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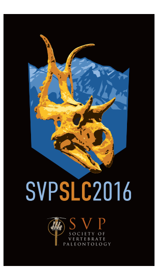
A NEW ATOPOSAURID CROCODYLOMORPH FROM THE MORRISON FORMATION (UPPER JURASSIC) OF WYOMING, USA

John R. Foster



Theme Issue
An Ecosystem We Thought We Knew—
The Emerging Complexities of the Morrison Formation
SOCIETY OF VERTEBRATE PALEONTOLOGY
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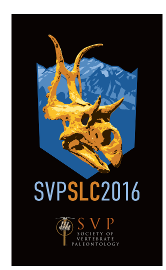

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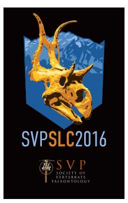

Cover

The Little Houston Quarry (Mammal Pit), in the lower middle right of the photograph, is in the Morrison Formation of the northwestern Black Hills, Crook County, Wyoming, which yielded the crocodyliform jaw described here.

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A New Atoposaurid Crocodylomorph from the Morrison Formation (Upper Jurassic) of Wyoming, USA

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ABSTRACT

A left mandible of a small crocodyliform found in the Upper Jurassic Morrsion Formation of northeastern Wyoming represents the first occurrence of the atoposaurid *Theriosuchus* in North America. The specimen demonstrates lower jaw morphology, including heterodonty (as indicated by alveolus shape), similar to *Theriosuchus* and *Knoetschkesuchus*, but autapomorphies and a unique combination of characters among these taxa indicate that it is a distinct, new species of *Theriosuchus*.

INTRODUCTION

Fossil crocodylomorphs are diverse in the Upper Jurassic Morrison Formation of western North America, with seven species of terrestrial and semi-aquatic forms occurring, with collective widespread distribution and high abundance (e.g., Clark, 2011; Pritchard and others, 2013; Foster and McMullen, 2017). In 2004, the left mandible of a small crocodyliform was collected from the Little Houston Quarry in the Morrison Formation of the Black Hills, northeastern Wyoming (figure 1). This specimen was found along with a diverse assemblage of dinosaurs and microvertebrates, the latter including mammals, fish, amphibians, a lizard, sphenodontians, the choristodere *Cteniogenys*, and turtles, among others (Foster, 2001). The dinosaurs included particularly abundant basal neornithischians, theropods, and diplodocine and camarasaurid sauropods. The crocodyliform specimen was initially described as a juvenile goniopholidid that would have demonstrated strong allometric growth in the relative elongation of the lower

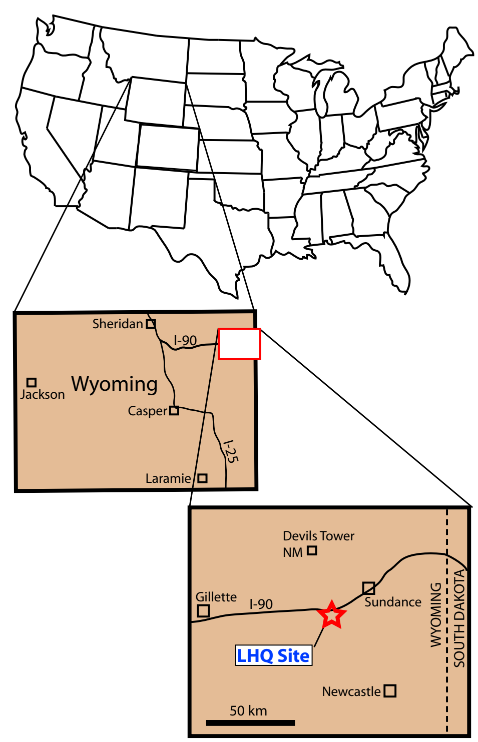

Figure 1. Location of Little Houston Quarry (LHQ) in Crook County, northeastern Wyoming, USA.

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jaw through ontogeny (Foster, 2006). Re-examination of the specimen (MWC 5625) indicates heterodonty in the lower jaw and strong similarities to *Theriosuchus*, and a redescription is provided here.

INSTITUTIONAL ABBREVIATIONS

MWC – Museums of Western Colorado, Dinosaur Journey Museum, Fruita, Colorado; BMNH – The Natural History Museum, London, England.

SYSTEMATIC PALEONTOLOGY

Crocodylomorpha
Crocodyliformes
Neosuchia
Mesoeucrocoylia
Atoposauridae
Theriosuchus Owen, 1879
Type species – *T. pusillus*
Theriosuchus morrisonensis sp. nov.
Figures 2 and 3

LSID. urn:lsid:zoobank.org:act:DAB8542A-7444-4026-9460-7735F0143C82

Type Specimen

MWC 5625, left mandible, nearly complete but missing teeth.

Type Locality

Little Houston Quarry (Mammal Pit), Crook County, Wyoming (Foster and Martin, 1994; Foster, 2001).

Type Horizon

Morrison Formation undifferentiated; thin local Morrison section of only ~23 m (Mapel and Pillmore, 1963); exact stratigraphic level and intraformational correlation with other localities in Wyoming unknown.

Etymology

For its occurrence in the Morrison Formation.

Diagnosis

Theriosuchus species with the following unique combination of characters (*denote autapomorphic for species relative to *Theriosuchus* and *Knoetschkesuchus*): greatly enlarged D2 and D3 alveoli*; dramatic reduction in mesiodistal diameter of alveoli from D3 to D4*; overall structure of mandible similar to *T. pusillus* in depth:length ratio, lack of external mandibular fenestra, retroarticular process angle, and dentary dorsal profile in two “waves” in lateral view; however, dentary nutrient foramina row and symphysis orientation relative to tooth row both more similar to *K. guimarotae*.

Revised Description (modified from Foster, 2006)

Specimen MWC 5625 is 141 mm long, with a pitted to rugose lateral surface and a relatively deep dorsoventral dimension (figure 2). The lingual side of the jaw (particularly along the ventral margin) is not well preserved in the central area, but the articular region and the rostral third are in good condition. The tooth row is relatively short. There are alveoli for 16 teeth, although all teeth are missing, and the lateromedial widths of the alveoli for the caudal seven of those teeth have been reduced somewhat by postmortem crushing. There is no external mandibular fenestra. In lateral view, the retroarticular process is short, and its dorsal surface is steeply inclined in a caudoventral direction. Although sutures of the bones of the lower jaw are difficult to distinguish in many areas, the splenial is involved in the caudal part of the oval symphysis. A deep foramen intermandibularis oralis occurs just caudal to the symphysis. A row of foramina extends along the occlusal surface of the dentary just lingual to the alveoli of D2 to D9 (figure 3). The edges of the alveoli are vertically festooned around D2 through D5 and are flat posterior to that.

There is slight damage to the anterior end of the dentary so the nature of the alveolus for D1 is obscured to some degree. Diameters of alveoli D2 and D3 are greatly enlarged relative to surrounding tooth positions; diameters of D4 through D9 alveoli are significantly reduced; and mesial-distal diameters of D10 through D16 are somewhat enlarged, some as large as D2 and D3 (table 1; figure 3). Despite some mediolateral crush-

Figure 2. *Theriosuchus morrisonensis* (n. sp.), specimen MWC 5625, left mandible. (A) Lateral (labial) view. (B) Medial (lingual) view. (C) Occlusal view; note enlarged dentary teeth D2 and D3, small circular D4 through D9, and slightly crushed but large and elongate D10 through D16. Scale bars = 5 cm. Abbreviations: D1, dentary alveolus 1; dedw, "waves" in dorsal edge of dentary; nfr, nutrient foramina row; rap, retroarticular process; sd, external sculpturing of dentary; sym, symphysis.

ing of the jaw posterior (caudal) to D8, the mesial-distal diameters of the alveoli do not appear to have been significantly altered, and the crushing appears to have been relatively minor at the caudal end of the tooth row. Alveoli for D10 through D16 are so significantly elongate mesial-distally, compared to their labiolingual diameter, that even prior to crushing, the alveoli for these posterior tooth positions appear to have been very different in shape compared with more anterior (rostral) ones. Given that the preserved widths of D10 through D16 are about 1 mm each, with a mesiodistal length of ~3 to 4 mm for each, and about 1 mm of labiolingual crushing, these alveoli still appear to have been nearly twice as long mesiodistally as wide labiolingually.

Thus, from the moderate-sized D1 alveolus posteriorly: D2 and D3 are very large and nearly circular, D4 through D9 are very small and circular, and D10 through D16 are seemingly large and elongate-oval

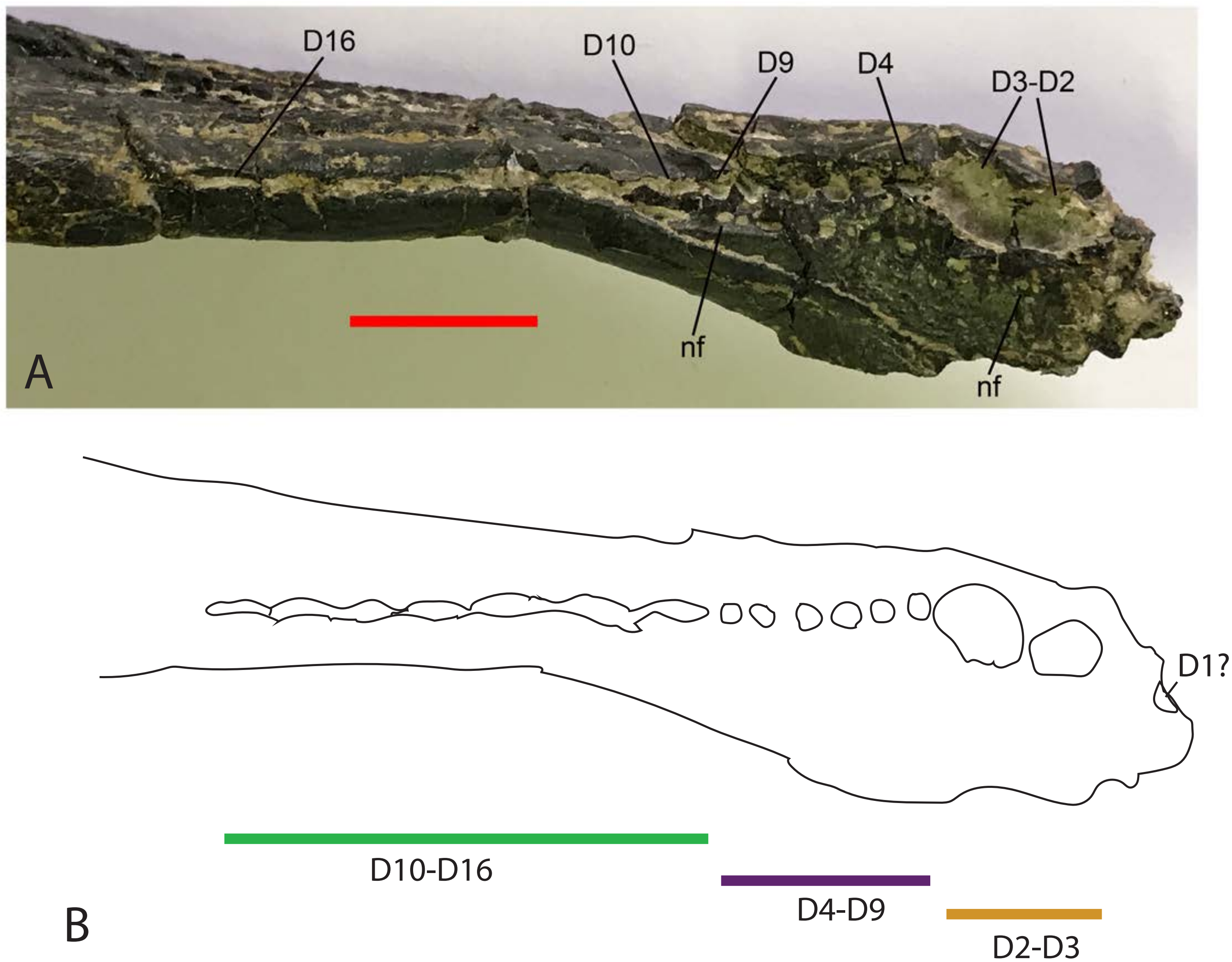

Figure 3. Close-up of anterior third of mandible, specimen MWC 5625, showing diversity of tooth alveoli; dentary tooth alveolus D1 difficult to distinguish; dentary alveoli D2 and D3 greatly enlarged and roughly circular, D4 through D9 roughly circular but greatly reduced in diameter, and D10 through D16 mesiodistally elongate in occlusal view. (A) Photo with some key alveoli labeled; nf = nutrient foramina at anterior and posterior end of row; scale bar (red) = 1 cm. (B) Tracing of jaw and alveoli with color coded zones of similar alveolar shapes below. Note that spaces between positions D13 through D14 and D15 through D16 have very thin septae, indicating minimal labial-lingual crushing; remaining alveoli in positions D10 through D16 may have been confluent.

shaped (figure 3; table 1). The interalveolar spaces between positions D10 through D16 appear to have extremely thin septae (at least three positions) or to lack them entirely (confluent), a feature still apparent despite some crushing. The preserved septae are oriented diagonally between alveoli due to crushing (originally perpendicular to the tooth row), but they are generally only about 1 mm in length, again suggesting that teeth D10 through D16 were laterally compressed. These great size differences and apparent change in shape suggest that the tooth row exhibited significant heterodonty and that the dentary possessed at least three tooth types with conical teeth anteriorly and possibly laterally compressed teeth posteriorly.

Table 1. Mesiodistal diameters of dentary alveoli in MWC 5625 (in mm).

Dentary Alveoli	Mesiodistal Diameters
D1	2.1
D2	3.2
D3	4.0
D4	1.5
D5	1.4
D6	1.4
D7	1.2
D8	1.5
D9	1.2
D10	2.7
D11	4.2
D12	4.2
D13	2.9
D14	3.3
D15	2.6
D16	3.3

DISCUSSION AND CONCLUSIONS

The specimen was found in an abandoned channel-fill pond deposit in interbedded laminated siltstone and green claystone (Foster and Martin, 1994; Foster, 2001). This is a dense bone bed preserving microvertebrate bones (e.g., jaws of mammals) and macrovertebrate bones (e.g., articulated sauropods) in the same layer and just centimeters away from each other. The abandoned channel deposit occurs as an elongate, laterally restricted deposit that lies stratigraphically just above a convex-bottomed channel sand, and it consists of two 1- to 10-cm-thick laminated siltstone beds with many aquatic, semi-aquatic, and terrestrial taxa mixed in the same layers. Charophytes, horsetails, bivalves, and other non-vertebrate taxa recovered from the deposit are also indicative of a relatively wet environment. Teeth of possible goniopholidids as well as unidentified crocodylomorph osteoderms are also found in the deposit.

Specimen MWC 5625 was originally described as a juvenile goniopholidid that would have undergone dramatic allometric growth in its lower jaw through ontogeny (Foster, 2006). I proposed that Morrison goniopholidids would have greatly increased the relative length of their tooth row and greatly reduced the relative depth of their lower jaw (greatest mandible depth/overall mandible length) as they grew to adult size. In both these ratios, however, specimen MWC 5625 is well off the trend lines set by a sample of Morrison goniopholidids (*Amphicotylus* and *Eutretauranosuchus*) and a growth series of the modern *Alligator* (figure 4). The apparent growth pattern collectively shown by those three taxa was in fact the reverse of what would have been required to turn the individual represented by specimen MWC 5625 into an adult (Foster, 2006). And in shape of the symphysis of the lower jaws, specimen MWC 5625 in fact plotted among the alligators and nowhere near the region of goniopholidids of having a more anteroposteriorly elongate symphysis (Foster, 2006). My own graphs in that paper (Foster, 2006) suggested, however, that *Alligator* at least did not undergo such dramatic allometric growth from the same small size up to that of the largest Morrison specimen, and even the trend among the known Morrison goniopholidids (though all are significantly larger than specimen MWC 5625) did not suggest dramatic changes.

In re-examining the specimen and data in that paper, it is clear that specimen MWC 5625 shares characters with the atoposaurid crocodyliform *Theriosuchus*, which was first named from the Purbeck (Lower Cretaceous) of England (Owen, 1879; Salisbury, 2002) and has since had members of its genus or close relatives show up in Asia, Portugal, Spain, Romania, and possibly (from teeth) in a few other places, usually in the Late Jurassic to Early Cretaceous (Martin and others, 2010; Young and others, 2016) but also ranging into the Late Cretaceous. *Theriosuchus* was a small neosuchian with a short and triangular-shaped skull (top view) with large eyes and a short, narrow snout (Salisbury, 2002; Martin and others, 2014).

Specimen MWC 5625 is relatively large and differs from the dentary of *Knoetschkesuchus* from Portugal in lacking an external mandibular fenestra and in having a mandible less elongate relative to its maximum depth (figure 4; Schwarz and Salisbury, 2005; Schwarz and

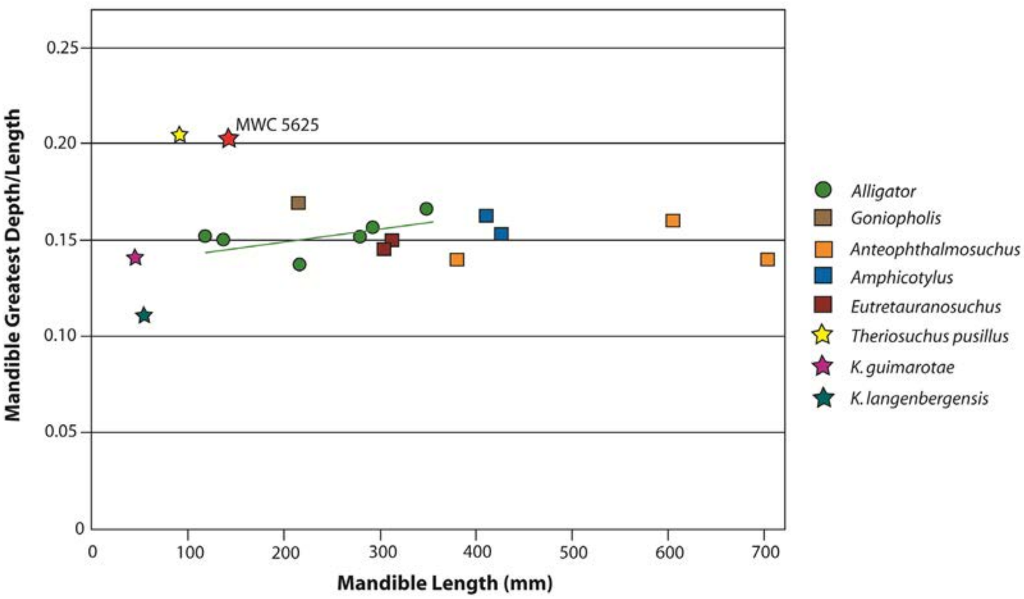

Figure 4. Comparison of mandible greatest depth to total length, by size, for: the atoposaurids *Theriosuchus pusillus*, *T. morrisonensis* (specimen MWC 5625, labeled), and *Knoetschkesuchus* (stars), several goniopholidids (squares), and a growth series of *Alligator* (circles), showing greater mandible depth:length of *Theriosuchus*. Green trendline is for *Alligator* series. Length of *T. pusillus* mandible estimated due to missing tip in BMNH 48328. Modified and updated from Foster (2006).

others, 2017). Based on alveolar diameters, specimen MWC 5625 also appears to have had more pronounced heterodont dentition anteriorly than *Knoetschkesuchus*. It differs from *Atoposaurus*, *Alligatorium*, and *Alligatorellus* in lacking homodont dentition and from *Alligatorium* and *Alligatorellus* specifically in lacking the external mandibular fenestra and smooth external surface of the mandible, respectively (Tennant and Mannion, 2014; Tennant and others, 2016). Specimen MWC 5625 also differs from species of *Sabresuchus* in lacking a lateral dentary concavity for reception of an enlarged 5th maxillary tooth, in lacking a diastema between D7 and D8, in lacking as short a symphysis, in not having all dentary teeth in a continuous groove, and in not having the occlusal surface of the dentary entirely lacking nutrient foramina (Tennant and others, 2016). Turner (2015) found species of *Theriosuchus* and *Alligatorium* to form an atoposaurid clade, although another recent analysis has suggested that Atoposauridae may be restricted to *Atoposaurus*, *Alligatorium*, and *Alligatorellus*, and that traditional species of *Theriosuchus* formed a polyphyletic group (Tennent and others, 2016). The same latter analysis found, however, that *Theriosuchus pusillus* and *Knoetschkesuchus* at least were sister taxa.

Specimen MWC 5625 is most similar overall to a referred lower jaw of *Theriosuchus pusillus* (specimen BMNH 48328; figure 5) illustrated by Salisbury (2002). Although the anterior tip of that specimen is missing, an estimation of the full jaw length suggests that the depth:length ratio of the mandible is very similar to MWC 5625 (figures 4 and 5). Additionally, the apparent tooth row length, external sculpturing, and retroarticular process of MWC 5625 are all most similar to *T. pusillus*; the symphysis length and orientation and the dentary dorsal profile with two "waves" also are similar to *Theriosuchus* (figure 5).

Specimen MWC 5625 possesses the following characters from the generic diagnosis of *Theriosuchus* in Young and others (2016). The folloing numbered list refers to the corresponding character numbers in Young and others (2016), and the missing character numbers relate to characters not preserved in the mandible: (1) heterodont dentition with pseudocaniniform and likely labiolingually compressed teeth (judging from alveoli); (5) some of the dentary alveoli form a confluent chain from dentary alveolus D4 through D8 (D10 through D16 in MWC 5625); (7) dentary alveolar size strongly heterogeneous; and (8) external surface of dentary is ornamented with heterogeneously spaced pits, ventrolaterally rugose. Specimen MWC 5625 appears to differ in lacking a notch in the dentary for the enlarged 5th maxillary tooth (character 6 in Young and others, 2016) and in seeming to lack a progressive reduction in alveolus size from D4 through D6 (character 3; instead

Figure 5. *Theriosuchus* mandibles compared. (A) Referred left mandible of *Theriosuchus pusillus* (specimen BMNH 48328) from the Purbeck Formation, England, showing depth:length ratio, short tooth row, and steep dorsal edge of retroarticular process. Also note heterodont dentition and "waves" of dorsal edge of dentary. Scale numbered in cm. Photo courtesy of D. Schwarz (Museum für Naturkunde, Berlin, Germany). (B) Left mandible holotype of *T. morrisonensis* (MWC 5625), Morrison Formation, Wyoming, showing similar morphology. Scale bar = 5 cm.

MWC 5625 demonstrates dramatic reduction in diameter from D3 through D4).

The external sculpting of the mandible and heterodonty were also characters listed in the revised diagnosis of *Theriosuchus* in Tennant and others (2016). The revised diagnosis of *T. pusillus* includes three mandibular characters that MWC 5625 matches: heterodont dentition (apparent indirectly in MWC 5625), absence of a mandibular fenestra, and dorsal edge of dentary with two dorsally projecting "waves" in lateral view. Specimen MWC 5625 lacks all mandibular characters listed by Tennant and others (2016) for a single speciment assigned to *Theriosuchus* sp. (Young and others, 2016) from the Middle Jurassic of the Isle of Skye, Scotland.

The mandibular configuration and combination of characters of MWC 5625 distinctly separate the specimen from goniopholidids, shartegosuchids, and protosuchids/sphenosuchians and suggest that MWC 5625 is within the genus *Theriosuchus*, closest to *T. pusillus* (also illustrated by Salisbury, 2002, and Schwarz and others, 2017); however, it differs from that genotype species in having greatly enlarged D2 and D3 alveoli and having the splenial more evenly distributed dorsoventrally along the symphysis (not restricted to dorsal part). Specimen MWC 5625 also differs from *T. pusillus*, and is similar to *Knoetschkesuchus guimarotae*, in hav-

Table 2. Matrix for mandible characters (201 through 242) from Tennant and others (2016) for *Theriosuchus morrisonensis* (specimen MWC 5625), compared with two closely related taxa.

Theriosuchus morrisonensis (scored here)			
201	211	221	231
1012210???	?00?011111	[0,1][0,1]12111000	11100100?0 ?1
Theriosuchus pusillus (from Tennant and others, 2016)			
201	211	221	231
1112110???	?12?101111	2111010	11110200?? 01
Knoetschkesuchus guimarotae (from Tennant and others, 2016)			
201	211	221	231
1111111101	120101111	2111010	101002000? 01

ing a line of foramina lingual to the tooth row on the occlusal surface of the dentary from D2 through D9 and in having a symphysis parallel in line to the tooth row.

Characters that make MWC 5625 unique among *Theriosuchus* and *Knoetschkesuchus* specimens include: (1) very large D2 and D3, relative to D4 through D9, and (2) dramatic reduction in diameter from alveoli D3 through D4.

Specimen MWC 5625 is too incomplete to run a meaningful phylogenetic analysis (only 35 of 329 characters known from Tennant and others [2016]; table 2), and preliminary assessments in TNT software and using the datasets of Turner (2015) and Tennant and others (2016) show it to be rather unstable within Neosuchia. However, its unique features and combination of numerous characters shared with the closely related *Theriosuchus pusillus* and *Knoetschkesuchus guimarotae* (Turner, 2015; Tennant and others, 2016) suggest that, if more complete, *Theriosuchus morrisonensis* (MWC 5625) would likely be found to lie within this clade, possibly as the sister taxon to *T. pusillus*.

This is the first occurrence of *Theriosuchus* in the Late Jurassic of North America and is a new crocodyliform species for the Morrison Formation. Although isolated teeth from the Early Cretaceous Cedar Mountain Formation have been referred to atoposaurids (Cifelli and others, 1999), until now no confirmation of *Theriosuchus* or close relatives has been found on this continent. The discovery thus strengthens biotic ties once again between the Morrison Formation and the Late Jurassic–Early Cretaceous of Europe (e.g., Mateus, 2006). This new occurrence also increases the diversity of crocodylomorphs in the Morrison Formation to eight taxa, with now at least two goniopholidids (*Amphicotylus*, *Eutretauranosuchus*), two shartegosuchids (*Fruitachampsa* and an unnamed form), two hallopodid sphenosuchians (*Hallopus*, *Macelognathus*), this new species of *Theriosuchus*, and a possible protosuchian (*Hoplosuchus*). The diversity of crocodylomorphs in the Late Jurassic–Early Cretaceous of Europe may have been even higher.

Atoposaurids appear to have been terrestrial or semiaquatic, depending on the species (Tennant and Mannion, 2014). With little of the postcranial skeleton known, the specific ecology of *Theriosuchus* is not clear, but the environmental setting of *Knoetschkesuchus guimarotae* in estuarine lagoons and swamps (Schwarz and others, 2017) suggests that that species at least was semi-aquatic. The occurrence of *T. morrisonensis* in an abandoned channel pond deposit in the apparently wetter northern region of the Morrison Formation (Turner and Peterson, 2004; Foster and McMullen, 2017) aligns with the wet paleoenvironmental settings of *K. guimarotae* and *T. pusillus* and may indicate that *T. morrisonensis* too was semi-aquatic in its habits.

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