A Late Cretaceous (Turonian–Coniacian) high-latitude turtle assemblage from the Canadian Arctic

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Abstract: Three turtles are present in a Turonian–Coniacian age high-latitude vertebrate assemblage from Axel Heiberg Island: *Borealochelys axelheibergensis* gen. et sp. nov., a generically indeterminate euctyodire, and a trionychid. The assemblage differs from most Late Cretaceous turtle assemblages from North America in that members of the Paracryptodira are absent. The absence of this group is interpreted as a result of latitudinal differentiation of turtle assemblages in North America during the Late Cretaceous. The level of diversity of turtles in the Axel Heiberg assemblage is comparable to that of mid-latitude assemblages associated with a mean annual paleotemperature of 14 °C, adding to the evidence for high mean annual temperatures at high latitudes during Turonian–Coniacian times.

Résumé : Trois tortues sont présentes dans un assemblage de vertébrés (Turonien–Coniacien) provenant d’une latitude élevée, l’île Axel Heiberg : *Borealochelys axelheibergensis*, n. gen., n. sp., un euctyodire génériquement indéterminé et un trionychidé. L’assemblage diffère de la plupart des assemblages de tortues de l’Amérique du Nord en ce que les membres de Paracryptodira sont absents. L’absence de ce groupe est interprétée comme une différenciation latitudinale des assemblages de tortues en Amérique du Nord au Crétacé tardif. Le niveau de diversification de l’assemblage Axel Heilberg est comparé aux assemblages à latitudes moyennes associées à une paléotemperature moyenne annuelle de 14 °C, ajoutant aux évidences de températures moyennes annuelles élevées à l’époque du Turonien–Coniacien.

Introduction

Nonmarine vertebrates of Turonian–Coniacian age from Axel Heiberg Island (Canadian Arctic) were first reported by Tarduno et al. (1998), and fish from the locality were described by Friedman et al. (2003). A striking aspect of the faunal assemblage is the abundance of ectothermic reptiles, particularly champsosaurs and turtles. Such reptiles are absent in other Late Cretaceous high-latitude assemblages (Fiorillo and Gangloff 2001; Rich et al. 2002). The occurrence of ectothermic reptiles in the Axel Heiberg locality was interpreted as evidence that the Axel Heiberg fossil assemblage was formed during a period of unusual climatic warmth (Tarduno et al. 1998). In particular, based on the thermal tolerance of their modern analogues, crocodiles, the presence of large champsosaurs suggested that the mean annual temperature was in excess of 14 °C. This estimate is consistent with oxygen-isotope analyses of foraminifera from several deep-sea deposits which indicate extreme warmth during the Late Turonian (Huber et al. 2002; Wilson et al. 2002). In this paper, turtle fossils from the Axel Heiberg Island locality are described and the biogeographic and paleoclimatological significance of this assemblage is discussed.

The vertebrate material was recovered from a single locality near Expedition Fiord (79° 23.5′N, 92°10.9′W). The paleolatitude of the locality is estimated to be 71°N (Tarduno et al. 2002). The material occurs in a 3 m thick unit of siltstone and shale that is stratigraphically positioned between the top of the Strand Fiord basalts and the base of the marine shale of the Kanguk Formation. 40Ar/39Ar radiometric age data on underlying basalts, magnetostratigraphic data, and ammonites and inoceramids from overlying sediments constrain the fossil assemblage to the Turonian–Coniacian. Sedimentology of the unit indicates deposition in a bay or estuary, although the champsosaurs, turtles, and fish suggest a freshwater environment.

Material from the Expedition Fiord locality is housed in the collections of the University of Rochester (UR).

Systematic paleontology

Testudines Batsch, 1788

Eurypmorphidae Gaffney, 1975

Family Incertae sedis

*Borealochelys axelheibergensis* gen. et sp. nov.

Holotype: UR 00.100, anterior portion of shell including the nuchal, neurals one to five, right peripherals one and two, left peripherals one to seven, right first and second costals, left first to fifth costals, and associated hyoplastron.
DIAGNOSIS: A euctodire similar to “macrobaenids” and “sinemydids” in having a low-domed shell with expanded posterolateral peripherals, differing from macrobaenids and sinemydids but similar to Xinjiangchelys in having a more extensive plastron; differing from Judithemys and Anatolemys in that carapace is convex, a mid-dorsal depression is absent, twelfth marginal scutes restricted to the pygal, and the inguinal buttress of the hyoplastron is bowed inwards; similar to Judithemys and different from Anatolemys in lacking an upturned lateral edge of the carapace and lacking plastral fenestrae; differs from that of Judithemys in that a nuchal emargination is absent, the cervical scute is narrower, the nuchal bone is longer, and the first dorsal rib is long and forms the sharp edge of a ridge extending to the hyoplastron.

ETYMOLOGY: The generic name refers to the high-latitude occurrence of the turtle. The specific name refers to Axel Heiberg Island.

REFERRED SPECIMENS: UR 97.100, partial carapace, including the nuchal, neurals one to seven, the medial ends of left costals one to seven, the first to seventh right costals, and the first to ninth peripherals; UR 03.00, carapace, missing only the posterior edge; UR 97.101, posterior end of carapace including costals six to eight, neural six, the pygal region, left peripherals nine to eleven, and right peripherals eight to eleven; UR 00.108, isolated hyoplastron; UR 00.106, isolated hypoplastron; UR 97.110, isolated femur.

DESCRIPTION: Borealocheles axelheibergensis is represented by four partial shells (Fig. 1) that allow for a nearly complete reconstruction of the carapace (Fig. 2). As in many primitive euctodires from Asia and North America included in the “Macrobaenidae” (Parham and Hutchison 2003) or Sinemydidae (Brinkman 2001), the carapace is oval in outline, longer than wide, and widest in the inguinal region. The anterior edge is rounded, not showing an anterior projection as in baenids or

Fig. 1. Carapace of Borealocheles axelheibergensis, with sutures and sulci drawn on the specimen. (A) Specimen UR 97.100 in dorsal and ventral views. (B) Specimen UR 00.100. (C) Specimen UR 97.101. (D) Specimen UR 10.15.3. Scale bars = 2 cm.
a nuchal emargination as in most macrobaenids (Parham and Hutchison 2003). The posterior end is rounded. The dorsal surface of the carapace is gently convex, lacking the mid-dorsal depression typically present in macrobaenids. The surface of the shell is smooth as is typical in Late Cretaceous macrobaenids.

Fenestrae are absent between the peripherals and costals, indicating that the specimens are from fully mature individuals. As reconstructed, the carapace is 18 cm long. Thus, *B. axelheibergensis* would have been comparable in size to most Early Cretaceous sinemydids, such as *Ordosemys* (Brinkman and Peng 1993), and approximately half the length of Late Cretaceous macrobaenids, such as *Judithemys* (Parham and Hutchison 2003).

The nuchal of *B. axelheibergensis* is relatively long, its length being greater than its width as measured at the anterior end of the carapace. In contrast, the opposite condition is typically observed in macrobaenids.

Eight neural plates are present in *Borealochelys*. The first neural is rectangular and the second to fifth are hexagonal with short anterolateral edges. The length of the first neural is subequal to (Fig. 1A) or shorter than (Fig. 1B) the length of the second. The seventh neural is smaller than the adjacent neurals. The eighth neural, preserved only in specimen UR 10.15.3, has a trapezoidal shape with a wide distal end.

The anterior peripherals lack upturned anterolateral edges such as are typically present in macrobaenids. Peripheral one is a subtriangular element. The length of the contact between the first and second peripherals is subequal to the length of the anterior edge of the first peripheral. Peripherals three to six are narrow when seen in dorsal view. The posterior peripherals are mediolaterally elongate, giving a flared appearance to the posterior end of the carapace, a characteristic feature of macrobaenids.

The pattern of sulci and proportions of scutes are generally similar to those of macrobaenids and other primitive eucryptodires. The cervical scute is rectangular and the central scutes are wide and have strongly angled lateral edges. Also, the position of the pleural–marginal sulci relative to the peripheral–costal sutures is similar to the condition in macrobaenids: anteriorly and posteriorly the sulcus is located on the peripherals, while the marginal–pleural sulcus and peripheral–costal sutures are close together on peripherals four and five. *Borealochelys axelheibergensis* differs from macrobaenids and most primitive eucryptodires in that the twelfth marginal scutes do not extend onto the suprapygal.

The inner surface of the shell is exposed in specimen UR 97.100 (Fig. 1A). Eight centra are visible. All these have a ventral keel, although this is subdued on the more posterior centra. The first dorsal centrum has a concave articular surface that faces strongly anteriorly. The first dorsal rib is a long element that forms the anterior edge of a sharp crest that extends from the vertebral column to the pit for the anterior edge of the plastral buttress.

The carapace articulates with the plastron via a series of pits that form a broad arc extending from near the anterior edge of the second peripheral to the eighth peripheral (Fig. 1A). The anteriormost pit is deep and oval-shaped and is bordered by the second peripheral laterally and the first costal and first dorsal rib medially. It is located farther medial to the edge of the shell than in macrobaenids (Parham and Hutchison 2003). Successively smaller pits are present along the medial edge of peripherals three and four. Peripheral five has a sharp medial edge. Pits for the lateral edge of the hypoplastron are present along peripherals six to eight. The most posterior of these pits, located ventrally on the eighth peripheral, is slightly larger than the anteriormost pit on peripheral two.

The plastron is represented by the hypoplastron of the type specimen (Fig. 3B) and two isolated hyoplastra. The hyoplastra are referred to *B. axelheibergensis* because the

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Fig. 2. Reconstruction of the carapace and plastron of *Borealochelys axelheibergensis*. Scale bar = 2 cm.
shape of the articular surface on the lateral edge of the element corresponds with the series of pits on specimen UR 00.100 that articulated with the hyoplastron. Pegs for articulation with the plastron are most strongly developed anteriorly and are missing for a short distance adjacent to the hypoplastral suture. The region of the hypoplastron without pegs would have opposed the knife-like medial edge of peripheral five. There is no development of fenestrae between the hypoplastron and any of the adjacent elements. The region of the axillary buttress is preserved only in specimen UR 00.108 (Fig. 3A). A well-developed, vertical buttress is absent. The medial edge of the axillary buttress of the plastron is bowed inwards, a feature seen in no other primitive eucryptodire. The humeral–pectoral sulcus is located midway along the anterior lobe of the hyoplastron, well anterior to the axillary notch. The pectoral–abdominal sulcus extends across the hyoplastron just anterior to the sutural surface for the hypoplastron. Sulci for the submarginal scutes are lightly impressed. These sulci are located near the lateral edge of the hyoplastron, so the scutes would have been mediolaterally narrow.

The hypoplastron of the type specimen, UR 00.100, is similar to the hyoplastron in that a well-developed buttress is absent. Also, as in the hyoplastra, sutural surfaces along the edge of the bone indicate that fenestrae are absent. A series of pegs are present on the lateral edge of the hypoplastron for articulation with the carapace. The pegs are absent in the area that would have opposed peripheral five and become successively more developed towards the buttress. The abdominal–femoral sulcus curves gently from the median edge of the bone to the inguinal notch. Infra marginal sulci are lightly impressed. Both the hyoplastra and hypoplastra have an extensively developed ventral surface. Consequently, the plastron, as reconstructed on the basis of these elements (Fig. 3B), would have covered much of the ventral surface of the shell. In the extensive development of the plastron, B. axelheibergensis is different from macrobaenids and sinemydids but similar to Jurassic eucryptodires, such as Xinjiangchelys (Peng and Brinkman 1993).

Two postcranial elements, a femur and an ilium, are tentatively attributed to B. axelheibergensis because they are comparable to those of other primitive eucryptodires. The ilium (specimen UR 97.121) has a tall, straight shaft and an expanded dorsal blade similar to that of Dracochelys (Brinkman 2001). The femur is similar to the femur of macrobaenids in being relatively straight (Fig. 4A).

**DISCUSSION:** B. axelheibergensis is interpreted as a eucryptodire because the position of the sulcus between the femoral and abdominal scutes on the hyoplastron indicates that a mesoplastron was absent. In paracryptodires, this sulcus is on the well-developed mesoplastron. Borealochelys is similar to primitive eucryptodires generally included in the Macrobaenidae in the presence of a characteristic low-domed, elongate, oval, shell with wide posterior-lateral peripherals. The plastron of Borealochelys differs significantly from that of macrobaenids, however, in that the ventral surface is more extensively developed. In the extensive development of the ventral surface of the plastron, B. axelheibergensis is similar to primitive eucryptodires, such as Xinjiangchelys (Peng and Brinkman 1993). Thus two interpretations of relationships of B. axelheibergensis are possible: it may be a macrobaenid with a highly modified plastron, or it may be a representative of a separate lineage of eucryptodires that retained a primitive plastron.

To test these alternative interpretations, B. axelheibergensis was compared to other Late Cretaceous macrobaenids. The Macrobaenidae was most recently reviewed by Parham and Hutchison (2003). They recognized three Late Cretaceous macrobaenids: Paratalassemys from the Cenomanian of central Asia, Anatolemys from the Turonian of central Asia, and Judithemys from the Campanian of North America. Borealochelys is similar to Judithemys in lacking an upturned lateral edge of the carapace and lacking plastral fenestrae. Both features are present in Anatolemys and are widely distributed in Early Cretaceous taxa that have been aligned with the macrobaenids (e.g., Dracochelys, Ordosemys). Thus the absence of an upturned lateral edge of the carapace can be interpreted as a character that supports a macrobaenid relationship close to Judithemys. The carapace of Borealochelys...
differs from that of *Judithemys* as follows: (i) a nuchal emargination is absent, (ii) the cervical scute is narrower, (iii) the nuchal bone is longer, (iv) a mid-dorsal depression is absent, (v) the pygal is elongate and the twelfth marginal scutes do not extend onto the suprapygal, and (vi) the first dorsal rib is long and forms the sharp edge of a ridge extending to the hyoplastron. Because the nuchal emargination is only weakly developed in *Judithemys*, this difference is likely not of great significance. The presence of a long dorsal rib forming the edge of a crest that extends to the axillary buttress and narrow cervical scute are features that can be interpreted as primitive relative to *Judithemys*, since they are widespread in primitive eucryptodires. In the absence of a mid-dorsal depression and restriction of the twelfth marginal scutes to the pygal, *Borealochelys* also differs from *Anatolemys*, and, where known, other macrobaenids. Thus the absence of plastral fenestrae and the lack of an upturned anterolateral edge on the carapace support a close relationship between *Borealochelys* and *Judithemys*. The phylogenetic significance of these characters seems weak, however, when compared to the differences in the plastron and other features of the carapace. As a result, *Borealochelys* is interpreted as a member of a lineage of eucryptodires that retains a primitive plastron.

**Family Incertae sedis**

**Gen. et sp. indet.**

**MATERIAL:** UR 00.109, isolated hyoplastron.

**DESCRIPTION AND DISCUSSION:** A single isolated hyoplastron, specimen UR 00.109 (Fig. 5), differs from that of *Borealochelys* in having a vertical inguinal buttress, wider inframarginal scutes, and the second marginal extending to the hyoplastron. This specimen is referred to the Eucryptodira because the sulcus marking the contact between the humeral and abdominal scutes is located on the hyoplastron, indicating that a well-developed mesoplastron is absent. Affinities within the Eucryptodira are uncertain, although the combination of pegs along the lateral edge of the plastron indicating a loose connection with the carapace and extensive ventral surface suggests that it was from a turtle closely related to *Borealochelys*. 

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**Fig. 4.** Postcranial elements of turtles from the Axel Heiberg locality. (A) Femur attributed to *Borealochelys axelheibergensis*, specimen UR 97.110. (B) Trionychid femur, specimen UR 00.102. (C) Trionychid cervical vertebra, specimen UR 00.113. Scale bars = 5 mm.

**Fig. 5.** Hyoplastron of eucryptodire gen. et sp. indet. specimen UR 00.109. Scale bar = 2 cm.
Family Trionychidae
Gen. et sp. indet.

MATERIAL: UR 00.106, distal end of costal; UR 97.104, lateral end of hypoplastron; UR 97.101, humerus; UR 00.102, femur; UR 97.114, partial first costal; UR 00.113, cervical vertebra.

DESCRIPTION AND DISCUSSION: All the trionychid material is consistent with the presence of a single taxon of small size. Sculpture on the carapace elements (Figs. 6A, 6B) consists of a network of ridges that varies little across the shell. From comparison with specimens of Aspideretoides foveatus from the late Campanian of Alberta, the trionychid would not have exceeded 25 cm in width. The femur and humerus (Fig. 4B) are similar to those of later trionychids in being strongly curved. The cervical vertebra (Fig. 4C), likely the seventh, is elongate, has a weak midventral ridge, and a has divided posterior cotyle as is generally the case in trionychids.

Discussion

Late Cretaceous high-latitude vertebrates from North America are of particular interest because they help define patterns of latitudinal differentiation of vertebrate assemblages and the relationships between climate and vertebrate distributions. As well, because interchange between Asia and North America would have been via a high-latitude connection, vertebrate assemblages from high latitudes are significant in defining the patterns of interchange between Asia and North America.

The presence of primitive eucryptodires (B. axelheibergensis and the possibly related indeterminate eucryptodire) in the Axel Heiberg fossil assemblage suggests that a taxonomically distinct, high-latitude turtle assemblage may have been present in North America during the Late Cretaceous, reflecting an earlier migration of Asian turtles into North America. The timing of this migration event is not phylogenetically constrained but may be associated with the high temperatures of the mid-Cretaceous, since other turtles with Asian affiliations first appear in North America during this time (Hirayama et al. 2000; Hutchison 2000). Additional data on the phylogenetic position of Borealochelys will be necessary to verify the validity of this hypothesis.

The absence of paracryptodires (Baenidae plus Pleurosternidae) in the high-latitude Axel Heiberg fossil assemblage may also be a reflection of latitudinal differentiation of Late Cretaceous turtle assemblages. Paracryptodires are diverse and abundant in most Late Cretaceous North American turtle assemblages (e.g., Hutchison and Archibald 1986; Brinkman 2003). Exceptions are the turtle assemblages of eastern North America (Gallagher 1993) and the late Campanian – early Maastrichtian Horseshoe Canyon Formation of south-central Alberta (Brinkman 2003), both of which have well-documented turtle assemblages containing only eucryptodires. The interior seaway could have been a barrier limiting exchange between the eastern and western parts of the continent and thereby...
resulting in the absence of paracryptodires in the Late Cretaceous of New Jersey, but no such physical barrier is present that could account for the absence of paracryptodire turtles in the Horseshoe Canyon Formation of Alberta. Indeed, they are present in both earlier and later assemblages in this area (Brinkman 2003). Brinkman (2003) suggested that, west of the interior seaway, the distribution of turtles is controlled by climate, and that the Horseshoe Canyon turtle assemblage represented a northern turtle assemblage. The absence of paracryptodires in this assemblage and in the Axel Heiberg assemblage suggests that paracryptodires did not extend as far north as eucryptodires during the Cretaceous. A climate-controlled limit to the northern distribution of paracryptodires could explain why they are not present in Asia: because the land bridge is at high latitude, paracryptodires never reached it.

The presence of at least three turtle taxa in the Axel Heiberg locality, a high-diversity assemblage considering the northerly paleogeographic position of the locality above the Polar Circle, supports the interpretation that the Turonian–Coniacian interval was a period of thermal maximum. Brinkman (2003) showed that changes in the diversity of turtles through the Late Cretaceous of Alberta correlated with changes in mean annual temperature during this time (Fig. 7) and suggested that changes in diversity of turtles in the Late Cretaceous of Alberta were the result of climate-controlled shifts of a Late Cretaceous turtle diversity gradient. Thus comparison of the level of diversity of turtles in the Axel Heiberg locality with assemblages from south-central Alberta provides a basis for interpreting the climate associated with this high-latitude assemblage relative to the sequence preserved in Alberta. The diversity of turtles in the Axel Heiberg assemblage is generally comparable to that of the latest Campanian lower Horseshoe Canyon Formation, which has four taxa. Total turtle diversity of the Axel Heiberg assemblage is lower (three rather than four taxa present), but diversity at a single locality is higher, since no more than two taxa have ever been recovered from a single locality in the lower unit of the Horseshoe Canyon Formation. Diversity and abundance of turtles in the Axel Heiberg assemblage are much greater than in the upper Horseshoe Canyon Formation, which was deposited during the early Maastrichtian, a time of relatively low mean annual temperatures (Fig. 7). Leaf-margin analysis (Upchurch and Wolfe 1993) indicates that, during the late Campanian, the mean annual temperature was 23 °C at a paleolatitude of 30°N and the latitudinal temperature gradient was 0.3 °C per degree latitude. Because south-central Alberta was located at about 60°N paleolatitude (Scotese and Golonka 1992), the mean annual temperature for the latest Campanian in Alberta would have been 14 °C. A somewhat warmer mean annual paleotemperature of 17 °C for this region has been proposed on the basis of analysis of oxygen and carbon isotope from contemporaneous marine invertebrates of the Bearpaw Formation in Saskatchewan (Forester et al. 1977). Thus the turtle diversity of the Axel

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**Fig. 7.** Comparison of (A) turtle diversity and (B) temperature based on leaf margin data for the Late Cretaceous of south-central Alberta. The turtle diversity curve has been updated from Brinkman (2003) to include recently identified taxa from the Edmonton Group. The temperature curve is from Upchurch and Wolfe (1993, their Fig. 6), with the scale modified for 60°N paleolatitude (pl.), the approximate paleolatitude of south-central Alberta, by using a latitudinal gradient of 3 °C. Time axis is not to scale. DMT, Drumheller marine tongue; Fm, Formation; Gp, Group.
Heiberg fossil assemblage suggests that a mean annual temperature of at least 14 °C characterized the Turonian–Coniacian interval at a paleolatitude of 71°N, reinforcing similar conclusions reached earlier on the basis of the presence of large body-sized champsosaurs (Tarduno et al. 1998).

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References


