

# 5<sup>th</sup> Triennial Mosasaur Meeting

- a global perspective on Mesozoic marine amniotes

Museum of Evolution, Uppsala University  
Uppsala, Sweden  
May 16-20, 2016

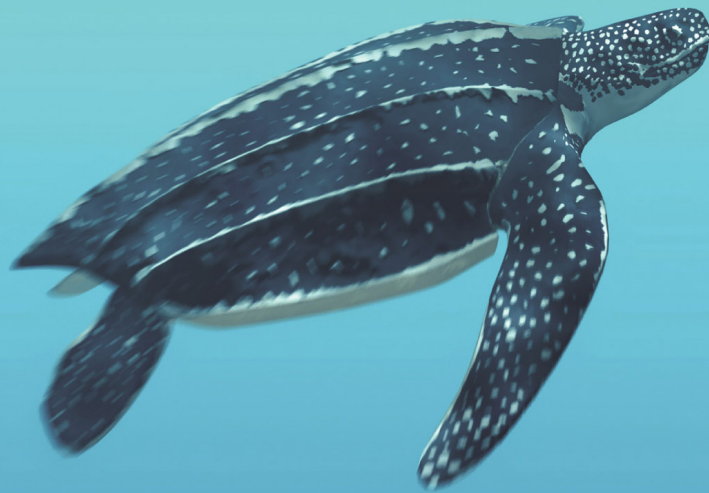


Illustration by Stefan Sølberg

# 5th Triennial Mosasaur Meeting



*A global perspective on Mesozoic marine amniotes*

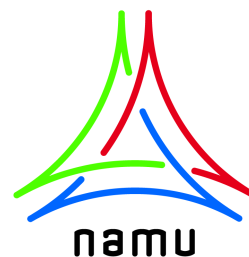
**May 16–20, 2016**  
**Museum of Evolution, Uppsala University**  
**Uppsala, Sweden**

## **Program and Abstracts**

Benjamin P. Kear, Johan Lindgren & Sven Sachs, Editors



**UPPSALA  
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**namu**

natur | mensch | umwelt

**5th Triennial Mosasaur Meeting –  
a global perspective on Mesozoic marine amniotes  
May 16–20, 2016  
Museum of Evolution, Uppsala University  
Uppsala, Sweden**

**Schedule of Meeting Events**

**TUESDAY MORNING, MAY 17, 2016**

**TECHNICAL SESSION I, 10:30–12:00**

**Moderator: Alexandra Houssaye**

- 10:30 **Lindgren, J., Kear, B.P. & Sachs, S.** A BRIEF INTRODUCTION TO THE 5TH TRIENNIAL MOSASAUR MEETING
- 10:40 **Ebbestad, J.O.R.** CARL WIMAN AND THE FOUNDATION OF MESOZOIC VERTEBRATE PALAEONTOLOGY IN SWEDEN
- 11:00 **Everhart, M., Jagt, J.W.M., Mulder, E.W.A. & Schulp, A.S.** MOSASAURS – HOW LARGE DID THEY REALLY GET?
- 11:30 **Polcyn, M.J., Bardet, N. & Paramo-Fonseca, M.** MORPHOLOGICAL EVOLUTION OF THE MOSASAUR SKULL: NEW SPECIMENS, APPROACHES, AND INSIGHTS

**TUESDAY AFTERNOON, MAY 17, 2016**

**TECHNICAL SESSION II, 13:00–16:30**

**Moderator: Michelle Campbell**

- 13:00 **Allemand, R., Bardet, N., Houssaye, A. & Vincent, P.** VIRTUAL RE-EXAMINATION OF A PLESIOSAURIAN SPECIMEN (REPTILIA, PLESIOSAURIA) FROM THE LATE CRETACEOUS (TURONIAN) OF GOULMIMA, MOROCCO THANKS TO COMPUTED TOMOGRAPHY
- 13:30 **Jagt, J.W.M., Jagt-Yazykova, E.A., Kaddumi, H.F. & Lindgren, J.** AMMONITE DATING OF LATEST CRETACEOUS MOSASAURS FROM JORDAN – PRELIMINARY OBSERVATIONS
- 14:00 **Roberts, A.J., Druckenmiller, P.S., Delsett, L.L. & Hurum, J.H.** A FRESH LOOK AT *COLYMBOSAURUS* (SEELEY, 1874), WITH NEW INFORMATION FROM THE SLOTTSMØYA MEMBER, AGARDHFJELLET FORMATION, SVALBARD
- 14:30 COFFEE BREAK
- 15:00 **Polcyn, M.J. & Bell, G.L.** A REASSESSMENT OF TWO PROBLEMATIC KANSAS MOSASAURS

- 15:30 **Sachs, S., Niedźwiedzki, R., Kędzierski, M., Kear, B.P., Jagt-Yazykova, E. & Jagt, J.W.M.** A REASSESSMENT OF HISTORICAL PLESIOSAURIAN SPECIMENS FROM THE TURONIAN (LOWER UPPER CRETACEOUS) OF THE OPOLE AREA, SOUTHWEST POLAND
- 16:00 **Zverkov, N.G., Averianov, A.O. & Popov, E.V.** BASICRANIUM OF AN ELASMOSAURID PLESIOSAUR FROM THE CAMPANIAN OF EUROPEAN RUSSIA

## **WEDNESDAY MORNING, MAY 18, 2016**

### **POSTER SESSION, 10:00–12:00**

- P1 **Bardet, N. & Galoyer, A.** THE LOST WORLD OF GEORGES CUVIER: MOSASAURIDS FROM THE CAMPANIAN MEUDON CHALK (FRANCE)
- P2 **Grigoriev, D.V.** RECONSTRUCTION OF INNER EAR SHAPE AND SIZE OF *MOSASAURUS*
- P3 **Pellegrini, R.A. & Beatty, B.L.** HISTOLOGY OF *MOSASAURUS MAXIMUS* PTERYGOID DENTITION AND ITS ATTACHMENT TISSUES
- P4 **Sachs, S., Hornung, J.J., Lallensack, J.N. & Kear, B.P.** EVIDENCE FOR A *SIMOLESTES*-LIKE PLESIOSAURIAN FROM THE BERRIASIAN (LOWER CRETACEOUS) LIMNIC-BRACKISH BÜCKEBERG GROUP OF NORTHWESTERN GERMANY
- P5 **Sachs, S., Lindgren, J. & Kear, B.P.** RE-DESCRIPTION OF *THALASSOMEDON HANINGTONI* – AN ELASMOSAURID FROM THE CENOMANIAN OF NORTH AMERICA

## **WEDNESDAY AFTERNOON, MAY 18, 2016**

### **TECHNICAL SESSION III, 13:00–16:30**

**MODERATOR: Sven Sachs**

- 13:00 **Mulder, E.W.A. & Jagt, J.W.M.** A NOTE ON THE ?CHELONIID TURTLE *GLYPTOCHELONE SUYCKERBUYKII* (UBAGHS, 1879) FROM THE UPPERMOST MAASTRICHTIAN OF THE NETHERLANDS
- 13:30 **Vincent, P., Allemand, R., Taylor, P.D., Suan, G. & Maxwell, E.** NEW INSIGHTS ON THE SYSTEMATIC AND PALEOECOLOGY OF A GERMAN PLESIOSAURIAN FROM THE TOARCICAN OF HOLZMADEN
- 14:00 **Grigoriev, D.V.** MOSASAURS OF RUSSIA AND ADJACENT TERRITORIES
- 14:30 COFFEE BREAK
- 15:00 **Polcyn, M.J., Bardet, N., Amaghazaz, M., Gonçalves, O.A., Houssaye, A., Jourani, E., Kaddumi, H.F., Lindgren, J., Mateus, O., Meslouhf, S., Morais, M.L., Pereda-Suberbiola, X., Schulp, A.S., Vincent, P. & Jacobs, L.L.** AN EXTREMELY DERIVED PLIOPLATECARPINE MOSASAUR FROM THE MAASTRICHTIAN OF AFRICA AND THE MIDDLE EAST



- 15:30 **Street, H.P. & Caldwell, M.W.** A REEXAMINATION OF MOSASAURINI BASED ON A SYSTEMATIC AND TAXONOMIC REVISION OF *MOSASAURUS* (SQUAMATA: MOSASAURIDAE)
- 16:00 **Kear, B.P.** POLAR DISPERSAL PATTERNS AMONGST AUSTRALIAN EARLY CRETACEOUS POLYCOTYLID PLESIOSAURIANS

## **THURSDAY MORNING, MAY 19, 2016**

### **TECHNICAL SESSION IV, 9:00–12:00**

**Moderator: Nathalie Bardet**

- 9:00 **Augusta, B.G., Polcyn, M.J., Zaher, H. & Jacobs, L.L.** A GRAVID CONIASAUR (*CONIASAURUS* SP.) FEMALE FROM THE UPPER CRETACEOUS OF TEXAS (USA) AND THE DEVELOPMENT OF DOLICHOSAURS
- 9:30 **Jagt, J.W.M., Barten, L. & Barten, J.** STATE OF PREPARATION OF MOSASAUR ‘LARS’ (*MOSASAURUS HOFFMANNI*) FROM THE MAASTRICHTIAN TYPE AREA, SOUTHEAST NETHERLANDS
- 10:00 COFFEE BREAK
- 10:30 **Lindgren, J.** ANALYSING FOSSIL SOFT TISSUE STRUCTURES: CHALLENGES AND APPROACHES
- 11:00 **Tanimoto, M., Shinzoy, T., Sato, M., Hamazuka, H. & Konishi, T.** A POTENTIAL HALISAURINE (MOSASAURIDAE: HALISAURINAE) TOOTH FROM THE IZUMI GROUP OF SOUTHWEST JAPAN
- 11:30 **Lively, J.R.** THE EVOLUTION AND VARIATION OF BASAL MOSASAURINAE BASED ON A SPECIMEN-LEVEL PHYLOGENY OF “*CLIDASTES*”

## **THURSDAY AFTERNOON, MAY 19, 2016**

### **TECHNICAL SESSION V, 13:00–15:00**

**Moderator: John W. M. Jagt**

- 13:00 **Dumont, M. & Houssaye, A.** WHAT THE 3D VASCULAR SYSTEM OF SQUAMATE BONES CAN REVEAL ABOUT SECONDARY ADAPTATION TO AN AQUATIC LIFE
- 13:30 **Neenan, J.M. & Benson, R.B.J.** EVOLUTION OF THE SAUROPTERYGIAN INNER EAR
- 14:00 **Campbell, M., Japundžić, D., Krizmanić, K. & Caldwell, M.W.** A NEW GENUS OF TETHYAN DOLICHOSAURID FROM THE TURONIAN OF CROATIA
- 14:30 **Houssaye, A. & Klein, N.** MARINE REPTILE BONE MICROANATOMICAL FEATURES – HOW TO INTERPRET THIS HIGH DIVERSITY?

**5th Triennial Mosasaur Meeting –  
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**ABSTRACTS**

**(Alphabetical by Surname)**

**VIRTUAL RE-EXAMINATION OF A PLESIOSAURIAN SPECIMEN (REPTILIA, PLESIOSAURIA)  
FROM THE LATE CRETACEOUS (TURONIAN) OF GOULMIMA, MOROCCO THANKS TO  
COMPUTED TOMOGRAPHY**

Rémi **Allemand**<sup>1,2\*</sup>, Nathalie **Bardet**<sup>1</sup>, Alexandra **Houssaye**<sup>2</sup> & Peggy **Vincent**<sup>1</sup>

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Turonian deposits of Goulmima, Er-Rachidia, Southern Morocco have yielded a diverse marine vertebrate fauna, including chondrichthyans, bony fishes and large marine reptiles such as plesiosaurs, mosasaurs and turtles. These fossils are included in ovoid calcareous nodules that are difficult to prepare. Moreover, bones may be partially or totally dissolved, making their study difficult. Using computed tomography, we have reconstructed the entire skull anatomy of the specimen SMNS 81783, one of the rare plesiosaurian specimens found in this locality and more generally in Africa. The digital 3D reconstruction of the skull and mandible offers for the first time the possibility to exhaustively describe this specimen. The newly evidenced following anatomical characters confirm that it belongs to the Elasmosauridae: 1) a slender triangular skull; 2) a beak index equal to 42 %; 3) a temporal fossa estimated to occupy about 40 % of the skull length; 4) a long process of the premaxillae extending posteriorly to meet the parietal above the orbit and separating the frontals; 5) a margin of the temporal fenestra lacking obvious contribution from the frontal. A preliminary phylogenetical analysis confirms its elasmosaurid affinity. The new anatomical information

provided by the digital reconstruction also permits to discuss the relationships of the specimen with *Libonectes atlasense* and *Libonectes morgani*. The presence of stapes and pineal foramen in SMNS 81783, previously considered absent among this group, are also discussed.

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**A GRAVID CONIASAUR (*CONIASAURUS* SP.) FEMALE FROM THE  
UPPER CRETACEOUS OF TEXAS (USA) AND THE DEVELOPMENT  
OF DOLICHOSAURS**

Bruno G. **Augusta**<sup>1</sup>, Michael J. **Polcyn**<sup>2</sup>, Hussam **Zaher**<sup>1</sup> & Louis L. **Jacobs**<sup>2</sup>

<sup>1</sup>Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil

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*Coniasaurus* Owen, 1850 is a dolichosaurid genus previously reported from the Upper Cretaceous (Cenomanian-Santonian) rocks of England (Kent, East Sussex and West Sussex), USA (Colorado, Kansas, South Dakota and Texas), Germany (North Rhine-Westphalia) and perhaps Australia (Queensland). Most described material comprises incomplete cranial remains and some associated vertebrae. Here we report a new specimen of an adult female and several embryos from the Upper Cenomanian *Sciponoceras gracile* Biozone (~94.5 Ma) of the Britton Formation, Eagle Ford Group northwest of Dallas, Texas. The bones were found in siderite concretions and as isolated elements recovered by screen washing. This is the most complete *Coniasaurus* specimen known so far, the adult including cranial (portions of the frontal, parietal, right quadrate, maxilla, dentary, and posterior mandible), axial (3 cervical, 36 dorsal and 28 caudal vertebrae and isolated ribs), and appendicular (humerus, femur, tibia, fibula?, and phalanges, including one ungual) remains. Embryos are represented by cranial (partial frontals, premaxilla, and tooth bearing elements), axial (cervical, dorsal and caudal

vertebrae), and a few indeterminate limb remains. This specimen can be assigned to the genus *Coniasaurus* by possession of a heterodont dentition with pleurodont tooth implantation; large, swollen tooth crowns with large labial sulcus; tooth apices posteriorly recurved; anteriormost teeth less robust than the posteriormost; well developed zygosphenes-zygantrum articulations; and neural arch of the dorsal vertebrae notched laterally. Comparisons of the embryonic and the adult elements reveal ontogenetic trends: 1) The fusion of the intercentrae with the cervical hypapophyses (unfused in the embryos); 2) The development of a lateral notch in the neural arch of the dorsal vertebrae (the neural arches are flattened in the embryos); 3) Grooves on the cristae cranii of the frontals becoming less conspicuous through development; 4) The increase in proportional size and curvature of the tooth apices in the adult. Furthermore, comparison with additional isolated specimens of putatively different ontogenetic stages, reveals significant changes in tooth morphology through ontogeny and thus calls into question species level identifications and diagnoses depending on dental characters alone. This is the first report of embryos in a dolichosaurid. Viviparity has been reported in the basal mosasaurid taxon *Carsosaurus marchesetti*; however, viviparity in a dolichosaur squamate suggests that this condition may have evolved in the common ancestor of dolichosaurids and mosasaurids. The adult female is the most complete and well preserved *Coniasaurus* specimen thus far reported, and thus allows detailed description of a series of additional characters that have been previously coded as missing in most phylogenetic analyses that include this taxon. The new specimens provide a unique opportunity for anatomical comparison with other Upper Cretaceous marine squamates and refinement of the phylogenetic relationships of dolichosaurids. This research was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) to B.A. and Fundação de Amparo à Pesquisa do Estado de São Paulo (BIOTA/FAPESP 2011/50206-9) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 306777/2014-2) to H.Z.

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**THE LOST WORLD OF GEORGES CUVIER: MOSASAURIDS FROM THE  
CAMPANIAN MEUDON CHALK (FRANCE)**

Nathalie **Bardet**<sup>1\*</sup> & Alain **Galoyer**<sup>2</sup>

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The Late Campanian white Chalk of Meudon, a city located in the suburbs of Paris (France), has yielded during the 19<sup>th</sup> century several mosasaurid remains consisting mainly in isolated teeth, most being nowadays lost. These specimens, which history is associated to the most famous French palaeontologist of that time like Georges Cuvier, Paul Gervais and Albert Gaudry, represent the earliest mosasaurid discoveries from France. As such, they are precious and unique testimonies of a nowadays “lost world”. In this work, an historical approach has been privileged, focusing on the history of these discoveries and how they were originally perceived and interpreted by Cuvier and others. In total, about fifteen specimens were originally described or mentioned, of which currently only half have been localized in the Palaeontology and Geology collections of the MNHN of Paris. The recovered material has been recently revised and most specimens referred to an indeterminated species of the tylosaurine *Tylosaurus*. However, it should be pointed out that, according to original descriptions and drawings of specimens now lost, *Plioplatecarpus* and possibly *Prognathodon* were also part of this Late Campanian mosasaurid fauna.

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**A NEW GENUS OF TETHYAN DOLICHOSAURID FROM THE  
TURONIAN OF CROATIA**

Michelle **Campbell**<sup>1</sup>, Dražen **Japundžić**<sup>2</sup>, Katarina **Krizmanić**<sup>2</sup> & Michael **Caldwell**<sup>1</sup>

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Until recently, knowledge of dolichosaurids (Ophidiomorpha, Squamata) consisted primarily of Cenomanian and Santonian finds from the Western Tethys. However, recent discoveries are changing this traditional understanding, with fossils from sediments as old as the Aptian or Barremian, and as young as the Campanian or even Maastrichtian. Spatially, dolichosaur diversity remains concentrated in the Western Tethys (Southern Europe and the Levant), but specimens have also been recently reported from North America, Japan, Australia, Patagonia, and Central Asia. This indicates that our understanding of the evolution of this group needs to be re-evaluated, as they show a much more temporally and geographically diverse pattern than previously indicated. We report here on a new dolichosaur from the Turonian of Croatia which helps to fill the Cenomanian-Santonian gap in the stratigraphic distribution of this group. The new specimen was discovered in 2008 on the Island of Dugi Otok, Croatia (Turonian; U. Cretaceous). Though heavily weathered at the time of its discovery, the articulated specimen was nearly complete from the anterior of the pelvis to the anterior cervical vertebrae. Unfortunately, after two years of further weathering on the shoreline, it now consists of a worn impression and a few fragmentary bones. The remaining elements include the majority of the cervical and dorsal vertebrae, fragments of the dorsal ribs, and an exquisitely preserved right forelimb. Impressions from the cervical and most of the dorsal ribs are present, as is the impression of the left forelimb, pectoral girdle and cranium. The tail,

pelvis and hind limbs have been lost. The individual, which would have been roughly a metre in length, has a distinctively long, cylindrical body with 8-10 cervical vertebrae and at least 23 dorsal vertebrae with posteriorly curved ribs. This is consistent with other long-bodied ophidiomorphs, and the length of the neck (> 7 cervical vertebrae) implies that the animal can be assigned to the family Dolichosauridae. Assessment of the forelimb suggests that a new taxon is represented, showing unique features of the paddle-like morphology. The articulated manus is particularly distinctive, exhibiting a broad, flattened first metacarpal similar to that found in the mosasauroid clade Mosasaurinae.

The importance of this find stems not only from the recognition and description of a new genus, but also the fact that it expands the known morphological, temporal and geographic variation of the dolichosaur lineage. Additionally, the unique anatomy of the forelimb gives valuable insight into the evolution of aquatic characteristics in Cretaceous marine squamates.

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## **WHAT THE 3D VASCULAR SYSTEM OF SQUAMATE BONES CAN REVEAL ABOUT SECONDARY ADAPTATION TO AN AQUATIC LIFE**

Maïtena **Dumont**<sup>1,2</sup> & Alexandra **Houssaye**<sup>2</sup>

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Squamate is a group showing several forms that adapted to aquatic lifestyles. Besides, marine squamates exhibit distinct types in their ecological habitat, swimming modes but also physiology. Bone vascularization is considered as a printer of bone mechanical properties and

animal growth speed (and thereby provides information about animal metabolism). Major changes should thus occur in the cortical bone of the aquatic squamates, according to their different locomotor, ecological and physiological adaptations. To analyze them, we used synchrotron micro-tomography to qualify and quantify in three-dimensions the vascular bone network of marine squamates and of their terrestrial sister groups. As our comparative research involves snakes, we focused our study on vertebrae. Here we present preliminary results on the vascularization pattern of the vertebral cortex of a few mosasauroids and ophidiomorphs: the pythonomorph from Touraine, *Carentonosaurus*, the mosasaurs *Tethysaurus* and *Eonatator*, the snake *Palaeophis*, and modern *Varanus* and *Python*. Three-dimensional vascular organizations of these different forms are compared with previous (2D) histological observations. Differences in vascular orientation and density are clearly observed from a few radial vascular canals in terrestrial forms to dense longitudinal organization in aquatic mosasauroids. This study permits to confirm and further extend data based on previous studies, and delivers a more detailed quantification of the changes in the vertebral cortex structure associated with secondary adaptation to an aquatic life.

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## **CARL WIMAN AND THE FOUNDATION OF MESOZOIC VERTEBRATE PALAEONTOLOGY IN SWEDEN**

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In 1908, Carl Wiman of Uppsala University, Sweden, discovered rich horizons with Triassic vertebrate remains in Spitsbergen on Svalbard, Norway. This marked the beginning of vertebrate palaeontology as a science in Sweden, subsequently developed mainly through the

collection and study of non-Swedish fossil remains. Wiman's accomplishments, resolute personality and a tight network of influential friends and supporters enabled him to become the first person in Sweden to hold a university chair in Palaeontology and Historical Geology. He also managed to amass large numbers of unique fossil vertebrate specimens culminating in an extensive Chinese collection of both world famous dinosaurs and Neogene mammals deposited at Uppsala University. Joint scientific Sino-Swedish collaboration and a deliberate Swedish scientific agenda ensured this unprecedented situation in an opportune moment. Governmental support and initiative allowed Uppsala University and Carl Wiman's Palaeontological Institute to erect a museum building dedicated foremost to the Chinese material, now known as the Lagrelius Collection in recognition of the patron behind Wiman's ambitious endeavours. In addition, the museum served as a permanent repository for seminal collections of Mesozoic fossils from Svalbard and North America. Collectively, these represent a landmark research and teaching resource that remains of intense scientific interest even today.

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## **MOSASAURS – HOW LARGE DID THEY REALLY GET?**

Michael **Everhart**<sup>1</sup>, John W.M. **Jagt**<sup>2</sup>, Eric W.A. **Mulder**<sup>2,3</sup> & Anne S. **Schulp**<sup>2,4,5</sup>

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The recent blockbuster film *Jurassic World*, featuring a CGI animation of a rather large “mosasaur”, prompted us to reflect on the ultimate size mosasaurs could *really* attain. The possibly 60 m sea monster as displayed at the “Jurassic [Sea] World” theme park in the film markedly exceeds the size of any known mosasaur specimen. Given the interest the film has generated, we feel that a review of extremely large mosasaur fossils is warranted here, if only to put film-star mosasaurs in perspective. Mosasaurs evolved during the latter part of the Cretaceous from small shore-dwelling reptiles into a wide variety of species to exploit a wide variety of niches – and ranging in size from the diminutive *Carinodens* to the largest tylosaurines and mosasaurines which exceeded 15 m in length.

The estimated body length of 17,6 m referred to by Lingham-Soliar (1995) is based on extrapolations on the “Hageman” specimen in the NHMM collections (NHMM 009002), a 920-mm-long portion of dentary with 13 tooth positions, which must have belonged to a considerably larger specimen than the holotype. The Natuurhistorisch Museum Maastricht collection also hosts a quadrate that is about 150% the average size of this bone in an “adult” *Mosasaurus hoffmanni*. This specimen, NHMM 003892, is 215 mm tall, and may represent an mosasaur that was close to 18 m in total length. The Penza *Mosasaurus* sp. specimen reported by Grigoriev (2014) from Russia is also in the 17 m size range, as well as *Tylosaurus* (*Hainosaurus*) *bernardi* from Belgium.

In the Western Interior Seaway of North America, *Tylosaurus proriger* had reached lengths of 15,8 m or more by the Early Campanian, based on the Bunker specimen (KUPV 5033) from western Kansas and similarly sized remains from Texas and Manitoba. Fragments of larger individuals have been reported but are not well documented.

Given enough time, and supported by a little help from Archimedes, mammals which adapted to aquatic life eventually reached body sizes well beyond those of the largest mosasaurs, although those marine mammals adapted to a planktonivorous lifestyle. So would

a 60-metre mosasaur be a biological possibility at all? Or would the squamate Bauplan hit the biomechanical constraints at a lower length already? The curve of the largest mosasaur body lengths did not show any indication of “plateauing” towards the K/Pg boundary. Had they not gone extinct, would the hypothetical Eocene giant “Killer Mosa” have discouraged any mammal moving into the marine realm?

## References

- Grigoriev, D. V. (2014) Giant *Mosasaurus hoffmanni* (Squamata, Mosasauridae) from the Cretaceous (Maastrichtian) of Penza, Russia. Proceedings of the Zoological Institute RAS 318(2): 148–167.
- Lingham-Soliar, T. (1995) Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, Upper Maastrichtian of the Netherlands. Philosophical Transactions of the Royal Society of London B347: 155–172.
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## MOSASAURS OF RUSSIA AND ADJACENT TERRITORIES

Dmitry V. Grigoriev

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Russia and adjacent territories, including Ukraine, Kazakhstan, Uzbekistan, and Azerbaijan makes up one-seventh of the land mass. In the Cretaceous, large parts of the European Russia and Siberia were covered by the epicontinental seas. In spite of this the fossil record of the marine reptiles including mosasaurs from Russia and neighbouring countries is still scarce.

The last summaries of mosasaur remains from this territory were published by Pervushov

*et al.* (1999) and Storrs *et al.* (2000). The taxa list provided by those authors was not documented by description and illustration of actual fossils.

Study of mosasaurs in Russia began in 19th century with the description of caudal vertebra from the Upper Cretaceous of Saratov Region (Sintsov, 1872). In recent years new mosasaur specimens have been collected from more than 62 localities from different parts of the country, of which one Cenomanian, one Turonian, two Santonian, 22 Campanian, and 36 Maastrichtian. The majority of known specimens are represented by isolated bones of the skull and postcranial skeleton. More or less complete skeletons which are currently preserved are very rare. Such findings include a partial skeleton of *Prognathodon lutugini* from the Campanian beds in Eastern Ukraine (Grigoriev, 2013), incomplete skull of *Mosasaurus hoffmanni* from the upper Maastrichtian deposits of Penza (Grigoriev, 2014), and a partial skeleton of presumably *M. hoffmanni* from the Maastrichtian beds in Saratov Region (Bayarunas, 1914). About 88% of all bone remains come from Volga River Basin (Penza, Saratov, and Volgograd regions).

Latest most significant findings are the frontal bone of *Clidastes propython* from Saratov Region (Grigoriev *et al.*, 2015), part of vertebral column of Tylosaurinae indet. from Turonian (?) of Russian Far East (Chukotka Region), anterior part of muzzle attributed to *Prognathodon* sp. from the Maastrichtian deposits of Crimean Peninsula.

Studied mosasaurs are represented by *M. hoffmanni*, *P. lutugini*, *C. propython*, *Carinodens belgicus*, *Prognathodon* sp., *Mosasaurus* sp., *Clidastes* sp., *Plioplatecarpus* sp., *Halisaurus* sp., Mosasaurinae indet., Tylosaurinae indet., Plioplatecarpinae indet., Russellosaurina indet., and Mosasauridae indet.

The work was supported by the Russian Scientific Fund Project 14-14-00015.

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## RECONSTRUCTION OF INNER EAR SHAPE AND SIZE OF *MOSASAURUS*

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Study of the inner ear morphology is crucial for understanding the vertebrate locomotion and

behavior. There are only few publications with description of inner ear structures in mosasaurs. The present study reconstructs the bony labyrinth endocast of *Mosasaurus* based on high resolution CT scans of articulated prootic, opisthotic, and supratemporal (ZIN PH 63/90) from the upper Maastrichtian beds of Rasstrigin locality (Volgograd Region, Russia). The studied specimen lacks the supraoccipital and thus the reconstruction of some endocast elements, including parts of vestibule, anterior and posterior semicircular canals (ASC and PSC) is incomplete. The skull length of the studied individual of *Mosasaurus* was estimated based on the length of articulated prootic and supratemporal.

ZIN PH 63/90 belong to the subfamily Mosasaurinae, while the previous studies have shown structures of the inner ear solely for the clade Russellosaurina (Tylosaurinae + Plioplatecarpinae): *Tylosaurus nepaeolicus*, *Platecarpus tympaniticus* (Georgi, 2008), *Platecarpus* sp. (Georgi, 2008; Yi, 2012), and *Plioplatecarpus peckensis* (Cuthbertson *et al.*, 2015). These species are older (from upper Coniacian to Campanian) and smaller than *Mosasaurus* sp. from Rasstrigin locality. Approximate body size of the previously studied species vary from 5.5 m (*P. tympaniticus*) to 8–9 m (*T. nepaeolicus*) (Everhart, 2002; Konishi *et al.*, 2012), while the length of the Rasstrigin specimen is estimated as 14 m.

ASC and PSC meet at an angle of 72.4°, ASC and LSC (lateral semicircular canal) meet at an angle 83.9°, and PSC and LSC meet at an angle 87.2°. LSC length is 25.3 mm. Absence of the fragment of the bony labyrinth does not allow to measure ASC and PSC length. Despite that it is possible to conclude that *Mosasaurus* inner ear is different from the previously described taxa. ASC and PSC have distinct dorsal compression. Ampullae of PSC and LSC are separated from each other while in other species they seem to be fused. However, it could be a matter of different states of preservation. The part of LSC enclosed in prootic is extremely thin (in the thickest region it is 0.41 mm), while in the adjacent opisthotic part it is wider more than five times (2.36 mm). It could be some kind of pathology that may hinder the movement of endolymph inside LSC which in turn could have affection on yaw movements (left-right in horizontal plane) of the head.



Also this study confirms that canal size does not appear to have been adapted to increase or decrease sensitivity (like in cetaceans) (Cuthbertson *et al.*, 2015) because the relative length of LSC in *Mosasaurus* is very close to *Platecarpus* and *Varanus* (Yi, 2012).

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**MARINE REPTILE BONE MICROANATOMICAL FEATURES –  
HOW TO INTERPRET THIS HIGH DIVERSITY?**

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If marine reptiles are nowadays relatively poorly diversified, this was not the case during the Mesozoic when a high number of very different forms inhabited the seas. Despite natural convergences associated with secondary adaptation to an aquatic life, this change of habitat also led to specific types of specializations, between shallow water taxa still able to occasionally locomote on land and open-marine forms totally independent from the terrestrial environment, but also between surface swimmers and deep divers, ambush or pursuit predators, giant and smaller forms.... This is notably true for inner bone structure specializations. Bone microanatomy is considered to be strongly associated with bone functional requirements and is thus a powerful tool to understand bone adaptation to functional constraints and to make functional inferences on fossil taxa. Two major microanatomical specializations were described in aquatic amniotes, referred to as bone mass increase and a spongy "osteoporotic-like" organization respectively. Recently, the bone microanatomy of various marine reptile groups was investigated in detail and revealed that numerous intermediary (and some contradictory) patterns occur between extremes in these specializations. Moreover these taxa display various distributions of these specializations in their skeleton. Here we propose, based on the analysis of the various microanatomical patterns observed in long bones, vertebrae and ribs of a large sample of marine reptiles, to illustrate and discuss this variability and the distinct types of microanatomical adaptations to

various marine ecologies.

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**STATE OF PREPARATION OF MOSASAUR ‘LARS’ (*MOSASAURUS HOFFMANNI*) FROM THE  
MAASTRICHTIAN TYPE AREA, SOUTHEAST NETHERLANDS**

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Currently, the fragmentary mosasaur skeleton (estimated c. 40 per cent, inclusive of the skull), recovered in April-September 2015 from the Emael Member (Maastricht Formation; late Maastrichtian, *Belemnitella junior* Cephalopod Zone) at the ENCI-HeidelbergCement Group quarry (Maastricht), is the main attraction in the new Sciencelab at the Natuurhistorisch Museum Maastricht. Since the opening of this permanent laboratory (January 16, 2016), volunteers and museum staff have been preparing two principal pieces. One is large chunk of matrix, of around 90 kg, that has yielded fairly numerous flipper bones, two pieces of a pterygoid jaw (with two teeth, one preserved *in situ*) and what appears to be the left squamosal. Of note is that at least four of the flipper bones from this block show healed lesions, with scar tissue, indicative of some kind of encounter during life. The main piece (‘skull block’) has now been completely freed from its protective plaster jacket and framed in so as to avoid diagonal cracks to develop further and lead to bone damage and possible loss of material. A partial upper jaw (left) is exposed, the right jaw apparently being displaced and situated underneath; the premaxilla has not yet been recognised. The lower jaws are also documented, but these have suffered considerable damage during lifting and transportation,

although all broken pieces have been salvaged. More of the skull appears to be sitting in this block; on one end, at least two cervical vertebrae have now been exposed, together with other bones that have yet to be identified. To date, we have not seen any shoulder girdle elements, nor quadrate(s), but all bones now freed from the matrix clearly show this to be a subadult individual of *Mosasaurus hoffmanni*, the commonest mosasaur taxon in the area. Volunteers and museum staff working at the Sciencelab (on regular working days [with the exception of Mondays] and during weekends) wear headsets to allow them to communicate with the public. Visitors can use four cameras to zoom in on specific parts of the blocks under preparation, and on another screen videos are shown of the quarry, highlighting several issues of fossil content, the history of the name ‘Maastrichtian’ and mosasaurs in general. At a later date, more detailed information on the mode of life of mosasaurs, their skeletal structure and other anatomical details, will be made available to the public to add to the ‘hands-on experience’.

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#### **AMMONITE DATING OF LATEST CRETACEOUS MOSASAURS FROM JORDAN – PRELIMINARY OBSERVATIONS**

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Recently, Ahmad *et al.* (2015) have recorded three ammonoid taxa (Cephalopoda) from upper lower Maastrichtian rocks in the Outhriate area, Jordan (*Gansserina gansseri* Planktonic Foraminifer Zone, c. 20 m below the Cretaceous-Paleogene boundary), namely *Hauericeras* sp., *Libycoceras acutodorsatus* and *Baculites ovatus*. The second of these is also known from the upper Maastrichtian of Baluchistan (Pakistan) and Iran (see Fatmi & Kennedy, 1999), while the last-named is both long ranging (late Campanian-late early Maastrichtian) and widely distributed. New material, collected by one of us (HFK) and co-workers, from the Muwaqqar Chalk Marl (MCM) at Harrana, includes medium-sized indeterminate baculitids, the sphenodiscid *Libycoceras acutodorsatus* and two pachydiscids, *Pachydiscus* aff. *dossantoi* and *Menuites fresvillensis*. Of these, the former occurs also in the United Arab Emirates/Oman border area, in strata of (late) early to early late Maastrichtian age (Kennedy, 1995) and from unspecified Maastrichtian levels in Brazil and Nigeria. The latter is a late Maastrichtian index species, with records from central Chile, Europe, South India, Pakistan, Australia, Madagascar and South Africa (Ward & Kennedy, 1993; Kennedy & Klinger, 2006; Salazar *et al.*, 2010). Comparison with the Maastrichtian type area suggests correlation with the middle/upper Maastricht Formation (Emael and Nekum members) and the upper Kunrade Formation. From these levels the following mosasaur genera are known to date: *Mosasaurus*, *Prognathodon*, *Plioplatecarpus* and *Carinodens*. Coeval strata of the Muwaqqar Marl Formation at Harrana have yielded remains of *Prognathodon*, '*Platecarpus*', *Mosasaurus* and *Carinodens* (Kaddumi, 2009; Lindgren *et al.*, 2013).

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## **POLAR DISPERSAL PATTERNS AMONGST AUSTRALIAN EARLY CRETACEOUS POLYCOTYLID PLESIOSAURIANS**

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Polycotylids were a predominately Late Cretaceous radiation of large-skulled

“pliosauromorphs” whose remains are found globally after a sudden appearance in the rock record at around the Aptian-Albian boundary. The stratigraphically oldest fragmentary polycotylid fossils occur in Aptian polar epeiric sediments of what is now southern Australia (Kear 2005). Cladistic topologies have additionally referred several coeval “pliosauromorph” taxa scored from associated or articulated skeletons: the early Aptian “*Leptocleidus*” *clemai*; and early Aptian–earliest Albian *Umoonasaurus democyllus*. Unfortunately, the osteology of these archetypal species has not been sufficiently documented, and indisputable polycotylids from sympatric strata have yet to be formally described. Moreover, the Gondwanan emergence of Polycotylidae has been contested by the recognition of early Albian remains from Boreal high-latitude deposits in North America (Druckenmiller & Russell 2009). To explore these palaeobiogeographical scenarios and provide a comprehensive appraisal of the Australian fossils, a sequence of S-DIVA, Bayesian Binary MCMC, and Lagrange optimization analyses were implemented across parsimony and Bayesian tree topologies derived from taxon-rich datasets of Plesiosauria. The results confirmed a Gondwanan polar dispersal deep within the polycotylid lineage, although seminal migrations amongst leptocleidians seem to have occurred from the northern hemisphere across the palaeo-Atlantic and Tethyan margin. Updated anatomical information for Australian polycotylids has further identified a new Gondwanan high-latitude taxon from the upper Albian Allaru Mudstone of Queensland. The unequivocal phylogenetic positioning of this specimen renders it amongst the most basal austral exemplars of the clade.

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## **ANALYSING FOSSIL SOFT TISSUE STRUCTURES: CHALLENGES AND APPROACHES**

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The fossil record is capable of exceptional preservation. On rare occasions, labile and decay prone tissues, such as skin, are preserved as organic residues and/or phosphatized remains with a high degree of morphological fidelity (sometimes revealing minute histological details). These unusual findings yield information on traits of ancient organisms not normally available to the scientific community, and are thus invaluable resources for enhancing our understanding of the biology and ecology of extinct animals. However, analysing fossil soft tissue structures is not a straightforward process, and hence caution needs to be exercised in this endeavour. Additionally, although the methodological advances and sophisticated new tools of molecular biology and analytical biochemistry have provided access to novel sources of geobiologically relevant information, the data produced are often ambiguous and thus difficult to interpret. This evokes excitement but potentially also overenthusiasm, which in turn may result in overconfidence in both the results and methods being employed.

Here, I address conceptual and methodological issues related to the interpretation of biomolecular remains detected in fossilised animal soft tissues. As a framework, I present molecular and ultrastructural data obtained from an array of ‘carbonized’ fossils, including marine amniote skin and various controls, such as cephalopod ink sacs, leaves and wood. Over the last few years, my team and I have used a suite of sensitive chemical, molecular and structural techniques, including alkaline hydrogen peroxide oxidation, infrared (IR) microspectroscopy, field emission gun scanning electron microscopy (FEG-SEM), transmission electron microscopy (TEM), and time-of-flight secondary ion mass spectrometry (ToF-SIMS) to investigate exceptionally preserved fossils. Our integrated approach have revealed that

complex series of taphonomic pathways, incorporating both organic and geochemical agents, probably contribute to the replacement of original tissues by authigenic minerals, as well as the retention of endogenous biomolecules in multimillion-year-old animal remains. Moreover, by combining multiple independent analytical techniques the precision of the data collected is greatly improved, which in turn augment the accuracy of the interpretations. A more widespread understanding of the processes leading to exceptional preservation, as well as the pros and cons of the methods employed, will reduce the risk of introducing spectacular, yet insufficiently supported claims propagating in the literature.

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**THE EVOLUTION AND VARIATION OF BASAL MOSASAURINAE BASED ON A  
SPECIMEN-LEVEL PHYLOGENY OF “*CLIDASTES*”**

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I examine the relationships of and variation within species of *Clidastes* to better understand the early evolution of the clade Mosasaurinae. The mosasaurines are a clade of marine squamates that includes the genera *Dallasaurus*, *Clidastes*, *Mosasaurus*, *Plotosaurus*, *Prognathodon*, *Plesiotylosaurus*, and *Globidens*. The oldest and most basal mosasaurine, *Dallasaurus turneri*, is known from the Turonian of Texas. By the Maastrichtian, mosasaurines are the most diverse and disparate clade of marine squamates. Despite this high diversity and an abundance of specimens, a number of phylogenetic and taxonomic issues within the clade are unresolved. One of those issues is the paraphyly of the genus *Clidastes*, based on a number of published phylogenetic hypotheses. The original type species was *Clidastes iguanavus*, the holotype of which is a non-diagnostic, isolated vertebra. *Clidastes propython* was designated as

the replacement type species for the genus. Other currently-recognized species within the genus include *Clidastes liodontus*, *Clidastes moorevillensis*, and an unnamed taxon from the Campanian of Texas. The type specimen of *Clidastes liodontus* was housed at Bayerische Staatssammlung für Paläontologie, is presumed to have been destroyed during the Second World War, and was not figured in the publication describing it. *Clidastes moorevillensis*, as it is referred to in recent publications, was originally designated as *Clidastes liodontus moorevillensis* in an unpublished thesis and has never been formally described. Traditionally, those species of *Clidastes* were diagnosed based on characters of the frontal and quadrate.

To better understand the evolution and systematics of *Clidastes*, I scored morphological characters of over 40 specimens of *Clidastes*, as well as other species of mosasaurines. I then performed specimen-level phylogenetic analyses, using both traditional character scorings from previous studies and character states that more precisely describe the anatomy of a given specimen. For example, I scored the absolute number of maxillary teeth for the latter analysis, contra to the first analysis in which each character state is represented by a range of tooth counts. Characters I found that vary intraspecifically within species of *Clidastes* include the length of the premaxilla-maxilla suture, the number of teeth in the maxilla and dentary, sculpturing of the frontal, and the dimensions of the quadrate stapedial pit. Those characters do not vary to the same degree in plioplatecarpines or tylosaurines. The paraphyly of “*Clidastes*” with respect to the rest of Mosasaurinae (exclusive of *Dallasaurus turneri*) is supported by both of my analyses. In the second analysis, I used characters that capture the variation observed within “*Clidastes*” specimens. A decrease in the resolution of the phylogenetic hypothesis resulted, producing a basal polytomy within Mosasaurinae. In the most parsimonious trees from that analysis, specimens of the various “*Clidastes*” species did not group into monophyletic clades. This is likely because there are more characters that vary intraspecifically, overlapping with specimens of other species, than there are apomorphic character states that unite each species. Depending on the preferred phylogenetic hypothesis, at least two interpretations can be drawn from these results. One possible conclusion is that

there are at least three highly variable species of basal mosasaurine that cannot be united under a single genus if monophyly is the organizing taxonomic principle. Another possible conclusion is that, to the exclusion of *Dallasaurus turneri*, there is a single, highly variable basal mosasaurine lineage within the Western Interior Seaway and Gulf Coastal Region from which we are sampling in Coniacian to Campanian strata. If this is the case, individual species within that lineage may not be distinguishable.

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**A NOTE ON THE ?CHELONIID TURTLE *GLYPTOCHELONE SUYCKERBUYKII* (UBAGHS, 1879)  
FROM THE UPPERMOST MAASTRICHTIAN OF THE NETHERLANDS**

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Until the mid-1950s, the holotype carapace (dorsal and ventral side, but skull lacking, collected in 1877; Institut royal des Sciences naturelles de Belgique collections, Brussels) of *Chelonia suyckerbuykii* Ubaghs, 1879 (p. 249, pls 6, 7), was the sole articulated individual on record of the ?cheloniid genus *Glyptochelone* Dollo, 1903. Ubaghs (1879, p. 264) was not particularly specific about the exact locality, describing it as ‘... une carrière non loin de Fauquemont, sur le versant du plateau de la rive gauche de la Geul’. This means the environs of Valkenburg aan de Geul, possibly in a westerly direction, towards Geulhem. His list of associated invertebrate fossils (gastropods, bivalves and echinoids) places the level which produced the holotype carapace in the higher portion of the latest Maastrichtian Meerssen

Member (Maastricht Formation) in the area, some metres below the Cretaceous-Paleogene (K/Pg) boundary which equates with the Berg en Terblijt Horizon. A second specimen, much damaged by the excavator, was discovered at the 'Kalkmergelmaatschappij St. Pietersberg' quarry (Van der Zwaan quarry), on the western margin of the Sint-Pietersberg on July 30, 1955. The level from which it came is the uppermost portion of the Meerssen Member (*Lockhartia* Benthic Foram Zone), of latest Maastrichtian age (*Belemnella kazimiroviensis* Cephalopod Zone) (see Hofker, 1955). According to Krutzler (1957), this specimen (NHMM 004548) consisted of the pygale, three associated neurals, numerous fragments of costals and marginals of the dorsal carapace, two pieces of both hypoplastra and fragments of both hypoplastra of the plastron as well as a fragmentary caudal vertebra and a near-complete shoulder girdle (minus the left coracoid). Until the mid-1980s the dorsal elements of this specimen were mounted on display; today, only the plastron (still embedded in matrix) is in the permanent museum exhibit. Unfortunately, the shoulder girdle of NHMM 004548 has not been traced in the collections, although Hofker's 1955 (see also 1957) benthic foram sample survives. This find has never entered the scientific literature, a shortcoming which we here wish to rectify by describing the available skeletal elements of NHMM 004548. Although apparently typical of the Meerssen Member, isolated material is on record from deeper levels of the Maastricht Formation at Neercanne (Belgium) and Cadier en Keer (the Netherlands) and of a smaller-sized individual from the 'Assise de Spiennes' (upper Maastrichtian, but markedly predating the Meerssen Member), collected in Hainaut, southern Belgium, in 1899 (compare Krutzler, 1955).

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## EVOLUTION OF THE SAUROPTERYGIAN INNER EAR

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Sauropterygia were an extremely successful radiation of marine reptiles that dominated aquatic environments globally for virtually the entire Mesozoic. Triassic sauropterygians are characterised as being widely diverse and disparate, with nearshore forms: placodonts, pachypleurosaurs, and nothosaurs; as well as the open-water pistosaurs. These sauropterygian groups died out at the Triassic-Jurassic (T/J) boundary. However, Plesiosauria, a pelagic sauropterygian group, crossed the T/J boundary and persisted for the remainder of the Mesozoic. As an independent replicate of the evolutionary transition to pelagic life in tetrapods (seen elsewhere in e.g. cetaceans, ichthyosaurs and chelonoids), sauropterygians provide valuable data on general patterns of the transition from terrestrial/semi-aquatic to obligate aquatic life. We are currently studying the evolution of the inner ear (containing the labyrinth organ of balance and orientation) in sauropterygians to determine how its morphology, and therefore function, changed during the nearshore to open water transition,



and among the distinct long and short-necked morphotypes that evolved repeatedly.

Computed tomographic (CT) models of 22 sauropterygian labyrinths representing their entire evolutionary history indicate a morphological transition between nearshore, Triassic taxa and open water plesiosaurians of the Jurassic–Cretaceous. Triassic sauropterygians possess anteroposteriorly elongate labyrinths, with narrow canal diameters, and anterior and posterior canals that turn ventrally at the dorsal end of the crus, producing an ‘M’-shaped morphology. In contrast, plesiosaurs have bulbous labyrinths with thicker canals and a rounded, horizontal junction of the anterior and posterior canals dorsal to the crus (in most taxa). Initial results show that, with the exception of the basal, near-shore placodonts, sauropterygian labyrinth diameters scale positively and significantly with skull size (basicranial length) and proportional neck length; thus taxa with shorter necks have smaller labyrinths relative to body size. Labyrinth size reduces in response to the evolution of pelagic life, and is further reduced in response to reduction in neck function. Placodont labyrinths are proportionally larger than in eosauroptrygians, with intermediate and long-necked taxa exhibiting reduced ears, and pliosauromorphs, with cetacean-like body proportions, having the proportionally smallest labyrinths. This mirrors the condition seen in cetaceans, which also evolved reduced labyrinths and neck lengths with increasing degrees of aquatic adaptation and underlines an apparently general feature of sensory adaptation in marine tetrapods.

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## **HISTOLOGY OF *MOSASAURUS MAXIMUS* PTERYGOID DENTITION AND ITS ATTACHMENT TISSUES**

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The pterygoid of *Mosasaurus hoffmani* has been examined in regards to tooth replacement and attachment, but no images of histological sections of the element with teeth *in situ* are widely known. Here, we present histological sections of the right pterygoid of the very closely related *M. maximus* (NJSM 11053, one of two classic, largely complete skulls in the collections of the New Jersey State Museum, both excavated in Sewell, New Jersey, USA), and test the assumptions and expected results from previous non-histological examinations of the pterygoid element of *M. hoffmani*. Caldwell *et al.* (2003) showed alveolar bone to be Woven Fibered Bone comprising the interdental plate (and therefore lining the tooth socket) of marginal tooth bearing elements, which in turn are made up of Fibrolamellar Bone. Gross examination of various mosasaur pterygoids led Caldwell (2007) to conclude that the socket of that element wasn't comprised of a complete circle around the tooth, but was rather a three-sided socket similar to that of snakes. Thin-sections NJSM 11053-1 through 11053-5 and to a lesser extent, 11053-8 and 9, show the labial zone of their respective pterygoid tooth and surrounding element tissues. The bone here appears to be fibrolamellar throughout. As Caldwell (2007) surmised, there is no discernible alveolar bone labial wall to the tooth socket in any of these sections. When investigating the lingual side of this specimen, nothing but continuous fibrolamellar bone was found as well, making it indistinct whether the alveolar bone is absent there too, or whether the alveolar bone and tooth bearing element were integrated and indistinguishable. Regardless, we can confirm that no labial wall of alveolar bone exists on the tooth sockets of the pterygoids of mosasaurs, as proposed by Caldwell (2007).

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## **MORPHOLOGICAL EVOLUTION OF THE MOSASAUR SKULL: NEW SPECIMENS, APPROACHES, AND INSIGHTS**

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In recent years, phylogenetic analyses have failed to reach consensus regarding the position of mosasaurs within squamata, and increasingly, analyses of internal relationships amongst mosasaurs have yielded a number of alternate arrangements. Large composite matrices underpinning these analyses derive from different sources of varying taxonomic scope; however, fundamental reassessment of characters and coding has been hampered by the absence of well-preserved basal mosasaur specimens on one hand and the highly derived nature of geologically younger mosasaurids which dominate these analyses on the other. In this talk we present new morphological data for the snout and dermal palate, suspensorium, quadrate, braincase, and other aspects of the skull, based on multiple Turonian mosasaur taxa, showing transitional and previously undocumented morphology. We employ both CT data of exceptionally well preserved, nearly 3-dimensional specimens, and disarticulated prepared

specimens, and comparisons with a broad range of squamate taxa, highlighting issues of character construction, coding, polarity, and outgroup decisions used in previous analyses. We also present inference of evolutionary sequences of morphology leading to the derived condition seen in advanced mosasaurs, shedding light on the early evolution and cladogenesis of major clades of more derived mosasaurs and the phylogenetic position of mosasaurs within Squamata. In this phylogenetic context, we also show broader patterns of homoplasy in derived forms, most broadly driven by shared adaptations to life in water and overprinted with optimization for prey preference and feeding style in certain taxa.

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## **A REASSESSMENT OF TWO PROBLEMATIC KANSAS MOSASAURS**

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We present here a reassessment of YPM40383, considered a basal mosasaurid by Bell (1997) and USNM3777, referred to *Clidastes (Eonatator) sternbergii* by Russell (1967). The skull of YPM40383 is nearly complete but dorsoventrally crushed, and would have been narrow and elongate. There are 23 maxillary, 16 pterygoid, and 5 premaxillary tooth positions. All teeth are simple recurved cones with smooth enamel and no carinae. The nasal process of the premaxilla is broad and contacts the maxilla to the 7th tooth position, its margins converge posteriorly and does not reach the frontal, but is instead embraced by narrow paired nasal bones, which underlie the premaxilla anteriorly and which become increasingly broader posteriorly, overlaying the anteromedial frontal. The frontal and prefrontal form the posterior narial margin. The septomaxillae are broadly exposed in dorsal view posteriorly to at least the

13th maxillary tooth position. The frontal is broad antorbitally, constricted supraorbitally, and bears sharp posterolateral alae. There is no median ridge. The parietal table is broadly subrectangular, narrowing posteriorly, and the pineal foramen is anteriorly located. A thin bony shelf is present between the diverging parietal rami, which in turn bear vertically oriented articulations with the supratemporals on their posterolateral surface and expanded paroccipital contact ventrally. The squamosals are tear-drop shaped with no ascending process. The quadrate has an elongate suprastapedial process, the tympanic alae are thin-walled and form a deep bowl with a modestly developed posteroventral ascending process. The mandibular condyle is convex. The vertebral column is preserved to the pygals. The condyles of the cervicals are dorsoventrally compressed, synapophyses extending below the ventral cotyle margin in the anterior series. Vertebrae increase in relative height through the column and none bear zygosphenes or zygantra. No mandibles or appendicular elements are preserved. USNM3777 is more fragmentary but preserves the articulated anterior snout (with paired nasals embracing the premaxilla visible), a significant portion of the frontal and parietal, parts of the pterygoids, braincase and both mandibles, and a single dorsoventrally compressed vertebral condyle. The skull roof elements are strikingly similar to YPM40383 but different from nominal species of *Eonatator*, all of which have a distinctly triangular parietal table. USNM3777 can be differentiated from YPM40383 by possession of 4 premaxillary tooth positions, at least 24 in the maxilla. the external nares begins at the 11th tooth position, and the more posterior position of pineal foramen. The two taxa share with Halosaurinae, the broad nasal process of the premaxilla and its elongate maxillary suture, posterior entrance of vidian canal at the basioccipital-basisphenoid suture, dorsoventral compression of the cervical series, parietal rami expanded contact with paroccipital process of opithstotic and a lack of zygosphenes and zygantra throughout the column (indicated by YPM40383), but can be differentiated from more derived halosaurines by retention of a relatively plesiomorphic configuration of the quadrate and no median ridge on the frontal. The unique combination of characters justify erection of two new closely related species, together the sister taxon of more

derived halisaurines.

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## AN EXTREMELY DERIVED PLIOPLATECARPINE MOSASAUR FROM THE MAASTRICHTIAN OF AFRICA AND THE MIDDLE EAST

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Fieldwork in the Maastrichtian of Angola, Morocco, and Jordan has yielded new specimens of the enigmatic mosasaur "*Platecarpus*" *ptychodon*, a form named on the basis of isolated teeth from Morocco. The new material includes articulated, associated, and isolated specimens from multiple individuals and reveals remarkable adaptations of the skull and postcranial skeleton that are convergent with certain stages of odontocete cetacean evolution. This unique mosasaur possesses a narrow elongate snout with closely spaced interlocking moderately heterodont teeth, accommodated by pits on the opposing jaw, extremely retracted bony nares, maxillae telescope posteriorly and broadly overlap the prefrontals, reduction of the frontal, elongate parietal and robust temporal arcade. Increased accommodation space for temporal musculature and proportions of the skull suggest optimization for high velocity jaw closure. Extreme adaptations yield an essentially akinetic skull. These include a long, dorsoventrally deep, premaxillary-maxillary suture, immobile contact of the prefrontal with the maxillae and skull roof, frontal-parietal sutural complexity, the postorbitofrontal-jugal-ectopterygoid-pterygoid contact is robust and immobile, and the contacts of the braincase-supratemporal-parietal-squamosal complex eliminates rotation around the metakinetic axis. Postcranial adaptations include a prominently downturned tail, suggesting presence of a well developed fluke and the forelimb morphology indicative of a high-aspect-ratio control surface as would be predicted for a high-performance swimmer. The new material does not support referral to the genus *Platecarpus* but instead supports a close relationship with *Goronyosaurus*, those two taxa recovered as the sister taxon of *Selmasaurus*, a clade that appears to have diverged relatively early in the evolutionary history of plioplatecarpine mosasaurs.

**A FRESH LOOK AT *COLYMBOSAURUS* (SEELEY, 1874), WITH NEW INFORMATION  
FROM THE SLOTTSMØYA MEMBER, AGARDHFJELLET FORMATION,  
SVALBARD**

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*Colymbosaurus* is a genus of long-necked plesiosaurian represented by two valid species; *C. megadeirus* from the Upper Kimmeridge Clay Formation (Kimmeridgian–Tithonian) of the United Kingdom and *C. svalbardensis* from the Slottsmøya Member of the Agardhfjellet Formation (Tithonian) of Svalbard, Norway. Morphologically characterizing *Colymbosaurus* has been problematic due to a lack of articulated skeletons, including the near absence of cranial material. Here we present data on the most complete specimen (PMO 222.663) of *C. svalbardensis* from the Slottsmøya Member yet found, which preserves the posterior half of the axial skeleton, portions of the pectoral and pelvic girdle and all four limbs. A comparative morphological analysis of PMO 222.663 was conducted following an extensive examination of congeners held in British museums and at the University of Oslo Natural History Museum, and a phylogenetic analysis was conducted.



The analysis resulted in newly-recognized diagnostic features for *Colymbosaurus* that include; mid-cervical vertebrae that are marginally anteroposteriorly shorter than dorsoventrally tall and lacking a longitudinal ridge on the lateral surface; mid-caudal centra that are sub-rectangular in anterior view due to a flat ventral surface and possessing widely-spaced chevron facets; an extensive postaxial flange on the propodials; a diamond-shaped fibula in dorsal view; a proximodistally short ulna that is anteroposteriorly wider than the radius. New diagnostic characters for *C. svalbardensis* include; proximodistally short hind limb epipodials; mid-dorsal vertebrae with a taller than wide neural canal; a relatively gracile femoral shaft compared to *C. megadeirus*. The strict consensus tree from the phylogenetic analysis recovered robust support for both species of *Colymbosaurus* as sister taxa. Ongoing studies of other recently discovered material from the Slottsmøya Member promises to expand the diversity and clarify the phylogenetic relationships within Cryptoclididae across the Jurassic-Cretaceous boundary.

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**EVIDENCE FOR A *SIMOLESTES*-LIKE PLESIOSAURIAN FROM THE BERRIASIAN  
(LOWER CRETACEOUS) LIMNIC-BRACKISH BÜCKEBERG GROUP  
OF NORTHWESTERN GERMANY**

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The middle to late Berriasian Bückeberg Group of northwestern Germany has yielded a number of plesiosaurian fossils. These include Europe's most complete Lower Cretaceous plesiosaurian, *Brancasaurus brancai*, in the fine grained, argillaceous Isterberg Formation near Gronau in Westfalen. Recently a second taxon, *Gronausaurus wegneri* was identified from the same locality and stratum (Hampe 2013). A higher diversity in the Bückeberg Group plesiosaurian assemblage is indicated by pliosauiromorph and other plesiosaurian vertebrae from strata in the upper part of the sequence (see e.g. Koken 1896; Hornung *et al.*, 2013), and both vertebrae and rib components described as *Plesiosaurus degenhardti*, from sandstones of the more marginal Deister Formation near Obernkirchen, Lower Saxony (Koken 1896).

The only plesiosaurian cranial remains thus far documented from the Bückeberg Group were with the holotype specimens of *B. brancai*, and *G. wegneri*. These collectively characterize the classical "plesiosauiromorph" morphology of a comparatively small head, long neck and slender conical teeth. Here we report on a newly discovered incomplete mandible representing a large-skulled, macrophagous plesiosaurian found within the coarse-grained nearshore facies from the Deister Formation of the Bückeberge range, probably near Obernkirchen. The more complete mandibular ramus of this specimen measures 315 mm. It also displays a terminal rosette-like procumbent tooth array in the symphyseal region, which is curiously reminiscent of Lower Jurassic rhomaleosaurids and the Middle Jurassic pliosaurid *Simolestes vorax*. The tooth rosette has a maximum diameter of 90 mm and comprises five large circular to ovoid alveoli and a smaller caudalmost alveolus. The most complete second alveolus on the left side measures 15 mm in labiolingual diameter. A prominent lateral concavity at the caudal end of the rosette probably accommodated a large caniniform tooth from the upper jaw. Comparison of the Deister Formation "pliosauiromorph" mandible with

those of *Simolestes vorax* suggests a maximum cranial length of about 600 mm.

As is typical for the Deister Formation sandstones, the "pliosauromorph" jaw is preserved as a highly detailed, undeformed impression remaining after removal of the soft, clay-like replacement of the skeletal material. This preservation mode commonly preserves structures in 3D, including in this case details of the vascular canals, dental lamina foramina and caudomedial symphyseal articulation. As a method to obtain a positive representation of these specimens, classically artificial casts in gypsum or latex were prepared. We employed photogrammetry to create a high-resolution 3D model, which then was inverted in order to generate a digital cast of the specimen.

Although incomplete, the Deister Formation "pliosauromorph" provides new insights into the surprising diversity of the Bückeberg Group plesiosaurian assemblage, which occupied limnic to brackish epicontinental settings incorporating only temporary connections to the sea. The sauropterygians competed in their role as aquatic predators with an abundant crocodilian fauna.

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**RE-DESCRIPTION OF *THALASSOMEDON HANINGTONI* – AN ELASMOSAURID FROM THE  
CENOMANIAN OF NORTH AMERICA**

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*Thalassomedon haningtoni* is one of the most thoroughly documented elasmosaurids. The type specimen, a nearly complete skeleton representing an osteologically mature individual with a well preserved postcranium (but damaged skull) was found in Cenomanian strata of the Graneros Shale in Colorado, USA. The only comprehensive description of this specimen produced so far is that of Welles (1943); however, his interpretations are contentious and require substantial updating relative to subsequent elasmosaurid discoveries. A second specimen of *T. haningtoni* is also known from the Cenomanian Graneros Shale of Nebraska, USA. This skeleton comprises a well preserved skull and articulated series of cervical, pectoral and a few dorsal vertebrae. Welles (1970) briefly mentioned the Nebraska *T. haningtoni* material in a newspaper article, and both Carpenter (1999) and Sato (2002) provided an interpretation of its skull. The osteologically immature elasmosaurid remains of *Alzadasaurus riggsi*, found likewise in Cenomanian strata of the Belle Fourche Formation in Montana, USA, was referred to *T. haningtoni* by Carpenter (1999); however, most of these remains are fragmentary and heavily distorted and they are insufficient for a confident diagnosis. It

therefore cannot be referred to *Thalassomedon* with certainty and is best considered a *nomen dubium*.

Since Welles' (1943) original documentation of *T. haningtoni* is flawed, and a detailed account of the Nebraska specimen has not yet emerged, we reassessed the material first-hand in order to interpret its character states and phylogenetic implications. The postcranial elements of both, the Colorado holotype and Nebraska specimen, are virtually undistorted, and reveal classical elasmosaurid traits, including a convex ventrolateral edge of the orbit, a ventral notch and longitudinal lateral ridge on the craniad cervicals, and transversally narrow cervical ribs (see Sachs & Kear, 2015). The teeth, which bear fine apicobasal enamel striations, are pristinely preserved in the Nebraska specimen. Salient cranial features include a prominent dorsomedian ridge on the premaxilla, ventromedian crest on the mandibular symphysis, dome-shaped parietals, and circular external nares. Moreover, the co-ossified atlas-axis complex (which is better preserved in the Nebraska specimen), bears a prominent hypophyseal ridge, and the craniad cervical centra are amphicoelous. The interclavicle is also fused with the clavicles and bears a prominent midline keel, the propodials are of near equal length but the femur is more slender than the humerus. Finally, a prominent craniolateral cornu is present on the pubis whereas a pelvic bar is absent.

In conclusion, the superb preservation of the Colorado holotype and referred Nebraska specimen of *T. haningtoni* establish a morphological benchmark for this taxon that will be applied for determination of the contentious phylogeny of elasmosaurids and their clade boundaries. Insights into biomechanics and palaeobiology of these quintessential Cretaceous plesiosaurians are also underway.

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**A REASSESSMENT OF HISTORICAL PLESIOSAURIAN SPECIMENS  
FROM THE TURONIAN (LOWER UPPER CRETACEOUS) OF THE OPOLE AREA,  
SOUTHWEST POLAND**

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In 1897, Richard Leonhard presented brief descriptions and some illustrations of a few plesiosaurian remains (teeth and a supposed phalanx) from the lower Turonian of the Opole area (southwest Poland). Leonhard assigned the teeth to *Polyptychodon interruptus* and established a new genus, *Plesiosauridarum* (a species name was not supplied, making this a *nomen nudum*), for the supposed phalanx. Until recently, the whereabouts of all these specimens were unknown. However, during a recent survey of several Polish and German collections, most of Leonhard's specimens could be relocated. Furthermore, other historical, still undescribed specimens (i.e., a tooth and paddle element) were encountered, and these supplement Leonhard's material. Most of the original material has probably been found in now abandoned quarries in the area. Active quarrying is done at the Odra Nowa quarry in the Opole city area, but so far no plesiosaurian remains have been collected there. In total, four slender pliosauiromorph teeth from the Opole area are available for study. These differ from the typically more massive teeth of Late Cretaceous pliosaurids (*Brachauchenius*/*Megacephalosaurus*) and the pliosauiromorph teeth from coeval strata in the Bohemian Cretaceous Basin (Czech Republic; see Kear *et al.*, 2014). However, a closely similar tooth crown has recently been described from the upper Turonian of the Saxonian Cretaceous Basin (eastern Germany; see Sachs *et al.*, 2016). Generic placement of isolated pliosauiromorph teeth from Cretaceous strata to the genus *Polyptychodon* is commonly seen in old literature sources. However, this taxon is, in fact, a *nomen dubium* (see Madzia, 2015). *Polyptychodon* has long been considered to be a late pliosaurid, but the slenderness of some referred tooth crowns, including those from Opole, indicate that these might rather derive from polycotylids (see Sachs *et al.*, 2016). The presence of similar teeth in Turonian strata in Germany and Poland indicate that some pliosauiromorph taxa had a wider distribution than previously recognised.

The paddle element (probably a mesopodial) is not diagnostic at the family level and Leonhard's *Plesiosauridarum* (which, so far, could not be traced) is a mosasauroid vertebra. In order to date these early finds, powdered rock samples for calcareous nannoplankton studies were scraped from the matrix or the infill of dentin canals. Light microscope studies have demonstrated nannofossil assemblages of 32 taxa, dominated by *Watznaueria barnesae*. Based on the presence of the stratigraphically youngest species, *Quadrum gartneri*, the samples appear to be not younger than nannofossil zone UC7, i.e., probably represent the lower (lower middle?) Turonian (see Burnett, 1998).

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**A REEXAMINATION OF MOSASAURINI BASED ON A SYSTEMATIC  
AND TAXONOMIC REVISION OF *MOSASAURUS*  
(SQUAMATA: MOSASAURIDAE)**

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The name Mosasaurini has come and gone from the literature, referring to more and less inclusive groupings genera within the subfamily Mosasaurinae, and generally includes *Mosasaurus* and its closest relatives to the exclusion of genera such as *Prognathodon* and *Globidens*. Previous phylogenetic analyses of Mosasaurinae (e.g. LeBlanc *et al.*, 2012) only considered three species of *Mosasaurus*, which has been common practice since Bell (1997). The use of the same three species is problematic because those taxa represent only a tiny fraction of the nearly 50 species that have been referred to the genus since its erection (Mantell, 1829). However, most of these species are now considered invalid. The study presented here is the most comprehensive treatment of *Mosasaurus* to date and began with the consideration that thirteen species, in addition to the type species *M. hoffmannii*, could potentially be valid. For greater context of the position of *Mosasaurus* within Mosasaurinae, this study also encompassed related genera within the subfamily, such as *Moanasaurus* and *Plotosaurus*.

The preliminary step in this study was to revise the diagnoses for *Mosasaurus* and its type species. Neither the erection of the genus (Conybeare, 1822), nor that of *M. hoffmannii* (Mantell, 1829) were accompanied by a diagnosis, and the concept of both taxa remained vague. Precise diagnoses provide the foundation for the morphological analyses in which

various potentially valid species were compared to the *Mosasaurus* paradigm. The results of the morphological analysis indicate that only two of the thirteen species evaluated are valid and similar enough to *M. hoffmannii* to remain in the genus.

The phylogenetic analysis recovered a monophyletic clade comprising the mosasaurine taxa examined for this study. The phylogenetic analysis also supported the morphological analysis in that a monophyletic *Mosasaurus* was found to be restricted to *M. hoffmannii*, *M. lemonnieri*, *M. missouriensis*, and a new species. Another interesting result from the phylogenetic analysis is that *Moanasaurus* was found to be more diverse and wide-spread than previously recognized. Even as *Mosasaurus* is found to be less speciose than previously thought, Mosasaurini is now recognized as a diverse clade that radiated rapidly from the late Campanian until the End-Cretaceous mass extinction event.

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**A POTENTIAL HALISAURINE (MOSASAURIDAE: HALISAURINAE) TOOTH  
FROM THE IZUMI GROUP OF SOUTHWEST JAPAN**

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Tanimoto *et al.* (2013) described mosasaur diversity in the Izumi Group of southwest Japan based on the material of five specimens from Takinoike, Izumisano City, Osaka Prefecture. Permanently curated at the Osaka Museum of Natural History, OMNH MV89 and OMNH MV90 represent small mosasaur teeth with striation-like prisms, whereas OMNH MV91 and OMNH MV92 represent larger teeth with broader/coarse prisms. Tanimoto *et al.* (2013) suggested that differences of these four teeth may indicate ontogenetic stages of a single mosasaur taxon. Tanimoto *et al.* (2016) further suggested a possibility that these teeth may pertain to a mosasaurine taxon similar to or same as *Mosasaurus prismaticus*. The recently erected *Phosphorosaurus ponpetelegans* from Hokkaido, northern Japan represents the first record of halisaurine mosasaurs from Japan (Konishi *et al.*, 2015). Derived from the same vicinity and the stratigraphic level as the holotype of *Mosasaurus hobetsuensis*, presence of halisaurines in the otherwise mosasaurine-rich Hakobuchi Formation in Hokkaido provides a unique

opportunity to re-evaluate mosasaur diversity in the Izumi Group of southwest Japan. Based on the striation-like prisms, the strong curvature and its small size, OMNH MV92 is here reinterpreted to pertain to an indeterminate species of Halisaurinae, which is most likely to be a more accurate identity of the specimen than it representing an immature individual of *M. prismaticus*-like mosasaurine. The reassignment of OMNH MV92 to Halisaurinae would broaden the range of spatial, and most likely temporal, distribution for halisaurines in the northwestern Pacific realm during the latest Cretaceous. At the same time, the proposed taxonomic reassignment to the specimen well corroborates the common occurrence of halisaurines and mosasaurines in many Maastrichtian strata across the globe.

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**NEW INSIGHTS ON THE SYSTEMATIC AND PALEOECOLOGY OF A GERMAN  
PLESIOSAURIAN FROM THE TOARCICAN OF HOLZMADEN**

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The Posidonien-Schiefer (Toarcian) of Holzmaden, Baden-Württemberg in south-western Germany has yielded many excellently preserved plesiosaurian specimens and received considerable research attention. The plesiosaurs found within these deposits are always significantly outnumbered by ichthyosaurs and close examination of these rare specimens is crucial to a better understanding of the diversity of Plesiosauria in this very peculiar ecosystem. The German plesiosaurian specimen SMNS 51943 found in this area is a juvenile individual consisting of a partial, crushed skull and an exquisitely preserved postcranial skeleton. Its anatomical characters seem to differ from the long-necked plesiosauroids *Microcleidus brachypterygius* and *Seeleyosaurus guilelmiimperatoris* that are the most abundant taxa within the plesiosaurian assemblage. However, the juvenile status of this specimen makes comparisons with other taxa problematic and features potentially less

influenced by the ontogenetic status will be discussed in term of taxonomical utility. The excellently preserved post-cranial skeleton also contains gastric contents and enigmatic structures around the back and hindlimb of the animal, which could provide new insights on the paleoecology of plesiosaurs.

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### **BASICRANIUM OF AN ELASMOSAURID PLESIOSAUR FROM THE CAMPANIAN OF EUROPEAN RUSSIA**

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The braincase of elasmosaurid plesiosaurs is poorly known despite numerous relatively complete and well-studied skeletons.

Thereby a new find of an elasmosaurid basicranium from the Rybushka Formation (mid-Campanian) of Saratov Region, Russia, is of great interest. The specimen, attributed to an elasmosaurid plesiosaur, possess an elongated plate-like median keel of the parasphenoid and the condyle demarcated from the rest of the basioccipital by a deep groove.

The studied basicranium is characterized by a number of peculiar features: extremely anteroposteriorly elongated pituitary fossa, single anterior foramen for the internal carotid arteries, reduced clinoid process, and deep channel on the basioccipital process. These

features indicate profound morphological changes of the brain and head vessels compared with the other known plesiosaurs.

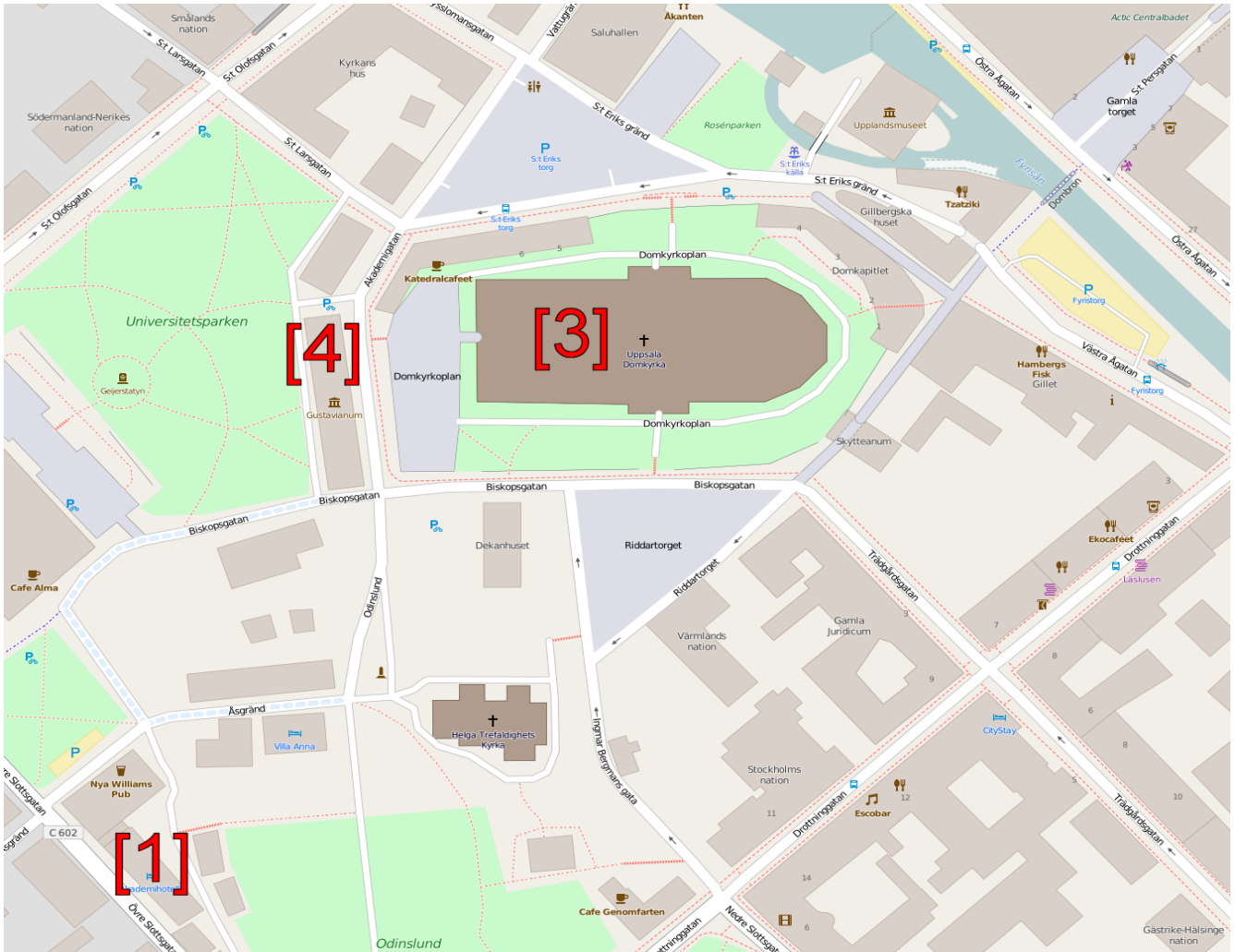
Because of its hidden position, the pituitary fossa is rarely described in amniotes. However, the foramen for the anterior exit of the internal (cerebral) carotid artery is paired in most described amniotes. In all hitherto known sauropterygians these foramina are widely spaced (e.g. Rieppel, 1994; Druckenmiller, 2002; Sato *et al.*, 2011). The single anterior foramen for the internal (cerebral) carotid was recently described in a new aristonectine elasmosaurid *Alexandronectes zealandiensis* (Otero *et al.*, 2016). This feature is a potential synapomorphy for derived elasmosaurids.

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# FIELD TRIP



Source: <http://www.openstreetmap.org>

The field trip start at about 10 am on May 20 outside of Akademihotellet [1]

## First stop

Gamla Uppsala Museum [2]

Disavägen, 754 40 Uppsala  
[[https://en.wikipedia.org/wiki/Gamla\\_Uppsala](https://en.wikipedia.org/wiki/Gamla_Uppsala)]

One of Scandinavia's most noteworthy cultural environments. We will look at finds from archaeological digs and Viking burial mounds, and we will also eat lunch there.





Source: <http://www.openstreetmap.org>

## Second stop

Uppsala domkyrka [3]

Domkyrkoplan, 753 10 Uppsala  
[\[https://en.wikipedia.org/wiki/Uppsala\\_Cathedral\]](https://en.wikipedia.org/wiki/Uppsala_Cathedral)

The Uppsala cathedral dates to the 13th century and is the tallest church in Sweden. Here we will have a look at the holotype of Homo sapiens.

## Third stop

Museum Gustavianum [4]

Akademigatan 3, 753 10 Uppsala  
[\[https://en.wikipedia.org/wiki/Gustavianum\]](https://en.wikipedia.org/wiki/Gustavianum)

The museum is housed in Uppsala University's oldest preserved building with the anatomical theatre on the roof. Exhibited at the museum are, among other things, discoveries from the Viking period, and in the garden you will find a collection of local runestones.