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A new species of trionychid turtle from the Upper Cretaceous (Campanian) Fruitland Formation of New Mexico, USA

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Abstract.—New shell material of a trionychid turtle from the Upper Cretaceous (upper Campanian) Fossil Forest Member of the Fruitland Formation of northwestern New Mexico represents a new species, *Gilmoremys gettyspherensis*. The material consists of right costals I–III, V, VI, and VIII, left costals V, VII, and VIII, the left half of the entoplastron, the right hypo- and xiphiplastron, and the left hyo-, hypo-, and xiphiplastron. The specimen shows great similarities to the Late Cretaceous (Maastrichtian) trionychid *Gilmoremys lancensis* (Gilmore, 1916) by having a relatively thin shell, carapacial sculpturing consisting of fine pits combined with extended sinusoidal ridges or grooves, free costal rib ends, presence of a preneural, a distally constricted costal I and distally expanded costal II, two lateral hyoplastral processes, low hyoplastral shoulders, and full midline contact of the elongate xiphiplastra, but differs by being smaller, having raised sinusoidal ridges on the carapace instead of grooves, less distally expanded costals II, and less elongate xiphiplastra. Phylogenetic analysis places *Gilmoremys gettyspherensis* n. sp. as sister to *Gilmoremys lancensis* near the base of the clade Plastomenidae. Like the majority of previously described plastomenid materials, the type specimen of *Gilmoremys gettyspherensis* n. sp. was collected from a mudstone horizon, suggesting a preference for ponded environments.

UUID: http://zoobank.org/e7165061-d86b-46b7-a1f8-c31f5a8ed628

Introduction

Continental sediments of upper Campanian (Upper Cretaceous) age are broadly exposed throughout Canada, Mexico, and the United States and have yielded exceptionally rich turtle faunas consisting of adocids, chelydroids, helochelydrids, macrobaenids, nanhsiungchelyids, trionychids, and paracryptodires (see Brinkman, 2003, 2005; Brinkman and Rodriguez de la Rosa, 2006; Hutchison et al., 2013; Sullivan et al., 2013; Lively, 2016; and Lyson et al., 2017 for recent summaries). Soft-shelled turtles (Pan-Trionychidae) are an important component of these faunas, but the majority of finds are fragmentary, making it difficult to rigorously assess their alpha taxonomy and phylogenetic relationships (Vitek and Joyce, 2015). The pan-trionychid faunas from the late Campanian of Alberta, New Mexico, and Utah are the best understood to date. The Oldman and Dinosaur Park formations of Alberta, Canada, have yielded particularly rich material, including complete shells and skeletons, that allows recognition of four taxa, the plastomenid *Aspideretoides foveatus* (Leidy, 1857), the trionychine *Axestemys splendidus* (Hay, 1908), and the indeterminate '*Trionyx*' *allani* (Gilmore, 1923) and '*Trionyx*' *latus* (Gilmore, 1919) (Gardner et al., 1995; Brinkman, 2005; Vitek, 2012; Vitek and Joyce, 2015). (The pan-trionychid fauna of the Fruitland and Kirtland formations of New Mexico, by contrast, mostly consists of fragments that hint at the presence of at least

four trionychids, in particular two unnamed taxa and the indeterminate '*Trionyx*' *austerus* (Hay, 1908) and '*Trionyx*' *robustus* (Gilmore, 1919) (Sullivan et al., 2013; Vitek and Joyce, 2015). The Kaiparowits Formation of neighboring Utah has so far yielded mostly fragmentary remains of four unnamed pan-trionychids with uncertain affinities (Hutchison et al., 2013; Vitek and Joyce, 2015). Although the turtle faunas of Alberta, New Mexico, and Utah are broadly contemporaneous (Roberts et al., 2005, 2013), clear faunal links are still missing with the exception of an unnamed taxon with a striated carapace reported from the lower Kirtland Formation of northwestern New Mexico (Plastomeninae indet. of Sullivan et al., 2013) and the Kaiparowits Formation of southern Utah (Trionychidae indet. type B of Hutchison et al., 2013). The purpose of this contribution is to formally name this taxon as a new species of plastomenid pan-trionychid based on a nearly complete shell from the Fossil Forest Member of the Fruitland Formation of northwestern New Mexico. In addition, we provide an initial assessment of the phylogenetic relationship of the new species and discuss biogeographic and paleoecological implications.

Geologic setting

Vertebrate fossils, including abundant remains of turtles, have been recovered from the upper Fruitland and lower Kirtland

formations for more than a century. These remains have traditionally been grouped into the 'Hunter Wash Local Fauna,' defined as the fossiliferous horizons in the upper 12.2 meters of the Fruitland Formation and the lower 16.8 m of the Kirtland Formation in the Hunter Wash area (Clemens, 1973; Sullivan and Lucas, 2003, 2006). This definition, however, is dependent on the recognition of a clear interformational contact. Considerable disagreement persists over the nature and stratigraphic location of the contact between the Fruitland and Kirtland formations. As first defined, the Fruitland/Kirtland contact was recognized as gradational, though the Fruitland Formation was observed to be typically sandier than the overlying Kirtland Formation (Bauer, 1916). Later work by Fassett and Hinds (1971) examined the contact in outcrop and subsurface logs across the San Juan Basin and defined the contact as the top of the highest coal or carbonaceous shale. This definition was largely followed by later work (Fassett, 2000, 2010), though the gradational nature of the contact between the lower shale member of the Kirtland formation ('Hunter Wash Member' of Hunt and Lucas, 1992) and the upper Fruitland Formation make the definition geologically useless, with the only easily definable contact at the base of the overlying Farmington Sandstone Member ('Farmington Member' of Hunt and Lucas, 1992). Other attempts to define the contact (e.g., Hunt and Lucas, 1992; Lucas et al., 2006) have placed the top of the Fruitland at the base of the 'Bisti Member' or 'Bisti Bed,' an indurated but laterally discontinuous sandstone horizon. Regardless of the definition used, the *Gilmoremys gettyspherensis* type locality (DMNH loc. 5812) is stratigraphically below the Bisti Bed by at least 10 m and falls comfortably within the Fruitland Formation, within the recognized horizons of the Hunter Wash Local Fauna.

The locality is likely bracketed by dateable ash horizons, one in the lower horizons of the Fruitland Formation just above its contact with the underlying Pictured Cliffs sandstone ('Dog Eye Pond' [DEP] ash of Fassett and Steiner, 1997) and the other in the lower Kirtland Formation (Ash 2 of Fassett and Steiner, 1997). The originally published dates for both of these ashes, 75.56 ± 0.41 Ma and 74.56 ± 0.13 Ma, respectively (Fassett and Steiner, 1997), have more recently been recalculated using updated standards. Interestingly, these recalculations are in marked disagreement: DEP = 75.16 ± 0.41 Ma and Ash 2 = 74.17 ± 0.13 Ma (Roberts et al., 2013); DEP = 76.029 ± 0.41 Ma and Ash 2 = 75.023 ± 0.13 Ma (Fowler, 2017). Refining the geochronology of the Fruitland Formation through identification and dating of new ash beds, and redating known ash beds, is imperative for the comparison of the Hunter Wash Local Fauna with other Western Interior Basin faunas. Regardless of the precise date, all published and recalculated ages firmly place the type locality in the late Campanian.

The holotype specimen was recovered from a blocky, carbonaceous mudstone horizon likely representing a ponded, overbank depositional environment located in San Juan County, New Mexico, USA (Fig. 1). Disarticulation of the carapace and plastron, accompanied by the vertical displacement and irregular orientation of recovered elements at the site, suggests soft sediment bioturbation typical of shallow pond or slow water environments on a fluvial floodplain. It is likely the postmortem remains settled to the bottom of a low-energy, shallow-water environment and experienced in situ disarticulation with negligible transport.

Materials and methods

All materials used herein were collected over the course of the past decades by independent teams from several institutions from Upper Cretaceous (Campanian) sediments exposed in New Mexico and Utah. Previously published materials from New Mexico (Sullivan et al., 2013) and Utah (Hutchison et al., 2013) are housed at the State Museum of Pennsylvania and Utah Museum of Natural History, respectively. New material presented herein is housed at the Denver Museum of Nature and Science.

Repositories and institutional abbreviations.—Types, figured, and other specimens examined in this study are deposited in the following institutions: Denver Museum of Nature and Science (DMNH), Denver, Colorado, USA; State Museum of Pennsylvania (SMP), Harrisburg, Pennsylvania, USA; Utah Museum of Natural History (UMNH), Salt Lake City, Utah, USA.

Systematic paleontology

Testudinata Batsch, 1788, sensu Joyce et al., 2004
Trionychidae Gray, 1825, sensu Joyce et al., 2004
Gilmoremys Joyce and Lyson, 2011

Type species.—*Aspideretes lancensis* Gilmore, 1916.

Gilmoremys gettyspherensis new species
Figures 2, 3

Holotype.—DMNH EPV.125905, a partial, disarticulated shell consisting of right costals I–III, V, VI, and VIII, left costals V, VII, and VIII, the left half of the entoplastron, the right hypo- and xiphiplastron, and the left hyo-, hypo-, and xiphiplastron (Figs. 2, 3); DMNH loc. 5812, North Escavada Study Area, San Juan County, New Mexico, USA (Fig. 1); Fossil Forest Member, Fruitland Formation, late Campanian, Late Cretaceous.

Diagnosis.—*Gilmoremys gettyspherensis* n. sp. can be diagnosed as a representative of Pan-Trionychidae, among other characters, by the absence of peripherals, pygals, and scutes, and as a representative of *Gilmoremys* by a relatively thin shell; carapacial sculpturing consisting of fine pits combined with extended sinusoidal ridges or grooves that cross the length of several carapacial elements; costal ribs that protrude beyond the margin of the carapacial disk; the inferred presence of a preneural; a distally constricted costal I and distally expanded costal II; two lateral hyoplastral processes; low hyoplastral shoulders (i.e., anteriorly protruding lappets); and full midline contact of the elongate xiphiplastra. *Gilmoremys gettyspherensis* n. sp. can be differentiated from *Gilmoremys lancensis* by smaller size; the presence of raised sinusoidal ridges, not grooves; less distally expanded costal II; and less elongate xiphiplastra.

Occurrence.—San Juan County, New Mexico, USA, Fossil Forest Member, Fruitland Formation, late Campanian, Late Cretaceous (type occurrence); San Juan County, New Mexico,
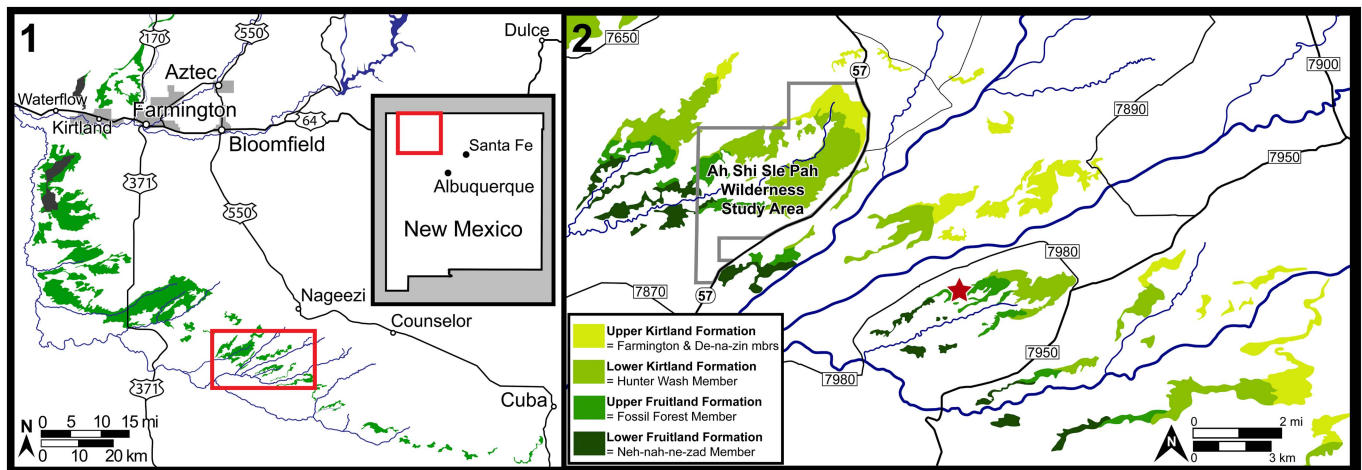
Figure 1. Location of DMNH loc. 5812, type locality of *Gilmoremys gettyspherensis* n. sp. (**1**) Overview of surface exposures (green) of the upper Campanian Fruitland and Kirtland formations in the San Juan Basin of northwestern New Mexico; (**2**) approximate placement of DMNH loc. 5812 (star) in the upper horizons of the Fruitland Formation in the North Escavada Study Area.

USA, Hunter Wash Member, Kirtland Formation, late Campanian, Late Cretaceous (Plastomeninae indet. of Sullivan et al., 2013, fig. 20.17); Kane and Garfield County, Utah, USA, Kaiparowits Formation, late Campanian, Late Cretaceous (Trionychidae type B of Hutchison et al., 2013, fig. 13.17).

Description.—The carapace of DMNH EPV.125905, the type specimen, includes right costals I–III, V, VI, and VIII, left costals V, VII, and VIII (Fig. 2). All elements with the exception of the nuchal, the preneural, the neurals, and costals IV are therefore present. The available elements indicate that the outline of the carapace was rounded, with the exception of a broad but shallow pygal notch formed by costals VIII. Although the costal rib is only completely preserved for right costal VI, well-developed breaks along the distal ends of all other preserved costals indicate that all costal ribs would have protruded significantly beyond the margins of the carapacial disk. We estimate the carapacial disk to have been about 22.5 cm along the midline, including the nuchal. The costals vary from about 3.5 mm in thickness toward the midline to about 4.5 mm toward their margins, not including the ribs. The margins of the costals are rounded and show no evidence for 'splitting' (i.e., separation of surficial and deepest layers of the costal by a trough). The carapace is primarily decorated by a surface pattern consisting of blunt, circular depressions that fade toward the midline. In addition, the carapace is decorated by a series of sinuous ridges that are arranged parallel to the midline and span the length of three to four costals. The ridges are faint and few on costals I, but they become increasingly dense and distinct toward the back of the carapace.

The nuchal is not preserved, but its preserved sutural attachment site with right costal I suggests that the metaplastic portion of the nuchal formed a callosity about half the width of the carapacial disk and that suprascapular fontanelles were absent. The neural series, including the preneural, is not preserved in DMNH EPV.125905, but the medial margins of the available costals provide enough information to allow reconstruction of the most important aspects. The presence of two facets along the medial edge of costal I indicate the presence

of a preneural, which was shorter than neural I. The width of this bone is unknown. Costals II, V, and VI have two facets as well, of which the anterior is shorter than the posterior one. This allows the inference that neurals I–VI were hexagonal and had short posterior sides. The medial margins of costal VII are unfortunately damaged and it is therefore unclear whether neural VII was square (i.e., laterally only contacted costals VII) or hexagonal with short posterior sides. The anteromedial margins on both costals VIII clearly hint at the former presence of a small neural VIII. There is an apparent gap between the anterior three and posterior four available costals, and DMNH EPV.125905 can therefore be reconstructed with confidence to have had eight pairs of costals. Costals I are slightly bowed to the anterior and narrower distally than proximally. Costals II mediate between the anteriorly oriented costals I and the straight costals III and are therefore expanded distally. Costals III, V, VI, and likely costal IV are similar in proportions, expand only slightly distally, and mediate between the anteriorly directly anterior costals and the posteriorly oriented posterior costals. Costals VII are clearly directly posterolaterally, have similar anteroposterior dimensions to the more anterior costals, but are noticeably shorter. Costals VIII are slightly broader than long, have the greatest anteroposterior dimensions of the costal series, contact one another along the midline for much of their anteroposterior length, and frame the shallow pygal notch.

No thoracic vertebrae are preserved in DMNH EPV.125905. The ribs of all available costals are greatly eroded, with the exception of right costal VI, which still preserves much of the distal end of its rib. It appears all but certain by reference to the available scars that all costal ribs extended significantly beyond the margin of the carapacial disk. Whereas costal rib VII clearly did not underlap costal VI, costal rib VIII may have underlapped costal VII.

The plastron of DMNH EPV.125905 includes the left half of the entoplastron, the right hypo- and xiphiplastron, and the left hyo-, hypo-, and xiphiplastron (Fig. 3). The entoplastron is greatly damaged medially, and it is therefore not possible to assess the original shape of this bone with confidence. We here nevertheless conclude by reference to other trionychids with an
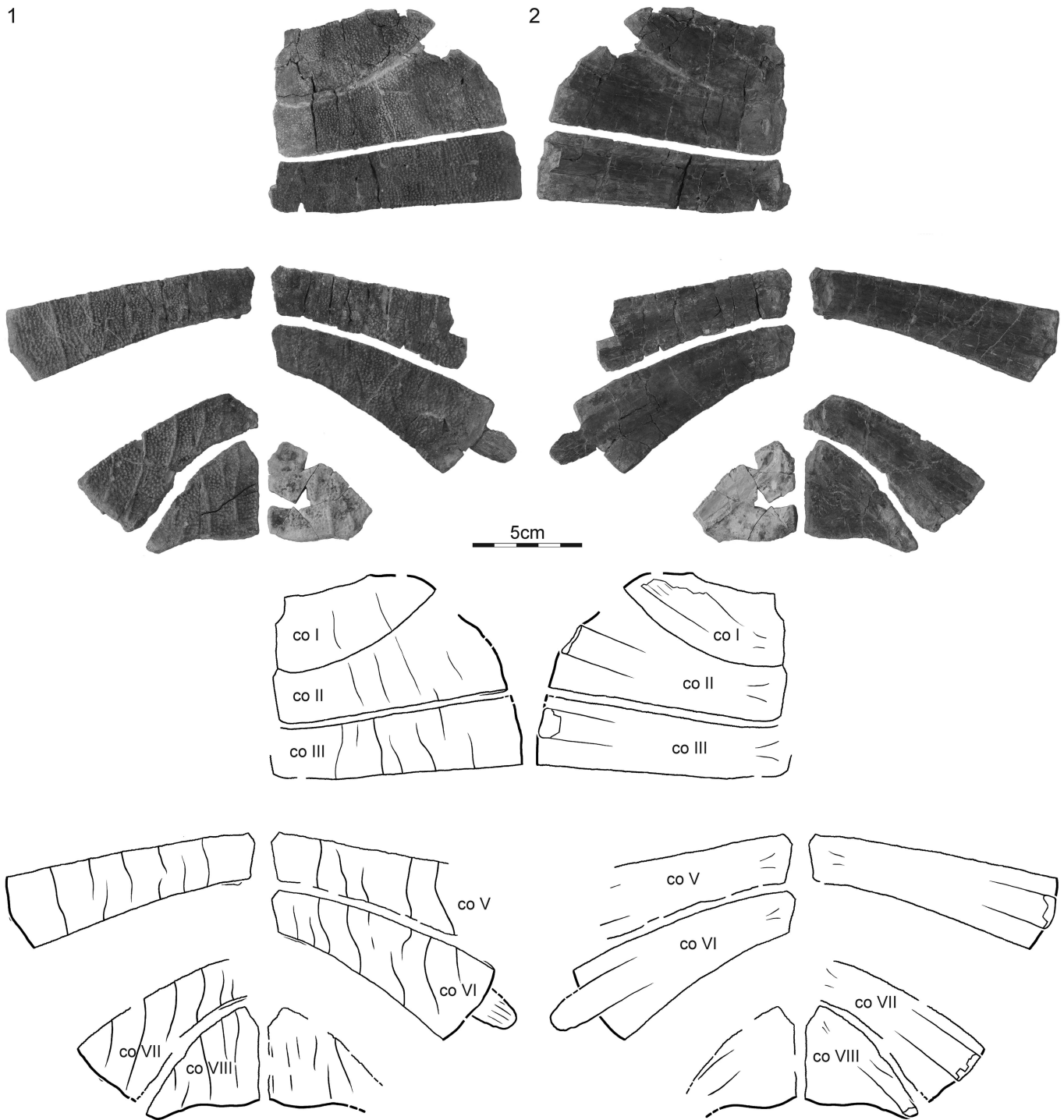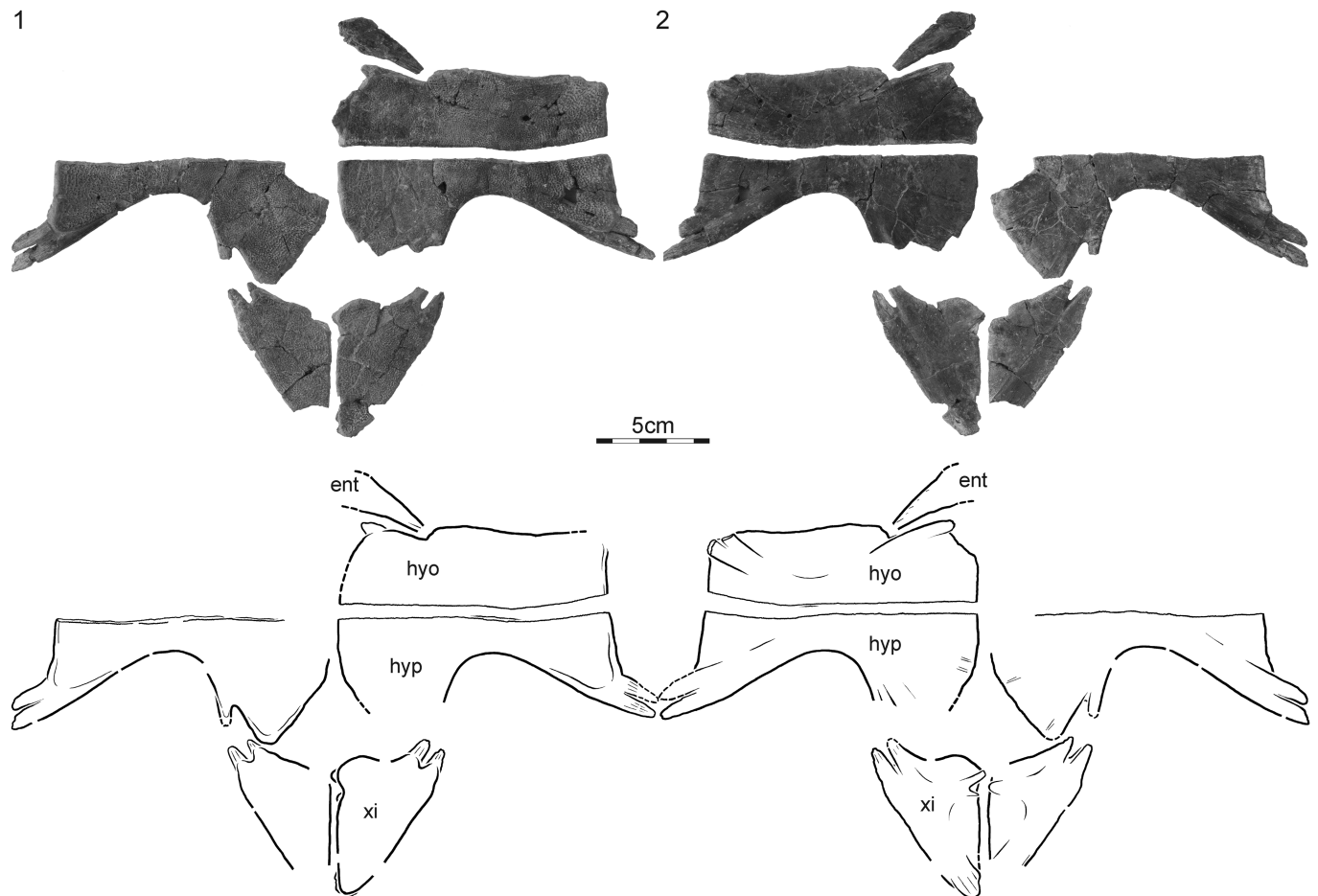
Figure 2. DMNH EPV.125905, *Gilmoremys gettyspherensis*, holotype, Late Cretaceous (late Campanian) of New Mexico. (**1**) Photograph and illustration of carapace in dorsal view; (**2**) photograph and illustration of carapace in ventral view. co = costal bone.

entoplastral callosity that enough is preserved to infer that such a callosity is absent.

Much of the hyo-, hypo, and xiphiplastra are covered by broad callosities that are decorated with a fine pattern of low, raised tubercles that are particularly closely packed near the inguinal buttresses, but otherwise coalesce in groups of twos or threes. The strap-like processes that form the deep tissue component of these bones are fully exposed along the lateral margins of the hyo- and hypoplastron but are otherwise partially

to fully covered by metaplastic bone. Whereas it is apparent that the xiphiplastra contacted one another along their full anteroposterior length, the hyo- and hypoplastra at best had a blunt midline contact.

The lateral processes of the only available hyoplastron are damaged, but the cross section of the break indicates that two processes were present. A single, medial process is apparent along the anteromedial margin of the hyoplastron that protrudes just beyond the margin of the metaplastic bone. The hyoplastral

Figure 3. DMNH EPV.125905, *Gilmoremys gettyspherensis*, holotype, Late Cretaceous (late Campanian) of New Mexico. (**1**) Photograph and illustration of plastron in ventral view; (**2**) photograph and illustration of carapace in dorsal view. ent = entoplastron; hyo = hyoplastron; hyp = hypoplastron; xi = xiphiplastron.

callosity is otherwise rectangular in shape and shows a modest anterior lappet that lightly embraces the entoplastron. The hypoplastra have two well-developed lateral processes and two faintly developed posterior processes for articulation with the xiphiplastron, but we can only discern faint traces of fine, medial processes. The hypoplastra form a triangular median fontanelle. The xiphiplastra have two anterior processes that interfinger with the hypoplastral processes and a single posteromedial process. The left xiphiplastron furthermore has two anteromedial processes that interfinger with a single anteromedial process of the right xiphiplastron.

Etymology.—In reference to the 'Gettysphere,' a circle of positive energy that surrounded Mike Getty, finder of the type specimen and recently deceased paleontologist, preparator, friend, and human being extraordinaire. Though figurative, the Gettysphere was a place, and the species epithet is therefore formed with the ending '-ensis.'

Phylogenetic analysis

We explore the phylogenetic relationships of *Gilmoremys gettyspherensis* n. sp. by incorporating it into the character/taxon matrix of Joyce and Lyson (2017), which in turn is based on the successive phylogenetic analyses of Meylan (1987), Joyce et al. (2009, 2016), Joyce and Lyson (2010, 2011), and Brinkman et al. (2017). To help resolve relationships, we added a single character (character 95) to the matrix that encodes the absence (0) or presence (1) of well-developed anteroposterior striation in the carapace of adults. The final data file, which includes the character/taxon matrix consisting of 95 characters scored for 37 taxa, the full list of characters and character states, and the backbone constraint, is provided in Supplemental data set 1.

We performed a parsimony analysis using the software TNT (Goloboff et al., 2008). Characters 1, 3, 5, 14, 20, 22, 41, 54, 79, 81, and 94 form morphoclines and were therefore ordered. Whereas the relationships of all extant trionychids were constrained using the molecular topology of Le et al. (2014), all fossil trionychids were allowed to float. Following the recommendations of Goloboff et al. (2017), characters were lightly weighted using a k factor of 12. The matrix was subjected to 1,000 replicates of random addition sequences followed by a second round of tree bisection-reconnection. The strict consensus tree resulting from the six equally most parsimonious trees with a score of 12.79441 is provided in Figure 4. The full strict consensus tree, common synapomorphies, and Bremer support values are provided in Supplemental data set 2.
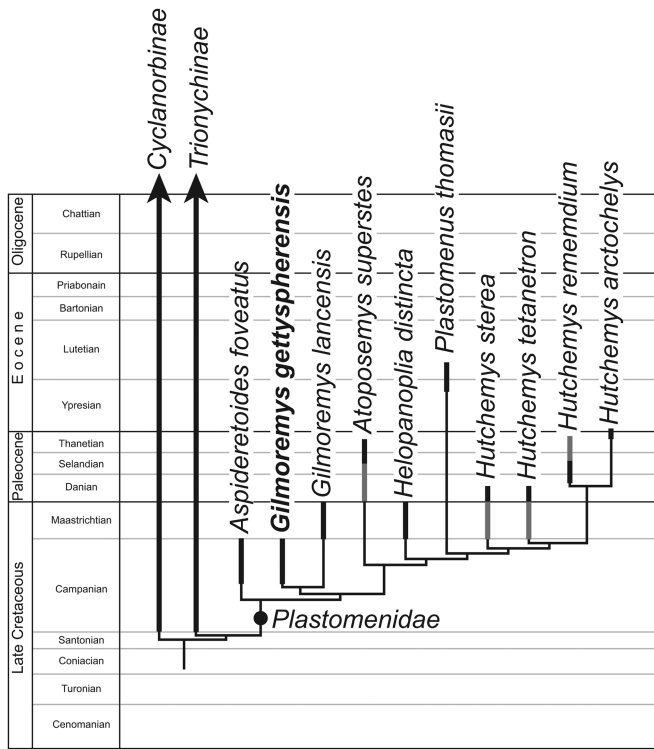
Figure 4.   Time-calibrated strict consensus cladograms retrieved from the phylogenetic analysis performed herein. The full tree is provided in Supplementary data set 2.

Discussion

Alpha taxonomy.—Although a total of 14 fossil trionychid species have been named from Campanian sediments exposed throughout North America, only six are currently recognized as valid (Gardner et al., 1995; Vitek, 2012; Sullivan et al., 2013; Vitek and Joyce, 2015): *Aspideretoides foveatus* (Leidy, 1857), *Axestemys splendidus* (Hay, 1908), 'Trionyx' allani (Gilmore, 1923), 'Trionyx' austerus (Hay, 1908), 'Trionyx' latus (Gilmore, 1919), and 'Trionyx' robustus (Gilmore 1919).

Gilmoremys gettyspherensis n. sp. resembles *Aspideretoides foveatus* (as described by Gardner et al., 1995; Brinkman, 2005) in overall size, outline of the carapace, and presence of a preneural, but *Aspideretoides foveatus* differs, among other characters, by being thicker shelled and by possessing a carapacial surface texture consisting of coarse pits that fade toward the midline, fewer neurals, smaller costals VIII, a broader entoplastron, only a single lateral hyoplastral process, and only poorly developed xiphiplastral callosities.

Gilmoremys gettyspherensis n. sp. resembles *Axestemys splendidus* (as described by Gardner et al., 1995) in carapacial outline, presence of a preneural, proportions of costals VIII, and the overall arrangement of the hyo-, hypo, and xiphiplastra. However, *Axestemys splendidus* differs by being about twice as large, by being thicker shelled, by having a coarsely netted carapacial surface ornamentation, fewer neurals, and less elongated xiphiplastra, and by lacking hyoplastral shoulders.

Gilmoremys gettyspherensis n. sp. resembles 'Trionyx' allani (as described by Gardner et al., 1995) in the overall arrangement of the carapace, including presence of a preneural,

but 'Trionyx' allani differs substantially by being about twice as large, having a coarsely netted carapacial sculpturing, possessing open suprascapular fontanelles, and exhibiting substantially smaller plastral callosities that lack a surface ornamentation.

Gilmoremys gettyspherensis n. sp. resembles 'Trionyx' latus (as described by Gardner et al., 1995) in overall size and number of neural elements, but 'Trionyx' latus differs by lacking a sutural contact between the nuchal and the remaining carapacial disk, exhibiting well-developed suprascapular fontanelles, lacking a preneural, possessing a finely knit carapacial surface sculpturing that is not developed along the margins of the shell, and having significantly smaller costals VII and VIII.

Gilmoremys gettyspherensis n. sp. resembles 'Trionyx' robustus (as described by Gilmore, 1919) in overall carapace outline, presence of a preneural, and proportions of costals VIII, but 'Trionyx' robustus differs by being about twice as large, being thick shelled, having a carapacial surface sculpturing consisting of deep, rounded pits, and having much better developed hyo/hypoplastral callosities that fully cover the medial and lateral processes.

The morphology of 'Trionyx' austerus (as described by Hay, 1908) is still poorly characterized, but this taxon can nevertheless be easily distinguished from *Gilmoremys gettyspherensis* n. sp. by being much larger and extremely thick shelled.

These comparisons highlight that *Gilmoremys gettyspherensis* n. sp. can be distinguished easily from all previously named Campanian taxa from North America.

Although up to eight fossil trionychids may compose the Maastrichtian trionychid assemblage of North America (Holroyd et al., 2014), only six are currently recognized by name (Vitek and Joyce, 2015): *Axestemys splendida* (Hay, 1908), *Gilmoremys lancensis* (Gilmore, 1916), *Helopanoplia distincta* Hay, 1908, *Hutchemys sterea* (Hutchison, 2009), *Hutchemys tetanetron* (Hutchison, 2009), and 'Trionyx' beecheri Hay, 1904. The two named Maastrichtian species of *Hutchemys* (as described by Hutchison, 2009) are easily distinguished from *Gilmoremys gettyspherensis* n. sp., among others, by being smaller and thicker shelled, by exhibiting a pitted shell sculpturing, and, most significantly, by possessing well-developed hyoplastral shoulders that suturally articulate with well-developed entoplastral callosities. *Helopanoplia distincta* (as described by Joyce and Lyson, 2017) most readily differs from *Gilmoremys gettyspherensis* n. sp. by being larger, by lacking free rib ends for costal ribs I–VI, by exhibiting a carapacial and plastral surface sculpturing that ranges from netting to isolated tubercles, by only possessing only a single lateral hyoplastral process and much more broadly developed hyo-, hypo-, and xiphiplastral callosities. Differences with *Axestemys splendida* are already listed. 'Trionyx' beecheri (as described by Hay, 1908; personal observation of the type specimen) finally differs by possessing a carapacial surface texture consisting of fine netting, a plastral texture consisting of fine raised tubercles, and large hyo/hypoplastral callosities that cover the lateral processes completely.

Gilmoremys gettyspherensis n. sp. broadly overlaps in morphology with *Gilmoremys lancensis* (as described by Joyce and Lyson, 2011): both species have a relatively thin shell, carapacial sculpturing consisting of fine pits combined with

extended sinusoidal ridges or grooves, costal ribs that protrude beyond the margin of the carapacial disk, a preneural, distally constricted costal I and distally expanded costal II, two lateral hyoplastral processes, only slightly developed hyoplastral shoulders, and full midline contact of the elongate xiphiplastra. It is therefore not surprising that our phylogenetic analysis retrieves them as immediate sisters (see the following). A small number of systematic differences are nevertheless apparent: the Maastrichtian material is consistently larger, costals II are more expanded distally, the xiphiplastra are more elongated, and most significantly, the sinusoidal ornamentation is developed in the form of grooves, not elevated ridges. We find the available character evidence to be sufficient to establish a new species for the Campanian morphotype that we herein name *Gilmoremys gettyspherensis*.

The comparisons made in the preceding highlight that *Gilmoremys gettyspherensis* n. sp. is the only known named species from the Late Cretaceous of North America to have surface sculpturing consisting of raised ridges. The only other previously reported material with such ridges has been reported from the Campanian of New Mexico (Plastomeninae indet. of Sullivan et al., 2013) and Utah (Trionychidae indet. type B of Hutchison et al., 2013). The most informative figured specimen from Utah is a left costal VIII (Hutchison et al., 2013, fig. 13.17c) that corresponds fully with that of the holotype of *Gilmoremys gettyspherensis* n. sp. by being wider than long and exhibiting well-developed raised ridges. The previously described specimen from New Mexico, recovered from the lowermost horizons of the Kirtland Formation (Hunter Wash Local Fauna) is a partial shell. The preserved costals once again exhibit well-developed raised ridges (Sullivan et al., 2013, fig. 20.17a, b). The preserved portion of the hyo/hypoplastra (Sullivan et al., 2013, fig. 20.17c, d) are consistent with the holotype of *Gilmoremys gettyspherensis* n. sp. in regard to sculpturing, but the hyoplastral shoulder is better developed. As this specimen appears to be slightly larger than the holotype, this difference can be attributed to a greater ontogenetic age. We therefore refer the previously described material from New Mexico and Utah to *Gilmoremys gettyspherensis* n. sp. with confidence.

Phylogenetic relationships.—Our phylogenetic analysis resulted in six equally parsimonious trees. The relationships among plastomenid soft-shelled turtles are fully resolved in the strict consensus tree (Fig. 3), highlighting that the six equally parsimonious trees did not reveal any topological conflict within this clade. The topology generally resembles those of previous analyses (e.g., Joyce and Lyson, 2011, 2017; Joyce et al., 2016) with exception of a more derived placement of *Atoposemys superstes* (Russell, 1930) as the sister to the *Helopanoplia*/*Hutchemys* clade and placement of *Gilmoremys gettyspherensis* n. sp. as sister to *Gilmoremys lancensis*. A literal interpretation of the tree implies that at least three plastomenid taxa existed during the Campanian: *Aspideretes foveatus*, *Gilmoremys gettyspherensis*, as the ancestral lineage of the clade formed by *Atoposemys superstes*, *Helopanoplia distincta*, *Hutchemys* spp., and *Plastomenus thomasii* (Cope, 1872). This number is certainly too conservative as an additional, unnamed plastomenid has been reported from the late Campanian of

Utah (*Helopanoplia* sp. of Hutchison et al., 2013) and as some previously described species from the Campanian of North American exhibit plastomenid characteristics, in particular '*Trionyx*' (originally *Plastomenus*) *robustus* (Gilmore, 1919). We therefore infer with confidence that the group originated prior to the late Campanian.

The hypothesized sister group relationship between the Campanian *Gilmoremys gettyspherensis* n. sp. and the Maastrichtian *Gilmoremys lancensis* is not surprising, as the morphology of these two species corresponds broadly. As the Campanian morphotype does not exhibit any characters that must be inferred to be apomorphic, it is possible to conclude that it may represent the ancestral morphology of the Maastrichtian morphotype and that the two form a single, persistent anagenetic lineage. This assertion can be tested in the future by finding both morphotypes in contemporaneous sediments.

It is relatively easy to establish the presence of *Gilmoremys gettyspherensis* n. sp. in a fauna, as the shells of adults are decorated by sinusoidal ridges. Although the study of turtle remains from the Campanian of New Mexico and Utah is still in its infancy, we here document multiple specimens referable to *Gilmoremys gettyspherensis* n. sp. Although the fossil turtle faunas of more northern basins of the Western Interior, in particularly those in Alberta and Montana, have been sampled heavily and are much better understood (see Brinkman, 2005 for a summary), we are unaware of any fragments of *Gilmoremys gettyspherensis* n. sp. reported from those localities. We therefore conclude that this taxon was restricted to the southern basins during the late Campanian.

The majority of plastomenid remains are recovered from siltstone and mudstones and the group is therefore often believed to have preferred ponded environments (e.g., Joyce and Lyson, 2017). The discovery of the type specimen of *Gilmoremys gettyspherensis* n. sp. in a mudstone once again confirms this conclusion.

Acknowledgments

Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.7h9p04r.