

## The oldest articulated mosasaurian remains (earliest Turonian) from Germany

### Die ältesten artikulierten Mosasaurier-Überreste (frühestes Turonium) aus Deutschland

#### Schatzfund\*

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#### Abstract

The Turonian was a seminal time in the evolution of Mosasauria, a clade of active lizards that came to dominate Late Cretaceous oceans until their demise at the Cretaceous–Palaeogene boundary. It saw in that time the mosasauroids increase in body size, become at last fully aquatic, and disperse throughout much of the world, while their sister-group, the long-necked dolichosaurs, largely went extinct. Yet a paucity of fossils from this crucial time obscures the beginning of their radiation. On this background we report the discovery of the oldest articulated mosasaurian remains from continental western Europe, namely from the uppermost Cenomanian–lowermost Turonian Hesseltal Formation near Halle/Westfalen, Germany. We also review the taxonomic allocation of dolichosaur remains – *Coniasaurus crassidens* and *Dolichosaurus longicollis* – previously described from a slightly older level at the same locality, the DIMAC quarry. The new specimen derives from the lowermost Turonian *Watinoceras* bed, comprises an articulated tail and is referred to Mosasauroida indet. Vertebral proportions suggest some adaptation away from the primitive anguilliform mode of propulsion and toward greater capacity for sustained swimming. Deductions based on degree of articulation and palaeoenvironment suggest that the animal died far out at sea, which is consistent with improved swimming abilities as well. In contrast, the previously described dolichosaur material comprises exclusively isolated bones or bone fragments, which may have been transported some distance to the site during a phase when the sea-level was lower. The new find highlights the potential of the Hesseltal Formation generally and especially the DIMAC quarry to produce important vertebrate fossils that may throw further light on early mosasaurian evolution.

**Key words:** Cenomanian–Turonian, Hesseltal Formation, DIMAC quarry, Mosasauroida, *Coniasaurus*, *Dolichosaurus*, swimming ability

**Schlüsselwörter:** Cenomanium–Turonium, Hesseltal-Formation, Steinbruch DIMAC, Mosasauroida, *Coniasaurus*, *Dolichosaurus*, Schwimmanpassung

\*Nach dem Denkmalschutzgesetz NRW § 17 "Schatzregal" gehen Fossilien von besonderer wissenschaftlicher Bedeutung bei ihrer Entdeckung in das Eigentum des Landes NRW über. Werden Fossilien entdeckt, die unter

diese Kategorie fallen könnten, muss umgehend die zuständige Untere Denkmalbehörde (Gemeinde) oder das Referat Paläontologie des LWL-Museums für Naturkunde, Münster informiert werden.

### Kurzfassung

Das Turonium war eine entscheidende Zeit in der Evolution der Mosasauria, einer Gruppe von aktiven Echsen, die in der späten Kreide die Ozeane dominierten, bis sie schließlich an der Kreide-Paläogen-Grenze verschwanden. Es scheint, als hätten die Mosasaurier in dieser Zeit an Körpergröße zugenommen und als wären sie schließlich vollständig aquatisch geworden, während ihre Schwestergruppe, die langhalsigen Dolichosaurier, weitgehend ausstarben. Der Mangel an Fossilien aus dieser Zeit verschleiern allerdings den Beginn ihrer Radiation. Vor diesem Hintergrund berichten wir über die Entdeckung des ältesten, artikulierten Mosasaurier-Materials aus dem kontinentalen Bereich Westeuropas, hier aus dem obersten Cenomanium–untersten Turonium der Hesseltal-Formation bei Halle/Westfalen. Weiterhin wird die taxonomische Zuordnung von Dolichosaurier-Material – *Coniasaurus crassidens* und *Dolichosaurus longicollis* – aus etwas älteren Ablagerungen der gleichen Fundstelle, des Steinbruchs DIMAC, überprüft. Das vorgestellte Stück stammt aus der *Watinoceras*-Schicht im untersten Turonium, umfasst einen artikulierten Schwanz und wird als Mosasauroida indet. eingeordnet. Die Proportionen der Wirbel zeigen Anpassungen, die über die primitive anguilliforme Undulation als Vortrieb hinausgehen und vielmehr eine erweiterte Fähigkeit zu ausdauerndem Schwimmen anzeigen. Die Artikulation des Stückes und die Paläoumgebung erlauben die Schlussfolgerung, dass das Tier auf offener See starb, was gleichermaßen eine verbesserte Schwimmfähigkeit voraussetzt. Im Gegensatz dazu umfasst das bisher beschriebene Dolichosaurier-Material nur isolierte Knochen oder lediglich Fragmente, die zu einer Zeit, als der Meeresspiegel niedriger war, vermutlich über eine gewisse Distanz transportiert worden sind, bevor sie abgelagert wurden. Der neue Fund zeigt, dass die Hesseltal-Formation, vor allem im Steinbruch DIMAC, das Potential hat, weitere wichtige Wirbeltierfossilien zu liefern und damit mehr Licht auf die frühe Evolution der Mosasaurier zu werfen.

### Introduction

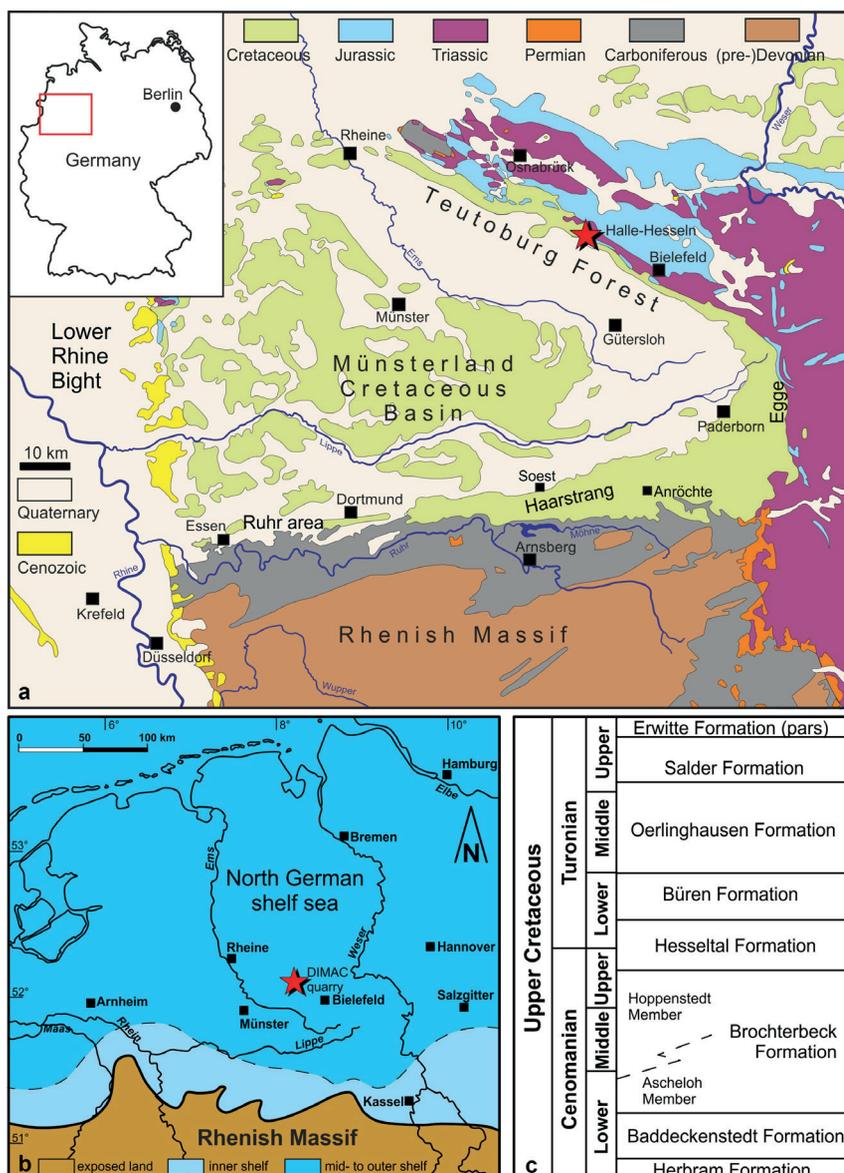
Mosasauria Marsh, 1880 is a clade of medium- to large-bodied semiaquatic or aquatic lizards whose known evolutionary history is confined to the Late Cretaceous (e.g., Williston 1898; Russell 1967; Polcyn et al. 1999; see also Evans et al. 2006). The earliest and most primitive representatives of the clade are less than 1.5 m in total length. They include Cenomanian species traditionally assigned to Dolichosauridae (e.g., Nopcsa 1908; Romer 1956; Carroll 1988) as well as basal mosasauroids – the latter traditionally assigned to Aigialosauridae – that might be related to different lineages of Mosasauridae (Bell & Polcyn 2005; Polcyn & Bell 2005; see also

Madzia & Cau 2017; Simões et al. 2017b). Most of these primitive representatives are found in Cenomanian strata of the Western Interior Seaway and adjacent regions of North America (Bell et al. 1982; VonLoh & Bell 1998), the English Chalk (Owen 1851), Germany (Diedrich 1997, 1999), Slovenia (Meyer 1860; Seeley 1881; Kornhuber 1893; Caldwell & Palci 2010), Croatia (Kornhuber 1873, 1901; Gorjanović-Kramberger 1892), and the Levant (dal Sasso & Pinna 1997; dal Sasso & Renesto 1999; Polcyn et al. 1999, 2003). A further dolichosaur specimen, from Kazakhstan, may be Cenomanian or Turonian in age (Averianov 2001); a Cenomanian specimen from the Saxonian Cretaceous Basin of Germany, initially referred to a dolichosaur (Geinitz 1871–1875), has not been confirmed (Sachs et al. 2017). Only the taxon *Coniasaurus* has been reported from the Cenomanian outside of the central Tethys and the European epicontinental shelf seas (Bardet et al. 2008), namely from the Western Interior Seaway and the Texas Gulf Coast (Bell et al. 1982; Liggett et al. 2005; Shimada et al. 2006; Cumbaa et al. 2010; Nagrodski et al. 2012). Many of these species are considered to have been semiaquatic or at best shallow-water dwellers (e.g., Jacobs et al. 2005; Ifrim et al. 2008).

A dramatic change took place during the approximately 4 million years of the succeeding Turonian. Many dolichosaurs went extinct, although there are reports, almost exclusively of fragmentary vertebrae, from younger horizons (Rage 1989; Shimada & Bell 2006; Shimada et al. 2007; Shimada & Ystesund 2007; Scanlon & Hocknull 2008; Paparella et al. 2018), while the geographic range of mosasauroids expanded substantially (Bardet et al. 2008; Jacobs et al. 2009; Polcyn et al. 2014). Primitive and more advanced mosasauroids are documented in the Turonian of North America (Bell & VonLoh 1998; Bell & Polcyn 2005; Polcyn & Bell 2005; Polcyn et al. 2008; Smith & Buchy 2008; Buchy & Smith 2011; Schumacher 2011), South America (Páramo-Fonseca 2000), and south-central Africa (Lingham-Soliar 1994) and are further found in a variety of Tethyan or European sites: England (Street & Caldwell 2014), Italy (Palci et al. 2013), Czech Republic (Zázvorka 1965; Ekrt et al. 2001; Wiese et al. 2004; Kear et al. 2014), and North Africa (Bardet et al. 2003). It is not yet clear how the Cenomanian occurrence of a mosasaurid reported by Grigor'ev et al. (2009) from south-western Russia fits into this story.

Biogeographic and ecomorphological expansion of mosasauroids continued into succeeding ages (Lindgren 2004; Polcyn et al. 2008, 2014). By the Campanian, highly aquatic mosasauroids of traditional aspect are found globally, including occurrences in much of Europe (Russell 1967), the East Coast of North America (e.g., Cope 1868; Miller 1955), Japan (Caldwell et al. 2008), New Zealand (Hector 1874), Antarctica, Argentina (e.g.,

**Figure 1:** Regional and geological framework of the Münsterland Cretaceous Basin (MCB). **a** Geological map of the study area and location of the Halle-Hesseln section (red star), the source of WMNM P64161. The DIMAC quarry is located near Hesseln in the municipality of Halle (North Rhine-Westphalia), Germany (map modified after Hiß 1995). **b** Palaeogeography of northern Germany during the Late Cenomanian (modified after Hiß 1995). **c** Chrono- and lithostratigraphy of the lower Upper Cretaceous in the northern part of the MCB (compiled after Niebuhr et al. 2007).



Fernández & Martin 2009; Fernández & Gasparini 2012), and Venezuela (Sánchez-Villagra et al. 2008). A further report from the Upper Cretaceous of Brazil is as yet uncorroborated (Branner 1890). Mosasaurs evolved some distinctive ecomorphological forms, including probable shell-crushers (Schulp 2005). And while Williston's (1904) speculation that mosasaurs regularly bred in freshwater has not found much support, fresh- or brackish water dwellers have in fact been discovered (Everhart 2005; Makádi et al. 2012). Some species achieved extraordinary size, at least 12 m in the case of *Tylosaurus proriger* (Cope, 1869a) (Everhart 2002) and more in other species (Everhart 2005). Mosasaurs went extinct at the end of the Cretaceous (e.g., Bardet 1994; Everhart 2005; Benson et al. 2009; Polcyn et al. 2014).

The patchy record of early mosasaurs has complicated the interpretation of their origins, quite apart from the differing perspectives on the nearest extant relatives

of Mosasauria (Osborn 1899; Fürbringer 1900; Nopcsa 1908; Camp 1923; Caldwell et al. 1995; Lee 1997; Conrad 2008; Gauthier et al. 2012; Reeder et al. 2015; Simões et al. 2017a). On this background, we report on a largely complete, articulated tail of a primitive mosasaurian from the lowermost Turonian of the DIMAC quarry between Halle and Hesseln, North Rhine-Westphalia, Germany (Fig. 1). In this paper, we describe the specimen, ascertain its phylogenetic affinities, and discuss the place of the animal that produced it in the history of mosasaurian locomotor evolution. This is the first partial skeleton known from continental western Europe during the early phase of mosasaurian evolution. It complements reports of isolated dolichosaur skeletal material from the region (Diedrich 1997, 1999) and highlights the potential for future discoveries in the mid-Cretaceous of Germany to shed light on the early evolutionary and dispersal history of Mosasauria.



**Figure 2:** Panoramic view of the inverted stratigraphy of the lower Upper Cretaceous strata at the DIMAC quarry. The Hesseltal Formation spans the uppermost Cenomanian and lowermost Turonian.

### Material and methods

The specimen was discovered by Marco Castens (Bielefeld) in dark grey marls of the Hesseltal Formation of the DIMAC quarry (see ‘Geological setting’ below), specifically in the *Watinoceras* bed (Figs 2, 3) of the lowermost Turonian (personal communication M. Castens, March 2017; cf. Hiß et al. 2010). The particular block of rock in which it was discovered has been stripped. However, the site was photographed, and the find was reported to the LWL-Museum of Natural History in Münster (WMNM). According to the law for the preservation of monuments for the state of North Rhine-Westphalia, DSchG NRW (§17 ‘Schatzregal’), it was classified as an important find for the fossil record of Westfalen-Lippe and thus became the property of North Rhine-Westphalia. Subsequently, it was assigned to WMNM, which houses it under accession number WMNM P64161. It was prepared at WMNM.

### Comparisons and palaeoecology

The specimen was compared in detail to other basal mosasaurians, particularly dolichosaurs previously described from the same quarry, and basal mosasauroids. Palaeoecological conclusions are based on a thorough review of the relevant geological literature on the palaeoenvironment as well as morphometric comparisons with the tails of other mosasaurians.

### Geological setting

The strata of the Münsterland Cretaceous Basin (MCB; Fig. 1a) in north-western Germany form an important element of the sedimentary and palaeontological record of the Boreal Cretaceous Realm in north-western Europe. Early surveys on their stratigraphy and fossil content thus date back well into the 19<sup>th</sup> century (e.g., Roemer 1841; Strombeck 1859). However, until the late part of the Early

Cretaceous, the MCB was still a non-depositional area to the north of the Rhenish Massif. A major sea-level rise during the Albian caused an onlap of nearshore and hemi-pelagic strata onto the northern part of the Rhenish Massif, transforming the Münsterland into a depositional area as a part of the wide north German epicontinental shelf sea (start of the 2nd sedimentary megacycle of Hiß et al. 2005; see synopsis by Wilmsen and Wiese 2008). A second major phase of this transgressive interval occurred during the Cenomanian to early Turonian when the coastline shifted far southwards and pelagic facies prevailed over much of the basin (e.g., Hiß 1982; Wilmsen et al. 2005; Berensmeier et al. 2018) (Fig. 1b). In connection with tectonic inversion at its north-eastern margin (‘Teutoburger Wald’, or Teutoburg Forest), the MCB experienced considerable subsidence during the Coniacian to early Campanian and a gradual withdrawal of the sea during the remainder of the Campanian (e.g., Voigt et al. 2008a). Today, the MCB is a bowl-shaped geomorphological and tectonic basin bordered in the north/northeast by the Teutoburg Forest (Osning), in the east by the Egge Mountains and in the south by the low-lying mountain ranges of the northern part of the Rhenish Massif (Ruhr area and northern Sauerland). The studied section at Halle-Hesseln is located in the central part of the Teutoburg Forest in the northern part of the MCB (Fig. 1a).

The quarry of DIMAC GmbH in Halle-Hesseln exposes strata of late early Cenomanian to early Coniacian age (Figs 1c, 2). It was recently restudied by Richardt (2010) and Kaplan (2011). The tectonically inverted succession starts with hemipelagic nodular limestones of the Ascheloh Member (upper lower Cenomanian) of the Brochterbeck Formation, followed by a thick succession of pelagic limestones of the Hoppenstedt Member (middle to lower upper Cenomanian, Fig. 1c). A conspi-

**Figure 3:** Strata of the Hesseltal formation at DIMAC quarry. Specimen WMNM P64161 was found at the *Watinoceras* bed. (Photo by Marco Castens, Bielefeld)



cuous facies change in the middle upper Cenomanian, corresponding to an intermittent short-term sea-level fall, forms the base of the uppermost Cenomanian-lowermost Turonian Hesseltal Formation. The Hesseltal Formation (Niebuhr et al. 2007, locally also known as 'Schwarzbunte Wechselfolge', 'Schwarzschiefer-Fazies', 'Rotpläner', or 'Schwarzweiße Wechselfolge') consists of alternating layers of dark (black, grey, reddish, greenish-grey) marls, clayey marlstones and greenish-grey or light grey limestones and marly limestones (Figs 2, 3). Up-section, a thick sequence of grey to white, fine-grained marly limestones and limestones of the Büren, Oerlinghausen, Salder and Erwitte formations continue the section in the DIMAC quarry into the lower Coniacian (Kaplan 2011) (Fig. 1c).

The Hesseltal Formation is known from offshore settings in northern Germany and outcrops are mainly restricted to the northern margin of the MCB (Teutoburg Forest) and to the low mountain ranges in Lower Saxony and Saxony-Anhalt. The black shales of the Hesseltal Formation represent the regional expression of the anoxic phase of the worldwide Ocean Anoxic Event 2 (OAE 2; Schlanger & Jenkyns 1976; Cetaan et al. 2008). The onset of OAE 2 was related to a large-scale magmatic episode (Kerr 1998; Turgeon & Creaser 2008; Du Vivier et al. 2014) and resulted in the formation of organic-rich sediments on a global scale, accumulating under dys- to anoxic conditions (e.g., Schlanger et al. 1987; Wignall 1994; Jenkyns 2010), and a major positive carbon stable isotope excursion that can be used for chemostratigraphic calibration and correlation (e.g., Gale et al. 1993; Paul et al. 1999; Tsikos et al. 2004). OAE 2 was associated with a major sea-level rise across the Cenomanian-Turonian boundary that culminated in a global earliest Turonian maximum flooding interval (K140 mfs of Sharland et al. [2001] on the Arabian Plate; 93.5 Ma

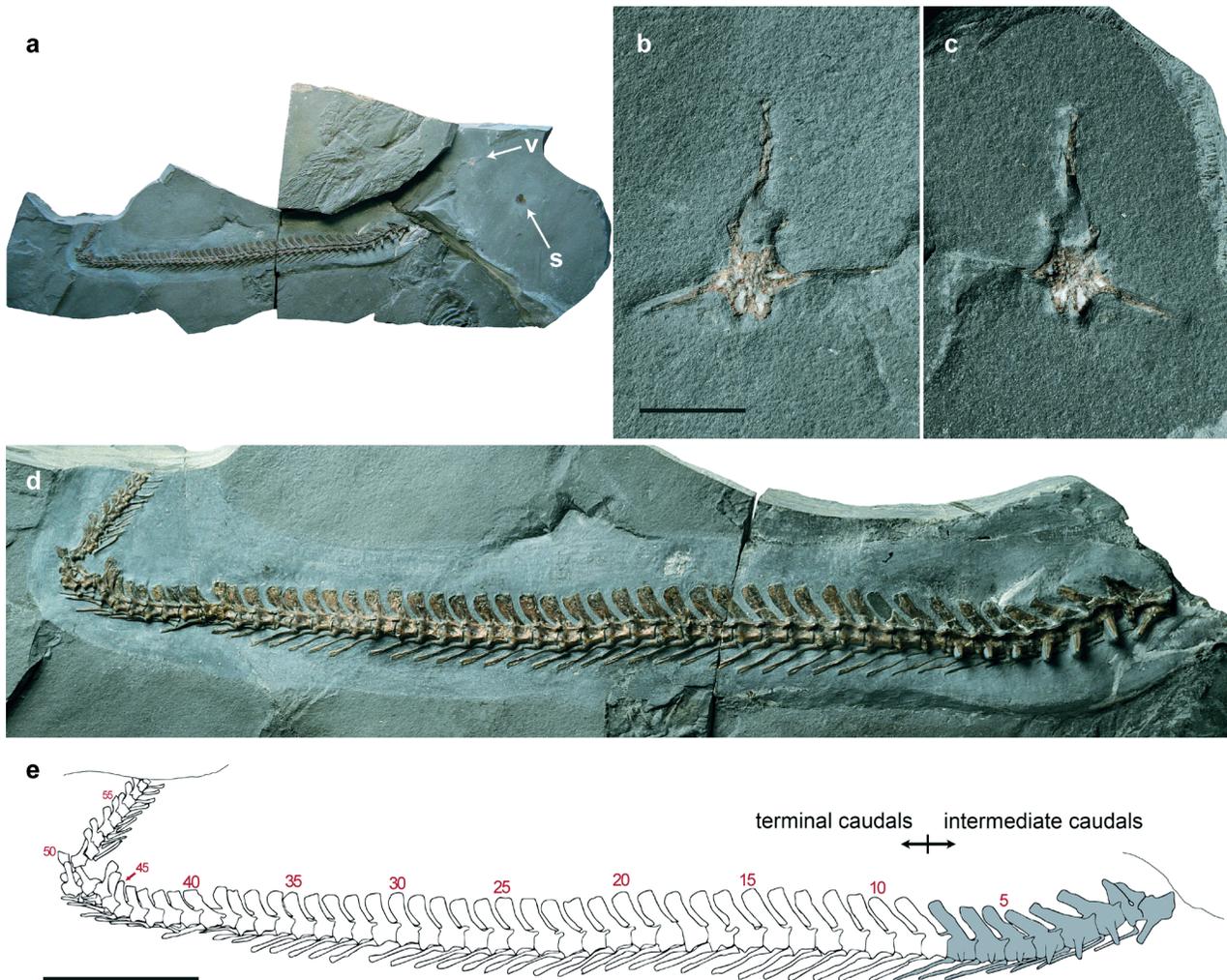
maximum flooding in the eustatic charts of Haq [2014]). The earliest Turonian maximum flooding corresponds to the *Watinoceras* bed at DIMAC, the layer in which the mosasauroid specimen described here was discovered. The Hesseltal Formation has been studied in detail by Voigt et al. (2007, 2008b), including high-resolution chemostratigraphic analyses.

#### *Morphometrics*

Centrum length (CL) was measured at mid-height on the centrum (excluding the condyle). Centrum height (CH) cannot be measured in the same way as in previously studied mosasauroids (Lindgren et al. 2011a) because the dorsal part of the centrum is incompletely exposed in most cases. Instead, we measured CH from the base of the centrum at the cotyle vertically to the dorsoventral level of the deepest part of the notch separating the prezygapophysis from the centrum. This measurement is most consistently measurable and closely approximates CH as measured by Lindgren et al. (2011a). Conceivably, this measurement of CH overestimates true CH distally in the tail, as the prezygapophysis shift to a position dorsal to the centrum. Hemal arch length (HAL) was measured along the right or left side (whichever was better exposed) from the edge of the articulation facet with the centrum to the distal tip. Because the vertebrae are laterally embedded in the slab, centrum width (CW) cannot be measured without CT scans, which have not yet been attempted for LWL P64161.

#### *Abbreviations*

BMB – Booth Museum of Natural History, Brighton, UK  
 BMNH – Natural History Museum, London, UK  
 WMNM – LWL-Museum of Natural History, Münster, Germany



**Figure 4:** Largely articulated section of tail of WMNM P64161, preserving 61 complete or partial vertebrae with hemal arches. **a** Overview of the specimen, showing position of isolated vertebra (v) and ganoid scale (s). **b, c** Isolated vertebra of WMNM P64161, broken transversely, showing tall neural spine, long transverse processes, and peduncles for hemal arch. **d, e** Photograph and interpretive outline drawing, respectively, of WMNM P64161, articulated vertebral column. Vertebra numbers are above neural spines and refer to the articulated series. Grey-shaded vertebrae are intermediate caudals. Scale bars: b, c = 1 cm; d, e = 5 cm.

### Systematic palaeontology

Squamata Oppel, 1811  
 Mosasauria Marsh, 1880  
 Mosasaurioidea Gervais, 1853  
 Mosasaurioidea indet.

#### Description

The specimen comprises a section of tail with 61 vertebrae, all but one of which are almost perfectly articulated and preserved in lateral view (Fig. 4). They can be divided into nine intermediate caudal vertebrae (Fig. 4e, grey), or those possessing transverse processes (=caudal ribs) and a hemal arch, and 52 terminal caudal vertebrae, or those possessing a hemal arch but no transverse processes (Russell 1967). Pygals, those vertebrae at the base of the tail possessing transverse processes but no hemal arch, are not preserved. The length of the articulated series measured along the vertebral axis is about 404 mm. The

distal-most preserved vertebra is incomplete, and the tail would have continued onto an uncollected slab (see below). An additional slab, comprising part and counterpart, contains an isolated proximal caudal vertebra split transversely along a bedding plane.

**Intermediate caudal vertebrae:** The isolated vertebra (Fig. 4b, c) has not been fully prepared but has a triangular outline, with a tall neural spine and long transverse processes. It is taken to be the anterior-most of the preserved vertebral series. It is unknown whether it once articulated with the first-preserved vertebra of the larger slabs or was located more proximally. The ventral margin of the centrum evinces a notch bounded by two narrow ventral projections, suggestive of peduncles for a hemal arch. Thus, it pertains to the intermediate series. The term 'intermediate', however, should not be taken to imply that the vertebrae in question are found in the middle of the tail (see below).

The first vertebrae of the articulated series are robust (Fig. 4d, e). The first two neural spines are damaged, but subsequent neural spines taper only slightly toward their tip. The spines are laterally compressed, slightly thicker basally than apically, and the anterior and posterior margins are straight and strongly inclined distally. The tip is flat and perpendicular to said margins; it evinces a thin, well-finished cap, presumably of bone, suggesting the animal was ontogenetically advanced. Due to erosion, perhaps as a result of the splitting of the shale, the cap is clearly visible only on a few vertebrae (such as the 4<sup>th</sup> and 19<sup>th</sup> of the articulated series).

Both pre- and postzygapophyses are well developed. The postzygapophyses project more strongly posterior to the margin of the centrum than the prezygapophyses do anteriorly. The articular facets are inclined medially, but due to articulation and/or damage, their precise shape and orientation cannot be specified. The prezygapophyses project strongly laterally as well as anteriorly. The 1<sup>st</sup> and 3<sup>rd</sup> vertebrae of the articulated series show that the right and left prezygapophyses were clearly separated by a notch in the neural arch. There is no evidence of a zygosphenon on any vertebra, and so presumably zygantra are also absent. A prominent interzygapophyseal ridge, rising slightly posteriorly, connects the pre- and postzygapophyses on the lateral surface of the neural arch.

The centrum is procoelous and slightly depressed, such that the exposed cotyle of the first vertebra of the articulated series is oval in outline. On the first eight vertebrae of the articulated series there is a strong pair of transverse process that project laterally and slightly ventrally from the centrum. Together with the isolated vertebra, this makes nine intermediate caudals. The processes diminish gradually in size from about 10 mm on the first vertebra to about 6 mm on the 8<sup>th</sup> vertebra. Their orientation also appears to shift from ventrolateral (~45°) to more nearly lateral (~20°); however, comparison with the isolated, transversely split vertebra suggests that the ventral component might be artifactually magnified by small breaks. The processes are abruptly absent on the 9<sup>th</sup> and more posterior vertebrae of the articulated series. The facets for the hemal arches are large protuberances located entirely on the preceding vertebra. They retain a connection, however, to the posterior margin of the vertebra (Gauthier et al. 2012, character 475).

Hemal arches articulated with all vertebrae in the articulated series. The hemal arches of the anterior caudal vertebrae are long (longer than the appertaining neural spines) and slender, with greatly expanded proximal articular processes. They grow slightly more robust posteriorly. They also increase in length from the first-preserved to the tenth. Thereafter, they decrease

in length at a slightly increasing rate. Hemal arches are almost always lacking on the first post-sacral vertebrae in squamates, including basal mosasauroids (Smith & Buchy 2008). The absence of any pygal vertebrae indicates that the tail WMNM P64161 is incomplete.

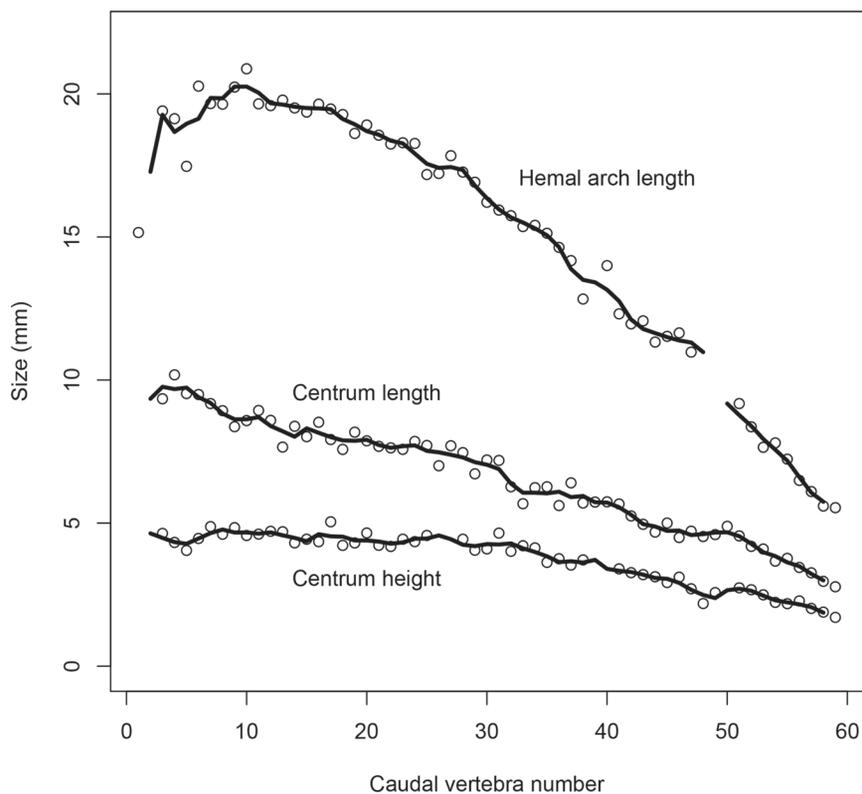
Terminal caudal vertebrae: The vertebrae undergo a number of changes behind the intermediate caudal vertebrae. As above, however, the word 'terminal' should not be taken to imply that these vertebrae were necessarily found only at the distal end of the tail; in fact, most of the tail, as preserved, consists of terminal caudals.

The neural spines grow longer absolutely and with respect to centrum length, before decreasing again in the posterior half of the tail. By the 11<sup>th</sup> and 12<sup>th</sup> vertebrae of the articulated series, they begin to expand slightly distally rather than tapering. This trend reaches a maximum distally in the tail, where the neural spine has twice the anteroposterior length distally as proximally. Meanwhile, the proximal part of the neural spine becomes rod-shaped. The posterior corner of the tip of the neural spine becomes slightly rounded, a shape that becomes more prominent posteriorly. Concomitantly, the anterior and posterior margins of the spine become anteriorly concave, so that the distal half of the neural spine becomes more dorsally directed rather than posterodorsally. The flattened tip of the neural spine thus becomes nearly horizontal. This change in orientation reverses in the distal third of the preserved segment, so that the tip is directed posterodorsally again.

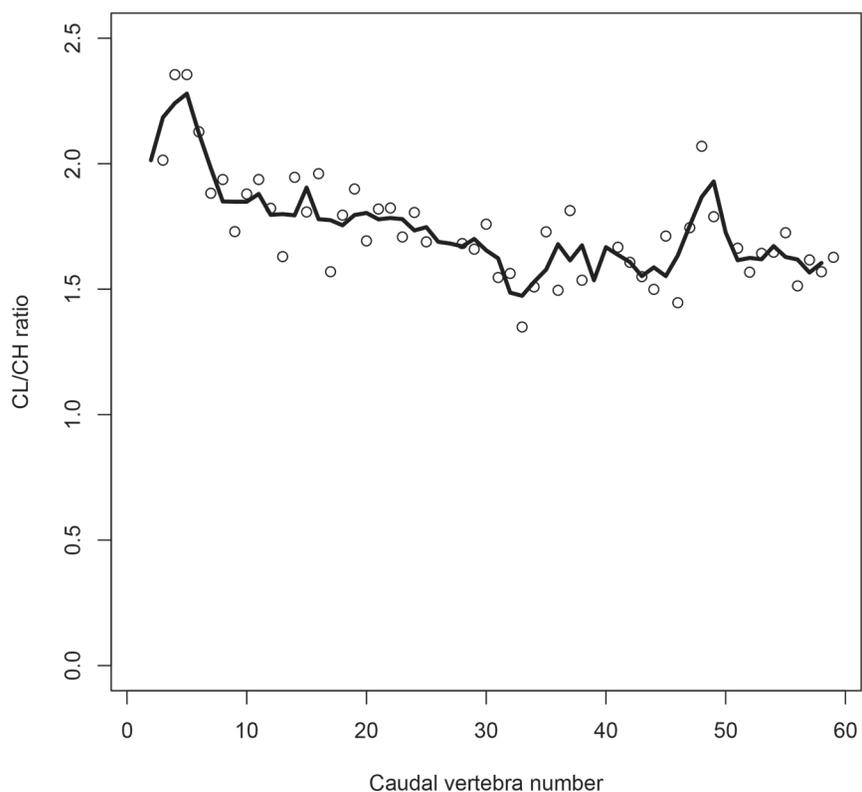
Pre- and postzygapophyses become reduced in prominence posteriorly, but to different extents. The postzygapophyses – which on the anterior caudals projected strongly behind the margin of the centrum – are gradually reduced to small protuberances along the posterior margin of the neural spine. The last vertebra with a trace of an articular surface is the 42<sup>nd</sup> in the articulated series; thereafter, postzygapophyses appear to be completely absent. Prezygapophyses, on the other hand, are present on all of the preserved caudal vertebrae. However, they too diminish considerably in prominence, no longer projecting anteriorly or laterally beyond the margin of the centrum. On the posterior-most vertebrae they do not even reach the level of the centrum's anterior margin. They become closely apposed medially, and the notch between them disappears. The interzygapophyseal ridge becomes indistinct posteriorly, and as the postzygapophyses disappear, it begins to curve dorsally, ascending the lateral surface of the neural spine to some extent. This leads to the formation of a groove on either side of the anterior margin of the neural spine.

On the first vertebra on which transverse processes are lacking (the 9<sup>th</sup> of the articulated series), there are lateral

**Figure 5:** Morphometric trends in the vertebrae of the articulated section of WMNM P64161: centrum length (CL), centrum height (CH), and hemal arch length (HAL). The thick lines are 3-point moving averages, which more clearly show the trends. See text for explanation of potential bias in CH measurement posteriorly.



**Figure 6:** Change in the ratio of centrum length (CL) to centrum height (CH) along the articulated section of WMNM P64161. In the first half of the tail, the ratio declines from over 2.0 to about 1.7, whereas in the second half it only declines to 1.6. The thick line is a 3-point moving average, which more clearly shows the trends.



foramina (one on each side, presumably) in the same position. These can be recognised on nearly all of the vertebrae until the preserved end of the tail.

The hemal arches become longer and more robust posteriorly. Distally in each arch, they expand in anteroposterior length and, at least on the middle vertebrae of the articulated series, appear to become compressed. On more posterior vertebrae,

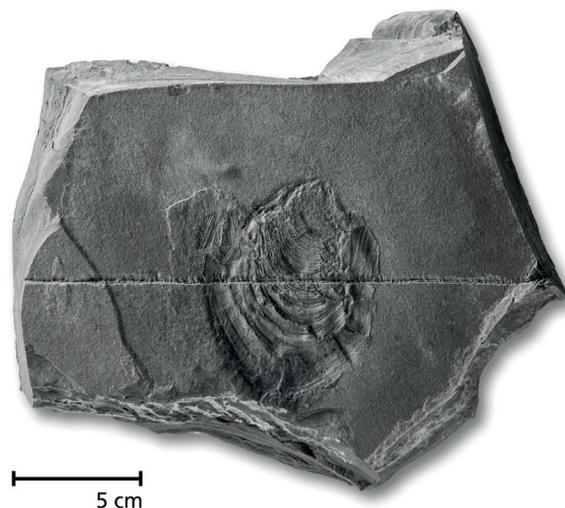
however, even the distal extent of the hemal arch is rod-shaped. The hemal arches of vertebrae 43–45 are disarticulated and show that the proximal articulations are clearly separated. By the 50<sup>th</sup> vertebra, however, similarly disarticulated hemal arches show that the proximal articulations become very closely spaced, just like the prezygapophyses approach one another medially.

**Morphometric trends:** Throughout the articulated tail section, CL decreases regularly from about 10 mm to 2.8 mm, the rate of decrease increasing slightly in the posterior half (Fig. 5). CH decreases very slightly in the first half, from about 4.7 mm to 4.1 mm, then more rapidly in the posterior half, to 1.7 mm. The greater rate of decrease in CL in the first half leads to a drop in the ratio CL/CH from around 2.0 to 1.7, thereafter it decreases only slightly until the preserved end of the tail, where the ratio is about 1.6 (Fig. 6). If CH is biased to higher values posteriorly in the tail (see above), then it is possible that the true CL/CH ratio flatlines or even rises slightly posteriorly. The particularly high value on vertebra 48 is probably an artefact resulting from a measurement of CH that is much too low (the vertebra in question is located in the 'kink' and so is difficult to measure accurately). HAL, as noted above, rises from 15.2 mm to 20.9 mm from the first to tenth preserved caudal; thereafter, it decreases at a regular and increasing rate until the posterior end, where HAL is 5.5 mm.

Estimates of the ratio of centrum length dorsally to centrum length ventrally are noisy but do not show a sustained positive departure from 1 at any point in the preserved column (data not shown). In fact, there may be a tendency for the ratio to decline below 1 in the distal third of the preserved column (i.e., ventral centrum length exceeds dorsal centrum length). In view of the noise and the difficulty of accurately measuring these embedded vertebrae, we do not accord this apparent decline any special significance. There is in any case no evidence that dorsal centrum length exceeds ventral centrum length in the preserved column, i.e., the vertebrae were nowhere 'wedged'.

#### Taphonomy

The earliest Turonian maximum flooding corresponds to the *Watinoceras* bed at DIMAC. This bed represents the uppermost thick, organic-rich horizon of the Hesseltal Formation in the DIMAC quarry (Richardt 2010); the 2-cm-thick slab, on which WMNM P64161 is preserved, is finely laminated and shows no clear evidence of bioturbation on fresh breaks. Several partially preserved bivalves are associated with WMNM P64161 and occur nearly on the same bedding plane. One is next to the middle section of the vertebral column (Fig. 4a), whereas the other is found sub- or superjacent to the proximal preserved end of the column (Figs 4a, 7). They are classified as *Mytiloides* sp., an inoceramid genus typically found in uppermost Cenomanian and Turonian strata (cf. Tröger 2009). The specimens are close to *Mytiloides hattinii* Elder, 1991, an index form characterising the Cenomanian–Turonian boundary interval (Kennedy et al. 2000; see Kaplan [2011] on problematical specific



**Figure 7:** *Mytiloides* sp., preserved in nearly the same bedding plane as WMNM P64161.

differentiation of different *Mytiloides* species at the DIMAC quarry). While bioturbation in other parts of the *Watinoceras* bed suggest that oxic conditions were sufficient at times to support a benthos of some kind, the finely laminated character of the slab, on which WMNM P64161 is preserved, and the absence of benthic taxa other than inoceramids, which are known to have tolerated low-oxygen conditions (Hilbrecht & Dahmer 1991; MacLeod & Hoppe 1992; Ifrim et al. 2008), suggest that a benthos was largely lacking at the time the specimen was embedded. There is also a large ganoid scale, about 10 mm in diameter, on the bedding plane (Fig. 4a, s), indicating that a nekton was present apart from ammonites and the specimen in question.

Of the 61 vertebrae comprising the specimen, 60 are largely articulated (Fig. 4d, e). The cranial end of the articulated portion of the tail is located at a crack, caused by the rock fragmentation procedure at the quarry. The laterally contiguous rock sample was recovered. It contains no further articulated vertebrae, but only an isolated one (Fig. 4a, v), thus suggesting that the specimen was indeed an isolated tail that came to rest on the sea floor. The articulated portion consists of a proximal and a distal section separated by a kink. The proximal section comprises 45 vertebrae. Posteriorly, this line is interrupted by five more or less displaced vertebrae, which lead to the distal articulated section, consisting of nine fully articulated vertebrae. This distal section is rotated 180° around the longitudinal axis and folded forward about 120° over the top of the proximal articulated section. The tip of the tail was not recovered; the specimen ends at a crack without further fitting pieces.

Major disarticulations affecting the specimen are restricted to its terminal ends. Whereas the main section of articulated vertebrae lies in a straight line, the distal

section with the lower mass was rotated and folded. The five anterior-most vertebrae turn slightly dorsally ( $< 30^\circ$ ) with respect to the main axis of the column. The isolated vertebra is separated from the rest of the tail by about 9 cm and also apparently located out of line with the main axis.

The articulation of the specimen, such as it is, must be original. The separation of the tail from the rest of the body, and of the isolation of the proximal vertebra from the rest of the tail, occurred either (1) prior to embedding or (2) subsequent to it. Under the first hypothesis, the minor disarticulation was enabled by decomposition of the soft-tissue and occurred prior to or during settling onto the seafloor. Considering the generally stagnant depositional environment, this hypothesis appears on its face to be more plausible. With regard to the second hypothesis, the absence of evidence of bioturbation in the immediate vicinity of the specimen makes bioturbation an unlikely explanation for the separation of the body, even if bioturbators could selectively move the body. However, without a more detailed study, it is not possible to exclude the possibility that a scavenger may have entered the low-oxygen zone and caused this separation.

## Discussion

### *Systematic position of the DIMAC quarry mosasaurians*

**Early Turonian-aged WMNM P64161:** The interpretation of some characters of WMNM P64161 could depend on what fraction of the tail the specimen represents, and unfortunately this must remain inconclusive. The known number of intermediate caudal vertebrae (9) is relatively low and therefore might suggest, by comparison with other mosasaurians, that a significant portion of the tail ( $\geq 20$  vertebrae) is missing. Namely, numerous mosasaurians have a high number (c. 25 or more) of intermediate vertebrae:  $\geq 32$  in a referred specimen of the dolichosaurid *Dolichosaurus longicollis* Owen, 1851 (Caldwell 2000), c. 26 in a referred specimen of the dolichosaurid *Adriosaurus suessii* Seeley, 1881 (Lee & Caldwell 2000), 28 in a specimen of the mosasaur *Platecarpus tympaniticus* Cope, 1869b (Konishi et al. 2012), and c. 24 in the mosasaur *Eonator sternbergii* (Wiman, 1920) (Bardet & Pereda Suberbiola 2001; personal observation KTS, June 2004). In addition to these potentially missing intermediate caudals, there would be at least 1–2 pygals, the primitive number for Mosasauria (Smith & Buchy 2008). Furthermore, in other mosasaurs, a large number of pygals is found instead of intermediates – e.g., 28–37 in *Plotosaurus bennisonii* (Camp, 1942) (Lindgren et al. 2007) – so that the combined number of pygals and intermediates

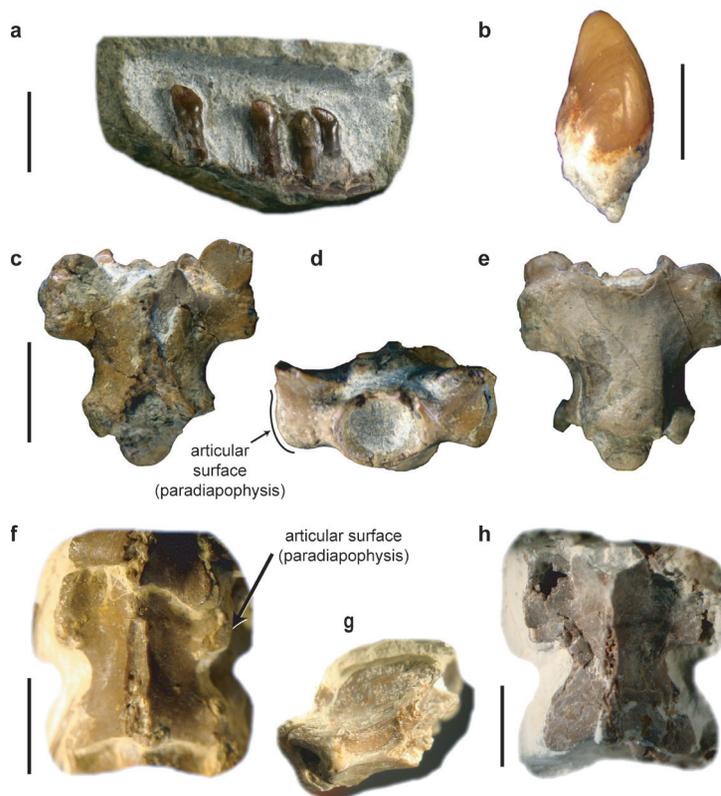
is not very different from the aforementioned taxa. On the other hand, some basal mosasaurians have fewer intermediates (and a primitively low number of 1–2 pygals): 22 intermediates in the dolichosaurid *Aphanizocnemus libanensis* dal Sasso et Pinna, 1997 (dal Sasso & Pinna 1997), a mere eight in *Pontosaurus kornhuberi* Caldwell, 2006 (cf. Caldwell & dal Sasso 2004), and 14 in the basal mosasauroid *Vallecillosaurus donrobertoi* Smith et Buchy, 2008 (Smith & Buchy 2008).

Furthermore, there is no clear difference in the orientation or morphology of the anterior-most transverse processes that would provide more information (Etheridge 1967). Finally, HAL does not provide much guidance. HAL peaks around the 10<sup>th</sup> caudal of the articulated series in WMNM P64161 (Fig. 6). But whereas HAL peaks around the 20<sup>th</sup> (absolute) caudal in *Vallecillosaurus donrobertoi* (Smith & Buchy 2008), it decreases monotonically from the 1<sup>st</sup> caudal in *Pontosaurus kornhuberi* (based on Caldwell 2006: fig. 8). In other primitive mosasaurians, the tail is incomplete, the hemal arches obscured by the centra, or the character has not been examined in detail, so that the primitive state for Mosasauria or Mosasauroida is uncertain. Therefore, whether few or many caudal vertebrae are missing in WMNM P64161 remains unknown.

Still, a number of phylogenetically relevant characters are present. Several features of WMNM P64161 are considered synapomorphies of Mosasauria, such as the vertical intervertebral articulations, the elongate, posteriorly inclined neural and hemal arches, and the reduced postzygapophyses in the distal part of the tail (e.g., deBraga & Carroll 1993; Smith & Buchy 2008).

Further characters suggest that WMNM P64161 pertains to Mosasauroida, the stem-based clade, according to Madzia and Cau (2017), encompassing taxa formerly assigned to Aigialosauridae and Mosasauridae. First, the ratio of neural spine length to length of the appertaining vertebral centrum ranges consistently between 1.6 and 1.7 over much of the tail. This value is intermediate between the value for basal mosasauroids like *Opetiosaurus bucchichii* Kornhuber, 1901 and *Vallecillosaurus donrobertoi* (c. 1.9) and that for dolichosaurs like *Adriosaurus suessii* and *Pontosaurus kornhuberi* (c. 1.5–1.6), though closer to the latter (Smith & Buchy 2008). Second, the neural spines are broad, especially distally in the tail, compared with the length of the appertaining centra. While the neural spines can be very broad proximally in Dolichosauridae (e.g., *Pontosaurus kornhuberi*), they are distally narrow. The ratio of neural spine length (measured just below and perpendicular to the distal end of the neural spine) to centrum length is: 0.27 on the 50<sup>th</sup> caudal in *Pontosaurus kornhuberi*, 0.16 on the 53<sup>rd</sup> caudal in *Aphanizocnemus libanensis*,  $< 0.3$  on

**Figure 8:** Comparison of previously described dolichosaur material from the DIMAC quarry with dolichosaur type material. **a** WMNM P19913, left dentary referred to *Coniasaurus crassidens*. Scale: 5 mm. **b** WMNM P22141, isolated tooth referred to *Coniasaurus crassidens* in mesial view. Scale: 1 mm. **c–e** WMNM P21960, dorsal vertebra referred to *Dolichosaurus longicollis* in dorsal, anterior, and ventral views, respectively. Scale: 5 mm. **f** Dorsal vertebra of type specimen, BMNH 49002, of *Dolichosaurus longicollis* in dorsal view. Scale: 5 mm. **g** Dorsal vertebra of type specimen, BMNH 44141, of *Coniasaurus gracilodens* in left lateral view. **h** Dorsal vertebra of type specimen, BMB 7155, of *Coniasaurus crassidens* in dorsal view. Scale bars: 5 mm.



the 53<sup>rd</sup> caudal in *Adriosaurus suessii*, <0.4 on the first vertebrae of the distal articulated tail in *Opetiosaurus buccichii*, and 0.39 on the 51<sup>st</sup> caudal in *Vallecillosaurus donrobertoi*. In contrast, the ratio is consistently 0.67–0.69 from the 20<sup>th</sup> to 50<sup>th</sup> preserved caudal in WMNM P64161, a higher ratio it shares with many mosasaurs: e.g., 0.70 on the 35<sup>th</sup> caudal in *Eonatator sternbergii* (KTS pers. obs.), c. 0.5 in the distal tail of *Halisaurus arambourgii* Bardet, Pereda Suberbiola, Iarochene, Bouya et Amaghazaz, 2005 (Polcyn et al. 2012), c. 0.7 in the distal tail of *Prognathodon* sp. (Lindgren et al. 2013), and c. 0.9 in *Platecarpus tympaniticus* (Konishi et al. 2012). Third, the ‘angling’, or shift in orientation, of the neural spines at mid-height in the distal part of WMNM P64161, while subdued, is reminiscent of the more significant shift seen in the fluke in some advanced mosasaurs (Lindgren et al. 2011a). The flat distal end of the neural spine becomes nearly horizontal. This angling is effectively absent in the dolichosaurids *Pontosaurus kornhuberi*, *Aphanizocnemus libanensis* and *Adriosaurus suessii* and in the basal mosasauroids *Opetiosaurus buccichii* and *Vallecillosaurus donrobertoi*, suggesting the possibility that WMNM P64161 comes from an animal closer to traditional mosasaurs than aigialosaurs.

In summary, there is sufficient evidence to refer WMNM P64161 to ‘Mosasauroida indet.’ Clearly, more complete material will be necessary before a firmer phylogenetic conclusion can be drawn. It may be worth noting that of the major mosasaur lineages that were probably present in the Turonian, the mosasaurines and

halisaurines have fused hemal arches (a derived feature), whereas members of Russellosaurina, like WMNM P64161, do not (a primitive feature).

#### Previously described late Cenomanian dolichosaurs:

Thus far only two aquatic squamate taxa have been reported (Diedrich 1997, 1999) from the DIMAC quarry: *Coniasaurus crassidens* Owen, 1851 and *Dolichosaurus longicollis*, both named based on specimens from the English Chalk. The former is represented by an isolated left dentary fragment with four teeth, WMNM P19913 (Fig. 8a), and an isolated tooth, WMNM P22141 (Fig. 8b), both found in different scour-marks at the base of the *plenus* bed in the lower part of the Hesseltal Formation (Diedrich 1999); the latter by an isolated dorsal vertebra lacking the neural spine, WMNM P21960 (Fig. 8c–e). In the case of the dentigerous specimens, the tooth morphology is highly distinctive. The teeth are bulbous with a mesiodistally expanded crown that rises distally to a blunt, posteriorly directed apex, and the lingual surface is heavily striated (Diedrich 1999). These features form part of the diagnosis of *Coniasaurus crassidens* (Caldwell and Cooper, 1999); the lack of a labial sulcus on the isolated tooth might raise questions about the identity, but the morphology appears consistent with variation seen in the type series (Owen 1851; personal observation KTS, May 2013; Caldwell & Cooper 1999). Thus, reference to *Coniasaurus crassidens* is well supported.

In the case of the vertebra of WMNM P21960, assignment was supported solely by biogeography (since only

*Coniasaurus* and *Dolichosaurus* had been described so far to the north) and general morphological resemblance, without a detailed comparison of the vertebrae of *Coniasaurus crassidens* or *Dolichosaurus dorsalis* (Diedrich 1999). Personal observation (KTS, May 2013) of the type material of both species suggests that the vertebrae of *Dolichosaurus dorsalis* show some distinctive features. The paradiapophysis on nearly all preserved dorsal vertebrae of the holotype, BMNH 49002, is particularly dorsoventrally elongate. This leads to a squaring of the anterolateral corner of the vertebrae (Fig. 8f), a feature found also in dorsal vertebrae of the holotype of *Coniasaurus crassidens*, BMB 7155 (Fig. 8h). In BMNH 49002, however, the paradiapophysis, including its articular surface, is expanded above the level of the interzygapophyseal ridge onto the dorsal surface of the neural arch (Fig. 8f); the functional significance of this highly unusual feature is unknown, but it appears to be absent in BMB 7155 and in the holotype of *Coniasaurus gracilodens* Caldwell, 1999, BMNH 44141 (Fig. 8g). The absence of this apparent autapomorphy in WMNM P21960 suggests that reference to *Dolichosaurus dorsalis* may be incorrect, but a firm identification will have to be based on more complete material. It is notable that the only cranial material from the same horizon as the vertebra is referable to *Coniasaurus crassidens* (see above).

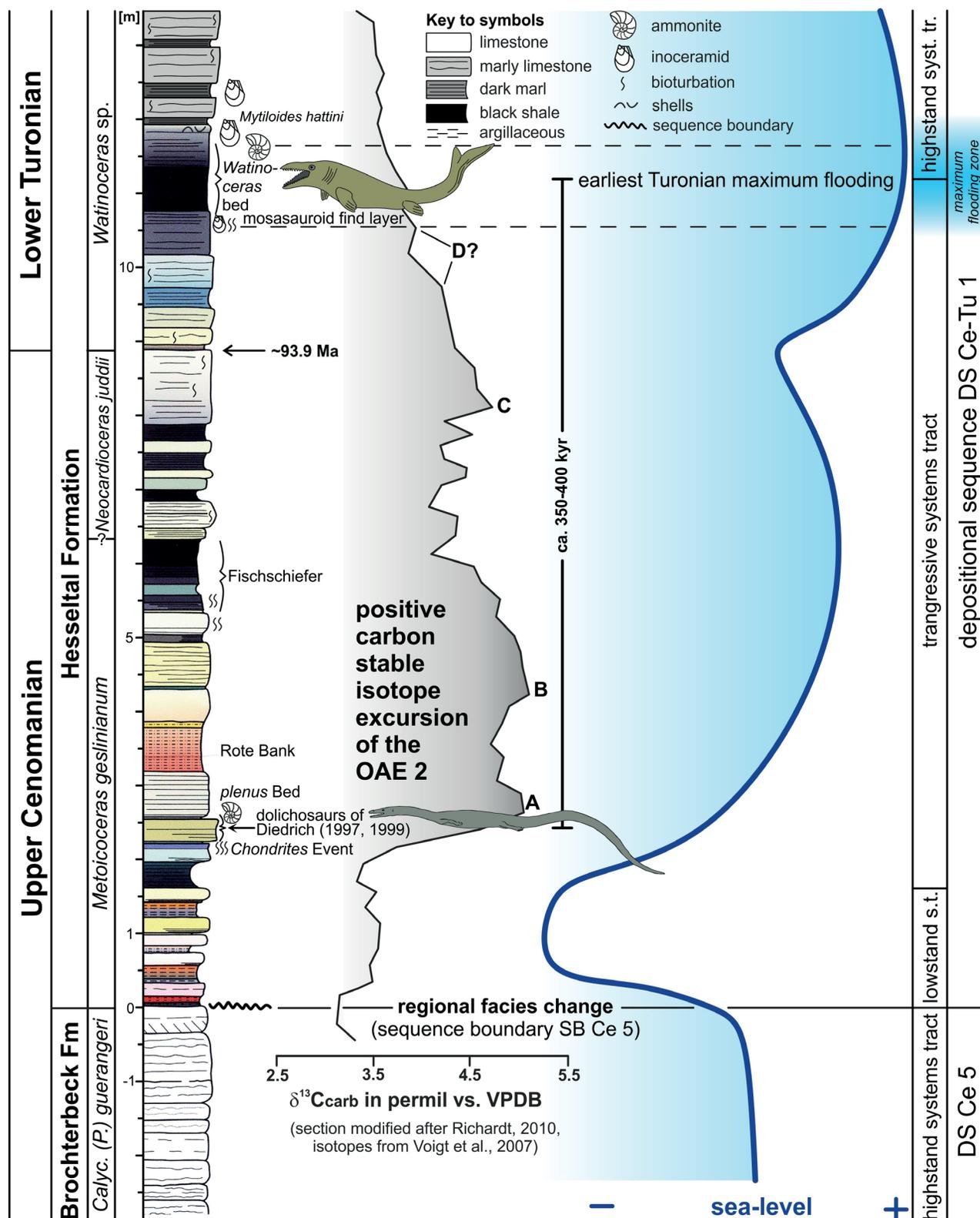
#### *Palaeoecology*

**Palaeoenvironment and palaeoautecology:** Mosasauroians were secondarily aquatic tetrapods, and the general open-marine environment represented by the DIMAC quarry is consistent with this. The dolichosaur material described earlier from this quarry derives from scours at a condensation horizon coincident with the so-called 'Puzosia event' near the base of the Hesseltal Formation, below the *plenus* Bed (Diedrich 1997, 1999, 2001) (Fig. 9). This horizon may represent a short-lived regressive phase, where bioturbation was abundant and fossil remains were concentrated by currents in scours (Diedrich 1997, 1999; Richardt 2010). However, Richardt (2010) did not recognise the *Puzosia* event identified by Diedrich (1997, 1999, 2001), and the stratigraphic interval belongs in general to the initial phase of a major transgression (the *plenus* transgression of authors, early transgressive systems tract of depositional sequence DS Ce-Tu 1; see Fig. 9). A sea-level fall occurred somewhat earlier, evidenced by the conspicuous facies change at the boundary of the Brochterbeck and Hesseltal formations (sequence boundary SB Ce 5; see Janetschke et al. [2015] for details on the regional early Late Cretaceous sequence stratigraphy). However, even during this short-lived phase of falling and low sea-level, the shoreline

was many tens of kilometres away (e.g., Hiß 1982), and the finds of Diedrich (1997, 1999) derive anyways from the lower part of the succeeding transgressive interval (Fig. 9).

In contrast, WMNM P64161 derives from dark marls of early Turonian age, specifically from the *Watinoceros* bed (Fig. 9). The latest Cenomanian–early Turonian transgression proceeded stepwise (Richardt et al. 2013) and, at the DIMAC quarry, a first intermittent maximum is reflected by the thick black shales of the Fischechiefer in the uppermost Cenomanian (Fig. 9). After a brief intermittent halt of transgression in the Cenomanian-Turonian boundary interval, sea-level rise accelerated into the earliest Turonian, culminating in the earliest Turonian maximum flooding, a global event. At DIMAC, this maximum flooding corresponds to the *Watinoceros* bed and thus the greatest distality during depositional sequence DS Ce-Tu 1 at DIMAC, with water depth and distance to the nearest shoreline certainly exceeding 100 m and 100 km, respectively. Ocean currents have not, to our knowledge, been studied in detail in the vicinity of the Teutoburg Forest. However, the coupled global climate model of Trabucho Alexandre et al. (2010) for the latest Cenomanian produced southward and south-westward sea-surface currents in the MCB of <10 cm/s. A south-westward palaeo-circulation for north-western Europe during the Cenomanian-Turonian boundary interval has also been reconstructed by Du Vivier et al. (2014). These currents were then moving toward the nearest shoreline, i.e. the Rhenish Massif, not away from it. The next closest subaerial exposures were thus on the Fennoscandian Shield, well over 500 km to the north-northeast.

It is noteworthy that the skeletal elements assigned to *Coniasaurus* and *Dolichosaurus* (Diedrich 1997, 1999) are isolated bones, whereas WMNM P64161 is a partial skeleton. The kind of transport that Diedrich (1997, 1999) envisaged for the former evidently did not occur with the latter, which is consistent with the different sequence stratigraphic positions of the layers in which they were found: current-swept early transgressive systems tract for the disarticulated elements and undisturbed maximum flooding conditions for the articulated specimen described herein. With regard to aquatic adaptations, the most conservative of the two taphonomic hypotheses above is that the tail of WMNM P64161 was lost by a decomposing, floating carcass and that the animal that bore it did not die immediately above the seafloor where it was emplaced. If we assume that the carcass was transported from a near-shore environment of the southern Fennoscandian Shield 500 km away and that a sustained ocean current of 10 cm/s obtained, it would have taken the carcass 57.9 days to reach the position of the DIMAC quarry. In the experiments of Richter and Wuttke (2012),



**Figure 9:** Section of the stratigraphic interval yielding the mosasauroid fossil (modified after Richardt 2010) including carbon stable isotopes (cf. Voigt et al. 2007) and eurybatic sea-level curve. Cenomanian-Turonian boundary age after Ogg & Hinnov (2012); the age difference between the two layers yielding mosasaurians is ca. 350-400 kyr according to the cyclostratigraphic model of Oceanic Anoxic Event (OAE) 2 by Voigt et al. (2008a).

who studied the disarticulation sequence in an immersed carcass of the spiny-tailed iguanid lizard *Oplurus cuvieri* (Gray, 1831), disarticulation was first found in the snout and middle of the tail (after the 8<sup>th</sup> caudal vertebra); the skeleton was almost completely disarticulated after 56 days, with only some of the appendicular elements (particularly hands and feet, and a few vertebrae) remaining in articulation. It is therefore highly implausible that the articulated tail came from so far. Thus, the animal represented by WMNM P64161 must have died at open sea and can be regarded as an open-water dweller. Ifrim et al. (2008) gave similar calculations in support of their hypothesis that the articulated mosasauroids of Vallecillo, Mexico, were open-water rather than near-shore dwellers.

To summarise, in case of the DIMAC specimens referred to *Coniasaurus* and *Dolichosaurus*, the circumstances may indicate that the isolated vertebra and dentigerous material derived from animals that may have died far from the present-day quarry and were carried thither by bottom currents associated with the sea-level fluctuations following the mid-late Cenomanian sequence boundary SB Ce 5. The partial skeleton described here, in contrast, represents an animal that died, and presumably lived, much closer to it and was buried parautochthonously. This, in turn, would be consistent with a significant enhancement of the swimming abilities of this mosasauroid in comparison with Dolichosauridae, which have been considered denizens of near-shore (Caldwell & Cooper 1999; Jacobs et al. 2005), crevice-filled, possibly reefal environments (Caldwell 1999), similar to some extant sea-snakes (Caldwell 2000). It may be speculated that the environmental pressure exerted by the major transgressions during the latest Cenomanian-early Turonian helped to precipitate the extinction of the dolichosaurs and the adaptive radiation of Mosasauroidea.

Swimming capabilities in marine reptiles: Among aquatic vertebrates, there are substantial differences in the mode of locomotion that influence the ability of an animal to catch prey, amongst other things. As characterised by Massare (1988), these modes form a progression, in which the proportion of the body used to generate thrust or propulsion, is increasingly limited to the tail: anguilliform (or axial undulatory), in which propulsive waves pass through most of the body, the amplitude increasing posteriorly; subcarangiform (or axial subundulatory), in which the anterior part of the body is held stiff; carangiform (or axial suboscillatory), in which only the hind third of the body experiences undulation; and thunniform (or axial oscillatory), in which only the tail and its peduncle are moved.

Massare's (1988) study of body shape and drag concluded that mosasaurs were only capable of relatively low sustained swimming velocities – lower than ichthyosaurs and plesiosaurs, and considerably lower than extant cetaceans. Massare (1988) assumed an axial undulatory mode of locomotion for them, but sensitivity tests showed that the results were not particularly dependent on this point. In combination with the relatively long, presumably flexible bodies, a presumably deep caudal peduncle, and large, low aspect ratio tail, Massare (1988) concluded that mosasaurs were more likely optimised for transient or burst swimming, rather than for sustained swimming. Thus mosasaurs would have been ambush predators rather than roaming hunters.

Aspects of Massare's (1988) quantitative model were improved by Motani (2002), who, nevertheless, found that the mosasaur *Platecarpus* was significantly slower than ichthyosaurs. More recent specimen-based work has also questioned the conclusion that mosasaurs were anguilliform or subcarangiform. First, palaeopathological work has suggested that the highest stress induced by locomotion was concentrated in the proximal part of the tail (Mulder 2001). In particular, a number of specimens of the plioplatecarpine mosasaur *Plioplatecarpus marshii* Dollo, 1882 show ligamentous ossification (also called diffuse idiopathic skeletal hyperostosis) of the pygal vertebrae, in this case fusion of adjacent centra by bony overgrowths that do not distort the internal structure of the vertebrae, unlike hyperostosis due to infection. Similar observations have been made in extant whales (Mulder 2001). In and of itself, this may not be surprising, since wave amplitude increases posteriorly in the body (see above). But an additional palaeopathological study of *Platecarpus* and *Tylosaurus* found common evidence in these taxa of decompression syndrome, which would result from returning to the surface from deep dives (Rothschild & Martin 1987). A movement from shallow to deep to shallow water again is suggestive of more sustained swimming capabilities.

More recently, extensive studies of exceptionally preserved mosasaur specimens have revealed new details about the anatomy and aquatic adaptations of mosasaurs. The scales of many mosasaurs, such as *Tylosaurus proriger* (Snow 1878), *Ectenosaurus clidastoides* Merriam, 1894 (Lindgren et al. 2011b), *Plotosaurus bennisonii* (Lindgren et al. 2009) and possibly the dolichosaur *Pontosaurus kornhuberi* (Caldwell 2006), were provided with longitudinal keels. These are apparently absent in the primitive mosasauroids *Vallecilloosaurus donrobertoi* (Smith & Buchy 2008) and *Aigialosaurus dalmaticus* Gorjanović-Kramberger, 1892 (Gorjanović-Kramberger 1892) and may have reduced pressure drag (Lindgren et al. 2009; Palmer & Young 2015). The

dermis on the body of *Ectenosaurus clidastoides* was provided with superimposed, cross-woven layers of helical fibres, thought to reduce surface deformation and therefore frictional drag (Lindgren et al. 2011b). Finally, mosasaurs apparently possessed a semilunate, hypocercal caudal fluke, the vertebral column bending downward to support the ventral lobe. This conclusion is supported by the dimensions of the individual vertebrae in the vicinity of the peduncle (Osborn 1899; Wiman 1920) or terminal vertebrae, which are longer dorsally than ventrally, or 'wedged' in the terminology of Lindgren et al. (2007). Presumably, a fleshy dorsal lobe complemented the ventral lobe dorsally (Lindgren et al. 2011a, 2011b). Moreover, the orientation of the hemal arches in taxa where these are fused has suggested that the peduncle was reduced in dimensions in comparison with the proximal part of the tail. The vertebral proportions, in particular the CL/CH ratios, are similar to those of carangiform swimmers like certain sharks (Lindgren et al. 2011a, 2011b). A specimen of *Prognathodon* with exceptional soft-tissue preservation decisively demonstrated these inferences (Lindgren et al. 2013).

A resolution of these partly contradictory results is wanting. One model parameter worth emphasising in this context is metabolic rate (Motani 2002). Energy can be used for growth, maintenance, reproductive investment, and movement (work). Massare (1988) assumed that mosasaurs, like extant 'reptiles', had a metabolic constant (i.e., the intercept of the mass–metabolic rate power law) in the range of 11.6–29.0. Extant mammals have a metabolic constant an order of magnitude higher (Withers 1992). However, monitor lizards (*Varanus*) have a greater maximum metabolic rate and endurance than other extant lizards (Clemente et al. 2009). Oxygen isotope ratios (Bernard et al. 2010; Harrell et al. 2016) as well as bone tissues in mosasaurine mosasaurs (Houssaye et al. 2013) are furthermore consistent with a higher metabolic rate than previously assumed by Massare (1988) or Motani (2002), although it is worth noting that Motani (2002) excluded a metabolic rate like that of extant reptiles on theoretical grounds. A higher total power output would allow for more energy to be expended on work like sustained (aerobic) swimming. Further work should test the extent to which an increased metabolic rate in Mosasauria might contribute to explain the contradictions of theory and anatomy in that clade.

Morphometrics and palaeoautecology: Lindgren et al. (2007) proposed a four-part functional division of the tail in mosasaurs. From proximal to distal, these are: the tail stock or base, corresponding to the pygal vertebrae, which possess transverse processes but lack hemal arches

(Russell 1967); a displacement unit, corresponding to most of the intermediate caudal vertebrae; a peduncle, comprising the last few intermediate caudals; and a fluke, corresponding to the terminal caudals. A shifting in the orientation of the neural and hemal spines is associated with the caudal peduncle (Lindgren et al. 2011a). While any shift in orientation of the hemal spines could not be recognised clearly in WMNM P64161 due to the fact that they are not fused to the centra, there is only a slight indication in the morphology of the neural spines for any regional differentiation in function. In this respect, WMNM P64161 appears similar to the tail of primitive mosasauroids rather than mosasaurs of traditional aspect. In particular, in WMNM P64161 as in 'aigialosaurs', the number of intermediate caudal vertebrae, while probably exceeding the number of pygals, is also probably much lower than the number of terminal caudals.

The tail in WMNM P64161 shows some transformation toward a mosasaur pattern of vertebral proportions, with a decreasing CL/CH ratio in the proximal half and then a stable (or possibly increasing) ratio in the distal half, but the absolute values are considerably higher (because the individual vertebrae are relatively longer) and thus more primitive (deBraga & Carroll 1993) than in the mosasaurs and extant carangiform swimmers studied by Lindgren et al. (2011a, b). Additionally, CW/CH ratios tend to rise near the caudal peduncle in mosasaurine mosasaurs and may play an important role in stabilising the vertebral column during fluke excursion (Lindgren et al. 2011a). In view of the absence for any evidence of a caudal peduncle, we expect that these ratios, when studied in WMNM P64161, will not show the mosasaurine pattern.

The elongated, posteriorly inclined neural spines in WMNM P64161 are consistent with an increased lateral profile of the tail that would contribute to greater propulsion. Soft-tissue preservation in the primitive mosasauroid *Vallecillosaurus donrobertoi* suggests that the dorsal caudal fin was more extensive than the ventral fin (Smith & Buchy 2008), potentially an intermediate state in the evolution of a typical hypocercal caudal fluke in mosasaurs (Lindgren et al. 2011a). There is no evidence of vertebral 'wedging' in the preserved caudal skeleton of WMNM P64161, suggesting that a well-developed caudal fluke was absent. Without soft-tissue preservation, it is impossible to make definite statements about the shape of the tail in the animal to which WMNM P64161 belonged. However, available evidence suggests some adaptation away from the primitive anguilliform mode of locomotion presumably used by the facultatively aquatic ancestors of Mosasauria, although a carangiform or thunniform mode associated with a semilunate caudal fluke can safely be excluded for WMNM P64161.

## Conclusion

WMNM P64161 is too incomplete to permit a firm taxonomic identification, yet it is clearly referable to Mosasauria and probably to Mosasauroidae. Furthermore, its age places it at the beginning of the mosasauroid radiation, which is marked by an increase in body size, improved swimming capabilities and dispersal to large parts of the world. The vertebral proportions of WMNM P64161 imply adaptation away from the primitive mode of locomotion in aquatic squamates, anguilliform swimming, and in the direction of animals that could sustain high rates of swimming. It is noteworthy, furthermore, that this articulated specimen became embedded on the sea-floor in fine-grained offshore facies at least 100 km from the shore. This, in turn, suggests it lived and died far from shore, which is consistent with the improved swimming capabilities suggested by the vertebral proportions. While there is no evidence for a caudal peduncle or well-developed hypocercal tail in WMNM P64161, the animal was apparently more advanced than the dolichosaurs previously described from slightly older Cenomanian horizons in same quarry. Regardless, the find highlights the potential for discoveries in the DIMAC quarry to shed light on this seminal time in mosasaurian evolution.

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