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Earliest record of the genus *Tylosaurus* (Squamata; Mosasauridae) from the Fort Hays Limestone (Lower Coniacian) of western Kansas

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Fossil vertebrates are extremely rare in the Fort Hays Limestone member of the Niobrara Chalk in comparison to the rich variety of well-preserved fish, turtles, mosasaurs, pteranodons, and toothed birds collected from the overlying Smoky Hill Chalk, and to a lesser extent, the underlying Carlile Shale. Although mosasaurs are well documented from the Smoky Hill Chalk (Upper Coniacian – Lower Campanian), and occur rarely in the Carlile Shale (Middle Turonian), they had not been previously reported from the intervening Fort Hays Limestone (Lower Coniacian). Here we report the remains of a mosasaur (FHSM VP-2297) preserving 14 articulated vertebrae, the left coracoid, ribs, and fragments of sternal cartilage collected by M.V. Walker in 1967 from Ellis County, Kansas. Serrated bite marks on several of the ribs are attributable to the anacoracid shark, *Squalicorax falcatus*, and suggest post-mortem scavenging of the remains. The specimen is identified as *Tylosaurus* sp. on the basis of the characteristic shape of the coracoid and represents the earliest documented occurrence of that genus. It is also the first record of a mosasaur in the Fort Hays Limestone and preserves the earliest evidence of scavenging on mosasaur remains by *Squalicorax*.

Keywords: Mosasaur, Squalicorax, Niobrara, Western Interior Sea.

INTRODUCTION

The Fort Hays Limestone was deposited during the maximum transgressive phase of the Niobrara Cyclothem when the Western Interior Sea covered the middle of North America (Hattin 1982). It ranges from 45 to 80 ft. (17-24 m) in thickness and consists of several relatively resistant beds of chalky limestone separated by thin layers of chalky shale (Frey 1972). The water was relatively deep, well aerated and far enough from shore as to be beyond the influence of terrestrial sediments (Ibid.).

Although rich in invertebrate remains (Miller 1968, 1969; Frey 1972), the Fort Hays Limestone has produced few vertebrate specimens since the first collections were made in the early 1870s. In 1874 Benjamin F. Mudge, a pioneer in Kansas paleontology, collected the fragmentary remains of an elasmosaurid plesiosaur from the Fort Hays Limestone of Jewell County, in north-central Kansas (Williston 1906). Later, Mudge (1876, p. 214) would describe the Fort Hays Member of the Niobrara Formation, saying, "Its fossils are *Inocerami,* fragments of *Haploscapha* [rudists], *Ostrea,* with occasional remains of fish and Saurians. The vertebrates are so rare that we never wasted our time in hunting them in this stratum; still, our largest Saurian [plesiosaur], *Brimosaurus* of Leidy, was found in it in Jewell County." Williston (1897, p. 237) had mentioned the plesiosaur discovered by Mudge in the Fort Hays Limestone, and noted that "mosasaurs and pterodactyls seem to be wholly wanting."

The plesiosaur remains collected by Mudge are cataloged as YPM 1640 in the Yale Peabody Museum collection and were initially described as the type specimen of *Elasmosaurus nobilis* by Williston (1906).

Although the specimen is now considered to be "Elasmosauridae indeterminate" by Storrs (1999), it does have some lasting value as an indicator of the scarcity of vertebrate remains in this member. Williston (1906, p. 233; see also pl. IV) wrote, "The specimen, notwithstanding what [damage] it has suffered, is of much interest since it is the only vertebrate I have any knowledge of from the [Fort] Hays limestone."

Almost a hundred years later, there are still quite few vertebrate remains known from the Lower Coniacian in Kansas. The type specimen of *Micropycnodon kansasensis* was collected from the Fort Hays Limestone in Rooks County (Hibbard and Graffham 1941). Although Frey (1972) mentioned that the teeth of sharks, including those of "shell crushers" (*Ptychodus*) are "common locally," he only identified the genus *Squalicorax*. However, he (Ibid., pl. 9, fig. 2) did illustrate the teeth of three sharks: *Squalicorax falcatus*, *Cretoxyrhina mantelli*, and *Cretalamna appendiculata*. Three additional chondrichthyans (*Ptychodus mortoni*, cf. *Scapanorhynchus* sp., and *Paranomotodon* sp.) were reported by Shimada (1996). Shimada and Everhart (2003) provided the most recent summary of vertebrates (mostly sharks and bony fish) previously collected from the Fort Hays Limestone and reported the first occurrence of *Ptychodus mammillaris* and *Enchodus* cf. *E. shumardi*. Because of their rarity, any identifiable vertebrate remains from the member are noteworthy. Until now, however, the plesiosaur remains (YPM 1640) collected by Mudge in 1874 represented the only known marine reptile collected from this member (Williston 1906).

The discovery of the well-preserved remains of a mosasaur in the Fort Hays Limestone establishes the presence of these marine lizards in this portion of the Western Interior Sea during early Coniacian time. Although overlooked in the collection for almost 40 years, the specimen is important to our understanding of the early diversification of mosasaurs and the paleoecology of the Late Cretaceous marine environment covering the midwest region.

Abbreviations: FHSM – Fort Hays State University, Sternberg Museum of Natural History, Hays, Kansas; KUVP – University of Kansas Vertebrate Paleontology Collection, Lawrence, Kansas; and, YPM – Yale Peabody Museum, Yale University, New Haven, Connecticut.

Material

FHSM VP-2297 is an articulated series of mosasaur vertebrae including a fragment of the 6th cervical, a complete 7th cervical and 13 complete dorsals that extend from near the base of the neck to the mid-back of a sub-adult or adult mosasaur, with associated ribs, the left coracoid and preserved sternal cartilage (Fig. 1). The posterior end of the 13th dorsal vertebrae is damaged. All of the vertebrae are slightly flattened dorso-ventrally and are preserved in ventral view in a thin layer of limestone. The anterior-most complete cervical vertebra (C7) is about 5 cm in diameter by 7 cm long, with a small, raised hypapophysis visible on the ventral surface. The vertebrae gradually increase in size with the posterior-most vertebra measuring about 6 cm in diameter by 8 cm long. The dorsal sides of the vertebrae are not visible on the underside of the limestone matrix. The nearly complete left coracoid is preserved in lateral view (Fig. 2) and there are a number of flattened pieces of preserved (calcified) sternal cartilage included in the remains. The bones are dark gray to black. The cartilage is lighter in color than the bones and has a pitted appearance (Fig. 3). Little additional preparation is evident and the limestone matrix is still attached to many of the bones and cartilage. The specimen measures approximately 1.2 m (4 ft.) in length and represents a mosasaur that would have been about 6.7 m (22 ft.) long.

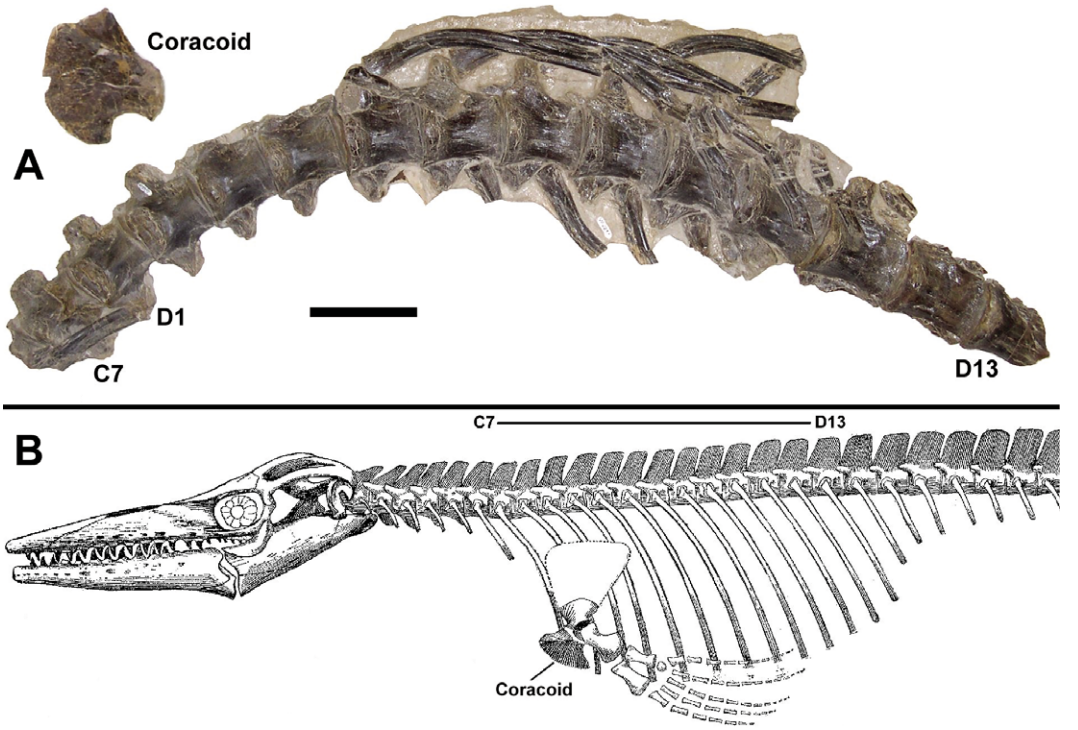

Figure 1. A. The vertebral column, left coracoid, and associated ribs of FHSM VP-2297 in ventral view, anterior to the left. C7 = last cervical vertebra; D1 and D13 = dorsal vertebrae. Scale bar = 10 cm. B. Left lateral view of the anterior skeleton of *Tylosaurus proriger*, adapted from Williston (1898), showing relative positions of the remains of FHSM VP-2297.

Figure 2. A. Left coracoid of VP-2297 in lateral view, anterior to the left. The estimated length of the mosasaur is 6.7 m. B. Left coracoid of a 5.8 m *Platecarpus tympaniticus* (FHSM VP-322) in lateral view. Scale bar = 10 cm.

Locality and stratigraphy

The specimen was discovered in north-central Ellis County on the south side of the Saline River (Fig. 4) near the top of the Fort Hays Limestone (Frey 1972). Detailed locality information is on file at the Sternberg Museum of Natural History. A museum exhibit label states that the specimen was originally identified as a "section of caudal (tail) vertebrae of a swimming reptile." Records indicate that it was collected by M.V. Walker and others on June 22, 1967 from the "Upper" Fort Hays Limestone. This portion of the Niobrara Chalk is considered to be early Coniacian in age and probably represents a period when the transgression of the Niobrara Cyclothem in the Western Interior Sea was near its greatest extent (Frey 1972). The preservation of the upper surface of the specimen is excellent, and appears to have been exposed naturally by weathering. The remains were collected together with a thin (1-2 cm) layer of the underlying limestone. The locality provided by Walker in the museum records includes a natural exposure

Figure 3. Fragments of sternal cartilage and ribs of VP-2297. Note the distinctive pitted appearance of the cartilage. Scale bar = 10 cm.

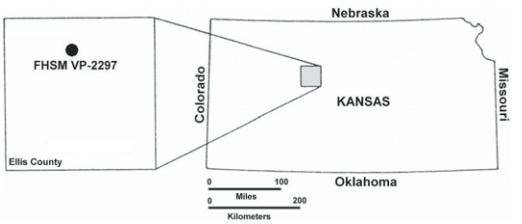

Figure 4. Approximate locality of FHSM VP-2297 in north-central Ellis County, Kansas.

of Fort Hays Limestone along a minor tributary of the Saline River and preserves evidence of the past operation of a small limestone quarry. Exposures of the contact between the Fort Hays Limestone and the overlying Smoky Hill Chalk trend from southwest to northeast (Hattin, 1982, fig. 1) in Ellis County. The contact is readily visible at the top of a roadcut about 10 km northeast of this locality where US highway 183 crosses the Saline River.

Discussion

Mosasaurs (Squamata; Mosasauridae) are an extinct group of marine lizards that flourished worldwide during the final 25 million years of the Late Cretaceous. The remains of mosasaurs are known from all continents, are preserved in marine sediments of Turonian through late Maastrichtian age, and are especially abundant and complete in the Smoky Hill Chalk Member (Upper Coniacian through Lower Campanian) of the Niobrara Chalk in western Kansas (Everhart 2001). Three mosasaur specimens including vertebrae and a jaw fragment identified as cf. *Clidastes* (Martin and Stewart 1977), and a plioplatecarpine frontal (KUVP 97200; Everhart 2005a) from the Fairport Chalk Member (Middle Turonian) of the Carlile Shale are in the University of Kansas collection. However, no mosasaur remains had been documented from the intervening Fort Hays Limestone (Lower Coniacian) in more than 130 years of collecting. This interval (approximately 2 million years) represents a critical and poorly understood period during the early evolution of mosasaurs.

Five species of mosasaurs (*Clidastes liodontus*, *Platecarpus tympaniticus*, *P. planifrons*, *Tylosaurus nepaeolicus*, and *T. kansasensis*) are documented from the basal portion of the Smoky Hill Chalk (Upper

Coniacian), although their earliest stratigraphic occurrence has been the subject of some question (Williston 1898; Russell 1967; Everhart 2001, 2002, 2005b). The biostratigraphy of mosasaurs in the Smoky Hill Chalk was most recently revised by Everhart (2001) on the basis of several new specimens. Everhart, Everhart and Bourdon (1997) reported the earliest occurrence of *Clidastes liodontus* from a complete skull and dorsal vertebrae (FHSM VP-13809) discovered in the chalk near Hattin's (1982) marker unit 4. Martin and Stewart (1977) identified two specimens of mosasaur vertebrae (KUVP 6176 and 27032) and a jaw fragment (KUVP 25869) from the Fairport Chalk Member of the Carlile Shale as cf. *Clidastes*. According to Polcyn (pers. com., 2004), however, the caudal centrum (KUVP 27032) is "clearly russellosaurine" and the jaw fragment is not diagnostic. Russell (1967) suggested that the range of *Platecarpus* probably extended to the base of the Smoky Hill Chalk. A mosasaur frontal (KUVP 97200) collected from the Carlile Shale of Ellis County has been identified as cf. *Platecarpus* (Polcyn, pers. com., 2004). Williston (1898) noted that *Tylosaurus* was present at the lowest levels of the chalk and Everhart (2005b) described a new species (*Tylosaurus kansasensis*) from several specimens, including the holotype (FHSM VP-2295), collected just above the contact of the chalk with the Fort Hays Limestone. Although *Tylosaurus nepaeolicus* is present in the lower Smoky Hill Chalk, *T. kansasensis* is the most commonly occurring species near the contact with the Fort Hays Limestone (Everhart, 2005b). The undescribed remains of tylosaurine mosasaurs are known from the Turonian of Texas (Bell, pers. com., 2004), and mosasaur remains also occur in the Lower Coniacian of Texas (Polcyn, pers. com., 2005).

The characteristics of the vertebrae of VP-2297 are consistent with those of *Tylosaurus*, but they cannot readily be distinguished from those of *Platecarpus* as preserved in ventral view. As they are compressed dorso-ventrally, it is not possible to differentiate between *Platecarpus* and *Tylosaurus* on the basis of the shape of the condyle and cotyle. The longest vertebrae in the series are the most posterior (mid-back) in the series, consistent with the observations of Russell (1967, p. 77) for both *Platecarpus* and *Tylosaurus*. The large size of the specimen, however, argues favorably for *Tylosaurus* and it is the genus most commonly collected in the basal Smoky Hill Chalk (pers. obs.).

The left coracoid is the only bone in the specimen that can be positively identified as *Tylosaurus*, in this case both by its distinctive shape (Fig. 3A) and relatively smaller size compared to that of *Platecarpus* (Fig. 3B; Russell 1967). Although the glenoid fossa is slightly damaged, the rest of the fan-shaped bone is nearly complete, measuring 13 cm in width by 10.5 cm in height. The expanded medial edge of the coracoid is thickened and rough where it would have been attached to the cartilaginous epicoracoid (Osborn 1899). The shape and location of the coracoid foremen are consistent with the descriptions and figures of a *Tylosaurus* coracoid provided by Williston (1898, p. 146, fig. LV) and Russell (1967, p. 85-86, fig. 45). In addition, the coracoid of FHSM VP-2297 shows no indication of emargination whereas the coracoids of the co-occurring genera (*Platecarpus* and *Clidastes*) are distinctly emarginate.

FHSM VP-2297 represents the presence of an adult mosasaur in mid-ocean, hundreds of kilometers from the nearest coast. Although it is possible that the remains were the result of a drifting carcass that finally came to rest far from the original place of death (Carpenter 1996), the articulation of the vertebrae and ribs, and the presence of soft tissue (sternal cartilages) argues for a relatively short period of decomposition prior to reaching the sea floor. The taphonomy of the remains is quite

similar (missing head and neck, limbs and tail) to a mosasaur specimen (FHSM VP-13746**)** reported by Everhart (2004) as being scavenged by two species of shark. Serrated bite marks attributable to the anacoracid shark, *Squalicorax falcatus*, are present on several ribs of FHSM VP-2297, indicating that the remains had been scavenged (Schwimmer, Stewart and Williams 1997). The taphonomy of FHSM VP-2297 suggests that it is the remains of a severely scavenged carcass that was missing head, neck, tail and limbs by the time it reached the sea bottom, similar to the condition of other scavenged mosasaur specimens described by Everhart (2004) from the overlying Smoky Hill Chalk. This specimen also preserves the first evidence of the co-occurrence of the genus *Tylosaurus* and *Squalicorax* in the Lower Coniacian of Kansas.

The early presence of mosasaurs in Kansas in the Middle Turonian Fairport Chalk Member of the Carlile Shale, and their abundance in the Smoky Hill Chalk and Pierre Shale raises the question of why more of their remains have not been collected from the Fort Hays Limestone. The paucity of vertebrate remains, however, is not limited to marine reptiles, but also includes fishes, pteranodons, and birds that are known from above and below the member. Because the sea in the area of deposition was apparently well aerated and circulated (Frey 1972), and supported a diverse invertebrate community (Miller 1968, 1969; Frey 1972), some other explanation appears to be required. A collecting bias may be partially responsible as noted by Mudge (1876) whereby collectors have preferentially sought more productive horizons. Since the late 1860s, most of the fossil collecting that has been done in Kansas has focused on the highly fossiliferous Smoky Hill Chalk, especially during the 1870s and the "bone wars" between E.D. Cope and O.C. Marsh (Everhart 2005a). Many of the localities where the Fort Hays Limestone crops out are difficult places to collect because the exposures are more or less vertical. In addition, the limestone is generally more resistant to weathering than either the Carlile Shale or Smoky Hill Chalk, and new remains are less likely to erode out over the same period of time than in other units. The most likely reason, however, is that the area where the Fort Hays Limestone was deposited was probably in deeper water, farther from shore during the height of the Niobrara Cyclothem than either the Carlile Shale or Smoky Hill Chalk, and may not have been a preferred environment for many larger vertebrates.

Conclusion

Although the presence of mosasaurs would be expected in the Fort Hays Limestone, they had not been documented in more than 135 years of collecting. FHSM VP-2297 represents both the first mosasaur remains documented from the Fort Hays Limestone and the earliest known remains of the genus *Tylosaurus*. It also provides the first evidence of an interaction (scavenging) between *Tylosaurus* and anacoracid sharks (*Squalicorax*) from the Lower Coniacian. As such, it adds significantly to our understanding of the paleoecology of the Western Interior Sea during early Coniacian time.

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