

# A PARTIAL SKELETON OF THE BASAL MOSASAUR *HALISAURUS PLATYSPONDYLUS* FROM THE SEVERN FORMATION (UPPER CRETACEOUS: MAASTRICHTIAN) OF MARYLAND

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**ABSTRACT**—A new specimen of the basal mosasaur *Halisaurus platyspondylus* from the Severn Formation of Prince Georges County, Maryland (Upper Cretaceous: middle Maastrichtian) represents the most complete partial skeleton of this uncommon taxon to be described to date. The characteristic dorsoventral compression of the vertebral centrum is most pronounced in the anterior trunk vertebrae, and the centra of the posterior trunk vertebrae exhibit proportions more similar to those in other mosasaurs such as *Plioplatecarpus*. The postorbitofrontal forms its primary contact with the frontal rather than the parietal, and the supraoccipital is firmly attached to the ventral side of the parietal. The plane of articulation between the parietals and supratemporal is neither vertical (as in Varanidae) nor horizontal (as in Mosasauridae), but forms an angle of about 55 degrees with the horizontal. The quadrate bears a long, ventrally-flared suprapedial process but appears to lack an infrapedial process. Close similarities in the structure of the frontal and parietal with "*Clidastes*" *sternbergii* support referral of the latter to *Halisaurus*, but reference of *Phosphorosaurus ortliebi* to *Halisaurus* is questionable. *Halisaurus* has been recorded from the Santonian to the late Maastrichtian.

## INTRODUCTION

**T**HE HOLOTYPE of *Halisaurus platyspondylus* Marsh, 1869, (YPM 444) was collected by John G. Meirs from late Maastrichtian strata of the upper New Egypt Formation in the pit-mine of the Cream Ridge Marl Company near Hornerstown, Upper Freehold Township, in Monmouth County, New Jersey (Baird, 1986a, 1986b). Marsh (1869, p. 396) described it as comprising a posterior cervical vertebra, an anterior thoracic vertebra, a right splenial (which is actually a left angular; Baird, 1986a), and a portion of the "base of the skull" (basioccipital and basisphenoid). Marsh did not provide any figures in his original account, but Baird (1986a, fig. 1) has since published photographs of this material. In his brief description, Marsh (1869, p. 395) particularly noted the dorsoventral flattening of the centra that gives the intercentral articular surfaces a "very transversely elliptical outline."

Marsh (1870) substituted the generic nomen *Baptosaurus* for *Halisaurus* to avoid confusion with *Halosaurus* Johnson, 1864, a genus of teleostean fish. However, this substitution is not valid under the ICZN rules concerning homonymy. Subsequently, two additional species of *Baptosaurus*, *B. fraternus* Cope, 1869–1870, and *B. onchognathus* Merriam, 1894, were named. The former is probably a subjective junior synonym of *Plioplatecarpus depressus*, and the holotype of the latter was destroyed during World War II (Russell, 1967). The invalid generic nomen *Baptosaurus* remained in general use until the 1950s (McDowell and Bogert, 1954), but Romer (1956) reintroduced the correct name *Halisaurus*.

Russell (1970) referred mosasaurid material from the Mooreville Chalk (formerly Mooreville Member of the Selma Formation) in Alabama to *Halisaurus* on the basis of its distinctive vertebral structure. He also noted the close similarity between the frontals from the Mooreville Chalk and those of "*Clidastes*" *sternbergii* Wiman, 1920, from the Smoky Hill Member of the Niobrara Chalk (Santonian) in Kansas. On this basis, Russell argued that the latter taxon should be referred to *Halisaurus*. He proposed a new combination, *Halisaurus sternbergi* to include both the holotype of "*Clidastes*" *sternbergii* and the material from the Mooreville Chalk. Additional undescribed specimens, similar to but not necessarily conspecific with *H. sternbergi*, were reported by Bell (1997).

Lingham-Soliar (1996) referred *Phosphorosaurus ortliebi*

Dollo, 1889, from the upper Maastrichtian "Craie phosphatée" of Ciply (Belgium), to *Halisaurus*. *P. ortliebi* had previously been synonymized with *Plioplatecarpus* by Russell (1967), presumably on the basis of the very large, anteriorly placed parietal foramen. However, the quadrates of this form differ considerably from those of *Plioplatecarpus* (Lingham-Soliar, 1996, fig. 5). Lingham-Soliar (1996) reassigned *Phosphorosaurus* to *Halisaurus* based on the structure of the frontal, which closely resembles that of *Halisaurus sternbergi* (e.g., Russell, 1970, fig. 165). However, *Phosphorosaurus* differs from *Halisaurus* in several cranial features, and its referral of that taxon is problematical (see below).

Although various isolated bones from Maastrichtian-age strata in the eastern United States have been referred to *Halisaurus platyspondylus* over the years, this taxon "remains one of the rarest and least well-known of the mosasaurs" (Baird, 1986a, p. 72). The new specimen reported here, USNM 442450, comprises, for the first time, numerous associated cranial and postcranial bones of a single individual. It represents a remarkable find because partial skeletons of mosasaurs from the Late Cretaceous marine strata exposed along the Atlantic coast from New Jersey to the Carolinas are rare (Baird, 1986a). USNM 442450 was collected by Dr. Peter M. Kranz (Washington, DC) from mid-Maastrichtian strata of the Severn Formation in a temporary exposure south of Oxon Hill, just north of Kerby Hill Farm along Indian Head Highway (MD-210), in Prince Georges County (Maryland) in 1989. The bones were preserved in a poorly consolidated, glauconitic sandy matrix that was easily removed using a dental pick and soft brush after initial consolidation of the bones with acrylic resin (Acryloid B 72).

**Institutional abbreviations.**—FMNH, The Field Museum, Chicago; NJSM, New Jersey State Museum, Trenton; NMC, Canadian Museum of Nature, Ottawa; USNM, National Museum of Natural History, Washington, DC; YPM, Peabody Museum of Natural History, Yale University; YPM-PU, former Princeton University collection, now housed in the Peabody Museum of Natural History at Yale University.

## SYSTEMATIC PALEONTOLOGY

Family MOSASAURIDAE Gervais, 1853

Genus HALISAURUS Marsh, 1869

*Baptosaurus* MARSH, 1870 (invalid substitute nomen)

*Type species.*—*Halisaurus platyspondylus* Marsh, 1869.

*Referred species.*—*Halisaurus sternbergi* (Wiman, 1920).

*Diagnosis* (modified from Bell [1993, 1997]).—Prefrontals extend far anteriorly, forming about one-half of lateral narial margin; maxilla lacking recurved posterolateral wing; ventral rim of parietal foramen supported by raised boss attenuated posteriorly into triangular ridge; plane of parietal-supratemporal contact oblique, forming an angle of about 55 degrees with the horizontal; quadrate exhibiting “question mark” lateral profile; expanded ventral termination of suprastapedial process articulating with, but not fusing to, a horizontal facet immediately above articular condyle; infrastapedial process apparently absent; quadrate ventral articulation gently domed, convex in any view; coronoid with greatly expanded posterior wing; surangular reaches posteriorly only to midpoint of the glenoid on the dorsal edge of the ramus, leaving the articular to form the bulk of glenoid surface; dorsal margin of articular contribution to glenoid strongly convex; vertebral centra dorsoventrally compressed, cotyles/condyles subrectangular in outline; synapophyses of posterior cervical and anterior trunk vertebrae flare distally and project well below the ventral rim of centrum.

#### HALISAURUS PLATYSPONDYLUS Marsh, 1869

*Diagnosis* (modified from Bell, 1993).—Premaxillary rostrum with large foramina; median keel on dorsal surface of frontals well-developed anteriorly; replacement teeth form in subdental crypts; external nares broadly rounded and wide posteriorly; surangular-articular suture passes posteroventrally from the dorsal rim of the jaw, tracing a broad arc across the lateral surface of the ramus.

#### DESCRIPTION OF *H. PLATYSPONDYLUS*

*Skull.*—USNM 442450 comprises both frontals, parietals, and prefrontals, a partial braincase, left quadrate, both pterygoids, partial mandibular rami, 26 vertebrae, ribs, and other indeterminate fragments of bone.

The coalesced frontals were broken into several pieces during collection, and are incomplete anteriorly. Nevertheless, enough is preserved to establish that they closely resemble the frontals in other specimens referred to *Halisaurus*, such as FMNH PR 195 (Russell, 1970) and YPM-PU 18818 (Baird and Case, 1966). The supraorbital margins of the frontals extend more or less parallel to each other. Ventrally, each frontal is extensively excavated anterolaterally for the reception of the prefrontal and bears a much more shallow, less extensive depression for articulation with the postorbitofrontal posterolaterally. Both surfaces are fluted, indicating firm sutural attachments in life. They are not confluent, indicating that the postorbitofrontal and prefrontal were not in contact with each other, and that each frontal formed a very short segment of the supraorbital border. Although a piece of the posteromedian portion of the frontal “shield” is missing, the edges of a prominent triangular boss are visible on its dorsal surface. Anterior to this boss, the median ridge is represented only by a slight rise on the dorsal surface, which becomes much more pronounced more anteriorly, where it forms a distinct, rounded keel. The dorsal surface of each frontal bears fine radial striations. The transverse frontoparietal suture, which lacks only a short section at the midline, is essentially indistinguishable from that of YPM-PU 18818 (Baird and Case, 1966, fig. 1A).

The right prefrontal is nearly complete, and the left is represented only by its central portion. The horizontal posterior ramus of the prefrontal bears a modest supraorbital process, comparable in size and shape to that in *Platecarpus ictericus* (Russell, 1967, fig. 83). The prefrontal projects far anteriorly to about the midpoint of the external naris. The preserved, broadly rounded rim indicates that the naris was unusually wide posteriorly (Fig. 1). The lateral surface of the vertical lamina of the prefrontal

bears a distinct facet for the reception of the maxilla. The shape of its edge indicates that the maxilla lacked the posterodorsally reflected lappet present in most other mosasaurs (Bell, 1997).

The central portion of the co-ossified parietals forms a raised “table” with an almost flat dorsal surface. The larger, anterior triangular portion of this table is set off from a smaller, posterior subrectangular portion by a constriction. Anteriorly, it bears a large pineal foramen that is separated from the frontoparietal suture by a distance about equal to its diameter. The foramen passes posteroventrally into the cranial cavity at an angle of about 15 degrees to the vertical plane. Ventrally, the rim of the foramen is supported by a raised boss that tapers posteriorly into a long, prominent triangular tongue of bone separated from the remainder of the ventral surface by deep lateral furrows (Fig. 2). In other mosasaurs in which the structure of this area is known (such as *Plioplatecarpus* and *Platecarpus*), the ventral margin of the foramen is not conspicuously raised, and its posterior margin turns posteriorly into a triangular trough on the ventral surface of the parietal. The bladelike supratemporal rami are oriented approximately vertically as they diverge from the central plate of the parietal. However, in contrast to other known mosasaurs, in which the rami have assumed an approximately horizontal orientation posteriorly, the rami of USNM 442450 form an angle of about 55 degrees with the horizontal plane at their posterior ends. The thickened posterior end of each supratemporal ramus bears a ventral facet for contact with the paroccipital process. Laterally, it bears a long, horizontal, triangular facet for articulation with the supratemporal. Postmortem compression has displaced the anterior process of the supratemporal to expose a relatively smooth surface that hints at the possibility of some anteroposterior movement between the suspensorial ramus and supratemporal.

The right pterygoid (Fig. 3), which lacks only the distal end of its quadratic process, and fragments of the left pterygoid are preserved. In overall form, the pterygoid resembles that of *Platecarpus*. The quadratic process expands posteriorly to form a vertical blade. A raised ridge on the palatal ramus bears nine teeth, the anterior and posterior of which are smaller than the more central teeth, which are similar in size to the marginal teeth.

The complete left quadrate (Fig. 4) closely resembles that of *Halisaurus sternbergi* (Wiman, 1920, fig. 5) and is similar to that of *Phosphorosaurus ortliebi* (Dollo, 1889; Lingham-Soliar, 1996), although neither quadrate is complete in the holotype of the latter. In contrast with other mosasaurs, where the circular or oval tympanic rim is uniformly curved in lateral view, the rim in USNM 442450 is slightly concave anteriorly, but abruptly turns posteriorly in a tight arc to join the nearly straight dorsal margin. This results in a profile resembling a question mark (Bell, 1997), similar to that in *Halisaurus sternbergi*. The expanded ventral termination of the large suprastapedial process articulates with, but apparently is not fused to, a transversely oval, horizontal shelf immediately above the distal articular condyle. A thick flange bearing coarse fluting projects posteromedially from the condylar base posterior to this shelf; it may be homologous to the infrastapedial process in other mosasaurs, but its orientation relative to the suprastapedial process makes this doubtful.

Only the posterior portion of the braincase (Fig. 5) is preserved. The occipital condyle resembles those of *Platecarpus* and *Plioplatecarpus* in outline, and is not compressed dorsoventrally. The prootic bears a well-developed otosphenoidal crest. In contrast to many mosasaurs, but as in derived Mosasaurinae (*Mosasaurus*, *Plesiotylosaurus*, *Plotosaurus*, and *Prognathodon*; Russell, 1967), the supraoccipital is firmly attached to the parietals.

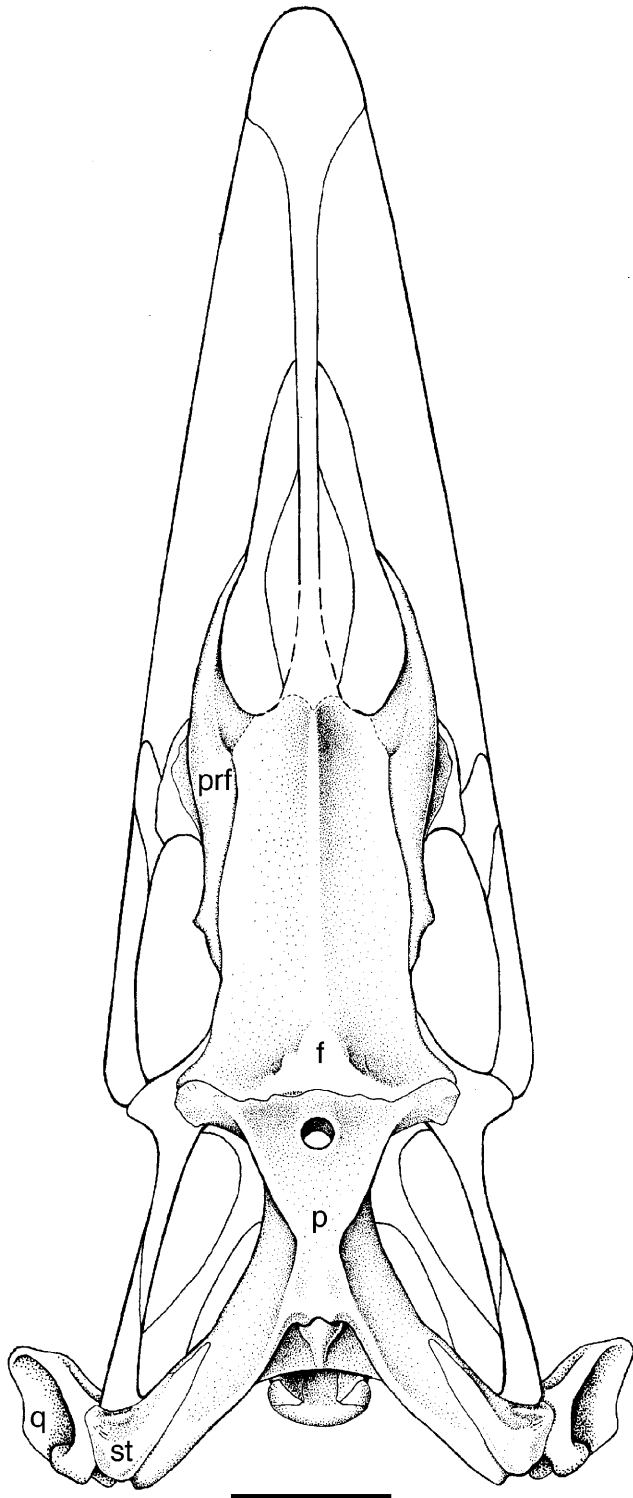


FIGURE 1—*Halisaurus platyspondylus*, USNM 442450, reconstruction of skull in dorsal view. Unshaded portions based on the holotype of *Halisaurus sternbergii* (Wiman, 1920). Abbreviations used in the figures: an, angular; ar-pra, articular-prearticular; bo, basioccipital; bp.p, basiptyergoid process; ec.p, ectopterygoid process; eo, exoccipital; f, frontal; fa.d, facet for dentary on lateral surface of splenial; f-p.su, frontoparietal suture; gl.f, glenoid facet; op, opisthotic; ot.cr, otosphenoidal crest; p, parietal; prf, prefrontal; q, quadrate; q.p, quadrate process; sa, surangular; so, supraoccipital; sp, splenial; s.p, suprastapedial process; st, supratemporal; t.c, tympanic crest. Scale bar equals 5 cm.

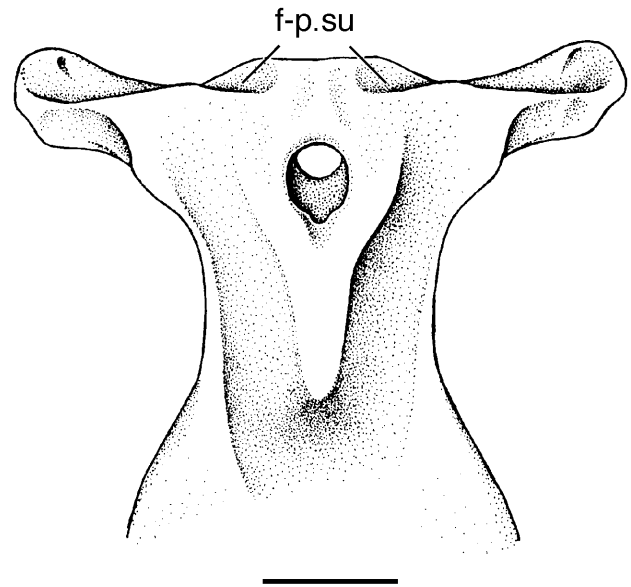


FIGURE 2—*Halisaurus platyspondylus*, USNM 442450, ventral view of parietals (slightly restored) showing the raised boss surrounding and tongue-like thickening behind the pineal foramen. Scale bar equals 2 cm.

Neither lower jaw is complete, but there is enough complementary information from both mandibular rami to permit reconstruction of most constituent bones (Fig. 6). Only the dentary and coronoid are not preserved on either side. Although the glenoid surface is formed by both the articular and the surangular, *Halisaurus* is unusual among mosasauroids in that the surangular reaches only to the midpoint of the glenoid on the dorsal edge of the ramus (see Bell 1997, character 79); hence the contribution of the surangular is considerably smaller than that of the articular. This may represent a plesiomorphic condition. However, unlike in other halisaurines, where the suture drops straight ventrally from this point and then curves anteriorly (Bell, 1993) the surangular-articular suture of USNM 442450 passes ventroposteriorly, tracing a broad arc as it turns ventrally and finally anteriorly. At the posterolateral end of the glenoid facet, the dorsal edge of the articular rises to form a stout conical process. The thickened retroarticular process is squared off posteriorly and is strongly inflected, assuming a nearly horizontal orientation. The form of the joint between the articular and splenial is virtually identical to that figured for *Platycarpus* (Russell, 1967, fig. 28).

**Vertebrae.**—Although the atlas and axis are missing, the remaining cervical vertebrae are present and well preserved (Fig. 7). Two anterior thoracic vertebrae, one bearing a prominent midventral tubercle, probably represent T1 and T2 or T3. Based on comparisons with a complete presacral vertebral column of *Plioplatecarpus* (NMC 11035; Holmes, 1996), the remaining 14 dorsal vertebrae form a more or less continuous series from approximately T10 to T23, the latter probably at or close to the sacrum (Table 1), although a shift anterior or posterior by a few segments would not be incompatible with the morphology observed. The anterior seven vertebrae of this series are generally well preserved and complete, but the rest lack the neural arches and transverse processes. Only a few caudal vertebrae are preserved, comprising two pygals, two anterior caudals, and one posterior caudal.

Zygosphenes and zygantra are absent. The synapophyses are unusually large in the anterior portion of the vertebral column,



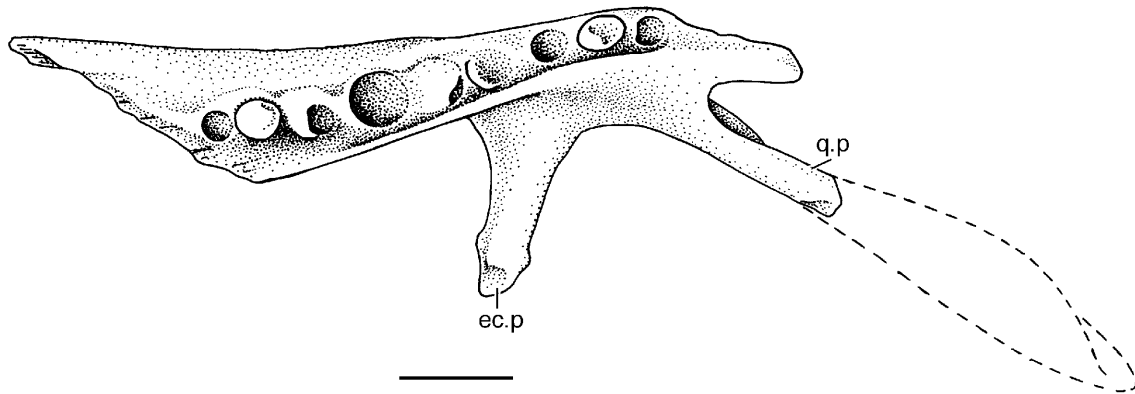


FIGURE 3—*Halisaurus platyspondylus*, USNM 442450, right pterygoid in ventral view. Scale bar equals 2 cm.

and flare distally to project well below the ventral rim of the centrum in the posterior cervical and anterior thoracic region. The diagnostic dorsoventrally compressed, subrectangular outline of the condyle is apparent throughout the preserved column, although it is most pronounced anteriorly (see Table 1). For example, the ratio of condylar width to height averages 0.54 in the preserved cervical vertebrae (compared with 0.77 for the equivalent series of vertebrae in *Plioplatecarpus*, NMC 11035), whereas this ratio is 0.62 (0.79 in *Plioplatecarpus*) in the mid-trunk vertebrae (T10–T13). In the posterior trunk vertebrae (T18–T21), it increases to 0.74 (0.88 in *Plioplatecarpus*). Dorsoventral compression of the vertebral centrum, rather than a circular condylar outline, is a common condition among varanoid lizards, and probably represents the plesiomorphic condition for this group. However, the width/height ratio for the condyle generally does not exceed 4:3 in the latter (Bell, 1997), and the ratio of 2:1 in *Halisaurus* may represent a derived condition.

On the thoracic vertebrae (Fig. 8), the prezygapophyses are connected to the synapophyses by a thick web of bone that becomes more pronounced posteriorly, and, on mid-thoracic vertebrae, bears a sharp ridge along its curved anterolateral border. A similar feature is present in *Plioplatecarpus primaevus* (R. B. H., unpublished data), but the ridge is not as pronounced.

Neural and hemal arches are not preserved on any of the caudal vertebrae. However, enough of the bases of the hemal

arches is visible to indicate that, unlike in rasselosaurines (*Tylosaurus* + *plioplatecarpines*; Bell, 1997) and varanoids generally, the arches were fused to the centrum.

#### DISCUSSION

*Skull structure and phylogenetic relationships.*—Various authors (Russell, 1967; Carroll and deBraga, 1992; deBraga and Carroll, 1993; Bell, 1993) have argued that the skull of *Halisaurus* is more primitive than that of any other known mosasaurid, and, in several important features, is more similar to that of varanoid lizards. According to deBraga and Carroll (1993), the postorbitofrontal of *Halisaurus*, as in varanoid lizards, is firmly attached to the parietal and only loosely connected to the frontal. The vertical supratemporal ramus of the parietal is firmly sutured to the supratemporal laterally and to the paroccipital process medially. The supratemporal arcade, comprising the supratemporal, squamosal, and postorbitofrontal, forms a rigid structural link between the suspensorium and parietal. Because the braincase is firmly attached to the ventral surface of the parietal, the parietal-braincase-temporal arcade can be considered a single structural unit. deBraga and Carroll (1993) argued that movement at the frontoparietal suture was possible when forces transferred from the pterygoid to the palatine and maxilla resulted in elevation or depression of the snout relative to the posterior part of the skull. The quadrate, which is firmly attached

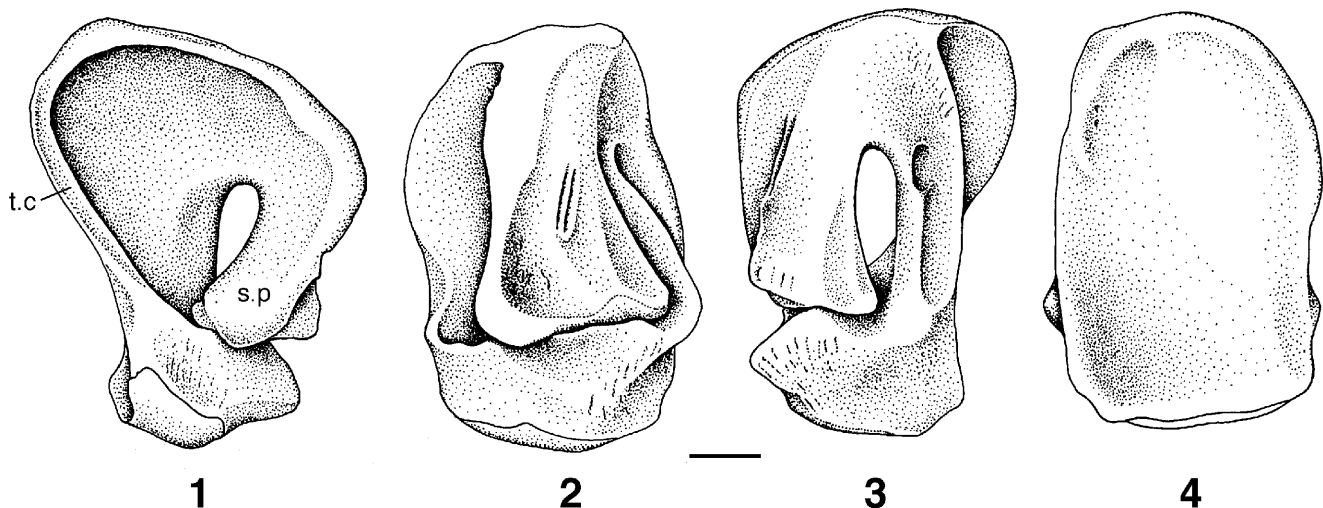


FIGURE 4—*Halisaurus platyspondylus*, USNM 442450, left quadrate in 1, lateral, 2, posterior, 3, medial, and 4, anterior views. Scale bar equals 1 cm.

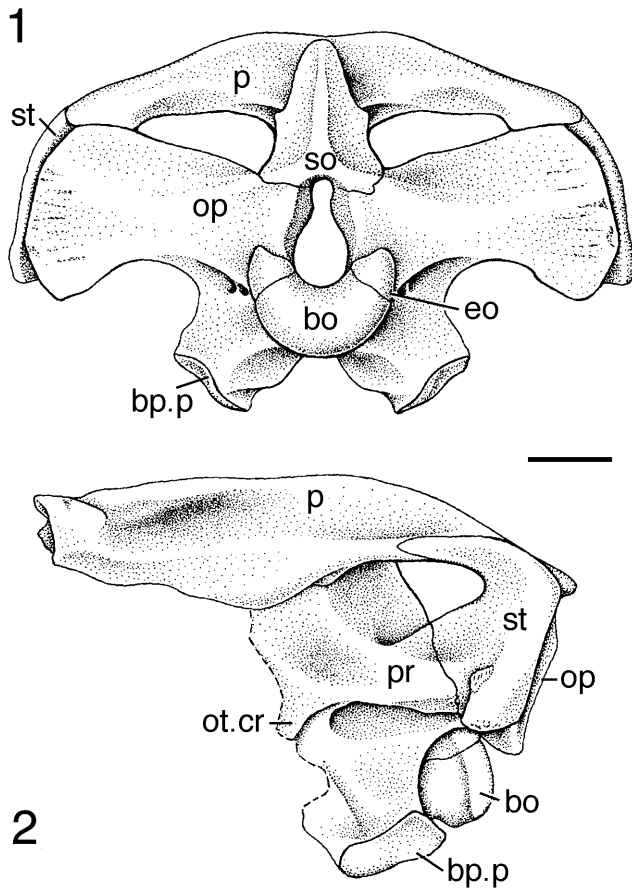


FIGURE 5—*Halisaurus platyspondylus*, USNM 442450. Reconstructed braincase in 1, occipital and 2, left lateral views. Scale bar equals 2 cm.

to the pterygoid, could have moved anteroposteriorly about its dorsal point of articulation, producing protraction and retraction of the jaws as in extant *Varanus* (Frazzetta, 1962). In mosasaurs other than *Halisaurus*, the postorbitofrontal primarily attached to the frontal rather than the parietal. The short supratemporal ramus of the parietal has a horizontal orientation and forms an unfused, overlapping contact with the supratemporal. Unlike the condition in varanoid lizards and *Halisaurus*, the occipital unit of the braincase could have rotated about an anterior transverse axis as a consequence of its loose dorsal contacts with the ventral surface of the conjoined parietals and lateral contacts with the supratemporal processes of the parietal through their unfused contacts with the supratemporals. This movement could have been transmitted through the temporal arcade to the frontal, producing elevation or depression of the snout. A significant consequence of this unique mechanical linkage is the effective decoupling of the quadrate, and therefore jaw protraction/retraction, from the mesokinetic system (Russell, 1964).

The new specimen demonstrates that, contrary to previous claims, the skull of *Halisaurus* does not exhibit a structure suggestive of kinesis like that hypothesized for varanoids, but rather shows a mosaic of varanoid and mosasauroid features of uncertain biomechanical significance. *Halisaurus* resembles more derived mosasaurs in the postorbitofrontal forming its primary contact with the frontal rather than with the parietal, and in the presence of a short supratemporal ramus of the parietal that forms a loose articulation with the supratemporal. However, the orientation of the supratemporal process is neither horizontal (as in more derived mosasaurs) nor vertical (as in varanoids), but is oblique, with the plane of its dorsolateral surface forming an angle of about 55 degrees with the horizontal. Unlike the condition in most mosasaurs, the occipital unit of the braincase is firmly attached to the ventral surface of the parietal, precluding any dorsoventral movement. Some of these features appear to be plesiomorphic, and, if considered together, the character complex could be interpreted as representing a stage transitional between varanoids and more derived mosasauroids, although it is incompatible with either hypothesized kinetic system.

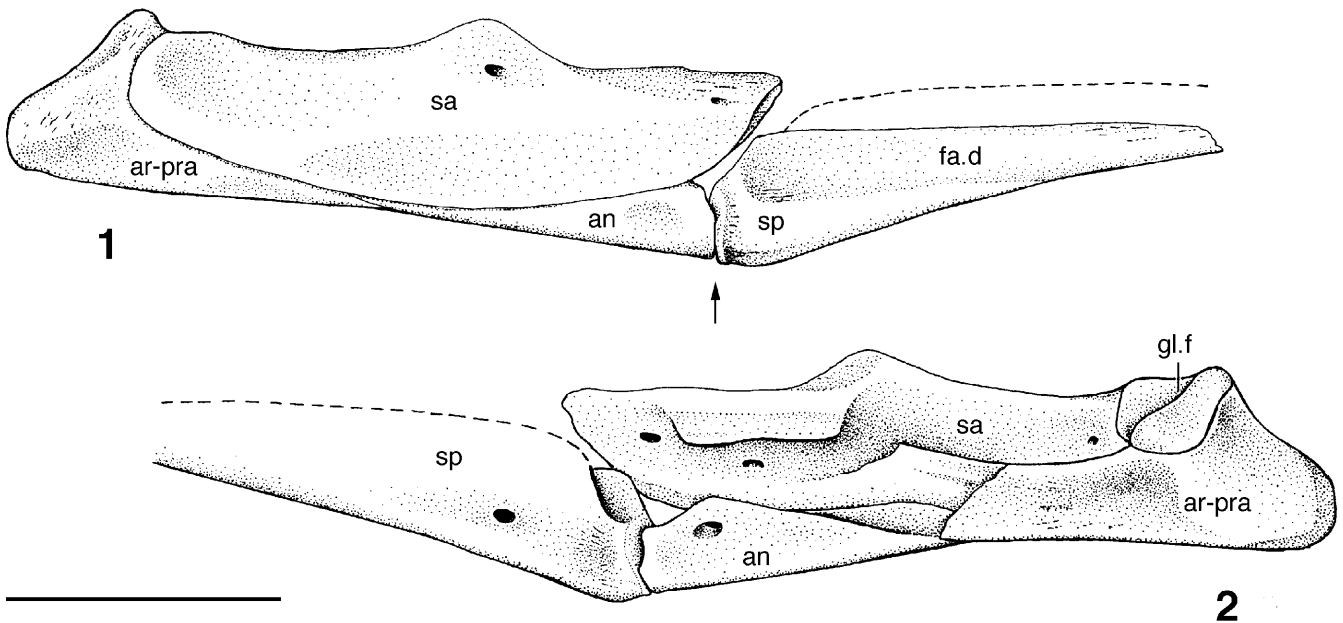


FIGURE 6—*Halisaurus platyspondylus*, USNM 442450. Partially reconstructed right mandibular ramus in 1, lateral and 2, medial views. Arrow denotes intramandibular joint. Scale bar equals 5 cm.

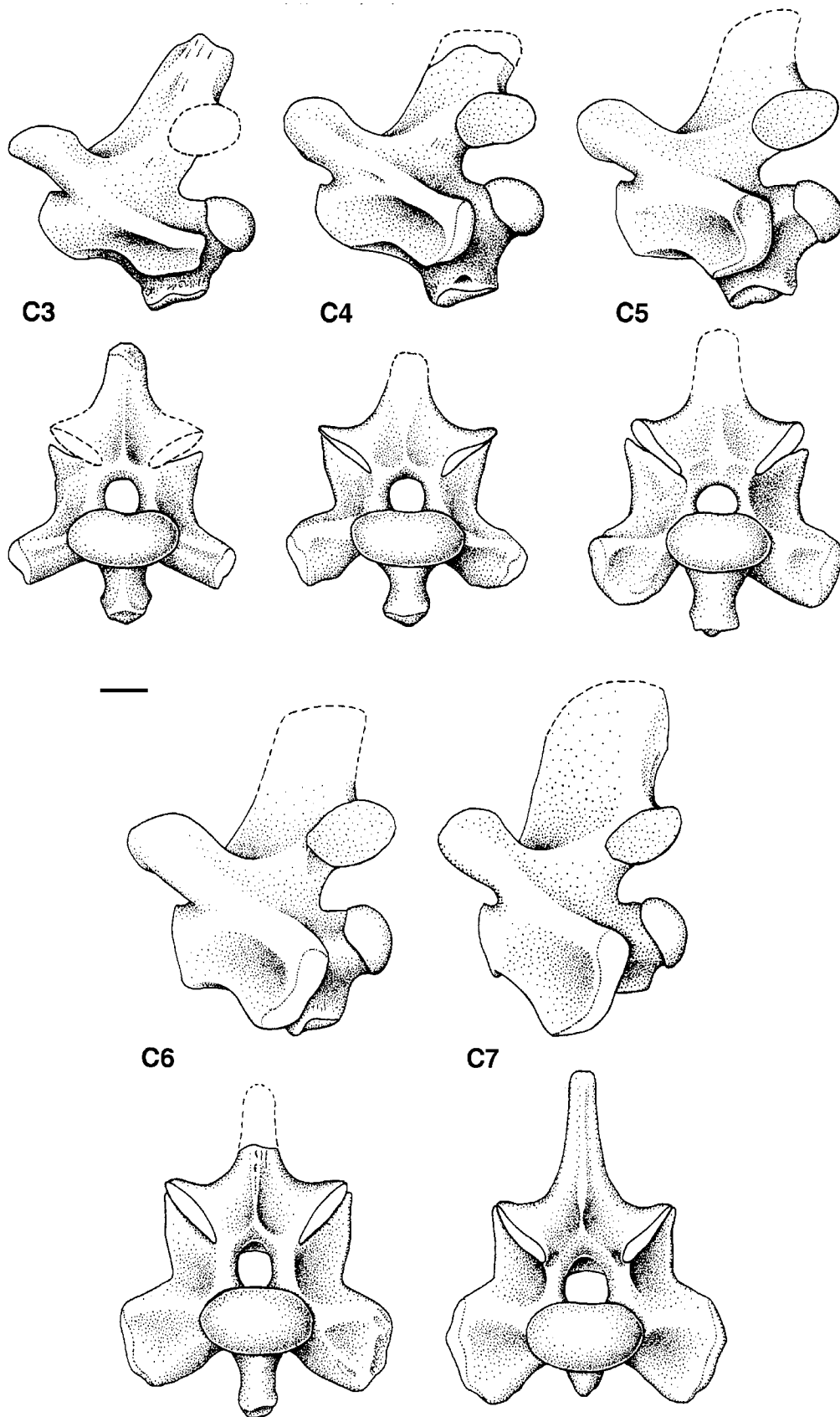


FIGURE 7—*Halisaurus platyspondylus*, USNM 442450. Cervical vertebrae (C3-7) in left lateral view (top) and posterior view (bottom). Scale bar equals 1 cm.

TABLE 1—Measurements (in mm) of vertebrae of *Halisaurus platyspondylus*, USNM 442450. Centrum height and width measured at condyle.

Vertebra	Centrum length	Centrum width	Centrum height	Centrum height/width
C3	52	27	13.5	0.50
C4	55	29.5	13.5	0.46
C5	55.5	27	15	0.56
C6	54	28	16	0.57
C7	52	29	17	0.59
T1	51.5	29.5	17.5	0.59
T10	48	30	18	0.60
T11	47.5	31	19.5	0.63
T12	48	30	19.5	0.65
T13	47	33	20	0.61
T14	49	32	21	0.66
T15	50	32.5	22	0.68
T16	51	33	23	0.70
T17	53	33.5	26	0.78
T18	50.5+	34.5	26	0.75
T19	48+	33.5	26	0.78
T20	51	34	24	0.71
T21	50	34	24	0.71
T22	54	—	—	—
T23	53	33+	26.5	—
ant. pygal	42+	31	27	0.87
post. pygal	36	33	27	0.82
ant. caudal	33	30	29	0.97
ant. caudal	29	28	25	0.89
post. caudal	20.5	20	16	0.80

*Classification of Halisaurus.*—Bell (1993), accepting the identification of H. D. Sues, referred USNM 442450 to *Halisaurus*, along with specimens NJSM 12146 and 12259. Vertebral structure alone is sufficient to confirm this identification. Since no differences between USNM 442450 and the fragmentary type of *H. platyspondylus* are apparent, the specimen is assigned to this species. Other isolated halisaurine bones from the Upper Cretaceous of Maryland and New Jersey have been assigned to *H. platyspondylus* (Baird, 1986b; Baird and Case, 1966; Bell, 1993). Specimens identified from other localities (Bell, 1993; Caldwell and Bell, 1995; Russell, 1970; Wiman, 1920) are excluded here from consideration pending further study.

Since the new find is more complete than the holotype of *Halisaurus platyspondylus*, it permits evaluation of other mosasauroid taxa that have been referred to *Halisaurus*. Numerous similarities between USNM 442450 and "*Clidastes*" *sternbergii* Wiman, 1920, particularly in the structure of the parietal, the position of the parietal foramen, and the structure of the quadrate support referral of the latter to *Halisaurus* (Russell, 1967, 1970). The reassignment of *Phosphorosaurus ortliebi* Dollo, 1889 to *Halisaurus* by Lingham-Soliar (1996) is questionable. Although the frontals are similar in the two taxa, especially in the absence of supraorbital emarginations (Lingham-Soliar, 1996), *Halisaurus* bears a median frontal keel only anteriorly, rather than a median crest that runs prominently the full length of the frontal as in *Phosphorosaurus*. Unlike USNM 442450 and *Halisaurus sternbergii*, *Phosphorosaurus* has a much larger pineal foramen located at the frontoparietal suture. However, in one specimen of *Halisaurus* cf. *H. sternbergii* (USNM 3777; Bell, 1993), the foramen is situated very close to this suture, but the same character-state occurs convergently in several other mosasauroid taxa (see Bell, 1993). Variation in size and relative position of the pineal foramen is not unexpected because the foramen represents a remnant of the large median fontanelle between the frontals and parietals in early developmental stages of extant lepidosaurs (Rieppel, 1992) and would not, in its self, preclude close relationship between *Halisaurus* and *Phosphorosaurus*. The incomplete quadrates of the holotype of *P. ortliebi* (Dollo, 1889, pl. 10, figs. 10, 11; Lingham-Soliar, 1996, fig. 5) closely resemble,

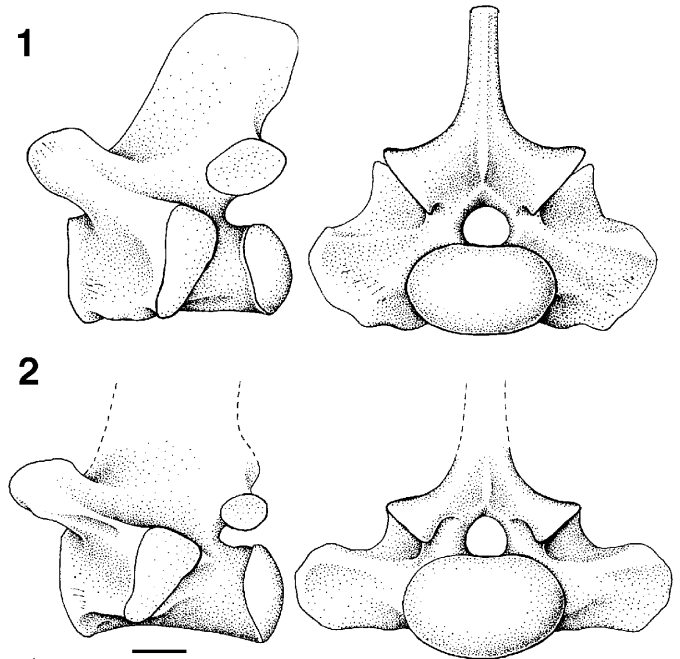


FIGURE 8—*Halisaurus platyspondylus*, USNM 442450. Dorsal vertebrae in left lateral view (left) and posterior view (right). 1, Anterior dorsal vertebra (T1 or T2). 2, mid-dorsal vertebra (probably T12). Scale bar equals 1 cm.

as far as preserved, those of USNM 442450 and *Halisaurus sternbergii* (Wiman, 1920, fig. 5). However, as reconstructed by Lingham-Soliar (1996, fig. 1), the quadrate more closely resembles that of *Prognathodon* (e.g., Dollo, 1889, pl. 10, figs. 8, 9). The parietals of *Phosphorosaurus* differ from those of USNM 442450 (see above) in the presence of a deep, elliptical fossa on the ventral surface. Additional material, especially vertebrae, is needed to resolve the status of *Phosphorosaurus ortliebi*, and we retain this taxon as distinct at the present time.

The skull of USNM 442450 shows some arguably plesiomorphic characters, but its overall structure, comprising a mosaic of mosasaurid and varanoid features, represents an intermediate pattern of uncertain phylogenetic significance. Although the pronounced dorsoventral compression of the vertebral centra is possibly plesiomorphic, it is more pronounced than in any of the hypothesized outgroups (Bell, 1993, 1997), and may well represent an autapomorphic condition.

*Type.*—Holotype, YPM 444. New Egypt Formation (Upper Cretaceous: upper Maastrichtian), pit-mine of the Cream Ridge Marl Company near Hornerstown, Monmouth Co., New Jersey.

*Occurrence.*—As noted by Caldwell and Bell (1995), *Halisaurus* had a wide stratigraphic and geographic distribution. The holotype of *H. platyspondylus* (YPM 444) was collected from the Upper Egypt Formation (upper Maastrichtian) of New Jersey, but specimens referable to *Halisaurus* have also been reported from strata of roughly equivalent age in Belgium (Lingham-Soliar, 1994), Niger (Lingham-Soliar, 1991), the Severn Formation of Maryland (Baird and Case, 1966 [as "Navesink"]; Baird, 1986b), the Navesink Formation (lower Maastrichtian) of New Jersey (Bukowski, 1983), the Mount Laurel Formation (lower Maastrichtian) of Delaware (Baird, 1986b), the Merchantville Formation (lower Campanian) of Delaware (Baird, 1986b), the Mooreville Chalk (lower Campanian) of Alabama (Russell, 1970), the lower to middle Campanian of Texas (Caldwell and Bell, 1995), the Niobrara Formation (Santonian) of



Kansas (Baird, 1986b; Merriam, 1894; Russell, 1970; Wiman, 1920), and the Santonian of east-central Peru (Caldwell and Bell, 1995). Although some of these identifications are based only on isolated vertebrae (e.g., Baird, 1986a, 1986b; Caldwell and Bell, 1995), more extensive skeletal remains are known from a number of localities ranging in age from the Santonian (Russell, 1970) to the late Maastrichtian. If correctly identified in each instance, these records indicate an unusually long stratigraphic range for *Halisaurus*, possibly appearing soon after the first reported occurrence of the Mosasauridae in the Turonian of Britain (Woodward, 1905) and persisting to the late Maastrichtian. Other known mosasaurid genera generally exhibit more restricted stratigraphic ranges (Bell, 1993, 1997).

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## REFERENCES

- BAIRD, D. 1986a. *Halisaurus* and *Prognathodon*, two uncommon mosasaurids from the Upper Cretaceous of New Jersey. *The Mosasaur*, 3: 37–45.
- . 1986b. Upper Cretaceous reptiles from the Severn Formation of Maryland. *The Mosasaur*, 3:63–85.
- , AND G. R. CASE. 1966. Rare marine reptiles from the Cretaceous of New Jersey. *Journal of Paleontology*, 40:1211–1215.
- BELL, G. L., JR. 1993. A phylogenetic revision of Mosasauroida (Squamata). Unpublished Ph.D. dissertation, University of Texas at Austin, Austin, 293 p.
- . 1997. A phylogenetic revision of North American and Adriatic Mosasauroida, p. 293–332. In J. M. Callaway and E. L. Nicholls (eds.), *Ancient Marine Reptiles*. Academic Press, San Diego.
- BUKOWSKI, F. 1983. *Halisaurus platyspondylus*—the third reported occurrence of this mosasaur in New Jersey. *The Mosasaur*, 1:119–121.
- CALDWELL, M. W., AND G. L. BELL, JR. 1995. *Halisaurus* sp. (Mosasauridae) from the Upper Cretaceous (?Santonian) of east-central Peru, and the taxonomic utility of mosasaur cervical vertebrae. *Journal of Vertebrate Paleontology*, 15:532–544.
- CARROLL, R. L., AND M. DEBRAGA. 1992. Aigialosaurs: Mid-Cretaceous varanoid lizards. *Journal of Vertebrate Paleontology*, 12:66–86.
- COPE, E. D. 1869–1870. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. *Transactions of the American Philosophical Society*, N. S., 14:1–252.
- DEBRAGA, M., AND R. L. CARROLL. 1993. The origin of mosasaurids as a model of macroevolutionary patterns and processes. *Evolutionary Biology*, 27:245–322.
- DOLLO, L. 1889. Première note sur les mosasauriens de Mesvin. *Bulletin de la Société Belge de Géologie, de Paléontologie, et d'Hydrologie*, 3:271–304.
- FRAZETTA, T. H. 1962. A functional consideration of cranial kinesis in lizards. *Journal of Morphology*, 111:287–319.
- GERVAIS, P. 1853. Observations relatives aux reptiles fossiles de France. *Comptes Rendus de l'Académie des Sciences Paris*, 36:374–377, 470–474.
- HOLMES, R. 1996. *Plioplatecarpus primaevus* (Mosasauridae) from the Bearpaw Formation (Campanian, Upper Cretaceous) of the Western Interior Seaway. *Journal of Vertebrate Paleontology*, 16:673–687.
- JOHNSON, J. Y. 1864. Descriptions of three new genera of marine fishes obtained at Madeira. *Proceedings of the Zoological Society of London*, 1863:403–410.
- LINGHAM-SOLIAR, T. 1991. Mosasaurids from the Upper Cretaceous of Niger. *Palaeontology*, 34:653–670.
- . 1994. The mosasaur *Plioplatecarpus* (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 64:177–211.
- . 1996. The first description of *Halisaurus* (Reptilia Mosasauridae) from Europe, from the Upper Cretaceous of Belgium. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 66:129–136.
- MARSH, O. C. 1869. Notice of some new mosasauroid reptiles from the green sand of New Jersey. *American Journal of Science*, ser. 2, 48: 392–397.
- . 1870. [Remarks on *Hadrosaurus minor*, *Mosasaurus crassidens*, *Liodon laticaudus*, *Baptosaurus*, and *Rhinoceros matutinus*.] *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1870: 2–3.
- MCDOWELL, S. B., JR., AND C. M. BOGERT. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. *Bulletin of the American Museum of Natural History*, 105:1–142.
- MERRIAM, J. C. 1894. Ueber die Pythonomorphen der Kansas-Kreide. *Palaeontographica*, 41:1–39.
- RIEPEL, O. 1992. The skull in a hatchling of *Sphenodon punctatus*. *Journal of Herpetology*, 26:80–84.
- ROMER, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago, 772 p.
- RUSSELL, D. A. 1964. Intracranial mobility in mosasaurids. *Postilla*, 86: 1–19.
- . 1967. Systematics and morphology of American mosasaurids (Reptilia, Sauria). *Bulletin of the Peabody Museum of Natural History, Yale University*, 23:1–241.
- . 1970. The vertebrate fauna of the Selma Formation of Alabama, Pt. VII, The Mosasaurids. *Fieldiana: Geology Memoirs*, 3:363–380.
- WIMAN, C. 1920. Some reptiles from the Niobrara Group in Kansas. *Bulletin of the Geological Institution of the University of Upsala*, 18: 11–18.
- WOODWARD, A. S. 1905. Note on some portions of mosasaurian jaws obtained by Mr. G. E. Dibley from the Middle Chalk of Cuxton, Kent. *Proceedings of the Geologists' Association London*, 19:185–187.

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