Late Cretaceous and early Paleocene turtles of the Denver Basin, Colorado

J. Howard Hutchison and Patricia A. Holroyd*

Museum of Paleontology, 1101 Valley Life Sciences Building, University of California, Berkeley, CA 94720-4780, U.S.A.

Author to whom correspondence should be addressed: pholroyd@uclink4.berkeley.edu.

ABSTRACT

The record of turtles in the Denver Basin spans four formations (Fox Hills, Laramie, Arapahoe, and Denver) that range from Late Cretaceous (Lancian) to early Paleocene (Puercan) in age. We recognize at least fifteen distinct, although fragmentary, species-level taxa, including Pleurosternidae (*Compsemys*), Baenidae (*Neurankylus, Plesiobaena, Stygiochelys,* and *Palatobaena*), Kinosternia (*Hoplochelys*), Adocidae (*Adocus*), Nanhsiungchelyidae (*Basilemys*), Trionychidae (*Axestemys, Aspideretoides, Helopanoplia,* and another plastomenine), Macrobaenidae, and Chelydridae. Notable among these are the best-preserved skull of *Compsemys*, a new chelydrid genus, the most northerly confirmed record of *Hoplochelys*, and the most southerly records of *Helopanoplia, Stygiochelys,* and Macrobaenidae in the Rocky Mountain region. We also present evidence for synonymy of *Paleotrionyx* and *Conchochelys* with *Axestemys*, and the first cranial material assignable to *Axestemys*. The early Paleocene (Puercan) part of the Denver Formation yielded the most diverse assemblage, followed by the Cretaceous (Lancian) part of the Denver Formation and Laramie Formation. The Cretaceous samples are not demonstrably different from more northerly comparable faunas, but the more diverse Paleocene part of the Denver Formation exhibits a unique combination of taxa compared to contemporaneous faunas to the north and south.

KEY WORDS: Chelonii (= Chelonia), Paleocene, Cretaceous, biogeography, Denver Basin, Arapahoe Formation, Fox Hills Sandstone, Denver Formation, Laramie Formation.

INTRODUCTION

Most of our knowledge of latest Cretaceous to early Tertiary nonmarine turtle faunas of North America comes from the Rocky Mountain region, stretching latitudinally from southern Canada to Texas (e.g., Estes, 1964; Hutchison and Archibald, 1986; Bryant, 1989; Holroyd and Hutchison, 2002; Williamson and Lucas, 1993; Kues, 1993; Tomlinson, 1997). Those of Alberta, Montana, Wyoming, and New Mexico are the most diverse and best known. Throughout this area and temporal interval, the turtle faunas are highly diverse, dominated by aquatic taxa, and moderately homogenous in taxonomic composition. Biogeographic provincialism in a variety of organisms and on a variety of scales, however, has been suggested to have existed in this time period (e.g., Lehman, 1987, dinosaurs; Nichols
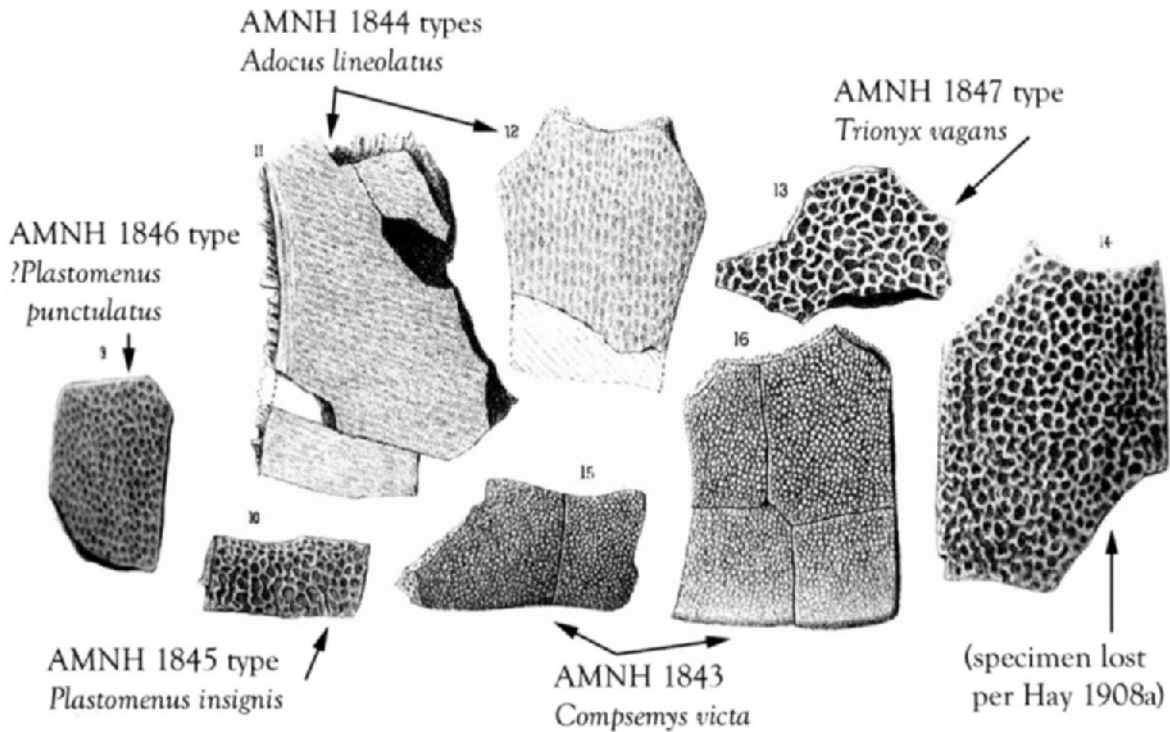
and Fleming, 1990, pollen; Holroyd and Hutchison, 2002, turtles).

The central latitudinal position of the Denver Basin, Colorado, within the Rocky Mountain corridor occupies a notable gap between the northern and southern faunas. Cope (1869) described the first fossil turtles from the Denver Basin and figured them all in 1875 (modified here as Fig. 1). Knowledge of the turtle faunas of the Denver Basin remained unchanged until the present, except for addition of a baenid by Archibald and Hutchison (1979). They remain among the most poorly sampled assemblages in the Rocky Mountain region. In addition to biogeographic insights that can be gained by a better understanding of the Denver Basin turtle fauna, these records can provide useful

Bijou Creek turtle fauna
40 mi east of Denver

1 cm

AMNH 1844 types
Adocus lineolatus

AMNH 1847 type
Trionyx vagans

AMNH 1846 type
*?Plastomenus
punctulatus*

AMNH 1845 type
Plastomenus insignis

AMNH 1843
Compsemys victa

(specimen lost
per Hay 1908a)

Figure 1. Bijou Creek turtle fauna, modified after Cope (1875, pl. 6); Cope's original identifications are shown in small type (upper right). *9*, Plastomeninae, indet. [= *Plastomenus punctulatus*]; *10*, Plastomeninae, indet. [= *Plastomenus insignis*]; *11* and *12*, *Adocus* sp. [= *A. lineolatus*]; *13* and *14*, Trionychidae, indet. [= *Trionyx vagans*]; and *15* and *16*, *Compsemys victa* [= *C. victus*].

information on changes in local hydrology, climate, and biostratigraphy here as they have elsewhere (e.g., Holroyd et al., 2001; Holroyd and Hutchison, 2000, 2002; Hutchison, 1982, 1992, 2000).

Here we report on the collections of fossil turtles from geographically and stratigraphically constrained localities in the Denver Basin, representing the Late Cretaceous (Lancian North American Land Mammal Age) and early Paleocene (Puercan NALMA). Although many of the specimens are fragmentary in nature, they are valuable as the first records of many taxa in the Denver Basin. In many cases, these records also represent the only fossils that are likely to be recovered from the localities, as they were exposed during the course of construction and are now lost or covered. The stratigraphic framework and age assessments for the discussions below follow Raynolds (2002) and Eberle (this

issue). The Denver Formation comprises part of the D1 sequence in the Denver Basin. This sequence is divided into Lancian and overlying Puercan components.

Abbreviations used: AMNH — American Museum of Natural History, New York, New York; DMNH — Denver Museum of Nature & Science, Denver, Colorado; NALMA — North American Land Mammal Age; UCM — University of Colorado Museum, Boulder, Colorado; UCMP — University of California Museum of Paleontology, Berkeley, California; and UW — University of Wyoming, Laramie, Wyoming.

SYSTEMATIC PALEONTOLOGY

**Order Chelonii Brongniart, 1800
Cryptodiramorpha Lee, 1995**

Pleurosternidae Cope, 1868
Compsemys Leidy, 1856
Compsemys victa Leidy, 1856
Figures 1.15–1.16 and 2A–D

Referred material.—Laramie Formation, Lancian — DMNH loc. 2364: DMNH 42938, peripheral margin fragment. UCM loc. 73175: UCM 38798, two plastron fragments. UCM loc. 77062: UCM 38777, two neurals; UCM 38778, peripheral fragment and hyo- or hypoplastron fragment; UCM 38779, costal fragments; and UCM 42343, neural and distal costal. UCM loc. 78193: UCM 42317, plastron fragment. Denver Formation (D1 sequence), Puercan — DMNH loc. 2387: DMNH 45197, shell fragment. DMNH loc. 2397: DMNH 45118, four peripherals and shell fragments. DMNH loc. 2549: DMNH 45140, three carapace fragments. DMNH loc. 2550: DMNH 45135, peripheral. DMNH loc. 2558: DMNH 44624, hypoplastron fragment. DMNH loc. 2560: DMNH 45134, four shell fragments. DMNH loc. 2561: DMNH 45181, fragment of a bridge peripheral. DMNH loc. 2598: DMNH 45080, crushed partial shell. UCM loc. 77267: UCM 85954, neural. UCM loc. 77275: UCM 85953, peripheral 10. UCM loc. 78192: UCM 63527, costal 1. UCM loc. 82126: UCM 37761, peripheral 7. UCM loc. 83196: UCM 49223, relatively complete but partially crushed skull lacking the left temporal area and parts of the posterior margin, most of the right and left dentaries. "Bijou Creek" (locality and formation unknown): AMNH 1843, two peripheral fragments.

Description.—The skull, UCM 49223, is deep, triangular in dorsal view, and tapers to a point anteriorly. The orbits are small, widely spaced, and vertically oriented. The tympanic cavity is small and enclosed posteriorly by contact of the quadrate and squamosal. The nasal opening is small and overhung by the nasals. The premaxillae turn down to form a sharply pointed beak. The triturating surface has a medial ridge lateral to the palatines and broadens anteriorly. The nasals are large, and there is a large dorsal exposure of the prefrontals. The frontals are isolated from the orbits and contact the nasal anteriorly, prefrontals and postorbitals laterally, and parietals posteriorly. There is no cheek emargination and probably little temporal emargination. The foramina posterior canalis carotici interni are exposed ventrally and lie lateral to the anterior part of the basisphenoid. Estimated skull length of UCM 83196 is 80 mm. The lower jaws are hooked anteriorly with their tip fitting into a pit in the premaxillae. UCM 83196 is the specimen reported by Hutchison and Archibald (1986) to be under study by Gaffney.

The associated measurable peripherals of DMNH 45118 have the following free margin lengths: peripheral 2 = 26.8 mm; peripheral 4 = 31.5 mm; and peripheral 8 = 30.0 mm. The central neural (UCM 38777, probably neural 2) is hexagonal, smooth, flat, about equidimensional, and has a midline length of 24 mm. The latter would yield a carapace length of about 292 mm. The first neural under the same number is 28.1 mm long. The proximal part of peripheral 10 (e.g., Fig. 1.16) exhibits the typical restricted peripheral contact of costal 8 to peripheral 10. The remaining shell fragments exhibit the fine, regular, and low, beaded and ridged pattern characteristic of *Compsemys* (Fig. 1.15–1.16).

Discussion.—Gaffney (1972, p. 291) synonymized all the previously named taxa under the single species *Compsemys victa*. While the shell fragments are unremarkable, the skull (Fig. 2) is the first reported for *Compsemys*. Although the Denver Basin skull was not associated with a shell, the distinctive finely beaded and ridged sculpture of the shell is replicated on the skull roof. Moreover, we can confirm this association based on an associated skull and shell (UCMP 131103) known from the Tullock Member of the Fort Union Formation of eastern Montana.

Using the phylogenetic scheme of Gaffney and Meylan (1988), the skull falls within the Cryptodiramorpha Lee, 1995 (= Cryptodira of Gaffney and Meylan, 1988) in having a processus trochlearis oticum and a processus pterygoideus externus that is flattened laterally. It falls within the Selmacryptodira in having the middle ear floored ventrally, absence of teeth, and closure of the interpterygoid space. The skull resembles the Daiocryptodira in the anterior mutual contact of the pterygoids, enclosure of the incisura columellae, and absence of the dorsal process of the epiplastron. It resembles pleurosternids in the broad contact of the squamosal and parietal (from UCMP 131103 and independently derived in Baenina), broad anterior triturating surface, large dorsal lappet of the prefrontal, and similar sculpture of the skull and shell. The shell more closely resembles that of the pleurosternids in the sculpture, loss of the cervical scale, broad mutual contact of the mesoplastra, and broad plastral lobes. *Compsemys* may thus be considered as either a basal taxon of the Daiocryptodira or a highly derived member of the Pleurosternidae with independent development of the supposed apomorphous daiocryptodiran characters, none of which is unique to the Daiocryptodira.

The extensively roofed-over skull, acutely pointed rostrum and jaws (UCMP 131103), and clo-
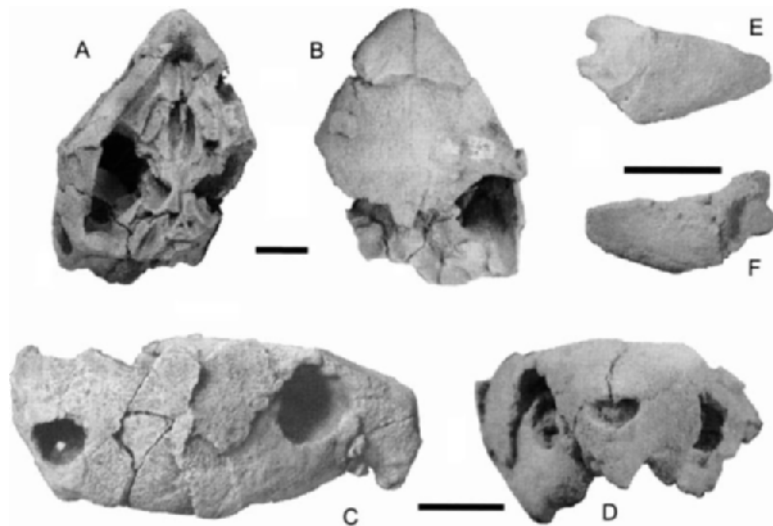
Figure 2. *Compsemys victa* skull and mandible, UCM 49223. Skull in ventral (*A*), dorsal (*B*), lateral (*C*), and anterior (*D*) views. Partial right dentary in lateral (*E*) and medial (*F*) views. All scale bars = 2 cm.

sure of the tympanic opening posteriorly functionally resembles extant *Platysternon* Gray, 1831 (Gaffney, 1979, figs. 221–222) and some chelydrids (Gaffney, 1979, figs. 219–220). The skull was apparently not retractable into the shell, and the simple but sharply pointed jaws indicate a carnivorous turtle.

The shell, however, is derived in some aspects (e.g., first peripherals meet in front of the nuchal) and primitive in others (e.g., well-developed mesoplastra, strong plastral buttresses). The high-domed and smoothly curved shell of *Compsemys* (Gilmore, 1919, pl. 4) more closely resembles the general shell shape of extant *Emydoidea* (Gray, 1870). This combination of skull and shell shape is unique. The globose shell as well as the usual presence of the more complete specimens in fine-grained sediments suggests a quiet-water turtle. *Compsemys* in North America ranges in age from Turonian (Eaton et al., 1999) to mid-Paleocene (JHH, personal observation), and Broin (1977, p.

5) reported it from the Paleocene of France.

Baenidae Cope, 1882
Baenini (Cope, 1882) Gaffney and Meylan, 1988
Neurankylus Lambe, 1902
Neurankylus eximius Lambe, 1902

Referred material. — Denver Formation (D1 sequence), Lancian — DMNH loc. 2368: DMNH 45240, plastron and partial carapace.

Discussion. — The plastron from Westmore Golf Course exhibits the typical broad and rounded anterior and posterior lobes and restricted extragular scales of *Neurankylus* (Gaffney, 1972, fig. 38). Another related species, *Hayemys latifrons* (Hay, 1908a) is also known from the Late Cretaceous but only from its skull. Some of the shells referred to *Neurankylus* may ultimately prove to belong to *Hayemys*. Only a single species of *Neurankylus*, *N. eximius*, is currently recognized (Gaffney, 1972; Brinkman and Nicholls, 1993a), and material referred to it ranges

in age from Campanian (Brinkman and Nicholls, 1993a) to mid-Paleocene (Torrejonian NALMA, Sullivan and Lucas, 1986).

Baenodd Gaffney, 1972
Plesiobaena Gaffney, 1972
Plesiobaena cf. *P. antiqua* (Lambe, 1902)

Figures 3, 4B, and 6A

Referred material. — Laramie Formation, Lancian — UCM loc. 78193: UCM 49318, fused posterior part of skull. UCM loc. 80013: UCM 43677, anterior part of shell. Denver Formation (D1 sequence), Puercan — DMNH loc. 2559: DMNH 44628, plastron lacking anterior tip.

Description. — Of the Cretaceous specimens, the posterior part of the skull (UCM 49318, Fig. 4B) is co-ossified, indicating an adult. The small size of the skull, small relative size of the condyles, and general morphology most closely resemble that of *Plesiobaena antiqua*. The anterior part of the shell, UCM 43677 (Fig. 6A), is co-ossified, thus obscuring the sutures. The scalation of the marginals is simple and lacks the extra cervical and prepleural scales present in the Baenini; the cervical scale is broad as in *Plesiobaena antiqua* and unlike *Neurankylus*. The anterior lobe closely resembles that of *P. antiqua*, as figured by Gaffney (1972, p. 11).

Of the Paleocene specimens, the plastron of DMNH 44628 (Fig. 3) has the sutures mostly fused or in the process of fusion, indicating an adult turtle with an estimated plastral length of about 270 mm. The bridge area is longer than the anterior and posterior lobes. The anterior lobe converges evenly toward the anterior point while the posterior lobe is rectangular with a broad and shallow anal notch. The sulci are finely incised or indeterminate in
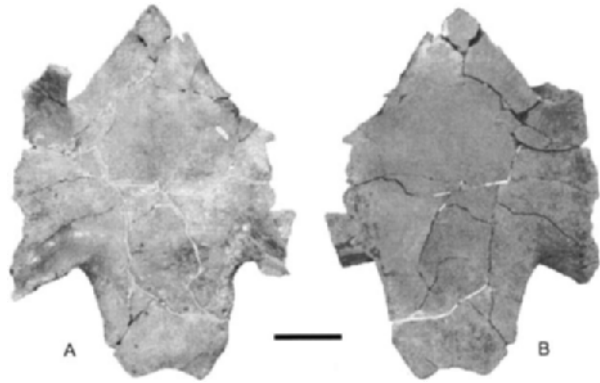
Figure 3. *Plesiobaena* cf. *P. antiqua*, DMNH 44628, plastron. *A*, dorsal and *B*, ventral views. Scale bar = 5 cm.
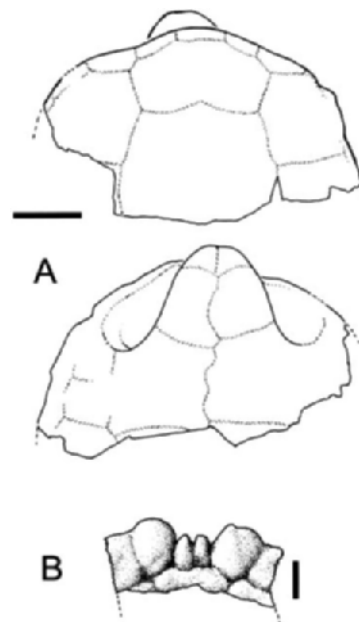

Figure 4. *A*, *Stygiochelys estesi*, UCM 48218, skull, ventral view; and *B*, *Plesiobaena* cf. *P. antiqua*, UCM 49318, skull in ventral (above) and posterior views. Both scale bars = 1 cm.

Figure 5. *Palatobaena bairdi*, UCM 49229, right dentary, dorsal (above) and lateral views. Scale bar = 1 cm.

Figure 6. Baenidae. *A*, *Plesiobaena* cf. *P. antiqua*, UCM 43677, anterior part of shell in dorsal (above) and ventral views; scale bar = 5 cm. *B*, Eubaenina indet., UCM 45124, anterior half of nuchal, dorsal view; scale bar = 1 cm.

several places. The humeral-pectoral sulcus lies well forward and is broadly anteriorly concave.

Discussion. — *Plesiobaena* is a rather generalized and long ranging (Campanian–Tiffanian; Gaffney, 1972) baenid known only from the Rocky Mountain region. Of the four baenid genera known from plastra in the early Paleocene, DMNH 44628 differs from *Neurankylus* Lambe (1902), *Eubaena* Hay (1908a), and *Stygiochelys* Gaffney and Hiatt (1971) and resembles *Plesiobaena* in the broad and rectangular posterior lobe, long bridge, strongly anteriorly

tapering anterior lobe, and anteriorly situated and broadly anteriorly concave pectoral-humeral sulcus. Of the two described species, *P. putoria* Gaffney, 1972 is known from the mid-Paleocene Torrejonian and Tiffanian NALMAs of Wyoming. *P. antiqua* is known from the Late Cretaceous of Alberta (mid-Campanian), Wyoming and Montana (Maastrichtian), as well as the early Paleocene (Puercan) of Montana (Gaffney, 1972; Hutchison and Archibald, 1986). The two species of *Plesiobaena* are not diagnosed on shells but are referred based on age. A fifth genus, *Palatobaena*, is known only from skull and jaws.

Plesiobaena sp.

Referred material.—Denver Formation (D1 sequence), Puercan — UCM loc. 82126: UCM 48399, partial plastron.

Description.—The partial plastron of UCM 48399 is poorly preserved and lacks much of the posterior lobe, bridge areas, and much of the edge of the anterior lobe. It has an estimated length of about 210 mm and is co-ossified.

Discussion.—Narrow anterior lobe and long bridge are characteristic of *Plesiobaena*, but this specimen differs from known species in being about 25 percent smaller in size. These distinctions may represent another species, different sex, or individual variation, although the first two options seem more likely based on comparisons to similar size disparities in the UCMP collection from Montana.

Baenini (Cope, 1882) Gaffney and Meylan, 1988
Eubaenina (Williams, 1950) Gaffney, 1972
Stygiochelys Gaffney and Hiatt, 1971
Stygiochelys estesi Gaffney and Hiatt, 1971
Figure 4A

Referred material.—Denver Formation (D1 sequence), Puercan — UCM loc. 77277: UCM 48218, skull. UCM loc. 77275: UCM 43739, posterior part of skull and isolated skull fragments.

Discussion.—The virtually complete skull UCM 48218 (Fig. 4A) agrees closely with that of *Stygiochelys estesi* figured by Gaffney (1972, figs. 20–21 and 58; 1979, fig. 163). The Denver specimens are the most southerly records thus far of the genus with Montana as the most northerly record. The genus is only known from the Lancian and Puercan.

Palatobaena Gaffney, 1972
Palatobaena bairdi Gaffney, 1972
Figure 5

Referred material.—Denver Formation (D1 sequence), Puercan — UCM loc. 82126: UCM 37738, skull and lower mandible fragments; UCM 49229, left dentary; and UCM 49230, right lower mandible. UCM loc. 77275: UCM 49224, right and left dentary.

Discussion.—*Palatobaena* is a peculiar brevirostrine baenid with broad triturating surfaces (Fig. 5) generally interpreted as a molluscivorous adaptation (Archibald and Hutchison, 1979). The genus has two recognized species, one of which occurs in Eocene (Wasatchian NALMA) strata. The other, *P. bairdi*, ranges in age from late Maastrichtian (Lancian NALMA) to mid-Paleocene (Tiffanian NALMA). This genus is known only from skulls and

jaws, although some of the shell taxa unknown from skulls may eventually prove to belong to this form. *P. bairdi* from the Denver Formation was mentioned previously by Archibald and Hutchison (1979, p. 177).

Eubaenina indet.
Figure 6B

Referred material.—Denver Formation (D1 sequence), Lancian — DMNH loc. 2389: DMNH 45124, distal half of nuchal.

Description and discussion.—A subadult (unfused) nuchal lacking the posterior moiety, UCM 45124 (Fig. 6B), exhibits the presence of prepleural sulci and the four scales between the first marginals typical of the Baenini. The lateral set of these four scales is not reduced or displaced toward the free margin as in Baenina and *Eubaena* Hay, 1908a (UCMP 107617) but are larger than the central set as in *Stygiochelys* (UCMP 113316), "*Baena*" *hatcheri* Hay, 1908a (Gaffney, 1972, fig. 43), and *Boremys pulchra* (Gilmore, 1935, fig. 9, pl. 15). Of these last three taxa, UCM 46124 most closely resembles the pattern in "*B.*" *hatcheri*. However, the extent of morphologic variation in this area of the shell is not well understood in most of these taxa, and the shell of the eubaenine *Palatobaena* is unknown.

Baenodd indet.

Referred material.—Denver Formation (D1 sequence), Lancian — UCM loc. 77283: UCM 34643, poorly preserved part of top of carapace. UCM loc. 77283: UCM 96593, parts of two fused bridge peripherals. Denver Formation (D1 sequence), Puercan — DMNH loc. 2402: DMNH 45119, carapace fragments. DMNH loc. 2549: DMNH 45138, posterior peripheral. UCM loc. 77275: UCM 85953, central part of poorly preserved plastron.

Discussion.—The various shell fragments exhibit morphologies typical of members of the Baenodd Baenidae (e.g., division of the first vertebral, supernumary cervical/marginal scales, strong serration of posterior peripherals, carapacial fontanelles, contact of vertebral 5 with the shell margin, and/or fusion of the narrow plastral lobes). We made no attempt to further identify the taxa in light of the poor understanding of the shells of several members of this group.

Baenidae, genus and species indet.

Referred material.—Laramie Formation, Lancian — UCM loc. 77062: UCM 42347, dorsal part of carapace and plastron fragment. Denver Formation (D1 sequence), Lancian — DMNH loc. 2372: DMNH

43155, fragment of buttress area of plastron. Denver Formation (D1 sequence), Puercan — DMNH loc. 2387: DMNH 43188, proximal costal 1. DMNH loc. 2401: DMNH 45121, hyo- or hypoplastron fragment and costal fragments. DMNH loc. 2553: DMNH 44620, carapace fragment with part of neural area and other fragments. DMNH loc. 2561: DMNH 44627, shell fragments. DMNH loc. 2563: DMNH 45100, carapace fragments. DMNH loc. 2591: DMNH 46649, humerus lacking proximal end. UCM loc. 77275: UCM 85952, carapace fragments. UCM loc. 82126: UCM 37760 (in part), fragment of opisthotic part of skull; UCM 37767, plastron fragments; and UCM 37762, proximal costal and part of costal 1.

Discussion. — Various shell, limb and skull fragments are included here based on fusion of the bones, lack of distinctive sculpture, or general similarity to baenids.

Polycryptodira Gaffney, 1984
Macrobaenidae Sukhanov, 1964
Macrobaenidae, genus and species indet.
Figure 7G

Referred material. — Denver Formation (D1 sequence), Puercan — UCM loc. 82126: UCM 37760 in part, ventral moiety of bridge peripheral.

Description. — An isolated bridge peripheral (UCM 37760, Fig. 7G) lacking the dorsal moiety has a roughly triangular cross section, strongly upturned lateral carina, and a distinctly rounded pit in the central area for the costal rib end. The ventromedial margin is marked by a shallow, matrix-filled trough about three-quarters of the total length. The length of UCM 37760 is 45 mm.

Discussion. — The large size, thick cross section, lack of well-developed suture with the plastron, and distinctly rounded pit for the rib end are consistent with reference to the Macrobaenidae. Macrobaenids are reported from the Campanian to late Paleocene (Clarkforkian NALMA) in North America (e.g., Holroyd and Hutchison, 2002; Holroyd et al., 2001) and Early Cretaceous to Paleocene of Asia (Sukhanov, 2000).

Cryptodira Cope, 1868
Chelydridae (Agassiz) Gray, 1870
Denverus middletoni, new genus and species
Figures 8 and 9

Type. — UCM 48400, left hyoplastron, right hypoplastron, right and left peripheral 7, left peripheral 6 and 8, three neurals, eight partial costals, one partial suprapygal, and shell fragments.
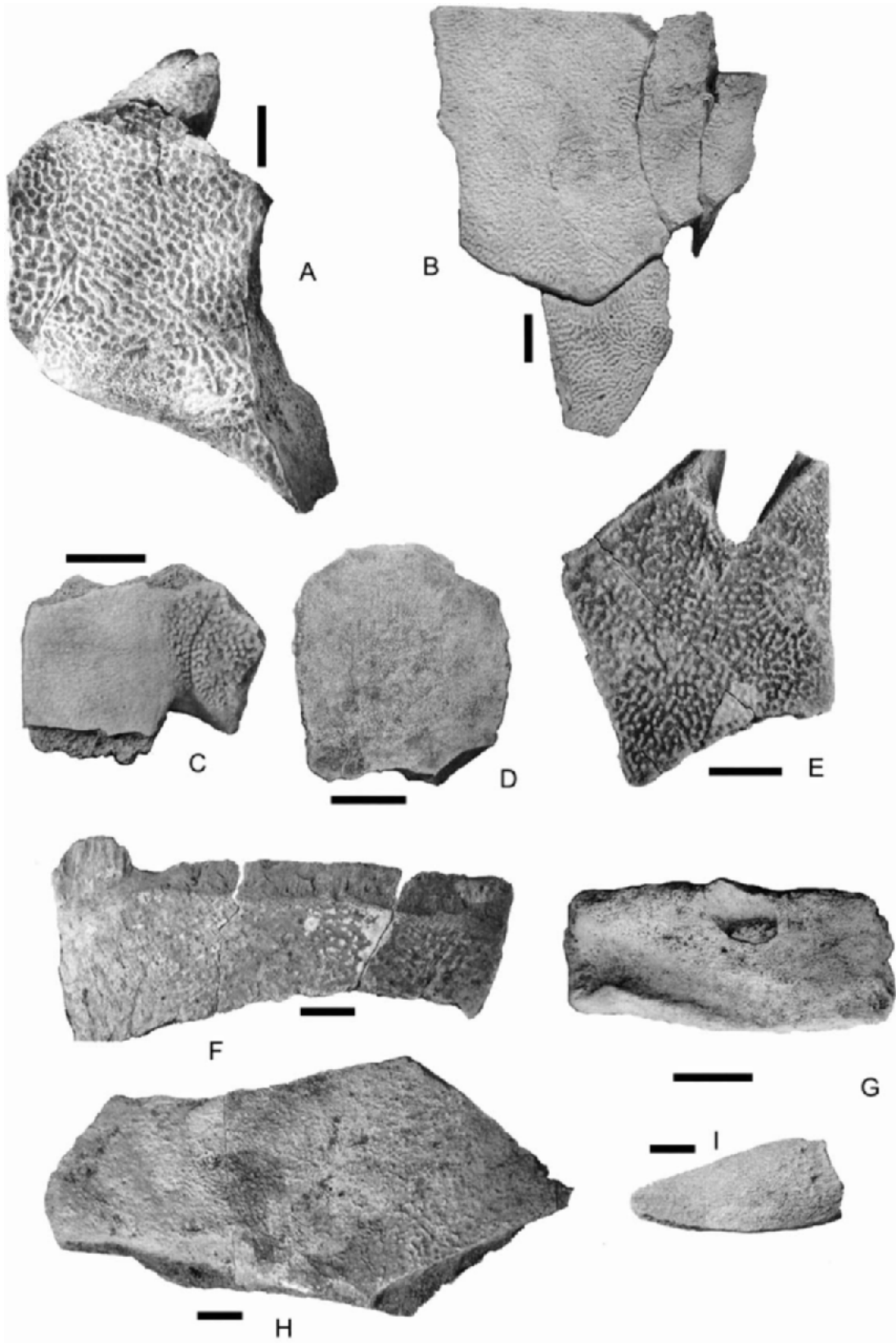
Type locality. — UCM locality 79013, El Paso County, Colorado, Denver Formation (D1 sequence), Puercan.

Diagnosis. — Plastron without fontanelles; bridge area of plastron relatively wide, hyoplastral buttress terminates at peripheral 2; hypoplastral buttress terminates in middle of peripheral 7; lateral length of hypoplastron as long or longer than medial length; plastron attached to carapace with gomphotic sutures; bridge peripherals inflated with bone between dorsal and ventral arms medially; neurals thick centrally, thin laterally, and forming a central carina; dorsolateral and lateral carina present; area below posterodorsal part of pleural scales thickened; costals with coarse corrugations extending posterior to the interpleural sulci. Denverus resembles Protochelydra Erickson, 1973 and Chelydropsis Peters, 1868, and it differs from extant Chelydra Schweigger, 1812 and Macroclemys Gray, 1855 in the lack of plastral fontanelles, presence of well-developed pits in the bridge peripherals for reception of the plastral digitations, and anterior extent of the hyoplastral buttress. It differs from Chelydropsis and Protochelydra in the relatively greater anteroposterior thickness of the bridge, strong development of the dorsal and dorsolateral carina, and hypoplastral buttress terminating on peripheral 7 rather than peripheral 8.

Referred material. — Denver Formation (D1 sequence), Puercan — DMNH loc. 2549: DMNH 45139, proximal costal.

Etymology. — Denverus for Denver Basin and middletoni for Mike Middleton, who collected the specimen.

Description. — The associated specimen (UCM 48400) preserves parts of the plastron and carapace. The hyo- and hypoplastra are similar in shape and have coarse medial and lateral sutures (Fig. 8C). Faintly impressed sulci for the abdominal scales cross the medial part of the bridge areas and do not extend to the plastral midline. A couple of the notches between the lateral dentations appear to be passages for musk ducts. The sulci for the inframarginals are very weak, but at least two (and probably three) inframarginals were present on each side. The femoral-anal sulcus crosses the posterior tip of the hypoplastron. The central carina extends at least from neural 1 to the suprapygal area. The peripherals 3 and 5–8 are represented (Fig. 9). Peripheral 3 has a slanting trough for reception of the costal 1 rib end and long narrow trough for the terminal extension of the hyoplastral buttress. The hyoplastral buttress extends anteriorly across peripheral 3 and probably terminates on peripheral 2. Peripher-

als 5–8 contribute to part of the plastral-carapace articulation and preserve a line of shallow pits to receive the plastral dentations. These also exhibit a lateral carina and have large pits to receive the rib ends of the costals. The angle between the dorsal and ventral arms of peripherals 5–8 are filled in with bone, making them quite stout. The marginal scales extend nearly to the top of the peripherals, and the pleural-marginal sulcus is marked by a distinct step. The costal fragments (Fig. 8A–B) exhibit a raised area near the posterodorsal corner of the pleural scales. A bend in the arch of the costal occurs at the vertebral-pleural sulcus with a thickening of the costal just lateral to the sulcus, thus indicating the presence of dorsolateral carina. Coarse corrugations emanate posteriorly from the interpleural sulci on some costals (Fig. 8B). The neurals are thick in the center and have a central carina but thin greatly laterally (Fig. 8D).
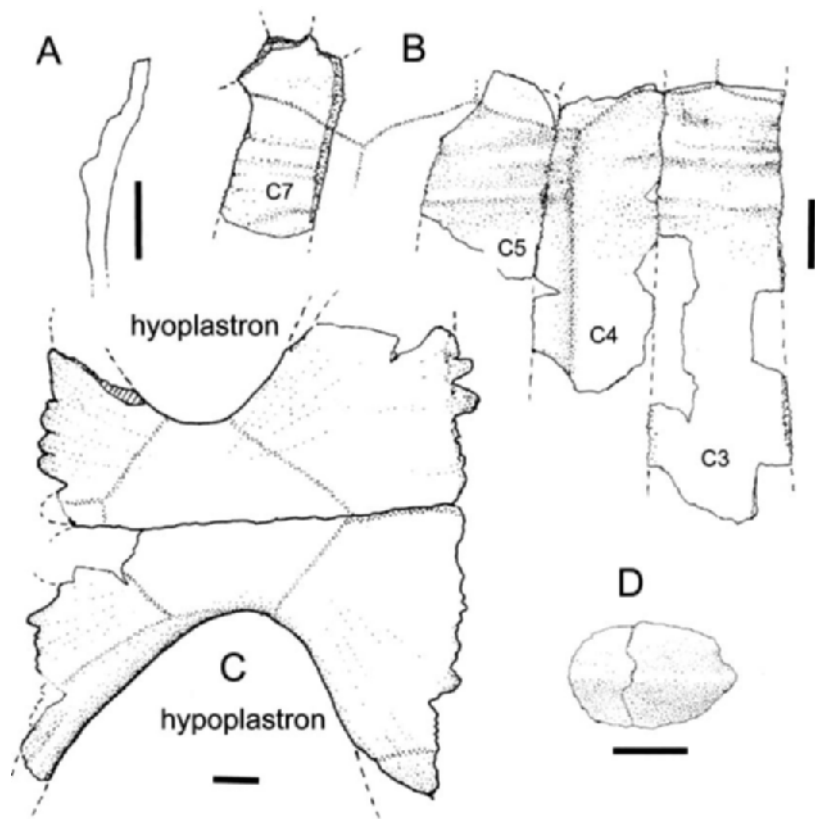
Figure 8. *Denverus middletoni,* n. gen. and n. sp. UCM 48400, type. *A,* Right costal 5, outline of anterior suture. *B,* Right costals 3–5 and 7, external views. *C,* Left hyoplastron (reversed) and right hypoplastron, ventral views. *D,* Neural 1, dorsal view. All scale bars = 1 cm.

Figure 7, facing page. *Basilemys* cf. *B. sinuosa; A,* DMNH 33304, plastron fragment, ventral view. *Helopanoplia* cf. *H. distincta; B,* UCM 42334, hypoplastron and anterior part of xiphiplastron fragments, and *E,* DMNH 45108, xiphiplastron fragment, ventral views. *Hoplochelys crassa;* DMNH 45102, costal fragment, external view. *Axestemys* cf. *A. puercensis; F- H,* DMNH 44622, plastron fragments, and *I,* ungual phalanx, ventral views; Macrobaenidae indet.; UCM 37760, partial bridge peripheral, medial view. All scale bars = 1 cm.
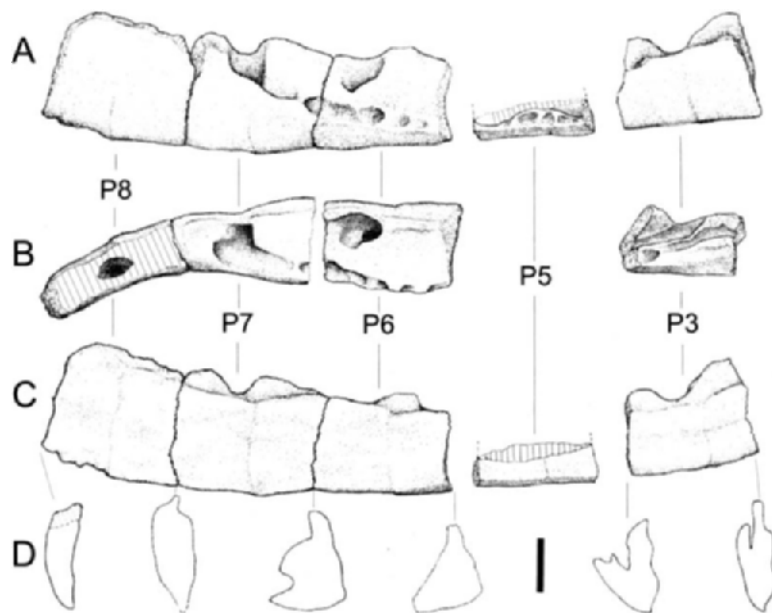
Figure 9. *Denverus middletoni,* n. gen. and n. sp. UCM 48400, type, left peripherals 3, peripherals 6–8, and right peripheral 5. *A,* Medial views (peripheral 5 reversed). *B,* Dorsal views of peripherals 6–8 and dorsomedial view of peripheral 3. *C,* External views (peripherals 3 and 6–8 reversed). *D,* Outlines of interperipheral sutures. Scale bar = 1 cm.

Discussion.—*Denverus* differs from the taxon noted in the Fort Union Formation of Montana (Chelydridae gen. indet. of Hutchison and Archibald, 1986) and the chelydrid described by Estes (1964) as "near *Pseudemys?*", both of which lack development of dorsal carina and medial thickening of the bridge peripherals.

Kinosternia Gaffney and Meylan, 1988
Hoplochelys Hay, 1908a
Hoplochelys crassa (Cope, 1888)
Figure 7D

Referred material.—Denver Formation (D1 sequence), Puercan — DMNH loc. 2550: DMNH 45102, costal fragment. UCM loc. 82126: UCM 37758, peripheral 1, partial nuchal, four peripheral fragments, two coastal fragments, and hyo- or hypoplastron fragment.

Description.—The nuchal, UCM 37758, exhibits the thickened edge, concave anterior margin, overlap of the first pleural, well-developed cervical scale, and broken base of a strong costiform process. The first peripheral of the same specimen has a free margin length of 32.7 mm and exhibits a trough on the upper medial side for reception of the costiform process of the nuchal. These measurements yield an estimated carapace length of 260 mm. Fragments of articulated peripherals 7–8 have a globose cross section, small upturned lateral carina, and slender extension of the posterior buttress onto the anterior part of peripheral 8. All show a finely porous and matte surface texture.

Discussion.—The previously known range of *Hoplochelys* was limited to New Mexico and Texas and chronologically from Late Cretaceous (Lehman, 1981) to mid-Paleocene (Torrejonian NALMA; Sullivan and Lucas, 1986). The species described by Hay (1908b) from the Fort Union Formation of Montana as *Hoplochelys caelata* is a chelydrid, and Hutchison and Archibald's (1986) report of a *Hoplochelys*-like form from the Late Cretaceous Hell Creek Formation remains an undescribed new genus (Holroyd and Hutchison, 2002). In New Mexico, three species of *Hoplochelys* are described from the same level (50 feet above the base of the Puerco beds) of the Puercan part of the Nacimiento Formation: *H. crassa* (Cope, 1888), *H. bicarinata* Hay, 1910, and *H. loqueata* Gilmore, 1919. We consider the differences separating them as either trivial or representative of individual variation, and these three species are synonymized here under *H. crassa*. The Denver specimens fall within the size range of, and are indistinguishable from, *H. crassa*.

Adocidae Cope, 1870
Adocus Cope, 1868
Adocus sp. indet.
Figure 1.11–12

Referred material.—Laramie Formation, Lancian — UCM loc. 73175: UCM 13747a, plastron fragments. UCM loc. 77062: UCM 38776, peripheral and costal fragments; UCM 42330, costal fragments; UCM 42312, costal; UCM 42331, peripheral 1, peripheral 1 or 2, two costal fragments; and UCM 42346, bridge peripheral fragment. Arapahoe Formation (D1 sequence), Lancian — Bijou Creek: AMNH 1844 (holotype of *A. lineolatus*), neural and plastron fragment. Denver Formation (D1 sequence), Lancian — DMNH loc. 2389: DMNH 45123, proximal costal fragment and shell fragments; DMNH 45127, shell fragment; DMNH 45141, shell fragment; and DMNH 45142, five shell fragments. DMNH loc 2486: DMNH 45128, two shell fragments. Denver Formation (D1 sequence), Puercan — DMNH loc. 2485: UCM 45122, two shell fragments. DMNH loc. 2596: DMNH 44630, three unsculptured shell fragments. Denver Formation (D1 sequence), age uncertain — UCM loc. 83069: UCM 48398, seven shell fragments.

Description.—The fragments usually exhibit the fine, wavelike surface sculptural pattern and finely incised sulci typical of adocids. The two most complete peripherals (UCM 42331), a peripheral 1 and peripheral 1 or 2, have free margin lengths of 61.6 and 47.1 mm, respectively. The only relatively complete costal (UCM 42312) has a width of 120 mm and proximal length of 48.3 mm.

Discussion.—The type of *Adocus lineolatus* Cope, 1874a is from the Denver Basin, and what little is known (Fig. 1.11–1.12) from this species was described by Cope (1875, p. 263, pl. 7., figs. 11–12) and discussed by Hay (1908a, p. 247). The type material is not specifically diagnostic, as recognized by Hay (1908a), who nonetheless conservatively retained the species. Where known from elsewhere, *Adocus* is a large turtle (carapace length up to 670 mm; Gilmore, 1919) with a fine, wavelike sculpture (Gilmore, 1919, pl. 5). *Adocus* has a stratigraphic range from Coniacian–Santonian (Eaton et al., 1999) to mid-Paleocene (Tiffanian NALMA; Hutchison, 1998). Much of the skeleton was described by Meylan and Gaffney (1989) and the shell by Hay (1908a) and Gilmore (1919). Only a single genus of the Adocidae, *Adocus*, is currently recognized in North America. *Adocus* was also reported from Asia, but all of these Asian specimens are now assigned to other related genera (Sukhanov, 2000, p. 333).

Nanhsiungchelyidae Yeh, 1966
Basilemys Hay, 1902
Basilemys cf. *B. sinuosa*
Riggs, 1906
Figure 7A

Referred material.—Laramie Formation, Lancian — DMNH loc. 612: DMNH 17678, peripheral fragments. DMNH loc. 2364: DMNH 42935, peripheral or plastron fragment; and DMNH 42936, shell fragment. Denver Formation (D1 sequence), Lancian — DMNH loc. 1513: DMNH 44609, fragment of a peripheral free margin. DMNH loc. 1926: DMNH 33304, parts of costals and plastral fragment.

Description.—All the shell fragments exhibit the distinctive sculpture (Hay, 1908a, pl. 34, fig. 1) of the Nanhsiungchelyidae. The most complete specimen, DMNH 33304, preserved part of the plastral buttress area of the plastron (Fig. 7A) and a significant portion of several costals lacking their distal ends. However, the anteroposterior length, measured near the distal end of one of the more complete costals, measures 97 mm, giving an estimated carapace length of about 693 mm. The peripheral and plastral margin fragments are greatly thickened.

Discussion.—The large size, distinctive sculpture, and thickened free margins of the shell and plastron are characteristic of the only known North American nanhsiungchelyid, *Basilemys*. There are four described species of the genus, two from the Campanian (Judithian NALMA) and two from the Maastrichtian (Lancian NALMA), *B. praeclara* Hay, 1910 and *B. sinuosa* (Brinkman and Nicholls, 1993b). The last two species are latest Cretaceous (Lancian) and were considered as valid sister taxa by Brinkman and Nicholls (1993b). They can be distinguished, however, only by differential development of the epiplastral beak and some differences in the associated scales. Brinkman and Nicholls did not explore the possibility that these differences represent sexually dimorphic features, as observd in many testudinids. Sufficient material probably exists to test this hypothesis by comparing the correlation of epiplastral beak development with possible dorsal arching of the central plastral area that might be expected in male plastra. If synonymous, *B. sinuosa* would be the senior synonym. Here we conservatively assign the Denver Basin material to *Basilemys* cf. *B. sinuosa*, as the referred material lacks those features necessary for their assignment to either species.

This large, broadly domed, elephantine-footed turtle with complex triturating surfaces of the jaws (Brinkman, 1998) is interpreted as a terrestrial herbivore. The genus is restricted to North America,

but it was reported previously from Asia. These latter records are now referred to other, related taxa (Sukhanov, 2000, p. 339). *Basilemys* ranges in age from Coniacian-Santonian (Eaton et al., 1999) to Maastrichtian (Hutchison and Archibald, 1986; Holroyd and Hutchison, 2002). This genus is one of the few turtle genera in the Rocky Mountain region to have become extinct at the Cretaceous/Tertiary boundary.

Trionychidae (Fitzinger, 1826)
Lydekker, 1889

The Trionychidae is a highly diverse, variable, and complex group fraught with taxonomic problems. The problems arising from individual variation have been amply demonstrated by variational studies (e.g., Webb, 1962; Dalrymple, 1977; Gardner and Russell, 1994). Problems of interpreting ontogenetic, individual, facultative, and sexual variation are daunting even with complete specimens. Given the fragmentary nature of most of the material from the Denver Basin and need for significant revisions of the many nominal fossil taxa, we do not attempt to identify the majority of the specimens below family levels. Nonetheless, there are sufficiently complete and distinctive specimens in the Denver Basin assemblages to allow recognition of the following taxa.

Subfamily Plastomenini Hay, 1908a
Helopanoplia Hay, 1908a
Helopanoplia cf. *H. distincta* Hay, 1908a
Figures 7B, E and 11E-F

Referred material.—Laramie Formation, Lancian — UCM loc. 73175: UCM 13747b, hyo- or hypoplastron fragment and two costal fragments. UCM loc. 77062: UCM 38725, most of right dentary and symphyseal part of left dentary; UCM 42334, medial and lateral parts of hypoplastron and anterior fragment of xiphiplastron; and UCM 42341, plastral and costal fragments. Denver Formation (D1 sequence), Lancian — DMNH loc. 1513: DMNH 45108, anterolateral quadrant of the left xiphiplastron. DMNH loc. 2389: DMNH 45126, medial part of a left hyoplastron.

Description.—The fragment of the xiphiplastron (UCM 45108, Fig. 7E) exhibits a sculpture of well-defined short ridges and fine pedicels that extend to the free and hypoplastral margins. The suture with the hyoplastron is well formed with a deep notch for the xiphiplastral process of the hypoplastron. The bone is stout with no distinct thinning toward the free or hypoplastral margins. The other plastral fragments are not diagnostic, except for the distinctive pedicellate sculpture. Parts of the plastron of

UCM 42334 exhibit the strong hyo-xiphiplastral suture, thick bones, and extensive coverage of the external surfaces by sculpture, usually to the edge of the exposed bones, that indicates the presence of a moderately large plastomenine turtle. The surface sculpture consists of a dense pattern of vermiculate ridges that may form isolated pedicels typical of *Helopanoplia*. The medial edges of the hypoplastron end bluntly but do not form a suture with its counterpart as in *Plastomenus* Cope, 1873, thus indicating the presence of a medial fontanelle as in *Helopanoplia* (see Holroyd and Hutchison, 2002, fig. 1*J*).

A partial mandible consisting of most of the right dentary and part of the left (Fig. 9*E*–*F*) also is referred to *Helopanoplia*. The triturating surface of the dentary is fused to its counterpart for essentially its entire length, thus forming a shallow trough narrowing gradually to a rounded end. The symphysis has an estimated length of 37 mm and estimated width across the dentaries of 35 mm. The depth of the triturating area of the dentary shallows steadily anteriorly to a knife-edge. Other known plastomenines are also characterized by a long symphysis. The size and shape of the mandible, coupled with its recovery from the same locality as the plastral parts of UCM 42334, suggest that it is referable to *Helopanoplia* sp., the first such mandible to be ascribed to the taxon.

Discussion.—*Helopanoplia* is a large (carapace length about 480 mm; Holroyd and Hutchison, 2002) trionychid known only from the Lancian of North America. It is the only latest Cretaceous trionychid genus that fails to cross the Cretaceous–Tertiary boundary. Originally described on very fragmentary material from the Lance Formation of Wyoming (Hay, 1908a), it is distinguishable based on the sculpture of the plastron and sometimes parts of the carapace. The sculpture consists of a pattern of distinct pustules instead of the typical pattern of pits and ridges. Hutchison and Archibald (1986) and Holroyd and Hutchison (2002, fig. 1*J*) referred additional material, but the sample contained no non-shell elements. The absence of fully developed pedicellate sculpture in some specimens may represent individual variation, ontogenetic variation, or slightly more primitive morphology than those specimens from the Hell Creek–Lance Formations. This assumption is supported by the presence of plastral fragments with typical pustulate surface morphology from the same locality. Assignment to the Plastomenini is based on its more fully ossified shell structure, as shown by specimens referred to this genus by Holroyd and Hutchison (2002).

Plastomenine A

Referred material.—Denver Formation (D1 sequence), Puercan — DMNH loc. 2596: DMNH 45111, costal fragment.

Description.—DMNH 45111 is a segment from a costal preserving both intercostal sutures. It is thick (4.0–5.2 mm) at sutures and exhibits 16 mm longitudinal distance between the sutures. The sculpture is well organized into ridges and the rib tract is strong and well elevated.

Discussion.—The morphology of the costal fragment is distinctive and inseparable from that of "Plastomenine type A" of Hutchison and Archibald (1986) and Holroyd and Hutchison (2002, fig. 1*K*). Plastomenine A is a small (carapace length about 165 mm), high-domed, stoutly constructed, and full-plastroned trionychid that ranges in age from Lancian to Puercan.

Plastomeninae, genus and species indeterminate
Figure 11G–H

Referred material.—Denver Formation (D1 sequence), Lancian — DMNH loc. 1513: DMNH 45109, costal fragment. Denver Formation (D1 sequence), Puercan — DMNH loc. 2387: DMNH 45110, plastron fragment. DMNH loc. 2398: DMNH 45114, costal 6, partial costals 5–6, proximal costal and neural. DMNH loc. 2562: DMNH 45105, distal costal fragment. UCM loc. 77275: UCM. 47585, right and left dentary.

Description.—Only the dentaries (UCM 47585, Fig. 11*G*–*H*) are of special note. They are fused at the symphysis into a shallow scoop that incorporates nearly all of the triturating surfaces. The symphysis is 25.9 mm long and the width across the dentaries is 29.5 mm, and it is distinctly shorter than the comparable specimen of *Helopanoplia* described above. In lateral profile, the dentary tapers to a relatively sharp edge anteriorly and has a slightly concave ventral margin of the anterior moiety.

Discussion.—The above carapacial materials are included here on the basis of the small to moderate size, abrupt termination of the free margins, short rib extensions, relatively greater thickness, and fine pit-and-ridge sculpture generally more suggestive of the plastomenine than trionychine trionychids. The dentary is included here on the basis of its long symphysis, which incorporates nearly all of the triturating surface.

In addition to the above material, Cope (1875) described the types of two nominal species from the Bijou Creek area in the eastern Denver Basin, *?Plastomenus punctulatus*, AMNH 1845 (Fig. 1.9;

Cope, 1875, p. 94 and 261, pl. 6, fig. 9) and *?P. insignis*, AMNH 1846 (Fig. 1.10; Cope, 1875, p. 95 and 261, pl. 6., fig. 10). Hay (1908a, p. 469) and Gardner et al. (1995, p. 640) noted that the specimens are generically indeterminate, and we concur that these species are *nomina vana*.

Subfamily Trionychinae (Fitzinger, 1826) Meylan, 1987
Axestemys Hay, 1899
Axestemys cf. *A. puercensis* (Hay, 1908a)
Figures 7F, H–I and 11A–D

Referred material.—Denver Formation (D1 sequence), Puercan — DMNH loc. 2387: DMNH 43187, glenoid area of scapula-coracoid. DMNH loc. 2546: DMNH 44622, plastron fragments and ungual phalanx. DMNH loc. 2558: DMNH 44623, costal and plastron fragments; and DMNH 45130, three phalanges and shell fragments. UCM loc. 78182: UCM 49228, symphysis and most of left dentary. UCM loc. 82126: UCM 34119, ungual phalanx; UCM 34134, distal humerus; UCM 37755, 15 costal fragments and half of cervical vertebra; and UCM 49231, skull fragments including partial parietal, most of right maxilla, and part of inner ear.

Description.—The presence of a very large trionychine turtle in the Paleocene (Puercan) part of the Denver Formation (D1 sequence) is indicated by phalanges, parts of the carapace, plastron, humerus, scapula, dentary, and skull. The very large size of the non-shell elements and large size and reduced sculpture of the shell elements suggests that they all belong to a single taxon, best referred to *Axestemys*.

Fragments of the skull (UCM 49231) preserve part of the otic capsule, parietal roof, and part of the right maxilla (Fig. 11A–B). The maxilla is massive, short and deep, and with a broad trough-like triturating surface and strong lateral marginal ridge. The dentary (UCM 49228; Fig. 11C–D) is massive, with a rounded anterior margin of the symphysis. The symphysis is shorter anteroposteriorly than the maximum width of the triturating surface posterior to the symphysis. In lateral profile, the dentary is deep, but it rises steeply at about a 45 degree angle at the symphysis. The external edge of the triturating surface forms a sharp ridge offset distally on a flat-sided lip from the body of the dentary.

The three phalanges of DMNH 45130 range in length from 32.1 to 48.7 mm. The scapula-coracoid fragment (DMNH 43187) measures 48 mm across the glenoid. The distal end of the humerus (UCM 34143) is massive and measures 75 mm across the distal end. The large ungual phalanx associated with the

plastron fragment (DMNH 44622, Fig. 7I) is 43 mm long and 17 mm in its greatest proximal diameter, is bifaceted, with the dorsal surface forming a ridge. Another ungual phalanx (UCM 34119) is still larger (58.3 mm long and 23.4 mm wide).

DMNH 44622 preserves part of the probable medial edge of the large hyo- or hypoplastron. The sculpture is subdued and consists of very low pustules and ridges that fade into a decussating surface. There is a narrow (5–11 mm) but distinct tapering lip along the preserved edge that feathers to the free edge. A flattened and weakly fluted spike (about 11 mm long and slightly wider) protrudes from the free edge.

The most complete material, DMNH 44623, represents a large turtle with an estimated carapace length of 50–60 cm. The sculpture of the carapace fragments consists of open but subdued and low ridges and pits. The only complete element, a neural, is 60 mm long at the midline and 6.5 mm thick at the lateral suture. The costal fragments have a tapered and wide unsculptured zone along the free margins and with long rib extensions. The maximum thickness of a partial costal near the distal end and through the rib tract is 17 mm. A hyoplastron or hypoplastron fragment has a distinct but low sculpture that becomes disorganized and then absent toward the medial edge. It has maximum thickness of 19.8 mm in the bridge area, thinning to 13 mm toward the medial edge.

Discussion.—The systematic placement and content of *Axestemys* are in dispute. Cope's (1872) original type series of *Axestus* (= *Axestemys*) *byssina*, from the Eocene Bridger Formation, consists primarily of appendicular elements plus a xiphiplastron (Cope, 1884, p. 116, pl. 15, figs. 1–12; Hay, 1908a, fig. 608, pl. 104, fig. 4). Broin (1977, p. 131) mentioned that *Axestemys*, *Conchochelys* Hay 1905, and maybe *Paleotrionyx* Schmidt 1945 are possible synonyms. Kordikova (1994, p. 6) considered it a genus of the tribe Ulutrionychini Kordikova, 1994, recognized two subgenera (*Axestemys* and *Eurycephalochelys* Moody and Walker, 1970), and placed *Paleotrionyx* Schmidt, 1945 and *Conchochelys* as synonyms of *Axestemys*. Ckhikvadze (2000, p. 210) placed *Axestemys* as a subgenus of the extant genus *Rafetus* Gray, 1864 (Tribe Rafetini) and recognized *Paleotrionyx* (with *Conchochelys* as a possible synonym) as a distinct genus. Despite the large size of the type of *Axestemys*, he thought that the adults would lack the scapular fontanelle and that a preneural was not present.

Our knowledge of the carapace rests on referred material by Hay (1908a, p. 509, fig. 669),

who restored the anterior neural areas as lacking a preneural, but other interpretations are equally likely. What the above-listed authors overlooked was a short paper by Gaffney (1979) describing the shell and some appendicular elements of a very large trionychid, UW 2382, with carapace length of 970 mm. Gaffney noted the similarity of morphology, size, and sculpture of this specimen to *Axestemys* and *Paleotrionyx* but placed them both in *Trionyx* Geoffroy Saint-Hilaire, 1809, *sensu lato*. This specimen retains a preneural and scapular fontanelles, thus disproving fontanelle loss with age. The presence of the preneural also negates its placement in *Rafetus* as proposed by Ckhikvadze (2000).

Paleotrionyx puercensis (Hay, 1908a; Hay, 19-8a, p. 499, figs. 654–655, pl. 94, figs. 1–3, pl. 104, figs. 2–3) from the Puercan of New Mexico and *Paleotrionyx quinni* Schmidt, 1945 (Schmidt, 1945, p. 2, fig. 1) from the late Paleocene of Colorado resemble UW 2382 in presence of preneural, scapular fontanelles, shape of nuchal, 7–8 neurals with neural 6 quadratic, and reduced carapace with large and long rib extensions. They differ from UW 2382 in smaller carapace length (*P. puercensis* = 330 mm; *P. quinni* = 70 mm), better development of the sculptural pattern, and less feathering of the costal margin. The smaller size and better pattern may well be interpreted as juvenile features. In any case, the general paedomorphy of the shell, even in adults, may be used as an apomorphy of these turtles, although those features are not unique to the group. Those features, coupled with the general similarity in others, justify including them within a single genus, *Axestemys* Hay, 1899, which has priority over *Paleotrionyx* Schmidt, 1945.

Another North American taxon, *Conchochelys admirabilis* Hay, 1905 (Hay, 1908a, p. 483, pl. 88, figs. 1–3), is known only from a relatively complete but poorly preserved skull from the Puercan of New Mexico. Broin (1977), Kordikova (1994), and Ckhikvadze (2000) have grouped it with *Axestemys*. This is a viable assumption, based on the large size of the skull (basilar length of 127 mm; width of 111 mm, fide Hay, 1908a), brevirostrine shape, and occurrence in the same rock unit as *Axestemys*-like shells (i.e., *Paleotrionyx puercensis*). The Denver skull fragments agree with *Conchochelys* in morphology to the extent that they can be compared (depth of maxilla, shape of triturating surface, shortness of rostrum judged from dentary, and size). We consider *Conchochelys* as a synonym of *Paleotrionyx puercensis*, and thus it is a synonym of *Axestemys*.

The phalanges and massive dentary from the Denver Basin closely resemble those of a large tri-

onychine from the Fort Union Formation (Tullock Member, Puercan) in the UCMP collections (UCMP 125815) represented by a forearm and crushed partial skull and jaws. The skull width to length ratio of UCMP 125815 compares favorably with those of *Conchochelys* (89% and 87%, respectively).

The immense size of this turtle indicates large areas of open water in the Denver Basin during the Paleocene. The genus, with the synonymies included, ranges from Montana to New Mexico and from earliest Paleocene to early middle Eocene (Puercan to Bridgerian NALMAs) in age.

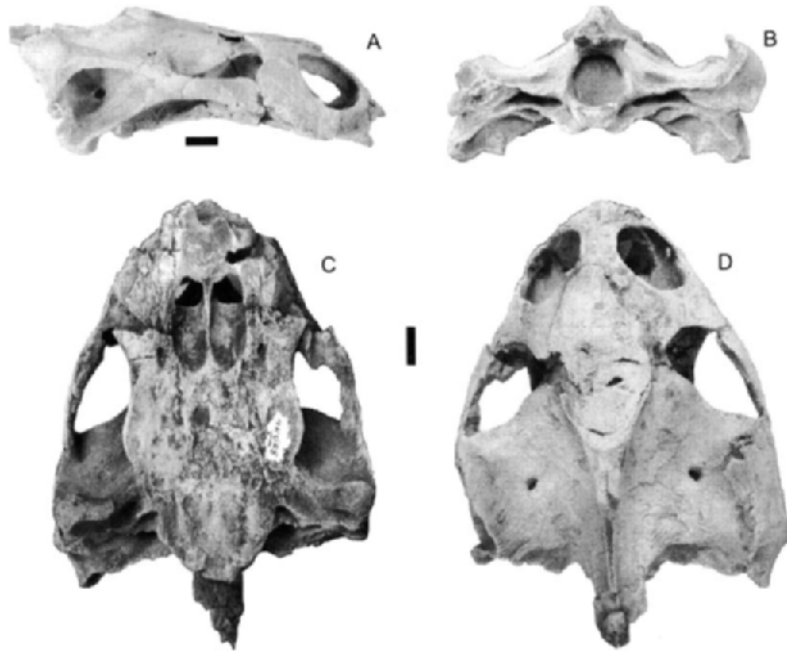## *Aspideretoides*
Gardner, Russell, and Brinkman, 1995
Aspideretoides sp.
Figure 10

Referred material.—Fox Hills Sandstone, Late Cretaceous — DMNH loc. 2300: DMNH 44605, skull.

Description.—The greater portion of an adult skull, DMNH 44605 (Fig. 10), is virtually uncrushed but lacks the triturating surfaces of the maxillae, tip of the rostrum and termini of the basioccipital, supraoccipital, and left squamosal. Co-ossification, erosion, hardener, dirt, or cracks obscure the positions of most of the sutures. A sandstone cast of the inner surface of the nasals appears to preserve their shape. The skull is relatively broad in relation to its length (basilar length estimated at 104 mm and width across the quadrates is 77 mm), and the preorbital region is short. There is moderate emargination of the apertura narum externum laterally. The parietal contributes about 30 percent or more to the processus trochlearis oticum. The intermaxillary foramen is only preserved on its posterior margin, but it is narrower and is well forward of the internal narial apertures. The maxillae meet posterior to the intermaxillary foramen and are only separated by the vomer near internal narial apertures.

Discussion.—The relatively short preorbital region and other details exclude *Plastomenus* Cope, 1873 and probably other plastomenines. Meylan (1987) revised the systematics of extant trionychids, and comparison of his character states in extant taxa with the fossil yields the following relationships. The emargination of the external nares indicates the Trionychinae. The contribution of the parietal to 30 percent or more of the processus trochlearis oticum indicates inclusion in the tribe Trionychinini. The relatively small size of the intermaxillary foramen in comparison to the internal nares and lack of separation of the maxillae by the vomer

Figure 10. *Aspideretoides* sp., DMNH 44605, skull in lateral (*A*), posterior (*B*), ventral (*C*), and dorsal (*D*) views. Both scale bars = 1 cm.

indicates membership in the subtribe Trionychina rather than Apalonina.

Meylan (1987) did not include fossil taxa in his analysis, even when some were known from complete skeletons. Most fossil trionychids are described from shell elements while a few others were only described from skulls. The systematics of the fossil taxa are poorly understood, but only two genera of trionychines (*Apalone* Geoffroy Saint-Hilaire, 1809 and *Aspideretoides* [including *Eugenichelys* Ckhikvadze, 2000, *Hummelichelys* Ckhikvadze, 2000] are currently recognized from the Late Cretaceous of North America. The Fox Hills specimen lacks the diagnostic separation of the maxillae by the vomer and enlarged intermaxillary foramen of *Apalone*, so an assignment to *Aspideretoides* seems more appropriate.

Skulls of only two species of *Aspideretoides* are known [A.
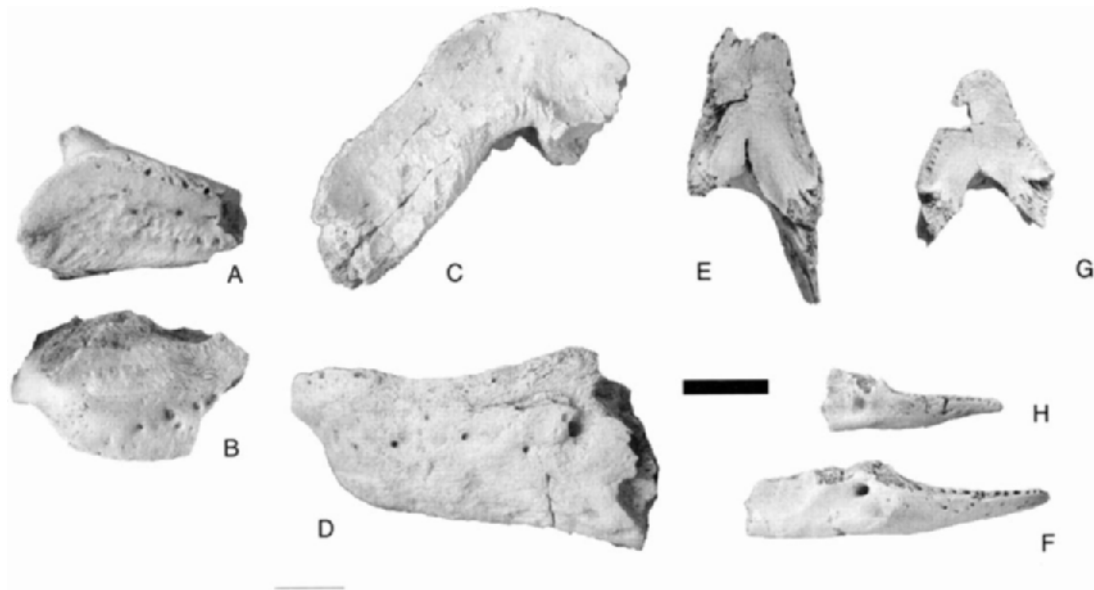
Figure 11. Trionychidae maxilla and dentaries. *Axestemys* cf. *A. puercensis*, *A-B*, UCM 49231, partial right maxilla in ventral (*A*) and right lateral (*B*) views; *C-D*, UCM 49228, dentary in dorsal (*C*) and left lateral (*D*) views. *Helopanoplia* cf. *H. distincta*; *E-F*, UCM 38725, dentary in dorsal (*E*) and lateral (*F*) views. Plastomenine indet.; *G-H*, UCM 47585, dentary in dorsal (*G*) and left lateral (*H*) view. In dorsal view, dentaries are at the foramen dentofaciale majus. Specimens scaled to same magnification; scale bar = 2 cm.

foveatus (Leidy, 1856) and *A. splendidus* Hay, 1908a], and both were figured and described by Gardner et al. (1995). The skull of *A. foveatus* (Gardner et al., 1995, fig. 5) is distinctly narrower (more elongate), smaller (basicranial length of 55–75 mm), and with relatively smaller orbits than DMNH 44605, but otherwise generally resembles it. The skull of *A. splendidus* (Gardner et al., 1995, fig. 6) more closely resembles the Fox Hills specimen in relative width, shape, and size of the internal nares and intermaxillary foramen, basicranial length (110–120 mm), and probably width of the maxillary triturating surfaces. Gardner et al. (1995) placed *Aspideretoides* between the Trionychina and Apalonina of Meylan (1987) on the basis of the vomer reaching the intermaxillary foramen dorsally as in Apalonina but not dividing the maxilla ventrally as in the Trionychina. Matrix and preservation of the Fox Hill specimen preclude determination of the dorsal contact of the vomer and intermaxillary foramen. The Late Cretaceous age and general similarities of the Fox Hills specimen to that of *A. splendidus* suggest assignment to the genus *Aspideretoides*.

Marsh (1896, p. 527) listed "*Trionyx*" [= *Aspideretoides*] *foveatus* from the "Ceratops beds near Denver", but Hay (1908a, p. 488) suggested that the specimens probably belonged to *Aspideretes beecheri* Hay, 1904. Neither Hay nor we have seen this material.

Trionychinae indet.

Referred material.—Laramie Formation, Lancian — UCM loc. 77062: UCM 96592, shell fragments. UCM loc. 90152: UCM 60001, large distal costal. Paleocene Denver Formation (D1 sequence), Puercan — DMNH loc. 2551: DMNH 44606, costal fragments. DMNH loc. 2558: DMNH 44625, carapace fragments. DMNH loc. 2563: DMNH 44621, costal fragments.

Discussion.—Included here are generally undiagnostic carapace fragments that show an unsculptured, tapered free margin of the costals and usually large size, unlike plastomenines. Of these, UCM 60001 is the most distinctive in having a relatively abrupt but tapered edge, a sculpture of very well defined pits and ridges that become more linear distally, and large size (distal length 104 mm). It strongly resembles the costals of "*Aspideretes*" *reesidei* Gilmore, 1919 (Gilmore, 1919, pl. 20) and *Aspideretoides foveatus* (Gardner et al., 1995, fig. 3A).

Trionychidae, subfamily undetermined
Figure 1.13–1.14

Referred material.—Laramie Formation, Lancian — DMNH loc. 1928: DMNH EPV 33354, shell

fragments; and DMNH 45112, three shell fragments. DMNH loc. 2347: DMNH 42919, neural. DMNH loc. 2364: DMNH 42937 costal fragment. UCM loc. 71106: UCM 12644, two plastron fragments. UCM loc. 73175: UCM 13748, two costal fragments; and UCM 38820, two costal fragments. UCM loc. 77062: UCM 38780, two costal fragments; UCM 38793, costal; UCM 42277, costal fragment; UCM 42336, costal fragments; and UCM 42345, distal costal fragment. Denver Formation (D1 sequence), Lancian — DMNH loc. 1513: DMNH 29476a, two costal fragments. DMNH loc. 2372: DMNH 45104, costal fragment; and DMNH 43151, neural. DMNH loc. 2389: DMNH 45125, two costal fragments. UCM loc. 77283: UCM 34642, posterior quadrant of carapace including parts of costal 6–8 and neurals 6–8. UCM loc. 77284: UCM 38056, costal fragment; and UCM 96594, costal fragments. Denver Formation (D1 sequence), Puercan — DMNH loc. 2387: DMNH 43189, two shell fragments. DMNH loc. 2400: DMNH 45117, shell fragments and proximal tibia. DMNH loc. 2402: DMNH 45120, two shell fragments. DMNH loc. 2549: DMNH 45137, nuchal fragments and costal fragment. DMNH loc. 2550: DMNH 45103, medial part of right hyoplastron; and DMNH 45136, two costal fragments. DMNH loc. 2560: DMNH 45133, costal fragments. DMNH loc. 2563: DMNH 44621, shell fragments; and DMNH 45132, shell fragments. UCM loc. 75992: UCM 38048, nuchal. UCM loc. 77275: UCM 85953, shell fragments. UCM loc. 82126: UCM 34121, glenoid region of scapula-coracoid; and UCM 37768, costal fragment. UCM loc. 77267: UCM 85951, carapace fragments. UCM loc. 78192: UCM 63526, left hyo-hypoplastron.

Description.—While most of the material is not particularly distinctive, a few specimens are worth noting for their morphology or completeness. UCM 63526 consists of a nearly complete and partly fused and stout left hyo- and hypoplastron with the ventral surface extensively covered by sculpture. The surface sculpture consists of a fine vermiculate pattern of ridges. The hyoplastron has one large anterolateral process (spike) and the anterior margin between the lateral process and entoplastral process is nearly straight. The lateral margin of the two bones between their lateral processes terminates abruptly without thinning. The medial margins of the bones form a narrow tapering edge. There are no medially extending processes from the medial margins. The hypoplastron is broken away along the anteromedial margin of the inguinal notch, but the medial part apparently turned sharply posteriorly in that area. There is a tight, straight, and fluted xiphiplastral suture medial to

the xiphiplastral notch. The posterolateral process is strong and twinned.

UCM 42345 consists of the distal part of a posterior costal and exhibits a fine sculpture of shallow pits and a narrow obtusely tapered free margin. Three longitudinal corrugations cross the surface. UCM 34642 consists of part of the posterior left quadrant of the carapace with neural 6-8 and parts of costals 6-8. The sculpture consists of well-defined pits and ridges but no longitudinal corrugations. The posterior margin of the carapace was apparently broadly convex with moderately large costal 8 in the shape of a right triangle. There is a narrow, unsculptured and feathered edge at the free margin with probably long rib extensions. Neural 6 is quadratic, and neural 7-8 are hexagonal with the short side anterior.

Discussion.—The bulk of the material included here is only diagnostic to family. However, some of the specimens noted above eventually may be identifiable to genus or species when the general taxonomy of the many nominal taxa from the Late Cretaceous and Paleocene is better known, or more complete material is recovered from the Denver Basin. The thick and well-calloused hyo-hypoplastron and strong xiphiplastral articulation of UCM 63526 is plastomenine-like, but the contour of the anterior margin of the hyoplastron resembles trionychines.

The type (AMNH 1847) of *Aspideretes? vagans* (Cope, 1874b, pl. 6, figs. 13-14; Fig. 1.13-1.14) from Bijou Creek, forty miles east of Denver, is based on a costal fragment, is not diagnostic, and is considered a *nomen dubium* (Hay, 1908a, p. 497, pl. 96. fig. 3).

Cryptodira indeterminate

Referred material.—Laramie Formation, Lancian — DMNH loc. 1928: DMNH 45113, humerus shaft. DMNH loc. 2370: DMNH 42944, humerus? shaft. Denver Formation (D1 sequence), Lancian — DMNH loc. 1513: DMNH 29476, ?scapula fragment; and DMNH 29477, shell fragment. DMNH loc. 2372: DMNH 43152, shaft of distal part of humerus. Denver Formation, early Paleocene — DMNH loc. 2398: DMNH 45115, xiphiplastron? fragment and carapace fragment; and DMNH 45116, costal fragment. DMNH loc. 2558: DMNH 45106, shell fragments. DMNH loc. 2563: DMNH 45131?, plastron fragment. DMNH loc. 2591: DMNH 44629, shell fragments. UCM loc. 82126: UCM 37769, carapace fragment.

Discussion.—The fossils included here are generally too fragmentary to identify. Some of the limb material may be assignable, but the detailed limb morphology of most fossil taxa is unknown or poorly described. Because there is no evidence from any of the identifiable turtles in the Denver Basin of the presence of pleurodiramorph turtles, we assume the above are cryptodiramorphs. Wright and Lockley (2001, p. 7-8, fig. 5) reported probable turtle tracks from the Laramie Formation from the Leydon Gulch locality near Golden, but they did not suggest possible taxonomic affinities. Bishop (2002) reported sea-turtle nesting structures from the Fox Hills Sandstone that are of an appropriate size to have been made by the sea turtle, *Protostega.* The collections we studied, however, do not have evidence of this taxon.

DISCUSSION

Stratigraphically successive turtle assemblages from the Denver Basin allow important insights into regional biogeography, the nature of latest Cretaceous to early Paleogene turtle associations, and how Laramide evolution of the Denver Basin differed from that of other areas in the Rocky Mountain Interior. Four formations in the Denver Basin (Fox Hills, Laramie, Arapahoe, and Denver) yield turtles (Table 1). Despite the fragmentary nature of many of these fossils, at least fifteen species-level taxa are recognized, including a pleurosternid (*Compsemys*), four to six baenids (*Neurankylus*, two species of *Plesiobaena, Stygiochelys, Palatobaena*, and probably another eubaenine), a kinosternian (*Hoplochelys*), an adocid (*Adocus*), a nanhsiungchelyid (*Basilemys*), four to six trionychids (*Axestemys, Aspideretoides, Helopanoplia*, and other unidentified plastomenines and trionychines), a macrobaenid, and a new genus of chelydrid. The basin also yielded a surprising number of skulls, including partial or nearly complete skulls of *Compsemys, Plesiobaena, Stygiochelys, Palatobaena, Axestemys*, and *Aspideretoides* and lower jaws of several of these plus *Helopanoplia* and an unidentified plastomenine.

The richness of the formations varies widely, with the Paleocene (Puercan) part of the Denver Formation (D1 sequence) being the most diverse, followed by the Cretaceous (Lancian) part of the Denver Formation (D1 sequence) and Laramie Formation. The Cretaceous units are less diverse and similar in taxonomic composition to other latest Cretaceous (Lancian) faunas from the northern Rocky Mountains. The relatively low number of taxa recognized from the Cretaceous formations is a combination of the small number of specimens from the Arapahoe Formation and Fox Hills Sandstone and the unfortunate fact that diagnostic ele-

Table 1. Distribution of taxa in formations of Denver Basin. Stratigraphically lowest is to left.

	Fox Hills Cretaceous	Laramie Cretaceous	Arapahoe (D1) Cretaceous	Denver (D1) Cretaceous	Denver (D1) Paleocene
Compsemys victa		X			X
Neurankylus eximius				X	
Plesiobaena cf. *P. antiqua*		X			
Plesiobaena sp.					X
Stygiochelys					X
Palatobaena					X
Eubaenina				X	
Baenodd				X	X
Baenidae indet.				X	X
Hoplochelys crassa					X
Adocus sp.		X	X	X	X
Basilemys		X		X	
Helopanoplia		X		X	
Plastomenine A					X
Plastomenine indet.				X	X
Axestemys sp.					X
Aspideretoides sp.	X				
Trionychinae indet.		X			X
Trionychidae indet.		X		X	X
Macrobaenidae					X
Denverus middletoni					X

ments for some diverse groups (i.e., Baenidae and Trionychidae) have not yet been recovered in these assemblages. Notable records from Cretaceous strata are the southernmost reports of *Helopanoplia* and *Aspideretoides*.

The Paleocene part of the Denver Formation (D1 sequence) is rich enough in specimens to show differences from comparable faunas in the north and from faunas in New Mexico and Texas. The Denver Basin Puercan fauna documents the most southerly records of *Stygiochelys*, *Plesiobaena*, Plastomenine A, chelydrids, and macrobaenids. *Plesiobaena*, chelydrids, and macrobaenids also probably occur in the Paleocene Nacimiento Formation (Puercan–Torrejonian NALMAs) of New Mexico (JHH, personal observation). The upper part of Denver Formation provides the most northerly confirmed record of *Hoplochelys*, which is a common element in the Nacimiento Formation but absent or extremely rare in northern faunas. While most of the taxa, if more completely known, could be referable to

named taxa, the chelydrid appears to be new. The Puercan fauna of the Denver Basin thus appears to be transitional between the early Paleocene faunas to the north and south and also may have some elements endemic to the area. Much additional collecting is needed to get a firm grip on the nature of the Denver Basin faunas and their role in interpreting the latitudinal and biostratigraphic significance of these faunas.

Paleontologic data also can provide insights into the geologic evolution of the basin and can be particularly helpful in an urban setting such as the Denver Basin, where outcrops and localities are more opportunistic than those encountered in the more frequently studied badlands settings. As discussed in greater detail elsewhere (Hutchison, 1998; Holroyd and Hutchison, 2000; Holroyd et al., 2001; Holroyd and Hutchison, 2002), the taxonomic composition and relative abundance of turtle faunas can provide insights into the quality and type of aquatic environments that occurred in an area. Turtle fossils

are particularly well suited for this purpose for a number of reasons. First, aspects of habitat preference are known for a large number of fossil species based on ecomorphology. Second, turtles are readily identifiable to at least family, and often genus, from even highly fragmentary remains. Third, turtle bone is dense and preserves well and so is common in the fossil record. Fourth, the density of turtle bone often permits it to be redeposited at some distance from where the animal may have died. This last point is important to understand when looking at fossil turtle assemblages. Articulated or relatively complete remains are not likely to be deposited far from where the animal died, and probably they reflect its original habitat. Mixed assemblages of fragmentary fossils, however, probably are derived from a larger area and thus can reflect small-scale variability in the local habitats (e.g., within a valley or river drainage). As such, these more fragmentary assemblages can tell us something about the diversity of aquatic habitats in an area that geologic information from a single site cannot. In an urban setting with limited outcrops, such as that seen in the Denver Basin, these assemblages can help us to understand what other types of habitats were present and how common they might be, even when much of the geologic record is obscured by development or other cover.

Comparisons of assemblages from the Laramie Formation and Cretaceous parts of the Denver Formation with other latest Cretaceous samples from the northern Rockies (Holroyd and Hutchison, 2002) suggest that trionychids are somewhat less common than expected, suggesting that the sandy-bottomed channels these taxa often prefer were less common. Typically, trionychids are virtually ubiquitous, occurring in between 70 and 90 percent of all localities in other Late Cretaceous assemblages. In samples from the Denver Basin, trionychids occur in 63 percent of localities in the Laramie Formation and only 27 percent of Cretaceous localities in the Denver Formation.

For the Puercan, other areas are less well known, so comparisons are more limited. Puercan turtle assemblages have not been formally described from anywhere in Wyoming, and samples from the San Juan Basin of New Mexico, while extensive, are still under study. The only well-known Puercan turtle assemblage published to date is that from the Tullock Member of the Fort Union Formation in eastern Montana (Hutchison and Archibald, 1986). As in the Cretaceous, overall taxonomic composition is similar between the two areas, although *Hoplochelys* is lacking in the more northerly fauna, and plasto-

menines type B and C have not yet been recognized in the Denver Basin. Table 2 shows differences in relative abundance at the family level between the Paleocene part of the Denver Formation and the Tullock Member of the Fort Union Formation. As in the Cretaceous, trionychids are somewhat less common than might be expected. More striking, however, is the difference in the relative abundance of chelydrids and macrobaenids. The comparative lack of macrobaenids in the Denver Basin is probably attributable to its distance from the ancient coastline. In North America, macrobaenids tend to be more common in areas of the coastal plain (Holroyd and Hutchison, 2002), and development of the Cannonball Sea in the northern Great Plains during the earliest Paleocene may have provided habitats conducive to greater macrobaenid abundance in Montana.

To some extent, the differences observed between the Denver Basin and areas in the northern Rockies can be attributed to the relatively smaller sample sizes per locality in the Denver Basin, although the extremely low percentages of trionchyids in both units of the Denver Formation are not likely to be due simply to sampling. Rather, it is more probable that the Denver Formation and the paleo-habitats it represents had comparatively few of the environments favored by trionychids. Trionychids (with the exception of *Helopanoplia*) tend to favor sandy-bottomed, fast-moving waters (Hutchison and Archibald, 1986; Bryant, 1989). The diversity of trionychids present, particularly the immense *Axestemys*, attest to the presence of these favored habitats, but such habitats may have made up only a small component of the landscape given their low relative abundance. Alternatively, these differences in relative abundance may reflect some latitudinal gradient that will only become apparent once more southerly faunas are better known. Finally, there may be some type of non-random exposure or recovery bias that is not apparent from available data.

In sum, turtle faunas from the Denver Basin provide important new insights into latest Cretaceous to early Paleocene patterns of biogeographic diversity. Given the comparatively short period over which collecting has been done, these finds suggest that the Denver Basin may ultimately prove to yield one of the best turtle faunas in the Rocky Mountain region and, certainly, one of the most intriguing.

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Table 2. Comparison of relative abundance of early Paleocene occurrence records between Denver Formation (D1 sequence; total number of localities = 30) and Tullock Member of Fort Union Formation (total number of localities = 137; data from Hutchison and Archibald, 1986).

Family	Denver Fm. (Puercan part) n	%	Fort Union Fm. (Tullock Mbr.) n	%
Baenidae	13	43.33	61	44.53
Chelydridae	1	3.33	31	22.63
Macrobaenidae	1	3.33	42	30.66
Adocidae[1]	3	10.00	19	13.87
Kinosternia[2]	2	6.67	3	2.19
Trionychidae	16	53.33	117	85.40
Pleurosternidae[3]	12	40.00	50	36.50

[1] Dermatemydidae of Hutchison and Archibald (1986)
[2] Kinosternidae of Hutchison and Archibald (1986)
[3] ?Family (*Compsemys*) of Hutchison and Archibald (1986)

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