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Mosasaurs from Germany – a brief history of the first 100 years of research

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Abstract

In Germany, mosasaur remains are very rare and only incompletely known. However, the earliest records date back to the 1830s, when tooth crowns were found in the chalk of the Isle of Rügen. A number of prominent figures in German palaeontology and geosciences of the 19th and 20th centuries focused on these remains, including, among others, Friedrich von Hagenow, Hermann von Meyer, Andreas Wagner, Hanns Bruno Geinitz and Josef Pompeckj. Most of these works were only short notes, given the scant material. However, the discovery of fragmentary cranial remains in Westphalia in 1908 led to a more comprehensive discussion, which is also of historical importance, as it illustrates the discussions on the highly controversial and radical universal phylogenetic theory proposed by Gustav Steinmann in 1908. This theory saw the existence of continuous lines of descent, evolving in parallel, and did not regard higher taxonomic units as monophyletic groups but as intermediate paraphyletic stages of evolution. In this idea, nearly all fossil taxa form part of these lineages, which extend into the present time, and natural extinction occurs very rarely, if ever. In Steinmann's concept, mosasaurs were not closely related to squamates but formed an intermediate member in a anagenetic chain from Triassic thalattosaurs to extant baleen whales. The newly found specimen led Josef Pompeckj to write a vehement rebuttal to Steinmann's theory, published in 1910, showing that his conclusions were conjectural and speculative, being based on convergence and not supported by scientific evidence. This particular specimen, housed in Göttingen, later also inspired a piece of palaeoart by Franz Roubal under the instructions of Othenio Abel.

With the exception of a vertebra from the Campanian of former East Prussia (now Russian Federation), and a possible vertebra from the Cenomanian of Dresden, Saxony, all datable material – today partly lost – originated from the northern part of present-day Germany and stratigraphically from the Campanian–Maastrichtian. The purported record from the Cenomanian of Bavaria (southeastern Germany) was most probably an error, based on Upper Jurassic crocodilian material.

Keywords: Mosasaurs, Upper Cretaceous, Germany, historical overview

Introduction

In general, mosasaur remains are rare in German Cretaceous strata and the record is limited to fragmentary specimens, mostly tooth crowns. The majority of these specimens were found before World War II. Some of them were lost during the war, others were kept in private collections and never went into a public repository. Only a part of the available material has recently been redescribed and taxonomically reassigned, most notably the specimens of the von der Marck Collection, which are now housed in the Geomuseum of the University of Münster (Sachs, 2000; Caldwell & Diedrich, 2005). In the present publication we provide a chronological overview of published mosasaur specimens found in Germany prior to 1945 (the localities are shown in Fig. 1). For the sake of completeness, we also include a specimen that was described from former East Prussia, today part of the Russian Federation (Kaliningrad Oblast), but part of the German Empire at the time when the specimen was found and described. However, we only include records for which at least basic information on specimen, age and locality was available. Unsubstantiated and cursory remarks on occurrences, for example those by Roemer (1841) and Goldfuss (1844) for the area of Aachen, North Rhine-Westphalia, close to the Maastrichtian type region, are generally not included. In addition, the lives, scientific backgrounds and views of notable people who were involved in these discoveries will be briefly described and discussed, as well as the impact some of these finds had on contemporary frontier topics in palaeontology.

Institutional abbreviations

GG Institute of Geography and Geology, University of Greifswald
GPIM Geomuseum of the University of Münster
GZG Geoscience Centre, University of Göttingen
SaK Senckenberg Naturhistorische Sammlungen Dresden
UBG University library Greifswald

Chronology

1830–1840s: Friedrich von Hagenow – Maastrichtian of the Isle of Rügen

Karl Friedrich von Hagenow (1797–1865; Fig. 2A) was born into an aristocratic family and grew up in Western Pomerania (Beyrich, 1866; Pyl, 1866). At an early age von Hagenow's tutor

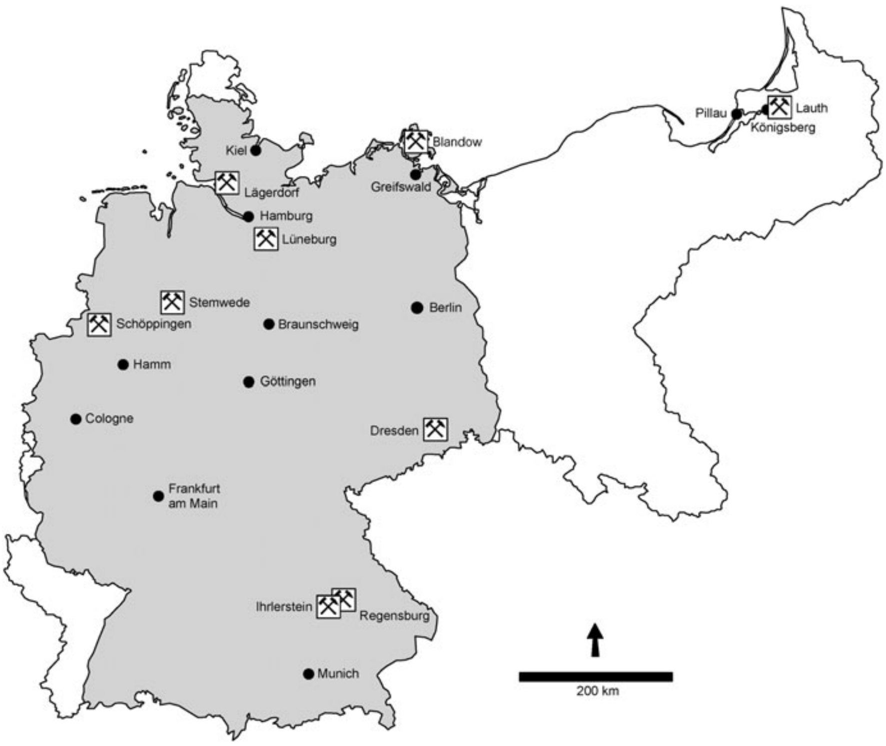

Fig. 1. Map of Germany showing the territory of 1871–1918 (white) and since 1945 (grey). Major cities and important places referred to in the text are indicated. The mining symbol refers to fossil localities.

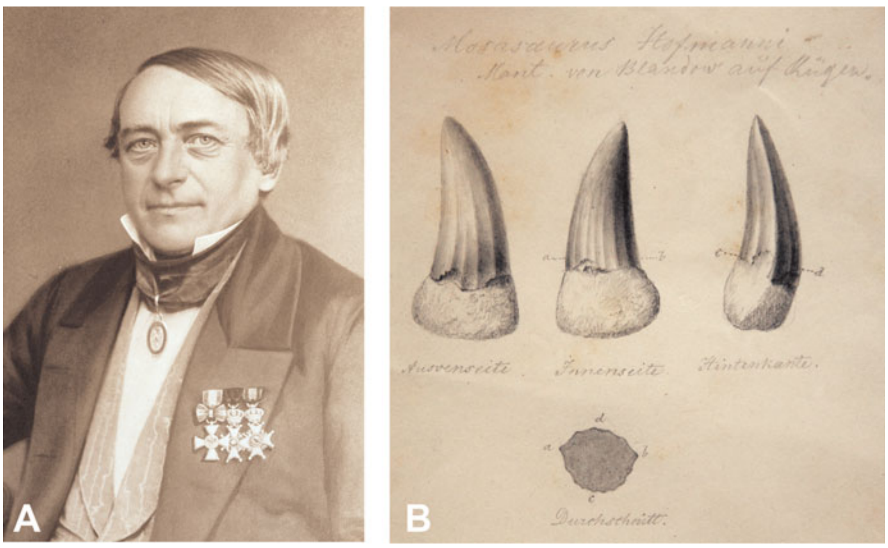

Fig. 2. (A) Friedrich von Hagenow (GG archives, modified). (B) Drawing of a mosasaur tooth crown from Blandow on the Isle of Rügen by von Hagenow (unpublished manuscript, UBG).

(and later stepfather), Gustav Salomon Tillberg (1777–1859), aroused his interest in natural sciences and arranged that he could attend the University of Greifswald in 1809, when the gifted boy was only 12 years old. His principal studies included mathematics, mechanics and ornithology. Von Hagenow had a lifelong vivid interest in prehistory and he carried out the topographical surveying of Neu-Vorpommern (formerly Swedish Pomerania) between 1825 and 1828, for which in 1830 he obtained an honorary doctoral degree from the University of Greifswald. In 1832 von Hagenow purchased a grant licence for the exclusive chalk exploitation on the peninsula of Jasmund, Isle of Rügen (von Hagenow, 1838). In the same year he opened a chalk factory in his place of residence at Greifswald with machines and equipment that he personally designed (Boll, 1865; Habetha, 1939; J. Ansorge & M. Reich unpublished data). As an additional gain of the precipitate chalk production von Hagenow amassed one of the largest collections of chalk fossil of his time, which contained around 100,000 specimens by the end of the 1830s (von Hagenow, 1839).

From this von Hagenow's most eminent opus resulted, the *Monographie der Rügen'schen Kreide-Versteinerungen* (*Monograph on the Cretaceous fossils from Rügen*) of which three volumes were published, dealing with invertebrate fossils (von Hagenow, 1839, 1840, 1842). A fourth volume that should have included the arthropod and vertebrate fossils was never completed due to the delayed return (after 5 years) of fish material sent on loan to Louis Agassiz (Paris and Neuchâtel) and von Hagenow's deteriorating eyesight after 1846. However, some illustrations had been finished, which are preserved as manuscripts in the Greifswald University library (Reich & Frenzel, 2002). Among them is the drawing of a well-preserved crown of a marginal mosasaur tooth from the Lower Maastrichtian chalk of Blandow on the Isle of Rügen (Western Pomerania, north-eastern Germany) that was prepared on the basis of material von Hagenow collected in the 1830s (see also Reich & Frenzel, 2002: pl. 2, fig. 4). This drawing is the earliest unambiguous document of a mosasaur fossil found in Germany. Later authors, especially Deecke (1895, 1907), commented briefly on the existence of mosasaur tooth crowns in the collection of von Hagenow. However, most of his material from the chalk of Rügen was destroyed at Stettin (now Szczecin, Poland) during World War II (Voigt, 1959; Steinich, 1965; pers. comm. W. Filipowiak, 1997), and only a few specimens (long-term loans before 1945) survived at Greifswald University, including a single fragment of a mosasaur tooth crown (Reich & Frenzel, 2002), which is not identical to the splendid specimen figured by von Hagenow (in his estate). Recently, Jagt et al. (2006) proposed that von Hagenow's specimen might represent another individual of the tylosaurine *Hainosaurus* 'sp. 2', which had been described earlier from the Lower Maastrichtian of Poland (Jagt et al., 2005). However, for reasons discussed in Hornung & Reich (2014), it seems more probable that it can be referred to a species of *Mosasaurus* Conybeare in Parkinson, 1822, most probably to *M. hoffmanni* Mantell, 1829. This is congruent with the assignment von Hagenow made on his original illustration (Fig. 2B).

1853–1856: Hermann von Meyer and Andreas Wagner – Turonian/Cenomanian of the Regensburg area

In 1853 Hermann von Meyer briefly mentioned an incomplete reptilian tooth crown allegedly from the Regensburger Grünsand[stein] (now Regensburg Formation, Turonian/Cenomanian; see Wilmsen et al., 2009) found by Professor Karl Emil von Schafhäutl (1803–1890) at an uncertain locality in the vicinity of Regensburg (Bavaria, southeast Germany) (von Meyer, 1853).

Christian Erich Hermann von Meyer (1801–1869; Fig. 3A) was born, grew up and lived for most of his life in Frankfurt am Main (Zittel, 1870). From 1822 to 1827 he studied natural sciences, and geology and mineralogy in particular, at Heidelberg, Munich and Berlin. In 1837 he accepted a position in the financial administration of the German parliament, where he worked for the rest of his career. Perhaps on recommendation of his childhood friend, the well-known chemist Friedrich Wöhler (1800–1882), the University of Göttingen offered him a professorship of Geology and Palaeontology in 1860, which, however, he turned down in order to be able to continue to work independently. Von Meyer carried out all of his voluminous scientific work in his spare time. He did not maintain a significant personal fossil collection, but instead worked on material sent to him by collectors and fellow scientists. Specialising in vertebrates, but with a focus on 'saurians', he is today considered the father of vertebrate palaeontology in Germany and one of the most preeminent figures of his days in this field of science. Hermann von Meyer was the co-founder and co-editor of the journal *Palaeontographica* (founded in 1846) and was a skilful artist who drew all the illustrations for his publications himself (Keller & Storch, 2001).

Von Meyer named some of the most famous fossil vertebrate taxa, including the first dinosaur found in Germany, the sauropodomorph *Plateosaurus engelhardti* von Meyer, 1837, and the first fossil of a Mesozoic bird, the feather of *Archaeopteryx lithographica* von Meyer, 1861. In 1832, he also – independently from Richard Owen – recognised that all genera of dinosaurs then known formed a distinct group (von Meyer, 1832, p. 210), although his proposal to name them 'Pachypodes' (von Meyer, 1845) never caught on. His work and style of thinking was that of a practical observer; it shows few, if any, indications of having been influenced by subjective theories, philosophies or religious beliefs. He observed the occurrences of extinction and gradual changes in the organisms at an early stage of his research (von Meyer, 1832), although he did not try to elaborate on them in a theoretical way or to unify them in a major hypothesis. Nonetheless he rejected the concept of catastrophism and considered the emergence of new species as a continuous, gradual and natural process (von Meyer, 1832, 1852; Hertler, 2001; Keller & Storch, 2001).

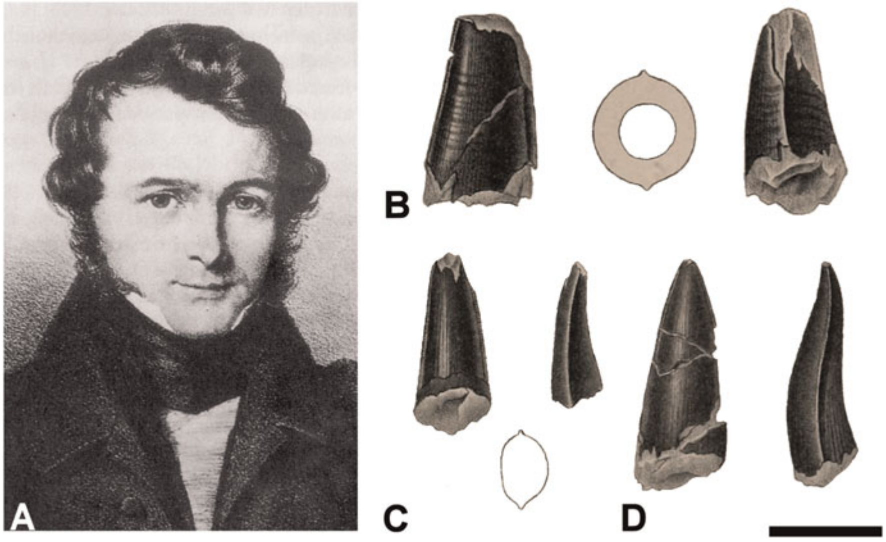

Fig. 3. (A) Hermann von Meyer (from Langer 1997, modified). (B) tooth crown referred to Liodon anceps*? by Wagner (1853) found nearby Regensburg. (C) Holotype tooth crowns of* Liodon paradoxus *found in Ihrlerstein, formerly Neukelheim (from Wagner 1853). Scale bar equals 2 cm.*

In the debate following the publication of Charles Darwin's *On the Origin of Species* (1859) he remained rather neutral and non-committed. Consequently, he did note the presence of true feathers but also of skeletal differences between *Archaeopteryx lithographica* and extant birds as a matter of fact, yet did not dwell on their meaning for evolution (Wellnhofer, 2001).

His work included occasional references to mosasaurs (von Meyer, 1832, 1853, 1856, 1860), especially to the material from the Maastricht area. In 1832 he proposed the species name *Mosasaurus camperi* for all mosasaur material then known from England (UK), Maastricht (the Netherlands) and New Jersey (USA). However, *M. camperi* is a junior synonym of *M. hoffmanni* Mantell, 1829 (see Bronn, 1838; Spamer et al., 1995).

Wagner (1853) formally described the tooth crown that was found by von Schafhäutl (Fig. 3B) and donated by him to the Geognostische Sammlung des Staates Bayern (Geognostic Collection of the State of Bavaria) at Munich.

Johann Andreas Wagner (1797–1861) studied natural sciences, in particular zoology, at Würzburg and Erlangen. At the beginning of his academic career he worked on extant molluscs. In 1832, Wagner was appointed professor in Munich, in charge of the zoological cabinet that also included the palaeontological collection. Besides extensive studies on extant mammals and birds, his work focused on extinct faunas and in particular the fossils found in Bavaria. Wagner was a conservative with a strong faith in Christianity, and a fierce and derisive opponent of the theory of descent as proposed by Darwin in 1859 (von Martius, 1862). He considered this to be scientific fantasy, entirely devoid of evidence. In an ironic twist of historical fate, he was the first to describe scientifically two of the most iconic evidences for evolution which turned up during this time of scientific revolution, although he did not recognise their meaning, nor was even eager to diminish their significance. In the last year before his death, he described a theropod dinosaur from the Upper Jurassic Solnhofen limestones, which he had earlier named *Compsognathus longipes* Wagner, 1859 and which he considered to be a giant, bipedal lizard (Wagner, 1861a). Shortly afterwards, in a story that is more extensively told by Wellnhofer (2009), his assistant, Carl Albert Oppel (1831–1865), showed him a sketch of a new 'reptile with feathers' that had been found in the same strata and offered for sale by its proprietor. This specimen was sold shortly afterwards to the British Museum in London, where it became known as the London specimen of *Archaeopteryx lithographica*, a taxon originally based on von Meyer's (1861) single feather. Without the opportunity to study the original specimen, Wagner dismissed the transitional nature of the specimen, and the impressions surrounding the bone being evidence of feathers, considering it a 'reptile with special adornments', and proposed the name *Griphosaurus* ('miracle lizard') for it (Wagner, 1861b). Near the end of the year of these important discoveries, in December 1861, Wagner died. The fact that *Compsognathus longipes* was a dinosaur – in fact the most complete one known at the time – and the implications of its similarity with *Archaeopteryx lithographica,* were shortly after extensively elucidated by Gegenbaur (1863), Cope (1867) and, most prominently, Huxley (e.g. 1868, 1870).

Wagner (1853) referred the tooth fragment found by Professor von Schafhäutl to *Liodon anceps*? Owen, 1841 in Owen (1840–1845) on account of morphological similarities to the teeth of that taxon described and illustrated by Owen (1840–1845). Two other tooth crowns (Figs 3C and D) from Neukelheim (now Ihrlerstein, Bavaria), also supposed to be from the Regensburg Formation, were considered to be a distinct new species by Wagner (1853), and named *Liodon paradoxus*. Although these teeth did not closely resemble Owen's (1840–1845) teeth of *L. anceps,* Wagner (1853) supposed that they could be pterygoid teeth of that taxon. The same teeth were further discussed by von Meyer (1856). He agreed with Wagner's (1853) generic assignment, but questioned the taxonomic validity of *L. paradoxus* since that species had been established on the basis of only minor differences to the other tooth from the Regensburg Greensand that Wagner (1853) referred to *L. anceps*?. In all probability, the material was destroyed together with many other specimens from the Munich collection by bombing raids in 1944 (e.g. Nothdurft et al., 2002).

Although suffering from loss of material and incomplete original data, today a mosasaur affiliation of von Meyer's and Wagner's material can almost certainly be ruled out. Schlosser (1881, p. 58) listed '*Liodon anceps* und *paradoxus* Wagner [1853]. [...] Taf. III, fig. 6-13' as '*Dacosaurus maximus* Quenst' (sic! – the correct taxon name is *Dakosaurus maximus* (Plieninger, 1846), see Young et al., 2012) and claimed that the remains of matrix on 'two' of the teeth (which apparently belonged to a larger set of specimens than those figured by Wagner (1853)) from Ihrlerstein (Neukelheim)) indicated that they are Upper Jurassic in age rather than Upper Cretaceous. Fraas (1902, pl. II, figs.: 1, 12–14) figured a partial dentary and a tooth from the Upper Jurassic of Schnaitheim as '*Dacosaurus paradoxus* Wagner em. Fraas'. This material shows close similarity to the now lost teeth figured by Wagner (1853, pl. 3, figs. 9–13), supporting a Upper Jurassic age and an assignment to *D. maximus*, representing teeth from the rostral part of the jaws (Young et al., 2012).

The third tooth, first described by von Meyer (1853), referred to *L. anceps*? by Wagner (1853, pl. 3, figs. 6–8), included summarily in *D. maximus* by Schlosser (1881) and Fraas (1902, p. 7), but not by Young et al. (2012), lacks precise age and locality data, but was assumed by Wagner (1853, p. 21) to have come from the same area and stratum based on its appearance. Its morphology is also consistent with that of the massive, cone-shaped caudad teeth of *D. maximus* (see Mason, 1869; Young et al., 2012). The robust tooth crown, which may be reconstructed to a height of about 60 mm based on the data supplied by Wagner (1853), would have been unusually large for a Turonian or Cenomanian mosasauroid but fits the dimensions and morphology of *D. maximus* well.

1858: Wilhelm von der Marck – Campanian Schöppingen

Johann Wilhelm Carl Theodor Matthias von der Marck (1815–1900) was a pharmacist at Hamm in Westphalia. He had a vivid interest in various fields, such as agronomy, botany, chemistry, meteorology, pharmacy, prehistory, geology, mineralogy and palaeontology, and published, between 1845 and 1894, a total of 130 works (Riegraf, 1995). His first palaeontological paper, a short note on petrified wood found near Siegburg, appeared in 1849 (von der Marck, 1849). Wilhelm von der Marck is well known for his studies on Campanian fishes from Sendenhorst. Fossil reptiles were only considered in his 1858 publication *Ueber einige Wirbelthiere, Kruster und Cephalopoden des Westfälischen Kreide* (*On some vertebrates, crustaceans and cephalopods of the Westphalian Cretaceous*, von der Marck, 1858) and a later popular publication (von der Marck, 1892). Von der Marck (1858) summarised the discoveries made at the Schöppinger Berg (near Schöppingen, North Rhine-Westphalia, western Germany) between 1853 and 1857 (these specimens are from the Upper Campanian Coesfeld Formation). He reported that an articulated series of procoelous vertebrae was found around 1853. In the summer of 1857 two more specimens were discovered at the Schöppinger Berg, a fragment of a lower jaw (a dentary with damaged teeth) and a block with four procoelous vertebrae and eight ribs. Furthermore von der Marck (1858) mentioned another series of five to six dorsal vertebrae from the collection of Kreisrichter (district judge) Ziegler at Ahaus. Today, the University of Münster houses some mosasaur specimens from the Schöppinger Berg. Among the material from the axial skeleton there is a slab with 11 partially damaged neural spines of dorsal vertebrae and most of one centrum (GPIM A.3D2; see Fig. 4A, here referred to as specimen A). Another specimen (same specimen number GPIM A.3D2; here referred to as specimen B) includes four caudal vertebrae in two slabs (see Sachs, 2000, fig. 4). These specimens are part of the von der Marck Collection, but it is not documented when each was collected. Judging from von der Marck's (1858) description as a block with four procoelous vertebrae, about one cubic foot in size, it seems plausible that GPIM A.3D2 (specimen B) is the one found in 1857. Likewise GPIM A.3D2 (specimen A) might be the one found around 1853 but may have suffered some damage since von der Marck's description. Unfortunately, this cannot be proved since von der Marck (1858, 1892) did not figure the reptilian specimens. The whereabouts of the vertebrae from the Ziegler Collection are unclear, whereas the dentary fragment went to Teylers Museum in Haarlem (the Netherlands) (von der Marck, 1892). Von der Marck asked Hermann von Meyer (see above) to identify the specimens. Meyer believed that the jaw fragment belonged to *Mosasaurus gracilis* Owen, 1851 and the other specimens to *Mosasaurus camperi* von Meyer, 1832. Recently Sachs (2000) and Caldwell & Diedrich (2005) redescribed the available mosasaur material from the Schöppinger Berg. Sachs (2000) identified the specimens as Mosasauria indet. (not as ?*Plioplatecarpus*, nor as ?*Leiodon* sp. as stated by Caldwell & Diedrich, 2005), whereas Caldwell & Diedrich (2005) referred to GPIM A.3D2 (specimen A) as cf. *Clidastes* sp. GPIM A.3D2 (specimen B) was not included in the study of Caldwell & Diedrich (2005); it was assigned to Mosasauria indet. by Sachs (2000). Neither Sachs (2000) nor Caldwell & Diedrich (2005) discussed the jaw fragment that went into the collection of the Teylers Museum.

1875: Hanns Bruno Geinitz – Cenomanian of Dresden

Alleged mosasaur material from the Cenomanian of Saxony (eastern Germany) was described in 1875 by Hanns Bruno Geinitz. Geinitz (1814–1900; Fig. 4B) studied natural sciences at the universities of Berlin and Jena, and later rose through the academic and administrative ranks at Dresden. In 1846 he was appointed inspector of the royal mineral collection, in 1850 he was appointed professor at the Königliche

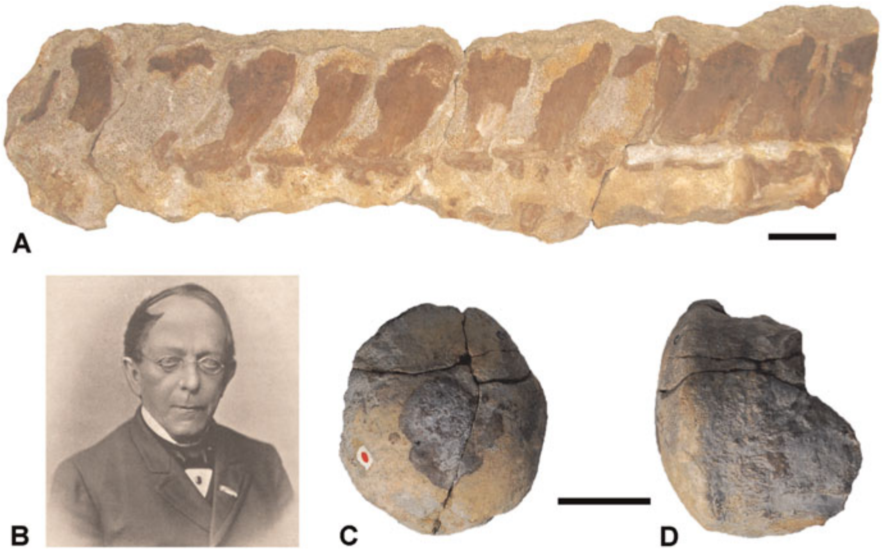

Fig. 4. (A) cf. Clidastes *sp., slab with neural spines (GPIM A.3D2, specimen A) from the Upper Campanian of the Schöppinger Berg. (B) Hanns Bruno Geinitz (GZG archives, modified). Possible squamate vertebra SaK 1748 from the Cenomanian of Dresden in (C) articular and (D) lateral views. Scale bars equal 5 cm (A) and 2 cm (C, D).*

Polytechnische Schule (Royal Polytechnical School), and finally, in 1857 became director of the Königliches Mineralogisches und Geologisches Museum (Royal Museum of Mineralogy and Geology) until his retirement in 1894 (Geinitz, 1900; Grunert & Grunert, 2001). His major contributions dealt with a wide range of fossils (e.g. Geinitz 1846, 1861–1862) and other aspects of geosciences. He extensively worked on local fossil occurrences, whereas his most important contributions to local Cretaceous palaeontology, e.g. *Das Quadersandsteingebirge oder Kreidegebirge in Deutschland* (*The ashlar sandstone stratum or Cretaceous stratum in Germany*) and *Das Elbthalgebirge* (*The Elbe Valley stratum*), were published in several volumes (Geinitz 1849–1850, 1871–1875, 1872–1875). In the first part of the latter work some fragmentary teeth found in the Upper Cenomanian Döltzschen Formation at Dresden-Plauen and at the Gamighügel in Dresden were described and figured (Geinitz 1871–1875: pl. 65, fig. 45; modern collection numbers SaK 3402 and SaK 7818). Geinitz tentatively referred them to *Leiodon anceps*? because of a similar morphology to a tooth depicted by Owen (1850, pl. 38, figs. 8, 9). However, the general morphology differs from that of mosasaur teeth (i.e. labiolingually compressed shape and lack of enamel ornamentation) and they may probably be attributed to enchodontid actinopterygians (Kear et al., 2013). Another fragmentary specimen from Dresden-Plauen was described and figured by Geinitz (1871–1875: pl. 66, fig. 1, modern collection number SaK 1748) as the proximal end of a reptilian humerus. It bears a convex articular surface and might be a very fragmentary procoelous vertebral centrum (Figs 4C and D), typical of a squamate (Kear et al., 2013).

1885: Henry Schroeder – Campanian of East Prussia

In 1885 Henry Schroeder published a description of Upper Cretaceous marine reptile remains from the Baltic, including specimens from East and West Prussia and from Sweden (Schroeder, 1885a). Henry Schroeder (1859–1927) grew up in East Prussia. He was born in Pillau (now Baltisk, Russian Federation) and attended the grammar school at Königsberg (now Kaliningrad, Russian Federation). From 1883 to 1924, Schroeder was Landesgeologe (state geologist) at the Preussische Geologische Landesanstalt (Prussian Geological Survey) at Berlin. In 1920 he became director of the collections department, which included the stratigraphical, geological, palaeozoological and palaeobotanical collections and the library of the Geological State Museum of the survey (Schmierer, 1928). One of his major tasks was to reorder the systematic palaeontological collection stratigraphically. Schroeder started his early career with contributions on local geology and stratigraphy (e.g. Schroeder, 1882); his later studies focused to a large degree on fossil vertebrates and in particular on Cenozoic mammals. Schroeder's work on Mesozoic tetrapods included nothosaurs and temnospondyls from the Triassic and marine crocodiles from the Lower Cretaceous.

Among the East Prussian material Schroeder (1885a,b) described, only a single isolated, partly damaged, strongly procoelous vertebra could be assigned to a mosasaur (see Schroeder, 1885a, pl. 17, fig. 1; see Fig. 5A here); all other specimens belonged to plesiosaurs. The mosasaur vertebra represents an intermediate caudal centrum (sensu Russell, 1967, showing haemapophyses as well as the bases of caudal ribs) that was found in an local erratic boulder (from the 'Mucronaten-Senon' = lower Upper Campanian) in a sand and gravel pit east of Lauth near Königsberg. Upper Campanian strata are widespread in the subsurface of former East Prussia (e.g. Gagel & Kaunhowen, 1900; Spulski, 1910) and therefore local glacial erratic boulders (Geschiebe) of the same age are also very common (e.g. Schroeder, 1882). The specimen was kept in the Ostpreußisches Provinzial-Museum (East Prussian Provincial Museum) at Königsberg; its current whereabouts are unknown. Schroeder (1885a,b) referred the specimen to *Mosasaurus camperi* (= *M. hoffmanni*), on account of a similarity to a vertebra figured by Cuvier (1824). Although he correctly described the

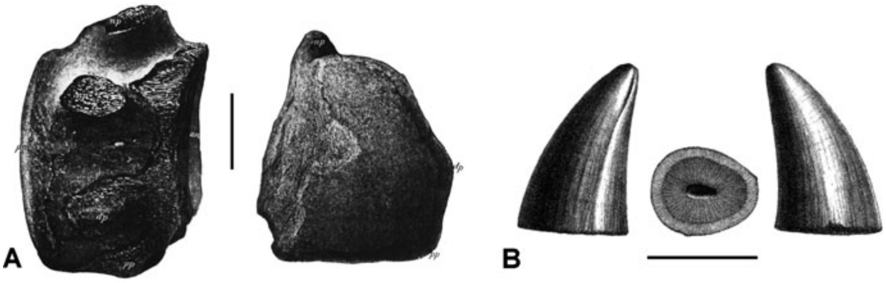

Fig. 5. (A) Mosasauridae indet., caudal vertebra from the Upper Campanian of former East Prussia (from Schroeder, 1885a). (B) Mosasaurus*?* alseni *Stolley, 1892, tooth crown, uppermost Santonian to Lower Campanian of Lägerdorf (from Stolley, 1892). Scale bar equals 3 cm.*

vertebra as a caudal, he erroneously interpreted the preserved ventral (haemapophyseal) and lateral (caudal rib) bases of processes as parapophyses and diapophyses, respectively. Judging from Schroeder's (1885a, pl. 17, fig. 1) illustration, the vertebra apparently suffered crushing, which resulted in the asymmetric right lateral exposure of the opposite left base of the neurapophysis and a ventral displacement of the right bases of the neurapophysis and caudal rib. It lacks diagnostic characters and cannot be further identified at the generic level.

1892: Ernst Stolley – Campanian of Lägerdorf

In 1889 two reptilian teeth were found at the Alsen chalk pit (uppermost Santonian to Lower Campanian) near Lägerdorf (Holstein, northern Germany). They stirred some local interest (including press reports) and were finally donated by the pit owner, Mr Alsen, to the geological collection of the Christian-Albrechts University at Kiel. Ernst Stolley included them in his doctoral thesis *Die Kreide Schleswig-Holsteins* (*The Cretaceous of Schleswig-Holstein*), which was completed in 1891 at Munich University and published the following year (Stolley, 1892).

Ernst Stolley (1869–1944) studied geology and palaeontology at Kiel and Munich, and was later a professor of geology and palaeontology at the Technische Universität (Technical University) at Braunschweig (Brunswick) from 1901 to 1935. He was one of the most eminent experts on Cretaceous strata in northern Germany and vicinity. His palaeontological work mostly focused on belemnites and stratigraphy, but he also covered a wide range of other topics, including Triassic fishes. Most of his collections and scientific estate was destroyed within months of his death, when the Braunschweig University was hit during a bombing raid in 1944 (Dorn, 1944), although the mosasaur tooth crowns survived at Kiel University.

Stolley (1892) gave an extensive description of the teeth and figured one of them accurately (Fig. 5B; Hornung & Reich, 2014). Having noted differences to the teeth of *Mosasaurus hoffmanni*, he established a new species which he reluctantly referred to the genus as *M.*? *alseni*. Despite the good description, this taxon seems to have been forgotten in the following decades. A reassessment of the specimens (Hornung & Reich, 2014) has resulted in a reassignment to *Tylosaurus* sp., morphologically close to *Tylosaurus ivoensis* (Persson, 1963), from the Lower Campanian of southern Sweden (Lindgren & Siverson, 2002). However, based on the fact that congruence in the marginal tooth morphology of tylosaurines may not be sufficient to diagnose species reliably (Lindgren & Siverson, 2002) and in view of the small sample, *Mosasaurus*? *alseni* is considered a *nomen dubium* instead of an unambiguous senior synonym of *T. ivoensis* (for more details, see Hornung & Reich, 2014).

1902: August Wollemann – Campanian of Lüneburg

Ernst August Wollemann (1862–1920) was a geologist and a teacher. After studying natural sciences and finishing his doctoral studies at Würzburg University in 1887, he returned to his home region in Lower Saxony and became a teacher in Braunschweig. August Wollemann was an active member of the Verein für Naturwissenschaft in Braunschweig (Braunschweig Association for Natural Sciences) as well as a correspondent of the Prussian Geological Survey. His geological studies were focused mainly regionally with publications on Cretaceous invertebrates (primarily molluscs, e.g. Wollemann, 1900, 1906, 1908). Besides this, he also wrote school geography books (e.g. Wollemann, 1905, 1910). In 1902, Wollemann published a descriptive overview of the Cretaceous fauna of Lüneburg (Lower Saxony, northern Germany) in which he briefly mentioned two incomplete, isolated reptilian teeth from the *Belemnitella mucronata* cephalopod zone (lower Upper Campanian), which he tentatively referred to *Mosasaurus*. Unfortunately, Wollemann (1902) did not describe nor illustrate the specimens so his assignment cannot be verified. He did not specify the collection in which the specimens were housed either. They are not present in the collection of the Naturkundemuseum (Natural History Museum) in Lüneburg (pers. comm. R. Erbguth, 2013) and so their current whereabouts is unknown.

1910: Josef Pompeckj – Campanian of Haldem

The most complete cranial remains of a mosasaur found to date in Germany comprises a partial right maxilla with teeth and associated left postorbitofrontal and two pterygoid teeth (GZG.V.10024) found during a geological fieldtrip by the University of Göttingen in April 1908 and described by Josef Pompeckj in 1910. The original description by Pompeckj

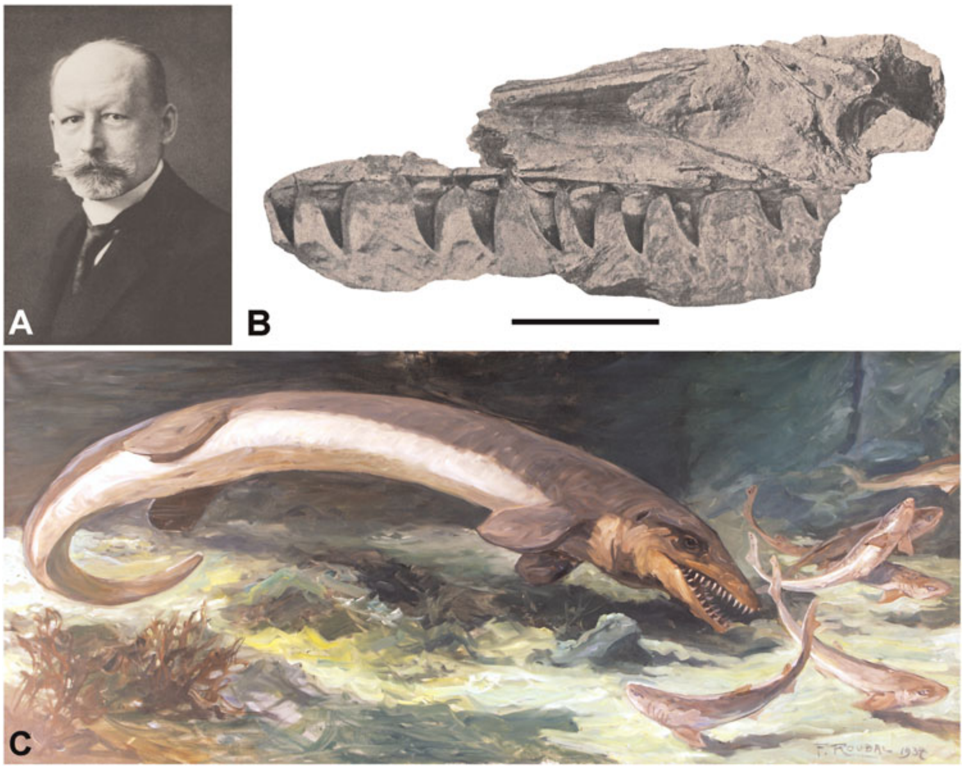

Fig. 6. (A) Josef Felix Pompeckj (GZG archives, modified). (B) Cranial remains of a mosasaur from the Upper Campanian of Haldem (GZG.V.10024), referred to as Mosasaurus *cf.* mosasauroides *by Pompeckj (1910). (C) Painting of* Mosasaurus *with sharks, inspired in part by the Haldem specimen, by Franz Roubal under instructions of Othenio Abel (1937, oil on canvass, ca. 230 × 105 cm, GZG.A.5440).*

(1910) also stated the presence of a cervical vertebra and rib fragments, although these elements are missing today.

Josef Felix Pompeckj (1867–1930; Fig. 6A) studied geology and palaeontology at the University of Königsberg (Kaliningrad) and subsequently held positions at various universities in Germany. His long and successful career included professorships at Hohenheim (from 1904), Göttingen (from 1907) and Tübingen (from 1913). Finally, in 1917, he was offered a position at the Friedrich-Wilhelms University (today Humboldt-University) in Berlin as professor of geology and palaeontology, and director of the associated Geologisch-Paläontologisches Museum (today the Museum für Naturkunde (Museum of Natural History)). In 1923 he became dean of his faculty and was elevated to rector of the university in 1925. He stayed at Berlin for the rest of his life (Hennig & Roethe, 1930; Krüger, 2001).

The remains Pompeckj (1910) described were found in Haldem (now a part of the community of Stemwede, North-Rhine Westphalia, northwestern Germany) in a yellowish sandy limestone of the uppermost Campanian Stemwede Formation (Fig. 6B). Pompeckj compared the maxillary fragment to various genera of mosasaurs and concluded that it showed closest similarities to *Mosasaurus mosasauroides* (originally *Leiodon mosasauroides* Gaudry, 1892). This species, based on a skull fragment comprising the rostrad portions of the cranium and mandibles, from the Maastrichtian of the Basses-Pyrénées in southwestern France, is poorly known and may – based on the specialised, highly trenchant dental morphology – represent a distinct genus (Lingham-Soliar, 1993; LeBlanc et al., 2012). Although sharing labiolingually compressed marginal teeth, this feature is much more pronounced in the French specimen, along with other differences (see Hornung & Reich, 2014). Lingham-Soliar (1993) re-included *L. mosasauroides* in his concept of the genus *Liodon* (= *Leiodon*) and followed Pompeckj (1910) in referring GZG. V.10024 tentatively to this species without further comments, a view that was repeated by Sachs (2000).

A reassessment of the specimen showed that it is referable to the tylosaurine genus *Hainosaurus* Dollo, 1885 (for details see Hornung & Reich, 2014). Curiously, Pompeckj (1910, p. 125) compared the Haldem specimen also to this genus but dismissed a reference to it on the basis of differences in the tooth morphology. In fact, the dental morphologies are quite similar, however the teeth in *Hainosaurus* were described very inadequately until recently (Lindgren, 2005).

In addition to the description of the Haldem specimen Pompeckj (1910) also provided a summary of the contemporary knowledge on mosasaur morphology and habits. This is the most comprehensive work on their palaeobiology resulting from the discovery of a mosasaur in Germany until today. Aside from compiling the results from major works on mosasaurs, especially by Louis Dollo (1857–1931), Georg Baur (1859–1898), Edward Drinker Cope (1840–1897), John Campbell Merriam (1869–1945), Henry Fairfield Osborn (1857–1935), Samuel Wendell Williston (1852–1918), Dragutin Gorjanović-Kramberger (1856–1936) and Andreas Kornhuber (1824–1905), Pompeckj added his own ideas on mosasaurs, especially on the question of their palaeobiogeography and extinction. He paid special attention to locomotion, pointing out that the main locomotory organ was the tail, which mosasaurs might have used in meandering motions similar to newts. Furthermore, he concluded that the front limbs were used to steer and balance the position in the water, similar to bilge keels on ships. Other subjects included diving capacity, reproduction, feeding and relationships to aigialosaurs and extant lizards.

Most significantly, Pompeckj's essay on mosasaur palaeobiology is interwoven with a critical discussion of a then new phylogenetic theory, published by Gustav Steinmann two years earlier.

Johann Heinrich Conrad Gottfried Gustav Steinmann (1856–1929), born in Braunschweig (Brunswick), studied chemistry, mineralogy, geology and zoology at the universities of Braunschweig and Munich. He completed a doctoral thesis on fossil hydrozoans in 1877 and a habilitation on the regional geology of Bolivia in 1880. Following affiliations with the universities of Strasbourg and Jena, he was appointed professor in Freiburg im Breisgau in 1886. In 1906, Steinmann became head of the newly founded institute of geology and palaeontology at the University of Bonn, which he developed during the following years as an effective administrator (Wilckens, 1930). Today, the institute bears his name and is still located in buildings that he commissioned.

He was an accomplished scientist, enormously productive and versatile in his fields. However, his ideas received a mixed reception. Although some parts of his work – especially in regional geology – are still considered groundbreaking, others have not found acceptance (Seibold & Seibold, 2010) and may be considered eccentric.

In 1908 Steinmann published his book *Die geologischen Grundlagen der Abstammungslehre* (*The Geological Foundations of the Theory of Descent*), in which he proposed an unorthodox phylogenetic theory. Citing the alleged lack of species that are transitional in morphology between higher systematic categories, Steinmann denied the monophyletic origins and subsequent diversification of these groups. He regarded the higher categories (genera, families, etc.) as different 'levels of organisation' that were superimposed by changing environmental conditions to independently evolving, anagenetic successions of species ('Abstammungslinien' or 'lines of descent'). Therefore he found characters defining and separating those higher categories not meaningful for the reconstruction of phylogeny but proposed to use features like external morphology or ornamentation for this purpose. He also considered extinction, as a natural phenomenon, extremely uncommon and an exception, suggesting that almost all fossil species are included as intermediate mutations somewhere in the chains of the lines of descent, leading to extant species.

As a consequence of those principles, he radically regrouped the organisms in a system he deemed to reflect serial and anagenetic phylogeny. This regrouping saw, for example, the ascidians (Tunicata) as a group of shell-less molluscs that had descended from rudistid bivalves (Steinmann, 1908, p. 174ff.; in contrast Jaekel, 1915, p. 67). This lineage was based on the superficial, entirely function-related, similarities between ascidians and rudists, and the desire to include the rudists in a persisting evolutionary lineage instead of being an extinct clade. However, he completely disregarded the numerous differences between those two groups that are not functional.

The same is true for the system he unfolded for the amniotes. He distinguished between the (extant), 'primitive' reptiles, in which he included the turtles, crocodilians, lizards and snakes, and the relatively advanced 'metareptiles'. Within the reptiles, he saw an anagenetic continuity towards the turtles via rhynchosaurs and placodonts, while he assumed direct ancestry of the remainder within the non-amniote basal tetrapods (e.g. the genera *Archegosaurus* and *Eryops* for longirostrine and latirostrine crocodilians, respectively; Steinmann, 1908, p. 214). The metareptiles were considered by him to represent the ancestors of birds and mammals. The distinction from the primitive reptiles was based on his – rather avant-garde – suggestion that the metareptiles, including dinosaurs, pterosaurs and various marine taxa, had elevated rates of metabolism and were potentially endothermic. With basal synapsids or therapsids not yet defined, he suggested that the metareptiles split into a dichotomy between the ancestors of birds (Avireptilia) and those of mammals (Mammoreptilia). Again he drew the line between the two entirely deliberately, for example he proposed the sauropod genus *Diplodocus* to have belonged to the Avireptilia, being a potential bird ancestor, while he referred the sauropod genera *Cetiosaurus*, '*Camerosaurus*' (sic! = *Camarasaurus*), '*Brontosaurus*' (= *Apatosaurus*) and '*Morosaurus*' (= *Camarasaurus*) to the Mammoreptilia. He justified this by a 'complete' dentition in the latter, while *Diplodocus* had teeth only in the rostral part of the jaws (Steinmann, 1908, p. 220).

Other 'mammoreptiles' included ceratopsians (which he renamed 'Homoeopoda'), pterosaurs, ichthyosaurs, plesiosaurs and 'thalattosaurs'. Theropods, ornithopods and stegosaurs were included in the Avireptilia (Steinmann, 1908, p. 220f.).

Steinmann's proposal – although claiming to solve inherent problems of the classical, monophyly-based theory – had a number of flaws. The most important of these were the opportunistic use or even total ignorance of the principle of homology and the employment of a highly random concept of homoplasy. The criteria to distinguish between phylogenetically relevant character transition and functionally induced convergence were entirely arbitrary and not justified.

With regard to mosasaurs, Steinmann hypothesised that they were an intermediate member in a phylogenetic lineage ranging from the Triassic 'mammoreptilian' thalattosaurs (which he expanded to include mosasaurs) to extant baleen whales (Mysticeti) based on a rough comparison of cranial features such as a rounded occiput, oblique nasal ducts, a flexible mandibular symphysis and similar morphology of the quadrate in 'thalattosaurs' and the bulla tympanica in whales. He also cited reduced metapodials, weak hyperphalangy and absence of polyphalangy in the forelimb as shared characteristics. He brought forward similar arguments to link plesiosaurs phylogenetically with toothed whales (Odontoceti), and ichthyosaurs with dolphins (Delphinoidea).

Pompeckj (1910, p. 132ff.) rejected a phylogenetic linkage of mosasaurs either to the Triassic Thalattosauria or to cetaceans. He pointed out that the alleged 'synapomorphies' in the cranial morphology between these clades are also present in other mammal groups or were wrongly identified. With regard to the vertebral series and forelimbs, he argued that those of mosasaurs show major differences to those of whales, which cannot be explained by environmental changes, as the locomotory requirements of mosasaurs and whales were essentially the same. As the most important argument he cited the differences in the proportions of the forelimbs, with whales having a proportionally much more elongate zeugopodium, which would have required an inexplicable reversal from the short zeugopodium in mosasaurs. He stated that it is more parsimonious to deduce forelimb morphology in whales from terrestrial mammals than from marine reptiles.

Pompeckj (1910) also delved into possible reasons for mosasaur extinction. Listing the known temporal and spatial relationships of mosasaur occurrences known at this time, he considered a shift of mosasaur localities through time and therefore a 'wandering' of the presence of mosasaurs across the globe (a view which cannot be upheld by present-day data). He proposed that their occurrence was bound to shallow, coastal regions (which is probable, although there may be a certain preservational bias for pelagic deposits). After considering potential but hypothetical environmental changes (especially to fluvial environments, which he had proposed as spawning grounds), increased predatory pressure by actinopterygians to juvenile mosasaurs, feeding competition by sharks or 'disadvantageous' gigantism, he considered these possibilities as conjectural or insufficient. In conclusion he saw the most probable reason for the extinction in an 'over-specialisation', hypothesising a 'depletion' of a somehow predetermined reservoir of the Umprägungsfähigkeit (ability to transform) of species. He envisaged a natural 'expiry' of taxa rather than their 'annihilation' (Pompeckj, 1910, p. 140).

The specimen from Haldem was incorporated in the Göttingen collections, where Pompeckj was professor of geology and palaeontology at the time of the discovery. A few decades later, his successor Othenio Abel (1875–1946) undertook a major effort to renew an inclusive view of the fossil biosphere, coining (together with Louis Dollo) the concept of palaeobiology. In his function as the head of the palaeontological department in Göttingen, he also fostered the popularisation of these concepts by designing an exhibit on palaeobiology and he commissioned the Austrian painter, sculptor and palaeoartist Franz Roubal (1889–1969) to create a series of large formatted paintings and sculptures of extinct animals (Reich & Reitner, 2004). One of these was a reconstruction of a mosasaur hunting on sharks, created in 1937 (Fig. 6C) and published by Abel (1939). Today the specimen is on display at the Geoscience Museum at Göttingen (Reich et al., 2013), next to the framed oil painting by Roubal.

1915: Karl Gripp – Coniacian to Campanian of Lägerdorf

In 1915 Karl Christian Johannes Gripp (1891–1985) published a note on a series of mosasaur vertebrae found in Lägerdorf, Holstein. Gripp studied geology at Göttingen, Kiel and Grenoble. From 1927 to 1934 he was professor of geology at the University of Hamburg. From 1940 to 1958 Gripp was affiliated with the University of Kiel, where he eventually became director of the Geological Institute. Gripp's research focused mainly on Quaternary geology, but he also published several books on the regional geology of northern Germany (e.g. Gripp, 1933, 1964). Furthermore, he had a lifelong interest in Arctic geology and participated in expeditions to Svalbard and Greenland (von der Brelie, 1985; Prange, 1991). In 1927 Gripp was a member of an expedition to Svalbard, which discovered parts of an enigmatic Lower Triassic ichthyosaur that Wiman (1928) named *Grippia longirostris* in honour of Karl Gripp. Gripp (1915) mentioned a series of 19 procoelous, laterally compressed caudal vertebrae. He did not present a formal description nor an illustration, but noted a similarity to the caudal vertebrae of *Mosasaurus*. The specimen was donated to the Museum of Mineralogy and Geology at Hamburg, but is not present in the collection of the Institute of Geology and Palaeontology in Hamburg (S. Sachs, pers. obs., 2012). Thus, these vertebrae were probably destroyed in 1943, as were other specimens housed in the geological institute in Hamburg (see also Hillmer, 2006, p. 3). The exact age of the vertebrae cannot be provided because the strata exposed at Lägerdorf range from the Middle Coniacian to the Upper Campanian (Schulz et al., 1984) and Gripp (1915) did not provide stratigraphic information.

Conclusions

Despite the rarity of mosasaur remains in Germany, a handful of specimens were described between the 1830s and 1945. Among their investigators were prominent figures of German palaeontology and geosciences of their time.

The first mosasaur specimen known from Germany was a tooth from the Lower Maastrichtian of the Isle of Rügen that was illustrated around 1840 for an uncompleted publication of von Hagenow.

The historically most significant episode linked to a mosasaur specimen from Germany is the discussion of Steinmann's (1908) aberrant phylogenetic theory by Pompeckj (1910) in the course of his description of the hitherto most complete material, cranial fragments from the Upper Campanian of Haldem, North-Rhine Westphalia.

According to Steinmann's (1908) idea, extinction only rarely took place, but instead parallel, continuous anagenetic lineages existed, incorporating most if not all fossil taxa as intermediate members, terminating in present-day species. In this concept the mosasaurs would form an intermediate member in a chain from Triassic thalattosaurs to extant baleen whales.

Pompeckj strongly disagreed with Steinmann's theory and demonstrated that these conclusions were conjectural, speculative, based on convergence and not supported by scientific evidence. Pompeckj (1910) also discussed the palaeobiogeography and possible reasons for the extinction of the mosasaurs, concluding in a 'vitalistic' view, that clades may 'deplete' a 'predetermined reservoir' of transmutational capacity, becoming in the end the victim of 'over-specialisation'.

Several specimens which were described in the first 100 years of research are unfortunately lost or destroyed. These sadly include the first tooth illustrated by von Hagenow and the vertebrae from Lägerdorf, Holstein, mentioned by Gripp (1915). The teeth, supposed to represent mosasaurs from the Turonian/Cenomanian of Bavaria (von Meyer, 1853, 1856; Wagner, 1853), were most probably those of a Upper Jurassic marine crocodilian (Schlosser, 1881; Fraas, 1902), and are also lost. These fates underscore the importance of preserving all available information that remains of these early discoveries.

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