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NEW MATERIAL OF *BOREALOSUCHUS* FROM THE BRIDGER FORMATION, WITH NOTES ON THE PALEOECOLOGY OF WYOMING'S EOCENE CROCODYLIANS

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ABSTRACT

The Eocene Green River and Bridger Formations of Wyoming represent lacustrine and fluvial environments noteworthy for an extremely diverse crocodylian fauna (at least eight species in seven genera). This paper discusses a fragmentary crocodylian jaw from the Bridger Formation, and also notes possible ecological partitioning among these sympatric crocodylians. The jaw fragment can be assigned confidently to *Borealosuchus* based on the exclusion of the splenial from the mandibular symphysis and the presence of occlusal grooves between the alveoli, and it is referred tentatively to *Borealosuchus cf. B. wilsoni*. To examine the paleoeology of these crocodylians, variables based on habitat, body size, and inferred diet were formulated and species placed within respective categories. The research found that while there were more sympatric crocodylians in the early to mid Eocene of Wyoming than in any present-day biota, direct interspecific competition for resources is presumed to have been relatively low.

Introduction

The early to mid Eocene of Wyoming (represented extensively by the Green River and Bridger Formations) is exemplified by a diversity of aquatic reptiles (Bartels, 1993), and especially, crocodylians (Class Eusuchia). These formations are stratigraphically contiguous and roughly represent the same point in geologic history. The primary difference between the two is mode of deposition; the Green River is characterized by finely laminated marls indicative of a lacustrine environment (Eugster and Surdam, 1973), whereas high-energy sandstones from a fluvial habitat typify the Bridger.

At least eight different crocodylians are known from these formations. Some estimates are much greater, though recent work (especially that of Brochu, 1997) has synonymized several problematic taxa.

This paper introduces a new fragmentary mandibular specimen of *Borealosuchus* cf. *B. wilsoni* from the mid-Eocene Bridger Formation of Wyoming. In addition, new research and a literature review seek to examine possible ecological relationships among the many sympatric crocodylian of the Green River.

The new crocodylian material described herein (hereafter referred to as Tate 2070) was originally donated to the East Tennessee State University Natural History Museum (ETMNH) by a local surgeon who collected the specimen in situ while on a fly-fishing trip in Le Barge, Wyoming. After laboratory preparation and with the donor's permission, the specimen was transferred to the Tate Museum for permanent repository.

Review of Included Taxa

Allognathosuchus cf. *A. polydon* – Originally described by Cope in 1873 as *Crocodylus polydon*, Mook (1921a) established the revised genus. *Allognathosuchus polydon* was originally described from a single lower jaw 21 cm in length that adheres to an alligatoroid form, dentary curvature along the anterior portion of the ramus and varying tooth shapes (Brochu, 2004). There is doubt that the Wasatchian *Allognathosuchus* represents *A. polydon*, though the presence of the genus is unquestioned (pers. comm. with C.A. Brochu).

Borealosuchus wilsoni – Brochu (1997) erected the *Borealosuchus* genus to revise earlier (incorrect) inclusions of fossil crocodiles within the Cretaceous - Paleocene genus *Leidyosuchus*. *Borealosuchus wilsoni*, like other members of the genus, has an oddly shaped skull, wide at the posterior and very narrow anteriorly. Brochu (1997) also includes the Bridger *Diplocynodon stuckeri* within *B. wilsoni*, though this synonymy is questioned by Zonneveld *et al.* (2000).

Brachyuranochampsia eversolei – Described by Zangerl (1944), *B. eversolei* is a Bridgerian taxon known from a nearly complete skull without lower jaws. The skull is triangular in shape and resembles the general crocodylid morphology of extant crocodylians. The holotype is medium size, with a skull length of 39 cm. Another species of *Brachyuranochampsia*, *B. zangerli*, has since been synonymized with "*C.*" *affinis* (Brochu & McEachran, 2000).

"*Crocodylus*" *acer* – Mook (1921b) fully described the skull of "*Crocodylus*" *acer* briefly named by Cope in 1882. Originally described from Utah, Bartels (1993) identifies the species from the Green River of Wyoming. The skull length of the holotype is 38.7 cm (Mook, 1921b) and the specimen very much resembles that of the extant slender-snouted crocodile, *Mecistops* (= *Crocodylus*) *cataphractus*, in overall shape.

"*Crocodylus*" *affinis* – Mook (1921a) described a very complete skull of "*Crocodylus*" *affinis* (Marsh) from the Bridger Formation of Wyoming. As with "*C. acer*" above, this species is listed in quotation marks to note its withdrawal from the genus *Crocodylus*. Brochu (2003) noted that the original inclusion within this genus was based on plesiomorphic conditions of Crocodylia found in the specimens, and not apomorphic states found in *Crocodylus*. Regardless, "*C.*" *affinis* is a relatively large crocodylian (skull length approximately 45 - 50 cm) that does, at least superficially, resemble many members of extant *Crocodylus*.

Pristichampsus vorax – Arguably the strangest and most specialized of the Eocene crocodylian, Langston (1975) described a very complete skull (and associated remains) of *P. vorax*. *Pristichampsus* is interpreted to have been a largely terrestrial crocodile genus with a dorsoventrally tall skull and ziphodont den-

tion. Zonneveld *et al.*, 2000 describe isolated ziphodont teeth from the Green River Formation and assign them to this species.

Procaimanoidea kayi – Mook (1941) described *Hassiacosuchus kayi* (a European genus) from the Bridger beds of Wyoming. Wassersug & Hecht (1967) referred the material to *Procaimanoidea*. The species is small (total length less than 2 m) and shares some characteristics with Alligator (Brochu, 1999). In addition to its occurrence in the Bridger, it is also known from the Green River Formation.

Tsoabichi greenriverensis – Brochu (2010) reports this newly described small alligatorid from the Wasatchian Green River Formation. Some fossils previously assigned to *Procaimanoidea* have been included in the new genus and species and the taxon is likely related to the modern caimans.

Sympatric Crocodile Species in the Modern World

With 23 crocodylian species extant today, some regions of the world boast far more diversity than others, notably, areas of South America and islands in Southeast Asia. In a few of these areas, up to four or five crocodylian species inhabit roughly sympatric distributions. In each of these modern cases, however, ecological partitioning is present to the exclusion of regular interspecific competition. Examples of such partitioning include differing habitat preference, prey utilization, and life history strategies (Ross, 1989).

Concerning feeding behavior, Marioni *et al.* (2008) observed sympatric caimans (one small and one large species) during the Amazonian dry season. Despite an expectation for interspecific competition, the frequency was observed to be low due to differing modes of prey capture and microhabitat utilization during the stressful season.

Abercrombie *et al.* (2001) used computer modeling to observe survivability in hypothetical sympatric crocodiles during “catastrophic” events affecting reproduction. They concluded that large species dominate a habitat until a catastrophe severely reduces both populations, in which the smaller species will rebound quicker and dominate the habitat for some time. This has been observed in the wild with overhunted large species of crocodiles and subsequent colonization of smaller caimans (Platt & Thorbjarnarson, 2000).

Clearly, while some modern methods and observations should apply to the fossil herpetofaunas, something unique was occurring to facilitate such a high diversity of sympatric Eocene crocodylians. This has been seen several times in the geologic past such as in Cretaceous crocodyliforms (Serenó & Larsson, 2009) and among Miocene crown-group crocodylians (Salas-Gismondi *et al.*, 2007), to name a couple. In each of these cases, some crocodiles were extremely specialized to a point far surpassing that seen in the modern world.

The following analysis is not meant to be definitive, but seeks to make general observations regarding the likely paleoecology of Wyoming's sympatric Eocene crocodylian based on inferred diet, habitat choice, and maximum body size.

Materials and Methods

Paleoecological Analysis

To put the Green River and Bridger crocodylian into an ecological perspective, a table was formulated to account for the variables used. Gross morphology of relative tooth shape and size, along with skull shape were used as the basis for presumed dietary habits. More robust teeth and/or brevirostran skull shape were assumed to aid in capture of a more mixed diet, whereas gracile teeth and longirostran skulls are more indicative of a piscivorous lifestyle (Ross, 1989).

Presumed habitat choice was based on the sediments in which the fossils were found. As previously noted, the Green River Formation is thought to have been a low-energy, lacustrine habitat and the Bridger was a much more dynamic, fluvial one.

Overall size of the species is the most precarious of the variables used, and should be noted with caution. In many cases, species are known from few or fragmentary specimens, so average or maximum size of the animal are questionable. This and other assumptions are further explained below.

Assumptions

As with much paleoecological interpretation, some assumptions are inescapable. To avoid some subsequent criticism, these deserve to at least be stated with remarks:

1) The fossil specimens represent an average adult size. With some taxa used, a substantial fossil record is known, and thus the overall body

size is reasonably ascertained. While Brochu (pers. comm.) recommends some osteological characters to deduce ontogenetic maturity, this assumption will have to be maintained for fragmentary specimens;

2) Depositional sediments represent a fairly accurate indicator of habitat. While the fluvial habitat is a bit more tenuous (as high energy environments have the ability to transfer specimens leading to a depositional bias, as is probably the case with the terrestrial *Pristichampsus vorax*; Langston, 1975), the lacustrine sediments of the Green River Formation should adequately represent taxa present (Eugster & Surdam, 1973). Further, some taxa found more frequently (or exclusively) in the Bridger Formation than in the Green River can be adequately assumed from that environment;

3) Skull shape and tooth morphology can interpret the crocodylians' diet. This is not intended to be a blanket assertion, but merely represents generalities about the animals' behavior. Though this generality is contested by C.A. Brochu (pers. comm.), the author follows Pierce *et al.*, 2008 in that while skull shape may not always reflect phylogenetic history, it at least can provide very basic ecological and dietary information;

4) The Green River and Bridger Formations are not contemporaneous, but represent a very narrow interval of time with little generic faunal interchange. While these two units are not ecologically or chronologically the same, together for the purpose of this study, they do represent a narrow window of geologic time (Wasatchian - Bridgerian) and regional area, while illustrating substantial faunal overlap.



Figure 1. Tate 2070, lingual view before tooth repair. Anterior is to the left. Photography by the author. Courtesy of Tate Geological Museum, Casper College, Wyoming.



Figure 2. Tate 2070, labial view. Anterior is to the right. Photography by the author. Courtesy of Tate Geological Museum, Casper College, Wyoming.

Results

Tate 2070

Lingual and labial views of Tate 2070 are in figures 1 and 2 (respectively). Though only the anterior right mandible is preserved, this is one of the most diagnostic portions of the crocodylian osteology (Brochu, 1999). Based on Brochu (2000), the symphysis extends posteriorly approximately to the 4th dentary alveolus. Also, though the splenial is not preserved, the scar of its anterior portion on the dentary shows that it did not participate in the mandibular symphysis. In addition, deep occlusal grooves are present between the anterior alveoli; these characteristics exclude all North American Eocene

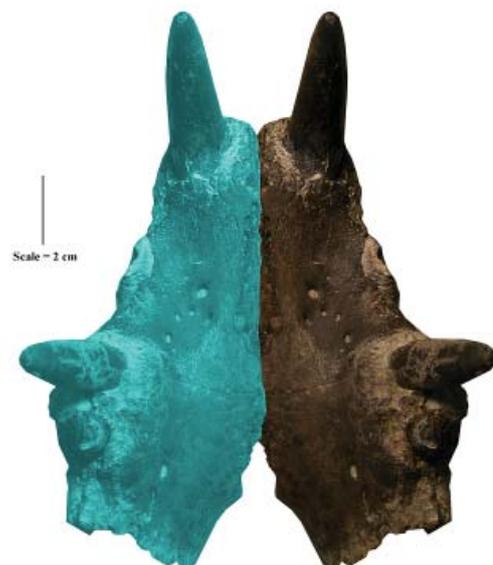


Figure 3. Reconstruction of symphyseal region of lower jaw using Tate 2070 and its reflected image (blue). Anterior is up. Photography by the author. Courtesy of Tate Geological Museum, Casper College, Wyoming.

	SIZE/DIET		
HABITAT	Large Piscivore	Small-mid size Mixed	Large Mixed
Fluvial:	" <i>Crocodylus</i> " <i>acer</i> , <i>Borealosuchus wilsoni</i> (?)	<i>Brachyuranochampsa eversolei</i> , <i>Allognathosuchus polyodon</i>	" <i>Crocodylus</i> " <i>affinis</i>
Lacustrine:	<i>Borealosuchus wilsoni</i> (?)	<i>Tsoabichi greenriverensis</i> , <i>Procaimainoidea kayi</i>	" <i>Crocodylus</i> " <i>affinis</i>
Terrestrial:			<i>Pristichampsus vorax</i>

Table 1. Purported habitat and diet of sympatric Eocene Green River and Bridger crocodylians.

taxa except *Borealosuchus* sp. (Brochu, 1997). Further, the intact teeth are long and gracile and possess thin striae oriented longitudinally from base to tip, additional support for the generic identification (Zonneveld *et al.*, 2000).

The anterior reconstruction of the fragment (figure 3) shows a restored symphyseal region of the mandibles of *Borealosuchus* sp. This illustrates the narrowness of the anterior region of the snout, but also the sharp angle moving toward the posterior of the skull, a strange shape not seen in extant crocodiles (pers. obs.).

Paleoecological Analysis

Table 1 shows the purported placement of all conclusive Green River and Bridger crocodylian taxa, based on the criteria mention above. Some taxa are listed among more than one habitat based on their presence in the fossil record of both formations. The terrestrial habitat is devoid of known crocodylians, except for *Pristichampsus vorax*.

Discussion

Borealosuchus cf. *B. wilsoni*

Tate 2070 is hereby referred to as *Borealosuchus* cf. *B. wilsoni*, the generic designation based on the exclusion of the splenial from the mandibular symphysis and the presence of occlusal grooves between the anterior alveoli, and is being tentatively conferred to *B. wilsoni* based on its known presence in the Bridger Formation ("*Diplocynodon stuckeri*", Mook 1960). This designation should be held cautiously, however, as the fragmentary nature of Tate 2070 precludes absolute species identification.

Based on the proportions of Mook (1959), the animal represented by Tate 2070 can be estimated to have had a skull length of approximately 70 cm, and a maximum skull width (between the distal-most portions of the quadrates)

of more than 35 cm. The anterior width of the rostrum, however, is estimated to have been less than 6 mm (figure 3). This extreme lessening of width from posterior to anterior implies an ecological role substantially different from that seen in any extant crocodile. Based on the gracile teeth and this "needle-nose pliers" shaped rostrum, it is speculated by this author that this animal was some sort of large, highly specialized piscivore.

Crocodylian Paleoecology

Overall, when observing the likelihood of interspecific competition between Wyoming's Eocene crocodylians, it is here presumed to have been low under normal circumstances. Even in broad categories where the crocodiles appear to occupy a similar ecological role (*i.e.* "*Crocodylus*" *acer* and *Borealosuchus wilsoni*), skull morphology suggests that the feeding ecologies were still quite different (in the unique skull morphology of *B. wilsoni* mentioned above, to the more gradually tapering condition in "*C.*" *acer*, Mook 1921b).

Further, the generalized category occupied by *Allognathosuchus polyodon*, *Brachyuranochampsa eversolei*, *Procaimainoidea kayi* and *Tsoabichi greenriverensis* (fluvial, small – medium body size, mixed diet) still does not necessitate the presence of regular interspecific competition. *Brachyuranochampsa eversolei* is much more "crocodile-like" (in the familial sense), whereas *A. polyodon* and *P. kayi* are much more "alligator-like" in gross morphology. Also, adult *P. kayi* and *T. greenriverensis* were likely much smaller than *A. polyodon*, thus potentially leading to a dynamic similar to that discussed by Marioni *et al.* (2008) regarding modern caimans in which the 2 disparately-sized sympatric species simply do pursue the same prey, and thus avoid competition for resources.

"*Crocodylus*" *affinis* appears to have been the top predator in the aquatic Green River and Bridger ecosystems, as its remains are found in relative completeness in both the Green River (Zonneveld *et al.*, 2000) and Bridger Formations (Mook, 1921a), and could be quite large (estimated skull lengths greater than 50 cm).

In the absence of direct fossil, a precise and detailed paleoecological interpretation is simply not possible at this point. However, given the relatively substantial fossil material of the Green River and Bridger crocodylians, it can be reasonably surmised that ecological partitioning played an integral role in the evolution of such a diverse crocodylian fauna.

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