

Two New Plastomenine Softshell Turtles from the Paleocene of Montana and Wyoming

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ABSTRACT

The many fossil turtle remains collected by Princeton University throughout the 1950s and 1960s from Paleocene sediments in Montana and Wyoming include two new species of plastomenine softshell turtles (Trionychidae) that are referred to *Hutchemys* gen. nov., which corresponds to the previously used informal taxon “Plastomenine Type A.” *Hutchemys* is unique among trionychids in having a broadly rounded entoplastron that is underlain by a large rectangular callosity and fully immobilized through lateral processes of the hyoplastra. *Hutchemys rememidium* sp. nov. is documented by specimens from the Torrejonian of Montana and the Tiffanian of Wyoming, whereas *Hutchemys arctochelys* sp. nov. is only known from a collection of shells from a single Clarkforkian locality in Montana. The holotype of a third taxon, *Aspideretes nassau* Hay 1908, is diagnostic for *Hutchemys*, but cannot be diagnosed to the species level and is thus considered a *nomen dubium*. A phylogenetic analysis places the new species in a clade that is sister to *Plastomenus* aff. *thomasi* along the phylogenetic stem of Cyclanorbininae, thus tentatively confirming monophyly of Plastomeninae and a close relationship to cyclanorbines. However, given that many supposedly diagnostic postcranial characters of Plastomeninae are often found among trionychines as well, in particular characters pertaining to the extensively ossified plastron, we suggest that a wide and rounded entoplastron is a more useful character in diagnosing this clade. Representatives of *Hutchemys* seem to have preferred swampy habitats and their shell converges on that of testudinoid or pleurodiran pond turtles in the degree of ossification and the presence of an anterior plastral hinge.

KEYWORDS

Trionychidae, Plastomeninae, *Aspideretes nassau*, *Hutchemys arctochelys*, *Hutchemys rememidium*, Paleocene.

Introduction

Softshell turtles (Trionychidae) are a highly enigmatic clade of reptiles characterized by a reduced shell, the loss of nearly all scales and scutes, and the development of a proboscis (Ernst and Barbour 1989). Trionychids generally prefer riverine habitats and are thus commonly found in fluvial and near-shore marine sediments. Furthermore, because of the unique surface texture and subsur-

face structure (Scheyer et al. 2007) of the shell, trionychids are easily recognized in the fossil record.

Although only three or four extant trionychid species are currently recognized in North America (Ernst and Barbour 1989), trionychids were highly diverse on this continent throughout the Late Cretaceous (Campanian and Maastrichtian) and Paleogene (Hay 1908). Unfortunately, the alpha taxonomy of the group is still rather chaotic and has not been reviewed since Hay (1908). This

is partially the result of the plethora of names that were created on the basis of extremely fragmentary material during the second half of the 19th century. Our informal review of the alpha taxonomy of named North American fossil trionychid species revealed almost 100 names, most of which should be considered *nomina dubia* by current standards.

Despite the surfeit of taxa, a consensus has emerged over the course of the last century that approximately 20 fossil trionychid species from the Late Cretaceous to Eocene of North America form a natural entity, variously called Plastomenidae or Plastomeninae, that is phylogenetically distinct from the two primary clades of living trionychids, namely Trionychinae and Cyclanorbinae (Hay 1902, 1908; Hummel 1929; Mlynarski 1976). More recent work by some of us (Joyce and Lyson, In press) placed the type species of *Plastomenus*, *P. aff. thomasi* Cope 1873 along the phylogenetic stem of Cyclanorbinae. However, because that analysis included only one plastomenine species, it is not clear whether Plastomeninae is a monophyletic clade or a paraphyletic assemblage of stem cyclanorbines. Furthermore, it remains unclear whether this phylogenetic position is the result of limited taxon sampling.

In a series of papers, Hutchison and colleagues recognized at least three distinct lineages of Plastomeninae, which they informally referred to as Plastomenine types A, B and C (e.g., Hutchison and Archibald 1986; Holroyd and Hutchison 2002; Hutchison and Holroyd 2003). However, because formal species were not named, it remains uncertain how this informal system relates to the approximately 20 previously named Plastomenine species, except that Holroyd and Hutchison (2002) noted that *Helopanoplia distincta* Hay 1908 represents a fourth plastomenine lineage independent from plastomenines type A, B and C. Nevertheless, of the informally named taxa, plastomenine type A is striking in that the entoplastron is heavily ossified, rectangular and fully immobilized through lateral processes of the hyoplastra (Holroyd and Hutchison 2002) and thus can readily be identified.

Throughout the 1930s to 1960s, expeditions led by staff from Princeton University collected many Paleocene vertebrate fossils from the Williston and Powder River basins of Montana and

Wyoming, including a significant number of well-preserved turtles, most of which now reside at the Peabody Museum of Natural History at Yale University (YPM). Although some of these turtles have been studied (e.g. Gaffney 1972; Estes 1975, 1976), the excellently preserved plastomenine skeletons remain undescribed, even though they can clearly be diagnosed as Plastomeninae type A. Our purpose here is to remedy this situation by providing comprehensive descriptions of these specimens, to formally name two new species, to investigate their phylogenetic relationships, and to discuss at least one previously named species of Plastomeninae type A. We also establish a new taxon, *Hutchemys*, to replace Plastomeninae type A with a formal name.

Materials and Methods

The study by Meylan (1987) remains the most comprehensive phylogenetic analysis of Trionychidae based on morphology to date. Engstrom et al. (2004) later expanded on this analysis by integrating the morphological data with extensive molecular data. The analysis of Meylan (1987) consists of 113 characters, of which 66 pertain to variation found within Trionychidae, whereas the rest resolves the placement of Trionychidae within Cryptodira. To investigate the phylogenetic placement of the plastomenine type species *Plastomenus aff. thomasi* within Trionychidae, Joyce and Lyson (In press) extracted these 66 informative characters and assessed the phylogenetic position of this fossil taxon using a molecular scaffold as informed by Engstrom et al. (2004). The number of extant species was reduced by three relative to the analysis of Meylan (1987), because molecular sequence data does not exist for them (Engstrom et al. 2004) and because they consequently cannot be part of a molecular scaffold.

To assess the phylogenetic position of the two new species named herein and to test the monophyly of Plastomeninae, we added 10 characters to the analysis of Meylan (1987), for a total of 76 characters. Several characters in Meylan's analysis do not have discrete character states, but rather polymorphic character states. For instance, character 14 pertains to the number of neurals present in the carapace, but character state 0 is nine neurals, 1 is eight or nine neurals, 2 is eight neurals, and so on. Given that our

sample is too small to allow a statistical assessment of variation, we scored our species as non-polymorphic, if all available specimens of the new genus show the same character state. See our revised character list (Appendix 1) and our character matrix (Appendix 2).

We analyzed the matrix (Figure 1) with PAUP*, v. 4.0b10 (Swofford 2002), using Meylan's (1987) polarity assessments. Following the analysis of Joyce and Lyson (In press), all characters were run unweighted and unordered and the conservative molecular consensus tree of Joyce and Lyson (In press) was used as a topological constraint. We used the tree bisection and reconnection (TBR) heuristic algorithm for all analyses and each analysis was run for 100,000 replicates. Minimum branch lengths were set to collapse. Support for each node was measured by calculating bootstrap frequencies (Felsenstein 1985) with 1000 bootstrap replicates and 100 random sequence addition replicates. Bootstrap frequencies greater than 70% are considered strong support (Hillis and Bull 1993).

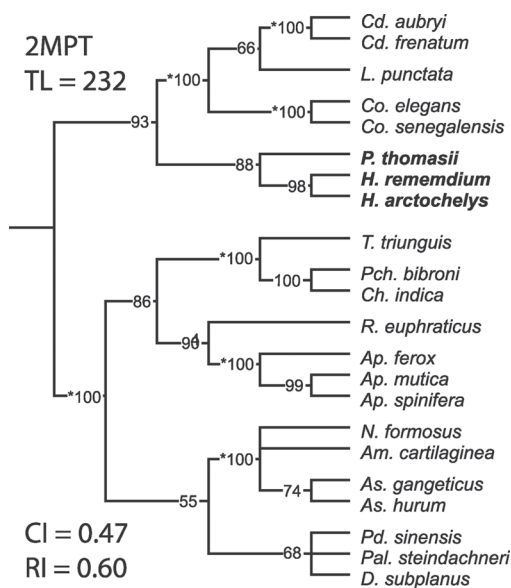


FIGURE 1. The strict consensus topology resulting from the phylogenetic analysis presented herein. Numbers below nodes are support values obtained from 1000 bootstrap runs. Nodes that were constrained automatically received 100% bootstrap values and are consequently denoted with an asterisk. *Abbreviations:* CI, consistency index; MPT, maximum parsimonious tree; RI, retention index; TL, tree length. Refer to Appendix 1 for complete species names.

Institutional acronyms are as follows: UCMP, University of California Museum of Paleontology, Berkeley, California, USA; YPM PU, Yale Peabody Museum of Natural History, Princeton University Collection, New Haven, Connecticut, USA.

Systematic Paleontology

Testudines Batsch, 1788

Cryptodira Cope 1868

Trionychidae Gray 1825

Plastomeninae Hay 1902

Remarks. In our opinion, an assignment of species to Plastomeninae according to the traditionally used characters is currently not desirable, because most of these characters occur widely among representatives of Trionychinae as well (see Discussion below for more details). Instead, we prefer a phylogenetic definition of the term Plastomeninae, as all turtles more closely related to *Plastomenus* aff. *thomasii* than any extant trionychid species, but we refrain from providing a formal definition of that term. Our assignment of *Hutchemys* to Plastomeninae is thus based solely on the phylogenetic position presented herein of this taxon as sister to *P.* aff. *thomasii*.

Hutchemys Joyce, Revan, Lyson and Danilov, gen. nov. Figures 2–9

Synonymy. "Plastomenine" type A: Hutchison and Archibald 1986:5–7, 12; Holroyd and Hutchison 2002:184; Plastomenine A: Holroyd and Hutchison 2002, table 3, 5; Hutchison and Holroyd 2003:132; Plastomeninae type A: Holroyd and Hutchison 2002, table 4.

Etymology. *Hutch*, in honor of John Howard Hutchison, an eminent turtle paleontologist, affectionately called "Hutch" by many, and the discoverer of this taxon. *Chelys*, Greek for turtle.

Type species. *Hutchemys rememidium* sp. nov.

Included species. *Hutchemys rememidium* sp. nov., *H. arctochelys* sp. nov., and an unnamed species from the Tullock Formation (see Remarks below and Figure 10).

Diagnosis. *Hutchemys* can be diagnosed as a representative of Trionychidae by the following list of synapomorphies: loss of peripherals, presence of wide nuchal, presence of a preneural, plastron consisting of several deep straps and surficial callosities, deep layer of entoplastron boomerang-shaped, shell sculptured and lacking epidermal scutes. Relative to all previously named trionychid taxa, including all previously named plastomenines, *Hutchemys* is unique in having two autapomorphies: (1) entoplastron covered ventrally by a well-developed, square callosity that is fully surrounded and immobilized laterally by anteriorly projecting bony flaps of the hypoplastron; and (2) trionychid

sculpturing well developed along margins but dissipates towards the center of the carapace and plastron. Several additional characters further help diagnose this clade, but they are not unique to this taxon: plastral bones fully connected to form single shield with no fontanelles (also occurs in other plastomenines, *Apalone* spp. and *Pelodiscus sinensis*), margins of the costals thickened and often split laterally (occasionally found in other plastomenines and trionychines), bridge region of the plastron have peripheral ossifications in large and, presumably, mature individuals (also occurs in the plastomenine *Helopanoplia distincta*).

Remarks. Hutchison and coauthors (Hutchison and Archibald 1986; Holroyd and Hutchison 2002; Hutchison and Holroyd 2003) mention that the shell of Plastomeninae type A is ovate, well ossified, notably small (carapace length about 165 mm), unusually high domed, and has peripheral ossifications in the area of the plastron–carapace contact. Many of these characters are apparent in the only published figure, which is a simplified line drawing (Holroyd and Hutchison 2002, fig. 2K) based on UCMP 130000 from the Paleocene Tullock Formation of Montana (Hutchison and Archibald 1986, table 3). We suspect that UCMP 130000 represents a different species, given that both species we describe herein have an octagonal neural 2 and rectangular neural 6, but because we have not personally examined UCMP 130000 we cannot comment further on its identity.

Hutchemys sp.

Synonymy. *Aspideretes?* *nassau* sp. nov.: Hay 1908:498, text fig. 653; *Trionyx nassau*: Hummel 1932:81; *Paleotrionyx* or *Aspideretes*: Schmidt 1945:4.

Holotype. YPM PU 11566.

Type locality and horizon. Duffy's Ranch, Sweet Grass County, Montana, USA; Torrejonian or Tiffanian; Fort Union Formation.

Remarks. *Aspideretes?* *nassau* is based on a single specimen that consists of the posterior 80% of a carapace. The locality information for this find is extremely vague. The associated labels only indicate "Fort Union (Paleocene), Duffy's Ranch, 18 mi from Melville, Sweetgrass Co, Montana." Additional locality information cannot be found in the archives of YPM. Duffy is a rather common family name in Montana today, but using current land ownership maps we were unable to find a ranch within 20 miles of Melville associated with that name. Within 20 miles of Melville, Paleocene age strata of both the Lebo and Tongue River members of the Fort Union Formation are broadly exposed and both members are likely exposed on most ranches. The holotype of this taxon is thus at best associated with the Torrejonian or Tiffanian. Before our study, *nassau* was assigned to ?*Aspideretes* (Hay 1908), *Trionyx* (Hummel 1932), and *Paleotrionyx* or *Aspideretes* (Schmidt 1945), but was never affiliated with Plastomeninae.

The holotype is heavily fractured and the surface texture looks as if it was scraped with a stiff metal brush. Finally, what remains is embedded in a dark-colored plaster matrix, making it difficult to study the specimen and assess what has been reconstructed. Nevertheless, a few features are apparent that

allow diagnosis of *nassau* as the only previously named taxon of *Hutchemys*. In particular, the distal ends of all available costals, with the notable exception of the eighth, have distally thickened and split margins, i.e., the costals separate distally into a more superficial, ornamented layer and a deeper visceral layer. More importantly, as Hay (1908) noted, the ornamentation consists of uneven ridges that run parallel to the rim of the carapace, but fade towards the interior of the specimen. The carapace seems to have a squared pygal notch. Other features, such as the arrangement of the neurals, cannot be established with confidence.

Of the two new species of *Hutchemys* named herein, *H. nassau* resembles *H. rememidium* in the distribution of the symmetrically split costal margins and the squarish pygal notch, but these two characters are not diagnostic by themselves, because they occur in other taxa (e.g., *Aspideretoides foveatus*, Gardner and Russell 1994). However, *H. nassau* resembles both species named here in the reduction of the trionychid surface sculpturing along the center of the carapace, a character that is unique among Trionychidae. We are confident in diagnosing the type of *H. nassau* as belonging to *Hutchemys*, but it is not sufficiently diagnostic to warrant detailed comparison to other plastomenines and we thus consider the name a *nomen dubium*.

Hutchemys rememidium Joyce, Revan,
Lyson and Danilov, sp. nov.
Figures 2–4

Etymology. *Rememidium*, Latin for medicine, in reference to the type locality near Medicine Rocks, Montana, USA.

Holotype. YPM PU 16795, a nearly complete postcranial skeleton (Figures 2 and 3).

Type locality and horizon. T3N R60E, Fallon County, Montana, USA; Ekalaka Member, Fort Union Formation (Torrejonian). More detailed locality information is archived at YPM.

Referred specimens. YPM PU 14985, the posterior half of a carapace (Figure 4A–D), Cedar Point Quarry, Wyoming, USA (Tiffanian 3); YPM PU 16781, right hyo/hypoplastron (Figure 4E–F), Ekalaka Member (Medicine Rocks; Torrejonian 3).

Diagnosis. *Hutchemys rememidium* sp. nov. is diagnosed by the following three autapomorphies and at the same time distinguished from *Hutchemys arctochelys* sp. nov.: (1) nuchal sharply notched; (2) distal margins of costals 1 to 7 evenly split; and (3) neural 1 small and circular. Several additional characters further help diagnose this clade, but they are not unique to this species: pygal notch rectangular (a symplesiomorphy widely found among trionychids); costals 8 wider than long (also seen in cyclanorbines and other plastomenines); neural 3 octagonal (synapomorphy with *Hutchemys arctochelys*); carapace without a waist; sculpturing on visceral surfaces of costals absent; posterior flap of hypoplastron absent (symplesiomorphies relative to *Hutchemys arctochelys*).

Remarks. The specimens referred to *Hutchemys rememidium* were collected from two primary localities. The holotype YPM PU 16795 and the isolated hyo/hypoplastron YPM PU 16781 were both collected in Fallon County, Montana, from the

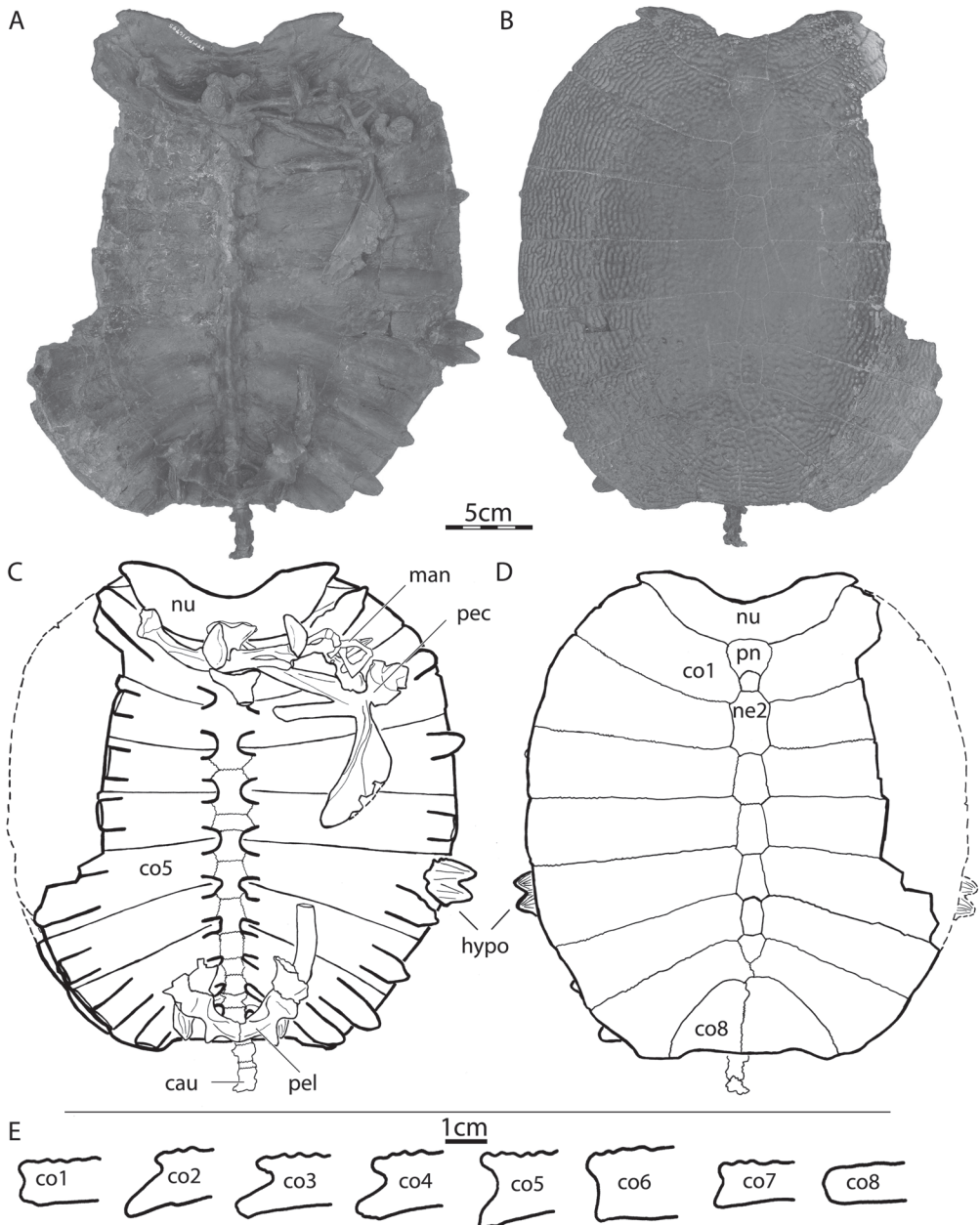


FIGURE 2. YPM PU 16795, holotype of *Hutchemys rememidium* sp. nov. **A.** Ventral view of carapace. **B.** Dorsal view of carapace. **C.** Ventral view of carapace. **D.** Dorsal view of carapace. **E.** Left margins of costals 1 to 8. *Abbreviations:* cau, caudal column; co, costal; hypo, lateral processes of left hypoplastron; man, manus; ne, neural; nu, nuchal; pec, pectoral girdle; pel, pelvis; pn, preneural.

Medicine Rocks Sandstone, a unit that was originally mapped as part of the Tongue River Member of the Fort Union Formation. More recent work, however, has shown that the Medicine Rocks Sandstone is bounded by unconformities and it has thus been designated as its own unit, now called the Ekalaka Member of the Fort Union Formation (Belt et al. 2002). YPM PU 16781 is from "Locality 1," which Sloan (1970) grouped with

other localities into an assemblage named Medicine Rocks I. A tentative Torrejonian 3 age is typically given on the basis of the mammalian assemblage found at that site (e.g., Lofgren et al. 2004). The exact locality of the holotype is uncertain and the specimen thus could have originated from anywhere within the Ekalaka Member. Given that the Ekalaka Member only contains pollen of the Pollen Zone 3 (Belt et al. 2002), we tentatively

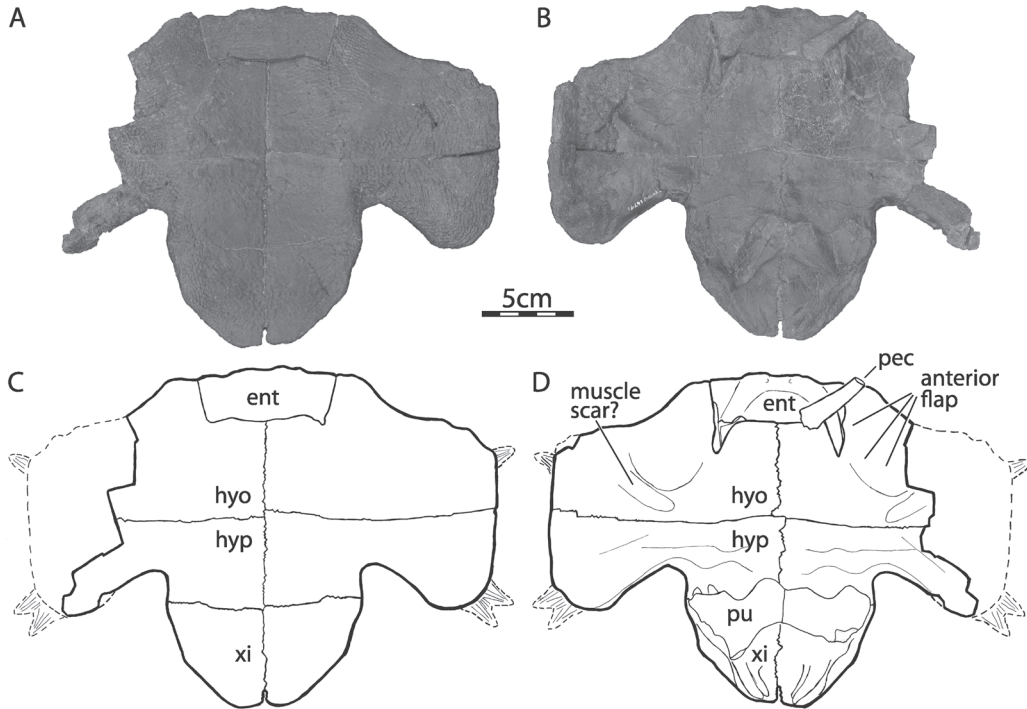


FIGURE 3. YPM PU 16795, holotype of *Hutchemys rememidium* sp. nov. **A.** Ventral view of plastron. **B.** Dorsal view of plastron. **C.** Ventral view of plastron. **D.** Dorsal view of plastron. *Abbreviations:* ent, entoplastron; hyo, hyoplastron; hyp, hypoplastron; pec, pectoral girdle; pu, pubes; xi, xiphiplastron.

assign the holotype to the Torrejonian in general. The partial carapace YPM PU 14985 was collected from Cedar Point Quarry in Wyoming and the associated mammals allow attribution to Tiffanian 3 (Lofgren et al. 2004).

Description. *Carapace.* The carapace of the holotype, YPM PU 16795, is remarkably well preserved, with only the distal halves of the right costals 2 through 4 missing (Figure 2). The sculpturing is clearly visible on the dorsal surface and all sutures are visible. Most of the bony disk is intact, and thoracic vertebrae 1 through 9 remain in articulation with the ventral surface of the carapace. The distal ends of costal ribs 1 to 3 and 5 to 7 are visible in dorsal view, protruding from the left side of the carapace, although most are broken or worn. Postcranial elements of the skeleton, including two cervical vertebrae, one intact manus with associated radius and ulna, the articulated right shoulder girdle, the partially complete left shoulder girdle, and the pelvic girdle are preserved in articulation with the carapace. The two prongs from the lateral edge of the left hypoplastron broke off and are now attached to the right edge of costal 5, between costal ribs 4 and 5. In contrast, the referred carapace YPM PU 14985 consists of the well-preserved posterior half of a carapace, including costals and neurals 4 through 8 (Figure 4A–D).

The length of the holotype carapace is approximately 290 mm along the midline and is thus notably smaller than all available specimens of *Hutchemys arctochelys*, but significantly larger than *Plastomenus* aff. *thomasii*, which is approximately 220 mm (Hay 1908). YPM PU 14985 is about 10% smaller than the holo-

type. Although we are unaware of any studies that clarify how to assess the ontogenetic stage of trionychid turtles, we note that the astragalus and calcaneum are fused and thus the holotype seems to represent a fully-grown specimen.

The carapace of the holotype is oval, posterolaterally convex, and has a distinct, squarish pygal notch (Figure 2). The type and the referred carapace are well enough preserved to reveal that the carapace is higher domed than in extant *Apalone*, but less than in extant *Lissemys*. The ratio of maximum length to width is approximately 1.2:1. The dorsal side of the carapace displays the distinct sculpturing characteristic of trionychids. This sculpturing consists of a pattern of interlocking ripples that roughly follows the outline of the carapace margin. These ripples are small, low profile ridges with smooth apices, many of which connect to form a network of irregularly spaced ripples. The pattern is more unidirectional on the sides of the carapace, where it runs anteroposteriorly. The sculpturing is most prominent around the perimeter of the carapace. Moving inward from the perimeter, the pattern remains distinct up to about two-thirds from the edge of the carapace, where the ripples become less pronounced and eventually fade altogether as they approach the neurals.

A distinctive feature of *Hutchemys rememidium* is the split margins of the costals, best seen in the holotype (Figure 2E). This split is the result of the formation of a projecting lip around the perimeter of the dorsal and ventral surfaces of the costals, with an indented groove between the two edges. The protruding distal ends of the costal ribs are included in the visceral lip.

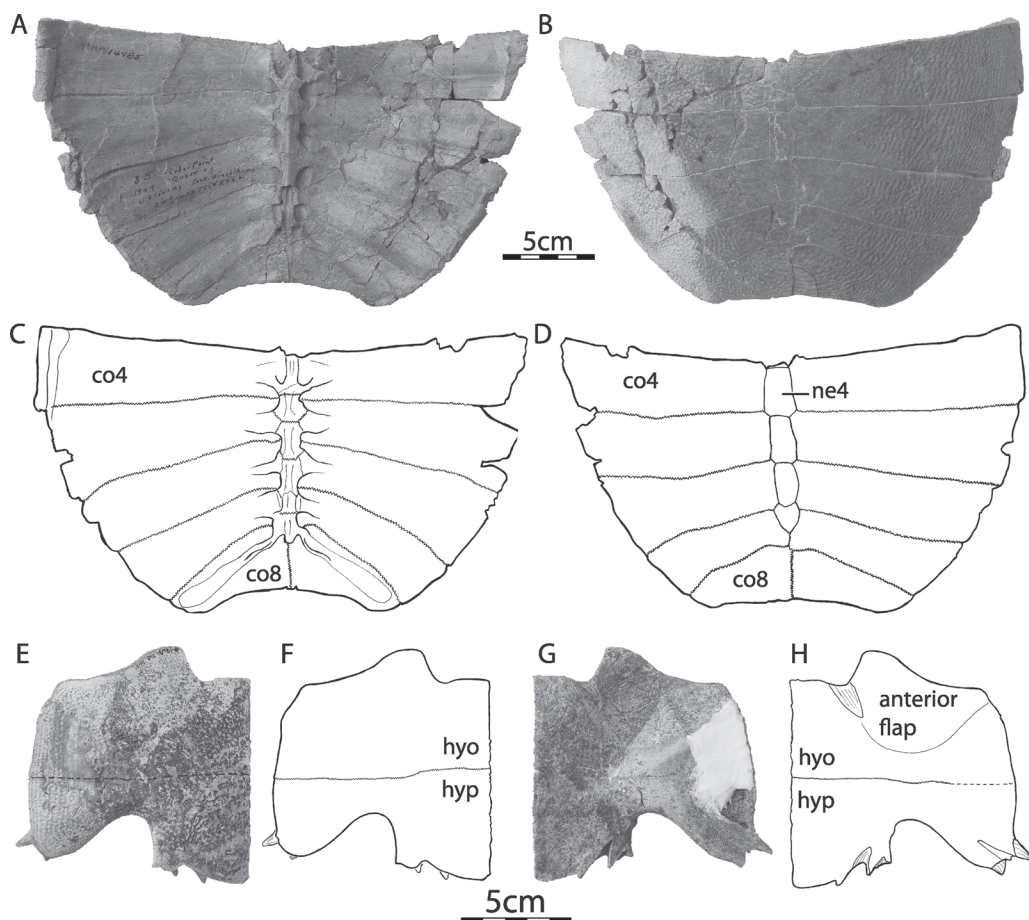


FIGURE 4. Paratype of *Hutchemys rememidium* sp. nov. **A.** YPM PU 14985, ventral view of carapace. **B.** YPM PU 14985, dorsal view of carapace. **C.** YPM PU 14985, ventral view of carapace. **D.** YPM PU 14985, dorsal view of carapace. **E.** YPM PU 16781, ventral view of right hyo/hyoplastron. **F.** YPM PU 16781, ventral view of right hyoplastron–hyoplastron. **G.** YPM PU 16781, dorsal view of right hyoplastron–hyoplastron. **H.** YPM PU 16781, dorsal view of right hyoplastron–hyoplastron. *Abbreviations:* co, costal; ne, neural; hyo, hyoplastron; hyp, hypoplastron.

The split originates along the middle of costal 1, is intensely developed from costals 2 to 5, and terminates along the middle of costal 7. The posterior border of costal 8 displays a simple rounded edge that is noticeably thinner than the rest of the carapace margin, except for the nuchal region closest to the midline. Split edges are also apparent in *H. arctochelys*, but the distribution is different (see below).

Nuchal. The nuchal is broad and deeply inset into the carapace for most of its length (Figure 2). The lateral tips of the nuchal extend for 10 mm as gently curved projections that protrude slightly from the front of the carapace. The nuchal is rather unique relative to other trionychids in that it is crescent-shaped, because of an extremely deep nuchal notch. The nuchal notch is only poorly developed in *Hutchemys arctochelys* and absent in *Plastomenus* aff. *thomasi*. The ratio of width to length of the nuchal bone in the holotype is approximately 5:1. The nuchal bone is approximately 129 mm wide when measured at its

greatest width, and the length from the anterior edge to the first neural is approximately 25 mm. A distinct ridge is developed along the posterior contact with costal 1, but there is no indication that this ridge was once expanded to form a second costiform process, as in Cyclanorbinae. The relative position of the anterior edge of the first thoracic vertebra to the nuchal is obscured. There is no evidence of a prenuchal bone, suprascapular fontanelles, or even suprascapular pits (i.e., an indication of suprascapular fontanelles that were closed by a thin sheet of bone). Given that no plastomenine has yet been described with suprascapular fontanelles, we presume that these were generally absent.

Neurals. A preneural and seven clearly defined neurals are preserved in the holotype, YPM PU 16795, whereas YPM PU 14985 only preserves what seem to be the posterior four elements (Figures 2, 4A–D). A fine but clear suture divides the well-developed preneural from the reduced, rounded neural 1.

Neural 2 is the longest neural element and is octagonal in outline, a distinctive feature of *Hutchemys rememidium* and *H. arctochelys*. Another reversal of the neural orientation occurs at neural 6, which has a slightly distended rectangular shape and slightly convex anterior and posterior sides. Neurals 3 through 5 are hexagonal with the short sides situated posteriorly. Neural 7 is pentagonal and distinctly wider than neural 6. Many other species of trionychids show great variability in their neural counts and the placement of the neural reversal (Meylan 1987; Gardner and Russell 1994). However, we note that the neural count and development is identical among the four specimens of *Hutchemys* available to us.

Costals. Eight pairs of costals are present, which display a slight widening toward the margin of the carapace (Figures 2, 4A–D). The costals are ossified along almost the entire length of the underlying ribs. The shape of costals 1 is unique, because of the deeply indented nuchal, which encroaches on their anterior edge (Figure 2A, C). The result is that the anterior margin of costals 1 is concave and follows the curvature of the nuchal. Costals 2 and 3 display a reduced degree of concavity compared to costals 1, and costals 4 extend laterally from the neurals in a straight line. After costals 4, the direction of curvature is reversed, and the costals become more convex with respect to the anterior margin of the carapace. This creates the oval shape of the carapace, which terminates in a pair of well-developed and triangular costals 8. Costals 7 partially contact one another along the midline, whereas costals 8 contact one another fully. Unlike *Hutchemys arctochelys*, costals 8 are wider than long. The articulated pelvis of the holotype reveals that costals 8 were developed well enough to roof the ilium, as is seen in Cyclanorbinae. However, unlike cyclanorbines, there is no evidence of a depression for the attachment with the ilia in either specimen (Figure 4C).

Plastron. The plastron of the holotype, YPM PU 16795, is generally well preserved, but epiplastra and much of the right portion of the hyo- and hypoplastra and the dorsal surface of the left hyo- and hypoplastra are missing (Figure 3). The distal ends of the left hypoplastral processes are broken, perhaps from compaction, and are now preserved attached to the carapace (Figure 2). Parts of the pectoral and pelvic girdle remain attached to the visceral surface of the plastron. The referred plastron of YPM PU 16781 is also well preserved, but only consists of the right hyo- and hypoplastron (Figure 4E–H). In the holotype, the sculpturing on the ventral surface of the plastron is similar to that of the carapace in structure, but the pattern is much finer and thus less pronounced. The ripple pattern is most recognizable around the perimeter, but soon becomes completely effaced towards the center. The anteriormost and posteriormost regions of the plastron have a shallow punctate pattern made up of tiny circular impressions. These quickly fade moving toward the hypo-xiphial union from either direction. The bridge region displays the most prominent patterning. In the holotype the pattern resembles the ripple-like pattern observed on the carapace, but it is more disorderly and less distinct, especially towards the middle of the plastron. In the referred specimen, YPM PU 16781, the pattern resembles rows of fine circular impressions. The plastron of the holotype is approximately 195 mm long (excluding the epiplastra) and 240 mm wide. The referred specimen is significantly smaller, by about 20%. Since the epiplastra are missing from the specimen, the number of plastral callosities cannot be determined with confidence. However, Holroyd and Hutchison (2002, fig. 2K) figured a plastron

of *Hutchemys* sp. with extremely well-developed callosities on the epiplastra, the specimens discussed by Kays et al. (1996) have epiplastral callosities, and we thus feel justified in speculating that *Hutchemys rememidium* had seven callosities as well, using the counting method of Meylan (1987). The bridge is well developed relative to other trionychids because of the development of a large anterior hyoplastral flap (see below).

Entoplastron. The entoplastron is only preserved in the holotype, although much of its outline can be discerned in YPM PU 16781 (Figures 2, 4E–F). When viewed from the ventral side, the entoplastron is roughly rectangular, with a length of 30 mm and a width of 80 mm. The medial portion of the anterior edge of the entoplastron has a shallow sinuous curve that slightly protrudes from the rest of the entoplastron. The lateral margins of the entoplastron are straight, but converge slightly towards the posterior. The posterior edge features a medial portion with a shallow convex curve flanked by a short, straight segment on each side. The posterior edge of the entoplastron also seems to be raised from the rest of the ventral surface of the plastron, but this feature could be an anomaly resulting from crushing and we presume that the entire plastron once was flush.

In dorsal view, the deep inset of the entoplastron is more striking. As with many other portions of the trionychid shell, a deeper laminar portion can be discerned from the more superficial ossified dermis (i.e., metaplastic bone). Despite the massive rectangular outline of the dermal component, a boomerang-shaped entoplastron is apparent in dorsal view, which generally resembles the entoplastron of trionychids. Similar observations can be made for the hyoplastron, where the typical, slim outline of this element, as seen in other trionychids, is elevated relative to an anterior flap. The original boomerang portion of the entoplastron is less angular than in other trionychids, but rather forms a rounded crescent. The anterior edge is flat and expanded and forms the anterior protrusions that are visible in ventral view. The two lateral side branches curve posteriorly and their distal ends lie against the anterolateral portion of the hyoplastron, as in other trionychids. However, the large anterior flap of the hyoplastron fully encloses the entoplastron laterally and forms a suture with the metaplastic portion of that element thus rendering the entoplastron completely immobile relative to the hypoplastra (Figure 3B, D). This feature is unique for representatives of *Hutchemys*.

Hyoplastron and hypoplastron. The hyoplastron and hypoplastron both have well-developed callosities and are sutured, but not fused, to one another along their entire length. As described above (see entoplastron), there is a faint, though clear, contoured line that starts at the posterior end of the entoplastral processes and extends laterally towards the end of the hyoplastron on the dorsal surface, which mimics the outline of the hyoplastron in other trionychids (Figures 3B, D; 4G, H). The line is concave with respect to the anterior edge of the plastron, and curves deeply into the hyoplastron before curving upward and outward along its lateral extension. Anterior to this line, the hyoplastron forms an expansive “flap” that widens the bridge and reaches anterior to fully lock in the entoplastron.

Another surface feature on the visceral side of the hyoplastron is a pair of shallow but wide grooves in the bridge region behind the aforementioned contour line that perhaps are muscle attachment sites (Figure 3B, D). The grooves start on the upper distal portion of the hyoplastron and extend posteriorly at an angle toward the hyo-hypoplastral union. The end of the groove approaches the suture about halfway along its length,

but does not come into contact with the suture. Two additional, subtle contour lines are apparent on the dorsal surface of the hypoplastron with a subtle wave-like profile (Figure 3B, D). These lines run roughly parallel across the hypoplastron approximately 1.5 cm apart. The anterior of these lines follows the lateral extension of the plastron just above where the two xiphiplastral processes are integrated into the hypoplastron. The line quickly fades as it diverges from the midline of the plastron. This contour takes the form of a slightly raised line. The second line is wavier than the first, and instead of a raised line it consists of a slight depression along the posterior portion of the hypoplastron. The line spans the width of the hypoplastron right under the first line, and terminates where it follows the lateral extension of the posterior process.

The bridge portions of the hyoplastra and hypoplastra are not well preserved in either specimen. Yet, the space between the damaged lateral processes of the hyoplastron and two distinct lateral processes of the hypoplastra are completely filled by metaplastic callosities. However, whereas it is unclear to us whether the lateral processes of the hyoplastron protruded laterally, the distal ends of the two hypoplastral processes are free (Figures 2 and 3). Other processes are nearly fully obscured, although a single pair of medial processes of the hypoplastron is hinted at in visceral view. The lateral aspects of the plastron are only poorly preserved in the holotype specimen. Given that the lateral edge is greatly thickened in the holotype specimen but not in the paratype plastron, apparently some type of peripheral ossification occurs in larger individuals. Whether the dermal pattern was expressed on the dorsal side of the plastron, as is seen in *Hutchemys arctochelys*, is unclear.

Xiphiplastra. The xiphiplastra have large callosities and are in full sutural contact with the hypoplastron anteriorly (Figure 3). The dorsal suture joining the two hypoplastra to the xiphiplastra is obscured by the remains of the pubis in the holotype, but is clearly visible in the referred specimen, YPM PU 16781. In ventral view, the suture is nearly linear in the holotype and slightly sinuous along the lateral edge in the referred specimens. However, in dorsal view, the suture is straight along the medial half, but the xiphiplastron produces two processes that protrude deeply into the hypoplastron thus locking the joint (Figures 3B, D; 4E–H). As in *Cyclanorbinae*, the most lateral aspect of the contact is formed by a process from the hypoplastron. Medially, the xiphiplastra contact one another along a straight suture. As with the other plastral elements, though much more faintly, it is possible to distinguish between a superficial metaplastic layer and deeper structures consisting of processes. As in other trionychids, these indicate that the xiphiplastra contact one another along a posterior pair of forked and interdigitating processes.

Vertebrae and girdles. Only the holotype preserves non-shell postcranial remains (Figures 2A, C; 3B, D). On the anterior portion of the ventral surface of the carapace, the left shoulder girdle is nearly fully preserved with the acromion processes, coracoid and scapula intact. The fully articulated left manus, radius, ulna and humerus were separated from the shoulder girdle and are not in contact with the carapace. The right forelimb is dislocated and less complete. The elements of the right shoulder girdle are missing, and the humerus, radius and ulna extend from the right side of the carapace across to the left side, where the phalanges of the right manus lie below the left shoulder girdle. Two dislocated cervical vertebrae are preserved in contact with the forelimbs and the first thoracic vertebra, obscuring the

region immediately posterior to the nuchal bone up to the second body vertebra. The ischium and the lower parts of the pubis lie below costal 8 and contact the sacral vertebrae posteriorly. Parts of the ilia are also present and are in contact with the carapace. The ischium is joined at the middle, and it can be observed on the plastron where the rest of the pubis is preserved that the interpubic suture is also roughly situated along the midline. The sockets for the attachment of the hind limbs are visible, but the limbs themselves, though articulated, were not preserved in contact with the pelvic girdle. The two hind limbs, including femur, tibia, fibula, metatarsals, tarsals and phalanges, are complete except for the absence of some claws and phalanges. A few caudal vertebrae extend beyond the posterior edge of the carapace, although they are not in contact with the surface of the carapace itself.

Vertebrae and ribs. Only two poorly preserved cervical vertebrae are preserved in the retracted position (Figure 2). The eighth is partially covered by a limb and only the posterior half of the seventh is preserved. From what can be seen, the eighth resembles that of other trionychids, in particular in lacking a well-formed posterior central articulation and by having well-developed postzygapophyses. However, the vertebrae are too damaged to discern any other morphology, including the development of ventral processes.

The thoracic vertebrae are in good condition except for some minor damage to the first two vertebrae. As in all trionychids, they possess strong lateral contacts with the rib heads and contact two ribs each. With exception of the ninth thoracic ribs (the ribs of costals 8), all ribs have well-developed heads. The ninth ribs have relatively reduced heads, but distally the ribs are as well developed as the more anterior ones. The 10th thoracic rib is fully reduced and two pairs of sacral ribs are present.

Pectoral girdle. The left pectoral girdle is complete but crushed (Figures 2A, C; 3B, D). The acromion, scapula and coracoid can be distinguished and are articulated with minimal breakage. The right coracoid is slightly chipped along its edge, but the laterally flared extension of the bone is mostly intact. It is not possible to establish the relative length of the three pectoral processes, because all are damaged distally. Also, because of the compression and warping of the pectoral girdle during preservation, the angles between the different elements cannot be assessed accurately.

Pubis and ischium. The pelvis is only poorly preserved, with parts remaining attached to the plastron and carapace and other remaining free (Figures 2A, C; 3B, D). Clearly, however, there is significant separation between this anterior portion of the pubis and the ischium across the open thyroid fenestra, the ischia do not introduce into the thyroid fenestra, and the pectineal processes and the interpubic suture lay in the same plane. Metischial processes are present and distinct on this specimen. The pair of processes extends posteriorly from the ischium and a slight concavity forms on the outline of the ischium on either side of the processes. The ilia are attached to the carapace as well as the rest of the pelvic girdle. It is difficult to make out any medial curvature along the ilia because of their orientation, although “thelial processes” are present (see Joyce 2007 for discussion of thelial processes).

Appendicular skeleton. No characters that pertain to the long bones have been described so far for trionychid turtles and we cannot find any significant variation. Unfortunately, no manus or pes is well enough preserved to determine the phalangeal formula or the count of claws.

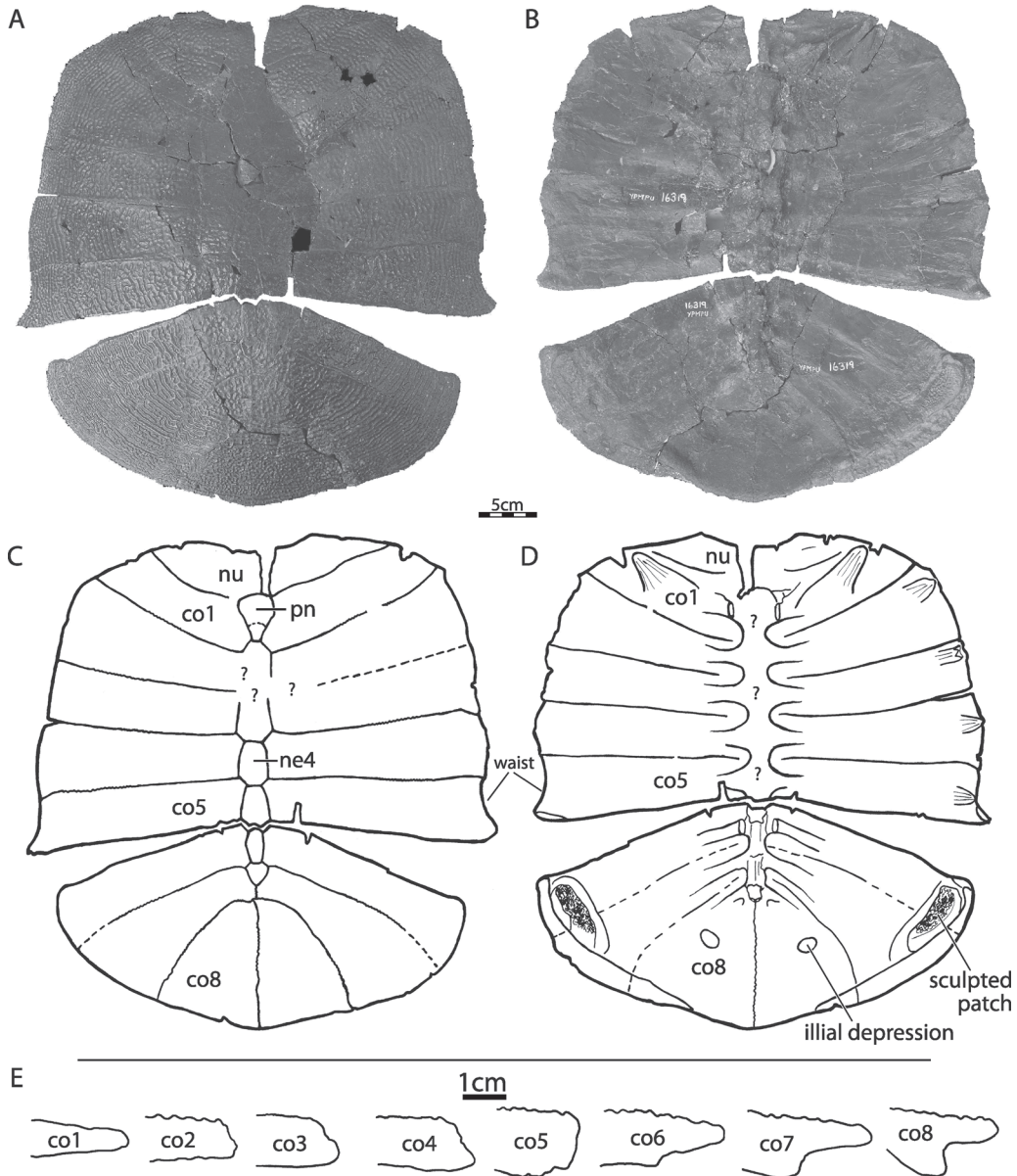


FIGURE 5. YPM PU 16319, holotype of *Hutchemys arctochelys* sp. nov. **A.** Dorsal view of carapace. **B.** Ventral view of carapace. **C.** Dorsal view of carapace. **D.** Ventral view of carapace. **E.** Illustrations of the right margins of costals 1 to 8. *Abbreviations:* co, costal; ne, neural; nu, nuchal; pn, preneural.

Hutchemys arctochelys Joyce, Revan,
Lyson and Danilov sp. nov.
Figures 5–9

Etymology. *Arctos* and *chelys*, Greek for bear and turtle, respectively, in reference to the type locality at Bear Creek.

Holotype. YPM PU 16319, a nearly complete carapace (Figure 5).

Paratypes. YPM PU 16320, nearly complete carapace (Figure 6); YPM PU 16321, nearly complete plastron lacking epiplastra (Figure 8); YPM PU 16322, nearly complete plastron lacking epiplastra (Figures 7A–D, 9); YPM PU 16238, partial plastron consisting of left hyoplastron, left xiphiplastron, and a partial left hypoplastron (Figure 7E–H) and various costal fragments. All paratypes were recovered from the same quarry as the holotype.

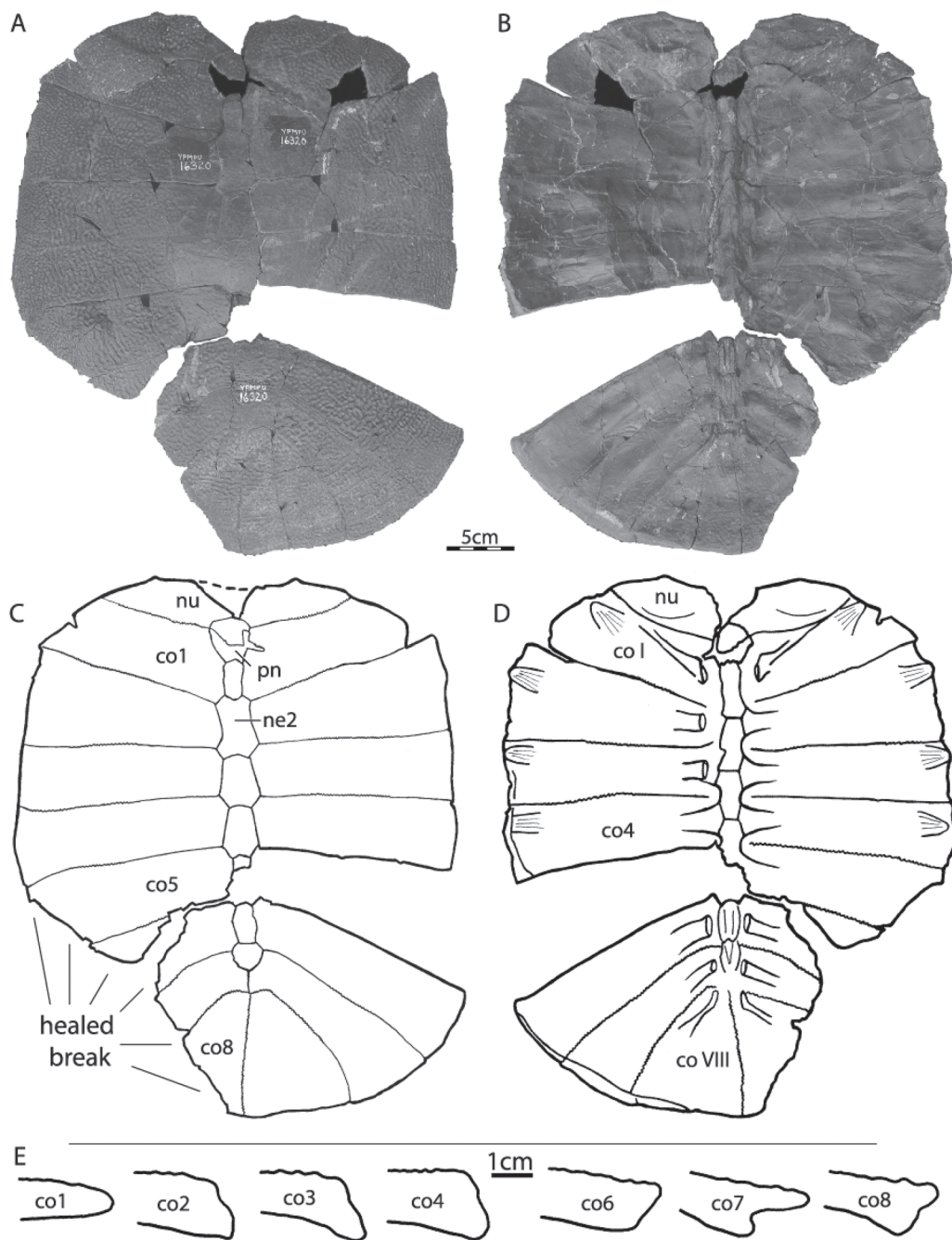


FIGURE 6. YPM PU 16320, paratype of *Hutchemys arctochelys* sp. nov. **A.** Dorsal view of carapace. **B.** Ventral view of carapace. **C.** Dorsal view of carapace. **D.** Ventral view of carapace. **E.** Illustrations of the right margins of costals 1 to 4 and 6 to 8. *Abbreviations:* co, costal; ne, neural; nu, nuchal; pn, preneural.

Type locality and horizon. Burns Mine, Washoe Area, Carbon County, Montana, USA; Tongue River Member, Fort Union Formation (Clarkforkian 1).

Diagnosis. *Hutchemys arctochelys* nov. sp. is diagnosed by the following list of autapomorphies and at the same time distin-

guished from *Hutchemys rememidium* sp. nov.: neural 1 elongate and subrectangular; carapace with a distinct waist at level of costals 5; costals 2 to 4 (sometimes costal 5) split evenly but costals 6 to 7 (sometimes costal 5) split asymmetrically with a greater dorsal than ventral aspect; limited surface sculpturing developed on visceral surfaces of costals 6 and 7 in some indi-

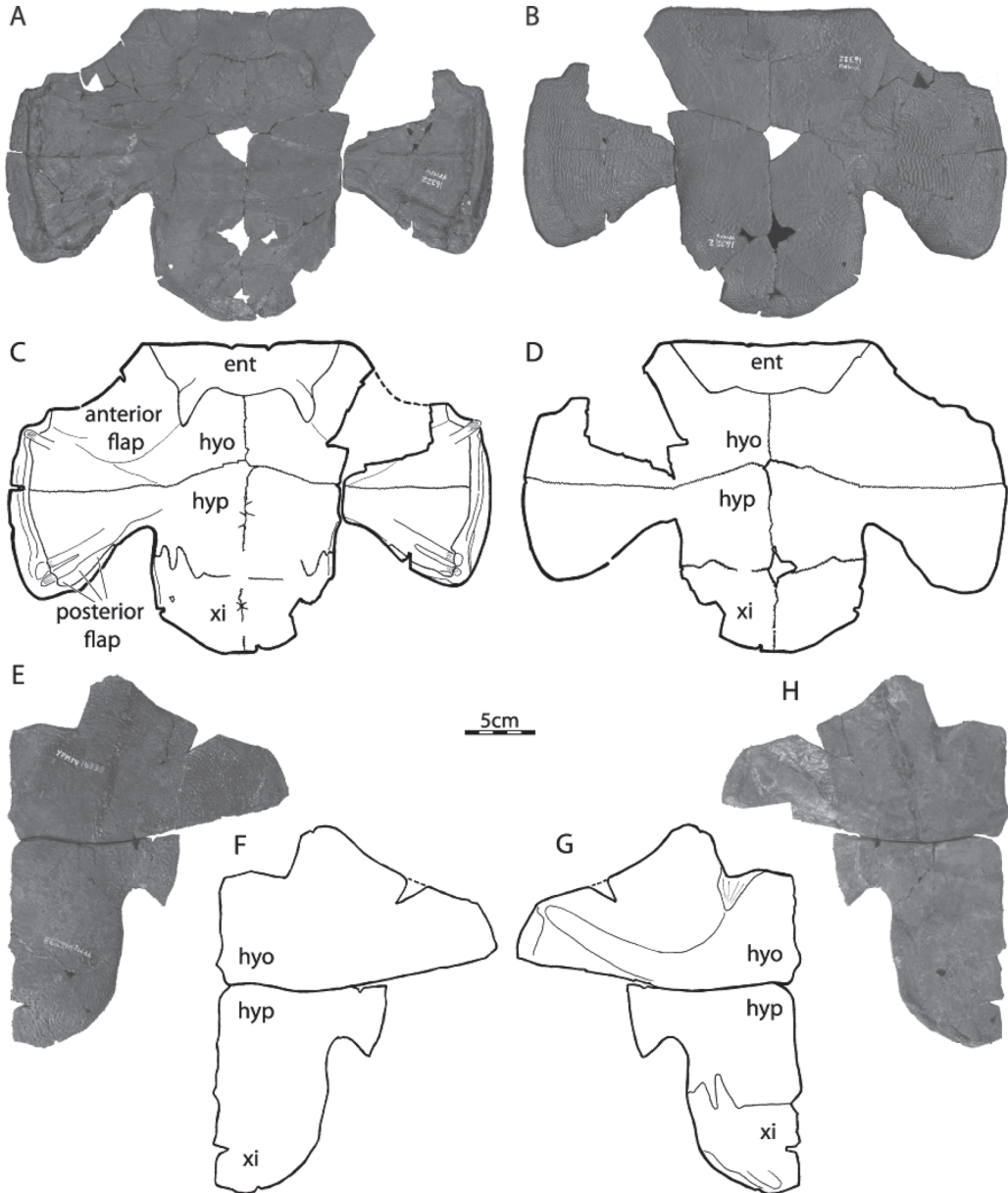


FIGURE 7. YPM PU 16322, paratype of *Hutchemys arctochelys* sp. nov. A. YPM PU 16322, dorsal view of plastron. B. YPM PU 16322, ventral view of plastron. C. YPM PU 16322, dorsal view of plastron. D. YPM PU 16322, ventral view of plastron. E. YPM PU 16238, ventral view of partial left plastron. F. YPM PU 16238, ventral view of partial left plastron. G. YPM PU 16238, dorsal view of partial left plastron. H. YPM PU 16238, dorsal view of partial left plastron. *Abbreviations:* ent, entoplastron; hyo, hyoplastron; hyp, hypoplastron; xi, xiphiplastron.

viduals; posterior flap of hypoplastron present. Furthermore, this taxon also has the following combination of characters: pygal notch absent, costals 8 longer than wide, ilial depression present on visceral side of costals 8 (generally found among cyclanorbines and other plastomenines); neural 3 octagonal (synapomorphy with *Hutchemys arctochelys*).

Remarks. All specimens referred to *Hutchemys arctochelys* originate from a single quarry that also produced remains of *Titanoides* spp., a rather complete skeleton of *Champsosaurus* sp. and multiple partial skeletons of a macrobaenid turtle. The locality is part of the Bear Creek Local Fauna and is attributed to the Tiffanian 1 (Lofgren et al. 2004).

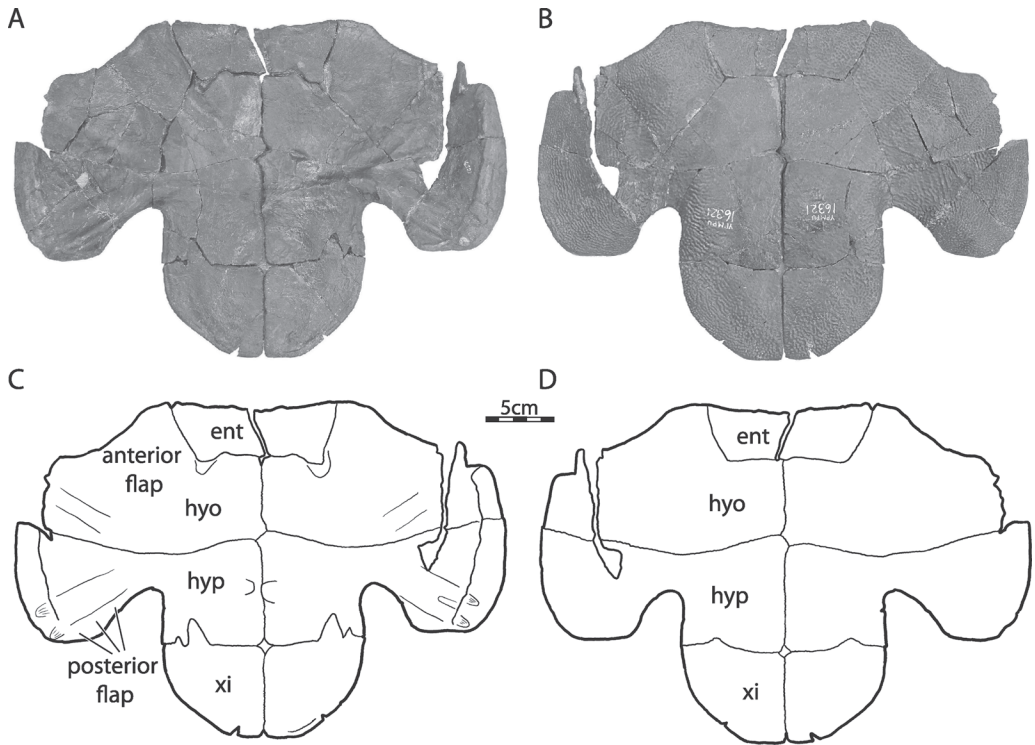


FIGURE 8. YPM PU 16321, paratype of *Hutchemys arctochelys* sp. nov. **A.** Dorsal view of plastron. **B.** Ventral view of plastron. **C.** Dorsal view of plastron. **D.** Ventral view of plastron. *Abbreviations:* ent, entoplastron; hyo, hyoplastron; hyp, hypoplastron; xi, xiphoplastron.

Description. *Carapace.* The carapace of the holotype, YPM PU 16319, is well preserved and only lacks small fragments that were lost during recovery (Figure 5). One of the paratype specimens, YPM PU 16320, at first sight seems to have lost much during recovery, because parts of the nuchal and neural 5 and right costal 5 are missing (Figure 6). However, even though significant distal portions of the left costals 5 through 8 are absent, the extension of trionychid-like sculpturing along the margins clearly reveals that these portions were lost during life, perhaps to an attack by a large crocodylian, and that the wound later healed. The sculpturing is easily visible on the dorsal surface and the sutures are generally clear. Some of the thoracic vertebrae remain in articulation, but they are generally poorly preserved.

The carapacial length of both the holotype and the paratype YPM PU 16320 is approximately 360 mm along the midline and is thus significantly larger than most described plastomenines, though smaller than the alleged plastomenine *Helopanopia distincta*. We are unable to assess the ontogenetic stage of these individuals. However, the large size combined with the fact that all individuals seem to be of the same size suggests that these are adult animals. All ribs end approximately at the same level as the more superficial costal callosities and are not visible in dorsal view. The outline of the carapace is generally oval, but a strange waist occurs at the level of the fifth costal, which is clearly preserved in both sides of the holotype, but not preserved in the paratype carapace. Only a shallow nuchal notch is present and a pygal notch is completely absent. The ratio of

maximum length to width is approximately 1.1:1, but this ratio is clearly much greater in life, because both carapaces are fully flattened.

The sculpturing on the dorsal surface of the carapace of both specimens greatly resembles that of *Hutchemys rememidium*, a pattern of interlocking ripples that roughly follows the outline of the carapace margin. However, the ripples dissipate less quickly toward the center of the carapace.

As in *Hutchemys rememidium*, *Hutchemys arctochelys* often has well developed “split margins,” but the distribution along the carapacial rim is different (Figures 5E, 6E). The margin of the nuchal and costals 1 is rounded and regular. In the holotype (Figure 5E) a symmetric split margin, i.e., a split margin where the dorsal protrusion is roughly equal to the ventral protrusion, is developed along nearly the entire length of costal 2, all of costals 3 and 4, and almost the full length of costal 5. At the end of costal 5, right at the level of the carapace’s waist, the margin starts to split asymmetrically, in that the dorsal portion is significantly better developed than the visceral portion. This asymmetry is continued for the full length of costals 6 and 7. The margin of costal 8 starts asymmetrically, turns symmetric halfway, and then loses the split for the posterior quarter. The margin is generally developed in the same way in YPM PU 16320, but costal 6 is symmetrically split (Figure 6E).

Nuchal. The nuchal is very broad, fully inset into the carapacial disk, and only displays a poorly developed and rather

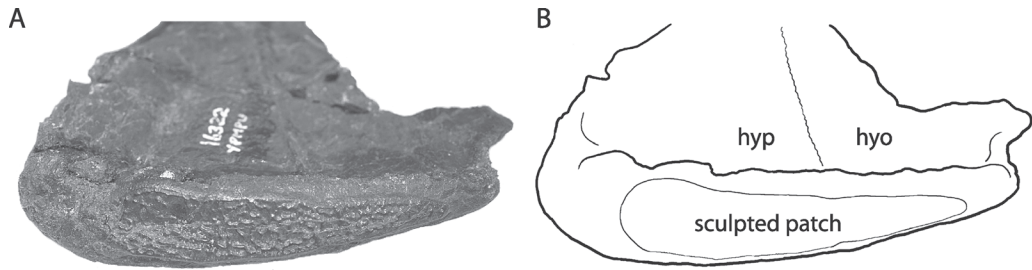


FIGURE 9. YPM PU 16322, paratype of *Hutchemys arctochelys* sp. nov. A. Right dorsolateral ventral view of right peripheral ossification of plastron. B. Right dorsolateral ventral view of right peripheral ossification of plastron. Abbreviations: hypo, hyoplastron; hyp, hypoplastron.

narrow anterior notch (Figures 5, 6). The ratio of width to length is approximately 5:1 in the holotype (35 mm deep and 180 mm wide) and 7:1 in the paratype carapace (estimated at 25 mm deep, because the anterior margin is broken, and 170 mm wide). A distinct ridge is developed where the nuchal contacts the first costal rib, but there is no evidence of a split costiform process. The first thoracic vertebra is absent and the relative position of its anterior margin to the nuchal cannot be estimated. No evidence is available for the presence of a pre-nuchal bone or the former presence of suprascapular fontanelles.

Neurals. The general count and development of the neural column in both specimens of *Hutchemys arctochelys* is generally similar to that of *H. rememidium* described above (Figures 5 and 6). In particular, the column consists of a large, anteriorly expanded preneural, an elongate and narrow neural 1, a distinctly elongate and octagonal neural 2, hexagonal neurals 3 through 5 with short posterior sides, elongate rectangular neurals 6, and a pentagonal neural 7. The total neural count (sensu Meylan 1987) is eight neural elements, including the preneural. The preneural is partially missing in the paratype specimen YPM PU 16320, thus exposing neural 1 anteriorly. The contact is strongly slanted towards the posterior, indicating that the preneural overlaps onto neural 1, thus making it seem smaller than it actually is below.

Costals. The number and development of the costals generally resembles that of *Hutchemys rememidium* (Figures 5 and 6). The complex split margin of the carapace is described above. Nevertheless, there are three notable differences. First, as mentioned above, the ribs are nearly fully enveloped by the overlying dermal bone and are thus not visible in dorsal view. Second, on the visceral side of costals 6 and 7 of the holotype specimen, patches are apparent near the margin of the specimen that correspond fully to the classic crenulated surface pattern of trionychid shell bones (Figure 5B, D). These patches are distinctly symmetrical in the holotype specimen, but are lacking completely in the paratype specimen YPM PU 16320. The patches are approximately 5 cm long, oval, and run parallel to the margin of the shell while fully straddling the suture between the sixth and seventh costal. Given that we are unaware of any other trionychid having surface sculpturing on the visceral side of the carapace, we do not have an immediate explanation. However, considering that the crenulated areas are situated within the deepest fold of the inguinal notch, it is possible that

the carapace is so greatly thickened in this area that it actually ossified the skin fold of the inguinal notch on the ventral side. It is unclear to us, however, why this feature is missing in the paratype specimen. The third difference pertains to the development of costals 8. In contrast to many other trionychids, including *H. rememidium*, costals 8 are extremely well developed, being longer than wide. Their midline length approximates the combined midline length of costals 4 through 7, as opposed to the combined midline length of costal 6 and 7 only in *H. rememidium*. As a result, the posterior region of the shell is fully rounded and there is not even a hint of a pygal notch. Furthermore, there is clear evidence of a groove for the ilium (Figures 5B, D and 6B, D), a feature that has mostly been noted for Cyclanorbinae (Meylan 1987).

Plastron. The same quarry that produced the holotype and paratype carapaces, YPM PU 16319 and 16320, also produced two and a half plastra, which are confidently assigned to *Hutchemys arctochelys* on the basis of their size, patterning and the complete lack of any other trionychid material from the same quarry. YPM PU 16321 and 16322 are nearly complete plastra that only lack their epiplastra and fragments that were lost during recovery (Figures 7A–D, 8 and 9). YPM PU 16238 only consists of a left hyoplastron, left xiphiplastron and most of the left hypoplastron (Figure 7E–H). The complete lack of epiplastra is mystifying, but given that other non-shell elements are also missing, it seems that they detached early and were removed from the carcasses. The plastron, excluding the epiplastra, is approximately 240 mm and 225 mm for YPM PU 16321 and 16322, respectively. Because of the lack of an entoplastron and damage to the posterior margin of YPM PU 16238, it is also not possible to measure this specimen, but we estimate that it is approximately 250 mm along the midline. As with *Hutchemys rememidium*, we assume that this taxon once had seven plastral callosities (sensu Meylan 1987).

The sculpturing on the ventral surface of the plastron varies extensively. As with the carapace, and similar to *Hutchemys rememidium*, the pattern is generally lost towards the center of the plastron. Along the rim of the posterior lobe, the pattern consists of unevenly placed, polygonal fields that connect to form an irregular netted pattern. The anterior plastral lobe, in contrast, has a pattern of irregularly placed pits that form a more regular network. The lateral halves of the bridges

display the most prominent pattern, ridges that run parallel to the lateral margin.

Entoplastron. In ventral view the entoplastron varies in shape between specimens (Figures 7 and 8). From what can be inferred, the entoplastron of YPM PU 16238 resembled that of *Hutchemys rememdium* by having straight margins that bow outward slightly toward the front. The two preserved entoplastra of YPM PU 16321 and 16322 expand much more significantly toward the anterior. The best preserved entoplastron, that of YPM PU 16321, is 38 mm deep and 135 mm wide at the anterior rim. The anterior margin is generally straight, but there is variation in the sinuosity of the posterior margin.

The dorsal aspect of YPM PU 16321 is completely homogenous, but that of YPM PU 16322 resembles that of *Hutchemys rememdium* in that the extremely faint outlines of the boomerang-shaped deeper portions of the entoplastron are visible relative to the more superficial metaplastic portions. As with the other species, the metaplastic portion of the entoplastron is laterally flanked by an anterior flap that is produced by the hyoplastron. Furthermore, deeper portions of the hyoplastron envelop the posterior entoplastral processes, thus fully immobilizing that element relative to the rest of the plastron.

Hyoplastron and hypoplastron. The hyoplastron and hypoplastron have extensive callosities and are sutured, but not fused, to each other along the midline. As above, the dorsal aspect of the hyoplastron of YPM PU 16321 is homogenous (Figure 8A, C), but the other two specimens show the phantom outline of a regular trionychid hyoplastron (Figure 7A, C, G–H). Anterior to this outline, the hyoplastron forms a massive anterior metaplastic flap that fully surrounds and immobilizes the entoplastron laterally.

The bridge region is unique. As with *Hutchemys rememdium*, the outlines of the lateral processes of both the hyo- and hypoplastra are visible and enough specimens are available to discern their original shape. YPM PU 16238 clearly reveals that the lateral process of the hyoplastron consists of a single prong, whereas the other two specimens clearly show two lateral prongs for the hypoplastron (Figures 7, 8). In both cases, the distal ends of the prongs are always enveloped in metaplastic bone and do not protrude laterally. Conversely, the entire space between the anterior hyoplastral prong and the posterior hypoplastral prongs is filled entirely by metaplastic bone. This webbing of bone apparently extended all the way to the lateral margin of the plastron, thickened, and started to develop a dorsal aspect, which expresses the characteristic skin sculpturing of the remaining parts of the shell (Figure 9). This morphology is often referred to as “peripheral ossification” (e.g., Holroyd and Hutchison 2002). Such peripheral ossification is known for some Cyclanorbinae, particularly *Lissemys* spp., but also occurs in *Helopanoplia distincta* (pers. obs. W. G. Joyce, of uncatalogued specimens housed at UCMP). Posterior to the lateral processes of the hypoplastra, a small posterior flap is developed that is lacking in *H. rememdium* (Figures 7A, C and 8A, C). The phantom remnants of a single medial hypoplastral process are apparent as well. Various other visceral surface ornamentations visible in *H. rememdium* cannot be discerned in any specimen. The relative proportions of the three-preserved plastra are different and much of this seems to be the result of the difference in length of the hypoplastron posterior to the inguinal notch. In YPM PU 16322 this portion of the hypoplastron (as measured parallel to the midline from the inguinal notch to the

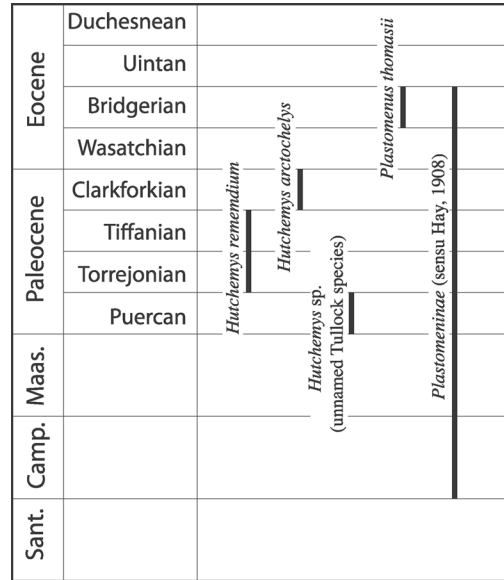


FIGURE 10. The stratigraphic distribution of taxa discussed in the text.

straight portion of the xiphiplastral contact) is only 21 mm, whereas that distance is 38 mm and 45 mm in YPM PU 16321 and YPM PU 16238, respectively. As a result, the latter two plastrons have significantly longer posterior plastral lobes.

Xiphiplastron. The xiphiplastron are in full sutural contact with the hypoplastron anteriorly and with one another medially (Figures 7 and 8). As with *Hutchemys rememdium*, the anterior suture with the hypoplastron shows only a minor sinuosity in ventral view, but in dorsal view two extremely well-developed lateral processes of the xiphiplastron protrude deeply into the hypoplastron. The most lateral aspect of the contact is formed by the hypoplastra, much as in Cyclanorbinae. Unlike *H. rememdium*, no remains of processes can be discerned in dorsal view.

Discussion

Phylogenetic Considerations

The preliminary phylogenetic analysis of Joyce and Lyson (In press) revealed that *Plastomenus* aff. *thomasi* should be considered a representative of the cyclanorbine stem group, but the question remains unanswered whether plastomenines are a monophyletic side branch of the cyclanorbine stem lineage or form a paraphyletic segment of that lineage. The latter arrangement would imply a more complex biogeographic history, in which the main lineage leading up to the crown group moved from Asia to North America and back to Asia again (Joyce and Lyson, In press).

Our phylogenetic analysis reveals that *Hutchemys* is monophyletic and placed as sister to *Plastomenus* aff. *thomasi*. Characters that support this hypothesis include: nuchal at least four times wider than long; single costiform processes (in DELTRAN); fusion of xiphiplastra (in DELTRAN); midline contact of hyoplastra, hypoplastra and xiphiplastra; and deep portion of entoplastron wide and rounded. Considering that the two new species described here, *Hutchemys rememdiium* and *H. arctochelys*, are morphologically rather disparate from *Plastomenus* aff. *thomasi*, this result provides some credence to the hypothesis that Plastomeninae (Plastomenidae sensu Hay 1908) may indeed represent a monophyletic side lineage unique to North America. For characters that support the placement of plastomenines along the phylogenetic stem of Cyclanorbinae, please refer to Joyce and Lyson (In press).

Although our phylogenetic analyses suggest that plastomenines are stem-cyclanorbines, the important question remains which characters can be considered unambiguously diagnostic for a monophyletic Plastomeninae. This is particularly important when assessing fossil trionychids known from less complete material, which is most of the material (Hay 1908). Traditionally, plastomenines were recognized by the higher degree of ossification of the plastron, in particular the partial to complete medial contact of the hyoplastra, hypoplastra and xiphiplastra and the development of hyoplastral shoulders (i.e., the anterior flaps that restrict the entoplastron laterally; Hay 1908). However, Hummel (1929) noted that these characters are also in fully mature individuals of some trionychines, particularly representatives of *Apalone*, but also *Pelodiscus sinensis*. We fully concur with this observation and particularly note the presence of a fully fused plastron and hyoplastral shoulders in adult individuals of *Apalone ferox* (e.g., AMNH 5931). However, our phylogenetic analysis, combined with a review of the North American fossil turtle literature (Hay 1908), reveals that the presence of an evenly rounded, wide entoplastron is unique to this clade. We thus suggest that the shape of the deep portions of the entoplastron are a better diagnostic character for the group, but note that the entoplastron is only rarely preserved in fossils.

Ecological Considerations

Although the material described here is only from the Paleocene, a series of papers indicate that *Hutchemys* (as Plastomeninae type A) occurred during the Maastrichtian as well (Hutchison and Archibald 1986; Holroyd and Hutchison 2002; Hutchison and Holroyd 2003). From our own observations on fragmentary trionychid material, *Hutchemys* seems to be the predominant type of trionychid in the Paleocene and is even known from mass burial sites (pers. obs. W.G. Joyce and T.R. Lyson of materials discussed in Kays et al. 1996). In contrast, this taxon is extremely rare in the Hell Creek Formation. Considering that modern trionychid species often show habitat preferences that restrict them either to large rivers or swamps (Ernst and Barbour 1989), the trend for *Hutchemys* to being rare in the Hell Creek Formation, but common in the Paleocene, correlates with the general shift from riverine to swampy facies during the Hell Creek to Fort Union transition (Murphy et al. 2003). This may indicate that *Hutchemys* preferred swampy habitats.

The carapace of *Hutchemys* generally resembles that of modern cyclanorbines, in that the bony carapacial disk is domed and forms most of the shell. The carapacial disk of trionychines is generally flattened and is only the central portion of a shell that is otherwise formed by leathery tissue (Meylan 1987). Conversely, the plastron of *Hutchemys* is extremely well ossified and even encroaches onto the dorsal aspects of the carapace (Figure 9). This feature is also present in some individuals of *Helopanoplia distincta* and could be evidence of a close relationship of these taxa. Such peripheral ossifications are also known in modern representatives of *Lissemys* spp., but the morphology is different in that the plastron of *Lissemys* spp. extend laterally and curve upward without any apparent thickening. Our phylogenetic analysis indicates that this arrangement is homoplastic. The plastron of *Hutchemys* is unique relative to other trionychids, in that the weak kinesis otherwise present between the entoplastron and epiplastra is converted to a fully kinetic hinge. Although we were not able to identify any epiplastra, the entoplastron and hyoplastra combined form a straight line along which the anterior or epiplastral flap of the plastron could hinge. The broadening of the entoplastron seen in other plastomenines could indicate that a

similar arrangement is developed there too, though not to the same degree as in *Hutchemys*. Meylan (1987) correctly deduced that all outgroups to Trionychidae have well ossified shells and that any reduction should be considered derived within Trionychidae. We nevertheless reason that the heavy ossification seen in plastomenines is secondary. We have one primary reason. In all well-ossified turtles, there are no signs of a differentiation of the plastron into a deep layer and a surficial layer formed by callosities. The development of these features is thus derived. In plastomenines, clear traces of the strap-like deep layers as seen in all other trionychids are always clearly visible. Although it is possible that stem trionychids developed this morphology in anticipation of later reduction and that it was retained in plastomenines, we think it to be significantly more reasonable to presume that these are leftovers from a reduced ancestor. As such, it is clear that plastomenines converged towards the heavily ossified and kinetic shells seen in various other groups of turtles, in particular pelomedusids and testudinoids. At the very least, this convergence can be explained by an increased need for protection against predators and underlines the great plasticity of the turtle shell.

Acknowledgments

We thank Pat Holroyd (University of California Museum of Paleontology), Carl Mehling (American Museum of Natural History), and Matt Carrano (United States Museum of Natural History) for generously providing access to collections in their care to W. G. Joyce and I. G. Danilov. Jacques Gauthier, Tom Near and Natasha Vitek (in alphabetical order) provided useful discussions, and Marilyn Fox helped with photography and preparation. This manuscript improved significantly thanks to comments from Don Brinkman, Jim Gardner, Jim Parham and an anonymous reviewer. Part of this contribution was the summer internship project of A. Revan and was funded by the Yale Peabody Museum of Natural History Summer Internship Program.

Received 16 February 2009; revised and accepted 16 June 2009.

Appendix 1: List of Characters Used in Phylogenetic Analysis

1–66. The first 66 characters are an extraction of characters from Meylan (1987) that are informative for trionychid relationships, including those flagged by Meylan as being autapomorphic for an extant taxon. In sequence, these correspond to the following characters of Meylan (1987): 1, 2, 3, 4, 5, 7, 8, 9, 10, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 23, 24, 25, 29, 32, 34, 36, 41, 42, 46, 48, 49, 51, 53, 54, 58, 59, 60, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 78, 87, 88, 90, 91, 92, 93, 95, 98, 100, 107, 109, 112, 113.

67. Development of surface sculpturing of carapace and plastron: 0 = all metaplastic portions of carapace and plastron have trionychid sculpturing; 1 = trionychid pattern grades towards the center of carapacial and plastral disk to a smooth pattern, as developed in *Hutchemys rememidium* and *Hutchemys arctochelys*.

68. Nuchal notch: 0 = anterior rim of nuchal convex or slightly notched; 1 = anterior rim of carapace with deep nuchal notch, as developed in *H. rememidium*.

69. Shape of neural 1 and 2 (neural 2 and 3 of Meylan 1987): 0 = neurals 1 and 2 hexagonal with short posterior sides; 1 = neural 1 circular to rectangular and neural 2 octagonal, as developed in *H. rememidium* and *H. arctochelys*.

70. Splitting of costals along distal margin: 0 = costal rim rounded or graded; 1 = dorsal rims split into separately protruding dorsal and visceral portions, as developed in *H. rememidium* and *H. arctochelys*.

71. Lateral notch in carapace at the level of costal 5: 0 = absent, lateral carapacial margin rounded; 1 = present, lateral carapacial margin shows a waist, as developed in *H. arctochelys*.

72. Skin callosity developed on the visceral side of costals 6 and 7: 0 = absent, visceral side smooth; 1 = present, visceral side sometimes develops a callosity, as seen in *H. arctochelys*.

73. Mid-line contact of hyoplastra, hypoplastra and xiphiplastra: 0 = hyo-, hypo- and xiphiplastra do not contact another fully, even in adults; 1 = hyo-, hypo- and xiphiplastra contact another fully along the entire mid-line in adults, as developed in *H. rememidium* and *H. arctochelys*.

74. Shape of deep portion of entoplastron: 0 = lateral branches of entoplastron more or less straight and merge anterior at a clear angle; 1 = entoplastron wide and rounded, as seen in *P. aff. thomasi*.

75. Mobility of entoplastron and anterior development of hyoplastron: 0 = lateral branches of entoplas-

tron abut loosely against hyoplastron, anterior rim of hyoplastron develops no anterior flap/shoulder; 1 = lateral branches of entoplastron abut loosely against hyoplastron, but hyoplastron develops an anterior flap/shoulder, as seen in *Plastomenus* aff. *thomasi*; 2 = entoplastron tightly integrated into anterior plastral lobe due to strong development of anterior flap/shoulder, as developed in *H. rememdium* and *H. arctochelys*.

Comment: This character forms a morphocline and may be ordered.

76. Peripheral ossification: 0 = lateral bridge ossification of plastron does not significantly extend beyond the lateral processes of hyo- and hypoplastron; 1 = lateral bridge ossification of plastron extends laterally beyond bridge processes of the hyo- and hypoplastron and ossifies the peripheral aspects of the shell, as seen in *H. arctochelys*.

**Appendix 2:
Data Matrix of Character Observations Used in Phylogenetic Analysis**

a = 0/1

Ancestor 110000000010
Cycloderma aubryi 2121411122221211211121132211221422131111222-12111112211212212110000000010
Pelochelys bibroni 322241131112113211221111311111122112111311310212111122322111121220000000000
Amyda cartilaginea 3222411211111221322111112112212111211211121021311212132112112120000000000
Cyclanorbis elegans 222141142122121111221111311221322131111112-122112211211212122210000000010
Rafetus euphraticus 322241241113123211221111121211121113112111110113212221331112122120000000000
Apalone ferox 322241231113324211221121113111121113111111101132122113311112212000000a0a0
Nilssonia formosus 2222411311111211122111231211221211131131111111311111113111111---2112212---0000000000
Cycloderma frenatum 211141112122122121111211321112214221311122132-122112112211212212110000000010
Aspideretes gangeticus 322141112111222311222111112112212111311311111112112111231121121120000000000
Aspideretes hurum 32214112111122311222111121311221211131131111111213111111311121121120000000000
Chitra indica 32324113111113111221121321111121112111211211310313001122322112121220000000000
Apalone mutica 422241211112324311222122213111212111311111112-112222211221111121220000000a0
Lissemys punctata 2111321122241221211112112111121122213111111211111111111111211211212000000011
Cyclanorbis senegalensis 322142102125-4-11111111322111113221311111132-1211111121121222210000000010
Pelodiscus sinensis 4222411111123242132221122131122122123113111112113112111221111121120000000000
Apalone spinifera 32224121111332431122212111311112111311211112-1132222112311111212200000000a0
Palea steindachneri 222241131111212211322211131312212112311311112-3131211---221111-2---0000000000
Dogania subplanus 42224113111120313222111213112212112321211111-11212211321121121120000000000
Trionyx triunguis 32224113111312321122111111311221211131211111101121?2211221111121120000000000
Plastomenus aff. *Thomasi* 42?141111224-3-1??1111?11???12-122223211111?????-211?????1?????0000001110
Hutchemys rememdium nov. sp. 42?14111122312212?2111????????????????????????????????????21??111100112?
Hutchemys arctochelys nov. sp. 42?14111122312212?1111??101111112?

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