteristic of larger (more mature) individuals.



Figure 17: Photograph of AMNH 3039 isolated costal with broken pieces aligned. **A**, dorsal surface; **B**, ventral.

AMNH 14588

Naomichelys (institutional diagnosis)

“turtle fragments from Cretaceous strata in Missouri. Collected Gaffney, March 1975

Near Lutesville, Bollinger Co., Missouri USA

Elements: collection of shell fragments.

Description: Fragments are notable for their pustule morphology. The raised bumps are well formed and uniformly dome shaped (without a flattened apex). Each bump is distinct with no coalescence (see Figure 18-B).

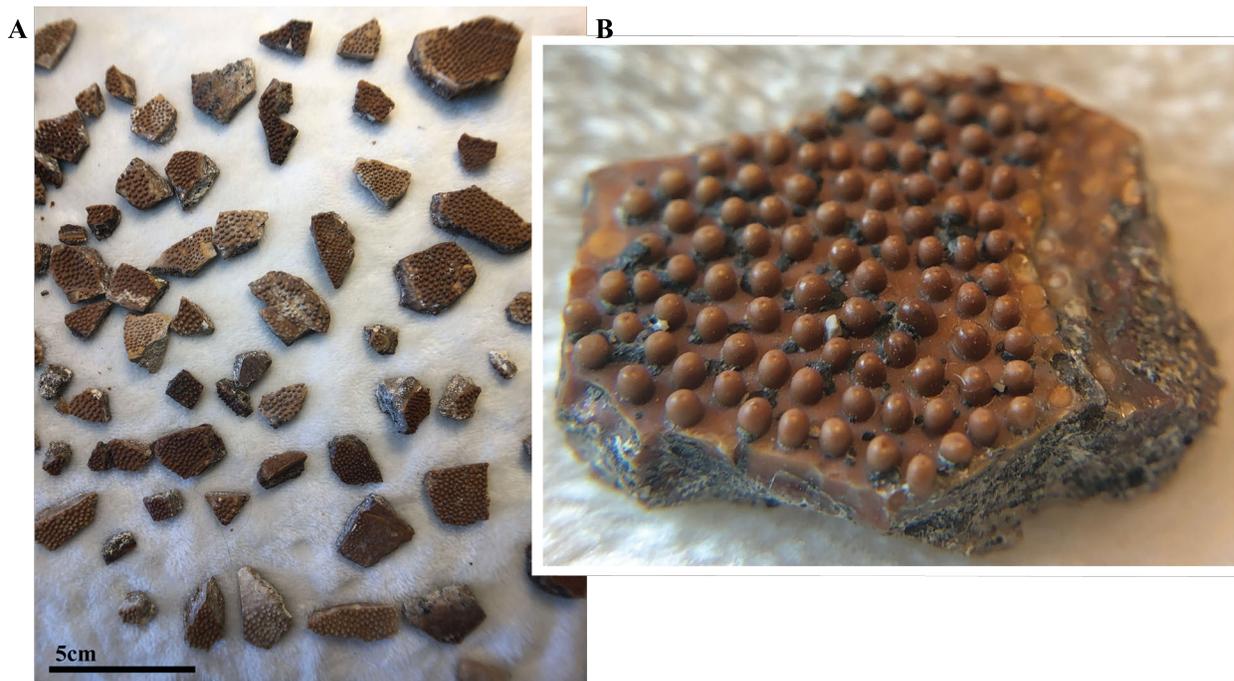


Figure 18: Bollinger Co, Missouri USA Cretaceous specimen AMNH 14588. **A**, Overview of shell fragments collected; and **B**, close up of shell patterning.

University of Texas at Austin (TMM)

TMM 40488-1

Compsemys sp. (original diagnosis)

Naomichelys (J.H. Hutchinson, 1989)

Milk River Fm. Cretaceous

Milk River, Alberta Canada

From National Museum of Canada, L.S. Russell

Element: two pieces of indet. Carapace fragment, one ~7cm x 3cm, the other ~1cm x 2cm

Description: Well-defined tubercles, many dislocated leaving rounded scars. The tubercles do not coalesce.

TMM 40945-5

Naomichelys sp.

Shell fragments

Upper Paluxy Formation, Lower Cretaceous

Triconodont Gully, Montague County, Texas USA

WL376 (Trinity Group, Albian)

Langston, 1974

Elements: Nine indeterminate plastron fragments, ranging in size from ~1cm to ~4cm

Description: Fragments are thin. One bears an unfused suture. Pustules are rounded with little dislocation. Only a few minor coalescing vermiculations are observed.

TMM 41649-2

Naomichelys shell fragments

Upper member Yucca Formation,

Lower Cretaceous

Quitman Mountains, Hudspeth County, Texas USA

Campbell, 1965

Elements: 19 indeterminate fragments of carapace or plastron

Description: Elements collected in blocks, one block cut for sectioning and showing cross section of pustules raising above surface. Sizes range from ~3cm to ~13cm. Other than cutting for sectioning, it does not appear that any preparation has been done on these specimens. Clearly defined vermiculations with no coalescing are present.

TMM 42866-1

cf. *Naomichelys* (TMM card diagnosis)

Compsemys (Herzog, this thesis)

Cretaceous, Georgetown

Texas Crushed Stone Quarry

Williamson County, Texas USA

Elements: Costal fragments

Description: This specimen is misdiagnosed. The shell pattern more closely matches *Compsemys*.

Oklahoma Museum of Natural History (OMNH)

OMNH 21865

Naomichelys sp.

Kane County, Utah USA

Wahweap Formation, Late Cretaceous, Campanian

Element: Osteoderm

Description: Well preserved complete osteoderm

comparable to FMNH PR 273 osteoderms. Some pustules,

and many surface scars from dislocation. The specimen measures ~1.5 cm x 1 cm at the base.



Figure 19: OMNH 21865 osteoderm

OMNH 28896

Naomichelys sp.

Emery County, Utah USA

Cedar Mountain Formation, Mussentuchit Member, Albian-Cenomanian

Element: Proximal right humerus

Description: Severely weathered proximal end matching gross morphology of FMNH PR 33895.

OMNH 66937

Naomichelys sp.

Big Horn County, Montana USA

Cloverly FM, Aptian-Albian

Elements: 62 shell fragments characteristic of helochelydrids. One nearly complete neural exhibiting longitudinal midline keel.

UCMP 324043

Chelonia Naomichelys

Montana Hill Co.

Judith River Fm. Campanian

M. Goodwin, 1981

Element: One small shell fragment

Description: Diagnostic by shell patterning only. Distinct tubercles, no coalescing, non-dislocated. Fragment measures approximately 1 cm x 1.5 cm.

UCMP 32404

Naomichelys

Liberty County, Montana USA

Judith River Formation, Campanian

L. Wright, 1981

Element: One small shell fragment

Description: Diagnostic by shell patterning only. Distinct tubercles, no coalescing, non-dislocated. Fragment measures ~1cm x 1.5cm

Smithsonian Institution, United States Natural History Museum (USNM)

USNM 546274

Naomichelys speciosa

Carbon County, Montana USA

Cloverly Formation, Albian

Collected 2010

Elements: 11 small fragments of shell

Description: Small fragments of shell (probably carapace). One fragment of costal is also included. The surface texture is typical of Cloverly Formation: slightly undulating with pustules with some coalescing towards suture edges.

USNM 546454

Naomichelys speciosa

Big Horn County, Wyoming USA

Cloverly Formation, Albian

Elements: Partial hypo/hyoplastron

Description: Mostly non-coalescing vermiculations along outer margin with some possible at anterior/posterior suture margin. Only one suture margin present on lateral edge, all others margins with broken edge. No obvious pattern of tubercles.

USNM 546760

Naomichelys speciosa

Big Horn County, Wyoming USA

Cloverly Formation, Albian

Elements: Nearly complete left epiplastron(?).

Description: Possible large bite marks are observed, suggesting predation. Well-developed pustulated surface, with little to no dislocation, and some coalescing near sutures perpendicular to margin.

USNM 546304

Naomichelys speciosa

Big Horn County, Wyoming USA

Cloverly Formation, Albian

Elements: Partial hyo/hypo plastron

Description: Worn and fragmented piece showing significant parallel striations/grooves on surface trending towards suture edge as seen in FMNH PR 3895. Pustules are low and spaced apart with little to no dislocation. No evidence of coalescing, but a general trend of alignment with the parallel striations/grooves is observed.

USNM 546436

Naomichelys speciosa

Carbon County, Montana USA

Cloverly Formation, Albian

Elements: Six small indeterminate fragments of shell

Description: Tubercles appear to be much more crowded together on four of the six fragments. One piece has a random coalescing pattern, and one piece has spaced out tubercles with some dislocation and scarring.

USNM 547234

Naomichelys speciosa

Big Horn County, Wyoming USA

Cloverly Formation, Albian

Elements: Partial hyoplastron

Description: Half to most of the pustules on this specimen have been dislocated. It is difficult to determine if a pattern was present due to the missing pustules.

USNM 547187

Naomichelys speciosa

Big Horn County, Wyoming USA

Cloverly Formation, Albian

Elements: One small indeterminate fragment of shell

Description: Tubercles appear to be much more crowded together as in 546436. One suture margin with no identifiable patterning. ~1cm x 2cm

USNM PAL 604955

Genus sp (as listed on specimen card)

Helochelydrid indet (Herzog 2019)

Prince Georges County, Maryland USA

Potomac Group, Patuxent Formation, Arundel Clay Member

Elements: Plastron fragment

Description: This specimen is not classified as helochelydrid. Most pustules are dislocated from shell surface. Some pustules are dislocated below surface of shell so that they appear as an indentation or pit. Nonetheless, the specimen is clearly a helochelydrid. Pustules on this specimen trend in a line parallel to the margin of bone without coalescing.

USNM PAL 487146

cf. Naomichelys speciosa?

Prince Georges County, Maryland USA

Potomac Group, Patuxent Formation, Arundel Clay Member

Kranz 1998.

Elements: Shell fragment

Description: Low rounded tubercles are general similar to other helochelydrids shell fragments. Matrix still present on the specimen obscuring low points between vermiculations.

USNM 357132

Naomichelys sp.

New Mexico USA

Upper/Late Cretaceous

Elements: Two indeterminate fragments of shell

Description: No pattern can be observed because the surface texture is obscured by matrix.

Yale Peabody Museum (YPM)

YPM 4900

Naomichelys (Family Baenidae) RH, July 1985

Testudinae? Emyninae?

Cloverly Formation, Late Cretaceous

Elements: Distal and proximal ends of right humerus. Missing shaft.

Description: Partially weathered proximal humerus, broken just distal to the articular surface.

Distal humerus exhibiting well-developed ectepicondylar foramen, ectepicondyle, entepicondyle, capitulum and trochlea. This specimen was collected apart from shell material with diagnostic helochelyrid patterning. However, overall morphology is consistent with that of *N. speciosa* FMNH PR 273.

YPM 5437

Naomichelys speciosa

Big Horn County, Montana USA

Cloverly Expedition 1965

Elements: partial (posterior) entoplastron, right and left humeral heads, proximal femur, carapace fragment, indeterminate bone fragment.

Description: Three elements are of interest for comparative anatomy. The entoplastron consists of posterior corner with single sulcus present running from the posterior corner, longitudinally, to the anterior truncated edge. This provides further support to the *N. speciosa* diagnosis (Hay 1908) of the scute arrangement on the entoplastron (Figure 20-A). The left and right proximal

humeri consist of a mostly complete head, and a partial lateral process is present on the left humerus (Figure 20-B, C).

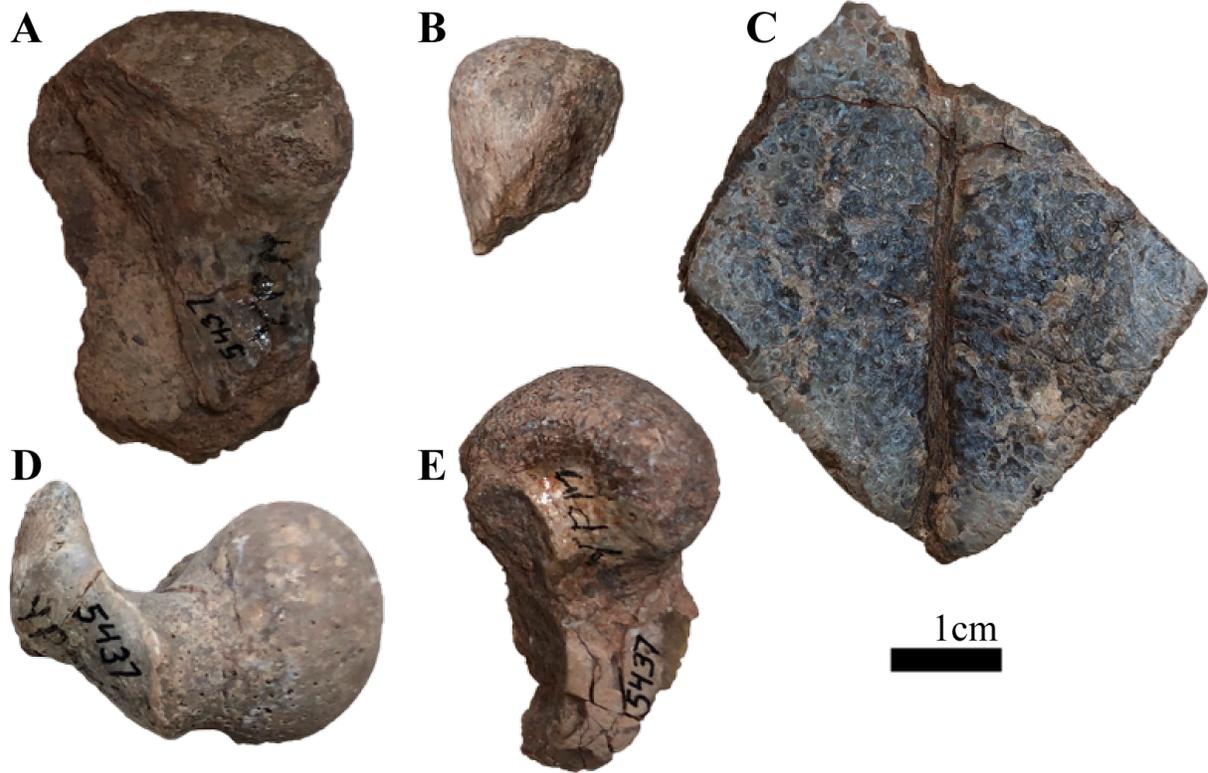


Figure 20: Fragments representing YPM 5437: **A**, proximal right femur in posterior view; **B**, proximal right fibula in lateral view; **C**, posterior portion of entoplastron in dorsal view; **D**, proximal left humerus in proximal view; **E**, proximal right humerus in dorsal view.

Qualitative Morphologic Analysis of Extant Specimens

To determine whether scute position and sulcus placement vary ontogenetically or individually, a qualitative morphologic analysis was performed in a series of specimens from the Herpetology Collections at the North Carolina Museum of Natural Sciences (NCSM). This review included visual confirmation of scute and sulcus placement on the plastral bones in a variety of species (see Table 4). The aim was to qualitatively assess the likelihood that scute positioning exhibits ontogenetic or pathologic variation. The plastron of each specimen was examined to ascertain conformity to the standard diagnosis by species, photographed, then scored as yes (conforms to standard for species) or no (does not conform). Particular interest was focused on the point at which the gular(s) joined with the humerals on the entoplastron, and if any variation occurred in the overlap of the pectorals, humerals and gulars relative to species diagnosis.

In some cases, specimens were preserved in ethanol with scutes in place. In these specimens the keratinous scutes were faded and partially transparent, making the underlying bones and sutures of the plastron discernable. Dry preservation of specimens results in shrinking and curling of scutes to reveal the underlying plastron sutures. Age of the individual at the time of death was unknown for the majority of specimens; therefore, ontogenetic variation within a species was explored by variation in body size as a proxy for age.

Table 4 Preserved specimens of extant species reviewed in the collections of the North Carolina Museum of Natural Sciences

Count	Species	Common Name
25	<i>Chrysemys picta</i>	Painted Turtle
2	<i>Clemmys guttata</i>	Spotted Turtle
20	<i>Deirochelys reticularia</i>	Chicken Turtle
2	<i>Glyptemys muhlenbergii</i>	Bog Turtle
2	<i>Graptemys kohnii</i>	Mississippi Map Turtle
14	<i>Kinosternon subrubrum</i>	Eastern Mud Turtle
9	<i>Sternotherus odoratus</i>	Common Musk Turtle
11	<i>Malaclemys terrapin</i>	Diamondback Terrapin
39	<i>Terrapene carolina</i>	Common Box Turtle
53	<i>Trachemys scripta</i>	Pond Slider
2	<i>Platysternon megacephalum</i>	Big-Headed Turtle
179	Total	

SYSTEMATIC PALEONTOLOGY

Systematic Paleontology

TESTUDINATA, Klein 1760, sensu Joyce et al 2004

MESOCHELYDIA, Joyce 2017

PERICHELYDIA, Joyce 2017

HELOCHELYDRIDAE, Nopcsa 1928

“Kate’s Ridge Taxon”

Holotype: “Kate’s Ridge Taxon” NCSM 33526 consists of a nearly complete isolated entoplastron, and one small fragment of shell.

Horizon and Locality – “Kate’s Ridge Taxon” was found eroding from the Cenomanian age Mussentuchit Member of the Upper Cedar Mountain Formation approximately 12-17 m above the Ruby Ranch contact. The locality lies within Emery County, UT and sits on State of Utah administered land. Institutional locality identity is NCPALEOUT06 and is restricted per State of Utah regulations. Access to additional details is available to qualified researchers through NCSM. The locality is 6-10 m upslope and adjacent to NCPALEOUT05, site of the recently described diminutive tyrannosaur *Moros intrepidus* quarry maximum age dated to 96.4 Ma (Zanno et al 2019). “Kate’s Ridge Taxon” is slightly younger based on superposition. Local lithology of light to medium grey mudstone and silty mudstone indicate a deltaic deposition, possibly within an ephemeral channel or oxbow with accumulation of a micro assemblage. Other taxon from this locality include dinosaur eggshell *Macroelongatoolithus* sp. fragments, gar scales, and crocodylomorph teeth and osteoderm fragments.

Diagnosis – “Kate’s Ridge Taxon” is a helochelydrid turtle diagnosed by the following autapomorphies (Fig. 21 A-E): entoplastron sub-rhombus shaped, margins subequal in length (Figure 21 – C); portions of three scutes represented on ventral surface; intergular scute represented by a sulcus forming a deep V that culminates at the posterior most corner; the arms of the V extend anteriorly to the bone margin. (Figure 21 -B); the center of the V represents the posterior portion of the intergular scute; the lateral left and right of the V represent overlapping the medial margins of the humeral scutes with no anterior humeral sulcus present; ventral surface marked by patterning diagnostic of helochelydrid turtles, with non-coalescing pustules on bone surface underlying the intergular scute and much reduced vermiculations over the bone surface area that would underlie the humeral scutes; dorsal surface exhibits a clearly defined ridge extending horizontally along the midline rhombus angle with a symmetrical sharp posterior downturn just prior to the midline on either side creating a deep V culminating prior to the most posterior point of the rhombus (Figure 21, D and E).

Remarks – The isolated entoplastron was selected to represent the holotype of “Kate’s Ridge Taxon” based on the presence of autapomorphies that can be directly compared to the type specimen of *Naomichelys speciosa* (AMNH 6136; see Figure 16), currently the only other North American helochelydrid named. The type specimen of *N. speciosa* consists of an isolated entoplastron. The most notable *N. speciosa* referred material consists of a nearly complete specimen (FMNH PR 273) and provides comparative material for the specimens referred to “Kate’s Ridge Taxon” listed below.

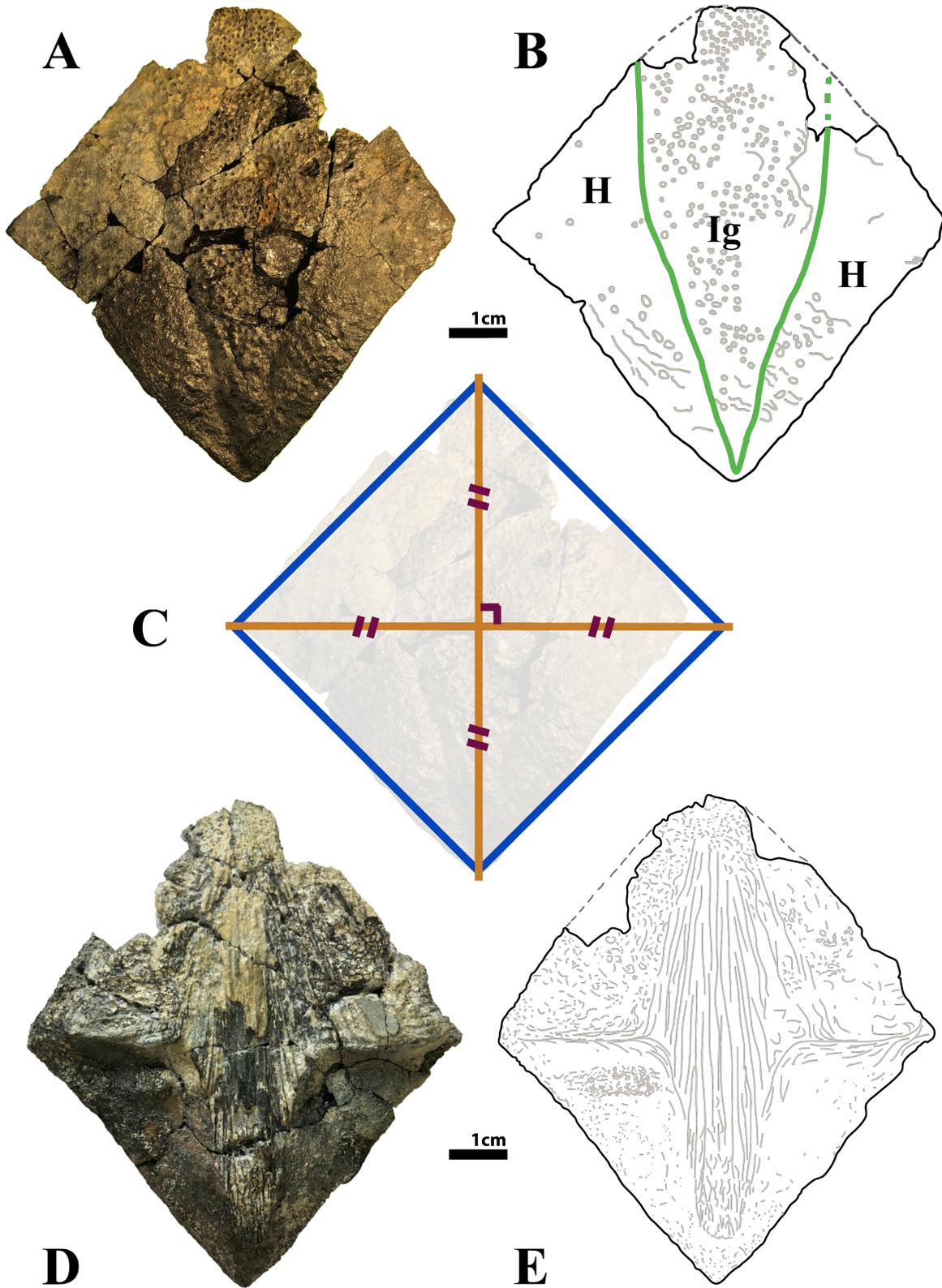


Figure 21: “Kate’s Ridge Taxon” **A** ventral view, **B** ventral view line drawing showing intergular (IG) and humerals (H) sulcus represented by green line, **C** rhombus overlay to highlight overall shape of entoplastron, **D** dorsal view, **E** dorsal view line drawing. Abbreviations: H=humeral, Ig=intergular.

Referred Material

“Dory” NCSM 33431

Consists of a poorly preserved partially complete carapace, plastron, skull and axial skeleton.

Specimen is highly fractured, dislocated and disarticulated.

Horizon and Locality: “Dory” was discovered as significant surface erosion in the Cenomanian age Mussentuchit Member of the Cedar Mountain Formation. The locality lies within Emery County, Utah and sits on federally owned land administered by the Bureau of Land Management. Quarry collection was done under permit UT13-017E. Institutional locality identity is NCPALEOUT07 and is restricted per Federal regulations. Access to additional details is available to qualified researchers through NCSM. Local lithology of light to medium grey mudstone and silty mudstone is near identical to that of “Kate’s Ridge Taxon.” No other taxa were detected from this locality. This site is within 100 meters direct line from NCPALEOUT06, the site of “Kate’s Ridge Taxon.”

Remarks: “Dory” is a helochelydrid turtle referred to “Kate’s ridge taxon” that exhibits the following additional autapomorphies likely to characterize the new genus: Skull parietal/squamosal/postorbital is diagnosed by surface patterning of small tubercles intermixed with larger diameter and taller spikes, and areas with adjacent raised round ridges that first depress inward, then rise close to the center to form a short rugose rounded spike (Figure 22). Additional preparation is still underway to clearly define elements, and uncover comparative material. The entoplastron has not been identified, but may still be present within unprepared material. This specimen is referred to “Kate’s Ridge Taxon” because it possesses the diagnostic

shell patterning of helochelydrid turtles, and due to its geographic and chronostratigraphic proximity to the holotype locality of the new Mussentuchit taxon “Kate’s Ridge Taxon”. These specimens are both recovered from the Mussentuchit Member of the Cedar Mountain formation, and their geographic proximity and lithology are nearly equivalent. However, it is recognized that more than one helochelydrid turtle species may be present in the Mussentuchit Member of the Cedar Mountain Formation, and without overlapping diagnostic skeletal material, this referral is tenuous.

FMNH PR 3895

Disarticulated incomplete carapace and plastron, left and right humerus, right pubis, phalanx, vertebra, astragalus, an additional poorly preserved proximal left humerus.

Horizon and Locality: FMNH PR 3895 was collected as part of a multitaxon bonebed located in Emery County, Utah and sits on Federally owned land administered by the Bureau of Land Management. Quarry collection was done by Peter Makovicky and crew. Elements and field jackets logged and mapped by Akiko Shinya. All materials are repositied in the vertebrate paleontology collection of The Field Museum of Chicago. Access to additional details is available to qualified researchers through FMNH. Quarry is situated within the Mussentuchit Member of the Cedar Mountain Formation and is in the process of being age dated. Lithology is of light to medium grey mudstone and grey to tan silty to sandy mudstone.

Remarks: FMNH PR 3895 is a helochelydrid turtle exhibiting the following additional autapomorphies likely to represent the genus: Nuchal with anterior vertebral I sulcus running

from left lateral edge to right marginal edge that near parallels the upturned shape of the nuchal notch; neural III is near flat and does not exhibit a midline keel; humeri lacking ectepicondylar foramen, poorly developed capitellum/trochlea, and a caput humerus with a dorso-posterior fossa (Figure 23 A-F). This specimen is referred to “Kate’s Ridge Taxon” based on its proximity to the localities of both the holotype, and referred specimen NCSM 33431 “Dory”. These three specimens are all recovered from the Mussentuchit Member of the Cedar Mountain formation, and their geographic proximity and lithology are nearly equivalent.

The available helochelydrid material collected from this quarry has been fully prepared and identified. One poorly preserved proximal left humerus was collected from the erosional surface. This left humerus is similar in size to the complete left and right humeri, but is missing the morphology that would confirm the diagnosis listed above. The remainder of the helochelydrid materials described from this locality likely represent a single individual based on quarry map clustering and preparation of multielement field jackets. The left and right hyoplastron were recovered overlapping one another within a field jacket also containing right costal II (Figure 22). The quarry was not exhausted at last excavation and additional materials may still be in situ. While several of the plastral bones are present, the entoplastron was not recovered (refer to Figure 13).



Figure 22: Field jacked containing “Kate’s Ridge Taxon” FMNH PR 3895 during preparation. Carapace and plastron elements outlined in pink and labeled.

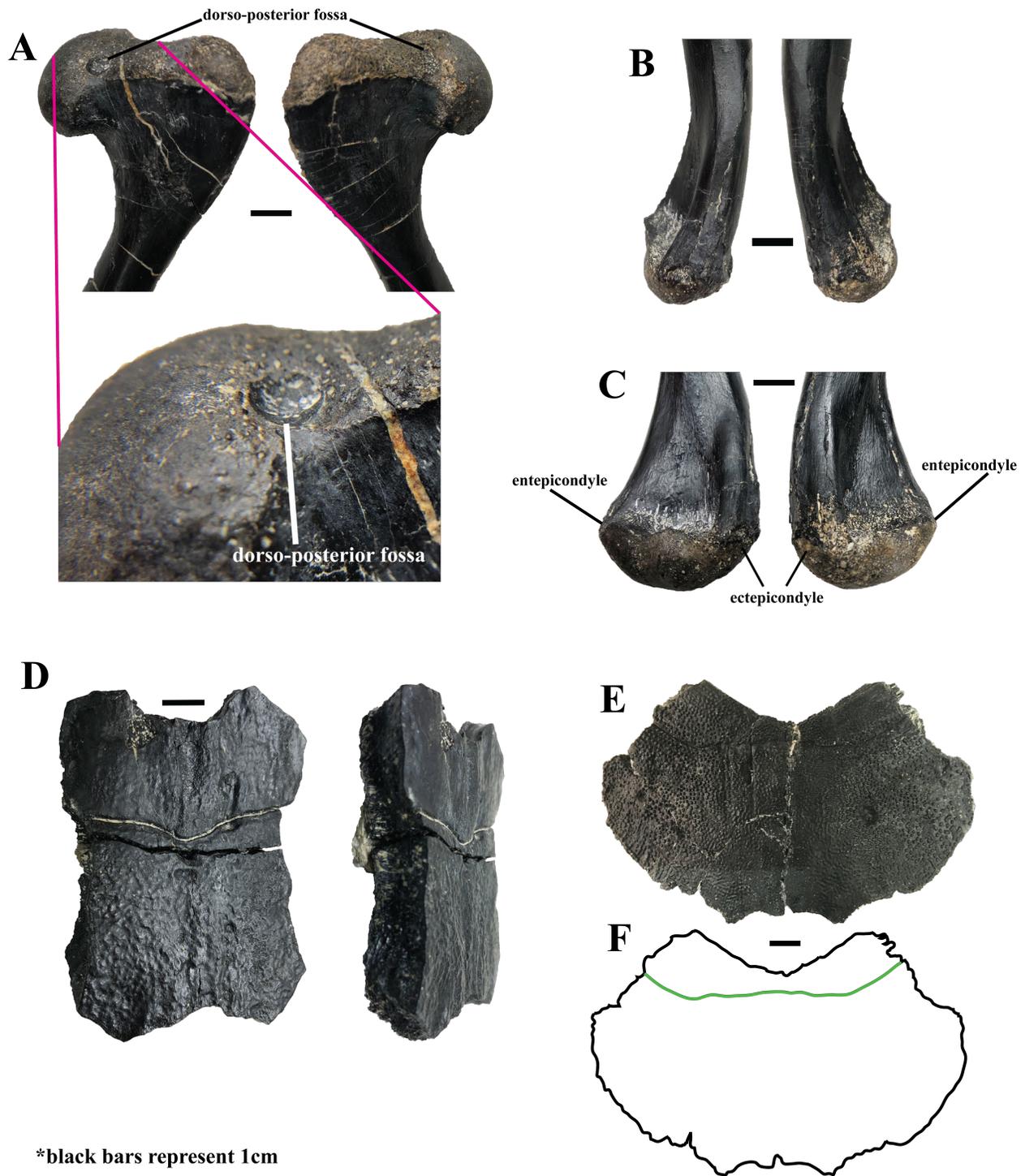


Figure 23: Illustrated examples of FMNH PR 3895 autapomorphies. A, proximal left and right humerus in dorso-posterior view; B, distal left and right humeri anterior view demonstrating lack of ectepicondylar foramen; C distal left and right humeri ventral view demonstrating poorly developed capitellum/trochea and lack of ectepicondylar foramen; D, neural III demonstrating near flat surface topography and lack of raised midline keel in dorsal and oblique dorsal view; E-F, nuchal dorsal view illustrating anterior vertebral I sulcus (green line)

COMPARATIVE OSTEOLOGY

“Kate’s Ridge Taxon” and referred specimens exhibit autapomorphies on the entoplastron, nuchal, and humerus. Here I describe these elements in the new “Kate’s Ridge Taxon” and compare autapomorphies observed with comparative material of both North American specimens and European taxa.

Entoplastron

Kate’s Ridge Taxon: NCSM 33526 is 78mm long x 73.5mm transversely (wide) and is nearly complete. Missing portions include approximately half of the left anterior margin between the corners, and one quarter of the right anterior margin. The ventral surface has missing bone along some of the fracture lines but without losing fidelity of the V-shaped intergular sulcus. The right arm of the V-shaped intergular sulcus is more pronounced than the left due to the missing surface bone. Helochelydrid patterning is best developed on the proximal most aspect and diminishes toward the periphery. The dorsal surface contains fewer missing bone fragments. There is a vertical ridge running the length of the midline that branches left and right laterally at the center demarking a thicker anterior half and a thinner posterior half. On the left posterior depression, a low rounded process of bone is present, but this feature is not mirrored on the right side.

Aside from recognizing the entoplastron and gular scute as a diagnostic helochelydrid feature, Nopcsa (1928) noted entoplastron variation in the then identified helochelydrid specimens as listed in Table 4.

Table 5 Helochelydrid entoplastral shape per Nopcsa 1928

Genus	Shape of Nuchal
<i>Helochelys</i>	nuchal is somewhat broader than long
<i>Helochelydra (anglica)</i>	as broad as long
<i>Naomichelys</i>	longer than broad
<i>Trachydermochelys (Plastremys)</i>	broader than long
<i>Tretosternum (Helochelydra bakewelli)</i>	posteriorly lyriform longer than broad

Comparative Osteology

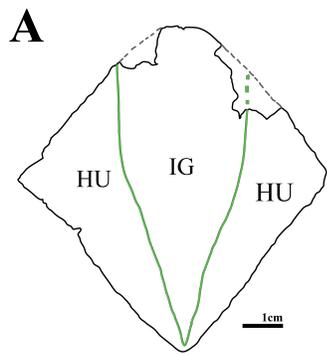
The turtle entoplastron and epiplastra are considered homologous with the interclavicle and clavicles of other reptiles and are thought to have been integral to the evolution of the plastron (Zangerl 1969, Rieppel 2013, Szczygielski and Sulej 2019). This hypothesis is supported by the entoplastral morphology seen in *Odontochelys* and the presence of an interclavicle in the stem turtle *Pappochelys*, which as noted by Schoch and Sues (2018) indicates that the possession of an interclavicle is the plesiomorphic condition for stem turtles. Early diverging specimens exhibit an entoplastron exposed at the anterior margin of the plastron, separating the left and right epiplastra. Plastral evolution indicates a general trend of the entoplastron moving posteriorly, with the left and right epiplastra migrating medially to meet at the midline. In some cases, the entoplastron is absent altogether, as in *Kinosternon* (Cadena et al., 2013 Fig 8.4).

In helochelydrid specimens, the entoplastron is present and located internal to the anterior plastral margin. Its shape is variable by species and presents as rhombus-, diamond-, or kite-shaped in outline. The helochelydrid entoplastron is joined by the left and right epiplastra on the anterior sutures and the left and right mesoplastra on the posterior sutures. The number of scutes represented in the entoplastron also varies by species; there are between three and seven scutes which include the following: intergular, right and left gular, right and left humeral, right and left

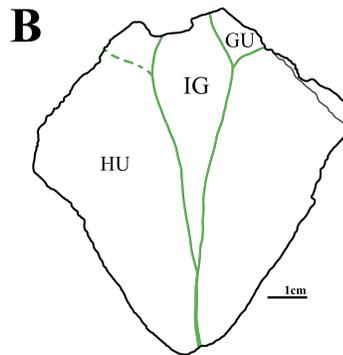
pectoral. The youngest European helochelydrid genus *Solemys* is the only taxon for which the pectoral scutes overlap onto the posterior most portion of the entoplastron.

North American helochelydrid specimens with preserved entoplastron are rare, and four are represented here (Figure 24, A-D): 1) “Kate’s Ridge Taxon” NCSM 33526 (Figure 24 A); 2) the holotype specimen of *N. speciosa* from the Kootenai Formation AMNH 6036 (Figure 24 B); 3) the posterior portion of cf. *Naomichelys sp.* from the Cloverly Formation YPM 5437 (Figure 24 C); and 4) cf. *N. speciosa* specimen of the Antlers formation FMNH PR 273 (Figure 24 D). Entoplastra from the Cloverly (YPM 5437), Antlers (FMNH PR 273), and Kootenai (AMNH 6036) Formations (Figure 24 B-H) uniformly exhibit medial contact of the left and right humeral scutes, whereas in “Kate’s Ridge Taxon,” the intergular divides the left and right humeral scutes along the entire length of the entoplastron. This represents an autapomorphy for the “Kate’s Ridge Taxon.” Additionally, the European helochelydrids *Solemys vermiculata* MCNA 7391 (Figure 24 E); *Helochelydra nopcsai* BMNH R171 (Figure 24 F); *Solemys gaudri* (Figure 24 G), *Trachydermochelys rutteri* cf. *Plastremys lata* (Figure 24 H) follow the *Naomichelys sp.* intergular morphology of a medial contact of left and right humeral scutes.

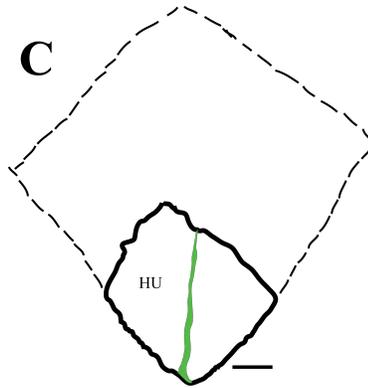
Figure 24: Helochelydrid entoplastra of North American and European specimens in ventral view. North American specimens have been viewed and photographed. European specimens redrawn from published materials. **A**, “Kate’s Ridge Taxon” from Mussentuchit Member of the Cedar Mountain Formation, Utah USA; **B**, type specimen of *Naomichelys speciosa* AMNH 6036 from Kootenai Formation of southern Montana, USA; **C**, cf. *N. speciosa* YPM 5437 from the Cloverly Formation of Montana, USA; **D** cf. *N. speciosa* from the Antlers Formation of Texas, USA; **E** *Solemys vermiculata* MCNA 7391 from Laño deposits of Burgose Spain, redrawn from Lapparent Broin and Murelaga (1999) and Pérez-García (2012); **F** *Helochelydra nopcsai* from Isle of Wight England BMNH R171, redrawn from Lapparent Broin and Murelaga (1999) and Pérez-García (2012); **G** *Solemys gaudri* redrawn from Lapparent Broin and Murelaga (1999), reconstruction of the plastral ventral face from several specimens of different sizes; **H** *Trachydermochelys rutteri* cf. *Plastremys lata* (Joyce, 2017) from the Upper Greensand of Melbury Down, near Shaftesbury, Dorset England, redrawn from Andrews 1920.



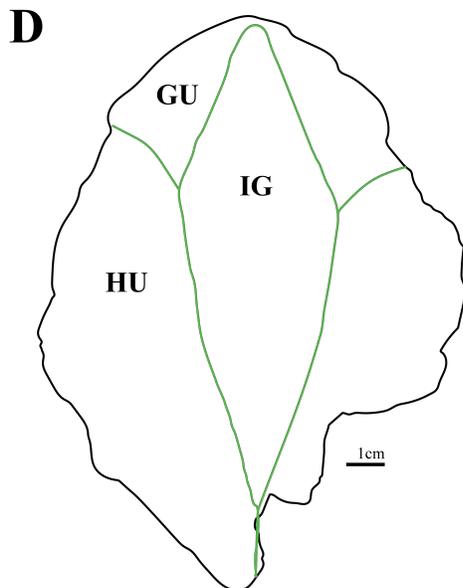
"Kate's Ridge Taxon"



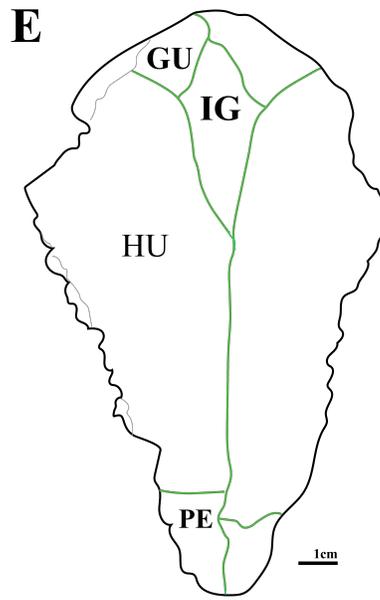
Naomichelys speciosa



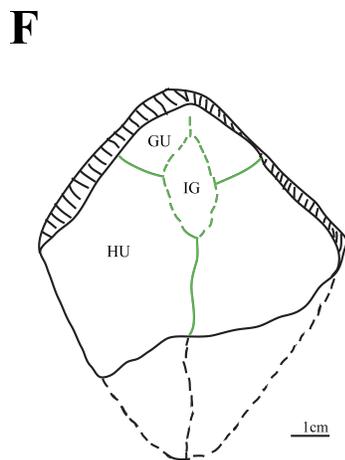
"Cloverly Turtle"



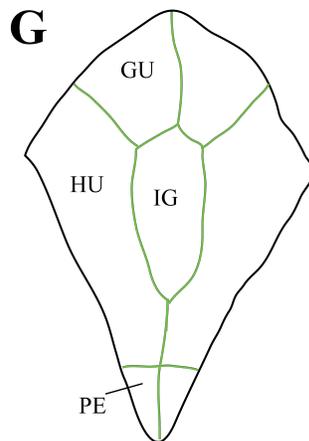
Naomichelys speciosa



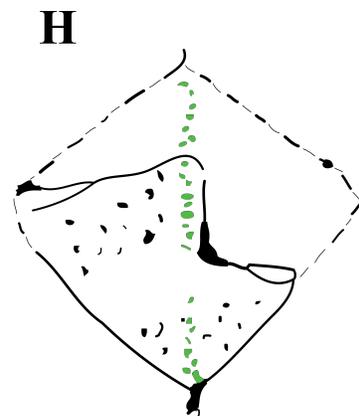
Solemys vermiculata



Helochelydra nopscai



Solemys gaudryi



Trachydermochelys rutteri

Nuchal

Kate's Ridge Taxon: Referred specimen FMNH PR 3895 nuchal is 6.2 cm wide near the anterior margin and 11.7 cm at its widest. Longitudinally it measures approximately 5.6 cm. The bone is slightly convex dorsally and exhibits a series of 4-7 mm round depressions possibly representing bite marks from predation. One of the larger depressions falls directly on the midpoint of the nuchal notch at the marginal edge. The dorsal surface is uniformly pustulated, with only a few pustules coalescing and some linear patterning along the anterior edge.

Comparative Osteology

The origin of the turtle carapace is enigmatic and has been debated in the literature for over a century. The main debate has focused on discerning the cellular genesis of carapace elements. The bones of the carapace could potentially develop from the axial skeleton, dermal ossifications, or a combination of both. While costals and neurals are associated with modification of ribs and vertebra, the nuchal is described as part of the 'thecal' shell (Scheyer 2007). The theca consists of elements of the inner dermal layer of ossification and epitheca are ossifications that develop more superficially in the dermis (Volker, 1913). The nuchal, pygal, and peripherals have also been described as true cutaneous ossifications from the neural and costal plates, derived from the endoskeleton (Goette, 1899). Specifically, the nuchal formed from osteoderm, and is the first anterior element of carapace (Rieppel in Brinkman et al. 2013). Additional support for this hypothesis is provided by Hirasawa (2013) who determined a purely endoskeletal origin of the neurals and costal plates, and exoskeletal components as nuchal, peripheral, suprapygal, pygal. In many extant turtles the nuchal is integral to the neck muscular system (Scheyer et al. 2013) and can be an indicator of feeding behavior, noted here to recognize

possible future investigations into the evolutionary purpose of the nuchal embayment of this group.

Helochelydrid turtles are recognized as having a well-defined nuchal notch or embayment that is formed by both the nuchal and the first peripheral (refer to Figure 5). Three North American helochelydrid nuchals are identified and described here (Figure 25 A-F). In cf. *N. speciosa* FMNH PR 273 the nuchal is partially reconstructed along the lateral and posterior margins, alterations that were made for the purpose of creating a ‘complete’ carapace for exhibition. The notch is notably deep, with the carapace reaching its anterior apex in peripheral II. Additionally, the median point of the anterior margin is markedly flattened proximally, so much so that the transition from dorsal to proximal to ventral surfaces form a hard turn or corner. Vermiculations continue from the dorsal surface to the proximal surface and are not present on the ventral side. Since the nuchal is partially reconstructed, complete descriptions of adjoining sutures as well as some of the scute sulci are not possible. The notable sulcus present here and on cf. “Kate’s Ridge Taxon” FMNH PR 3895 is the anterior margin of vertebral I scute. In FMNH PR 273 the sulcus makes an anteriorly raised arch approximately half to two-thirds anterior to the lateral midline across the width of the nuchal.

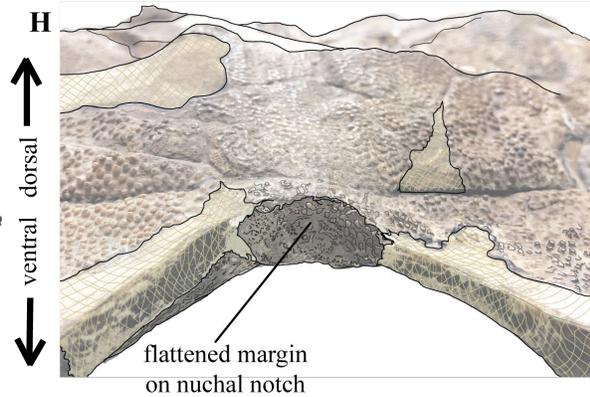
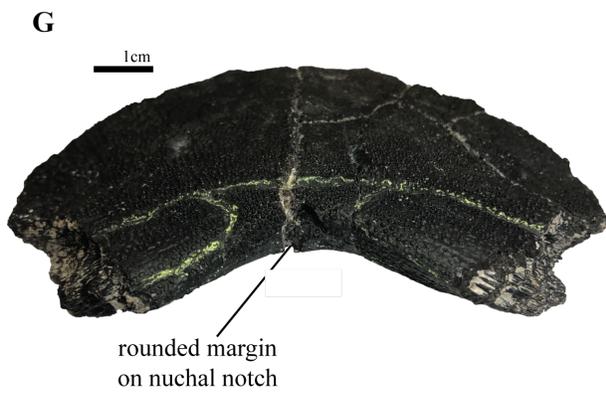
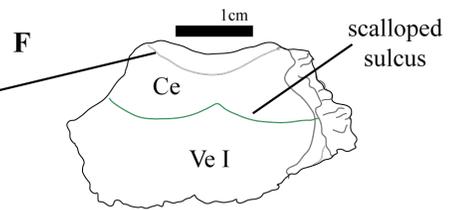
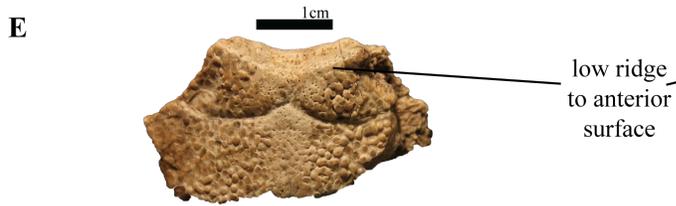
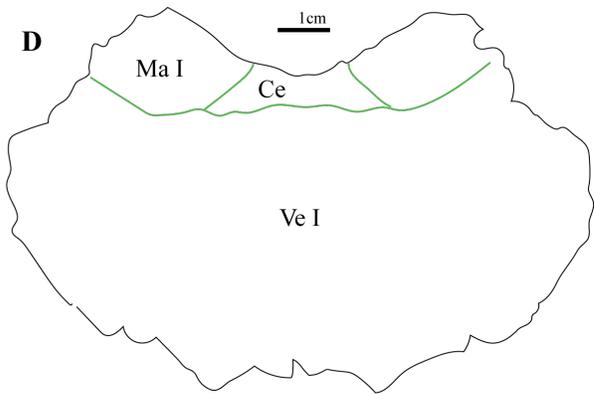
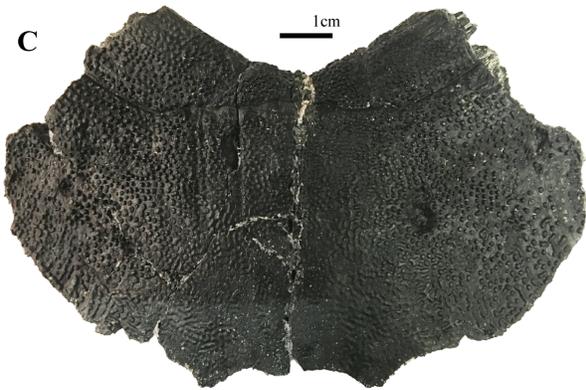
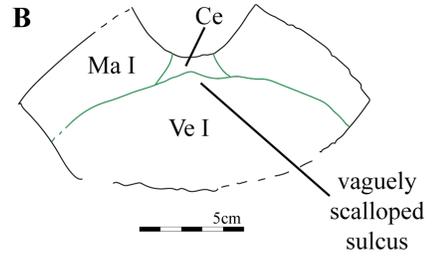
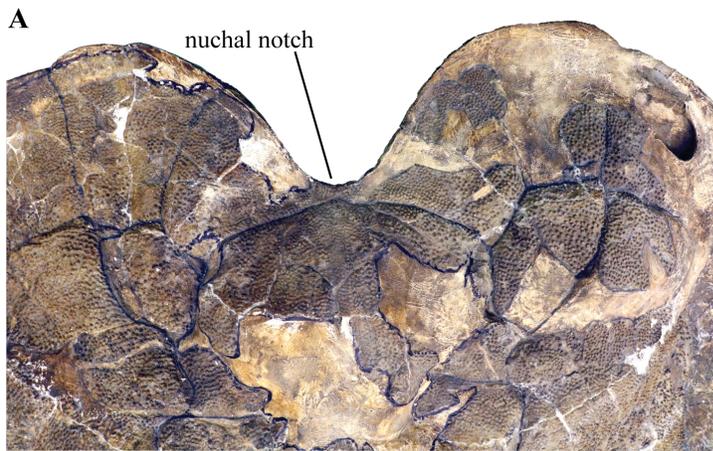
Kate’s Ridge Taxon (FMNH PR 3895) exhibits a nuchal embayment that gradually curves anteriorly and is likely shallower than in FMNH PR 276; however, the total depth of the notch is unknown. Peripherals of this specimen have been recovered but not successfully joined with their corresponding bones. The anterior margin is rounded across the dorsal to ventral plane and lacks the flattened median surface as in FMNH PR 273. Vermiculation continues from dorsal to ventral approximately two-thirds around the proximal surface. On the dorsal surface, sulci representing four scutes are present: the cervical, left and right marginals, and vertebral I.

The anterior sulcus margin of vertebral I makes a posteriorly depressed arch approximately two-thirds to three-quarters anterior to the lateral midline across the width of the nuchal.

A third partial nuchal was identified from the Cloverly Formation collections at the Oklahoma Museum of Natural History. OMNH 60387 is fragmentary but provides a partial marginal I sulcus. The limited width of the anterior margin is rounded from the dorsal to ventral surface with a mildly flattened proximal surface represented by a poorly defined low ridge, where vermiculations cease (Figure 25 C & F). The anterior vertebral I sulcus appears as a scalloped, laterally-trending depression with unknown endpoints. The midpoint is raised anteriorly then scoops downward (posterior) and laterally to the right and left.

A fragment of shell from NCSM 33431 “Dory” may represent a portion of the nuchal illustrating the morphology of this element for “Kate’s Ridge Taxon.”. Currently, this fragment appears to represent a small portion of the left, anterior-most margin of the nuchal. As is, this specimen exhibits similar anterior proximal curvature and vermiculation pattern to cf. “Kate’s Ridge Taxon” FMNH PR 3895. If confirmed through further preparation and joining with missing pieces, this specimen could provide additional support to the diagnosis of the nuchal.

Figure 25: North American nuchal specimens. **A** and **b** are FMNH PR 3895 photo and line drawing exhibiting the anterior border (sulcus) of vertebral I where it meets with the cervical and the first marginals (green line). **C** and **D** are FMNH PR 273 photo and line drawing where the green line represents the anterior sulcus of vertebral I. **E** and **F** are OMNH 60387 photo and line drawing where green line represents the sulcus between vertebral 1 and the cervical. Proximal margins are illustrated in: **G**, FMNH PR 3895; and **H**, FMNH PR 273.



Humerus

Kate's Ridge Taxon: The left and right humeri of the referred specimen FMNH PR 3895 are well preserved and complete. Left and right measurements are 117 and 119 mm in length; the laterally expanded proximal end is 47 and 45 mm wide; narrowest point of shaft is 12.5 and 13.3 mm; and the distal lateral expansion is 30 and 31 mm wide, respectively. The proximal humerus is approximately 45-50% transversely wider than the distal end, and tilts medially, whereas the distal end tilts slightly laterally.

Comparative Osteology

The entepicondylar foramen has been reported as a primitive amniote feature (Romer 1945) that serves as a passage of the medial nerve and brachial artery. It can be present in several forms, ranging from a shallow to deep canal along the distal end of the anterior humerus, to an enclosed foramen entering the humerus anteriorly and exiting the ectepicondyle ventrally. In some turtles, such as *Chelydra serpentina*, the foramen makes a deep rounded canal that is not completely enclosed. It is also said to correlate to positioning of the humerus within the skeleton and lifestyle (Weiland 1900; Nopcsa 1928).

Complete North American helochelydrid humeri are rare, but partial elements have been collected from a few localities. Comparative material is illustrated in Figures 26 A-E, and 27 A-E. Helochelydrids are generally considered to be purely terrestrial (Scheyer et al. 2015), although there has been some debate over a purely terrestrial or semi-aquatic lifestyle (Marmi et al. 2009). Terrestriality or aquatic lifestyle is a character state diagnostic in the humerus of turtles based on gross morphology (Weiland 1900) and more recently confirmed by microanatomy (Nakajima et al. 2014). The gross morphology of the terrestrial turtle humerus is sigmoidal in the dorso-ventral

plane, with the proximal end turned dorsally and the distal turned ventrally. The North American helochelydrid representatives illustrated in Figure 26 (A-E) conform to this morphology and support the hypothesis of a land-dwelling clade.

The best overall comparison here is between the Antlers Formation cf. *Naomichelys speciosa* FMNH PR 273 and the Mussentuchit humeri cf. “Kate’s Ridge Taxon”, FMNH PR 3895. Both have complete right and left humeri that show similar gross morphology, as well as distinctive traits. Both specimens exhibit a lateral process with a flattened ventral surface that bends medially when viewed proximally. The Antlers Fm. specimen is more robust with a thicker shaft as well as a more robustly developed epicondyle on the radial/ulnar articular surface. The distal anterior surface of FMNH PR 273 and YPM 4900 both have a well-developed groove that originates just proximal to the distal diaphysis and terminates as an ectepicondylar foramen that enters the bone near the distal end. The ectepicondyle is also pierced by a round foramen visible in ventral view and illustrated in Figure 27 (A-E). The cf. “Kate’s Ridge Taxon” FMNH PR 3895 lacks this feature and only a minor, shallow groove is present along the distal end of the anterior surface on the left humerus, and nearly absent on the right.

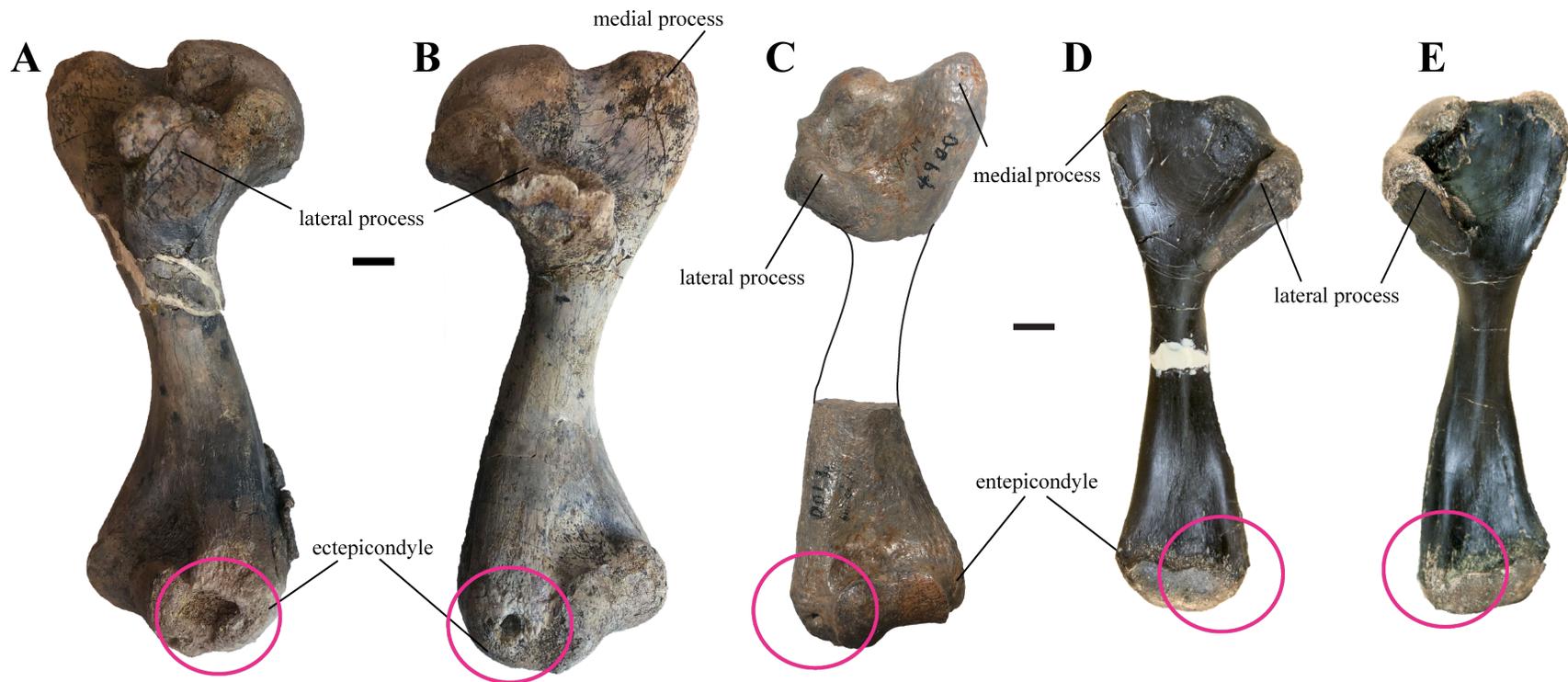


Figure 26: North American helochelydrid humeri with area of humeral ectepicondyle circled in pink to highlight presence or absence of ectepicondylar foramen. **A** left humerus of FMNH 273; **B**, FMNH PR 273 right humerus; **C** YPM 4900 proximal and distal ends positioned to virtually reconstruct estimation of missing shaft; **D**, FMNH PR 3895 left humerus; **E**, FMNH PR 3895 right humerus.

It is curious that the ectepicondylar foramen is absent in “Kate’s Ridge Taxon”, as it is seen in other basal turtles such as *Pr. Quenstedti*, *Pal. Talampayensis*, *C. antiqua*, *Mo. Efremovi*, and *Me. Platyceps* (Joyce et al. 2014).

One additional autapomorphy seen in cf. “Kate’s Ridge Taxon” FMNH PR 3895 is the presence of a ‘dorsoposterior’ fossa. The lack of this feature has been identified on three other specimens: two identified from the Cloverly Formation, and one from The Antlers (Figure 27). This feature is present on both the left and right humerus of FMNH PR 3895 and is therefore considered to be a character applicable to diagnosing the “Kate’s Ridge Taxon”.

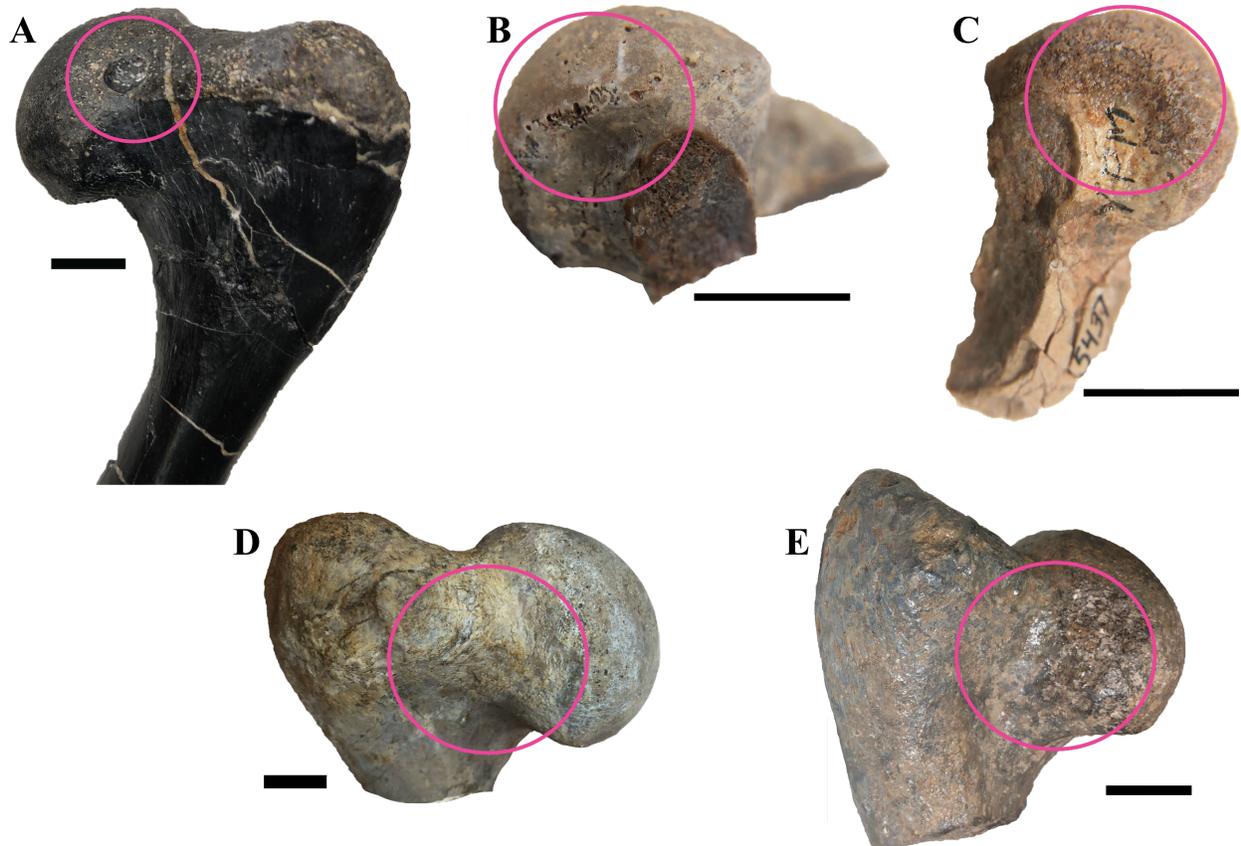


Figure 27: Proximal North American helochelydrid humeri with area of “dorsoposterior” humeral head circled in pink. Only on **A**, FMNH PR 3895 is there a distinct fossa present; **B & C** are YPM 5437 left & right proximal humeral head; **D** is FMNH PR 273 proximal right humerus; and **E** is YPM 4900 right proximal humerus. Black bars represent 1cm.

DISCUSSION

On the Status of “Naomichelys” and other North American Helochelydrids:

Joyce’s 2017 detailed review of early-diverging Mesozoic turtles include five key diagnostic characters for Helochelydridae: 1) doubled occipital tubercles formed by the pterygoid; 2) posterior squamosal fossa; 3) shell covered by tubercles; 4) V-shaped anterior peripherals; and 5) presence of an entoplastral (intergular) scute. Two of the five pertain to the skull and are confirmed in *cf. Naomichelys speciosa* FMNH PR 273, but cannot be evaluated in the holotype or referred specimens of “Kate’s Ridge Taxon” based on currently prepared material. The remaining three synapomorphies of Helochelydridae have been identified and confirmed in the “Kate’s Ridge Taxon” hypodigm (NCSM 33526 and referred specimens “Dory” NCSM 33431, and FMNH PR 3895).

Among the other helochelydrid specimens viewed for comparison, the vast majority are so fragmentary as to be identifiable as helochelydrid only by the diagnostic feature of ‘shell covered by tubercles.’ It is remarkable then, that three skeletally diagnostic specimens from a single formation collected within 3 miles of one another can be reported here. Unpublished and sequestered material mentioned in program abstracts indicate there are at least two additional undescribed, partially complete specimens referable to Helochelydridae from North America. Abstract publication from the 2010 Annual Meeting of the Society for Vertebrate Paleontology entitled “*Late Cretaceous Canadian Specimens of Family Solemydidae (Testudines) with Special Mention of a new Genus and Species*” reports the recovery of a ‘relatively complete’ shell from the (Santonian) Haslam Formation of Vancouver Island (Larson et al. 2010). This specimen is yet to be fully diagnosed and named and was not available for comparative analysis.

A second, possibly new species from the Cloverly Formation of Montana was reported at the 5th Turtle Evolution Symposium and the 75th Annual Meeting of the Society for Vertebrate Paleontology in 2015. This specimen (MOR 941) consists of “a large, diamond shaped entoplastron, which exhibits the distinctive solemydid surface ornamentation and an entoplastral (intergular) scute,” as well as elements of the carapace, plastron, cervical vertebrae, shoulder girdles, and right femur. It represents a smaller individual than FMNH PR 273 (Lawver 2015a; 2015b) and is referred to *Naomichelys*. Variation is noted as either ontogenetic or representative of a second distinct species of *Naomichelys*. This specimen is yet to be fully diagnosed and identified and was not available for comparative analysis.

From the data provided here, it is clear that *Naomichelys* was not the sole helochelyrid to exist in North America during the Cretaceous. Whether this is due to diversification of a single founder population, or represents multiple dispersals events from Europe is still unclear and needs further study—no biogeographical analyses of Helochelyridae has yet been undertaken. Description and diagnosis of the specimens presented here, in conjunction with expected forthcoming papers on specimens reported in proceedings volumes will provide more new data than already exists on North American helochelyrids.

The diagnosis here is based on comparative anatomy between the type specimen of *Naomichelys speciosa* (Hay, 1908) and “Kate’s Ridge Taxon” NCSM 33526. The placement and shape of scutes represented by sulci on the ventral surface represents a significant divergence from the *N. speciosa* holotype specimen, AMNH 6136, in which the intergular spans approximately $\frac{3}{4}$ the length of the entoplastron, and the left and right humerals meet at the midline on the bone’s posterior surface. In “Kate’s Ridge Taxon” the intergular spans the entire length of the entoplastron with no meeting of the left and right humerals at the midline. The

variation in scute arrangement on the entoplastron of *Naomichelys speciosa* in comparison to “Kate’s Ridge Entoplastron” also includes the apparent absence of a sulcus marking the separation of the humeral from the gular.

Based on the prevalence of helochelydrid shell material found in Cretaceous age sediments in North America, it has long been postulated that more than one species populated this continent. Specimens are reported from over twenty formations, and spans a time period of over 50 million years. The addition of this diagnostic material provides desperately needed data for understanding this enigmatic and contentious clade.

Ontogenetic Variation

Although exceptional preservation of soft tissues is known from the fossil record of turtles (Lindgren et al. 2017), the exact pattern of keratinous scutes overlying the bones of the turtle shell does not generally preserve. Fortunately, scute margins create a groove (sulcus) on the bone that preserves the pattern that would have existed in life. As a turtle grows, the bones and scutes grow relative to one another, and the plastron to carapace size ratio remains equivalent (Mosimann 1956). The hypothesis of this thesis suggesting a new species of helochelydrid is partially dependent on the placement and orientation of sulci representing scute margins. Ontogeny or pathology could play a role in this variation. To rule out the possibility that variation in scute patterning on the entoplastron was the result of individual pathology or ontogenetic variation (and could not therefore be used reliably as an autapomorphy diagnostic of the new taxon), I conducted a qualitative morphologic analysis of plastral scute patterning in extant terrestrial, semi-aquatic and aquatic freshwater turtles from the NCSM herpetology collection (see p. 44 in Materials and Methods). I inspected a total of 179 specimens representing

individuals from Emydidae, Kinosternidae, and Platysternidae in various stages of growth, ranging from hatchlings to adult for variation in scute positioning relative to the underlying bone. Overlying scute pattern is standardized for each species with regard to how each scute overlaps with the underlying bones, such as in the osteological standard for *Trachemys scripta* (Figure 28). For each species examined, I noted the presence or absence of variation with regard to scute placement and the underlying bone structure. The purpose of this analysis was to determine if there was any qualitative visible variation that would place the individual as an ‘outlier’ to the standard morphology of the species itself based on its systematic diagnosis.

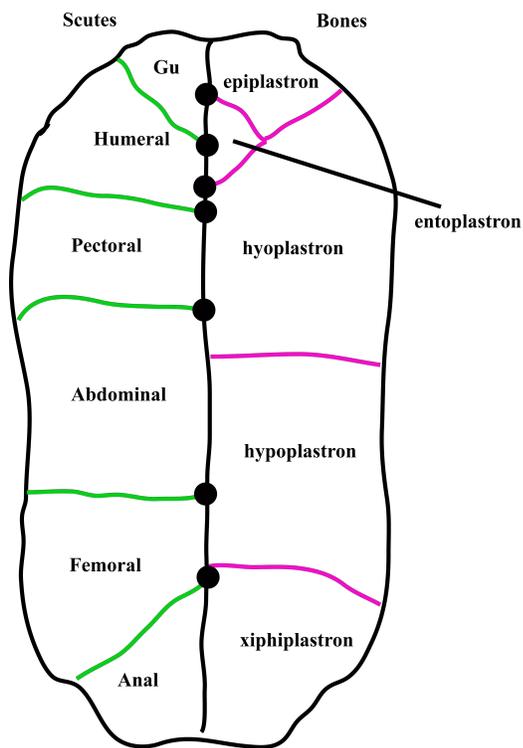


Figure 28 line drawing of *Trachemys scripta* standard arrangement of plastral bones and scutes

The plastron of these species all contain an entoplastral bone; however, they do not have an intergular scute. Scutes covering the entoplastron included gulars, humerals, and pectorals. In each species, the scutes are paired left and right except in *Kinosternon subrubrum* where the

gular is represented by a single scute. The point at which the gulars meet the humeral was noted in each species and compared between the available specimens for that species (represented as large black dots in Figure 28). In all specimens, the overall scute arrangement and relative size compared to underlying bone did not vary between differently sized individuals of the same species (ontogenetic) or between individuals of approximately the same size of the same species (individual variation). Each individual conformed to the standardized diagnosis for that species with regard to these traits. For example, the posterior-most point of the gular(s) always fell at or very near the anterior-most point of the entoplastron. They never overlapped onto the hyoplastron, regardless of growth stage, and no individual exhibited variation in this trait. This is the most salient parallel to my argument for the entoplastral diagnosis of the “Kate’s Ridge Taxon”. This investigation did not include quantitative morphologic statistical analysis, but provided qualitative visual evidence to support stability in scute arrangement on the plastral lobe of modern turtles.

Comprehensive analyses of morphological variation in fossil species is often overlooked due to the rarity of multiple representations of any individual species. However, Szczygielski *et al.* (2018) compiled data on 288 specimens of the Late Triassic terrestrial *Proterochersis* spp. This exhaustive study determined the presence of ‘significant’ shell variability through ontogeny, as well as evidence of abnormal scute layout. This variability included non-symmetry between left and right scute arrangements and variation in gular size and shape throughout ontogeny; however, the variability did not discount or oppose that of species diagnosis. Patterns of sulci arrangement were consistent on individual plastral bones within Szczygielski *et al.* (2018) sample of *Proterochersis* lending support to the use of these patterns as taxonomically significant in this study.

Aside from ontogenetic variability, abnormalities can be a product of external factors such as disease, dietary interruptions, or genetic defect. Some supporting evidence in published literature is available. In a large study of 3511 *Caretta caretta* (sea turtles), Türkozan et al. (2001) observed variability in carapace scutes, but noted that scute pattern in adults is stable. Additionally, Box Turtles (*Terrapene* spp.) show high incidence of shell variability and Vitek (2018) reported on methods to correlate variability of extant species to fossil material in order to determine species diversity from abnormalities. Important to this study, these variations represent as disparities in bilateral symmetry and three-dimensional morphospace. The ability to diagnose individuals to a species is not a factor.

These studies provide an important baseline for identifying and diagnosing fossil turtles and should be considered when classifying new species and its relative autapomorphies. However, much more research and analysis is needed. In the case of the Cedar Mountain Formation helochelydrids presented here, specimens are comparable in development to those reviewed from the Cloverly, Kootenai and Antlers Formation specimens and do not exhibit abnormalities in bilateral symmetry indicative of pathology or abnormal growth.

Sexual Dimorphism

The plastron of cf. *Naomichelys speciosa* FMNH PR 273 exhibits a plastral fontanelle that is unique among helochelydrids. The fontanelle has been described, but it remains enigmatic as to the significance, particularly as it might relate to diagnosing the species. First, this could be a character of the species itself. One European helochelydrid genus, *Solemys*, exhibits this character (Lapparent de Broin and Murelaga 1999). However, the presence of a plastral fontanelle is often thought of as an indicator of skeletal immaturity, or a feature that is lost

during ontogeny (Joyce 2014). FMNH PR 273 has been identified as a skeletally mature, relatively large helochelydrid adult having an ankylosed shell with undulating dorsal carapace surface.

Alternatively, sexual dimorphism could be seen as an alternative cause for this character. Modern male turtles are known to exhibit a concave plastron (Pritchard 2008), and in terrestrial turtles, males are usually larger (Berry and Shine 1980). Cadena et al. (2012) postulated that large size, long narrow posterior xiphiplastral tips with an anal notch, along with a concave plastron and posterior fontanelle to be sexually diagnostic features for males in fossil turtles. This diagnosis was based on specimens of platychelids exhibiting plastral variation where males and females were identified.

By the reasoning above, presence of the plastral fontanelle would be an indication that FMNH PR 273 is a male. Additionally, if this theory applies to Helochelydridae group, the plastron of “Kate’s Ridge Taxon” specimen FMNH PR 3895 would allow for diagnosis. Despite the plastron missing the right mesoplastron, and left hypo- and xiphiplastron, a plastral fontanelle is not evident. The plastral elements present exhibit sutural medial margins that indicate the right and left elements would be completely adjoining. While this hypothesis is poorly supported, the basis for future comparative analysis resides in the argument for the possibility of inaccurate species identification between individuals based on plastral morphology.

Paleoecology & Paleobiogeography

The habitat for *Naomichelys* has previously been posited as either entirely terrestrial or semi-aquatic. However, the case for terrestriality has become stronger through additional histological study (Scheyer et al. 2015). The specimens presented here provide more support of terrestriality via traits such as humeral shape (Wieland 1900; Nakajima et al. 2014) and presence of osteoderms (Scheyer et al. 2015; Joyce 2014). Helochelydrid turtles are known to inhabit deltaic and lacustrine environments and have been recovered from sediments representing ecosystems that thrived near the coast of the Western Interior Seaway. Additionally, several of the reviewed specimens exhibit predation such as bite marks and scoring on shell surfaces. Providing evidence that these turtles were an integral part of the food chain during this time. Surveys of the Mussentuchit Member that produced the specimens described here have also recovered skeletal fragments of large predatory crocodylomorphs; however, not enough skeletal material has been recovered for species identification.

Following the climate-mediated diversification hypothesis (Nicholson et al. 2015), at least one helochelydrid species likely migrated into North America through Europe. This is supported by the first occurrences in North America dated to Aptian age sediments from the Arundel Clay of Maryland (Kranz 1998) and the lack of helochelydrids identified in Asia. Additionally, phylogenetic relationships among helochelydrid species remain unresolved (refer to Figure 2), preventing quantitative biogeographical analyses. It is possible that more than one species of helochelydrid migrated to provide the population density observed in the Cretaceous of North America; however, equally likely scenarios include a single dispersal event from Europe into North America.

Helochelydrid turtles are both well known and obscure, mostly due to the nature and prevalence of fragmentary specimens. Attempting to accurately diagnose and describe a new species from North America has proved challenging due to the paucity of comparative material, and ambiguous character state present. Reviewing available extant material and referring to the literature on shell bone and scute variation provides clarification and support for the diagnosis presented here. Based on the widespread occurrences of helochelydrids in Cretaceous sediments of North America it seems likely that they were a successful and important part of the ecosystems (and food chains) where they lived.

SUMMARY

New helochelydrid material from the Mussentuchit Member of the Cedar Mountain Formation, represents a new species “Kate’s Ridge Taxon”. “Kate’s Ridge Taxon” is only the second definitive North American helochelydrid taxon yet described; prior to its discovery, all helochelydrid specimens were referred to *Naomichelys speciosa*, previously the singular helochelydrid known outside of Western Europe, or the larger group Solemydidae. Autapomorphies of the entoplastron of “Kate’s Ridge Taxon” render the taxon distinct from *N. speciosa* and include: intergular placement on the entoplastron, shape of vertebral I anterior sulcus on the nuchal, rounded anterior margin of the nuchal notch, absence of an entepicondylar foramen, and presence of a dorsoposterior fossa. Additionally, the referred specimen “Dory” NCSM 33431, which preserves axial, appendicular, and unprepared skull materials, will provide additional autapomorphies to solidify the status of this new taxon. Further preparation has the potential to yield an entoplastron to provide additional support for this diagnosis.

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