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Boremys (Testudines, Baenidae) from the latest Cretaceous and early Paleocene of North Dakota: an 11-million-year range extension and an additional K/T survivor

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BOREMYS (TESTUDINES, BAENIDAE) FROM THE LATEST CRETACEOUS AND EARLY PALEOCENE OF NORTH DAKOTA: AN 11-MILLION-YEAR RANGE EXTENSION AND AN ADDITIONAL K/T SURVIVOR

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ABSTRACT—For over a century, the baenid turtle *Boremys* has been recognized as being restricted to the Campanian of North America. Herein we describe new material of *Boremys* sp. from the Hell Creek Formation (Maastrichtian) and Fort Union Formation (Puercan) of southwestern North Dakota and eastern Montana, increasing the stratigraphic range of this taxon by 11 million years. The material was recovered from the base of the Hell Creek Formation to 14 m above the pollen-calibrated K/T boundary in the basal Fort Union Formation. Most of the specimens consist of isolated shell elements, which are easily misidentified as belonging to a kinosternid or chelydrid turtle, but complete shells are present as well. The presence of *Boremys* sp. in the Hell Creek formation increases the baenid taxonomic diversity of this particular rock unit to nine and the overall turtle diversity to 20 taxa, and the presence of *Boremys* sp. in the Fort Union Formation increases the number of baenid lineages that survive the K/T extinction event to eight.

INTRODUCTION

Baenidae is the most speciose group of latest Cretaceous (Maastrichtian) turtles (Gaffney, 1972; Hutchison and Archibald, 1986; Holroyd and Hutchison, 2002; Lyson and Joyce, 2009a, 2009b, 2010). The clade is endemic to North America and flourished during the latest Maastrichtian, in which eight taxa are currently recognized (Lyson and Joyce, 2009a, 2009b). In addition to being the most speciose, baenids are also among the most common turtles in the latest Cretaceous and earliest Paleocene (T.R.L. and W.G.J., field observ.).

The baenid *Boremys* spp. is a common turtle in the Campanian of Alberta and New Mexico. Brinkman and Nicholls (1991) revised this taxon and recognized two species, *Boremys pulchra* (Lambe, 1906a) and *Boremys grandis* Gilmore, 1935, both restricted to the Campanian. *Boremys pulchra* is smaller (shell length not exceeding 320 mm), possesses fewer supramarginals, and is found in the Dinosaur Park Formation of Alberta, whereas *B. grandis* is twice the size (shell length exceeds 320 mm) of *B. pulchra*, has a proliferation of supramarginal scutes, and is found in the Kirtland Formation of New Mexico (Brinkman and Nicholls, 1991). The rugose nature of the carapace and presence of supramarginal scutes makes this taxon highly diagnosable in the field. This, combined with the view that North American Maastrichtian sediments (e.g., Hell Creek, Lance, Denver, and Scollard formations) have been thoroughly prospected, indicated that *Boremys* spp. were restricted to the Campanian.

Here we report the presence of *Boremys* sp. in the Hell Creek (Maastrichtian) and Fort Union (Puercan) formations of south-

western North Dakota. We discuss explanations for why this highly diagnosable taxon has been overlooked in the Hell Creek formation, one of the most exhaustively collected North American rock units, and provide a species-level phylogenetic analysis of Baenidae.

Institutional Abbreviations—**CMN**, Canadian Museum of Nature, Ottawa, Ontario; **PTRM**, Pioneer Trails Regional Museum, Bowman, North Dakota; **SMP**, State Museum of Pennsylvania, Harrisburg, Pennsylvania; **TMP**, Tyrell Museum of Paleontology, Drumheller, Alberta; **USNM**, United States National Museum, Washington, D.C.; **YPM**, Yale Peabody Museum, New Haven, Connecticut.

Anatomical Abbreviations—**ab**, abdominal scale; **an**, anal scale; **asn**, anterior supernumerary scale; **ce**, cervical scale; **co**, costal; **eg**, extragular scale; **epi**, epiplastron; **ent**, entoplastron; **fem**, femoral scale; **gu**, gular scale; **hu**, humeral scale; **hyo**, hypoplastron; **hypo**, hypoplastron; **ma**, marginal scale; **mes**, mesoplastron; **ne**, neural; **ns**, nuchal scale; **nu**, nuchal; **pec**, pectoral scale; **pl**, pleural scale; **pne**, preneural; **psn**, posterior supernumerary scale; **py**, pygal; **spm**, supramarginal scale; **spy**, suprapygal; **ve**, vertebral scale; **xi**, xiphoplastron.

STRATIGRAPHIC AND GEOLOGIC SETTING

The material of *Boremys* sp. described herein was found from the base of the Hell Creek to 14 m above the pollen-calibrated K/T boundary in the basal Fort Union Formation (Bercovici et al., 2009) (Table 1). All of the material was found in sand or silty mudstone with either a channel or crevasse splay paleoenvironmental interpretation (Table 1).

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TABLE 1. Lithology, paleoenvironmental interpretation, and distance from the pollen-calibrated K/T boundary of PTRM field localities that yielded material of *Boremys* sp.

PTRM site no.	Lithology	Paleoenvironmental interpretation	Distance from the K/T Boundary
V89004	Sand	Channel	(-) 81.68 m
V92048	Sand	Channel	(-) 41.12 m
V92067	Sand	Crevasse splay	(-) 38.88 m
V00028	Sand	Channel	(-) ~25–65 m
V98027	Sand	Channel	(-) 12.07 m
V88004	Silty mudstone	Crevasse splay	(-) 10.61 m
V89003	Sand	Crevasse splay	(-) 8.40 m
V95008	Sand	Channel	(-) 6.00 m*
V96003	Silty mudstone	Crevasse splay	(-) 5.25 m
V02017	Sand	Crevasse splay	(+) 1.40 m
V99011	Sand	Channel	(+) 8.57 m
V99012	Sand	Channel	(+) 14.00 m

An asterisk (*) denotes the distance from the Hell Creek/Fort Union formational contact; a minus (-) or a plus (+) sign denotes distance below and above the K/T boundary, respectively.

Most of the elements preserved were found isolated (see below). However, two articulated shells from the Fort Union Formation (PTRM 16150 and PTRM 16156) were found at PTRM sites V99011 and V02017, respectively. Both localities are near the pollen-calibrated K/T boundary (Bercovici et al., 2009). PTRM 16156 was collected from a silty mudstone, sandstone sequence 1.40–1.63 m above the K/T boundary, whereas PTRM 16150 was located in a sandstone unit that extends from 8.57–14.10 m above the K/T boundary (Table 1). Since PTRM 16156 is more complete and therefore likely did not undergo much preburial transportation, site V02017 probably most closely approximates the paleoenvironment in which *Boremys* sp. lived.

PTRM site V02017 is an unusually fossiliferous Fort Union Formation (Puercan) locality that is several meters thick. An intensive, stratigraphically controlled screen-washing operation was undertaken for several years to recover vertebrate, plant, and pollen fossils (Bercovici et al., 2009). A total of 5404 kg of matrix was screen-washed, yielding a total of 5341 vertebrate specimens. Puercan mammals and Fort Union plant fossils are found throughout the site, starting between 72 and 95 cm above the pollen calibrated K/T boundary (Bercovici et al., 2009). The fossils are found in a fluvial sequence of sands and silty mudstones that are overlain by variegated beds. The site has yielded several turtles, including *Axestemys* sp., *Stygiochelys* sp., and *Neurankylus* sp., and abundant microvertebrate remains, including numerous species of mammals, lizards, salamanders, alligators, crocodiles, and fish, as well as numerous leaves (see Bercovici et al., 2009, for stratigraphic details for the fossils). PTRM 16156 was found 1.40–1.63 m above the pollen defined K/T boundary in fine- to medium-grained, unconsolidated sand that is weakly cross-bedded.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788

PARACRYPTODIRA Gaffney, 1975

BAENIDAE Cope, 1882

BAENODDA Gaffney and Meylan, 1988

BOREMYS Lambe, 1906b

Type Species—*Boremys pulchra* (Lambe, 1906a).

Species Included—*Boremys pulchra* (Lambe, 1906a); *Boremys grandis* Gilmore, 1935.

BOREMYS PULCHRA (Lambe, 1906a)

Holotype—NMC 1648; Dinosaur Park Formation, Dinosaur Provincial Park, Alberta; middle Campanian, Upper Cretaceous (Brinkman and Nicholls, 1991).

Referred Specimens—Campanian, Dinosaur Park Formation, Alberta: TMP 1999.55.223 (complete shell), TMP 2001.12.36 (articulated skeleton), USNM 10676 (complete shell), and specimens listed by Brinkman and Nicholls (1991). Campanian, Judith River Formation, Montana; see specimens listed by Brinkman and Nicholls (1991).

Diagnosis—See Brinkman and Nicholls (1991).

BOREMYS GRANDIS Gilmore, 1935

Holotype—USNM 12979; Kirtland Formation, New Mexico, U.S.A.; Upper Cretaceous (Campanian) (Brinkman and Nicholls, 1991).

Referred Specimens—Campanian, Kirtland Formation, New Mexico, U.S.A.: SMP VP-2820 (neural; Hunter Wash Member of Kirtland Formation), also see specimens listed by Brinkman and Nicholls (1991).

Diagnosis—See Brinkman and Nicholls (1991).

BOREMYS sp.

(Figs. 1–3)

Horizon and Locality—Hell Creek Formation, Maastrichtian, Montana and North Dakota; Fort Union Formation, Paleocene, North Dakota; numerous localities, see next section.

Referred Material—The following specimens are from the Hell Creek Formation localities in North Dakota (PTRM localities V89004, V92048, V92067, V00028, V88004, V98027, V89003, V95008, and V96003): PTRM 2944, neural 7?; PTRM 9406, neural fragment; PTRM 9800, costal 6? fragment; and PTRM 16155, costal fragment; all from V89004. PTRM 9802, neural 7?, from V92048. PTRM 10041, neural fragment; PTRM 9804, right costal 5?; PTRM 9404, fragment; all from V92067. PTRM 10021, neural 3, from V00028. PTRM 9386, neural fragment, from V88004. PTRM 10020, preneural?, from V98027. PTRM 16153, three costal fragments; PTRM 16152, unidentified element; PTRM 9796, suprapygal; PTRM 16151, right costal 1; PTRM 9799, costal; PTRM 9474, suprapygal?; PTRM 9443, neural fragment; all from V89003. PTRM 7072, nuchal, from V95008. PTRM 9471, posterior end of neural 1?, from V96003. The following specimens are from the Hell Creek Formation localities in Montana (unknown localities): YPM 57303, two peripherals and suprapygal, and YPM 57310, peripheral and two costals. The following specimens are from the Fort Union Formation localities in North Dakota (PTRM localities V02017, V99011, and V99012). PTRM 16150.01, anterior carapace; PTRM 16150.02, complete plastron; PTRM 8932, left costal 1; PTRM 16154, costal fragment; all from V99011. PTRM 8912, left costals 1 and 2, from V99012. PTRM 5350.74, nuchal; PTRM 16156, mostly complete shell lacking all but three peripherals, isolated peripheral, anterior caudal vertebra, and small shell fragments; all from V02017. The nuchal (PTRM 5350.74) was found in the same horizon within 25 cm of PTRM 16156 and is thought to belong to the same individual. This interpretation is supported by a perfect match of the suture and the sulci on the nuchal with that found on the carapace.

DESCRIPTION

The two Fort Union shells are mostly complete and they largely form the basis of this description. PTRM 16156 has a carapace length of 31.8 cm and a plastron length of 30 cm (Fig. 1). The carapace length of PTRM 16150.01 cannot be determined, but the length of the associated plastron (PTRM 16150.02) is considerably shorter (19.4 cm) than that of PTRM 16156 (Fig. 2).

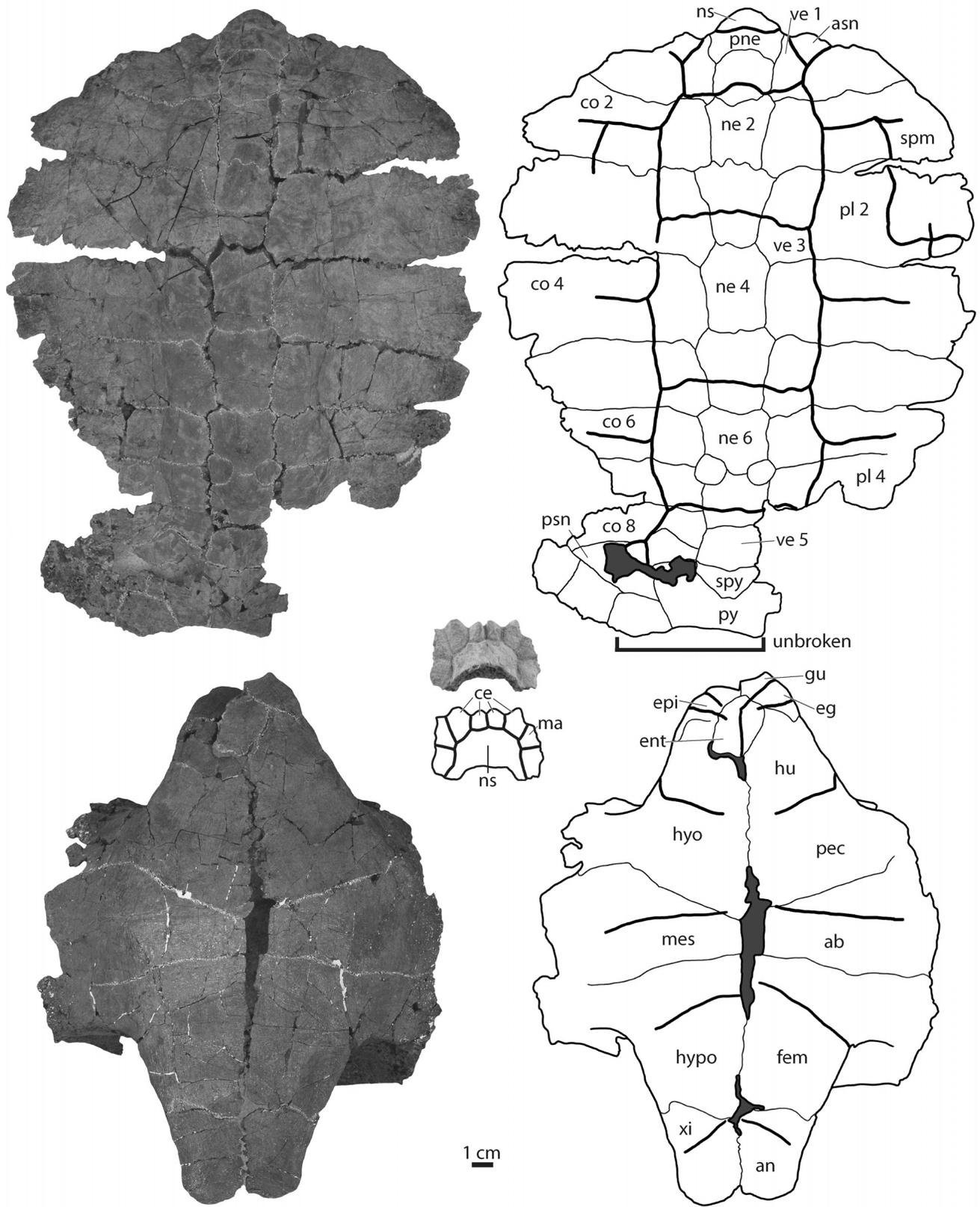


FIGURE 1. Shell of *Boremys* sp. from the early Paleocene (Puercan) PTRM field locality V02017. Photographs (left) and illustrations (right) of carapace (top), nuchal (middle), and plastron (bottom) of PTRM 16156. Thick lines are sulci and thinner lines are sutures.

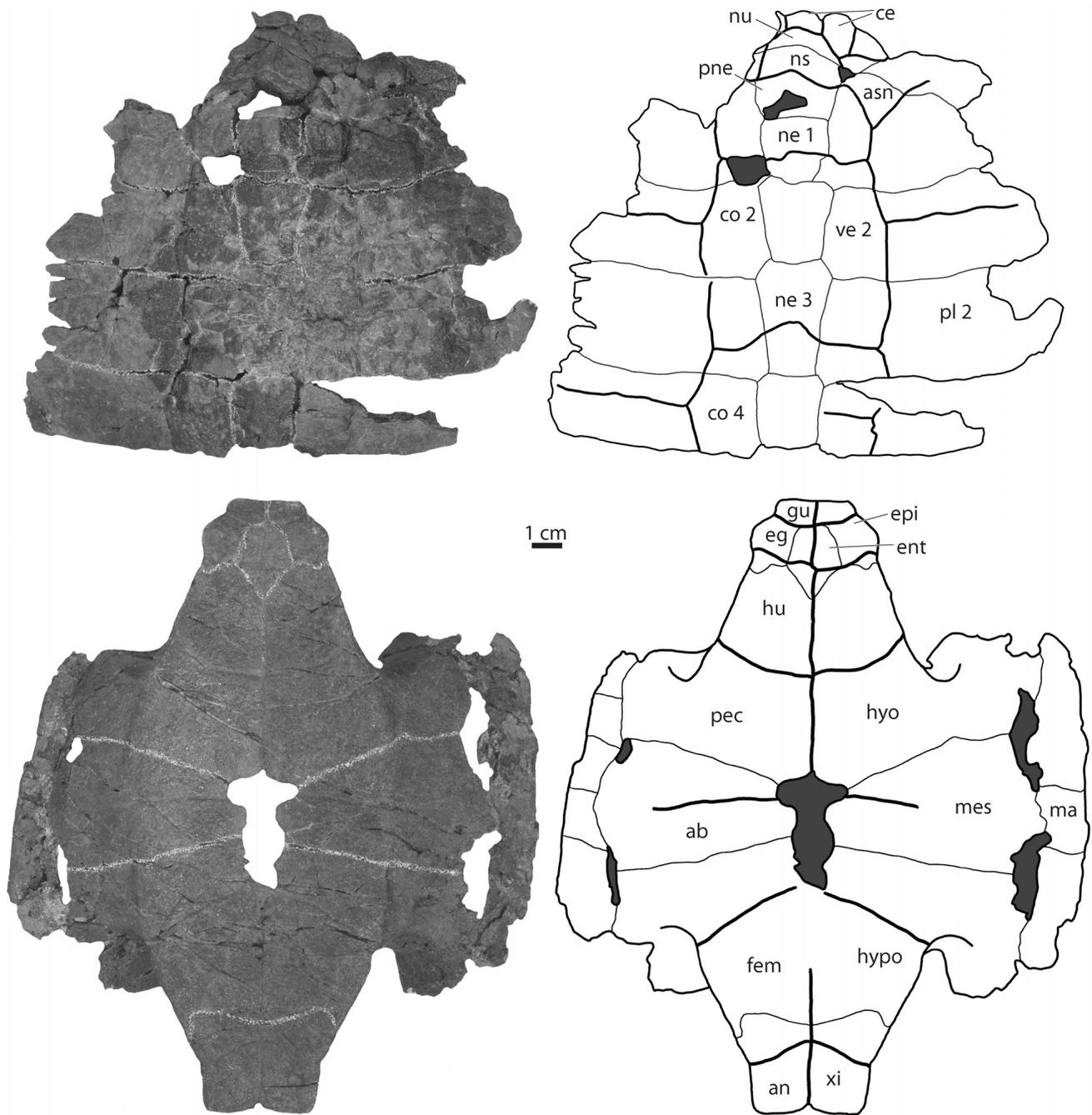


FIGURE 2. Shell of *Boremys* sp. from the early Paleocene (Puercan) PTRM field locality V99011. Photographs (left) and illustrations (right) of carapace (top) and plastron (bottom) of PTRM 16150. Thick lines are sulci and thinner lines are sutures.

Unlike material of *B. pulchra* of similar size from the Campanian (Brinkman and Nicholls, 1991), both individuals have open sutures. Central plastral fontanelles are present between the mesoplastra in both individuals. Given that such fontanelles are absent from all known Campanian specimens of *Boremys* and are not preserved in any Maastrichtian specimen, this may indicate skeletal immaturity, but the possibility remains that this is an autapomorphy of the Maastrichtian to Puercan lineage. Peripherals are missing in both specimens except for the left last three and one isolated peripheral in PTRM 16156. Neither carapace width nor scalloping of the posterior margin of the

shell can be determined. As in the Campanian *Boremys* spp., the carapace has a distinctive nodular surface texture. This nodular surface texture is strongest on the nuchal.

As in the material of Campanian *Boremys* spp., the anterior margin of the nuchal is weakly scalloped (Fig. 3). The nuchal bone shows some variation in the scute pattern, similar to *B. pulchra* (Brinkman and Nicholls, 1991) (Fig. 3). In the Puercan nuchal PTRM 16156.06 and the Maastrichtian nuchal PTRM 7072, the cervical scute is subdivided, whereas the cervical scute of the Puercan nuchal PTRM 16150.01 is not subdivided. In these three specimens the cervical scute lies entirely on the nuchal

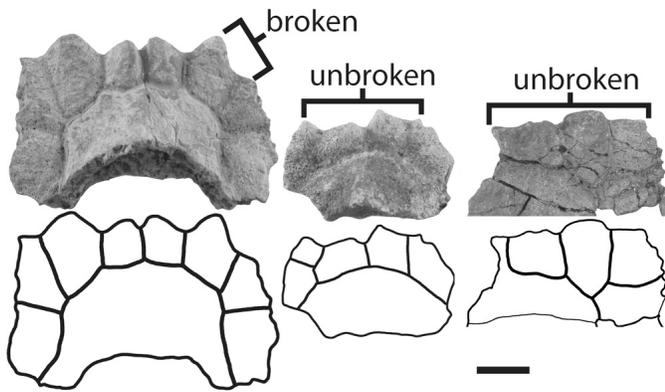


FIGURE 3. Nuchal bones from three individual *Boremys* sp. from the early Paleocene (Puercan) of North Dakota showing variation in scale morphology. Photograph (top) and illustration (bottom) of PTRM 16156 (left), PTRM 7072 (middle), and PTRM 16150 (right).

bone, as in *Boremys* spp. from the Campanian. A large nuchal scute is present in all *Boremys* material and, unlike other baenids with a nuchal scute (i.e., *Eubaena* sp. and *Stygiochelys* sp.), the nuchal scute covers the nuchal-preneural suture, instead of lying entirely on the nuchal bone. As in Campanian *Boremys* spp., large pronounced knobs are present along the nuchal and preneural contact, third neural, fifth neural, and along the contact between the sixth and seventh neurals, which correspond to rounded apices formed by the vertebral scutes. The shell is greatly thickened at the center of these knobs and isolated preneurals and odd numbered neurals can be identified as *Boremys* using this character. Five vertebral scutes are present. As in most other baenods, the first vertebral widens posteriorly and the vertebrals are slightly longer than wide. An anterior supernumerary pleural scale is present, similar to Campanian *Boremys* spp., *Stygiochelys* sp., and *Eubaena* sp. As in Campanian *Boremys* spp., a posterior supernumerary pleural scale is present as well. The sulci fade laterally; however, it is apparent that at least one row of supramarginal scales are present. As a result of the presence of supramarginal scales, the second pleural scale in PTRM 16156 is more than twice as long as wide.

A large, square preneural bone is present, as in Campanian *Boremys* spp., *Stygiochelys* sp., and some individuals of *Eubaena* sp. (T.R.L. and W.G.J., pers. observ.). The first neural is square and small. The second through sixth neurals are hexagonal in shape. Two small, round, supernumerary bones are present between the sixth and seventh neurals in PTRM 16156. A single suprapygal is present and is triangular in shape. The pygal is trapezoidal in outline and the suprapygal is deeply inserted into the pygal. The eighth costal is split and nine costals are therefore present in PTRM 16156. The ninth costal contacts two and a half peripherals. Rows of weak knobs are present along the costals approximately one-third of the distance from their lateral edge, corresponding to the medial extent of the supramarginals. These knobs occur on the contact between the first and second costals, on the third costal anterior to the contact between the third and fourth costals, on the contact between the fifth and sixth costals, and on the eighth costal anterior to the contact between the eighth and ninth costals.

Central plastral fontanelles are present in both preserved plastra. Both the anterior and posterior lobes are rectangular in shape. Large extragulars are present and they contact one another medially in PTRM 16150. The gular scutes also contact one another medially. In PTRM 16150 the extragular and humeral

sulcus is on the center of the entoplastron. This differs from the Campanian *Boremys* spp., where this sulcus is located on the anterior portion of the entoplastron (Brinkman and Nicholls, 1991). As in Campanian *Boremys* spp., the anal scute does not lap onto the hypoplastra. A small anal notch is present. The epiplastra and entoplastron are large. A distinct lateral projection is present on the epiplastra, as in the Campanian *Boremys* spp. Mesoplastra are present and extend medially to form the lateral edge of the central plastral fontanelle.

PHYLOGENETIC ANALYSIS

In order to test the character-based hypothesis that the material described herein belongs to *Boremys* spp., a maximum parsimony analysis was performed using the matrix of Lyson and Joyce (2009a, 2009b, 2010, 2011). A total of 106 osteological characters for 28 taxa, including 26 ingroup taxa, were analyzed. Eight characters were considered to represent morphoclines and were ordered (7, 14, 16, 18, 28, 33, 36, and 70). The remaining characters were run unordered and all characters were left unweighted. Missing data were scored as '?'. The complete matrix can be found in Appendix 1. A maximum parsimony analysis was performed on the data set using PAUP 4.0b10 (Swofford, 2002). *Proganochelys quenstedti* Baur, 1887 (as described by Gaffney, 1990) and *Kayentachelys aprix* Gaffney et al., 1987 (as described by Sterli and Joyce, 2007; Gaffney and Jenkins, 2010; and pers. observ. of postcranial material) were specified as the outgroup taxa and a branch-and-bound search was used with minimum branch lengths set to collapse. Support for each node was measured by calculating Bremer support values (Bremer, 1994) for each clade, as well as bootstrap frequencies (Felsenstein, 1985) with 10,000 bootstrap replicates and 100 random sequence addition replicates. Bootstrap frequencies >70% are considered strong support (Hillis and Bull, 1993).

The analysis resulted in eight most parsimonious trees with a tree length of 247 (consistency index [CI] = 0.4899, retention index = 0.7375, rescaled CI = 0.3613). The outcome of this analysis is identical to that of Lyson and Joyce (2011), with the only difference being the addition of the Hell Creek material of *Boremys* sp. described herein placed in a polytomy with *B. pulchra* and *B. grandis*. The phylogenetic analysis thus supports the identification of the material as belonging to *Boremys* spp (Fig. 4).

DISCUSSION

The described material can confidently be assigned to *Boremys* sp. based on the presence of several characters that it shares with previously described Campanian *Boremys* spp., including the presence of a nodular surface texture; a weakly scalloped anterior shell margin; distinct knobs on the nuchal-preneural suture, on the third and fifth neurals, and between the sixth and seventh neurals; lateral row of knobs on the costals; the presence of a preneural, supramarginals, anterior and posterior supernumerary scales; lateral epiplastra projections; and anal scutes that are located completely on the xiphiplastra. Several of these characters are also shared with *Denazinemys nodosa* (Gilmore, 1916), including the presence of a nodular surface texture, weakly scalloped anterior shell margin, anterior supernumerary scales, and anal scutes that are located completely on the xiphiplastron. However, the distinctive knobs in discrete locations, supramarginals, and posterior supernumerary scales are only found on *Boremys* spp. and we feel that this material is best referred to this taxon. Yet, we feel that the material cannot be diagnosed to the species level. Two species of *Boremys* are generally recognized and are differentiated from one another based on shell size and number of supramarginals (Brinkman and Nicholls, 1991). The material described herein likely belongs to juvenile individuals based on the presence of large plastral fontanelles and open

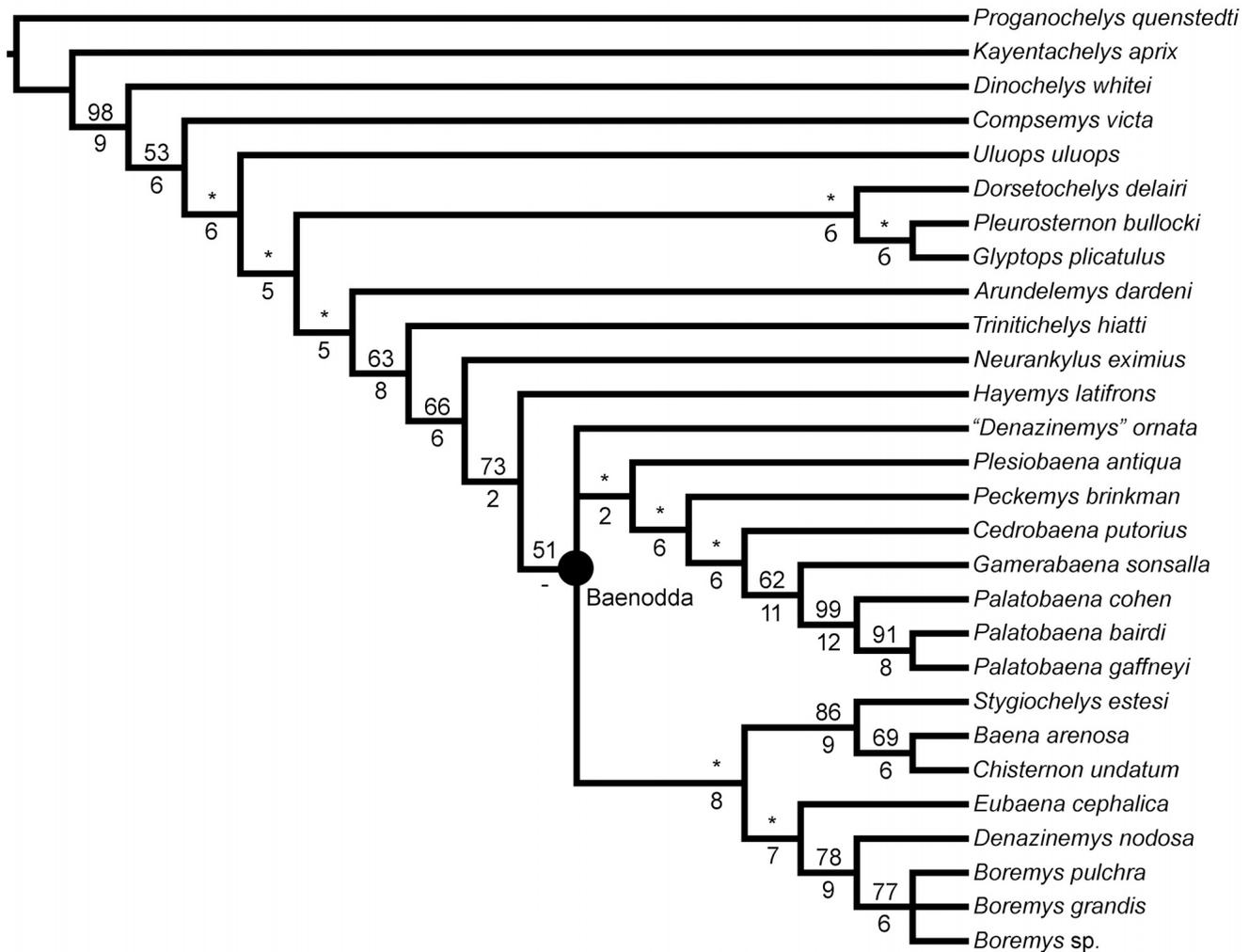


FIGURE 4. Phylogenetic hypothesis for the placement of Maastrichtian and Puercan materials of *Boremys* sp. based on a strict consensus of eight trees. The phylogenetic analysis places *Boremys* sp. in a polytomy with the two Campanian *Boremys* spp. Support for each node is measured using bootstrap frequency (top) and Bremer support for each clade (bottom). An asterisk (*) indicates bootstrap support of less than 50% and a dash (-) indicates a Bremer support of 0. See text for tree statistics and discussion.

sutures and therefore the adult size cannot be determined. Assuming that this taxon lost its fontanelles during ontogeny, a considerable adult size can be inferred, although it is not clear if it would have reached the large size seen in *B. grandis*. The second character that differentiates the two valid *Boremys* species is the number of supramarginals. However, the sulci fade laterally in the described material and the number of supramarginals cannot be estimated. It should be noted that the placement of the visible supramarginals on PTRM 16156 on costal III indicate a second row of supramarginals similar to that in *B. grandis*. However, we cannot be certain of this and we therefore cannot determine if the material belongs to *B. pulchra*, *B. grandis*, or to a new taxon. We thus conservatively identify the material as *Boremys* sp.

The stratigraphic range of *Boremys* spp. has long been recognized as being restricted to the Campanian Dinosaur Park, Judith River, and Kirtland formations (Lambe, 1906a; Gilmore, 1919; Gaffney, 1972; Brinkman and Nicholls, 1991; Brinkman, 2005). The presence of *Boremys* in both the Hell Creek and Fort Union formations is surprising for several reasons: (1) paleontologists have been collecting in the Hell Creek Formation for over 100 years and this formation contains one of the best understood

terrestrial vertebrate faunas; (2) *Boremys* spp. is thought to be a riverine turtle and therefore has a high preservation potential; and (3) the carapaces of *Boremys* spp. can easily be identified on the basis of their nodular surface texture and presence of supramarginals. It appears, however, that Maastrichtian or Puercan *Boremys* sp. was not recognized until now for several reasons. *Boremys* sp. differs from other baenids in having a relatively thin shell and its preservation potential is not as high as that of other baenids. In addition, all of the newly described material is completely unfused, indicating that the shells of late representatives of *Boremys* disarticulated more easily than those of contemporaneous baenids. Given these two observations, the chance of finding a complete shell is low. Through comparison with the two new Paleocene shells and previously published Campanian shells, it now is possible to confidently identify a number of isolated shell bones of this lineage, such as the nuchal, suprapygal, pygal, a few costals, and a few neurals. In particular, isolated nuchals and neurals show evidence of the prominent median knobs of the apex of the vertebral scutes, and the pygal and suprapygals exhibit a sharp keel. Indeed, many of the elements referred herein were originally misidentified by the authors as

belonging to the kinosternoid *Hoplochelys clark*, a taxon known to have a nodular surface texture as well (Knauss et al., 2011).

The Hell Creek and Fort Union *Boremys* sp. consists of only shell material, leaving open the possibility that it belongs to an already named skull taxon. Four Hell Creek and Fort Union taxa exist that are currently known from skulls only, including *Hayemys latifrons* Gaffney, 1972, *Gamerabaena sonsalla* Lyson and Joyce, 2010, *Cedrobaena putorius* (Gaffney, 1972), and *Eubaena cephalica*. Of these, only *E. cephalica* is predicted by our phylogeny to have had a shell with five pleural scales and, therefore, it appears plausible that the *Boremys* shells described herein belong to *E. cephalica*. A number of observations support this hypothesis. First, like the shells of the Hell Creek and Fort Union *Boremys* sp., the skull of *E. cephalica* has open sutures. By contrast, most other baenid taxa from the Hell Creek Formation are mostly known from fused shells and skulls. Second, the skull of *B. pulchra* and *E. cephalica* are very similar (Brinkman and Nicholls, 1991). The two taxa share the following characters: jugal excluded from the orbital margin; a well-developed contact between the pterygoids; deep posterior emargination; cheek region moderately emarginated and level with the ventral edge of the orbital margin; long preorbital length; a distinctive constriction of the maxilla just anterior to the orbits; a long midline oval scale located on the posterior end of the skull roof; absence of a lingual ridge; large nasals; opisthotic excluded from the stapedial foramen; very little exposure of the prefrontal on the dorsal skull roof; long symphysis joining rami of mandible; outward facing triturating surface on lower jaw, so when seen in lateral view the lingual ridge appears higher than the labial ridge; labial ridge of mandible slightly more pronounced anteriorly; coronoid forms relatively large portion of the posteromedial triturating surface; long, low splenial; and well-developed retroarticular process. The skull nevertheless differs in a number of characters. In particular, the skull of *B. pulchra* is significantly smaller than that of *E. cephalica*, and the latter species has an incipient secondary palate and a high maxillary height below the orbit, both of which are lacking in *B. pulchra*.

Considering the great similarity in the skulls of *B. pulchra* and *E. cephalica* and the phylogenetic clustering of the skull taxon *E. cephalica* within the contemporaneous postcranial material described herein, we normally would conclude that *E. cephalica* is the previously unrecognized Maastrichtian representative of the *Boremys* lineage. We have used similar argument to resolve the parataxonomy of numerous other baenid groups (Lyson and Joyce, 2010). However, a newly discovered locality in the lower third of the Hell Creek Formation of Slope County, North Dakota, allows us to conclude otherwise (Lyson and Joyce, unpubl. data). This locality has yielded several skulls of *E. cephalica* that are closely associated with shells that clearly differ from the *Boremys* shells described herein. For example, the new *E. cephalica* shell material is smooth, lacks the distinctive knobs found in *Boremys* spp., has deep, wide sulci, and also lacks supramarginal scutes. Thus, we are confident that the *Boremys* sp. shell material described herein does not belong to a previously named skull taxon.

The presence of *Boremys* sp. material in the Hell Creek and Fort Union formations extends the range of this lineage by 11 million years. Material of *Boremys* sp. is found throughout the Hell Creek Formation and at least 14 m above the pollen calibrated K/T boundary (Table 1). The presence of *Boremys* sp. above the K/T boundary increases the number of surviving baenid lineages to eight. Specifically, the Cretaceous baenids *Neurankylus eximius* Lambe, 1902, *Peckemys brinkman* Lyson and Joyce, 2009b, *C. putorius*, *Palatobaena cohen* Lyson and Joyce, 2009a, *E. cephalica*, *S. estesi*, and the lineages leading to *G. mckennai* and now *Boremys* sp. are hypothesized to have survived into the Paleocene. Only two baenid taxa, *G. sonsalla* and *H. latifrons*, appear to go extinct at the K/T boundary. These two taxa are each known

from a single skull and thus have a very poor fossil record. Thus these extinctions may not be 'real,' but rather an artifact of their poor sampling. Regardless, baenid turtles do very well across the K/T boundary.

The addition of *Boremys* sp. to the Hell Creek turtle fauna increases its baenid diversity to nine and the overall turtle diversity to 20. Baenids dominate the Hell Creek in both number of taxa and number of individuals. The Hell Creek baenid diversity is more than twice that in any other formation (e.g., Gaffney, 1972; Brinkman, 2005). The overall turtle diversity of the Hell Creek is comparable to that of the modern Mobile Bay region of Alabama, and baenids appear to play a similar ecological role as the Mobile Bay emydids. In particular, 10 emydids are currently found in southern Alabama and the overall turtle diversity for the bay and surrounding region is ca. 19 (Ernst and Barbour, 1989). Like the Mobile Bay emydids, the Hell Creek baenids have diverse triturating surfaces, indicating a certain degree of niche partitioning, which would help explain the high number of closely related taxa in a single formation.

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APPENDIX 1. Character-taxon matrix for the phylogenetic analysis of Paracryptodira performed in this study. Characters are listed in Lyson and Joyce (2009a, 2009b, 2010, 2011). Missing data are coded as ‘?’ **Abbreviations:** **A**, polymorphism for states 0 and 1; **B**, polymorphism for states 0 and 2.

<i>Proganochelys quenstedti</i>			
000000000	000000000	000000?00	000000000
00000?100	000000000	000000000	000000000
000000000	0?00000???	0???00	
<i>Kayentachelys aprix</i>			
000000000	0000010?0?	000000?00	000010000
000000000	000000000	000000000	0000000010
000000000	0000000???	000000	
<i>Dorsetochelys delairi</i>			
1000020010	0000120110	0010?00000	0??????????
???????????	???????????	0000000002	00111011??
??1?????1?	???????????	???????	
<i>Compsemys victa</i>			
0000020010	0000000001	0?0??00010	0001?00000
00010000?2	100000001?	000000?00?	00110110??
1?00?????11	011100000?	000010	
<i>Arundelemys dardeni</i>			
0000010010	000001021?	1101000010	01?????????
???????????	???????????	000000?0?	00110010??
01?0?????11	???????????	???????	
<i>Dinochelys whitei</i>			
?0000?0?00	0000010???	0??????????	??0?00000
0000000000	?101000000	00000?00??	001101?110
??0?00?210	000?000100	1???1?	
<i>Pleurosternon bullocki</i>			
10000200?0	0000120210	00100?0200	21??00000
0001000002	?0?0000000	0000001001	00111011??
0?00?00111	001?00?11	1?????	
<i>Glyptops plicatulus</i>			
1000020011	0000120210	001?000200	2000000000
0001000002	0100000000	000000000?	0011011110
1?00?00?11	0001000100	111011	
<i>Uluops uluops</i>			
0000010010	0000110010	0000000010	1??????????
???????????	???????????	00000?100000111010??	
0?10??01?	???????????	???????	
<i>Trinitichelys hiatti</i>			
0000010001	0001120210	111010001?	11????????00
?00100?002	100000?00?	0000000000	00111000??
0?00??0011	10?1011???	011?01	

Neurankylus eximius
 00?00??0?0 0000110??? 0010??01? 01?0?10000
 0001000000 1100000000 0000010100 0011?00010
 01?1111000 1001011101 011101

Hayemys latifrons
 00??0??0?0 0000001210 111??0101? 00?????????
 ?????????? ?????????? 000000000? 00111000??
 0?11??00? ??0???????? ???????

Plesiobaena antiqua
 0000011010 01B1121200 1110110110 1001011110
 1001000011 1011011011 0000000001 0011100101
 1111111000 0001111001 011101

Peckemys brinkman
 0000001011 0??1111110 1000110211 100111?1?0
 1000000001 11??0?1001 0000012001 00?????????
 ?????????? ??01111?? 0?????

Cedrobaena putorius
 0000011111 1??1111100 111010A211 1001???????
 ?????????? ?????????? 0000000010 10?????????
 ?????????? ?????????? ???????

Boremys pulchra
 01000?11?1 0101121?10 1110?00011 1010021101
 1011111101 1110111111 0000000001 0011100101
 1111100002 0001111010 011101

Boremys grandis
 ?????????? ?????????? ?????????? ??????21101
 1012111101 1110111111 ?????????? ??????????
 ??????????2 0001111010 011?01

Boremys sp.
 ?????????? ?????????? ?????????? ???????11?1
 ?0121111?1 1110111111 ?????????? ??????????
 ??????????2 0001111010 011101

Eubaena cephalica
 0101011101 1101101210 1110100011 10?????????
 ?????????? ?????????? 0000001101 00111001??
 1?11??000 00????????? ???????

Palatobaena cohen
 2000121010 1122011100 1110110011 1001111110
 ?001000011 10?111?011 1111011111 1011101101
 ??11??000 0001111?? 0????01

Palatobaena bairdi
 2000121010 1122111000 1000110011 10011?????
 ?????????? ?????????? 1111001112 1011101101
 ??11??00? ?????????? ???????

Palatobaena gaffneyi
 2001121010 1122111100 1000110111 10?????????
 ?????????? ?????????? 1111001112 10111011??
 ??11??00? ?????????? ???????

Stygiochelys estesi
 0010011000 1112121110 1111001111 11?????????
 ??1211?0?0 ?01?1??01? 0000001001 0011100101
 1111??000 0001111110 0??????

Baena arenosa
 0010011000 01?2121011 0001000011 1121011100
 1112010000 1011111011 0000000000 011110?101
 1111??000 0001111?? 011101

Chisternon undatum
 0010011000 1112121011 0101001111 1120011101
 1012110000 1011101011 0000000101 0111100101
 1111111000 0001111?? 011?01

Gamerabaena sonsalla
 0000111000 111100120? ??????10011 10?????????
 ?????????? ?????????? 00001?11?? 1?111001??
 1??1??00? ?????????? ???????

Denazinemys nodosa
 ?????????? ?????????? ?????????? ??????2110?
 1012110000 11101?1111 ?????????? ??????????
 ??????????2 0001111?? 0????01

Denazinemys' ornata
 ?????????? ?????????? ?????????? ??????1110?
 1001000000 10100?1011 ?????????? ??????????
 ??????????2 0001111?? 0????01

Downloaded by [Tyler R. Lyson] at 07:15 12 July 2011