RAPID COMMUNICATION

PELAGIC NEONATAL FOSSILS SUPPORT VIVIPARITY AND PRECOCIAL LIFE HISTORY OF CRETACEOUS MOSASAURS

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Abstract: Mosasaurs were large marine squamates that inhabited all of the world's oceans during the Late Cretaceous. Their success as apex predators has been attributed to their rapid acquisition of aquatic adaptations, which allowed them to become fully pelagic. However, little is known about the breeding biology of derived, flipper-bearing mosasaurs, as the record of neonatal mosasaur fossils is extremely sparse. Here, we report on the fragmentary cranial remains of two neonatal mosasaurs from the Niobrara Formation, referred to *Clidastes* sp. Comparison with other preliminary reports of neonatal mosasaurs reveals that these specimens are among the smallest individuals ever found and certainly represent the smallest known *Clidastes* specimens. The recovery of these extremely young specimens from a pelagic setting indicates that even neonatal mosasaurs occupied open oceanic habitats and were likely born in this setting. These data shed new light on the ecology of neonatal mosasaurs and illustrate the degree to which size-related taphonomic and collection biases have influenced our understanding of the early life history of these iconic marine reptiles.

Key words: mosasaur, viviparity, Niobrara, marine reptile, life history.

Mosasaurs (Squamata: Mosasauridae, *sensu* Bell and Polcyn 2005) were a clade of aquatic Mesozoic lizards that attained peak diversity during the Santonian and Maastrichtian, before going extinct during the end-Cretaceous mass extinction event along with many other vertebrate clades (Russell 1967; Jagt 2005; Jagt *et al.* 2008; Longrich *et al.* 2011; Polcyn *et al.* 2014). The larger, flipper-bearing mosasaurs exceeded the size of any extant lizards, ranging from 3 m to over 13 m in length, and were top predators in many Late Cretaceous marine ecosystems (Christiansen and Bonde 2002; Lindgren 2005). Although mosasaur remains have been discovered on all seven continents, a particularly diverse assemblage is known from the Late Cretaceous Niobrara Formation of western Kansas (Russell 1967). Remains of adult mosasaurs are abundantly preserved in the Smoky Hill Member of the Niobrara Formation, but discoveries of juvenile specimens are rare. This dearth of juveniles from the Niobrara led early workers to hypothesize that mosasaur birthing grounds were located elsewhere and that adults may have travelled inland via rivers and climbed ashore to lay eggs (Williston 1904). At the time, this scenario provided a compelling explanation for the rarity of young mosasaurs in marine fossil localities like the Niobrara, given that gravid representatives of other marine reptiles such as ichthyosaurs had been recovered from pelagic sediments, but mosasaurs had not (Shine 1985; Maxwell and Caldwell 2003). Since then, however, juvenile fossils have been found at sites populated by adult mosasaurs within the Niobrara and elsewhere (Bell and Sheldon 1986; Everhart 2002*a*, 2007). Everhart (2007) additionally noted that at least larger juvenile mosasaurs could not have been restricted to nearshore nurseries, as the Niobrara Formation was deposited several hundred kilometres from the nearest landmass.

Although the breeding ecology and early life history of mosasaurs has remained speculative for decades, recent preliminary discoveries and anecdotal reports have provided evidence supporting mosasaur viviparity,

suggesting that the lack of neonatal specimens in museum collections may be due to systematic collection and preservation biases, as opposed to being the result of baby mosasaurs exclusively inhabiting nearshore nurseries. Indeed, some recently recognized juvenile mosasaur material shows evidence of acid wear and may represent initially overlooked gut contents belonging to larger animals that were the original targets of fossil collectors (Everhart 2002*b*). Everhart (2002*a*) references 'foetal material' associated with an adult mosasaur from South Dakota and the basal mosasauroid *Carsosaurus marchesetti* from Slovenia, whereas Bell and Sheldon (2004) preliminarily reported a well-preserved gravid mosasaur (*Plioplatecarpus*) from South Dakota, apparently exhibiting multiple embryos inside its body cavity. However, beyond these inceptive

reports (none of which have been published beyond conference abstracts), no formal descriptions exist to provide support for viviparity in the derived clades of flipper-bearing mosasaurs. Although the report of a pregnant specimen of *Carsosaurus* (possibly a semi-aquatic mosasauroid; Caldwell and Lee 2001), and the discovery of the juvenile mosasaur *Tethysaurus* (Houssaye and Bardet 2013), indicate that viviparity may have arisen early in the evolutionary history of the Mosasauroidea, a pattern that may also hold true among ichthyosaurs (Motani *et al.* 2014), a specimen-based analysis of obligatorily aquatic, neonatal mosasaurs has yet to be undertaken.

Here, we describe the cranial remains of two extremely small mosasaur specimens from the Niobrara Formation of Kansas (Figs 1–3). The material represents the smallest
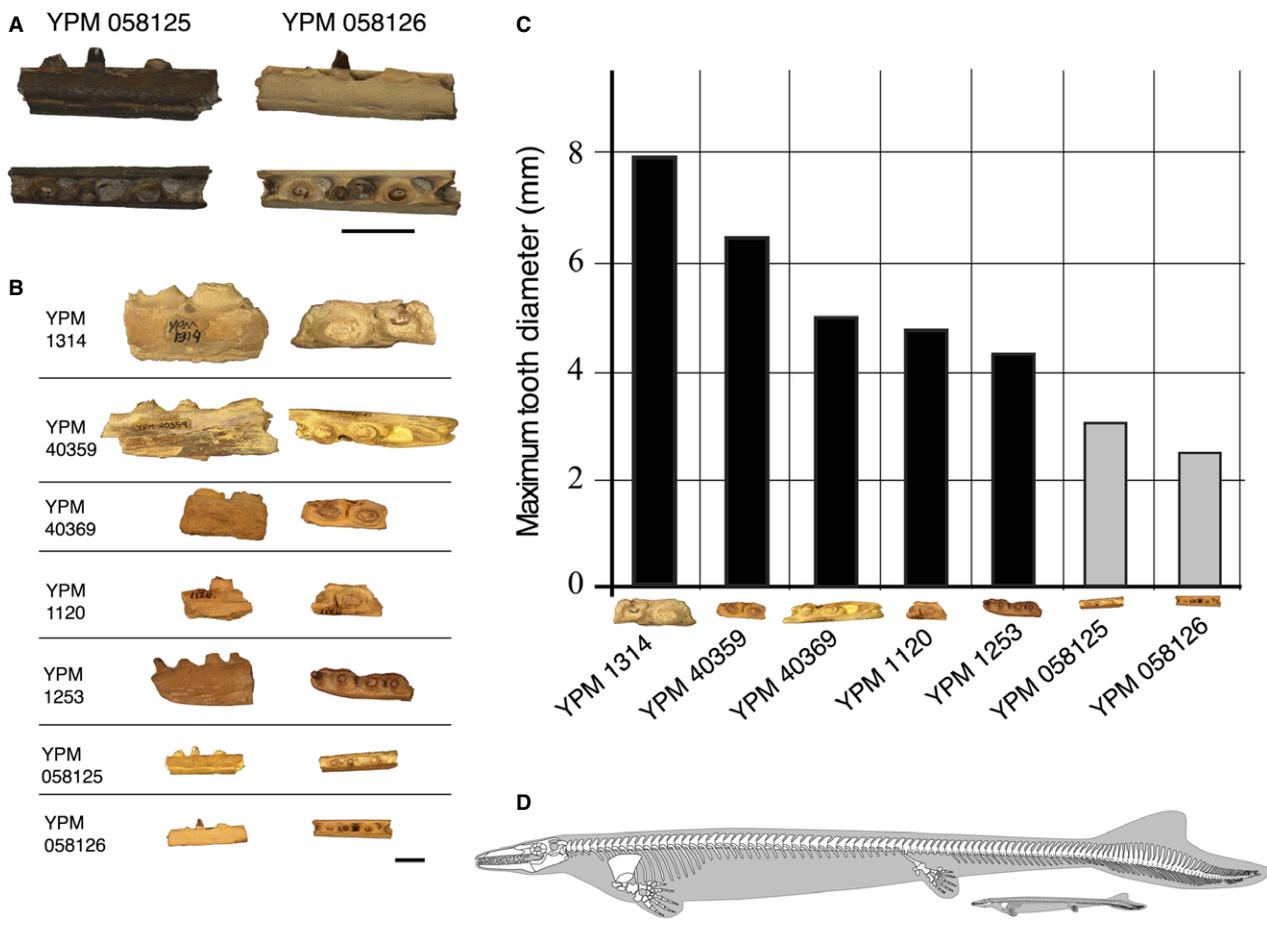
FIG. 1. The smallest mosasaurid remains from the Niobrara Formation, previously misidentified as toothed stem birds. A, lateral and dorsal view of the left dentary of *Clidastes*, YPM VP.058125; lateral and dorsal view of the left dentary of *Clidastes*, YPM VP.058126. Scale bar represents 1 cm. B, size comparison of several of the smallest *Clidastes* dentaries from the Niobrara Formation, in lateral (left) and dorsal (right) views. Scale bar represents 1 cm. The newly discovered specimens reported here (YPM 058125, YPM 058126) are by far the smallest. C, comparison of maximum tooth diameters for juvenile *Clidastes* from the Niobrara chalk. The newly discovered specimens (YPM VP.058125, YPM VP.058126) represent the smallest mosasaurids known from the Niobrara Formation and are currently the youngest *Clidastes* specimens ever found. D, estimated body length of neonatal mosasaurs (YPM VP.058125 and YPM VP.058126) relative to an adult specimen of *Clidastes liodontus*. The adult is 3 m in length; the neonate is 0.66 m in length (see text). Redrawn from Caldwell and Diedrich (2005, fig. 5) and Lindgren *et al.* (2011, fig. 12). Scale bar represents 1 m. Colour online.

mosasaur remains yet discovered from these sediments; probably collected in the nineteenth century, the specimens had until now been misclassified as 'Aves indeterminate' in the collections of the Yale Peabody Museum of Natural History. Numerous features of these specimens (including osteocementum and posterolingual tooth replacement), however, are diagnostic of Mosasauridae (Caldwell *et al.* 2003, Caldwell 2007), the clade including the flipper-bearing mosasaurs. These new specimens bolster the existing evidence for mosasaur viviparity and provide some of the first direct evidence in support of a pelagic ecology for flipper-bearing, neonatal mosasaurs. These data cast further doubt on classic hypotheses of mosasaur nurseries in nearshore habitats, and the rarity of this material affirms the effects of size-dependent preservation and collection biases influencing our understanding of the Mesozoic vertebrate fossil record.

MATERIAL AND METHODS

The material described here comprises two specimens: YPM VP.058125 and YPM VP.058126. The former specimen consists of an isolated partial left dentary, and the latter consists of ten cranial fragments, three of which are tooth bearing. Comparisons were made with other Niobrara mosasaurid material in the collections of the Yale Peabody Museum. Measurements were taken with digital callipers (iGaging) and given in millimetres.

GEOLOGICAL SETTING

The material presented here was collected from the Smoky Hill Member of the Niobrara Formation (Kansas,

USA). These chalks were deposited from the late Coniacian through the Early Campanian on the western shelf of the Western Interior Seaway (Everhart 2007).

Institutional abbreviation. YPM, Yale Peabody Museum of Natural History, New Haven, USA.

SYSTEMATIC PALAEONTOLOGY

Order SQUAMATA Oppel, 1811
Family MOSASAURIDAE Gervais, 1853
Subfamily MOSASAURINAE Gervais, 1853

Genus cf. CLIDASTES Cope, 1868

Type species. Clidastes propython Cope, 1869, p. 258; from the Early Campanian of the Mooreville Chalk of the Selma Group, Alabama, USA.

cf. *Clidastes* sp.

Specimen descriptions
YPM VP.058125 consists of a partial left dentary (Fig. 1); three complete tooth bases are preserved, with indications of one incomplete tooth base at each of the broken ends of the bone. Each tooth is encased in a spongy, bony base, and the grain of this tissue is oriented parallel to the long axis of each tooth. This bony base appears identical to the osteocementum base of mosasaurid and ichthyosaur teeth (Caldwell 2007; Luan *et al.* 2009; Maxwell *et al.* 2011). The teeth are not positioned exactly along the midline of the dental groove, but are instead positioned closer to the labial wall of the dentary. The crowns are labiolingually compressed. The anterior carina of the only preserved tooth crown is not

FIG. 2. Associated cranial material from a neonatal mosasaur (YPM 058126). A–C, partial surangular in: A, lateral; B, dorsal; and C, medial view. D–G, anterior fragment of a left splenial (?) in: D, ventral; E, lateral; F, dorsal; and G, medial view. H–J, dentary fragment in: H, ventral; I, medial; and J, lateral view. K–L, partial surangular in: K, medial, and L, lateral view. M–O, partial left dentary in: M, labial; N, dorsal; and O, lingual view. All scale bars represent 1 cm. Colour online.
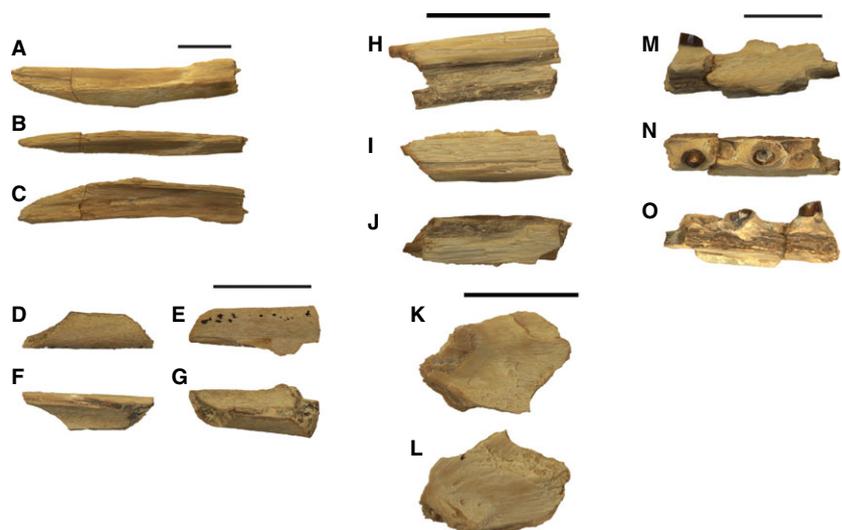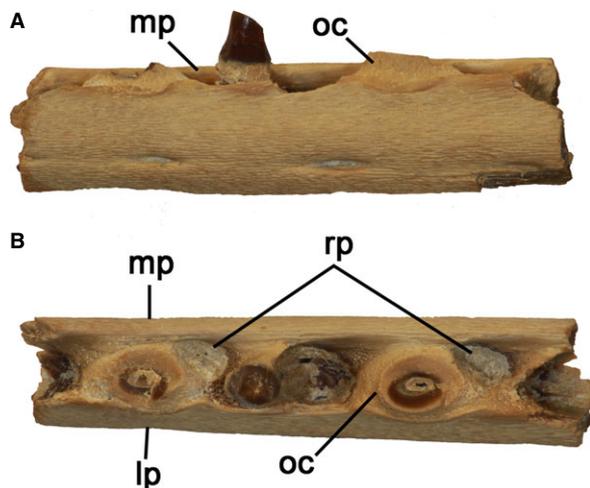
FIG. 3. Partial left dentary of YPM VP.058126 referred to *Clidastes sp.* in A, labial, and B, occlusal view. *Abbreviations*: lp, lateral parapet of dentary; mp, medial parapet of dentary; oc, osteocementum; rp, resorption pit. Rostral end on the left. Scale bar represents 1 cm. Colour online.

serrated. The labial surface of the tooth crown appears smooth, whereas the lingual surface has one or two incipient facets. There are thin, dark, closely spaced lines along the long axis of the tooth enamel. Based on the presence of a distinct anterior carina, lingual facets and fluting along the lingual surface of the dentary tooth crown, the specimen is attributed to *Clidastes* (following the dental features identified by Lindgren and Siverson 2004).

The alveolar margin of the dentary is straight, and the lateral and medial margins gradually taper anteriorly. The width of the dentary at its anterior end is slightly narrower than its width at the posterior end. A row of neurovascular foramina is preserved on the lateral surface for the mandibular division of the fifth cranial nerve. The medial surface bears a groove for the Meckelian canal. Roughly one quarter of the ventral surface is not preserved. The medial parapet of the dentary is even with the lateral parapet, which is typical of Mosasauridae (Bell 1997).

YPM VP.058126 consists of ten fragments, three of which are tooth bearing (Figs 2–3). The largest dentary fragment is from the left side of the jaw and is extremely similar to YPM VP.058125 (Fig. 1A). As in that specimen, this fragment contains three complete alveoli. Only the second crown is preserved, with the tip of the crown missing. The dentary is broken below the Meckelian canal. The long axis of the dentary is straight, as are the dorsal, lingual and buccal margins. The lingual and labial margins taper slightly at the anterior end of the fragment. The tooth bases consist of the same spongy bone tissue seen in YPM VP.058125, which extends across the entire width of the alveolar groove of the dentary. Neighbouring tooth bases are separated by large resorption pits (Fig. 3). These resorption pits would have housed replacement teeth and are positioned posteriolingually to the functional teeth, which is indicative of 'varanid type' tooth replacement, seen in all mosasaurids (Caldwell 2007). The preserved tooth crown is oval in cross section. Enamel is only present along the labial surface of the preserved tooth in the dentary fragment and is smooth. The second

dentary fragment also derives from the left dentary, containing two complete tooth bases and evidence for additional tooth bases at each end. The base of a tooth crown is preserved on the second dentary fragment, and there are carinae present on both the anterior and posterior sides of the tooth crown (a diagnostic feature of *Clidastes*; Russel 1967). These carinae divide the tooth crown roughly in half, but the lingual side is more convex in occlusal view than the buccal side. The carinae are not serrated (another feature diagnosing *Clidastes*; Russell 1967, Ikejiri and Lukas 2015). Another cranial element can be attributed to a partial surangular. The surangular fragment is long, thin and gently bowed, but lacks information about the anterior and posterior ends of the bone. An additional fragment probably represents the posterior end of the splenial. The other partial surangular preserves only the posterior-most portion, close to its articulation with the articular. The lateral surface is smooth. Based on tooth morphology, we also refer this specimen to *Clidastes* sp.

DISCUSSION

Until now, the material described here was tentatively assigned to an unspecified toothed stem bird. The superficial similarity between the toothed jaws of Niobrara stem birds such as *Ichthyornis* and *Hesperornis* and those of small mosasaurs has led to multiple instances of taxonomic confusion (Marsh 1880; Gregory 1952; Walker 1967; Gingerich 1972). Marsh (1880, p. 124) stated that 'the dentigerous portion of the lower jaw [of *Ichthyornis*] is so similar to that of some of the smaller Mosasauroid Reptiles, that, without other portions of the skeleton, the two could hardly be distinguished'. Indeed, Gregory (1952, p. 73) erroneously concluded 'the jaw assigned to *Ichthyornis*. . . is so closely similar to that of the mosasaur *Clidastes* in details of structure, that actual relationship rather than convergence is suggested. Its association with the bird skeleton seems extremely doubtful'. Although Gregory (1952) was incorrect in his diagnosis (Clarke 2004), the historical lack of neonatal mosasaurs from the Niobrara has hindered our understanding of the early life histories of these organisms.

We can confidently assign these fragmentary remains to neonatal mosasaurids based on the presence of osteocementum along the roots of the teeth and posterolingually positioned replacement pits (Caldwell 2007). Furthermore, the combined presence of enamel facets and nonserrated carinae along the anterior and posterior edges of the preserved tooth crowns is diagnostic of *Clidastes* (Lindgren and Siverson 2004). The maximal tooth diameter of the smaller individual described here (YPM 058126; 2.48 mm) is roughly 22% that of YPM 1324, the largest YPM *Clidastes* measured (11.35 mm; Fig. 1D). Although isometry between tooth dimensions and body length is unlikely, this ratio between adult and parturition size is comparable to other Mesozoic marine reptiles,

FIG. 4. Artist's interpretation of this study's principal conclusions, illustrating *Clidastes liodontus* giving live birth in an open pelagic setting ~85 million years ago, beneath the shadow of the toothed stem bird *Ichthyornis*. Illustration by Julius Csotonyi.

including the ichthyosaur *Stenopterygius quadriscissus* (Böttcher 1990), and the basal mosasauroid *Carsosaurus* (Caldwell and Lee 2001; O'Keefe and Chiappe 2011). While fragmentary remains may be useful for robust estimates of fossil body size (Field *et al.* 2013), in this instance, the lack of an effective aquatic crown group comparison for mosasaurids precludes the precise estimation of total body size for these specimens. However, if simplistic scaling and a ~22% ratio between adult and parturition size are assumed, then for a fairly average adult *Clidastes* length of 3 m, the total body length of the juveniles reported here would have been roughly 0.7 m.

Whereas some preliminary reports of neonatal mosasaurids do exist (Everhart 2002*a*), at least some of these occurrences probably represent partially digested remains and thus do not indicate conclusively that neonatal mosasaurids inhabited open-water settings. The baby *Clidastes* fossils reported here show no evidence of acid wear and represent important new evidence for marine viviparity and precociality in mosasaurs. The presence of these extremely young mosasaurids in an open pelagic setting supports the idea that *Clidastes* was precocial, likely giving birth to fully fledged swimmers able to survive alongside adults (Fig. 4). These data lend support to similar interpretations based on comparative osteohistology of juvenile and adult mosasaurids (Houssaye and Tafforeau 2012), although neonates were not included in that analysis. Even without direct observation of embryos *in situ*, the flipper-bearing mosasaurids were probably exclusively viviparous. Unlike modern sea turtles who come ashore to lay eggs, or basal, facultatively aquatic mosasauroids, more derived mosasaurids lost the ability to move on land: the presence of a streamlined body with an anteri-

orly deepened rib cage, the lack of any sacral attachment for the pelvis and the presence of a hypocercal tail would have rendered these mosasaurids obligatorily aquatic (Russell 1967; Caldwell and Palci 2007; Lindgren *et al.* 2010; Lindgren *et al.* 2011; Konishi *et al.* 2012; Lindgren *et al.* 2013). Mosasaurids would therefore have had to give birth to live young, as do other secondarily (and obligatorily) aquatic tetrapods (Maxwell and Caldwell 2003; Organ *et al.* 2009).

Uncontroversial representatives of the early ontogenetic stages of fossil taxa are at a premium in vertebrate palaeontology, where the potential for complex ontogenetic trajectories and the scarcity of intermediate growth stages documenting major anatomical transitions may lead to taxonomic confusion (Carr and Williamson 2004; Horner and Goodwin 2009; Scannella and Horner 2010; Longrich and Field 2012). We hope the neonatal *Clidastes* material described herein, which represents a previously unsampled ontogenetic stage, will be useful for future studies of mosasaur growth and ontogenetic change.

Sheldon (1990) examined the relative scarcity of baby mosasaurids in most localities containing large numbers of adult specimens and attributed the discrepancy to sampling bias. The results of that study indicated a substantial difference in the ratio of juveniles to adults between Alabama's Mooreville Chalk Formation and the Niobrara Formation, supporting some combination of preservation, collection, or identification bias against the preservation of juveniles in the Niobrara Formation. These results are similar to those of Brown *et al.* (2013), who illustrated a strong positive association between body size and both rate of preservation and skeletal completeness in Mesozoic terrestrial settings. Those data indicate that not only smaller bodied species, but also juveniles of larger bodied species exhibit significantly lower fossil preservation rates than do large adults. These taphonomic biases likely apply equally to marine mosasaur-bearing localities as to the terrestrial Cretaceous localities investigated by Brown *et al.* (2013). Given the historical collecting bias favouring large specimens in the Niobrara Formation (Everhart 2002*a*), as well as other classic Mesozoic localities in the American West, we consider it likely that future attention to collecting smaller remains from the Niobrara Formation and elsewhere will shed additional light on the ecology and life history of juvenile mosasaurs.

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