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New soft-shelled turtles (Plastomeninae, Trionychidae, Testudines) from the Late Cretaceous and Paleocene of North America

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Two new genera (*Derrisemys* and *Plastomenoide*s) and three new species (*D. sterea, P. lamberti, P. tetanetron*) of plastomenine trionychids from Montana and Wyoming are described. They are unique within the Trionychidae in having the entoplastron locked into notches in the hyoplastra and restricting midline kinesis. *D. sterea* occurs in the Lancian NALMA (North American Land Mammal Age) of Montana and Wyoming and Puercan NALMA of Montana. *P. tetanetron* occurs in the Puercan NALMA of Montana. *P. lamberti* occurs in the Torrejonian NALMA of Montana and Tiffanian NALMA of Wyoming and Utah. *Plastomenus acupictus* Hay 1907 from New Mexico is referred to *Derrisemys*. The age of *D. acupictus* is uncertain but is likely from early Paleocene (Torrejonian NALMA).

INTRODUCTION

Extant trionychines (Meylan 1987) as a group are highly specialized turtles which have lost the organized peripheral bones of the shell and developed extensive kinesis between most the bones of the plastron and between the carapace and plastron. Hay (1902:452) erected the family Plastomenidae (included only *Plastomenus* Cope 1873) for "Trionychia without fontanelles in the plastron behind the anterior border of the hyoplastra" Hay (1908:466) later noted that the Paleogene genus *Plastomenus* departed from the typical trionychid pattern of loosely connected plastral elements in having "the three hinder pairs of bones join their fellows closely at the midline" and "the hypoplastra are closely sutured to the hyoplastra and to the xiphiplastra." He further notes "there appears to have been little space between the entoplastron and hyoplastra." The epiplastron was unknown to Hay, but new material of *Plastomenus thomasi* (Cope) 1872 (UCMP 158800, Fig. 1) from the Bridger Formation reveal it to be reduced to a single spike. Subsequent authors have generally reduced the family to subfamily rank (Hutchison and Archibald 1986).

A variety of trionychids have come to light in recent decades in published lists or with cursory reference (Hutchison and Archibald 1986, Holroyd and Hutchison 2002) by informal appellations (e.g., Plastomenine A). Several new species of plastomenines described here from the Late Cretaceous (Lancian NALMA) and early and middle Paleocene of western North America have further dramatically reduced plastral kinesis by having the entoplastron develop a tight suture with the hyoplastra. This paper provides a formal nomenclature and brief diagnostic descriptions in order to simplify comparisons and reference to these taxa in taxonomic and non-taxonomic papers.

Terminological Conventions and Abbreviations—All measurements are in millimeters. Bone terminology follows Zangerl (1969). Anatomical abbreviations are used for serial elements, e.g., carapacial bones are denoted by a letter (**C** = costal, **N** = neural, **P** = peripheral) and position number (e.g., C2 for the second costal), with the lower numbers being more anterior.

The ages are given in terms of the international units and North American Land Mammal Ages (NALMA) following Berggren et al. (1995) and Woodburne (2004). Detailed locality descriptions available to qualified researchers through the respective institutions.

Institutional abbreviations: **AMNH**—American Museum of Natural History, New York; **NMMNH**—New Mexico Museum of Natural History, Albuquerque; **UCMP**—University of California Museum of Paleontology, Berkeley; **UMMP**—University of Michigan Museum of Paleontology, Ann Arbor; **YPM (PU)**—Yale Peabody Museum (Princeton University collection), New Haven.

SYSTEMATIC PALEONTOLOGY

ORDER: TESTUDINES Batsch 1788
FAMILY: TRIONYCHIDAE Fitzinger 1826
SUBFAMILY: PLASTOMENINAE Hay 1902

Diagnosis—Posterolateral arm of epiplastron reduced or absent, hyo-hypo-xiphiplastra without fontanelles and with patent sutures in adults.

Remarks—Although Hay (1908:466) erected the family Plastomenidae for the genus *Plastomenus*, it hardly justifies this status compared to other major groups within the Trionychidae such as the Trionychinae or Cyclanorbinae. Here it is treated as a subfamily until its detailed relationships to trionychids is better understood. A comparable diagnosis of *Plastomenus* is presented for comparison with the new taxa.

GENUS: *Plastomenus* Cope 1873

Type Species—*Trionyx thomasii* Cope 1872

Included Species—Type species and an undetermined number of nominal species (see Hay 1908) but probably including all the species named from the Eocene and some Paleocene species.

Diagnosis—Small to moderately large size (carapace length approximately 200–310 mm; entoplastral-xiphiplastral length approximately 140 mm); plastron with post-entoplastral fontanelle in adults; hyoplastron, hypoplastron and xiphiplastron sutured and completely calloused ventrally

but some midline kinesis possible; uncalloused epiplastron reduced to a simple spike (Fig. 1); entoplastron arched anteriorly, weakly to moderately calloused, not recessed or sutured to hyoplastra; interclavicular alae inserted into pits on the anterior margin of the hyoplastra; hyoplastron tapers laterally to a twinned point and not expanded anteriorly to enclose the lateral margin of the entoplastron; peripheral ossifications apparently absent in mature adults; pelvis extending beyond the bony confines of the carapace; carapace broadly domed and oval; eight costals that thicken and terminate abruptly or are somewhat tapered; rib ends compressed and short but usually extending beyond costal margins; C8 is large; nuchal is smoothly contiguous with costal margins and may or may not be marked by a small spur that is noticeably medial to the suture; nuchal lenticular and not emarginated anteriorly; preneural is present.

GENUS: *Derrisemys* gen. nov.

Type species—*Derrisemys sterea* sp. nov.

Included Species—Type species and *D. acupictus* (Hay 1907).

Etymology—From the Greek *derris*, leather coat; plus *emys*, turtle; and *sterea*, hard or three-dimensional.

Diagnosis—Small size (carapace length approximately 160 mm); plastron without post-entoplastral fontanelles in adults; hyoplastron, hypoplastron and xiphiplastron rigidly sutured and completely calloused ventrally; epiplastron subtriangular with short but distinct lateral arm, epiplastron well calloused; entoplastron transversely elongate with an obtusely angled anterior margin, calloused, recessed into anteromedial margin of the hyoplastra and sutured to hyoplastra laterally and posteriorly in adults; interclavicular alae inserted into grooves on the dorsal side of the hyoplastra; hyoplastron tapers posterolaterally to a single point and expands anteriorly to enclose the lateral margin of the entoplastron; hypoplastron fuses laterally to an elongate peripheral ossification in mature specimens; pelvis within the bony confines of the carapace; carapace distinctly domed and oval; eight costals that thicken and terminate abruptly; rib ends compressed, short, and usually not extending beyond the costal margins; C8 large; nuchal smoothly contiguous with costal margins and moderately narrow and deep; preneural absent.

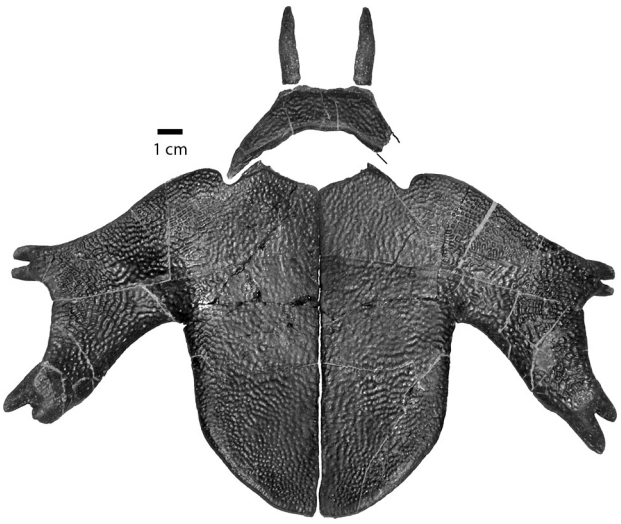


Figure 1. *Plastomenus thomasi* Cope 1872, UCMP 158800, ventral view of the plastron, left epiplastron digitally restored from the right side.

Derrisemys sterea sp. nov.

"Plastomenine" Type A: Hutchison and Archibald 1986:5
Plastomenine A: Holroyd and Hutchison, 2002:184:fig. 2K
Plastomenine A: Hutchison and Holroyd, 2003:132

Diagnosis—Hypoplastron bridge relatively wide and inguinal notch narrow; xiphiplastron about as long or longer than wide; hyo-hypoplastral suture angles anteriorly near the midline; hyo-xiphiplastral suture relatively straight; dorsal surface of C6-8 with shelf-like projection over the ventral surface at the distal margins.

Holotype—UCMP 130000, nearly complete carapace and plastron, fragments of scapula, coracoid and pelvis (Figs. 3–9). Collected by the author, 5 July 1984.

Type Locality—UCMP locality V84153, McCone County, Montana. Tullock Member of the Fort Union Formation, Puercan (Mantuan) NALMA, Zone Pu1, early Paleocene (Fig. 2).

Hypodigm—Late Cretaceous (Lancian NALMA). Hell Creek Formation, Garfield County, Montana. UCMP loc. V74117, UCMP 130002, complete right and medial part of left hyoplastra, juvenile; UCMP loc. V75181, UCMP 130102, hyoplastron; UCMP loc. V80092, UCMP 130093, medial part of left hypoplastron; UCMP loc. V82022, UCMP 130095, three medial and one lateral hypoplastral fragments; UCMP loc. V83046, UCMP 130094, left hypo-xiphiplastron; UCMP loc. V83153, UCMP 130101, medial hypoplastron.

Early Paleocene (Puercan NALMA). Hell Creek Formation, McCone County, Montana. UCMP loc. V65127, UCMP 130111, medial hypoplastron; UCMP 130110, hyoplastron fragment; UCMP 130109, medial hypoplastron and distal costal fragment; UCMP loc. V85085, UCMP 136100, crushed partial carapace and plastron.

Early Paleocene (Puercan NALMA). Tullock Member of the Fort Union Formation, Garfield County, Montana. UCMP loc. V77134, UCMP 129517, fragmentary middle portion of shell preserving the greater parts of C3–6, partial plastron consisting of compositely complete hyoplastron, hypoplastron and anterior xiphiplastron; UCMP loc. V84045, UCMP 130003, carapace fragments including complete or composite N1, N3–5, C1, C3–5 and fragments of nuchal and other costals.

Referred Specimens—Late Cretaceous (Lancian NALMA). Lance Formation, Niobrara County, Wyoming. UCMP loc. V65238, UCMP 173431, nuchal; UCMP loc. V5820, UCMP 173435, partial costal (Holroyd and Hutchison 2002).

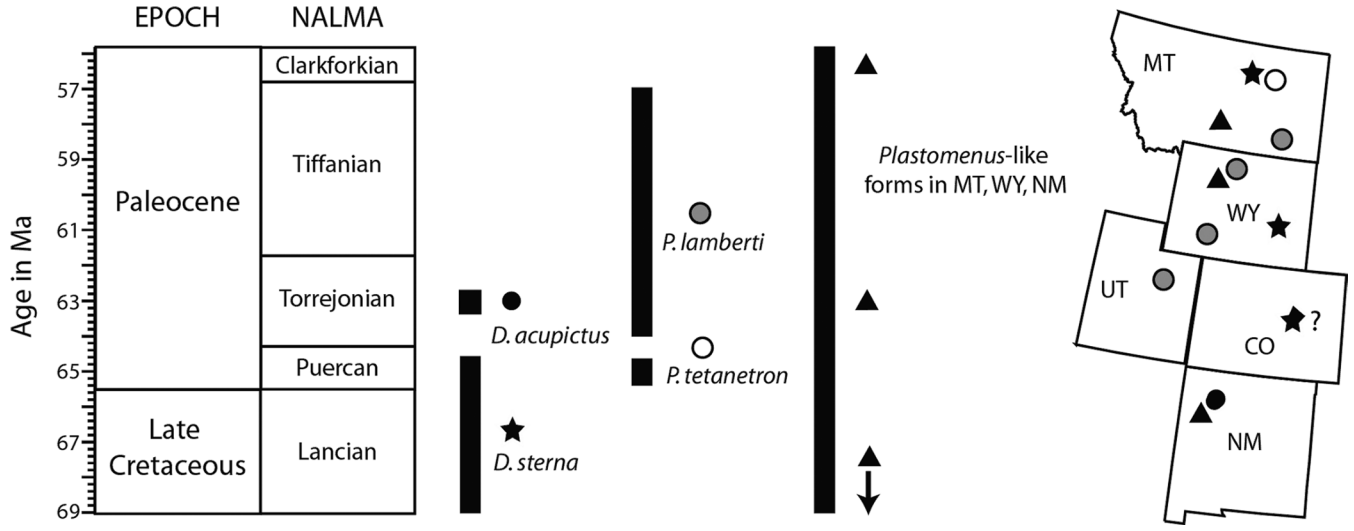


Figure 2. Distribution of *Derrisemys* and *Plastomenoides* in space and time. Partial range of *Plastomenus*-like plastomenines is also indicated but extends temporally (see text) into the Campanian and late middle Eocene (Duchesnean NALMA).

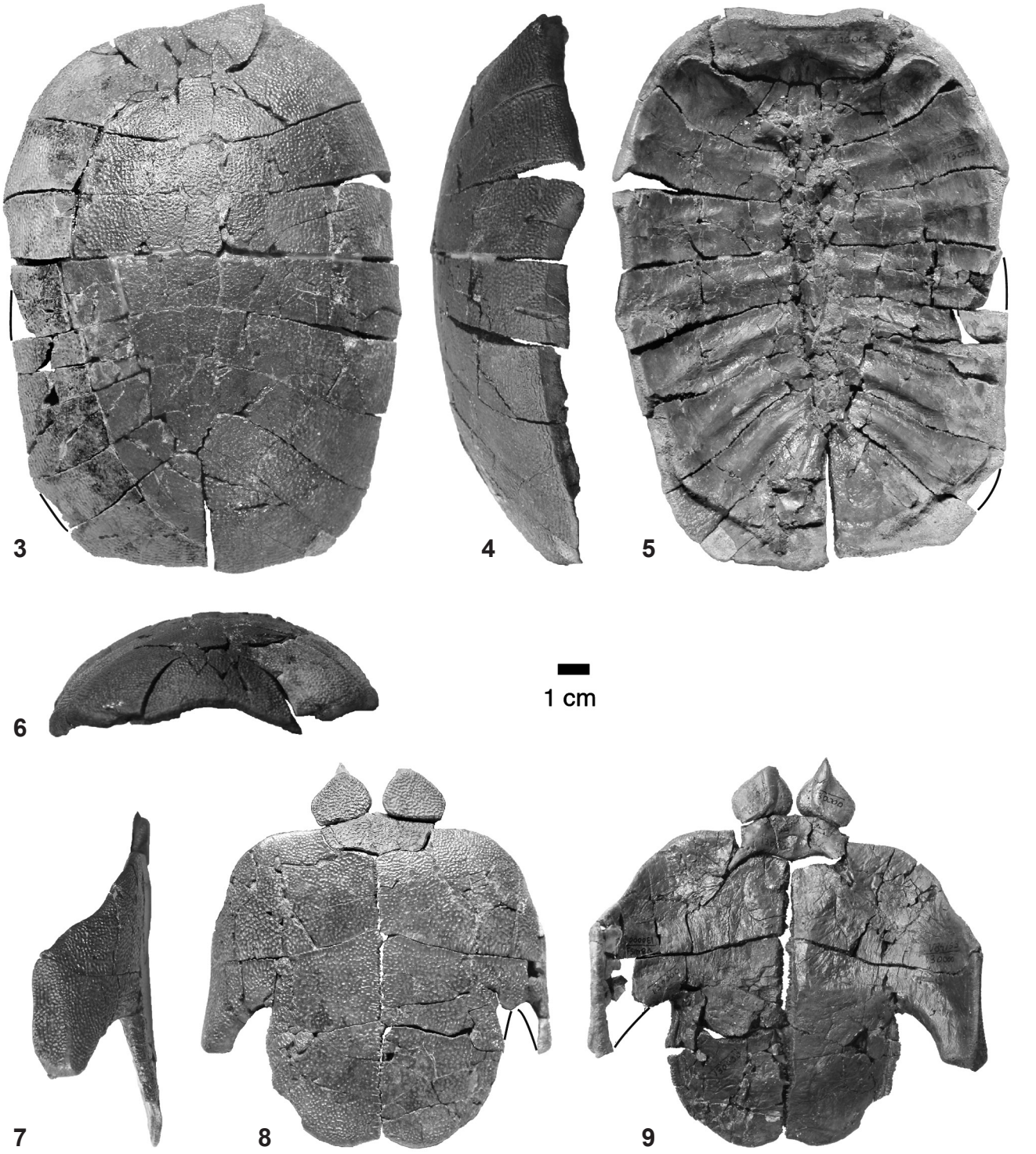
Description of the type—*Carapace* (dorsal view, Figs. 3, 4, 6): The carapace consists of eight pairs of costals, seven neurals and a nuchal. Its shape is narrowly subquadratic, being more angulated posteriorly. There is a distinct but shallow cephalic concavity that is confined to the nuchal. The entire dorsal surface is covered with a pattern of fine pits averaging about 7–8 pits per cm. Toward the lateral and posterior margins the pits deepen and tend to connect up meridianally to produce a fine lineal pattern of ridges and valleys. Aside from the delicate surface pattern, it is devoid of welts or carinae. The dorsal surface is smoothly convex. The rib terminations are not visible in dorsal view. The nuchal is slightly more than twice as wide as long externally but 16% wider on its ventral surface. The difference between the widths is reflected in a thick (9 mm) and finely dentate sloping suture with the first costal (C1). The superficial part of the suture (2+ mm) is normal to the external surface so that as it approaches the free margin it forms a distinct step-shaped joint with the C1. The free margin is shallowly concave and roughened but not patterned like the dorsal surface. The costiform process is indicated by a single raised ridge that just terminates against the C1 rib. The neurals are all longer than wide and form a continuous series from the nuchal to C7 where they terminate. Aside from their normally sagittal contacts, N1 articulates with C1–2, N2 with C2–3, N3 with C3–4, N4 with C4 only, N5 with C4–5, N6 with C5–6, and N7 with C6–7. C7–8 pairs are in mutual contact behind N7. The eighth costals are large.

Carapace (ventral view, Fig. 5): The vertebral centra are badly damaged by crushing but appear to be unkeeled and moderately convex ventrally. The rib heads are wide and flat as in other trionychids. The convex trace of the rib along the visceral surface of the costal plates is well defined and tapers to extinction distally before exiting the costal, except for C7–8. The rib trace on C7–8 remains undiminished until very close to the costal margin; only rib 8 extends slightly beyond the margin. The trace of rib 1 rises from the surface to form a sharp ridge where it meets the costiform process of the nuchal which inserts into a shallow pocket dorsal to the rib. The terminal articulation of C1–2 and C2–3 are complex and hook-like in ventral view. The trace of the ligament binding the first trunk vertebra to the nuchal resembles that in *Apalone* Rafinesque 1832. All the costals thicken distinctly toward the lateral margins. C1–2 have a rolled edge that is finely patterned dorsally. C3–6 are more truncate distally but with the exception of C6, the very slightly roughened surface slopes dorsally and slightly laterally. C7 has the thickest terminal edge (8 mm) and is truncate normal to its plane. Starting on the posterior part of C6 and extending onto C8, there is an eave-like projection of the dorsal part of the terminus over the ventral part. It reaches 12 mm at its maximum extent in the area of the C7–8 suture. The whole surface is finely and irregularly roughened and apparently housed a movable flap of fibrous connective tissue. The visceral and down-turned patterned dorsal surface of C8 converge to a more or less normal edge at the caudal-most part.

Plastron (ventral view, Figs. 8–9): The plastron is broadly anchor-shaped and turns up to vertical at the lateral margins. The posterior lobe is broad with a slight caudal notch. As on the carapace, the surface is fully patterned with pits and fine anastomosing ridges. All the bones except the epiplastra are joined by tight-fitting sutures. The epiplastra are subtriangular in shape. The contact of the epiplastra with the entoplastron is represented by a shallow and slightly spiral groove. Although the epiplastra were slightly separated from the body of the plastron when found, the best fits indicate that they contacted the anterolateral part of the entoplastron and apparently made slight contact with the hyoplastra. In this position, the epiplastra are mutually separated by about an 8–9 mm gap. The entoplastron is roughly rectangular,

more than twice as wide as long, with tight-fitting sutures on the lateral and posterior margins with the hyoplastra. The anterior margin is broadly convex with broad and slightly spiral grooves on either side of the midline for the epiplastra. The posterior margin is biconcave, turning sharply anterior at the lateral margins.

The hyoplastron is strongly transversely convex and roughly triangular in outline with the midline forming the



Figures 3–9. *Derrisemys sterea* gen. nov. et sp. nov. UCMP 130000 (Type). **3.** Carapace, dorsal view. **4.** Carapace, right lateral view. **5.** Carapace, ventral view. **6.** Carapace, anterior view. **7.** Plastron right lateral view. **8.** Plastron, ventral view. **9.** Plastron, dorsal view.

shortest side. The anterior margin is notched medially for the entoplastron, which, when articulated, forms a smoothly continuous margin that slopes sinuously posterolaterally. The anterior margin and the hyo-hypoplastral sutural converge to a single point laterally. The suture with the hypoplastron is finely dentate, broadly convex and thick (8.5 mm at the base of the bridge portion). The midline suture is coarser with generally vertically aligned dentations.

The hypoplastra are the thickest bones of the plastron (9.6 mm at the midline, 10.6 mm on the bridge). The bridge region occupies the lateral one half of the hypoplastron and turns sharply dorsally at its lateral extremity which appears to be formed by fusion with an elongate peripheral ossification. The posterolateral margin terminates in a thick blunt point. The medial part of the hypoplastron inscribes a parallelogram. The inguinal notch is acute (30°). The patterned surface curls around the margin on the medial side of the inguinal opening indicating the lack of a fleshy lobe. The xiphiplastron is about as broad as long with a distinctly convex free margin. The rolled edge of the inguinal opening disappears posteriorly.

Plastron (dorsal view, Fig. 9): The dorsal surface is marked by a series of incised and dentritic vascular grooves. A rounded ridge ("clavicular" trace) extends medially from the posterolateral corner of the epiplastron and then turns degrees anterolaterally and extends beyond the margin of the ventral surface and rapidly tapers to a sharp point. The trace of the "interclavicle" on the entoplastron forms a very slightly raised and anteriorly pointed V-shaped ridge. The lateral ends of the V extend beyond the body of the entoplastron as pointed spikes and insert into dorsally open notches in the hyoplastra. A faint and posteriorly tapering midline ridge lies between the arms of the V. The finely dentate suture of the hyoplastron and xiphiplastron is interrupted medial to the inguinal opening by a dorsally open notch for reception of a large triangular projection from the xiphiplastron.

Pelvis: The pelvis is not represented but judging from the long posterior extent of the eighth costals and indications of depressions for accommodation of the ilia, the pelvis was restricted to the confines of the carapace.

Description of the hypodigm—The hypodigm specimens, while generally resembling the type, provide an indication of individual and ontogenetic variation. Of the four hypodigm specimens, only two preserve portions of the carapace. One of these, UCMP 130003 is smaller than the type and subadult, judging from the porous and rounded contours of the free margins of the costals. Both have N1–5 reversed, UCMP 129517 is larger than the type and has C3–6 terminating in a truncate surface normal to the costal plane as in C6 of the type. The rib traces extend in both specimens to the ventral edge of the costals and probably extended a few mm beyond in the juvenile. The rib traces in the latter also widen rather than taper distally. Both specimens appear to have been more circular in outline than the type. UCMP 129517 preserves a significant part of the plastron and differs from the type in having a small entoplastral process just medial to the notch for the entoplastral alae. It also has a more sinuous and likely more kinetic suture with the entoplastron. The midline dentations on the hyoplastra, hypoplastra and xiphiplastra are less extensive with only very slight relief, suggesting greater midline kinesis. There is no peripheral ossification (at least not one fused to the plastron). The plastron has a generally broader curvature. The lateral margin of the hypoplastron is thickened and roughened as in the midline suture. A single dorsolateral projection of the hyoplastron extends laterally beyond the perimeter of the plastron. The hyoplastron of the juvenile UCMP 130002 resembles that of UCMP 129517 except that the midline suture is more distinctly dentate as in the type. The entoplastral suture medial to the alae notches is bluntly rounded, straight and slopes posteromedially. If not just individual variation, some of these differences may represent sexual dimorphisms.

Derrisemys acupictus (Hay 1907)

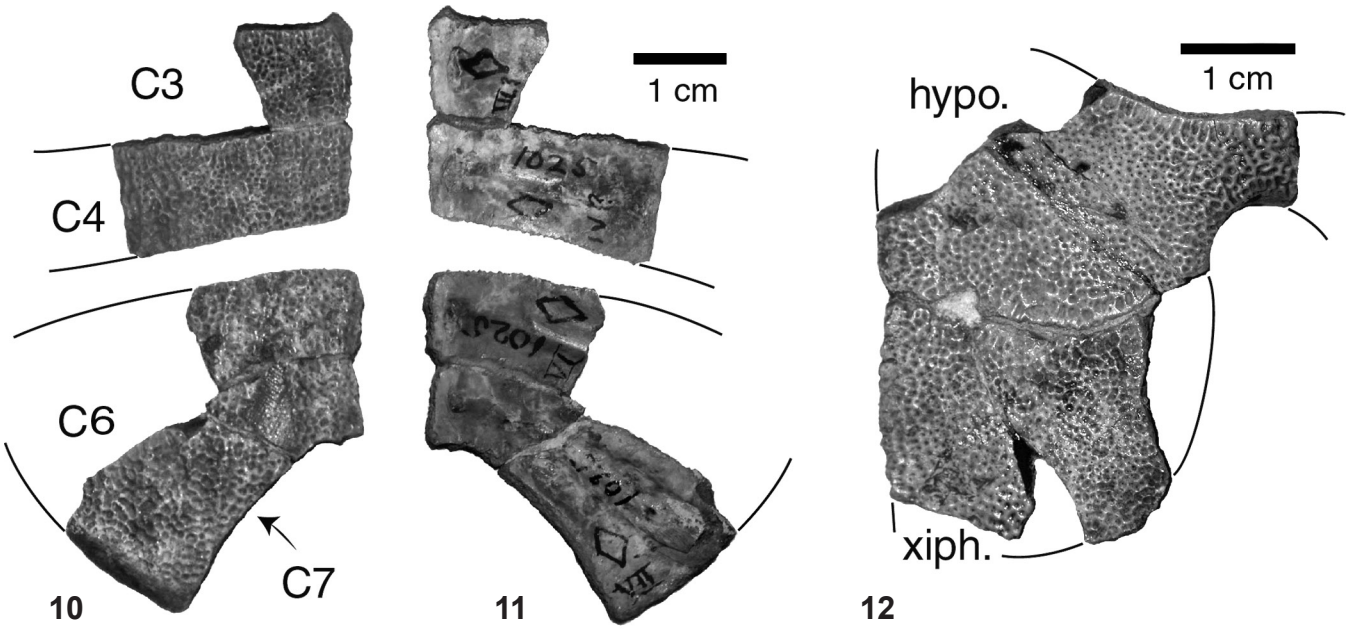
Plastomenus acupictus Hay: Hay 1907:852–853, fig. 8; pl. 54, figs. 1–3
Plastomenus acupictus Hay: Hay 1908:470, fig. 629
Plastomenus acupictus Hay: Hay 1930:106
Plastomenus acupictus Hay: Matthew 1937: 335–336
Plastomenus acupictus Hay: Sullivan and Lucas 1986:204 (prob. a *nomen dubium*)
Plastomenus acupictus Hay: Kues 1993:244

Holotype—AMNH 1025, costal fragments and incomplete hypoplastron and xiphiplastron (Figs. 10–12). Collected by David Baldwin.

Type Locality—New Mexico but type locality uncertain. The specimen was apparently found in Baldwin's collection containing mammals associated with the Torrejonian NALMA (Matthew 1937, Sullivan and Lucas 1986:204). Hay (1907) reported that they came from a region north of Santa Fe, New Mexico, but it seems more likely that they came from the vicinity of Torreon Wash, west northwest of Santa Fe in the southern San Juan Basin, Sandoval County, Nacimiento Formation. Williamson and Lucas (1993) divided that part of the Nacimiento Formation into the lower Ojo Encino and higher Escavada Members (Fig. 2). The Ojo Encino Member produces Torrejonian fossils.

Diagnosis—Hypoplastron bridge relatively narrow and inguinal notch wide; xiphiplastron distinctly shorter than wide; hyo-hypoplastral suture angles anteriorly near the bridge; hyo-xiphiplastral suture convex posteriorly; dorsal surface of C6–8 without shelf-like projection over the ventral surface at the distal margins.

Remarks—See Hay (1907) for description of this species. It is unlike the type specimen of *D. sterea*, but resembles the hypodigm specimens of *D. sterea* in that N6 in *D. acupictus* is quadratic. Sullivan and Lucas (1986:204) suggested that this species was a *nomen dubium*. Comparisons with the specimens attributed to *D. sterea* indicate *D. acupictus* is a diagnosable taxon based on the features of the type hypoplastron and xiphiplastron contra Sullivan and Lucas (1986).



Figures 10–12. *Derrisemys acupictus*, AMNH 1025 (Type). **10.** Right costals 3–4, 6–7, dorsal views. **11.** Right costals 3–4, 6–7, ventral views. **12.** Left hypoplastron and xiphiplastron, ventral view.

Derrisemys sp.

Hutchison and Holroyd (2003) referred fragmentary costals from the Puercan portion of the Denver Formation, Denver Basin of Colorado, to Plastomenine A. These are referable to *Derrisemys*, but are not sufficiently diagnostic to assign to species.

GENUS: *Plastomenoides* gen. nov.

Type Species—*Plastomenoides lamberti* sp. nov.

Included species—Type species and *P. tetanetron,* sp. nov.

Diagnosis—Small to moderately large size; plastron without post-entoplastral fontanelles in adults; hyoplastron, hypoplastron and xiphiplastron rigidly sutured and completely calloused ventrally; epiplastron subtriangular with short but distinct lateral arm, epiplastron well calloused; entoplastron transversely elongate with a relatively straight anterior margin, calloused, recessed into hyoplastra and sutured to hyoplastra laterally and posteriorly in adults; interclavicular alae inserted into grooves on the dorsal side of the hyoplastra; hyoplastron tapers laterally to a single point and expanded anteriorly to enclose the lateral margin of the entoplastron; peripheral ossifications apparently absent in mature adults; pelvis extending beyond the bony confines of the carapace; carapace broadly domed and oval to subrectangular; eight costals that thicken and terminate abruptly; rib ends compressed, short and may not extend beyond the costal margins; C8 moderate in size; nuchal not smoothly contiguous with costal margins and marked by a small spur or distinct change in angle near the suture; nuchal wide and shallow and distinctly emarginate; preneural present or absent.

Plastomenoides lamberti sp. nov.

Etymology—Named in honor of Marshall E. Lambert, collector, educator and founder of the Carbon County Museum.

Holotype—YPM (PU) 16795 (Figs. 13–16), plastron and carapace lacking only the right lateral margins, virtually complete limbs and girdles on the right side, left hind limb down to the tarsals and fragments of the left side of the girdles. Collected by M.E. Lambert, 1958.

Type Locality—Traweek Ranch, Fallon County, NW ¼, NW ¼, Section 36, T3N, R60E. Montana. Fort Union Group, Tongue River Formation, Medicine Rocks Sandstone. Torrejonian NALMA.

Diagnosis—Moderately large size (carapace length approximately 290–360 mm; entoplastral-xiphiplastral length approximately 230–320 mm), oval and longer than wide; preneural present or absent; cephalic emargination well within the confines of the nuchal; anterior margin of hyoplastron with a broad concavity; xiphiplastron distinctly wider than long.

Hypodigm—Torrejonian NALMA (early middle Paleocene). Tongue River Member of the Fort Union Formation. Burns Mine, Bear Creek-Washoe area, Carbon County, Montana. YPM(PU) 16238, partial carapace and plastron; YPM(PU) 16317, carapace; YPM(PU) 16320, partial carapace; YPM(PU) 16321, plastron; YPM(PU) 16322, partial plastron.

Referred Specimens—Early middle Paleocene (Torrejonian NALMA). Tongue River Member of the Fort Union Formation, Powder River County, Montana. UCMP loc. V86107, UCMP 197893, fragments of carapace and plastron; UCMP loc. V86108, UCMP 197894, nuchal and

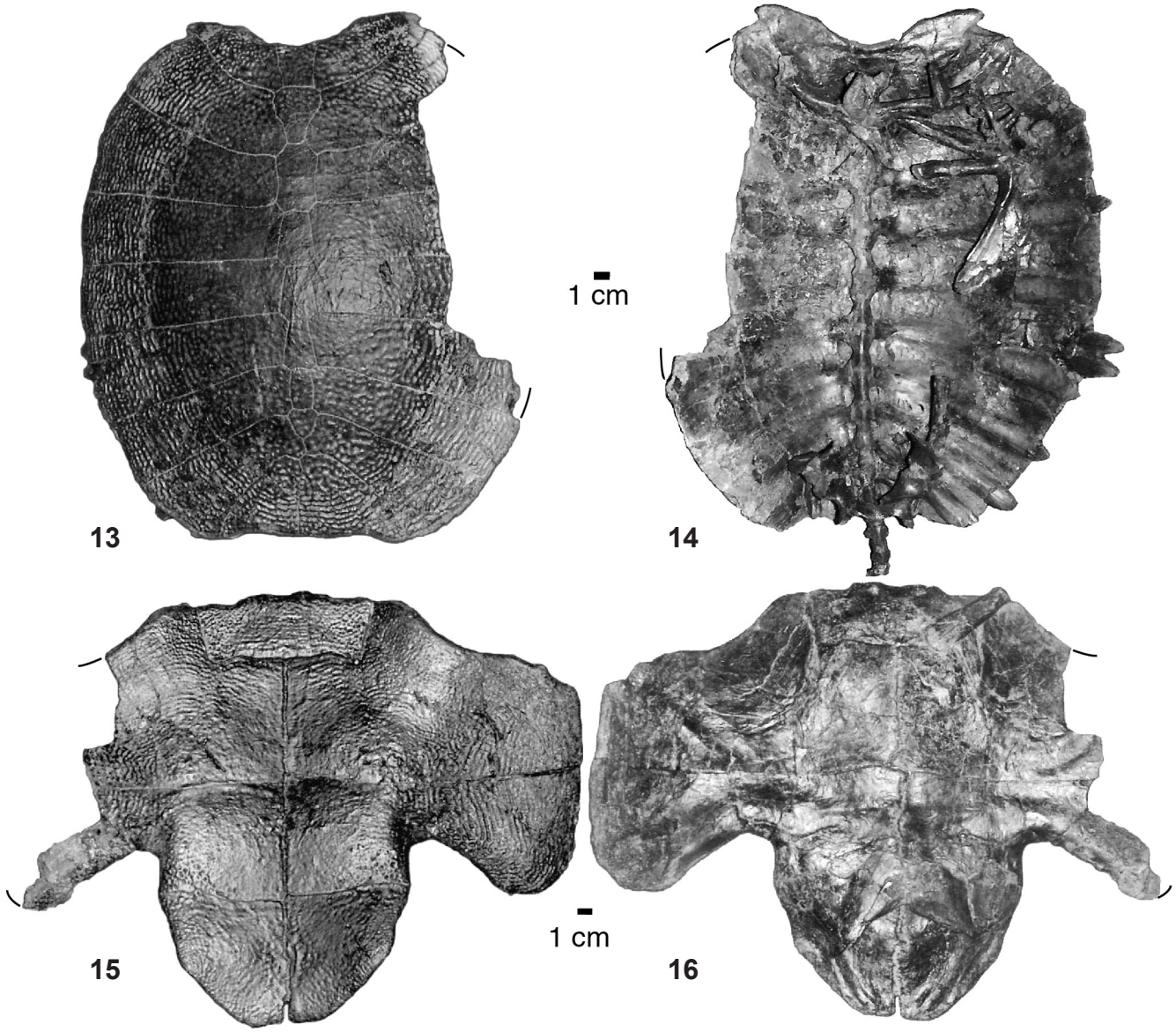
costal fragments of a subadult; UCMP loc. V86105, UCMP 197891, hyoplastron; UCMP loc. V86106, UCMP 197892, incomplete plastron and carapace lacking compositely only the lateral parts of the hyo-hypoplastron and distal top of the xiphiplastra.

Mid-Paleocene (Tiffanian NALMA). Fort Union Formation, Big Horn County, Wyoming. Cedar Point Quarry. UMMP V74588, most of the entoplastron, nuchal lacking lateral arm, lateral portion of hyoplastron.

Mid-Paleocene (Tiffanian? NALMA) Fort Union Formation, Sweetwater County, Wyoming. UCMP loc. V73136, UCMP 131053, medial hyoplastral fragment and three costal fragments; UCMP loc. V91014, UCMP 137199, incomplete carapace, plastron fragments.

Mid-Paleocene (Tiffanian NALMA), North Horn Formation, Carbon County, Utah. UCMP loc. V82063, UCMP 126292, juvenile posterior carapace starting at C6 and partial hyoplastron.

Description of the type specimen—The plastron is devoid of fontanelles, broadly anchor-shaped and only moderately turned up laterally. The ventral surface is fully patterned except for the projections of the inguinal and auxiliary buttresses. All the bones except the epiplastra are joined by tight-fitting dentate sutures. The dorsal surface is generally unmarked except in the center of the hyoplastron which is scored by some vesicular grooves. In ventral view the entoplastron is trapezoidal in shape with straight lateral sides that converge posteriorly at approximately a 28° angle. The



Figures 13–16. *Plastomenoides lamberti* gen. nov. et sp. nov., YPM (PU) 16795 (Type). **13.** Carapace, dorsal view. **14.** Carapace, girdles and caudal vertebrae, ventral view. **15.** Plastron, ventral view. **16.** Plastron, dorsal view.

posterior margin is approximately straight and the anterior margin is only slightly sinuous. In dorsal view the tips of the interclavicular arms extend posterior from the body of the entoplastron and are recessed into grooves in the dorsal surfaces of the hyoplastra.

The hyoplastron is deeply notched anteromedially for the entoplastron. The anterior free margin is continuous with that of the entoplastron and slopes via a concave margin posterolaterally. The axillary buttress is composed of a single anterolaterally directed fluted spike and is separated from the hyo-hypoplastral suture at about the same distance as that of the posterior margin of the entoplastron. The midline suture is patent and allows no space for medial fontanelles. It terminates laterally in a beveled edge.

The hypoplastra are the thickest bones of the plastron. The bridge region occupies the lateral half and terminates laterally in a beveled edge as in the hyoplastron. No evidence of a peripheral ossification. The inguinal buttress terminates in two thickened and fluted spikes. The inguinal notch is acute (24°). The patterned surface curls up to form the lateral perimeter but does not extend onto the dorsal surface. The transverse suture with the xiphiplastron is marked by only one slight irregularity in ventral view.

The xiphiplastron is about as wide as long. The dentate part of the inter-xiphiplastral suture fades out on the posterior third and there may have been a narrow gap between the bones distally.

The carapace is elliptical but concave at the cephalic and caudal ends. It has eight pairs of costals and seven contiguous neurals including N1. The nuchal is broadly C-shaped with a distinctly concave anterior margin. Toward the lateral margin of the nuchal there is a change in the perimeter outline that is marked by a short spike. The lateral tip of the nuchal is separated from the perimeter of C1 by a distinct notch. The neural series consists of a bell-shaped N1 (possibly including a fused preneural), octagonal N2, reversed hexagonal N3–N5, quadratic N6 and a pentagonal N7. The lateral margins of the costals thicken and end abruptly in the bridge region. The edges in the bridge area are bifurcated by a longitudinal groove. The rib tips where preserved are strongly compressed, short and extend a short distance beyond the costal margins. A shallow and broad rectangular caudal emargination marks the posterior margin of the carapace and is confined to the margins of the eighth costals which are not notably enlarged or reduced.

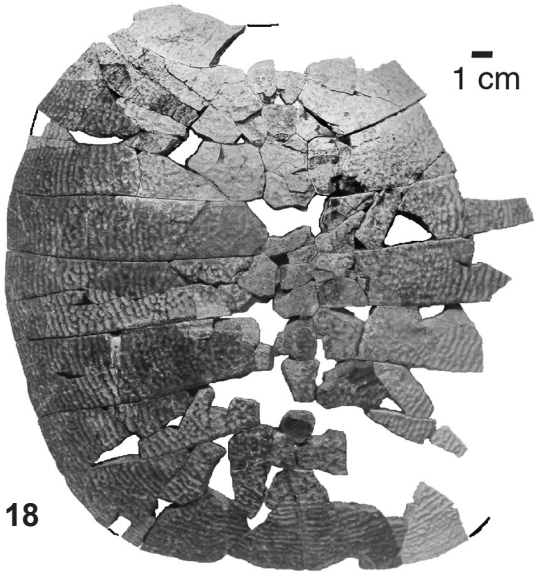
Description of the Hypodigm—The plastra from the hypodigm generally resembles the type specimen. However, the carapace of YPM(PU) 16319 (Fig. 17) is different and may represent an older individual. Carapace length is about 36 cm along the midline. The cephalic emargination is reduced in both depth and width and the caudal region, rather than being somewhat emarginated or straight, is convex, suggesting that the pelvis did not extend beyond the margins of the carapace. The most striking feature is that the distal margins of the costals have completely overgrown the tip of the ribs

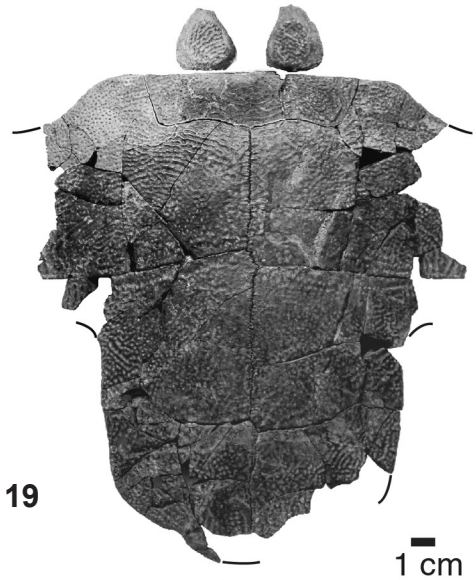
Figure 17. *Plastomenoides lamberti* gen. nov. et sp. nov. YPM(PU) 16319, carapace, ventral view.

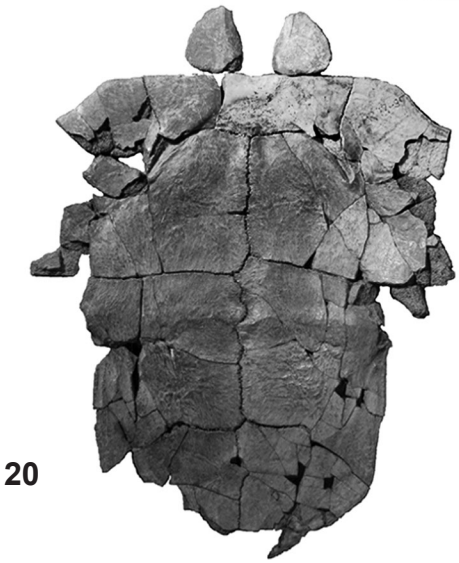
and the margins of C6–8 are curled ventrally, indicating that the typical fleshy margin of trionychids was absent.

Description of Referred Material—The epiplastron (UCMP 197898, Figs. 19–20) resembles that of *D. sterea* but the edges of the calloused area occupies only about half the ventral surface. The trace of the clavicle is L-shaped. The posterior margin of the entoplastron is usually biconcave. In dorsal view the tips of the interclavicular arms are recessed into broad somewhat rough-floored grooves in the dorsal surfaces of the hyoplastra. Most of the specimens preserving this groove (UCMP 197891, 197892) show the presence of a secondary short spike conjoined anteriorly to the principle interclavicular spike. The suture of the hyoplastron with the entoplastron is finely dentate, gently transversely convex and moderately thick (10.5 mm maximum in UCMP 197891). The midline suture is more coarsely dentate but the dentations are not distinctly aligned. The hypoplastra are the thickest bones of the plastron (13+ mm on the bridge, 7.7 mm at the midline in UCMP 197891). The xiphiplastron is slightly broader than long.

On the carapace, the lateral margin of the nuchal is marked by a bump (YPM (PU) 16795 (Figs. 13–16), UCMP 197898 (Fig. 18)) or short spike (UCMP 197894). The lateral tip of the nuchal is separated from the perimeter of C1 by a distinct notch in YPM (PU) 16795 (Figs. 13–16) and UCMP 197893 but not in UCMP 197894. UCMP 197898 preserves a similar pattern but N5 is quadratic, N6 is hexagonal normal, and N1 and the preneural are quadratic. A shallow rectangular caudal recess marks the posterior margin of the







carapace in the type and UCMP 197898 (Fig. 18) and is confined to the margins of the eighth costals, which are not notably enlarged or reduced.

UMMP 74588 resembles the hypodigm (YPM (PU) 16319) in the shape of the nuchal, position of the axillary spike on the hyoplastron, costal termination and broad entoplastron sutured to the hyoplastra. The side of the neural suture on the nuchal suggests but does not confirm that the N1 was not preceded by a separate preneural. The entoplastron differs from the hypodigm in having a broadly concave posterior and anterior margin. UCMP 126292 resembles the hypodigm in general proportions, although the region of the entoplastral sutures is broken away. The posterior carapace fragment of this specimen exhibits details not shown in the hypodigm. The eighth costals are of normal size and marked by a small V-shaped marginal notch but the posterior perimeter is otherwise transversely straight. N6 is quadratic and N7 is pinched off posteriorly by the mutual contact of the eighth costals. None of these differences appear at present to justify exclusion of the referred material to *D. lamberti.*

Plastomenoides tetanetron sp. nov.

"Plastomenine" Type B, Hutchison and Archibald 1986:5

Etymology—From the Greek *tetanos,* stiff, rigid; and *etron*, belly, abdomen.

Type Specimen—UCMP 125800, carapace and partial plastron (Figs. 21–24).

Type Locality—UCMP locality V81155, Tullock Member of the Fort Union Formation, Garfield County, Montana. Collected by the author.

Diagnosis—Small size (carapace length approximately 125 mm), subcircular and wider than long; preneural present; cephalic emargination virtually the width of the nuchal; anterior margin of hyoplastron without a broad concavity; xiphiplastron distinctly wider than long; the bridge region occupies less than half of the width of the plastron.

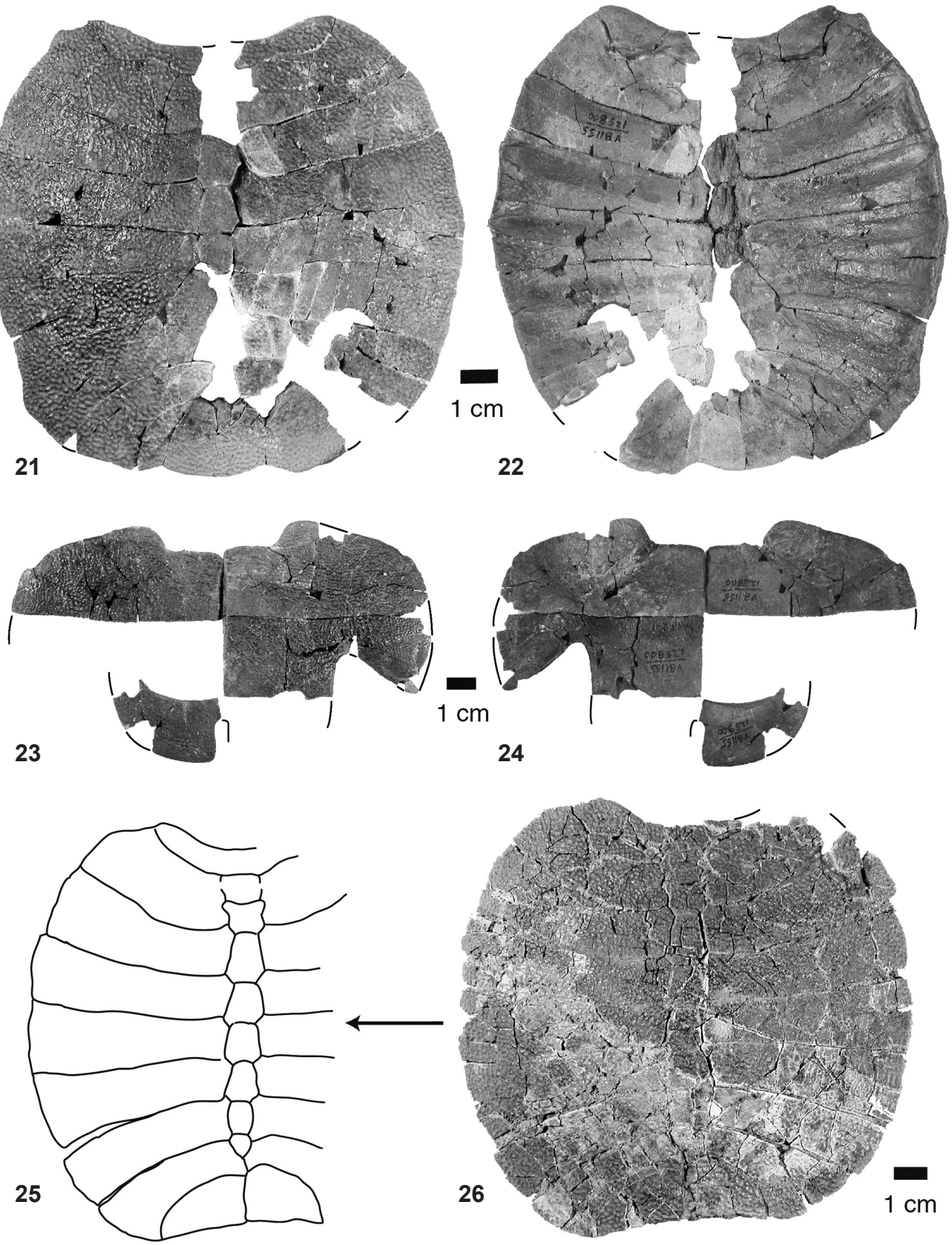
Hypodigm—Early Paleocene (Puercan NALMA) Hell Creek Formation, McCone County, Montana. UCMP loc. V91011, UCMP 137195, carapace.

Early Paleocene (Puercan NALMA) Tullock Member of the Fort Union Formation, Garfield County, Montana. UCMP loc. V76154, UCMP 117370, partial carapace; UCMP loc. V84060, UCMP 137198, shell fragments; UCMP loc. V91014, UCMP 137199, incomplete carapace, plastron fragments.

Early Paleocene (Puercan NALMA) Tullock Member of the Fort Union Formation, McCone County, Montana. UCMP loc. V91005, UCMP 137197, carapace fragments.

Description of the Type Specimen—The plastron is lacking the entoplastron and epiplastra, right hypoplastron

◀ **Figures 18–20.** *Plastomenoides lamberti* gen. nov. et sp. nov., UCMP 197898. **18.** Carapace, dorsal view. **19.** Plastron, ventral view. **20.** Plastron, dorsal view.



Figures 21–26. 21–24. *Plastomenoides tetanetron* gen. nov. et sp. nov., UCMP 125800 (Type). **21.** Carapace, dorsal view. **22.** Carapace, ventral view. **23.** Plastron, ventral view. **24.** Plastron, dorsal view. **25–26.** UCMP 130017, carapace. **25.** Trance of carapacial sutures. **26.** Dorsal view

and left xiphiplastron, while the carapace is complete except for the preneural, N1 and N5–7. The preserved morphology of the plastron is devoid of fontanelles posterior to the epiplastra and short. The ventral surface is fully patterned which also covers the projections of the inguinal and axillary buttresses. All the bones except the epiplastra are joined by tight-fitting dentate sutures. In ventral view, the position of the entoplastron is marked by a subrectangular emargination spanning the hyoplastra midline suture. The interclavicular ends project posterolaterally and insert into grooves in the dorsal surfaces at the corners of this emargination.

The hyoplastron is deeply notched anteromedially for the entoplastron. The anterior free margin was probably continuous with that of the entoplastron and slopes via a straight to broadly convex margin posterolaterally. The axillary buttress is composed of a single, mostly laterally directed spike, and is separated from the hyo-hypoplastral suture at about the same distance as that of the posterior margin of the entoplastron. The midline suture is patent and allows no space for medial fontanelles. The hyoplastron terminates laterally in a blunt and slightly convex margin.

The hypoplastra are the thickest bones of the plastron. The bridge region occupies less than half of the width of the hyo-hypoplastron and terminates laterally in a convex rounded margin. No evidence of a peripheral ossification is present. The inguinal buttress terminates coincident with the calloused surface and does not project. The inguinal notch is acute (23°). The patterned surface curls up to form the lateral perimeter but does not extend onto the dorsal surface. The transverse suture with the xiphiplastron is straight except for the interlocking lateral teeth.

The xiphiplastron is distinctly wider than long. The dentate part of the inter-xiphiplastral suture is absent on the posterior two-thirds and leaves a narrow gap between the bones distally.

The carapace is subcircular but concave at the cephalic end and nearly flat at the caudal end except for a pair of small notches. It has eight pairs of costals, a preneural and seven contiguous neurals including N1. The nuchal is broadly C-shaped with a distinctly concave anterior margin that extends nearly the full width of the nuchal. The neural series is incomplete but retains reversed coffin-shaped (hexagonal) N2–4. The lateral margins of the costals thicken at their ends. The preserved rib tips are strongly compressed and very short. The free margins of C6–7 are marked by an eave-like overhang of the dorsal surface. The caudal margin of the carapace is nearly straight except for small notches at the perimeter of the C7–8 sutures. The eighth costals are not notably enlarged or reduced.

Description of the Hypodigm—The hypodigm generally resembles the type in preserved parts and provides evidence for some parts missing in the type. UCMP 117370 and UCMP 130017 preserve additional neurals. The preneural is rectangular (UCMP 130017) to trapezoidal (UCMP 117370). N1 is rectangular in UCMP 117370 but is hexagonal in UCMP 130017. N2 is hexagonal in UCMP 117370 but octagonal in UCMP 130017. Both have N3–4 with a reversed hexagonal pattern. UCMP 130017 (Figs. 25–26) preserves a reversed hexagonal N5, quadratic N6, and pentagonal N7 with mutual contact of C7 behind N7. The posterior margin of the carapace in UCMP 130017 is slightly concave and includes all of the eighth costal margins.

DISCUSSION

The positioning and intimate contact of the entoplastron with the hyoplastra in *Derrisemys* and *Plastomenoides* is unique within the Trionychidae. Typically there is a loose and kinetic joint between the entoplastron plus epiplastra and the hyoplastra in *Plastomenus* trionychids in general and their sister taxon Carettochelyidae. The closure of plastral fontanelles, keystone placement and morphology of the entoplastron and isolation of the kinetic epiplastra thus marks a major departure from the typical trionychid pattern. The functional significance of these morphologies and detailed relationships of these taxa will be discussed in detail in a companion study.

Plastomenines are widely distributed in the western United States both geographically and temporally (Fig. 2). *Plastomenus*-like plastomenines are present in the Late Cretaceous (Gilmore 1917, Mateer 1981) and Paleocene (UCMP 130075, NMMNH P-22042). *Plastomenus* s. s. is present from the late Paleocene (Clarkforkian NALMA, UMMP V65240) to late middle Eocene (Duchesnean NALMA (Eaton et al. 1999)). *Derrisemys* and *Plastomenoides* are present in earliest Puercan NALMA and, while *Plastomenoides* is not definitely known from the Lancian NALMA, the degree of morphological separation between these taxa indicates a Cretaceous divergence. Thus by the latest Cretaceous and persisting into the early Paleocene, there are at least three clades of plastomenines in North America. These are reduced to one in the latest Paleocene with *Plastomenus* persisting into the late middle Eocene. *Plastomenus* has yet to be found in Uintan NALMA deposits of Wyoming and northern Utah and appears to retreat south to southern Utah (Eaton et al. 1999) during the last of its reign. Although the systematics of North American trionychines is in much need of revision, they also seem to exhibit a similar pattern of high diversity in the Lancian NALMA that persists into the early middle Eocene (Bridgerian NALMA), but then is reduced to a single genus.

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LITERATURE CITED

Batsch, A.J.G.C. 1788. Versuch einer Anleitung zur Kenntniss und Geschichte der Thiere und Mineralien. Vol. 1. Akaademische Buchhandlung, Jena. viii + 528 pp.

Berggren, W.A., D.V. Kent, C.C. Swisher, and M.-P. Aubry. 1995. A revised Cenozoic geochronology and chronostratigraphy. *Society for Sedimentary Geology (SEPM), Special Publication* 54:129–212.

Cope, E.D. 1872. Descriptions of some new Vertebrata from the Bridger group of the Eocene. *Paleontological Bulletin* No. 1:1–6.

Cope, E.D. 1873. Some extinct turtles from the Eocene strata of Wyoming. *Proceedings of the Academy of Natural Sciences, Philadelphia* 1873:277–279.

Eaton, J.G., J.H. Hutchison, P.A. Holroyd, W.W. Korth, and P.M. Goldstrand. 1999. Vertebrates of Turtle Basin local fauna, middle Eocene, Sevier Plateau, south-central Utah. *Utah Geological Survey Miscellaneous Publication* 99-1:463–468.

Fitzinger, L.J.F.J. 1826. Neue classification der Reptilien nach ihren Natürlichen Verwendtschaften nebst einer Verwandtschafts-Tafel und einen Verzeichnisse der Reptilien-Sammlung des k. k. Zoologischen Museum zu Weien. J.G. Hüber, Wien, viii+66 pp.

Gilmore, C.W. 1917. Vertebrate faunas of the Ojo Alamo, Kirtland, and Fruitland Formations. *U.S. Geological Survey Professional Paper* 98:279–308.

Hay, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. *U.S. Geological Survey Bulletin* 179.

Hay, O.P. 1907. Descriptions of seven new species of turtles from the Tertiary of the United States. *Bulletin of the American Museum of Natural History* 23:847–863.

Hay, O.P. 1908. The fossil turtles of North America. *Carnegie Institution of Washington Publication* 75:1–568.

Hay, O.P. 1930. Second bibliography and catalogue of the fossil Vertebrata of North America, v. I. *Carnegie Institution of Washington Publication* 390(2):1–1974.

Holroyd, P.A., and J.H. Hutchison. 2002. Patterns of geographic variation in latest Cretaceous vertebrates: Evidence from the turtle component. *In* J.H. Hartman, K.R. Johnson, and D.J. Nichols (eds.). The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous. *Geological Society of America Special Paper* 361:177–190.

Hutchison, J.H., and J.D. Archibald. 1986. Diversity of turtles across the Cretaceous/Tertiary boundary in northeastern Montana. *Palaeogeography, Palaeoclimatology, Palaeoecology* 55(1):1–22.

Hutchison, J.H., and P.A. Holroyd. 2003. Late Cretaceous and early Paleocene turtles of the Denver Basin. *Rocky Mountain Geology* 38(1):1–22.

Kues, B.S. 1993. Bibliographic catalogue of New Mexico vertebrate fossils. New Mexico *Museum of Natural History and Science Bulletin* 2:199–279.

Mateer, N.J. 1981. The reptilian megafauna from the Kirtland Shale (Late Cretaceous) of the San Juan Basin, New Mexico. Pp. 49–75 *in* S.G. Lucas, J.K. Rigby, Jr., and B.S. Kues. (eds.). Advances in San Juan Basin Paleontology. University of New Mexico Press, Albuquerque, New Mexico.

Matthew, W.D. 1937. Paleocene faunas of the San Juan Basin, New Mexico. *Transactions of the Philosophical Society* 30:1–510.

Meylan, P.A. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). *Bulletin of the American Museum of Natural History* 186:1–101.

Rafinesque, C.S. 1832. Description of two new genera of soft shell turtles of North America. *Atlantic Journal and Friend of Knowledge*, Philadelphia 1(2):64–65.

Sullivan, R.M., and S.G. Lucas. 1986. Annotated list of lower vertebrates from the Paleocene Nacimiento Formation (Puercan-Torrejonian), San Juan Basin, New Mexico. Journal of Herpetology 29:202–209.

Williamson, T. E. and S. G. Lucas. 1993. Paleocene vertebrate paleontology of the San Juan Basin, New Mexico. New Mexico Museum of Natural History and Science Bulletin 2:105–144.

Woodburne, M. O. (ed.). 2004. Late Cretaceous and Cenozoic mammals of North America. Biostratigraphy and Geochronology. Columbia University Press, New York. 391 p.

Zangerl, R. 1969. The turtle shell. Pp. 311–339 *in* C. Gans, A. Bellairs, and T.S. Parsons (eds.). Biology of the Reptilia, vol. I. Academic Press, New York.