

COMPLETE SPECIMENS OF THE EOCENE TESTUDINOID TURTLES *ECHMATEMYS* AND *HADRIANUS* AND THE NORTH AMERICAN ORIGIN OF TORTOISES

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Abstract—Newly described specimens of North American Eocene turtles provide valuable information on their morphology and, more specifically, variation, both intraspecific and ontogenetic. We describe several complete and nearly complete testudinoid (Testudinoidea) specimens, including juvenile specimens of *Hadrianus corsoni*, *H. majusculus*, *Echmatemys haydeni* and *E. naomi*. These specimens help us determine that the oldest and most basal tortoises are from the western United States, suggesting Testudinidae evolved in North America from one of the geoemydid-like forms in the genus *Echmatemys*, which have their lowest stratigraphic occurrence in the earliest Wasatchian North American land-mammal “age” (early Eocene, Ypresian, ~53 Ma).

INTRODUCTION

The genus *Echmatemys* was first named by Hay (1906) for *E. septaria* from the early middle Eocene (Bridgerian North American land-mammal “age”-NALMA) of Wyoming. Over the next two decades this genus rapidly grew to include all Eocene non-testudinid testudinoids in North America, with approximately 20 named species (e.g., Hay, 1908; Roberts, 1962). *Bridgeremys* was separated from this group by Hutchison (2006) and was suggested to be a stem-*Rhinoclemmys* or ancestral to it.

Here, we describe three new specimens of *Echmatemys* and *Hadrianus*, including cranial and juvenile material. We also look at variation in a modern species (*Gopherus agassizii*) to gain a better understanding of interspecific variation within testudinids. In addition to providing further information about these turtle taxa, we further explore the implications of these taxa and variation for the origin of tortoises (Testudinidae).

Institutional Abbreviations: **FOBU**, Fossil Butte National Monument, Kemmerer, Wyoming, USA; **IGM**, Geological Institute of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; **MSB**, Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UCB**, University of Colorado Museum of Natural History, Boulder, Colorado, USA; **USNM**, United States National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

VARIATION IN EXTANT *GOPHERUS AGASSIZII* (COOPER, 1863)

To gain a better understanding of variation in fossil testudinoids, it is important to understand the variation in modern living members. The issues surrounding this shell variation are important to understand testudinid taxonomy and phylogeny. Vlachos and Rabi (2018) and Vlachos (2018) analyzed testudinid relationships using a number of characters we suspect have a much higher degree of polymorphism than is indicated in their matrices. These were focused around the neural bones and gular scutes of these tortoises. To provide some assessment of the polymorphism in the characters of Testudinidae we examined a sample of 17 *Gopherus agassizii* in the collections of the Museum of Southwestern Biology to provide a baseline of testudinid variability. Most recent phylogenies place the genus

Gopherus as sister to all extant testudinids other than *Manouria*, making it a good example of a extant basal testudinid (e.g., Le et al., 2006; Fritz and Bininda-Emonds, 2007; Mautner et al., 2017; Takahashi et al., 2018; Vlachos and Rabi, 2018; Zhao et al., 2020). The *Gopherus agassizii* specimens discussed here come from Clark County, Nevada, USA, and are thus from a relatively small geographic area, limiting the possible impact of geographic variation on our assessment of intraspecific variation (polymorphism) in this sample.

In this sample of *Gopherus*, the shape of the neurals is highly variable, including every possible morphology in the character matrix of Vlachos and Rabi (2018, see their characters 86–90). The contacts and shapes of the costals and neurals vary considerably (Table 1). For example, neural 1 (character 86) is about equally often rectangular and hexagonal, and both hexagonal short sides facing anterior and short sides facing posterior were observed. Neural 2 (character 87) is more consistent, either octagonal or hexagonal in shape with the short sides facing anteriorly. Neural 3 (character 88) is extremely variable, with shapes including rectangular, hexagonal, with short sides anterior and posterior, or octagonal. Neural 4 (character 89) is rectangular, hexagonal, with short sides facing anteriorly, or octagonal. Despite suggestions that the shape controls the contacts (Vlachos, pers. com, 2018), the contacts are more consistent than the shape, mainly varying in the contacts of neurals 3-5.

It is worth noting that whereas the shape of the neurals and their contacts with the costals vary, all specimens have costal wedging present, as described by Hay (1908). Thus, we conclude that the shape of the neurals and the presence of costal wedging are two independently varying characters, contrary to Vlachos and Rabi (2018). Furthermore, the gulars both cover the entoplastron and not cover it in different specimens (Vlachos and Rabi, 2018, character 123), as seen in Lichtig and Lucas (2015c). The angle of the posterior corner of the gulars varies from 75° to 135°, covering two of the character states of Vlachos and Rabi (2018, character 124). In no specimen we examined did we find the costal-peripheral suture and pleural-marginal sulcus to not coincide, contrary to Vlachos and Rabi (2018, character 97). Indeed, our examination more than doubles the number of polymorphic characters in *Gopherus agassizii* from five to 11.

In addition, juvenile specimens examined have narrower nuchals and entoplastra. Part of the lengthening of the entoplastron is the retention of the long posterior process seen in many ontogenetically older geoemydids and emydids but absent in older testudinids (personal observation). This may

TABLE 1. Measurements of extant *Gopherus agassizii* from Clark County, Nevada, USA. Note the high variation in the neural formula as well as in the gular angle fitting all three states described in Vlachos and Rabi (2018). Less marked is the variation in the contacts of the neurals and the presence of an overlap of the gular scutes onto the entoplastron.

Specimen number	Gender	Neural formula	Contacts								Gulars overlap entoplastron	Gular angle	Notes	
			N1	N2	N3	N4	N5	N6	N7	N8				
MSB 66576	M	No carapace preserved										+	75°	
MSB 66589	M	No carapace preserved										-	90°	
MSB 66612	F	6A-8-4-8-47-8-4-6A	1	1, 2, 3	3	3, 4, 5	5	5, 6, 7	7	7, 8		-	130°	
MSB 66597	F	4-8-4-8-4-6A-6A-4	1	1, 2, 3	3	3, 4, 5	5	5, 6	6, 7	8 left, 7, 8 right		-	135°	
MSB 66598	F	4-8-4-8-4-6P-6A	1	1, 2, 3	3	3, 4, 5	5	5, 6, 7	7, 8	N8 absent		-	114°	
MSB 66569	F?	4-8-6A-8-6A-8-6A-6A	1	1, 2, 3	3	3, 4, 5	5	5, 6	6, 7	7, 8		-	123°	
MSB 66609	M	6P-8-6P-8-6A-6A-6P-4-4	1	1, 2, 3	3	3, 4, 5	5	5, 6, 7	7, 8	8		-		Extra neural present
MSB 66611	?	4-8-6P-4-6A-6A-6A-6E-8	1	1, 2, 3	3, 4	4	4, 5	5, 6	6, 7	7				Extra neural present
MSB 66563	?	4-8-6A-8-4-8-6A-6A	1	1, 2, 3	3	3, 4, 5	5	5, 6, 7	6, 7	7, 8		+		Costals 3 and 5 do not reach the peripherals
MSB 66554	?	6P-8-4-8-6A-6P-6P-6A	1	1, 2, 3	3	3, 4, 5	5	5, 6	6, 7	7, 8				
MSB 66538	F	4-8-6P-8-6A-6E-6A-4	1	1, 2, 3	3	3, 4, 5	5	5, 6	6, 7	7, 8		+		
MSB 66557	M	4-8-6A-8-8-4-6P-6A-6A	1	1, 2, 3	3	3, 4, 5	5	5, 6	6, 7	7, 8		+		
MSB 66556	M	6A-8-4-8-6A-6A-6A-6A	1	1, 2, 3	3	3, 4, 5	5	5, 6	6, 7	7, 8				
MSB 66567	?	6P-8-4-8-4-6A-6A-6A	1	1, 2, 3	3	3, 4, 5	5	5, 6	6, 7	7, 8				

indicate that some of the traits associated with the Testudinidae do not appear until later in testudinid ontogeny, while earlier in ontogeny there is a more geoemydid-like morphology.

Vlachos (pers. com., 2018) states that he has seen similarly high intraspecific variation in *Chelonoidis*. *Chelonoidis* is a significantly more derived taxon of testudinid, so, based on phylogenetic bracketing, we consider this high variation likely to be a trait of testudinids as a whole. This is not surprising given that high intraspecific variation has also been noted in the non-testudinid testundoids Geoemydidae (see Garbin et al., 2018 and references therein) and Emydidae (e.g., Jasinski, 2018; Vamberger et al., 2020). Furthermore, as stated by Bever (2008) and others, variability or the tendency to vary in various anatomical structures is a heritable trait. This variation was overlooked by Vlachos and Rabi (2018), which scores only 0.02% of their character-state entries as polymorphic. This results from their low sample sizes of extant testudinids, averaging 3.85 specimens per species where specified, including named references, where applicable.

SYSTEMATIC PALEONTOLOGY
Testudinidae Linnaeus 1758
***Hadrianus* (Cope, 1872)**
***Hadrianus majusculus* (Hay, 1904)**
Fig. 1-2

1874 ?*Hadrianus*: Cope, p. 36
 1904 *Hadrianus* Hay, p. 271
 1906 *Hadrianus*: Hay, p. 374
 1974 *Geochelone* (*Manouria*): Auffenberg, p. 171
 2015a *Hadrianus*: Lichtig and Lucas, p. 164

Referred material— UCB 76816, an incomplete shell, consisting of posterior portions of the carapace and plastron, and missing the anterior and posteriormost ends of the plastron, as well as most peripherals, the nuchal, and the pygal from the carapace (Fig. 2).

Diagnosis— Same as for genus.

Localities and age— Early Eocene Wasatchian (Wa-6) of the San Jose Formation of the San Juan Basin, New Mexico, USA and the Wasatchian (Wa-5) of the Willwood Formation of Wyoming, USA.

Description— The holotype of *Hadrianus majusculus*, YPM 2743 (Fig. 1), was described and illustrated by Hay (1904, 1908, fig. 472, plate 59), obviating the need for a detailed re-description, so only a brief overview is provided. The carapace is 530 mm long and at least 440 mm maximum width. It is crushed toward the left, with the midline greatly fractured as to obscure the shape and proportions of most of the neurals (Hay, 1908). The nuchal is approximately equal in length and width. Furthermore, the anterior portion of the two posterior neurals is rectangular, while the posterior one is hexagonal with the shorter sides facing anteriorly. The posterior of these may have been what Hay (1908) referred to as a third suprapygal, which we do not see in YPM 2743. The associated material includes an additional hexagonal neural of uncertain placement.

The plastron is also 530 mm long; with 180 mm of this made up by the anterior lobe, and 175 mm by the posterior lobe. The anterior lobe is slightly constricted at the gular-humeral sulcus, forming a very slight trilobed shape. The gulars overlap the entoplastron in this specimen. The entoplastron is relatively large and bell shaped, with the wider portion posterior. The posterior border of the entoplastron is closely approached by the humeral-pectoral sulcus overlapping the entoplastron slightly at the midline. The shapes of the pectoral scutes are significantly different than those in *Hadrianus corsoni*, where the humeral-pectoral and pectoral-abdominal sulci approach each other much more closely just medial to the axillary notch. The posterior lobe has a deep notch along the midline and a rounded posterior margin of the xiphiplastron. The lateral margin is constricted at

the femoral-anal sulcus in a manner similar to the anterior lobe at the gular-humeral sulcus.

UCB 76816 (Fig. 2) is an incomplete tortoise shell from the early Eocene Willwood Formation of Wyoming. It is identifiable as *Hadrianus majusculus* based on several features, including: (1) lack of costal wedging seen in other tortoises; (2) the posteriorly concave pectoral-abdominal sulcus which is absent in *Echmatemys* and *Bridgeremys*; and (3) the narrow base of the anterior lobe of the plastron relative to the base of the posterior lobe. The hyoplastron on UCB 76816 measures 20 mm long on the midline (based on the right side). The hypoplastron is 21 mm long at the midline. The posteriormost portion of the xiphiplastron is not preserved, so its length cannot be determined. The hyoplastron has four scute annuli, suggesting that this was an individual about 4 years old (see Zug, 1991).

The costals thicken lateral to the vertebral-pleural sulcus. Given the young ontogenetic age of this specimen, it suggests the absence of significant ontogenetic variation in costal wedging in *Hadrianus majusculus*. In addition, the striated surface sculpture of this species, which UCB 76816 possesses, is unique among the turtles of its type stratum, the San Jose Formation, making recognition of even fragmentary specimens possible.

Remarks— We do not consider crushing or other taphonomic deformation to be a likely cause of the lack of costal wedging in this species as that is a change in length, and we see no evidence of antero-posterior crushing in the individual elements in either of these specimens.

Hay (1908) pointed out that *Hadrianus majusculus* (YPM 2743) has unusual costal morphology relative to other Testudinidae, and summarized it in a list of measurements of the costal dimensions (Table 2). Only costal 7 is significantly narrowed proximally, rather than costals 2, 4, and 6, as in other Testudinidae. We disagree with the assessment that *Achilemys* is the most basal testudinid (Claude and Tong, 2004). Instead, we consider the most basal testudinid to be *Hadrianus* given the absence of the derived traits present in *Achilemys* and other testudinids. These features include the lack of costal wedging and the overlap of the pectoral scutes onto the entoplastron, features not seen in any testudinid other than *Hadrianus*. It is noted that more study needs to be done to better understand the ontogenetic changes of testudinoids, including those in *Hadrianus majusculus*.

***Hadrianus corsoni* (Leidy, 1871)**
Fig. 3-4

1871 *Testudo corsoni*: Leidy, p. 154
 1873 *Hadrianus corsoni*: Cope, p. 631

Revised diagnosis (modified from Lichtig and Lucas, 2015b)— A species of the genus *Hadrianus* with pectoral scutes barely posterior to the entoplastron. Abdominal scutes are less anteriorly elongated along the lateral edge than in *Hadrianus*

TABLE 2. Costal measurements in millimeters from Hay (1908) of the costals in the holotype of *Hadrianus majusculus* (YPM 2743).

Costal	Width proximally	Width distally
2	62	77
3	45	50
4	72	70
5	46	44
6	45	45
7	30	40
8	35	55

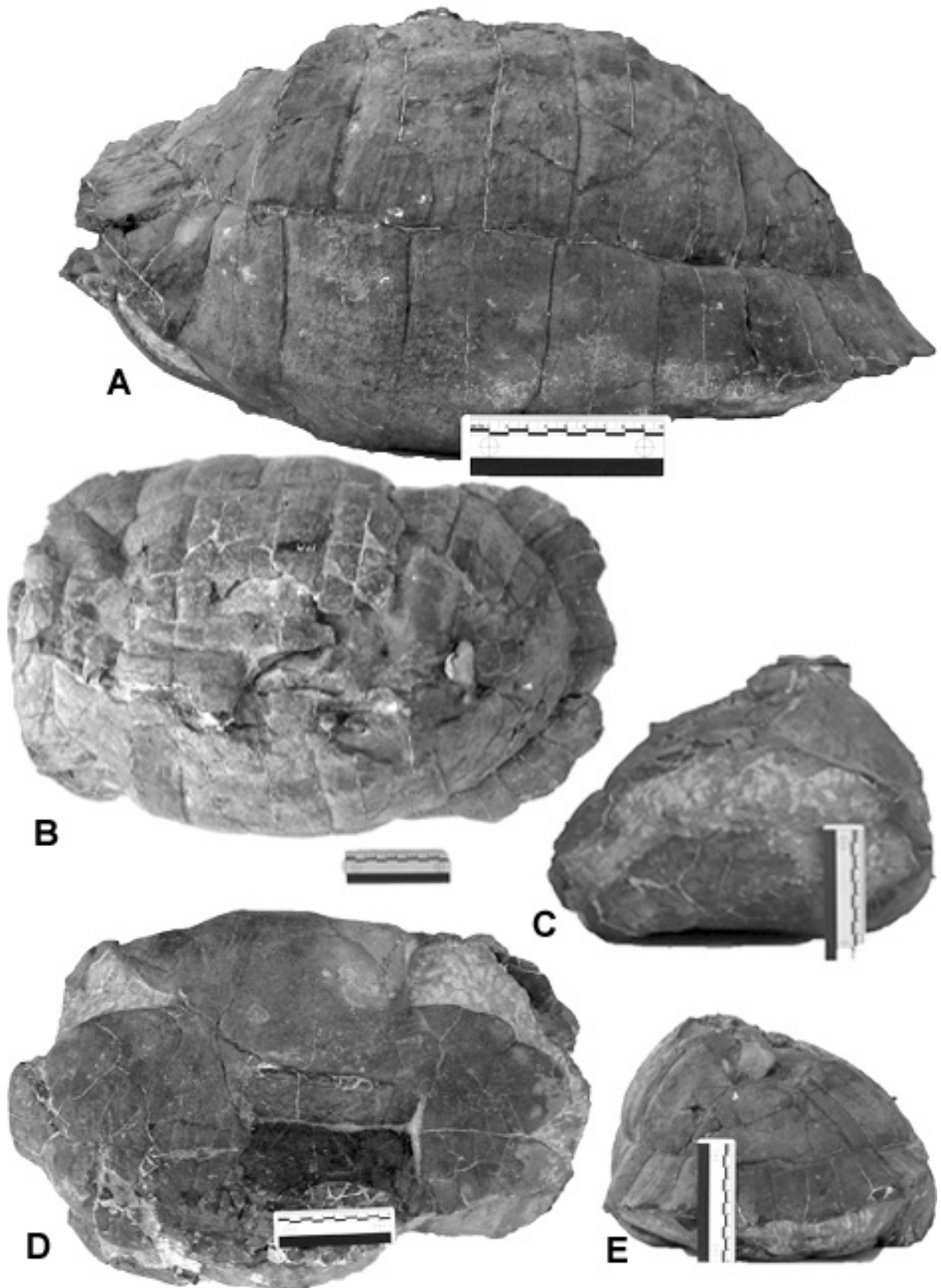


FIGURE 1. *Hadrianus majusculus*, holotype YPM 2743, nearly complete carapace and plastron: **A**, left lateral; **B**, dorsal; **C**, anterior; **D**, ventral; and **E**, posterior views.

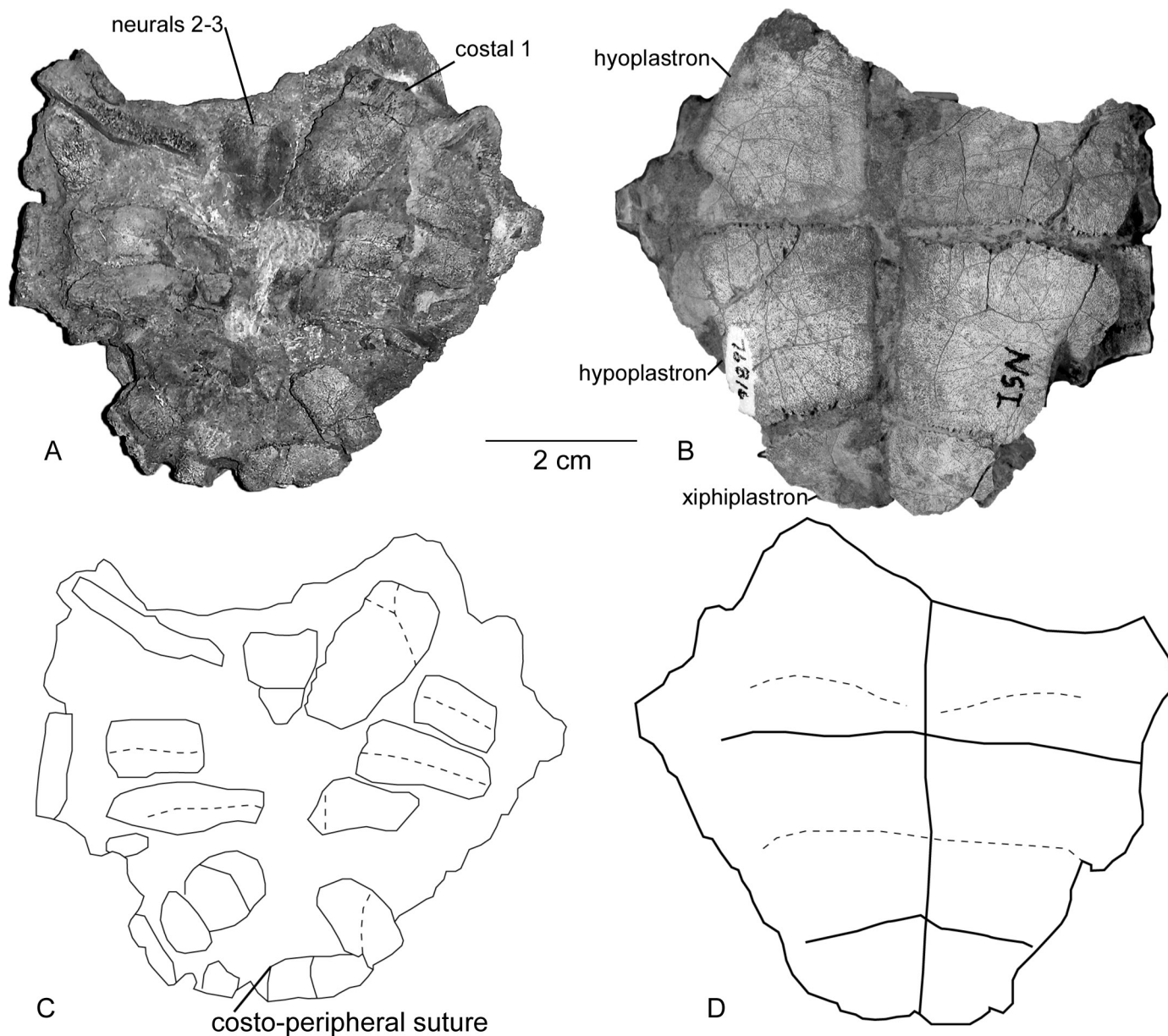


FIGURE 2. *Hadrianus majusculus*, juvenile, posterior portions of the carapace and plastron, UCB 76816: A, dorsal (of carapace) and B, ventral (of plastron) views; and C–D, line drawings in C, dorsal (of carapace) and D, ventral (of plastron) views.

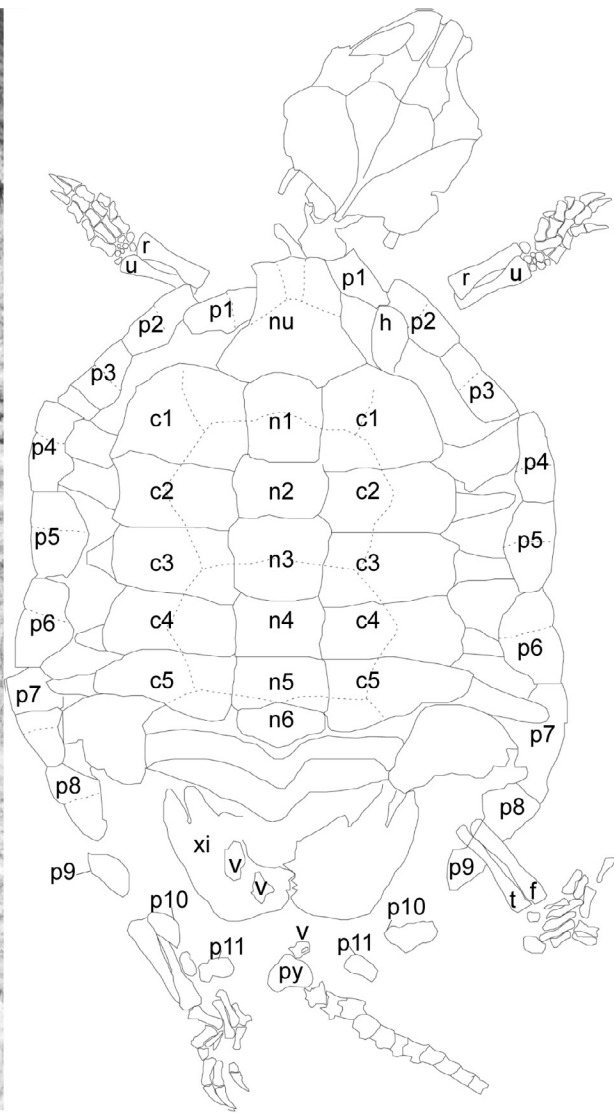
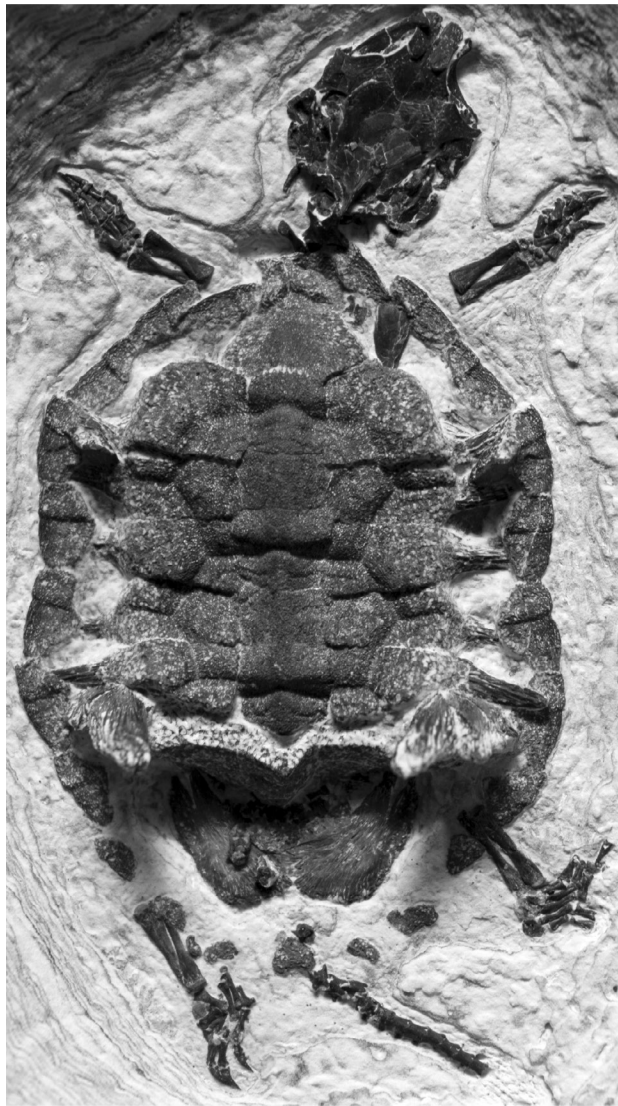
majusculus. Pectoral scutes are less than half as wide as the abdominal scutes along the midline. Peripherals are lower dorsally than in *H. majusculus* (Hay, 1908, p. 374). Furthermore, unlike *H. majusculus*, the posterior sutures of the epiplastron are nearly straight, and the costals show wedging in line with the definition of Hay (1908). Additionally, the genus *Hadrianus* differs from *Echmatemys* in the triangular shape of the postorbital in contrast to its broad, trapezoidal shape in *Echmatemys*.

New material—A hatching turtle identified by the authors as *Hadrianus* cf. *H. corsoni* (FOBU 14015, Green River Formation, Kemmerer, Wyoming, Figs. 3–4) is remarkably complete, including the skull, carapace, posterior two-thirds of the plastron, and incomplete limbs.

Skull—The skull (Figs. 3a, c, 4, A1) is 13 mm long and 9.7 mm wide, reaching a maximum width across the quadratojugals. Due to the preservation of the specimen, the majority of details in dorsal view are visible, but those laterally are obscured or not visible. Dorsally, the frontal contributes to the orbit, forming the posteromedial half of its dorsal margin. The frontals also have

a distinct anteromedial projection between the prefrontals. The orbits are anteriorly placed just behind the anterior tip of the rostrum. The parietals are large, forming most of the posterior portion of the skull roof. The postorbital is large and expanded laterally relative to *Echmatemys*, triangular, and sutured to the parietal and frontal. It forms the entire posterior margin of the orbit. The prefrontals are roughly rectangular, forming the dorsal anterior portion of the orbital margin. The maxilla forms much of the lateral margin of the nasal passage and the floor of the orbit. The squamosal and quadrate suture lies about halfway between the posterior margin of the postorbital and the posterior extremity of the supraoccipital. The details of these bones are obscured by crushing. The articular of each side of the mandible can be seen below the skull about 3 mm lateral to either side of the supraoccipital, with the left one being more abraded. No retroarticular process is visible on either side of the skull.

Carapace—The carapace (Fig. 3) is 40 mm long and 31.3 mm wide, including most of the bones. It has the distinct medial ridge seen in many juvenile testudinoids. The posterior three

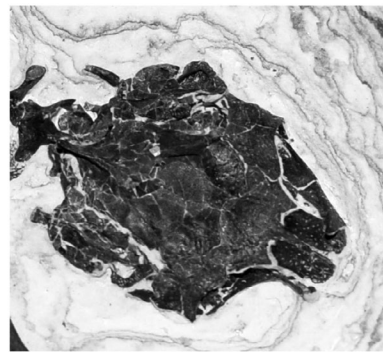


A

1 cm



B



C

FIGURE 3 (facing page). *Hadrianus corsoni*, articulated juvenile skeleton (still partially encased in matrix), FOBU 14015: **A**, dorsal view, with image of specimen (left) and line drawing (right); **B**, only existing image of the plastron in ventral view; and **C**, image of skull showing more of right lateral side, particularly region around the orbit. **Abbreviations:** c, costal; h, humerus; f, fibula; n, neural; nu, nuchal; p, peripheral; py, pygal; r, radius; t, tibia; u, ulna; and xi, xiphiplastron.

peripherals and the pygal are poorly ossified, and do not contact each other. This resembles the anterior-to-posterior formation of the peripheral bones noted in the embryos of *Trachemys* studied by Gilbert et al. (2001). Costal wedging is present, and the neurals and proximal portions of the costals show the typical striated surface sculpture associated with *Hadrianus*. The more distal portions of the costals, as well as the peripherals, show a more typical juvenile turtle surface sculpture. The sulci are deeply incised into the carapace. The nuchal is well developed, contacting neural 1, both first peripherals, and both first costals. Neural 1 is rectangular, measuring 6.3 mm long and 5.8 mm wide, contacts costal 1, and is crossed by the vertebral 1-vertebral 2 sulcus. Neural 2 is hexagonal, measuring 2.5 mm long and 8.1 mm wide, contacts costals 1 and 2, and is not crossed by any sulci. Neural 3 is hexagonal with short sides paralleling the midline near the crossing of the vertebral 2-vertebral 3 sulcus. It measures 5 mm long and 4.4 mm wide. Neural 4 is hexagonal, with extremely short anterior lateral sides so as to appear nearly rectangular, measuring 5 mm long and 5 mm wide. This neural lacks any crossing sulcus and is in contact with costals 3, 4 and 5, although the contact with costal 5 is quite small. Neural 5 is rectangular with very slight elongation anteriorly and posteriorly along the midline. Neural 5 is crossed by the vertebral 3-vertebral 4 sulcus. All three vertebral-vertebral sulci in this specimen bow anteriorly as they cross the midline, resulting in a slight “omega” shape. We consider that neural 6 is taphonomically tilted nearly vertical, so some of its features are obscured; but, it appears rectangular, with no apparent division of the lateral sides. This allows us to conclude that the neural formula up to neural 6 is 4-6A-6A-6A-4-4

The costals at their medial ends are 6.1, 3.1, 4.5, 3.2, 4 and 4 mm long, respectively. Costal 6 is missing the posterior margin on both sides, so this is its preserved length rather than its complete length. The distal rib tips (3.8 mm) are exposed beyond the costal plates, with a slight elongation near the inguinal buttress. The lateral margin of the carapace is slightly

concave between peripherals 5 and 6, although this lateral pinching may be a taphonomic feature. The carapace reaches its greatest width at the peripheral 6-peripheral 7 suture.

Plastron—The morphology of the hyoplastron and hypoplastron is known thanks to the preparation of the ventral side prior to recapping this side and preparing the dorsal side (Arvid Aase, pers. com., 2017) (Fig. 3B). The plastron is missing the epiplastron and entoplastron, but is otherwise complete. Both the hyoplastron-hypoplastron and the hypoplastron-xiphiplastron fontanelles are still open, with the former opening being especially large. The midline suture is loose and unfused in some areas. The inguinal buttress is well ossified between the distal third of costals 5 and 6 and was pushed through the carapace during burial and fossilization (Fig. 3a).

Caudal vertebrae—At least 13 procoelous caudal vertebrae are present, forming a relatively long tail (Fig. A6). These are slightly longer than tall, with the anterior and posterior processes less developed in the more posterior vertebrae. This appears to be almost the complete tail, potentially missing just the distal caudal vertebrae. However, despite appearances, the tail in FOBU 14015 is no longer relative to plastron width than that of an extant male *Pyxis planicauda* (Bonin, 2007) or *Agrionemys horsfieldii* (personal observation).

Forelimb—The forelimbs are nearly complete, but the right humerus is partially covered by the anterior peripherals. Both ulnae are 4.4 mm long with short, 6 mm long manus. The distal phalanges each have a small flexor tubercle (Fig. A2-A3). The development of this flexor tubercle is associated with walking behavior and is absent in species that primarily move by swimming (Lichtig and Lucas, in prep.). This corresponds to some of the observations of patterns of muscle modifications of Abdala et al. (2008). The phalangeal formula based on the left manus is 0-3-3-3-3.

Hind limb—The left hind limb is relatively complete, including a 5 mm long tibia and a 6 mm long pes. The distal phalanges of the pes lack a well-defined flexor tubercle. The

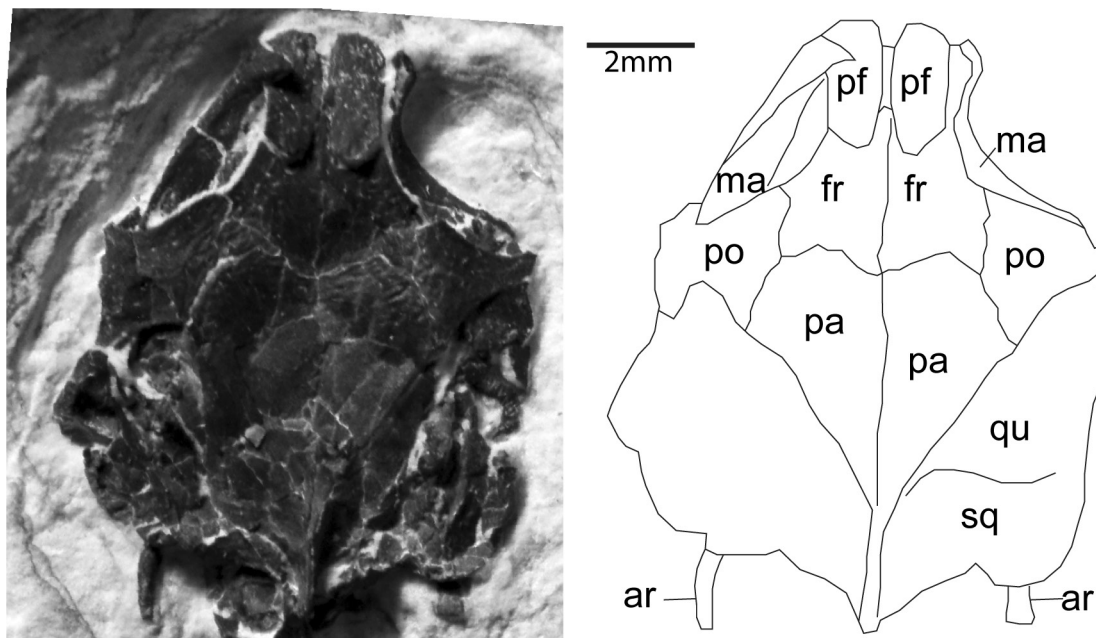


FIGURE 4. *Hadrianus corsoni*, juvenile skull, FOBU 14015, close up dorsal view of skull (left) and line drawing showing sutures of the dorsal view of the skull (right). **Abbreviations:** ar, articular; fr, frontal; ma, maxilla; pa, parietal; pf, prefrontal; po, postorbital; qu, quadrate; and sq, squamosal.

phalangeal formula of the pes is approximately ?-?-3-3-3 (Fig. A4-A5). Neither pes preserves the full digit 1 or 2.

Similar to that noted for *Hadrianus majusculus* above, more study is needed to better understand the changes through ontogeny of testudinids and *Hadrianus*, which may lead to more information about what these ontogenetic changes mean for the taxonomy and biology of these turtles.

Geoemydidae *Echmatemys* Hay, 1906

1871 *Emys*: Leidy p. 367

1871 *Emys*: Leidy p. 366

1873 *Emys*: Cope p. 625

1906 *Echmatemys* Hay p. 448

1908 *Echmatemys*: Hay p. 308

Type species– *Echmatemys septaria* (= *E. stevensoniana*).

Included species– The type species (*Echmatemys septaria*), together with *Echmatemys wyomingensis*, *E. uintensis*, *E. naomi* and *E. haydeni*.

Revised Diagnosis– Testudinoid turtles with the following unique characters: anterior three neurals longer than wide, anterior lobe of plastron enlarged anterior to the hyo-epiplastral suture, and musk glands usually present anterior to inguinal buttress.

Remarks– Our analysis supports the suggestion of J. H. Hutchison (pers. com., 2015) that *E. stevensoniana* and *E. septaria* are synonyms, as also suggested by Vlachos (2018).

Echmatemys haydeni (Cope, 1873) Fig. 5

1871 *Emys haydeni* Leidy p. 123

1871 *Emys haydeni* Cope p. 366

1871 *Emys wyomingensis* (in part) Leidy p. 367

1873 *Emys wyomingensis* (in part) Leidy p. 145 plate 9, fig. 6

1902 *Emys haydeni* Hay p. 448

Revised diagnosis– A species diagnosed from other *Echmatemys* by the long contact between marginal 1 and pleural 1 (Vlachos, 2018), the overlap of the posterior sulcus of vertebral 5 over the pygal, the lack of broadening of the suprapygals seen in *E. naomi* and the large medial extent of the inguinal buttress.

Referred specimen– An articulated skull, shell and limbs from the Green River Formation of Wyoming (TMP 2008.00.14, Fig. 5) provides the first documentation of the morphology of the skull of *Echmatemys haydeni*. Identification of this specimen was based on the long contact of marginal 1 and pleural 1 as well as the overlap of the posterior sulcus of vertebral 5 over the pygal not seen in *E. lativertebralis*. In addition, the large medial extent of the inguinal buttresses indicated by the protrusion between the costals, separating the costals nearly to the costal-neural sutures, is unusual and identical on both sides. This is seen in *E. stevensoniana*, *E. septaria*, and *E. haydeni* (Hay, 1908). We thus conclude that this specimen represents *E. haydeni*.

Skull– The skull is 31 mm long and 21 mm wide at its broadest point. It is dorsoventrally compressed, with most elements below the skull table obscured. Conversely, the skull table is complete with clear sutures. The frontals have greater exposure along the orbital margin than in *Hadrianus corsoni*. Furthermore, the postorbitals are reduced, with another bone (possibly the jugal) forming much of the ventral posterior margin of the orbit. The anterior process of the frontal is abbreviated relative to that of *Echmatemys naomi* (discussed below). The frontals lie rostrally, mainly between (medial to) the orbits, and extend caudally slightly beyond the caudal edge of the orbital rim. Additionally, the frontals in our specimen of *E. haydeni* project posteromedially between the parietals, allowing the parietals to project anterolaterally toward the orbital rim, also leading to the reduced postorbitals. This also makes the parietals prominent, extending between the orbits beyond their posterior

rim, distinctly farther than in *H. corsoni* and *E. naomi* (discussed further below).

Carapace– The carapace is complete, measuring 142 mm long, with the normal complement of scutes and bones seen in *Echmatemys* as described by Hay (1908). Five or six growth annuli are present on costal 1, indicating that this individual was at least five years old when it died (see Zug, 1991). Further study is still needed to better understand the ontogenetic changes of *Echmatemys* and what this may mean for these turtles.

Caudal vertebrae– The tail is more slender with smaller anterior and posterior processes of the neural arches than in *Echmatemys naomi* and slightly longer, at 29 mm length.

Limb Bones– The limbs are similar to, but more elongate in *Echmatemys haydeni* than in *E. naomi*. The relative length of the pes is 17.6% of the total carapace length in *E. haydeni* (TMP 2008.00.14) compared to 13.6% in *E. naomi* (FOBU 14014). The pes in *E. haydeni* measures 25 mm long, but in *E. naomi* is only 15 mm. The manus in *E. haydeni* is 12 mm long, similar to 11 mm in *E. naomi*. However, relative to total carapace length, the manus is shorter in *E. haydeni* (TMP 2008.00.14) at 8.5% compared to *E. naomi* (FOBU 14014) at 10%. This difference in hind limb morphology may indicate a difference in ecology between these two species. Conversely, the small sample size may mean this simply reflects two individual variants.

Echmatemys naomi (Leidy, 1871) Fig. 6

1908 *Echmatemys naomi* Hay p. 335, figs. 442-444

Revised diagnosis– A species of the genus *Echmatemys* diagnosed from other species of *Echmatemys* by the presence of a much longer than wide neural 1, the vertebral 4/vertebral 5 sulcus crosses the last neural, a wide suprapygals (Vlachos, 2018), and the lack of overlap of the pleurals over the nuchal.

Referred specimen– A nearly complete skeleton of *Echmatemys naomi* from the Green River Formation of Wyoming (FOBU 14014, Fig. 6A–C). The identification is based on the lack of overlap of the nuchal by the pleurals, neural 1 much longer than wide, vertebral 4/vertebral 5 sulcus over the last neural, and a wide suprapygals (based on Vlachos (2018) in part). This confirms the association of an isolated skull (USNM 17999, Fig. 7A–D), lacking the lower jaws, from the Bridger Formation in Wyoming, with this species.

Description of new material– FOBU 14014 is a nearly complete individual carapace with a length of 110 mm. The first costal shows four growth lines, so we estimate this turtle's ontogenetic age at death as approximately four years (see Zug, 1991). The carapace is similar to other published *Echmatemys naomi* (e.g., Hay, 1908). The caudal vertebrae outline a slightly shorter tail (28 mm long) than in *E. haydeni* (TMP 2008.00.14), but it is more robustly constructed, with large anterior and posterior processes relative to either *E. haydeni* (TMP 2008.00.14) or *Hadrianus corsoni* (FOBU 14015).

The skull is quite distinctive, being more robust (22.7 mm long and 16 mm wide) than *Echmatemys haydeni* (TMP 2008.00.14), with more pronounced prefrontals. The frontals have a more pronounced and larger anteromedial process along the midline reaching between the prefrontals. The right prefrontal is dislocated toward the left, covering part of the anterior process of the frontals. Furthermore, the postorbital is expanded, excluding the jugal from the dorsal margin of the orbit. The parietals form a posteriorly concave suture with the frontals, rather than being anteriorly concave with a posteromedial projection of the frontals between them, as in *E. haydeni*.

USNM 17999, an isolated skull (Fig. 7), was long suspected (e.g., Hirayama, 1984) to belong to *Echmatemys*, but until the discovery of an articulated specimen this could not be confirmed. Now that an articulated *E. naomi* has been identified (FOBU

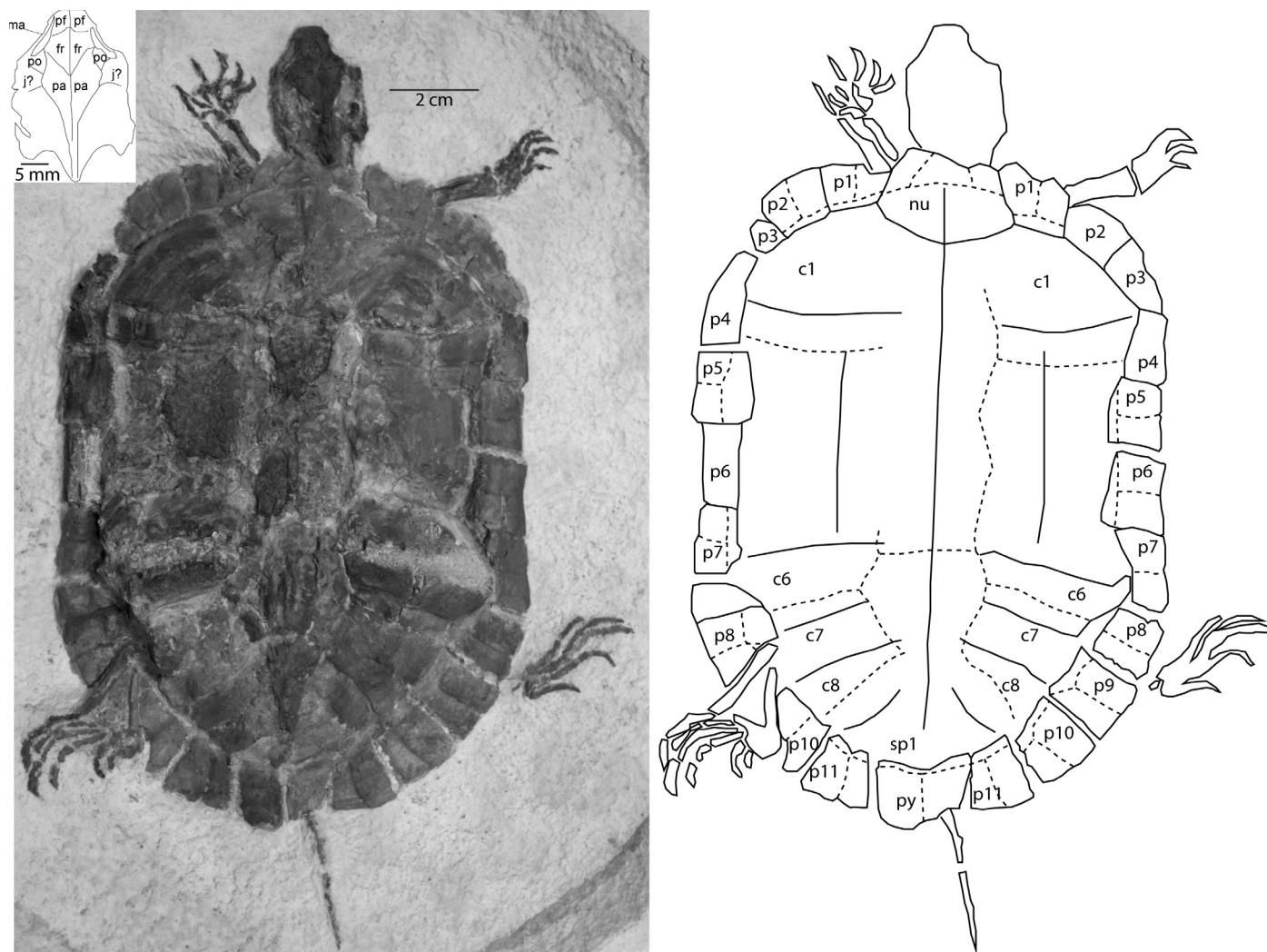


FIGURE 5. *Echmatemys haydeni*, articulated skeleton (still partially encased in matrix), TMP 2008.00.14 in dorsal view: Line drawing of dorsal aspect of skull based on original specimen (upper left); dorsal view of a cast of the specimen (lower left); line drawing of dorsal view of full specimen (right). **Abbreviations:** c, costal; fr, frontal; j?, ?jugal; ma, maxilla; nu, nuchal; pa, parietal; pf, prefrontal; p, peripheral; po, postorbital; py, pygal; spy, suprapygal.

14014), USNM 17999 can be referred to an individual of the same species. It is nearly identical in the overlapping portions to the skull in FOBU 14014, in the morphology of the skull table, and confirms some of the features discussed in FOBU 14014. Based on this cranial material, compared to *E. haydeni*, *E. naomi* has a distinctly enlarged frontal. The frontal extends distinctly caudal to the orbit, particularly posterolaterally. This also leads to reduced parietals, mainly in regard to their length, in *E. naomi* compared to *E. haydeni*.

USNM 17999 also preserves additional details of the remainder of the skull not visible in FOBU 14014. The maxilla in USNM 17999 has a single trituration surface and forms the anterior portion of the choana. The premaxillae are small and do not reach the choana. Instead, the vomer forms the anterior midline of the choana. The palatines form the posterior end of the choana and the medial edges of the suborbital fenestra. The pterygoids form only the posterolateral rim of the suborbital fenestra. Posteriorly, the pterygoids have a long, oblique suture with the pterygoid process of the quadrate and the basisphenoid. The quadrate is restricted to the posterior half of the fossa temporalis inferior. The basioccipital is well developed, forming the posteriormost preserved portion of the skull.

Remarks—The limbs of FOBU 14014 are similar to those

described by Hay (1908, p. 297, fig. 367–374) for an indeterminate *Echmatemys*, (YPM VPPU 011525), and the skull associated with these limbs (Hay, 1908, p. 297, pl. 45, figs. 11–13) is quite similar to the isolated adult skull described above (USNM 17999). These specimens were not associated with any shell material, so they could not previously be confidently identified without an articulated specimen of *E. naomi* for comparison. Although the frontal contribution to the orbital rim is slightly more prominent in YPM VPPU 011525 than in USNM 17999, other morphologic features agree between the two specimens. Therefore, we consider the skull and limbs (YPM VPPU 011525) Hay (1908) reported to be from *E. naomi* as well. With FOBU 14014 identified as an ontogenetically younger individual, more study is needed to better understand the ontogenetic changes of *Echmatemys* and *E. naomi*, in addition to comparing these to the ontogenetic changes in other testudinoids.

ECOLOGY OF EARLY NORTH AMERICAN TESTUDINIDS

Following the end-Cretaceous mass extinction, no terrestrial families of turtles survived, with the possible exception of meiolaniids in Australia and South America (Lichtig and Lucas, 2016). It has also been suggested that lindholmemydids

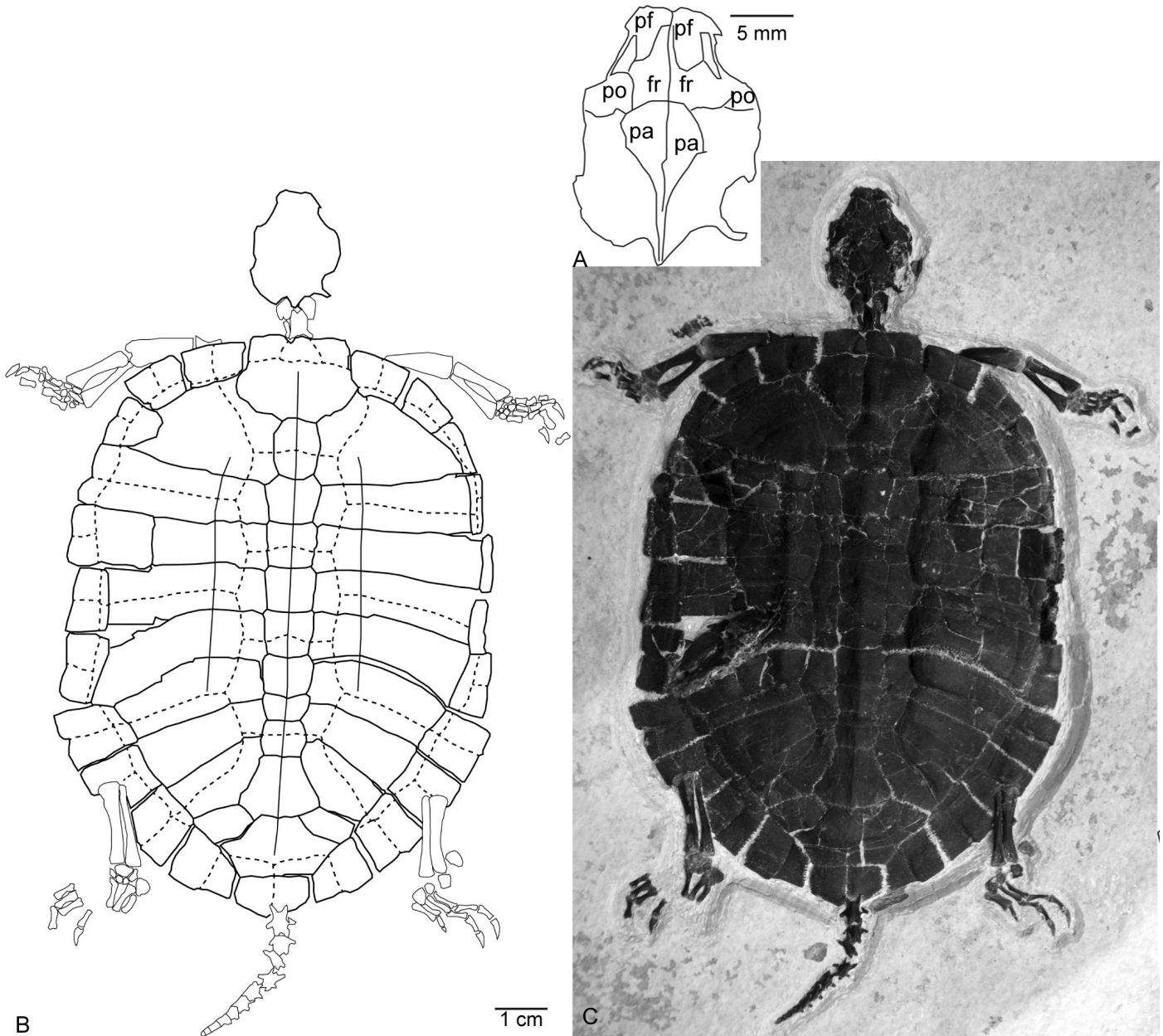


FIGURE 6. *Echmatemys naomi*, articulated skeleton (still partially encased in matrix), FOBU 14014, in dorsal view; A, magnified line drawing of skull; B, Line drawing of specimen, and C, Image of complete specimen. **Abbreviations:** c, costal; fr, frontal; j?, ?jugal; ma, maxilla; nu, nuchal; pa, parietal; pf, Prefrontal; p, peripheral; po, postorbital; py, pygal; spy, suprapygal.

might be an exception to this. We do not consider this likely, as the only published account of lindholmemydid (*Mongolemys elegans*) paleoecology by Cadena et al. (2013) suggests that these are aquatic to semi-aquatic turtles. Furthermore, based on the methods in Lichtig and Lucas (2017), we examined other lindholmemydids based on published reconstructions from Danilov (2003). This resulted in carapace-width-to-plastron-width ratios of 2-3, higher than any living terrestrial or even most semi-aquatic turtles. In addition, based on the statements and images of Cadena et al. (2013), the paratype of *Mongolemys elegans* (IGM 90/11) has the elongate femoral head suggested by Zug (1971) to be associated with swimming behavior. Thus, the end-Cretaceous extinction left at least the northern continents devoid of terrestrial turtles, possibly until the Eocene. The Paleogene transition by turtles to terrestriality was more challenging than it may at first seem (Natchev et al., 2015). Thus, Natchev et al. (2015) assert that most aquatic turtles find it difficult or impossible to swallow in the air (respire) on land.

Furthermore, Natchev et al. (2015) suggest that testudinoids may have been uniquely preadapted to fill this niche, given their well-developed muscular tongues. This may be why all extant, fully terrestrially adapted turtles are testudinoid turtles.

Basal testudinids have long been assumed to have an ecology similar to extant testudinids. This has been difficult to demonstrate given the absence of cranial or articulated limb material for *Hadrianus*. This assumption of uniform testudinid ecology is challenged by two facts. First is that *Manouria emys*, the most basal extant testudinid, has a distinct ecology (Natchev et al., 2015). This includes a distinct mode of food apprehension, breeding behavior, and a greater willingness to attempt subaqueous food capture. The second is that Scheyer and Sander (2007) found the histology of *Hadrianus* more in line with that of a semi-aquatic to aquatic turtle. This was suggested to be a carry over from their aquatic ancestors, but may reflect a more aquatic habitus in *Hadrianus* than previously recognized. This histology is similar to that observed for

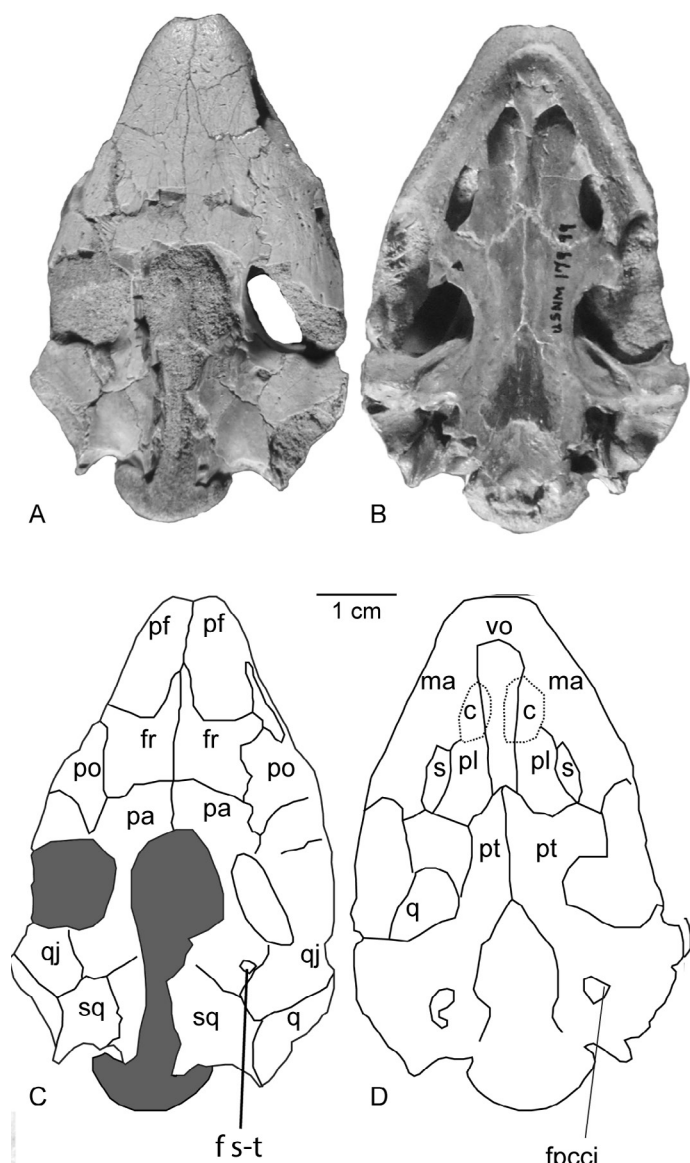


FIGURE 7. *Echmatemys naomi*, isolated skull, USNM 17999, in: **A**, dorsal and **B**, ventral views; **C**, line drawing of skull in dorsal view showing sutures; and **D**, line drawing of skull in ventral view showing sutures. **Abbreviations:** **bo**, basioccipital; **bs**, Basisphenoid; **c**, choana; **f s-t**, foramen stapedio-temporale; **fr**, frontal; **fpcci**, foramen posterius canalis carotici interni; **ma**, maxilla; **a**, parietal; **pf**, prefrontal; **pl**, palatine; **po**, postorbital; **pt**, pterygoid; **qj**, quadratojugal; **qu**, quadrate; **s**, suborbital fenestra; **sq**, squamosal; **vo**, vomer.

Rhinoclemmys pulcherima, which is aquatic as a hatchling and becomes terrestrial later in life (Webb, 2010). This could serve as a transitional form in the path to a fully terrestrial habitus. *Hadrianus* are near the base of a long stem leading to crown testudinids, so we need not assume they were exactly like extant or even fossil crown testudinids in their ecology. More material, particularly of the intermediate-sized individuals, is needed to further test this hypothesis.

AGE OF THE OLDEST TORTOISE

The oldest tortoises are stem-Testudinidae from the early Eocene of North America. The first recognition of Eocene tortoises in North America was that of *Hadrianus majusculus* by Cope (1874) from the late Wasatchian (Wa-5) of North America (Lichtig and Lucas, 2015a) (Fig. 8). This is the oldest reported

age Ma	Asia	North America	Europe
47	Arshantan LMA ?	Bridgerian LMA	Br-3 Br-2 Br-1b MP10 Grauvian LMA Fontainechelon ?
51	Bumbanian LMA	Hadrianus Wasatchian LMA	Br-1a Wa-7 Wa-6 MP 8+9 Neustrian LMA Wa-5 Wa-4
56	<i>Anhuichelys</i> Nongshanian LMA ?	<i>Echmatemys</i> Tiffanian LMA	Wa-3 MP7 Wa-2 MP6b Rivecourt LMA Wa-1 Cernaysian LMA MP6a

FIGURE 8 . Correlation chart showing the relative ages of proposed earliest testudinids (Testudinidae) and stem-testudinids. The tortoises with question marks indicate the possible ages of the unpublished Mongolian material. Correlations based on Lucas et al. (2003) and Smith et al. (2014). **Abbreviations:** **Br**, Bridgerian; **LMA**, land mammal age; **MP**, Mammal Paleogene zones; **Wa**, Wasatchian.

pantestudinid. *Echmatemys* comes from the same stratum. *Echmatemys* has been reported as far back as the base of the Wasatchian (Holroyd et al., 2001) (Fig. 8).

Purported stem-Testudinidae and -testudinids have been reported from the Eocene of Asia and Europe. This includes the recent revision of *Anhuichelys* (Tong et al., 2016) that concluded that this genus is a stem testudinid, rather than an emydid as previously proposed (Yeh, 1979). However, identifying *Anhuichelys* as a stem-testudinid was based on the false assumption that costal wedging is a unique trait of Testudinidae. In fact, it is known to occur in some emydid (e.g., some *Terrapene* specimens), making it more widespread in Testudinoidea. Furthermore, the shortened pectorals of *Anhuichelys* referenced by Tong et al. (2016) are actually relatively long compared to modern tortoises and not distinctly shorter than are found in emydid. The reputed hinging of the plastron is also questionable, as no undisputed testudinid has a kinetic anterior lobe, though this occurs in some members of both Emydidae and Geoemydidae, in addition to some other families such as Kinosternidae. Finally, the phylogenetic analysis of Tong et al. (2016) is suspect given that, by their own statement, minus either of two characters in their analysis –“Vertebrales 2-4: 0 wider than long, 1 longer than wide” and “Suture between the epiplastron and hyoplastron: 0 nearly perpendicular to body axis or backward laterally, 1 forward laterally”– the analysis finds a sister group relationship of *Anhuichelys* with *Platysternon*. This clade was found to be sister to both basal testudinids included in the analysis (*Lindholemys* and *Mongolemys*). Therefore, we conclude that *Anhuichelys* has no relevance to the origin of the Testudinidae. More recently, Vlachos and Rabi (2018) found that *Anhuichelys* was clearly not a testudinid, finding some ties

to the Emydidae as a sister taxon to the *Trachemys*+*Chrysemys* clade. This agrees with the original placement suggested by Yeh (1979).

Purported stem-Testudinidae have long been mentioned from Mongolia but have never been published (Holroyd and Parham, 2003). These come from the “Naran Bulak Formation of Khaichin Ula IV and the Tsagan Khushu localities” (Igor Danilov pers. com., 2016). Tsagan Khushu is of late Paleocene to early Eocene age in the Naran Bulak Svita, whereas Khaichin Ula IV is of middle Eocene age in the Khaychin Svita (Russell and Zhai, 1987) (Fig. 8). Without a published record it is difficult to assess this report.

Perez-Garcia et al. (2016) revised Europe’s oldest tortoises, naming *Fontainechelon* for the species “*Achilemys*” *cassouleti* (Claude and Tong, 2004). Perez-Garcia et al. (2016) suggested the specimen is from the early Eocene (MP 8–9), roughly equivalent to the late Wasatchian NALMA. This is counter to the original description, which placed it in MP 10, or approximately the Bridgerian NALMA (Fig. 8). There appears to be some confusion between the sites in that region of France. Thus, the application of the age of the “La Borie” locality to these specimens, which are from a different locality (“Saint-Papoul”), is not justified (Danilo et al., 2013). This is compounded by the fact that the compared North American taxa, *Hadrianus majusculus* and *H. corsoni*, are falsely stated to be significantly younger than they are and contemporaneous, although they are of different ages. Thus, *Fontainechelon* from France is younger than *Hadrianus* from North America.

We do not agree that *Fontainechelon* is the most basal testudinid, an assessment based on “the presence narrower and longer gular scutes; “wavy” humero-pectoral sulcus with medial part being convex anteriorly” (Vlachos and Rabi, 2018). *Achilemys* and *Hadrianus* have similar-sized gular scutes, each occupying approximately one-third of the length of the midline. The difference as coded seems to rely on the overlap (or lack thereof) of the gulars onto the entoplastron, rather than their size. Our examination of extant testudinids (see above) suggests that while the proportions are fairly stable, the overlap of the entoplastron is highly variable. The “wavy” sulcus is coded as present in a wide variety of taxa in the Emydidae, Geoemydidae and Testudinidae. There are a number of distinct morphologies within this, most of which are not particularly close to what is seen in *Hadrianus*. The closest comparison we are able to find is *Rhinoclemmys pulcherima*, a basal geoemydid close enough to be included in Testudinidae in some past molecular analyses (e.g., Spinks et al., 2004). It is also worth noting that while this character is quite distinct in mature individuals, it is completely absent in a three-month-old hatchling of *R. pulcherima* that has a transverse humeral-pectoral sulcus (pers. obs.). The more derived taxa within Testudinidae coded as possessing this characteristic are quite distinct, having a much lower degree of curvature to the humeral-pectoral sulcus and lacking the recurving to concave curvature anteriorly around the midline.

The hypothesis that Testudinidae entered North America from Asia during the second thermal maximum of the Eocene period (~52 Ma) was first proposed by Hutchison (1980). This was expanded upon in a subsequent review of Eocene turtle biostratigraphy and biogeography (Hutchison, 1998) and a review of the Willwood Formation turtle fauna (Holroyd et al., 2001). Hutchison (1980, 1998) and Holyroyd et al. (2001) identify three important events: (1) *Echmatemys*, in the broadest taxonomic sense, appears in North America by Wa-0; (2) *Baptemys* appears, likely an immigrant from south of Texas, at Wa-5; and (3) at this same horizon in the Willwood Formation, Testudinidae make an abrupt first appearance. We conclude *Echmatemys* (*sensu* Hay 1908) is an amalgamation of geoemydids including at least three distinct groups. These groups appeared in North America around the Paleocene-Eocene

thermal maximum and emigrated from North America to Europe and Asia by the earliest Bridgerian.

CONCLUSIONS

1. Complete articulated skeletons are described for *Hadrianus corsoni*, *Echmatemys haydeni*, and *E. naomi*, together with an incomplete shell of *H. majusculus*.

2. The appearance of stem-Testudinidae in North America does not support the hypothesis of *Hadrianus* emigrating from Asia. Furthermore, this helps explain the lack of precursors to Testudinidae in Paleogene rocks of Asia.

3. Given the earlier records relative to other continents of undisputed tortoises (e.g., *Hadrianus*), as well as the presence of stem members, Testudinidae likely originated in North America, subsequently immigrating to Europe and Asia during the late Wasatchian.

ACKNOWLEDGMENTS

We thank Arvid Aase and the staff of Fossil Butte National Monument for providing access to their specimens for study. We also thank Tonia Culver and the University of Colorado Museum of Natural History for access to their collections for this project. We thank Evan Vlachos, Edwin Cadena and an anonymous reviewer for their helpful reviews of an earlier version of this manuscript. The current version of the manuscript was reviewed by Daren Riedle, Adrian P. Hunt and Carl J. Franklin whose comments improved the content and clarity of this manuscript.

REFERENCES

- Abdala, V., Manzano, A. S., and Herrel, A., 2008, The distal forelimb musculature in aquatic and terrestrial turtles: phylogeny or environmental constraints?: *Journal of Anatomy*, v. 213, 2, p. 159-172.
- Auffenberg, W., 1974, Checklist of fossil land tortoises (Testudinidae): *Florida State Museum Bulletin*, v. 18, p. 121-251.
- Bever, G. S., 2008, Comparative growth in the postnatal skull of the extant North American turtle *Pseudemys texana* (Testudinoidea: Emydidae): *Acta Zoologica*, v. 89, p. 107-131.
- Bonin, F., Devaux, B., and Dupré, A., 2007, *Turtles of the world*. JHU Press.
- Cadena, E. A., Ksepka, D. T., and Norell, M. A., 2013, New material of *Mongolemys elegans* Khosatzky and Mlynarski, 1971 (Testudines: Lindholmemydidae), from the Late Cretaceous of Mongolia with comments on bone histology and phylogeny: *American Museum Novitates*, no. 3766, p. 1-28.
- Claude, J. and Tong, H., 2004, Early Eocene testudinoid turtles from Saint-Papoul, France, with comments on the early evolution of modern Testudinoidea: *Oryctos*, v. 5, p. 3-45.
- Cooper, J. G., 1863, *New Californian animals: Proceedings of the California Academy of Natural Sciences*, v. 2, p. 118-121.
- Cope, E.D., 1873, *Synopsis of new Vertebrata from the Tertiary of Colorado: obtained during the summer of 1873: U.S. Government Printing Office*. 19 p.
- Cope, E.D., 1874, *Report upon vertebrate fossils discovered in New Mexico, with descriptions of new species: U.S. War Department, Chief Engineer Annual Report, 43rd Congress, 2nd Session, House Executive Document 1, pt. 2; v. 2, pt. 2, Appendix FF, p. 589-606*.
- Danilo, L., Remy, J.A., Vianey-Liaud, M., Marandat, B., Sudre, J. and Lihoreau, F., 2013, A new Eocene locality in southern France sheds light on the basal radiation of Palaeotheriidae (Mammalia, Perissodactyla, Equoidea): *Journal of Vertebrate Paleontology*, v. 33, p. 195-215.
- Danilov, I. G., 2003, *Gravemys* Sukhanov and Narmandakh, 1983 (Testudinoidea: Lindholmemydidae) from the Late Cretaceous of Asia: *New data: PaleoBios*, v. 23, p. 9.
- Fritz, U. and Bininda-Emonds, O.R.P., 2007, When genes meet nomenclature: Tortoise phylogeny and the shifting generic concepts of *Testudo* and *Geochelone*: *Zoology*, v. 110, p. 298-307.
- Garbin, R. C., Ascarrunz, E., and Joyce, W. G., 2018, Polymorphic

- characters in the reconstruction of the phylogeny of geoemydid turtles: *Zoological Journal of the Linnean Society*, v. 184, p. 896–918.
- Gilbert, S. F., Loredó, G. A., Brukman, A., and Burke, A. C., 2001, Morphogenesis of the turtle shell: The development of a novel structure in tetrapod evolution: *Evolution & Development*, v. 3, p. 47–58.
- Hay, O.P., 1902, Bibliography and catalogue of the fossil Vertebrata of North America: U. S. Government Printing Office, 179, 868 p.
- Hay, O.P., 1904, On some fossil turtles belonging to the Marsh collection in Yale University Museum: *American Journal of Science*, v. 106, p. 261–276.
- Hay, O.P., 1906, Descriptions of two new genera (*Echmatemys* and *Xenochelys*) and two new species (*Xenochelys formosa* and *Terrapene putnami*) of fossil turtles: *Bulletin of the American Museum of Natural History*, v. 22, p. 27–31.
- Hay, O.P., 1908, The fossil turtles of North America: Carnegie Institute of Washington Publications, 75, 568 p.
- Hirayama, R., 1984, Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoidea); a preliminary result: *Studia Geologica Salanticensia*, v. 1, p. 141–157.
- Holroyd, P.A. and Parham, J.F., 2003, The antiquity of African tortoises: *Journal of Vertebrate Paleontology*, v. 23, p. 688–690.
- Holroyd, P.A., Hutchison, J.H., and Strait, S.G., 2001, Turtle diversity and abundance through the lower Eocene Willwood Formation of the southern Bighorn Basin: University of Michigan, *Papers on Paleontology*, v. 33, p. 97–107.
- Hutchison, J.H., 1980, Turtle stratigraphy of the Willwood Formation, Wyoming: Preliminary results: University of Michigan, *Papers on Paleontology*, 24, p. 115–118.
- Hutchison, J.H., 1998, Turtles across the Paleocene/Eocene epoch boundary in west-central North America; in Aubry, M-P, Lucas, S.G., and Berggren, W.A., eds., Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records. New York, Columbia University Press, p. 401–407.
- Hutchison, J.H., 2006, *Bridgeremys* (Geoemydidae, Testudines), a new genus from the middle Eocene of North America: *Fossil Turtle Research*, v. 1, p. 63–83.
- Jasinski, S. E., 2018, A new slider turtle (Testudines: Emydidae: Deirochelyinae: Trachemys) from the late Hemphillian (late Miocene/early Pliocene) of eastern Tennessee and the evolution of the deirochelyines: *PeerJ*, v. 6, e4338.
- Le, M., Raxworthy, C.J., McCord, W.P., and Mertz, L., 2006, A molecular phylogeny of tortoises (Testudines: Testudinidae) based on mitochondrial and nuclear genes: *Molecular Phylogenetics and Evolution*, v. 40, p. 517–531.
- Leidy, J., 1871, Report on the vertebrate fossils of the Tertiary formations of the West: *Annual Report of the United States Geological and Geographical Survey of the Territories*, v. 2, p. 340–370.
- Lichtig A.J. and Lucas S.G., 2015a, Juvenile *Echmatemys* (Testudines) from the Wasatchian of western North America: Taxonomic implications: *New Mexico Museum of Natural History and Science, Bulletin 67*, p. 139–144.
- Lichtig A.J. and Lucas S.G., 2015b, Turtles of the Eocene Huerfano Formation, Raton Basin, Colorado: *New Mexico Museum of Natural History and Science, Bulletin 67*, p. 153–160.
- Lichtig, A.J. and Lucas, S.G., 2015c, Turtles of the lower Eocene San Jose Formation, San Juan Basin, New Mexico, USA: *New Mexico Museum of Natural History and Science, Bulletin 67*, p. 161–177.
- Lichtig A.J. and Lucas S.G., 2016, Cretaceous nonmarine turtle biostratigraphy and evolutionary events: *New Mexico Museum of Natural History and Science, Bulletin 71*, p. 185–194.
- Lichtig, A.J., and Lucas, S.G., 2017, A simple method for inferring habitats of extinct turtles: *Palaeoworld*, v. 26, 3, p. 581–588.
- Linnaeus, C., 1758, *Systema Naturae*.
- Lucas, S.G., Holbrook, L.T., and Emry, R.J., 2003, *Isectolophus* (Mammalia, Perissodactyla) from the Eocene of the Zaysan Basin, Kazakstan and its biochronological significance: *Journal of Vertebrate Paleontology*, v. 23, 1, p. 238–243.
- Mautner, A.-K., Latimer, A.E., Fritz, U., and Scheyer, T.M., 2017, An updated description of the osteology of the pancake tortoise *Malacochersus tornieri* (Testudines: Testudinidae) with special focus on intraspecific variation: *Journal of Morphology*, v. 278, p. 321–333.
- Natchev, N., Tzankov, N., Wernebur, I. and Heiss, E., 2015, Feeding behavior in a ‘basal’ tortoise provides insights on the transitional feeding mode at the dawn of modern land turtle evolution: *PeerJ*, v. 3, e1172; DOI 10.7717/peerj.1172
- Perez-Garcia, A., Ortega, F. and Fuentes, E.J., 2016, Taxonomy, systematics, and diversity of the European oldest testudinids: *Zoological Journal of the Linnean Society*, v. 177, p. 648–675.
- Roberts, D.C., 1962, A study of *Echmatemys callopyge* from the Uinta Eocene of Utah, and its redefinition as a subspecies of *E. septaria*: *Bulletin of the Museum of Comparative Zoology*, v. 127, p. 375–399.
- Russell, D.E. and Zhai, R.-J., 1987, The Paleogene of Asia: Mammals and stratigraphy: *Memoires du Museum National d’histoire Naturelle*, v. 52, 488 p.
- Scheyer, T. M., and Sander, P. M., 2007, Shell bone histology indicates terrestrial palaeoecology of basal turtles: *Proceedings of the Royal Society of London B: Biological Sciences*, v. 274, p. 1885–1893.
- Smith, T., Quesnel, F., De Plöeg, G., De Franceschi, D., Métais, G., De Bast, E. and Dupuis, C., 2014, First Clarkforkian equivalent land mammal age in the latest Paleocene basal Sparnacian facies of Europe: fauna, flora, paleoenvironment and (bio) stratigraphy: *PloS One*, v. 9, 1, e86229.
- Spinks, P. Q., Shaffer, H. B., Iverson, J. B., and McCord, W. P., 2004, Phylogenetic hypotheses for the turtle family Geoemydidae. *Molecular phylogenetics and evolution*, v. 32, 1, p. 164–182.
- Takahashi, A., Hirayama, R., and Otsuka, H., 2018, Systematic revision of *Manouria oyamai* (Testudines, Testudinidae), based on new material from the upper Pleistocene of Okinawajima Island, the Ryukyu Archipelago, Japan, and its paleogeographic implications: *Journal of Vertebrate Paleontology*, v. 38, e1427594 (11 p.).
- Tong, H., Li, L., Li, D. S., Chen, L. M., Li, T., Yu, S.H., Yu, G.S., Cheng, X.Q. and Claude, J., 2016, A revision of *Anhuichelys* Yeh, 1979, the earliest known stem Testudinidae (Testudines: Cryptodira) from the Paleocene of China: *Vertebrata Palasiatica*, v. 54, 2, p. 156–179.
- Vlachos, E., 2018, A review of the fossil record of North American turtles of the clade pan-Testudinoidea: *Bulletin of the Peabody Museum of Natural History*, v. 59, p. 3–94.
- Vlachos, E. and Rabi, M., 2018, Total evidence analysis and body size evolution of extant and extinct tortoises (Testudines: Cryptodira: Pan-Testudinidae): *Cladistics*, v. 34, p. 652–683.
- Vamberger, M., Ihlow, F., Asztalos, M., Dawson, J. E., Jasinski, S. E., Praschag, P. and Fritz, U., 2020, So different, yet so alike: North American slider turtles (*Trachemys scripta*): *Vertebrate Zoology*, v. 70, 1, p. 87–96.
- Webb, M.R., 2010, Care and breeding of the Central American Wood Turtle *Rhinoclemmys pulcherimma manni*: Tortoise Trust, <http://www.tortoisetrust.org/articles/rhinoclemmys.html>.
- Yeh, H.K., 1979, Paleocene turtles from Anhui: *Vertebrata Palasiatica*, v. 17, p. 49–56.
- Zhao, Z., Heideman, N., Grobler, P., Jordaan, A., Bester, P., and Hofmeyr, M.D., 2020, Unraveling the diversification and systematic puzzle of the highly polymorphic *Psammobates tentorius* (Bell, 1828) complex (Reptilia: Testudinidae) through phylogenetic analyses and species delimitation approaches: *Journal of Zoological Systematics and Evolutionary Research*, v. 58, p. 308–326.
- Zug, G.R., 1971, Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles: *Miscellaneous Publications, Museum of Zoology, University of Michigan*, v. 142, p. 5–98.
- Zug, G.R., 1991, Age determination in turtles: *Society for the Study of Amphibians and Reptiles, Herpetological Circular*, v. 20, p. 1–28.



FIGURE A1. *Hadrianus corsoni*, FOBU 14015: Close up of dorsal view of the skull.



FIGURE A2. *Hadrianus corsoni*, FOBU 14015: Right forelimb.

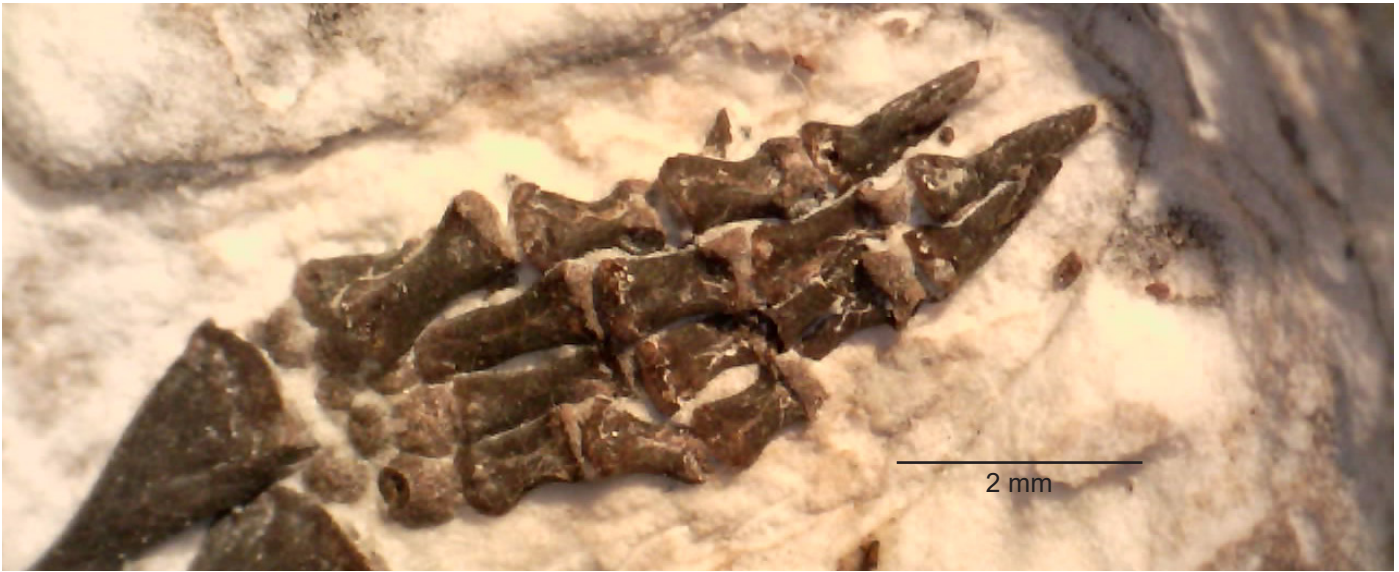


FIGURE A3. *Hadrianus corsoni*, FOBU 14015: Left manus and distal radius and ulna.



FIGURE A4. *Hadrianus corsoni*, FOBU 14015: Close up of the left pes.



FIGURE A5. *Hadrianus corsoni*, FOBU 14015: Close up of right pes, tibia, and fibula.

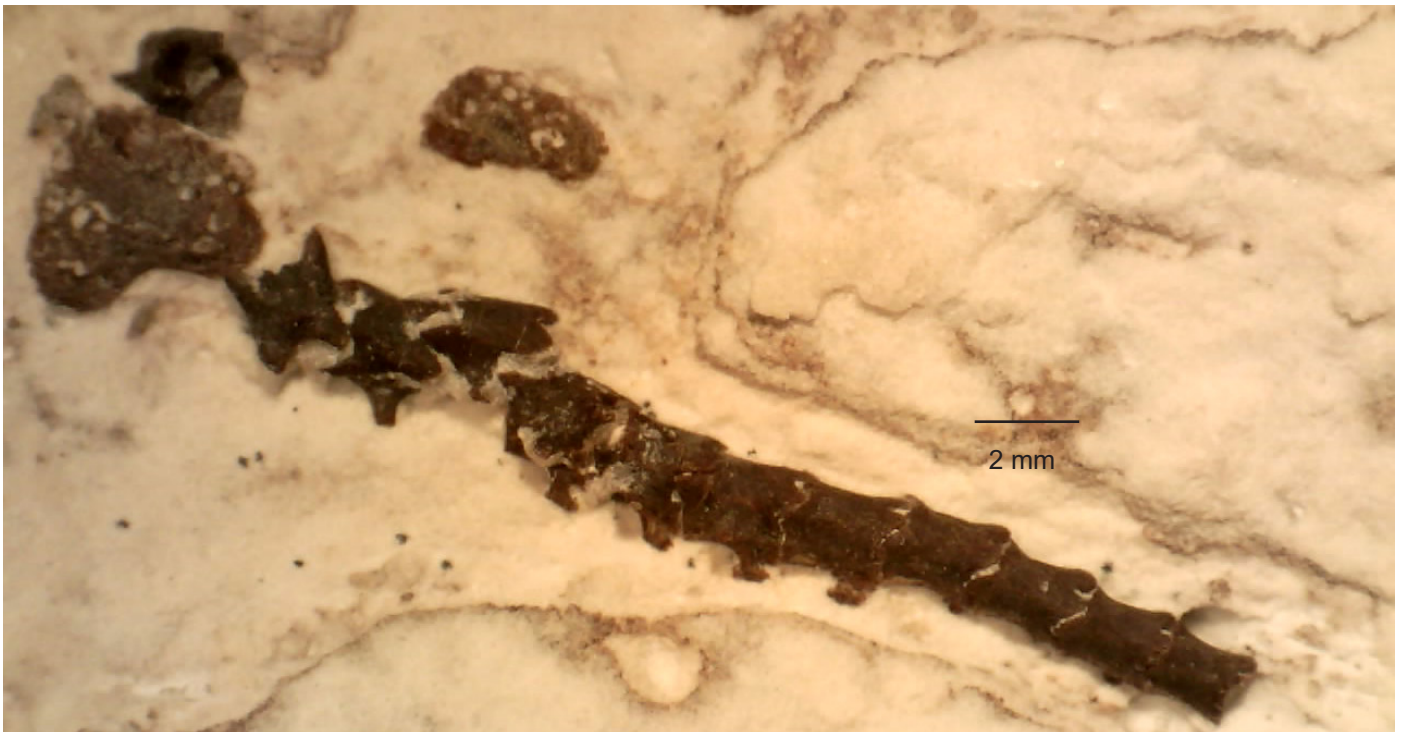


FIGURE A6. *Hadrianus corsoni*, FOBU 14015: Close up of caudal vertebrae, pygal, and the right p11.