New mosasaurid teeth (Reptilia: Squamata) from the Maastrichtian of Albaina (Laño quarry, Condado de Treviño)

Nathalie BARDET1*, Gorka MARTIN2, J. Carmelo CORRAL3, Xabier PEREDA SUBERBIOLA4 & Humberto ASTIBIA4

1 CR2P, UMR 7207 CNRS-MNHN-UPMC, Département Histoire de la Terre, Muséum National d’Histoire Naturelle, CP 38, 8 rue Buffon, 75005 Paris, France; bardet@mnhn.fr
2 Luberri, Oiartzungo Ikasgune Geologikoa Museoa, Pagoaldea pol. 41-42, 20180 Oiartzun; geoluberri@euskalnet.net
3 Museo de Ciencias Naturales de Alava/Arabako Natur Zientzien Museoa, Siervas de Jesús 24, 01001 Vitoria-Gasteiz, corral; arroyo@gmail.com
4 Universidad del País Vasco/Euskal Herriko Unibertsitatea, Facultad de Ciencia y Tecnología, Dpto. Estratigrafía y Paleontología, Apdo. 644, 48080 Bilbao; xabier.pereda@ehu.es; humberto.astibia@ehu.es

* Corresponding author

Bardet, N., Martin, G., Corral, J.C., Pereda Suberbiola, X. & Astibia, H. 2013. New mosasaurid teeth (Reptilia: Squamata) from the Maastrichtian of Albaina (Laño quarry, Condado de Treviño). [Nuevos dientes de mosasáuridos (Reptilia: Squamata) del Maastrichtiense de Albaina (Cantera de Laño, Condado de Treviño)]. Spanish Journal of Palaeontology, 28 (1), 69-78.

Manuscript received 2 October 2012
Manuscript accepted 8 March 2013 © Sociedad Española de Paleontología ISSN 2255-0550

ABSTRACT

We report on new mosasaurid remains, namely isolated teeth, from the Upper Maastrichtian shallow marine environment of Albaina in the Laño quarry (Condado de Treviño). The new specimens belong mostly to mosasaurines, i.e., *Mosasaurus hoffmanni*, *Prognathodon solvayi*, *Prognathodon sectorius*, and to the russellosaurine plioplatecarpine *Platecarpus cf. ictericus*. *Prognathodon solvayi* and *Platecarpus cf. ictericus* were previously known from Albaina. This is the first mention in the site of *Mosasaurus hoffmanni*, widespread in Maastrichtian outcrops located around palaeolatitude 30-40ºN, from New Jersey (USA) to Turkey passing through Europe where it is commonly found. *Prognathodon sectorius* has a comparable palaeobiographical distribution, though not so expanded, that *M. hoffmanni*, being known in the Maastrichtian of New Jersey (USA) and Europe and, since recently, in the Campanian of Navarre. With six different

RESUMEN

Se describen nuevos restos fósiles de mosasáuridos, que consisten en dientes aislados, procedentes de los depósitos marino-litorales del Maastrichtiense superior de Albaina, en la cantera de Laño (Condado de Treviño). El nuevo material pertenece principalmente a mosasáuridos, como *Mosasaurus hoffmanni*, *Prognathodon solvayi*, *Prognathodon sectorius*, y al plioplatecarpino russellosaurino *Platecarpus cf. ictericus*. En un trabajo previo se describió la presencia de *Prognathodon solvayi* y *Platecarpus cf. ictericus* en Albaina. Esta es la primera cita en el yacimiento de *Mosasaurus hoffmanni*, un taxón ampliamente distribuido en afloramientos maastrichtienses situados en paleolatitudes cercanas a los 30-40ºN, desde Nueva Jersey (EE. UU.) hasta Turquía, pasando por Europa donde sus restos se han descubierto en numerosas localidades. *Prognathodon sectorius* presenta una distribución paleobiogeográfica comparable, aunque no tan amplia, como
taxa reported here, Albaina is the richest outcrop in specific mosasaurid diversity from the Maastrichtian of southern Europe.

**Keywords:** Mosasauridae, Iberian Peninsula, latest Cretaceous, palaeobiogeography.

1. **INTRODUCTION**

Mosasaurid fossil remains are very scarce in the latest Cretaceous of the Iberian Peninsula. Though they were first described in Portugal at the end of the XIXth century (Sauvage 1897-1898), other discoveries date from the 1990s and more recently (see Bardet et al., 2008 for an overview). They mainly consist of isolated teeth and vertebrae and were known up to now exclusively from the Campanian-Maastrichtian of the Lusitanian Basin and the Basque-Cantabrian Region (see Bardet et al., 2008 for details), until their recent discoveries in the Maastrichtian of the External Zone of the Betic Cordillera (Bardet et al., 2013).

The Albaina fossiliferous site is located in the Laño quarry, in the Condado de Treviño, an exclave of the Burgos province inside Alava in the Basque Country, in the Northern part of the Iberian Peninsula. In the Laño quarry, two stratigraphic horizons within a continental to shallow marine succession of Late Cretaceous age are known (Baceta et al., 1999): the lower horizon contains the continental sites Laño 1 and 2, the upper horizon contains the Albaina site.

The fluvial beds of Laño, regarded as Late Campanian to Early Maastrichtian in age, have yielded a diverse vertebrate assemblage, which consists of nearly 40 species (at least 11 new taxa), including actinopterygians, amphibians, lizards, snakes, turtles, crocodyliforms, dinosaurs, pterosaurs and mammals (Astibia et al., 1999; Pereda Suberbiola et al., 2000).

The shallow marine vertebrate association of Albaina consists of about 35 species, including shark and rays (among them four new rhinobatoids), actinopterygians, mosasaurids and plesiosaurs, of Late Maastrichtian age (Bardet et al., 1999; Cappetta & Corral, 1999; Poyato-Ariza et al., 1999).

Mosasaurid remains from Albaina were previously reported by Bardet et al. (1997, 1999). They are referred to the mosasaurines *Prognathodon solvayi*, *Prognathodon sp.* (= *Leidodon anceps* and *Leidon* sp. of Bardet et al., 1997, 1999), *Mosasaurus* sp., indeterminate mosasaurs, and to the rutilusosaurine plioplatecarpine *Platecarpus* cf. *ictericus* (see Table 1).

Here we describe newly discovered specimens, namely isolated teeth, all found by one of us (G.M.) in the same Albaina horizon of the Laño quarry as the previously described ones. The specimens are kept in Luberri/Oiartzungo Ikasgune Geologikoa Museoa of Oiartzun.

**Institutional abbreviations.** IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; LU, Luberri, Oiartzungo Ikasgune Geologikoa Museoa, Oiartzun, Gipuzkoa; MCNA, Museo de Ciencias Naturales de Alava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Alava.

2. **LOCATION AND GEOLOGICAL SETTING**

The Laño-Albaina outcrop is located in a disused quarry, about 30 km south of Vitoria-Gasteiz, in the Basque-Cantabrian Region (Fig. 1). Locally, the outcrop is located on the southern limb of the Miranda-Treviño syncline and R includes both continental and shallow marine successions ranging in age from Late Campanian to Maastrichtian.

The Late Campanian marks a period of overall regression in the southern part of the Basque-Cantabrian Basin (Navarro-Cantabrian Trough), resulting in the emergence of littoral environments in some marginal areas and the deposition of fossil-rich deltaic sandstones in the southern limb of the Miranda-Treviño syncline (Fig. 2: L1A, L1B). But, despite an initially regressive phase in the Laño-Albaina zone (Sobrepeña Formation), the Maastrichtian was overall transgressive in the area, as can be deduced from rock exposures in both limbs of the Miranda-Treviño syncline. Limestones and fossiliferous marls (Puerto de Olazagutía Formation) containing echinoids, ammonites, inoceramids and other bivalves and shark teeth (Corral, 1996) indicate that shallow-marine environments were widespread in the northeastern part of the domain. The collected ammonites *Anapachydiscus fresvillensis* and *Baculites anceps* also indicate a Late Maastrichtian age (Santamaría & López, 1996).

In the southern outcrop of the Laño-Albaina quarry, marine rocks crop out in the upper part of the series. Thus,
the friable sandstones and mudstones of the Sobrepeña Formation are connected to yellow calcarenites with fish and mosasaur remains by means of a lag with vertebrate bone fragments and fish remains that will mark an intra-Maastrichtian unconformity (sensu Baceta, 1996). Invertebrate macrofossils in these calcarenites, whose diagenetic history has turned them to decalcified limestones with mouldic porosity, are scarce but layers of accumulated orbitoidids occur. This unnamed formation is considered to be equivalent to the Torme Formation in the Villarcayo area (North-Castilian Platform) (Berreteaga, 2008). This unit lacks good index fossils but selachian biostratigraphy may indicate a Late Maastrichtian age (Cappetta & Corral, 1999).

The Campanian-Maastrichtian interval includes the end of a regressive cycle and the beginning of transgressive period in the domain (Fig. 2). Upwards, carbonate rocks of Danian age indicate that a shallow marine platform lasted for a while in this part of the Basque-Cantabrian Basin.

### 3. SYSTEMATIC PALAEONTOLOGY

**Order** SQUAMATA Oppel, 1811  
**Family** MOSASAUROIDAE Gervais, 1853  
**Subfamily** MOSASAURINAE Gervais, 1853  
**Genus** *Mosasaurus* Conybeare, 1822  
*Mosasaurus hoffmanni* Mantell, 1829

#### Material and occurrence
LU–GMS/LAÑ004, a marginal tooth from the anterior part of the jaws; Albaina, Laño quarry, Condado de Treviño; Late Maastrichtian (Baceta et al., 1999; Cappetta & Corral, 1999) (Figs 3a-3b).

#### Description
The tooth preserved the enameled crown only. It has been found broken in numerous fragments and has been restored and reconstructed by one of us (J.C.C.). Though incomplete, the preserved part of the crown (39 mm high) is high and narrow, its height being more than twice the basalmost preserved length (estimated to about 15 mm). The posterior margin of the crown is almost straight in lateral view, without any pronounced curvature. It bears two marked carinae located anteriorly and posteriorly. Both being eroded it is impossible to see if they bear crenulations. The crown bears a well-marked U-shaped cross-section. The labial surface is slightly convex and bears 3 large prisms. The lingual surface is strongly convex, and bears indistinct prisms that do not reach the apex. The enamel is thick and smooth but longitudinally structured.

#### Discussion
The U-shaped cross-section of the crown is typical of the genus *Mosasaurus* (Russell, 1967), as well as is the longitudinally structured smooth enamel (N.B., pers. obs.). The respective position of the two carinae, the distinctive size of the labial and lingual surfaces, and the
reduced number of prisms on the labial surface indicate that this tooth was from the anterior part of the jaws (Lingham-Soliar, 1995). The high and slender shape of the crown, as well as a labial surface bearing 3 prisms and a lingual face with indistinct ones are typical characters of *Mosasaurus hoffmanni* (Lingham-Soliar, 1995).

This species is widespread in the Maastrichtian of Europe up to Turkey and is also known in the Campanian-latest Maastrichtian of North America (see Bardet, 2012 for details). It has a transatlantic palaeobiogeographical distribution around palaeolatitudes 30-40ºN (Mulder, 1999; Bardet, 2012).

**Genus** Prognathodon Dollo, 1889

*Prognathodon solvayi* Dollo, 1889

**Material and occurrence.** LU–GMS/LAÑ001, a marginal tooth probably from the median part of the jaws; LU–GMS/LAÑ005, a marginal tooth from the median part of the jaws; Albaina, Laño quarry, Condado de Treviño, Late Maastrichtian (Baceta et al., 1999; Cappetta & Corral, 1999) (Figs 3c-f).

**Description.** LU–GMS/LAÑ001 is a poorly preserved crown with a complete basal portion, but the apex and posterior part are broken. However, it can be deduced from its shape that its height was probably only one and half its basal length as in LU–GMS/LAÑ005 (see below). LU–GMS/LAÑ001 was probably only slightly posteriorly recurved. The crown is significantly laterally compressed, with subequal and slightly convex labial and lingual surfaces; subsequently, the basal cross-section is a long oval. Both surfaces bear well-marked and defined facets, probably 5 labially and 7 lingually. The anterior carina is eroded. Because the posterior portion of the crown is broken, the occurrence of a posterior carina cannot be confirmed. The enamel is thick, smooth and silky.

LU–GMS/LAÑ005 preserves only the crown, which is complete. It is 14 mm high and 9 mm long basally. This crown is only slightly posteriorly recurved and strongly laterally compressed. It bears two well-marked and anteroposteriorly aligned carinae, which bear minute crenulations. The labial and lingual surfaces are comparable in size so that the basal cross-section is an elongated oval. The labial surface is slightly convex and bears 5 well-marked facets, of which only 3 reach the apex. The lingual surface is also slightly convex and bears 6 well-marked facets; one reaches the apex. The enamel is smooth like in LU–GMS/LAÑ001, but because LU–GMS/LAÑ005 is a much smaller crown, it is thin and shiny.

**Discussion.** With their labial and lingual surfaces of comparable size, anteroposteriorly aligned carinae (in LU–
Figure 2. Stratigraphic section of the Laño quarry showing the main lithofacies and the location of the fossiliferous levels (modified from Gómez-Alday et al., 1999). L1A, L1B: continental vertebrate fossil sites; IMU: intra-Maastrichtian unconformity.
GMS/LAÑ005 only), and scarcely posteriorly recurved shape, these teeth probably come from the median part of the jaws. The small size of LU–GMS/LAÑ005 and the fact that its crown is complete without any trace of the root indicate that it is a fully erupted tooth belonging to a small individual. With a comparable number of strong facets on both the labial and lingual surfaces, as well as of a compressed basal cross-section, the above described teeth are very similar to those of Prognathodon solvayi (IRSNB R33 and IRSNB R107), type species of the genus and the only one having strongly faceted teeth (Dollo, 1889; Lingham-Soliar & Nolf, 1989). The two studied teeth, especially the larger one (LU–GMS/LAÑ001), are also quite similar to the tooth previously referred to P. solvayi from Albaina (Bardet et al., 1997, 1999).

Besides Albaina, Prognathodon solvayi is known from the Late Campanian of The Netherlands (Mulder et al., 1998) and the Early Maastrichtian of Belgium (Dollo, 1889; Lingham-Soliar & Nolf, 1989). Its occurrence in the Late Maastrichtian of Albaina is stratigraphically the youngest one and biogeographically the southernmost of this species.

Prognathodon sectorius (Cope, 1871)

**Material and occurrence.** LU–GMS/LAÑ002, a marginal tooth from the median part of the jaws; Albaina, Laño quarry, Condado de Treviño; Late Maastrichtian (Baceta et al., 1999; Cappetta & Corral, 1999) (Figs 3g-3h).

**Description.** LU–GMS/LAÑ002 is a complete crown of a fully erupted tooth. It is robust and triangular in lateral view (H = 25 mm, basal L = 18 mm), with a dental

**Figure 3.** Mosasaurid teeth from Albaina, Laño quarry, Condado de Treviño, Late Maastrichtian. a-b) Mosasaurus hoffmanni, LU – GMS/LAÑ004, marginal tooth in lingual (a) and labial (b) views. c-d) Prognathodon solvayi, LU – GMS/LAÑ001, marginal tooth in labial (c) and lingual (d) views. e-f) Prognathodon solvayi, LU – GMS/LAÑ005, marginal tooth in lingual (e) and labial (f) views. g-h) Prognathodon sectorius, LU – GMS/LAÑ002, marginal tooth in labial (g) and lingual (h) views. i-j) Platecarpus cf. icterus, LU – GMS/LAÑ003, pterygoid tooth in labial (i) and lingual (j) views. Scale = 1 cm.
Late Campanian of Navarre (Bardet 2012). Recently, this species has been described from the Early Maastrichtian of Belgium, the Late Maastrichtian & Corral, 1999) (Figs 3i-3j).

is strongly posteriorly recurved. It bears two very weak carinae located on the anterior part of the supposed lingual surface and on the posterior part of the supposed labial one. Both carinae are only developed on the upper half of the crown. The entire crown surface exhibit fine striations that reach the apex, more marked basally and on the posterior surface.

Discussion. The above mentioned combination of characters is the same observed in a marginal tooth from Albaina that was previously referred to Platecarpus cf. ictericus (Bardet et al., 1997, 1999), with the difference that LU–GNS/LAÑ003 is a pterygoid tooth.

This species is mainly known in the Santonian-Campanian of the Western Interior Seaway of North America (Russell, 1967). Its description in the Santonian-Campanian of France (Bardet et al., 1991) and the Maastrichtian of Albaina (Bardet et al., 1997, 1999) greatly enlarges both its palaeobiogeographical and stratigraphical distributions.

4. CONCLUSIONS

Despite intensive prospecting, the Laño-Albaina quarry is the only known fossil-rich marine outcrop in the southern limb of the Miranda-Treviño syncline. It richness may be related to a local palaeo-sea depression that allowed the accumulation and preservation of marine deposits. These new discoveries permit to expand the Laño-Albaina mosasaurid faunal list (see Table 1) by including the first mention here of Mosasauroidea tethysica and Prognathodon sectorius. Prognathodon solvayi and Platecarpus cf. ictericus were previously reported in Albaina (Bardet et al., 1997, 1999). As commonly seen in latest Cretaceous mosasaurid sites, the Albaina fauna predominantly consists of mosasaurine taxa. Moreover, these Maastrichtian mosasaurid faunas are typical of the Northern Tethys margin Palaeoprovince located around palaeolatitudes 30-40°N and differ significantly from those of the Southern Tethys margin around 20°N (Bardet, 2012). With six taxa reported here, Albaina is the richest Maastrichtian outcrop in mosasaurid remains from southern Europe.

ACKNOWLEDGMENTS

We dedicate this work to our dear friend and colleague Nieves López Martínez. Financial support provided by the Ministerio de Economía y Competitividad of Spain (project CGL2010-18851/BTE) and the Gobierno Vasco/ EJ (research group IT-320-10). This work is part of a palaeontological collaboration between the Universidad del País Vasco/E.H.U., the Centre National de la Recherche...
Scientific (CNRS, France) and the Muséum National d’Histoire Naturelle (MNHN, Paris). Finally, we thank Anne Schulp (Natuurhistorisch Museum Maastricht) for his constructive review, which permitted to improve our manuscript.

REFERENCES

Astibia, H., García-Garmilla, F., Orue-Etxebarria, X., Rodríguez-Lázaro, J., Buscalioni, A. D., Sanz, J. L. & Jiménez-Fuentes, E. 1987. The Cretaceous-Tertiary boundary in a sector of the south limb of the Miranda-Treviño synclinal: The first appearance of Chelonia and Archosaurus in the Basque Country. *Cretaceous Research*, 5, 15-27.

Astibia, H., Corral, J.C., Murelaga, X., Orue-Etxebarria, X. & Pereda Suberbiola, X. 1999. Geology and palaeontology of the Upper Cretaceous vertebrate-bearing beds of the Laño quarry (Basque-Cantabrian Region, Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Álava*, 14, Número especial 1, 1-380.

Bacerta, J.I. 1996. *El Maastrichtiense superior, Paleoceno e Ilerdiense basal de la Región Vasco-Cantábrica*: secuencias deposicionales, facies y evolución paleogeográfica. PhD Thesis, Universidad del País Vasco/Euskal Herriko Unibertsitatea (unpublished).

Bacerta, J.I., Pujalte, V. & Orue-Etxebarria, X. 1999. The vertebrate fossil-bearing sites of the Laño quarry (Basque-Cantabrian Region): stratigraphical and palaeogeographical context. *Estudios del Museo de Ciencias Naturales de Álava*, 14, Número especial 1, 13-28.

Bardet, N. 2012. Maastrichtian marine reptiles of the Mediterranean Tethys: A palaeobiogeographical review. *Bulletin de la Société géologique de France*, 183, 573-596.

Bardet, N., Bilotte, M., Christensen, W.K., Hansotte, M., Melchior, P. & Raynaud, C. 1991. Nouveaux restes et révisions de faunes exceptionnelles du Crétacé supérieur audois: les Belemnitellidae et Mosasauroidea des Corbières. *Bulletin de la Société d’Études scientifiques de l’Aude*, 91, 11-21.

Bardet N., Corral J.C. & Pereda Suberbiola X. 1997. Les mosasaures (Squamata) du Crétacé supérieur du Bassin basco-cantabrique. *Geobios*, 20, 19-26.

Bardet, N., Corral, J.C. & Pereda Suberbiola, X. 1999. Marine reptiles from the uppermost Cretaceous of the Laño quarry (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Álava*, 14, Número especial 1, 373-380.

Bardet, N., Pereda Suberbiola, X. & Ruiz-Omeñaca, J.I. 2008. Mesozoic marine reptiles from the Iberian Peninsula. *Geo-Temas*, 10, 1245-1248.

Bardet, N., Pereda Suberbiola, X., Corral, J.C., Baceta, J.L., Torres, J.A., Botantz, B. & Martin, G. 2012a. A skull fragment of the mosasaurid *Prognathodon* cf. *sectorius* from the Late Cretaceous of Navarre (Basque-Cantabrian Region). *Bulletin de la Société géologique de France*, 183, 117-121.

Bardet, N., Baeza-Carratalá, J.F., Diez-Díaz, V., Carbonell, A., García-Avila, M. & Giner, V. 2013. First occurrence of Mosasauroidea (Squamata) in the Maastrichtian (latest Cretaceous) of Alicante (Valencia Community, Eastern Spain). *Estudios geológicos* 69 (1) online, doi: 10.3989/egeo.40946.222

Berreteaga, A. 2008. *Estudio estratigráfico, sedimentológico y paleontológico de los yacimientos con fósiles de vertebrados del Cretácico final de la Región Vasco-Cantábrica*. PhD Thesis, Universidad del País Vasco/Euskal Herriko Unibertsitatea (unpublished).

Cappetta, H. & Corral, J.C. 1999. Upper Maastrichtian selachians from the Condado de Treviño (Basque-Cantabrian Region, Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Álava*, 14, Número especial 1, 339-372.

Conybeare, W.D. 1822. Fossil crocodiles and other saurians animals. In: *Outlines of Oryctology: An introduction to the study of fossil organic remains; especially those found in the British strata* (ed. Parkinson, J.). vii + 344 pp., London.

Cope, E.D. 1871. Supplement to the ‘Synopsis of the extinct Batrachia and Reptilia of North America’. *Proceedings of the American Philosophical Society*, 12, 41-52.

Corral, J.C. 1996. *Squalicorax pristodontus* (Agassiz 1843), selaco citado por M. Ruiz de Gaona en la Sierra de Urbasa (Navarra). Descripción de nuevo material en Álava. *Princes de Viana. Suplemento de Ciencias*, 14/15, 125-136.

Dollo, L. 1889. Note sur les vertébrés récemment offerts au Musée de Bruxelles par M. Alfred Lemonnier. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie*, 3, 181-182.

Floquet, M. 1998. Outcrop cycle stratigraphy of shallow ramp deposits, the Late Cretaceous series on the Castilian Ramp (Northern Spain). In: *Mesozoic and Cenozoic Sequence Stratigraphy of European Basins* (eds. Graciansky, P.C. de, Hardenbol, J., Jacquin T. & Vail, P.R.). SEPM, Special Publication, 60, 343-361.

Gaudry, A. 1892. Les Pythonomorphes de France. *Mémoires de la Société géologique de France*, 10, 13 pp., 2 pl.

Geervais, P. 1853. Observations relatives aux reptiles fossiles de France. *Comptes Rendus de l’Académie des Sciences Paris*, 36, 374-377 and 470-474.

Graciansky, P.C. de, Hardenbol, J., Jacquin T. & Vail, P.R.). SEPM, Special Publication, 60, 343-361.

Gómez Alday, J.J., Elorza, J., Pereda-Suberbiola, X., Murelaga, X. & Astibia, H. 1999. Taphonomy and Paleoecology of the Upper Cretaceous continental vertebrate-bearing beds of the Laño quarry (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Álava*, 14, Número especial 1, 43-104.

Lingham-Soliar, T. 1995. Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauroidea, Reptilia) from the Upper Cretaceous, Upper Maastrichtian of the Netherlands. *Philosophical Transactions of the Royal Society of London* B, 347, 155-180.
Lingham-Soliar, T. & Nolf, D. 1989. The mosasaur Prognathodon (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. Bulletin de l’Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 59, 137-190.

Mantell, G.A. 1829. A tabular arrangement of the organic remains of the county of Sussex. Transactions of the Geological Society of London, 2, 201-216.

Mulder, E.W.A. 1999. Transatlantic latest Cretaceous mosasaurs (Reptilia, Lacertilia) from the Maastrichtian type area and New Jersey. Geologie en Mijnbouw, 78, 281-300.

Mulder, E.W.A., Jagt, J.W.M., Kuypers, M.M.M., Peeters, H.H.G. & Rompen, P. 1998. Preliminary observations on the stratigraphic distribution of Late Cretaceous marine and terrestrial reptiles from the Maastrichtian type area (SE Netherlands, NE Belgium). Oryctos, 1, 55-64.

Oppel, M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. Joseph Lindauer, München.

Polcyn, M.J. & Bell, G.L., Jr. 2005. Russellosaurus coheni n. gen., n. sp., a 92 million-year old mosasaur from Texas (USA), and the definition of the parafamily Russellosaurina. Netherlands Journal of Geosciences, 84, 321-333.

Pereda Suberbiola, X., Astibia, H., Murelaga, X., Elorza, J. & Gómez-Alday, J.J. 2000. Taphonomy of the Late Cretaceous dinosaur-bearing beds of the Laño Quarry (Iberian Peninsula). Palaeogeography, Palaeoclimatolology, Palaeoecology, 157, 247-275.

Poyato-Ariza, F., Fielitz, C. & Wenz, S. 1999. Marine actinopterygian fauna from the Upper Cretaceous of Albaina (Laño quarry, northern Spain). Estudios del Museo de Ciencias Naturales de Álava, 14, Número especial 1, 325-338.

Russell, D.A. 1967. Systematics and morphology of American mosasaurs. Bulletin of Peabody Museum of Natural History, Yale University, 23, 1-241.

Santamaría, R. & López, G. 1996. Aspectos bioestratigráficos de los ammonites e inocerámidos (Bivalvia) del Albiense superior al Maastrichtiense de la Provincia de Álava. Revista Española de Paleontología, N° extraordinario, 148-159.

Sauvage, H.E. 1897-1898. Les vertébrés fossiles du Portugal. Contributions à l’étude des poissons et des reptiles du Jurassique et du Crétacé. Mémoires et Communications du Service géologique du Portugal, 1-46.

Schulp, A.S. 2006. On Maastricht mosasaurs. Publicaties van het Natuurhistorisch Genootschap in Limburg, 45, 1-140.

Schulp, A.S., Polcyn, M., Mateus, O., Jacobs, L. & Morais, M.L. 2008. A new species of Prognathodon (Squamata, Mosasauridae) from the Maastrichtian of Angola, and the affinities of the mosasaur genus Liodon. Proceedings of the Second Mosasaur Meeting, Fort Hays Studies Special Issue, 3, 1-12.
