

Osteology and taxonomy of *Mosasaurus conodon* Cope 1881 from the Late Cretaceous of North America

T. Ikejiri^{1,2,*} & S.G. Lucas³

¹ Department of Geological Sciences, University of Alabama, Tuscaloosa, Alabama 35487, USA

² Alabama Museum of Natural History, Tuscaloosa, Alabama 35487, USA

³ New Mexico Museum of Natural History and Science, 1801 Mountain Road N.W., Albuquerque, New Mexico 87104, USA

* Corresponding author. Email: ikejiri1859@gmail.com

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Abstract

Two well-preserved skeletons of *Mosasaurus conodon* Cope 1881 (Squamata, Mosasaurinae) from the Pierre Shale (late Campanian) of Colorado and the Bearpaw Shale (Late Campanian to Early Maastrichtian) of Montana are described. The two specimens are important because they provide new osteological information, especially on the skull (including jaws with teeth) and forelimbs, whereas those elements are largely missing in the holotype (AMNH 1380) of *M. conodon*. Morphological comparisons of the holotype with the two new specimens allow us to emend the diagnosis of the species in the genus *Mosasaurus*, primarily using tooth and forelimb morphologies. Teeth of *M. conodon* are unique in their combination of having a slender, gently recurved overall shape (similar to *Clidastes*) with no serration on the developed carinae (less developed in *Clidastes*). The tooth count of *M. conodon* tends to be low (14–15 in the maxilla, 16 in the dentary and eight in the pterygoid, respectively) when compared to other species, such as *Mosasaurus lemnionieri*, *Mosasaurus missouriensis* and *Mosasaurus hoffmanni*–*Mosasaurus maximus*. The forelimb is short in the species, characterised by a much lower number of the manual digital formula, $4(+1?)-4(+2?)-4(+1?)-4(+1)-2$ than other species of *Mosasaurus*. The forelimb bones are generally robust, especially the box-shaped humerus (width-to-length ratio 3/2). A variety of new morphological data support the conclusions that (1) *M. conodon* is a nominal species, (2) the European species *M. lemnionieri* is not a junior synonym and (3) one of the most complete skeletons of *Mosasaurus* from South Dakota (SDSM 452) is not assigned to *M. conodon* (but is likely to be *Mosasaurus* sp.). To date, *M. conodon* occurs only in North America during the late Campanian to early Maastrichtian.

Keywords: Plotosaurini, *Mosasaurus*, taxonomy, holotype, tooth morphology, palaeobiogeography

Introduction

The genus *Mosasaurus* (Reptilia, Squamata) is historically one of the best known mosasaur taxa from upper Campanian to Maastrichtian marine strata. A number of species of the genus have been recognised from six continents. These taxa include *Mosasaurus conodon* Cope 1881, *Mosasaurus missouriensis* Harlan 1834, *Mosasaurus maximus* Cope 1869, *Mosasaurus ivoensis* Persson 1963 (= *Tylosaurus ivoensis*?; see Lindgren & Siverson, 2002) and *Mosasaurus dekayi* Bronn 1838 from North America, as well as *Mosasaurus hoffmanni* Mantell 1829 and *Mosasaurus lemnionieri* Dollo 1889 from Europe (Russell, 1967; Machalski et al., 2003). The taxonomic status between the European and North American species, however, has been

problematic, and a few taxa have been synonymised and reestablished repeatedly, primarily due to poorly preserved and/or largely incomplete skeletons of the holotypes and a limited number of other associated specimens. For example, *M. maximus* and *M. dekayi* have been suggested to be junior synonyms of *M. hoffmanni* (Russell, 1967; Mulder, 1999; Harrell & Martin, 2014), whereas Lingham-Soliar (1995) determined *M. maximus* and *M. hoffmanni* are different species based on their quadrates and other bones.

Since it was named by Edward D. Cope in 1881, *M. conodon* has been one of the most commonly identified species of mosasaurs. It should be noted that the holotype, AMNH 1380, includes only some isolated cranial bones, lower jaw fragments with a few teeth, 12 cervical and anterior dorsal vertebrae, a

humerus and a shoulder bone (Fig. 1). This incomplete nature of the holotypic skeleton provides limited morphological information, which has posed challenges to the recognition of the species. Russell (1967) proposed two main ideas regarding the taxonomy of *M. conodon*: (1) the European *M. lemonnieri* is a junior synonym of *M. conodon* and (2) the fairly complete, articulated skeleton (SDSM 452) from South Dakota, which was unofficially named as the new species *Mosasaurus 'poultrney'* in an unpublished MSc thesis (Martin, 1953), is assigned to *M. conodon*. Notably, the newly established diagnosis for the species by Russell (1967) was based on the South Dakota specimen and a number of specimens assigned to *M. lemonnieri*, although some morphological features tend not to apply to the holotype. Bell (1993, 1997) in fact suggested that SDSM 452 is not *M. conodon*, but an indeterminate species of the genus. This identification allowed him to score only 51 characters out of 142 for that taxon in his cladistic analysis of the Mosasauridae, which possibly supported the idea that *M. conodon* was the basalmost taxon in the genus and closely related to *M. missouriensis*. Lingham-Soliar (2000) later stated that the North American *M. conodon* and the

European *M. lemonnieri* are taxonomically distinct. To date, many small to medium-sized mosasaurs from Campanian and Maastrichtian strata are often assigned to *M. conodon* in museum collections, often based solely on body size and/or stratigraphic occurrences. Clarification of the taxonomic assignment and diagnostic features of *M. conodon* is thus needed.

In 1998, a local landowner, Mr Allen Peterson, in Trinidad, southern Colorado, discovered a partial mosasaur skeleton, exhibiting some cranial bones, jaw elements, teeth and many postcranial bones, in the upper part of the Pierre Shale. This mosasaur specimen (TSJC 1998.2) displays a nearly identical size and morphology to the holotype of *M. conodon* (AMNH 1380), especially in its teeth, dentary, coracoid and humerus. Moreover, we here refer another undescribed skeleton with an articulated skull, forelimbs and presacral vertebrae (MOR 006) from the Bearpaw Shale in north-central Montana to *M. conodon*. These two new specimens allow us to present osteological information on the species that is largely missing in the holotype and thereby provide a better basis for comparing it with other closely related taxa.

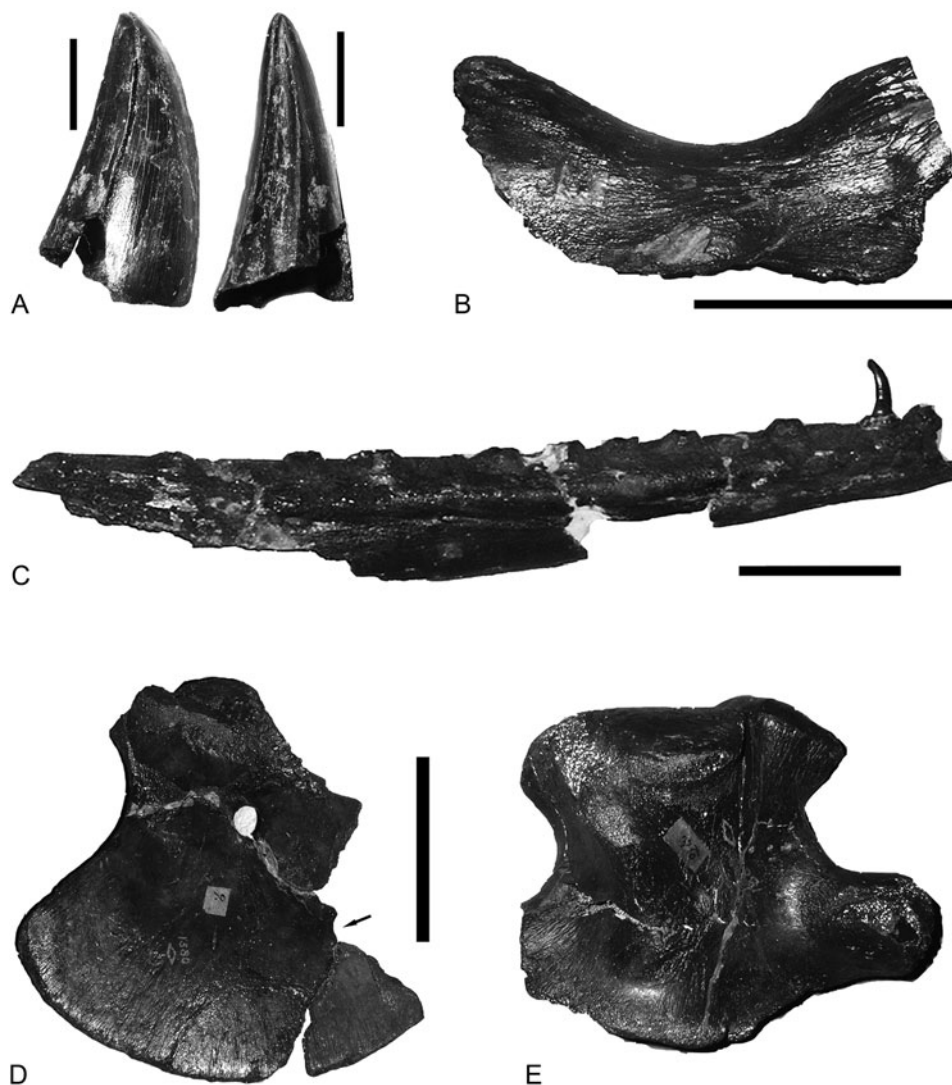


Fig. 1. Holotype of *M. conodon* (AMNH 1380). A, tooth in lateral and anterior views; B, right coronoid in lateral view; C, left dentary in medial view; D, coracoid; E, right humerus. The arrow in D indicates the position of the second coracoid foramen. Scale equals 1 cm in A and 10 cm in B–E.

This study mainly focuses on the diagnosis of *Mosasaurus conodon* based on specimen-based osteological comparisons, especially between the holotype and the two new specimens. The diagnoses for the species presented by Cope (1881) and Russell (1967) are reviewed and applied to a re-examination of *M. lemonnieri* and SDSM 452. Implications for biostratigraphic and palaeobiogeographic distributions of the species are then discussed.

The institutional abbreviations used in this report are as follows: AMNH – American Museum of Natural History, New York, USA; FHSM – Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas, USA; FMNH – Field Museum of Natural History, Chicago, USA; Goldfuss – Goldfuss-Museum, Institut für Paläontologie, Der Universität Bonn, Bonn, Germany; IRSNB – Royal Belgian Institute of Natural Sciences, Brussels, Belgium; KUVV – University of Kansas, Museum of Natural History, Lawrence, Kansas, USA; MNHN – Musée National d’Histoire Naturelle, Laboratoire de Paléontologie, Paris, France; MOR – Museum of the Rockies, Bozeman, Montana, USA; MSC – McWane Science Center, Birmingham, Alabama, USA; NHMM – Natuurhistorisch Museum Maastricht, Maastricht, USA; NHMUK – Natural History Museum, London, UK (formerly the British Museum of Natural History); NJSM – New Jersey State Museum, Trenton, New Jersey, USA; RMM – former Red Mountain Museum (paleontological collection now stored at MSC), Birmingham, Alabama, USA; SDSM – South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; TMM – Texas Memorial Museum, University of Texas, Austin, USA; TSJC – Loudon-Henritze Archaeology Museum, Trinidad State Junior College, Trinidad, Colorado, USA; UAM – University of Alabama Museums, Tuscaloosa, Alabama, USA; UNSM – University of Nebraska State Museum, Lincoln, Nebraska, USA; USNM – National Museum of Natural History, Washington, D.C., USA; YPM – Yale Peabody Museum, New Haven, Connecticut, USA.

The osteological abbreviations are as follows:

Cranial skeleton: **ax**, articular; **ba**, basioccipital condyle; **d**, dentary; **f**, frontal; **j**, jugal; **m**, maxilla; **oc**, occipital segment; **p**, parietal; **paf**, parietal foramen; **pm**, premaxilla; **pof**, postorbitofrontal; **pr**, prootic; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **sa**, surangular; **sp**, splenial; **sq**, squamosal.

Quadrate: **aa**, anterodorsal ridge of ala; **isp**, infrastapedial process; **ssp**, suprastapedial process.

Vertebrae: **CV**, cervical vertebra; **DS**, dorsal vertebra; **P**, pygal vertebra including a sacral vertebra; **CdC**, anterior caudal vertebra with chevron.

Appendicular skeleton: **cg**, glenoid condyle; **ect**, ectepicondyle; **hu**, humerus; **i**, intermedium; **mc**, metacarpal; **pc**, pectoral crest; **pf**, pisiform; **pgp**, postglenoid process; **r**, radius; **ra**, radiare; **ul**, ulna; **ula**, ulnare; **2-4**, 2-4 distal carpals.

Age and geological context

TSJC 1998.2 was collected from a construction site near the downtown of Trinidad, in south-central Colorado (NW1/4, NE1/4 Sec. 24, T33 S, R64 W) (Fig. 2). The layer yielding the bones is in the upper part of the Pierre Shale, about 45–60 m below the base of the overlying Trinidad Sandstone. Another medium-sized mosasaur, TSJC 1966.P.2, was collected from about 2 km east of the site. The beds containing the bones are characterised by greyish shale with indurated limestone concretions. The bone layer of TSJC 1996.P2 is about the same stratigraphic level as TSJC 1998.2. Following Lee and Knowlton (1917), the two skeletons are estimated to belong to either the *Baculites cuneatus* or *B. compressus* ammonite zones.

MOR 006 was found on US Fish and Wildlife Lands in Phillips County, north-central Montana (MOR locality number BS-136) (Fig. 2). Although precise locality and stratigraphic data are not available, the specimen was most likely collected from an upper Campanian horizon (P. Leiggi, written commun., 2002).

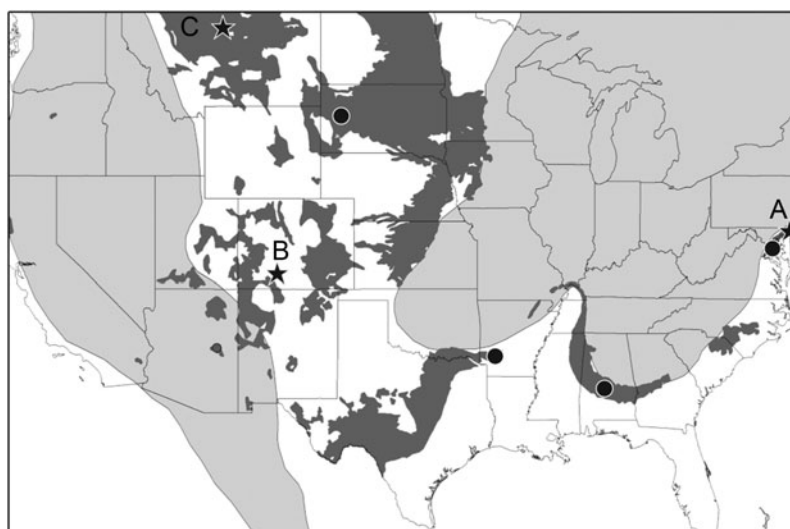


Fig. 2. Representative fossil sites of *M. conodon* in North America. Light grey areas indicate the Late Cretaceous (Campanian) landmass. Dark grey colour indicates distribution of Upper Cretaceous marine surface rock/strata. Letters for locality: A, the holotype (AMNH 1380) from New Jersey B, TSJC 1998.2 from Colorado; C, MOR 006 from Montana. A list of other specimens (dots) is explained in the text. The map is modified from Ikejiri et al. (2013).

Systematic palaeontology

MOSASAURIDAE Gervais, 1853
 MOSASAURUS Conybeare, 1822
 MOSASAURUS CONODON Cope 1881
Clidastes conodon, Cope 1881
 ?*Mosasaurus lemtonneri*, Dollo, 1889
Mosasaurus conodon, Baird & Case, 1966
Mosasaurus conodon, Russell, 1967
Mosasaurus lemtonneri, Russell, 1967
Mosasaurus conodon, Lingham-Soliar, 2000

Distribution

M. conodon is largely known from Upper Cretaceous strata of North America, which are associated with the Western Interior Seaway, the Gulf of Mexico and southern Atlantic Seaboard (Fig. 2). Fossils have been collected from various upper Campanian and lower Maastrichtian strata, such as the Navesink Formation (New Jersey), Severn Formation (Maryland), upper Pierre Shale (Colorado and South Dakota), Bearpaw Shale (Montana), Marlbrook Marl (Arkansas) and Demopolis Chalk (Alabama).

Emended diagnosis

Medium-sized *Mosasaurus* exhibiting the following combination of features: relatively narrow snout; slender maxilla and dentary; greatly expanded splenial ventroposteriorly; 13–14 maxillary teeth, 15–16 dentary teeth and eight pterygoid teeth; slender, transversely compressed teeth on premaxilla, maxilla and dentary; oval-shaped cross-section of teeth; no serration on well-developed carina(e); single anterior carina on teeth of anterior jaw (tooth pm1-maxillary tooth m4 and dentary tooth d1–d4 or d5), anterior and posterior carinae in m5 and m6 and d6 and d7, single posterior carina in m7–m14 and d8–d16; narrow posteroventral angle of jugal (70–80°); relatively large infrastapedial process placed low on posterior quadrate (c. 2/5 of total height from the mandibular articulation); large box-shaped humerus (ratio of total height-to-transverse width = 3:2); well-developed, hooked entepicondyle of humerus; strongly constricted medial surface of humeral mid-shaft; radius much larger than ulna; strongly concave proximal articular surface of intermedium; reduced digital formula in manus [4(+1?)–4(+2?)–4(+1?)–4(+1)–2] (much less than *M. hoffmanni*–*M. maximus* and SDSM 452).

Holotype

AMNH 1380, consisting of incomplete right dentary with one tooth, a few tooth fragments, coronoid, splenial, angular, articular, squamosal, 12 vertebrae (at least six cervical and four dorsal vertebrae), partial left (?) scapula, left coracoid, right humerus, right ulna and rib fragments (Fig. 1). It was most likely collected

from the Navesink Formation (upper Campanian to lower Maastrichtian) in Freehold, Monmouth County, New Jersey (Baird & Case, 1966; Gallagher, 1993).

Referred specimens

MOR 006, nearly complete skull and jaws except for coronoids (reconstructed), 41 articulated presacral to pygal vertebrae, left and right pectoral girdle bones, nearly complete articulated forelimbs except a few distal phalanges, ischia, many ribs and chevrons (from the Bearpaw Shale of north-central Montana); MOR 5051, partial left maxilla with four teeth (from the Pierre Shale); RMM 2204 (now stored at MSC), three isolated teeth, two pterygoid teeth, skull fragments, seven trunk and six caudal vertebrae (from the Demopolis Chalk of Lowndes County, Alabama); RMM 3037 (now stored at MSC), partial left dentary and lower jaw, pterygoids, 18 isolated teeth, coracoid, humerus (from lower Demopolis Chalk of Sumter County, Alabama); TSJC 1998.2, fairly large disarticulated skeleton, including incomplete skull with squamosal, postorbitofrontal and left paroccipital process, several partial jaw elements with teeth, six cervical vertebrae, 25 dorsal vertebrae, nine pygal vertebrae (including sacral?), nine intermediate caudal vertebrae, partial left coracoid, right coracoid, right humerus, ulna, radius, tibiae, three metacarpals, nine disarticulated phalanges and rib fragments; TSJC 1966.P.2, occipital condyle, posterior portion of lower jaw, most of the cervical and dorsal vertebrae, humerus, ulna, radius, three metacarpals, five phalanges, rib fragments, chevron (both TSJC specimens from the Pierre Shale of southern Colorado); UAM 1994.0008.0004, teeth and some cranial bones (from the Demopolis Chalk of Marengo County, Alabama); USNM 18255, partial right maxilla with tooth; USNM 11396, one cervical vertebra, 15 articulated trunk to pygal vertebrae, some caudal vertebrae, chevrons, partial scapula, ilia, pubes, ischia, ulna, phalanges, rib fragments (from the Marlbrook Marl of Hempstead County, Arkansas); USNM 18255, partial premaxilla and right maxilla, tooth, left humerus, partial coracoid and scapula, radius (from the Pierre Shale of Hughes County, South Dakota); USNM 336480, tooth (from the Severn Formation of Prince George's County, Maryland); YPM 1573, teeth, jaw fragments, three cervical vertebrae including atlas, ulna, radius (from the McLean Pits of Middletown, New Jersey).

Remarks on excluded specimens

Russell (1967, p. 135) referred 17 specimens to *M. conodon*. Some of these specimens are, however, too incomplete and/or fragmentary to identify to species level with certainty, such as AMNH 1387, 1395, 1397, ANSP 8469, 8480, 8501, 8502, 8504, 8509, and YPM 279, 1500 and 1510. AMNH 1395 consists of an isolated tooth, jaw fragments and a coracoid. The tooth, likely from the posterior portion of a jaw, does not resemble that of *M. conodon* because of its transversely compressed



Fig. 3. Skull of *M. conodon* (MOR 006) in lateral view. Scale equals 10 cm.

structure and carinae with serrations. Some isolated teeth of YPM 1573 are morphologically similar to TSJC 1998.2. USNM 11904 includes 14 trunk vertebrae, one sacral and some pygal vertebrae, a phalanx, a radius and two ribs. USNM 11396 consists of a partial scapula, all pelvic bones, two phalanges, and 15 dorsal, some pygal, and many caudal vertebrae, but these portions of the skeleton are not useful to identify *M. conodon*. USNM 18255 is a relatively small individual of *Mosasaurus*, and the two isolated teeth are greatly flattened transversely, similar to AMNH 1395. This tooth morphology indicates the two specimens do not assign to *Mosasaurus*. SDSM 452 is not assignable to *M. conodon*, a view we base on a number of morphological features as presented below.

Description

Skull

The nearly complete articulated skull of MOR 006 (Figs 3 and 4) indicates that *M. conodon* has a much more slender skull in

overall shape than *M. maximus* (TMM 313, NJSM 11053), *M. hoffmanni* (NMHNP AC. 9648), *M. missouriensis* (KUVV 1034) and *Mosasaurus* sp. (UNSM 77040). A small but deep concavity is located in the lateral margin near the mid-section of the frontal in MOR 006 (Fig. 4). This margin is weakly concave in *M. missouriensis* (Bell, 1997, p. 305; Williston, 1898, pl. 20; personal observation of KUVV 1034) and *M. maximus* (NJSM 11053, TMM 313), but absent in *M. hoffmanni* (see Lingham-Soliar, 1995, figs 4 and 6) and *M. lemonnieri* (Lingham-Soliar, 2000). The parietal of MOR 006 is relatively shorter anteroposteriorly and wider transversely than that of *M. lemonnieri*. The parietal-frontal suture is not clearly visible in the specimen, but a weak line is visible along the anterior margin of the parietal flares.

According to Bell (1997), a relatively small parietal foramen, defined as smaller than or equal to the area of the stapedia pit, is commonly found in *Mosasaurus missouriensis*, *M. maximus* and UNSM 77040 (*Mosasaurus* sp.), but the foramen is relatively large in *M. conodon* (MOR 006 and TSJC 1998.2). The two specimens exhibit an oval-shaped parietal foramen that is slightly elongated anteroposteriorly. A similar oval-shaped parietal foramen also appears in *M. maximus* (NJSM 11052; see Mulder, 1999; Lingham-Soliar, 1995, fig. 7) and *M. hoffmanni* (IRSNB R26; see Lingham-Soliar, 1995, fig. 6e), but the outline tends to be wider transversely, forming a nearly circular shape, as in *M. missouriensis* (KUVV 1034) and *M. lemonnieri* (IRSNB 3127 and 3211).

In MOR 006, the postorbitofrontal-squamosal ramus reaches the end of the supratemporal fenestra in *M. maximus*, *M. missouriensis* (Bell, 1997) and *M. lemonnieri* (Lingham-Soliar, 2000), as well as in MOR 006.

The posteroventral angle of the jugal is about 70–80° in MOR 006 (Fig. 3). This angle is smaller than in *M. lemonnieri* (85–95°: IRSNB 3127, 3189), *M. hoffmanni* (90–95°: NHMUK PV OR 11589, IRSNB R26), *M. maximus* (c. 90°: NJSM 11053)

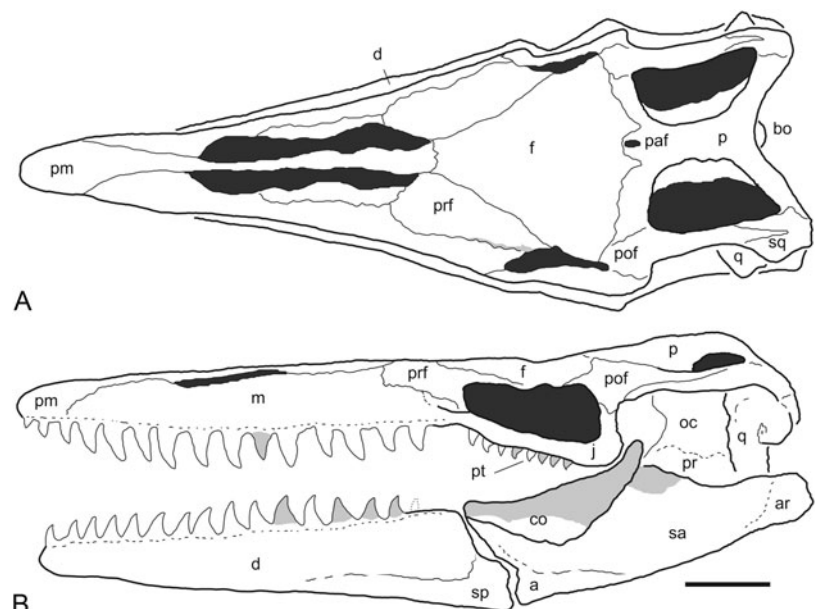


Fig. 4. Skull of *M. conodon* (MOR 006) in (A) dorsal and (B) lateral views. Light grey colour indicates missing or reconstructed portion in the original skull. Scale equals 10 cm. Osteological abbreviations are listed in the text.



Fig. 5. Braincase of *M. conodon* (MOR 006) in posterior view. Scale equals 10 cm.

and the holotype of *M. missouriensis* (c. 90°: Goldfuss 1327). In *M. conodon* (MOR 006), the posteroventral process of the jugal is greatly expanded posteriorly, which can be distinguished from *M. lemonnieri*, *M. hoffmanni* and *M. maximus*. This process is also positioned much higher in *M. conodon* (MOR 006) than it is in *M. lemonnieri* and *M. hoffmanni*.

The well-preserved squamosal has a robust overall structure with a circular cross-section in TSJC 1998.2. It bears a very shallow trench on the dorsolateral surface of the anterior wing, which differs from a much deeper trench in *M. lemonnieri* (Lingham-Soliar, 2000).

The well-preserved braincase of MOR 006 (Fig. 5) displays tightly sutured occipital elements. The basisphenoid is wide transversely and expanded to the anterior margin. The occipital condyle of MOR 006 has a nearly circular shape in posterior view.

The quadrate of MOR 006 has a rectangular-shaped dorsal end in anterior view and a relatively small suprastapedial process (Fig. 6). The notch of the suprastapedial process is

placed slightly above two-thirds of the total height of the quadrate. A relatively large infrastapedial process is located slightly below the mid-point of the overall quadrate height, which is about the same position as in *M. lemonnieri* (IRSNB 3189; see Lingham-Soliar, 2000, fig. 2) and *M. maximus* (NJSM 11052, 11053) but lower than in *M. hoffmanni* (ISRN B R26, NHMUK PV OR 11589: half to three-fifths of the overall height) and *M. missouriensis* (about half of the overall height). When compared to *M. maximus* (NJSM 11053), MOR 006 has a less-developed external ridge of the suprastapedial process. The stapedial pit of MOR 006 is large, with a nearly circular outline, as in other species of *Mosasaurus*.

The quadrates of MOR 006 are smaller than those of *M. missouriensis* and *M. maximus* relative to overall skull size (Table 1; Appendix 1). Based on the ratio of the quadrate height-to-dentary length, *M. conodon* (MOR 006) has a lower ratio (0.19) than *M. missouriensis* (0.22 in KUVF 1034) and *M. maximus* (0.23 in NJSM 11053), indicating that the former species has a relatively slender skull among species in the genus.

Jaws

MOR 006 has nearly complete upper and lower jaws, except for largely reconstructed coronoids (Figs 3 and 4). The entire structure of the lower and upper jaws is slender. The premaxilla of MOR 006 is narrow transversely when compared to other species of *Mosasaurus* (Fig. 7). The anterior end of the premaxilla is slightly pointed in MOR 006, which is similar to *M. lemonnieri* (Lingham-Soliar, 2000). The coronal cross-section of the premaxilla is nearly sub-rectangular, with nearly straight ventral and gently curved dorsal margins in rostral view. A well-developed median ridge runs along the anteroposterior axis on the ventral surface of the premaxilla, which reaches about half the height



Fig. 6. Left quadrate of *M. conodon* (MOR 006) in (A) posterior and (B) lateral views. Scale equals 10 cm. Osteological abbreviations are listed in the text.

Table 1. Comparisons of skull measurements in *Mosasaurus*.

	<i>M. conodon</i> MOR 006	<i>M. maximus</i> NJSM 11053	<i>M. missouriensis</i> KUVF 1034
Skull length (pm–ba)	977 mm	1,208 mm	1,110 mm
Dentary length (ventral margin)	620 mm	818 mm	609 mm
Skull height (q–pa)	200 mm	317 mm	224 mm
Skull width (q–q)	321 mm	329 mm	307 mm (sq–sq)
Quadrates height	115 mm	190 mm	135 mm
Frontal width	203 mm	260 mm	175 mm (pa–pa)
Length ration q:de	0.19	0.23	0.22

Osteological abbreviations are listed in Fig. 2.

of the tooth crown of pm1. The ridge does not directly contact the anterior-most tip of the premaxilla but stops near the anterior base of pm1 (Fig. 7C). The posterior end of the maxillo-premaxillary suture occurs above m6 and m7.

The slender maxillae of MOR 006 (Appendix 1) can be distinguished from fairly robust maxillae of *M. lemmnieri* and strongly broad bones of *M. hoffmanni* (Lingham-Soliar, 1995, 2000). In lateral view, MOR 006 shows that the dorsal and ventral outlines are relatively low and nearly parallel from near m4 to m14 or m15 (Figs 3 and 4). The lateral surface of the mid-maxilla is inclined about 80° from the horizontal in coronal cross-sectional view, although the medial surface is nearly perpendicular. A posterodorsal process is absent (or possibly damaged) in MOR 006, whereas it is reported in *M. missouriensis* (KUVF 1034) and *Mosasaurus* sp. (UNSM 77040) (Bell, 1997).

The very slender dentary in the holotype of *Mosasaurus conodon* (Fig. 1), which has been suggested to be diagnostic of the species by Cope (1881) and Russell (1967), is also seen in MOR 006 (Figs 3 and 4; Appendix 1). The slenderness is

morphologically similar to *Clidastes*, rather than to other species of *Mosasaurus*. In MOR 006 and AMNH 1380, the ventral margin of the posterior end of the dentary is greatly expanded ventrally (Fig. 8). In the cross-section of the mid-dentary, the lateral surface is convex, but the medial surface is slightly concave. A narrow, trench-like mandibular canal extends from nearly the anterior-most tip to the mid-portion of the dentary on the medial surface, being gradually expanded posteriorly. On the medial surface a small, oval-shaped concavity (10 × 20 mm in diameter) is placed below d7 and d8 (the arrow in Fig. 8). This feature is probably not pathological based on the smooth surface morphology and nearly identical size and relative position on both of the dentaries.

Tooth counts

MOR 006 has 14 teeth in the left maxilla and 15 in the right maxilla, including a dental alveolus. This discrepancy between left and right upper jaws indicates a small degree of intraspecific variation in *M. conodon*. Other species of *Mosasaurus* tend to have a higher tooth count (e.g. 16 in *M. maximus*), but *M. hoffmanni* and *M. missouriensis* (KUVF 1031) display a lesser number (14 teeth) (Table 3). Russell (1967) reported that *Clidastes liodontus* has 14–15 teeth, whereas *Clidastes propython* has 16–18 teeth.

Russell (1967, p. 133) reported that 17 teeth in the dentary, based on SDSM 452, is diagnostic of *M. conodon*, although Martin (1953) reported the jaw bones were largely reconstructed based on *Clidastes*. Both of the dentaries of MOR 006, however, have a total of 16 teeth (Tables 2 and 3). The same tooth count appears in *C. liodontus*, but *C. propython* tends to have a higher number (17 teeth) (Russell, 1967). Within *Mosasaurus*, the dentary holds a total of 16 teeth in *M. lemmnieri* (IRSNB specimens; Lingham-Soliar, 2000) and 15 teeth in *M. missouriensis*

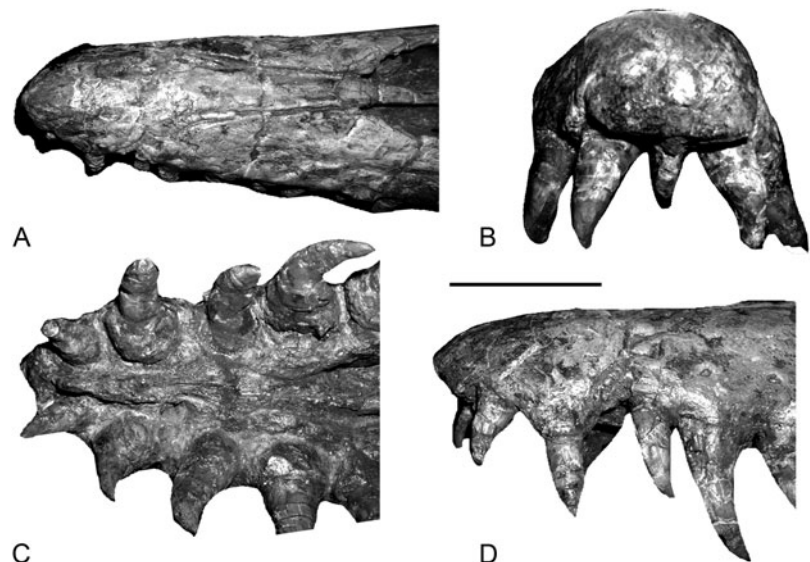


Fig. 7. Premaxilla of *M. conodon* (MOR 006) in (A) dorsal, (B) anterior, (C) ventral and (D) left lateral views. Scale equals 10 cm.



Fig. 8. Dentary of *M. conodon* (MOR 006) in medial view. Arrow indicates a depression (see explanation in text). Scale equals 5 cm.

(KUVV 1034). The more derived species, *M. hoffmanni*–*M. maximus* exhibits 14 teeth, which is the lowest number in the genus.

Russell (1967) stated that *M. conodon* has a total of 10 pterygoid teeth, but the specimen he based this on is not specified. Notably, MOR 006 has only eight in both pterygoids. *M. lemnioneri* (multiple IRSNB specimens?) has 11–12 pterygoid teeth (Lingham-Soliar, 2000), although eight teeth appear in *M. hoffmanni* (IRSNB R26; Lingham-Soliar, 1995) and *M. missouriensis* (KUVV 1032; Williston, 1898). *C. propyhton* (ANSP 10193; KUVV 1022) displays 13–14 pterygoid teeth.

Tooth morphology

In general, mosasaur teeth morphologically vary in (1) overall shape (curvature and robustness), (2) surface texture (smooth or faceted), (3) overall size, (4) position of a carina (when present), (5) serrations (if present) and (6) cross-sectional shape. The holotype of *M. conodon* (AMNH 1380) includes two well-preserved marginal teeth: one located in the anterior

portion of the right dentary and an isolated tooth crown (Fig. 1). The two teeth are slender and slightly recurved in overall shape, which is suggested to be one of the diagnostic features in the species (Cope, 1881; Russell, 1967). This overall tooth morphology in AMNH 1380 is nearly identical to several well-preserved teeth in TSJC 1998.2 (Fig. 9). In contrast, overall tooth shape is much more robust in *M. hoffmanni*–*M. maximus*. MOR 006 preserves most teeth in the nearly complete left and right upper and lower jaws, although the tooth surfaces are damaged by a high degree of pyrite mineralisation. In MOR 006, the two-thirds apicalmost portion of the teeth from the mid-portions of the jaws are more curved distally and also slightly curved lingually in *M. conodon* compared to *M. hoffmanni*–*M. maximus*. The teeth of *M. lemnioneri* in the mid-portion of the jaws are much straighter than those of *M. conodon*. Additionally the pm1, pm2, d1 and d2 teeth have a much stronger curvature than other teeth in the jaws of MOR 006.

The smooth tooth surface in AMNH 1380 (Fig. 1) has been suggested to be another diagnostic feature of *M. conodon* (Cope, 1881). This tooth morphology is also found in all preserved teeth in TSJC 1998.2 (Fig. 9) and *Clidastes* (Russell, 1967), as well as in *M. hoffmanni* (MNHN AC9648). In contrast, well-developed facets or striae occur in the holotypes of *M. maximus* (AMNH 1389) and *M. missouriensis* (Goldfuss 1327; illustrated in Harlan, 1834). Lingham-Soliar (2000) suggested that in *M. lemnioneri* the tooth facets are better developed in more mature than in immature individuals. However, to our knowledge, all known specimens of *M. conodon*, including the two largest, TSJC 1998.2 and AMNH 1380, commonly have a very smooth dental surface. This evidence indicates that the facet surface is absent throughout the postnatal ontogeny of *M. conodon*.

Tooth size is variable depending on its relative jaw position in MOR 006. The two premaxillary teeth are much slenderer than other teeth in the maxilla in MOR 006 (Table 2). M3 is

Table 2. Measurements (in millimetres) of teeth and variation in positions of carina in *M. conodon* (MOR 006).

Left upper jaw: premaxillary (1–2) and maxillary (3–16) teeth																
Tooth number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Crown height	32	28	36	35	30	28	34	29	32	31	?	27	?	?	?	?
Crown transverse width	16	18	22	22	21	24	28	26	29	28	?	26	?	?	?	?
Position of carina	?	A	A	A	A	AP	AP	?	P	P	?	P	?	?	?	?

Left lower jaw: dentary (1–16) teeth																
Tooth number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Crown height	22	29	31	45	47	42	46	41	47	?	44	45	45	39	37	?
Crown transverse width	15	15	15	26	29	27	29	29	28	?	28	21	23	19	18	?
Position of carina	A	A	A	A	?	AP	AP	A(?) P	P	?	P	P	P	P	P	?

A, anterior; P, posterior carina present.

Table 3. Tooth count in selected taxa of *Mosasaurus* and *Clidastes*.

	<i>M. conodon</i> MOR 006	<i>C. liodontus</i>	<i>C. propython</i>	<i>M. lemniereri</i> IRSNB 3127	<i>M. maximus</i> NJSM 11053	<i>M. hoffmanni</i> IRSNB R12, MNHN AC9648
Maxilla	14–15	14–15*	16–18*	15**	16	14***
Dentary	16	16*	17*	16**	14	14***

* Data from Russell (1967).

** Data from Lingham-Soliar (2000).

*** Data from Lingham-Soliar (1995).

the longest tooth, whereas more posterior teeth (m6–m12) are wider transversely, in the upper jaw, although a few posterior teeth are missing. Based on the sizes of the aveoli, tooth size gradually decreases from m6 to the distal teeth. In the dentary, d1 and d2 are relatively small and have much weaker recurvature than pm1 and pm2, whereas d5 is the longest tooth in the dentary of MOR 006. The tooth length from d4 to d13 is nearly sub-equal in MOR 006, which appears slightly different from *M. lemniereri* (IRSNB 3132), which has a more anterior position of sub-equal-sized teeth (from d3 to d11; Lingham-Soliar, 2000).

A mix of single and double carinae in jaws is suggested to be another diagnostic feature of *M. conodon* (Cope, 1881). The well-preserved maxilla and dentary of TSJC 1998.2 also display this morphology. In the partial left dentary of TSJC 1998.2, three teeth and two aveoli are exhibited, and the rostral-most tooth has a single anterior carina, the middle tooth has both anterior and posterior carinae, and the caudal-most tooth has a single posterior carina. Interestingly, a similar type of variation occurs in the premaxilla-maxilla and dentary of MOR 006 (Table 2). In the upper jaw, m4 and m5 have double carinae, but an extensively weathered tooth surface does not allow us to examine this feature in m6. Only an anterior carina is present

between pm1 and m4. Only the posterior carina is present from m6 to m10; the rest of the posterior teeth are missing in the maxilla. These features are unique to *M. conodon* or, at least, sharply different from *M. maximus*, *M. lemniereri* and *M. missouriensis*.

Well-preserved teeth in TSJC 1998.2 and AMNH 1380 show the absence of serrations under light microscopic examination (Fig. 10). Well-developed thin carinae in the Colorado specimen indicate that serrations are not worn or physically damaged. Such unserrated carinae are also known in *Clidastes* (Russell, 1967), but *M. conodon* tends to have better-developed edges. Highly developed serrations are, in contrast, commonly found in *M. lemniereri*, *M. hoffmanni* and *M. maximus*, including small (juvenile) individuals.

A transversely compressed cross-section of the teeth, characterized by nearly symmetrical lingual and labial circumferences, is also an autapomorphic feature in *Mosasaurus conodon*. This oval-shaped cross-section is found in all teeth on the premaxilla, maxilla and dentary of MOR 006. This feature is morphologically differentiated easily from a U-shaped cross-section in *M. hoffmanni*, *M. maximus* and *M. dekeyi*. In those species of *Mosasaurus* the distal carina is placed strictly labially, and the angle between the anterior and posterior carinae is less than 90° in the premaxillary teeth and gradually spread to the caudal teeth but never meets 180° nor an oval-shaped cross-section.

Based on a series of tooth morphologies, we suggest teeth, even isolated ones, are the most useful elements to identify *M. conodon*. *M. conodon* and *Clidastes* share morphologically very similar teeth in the jaws, but the former taxon displays

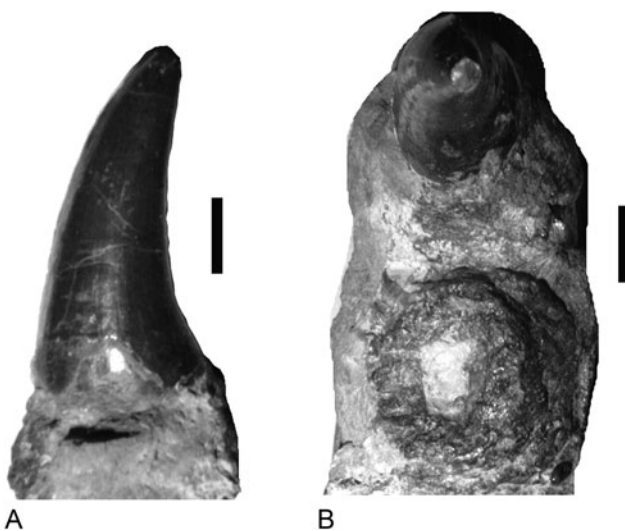
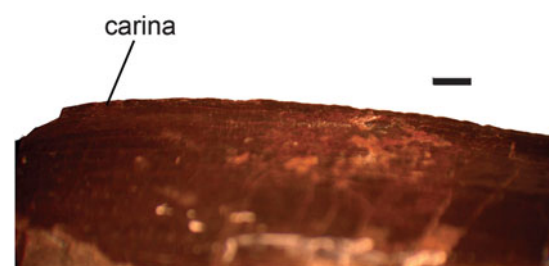
Fig. 9. Teeth of *M. conodon* (TSJC 1998.2) in (A) lateral and (B) dorsal views. Scale equals 1 cm.Fig. 10. Anterior carina of tooth of *M. conodon* (TSJC 1998.2) in side view under light microscopy. Scale equals 1 mm. Note about 0.2 mm of the edge is a carina with no serration.

Table 4. Comparisons of counts of vertebrae in mosasaurs (modified from Nicholls, 1988).

Taxon	CV	DS	P	CdC
<i>Tylosaurus proriger</i> ¹	7	23	7	?
<i>Hainosaurus bernardi</i> ²	10	>19	20	49
<i>Platecarpus</i> ¹	7	30	5	59
<i>Clidastes</i> ¹	7	35	7	70
<i>Plotosaurus tuckeri</i> ³	9	30	30	59
<i>Mosasaurus</i> sp. (SDSM 452)	7	38	8	21
<i>Mosasaurus</i> sp. (FMNH P26956)	7	32	9	?
<i>M. conodon</i> (TSJC 1998.2)	7	>25?	8 or 9	>10?
<i>M. conodon</i> (MOR 006)	7	35 (or 36)	?	?
<i>M. maximus</i> (TMM 313 and NJSM 11053) ⁴	7	24 (+8?)	9 or 10	?
<i>M. lemnionieri</i> ⁵	7	31–38	13–22	?15–40

Data sources: ¹Williston (1898, p. 143); ²Dollo (1882, p. 153); ³Camp (1942); ⁴Langston (1966, fig. 2); ⁵Lingham-Soliar (2000).

10–20% larger teeth due to larger overall body size and better-developed carinae than the latter taxon.

In *M. conodon* (MOR 006), the pterygoid teeth can be distinguished from all other teeth in the jaws based on: (1) the transversely wider base of the tooth crown than the crown length and (2) the absence of carinae. The latter characteristic is different from the holotype of *M. hoffmanni* (MNHN AC9648), which displays carinae. The apical one-fifth to one-fourth of the tooth crown is strongly curved and occasionally hooked in MOR 006.

Vertebrae

MOR 006 has 41 articulated presacral–pygal vertebrae. The cervical vertebrae indicate MOR 006 is 15–20% smaller than AMNH 1380. The two specimens show that cervical vertebrae have a more slender overall structure in *M. conodon* than in *M. hoffmanni* and *M. maximus*. In TSJC 1998.2 (*M. conodon*) the fourth cervical vertebra has the largest hypophyseal peduncle, although the seventh cervical vertebra has only a small pinched convexity, but lacks an articular surface. The posterior cervical vertebrae of TSJC 1998.2 and AMNH 1380 display a heart-shaped posterior face of the centrum with slightly concave dorsal and rounded ventral margins. The synapophyses are slightly elongated dorsoventrally in the cervical series in the genus *Mosasaurus*, but the expansion is weaker in *M. conodon* (AMNH 1380, MOR 006, TSJC 1998.2) than it is in *M. hoffmanni* and *M. maximus*. Cope (1881) listed the presence of the zygantrum as a diagnostic character of *M. conodon*. This accessory vertebral articulation is found in the mid-cervical to anterior dorsal vertebrae of MOR 006, TSJC 1998.2 and AMNH 1380, and is also reported in *M. lemnionieri* (Lingham-Soliar, 2000).

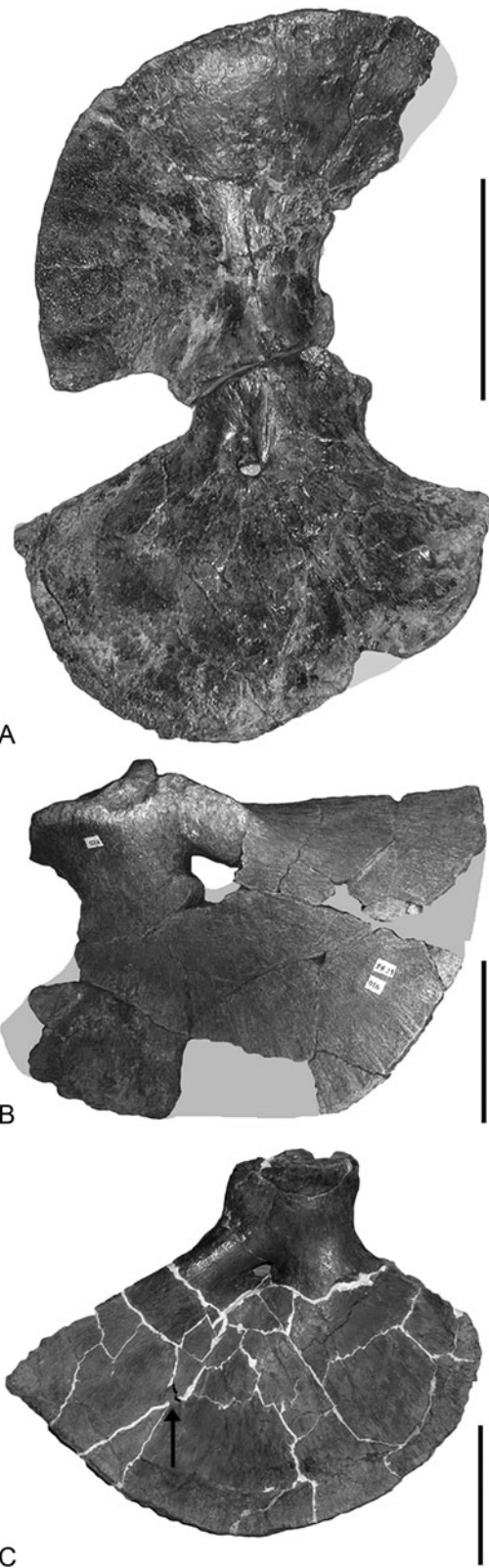


Fig. 11. Pectoral girdles of *Mosasaurus*. A, right coracoid (top) and scapula (bottom) of *M. conodon* (MOR 006); B, right coracoid of *M. conodon* (TSJC 1998.2); C, left coracoid of *Mosasaurus* sp. (FMNH P26956). Arrow indicates the second coracoid foramen. Grey colour indicates a missing portion. Scale equals 10 cm.

The total number of dorsal (trunk) vertebrae varies in various genera of mosasaurs (Nicholls, 1988). In the genus *Mosasaurus*, *M. conodon* tends to have a higher number (35 in MOR 006) (Table 4). SDSM 452 has one of the highest dorsal vertebral counts among specimens assigned to *Mosasaurus*. Lingham-Soliar (2000) reported 31–38 dorsal vertebrae in *M. lemnierii*, but the specimen(s) were not specified. The mounted skeleton of *M. maximus* (TMM 313) exhibits the smallest number (24 in total) in the genus, but, possibly, several vertebrae are missing (Langston, 1966, fig. 2).

Eight disarticulated pygal vertebrae of *M. conodon* (TSJC 1998.2) have a relatively large, elongate centrum, as do the posterior dorsal vertebrae. According to Osborn (1899), the transverse processes of the first pygal vertebra (aka. sacral) are more than twice as long as the synapophyses of the last dorsal vertebra in *Mosasaurus*, but the difference is 120–130% in TSJC 1998.2.

TSJC 1998.2 has several centra of the intermediate caudal vertebrae with fused chevrons. The shape of the centra exhibits a typical triangle shape in posterior view, which is evidently taller dorsoventrally than the transverse width.

Pectoral girdle

Nearly complete scapulae and coracoids are articulated in MOR 006 (Fig. 11A), although they are slightly flattened due to taphonomic processes. The scapula has about the same surface area as the coracoid. The long and straight medial margin of the scapula is in stark contrast to the short, strongly constricted lateral edge. The scapula and coracoid have about the same width in MOR 006 and AMNH 1380, but in SDSM 452 the scapula is slightly more emarginated than the coracoid. The scapula (MOR 006) has a rectangular-shaped coracoid articular head, which exhibits a weak convexity and many small pits. The anteromedial corner of the fan is greatly expanded, which contrasts with the reduced anterolateral corner. The medial margin is slightly damaged, but is nearly straight in MOR 006. The entire medial edge from the scapular head to the corner of the fan is thicker than the lateral edge, as in the coracoid.

The right coracoid of TSJC 1998.2 exhibits excellent three-dimensional preservation (Fig. 11B) and shares a number of morphological similarities with AMNH 1380, such as a relatively expanded medial border, a thicker medial margin of the fan (i.e. the thickest portion in the fan) and a well-developed ridge-like anterior margin on the proximal head.

Russell (1967) discussed variation in relative size between the lengths of the medial border of the coracoid fan and the circumference of an outer line of the fan among mosasaurs (e.g. ratio of the length-to-circumference: c. 0.33 in *Platecarpus* and *Tylosaurus*; larger than 0.33 in *M. conodon* and *Clidastes*). Three specimens of *M. conodon* show variation in the ratio ranging from c. 0.24 (AMNH 1380) to 0.28 (TSJC 1998.2) to 0.30 (MOR 006). Two other specimens of *Mosasaurus* sp. have a very similar ratio: 0.29 in FMNH P26956 and 0.31 in SDSM 452. Based on these data, the ratio is not useful for species-level taxonomic assignment among *Mosasaurus*. TSJC 1998.2 (Fig. 11B) has a relatively large coracoid foramen, as commonly seen in *Mosasaurus* and *Clidastes* in Mosasaurinae, but sharply different to its relatively small size in plioplacarpine mosasaurs.

A single coracoid foramen is usually found in most individuals among various mosasaur taxa, but a few specimens assigned to the genus *Mosasaurus* display two foramina. Notably, two coracoid foramina occur in the large individual of *Mosasaurus* sp. (FMNH P26956). The double coracoid foramina appear in only the left coracoid (Fig. 11C), but the right coracoid exhibits one regular foramen in the typical spot. The accessory second foramen is slightly larger in diameter than the typical anterior foramen. The coracoid of the holotype of *M. conodon* (AMNH 1380) is only about four-fifths complete, but a smooth natural edge, forming a part of a foramen, indicates the presence of this second coracoid foramen (arrow in Fig. 1D), which is at a nearly identical position, as seen in the Field Museum material. All preserved coracoids of MOR 006 and TSJC 1998.2 show only a single foramen, indicating intraspecific variation in *M. conodon*.

Limb bones

The right humerus of the holotype of *Mosasaurus conodon* (AMNH 1380) (Fig. 1E), is large and overall very robust.

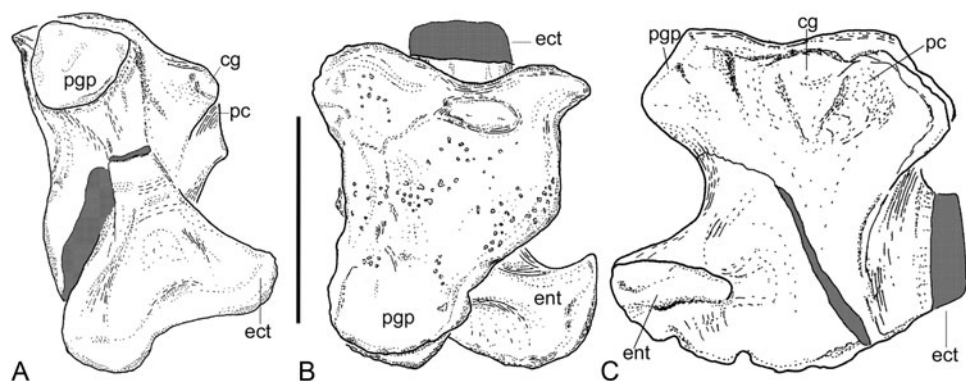


Fig. 12. Right humerus of *M. conodon* (TSJC 1998.2) in (A) anterior, (B) dorsal and (C) lateral views. Scale equals 10 cm. Osteological abbreviations are listed in the text.

The overall size and shape are nearly identical to the humerus of TSJC 1998.2 (Fig. 12). The two humeri have nearly cubic three-dimensional shape, with the ratio of 3:2.4:2 of the greatest height-to-anteroposterior breadth-to-transverse width at the ectepicondyle. The humerus of TSJC 1998.2 has a well-developed pectoral crest, as seen in AMNH 1380. The pectoral crest stops at nearly a quarter of the total length from the proximal end in TSJC 1998.2, which is much shorter than *M. hoffmanni* (IRSN R12; Lingham-Soliar, 1995, fig. 20). The anterior and posterior surfaces of the mid-shaft are strongly constricted, which is also similar to IRSN R12. The entepicondylar process is well-developed in TSJC 1998.2, which exhibits a hook-like medial end that is strongly curved, but *M. hoffmanni* (IRSN R12) has a much-less developed process.

MOR 006 has nearly complete, articulated forelimbs, which are relatively short and robust for the genus (Fig. 13). The ulna is smaller than the radius in *Mosasaurus*, but the size discrepancy in MOR 006 is greater than in other species, such as *M. hoffmanni* (NHMM 1993024; Lingham-Soliar, 2000, fig. 21) and SDSM 452. The radius of MOR 006 has a greatly expanded distal end. The mid-shaft is strongly constricted, and the least circumference is at about one-sixth of the total distance distal from the proximal end, which differs from it being located about the middle of the shaft as in SDSM 452 and *M. missouriensis* (KUPV 1032).

Based on the complete set of tarsals of MOR 006 (*M. conodon*) (Fig. 13), the manual formula is the same as in SDSM 452 (*Mosasaurus* sp.) and NHMM 1993024 (*M. hoffmanni*). The proximal end of the intermedium is strongly concave, as found in SDSM 452, but this expansion is much gentler in *M. hoffmanni*. The very elongate pisiform of MOR 006 also morphologically differs from that of *M. hoffmanni* (NHMM 1993024; Lingham-Soliar, 2000).

The manual digital formula can distinguish *Mosasaurus conodon* from at least a few other species of *Mosasaurus*. Although articulated manus are generally not common in any mosasaurs, MOR 006 has a nearly complete set except for perhaps four or five distal phalanges, based on relative size and articulation of preserved bones. The specimen allows an estimation of 4(+1?)–4(+2?)–4(+1?)–4(+1)–2 in the left manus (Fig. 13; Appendix 1). Notably, the formula of *M. conodon* is much less than that of SDSM 452, which has 9–10(?)–10–10(?)–4(?) (Martin, 1953). One specimen of *M. hoffmanni* (NHMM 1993024) exhibits 9–10–10–10–3 (Lingham-Soliar, 1995, fig. 21). Each of those metacarpals and phalanges in SDSM 452 and *M. hoffmanni* is relatively shorter than those of *M. conodon*.

The eight well-preserved, isolated phalanges of TSJC 1998.2 are relatively short for a mosasaur. The proximal and distal ends are greatly expanded, as is typically seen in *Mosasaurus*. Articular surfaces in the proximal and distal ends are smooth. In MOR 006, the proximal end is slightly convex, especially on metacarpals II–IV, although the distal ends are slightly concave

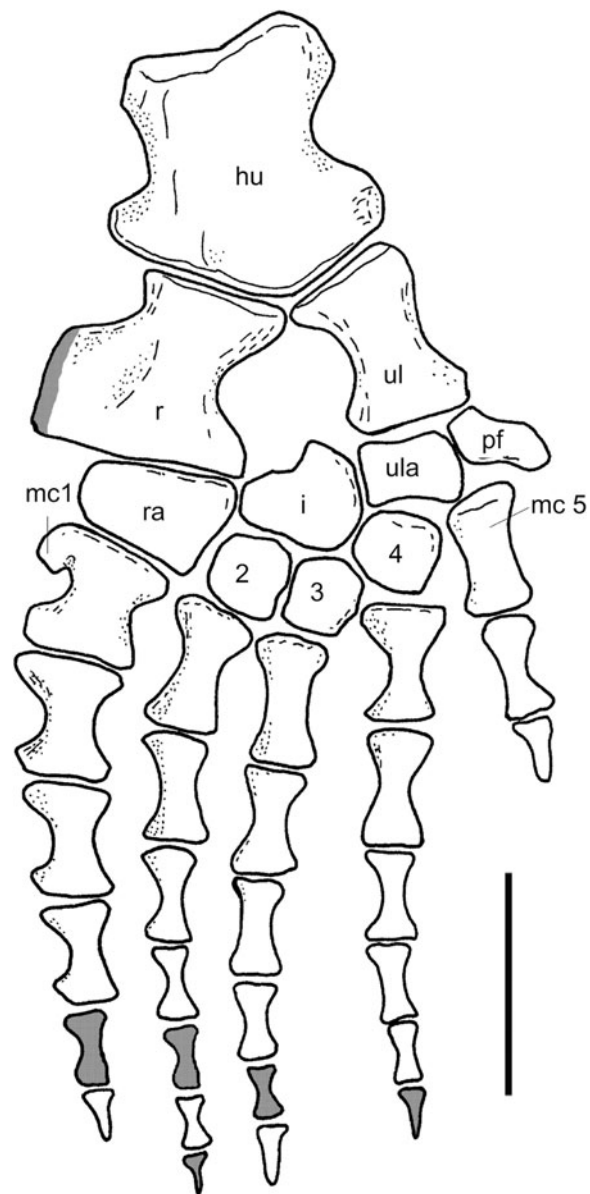


Fig. 13. Left forelimb of *M. conodon* (MOR 006). Light grey colour indicates missing portion. Scale equals 10 cm. Osteological abbreviations are listed in the text.

or flat (Fig. 13). Metacarpal I has a large, hook-like corner on the ventral margin of the proximal end, which appears in various taxa of Mosasaurini, such as *Mosasaurus*, *Plotosaurus* and *Clidastes*. *Mosasaurus*, however, has a much more strongly constricted mid-shaft than the two other genera. The ventral margin of the mid-shaft is also more constricted in all elements of digit I than is seen in digits II–IV in *M. conodon*, which also occurs in SDSM 452.

The well-preserved tibia has a greatly expanded mid-shaft in TSJC 1998.2. Both proximal and distal articular surfaces display a rectangular shape with a shallow concavity, which is in contrast to the flattened surface in *Clidastes*. The isolated fibula of TSJC 1998.2 also exhibits heavily built overall structure, with

Table 5. Comparisons of diagnostic morphological features for *M. conodon* with previous studies.

Cope (1881) Key specimen(s): AMNH 1380	Russell (1967) SDSM 452, AMNH 1380 and <i>M. lemonnieri</i>	This study AMNH 1380, MOR 006 and TSJC 1998.2
Large body size (about size of ' <i>Liodon validus</i> ')	Not used	Small–medium size <i>Mosasaurus</i>
NA	Tuberosity present(?) below stapedial pit on lower medial body of quadrate	Not included
NA	Suprastapedial and infrastapedial process small in lateral profile	Revised (placed above a third of the quadrate height)
Narrow splenial angular joint	Not included	Not included
Slender dentaries	Dentary very slender, as in <i>Clidastes</i> , dorsal and ventral margins converge gradually anteriorly, element comes to rounded tip anterior to first dentary tooth	Adapted from Russell
16 (plus two or three more) teeth on dentary	17 teeth on dentary	Revised (16 teeth on dentary)
NA	15 teeth on maxilla	Revised (14–15 teeth on maxilla)
NA	10 teeth on pterygoid	Revised (8 teeth on pterygoid)
NA	Ventral wing of coronoid well developed on medial surface of lower jaw	Not included
Subcircular teeth (in cross-section)	Same as Cope	Adapted from Cope
Bicarinate middle teeth	Not included	Uncertain if autapomorphy of the species
Teeth not faceted and smooth enamel	External facets narrow and more numerous than in <i>M. maximus</i>	Adapted from Cope & Russell
Anterior teeth have only anterior carina	Not included	Adapted from Cope (uncertain if autapomorphy of the species)
NA	Marginal teeth slenderer than in <i>M. missouriensis</i> , <i>M. maximus</i> and <i>M. ivoensis</i> , tips posteriorly recurved	Adapted from Russell
Coracoid has 'deep fissure' extending toward foramen	Not included	Not included
Humerus wider than long (height:width = c. 1.0)	Same as Cope	Height:width = 3:2
Eight cervicals?	Not included	Excluded
The presence of zygosphenes zygandra	Not included	Excluded (synapomorphy in Mosasaurini?)
Nearly circular vertebral articulations	Not included	Excluded
Chevron co-ossified with caudal vertebra	Not included	Excluded (synapomorphy in Mosasaurinae)

a prominent proximal end, which is thought to be a diagnostic character of *M. conodon* (Russell, 1967). Some disarticulated metapodials of TSJC can be separated into either elongate or short morphotypes. Based on an articulated manus and pes in SDSM 452, the metatarsals are slightly more elongate than the metacarpals.

Discussion and conclusions

Despite the incomplete and fragmentary nature of the holotypic skeleton (AMNH 1380), *M. conodon* is, we suggest, a nominal species for two main reasons. First, the elements preserved in the holotype are enough to allow referral of some other

specimens to the same species. Second, the holotype and the newly described specimens we here refer to *M. conodon*, especially MOR 006 and TSJC 1998.2, allow a review of previous diagnostic characters (Table 5) and thereby reinforce the diagnosis. These emended diagnostic characters can distinguish *M. conodon* from other species of *Mosasaurus*, such as *M. lemonnieri*, *M. hoffmanni*-*M. maximus* and *M. missouriensis*, as well as SDSM 452, as discussed below.

M. conodon differs from *M. lemonnieri*, as suggested by Lingham-Soliar (2000). Considerable differences appear in the tooth morphology, the tooth count in the maxilla, dentary and pterygoid (Table 3), and the position of the infrastapedial process in the quadrate. *M. conodon* displays very smooth tooth surfaces (no facets) and developed carinae without any serrations, as are also suggested to be diagnostic characters of *Clidastes* (Russell, 1967), which indicate plesiomorphic features in the lineage of Mosasaurini. In contrast, *M. lemonnieri* possesses well-developed facets and developed serrate carinae. Lingham-Soliar (2000) suggested these developed facets and serrations might occur during ontogeny in *M. lemonnieri*, without presenting specific data on juvenile specimens. Notably, the two specimens described above, AMNH 1380 and TSJC 1998.2, are fairly large for *M. conodon* (Table 1), and the presence of some fused cranial bones and rugose articular surfaces in appendicular bones indicates fully-grown individuals. Thus, comparisons of tooth morphology with other species of *Mosasaurus* should be relevant for taxonomic assignment.

M. hoffmanni-*M. maximus* can be differentiated from *M. conodon* by tooth morphology, especially the presence of well-developed serrations on the carinae. Their teeth are also morphologically different from those of *M. conodon* in cross-section. The two large species show a U-shaped cross-section instead of the transversely compressed, oval-shaped outline in *M. conodon*. The North American *M. maximus* tends to possess well-developed facets on the entire tooth surface. Some very large specimens assigned to *M. hoffmanni*, including the holotype, exhibit smooth tooth surfaces, as seen in *M. conodon* (personal observation in MNHNAC9648). Besides tooth morphology, there is an apparent difference body size. *M. conodon* is at least 20% smaller than one of the largest known specimens of *M. maximus* and *M. missouriensis* (based on skull length; Table 1). In *M. conodon*, the posteroventral process of the jugal is located higher on the vertical ramus, and the quadrate is small relative to the overall skull and jaw size; the ratio of quadrate (dorsoventral height)-to-dentary (anteroposterior length) is 0.19 in *M. conodon* and 0.23 in *M. maximus* (Table 1). *M. conodon* also exhibits a smaller manual phalangeal formula (Table 3) and a box-shaped humerus with a well-developed entepicondyle crest that is more heavily built than in *M. hoffmanni*-*M. maximus*.

The new Colorado and Montana specimens indicate that the nearly complete mounted skeleton, SDSM 452, should not be referable to *M. conodon* based on the following features found in the South Dakota specimen: a higher tooth count in

the pterygoid, a higher position of the infrastapedial process in the quadrate, gradually expanded splenial and ventral margin of the posterior dentary and a higher number of the manual digital formula (Fig. 13). The species-level taxonomic identification of SDSM 452 is difficult primarily due to the large amount of plaster reconstruction in the skull region (Martin, 1953). For now, we suggest that *Mosasaurus* sp. is a reasonable option for identification of SDSM 452, following Bell (1997).

The diagnosis of *Mosasaurus missouriensis* is currently not well understood, mainly due to the incomplete nature of the holotype. If KUVV 1034 (a fairly complete, well-preserved skull) is assigned to this species as suggested by Bell (1997), this species can be separated from *M. conodon* by fewer teeth in the pterygoid, a smaller number of the manual digital formula, a smooth tooth surface and a robust humerus.

Stratigraphically, *M. conodon* has one of the oldest records within the clade Potosaurini. A number of specimens listed above demonstrate that *M. conodon* occurs in upper Campanian to lower Maastrichtian strata. TSJC 1998.2 is one of the oldest known specimens in the species, which is estimated to be stratigraphically in the late Campanian *Baculites cuneatus/compressus* Biozone (c. 74 Ma; Ogg et al., 2012). There are difficulties in determining the precise stratigraphic levels of AMNH 1380 and MOR 006, although they must occur in late Campanian to early Maastrichtian strata (Gallagher, 1993; P. Leiggi, written commun., 2002), more precisely ranging through the *Exiteloceras jenneyi* (late Campanian) and *Baculites eliasi* (early Maastrichtian) ammonite zones (Gill & Cobban, 1973; Rice & Shurr, 1983). In the Gulf Coastal Plain, a number of specimens assigned to *M. conodon* are known only from the Demopolis Chalk, which is late Campanian to early Maastrichtian in age (Raymond et al., 1988; Ikejiri et al., 2013). This leads to the conclusion that *M. conodon* is from a different time interval to *M. maximus* in North America (Russell, 1967; Gallagher, 1993), as, to date, the two species have not yet been found in the same stratigraphic unit.

The European *M. lemonnieri* is mainly known from the late Maastrichtian age (e.g. the upper Maastrichtian Opoka of central Poland and upper Maastrichtian formations of the Netherlands; Lingham-Soliar, 2000; Machalski et al., 2003). If *M. conodon* and *M. lemonnieri* are phylogenetically closely related, as suggested by Lingham-Soliar (2000), the divergence of this clade to Europe might have happened before the Maastrichtian. To test this hypothetical scenario, a cladistic analysis including various taxa of Mosasaurini and detailed data of their stratigraphic occurrences will be needed.

To date, populations of *M. conodon* are palaeogeographically restricted to North America, including the Western Interior Seaway (the most northerly record in Phillips County, northeastern Montana), the Gulf Coastal Plain and the Mississippi Embayment areas (Russell, 1967; Kiernan, 2002; Ikejiri et al., 2013), and the Atlantic Seaboard area in New Jersey (Gallagher, 1993, 2002). However, some relatively small species of *Mosasaurus* from outside of North America, which are

established by mostly incomplete, fragmentary skeletons, are known, such as *M. hobetsuensis* and *M. prismaticus* from Japan (Suzuki, 1985a,b; Sakurai et al., 1999; Tanimoto, 2005), *M. beaugei* from Morocco and Syria (Bardet et al., 2004) and *M. mokoroa* from New Zealand (Welles & Gregg, 1971). Hopefully, the specimen-based study presented here will increase our knowledge of osteological information and help clarify some taxonomic problems and the phylogenetic relationships of various species of *Mosasaurus*.

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