

Article

Re-Evaluation of *Compsemys* and North American Compsemydids (Testudinata)

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Abstract

Compsemys is an enigmatic turtle first described over 160 years ago. Its taxonomic position has been uncertain, as many of the species placed in the genus have since been removed from it. For the last 30+ years, *Compsemys victa* has been the only recognized North American fossil species. New fossil specimens collected from the Paleocene in the United States necessitate a re-evaluation of the taxonomy of these turtles and call into question the long-held belief that only one species of *Compsemys* is valid in North America. Specimens from the Paleocene are far more complete than the holotype of *C. victa*, and all have been referred to this species based on a similar surface texture. Differences between material from the Cretaceous and Paleocene suggest multiple species of *Compsemys* are valid. In addition to the genotypic species *Compsemys victa*, *C. puericensis*, and *C. torreonensis* are both valid species from the Paleocene. Beyond surface sculpturing and texture, features of the carapace and plastron can be used to help differentiate the three species. North American *Compsemys* survived the Cretaceous–Paleogene mass extinction. Rather than being a monospecific genus, *Compsemys* diversified in the Paleocene. Not only does this suggest an increase in the diversity of North American compsemydids, but it also leads to the possibility of asymmetric or budding cladogenesis among *Compsemys* species during the Late Cretaceous and Paleocene, at least in the American Southwest.

Keywords: *Compsemys*; Compsemydidae; Testudines; Late Cretaceous; K–Pg boundary; Paleocene; Paleogene; evolution



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1. Introduction

Compsemys (sensu stricto) represents a group of fossil turtles known from North America. Records of the genus are known from Cretaceous and Paleocene strata in several western US states, north into Canada and south into Mexico, e.g., [1–5]. However, *Compsemys* has a complicated taxonomic history. *Compsemys victa* was first described by Leidy [6] based on fragmentary material from the Late Cretaceous in North Dakota. *Compsemys plicatulus* was later named by Cope [7] from the Late Jurassic Morrison Formation in Colorado and subsequently placed in the genus *Glyptops* by Hay [8] as *G. plicatulus*. This convention has been followed in some other studies, e.g., [1,4]. More recently, Joyce and Anquetin [5] synonymized *G. plicatulus* with *G. ornatus*. Other species of *Compsemys* were named from Paleocene strata in New Mexico. These include *C. parva* and *C. vafer* by Hay [9],

and *C. puercensis* and *C. torrejonensis* by Gilmore [10]. The type specimens of *C. puercensis* and *C. vafer* originate from the older, Puercan NALMA (North American Land Mammal Age) interval of the Nacimiento Formation, and that of *C. torrejonensis* originates from the younger, Torrejonian NALMA interval of the Nacimiento Formation in the San Juan Basin of northwestern New Mexico. The stratigraphic position of the type specimen of *C. parva* has been uncertain, but it is now considered to be within the Puercan–?Torrejonian NALMAs by Jasinski et al. [11]

The first major review of *Compsemys* by Gaffney [1] resulted in *C. victa* being considered the only valid species, which has been followed by most studies since, e.g., [4,5,12,13]. Additionally, some European species have been referred to the genus, including *Berruchelus russelli*, e.g., [5,14,15].

New material recently collected from the Late Cretaceous and Paleocene in New Mexico has called for a re-evaluation of *Compsemys*. This re-evaluation allows for a better understanding of the taxonomy of *Compsemys*, providing evidence of multiple species around the Cretaceous–Paleogene boundary. The current study also allows for a better understanding of these turtles and provides valuable new data for understanding the evolution and morphological variation within this extinct group.

2. Geological Setting

Compsemys victa was first named from material collected from the Maastrichtian Hell Creek Formation in central North Dakota [1,4,6,8]. The new material discussed herein comes from the San Juan Basin, New Mexico, where the specimens of the named North American Paleocene species were also collected (Figure 1). Paleocene species from the San Juan Basin of New Mexico include *C. puercensis* [10] and *C. vafer* [9] from the Puercan NALMA (North American Land Mammal Age) interval of the Nacimiento Formation, *C. parva* from the Puercan–? Torrejonian NALMA interval of the Nacimiento Formation, and *C. torrejonensis* from the Torrejonian NALMA interval of the Nacimiento Formation.

We consider *Berruchelus* to be valid (see Discussion below), so only North American records of *Compsemys* are considered for the stratigraphic distribution of these turtles. In addition to other species, numerous specimens have been referred to *Compsemys*, and more specifically to *C. victa*, over the years, mainly based on what was determined to be a unique surface sculpturing of the shell that was also found on isolated cranial material, see [4,12]. However, a specimen (UCMP 131103) consisting of shell material associated with skull material is known and was briefly mentioned and described by both Hutchison and Holroyd [12] and Lyson and Joyce [4]. The referral to the North American taxon *C. victa* was based on the presumed monospecific status of the genus at the time of those studies. Since *Compsemys* is no longer considered monospecific in this study, this material (UCMP 131103) may be referable to another species, diagnostic only to the genus level, or undiagnostic.

Brinkman [16] referred material from the Santonian in Alberta to ?*Compsemys*, but this material is considered here to be too incomplete to confidently refer to the genus. Similarly, Eaton et al. [17] listed the presence of *Compsemys* within the late Turonian Smoky Hollow Member of the Straight Cliffs Formation in south-central Utah based on shell surface texture, but this material is also considered too incomplete to confidently refer to *Compsemys*. Other material previously referred to *Compsemys*, see ref. [5], includes that from the Campanian in Coahuila (Mexico) [3,18], Texas [19], Utah [4,20], and New Mexico [4,13,21–24]; the Maastrichtian in Alberta (Canada) [4,16], Montana [1,8,25–27], North Dakota [4,6,28], Wyoming [8,28–31], and New Mexico [22,32,33]; the Puercan NALMA interval of the early Paleocene in Montana [4,26,27], Wyoming [4,34], Colorado [12], and New Mexico [9–11]; the Torrejonian NALMA interval of the early Paleocene in Montana [4,35]

and New Mexico [10,11]; the Puercan–Torrejonian NALMA interval of the early Paleocene in New Mexico [9,11]; the Tiffanian NALMA interval of the middle–late Paleocene in Texas [19]; and potentially the Tiffanian–Clarkforkian of the latest Paleocene–earliest Eocene in Colorado [36,37]. Most of these records are based on highly fragmentary material that is identified based exclusively, or almost exclusively, on its surface sculpturing. While this surface sculpturing or texture may be diagnostic to the generic level (see discussion below), these records must be re-evaluated and may not yet be diagnostic to any one species, particularly in the case of highly fragmentary material.

It is noted that, when discussing NALMA/NALVA, the majority of the ages belong to the North American Land Mammal Ages; however, the Kirtlandian was defined by Sullivan and Lucas [38,39] as a North American Land Vertebrate Age based on non-mammalian taxa. Additionally, the age of the Naashoibito Member of the Ojo Alamo Formation has been debated as to whether it is from the Edmontonian or the Lancian, e.g., [33,40]. In this paper, we consider it the Maastrichtian Age, within the Lancian NALMA.

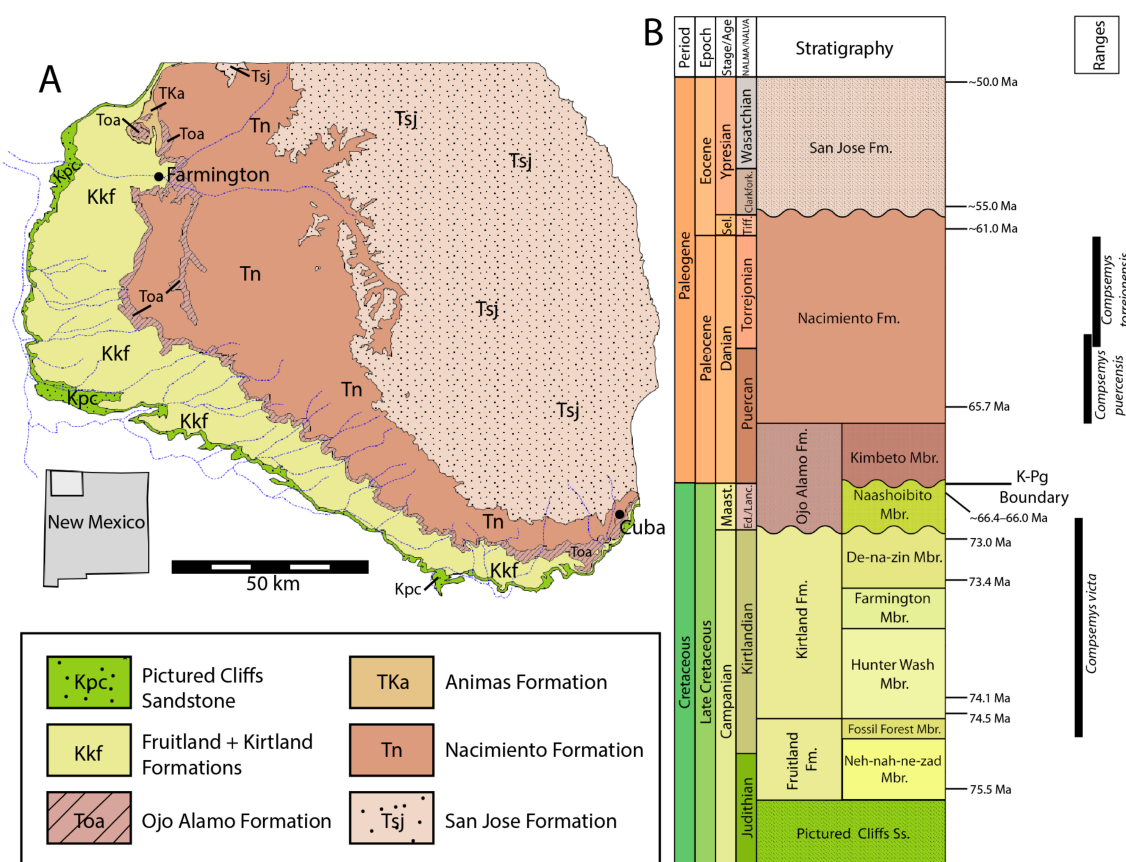


Figure 1. (A) Geologic map showing Late Cretaceous through Eocene strata of the San Juan Basin, where the type specimens of *Compsemys puericensis* and *C. torrejonensis* were collected. (B) Stratigraphic chart showing important strata of the San Juan Basin related to *Compsemys* specimens. Ranges of *Compsemys* spp. shown to the right. The figure pools information from multiple sources, including Lucas and Williamson [41], Williamson and Lucas [42], the Geologic Map of New Mexico [43], Sullivan and Lucas [38,39], Williamson and Weil [44], Williamson et al. [45], Fassett [46], Lucas et al. [47,48], Jasinski and Sullivan [49–51], Jasinski et al. [11,33,52,53], Lyson and Joyce [4], Koenig et al. [54], Sullivan and Jasinski [55], Williamson and Brusatte [56,57], Jasinski [58], Ksepka et al. [59], Lichtig et al. [60,61], and Flynn et al. [40]. Abbreviations: Clarkfork, Clarkforkian; Ed, Edmontonian; Lanc, Lancian; Ma, megaannum or million years ago; Maast, Maastrichtian; NALMA, North American Land Mammal Age; NALVA, North American Land Vertebrate Age; Sel, Selandian; Tiff, Tiffanian.

3. Materials and Methods

Fossils presented here are primarily from Cretaceous to Paleocene deposits in the San Juan Basin of New Mexico (Figure 1). Spanning from the Cretaceous to the Paleocene, the focal strata of the present study cross the Cretaceous/Paleogene boundary. Within the current study, we follow the morphological terminology of Gaffney [1], Ernst and Barbour [62], Jasinski [63–65], Jasinski et al. [66,67], and Joyce et al. [15].

For the taxonomic relationships of Compsemysidae, we follow the works of Pérez-García [68] and Tong et al. [69] in recognizing that *Berruchelus* is distinct from *Compsemys* (see discussion below). We also follow Pérez-García [70] and Pérez-García et al. [71] for the inclusion of only *Compsemys* and *Berruchelus* in Compsemysidae (see those works for arguments against the inclusion of other taxa within the family).

For those species within *Compsemys*, we follow a more restricted inclusion, where the only valid species are *C. victa*, *C. puercensis*, and *C. torrejonensis*. *Compsemys parva* [9] and *C. vafer* [9] are based on fragmentary shell material and are considered undiagnostic below the genus level and, therefore, nomina dubia. Other species are either considered nomina dubia or species within other genera (see discussion below).

4. Systematic Paleontology

Testudinata Batsch, 1788 [72].

Paracryptodira Gaffney, 1975 [73].

COMPSEMYDIDAE Pérez-García, Royo-Torres and Cobos, 2015 [74], (Joyce et al., 2021 [75]).

Included genus. *Compsemys* Leidy, 1856 [6].

Included species. *Compsemys victa* Leidy, 1856 [6] (type species of *Compsemys*); *Compsemys puercensis* Gilmore, 1919 [10]; *Compsemys torrejonensis* Gilmore, 1919 [10]; and *Berruchelus russelli* Pérez-García, 2012 [70].

Distribution. Campanian (Late Cretaceous) to Thanetian (late Paleocene) in North America and Thanetian (late Paleocene) in France [1,4–6,11,13,15,33,70,74].

Emended diagnosis. Adapted from Pérez-García et al. [74] and Joyce and Anquetin [5]. Note that the diagnosis is adapted from the diagnosis of *Compsemys* by Joyce and Anquetin [5], since their designation of *Compsemys* is equivalent to Compsemysidae listed here. The Compsemysidae are members of Paracryptodira through these symplesiomorphies: a midline contact of the nasals with modest lower and upper temporal emarginations (cranial characters from specimens referable to *Compsemys*, no cranial characters are known in *Berruchelus russelli*), the lack of a midline contact of the prefrontals, and large mesoplastra with a midline contact. The apomorphies include a dense surface texture, consisting of small, close-set keratin-covered tubercles and surrounding pits, that cover the skull and shell (carapace and plastron); a foramen posterius canalis carotici interni located halfway along the contact between the pterygoid and basisphenoid; and thickenings of the plastron medial to the bridges [most easily seen dorsally (internally)]. Compsemysidae can be differentiated from all other paracryptodires by possessing distinctly thickened skull bones; reduced temporal emarginations; expanded, rectangular quadratojugals; a postorbital contribution to the small, fully enclosed cavum tympani; a median, hooklike tomial process; an expanded secondary palate with a broad contribution from the vomer and palatines; a midline contact of peripheral I anterior to the nuchal combined with a loss of contact between costal I and peripheral I (also present in *Selenemys lusitanica*); large mesoplastra with an offset midline contact; a deeply sinuous midline plastral sulcus; and a deep anal (= xiphiplastral) notch. Compsemysids (*Compsemys* spp. and *Berruchelus russelli*) share the following features: oval and elongate shell with parallel to subparallel sides; a midline contact of peripheral 1 anterior to the nuchal combined with a loss of contact between

costal I and peripheral I (also present in *Selenemys lusitanica*); nuchal fully covered by first vertebral scute; first vertebral trapezoidal, and wider anteriorly than posteriorly; pleurals considerably overlapping onto peripherals; last pair of marginals covering posterior half of the pygal; relatively small extragulars, much smaller than larger gulars; gulars entering the anterior portion of the entoplastron; large mesoplastra with an offset midline contact; a deeply sinuous midline sulcus on the plastron; and a deep and conspicuous anal (=xiphiplastral) notch.

COMPSEMYS Leidy 1856 [6]

Figures 2–7

Type species. *Compsemys victa* Leidy, 1856 [6]

Other species. *Compsemys puercensis*, *Compsemys torrejonensis*.

Distribution. Late Cretaceous in Montana, North Dakota, and Wyoming, and Late Cretaceous to Paleocene in New Mexico. Additionally, based on fragmentary material identified mainly from surface sculpturing or texture to *Compsemys victa*, the genus is purportedly also present in the Late Cretaceous in Texas, Utah, Coahuila (Mexico), Montana, North Dakota, Wyoming, and Alberta (Canada); the early Paleocene (Puercan NALMA) in Montana, Wyoming, and Colorado; the early Paleocene (Torrejonian NALMA) in Montana; the middle to late Paleocene (Tiffanian) in Texas; and the middle to late Paleocene (Tiffanian–Clarkforkian NALMAs) in Colorado. As the surface sculpturing may not be diagnostic by itself, many of these records must be re-evaluated.

Emended diagnosis. Paracryptodiran turtles with granular tubercles (finely beaded and ridged) making up the surface sculpturing of the carapace, plastron, and dorsal skull roof; unusually large mesoplastra with a broad, but offset, midline contact; first peripherals meet medially anterior to nuchal, preventing nuchal from reaching the anterior margin of the carapace; flat anterior edge of the carapace (namely peripherals I and II), with potentially inconspicuous anteromedial projection between marginal I; square vertebrals II and III; broad posterior neurals; distinctly broad (wider than long) entoplastron; anteromedial projections of the pectorals, causing the humerals to be sub-triangular and thinner near their mid-length; a sinuous midline sulcus of the plastron; and a deep xiphiplastral notch (=anal notch) that varies from U-shaped to V-shaped. In addition to these shell characters, Lyson and Joyce [4] included several skull and cranial characters from a specimen (UCM 49223) they referred to *Compsemys victa*, herein referred to *Compsemys* sp., including no cheek emargination; rectangular quadratojugal; quadratojugal extends ventrally to a level even with mandibular condyles of quadrate, covering up these condyles; postorbital contributes to rim of cavum tympani; and a cavum tympani diameter less than the diameter of the orbit.

Notes. *Compsemys victus* (= *Compsemys victa*) was named by Leidy [6] from fragmentary shell material (USNM 960). Leidy [6]: (p. 312) named the species based on a type of surface sculpturing of the shell (i.e., carapace and plastron) he had not seen before, namely the “free surface of all the bones is thickly studded with granular tubercles, which give to it a shagreened appearance” (see also Figures 2C and 3). While the surface sculpture (i.e., surface texture or ornamentation) alone has been used for diagnosis before, the observance of multiple species with such surface sculpture makes this surface texturing diagnostic only to the genus level. This generic diagnosis applies to the valid species *C. victa*, *C. puercensis*, and *C. torrejonensis*. It includes information from other specimens potentially only referable to the genus *Compsemys* (e.g., UCM 49223 and UCMP 131103), which were previously referred to *Compsemys victa* (see discussion below).

Description. Species-level diagnoses of *Compsemys* are based solely on carapace and plastron material, so current cranial and non-shell post-cranial material cannot yet be referred below the genus level. Despite *C. victa* being the only species known from the

Cretaceous, we take a conservative approach in identifying isolated cranial material until a more complete shell and skull are found together and described. Presently, referral of cranial material is based on the same criteria used by Hutchison and Holroyd [12] and Lyson and Joyce [4], namely that surface sculpturing agrees among the shells and the surface of the skull. This surface sculpturing (Figure 3) consists of “small, close-set, enameled tubercles which produce the appearance of shagreen”, see ref. [8]: (p. 233). Characteristics of *Compsemys* indeterminate species cranial material are discussed by Lyson and Joyce [4] and includes: no cheek emargination; rectangular quadratojugal; quadratojugal extends ventrally to a level even with mandibular condyles of quadrate, covering up these condyles; postorbital contributes to rim of cavum tympani; and a cavum tympani diameter less than the diameter of the orbit. Additionally, they also noted post-cranial features, including: mesoplastra unusually large and with a broad midline contact; first peripherals meet medially in front of nuchal, preventing the nuchal from being exposed along the anterior margin of carapace; deep xiphiplastral notch present, varying from U-shaped to V-shaped; and sinuous midline sulcus on the plastron [4].

Other cranial material, in addition to that discussed by Hutchison and Archibald [26], Hutchison and Holroyd [12], and Lyson and Joyce [4], is known, including an incomplete set of lower jaws associated with shell fragments; several neurals, the proximal portion of several costals, and plastron fragments (NMMNH P-67478, Figure 4) from the Puercan NALMA interval of the Nacimiento Formation (San Juan Basin) in northwestern New Mexico. Shell fragments indicate referral to *Compsemys* but cannot be definitely assigned to any particular species. The lower jaws of NMMNH P-67478 are incomplete, missing the majority of the left dentary and all caudal (or posterior) elements, including the left articulation. The jaws have a maximum length of 28 mm, with the right side 13 mm wide at the caudal end and the posterior-most portion of the right side of the jaws is 5 mm wide. The dentary is large and makes up approximately half the total length of the jaws. The rostral-most point of the beak is strongly upturned dorsally, with a pronounced labial ridge. The extreme external side of this has a narrow (1.3 mm wide) band of surface sculpturing, indicating the origin of the overlying keratin sheath. Lingual (=medial) to this is a large, distinct lingual ridge that merges rostrally with its counterpart from the left side to form a midline ridge leading to the rostral-most point of the beak. The ventral side of the dentary has a deep, triangular channel, with its sides paralleling the dorsal outline of the beak. The angular and splenial are similar in size, each making up about half of the height of the coronoid eminence. The coronoid eminence is capped by a narrow coronoid. The Meckelian fossa is ventral to the coronoid eminence and angled nearly perpendicular to the plane of the splenial.

NMMNH P-67478 is the first described isolated lower jaw of *Compsemys* that is not associated with a skull. This lower jaw corresponds well with UCM 49223 (the skull described by Lyson and Joyce [4]) and possesses a similarly pointed beak. UCM 49223 is a nearly complete, but taphonomically deformed (partially crushed), skull lacking the left temporal area and portions of the posterior margin, and it includes nearly complete right and left dentaries, collected from the early Paleocene Denver Formation (Puercan NALMA, D1 sequence). NMMNH P-67478 represents a smaller and possibly younger individual than UCM 49223, as the mandible of the former is 5 mm wide as opposed to an estimated 15 mm wide in UCM 49223 based on the preserved length of the dentaries. Otherwise, UCM 49223 is difficult to compare to NMMNH P-67478, as the former has only the portion adjacent to the mandibular articulation, and the latter has only the anterior-most portion of this and forward (anterior).

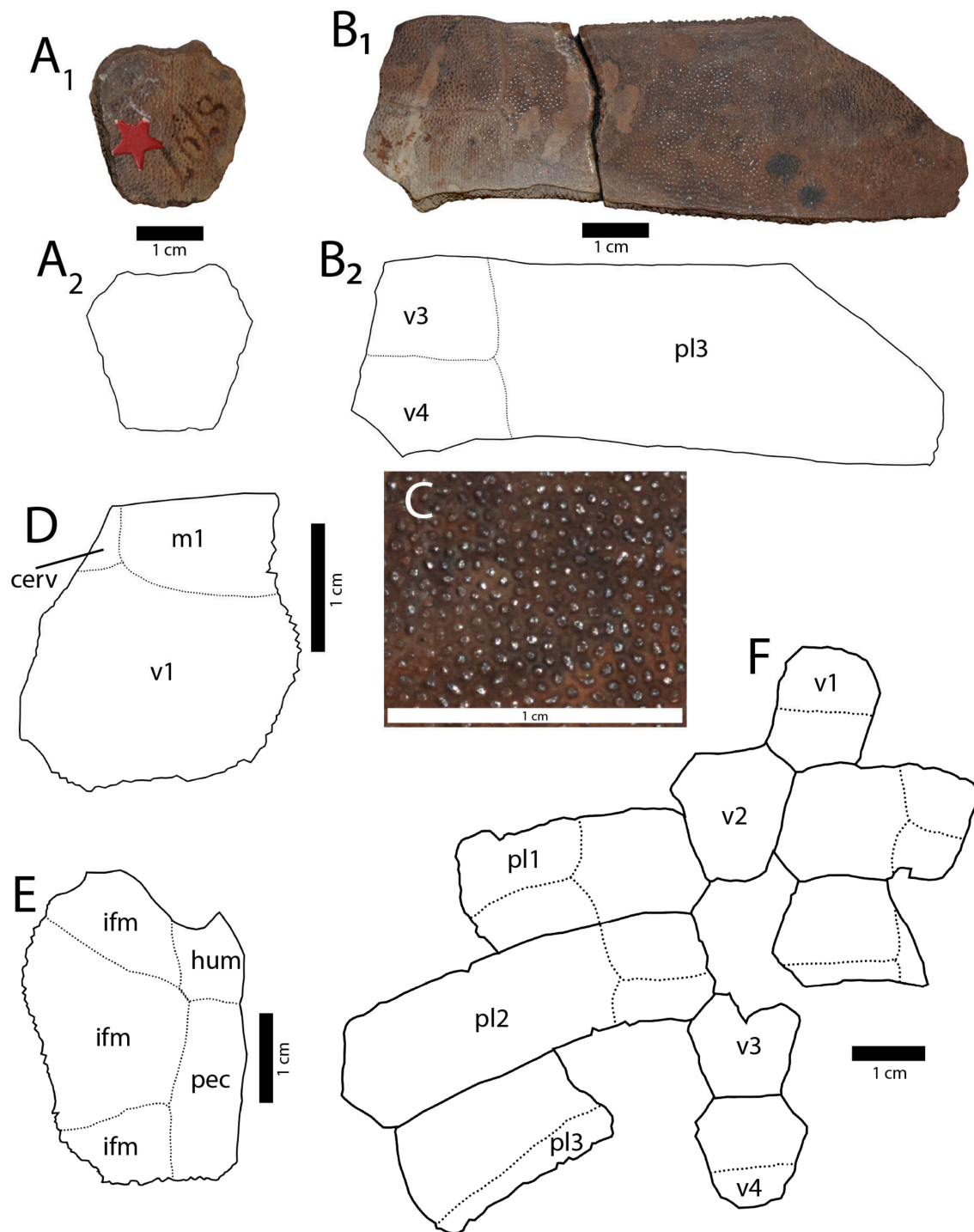


Figure 2. *Compsemys victa* from the Late Cretaceous in North America. (A–C) USNM 960 (holotype of *Compsemys victa*); (A) USNM 960 (holotype), neural IV in dorsal view, (A₁) photograph, (A₂) outline drawing; (B) nearly complete right costal V in dorsal view, (B₁) photograph, (B₂) outline drawing; (C) USNM 960 (holotype), close up of surface sculpturing. (D) AMNH 1085 (referred specimen), nearly complete right peripheral I in dorsal view; (E) AMNH 1015 (referred specimen), incomplete right hyoplastron in ventral view; (F) UCMP 194249 (referred specimen), fragmentary carapace in dorsal view. Abbreviations: cerv, cervical; hum, humeral; ifm, inframarginal; m, marginal; pec, pectoral; pl, pleural; v, vertebral. Scale bars = 1 cm.

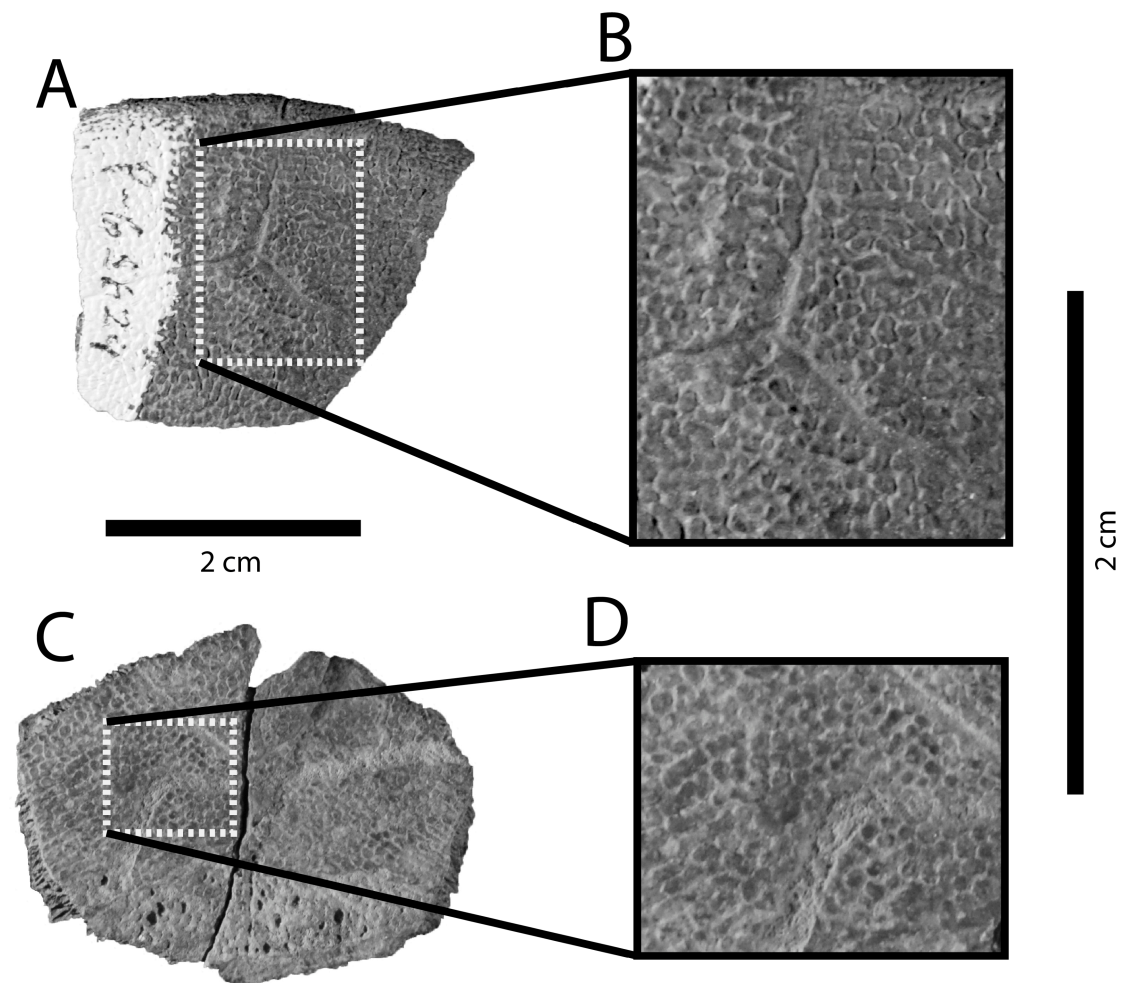


Figure 3. Surface sculpturing of *Compsemys*. (A) NMMNH P-65624, *Compsemys puercensis*, peripheral in dorsal view; (B) close up of surface sculpturing; (C) NMMNH P-67478, *Compsemys* indeterminate species, entoplastron in ventral view; (D) close up of surface sculpturing. Scale bars = 2 cm.

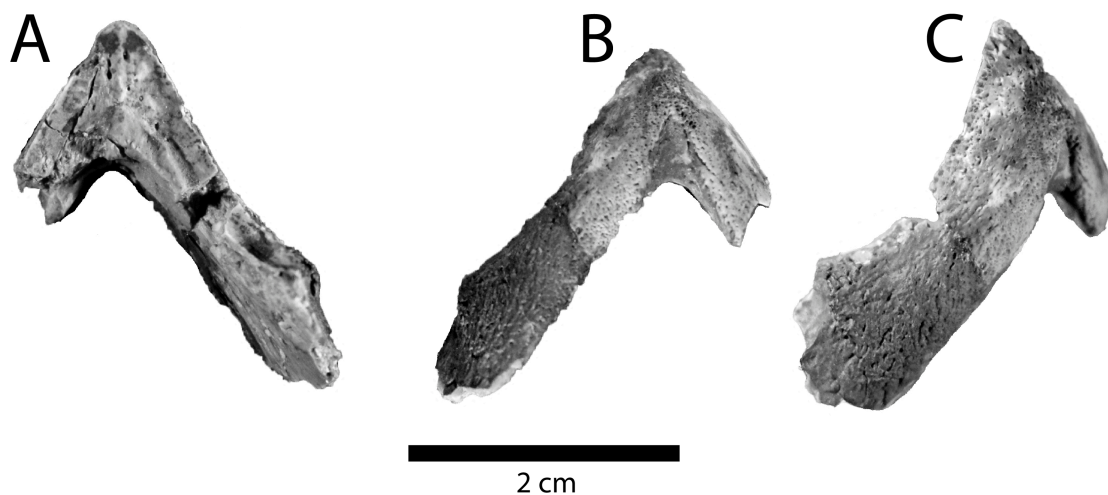


Figure 4. Incomplete lower jaws of *Compsemys* indeterminate species, NMMNH P-67478. (A) dorsal (=occlusal) view; (B) ventral view; (C) left lateroventral view. Scale bar = 2 cm.

COMPSEMYS VICTA Leidy 1856 [6].

Figure 2

Holotype specimen. USNM 960 [6], complete neural IV, nearly complete right costal V, and fragmentary right costal VIII (Figure 2A–C).

Type locality. Long Lake [6], 30 miles (ca. 50 km) southeast of Bismark, Burleigh County, central North Dakota. While Leidy [6]: (p. 312) stated that the holotype specimen (USNM 960) was found at Long Lake, Nebraska, it was actually from Long Lake, North Dakota. Referred material comes from Montana, see ref [8].

Type horizon and age. Hell Creek Formation, late Maastrichtian, Late Cretaceous.

Referred specimens. AMNH 998, bridge peripheral fragment (Lance Formation, Wyoming); AMNH 1015, incomplete right hyoplastron (Hell Creek Formation, Wyoming); AMNH 1085, nearly complete right peripheral I (Lance Formation, Wyoming); AMNH 6096, right costal VIII fragment (Hell Creek Formation, Montana); UCMP 19429, fragmentary carapace including neurals II and IV–V, fragmentary right costals I–III, incomplete left costals II–IV (left costal III complete) (Kaiparowits Formation, Utah). Other specimens previously referred to *Compsemys victa* based on surface sculpturing are only referable to the genus level, as the genus is not herein considered monospecific. However, it is noted that currently *C. victa* is the only valid Cretaceous species, and other Cretaceous material referable to *Compsemys* may eventually be referred to this species.

Diagnosis. *Compsemys victa* can be diagnosed as a member of *Compsemys* by the list of characters for the genus provided above. It differs from *C. puericensis* and *C. torrejonensis* in a more lateromedially (=horizontally) flattened humeral–pectoral sulcus; a longer contact (more than a single point contact) between the humeral and the inframarginal at its posterolateral (=caudolateral) side that restricts the pectoral from contacting the anterior-most inframarginal; a flat, transverse anterior border of neural II; and a latitudinally flattened vertebral III–IV sulcus. Differs further from *C. torrejonensis* by lacking notches on the anterior margin of the carapace at the cervical–marginal sulcus.

Description. USNM 960 (Figure 2A–C) consists of a complete neural IV, a nearly complete right costal V, and a fragment of costal VIII. Neural IV is hexagonal with a length of approximately 2.5 cm and is slightly longer than wide. The incomplete right costal V is missing the lateral portion but has the sulci for vertebrae III and IV and has an anteroposterior length of approximately 3.2 cm. There is a slight indent where the lateral sulci of vertebrae III and IV contact each other, similar to other *Compsemys*. The vertebral III–IV sulcus is flattened latitudinally, which is more similar to that of *C. puericensis*, and eventually curves anteriorly near the midline, whereas in *C. torrejonensis* this sulcus curves posteriorly. Both fragments have the distinct surface sculpturing used to identify fragmentary material as *Compsemys*. The fragmentary costal VIII also has this surface sculpturing, although it does not offer any other morphologic data. The material is relatively gracile, particularly compared to Paleocene *Compsemys* fossils.

Hay [8] referred several shell elements to *Compsemys victa*. Several of these fragments offer little morphologic data, including a fragmentary bridge peripheral (AMNH 998), an incomplete right hyoplastron (AMNH 1015), an incomplete right peripheral I (AMNH 1085), and a right costal VIII fragment (AMNH 6096). Little information can be gathered from AMNH 998 and 6096. They agree with the characteristic surface sculpturing of the type specimen (USNM 960). The first peripheral (AMNH 1085, Figure 2D) preserves the sulci separating the cervical, marginal I, and vertebral I scutes. There is no evidence of a notch on the anterior margin of the carapace between the cervical and marginal I scutes. This is similar to the condition seen in *C. puericensis* and distinguishes it further from *C. torrejonensis*. The bridge peripheral (AMNH 998) could be peripheral VIII, X, or XI based on the preserved sulci between the marginals and pleurals. It is more likely peripheral VIII or

X, although it agrees with other specimens referred to *Compsemys* and does not help further distinguish between the potential species. The incomplete right hyoplastron (AMNH 1015, Figure 2E), however, can help distinguish *C. victa* from other species of *Compsemys*. An elongated contact between the humeral and the inframarginal scute to its posterolateral edge restricts the pectoral from contacting the anterior-most inframarginal. While the hyoplastron is incomplete, it preserves the lateral portion of the humeral–pectoral sulcus, which shows a distinctly latitudinal, lateromedially flattened orientation. However, in *C. puercensis* and *C. torrejonensis*, the humeral–pectoral sulcus is distinctly angled anteriorly where it continues onto the entoplastron.

UCMP 194249 (Figure 2F) consists of a highly fragmentary carapace, including several neurals and costals, see [20]: (figure 13.1). Neurals II, IV, and V are hexagonal. Neural II has a flattened anterior border suggesting a neural I with a flattened posterior border and potentially more distinctly angled sides. Neural IV, preserved with the specimen, agrees with USNM 960, namely in its flattened to only slightly posteriorly concave curvature of the anterior border and being slightly longer than wide. Those of *C. puercensis* and *C. torrejonensis* are more distinctly curved, and that of *C. torrejonensis* is the most conspicuously curved. The vertebral III–IV sulcus is latitudinally flattened as it crosses neural V, further distinguishing *C. victa* from the Paleocene species. The remaining morphology of the neurals and preserved portions of the costals all agree with other preserved specimens of *Compsemys*, including the holotypes of *C. puercensis* (USNM 8544) and *C. torrejonensis* (USNM 8549).

COMPSEMYS PUERCENSIS Gilmore, 1919 [10].

Figure 3A,B and Figure 5

Holotype specimen. USNM 8544 [10], incomplete carapace including portions of peripherals II (left peripheral II complete), costals I–VI, neurals I–VI (neurals II–V complete), an incomplete nuchal, and an incomplete plastron including portions of the ento-, hyo-, meso-, hypo- (complete right hypoplastron), and xiphiplastra (complete right xiphiplastron) (Figure 5).

Type locality. “Four miles northwest of Kimbetoh (Kimbeto), on the north line of sec. 27, T. 23 N., R. 9 W.,” San Juan Basin, northwestern New Mexico, see ref. [10]: (p. 19).

Type horizon and age. “50 feet above the base” of the Nacimiento Formation, see ref. [10]: (p. 19), Paleogene, Paleocene (Puercan). Definitive specimens are from the Puercan NALMA, although some material from the Late Cretaceous may also be from this species, and one specimen from the early Torrejonian NALMA (NMMNH P-21602) suggests this species existed during that age as well.

Referred specimens. NMMNH P-21602, relatively complete left side of the carapace and incomplete plastron missing the entoplastron and posterior lobe (early Torrejonian interval of the Nacimiento Formation, San Juan Basin, New Mexico); NMMNH P-65624, carapace fragments; USNM 8528 (referred to *Compsemys parva* by Gilmore [10]), nearly complete carapace (missing lateral sections of the middle and anterior portions) and plastron missing lateral sections of the anterior portion and the bridges (Puercan interval of the Nacimiento Formation, San Juan Basin, New Mexico); USNM 8529 (referred to *Compsemys vafer* by Gilmore [10]), incomplete carapace (missing anterior portion) and nearly complete plastron (missing lateral sections of the anterior portion and much of the bridges) (Puercan interval of the Nacimiento Formation, San Juan Basin, New Mexico).

Diagnosis. *Compsemys puercensis* can be diagnosed as a member of *Compsemys* by the list of characters provided for the genus above. It differs from *C. victa* by having an anteriorly angled humeral–pectoral sulcus, a shorter contact (single-point contact) between the humeral and the inframarginal at its posterolateral (=caudolateral) side, a concave anterior border of neural II, and an anteromedially convex vertebral III–IV sulcus. It differs

from *C. torrejonensis* by having a flat anterior edge of the carapace with no notches; the vertebral III–vertebral IV sulcus crossing neural V; slightly more rounded anterior edge of the plastron; parallel to subparallel lateral edges of the posterior plastral lobe; straighter (i.e., less sinuous) humeral–humeral sulcus; convexly rounded (anteriorly) to anteromedially pointed femoral–anal sulci; and a less pronounced xiphiplastral notch (=anal notch) with sharply pointed posterior projections.

Description. USNM 8544 consists of the majority of the medial portion of the carapace through neural 6, although most of the costals and peripherals are not preserved, and a nearly complete plastron (Figure 5). The plastron preserves most portions on the right or left sides, although the entoplastron is not preserved and its proportions are only based on the general morphology of the elements preserved around it and referred specimens. Based on the type (USNM 8544) and referred specimens (USNM 8528 and 8529), the majority of the shell is known [10]. The nuchal is restricted from the anterior margin of the shell by the peripherals I. The neural formula for the first six neurals is ?4-6-6-6-6-6. Neural II has a concave anterior border, similar to *C. torrejonensis*, but is distinct from *C. victa*, whose neural II has a flat, transverse border. The vertebral I–vertebral II sulcus crosses neural I and the vertebral II–vertebral III sulcus crosses neural III. Of particular interest is the crossing of neural V by the vertebral III–vertebral IV sulcus, which is distinct from *C. torrejonensis*. The anterior margin of the carapace is relatively flattened when looking at the orientation of peripherals I and II and compared with referred specimens. Based on the preserved medial portion of the right entoplastron, the anteromedial margin would have been slightly elongate, giving it a more rounded outline in dorsal or ventral view. The sinuosity of the sulci running medially through the plastron is preserved on the right hyo- and mesoplastron, showing its offset nature from the sutures running medially between the paired elements of the plastron. The abdominal–femoral sulci are flat to convex (posteriorly), while the femoral–anal sulci are distinctly angled, with the medial portion angled anteromedially. While the posterior-most portion of the left xiphiplastron was reconstructed by Gilmore [10]: (pl. III), the complete right xiphiplastron is preserved and shows that the broad, sub-rounded anal notch would have been a natural morphological feature of *C. puercensis*. The anal notch is distinctly, but shallowly, notched with sharply pointed posterior projections bordering the notch.

The original material of *C. parva* (holotype USNM 6548) and *C. vafer* (holotype USNM 6551 and referred specimen USNM 6553) described by Hay [9] are undiagnostic to the species level and can only be referred to *Compsemys* indeterminate species. This also makes both *C. parva* and *C. vafer* nomina dubia. However, based on the more complete specimens referred to *Compsemys parva* and *C. vafer* by Gilmore [10]: (USNM 8528 as *C. parva* and USNM 8529 as *C. vafer*), these two species are probably synonymous with *C. puercensis*. USNM 8528 and 8529 agree with the above features of *C. puercensis*, particularly the crossing of neural V by the vertebral III–vertebral IV sulcus and the shape of the anterior and posterior margins of the plastron. NMMNH P-21601 and P-65624 are both made up of carapace fragments, but some of the neurals are preserved, allowing referral based on the vertebral III–vertebral IV sulcus. Although peripherals I are not preserved in the type specimen (USNM 8544, Figure 6), they are present in referred specimens (e.g., USNM 8528 and USNM 8529) and maintain the relatively flattened anterior margin of the carapace.

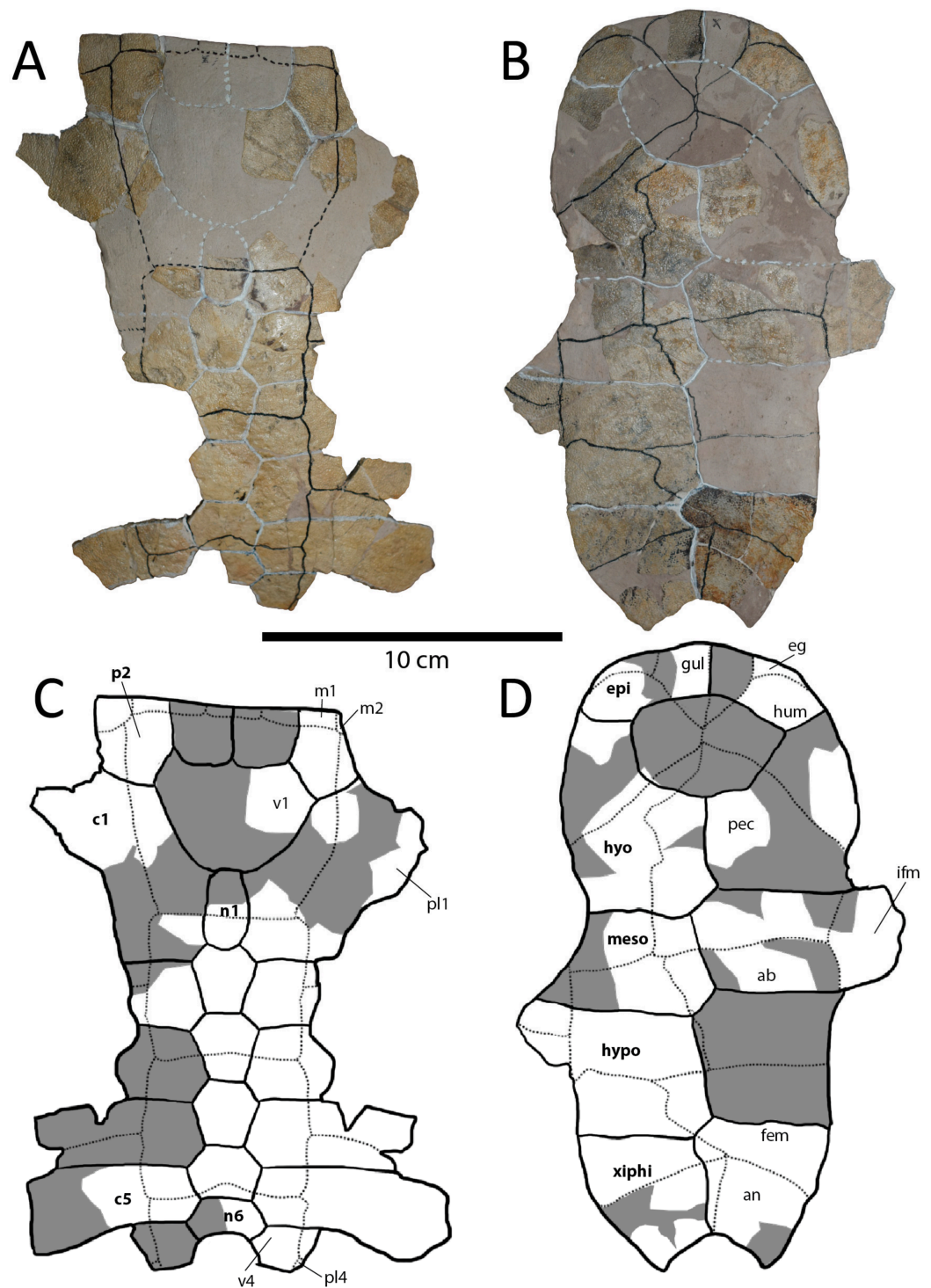


Figure 5. *Compsemys puercensis*, USNM 8544 (holotype), from the Puercan NALMA, Nacimiento Formation, northwestern New Mexico. (A) incomplete carapace in dorsal view; (B) nearly complete plastron in ventral view; (C) line drawing of incomplete carapace in dorsal view; (D) line drawing of nearly complete plastron in ventral view. Sutures (of bones) are marked by solid lines and sulci (of scutes) are marked by dotted lines in line drawings. White colors indicate preserved original bone material, while dark gray represents reconstructed portions. Abbreviations: ab, abdominal; an, anal; c, costal; eg, extragular; epi, epiplastron; fem, femoral; gul, gular; hum, humeral; hyo, hyoplastron; hypo, hypoplastron; ifm, inframarginal; m, marginal; meso, mesoplastron; n, neural; p, peripheral; pec, pectoral; pl, pleural; v, vertebral; xiphi, xiphiplastron. Bones are labeled in bold to the left, while scutes are labeled to the right. Numbers correspond to the number of the individual elements (i.e., first neural is n1; second marginal is m2). Scale bar = 10 cm.

Joyce and Anquetin [5] noted that the shells referred to various species of *Compsemys* by Gilmore [10] were originally made up of carapace and plastron fragments that were then reassembled. For the most part, the portions reconstructed by Gilmore [10] were mirrored by pieces that were preserved from the opposite side of the shell, and the fragments that were reassembled were, and currently are, considered to be from single individuals. From the information available, Gilmore did not assemble shells from multiple individuals. Therefore, the morphology shown here is considered accurate, although the entoplastron is not preserved in USNM 8544 (Figure 5) and, as it has no paired element, its morphology is more hypothetical based on referred specimens of *C. puericensis* (USNM 8528 and 8529). Although the entoplastron is not preserved, the morphology of the humeral–pectoral sulcus on the right hyoplastron suggests the pectoral covered a significant part of the entoplastron and reached to approximately its midpoint (relative to its length). The position of the sulcus between the pectorals usually lies anteromedially on the posterior portion of the entoplastron; however, it is reconstructed as coming from the right posterolateral margin of the entoplastron in USNM 8544 (see Figure 5). While this would be more distinct from other specimens of *Compsemys*, Gilmore [10] reconstructed this as such due to its position on the right hyoplastron. This placement also seems likely when compared to USNM 8549 (Figure 6), which shows a similar morphology immediately posterior to the entoplastron, although the pectoral–pectoral sulcus still enters the entoplastron medially on its posterior margin. Although the entoplastron is not preserved in USNM 8544, the posteromedially angled gular–hyoplastron sulci, the anteromedially angled humeral–pectoral sulci, and the small humeral–humeral sulcus, resulting in a short contact between the paired humerals, is consistent with *Compsemys*, or at least the Paleocene *Compsemys* specimens where entoplastra are known. This morphology is inferred to have been present in USNM 8544 and *C. puericensis* based on other referred specimens (e.g., NMMNH P-21602, USNM 8528 and 8529).

COMPSEMYS TORREJONENSIS Gilmore, 1919 [10].

Figures 6 and 7

Holotype specimen. USNM 8549 [10], nearly complete carapace and plastron, missing portions of both bridges, including the corresponding peripherals (Figure 6).

Type Locality. “Eight miles N. 60° E. of Kimbetoh (Kimbeto), in sec. 17, T. 23 N., R. 8 W.,” San Juan Basin, northwestern New Mexico, see ref. [10]: (p. 21).

Type horizon and age. “840 feet above base of the Puerco, in Torrejon,” Nacimiento Formation, see [10]: (p. 21), Paleogene, Paleocene (Torrejonian NALMA).

Referred specimen. SMP VP-832, majority of the anterior portions of a carapace (Figure 7) and plastron. SMP loc. 314, “Turtle City,” north De-na-zin Wash (northeast), from the Torrejonian interval of the Nacimiento Formation, San Juan Basin, New Mexico.

Diagnosis. *Compsemys torrejonensis* can be diagnosed as a member of *Compsemys* by the suite of characters provided for the genus above. It differs from *C. victa* and *C. puericensis* in having notches on the anterior margin of the carapace at the cervical–marginal I sulci and having the vertebral III–vertebral IV sulcus crossing neural VI. It differs further from *C. victa* in having an anteriorly angled humeral–pectoral sulcus, a shorter contact (single-point contact) between the humeral and the inframarginal at its posterolateral side, a concave anterior border of neural II, and an anteromedially convex vertebral III–vertebral IV sulcus. Lastly, it differs further from *C. puericensis* in having expanded or inflated lateral edges of the posterior plastral lobe; a highly sinuous humeral–humeral sulcus; flattened, latitudinally oriented medial portion and angled lateral portion of the femoral–anal sulci; and a strongly pronounced, deep xiphiplastral notch (=anal notch) with rounded posterior projections.

Description. USNM 8549 is a nearly complete carapace and plastron [10], missing only portions of the peripherals around both bridges and portions of the posterior of the carapace around neurals VI–VIII, costals VII–VIII, and a portion of the suprapygal (Figure 6).

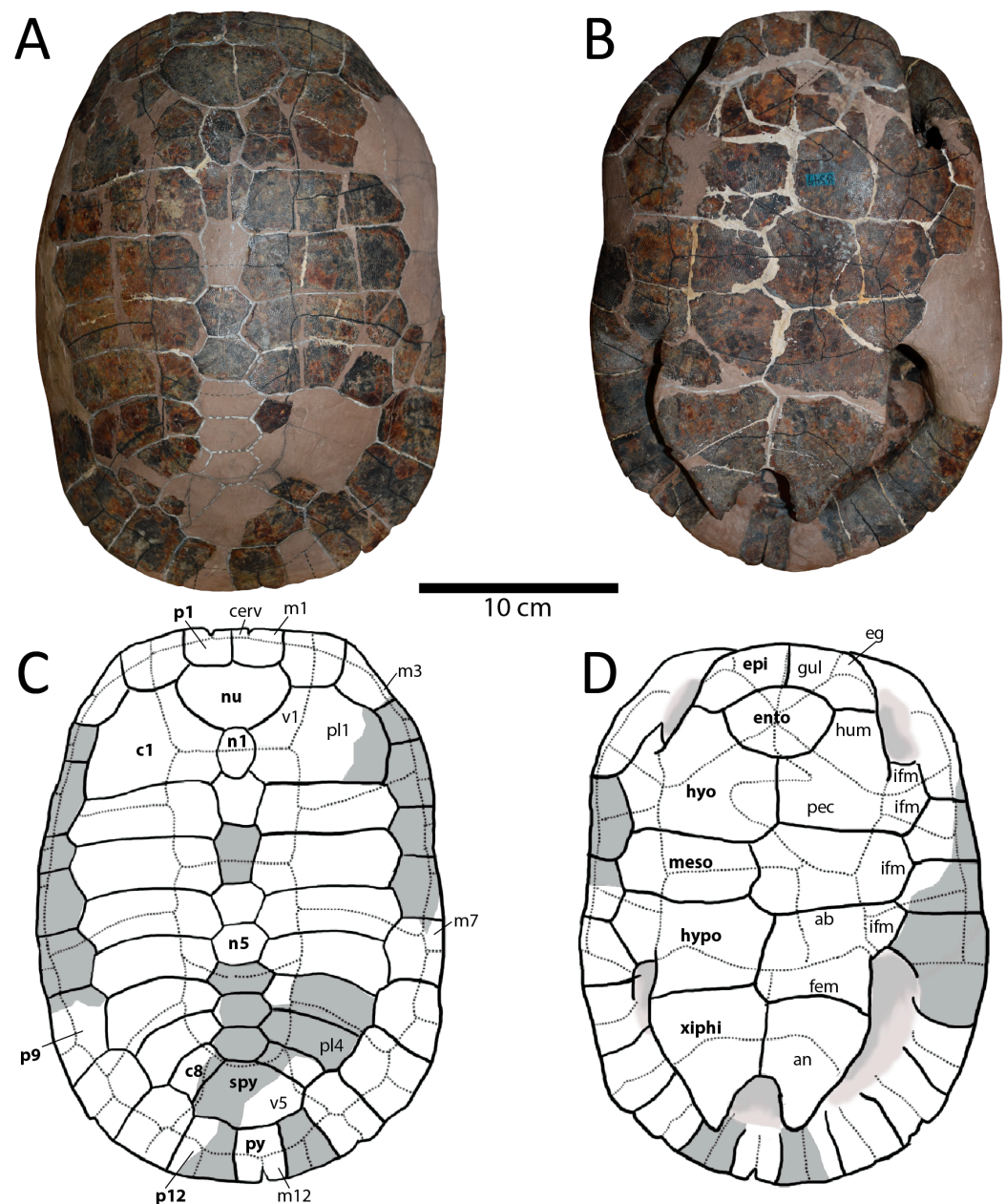


Figure 6. *Compsemys torrejonensis*, USNM 8549 (holotype), from the Torrejonian NALMA, Nacimiento Formation, northwestern New Mexico. (A) nearly complete carapace in dorsal view; (B) nearly complete plastron in ventral view; (C) line drawing of nearly complete carapace in dorsal view; (D) line drawing of nearly complete plastron in ventral view. Sutures (of bones) are marked by solid lines and sulci (of scutes) are marked by dotted lines in line drawings. White colors indicate preserved original bone material, while dark gray represents reconstructed portions, and light gray represents internal (visceral) surface. Abbreviations: ab, abdominal; an, anal; c, costal, cerv, cervical; eg, extragular; ento, entoplastron; epi, epiplastron; fem, femoral; gul, gular; hum, humeral; hyo, hyoplastron; hypo, hypoplastron; ifm, inframarginal; m, marginal; meso, mesoplastron; n, neural; nu, nuchal; p, peripheral, pec, pectoral; pl, pleural; py, pygal; spy, suprapygal; v, vertebral; xiphi, xiphiplastron. Bones are labeled in bold to the left, while scutes are labeled to the right. Numbers correspond to the number of the individual elements (i.e., first neural is n1; twelfth marginal is m12). Scale bar = 10 cm.

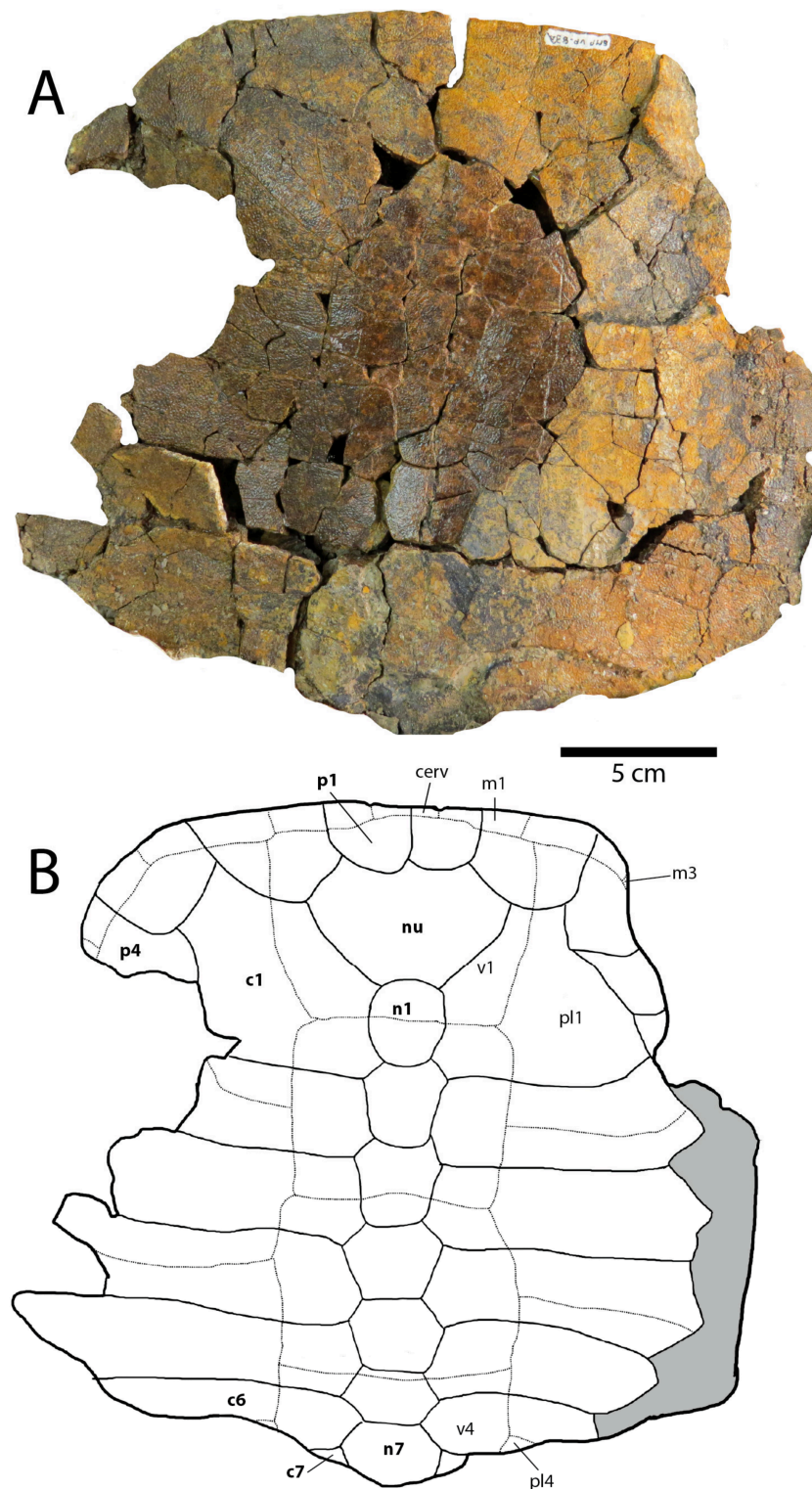


Figure 7. SMP VP-832, anterior portion of the carapace in dorsal view, referred to *Compsemys torrejonensis*, from the Torrejonian NALMA Nacimiento Formation, New Mexico. (A) anterior portion of carapace in dorsal view; (B) illustration of anterior portion of the carapace in dorsal view, sutures (of bones) are marked by solid lines, and sulci (of scutes) are marked by dotted lines. White colors indicate preserved original bone material, while gray represents internal (visceral) surface of the plastron below. Abbreviations: c, costal, cerv, cervical; m, marginal; n, neural; nu, nuchal; p, peripheral, pl, pleural; v, vertebral. Bones are labeled in bold to the left, while scutes are labeled to the right. Numbers correspond to the number of the individual elements (i.e., first neural is n1; second marginal is m2). Scale bar = 5 cm.

The nuchal is restricted from the anterior margin of the shell by the peripherals I. The posterolateral edges of the nuchal are distinctly rounded. The formula for the first six neurals is 4-6-6-6-6-6. Neural I is crossed by the vertebral I–vertebral II sulcus, and neural III is crossed by the vertebral II–vertebral III sulcus, whereas the vertebral III–vertebral IV sulcus crosses neural VI. Neural II has a concave anterior border, similar to *C. puercensis*, but is distinct from *C. victa*, whose neural II has a flat, transverse border. The anterior margin of the carapace has small notches between the cervical scute and the marginal I scutes, which are also present on the referred specimen SMP VP-832, although they are more inconspicuous in the former.

The plastron, nearly complete except for portions of the bridge, shows a morphology consistent with *Compsemys* (Figure 6). The humeral scutes are distinctly triangular and medially pinched. This leads to the entoplastron having distinct portions covered by the gular, humeral, and pectoral scutes. The anterior lobe of the plastron has relatively subparallel to constricted lateral edges, whereas the posterior lobe of the plastron is distinctly inflated. The pectoral–pectoral sulcus is extremely sinuous and far more prominent than in the *C. puercensis* holotype (USNM 8544, Figure 5) and any specimens referred to the latter species. The abdominal–femoral sulci are convexly rounded (posteriorly), whereas the femoral–anal sulci are angled laterally and flat medially. The anal notch is prominent and deep, with the edges bordered by pronounced but rounded posterior projections.

SMP VP-832 represents the greater anterior portion of a carapace (Figure 7), while the anterior portion of the plastron is present but currently unprepared. It agrees with the key features of *C. torrejonensis*, in particular the crossing of neural VI by the vertebral III–vertebral IV sulcus.

5. Discussion

5.1. Historical Taxonomic Overview

Compsemys was first named for *C. victa* based on highly fragmentary material [6]. The fragmentary nature of this material, and the original reliance on surface texture, led to numerous taxonomic issues for the taxon moving forward. This was followed by *Compsemys plicatulus* from the Late Jurassic Morrison Formation in Colorado, named by Cope [7], which was subsequently placed in the genus *Glyptops* by Hay [8] as *G. plicatulus*. Other species of *Compsemys* were eventually named from Paleocene strata in New Mexico, including *C. parva* and *C. vafer* by Hay [9], and *C. puercensis* and *C. torrejonensis* by Gilmore [10]. Some of the other species originally referred to *Compsemys* due to presumed similarities in surface texture (e.g., *Compsemys variolosus*, ?*C. ogmius*, and *C. imbricarius*) [76,77] were later placed in the taxon *Basilemys* [8,78,79].

Another early species referred to *Compsemys* was *Emys obscurus* from the Maastrichtian in North Dakota [6], which was subsequently referred to *Compsemys obscurus*, e.g., [9,80], and *C. victa* [4]. Hay [8] questioned the referral of the species to *Compsemys*. Indeed, the type specimen was said to have a smooth surface, which excludes it from *Compsemys*. Most species referred to *Emys* belong to various other genera, e.g., [63,65,81], thus the generic referral of *E. obscurus* to *Compsemys* is also incorrect, as *Emys* has been considered something of a wastebasket genus by numerous early turtle workers. The material, a costal fragment, is highly fragmentary, undiagnostic, and represents a nomen dubium, which is in agreement with Joyce and Anquetin [5].

One of the first major reviews of *Compsemys* was provided by Gaffney [1]. He hypothesized that differences among the New Mexican species (*C. victa*, *C. parva*, *C. vafer*, *C. puercensis*, and *C. torrejonensis*) were within the limits of population variation. He noted that the Cretaceous form, *C. victa*, was too fragmentary to differentiate it from the Paleocene species. He provisionally referred all of the species to *C. victa*, as it had been named first,

with the caveat that further information and specimens might eventually show there to be taxonomic differences. Additionally, he agreed with the generic placement of *Glyptops plicatulus* first suggested by Hay [8], thus not including it in *Compsemys*.

Lyson and Joyce [4] also reviewed the genus while describing an isolated skull from Colorado. This skull (UCM 49223), first reported by Hutchison and Holroyd [12], is from “Bijou Creek.” The stratigraphy, however, is uncertain, see ref. [12], particularly as Bijou Creek potentially has Cretaceous and Paleocene strata. It is likely from the Puercan (Paleocene) portion of the Denver Formation. Hutchison and Holroyd [12] referred it to *Compsemys* as it possessed sculpturing similar to that of the carapace and plastron. Additionally, they justified this referral based on known and associated skull and shell material (UCMP 131103) from the Puercan Tullock Member of the Fort Union Formation in Montana. In their study, Lyson and Joyce [4] agreed with the synonymies of Gaffney [4], while also synonymizing *Emys obscurus* and *Glyptops depressus* with *C. victa*, although they provided little to no justification. However, Joyce and Anquetin [5] surmised that the placement of *E. obscurus* in *C. victa* was probably based on the mistaken reference of a different specimen within the plate illustrated by Leidy [82]: (pl. 11, figures 5–7) and considered the former taxon a nomen dubium. Joyce and Anquetin [5] discussed *G. depressus* further but considered it a nomen dubium as well, agreeing with the findings of Gaffney [83].

Compsemys was recently discussed by Joyce and Anquetin [5], who agreed with the previous hypothesis of the genus as monotypic [1,4], that *C. victa* is the only valid species of North American *Compsemys*, and that all fragmentary material from Campanian to Paleocene age strata is referable to this species. They considered the shell surface texture (i.e., shell ornamentation) to be diagnostic and could be used to refer specimens to the genus. They also determined that *C. parva*, *C. vafer*, *C. puercensis*, and *C. torrejonensis* were nomina invalida and junior synonyms of *C. victa*. “*Compsemys*” *plicatulus*, which was attributed to *Glyptops* by Hay [8], was still placed within this latter genus by Joyce and Anquetin [5], although they determined that the surface sculpturing was not unique enough among basal paracryptodires, and they considered the name a nomen dubium. In their discussion of *Emys obscurus*, Joyce and Anquetin [5] determined it to be a nomen dubium due to the loss of the holotype and lack of similarities with other taxa. Furthermore, they considered *Glyptops depressus*, which Lyson and Joyce [4] also synonymized with *C. victa*, to likely be a synonym of *C. victa* based on several features of the carapace and plastron.

However, the *G. depressus* holotype (USNM 5731), purportedly from the Late Cretaceous in Colorado, is a heavily weathered carapace and plastron lacking all the peripherals and portions of the posterior side of the shell. Gaffney [83] felt it more sensible to consider it a nomen dubium, and Joyce and Anquetin [5] concurred. *Glyptops depressus* was synonymized with *C. victa* by Lyson and Joyce [4], but with no justification given. While it does have mesoplastra, *G. depressus* does not have sinuous plastral midline sutures. Additionally, Hay [8] mentioned that the surface sculpturing was similar to that of *G. plicatulus*, a species removed from *Compsemys* and moved to *Glyptops*, and whose generic placement has not since been altered. Joyce and Anquetin [5] considered *G. depressus* a nomen dubium, a finding we agree with here. *Compsemys plicatulus* is based on highly fragmentary material that Joyce and Anquetin [5] determined was more similar to *G. ornatus*, although they considered the species a nomen dubium based on the undiagnostic nature of the holotype (AMNH 6099), which we also agree with here. The removal of the Jurassic specimens from *Compsemys* (including those referred to *Glyptops*) means the specimens currently referred to *Compsemys* date from the Late Cretaceous to the Paleocene.

None of the characters in the revised diagnoses of *Compsemys* or *C. victa* by Joyce and Anquetin [5] are present in the holotype of *C. victa* (USNM 960), which includes several

shell fragments, including a neural (possible fourth) and two costals (a fragment of the ?fifth and eighth) (Figure 2A–C). Instead, the diagnosis for *C. victa* used by Joyce and Anquetin [5] uses referred specimens, in particular the holotype of *C. torrejonensis* (USNM 8549) and referred specimens with non-shell elements. *Berruchelus russelli* was named by Pérez-García ([70] based on a holotype nuchal (MNHN.F.BR 9110) and numerous other shell elements and fragments from the upper Thanetian (upper Paleocene) in France. Joyce and Anquetin [5], however, considered *B. russelli* referable to *Compsemys*, although we still consider them generically distinct (discussed further below).

There have also been other reports of *Compsemys* outside North America. *Trionyx bakewelli*, a taxon named by Mantell [84] from an isolated costal collected from the Grinstead Clay Member of the Tunbridge Wells Sand Formation (Early Cretaceous, middle–late Valanginian) on the Isle of Wight, UK [85], may be referable to *Compsemys*. *Platychelys(?) anglica* was named by Lydekker [86] from the left posterolateral portion of a carapace collected from the Purbeck Limestone Group (Early Cretaceous, Berriasian) on the Isle of Wight [85]. Both species were tentatively referred to *Compsemys* by Joyce et al. [87], with the caveat that they may represent a different genus (or genera) once more specimens and data are collected. Joyce [88] removed the two species from *Compsemys* and placed them in “*Helochelydra*” *bakewelli* and “*H.*” *anglica*, respectively, and neither of these species was mentioned by Joyce and Anquetin [5]. British fossil material previously referred to *Compsemys* (i.e., (“*Helochelydra*” *anglica* and “*H.*” *bakewelli*)) would have extended the genus back another 80 million years. However, all British fossil material that, at some point, was referred to *Compsemys* is now identified as belonging to a different lineage of turtles (i.e., Helochelydridae).

As currently interpreted, the entire fossil record of *Compsemys* lasted for approximately 25 million years. However, if these Early Cretaceous records are indeed referable to the genus, it would extend the genus back another 80 million years, which seems highly unlikely. It is more likely that this surface ornamentation, or similar sculpturing, has evolved multiple times. Gaffney [1]: (p. 291) also stated that the possibility of two fairly unrelated turtles developing similar surface sculpturing would not be that unusual. Indeed, the fact that multiple turtle genera are known for having small tubercles on the surface of their shells (e.g., *Glyptops*, *Helochelydra*, and *Naomichelys*) hints at this possibility. Helochelydrids, in particular, are known for a shell surface texture made up of tubercles [87,89–91]. The similar ways these textures are described makes it easier to deduce why workers have had difficulty referring fragmentary material to particular taxa. This is further supported by the fact that other species originally believed to have unique and similar surface texturing were moved to the nanhsiungchelyid *Basilemys*, another turtle with presumed distinct shell surface texture [8,78,79].

5.2. Morphology and Variation

Variation among turtles differs genotypically and phenotypically to varying degrees. While some taxa exhibit lesser amounts of intraspecific variation, others exhibit larger degrees, such as modern *Trachemys*, e.g., [63,92,93]. When taxa are named based on highly fragmentary material, and are diagnosed, completely or in large part, on something like shell surface texture, those taxa can quickly become trash-bin taxa. *Compsemys*, as noted above, has become one such turtle taxon. However, new fossil material, presented herein, including shell and cranial material, is referable to *Compsemys* based on surface texture and a shared morphology of shell elements. Moreover, specimens previously referred to *Compsemys victa* show variation in the sutures between bones and sulci between scutes. While some of this variation may represent sexual dimorphism and/or intraspecific variation, some undoubtedly represents interspecific variation (i.e., disparity).

While *Compsemys* was first named based on distinct sculpturing on the surface of the carapace and plastron, similar sculpturing among other turtles has caused some confusion in referring species to this genus (see further discussion above). For this reason, some species have moved between various genera, e.g., [4,58,94,95]. While the majority of previous diagnoses for *C. victa* did not include any of the features within the holotype of the species (USNM 960) and instead focused on features of referred specimens and those of specimens previously referred to other species, the holotype does preserve a few important features that allow for a more confident referral of a few other specimens to the species.

Surface sculpturing, previously used as a key feature of the genus, e.g., [8–10], and later as a key feature of the monotypic *C. victa*, is more correctly a generic character when viewed through the prism of interspecific variation within the genus. Although a shagreen-like surface texture with fine, granular tubercles is not part of the diagnosis presented by either Lyson and Joyce [4] or Joyce and Anquetin [5], it can be used to diagnose *Compsemys*. It is also different than that in *Berruchelus russelli*, which has a surface texture that is more variable and subdued.

Gilmore [10]: (figure 4) illustrated differences in the posterior lobes of the plastra of the four Paleocene New Mexican species and used these to help distinguish the species. Without a larger sample size, we infer that two Paleocene species are represented based on different morphologies across the shells, not only the posterior plastral lobes. In addition, differences in the anal notch may be due to intraspecific variation or dimorphism, particularly sexual dimorphism, see ref. [5]. However, taxonomically significant differences from the specimens Gilmore [10] reported include the vertebral III–vertebral IV sulcus (crossing neural V in *Compsemys puericensis* and neural VI in *C. torreonensis*) and the shape of the plastral lobes, among others. The placement of the vertebral III–vertebral IV sulcus mostly corresponds to the different NALMAs, with the majority of those individuals from the Puercan crossing neural V and those from the Torrejonian crossing neural VI. A single individual from the early Torrejonian NALMA (NMMNH P-21602) has its vertebral III–vertebral IV sulcus crossing the posterior-most portion of neural V, so the correlation is not perfect, and geologic age alone cannot be used for species referral. The morphology of *C. torreonensis* from the Torrejonian interval and that of *C. puericensis* from the Puercan interval (with possible extension into the earliest Torrejonian) suggest that *C. torreonensis* evolved in the Torrejonian and *C. puericensis* lived in the Puercan and became rare at the beginning of the Torrejonian before dying out. This is shown by the fact that, within the collections of the NMMNHS and SMP, of over 100 specimens in the Cretaceous and Paleocene referable to *Compsemys*, only one specimen from the Torrejonian NALMA portion of the Nacimiento Formation is referable to *C. puericensis*. The lone *C. puericensis* specimen from the Torrejonian NALMA is among 50 total *Compsemys* specimens (2%) from that age. This suggests slight overlap before leaving *C. torreonensis* as the only survivor, at least in the American Southwest.

Additionally, the morphology of *C. victa* suggests a closer relationship with *C. puericensis* than with *C. torreonensis*, including features from the anterior of the carapace and morphology of neural IV (longer than wide in *C. victa* and *C. puericensis*, wider than long in *C. torreonensis*), which is to be expected in a lineage undergoing cladogenesis. The changes in morphology through time, although some are slight, potentially show continued variation in an asymmetric or budding cladogenetic lineage, with the latest surviving *C. puericensis* living with the earliest *C. torreonensis*. It may possibly represent a type of sympatric speciation where competition led to *C. puericensis* being outcompeted by *C. torreonensis*, leading to the extinction of the former.

Joyce and Anquetin [5] discussed the shape of the anal notch within species of *Compsemys*, in particular Paleocene species, as this region of the plastron is not preserved in the

holotype of *C. victa* (USNM 960, Figure 2A–C), and apparent differences in their shapes were believed to be consistent with the sexual dimorphism seen in some extant turtles. While the anal notch in these turtles does not seem to fall into only two morphs, which would be suggestive of sexual dimorphism, further variation in the morphology of the anal notch may be due to ontogenetic or individual variation as well. A larger sample size of this portion of the shell in *Compsemys* is needed to determine the range of this morphology, and those of closely related species would also be useful in more fully understanding this morphologic variation, particularly as this lineage of turtles has no surviving members today. Regardless, other features also show variation, including the elongated contact between the humeral and the inframarginal scute that restricts the pectoral from contacting the anterior-most inframarginal, which is likely due to intraspecific (i.e., individual) variation, although more specimens are needed to confirm or refute this. Without the addition of more specimens, this feature is also maintained in the diagnosis of *C. victa* for the moment.

5.3. Taxonomic Relationships

Much of what has been previously written about *Compsemys* has focused on its phylogenetic placement and relationships, e.g., [1,4,8–10,12]. Pérez-García [70] and Pérez-García et al. [74] recovered *Berruchelus russelli* as sister to the monotypic *C. victa* in their phylogenetic analyses, with the latter study establishing Compsemydidae for this clade. The phylogenetic analysis by Pérez-García et al. [74] was also recently used by Joyce and Anquetin [5]. Since this latter study considered *C. victa* to be the only valid North American species within *Compsemys* at the time, they used the sister relationship between *B. russelli* and *C. victa* as a generic clade rather than familial, moving the former species into *Compsemys* and synonymizing the two genera. Other recent studies have yielded similar results, e.g., [14,15,75], and retained these species within *Compsemys*, although Pérez-García [68] and Tong et al. [69] kept the species in *Berruchelus*. Regardless, with *Compsemys* no longer considered monospecific in the present study, the sister relationship of *Berruchelus russelli* to *C. victa* has also changed. Because the three species of *Compsemys* share more apomorphies with each other than any do with *B. russelli*, these data suggest that *B. russelli* should remain in the genus *Berruchelus* and not be considered a species of *Compsemys*. The fragmentary nature of the material of *C. victa* makes determining its phylogenetic relationships difficult; however, if the three species of *Compsemys* are placed together at the generic level (as *Compsemys* spp.), they form a generic clade.

With their recognition of Compsemydidae, Pérez-García et al. [74] provided a diagnosis that included *Compsemys* and *Berruchelus russelli*. Based on the presence of *Berruchelus* and our diagnosis of *Compsemys* and the species therein, a revised diagnosis for Compsemydidae was needed, which we have provided above. Many of the features listed above for the diagnosis of *Compsemys* are also present in *Berruchelus*, including large mesoplastra, a nuchal that does not reach the anterior margin, and a deep xiphiplastral notch. There are distinct differences between the genera, though, including a broad suprapygal, neural 8 being broader posteriorly than anteriorly, an anteromedial projection of the nuchal between marginal I, square vertebrals II and III, strongly sinuous plastral midline sutures, and a more distinctly squared-off and flattened anterior plastral edge in *Compsemys*. Further specimens are needed to understand these relationships more fully. *Compsemys*, with the current recognition of three valid species, is closely related to *Berruchelus*, but the two are generically distinct. However, we maintain their inclusion in Compsemydidae (sensu, in part, [74]).

Since the work of Pérez-García et al. [74], other species have been placed within Compsemydidae. Recent studies by Joyce and Rollot [14], Joyce et al. [15], and Tong et al. [69] identified several previous or new species as compsemydids, including *Kallokibotion bajazidi*, *Selenemys lusitanica*, *Peltochelys duchastelii*, *Tongemys enigmatica*, *Calissounemys matheroni*, and *Riodevemys inumbragigas*. However, Pérez-García et al. [96] disagreed with the inclusion of taxa beside *Compsemys* and *Berruchelus russelli* in Compsemydidae, particularly making note of *P. duchastelii*, *R. inumbragigas*, and *S. lusitanica*, which had been recovered in the family by Joyce and Rollot [14]. Pérez-García et al. [96] considered these species to still be within Pleurosternidae. A sister relationship between *Selenemys lusitanica* and *Compsemys* was recovered by Tong et al. [69], although this seems unlikely, particularly if *Selenemys lusitanica* is, indeed, a pleurosternid, see ref. [71]. It is apparent that the phylogenetic relationships of compsemydids and pleurosternids still need more work, but for now we conservatively follow the memberships put forward (i.e., species included) by Pérez-García et al. [74], including *Compsemys* and *Berruchelus* in Compsemydidae. The other potential compsemydids mentioned above will need to be re-evaluated in light of these new taxonomic hypotheses for North American compsemydids.

Specimens previously referred to *Compsemys victa* must also be re-evaluated. The phylogenetic placement of *C. victa* was determined, at least partially, through the use of non-shell characters, including the use of specimens like UCM 49223. With multiple species now present within what was formerly a monospecific *Compsemys*, the specific identification of these specimens is important but may not yet be possible without more material. As UCM 49223 came from the Puercan NALMA interval of the Denver Formation in Colorado, it is likely that it is *C. puercensis*. However, without overlapping material, this specific identification is uncertain. If the same arguments are used for its new placement as those used by Hutchison and Holroyd [12] and Lyson and Joyce [4], then it can be referred to *Compsemys*, but not with certainty to any species.

5.4. Paleoeecology

Based on the resemblance of the skull and shell with that of the extant bigheaded turtle *Platysternon megacephalum*, *Compsemys* may have been carnivorous without the ability to retract its head within the shell, e.g., [4,5,12]. Indeed, the simple but sharply pointed jaws (on referred skulls) are indicative of a carnivorous lifestyle, e.g., [4,5,12]. As the majority of material previously referred to *Compsemys victa* comes from muddy overbank deposits, this aquatic turtle may have also preferred ponded habitats with quieter and gentler water systems, e.g., [1,4,5,12,26].

5.5. Evolution and the Cretaceous–Paleogene Mass Extinction Event

Compsemys specimens are less common from the Cretaceous in New Mexico, e.g., [13,33,38,39], compared to more common and complete material known from the Paleocene, e.g., [11,97]. This implies that *Compsemys* fossils become more prevalent after the K–Pg mass extinction event, at least farther south. Even looking at the collections of NMMNHS and SMP, these patterns are visible in the fossil material referred to *Compsemys*, even if most of it is made up of shell fragments only identifiable to the genus. These institutions, which have been actively collecting from Cretaceous and Paleocene strata in the San Juan Basin where *Compsemys* fossils are found, have 103 total catalogued specimens, with 24 (23.3%) coming from Cretaceous (Campanian–Maastrichtian) strata and 79 (76.7%) coming from Paleocene (Danian) strata. Hutchison and Archibald [26] found a different pattern, however, in northeastern Montana, with *Compsemys* being more common in the latest Cretaceous Hell Creek Formation compared to the early Paleocene Tullock Formation. These different patterns suggest that habitats changed in different ways across

the Cretaceous–Paleogene boundary in the north (Montana) compared to the south (New Mexico). Jasinski et al. [11] also showed that some turtles went extinct at or near the K–Pg boundary. This suggests that different regions transformed differently, and different turtles may have taken advantage and diversified, while others went extinct. Additionally, specimens of *Compsemys* tend to be smaller from the Cretaceous in New Mexico compared to Paleocene material from the state. This may also suggest changing ecological conditions in this region at this time. Although we note that it may also be sampling bias, with more *Compsemys* specimens known from the Paleocene compared to the Cretaceous in New Mexico.

6. Conclusions

Compsemys currently has three valid species, one from the Late Cretaceous (*C. victa*), and two from the Paleocene (*C. puericensis* and *C. torreonensis*). This taxonomic hypothesis is distinct from those of previous studies, which considered all North American compsemysids to belong to *Compsemys victa*, e.g., [1,4,5,12,14,15,69,70,74,87,97,98]. The findings of the current study suggest that specimens previously referred to *Compsemys*, including *C. victa*, must be re-evaluated. Much of the material previously referred to *C. victa* is now only definitively referable to *Compsemys* sp., as most specimens cannot be confidently referred to a distinct species. This suggests fragmentary material from the Late Cretaceous in North America previously referred to *C. victa*, is now referable to *Compsemys* indeterminate species, making the genus a survivor of the end-Cretaceous mass extinction.

Skull material from fossil turtles is rare from the Late Cretaceous in New Mexico, e.g., [11,13,33,64], and finding some associated with shell material will help determine more distinct differences between the species of North American compsemysids. Additionally, the lower number of *Compsemys* specimens from the Cretaceous in New Mexico compared to more common and complete material from the Paleocene suggests changing conditions in this region around the Cretaceous–Paleogene boundary. Different patterns in the occurrences of *Compsemys* (and North American compsemysids) in the northern and southern United States, based on the prevalence of fossil material, may suggest that habitats changed in different ways between the regions after the end-Cretaceous extinction event, changed asynchronously, or that different species (in different locations) coped in different ways. More time and specimens may provide additional information, and subsequent study of other specimens previously referred to *Compsemys victa* may provide further information on *Compsemys* and North American compsemysids, while also helping us further understand the phylogenetic relationships among compsemysids, pleurosternids, and other basal paracryptodires.

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Abbreviations

The following abbreviations are used in this manuscript:

Institutional Abbreviations

AMNH	American Museum of Natural History, New York, New York, USA
MNH.N.F.	Paleontology Collection of the Muséum National d'Histoire Naturelle, Paris, France
NMMNH	New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA
SMP	State Museum of Pennsylvania, Harrisburg, Pennsylvania, USA
UCM	University of Colorado Museum, Boulder, Colorado, USA
UCMP	University of California Museum of Paleontology, Berkeley, California, USA
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington D.C., USA

Anatomical Abbreviations

ab	abdominal	an	anal
c	costal	cerv	cervical
eg	extragular	ento	entoplastron
epi	epiplastron	fem	femoral
gul	gular	hum	humeral
hyo	hyoplastron	hypo	hypoplastron
ifm	inframarginal	m	marginal
meso	mesoplastron	n	neural
nu	nuchal	p	peripheral
pec	pectoral	pl	pleural
py	pygal	spy	suprapygal
v	vertebral	xiphi	xiphiplastron

Other Abbreviations

Clarkfork	Clarkforkian	Ed	Edmontonian
Lanc	Lancian	Ma	megaannum or million years ago
Maast	Maastrichtian	NALMA	North American Land Mammal Age
NALVA	North American Land Vertebrate Age	Sel	Selandian
Tiff	Tiffanian		

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