Giant Fossil Soft-Shelled Turtles of North America

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Abstract

Axestemys byssina—a large, potentially paedomorphic soft-shelled turtle (Trionychidae)—and a number of other of giant trionychids have been described, but no rigorous analysis has been undertaken to investigate their relationships. Because these trionychids are so unusual and occupy a broad Cretaceous-Eocene temporal range (70-46 myr), their study provides new insights into broad patterns of trionychid evolution. This project sets out to use all material previously assigned to *Axestemys* as well as previously undescribed material with traditional *"Axestemys"*-like characteristics to develop a concept of *Axestemys* that is meaningful in both a systematic and taxonomic context. *Axestemys cerevisia* sp. nov. and *A. montinsana* sp. nov. are established as new species, *A. byssina* and *A. splendida* comb. nov. are revised as a result of the description of new material, and *A. quinni* is reviewed and confirmed to be a member of *Axestemys. Eugenichelys robertemryi* is synonymized with *Axestemys byssina.* Phylogenetic analysis does not support the inclusion of *"Trionyx" puercensis* and *Conchochelys admiribalis*, previously hypothesized to belong to *Axestemys,* within the clade *Axestemys*. The taxon name '*Axestemys'* is best defined phylogenetically as a stem-based clade rather than a clade based on many of the characters traditionally ascribed to it, which are not consistently present throughout the clade. All members of *Axestemys* reach a gigantic size that is today found only in a few tropical trionychid species which independently evolved gigantism. The presence of *Axestemys* in North America indicates both a warmer climate and a higher trionychid diversity and disparity comparable to those of Recent species confined to tropical climates today.

Introduction

Soft-shelled turtles (Trionychidae) are a clade of highly modified aquatic turtles whose bony shells are covered by a layer of leathery skin. They lack several features common to other turtles, such as keratinous scutes, pygal bones, and an ossified bridge between the dorsal carapace and ventral plastron (Ernst and Barbour 1989). Recent diversity is limited to about 26 species distributed through North America, Africa, Asia, and the Indo-Australian archipelago (Ernst and Barbour 1989; Engstrom et al. 2004).

The trionychid fossil record extends at least as far back as the earliest Late Cretaceous in North America (Brinkman 2003). However, the evolutionary history of Trionychidae within North America is still unclear, partly because many taxa were named more than one hundred years ago based on fragmentary material with few or no characters considered diagnostic today (Hay 1908; Joyce et al. 2009). Nevertheless, despite the chaotic state of North American fossil trionychid systematics, it is clear that some fossil taxa developed a bizarre morphology within an already morphologically bizarre clade of turtles.

In particular, *Axestemys byssina*—a large, potentially paedomorphic trionychid — and a number of similarly modified taxa deserve further study. They present a good opportunity to explore potential influences on trionychid evolution that could produce giant species with such unusual morphological characters.

Edward Drinker Cope (1872) originally named the taxon '*Axestus byssinus'* based on a single, large xiphiplastron and some fragmentary non-shell postcranial bones. Unlike the rugose, sculptured xiphiplastra of all other North American trionychids known at that time, this specimen was covered by a smooth, unsculptured callosity. Later, Hay (1899) changed the generic name to '*Axestemys'* due to the fact that the name '*Axestus'* was already in use for a group of beetles. In his review of the fossil turtles of North America, Hay (1908) also referred several other hypoplastral and carapace fragments to *Axestemys byssina*. In the process, he described new characters found in this taxon, including a relatively large—but not gigantic—estimated size of 42 cm, the presence of suprascapular fontanelles and a smooth hyo-hypoplastral callosity similar to the smooth xiphiplastral callosity of the holotype specimen.

In subsequent decades other gigantic trionychids were described. Schmidt (1945) established the name *'Paleotrionyx'* and included *Paleotrionyx puercensis* and the new taxon *Paleotrionyx quinni* on the basis of large suprascapular fontanelles which separated the nuchal from the first costal. Gaffney (1979) described another gigantic fossil trionychid with similarly large suprascapular fontanelles, as well as a smooth border on the callosity covering the carapace and smooth hyo-hypoplastral callosity. He noted the similarities of this specimen to *Axestemys* and *Paleotrionyx*, but refrained from giving the specimen a name or making any taxonomic revisions.

Meanwhile, other scientists debated the systematics of *Axestemys* within Trionychidae. Some suggested that the shell-only *Axestemys* and *Paleotrionyx* and the skull-only taxon *Conchochelys* were synonymous within Trionychidae (de Broin 1977; Kordikova 1994). Others considered *Axestemys* a separate taxon from *Paleotrionyx* and placed *Axestemys* as a subgenus of *Rafetus* (Chkhikhvadze 2000).

Huthchison and Holroyd (2003) formally addressed the systematics of *Axestemys* when they described new, fragmentary skull and shell material that they assigned to *Axestemys* cf. *puercensis*. On the basis of the new material they synonymized *Paleotrionyx puercensis* and *Conchochelys admiribalis*. and this material in addition to Gaffney's (1979) unnamed turtle provided the basis for synonymizing *Axestemys* and *Paleotrionyx* (and therefore *Conchochelys*). Their study failed to support the placement of *Axestemys* within *Rafetus*. They suggested that "general paedomorphy of the shell" (Hutchison and Holroyd 2003:134) was an apomorphy for *Axestemys*.

However, there has been no cladistic analysis of any of these specimens, partly because many of the taxa, such as the type species, are based on material too incomplete to be useful in a phylogenetic analysis. Still, given previous work it seems probable that a clade exists which includes multiple gigantic fossil trionychids similar to *Axestemys byssina*.

Now, new material has made a re-evaluation and phylogenetic analysis of *Axestemys* possible. The purpose of this study is to use all material previously assigned to *Axestemys* as well as previously undescribed material with traditional "*Axestemys*"-like characteristics to develop a concept of *Axestemys* that is meaningful in both a taxonomic and systematic context. This project includes descriptions of new material attributable to *Axestemys byssina* and *A. splendida* nov. comb., as well as the establishment of two new taxa: *A. cerevisia* and *A. montinsana*. In addition, the phylogenetic relationships within *Axestemys* and among fossil and extant Trionychidae are investigated for the first time and used to test the hypothesis that *Axestemys* is a monophyletic clade of giant fossil trionychids.

There are a number of Eurasian specimens that have been referred to *Paleotrionyx* and/or *Axestemys* (Nessov 1997, De Broin 1977), which are not addressed here. This study focuses on potential North American representatives of *Axestemys*. Hopefully a clearer picture of what makes a North American trionychid *Axestemys* or not will provide insight for future studies of Eurasian trionychids.

This text follows Gaffney's (1972) terminology for skull features and Zangerl's (1969) for shell features. Institutional acronyms are as follows: AMNH = American Museum of Natural History, New York, New York; DMNH = Denver Museum of Nature and Science, Denver, Colorado; FMNH = Field Museum of Natural History, Chicago, Illinois; MRF = Marmarth Research Foundation, Marmarth, North Dakota; PTRM = Pioneer Trails Regional Museum, Bowman, North Dakota; TMP = Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; UCM = University of Colorado Museum, Boulder, Colorado; UM = University of Michigan Museum of Paleontology, Ann Arbor, Michigan; USNM = National Museum of Natural History, Washington, D.C., UW = University of Wyoming, Laramie, Wyoming; YPM = Yale Peabody Museum, New Haven, Connecticut.

Materials and methods

A morphological dataset was used to conduct a phylogenetic analysis. Morphological data were reproduced from a combination of Vitek's (2011) and Joyce and Lyson's (2011) matrix. The first is a slight revision of Joyce et al.'s (2009) extraction of characters from Meylan's (1987) matrix of osteological characters of extant trionychids.

The second includes eight additional characters added to Joyce et al's. (2009) matrix.

As a result of the conclusions of Vitek (in press), the scorings for specimens and synonyms of *Oliveremys uintaensis* were combined into a single taxon and scored as such. The plastomenid taxa *Gilmoremys lancensis, Hutchemys arctochelys, H. rememdium, H. sterea, H. tetanetron*, and *Plastomenus thomasii* (Joyce et al. 2009, Joyce and Lyson 2011) as well as the trionychines *Aspideretoides foveatus*, *A. splendida*, and *"Trionyx" egregius* (Gardner et al. 1995, Vitek in press) were included from previous analyses. For the purpose of this study, species historically considered part of *Axestemys* or displaying *"Axestemys"*-like characters were scored and added to the matrix. These species are: *Axestemys byssina*, *A. cerevisia, A. montinsana, A. quinni*, *"Axestemys" puercensis*, and *Aspideretoides allani*. The scoring of *A. allani* was based on the Gardner's (1992) scoring and the description of Gardner et al. (1995). Four new characters were added to the matrix in order to help resolve relationships among potential *Axestemys* taxa. A list of characters used in the analysis is in Appendix 1. The taxon/character matrix used in the analysis is in Appendix 2.

The parsimony analysis was conducted using PAUP* version 4.0b10 (Swofford 2003) with a strict consensus tree and fifty percent consensus tree (Fig. 1) generated from heuristic search with tree bisection and reconnection (TBR) branch-swapping and 100,000 replicates. All characters were run unordered, unweighted, and with no topological constraints. Minimum branch lengths were set to collapse. Polarity and a hypothetical-ancestor outgroup were based on Meylan's (1987) analysis

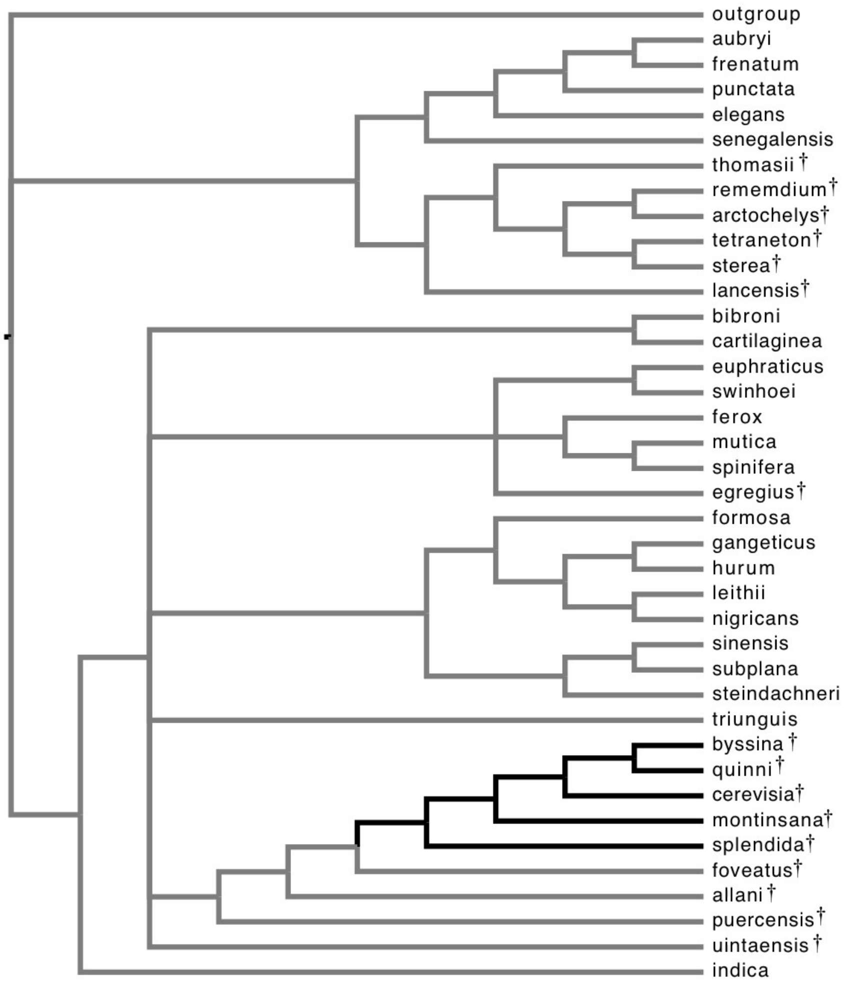

Figure 1. The 50 percent consensus tree topology of 6,571 most parsimonious trees resulting from a parsimony analysis of fossil and recent Trionychidae based on morphological data. 308 steps, CI = 0.3929, RI = 0.5917. *Axestemys* is designated in black. Daggers indicate extinct species.

Systematic Paleontology

Testudines Batsch 1788

Cryptodira Cope 1868

Trionychidae Gray 1825

Trionychinae Gray 1825

Axestemys Hay 1899 (converted clade name)

Definition: '*Axastemys'* is defined as the most inclusive clade containing the type species *Axastemys byssina* Cope 1872 but excluding *Aspideretoides foveatus* (Leidy 1856) as well as *Apalone, spinifera* (Le Sueur 1827) *Aspideretes gangeticus* (Cuvier 1825)*, Rafetus euphraticus* (Daudin 1802)*, Trionyx triunguis* (Forskal 1775)*, Cyclanorbis senegalensis* (Dumeril and Bibron 1835), *Plastomenus thomasii* (Cope 1872), *Chitra indica* (Gray 1831), and *Pelodiscus sinensis* (Weigmann 1835)

Reference Phylogeny: Fig. 1.

Composition: Type species*: Axestemys byssina* Cope 1872 USNM 4089. Referred species: *Axestemys cerevisia* sp. nov.*, Axestemys montinsana* sp. nov.*, Axestemys quinni* Schmidt 1945*, Axestemys splendida* comb. nov. (Hay 1908)

Diagnostic apomorphies: *Axestemys* can be diagnosed as a clade of trionychids with a carapace length 60 cm or longer.

Synonyms: *Axestus:* Cope 18872:462

Comments: *Axestemys* can be diagnosed as a member of Trionychinae by the following characters: a nuchal at least four times wider than long, a short plastral bridge, dorsal edge of apertura narium externum weakly emarginated, and absence of posterior costiform processes, peripherals, and depression on the eighth costals for articulation of the ilia.

Axestemys splendida comb. nov. (Hay 1908)

Figures 2-6

Type specimen

AMNH 3952, partial carapace.

Horizon and type locality

Judith River Group (Judithian), Judith River Basin, Montana

Referred material

Turtle Ridge Locality, Slope County, North Dakota, USA; Hell Creek Formation, Late Cretaceous (Maastrichtian): MRF 266, skull.

Big Turtle Cove Locality, Slope County, North Dakota, USA; Hell Creek Formation, Late Cretaceous (Maastrichtian):MRF 666, lower jaw; MRF uncatalogued 1, partial carapace and complete right hyo- and hypoplastron; MRF uncatalogued 2, field number BTC 10-28; MRF 700, preneural; MRF 631, costal 1; MRF 654, 676, costal; MRF 567, 675, 678 hyoplastron;MRF 699, partial pectoral girdle; MRF 586, MRF 661, femur.

Distribution

Judith River Group (Judithian), Alberta and Montana; Hell Creek Formation (Maastrichtian), North Dakota

Revised Differential Diagnosis

Characters that help differentiate the clade *Axestemys* but are not unique to this taxon include presence of a preneural, a single lateral hyoplastral process, and a maximum known carapace length at least 690 mm. Unlike Campanian specimens described by Gardner et al. (1995), Maastrichtian specimens of *Axestemys splendida* have maximum known basicranial length 205 mm and a smooth, unsculpted skull roof. From Gardner et al. (1995:636): “dorsomedian carapacial sculpture of larger individuals consists of high, narrow ridges bordering wavy, flat-bottomed, reticulate lacunae and (or) inosculating troughs; hypoplastral inguinal border thick; medial edge of xiphiplastral callosities in broad, unsutured medial contact in adults. Further differs from *Aspideretoides foveatus* as follows: length of epiplastral projections about one-quarter maximum hypoplastral width; epiplastral anterior projection wider and not tapered anteriorly; entoplastron gracile; skull wide, with broadly triangular face and blunt snout in dorsal view; face deep in lateral view; anterior edge of prefrontals shallowly emarginated laterally;...angle between anterior face of dentary symphysis and dorsal edge of labial ridge 30-40 degrees; dentary

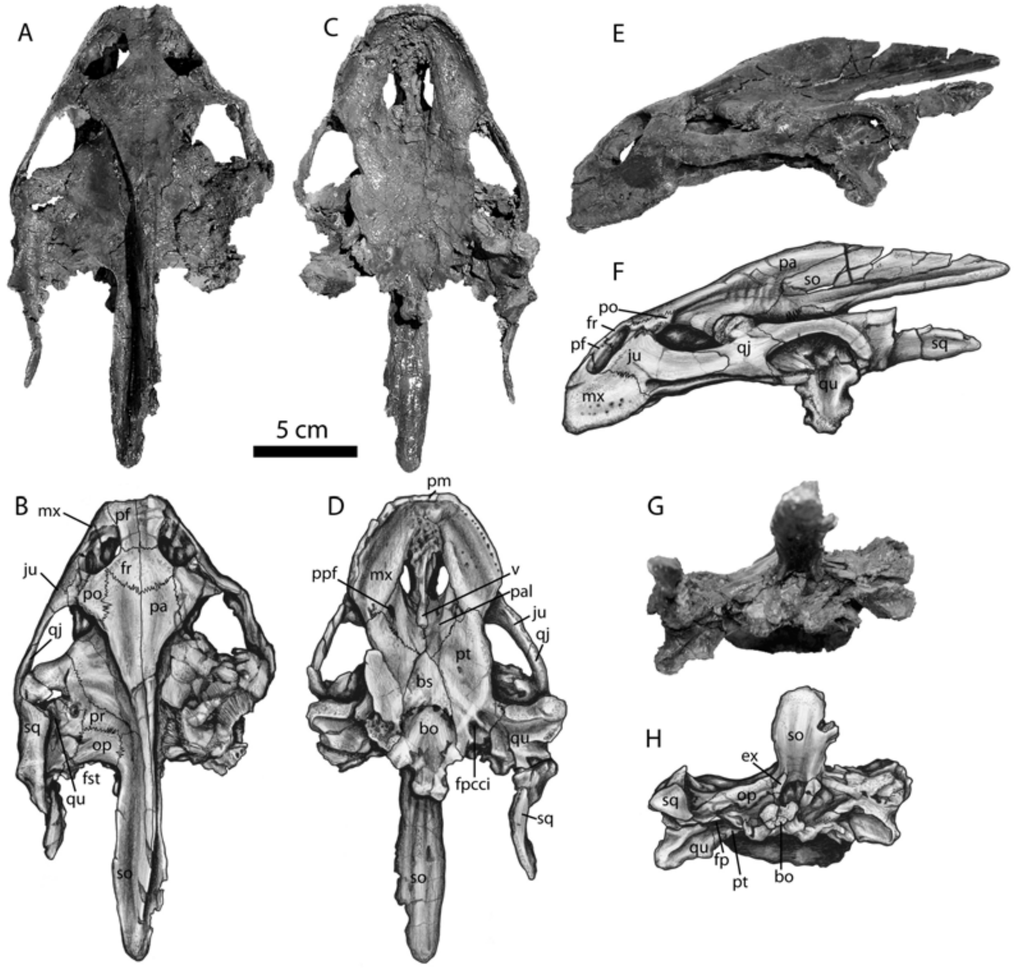

Figure 2. MRF 266, skull of *Axestemys splendida* from the Cretaceous Hell Creek Formation of North Dakota. A, photograph and B, illustration of dorsal view. C, photograph and D, illustration of ventral view. E, photograph and F, illustration of lateral view. G, photograph and H, illustration of posterior view. Abbreviations: bo = basioccipital, bs = basisphenoid, ex = exoccipital, fp = fenestra postotica, fpcci =foramen posterius canalis carotici intern, fr = frontal, fst = foramen stapedio-temporale, ju = jugal, mx = maxilla, op = opisthotic, pa = parietal, pal = palatine, pf = prefrontal, pm = premaxilla, po = postorbital, ppf = foramen palatine posterius, pr = prootic, pt = pterygoid, qj = quadratojugal, qu = quadrate, so = supraoccipital, sq = squamosal, v =

vomer.

pockets broad and deep. Further differs from *A. allani* in retaining sculpted plastral callosities and unfused hyo- and hypoplastron."

Description of new material

Cranium.— Figure 2. The right half of the skull has been crushed, and the secondary palate is broken, but the fossil is otherwise complete. From the premaxilla to the end of the supraoccipital, the skull is 20.5 cm long. The roof of the skull is smooth, unlike that of the Campanian specimens of this species (Gardner et al. 1995).

Premaxilla.— The premaxillae are fused into a single element. They make up part of the anterior margin of the skull, and are otherwise surrounded by the maxillae. They do not enter the apertura narium externum.

Maxilla.— The maxillae are deep and short. They make up part of the margin of the orbit and the apertura narium externum. They contact the prefrontals anterior to the orbit and along the anteriomedial margin of the orbit. They contact the jugal ventral to the orbit. The maxillae do not contact the frontals or quadratojugals. Ventrally, the maxillae form a wide, pitted primary palate that contacts the premaxilla. The vomer is visible, but the surface of the secondary palate is broken. To what extent the vomer contacted the maxillae is unknown. Matrix obscures the foramen intermaxillaris.

Prefrontal.— The prefrontal makes up part of the margin of the orbit and the apertura narium externum. The dorsal edge of the apertura narium externum is weakly emarginated laterally, but not at all emarginated medially. The prefrontal does not contact the palatine. In dorsal view, the prefrontals contact the maxillae laterally, the frontals posteriorly, and, within the orbit, the vomer.

Frontal.—The frontals are roughly trapezoidal. They make up the posteromedial margin of the orbit. On the skull surface they contact the prefrontals anteriorly and the parietals posteriorly. They have a short lateral contact with the postorbitals near the orbital margin. Within the orbit, the frontals remain unfused and contact the prefrontals in a suture that is relatively straight dorsoventrally. The sulcus olfactorius is present as a long ventral depression where the two frontals contact each other.

Parietal.— On the skull roof, the parietals contact the frontals anteriorly and the postorbitals anterolaterally. Unlike plastomenids, at no point do they participate in the orbital margin, either on the surface or within the skull. Within the upper temporal fossa, they contact the postorbital and prootic laterally and taper into the supraoccipital. The processus trochlearis oticum is composed of the quadrate, prootic, and parietal. The latter contributes to about 25% of the process. Anterior to the foramen nervi trigemini, the parietal forms part of the foramen margin, but its contacts with other elements are fragmented and unclear.

Postorbital.— The postorbitals are large and extend from the margin of the orbit to the upper temporal emargination. They are bounded by the parietals and the frontals medially and the jugals laterally. The contact between the jugal and the postorbital is obscured by cracks, but it is still clear that the postorbitals form the entirety of the surface of the postorbital bar, which is approximately half the diameter of the orbit.

Jugal.—The jugal forms part of the lateral margin of the orbit, where it contacts the maxilla anteriorly and the postorbital posteriorly. The postorbital prevents any contact between the jugal and parietal. The jugal contacts the quadratojugal along the temporal arch, but doest not contact the squamosal. The anterior limit of cheek emargination is formed by the jugal.

Quadratojugal.—The quadratojugal forms part of the temporal arch. Laterally, it comprises the posterior third of the arch, contacting the jugal anteriorly and the quadrate and squamosal posteriorly. Medially, the quadratojugal comprises about half of the inner surface of the temporal bar.

Squamosal.— The squamosal forms the lateral boundary of the upper temporal fossa. In lateral view, it contacts the quadratojugal anteriorly and the quadrate ventrally, roofs the cavum tympanum, and forms most of the antrum postoticum.

In dorsal view, the squamosal forms a small, accessory ridge along the top of the otic capsule, and contacts the quadrate and opisthotic medially along the length of the otic capsule. The squamosal probably contacted the paroccipital process of the opisthotic, but that region is broken. Posterior to the otic capsule, the squamosal forms a long, thin process.

Vomer.—The edges of the vomer are broken both within the orbit and in palatal view. The anterior contacts with the maxillae are either broken or obscured by matrix. In palatal view, the remains of the vomer extend between the internal choanae and partially separate the palatines. They do not contact the pterygoids.

Palatine.— In palatal view, the palatines contact the vomer anteriorly and form the posterior margin of the internal choanae anterolaterally. A single, large foramen palatinum posterius forms on either side of the palate at the contact between the maxillae and palatines. Posterolaterally, the palatines contact the pterygoids, and between the pterygoids the palatines have a short contact with the basisphenoid.

In lateral view, the palatine contacts the jugal and maxilla anteriorly, both within the lower temporal fossa and within the orbit. Posterior to the orbit, the medial margin of the palatine contacts the vomer ventrally, forms part of the wall of the braincase, and contacts the parietal dorsally. The posterior part of the braincase wall and the floor of the lower temporal fossa are fragmented. Although the palatine appears to be present there, its contacts with other bones in that region are unclear.

Pterygoid.—The pterygoid forms part of the floor of the lower temporal fossa, but the extent of this contribution and any possible contribution to the foramen nervi trigemini is unclear due to the highly fragmented bone in this region. In palatal view, the pterygoids have a long, crescent-shaped contact with the maxillae anteriorly, and a medial contact with the palatines, the basisphenoid. and the basioccipital. Posterolaterally, they contact the quadrates. The foramen posterius canalis carotici interni is surrounded by the pterygoid and positioned posteriorly in palatal view, below the basioccipital tubercule.

In posterior view, the pterygoid contacts the quadrate laterally, the opisthotic dorsally, and the exoccipital medially. The fenestra postotica is crushed, but there are no apparent process that would exclude the foramen jugulare posterius from the fenestra postotica, either from the pterygoid or the opisthotic.

Basisphenoid.— The basisphenoid is triangular, without any sort of constriction along the bone. It contacts the palatines anteriorly, the pterygoids laterally, and the basioccipital posteriorly.

Prootic.— In dorsal view, the prootic forms the majority of the processus trochlearis oticum. It contacts the parietal medially and the supraoccipital posteromedially along a short suture. Dorsally, it contacts the opisthotic, and laterally it contacts the quadrate. It forms almost the entirety of the foramen stapedio-temporale. Within the lower temporal fossa, the prootic forms the dorsal margin of the foramen nervi trigemini and contacts the parietal anteriorly. Posterior contacts are obscured.

Epipterygoid.— The region anterior to the foramen nervi trigemini is fragmented, and the location of the epipterygoid, if it is present, is unclear.

Opisthotic.— In dorsal view, the opisthotic forms the posterior margin of the skull between the squamosal and the supraoccipital. Anteriorly it contacts the prootic and medially it contacts the supraoccipital. Laterally it contacts the quadrate. Broken edges of the skull indicate that the opisthotic had a paraoccipital process that contacted the squamosal

In posterior view, the opisthotic contacts the exoccipital medially and the pterygoid ventrally. The opisthotic does not participate in any subdivision of the fenestra postotica (see above).

Quadrate.— The quadrate makes up most of the cavum tympani and encloses the columnella auris. In lateral view, the quadrate contacts the quadratojugal anteriorly, the squamosal anteriorly and posteriorly along the roof of the cavum tympani, and makes up the ventral margin of the cavum tympani. In dorsal view, the quadrate contacts the squamosal laterally and the prootic and opisthotic medially. It contributes to part of the lateral wall of the stapedio-temporal foramen. In ventral view, the quadrate contacts the quadratojugal anteriorly, the prootic anteromedially, the pterygoid posteromedially. and the squamosal posteriorly.

Basioccipital.— The basioccipital makes up the ventral third of the occipital condyle. In ventral view, it contacts the basisphenoid anteriorly and the pterygoids laterally. The basioccipital contacts the exoccipitals along the dorsal surface of the basioccipital tubercules. The exoccipitals prevent the basioccipital from participating in the foramen magnum.

Exoccipital.— The exoccipitals form the dorsal two-thirds of the occipital condyle. In posterior view, they form much of the lateral margin of the foramen magnum. The exoccipital contacts the opisthotic laterally, the pterygoid briefly ventrolaterally, and the basioccipital along the lateral edge of the dorsal surface of the basioccipital tubercules. The exoccipitals exclude the basioccipital from the foramen magnum.

Supraoccipital.— The high crista supraoccipitalis is composed of both the parietal anteriorly and the supraoccipital posteriorly. The supraoccipital is a long, T-shaped bone. In dorsal view, it contacts the parietal anteriorly and the prootic and opisthotic laterally. In posterior view, the supraoccipital forms the dorsal margin of the foramen magnum. It contacts the opisthotics laterally and the exoccipitals ventrolaterally.

Mandible.—Figure 3. Two partial mandibles were recovered from the same locality where the shells (described below) were found. The larger mandible (MRF 666, Figs. 3A-F) is complete except for a break between the two lateral halves of the jaw. The smaller mandible (MRF uncatalogued 1, Figs. 3G-J) preserves the complete anterior portion of the dentary, but nothing else.

The mandible has a broad, rugose triturating surface, particularly toward the posterior end of the dentary where the lingual ridge is enlarged into a broad dentary pocket. In lateral view, the triturating surface extends beyond the anterior margin of rest of the dentary, forming a lip on the dorsal part of the mandible. The coronoid process is relatively high, but much less so than that of *Gilmoremys lancensis* (Joyce and Lyson

2011).

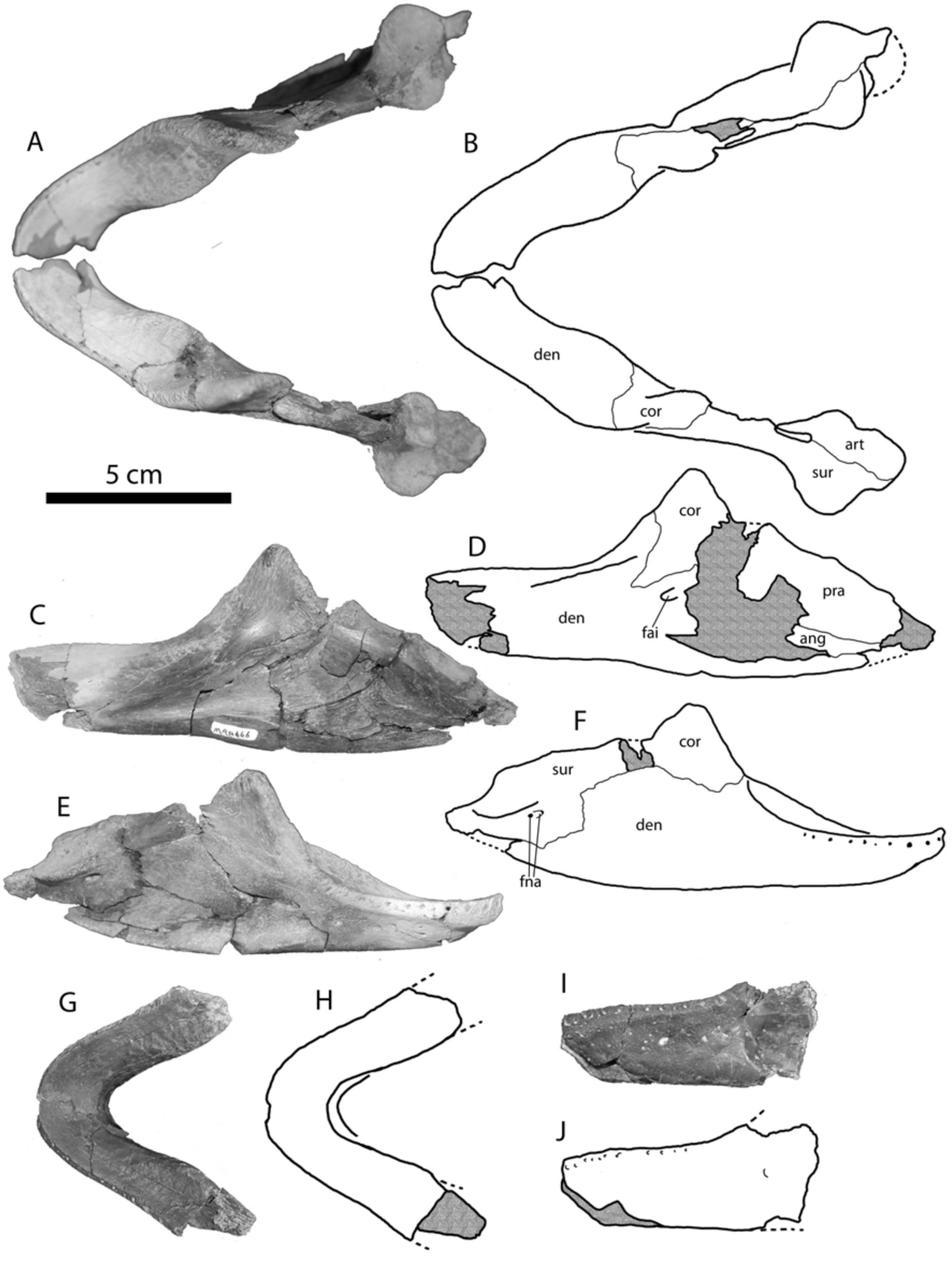
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Figure 3. Mandibles of *Axestemys splendida* from Cretaceous Hell Creek Formation of North Dakota. MRF 666, A, photograph and B, illustration of dorsal view. C, photograph and D, illustration of medial view. E, photograph and F, illustration of lateral view. MRF uncatalogued 2, G. photograph and H, illustration of dorsal view. I, photograph and J, illustration of lateral view. Abbreviations: ang = angular, art = articular, cor = coronoid, den = dentary, fai = foramen alveolare inferius, fna = foramen nervi auriculotemporalis, pra = prearticular, sur = surangular.

Dentary.—The dentary forms the anterior half of the jaw, including the triturating surface. In dorsal view the anterior margin of the dentary is bluntly rounded, without the elongation see in *Gilmoremys lancensis*. It lacks a symphyseal ridge, but has a pronounced lingual and labial ridge. It contacts the coronoid posteriorly. In lateral view, the posterior end of the dentary contacts the coronoid anterodorsally and the surangular posterodorsally. In medial view, most of the contacts between the dentary and other bones are obscured by a broken region posterior to the coronoid process. The dentary contacts the coronoid anterior to and ventral to the coronoid process, and the angular dorsally.

Angular.—Very little of the angular is visible. It contacts the dentary ventrally and the prearticular dorsally.

Surangular.—In lateral view, the surangular contacts the dentary anteroventrally. It probably contacted the coronoid, but the area between the two bones is missing. Two openings for the foramen nervi auriculotemporalis—one very large, and one smaller one inside the larger opening—are anteroventral to the area articularis mandibularis. In dorsal view, the surangular contacts the articular medially, makes up just over half of the area

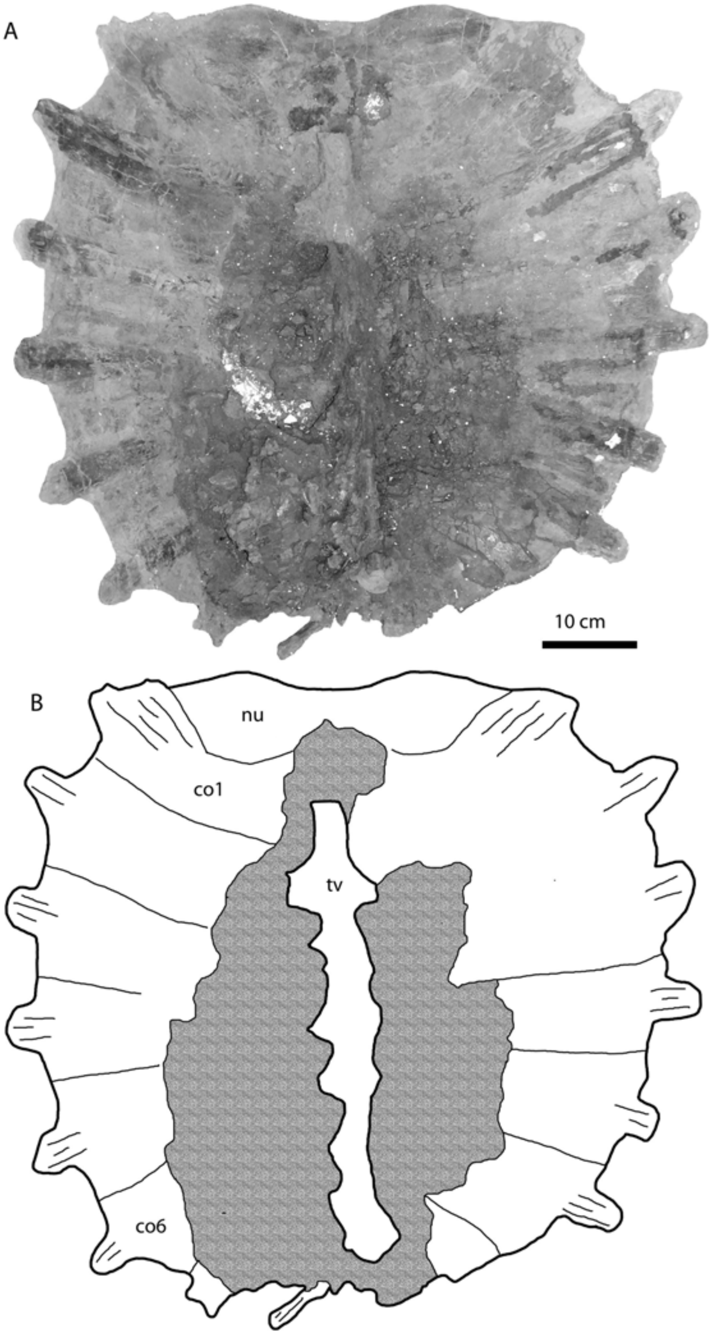

Figure 4. MRF uncatalogued 1, carapace of *Axestemys splendida* from the Cretaceous Hell Creek Formation of North Dakota. A, photograph and B, illustration of visceral view. Shaded areas indicate fragmented regions. Abbreviations: co = costal, nu = nuchal, tv = thoracic vertebrae.

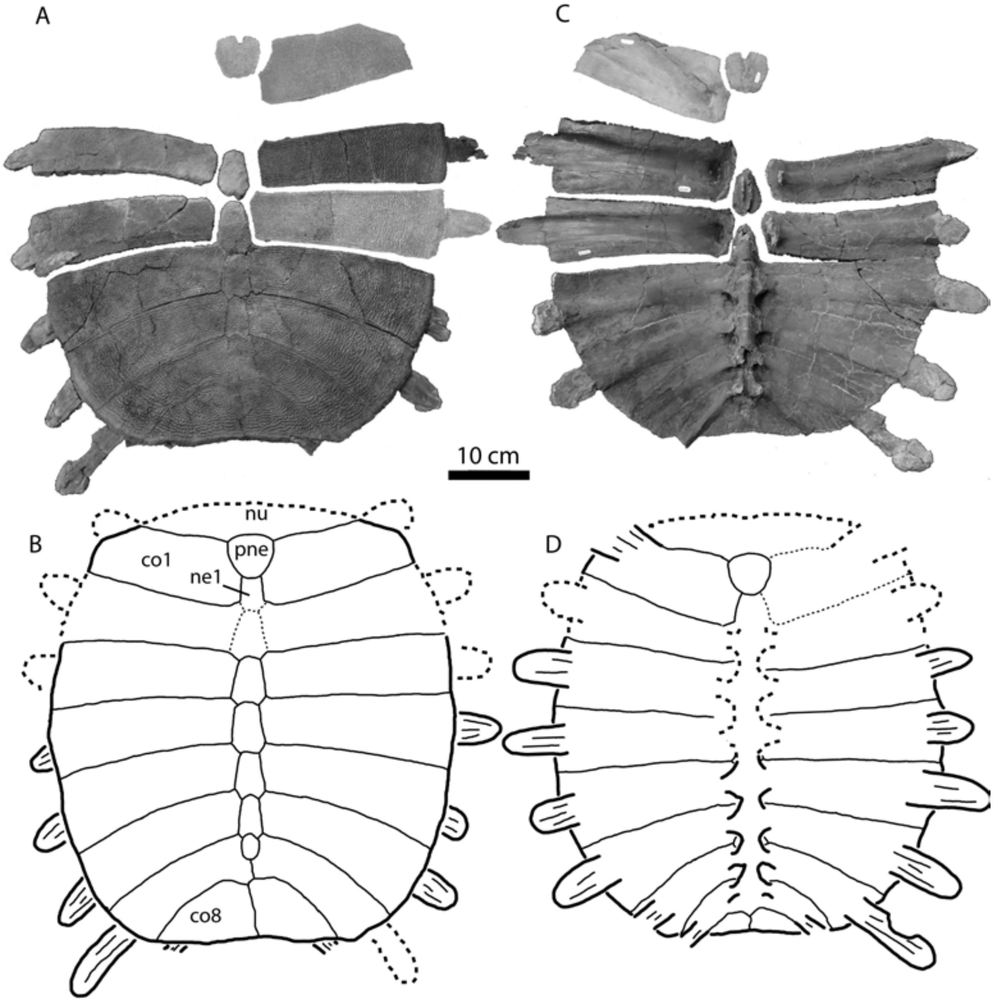

Figure 5. MRF uncatalogued 2, MRF 631, MRF 654, MRF 676, MRF 700, carapace of *Axestemys splendida* from the Cretaceous Hell Creek Formation of North Dakota. A, photograph and B, illustration of external view. C, photograph and D, illustration of visceral view. Abbreviations: co = costal, ne = neural, nu = nuchal, pne = preneural.

articularis mandibularis, and forms the lateral margin of the fossa Meckelii.

Coronoid.—The coronoid contacts the dentary anteriorly. In dorsal view it most likely contacted the surangular laterally and the prearticular medially, but the posterior region of the coronoid is broken.

Articular.—The articular is poorly preserved. In dorsal view it forms just under half of the area articularis mandibularis and contacts the surangular laterally.

Prearticular.—A large part of the prearticular is present, but contacts between the prearticular and other bones are poorly preserved. It contacts the angular ventrally.

Carapace.—Figures 4-5. Two partial carapaces were recovered from the same locality as the lower jaws (described above) and the hyo- and hypoplastra (described below). The larger carapace (MRF uncatalogued 1, Fig. 4) is 64 cm. long along the midline. The medial region of the larger carapace, including the neurals, weathered away before the specimen was discovered and collected, leaving only the nuchal and the lateral parts of the costals. Preparation exposed the ventral side of the carapace, but the dorsal side remains unprepared. The posterior half of the smaller carapace was found articulated, including left costals III and IV, and both costals V-VIII. The preneural, right costal I, III, and IV, were all found in the same quarry. A reconstruction of the complete carapace is approximately 55 cm long (MRF uncatalogued 2, Fig. 5). The larger carapace is circular in outline, while the smaller carapace probably had a subrectangular outline when complete. Neither has any kind of waist or significant emargination, unlike *Hutchemys arctochelys*. The lateral margins of the larger carapace are straight, while the posterior margin is incompletely preserved. The lateral margins and posterior border of the smaller carapace are straight.

Sculpturing on the smaller carapace is similar to that on the type specimen of *Axestemys splendida*. It consists of thin ridges in either a net-like pattern or in wavy lines with wide furrows in between. Near the sutures with other bones, the pattern becomes more regular, with straight lines of subrectangular pits surrounded by the same, thin ridges. Sculpturing covers all but a narrow, approximately 1 cm margin of the external surface of the carapace. Unlike *Hutchemys arctochelys*, the visceral portion of the carapace lacks a callosity and is completely smooth.

Nuchal.—The nuchal is approximately five times wider than long. Unlike cyclanorbines, MRF uncattalogued 1 lacks a posterior costiform processes and there is no evidence of a prenuchal. The anterior margin of the nuchal is slightly medially emarginated, but not to the extreme degree seen in the *"Trionyx" kansaiensis* or *Hutchemys rememdium* (Joyce et al. 2009; Vitek and Danilov 2010). The first thoracic vertebra is situated in the middle of the nuchal. The partially preserved nuchal of the larger carapace as well as the first costal (MRF 631) and preneural (MRF 700) of the smaller carapace indicate that the nuchal was completely sutured to the first costals and preneural without any suprascapular fontanelles. The first costal ribs overlap part the visceral surface of the nuchal.

Neurals.—Although not all of the neurals in either carapace are preserved, the posterior portion of the smaller carapace indicates that seven neurals were present in addition to a preneural (eight neurals with neurals 1 and 2 unfused in Meylan's terminology). The preneural is large and roughly trapezoidal. Neurals 3-6 are hexagonal with short posterolateral sides, and neurals 1 and 2 were probably similarly shaped. The posterior edge of neurals 5 and 6 are posterior to the posterior edge of costals 5 and 6, respectively. Throughout the neural column, there is no neural reversal. The seventh neural is reduced and oval-shaped.

Costals.—Eight pairs of costals are present. The distal margins of the costals are

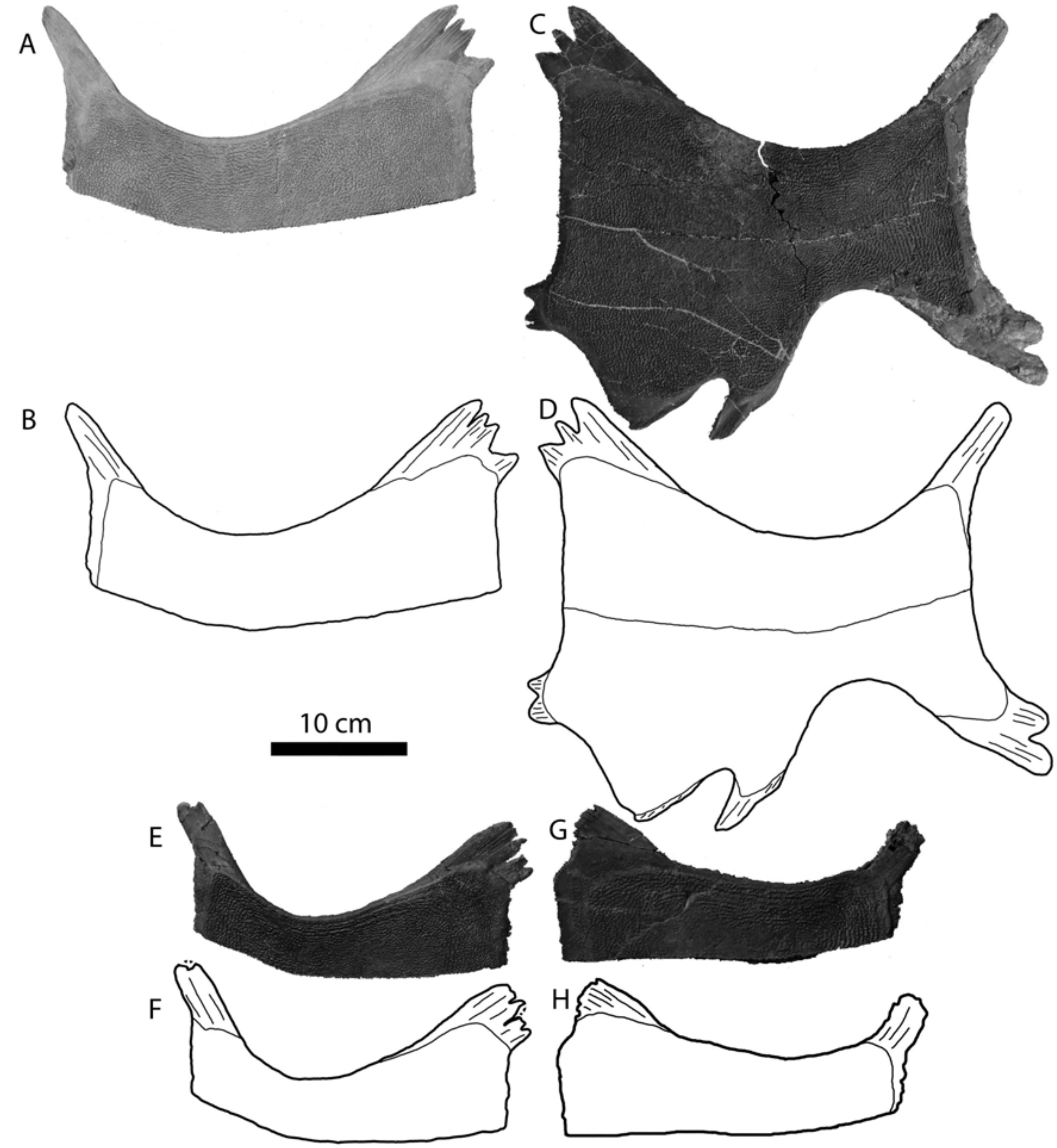

Figure 6. Hyo- and hypoplastra of *Axestemys splendida* from the Cretaceous Hell Creek Formation of North Dakota. MRF 678, right hyoplastron, A, photograph and B, illustration. MRF UNCAT, left hyo- and hypoplastron, C, photograph and D, illustration. MRF 675, right hyoplastron, E, photograph and F, illustration. MRF 567, left hyoplastron, G, photograph and H, illustration.

rounded. Rib ends extend as much as 10 cm from the margin of the smaller carapace and 6 cm from the margin of the larger carapace. The first pairs of costals have lateral margins neither reduced nor expanded, unlike fossil trionychid species such as Gilmoremys lancensis. The eighth pair is reduced and wider than long. Costals 7 meet partially at the midline, costals 8 meet entirely at the midline, and both costals 7 and 8 make up the posterior border of the carapace. The visceral surfaces of costals 8 are smooth, without a depression for the ilia.

Plastron.— Figure 6. A left hyo- and hypoplastron were found sutured together underneath the larger shell (MRF uncatalogued 1, described above). Three additional hyoplastra were found in the same quarry. No epiplastra, entoplastra, or xiphiplastra attributable to this species were recovered.

Both the hyo- and hypoplastra are covered in a sculptured callosity. The callosity does not cover the lateral and medial processes, nor does it form an anterior plastomenid-type "shoulder" or extend beyond the lateral processes. The sculpture pattern is a series of fine ridges that cross each other to form a net-like pattern, identical to the pattern on the carapace. The hyo- and hypoplastron are connected by a suture, but unlike *Apalone ferox* the two bones do not fuse together. The hyo-hypoplastral bridge is short, about one-quarter the maximum width of the hypoplastron. The hyo- and hypoplastra do not appear to have met at the midline.

The hyoplastra have a single lateral process and 3-4 medial processes. The single preserved hypoplastron has two lateral processes. The medial processes are divided up into a pair of anteromedial processes then a gap followed by two posteromedial processes that contact the xiphiplastra. Given the arrangement of posteromedial hypoplastral processes, the xiphiplastra can be inferred to have been lateral-most in the hypo-xiphiplastral contact.

Remarks

All of the bones from the Big Turtle Cove locality come from a single, small quarry. All of the trionychid material from the quarry comes in one of two sizes, each corresponding to the larger and smaller carapace described above. There are no extraneous trionychid bones from the quarry that do not correspond to these two individuals, either in terms of characters or in terms of "extra" bones such as two large right hyoplastra that would require two large individuals. In addition, the smaller isolated carapace bones (MRF 631, MRF 654, MRF 676, MRF 700) are identical to the smaller posterior carapace (MRF uncatalogued 2) in terms of size, sculpture pattern, and bone thickness. For these reasons, the smaller carapace bones are inferred as belonging to a single individual in Figure 5 despite not being found in articulation.

The described material is identical to *Aspideretoides splendidus* as described and diagnosed by Gardner et al. (1996), including characters that were not mentioned in the original diagnosis, such as a single lateral hyoplastral process (variably present in Campanian specimens such as TMP 2001.12.27) and relatively long rib extensions. The exceptions are the larger skull size and the absence of sculpturing on the skull roof in the newly described material. A 20.5 cm skull is a reasonable length for a skull of a taxon whose carapace is more than 60 cm in length and supports the inclusion of this new material in *Axestemys splendida.* Although sculpturing on the skull roof was considered diagnostic for this species and is absent in MRF 266, there is not sufficient justification to establish a new taxon that is identical to *A. splendida* with the exception of a single character whose variability is unclear.

Axestemys montinsana sp. nov.

Figures 7-12

Etymology

Mont-, Latin for 'mountain,' and *insana*, Latin for 'crazy,' in reference to the Crazy Mountains Basin in which the type specimen was discovered.

Synonymy

Axestemys cf. *A. puercensis*: Hutchison and Holroyd 2003:133, fig. 7F, H-I, 11A-D.

Type Specimen

UM 27029, a skull, partial lower jaw, partial carapace, fragmentary entoplastron, hyoplastron, and hypoplastron, xiphiplastron, five cervical vertebrae, a partial pelvic girdle, two humeri, a femur, and various disarticulated appendicular elements.

Horizon and Type Locality

Scarritt Quarry, (early Tiffanian, Ti2) Melville Formation, eastern Crazy Mountains Basin, Montana, USA. Discovered by E. Robinson, collected by D. R. Krause 1985 (pers. comm. D.R. Krause 2011; Scott and Krause 2006).

Referred material

PTRM Site V02017, Slope County, North Dakota, USA; Fort Union Formation, early Paleocene (Puercan; Bercovici et al. 2009): PTRM 5350.88, skull fragments; PTRM 5350.23, PTM 5350.24, lower jaw; PTRM 6030.07, PTRM 6030.08, epiplastron; PTRM 6030.01, entoplastron; PTRM 6030.03, hyoplastron; PTRM 6030.04, hypoplastron; PTRM 6030.02, hyo- and hypoplastron; PTRM 6030.05, PTRM 6030.06, xiphiplastron; PTRM 5350.21, PTRM 5350.22, PTRM 5350.30, PTRM 5350.108, cervical vertebra; PTRM 5350.91, PTRM uncat, pectoral girdle; PTRM 5350.25, humerus; PTRM 5350.21, pelvic girdle, PTRM 5350.77,5350.78, ilium; PTRM 5350.27, ischium, PTRM 5350.75, PTRM 5350.76, pubis; PTRM 5350.28, PTRM 5350.51, PTRM 5350.130, femur; PTRM 5350.122, tibia; PTRM 5350.47, PTRM 5350.110, PTRM 5350.117, 5350.117, PTRM 5350.121, phalange; PTRM 5350.43, PTRM 5350.105, claw

Colorado, USA; Denver Formation, early Paleocene (Puercan): UCM 49231, skull fragments; UCM 49228, partial dentary; DMNH 44623, costal and plastron fragments; UCM 37755, costal fragments and partial cervical vertebra; DMNH 45130, shell fragments and phalanges; DMNH 44622, plastron fragments and ungual phalanx; DMNH 43187, partial pectoral girdle; UCM 34134, humerus; UCM 34119, phalanx

Distribution – Denver Formation (Puercan) of Colorado, Fort Union Formation (Puercan) of North Dakota, and Melville Formation (Tiffanian) of Montana.

Diagnosis

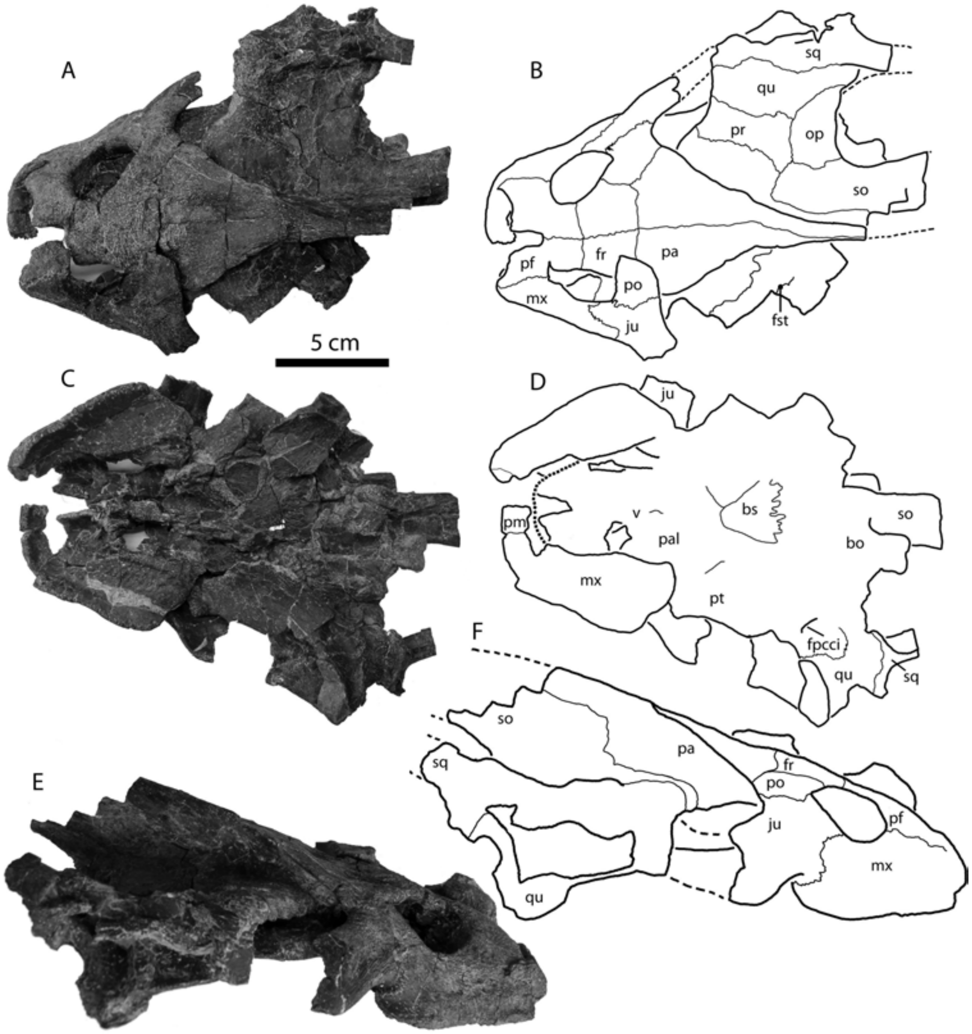

Figure 7. UM 27029, skull of *Axestemys montinsana* from the Paleocene Melville Formation of Montana. A, photograph and B, illustration of dorsal view. C, photograph and D, illustration of ventral view. E, photograph and F, illustration of lateral view. Abbreviations: bo = basioccipital, bs = basisphenoid, fpcci =foramen posterius canalis carotici intern, fr = frontal, fst = foramen stapedio-temporale, ju = jugal, mx = maxilla, op = opisthotic, pa = parietal, pal = palatine, pf = prefrontal, pm = premaxilla, po = postorbital, pr = prootic, pt = pterygoid, qu = quadrate, so = supraoccipital, sq = squamosal, v = vomer.

Axestemys montinsana is diagnosed as a member of *Axestemys* by a maximum carapace length of at least 60 cm; sculpturing on the skull roof; blunt, triangular skull; broad, rugose triturating surface; deep maxillae; preneural; and a single hyoplastral process. *A. montinsana* can be differentiated from other members of *Axestemys* by the unique combination of a wide, smooth, unsculptured border around the carapacial callosity; absence of suprascapular fontanelles; smooth hyo-hypoplastral callosity but sculptured xiphiplastral callosity; dorsal processes on cervical vertebrae.

Description

Cranium.— Figure 7. The skull has been severely crushed and flattened. Both quadratojugals are missing, as well as the left region of the skull posterior to the upper temporal fossa and much of the supraoccipital. The palate is heavily fragmented. The lower temporal fossa has been crushed underneath the upper temporal fossa and bones in that region are not visible. The exterior of the skull has a sculpturing pattern, similar to that found on the skull roof of Campanian specimens of *Axestemys splendida* (Gardner et al. 1995).

Premaxilla.— The premaxillae are fused into a single element, although the bone is broken into two unequal pieces. They form part of the anterior margin of the skull, and do not enter the apertura narium externum.

Maxilla.— The maxillae form parts of the ventral margins of the orbit and the lateral margin of the apertura narium externum. They contact the prefrontals between the apertura narium externum and the orbit. The maxillae contact the jugals within the ventral wall of the orbits as well as on the external surface of the skull ventral to the orbits. The maxillae do not contact the frontals or quadratojugals.

In ventral view the maxillae form a deep, pitted primary palate. They contact the premaxilla. The skull is broken along the contact between the maxillae and the pterygoids, although the maxillae appeared to contact the pterygoids along a brief posterior suture. The surface of the vomer and the anteromedial portions of the maxillae are missing. Contact between these bones, as well as the shape of the foramen intermaxillaris, is unclear.

Prefrontal.— The prefrontal forms the dorsal margin of the apertura narium externum and the anterior margin of the orbit. The dorsal edge of the apertura narium externum is weakly emarginated laterally and not at all medially. Within the skull, the prefrontals do not contact the palatines. In dorsal view, the prefrontals meet along the midline and contact the maxillae laterally and the frontals posteriorly. They may have contacted the vomer within the orbit, but this part of the skull has been sheared in two and the contact is unclear.

Frontal.—The frontals are roughly rectangular. On the skull surface, they contact the prefrontals anteriorly, form the posteromedial margin of the orbit, contact the postorbitals posterolaterally along a broad suture, and contact the parietals posteriorly. Within the orbit, the frontals contact each other in a sinuous suture along midline of the depression of the sulcus olfactorius.

Parietal.—In dorsal view, the parietals contact the frontals anteriorly and the postorbitals anterolaterally. Unlike the condition seen in plastomenids, the parietals do not contribute to the margin of the orbit. Within the upper temporal fenestra, the parietals contact the prootic and supraoccipital laterally. The parietal forms about 25% of the processus trochlearus oticum. The other 75% is composed of the prootic and quadrate.

Postorbital.— The postorbitals are large and form part of both the posterior margin of the orbit, the anterior limit of upper temporal emargination, and therefore the entire postorbital bar. The length of the bar is approximately half the width of the diameter of the orbit. The postorbitals contact the frontals anteromedially, the parietals posteromedially, and the jugals laterally.

Jugal.—The jugals forms the lateral margin of the orbits and the anterior limit of cheek emargination. They contact the maxillae anteriorly and the postorbitals posteriorly. The jugals are broken off before contact with the quadratojugals.

Squamosal.—In dorsal view the surface of the squamosal is crushed and somewhat fragmented. If a small, accessory ridge along the top similar to that seen in *Axestemys splendida* is present, it is obscured. The squamosal contacts the quadrate medially. In lateral view, the squamosal contacts the quadrate ventrally along the posterior margin of the cavum tympanum, but further contact between the two bones, as well as potential contribution of the squamosal to the antrum postoticum, is obscured.

Vomer.—Pieces of the vomer are present, including at least one fragment that contacts the parietals posterolaterally.

Palatine.—In ventral view, the palatines contact the vomer anteromedially and the maxillae laterally. Although the bones are separated, it appears that when the skull was complete the palatines contacted the pterygoids posterolaterally and the basisphenoid posteriorly. The location of the foramen palatinum posterius is obscured by the fragmentation of the palate.

Pterygoid.—The pterygoids are large bones that floor of the lower temporal fossa. They extend from anterior contact with the maxillae to posterior contact with the quadrates. They contact the palatines anteromedially, the basisphenoid posteromedially, and probably contacted the basioccipital posteromedially, although the latter contact is uncertain. The foramen posterius canalis carotici interni are surrounded by the pterygoids. Reconstructing their original position in relation to other skull features indicates that the foramen posterius canalis carotici interni were positioned posteriorly in palatal view, ventral to the basioccipital tubercule. The posterior view is deformed due to crushing, but the posterior margin of the skull made up by the opisthotic indicates that the foramen jugular posterius is confluent with the fenestra postotica.

Basisphenoid.— The basisphenoid is completely preserved, although it has broken away from most other bones along the sutures. It is bluntly triangular, with a long interdigitated posterior suture with the basioccipital. It contacted the pterygoids laterally and probably the parietals anteriorly.

Prootic.— In dorsal view, the prootic forms approximately one-third of the processus trochlearis oticum. It contacts the parietal medially, the quadrate laterally, and the supraoccipital and opisthotic posteriorly. The foramen stapedio-temporale lies between the prootic and the quadrate.

Opisthotic.— In dorsal view, the opisthotic contacts the prootic anteriorly, the quadrate anterolaterally, and the supraoccipital medially. It makes up part of the posterior margin of the skull. The opisthotic probably did not participate in any subdivision of the fenestra postotica (see above).

Quadrate.—In dorsal view, the quadrate is visible in the upper temporal fossa and

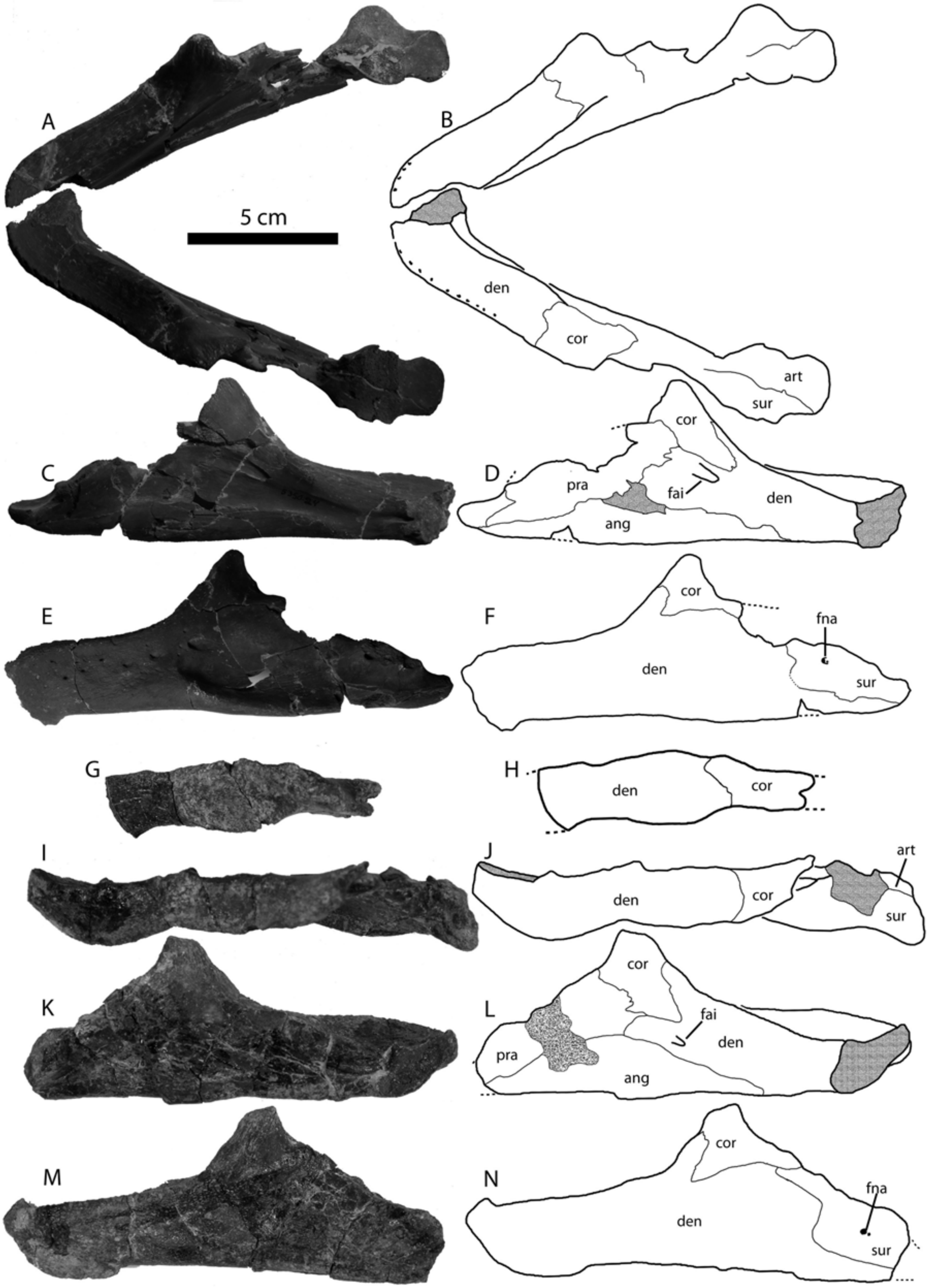
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Figure 8. Mandibles of *Axestemys montinsana.* PTRM 5350.23 and PTRM 5350.24, A, photograph and B, illustration of dorsal view. PTRM 5350.24, C, photograph and D, illustration of medial view. E, photograph and F, illustration of lateral view. UM 27029, G, photograph and H, illustration of right dentary pocket and coronoid in dorsal view. I, photograph and J, illustration of left half of dentary in dorsal view. K, photograph and L, illustration of medial view. M, photograph and N, illustration of lateral view. Abbreviations: ang = angular, art = articular, cor = coronoid, den = dentary, fai = foramen alveolare inferius, fna = foramen nervi auriculotemporalis, pra = prearticular, sur = surangular.

contacts the squamosal laterally, the prootic anteromedially, and the opisthotic posteromedially. It forms the lateral extent of the processus trochlearis oticum and makes up about half of the wall of the stapedio-temporal foramen. In lateral view, the quadrate forms most of the cavum tympani. Because the cavum tympani is crushed and distorted both dorsoventrally and anteroposteriorly, the contact between the quadrate and the squamosal within the cavum tympani is unclear

Basioccipital.—The basioccipital forms the ventral part of the occipital condyle. The basioccipital is broken into two pieces. The anterior fragment contacts the basisphenoid anteriorly along an interdigitated suture. Two basioccipital tubercules are partially preserved. Need to describe wether basioccipital is in or out of foramen magnum owing to exclusion by exoccipitals (the ancestral amniote condition in my estimation).

Exoccipital.— The exoccipitals form the dorsal two-thirds of the occipital condyle. They contact the basioccipital ventrally along the occipital condyle.

Supraoccipital.— Although flattened, the part of the crista supraoccipitalis that remains is high. The preserved part of the supraoccipital is T-shaped and contributes to much of the crista supraoccipitalis posteriorly, while the parietal forms the anterior part of the scrista supraoccipitalis. In posterior view, the supraoccipital forms the dorsal margin of the foramen magnum.

Mandible.—Figure 8. The mandible found in the Fort Union Formation is mostly complete, although it is broken into two pieces roughly along the midline. A partial dentary found in the Denver Formation. preserves the anterior margin of the mandible and part of the triturating surface. The holotype UM 27029 preserves a small fragment of the right dentary pocket and the coronoid process, as well as the left half of the mandible.

Dentary.—In dorsal view, the dentary has a short, rounded anterior margin. It lacks a symphyseal ridge. The lingual and labial ridges are both present and pronounced. The triturating surface is broad and rugose. Anteriorly, it extends past the anterior margin of the rest of the dentary, forming a dorsal lip. A large dentary pocket is present. In lateral view, the dentary contacts the coronoid posterodorsally and the surangular posteriorly. In medial view, the dentary contacts the coronoid posterodorsally and the prearticular posteriorly. The dentary contacts the angular along a long, interdigitated suture posteriorly, then posterodorsally along a long, straight suture.

The partial dentary (UCM 49228) found in the Denver Formation. is similar to the mandible from the Fort Union Formation in having a wide, rugose triturating surface in dorsal view and a lip formed by the triturating surface on the anterior of the mandible in lateral view.

Angular.—The angular covers approximately one-quarter of the medial surface of

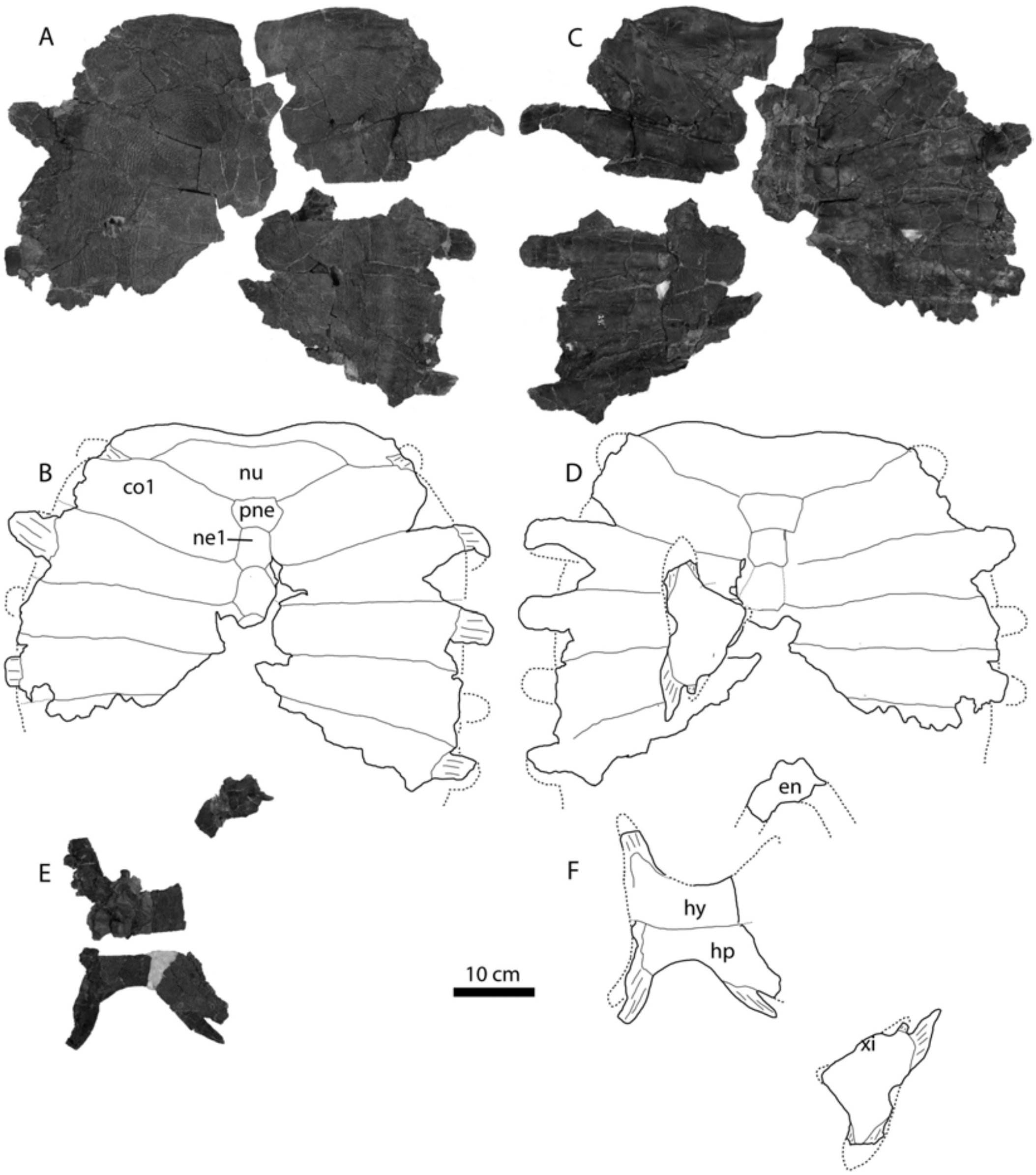

Figure 9. UM 27029, carapace and plastron of *Axestemys montinsana* from the Paleocene Melville Formation of Montana. A, photograph and B, illustration of carapace external view. C, photograph and D, illustration of carapace in visceral view and left xiphiplastron. E. photograph and F. illustration of plastron. Abbreviations: co = costal, en = entoplastron, hp = hypoplastron, hy = hyoplastron, ne = neural, nu = nuchal, pne =

preneural, xi = xiphiplastron

the mandible. It contacts the dentary anteriorly, the prearticular dorsally, and the articular posterodorsally.

Surangular.—In lateral view, the surangular contacts the dentary anteriorly and the coronoid dorsally. The foramen nervi auriculotemporalis is divided into two openings ventral to the articularis mandibularis, a smaller foramen within a larger foramen. In dorsal view, the surangular forms about half of the area articularis mandibularis.

Coronoid.—The coronoid process is high, with proportions more similar to *A. splendida* than to *Gilmoremys lancensis*. In medial view the coronoid contacts the dentary anteroventrally and the prearticular posteroventrally.

Articular.—The articular is partially preserved at the posteriomedial margin of the mandible. In dorsal view it forms approximately half of the area articularis mandibularis and contacts the surangular laterally. In medial view it forms the posterior margin of the mandible. The articular contacts the angular ventrally and the prearticular anteriorly.

Prearticular.—In medial view, the prearticular contacts the coronoid anteriorly and the articular posteriorly. Along a long ventral suture the prearticular contacts the dentary anteroventrally and the angular posteroventrally.

Carapace.—Figure 9. Most of the anterior half of the carapace is preserved in UM 27029 including the nuchal, preneural, neurals 1 and 2, and most of costals 1-5. The length at the midline from the anterior margin of the carapace to the anterior margin of costals 5 is 31 cm. The length of the carapace when complete is estimated to be approximately 64 cm. The outline of the preserved carapace is subrectangular. The anterior margin is slightly emarginated medially. The lateral margins may have been straight or scalloped—not enough is preserved to be sure. Unlike *Hutchemys sp?*, neither has any kind of waist or significant emargination, and the visceral side of the carapace is smooth.

A callosity covers most of the carapace bones, with the exceptions of the ends of the ribs that extend from the carapacial margin and the anterior and lateral parts of the nuchal. The medial part of the callosity is sculptured in a pattern of thin ridges that form subparallel ridges laterally and intersect to form broad, flat-bottomed, circular pits medially. At the lateral-most edges of sculpturing, the ridges may break up into smaller ridges or into a series of small, irregular pustules. A smooth band as wide as 64 mm makes up the lateral margin of the callosity. The costal fragments from the Denver Formation. such as DMNH 44622 and 44623 also preserve the unsculptured band around the border of the callosity. The pattern is similar to *Axestemys cerevisia*.

Nuchal.– The nuchal is 4.3 times wider than long and lacks both posterior costiform processes and a prenuchal. The anterior margin is slightly emarginated medially, but no more than the extent seen in *Axestemys splendida*. The first thoracic vertebra is situated in the middle of the nuchal. Suprascapular fontanelles are absent, and the suture between the nuchal, first costals, and prenuchal is complete. The ribs of the first costal overlap the lateral part of the suture between the nuchal and first costals.

Neurals.—A preneural (neural 1 in the terminology of Meylan 1987) and two neurals are preserved in UM 27029. The preneural is wider and shorter than the other neurals. Neurals 1-2 are hexagonal with short posterolateral sides. The isolated neural found in the Denver Formation (DMNH 44623) is similar in size and shape to neurals 1-2 in UM 27029; the former is 60 mm long and the latter is 58 mm long.

Costals.—UM 27029 preserves the first five costals, although costals 3-5 are incomplete. The distal edge of the costals is rounded. The free rib ends extend as much as

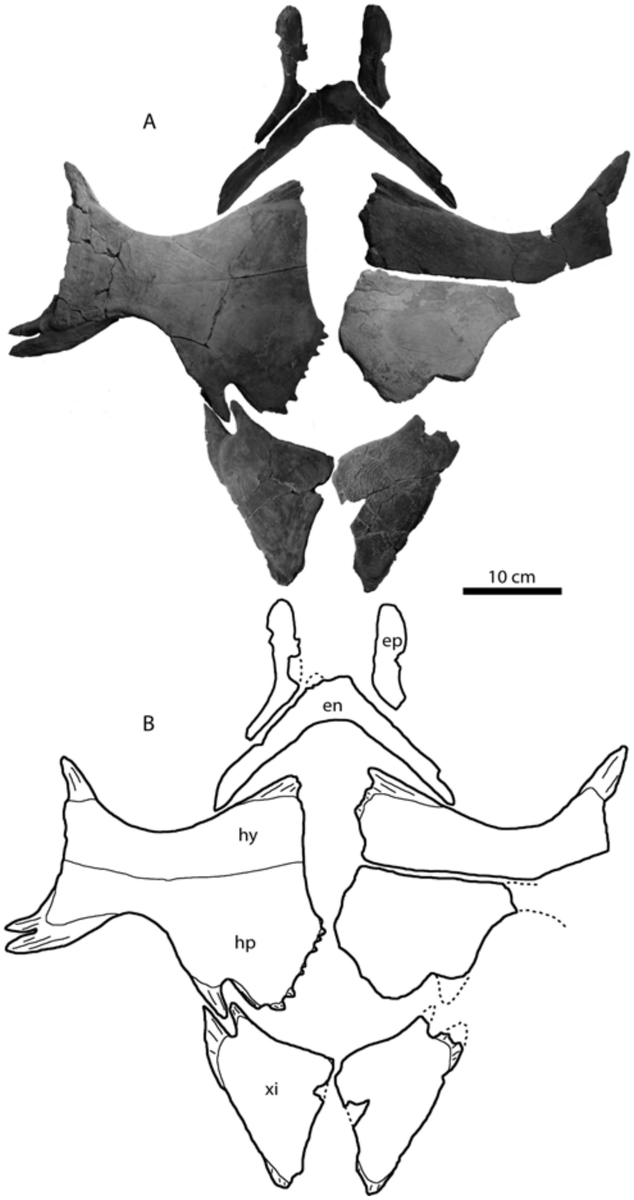

Figure 10. PTRM 6030.01-6030.08, plastron of *Axestemys montinsana* from the Paleocene Fort Union Formation of North Dakota. A. photograph and B, illustration. Abbreviations: en = entoplastron, ep = epiplastron, hp = hypoplastron, hy = hyoplastron, xi = xiphiplastron.

5.5 cm, but when complete could have extended further. The distal margin of costals 1 is about the same length as the medial margin.

Plastron.—Figures 9-10. The plastron has four callosities: one on each hyo- and hypoplastron and one on each xiphiplastron.

Epiplastron.—The epiplastra are bent at the point of anterior-most contact with the entoplastron, making them J-shaped. The part of the epiplastron anterior to the entoplastron is short, .24 times the width of the width of the hypoplastron.

Entoplastron.—The entoplastron is V-shaped, with an approximately 90 degree angle between the two arms of the V. Where the arms of the entoplastron meet, two small processes extend from the anterior edge of the bone with a small crescent-shaped gap between them. Unlike plastomenids or extant *Apalone* spp., the entoplastron is not sutured to the hyoplastron, nor is there a hyoplastral shoulder developed to accommodate extensive contact between the hyoplastron and entoplastron.

Hyoplastron and hypoplastron.—They hyo- and hypoplastron are connected by a suture, but do not fuse together. The callosity on the hyo- and hypoplastron is almost entirely devoid of sculpturing. Small pustules and ridges are present on the lateral-most sections of UM 27029, as well as faint sculpturing of a similar pattern on the hyoplastral bridge of DMNH 44623. The callosity covers most of the hyo- and hypoplastron, excluding the lateral and medial processes. In UM 27029, the callosity does not reach the lateral margin of the hyo- and hypoplastron, and in no specimen does it extend past the lateral processes. The hyo-hypoplastral bridge is short, just over one-quarter maximum hypoplastron width. There is no extensive midline contact between the two hyo- and hypoplastra.

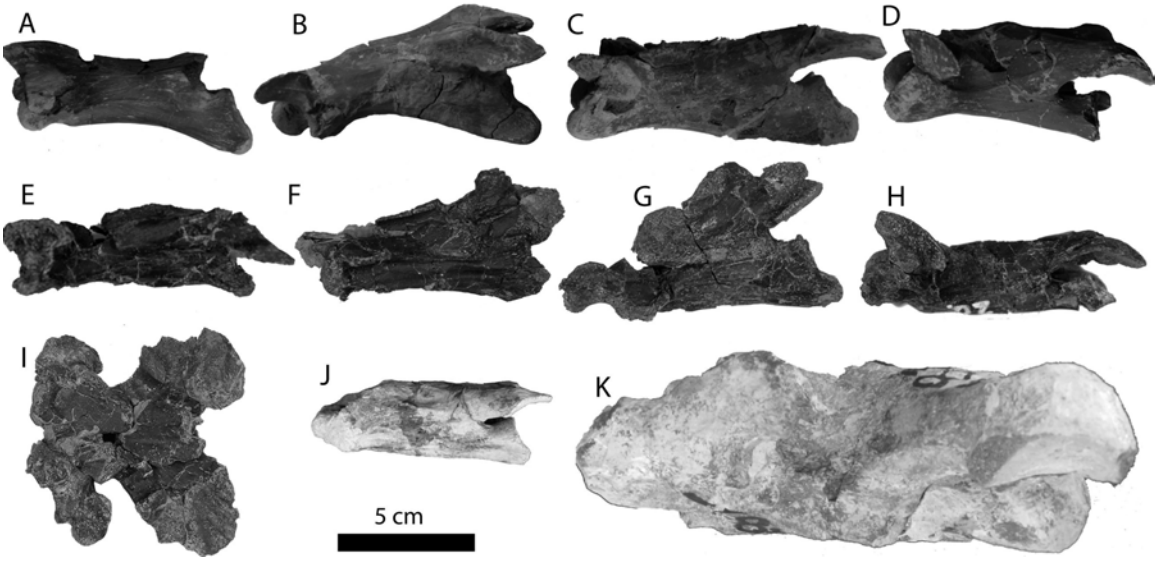

Figure 11. Cervical vertebrae of *Axestemys*. Lateral view of *A. montinsana* from the Paleocene Fort Union Formation of North Dakota, order unknown, A, PTRM 5350.22, B, PTRM 5350.30, C, PTRM 5350.108, D, PTRM 5350.21, seventh cervical vertebra. UM 27029, *A. montinsana* from the Paleocene Melville Formation of Montana, E-G, cervical vertebrae in lateral view, order unknown, H, seventh cervical vertebra in lateral view, I, eighth cervical vertebra in ventral view. J, seventh cervical vertebra in lateral view of *A. byssina* from the Eocene Bridger Formation. K, seventh cervical vertebra in lateral view of *A. cerevisia* from the Eocene Bridger Formation.

The hyoplastra have a single lateral process and 3-5 medial processes. The hypoplastra have two lateral processes. Medial hypoplastral processes consist of eight small processes distributed evenly along the posteromedial margin of the hypoplastron, followed by two larger posteromedial processes that articulate with the xiphiplastron.

Xiphiplastron.—The xiphiplastra are subtriangular, with a brief emargination at the lateral edge (UM 27029, Fig. 9) that disappears as the callosity covering the xiphiplastron becomes more extensive (PTRM 6030.05 and PTRM 6030.06, Fig. 10).

The callosity is covered by a sculpture pattern that consists of thin, uneven ridges that occasionally break down into shorter ridges and pustules. This pattern is similar to that seen in lateral sections of the carapace. At the hypo-xiphiplastral contact, the xiphiplastron is lateral-most. The xiphiplastra meet narrowly at the midline, although there is no or suture between the two xiphiplastra.

Non-shell postcranials.—Figures 11-12. Cervical vertebrae, pieces of both pectoral and pelvic girdles, and several appendicular elements, are preserved in specimens from all three formations. The appendicular elements are indistinguishable from those of *Apalone* spp. except for their large size. For example, ungual phalanges are as large as 5.8 cm long (DMNH 44622), at least 4.1 times the length of an ungual phalanx of an *Apalone ferox* specimen with a 16.2 cm carapace (YPM R 10574).

Cervical vertebrae.—UM 27029 preserves the 7th and 8th cervical vertebrae, as well as three other vertebrae of unknown number. PTRM 5350.21 is a 7th vertebra, and PTRM 5350.22, PTRM 5350.30, and PTRM 5350.108 are three vertebrae of uncertain order. The ventral surface of the 8th vertebra has a small posterior keel. Although the dorsal surfaces of three of the cervical vertebrae of UM 27029 are incomplete, dorsal processes are present on the posterior surface of the vertebrae (Fig. 11E, F, G). Small dorsal processes are also present on PTRM 5350.21 and PTRM 5350.30 (Fig 11B, D).

Pectoral girdle.—The coracoid is the longest of the three pectoral processes. The acromion process and the scapula are approximately the same length. The angle between the acromion process and the scapula is nearly 90 degrees, and the angle between the

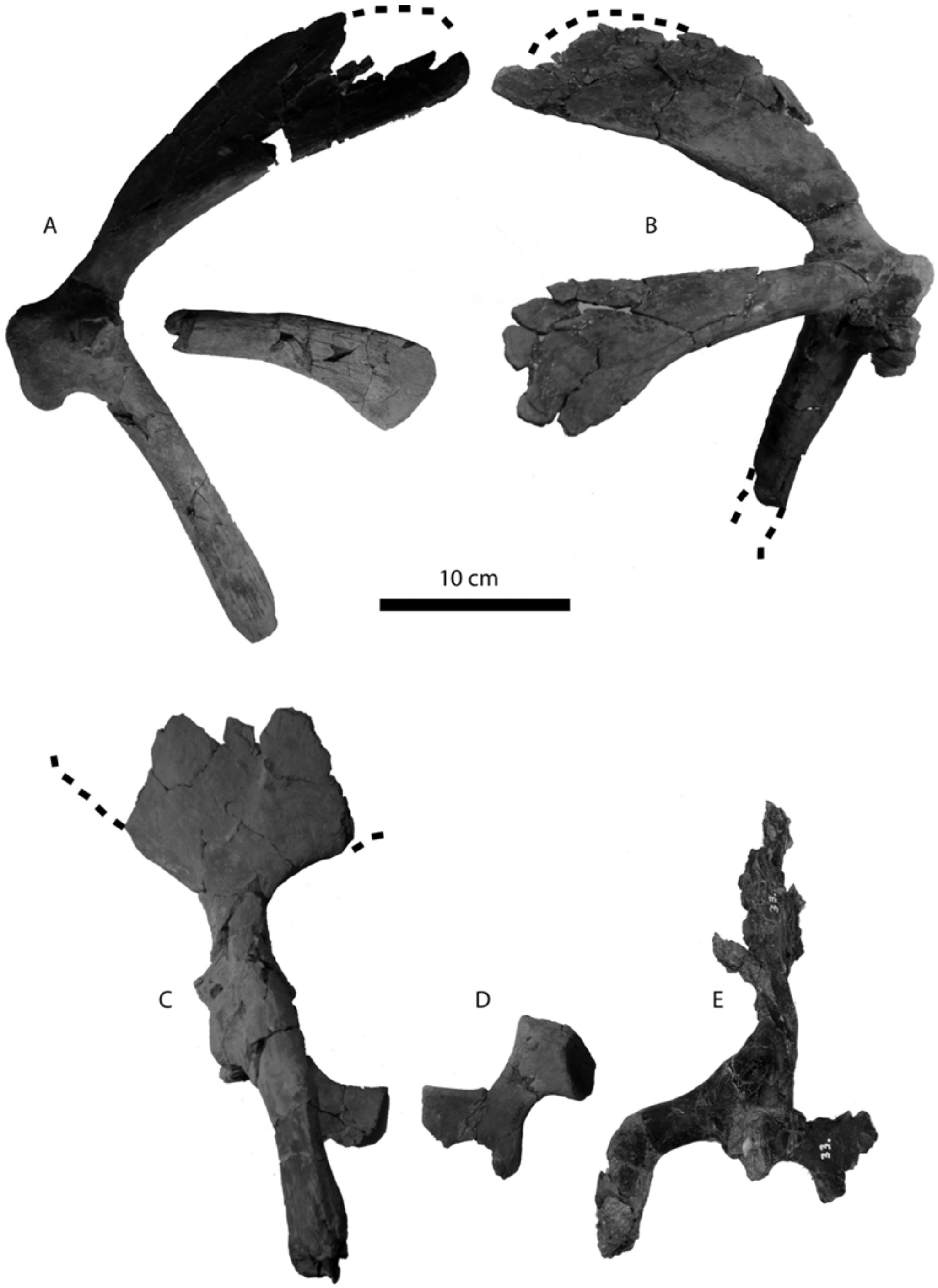

Figure 12. Pectoral and pelvic girdle of *Axestemys montinsana*. Pectoral girdle from the Paleocene Fort Union Formation of North Dakota, A, PTRM 5350.91, B, PTRM uncat,

C, PTRM 5350.31, pelvic girdle. D, PTRM 5350.27, ischium. E, UM 27029, pelvic girdle from the Paleocene Melville Formation of Montana.

acromion process and the coracoid is much less—20 degrees at most.

Pelvic girdle.—The anterior end of the pubis is incomplete in all specimens, but the ischium and ilium are entirely preserved in PTRM 5350.3 and UM 27029. There is no division of the obturator fenestra The ilia curve posteriorly, but not medially. The ischia do not extend into the obturator fenestra, but a distinct, medially curving metischial process is present outside of the thyroid fenestra.

Remarks

Although twelve trionychid taxa have already been named from Puercan-Tiffanian specimens, *Axestemys montinsana* differs significantly from all of them. Diagnostic characters include traditionally recognized characters, such as the presence of a preneural, the lack of significant medial plastral contact, lack of an anterior hyoplastral shoulder, and nuchal length:width ratio, as well as apomorphies found in other *Axestemys* taxa, such as the lack of sculpturing on the hyo- and hypoplastral callosity, the small double anterior processes on the entoplastron, the single lateral hyoplastral process, relatively long free rib ends, very large size, and the band of unsculptured callosity around the border of the carapace.

In particular, *A. montinsana* differs from the previously named Puercan taxon “*Axestemys” puercensis* in it is much larger size, lack of fontanelles, smooth band of unsculptured callosity around the carapace, and unsculptured hyo- and hypoplastra. Previously, the smooth band on the border of the carapace was considered a juvenile feature (Hutchison and Holroyd 2003), and size and the presences of fontanelles have often been considered juvenile features (Hutchison and Holroyd 2003; Meylan 1987). Therefore, the possibility that *Axestemys montinsana* represent adult specimens of *"Axestemys" puercensis* should be addressed.

The fontanelles seen in "*A." puercensis* and some other *Axestemys* taxa are different from the fontanelles seen in extant juvenile trionychids (see Systematics section of Results for further discussion), and are often retained in very large, presumably adult fossil trionychids, indicating that their presence is not related to ontogeny. Furthermore, it is unclear why the hyo- and hypoplastron would lose sculpturing almost entirely during growth while the sculpturing on the xiphiplastra remains intact. It is more likely that, as in *Oliveremys uintaensis*, the lack of sculpturing on certain plastral elements is a useful feature not related to ontogeny (Vitek in press). These character differences between *"A." puercensis* and *A. montinsana* are best explained as interspecific differences rather than ontogenetic variation.

The Denver Formation skull fragments described here and elsewhere (Hutchison and Holroyd 2003) and included in this taxon have been considered synonymous with *Conchochelys admiribalis* Hay 1905 based on their similar age, large size, deep maxillae, shape of the triturating surface, and short snout (Hutchison and Holroyd 2003). However, comparison of *C. admiribalis* with the more complete skull of UM 27029 shows that the two skulls are very different. *C. admiribalis* has a much narrower snout, smaller orbits, and a secondary palate that has moved the openings of the choanae posteriorly in ventral view. Most of the sutures on *C. admiribalis* are not visible, making more detailed comparison difficult, but from general skull shape it is clear that *Axestemys montinsana* and *C. admiribalis* are not synonymous.

Axestemys byssina Cope 1872

Figures 11J, 13-16.

Synonymy

Axestus byssinus: Cope 1872:462, 1873:616, 1884:116, pl. 15, figs. 1-12.

Eugenichelys robertemryi: Chkhikvadze 2008:90, fig. 7.

Type Specimen

USNM 4089, xiphiplastron, cervical vertebra, isolated ilium, several fragmentary appendicular elements.

Horizon and Type Locality

Black's Fork of Green River, (Bridgerian) Bridger Formation, Wyoming, USA.

Referred material

South Elk Creek, Big Horn County, Wyoming, USA; Wasatch Formation, Eocene (Wasatchian): USNM 12589, skull fragments, partial left dentary, left hyoplastron, right hypoplastron, left and right xiphiplastron.

East side of Elk Creek, Big Horn County, Wyoming, USA; Wasatch Formation, Eocene (Wasatchian): USNM 16174, fragmentary carapace, left and right hyo- and hypoplastra, partial epiplastron.

Upper Green River, Wyoming, USA; Bridger Formation, Eocene (Bridgerian): AMNH 1034, partial medial hypoplastron.

Wyoming, USA; Bridger Formation, Eocene (Bridgerian): AMNH 1046, partial medial hypoplastron, partial nuchal, partial costal 1, costal fragments.

Distribution

Wasatch Formation (Wasatchian), Bridger Formation (Bridgerian) of Wyoming.

Differential Diagnosis

Axestemys byssina is diagnosed as a member of *Axestemys* by a maximum carapace length of at least 60 cm, sculpturing on the skull roof, and a single lateral hyoplastral process. *A. byssina* can be differentiated from other member of *Axestemys* by the unique combination of suprascapular fontanelles; suture between lateral edge of nuchal and costals 1; wide, smooth border around carapacial callosity; highly reduced costals 8; and smooth hyo-hypoplastral and xiphiplastral callosities.

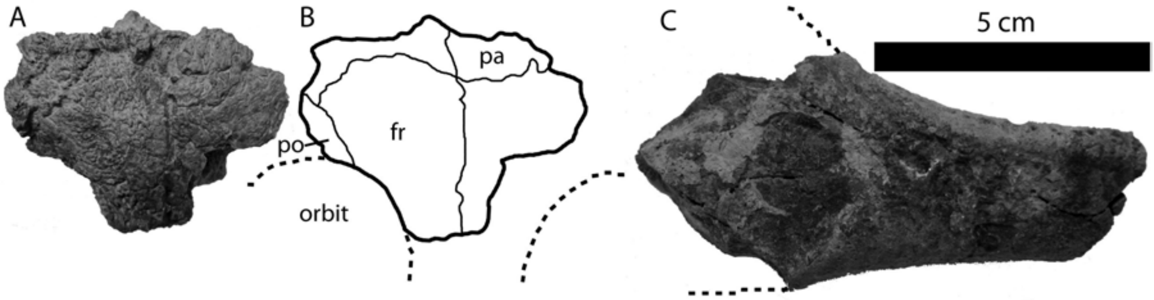

Figure 13 USNM 12589, skull fragments of *Axestemys byssina* from the Eocene Wasatch

Formation of Wyoming. A, Photograph and B, illustration of skull roof fragment. C, dentary fragment. Abbreviations: fr = frontal, pa = parietal, po = postorbital.

Description of new material

Skull.—Figure 13. A small piece of the skull roof and the margin of the orbit is preserved. The fragment contains parts of the frontals, parietals, and right postorbital. The surface is covered with a sculpture pattern of densely packed ridges, similar to the skull surface of *Axestemys montinsana* (UM 27029). Unlike *Plastomenus thomasii,* the parietals do not contribute to the margin of the orbit on the skull surface between the postorbital and the frontal, nor is the parietal contact with the orbit extended anteriorly (as in Joyce and Lyson 2011). In addition, the fragment comes from a large skull, with an orbit at least 28 mm in diameter.

Lower Jaw.—Figure 13. The dentary fragment is massive and resembles the anterior portion of the dentary of both *Axestemys montinsana* and *A. splendida.* The triturating surface is covered by matrix, but is wide and forms a lip in lateral view by extending beyond the anterior margin of the dentary.

Carapace.—Figures 14-15. The carapace of USNM 16174, when complete with the nuchal attached, was about 60 cm long at the midline. Only one neural can be distinguished: a reduced, irregularly shaped neural at the end of the neural column. Given its placement, it is likely neural 7. The anterior margin of the carapace is broadly convex and the lateral margins are straight. The posterior margin of the carapace has a steeply concave notch at the midline. The carapace itself is oval-shaped. The costals and neurals are fully covered in a callosity. The callosity only covers the posteromedial part of the nuchal. The callosity itself consists of an outer unsculptured band 24 mm wide and a medial sculptured area. The sculpturing pattern consists of large, subcircular, flat pits

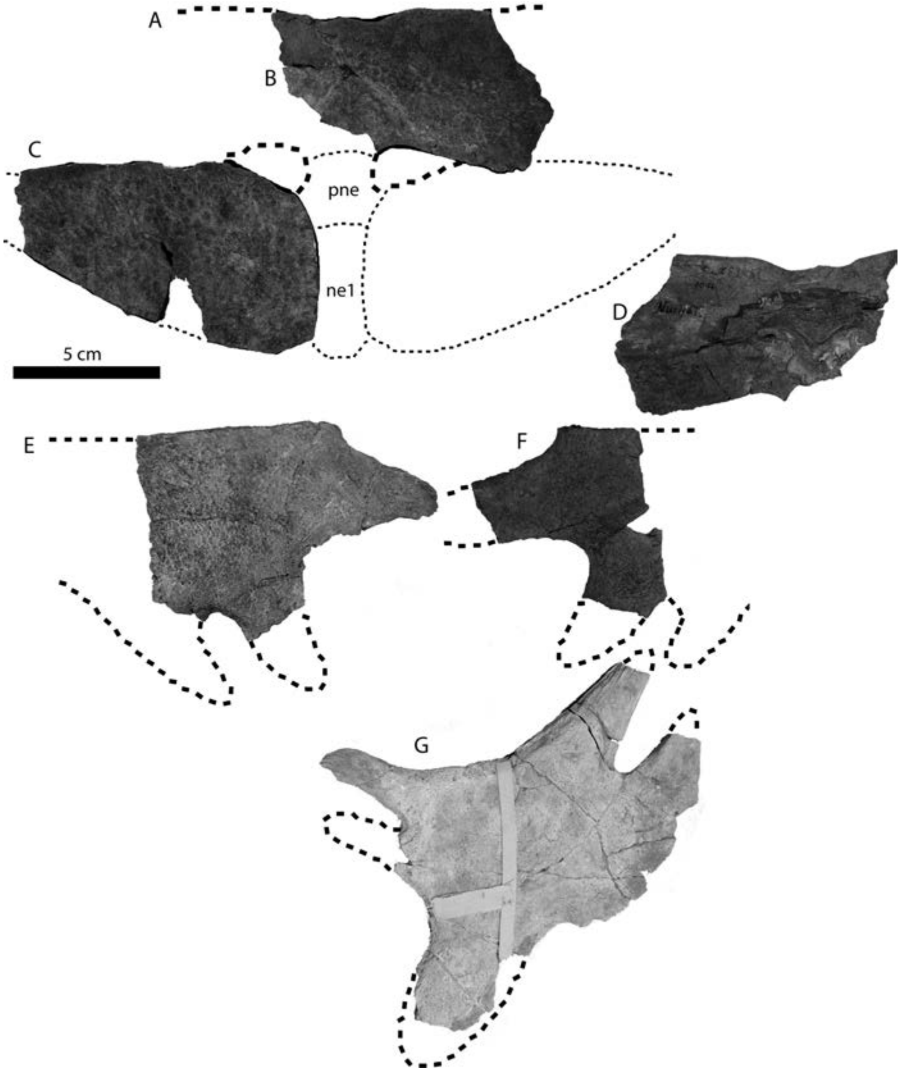

Figure 14. Photograph of *Axestemys byssina* material described by Hay (1908). A, reconstruction of nuchal region. AMNH 1046, B, partial nuchal in exterior view, C, costal 1, D, partial nuchal in visceral view, E, AMNH 1034, partial hypoplastron from the Eocene Bridger Formation of Wyoming. F. AMNH 1046, partial hypoplastron. G, USNM 4089, holotype xiphiplastron from the Eocene Bridger Formation of Wyoming. Abbreviations: ne = neural, pne = preneural.

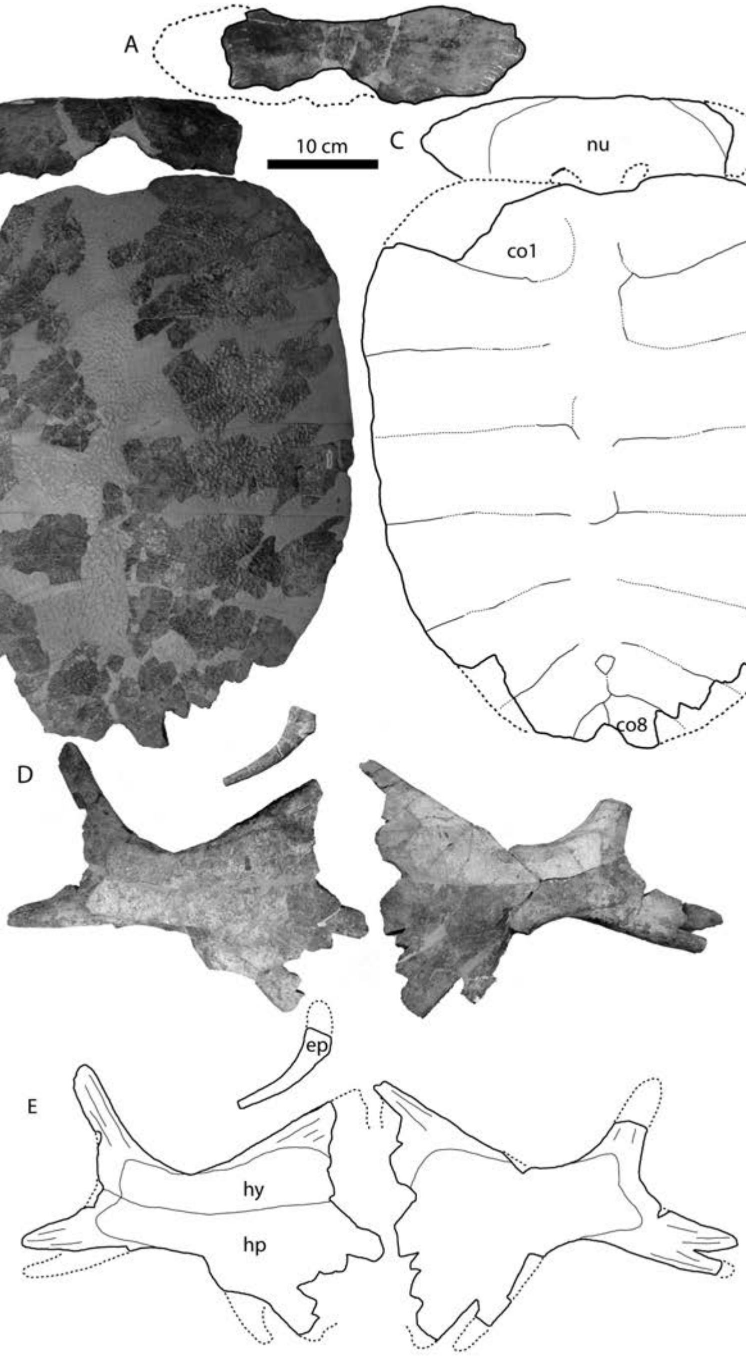

Figure 15. USNM 16174, carapace and plastron of *Axestemys byssina* from the Eocene Wasatch Formation of Wyoming. A, Photograph of nuchal in visceral view. B,

Photograph and C, illustration of carapace in external view. D, Photograph and E, illustraion of plastron. Abbreviations: co = costal, ep = epiplastron, hp = hypoplastron, hy = hyoplastron, nu = nuchal.

surrounded by thin, uneven ridges, with several areas where the ridges separate into short rows or larger, irregular shapes. Sculpturing on carapace fragments of AMNH 1046 is identical, including the unsculptured margin visible on at least one lateral costal fragment.

Nuchal.—The reconstructed nuchal based on USNM 16174 is about four times wider than long. Both partial nuchals in USNM 16174 and AMNH 1046 lack a posterior costiform process. Contact with the thoracic vertebra is in the middle of the nuchal. Although both nuchals are incomplete, each preserves a smooth section of the posteromedial margin, indicating an area of the margin not sutured to the first costal and therefore the presence of suprascapular fontanelles. The anteromedial margin of the partial costal 1 in AMNH 1046 also has a matching area for such fontanelles. The fontanelles are relatively small, and do not extend to the first costal rib as do the fontanelles in *Axestemys cerevisia, "A." puercensis,* and *A. quinni*.

Costals.—Eight pairs of costals are present, with the eighth pair reduced. All of the rib ends are broken off and it is unclear how far they extended from the carapace margin. The edge of the costals, where complete, are rounded. The seventh and eighth costals probably made up the posterior margin of the carapace, although that margin is fragmented. Due to this fragmentation, the width:length ratio of costals 8 is unclear. In USNM 16174 and AMNH 1046, the lateral margin of the first costal is just over half the size of the medial margin, but the lateral margin is not as radically constricted as in

Gilmoremy lancensis.

Plastron.— Figures 14-16. AMNH 1046, AMNH 1034, USNM 4089, USNM 12589, and USNM 16174 collectively preserve multiple xiphiplastra, hyo- and

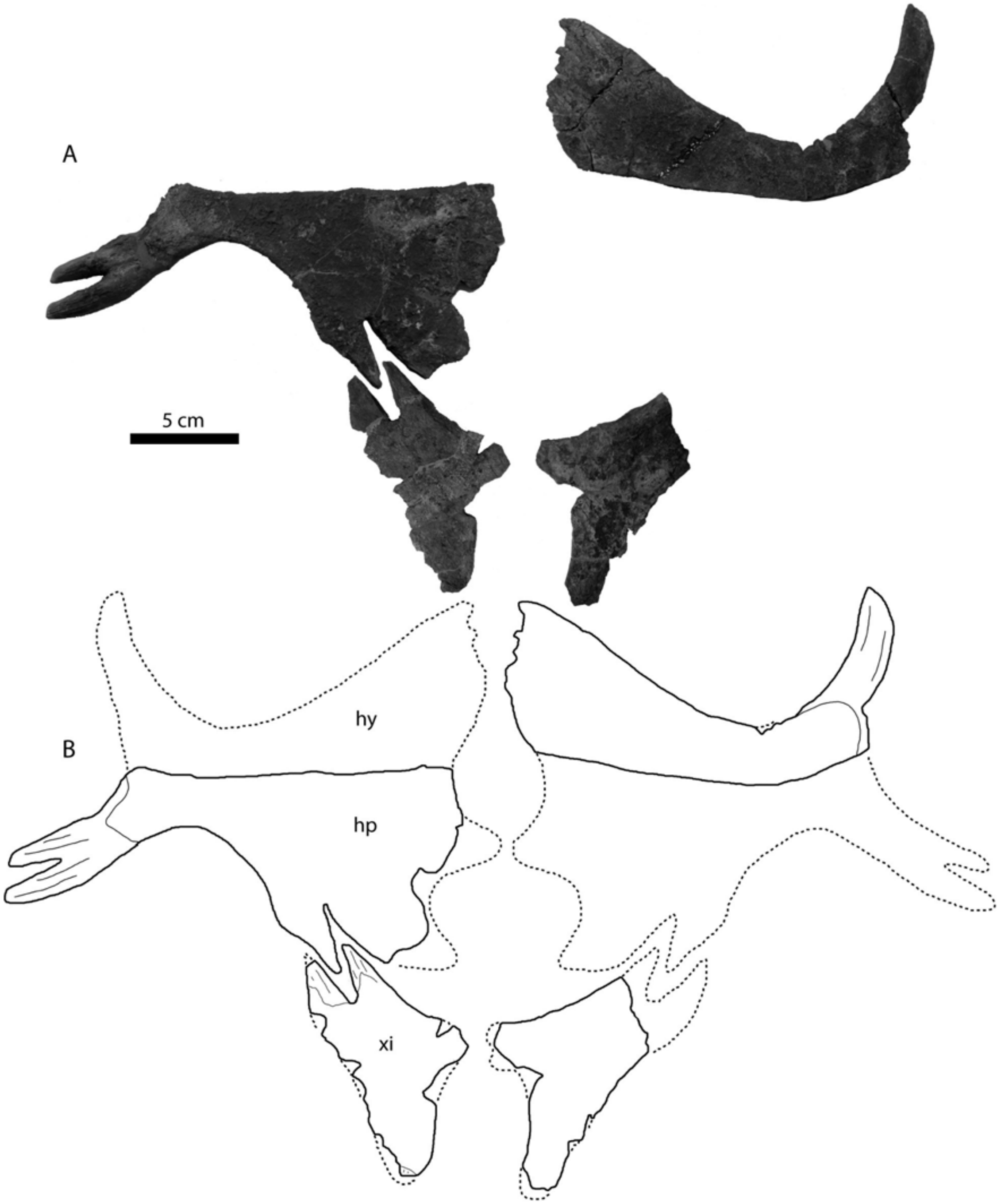

Figure 16. USNM 12589, plastron of *Axestemys byssina* from the Eocene Wasatch Formation of Wyoming. A, photograph and B, illustration. Abbreviations: hp = hypoplastron, hy = hyoplastron, xi = xiphiplastron.

hypoplastra, and a single partial epiplastron. No entoplastron has been found in these specimens. The plastra as they are preserved have four unsculptured callosities: one on each hyo- and hypoplastron and one on each xiphiplastron. The unsculptured callosities can be differentiated from bone by a smooth surface with occasional cross-hatching, described by Hay as "textile-like fibers of bony tissue" (Hay 1908:509) and compared to "woven linen" by Cope (1872:462).

Epiplastron.—The fragment of the epiplastron in USNM 16174 preserves just enough of the bone to indicate that it was j-shaped in Meylan's (1987) terminology.

Hyo- and hypoplastron.—The callosity covers much of the medial part of the hyo- and hypoplastron, including most of the medial processes, but does not extend as far as the lateral margin of the hyo- and hypoplastron. The lateral processes are left entirely bare. The hyo-hypoplastral bridge is short, about one-fifth the maximum hypoplastral width. Where the medial margin of the hyo- and hypoplastron is complete, there is no evidence for midline contact, nor is there an anterior hyoplastral shoulder for extensive contact with the entoplastron, unlike plastomenids. The hyoplastron has a single lateral process and several small hyoplastral processes. The exact number of processes on each specimen is unclear, although the hyoplastron in USNM 12589 has at least three. The hypoplastron has two lateral processes. In smaller specimens such as AMNH 1046 and 1034, the hypoplastron has a single large anteromedial process, followed by a large gap and two posteromedial processes that contact the xiphiplastron. The medial margin of

USNM 12589 and USNM 16174 is too fragmentary to be sure what kind of pattern the medial hypoplastral processes had, but a broken anteromedial process on the right hypoplastron of USNM 16174 indicates that the pattern seen in smaller specimens was probably conserved in larger specimens.

Xiphiplastron.—The xiphiplastra of *A. byssina* are not as narrow as the xiphiplastra of *Oliveremys uintaensis*, another Eocene trionychid with unsculptured xiphiplastra. The width across the narrowest part of the body of all xiphiplastra of *A. byssina* is at least one-third the length of the xiphiplastra along the lateral edge, whereas the width across the all the xiphiplastra of *O. uintaensis* is no more than one-fourth of the length. However, the overall shape of the xiphiplastra of *A. byssina* is also not as widely triangular as those in *Axestemys montinsana.* Rather, the xiphiplastra are intermediate, still roughly triangular in shape but more elongated, with an emargination along the lateral edge of the xiphiplastra that becomes less pronounced as a callosity grows to cover it. In addition to covering the lateral emargination, in larger, presumably older, individuals the callosity also grows to cover most of the processes on the xiphiplastron. In the xiphi-hypoplastral contact, the xiphiplastron is lateral-most. Hay (1908) reconstructed the xiphiplastra as meeting at the midline via two anteromedial processes, such as the kind reconstructed in the holotype (Fig. 14G), but there is no suture or other evidence to suggest extensive midline contact.

Non-shell postcrania.—A single cervical vertebra is preserved as part of the type specimen. Hay (1908) referred to it as the seventh. Unlike *Axestemys montinsana* and some other large trionychids (Meylan 1987), *Axestemys byssina* lacks dorsal procese on this cervical vertebra.

Remarks

In addition to describing *Axestemys byssina* based on USNM 4089, Hay (1908) referred the partial medial hypoplastron AMNH 1034 (Fig 14E) to *A. byssina* on the basis of its mention by Cope (1884) and the fact that both USNM 4089 and AMNH 1034 are covered by an entirely unsculptured callosity. This character was also the basis for Hay's referral of the shell fragments—including a partial hypoplastron—of AMNH 1046 (Fig 14B-D, F) to *Axestemys* and tentatively to *A. byssina*. None of these three specimens were found at the same site. Furthermore, the two referred specimens have no xiphiplastra and therefore no characters that overlap with the holotype.

However, the more complete material of USNM 12589 and USNM 16174 supports Hay's conclusion that there is single taxon present in the Eocene which has the same characters attributed to various specimens of *Axestemys byssina* and which is different from both *Axestemys cerevisia*, an Eocene taxon with callosified but unsculptured hyo- and hypoplastra, and *Oliveremy uintaensis,* another Eocene taxon with callosified but unsculptured xiphiplastra. In addition to the characters described above, it is likely that *A. byssina* also differs from *O. uintaensis* in the presence of a preneural, which *O. uintaensis* lacks. Hay supposed that *A. byssina* lacked a preneural, and none of the referred material preserves either a preneural or a first neural that would clarify whether or not that element is present. Nevertheless, a preneural is present in all more basal speciesof *Axestemys*. In the absence of direct evidence, it is more parsimonious to infer that *A. byssina* also had a preneural.

Axestemys cerevisia sp. nov.

Figure 17

Etymology

cerevisia, Latin for beer, in reference to the unusual method of data collection for the holotype specimen as reported by E.S. Gaffney: "The only information about the *in situ* position of the skeletal elements of this specimen is a field sketch made on a Coors beer six-pack container, another demonstration of the essential nature of this sort of field equipment" (Gaffney 1979:53).

Synonymy

Trionychidae gen. indet.: Gaffney 1979:53, fig.1-3;

Axestemys sp. indet.: Hutchison and Holroyd 2003:134.

Type Specimen

UW 2382, a carapace, plastron, partial pectoral and pelvic girdles, and one cervical vertebrae

Horizon and Type Locality

University of Wyoming Locality Number V-65004, NE 1/4 SE 1/4 Sec. 35, T 22N, R 113W, NE of Opal, Lincoln County, (Bridgerian) Bridger Formation, Bridger A, Wyoming, USA (Gaffney 1979).

Diagnosis

Axestemys cerevisia can be diagnosed as a member of *Axestemys* by a maximum

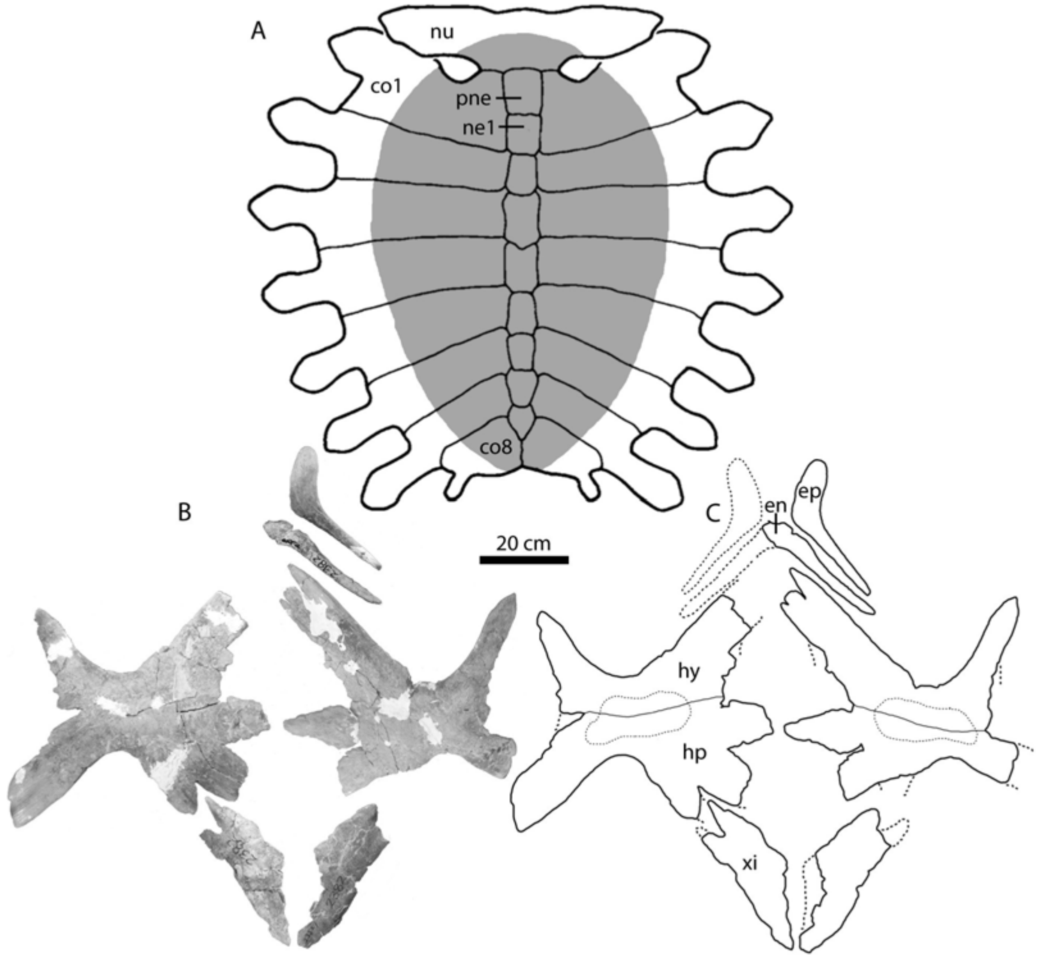

Figure 17. UW 2382, holotype of *Axestemys cerevisia* from the Eocene Bridger Formation of Wyoming. A, illustration of carapace. Gray area indicates limit of sculpturing. B, Photograph and C, illustration of plastron. Dotted line on hyo- and hypoplastra indicates limit of callosity. Abbreviations: en = entoplastron, ep = epiplastron, hp = hypoplastron, hy = hyoplastron. Carapace illustration modified from Gaffney, 1979.

known carapace length of 97 cm; preneural present; single lateral hyoplastral process. *A. cerevisia* can be differentiated from other member of *Axestemys* by wide, smooth border of carapacial callosity; open suprascapular fontanelles with no suture between posterolateral edge of nuchal and costals 1; smooth, reduced hyo-hypoplastral callosities; xiphiplastral callosities absent.

Description

Gaffney (1979) published a detailed description of the holotype specimen. Little needs to be changed or added to that description with the exception of the following: contrary to the previously published description, a small callosity is present on each hyo- and hypoplastron. It does not reach any of the margins of the bone or the processes. Its presence is indicated by a raised area in the middle of each element, which, unlike the bare, uncallosified bone, has a smooth surface with occasional cross-hatching, similar to that described in the plastron of *Axestemys byssina*. In addition, distinct dorsal processes are absent on the single preserved seventh cervical vertebra.

Remarks

The first article to mention this specimen (Gaffney 1979) provided locality and stratigraphic information, a description of the specimen, and a comparison with several other fossil and extant trionychids, but did not name the specimen. Instead, Gaffney referred the taxon to Trionychidae gen. indet, arguing that the state of trionychid systematics was so disordered at that time that assigning a name to the specimen would be meaningless.

Since then, revisions and phylogenetic studies of both fossil and recent trionychids (Meylan 1987; Gardner et al. 1995; Joyce and Lyson 2011; Joyce et al 2009; Vitek in press) have made inroads into examining phylogenetic relationships and providing a meaningful taxonomy within North American Trionychidae. Although much work remains to be done, the current state of trionychid systematics is at a point where it is now not only apparent that UW 2382 represents a unique species (Gaffney 1979), but that this taxon is a part of *Axestemys*. *Axestemys cerevisia* differs from *A. byssina*, another Bridgerian species of *Axestemys*, in having large, open suprascapular fontanelles that prevent a suture between the nuchal and the first costals, less extremely reduced eighth costals, the absence of a callosity on the xiphiplastra, and extensive reduction of the callosity on the hyo- and hypoplastron.

Results

Phylogenetic analysis

Parsimony analysis produced 6,571 most parsimonious trees of 308 steps. A strict consensus of all 6,571 trees showed poor resolution among almost all of the clades and failed to recover many otherwise well-established clades, such as Trionychinae, Apalonina, and Chitrini. Only Plastomenidae, *Apalone*, and *Axestemys* were recovered as well resolved clades. Relationships within Plastomenidae are identical to those found by Joyce and Lyson (2011) and relationships within *Apalone* are identical to the results of both morphological and molecular results (Meylan 1987, Engstrom et al. 2004). Within *Axestemys*, *A. byssina* and *A. quinni* are the most derived sister taxa. They, in turn, are sister to *A. cerevisia*, which formed a clade sister to *A. montinsana*, which formed a clade sister to *A. splendida*.

A fifty percent majority rule consensus tree (Fig. 1, CI = 0.3929, RI = 0.5917), recovered many traditionally recognized clades not present in the strict consensus tree. Cyclanorbinae + Plastomenidae is recovered as a single clade in agreement with previous analyses (Joyce et al. 2009; Joyce and Lyson 2010, 2011). Within Trionychinae, Meylan's (1987) Apalonina, Aspideretini, and Pelodiscini are recovered. Strangely, Meylan's (1987) Chitrini clade is broken up, with *Chitra indica* sister to all other Trionychinae, including *Pelochelys bibroni* and *Amyda cartilaginea*. Although these results differ somewhat from previous results (Meylan 1987, Engstrom et al. 2004), they have no bootstrap support and are considered preliminary results in an unstable tree. More work should be done to explore whether the results and lack of resolution are due to conflict within the data or to missing data within the matrix.

“Trionyx” egregius is recovered within Apalonina. *Oliveremys uintaensis* is recovered as a basal trionychine. *Aspideretoides foveatus, “Aspideretoides” allani*, and *“Axestemys” puercensis* were recovered as a polytomy outside of *Axestemys*.

Systematics

Phylogenetic analysis supports the hypothesis that *Axestemys byssina*, the type species of *Axestemys*, is part of a monophyletic group of giant fossil North American trionychids. This clade contains five species, discussed below.

Axestemys byssina shares with *Axestemys splendida*—the oldest and phylogenetically most basal representative of *Axestemys*—the plesiomorphic characters of a nuchal at least four times wider than long, a preneural, a single lateral hyoplastral process, the presence of four plastral callosities, and a short hyo-hypoplastral bridge. They and the other members of *Axestemys* share the local apomorphy of having an extremely large size, with carapaces at least 600 mm in length. A distinct category of giant trionychids of this size has been found within extant taxa (Pritchard 2001) and includes *Rafetus swinhoei, Chitra chitra, C. indica, Pelochelys bibroni,* and *P. cantorii* . *Pelochelys* and *Chitra* are considered sister taxa, and therefore it is likely that the distribution of gigantism in modern trionychids is the result of two independent evolutions of gigantic size. In addition, both the skull fragment referred to *A. byssina* and all skulls referred to *A. splendida* (with the exception of MRF 266) have sculpturing on the surface of the skull roof, a character not found in any extant or North American non-*Axestemys* fossil trionychid. These two apomorphies support the inclusion of *A. splendida* within *Axestemys* and help to diagnose the clade as a whole.

Axestemys montinsana can be included within *Axestemys* based on a sculptured skull roof and large carapace size. Furthermore, *A. montinsana* and all other more derived members of *Axestemys* have a callosified but unsculptured hyo- and hypoplastron and a wide unsculptured band on the border of the callosity covering the carapace (with the exception of *A. quinni*). Most trionychids have some sort of smooth border on the carapace, but these are usually no more than a few millimeters wide. The smooth border on the carapace of *A. montinsana* and other *Axestemys* taxa is several centimeters—an order of magnitude wider. *A. montinsana, A. cerevisia,* and *A. byssina* also share short twin anterior entoplastral processes. *A. quinni* does not have a preserved plastron, but it is possible that this taxon had a similarly shaped entoplastron.

Only *Axestemys splendida* and *A. montinsana* have reasonably complete skulls and mandibles. They are similar in many regards, with blunt and deep maxillae, large postorbitals, contact between the basisphenoid and palatines, a parietal that makes up more than twenty percent of the processus trochlearis oticum, a weakly emarginated dorsolateral edge of the aperatura narium externum, high crista supraoccipitalis and coronoid processes, wide and rugose triturating surfaces, and broad dentary pockets.

Axestemys cerevisia lacks a skull, but it can be included in *Axestemys* based on having the largest known carapace out of all five species and a lack of sculpturing on the hyo-hypoplastral callosity. *A. cerevisia* and all other more derived members of *Axestemys* have suprascapular fontanelles.

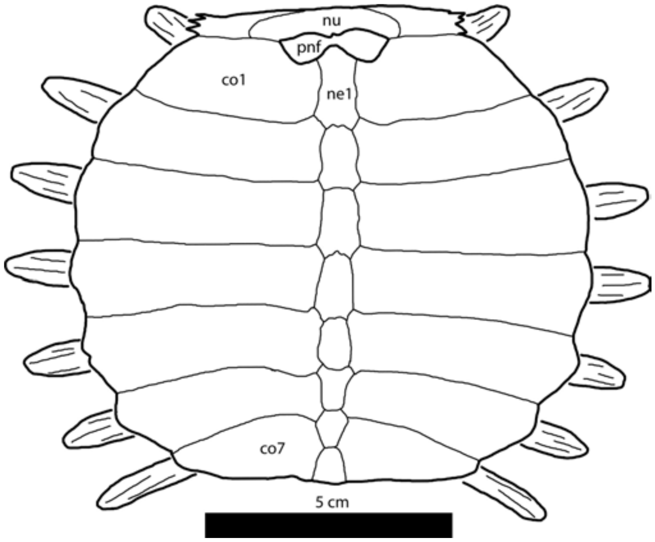

Figure 18. Illustration of YPM R 10890, carapace of a juvenile *Apalone mutica*.

Using the presence of suprascapular fontanelles to diagnose fossil taxa is hazardous because the presence of fontanelles is generally an ontogenetic character. Many juvenile trionychids have a loosely attached nuchal and large suprascapular fontanelles. During growth, the nuchal usually becomes more strongly sutured to the rest of the carapace and the fontanelles close. In the past, the presence of suprascapular fontanelles in large carapaces has been used to justify the character as diagnostic with the argument that if the carapace is large, then the individual had probably already reached adulthood and the suprascapular fontanelles would remain open throughout life (Gardner and Russell 1994). However, without a clear growth series in fossil trionychids and a wide range of adult sizes in extant trionychids (Meylan 1987, Pritchard 2001) it is difficult to quantitatively decide when a carapace is "big enough" to be considered an adult.

Comparison of the fontanelles in *Axestemys* with fontanelles in juvenile extant trionychids show that it is irrelevant whether or not the carapaces referred to *Axestemys* represent juveniles or adults. The nuchal suture pattern of *Axestemys* and the pattern in extant taxa with suprascapular fontanelles such as *Pelodiscus sinensis* and *Apalones spinifera* are very different. In extant trionychids such as *Apalone mutica* (e.g. YPM R 10890, Fig 18) the lateral edge of the nuchal sutures to the anterolateral edge of the first costals before the nuchal divides the suprascapular fontanelles to contact the neural, preneural, and/or first costals medially. In contrast, the large suprascapular fontanelles of *Axestemys cerevisia* and *Axestemys quinni* show that the nuchals of these taxa sutured to the preneurals and, in some cases, the anteromedial edge of the first costals between the two fontanelles before the nuchals sutured to the anterolateral edge of the first costals, if they formed a suture there at all. As far as is known, this nuchal suture pattern is unique to *Axestemys* and *"Axestemys" puercensis*.

Although the only specimen of *Axestemys quinni* (Fig. 19) lacks a skull, plastron, and non-shell postcranials, it can be referred to *Axestemys* based on its gigantic size and the presence of large suprascapular fontanelles which prevent contact between the nuchal

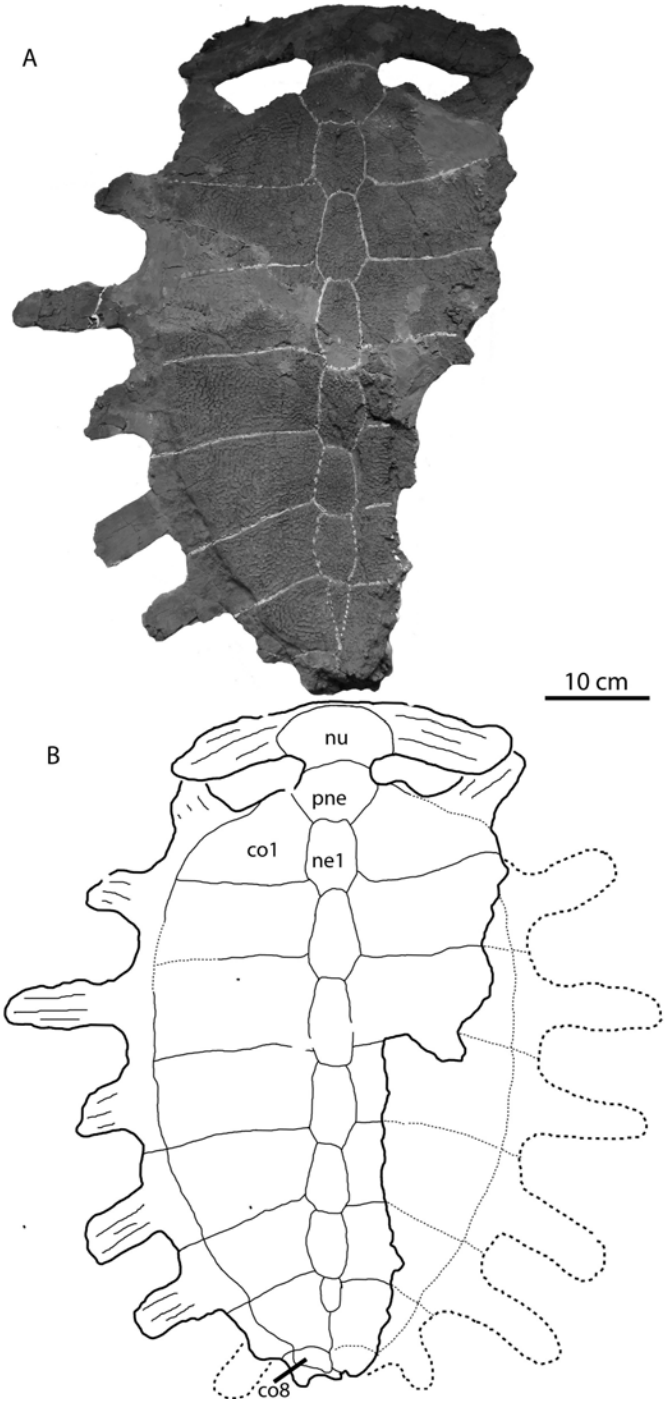

Figure 19. FMNH P 26641, holotype of *Axestemys quinni* from the Paleocene De Beque Formation of Colorado. A, Photograph and B, illustration of carapace. Abbreviations: co = costal, ne = neural, nu = nuchal, pne = preneural.

and first costals. It is unclear whether the large type of fontanelles was derived twice in *A. quinni and A. cerevisia,* or whether it was derived once in the common ancestor of *A. byssina, A. quinni,* and *A. cerevisia a*nd subsequently lost in *A. byssina. A. byssina and A. quinni*, the two most phylogenetically derived members of *Axestemys,* share the character of extremely reduced eighth costals. *A. quinni* has been considered a member of *Axestemys* for several years already, after Hutchison and Holroyd (2003) synonymized its original generic name *Paleotrionyx* with *Axestemys*.

One other giant North American taxon with unsculptured xiphiplastral and hyo-hypoplastral callosities has been named. Chkhikhvadze (2008) named *Eugenichelys robertemryi* based on specimen USNM 12589, a partial plastron as well as some skull fragments. He proposed that *E. robertemryi* differed from *Axestemys* in that the former came from older sediments. The two holotype specimens come from the Wasatch Formation and Bridger Formation, respectively. It is not uncommon for the ranges of fossil trionychid taxa to extend across ages as long or longer than the Wasatchian-Bridgerian, and without any morphological differences an age difference this small is not enough to justify a separate taxon. Examination of USNM 12589 shows no difference between this specimen and the holotype material of *A. byssina* or any other material referred to this taxon from both the Wasatch and Bridger Formations. *A. byssina* was named before *Eugenichelys robertemryi* and therefore has priority. For these reasons, *E. robertemryi* is synonymized with *A. byssina*.

"Axestemys" puercensis has been historically referred to the same genus as *Axestemys quinni* and *Axestemys cerevisia* based on its large suprascapular fontanelles which separate the nuchal from the first costals (Schmidt 1945, Hutchison and Holroyd 2003). It shares other characteristics with *Axestemys* such as a preneural, 7-8 neurals, and long rib ends extending from the edge of the carapace (Hutchison and Holroyd 2003). Long rib ends have previously been considered characteristic of *Axestemys* (Hutchison and Holroyd 2003), and there is evidence to suggest that retention of long rib ends at large sizes is a derived feature (Gardner and Russell 1994). However, long rib ends are also a juvenile feature of trionychids, and *"A." puercensis* is much smaller than all other *Axestemys* species (carapace length 330 mm). Therefore, use of long rib ends in adult specimens as evidence that *"A." puercensis* is a member of *Axestemys* may be conflating a possibly species-diagnostic character with an ontogenetic character.

It is possible that the holotype specimen represents a juvenile, and that adult individuals of the taxon grew large enough to be considered giant. However, the only described giant Puercan trionychid specimens differ from *"A." puercensis* in several characters, including smooth hyo- and hypoplastral callosities, the absence of suprascapular fontanelles of any kind, and a wide, smooth band on the lateral border of the carapace. These specimens were referred to *Axestemys montinsana*, and no intermediate specimens of the same age have been reported that would suggest an ontogenetic transition between the two taxa. Furthermore, there is no phylogenetic support for the inclusion of *"A." puercensis* within *Axestemys*. Without evidence that *"A." puercensis* reached gigantic size or developed other characters found in other species of *Axestemys*, the presence of open suprascapular fontanelles is not sufficient evidence to justify referring *"A." puercensis* to *Axestemys*.

Hutchison and Holroyd (2003) referred several shell and skull fragments from a large trionychid to *"A." puercensis*. On the basis of these fragments, the fact that they were found in the same rock unit as the skull-only taxon *Conchochelys admiribalis*, and the similarities between the skull fragments and *C. admiribalis*, the authors synonymized *C. admiribalis* and *"A." puercensis* and referred them both to *Axestemys*. New material described in this study indicates that these skull and shell fragments belong to *Axestemys montinsana* rather than to *"A." puercensis*, and that the skull of *A. montinsana* differs in several ways from *C. admiribalis*. Without these fragments, there is no evidence to suggest that *"A." puercensis* and *C. admiribalis* are synonymous, or that *C. admiribalis* should be included in *Axestemys.*

Discussion

The most recent review of *Axestemys* proposed that this clade can be identified as as a group of trionychids with generally paedomorphic shells, based on long free rib ends, the presence of suprascapular fontanelles, and a general reduction of carapacial and plastral callosities at large body sizes (Hutchison and Holroyd 2003). Trionychids as a whole are already considered to have some paedomorphic characters such as the loss of peripherals due to develomental truncation, although paedomorphosis does not otherwise appear to be an overwhelming factor in trionychid evolution (Meylan 1987).

Similarly, in *Axestemys* some of the characters seen in some of the species can be explained through paedomorphism. These characters are the relatively long rib ends seen in *Axestemys quinni* and *A. cerevisia*, the restriction of the hyo- and hypoplastral callosity and the absence of a xiphiplastral callosity in *A. cerevisia*, and the reduced carapacial callosity in *A. quinni*. However, these characters are not distributed throughout all of the taxa in *Axestemys*. The large, open suprascapular fontanelles in *A. cerevisia* and *A. quinni* are not homologous to the suprascapular fontanelles seen in extant juvenile trionychids, and without a growth series for fossil trionychids with the *A. quinni*-type nuchal attachment, it is unclear how this character is related to trionychid development. Other characters, such as smooth plastral callosities and a smooth carapacial border, do not appear to be caused by paedomorphosis. Therefore, while it is possible that paedomorphosis played a role in the evolution of more derived *Axestemys* taxa, it is not the principal factor influencing the evolution of *Axestemys*.

The systematics of *Axestemys* indicate that, contrary to historical precedent, it is not possible to diagnose *Axestemys* based solely on the characters exemplified by the type species *Axestemys byssina* or more derived taxa such as *A. cerevisia*. Traditional characters used to define *Axestemys*, such as large suprascapular fontanelles and smooth plastral callosities, are found in other non-*Axestemys* fossil taxa such as *"Aspideretoides" allani, "Trionyx" puercensis*, and *Oliveremys uintaensis*. With the exception of the presence of sculpturing on the skull roof, no characters that could define *Axestemys* are found throughout the entire group and nowhere else within trionychids. Gigantic size is an unsuitable character in the absence of other characters because it is found in other non-*Axestemys* taxa such as *Rafetus swinhoei, Chitra chitra, C. indica, Pelochelys bibroni,* and *P. cantorii* and the Cretaceous Eurasian *"Trionyx" kansaiensis* (Pritchard 2001; Vitek and Danilov 2010), and therefore gigantism must have evolved at least two other times beside that in *Axestemys*.

Axestemys is better thought of as a wholly extinct monophyletic side branch of gigantic trionychids whose other, more recognizeable characters developed gradually from a taxon that by all traditional accounts would not have been considered a part of the clade. The stratigraphic range of the clade is longer than previously supposed, now extending from the Campanian to the Bridgerian (Fig. 20).

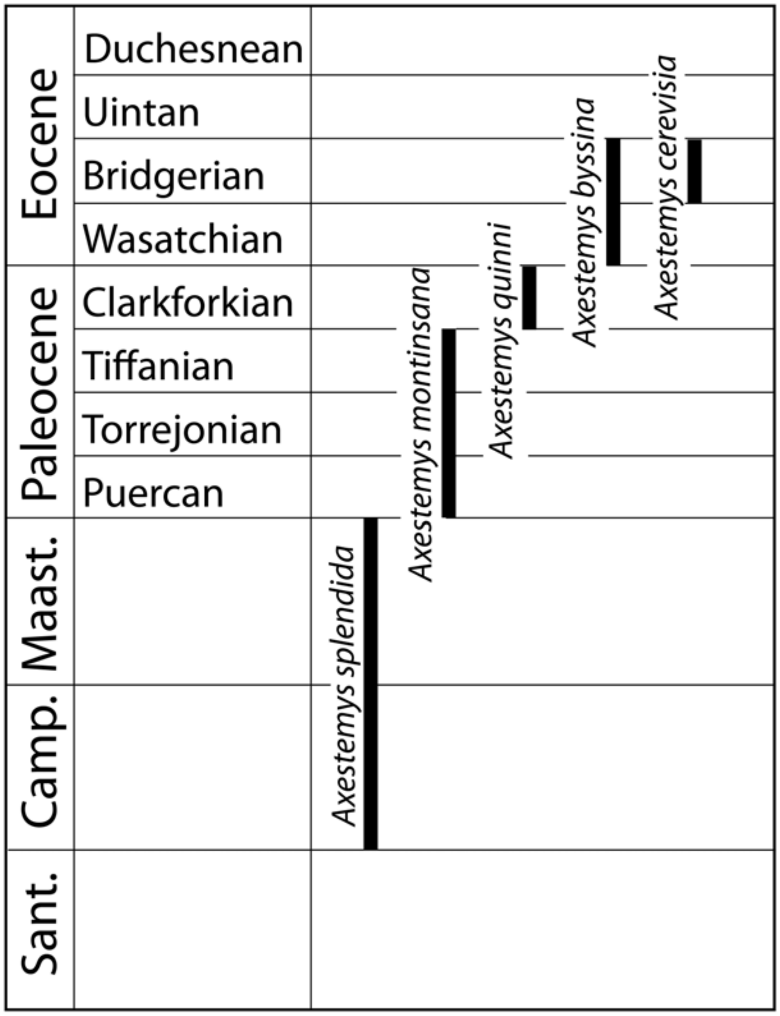

Figure 20. The stratigraphic distribution of taxa discussed in the text.

The monophyly of *Axestemys* suggests the possibility that gigantism developed once in North American trionychids and that gigantism was conserved in a single lineage for approximately 24 million years. However, until *Conchochelys admiribalis*—currently represented by a single large skull that may have belonged to a gigantic shell—is more fully understood, this hypothesis leaves some taxa unaccounted for.

Two factors could have influenced the evolution of giant fossil soft-shell turtles in North America. The first is climate. Trionychids, as poikilotherms, have a limit on their maximum body size imposed by the mean annual temperature of their environment (Head et al. 2009; Head 2010). Warmer temperatures allow larger body size. For example, Recent trionychid species that reach gigantic sizes are restricted to the tropics (Pritchard 2001, Ernst and Barbour 1989). The significantly warmer global climate 70-46 million years ago would have allowed a larger body size and would have made it possible for trionychids with meter-long shells to live in Wyoming.

The second factor is diversity and sympatry of trionychid taxa. Where multiple taxa are sympatric, they develop significant size differences (Pritchard 2001). Areas with higher diversity, may encourage size divergence and therefore gigantism. Today, the area with the highest sympatry includes one small, one large, and two giant trionychids. There, one of the giant species is hypothesized to avoid competition with the second taxa by inhabiting estuarine environments (Pritchard 2001). High diversity in western North America might have also encouraged the evolution of gigantic trionychids.

These two factors are in no way mutually exclusive. The island of Java, Indonesia, is both tropical and the area of highest diversity on earth in terms of trionychids, with four species living in sympatry. Western North America had a warm climate from the

Maastrichtian through the Bridgerian Eocene, and in at least some periods had high trionychid diversity.

Recent attempts to study fossil trionychid diversity in North America have been complicated by a hyperinflated number of species reported based on fragmentary and undiagnostic material (Gaffney 1979, Joyce et al. 2009). For example, at least twenty-three species have been named from the Bridger Formation alone. Of those, only four species have recently been reviewed and included in phylogenetic analyses that supports their designation as distinct and valid: *Plastomenus thomasii*, *Oliveremys uintaensis*, *Axestemys byssina*, and *Axestemys cerevisia* (Joyce and Lyson 2010; Vitek in press; this study).

However, even if all of the other nineteen species are later found to be invalid or synonymous with these four, the Bridger Formation trionychid fauna is still more diverse than the modern North American trionychid fauna and at least as diverse as Java, where four trionychid species are found in broad sympatry. Although much work remains in the project of revising the systematics of North American Cretaceous-Eocene fossil trionychids, future work regarding the diversity of taxa—and the wide range of size that seems to come with it—might be best compared to modern diversity in localities like Java, rather than the modern North American trionychid fauna.

Summary

The taxonomic revision and phylogenetic analysis of *Axestemys* revealed a clade containing five species. *Axestemys cerevisia* sp. nov. and *A. montinsana* sp. nov. are established as new species, *A. byssina* and *A. splendida* comb. nov. are included as a result of the description of new material, and *A. quinni* is reviewed and confirmed to be a member of the clade. Phylogenetic analysis does not support the inclusion of *"Trionyx" puercensis* and *Conchochelys admiribalis*, previously hypothesized to belong to *Axestemys*. *Eugenichelys robertemryi* is synonymized with *Axestemys byssina. Axestemys* is best defined in terms of common ancestry relationships rather than based on many of the characters traditionally ascribed to it. Nonetheless, all members of *Axestemys* reach a gigantic size that is today only found in a few tropical trionychids. The presence of *Axestemys* in North America indicates both a warmer climate and a higher trionychid diversity and disparity comparable with Recent tropical diversity.

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Appendix 1: List of characters

1-77: The first 77 characters are taken directly from Vitek's (2011) analysis. This analysis is based off of the analysis of Joyce et al. (2009) with some revisions to character wording and scoring.

78-84: Characters 78-84 are the seven new characters that Joyce and Lyson (2011) added to Joyce et al.'s (2009) matrix, taken directly from Joyce and Lyson (2011).

Character 85: Maximum adult carapace size greater than 600 mm: 0 = no; 1 = yes.

Character 86: hyo-hypoplastral callosity, if present, lacks sculpturing on more than 90 percent of its surface: 0 = no; 1 = yes.

Character 87: xiphiplastral callosity, if present, lacks sculpturing on more than 90 percent of its surface: 0 = no; 1 = yes.

Character 88: Nuchal sutures to preneural, and/or neural 1, before it sutures to anterolateral edge of costal 1: 0 = no 1 = yes.

Appendix 2: Data matrix

a=0/1 b=1/2 c=2/3 d=1/2/3

outgroup 00000 00100 00010 00000 00000 00000 00000 00000 00001 00011 00000 00000 00000 00000 00010 ?0000 00000 000

aubryi 10103 00111 1a0b0 10000 10021 10111 03110 20000 0111- 01011 00010 00101 10100 00000 00010 10000 00000 000

bibroni 21113 00300 0a011 00110 00020 00100 11000 10002 00200 10111 00111 11000 01011 00000 00000 20000 000a0 000

cartilaginea 21113 00200 00011 02110 00000 10111 01000 10010 00100 10211 10101 00010 01001 00000 00000 20000 00010 000

elegans 1110 30041 01a0b 00011 000020 01111 02110 20000 0001- 01111 11000 00101 01110 00000 00010 10000 00000 000

euphraticus 21113 01400 010b1 00110 00000 10100 01000 20010 00000 00221 11102 00001 01101 00000 00000 20000 00a10 000

ferox 21113 01300 012b1 00110 01000 20100 01000 20000 00000 00221 11002 00000 01101 00000 0a0a0 10000 00110 0-0

formosa 11113 00300 00010 00110 00120 10111 01000 20020 00001 00211 00--1 00011 01--- 00000 000?? ?0000 00010 000

frenatum 10003 00110 1a0b0 10000 10021 00111 03110 20001 1021- 01111 10010 00101 10100 00000 00010 10000 00010 000

gangeticus 21103 00200 0a1b0 01110 00000 10111 01000 20020 00001 00111 10002

00010 01010 00000 00000 20000 00a10 000

hurum 21103 00200 0a1b0 01110 00010 20111 01000 20020 00001 10211 00000 00010 01011 00000 00000 20000 00a10 000

indica 21213 00300 00010 00110 01021 00100 01000 10001 00200 20200 00111 11001 01011 00000 00000 20000 00a11 000

leithii 21103 00200 0a010 01110 00110 10111 01000 20020 00000 00211 00001 00010 01010 ????? ????? ????? ??a10 000

mutica 31113 01100 0a2b2 00111 01110 20101 01000 20000 0001- 00122 11001 00000 01010 00000 000a0 10000 00110 000

nigricans 21103 00200 000b- 01110 00100 10111 01000 10020 00201 00211 01001 00010 01010 ????? ????? ????? ??a10 000

punctata 10002 10111 1b0b0 10000 10010 00110 01110 20000 00101 00011 00000 00101 00110 00000 00011 10000 00010 000

senegalensis 21103 10010 12-40 00000 00021 10100 02110 20000 0021- 01011 00000 00101 11100 00000 00010 20000 00--0 000

sinensis 31113 00100 0b2b1 02111 00110 20111 01101 20020 00002 00211 10001 00000 01010 00000 00000 20000 00110 000

spinifera 21113 01100 012b2 00111 01000 20100 01000 20010 0001- 00222 11002 00000 01010 00000 000a0 10000 00110 000

steindachneri 11113 00300 0a0b0 02111 00020 20111 01001 20020 0001- 20212 00--1 00000 -1--0 00000 000?? ?0000 00010 000

subplana 31113 00300 00102 02111 00010 20111 01001 21010 0000- 00112 10001 00010 01011 00000 00000 20000 00010 000

swinhoei ---13 01400 0---- 00110 00100 10100 01100 20000 00000 00221 11--- 00001 -1
—1 ????? ????? ????? ??--1 000

triunguis 21113 00300 010b1 00110 00000 20011 01000 20100 00000 0011? 11001
00000 01010 00000 00000 20000 10a10 0-0

thomasii 31?0 30010 11b-c 0??00 00?00 ???01 -01111 21000 00??? ???-2 00??? ???
0? ????? 00000 01110 21001 ?1--0 000

rememdium 31?03 00101 110b0 1?100
0???? ????? ????? ????? ????? ????? ????? ????? ?10?? 11110 01120 1???? ?a010 000

arctochelys 31?03 00101 110b0 1?000
0???? ????? ????? ????? ????? ????? ????? ????? ????? 10111 11121 1???? ?1010 000

foveatus 31103 00300 011b1 00110 0?000 21110 ?1??0 10?00 00??1 ?2?12
1???? ????? ????? 000?0 00000 10??0 ?0a10 000

uintaensis 31113 01300 01?ca 00110 0?010 10100 00000 000?0 00a00 a0211 0110? ???
0? 01000 -0000 00000 200?0 00a10 010

tetraneton 31?03 00?00 11010 ???01
0???? ????? ????? ????? ????? ????? ????? ????? ????? 11010 01?20 ????? ??010 000

sterea 21?03 00101 11020 10001 0???? ????? ????? ????? ????? ????? ????? ????? ?????
10010 01120 ????? ?1110 000

lancensis 31?03 00?02 01020 ??110 0?121 20a11 02111 2000? 0001- 20211
00??? ????? ????? 00000 00?10 211?1 100a0 000

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