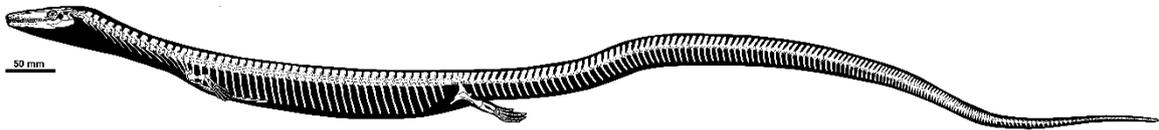


Bruno Gonçalves Augusta

Anatomia, taxonomia, ontogenia e filogenia de  
mosassaurianos basais (Squamata, Mosasauria)  
e suas implicações para a evolução de  
Anguimorpha



Anatomy, taxonomy, ontogeny and phylogeny  
of basal mosasaurians (Squamata, Mosasauria)  
and their implications to the evolution of  
Anguimorpha

Vol. 1 – Text

São Paulo

2019

Bruno Gonçalves Augusta

Anatomia, taxonomia, ontogenia e filogenia de mosassaurianos basais (Squamata, Mosasauria) e suas implicações para a evolução de Anguimorpha

Anatomy, taxonomy, ontogeny and phylogeny of basal mosasaurians (Squamata, Mosasauria) and their implications to the evolution of Anguimorpha

Thesis submitted to the Instituto de Biociências da Universidade de São Paulo, for obtaining the degree of Doctor of Philosophy in Zoology, subarea Vertebrate Paleontology.

**Advisor:** Dr. Hussam Zaher

**Internship supervisor:** Dr. Louis Leo Jacobs

São Paulo

2019

Augusta, Bruno Gonçalves

Anatomy, taxonomy, ontogeny and phylogeny of basal mosasaurians (Squamata, Mosasauria) and their implications to the evolution of Anguimorpha / Bruno Gonçalves Augusta; orientador Hussam Zaher. -- São Paulo, 2019.

315 f.

Tese (Doutorado) - Instituto de Biociências da Universidade de São Paulo, Departamento de Zoologia.

1. Mosasauria. 2. Dolichosauridae. 3. Cretaceous. 4. Coniasaurus. 5. Western Interior Seaway. I. Zaher, Hussam, orient. II. Título.

## Committee:

---

Prof. Dr.

---

Prof. Dr.

---

Prof. Dr.

---

Prof. Dr.

---

Prof. Dr. Hussam Zaher (advisor)

For Amanda Alves Gomes,  
my lovely and very patient wife, who supported me  
in more situations than I can even count,  
and for the future children we are going to have someday.

*Beautiful is what we see,*

*More beautiful is what we know,*

*Most beautiful, by far, is what we don't*

(Nicholas Steno, 1638-1686)

## Acknowledgements

First and foremost, I would like to thank my three advisors, mentors and good friends: Hussam Zaher, Michael Polcyn and Louis Jacobs. I am a very lucky man by having not only one, but three advisors, who helped me in many situations with advices, discussions, corrections and support. I am very grateful for developing my Ph.D. with three of the greatest paleontological minds I have ever known. Thank you.

The journey of developing a Ph.D. thesis is anything but easy, and the family support plays an essential role as an “invisible force” who constantly drives you forward. For this, I thank my parents, Virginia Célia Gonçalves and Mauricio Augusta, my brother Mauricio Gonçalves Augusta, my nephew Lucas Pacheco Augusta, my grandparents Iolanda Carlos Augusta and Laerte Augusta (*in memorian*) and my parents-in-law Elizabeth Alves Gomes and João Gomes Neto for providing me all the strength and love I needed so many times. But the greatest support I have had during this journey was definitely given by my wife, Amanda Alves Gomes, who stayed by my side during the whole process, helping me with emotional support, discussions and even image and text editions. Thank you, Amanda, this thesis is partly yours too and I love you.

The best part of being in an active laboratory is to exchange knowledge with so many good friends and admirable minds. This interchange is crucial for having new ideas and resolving many of the problems that arise during the thesis construction. I deeply thank active and former members of the MZUSP Paleontology and Herpetology labs, including Paulo Nascimento, Rosely Rodrigues, Melissa Rosa, Natan Brilhante, Wellton Pinto, Leandro Sanchez, Natasha Mezzacappa, Rafael Delcourt, Ana Bottallo, Karla Moya, Bruno Navarro, André Cataruzzi, Lucas Piazzentin, Ernesto Aranda, Rodolfo dos Santos, “Duzão”, Caio Geroto, Natália Friol, Paulo Machado, Paola Sánchez, Flávio Molina, Daniela Gennari, Felipe Grazziotin, Daniela França and Aline Benetti. I wish to especially thank Alberto Carvalho for all the support through these years (10 years from now!) and for being a very good friend of mine. And I thank again Hussam Zaher for allowing me to be part of these labs.

My internship at Southern Methodist University was the main core of this thesis, and I will be forever in debt to everyone involved with it. I would like to thank Diana Vineyard, Bonnie Jacobs, Dale Wrinkler, Bill Johnson, William Stenberg, Clarice do Couto and Alexander Herrera and especially Louis Jacobs and Michael Polcyn for allowing me to be part of the SMU Paleontological lab. You guys provided me four of the best months of my entire

life. I also thank the crew of the University of Texas High-Resolution X-ray CT Facility, Jessie Maisano and Matthew Colbert, for the support during the scanning of SMU and DMNH specimens.

Graduation Office at IB-USP provided substantial support during the whole process of this thesis development, and I would like to thank especially Lilian Parpinelli and Erika Takamoto for their “infinite” patience when answering so many of my questions. I have learned a lot with professors from the many classes I participated during the beginning of this Ph.D. process, so I would like to thank them all: Antônio Olinto, Maria Isabel Landim, Mário de Vivo, Chris Klingenberg, Suzana Ursi, Miguel Trefaut, Mônica Ragazzo, Taran Grant, Eduardo Santos, Luis Silveira and especially Peter Pearson, who inspired and supported me to write this thesis in English. I am also very thankful for all the important comments from my qualifying exam committee: Mário de Pinna, Luiz Anelli and Alberto Barbosa. And besides being a great friend of mine from a long time now, Felipe Elias is also an amazing paleoartist and kindly provided the coniasaur reconstructions seen here.

I also want to deeply thank all the curators from the many paleontological collections I was able to visit during graduation: Sandra Chapman (Natural History Museum – London), John Cooper (Booth Museum of Natural History – Brighton), Irene Zorn (Geologische Bundesanstalt – Wien), Ursula Göhlich (Natural History Museum – Wien), Cristiano Dal Sasso (Museo di Storia Naturale di Milano) and Deborah Arbull (Museo Civico di Storia Naturale di Trieste). In special, I would like to thank Tony Fiorillo (Perot Museum of Nature and Science – Dallas) for providing unrestricted access to the astonishing DMNH-1601 specimen. During my European trip I have had an essential housing support at Portogruaro, so I would like to thank Anna Ferraroni and her family (Paolo, Maria Elisabetta and Antonio Ferraroni) for kindly hosting me that time.

Finally, I would like to thank the financial support which made this thesis possible. This research was financed by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil CAPES (Finance Code 001) and Institute for the Study of Earth and Man (ISEM). I also thank Hennig Society for providing free access to the T.N.T. software and documentation.

## **Abstract**

Mosasauria is a clade of essentially Late Cretaceous marine reptiles. Although well known by several nicely preserved specimens, phylogenetic relationships of mosasaurians within Squamata are still a matter of intense debate. Most of the works discussing the relationships of mosasaurians in global contexts of squamates were based mainly on more derived taxa, including only few basal forms. Here the anatomy, phylogeny, ontogeny and taxonomy of the basalmost mosasaurian radiation, the commonly known “dolichosaurs”, is reviewed, mostly on the light of new and exquisitely preserved coniasaur remains from Texas. New remains described here encompass dozens of specimens, including a new species represented by a gravid female and several embryos. A revision of the genus *Coniasaurus* suggest it as encompassing four species: *C. crassidens*, *C. longicollis* (former *Dolichosaurus longicollis*), *C. gracilodens* and the new taxon described here. Contrary to what is observed in more derived forms, the patterns of tooth attachment in coniasaurs are very similar to those of varanooids, suggesting similarities between tooth attachment and implantation in snakes and derived mosasaurs to be the result of homoplasies. The evolution of the dolichosaurian postcranial anatomy is assessed, finding new diagnostic characters for several distinct lineages. A phylogenetic analysis of Mosasauria in a global matrix of squamates, including the largest sample of basal forms ever tested, consistently found the group to be closely related to Varanoidea, rejecting the hypotheses of the group being closely related either to snakes or lying in a more basal position among squamates. Results gathered by this thesis are expected to greatly contribute to the knowledge of this astonishing group.

**Keywords:** Dolichosauridae; Late Cretaceous; Western Interior Seaway; Postcranial anatomy; Varanoidea.

## Resumo

Mososauria é um clado formado essencialmente por répteis marinhos do Cretáceo Superior. Embora bem conhecido por diversos espécimes, as relações filogenéticas do grupo dentro de Squamata formam um tópico de intenso debate. A maior parte dos trabalhos discutindo o tema em análises globais de Squamata foram baseadas em táxons mais derivados, incluindo apenas poucas formas basais. Aqui, a anatomia, filogenia, ontogenia e taxonomia da irradiação mais basal do grupo, os “dolicossauros”, foi revista, principalmente à luz de novos restos fósseis de coniaossauros do Texas. Os novos fósseis descritos aqui englobam dezenas de espécimes, incluindo uma nova espécie representada por uma fêmea grávida e diversos embriões. Uma revisão do gênero *Coniasaurus* sugere que o mesmo engloba quatro espécies: *C. crassidens*, *C. longicollis* (antes *Dolichosaurus longicollis*), *C. gracilodens* e o novo táxon descrito aqui. Ao contrário do observado em formas mais derivadas, os padrões de fixação dentária nos coniaossauros é muito similar àqueles dos varanoídes, sugerindo que as similaridades observadas nestes padrões entre serpentes e mosassauros derivados resulta da ocorrência de homoplasias. A evolução do esqueleto pós-craniano dos dolicossauros foi avaliada, encontrando novos caracteres diagnósticos para diferentes linhagens. Uma análise filogenética de Mososauria em uma matriz global de Squamata, incluindo a maior amostragem de formas basais já testada, consistentemente encontrou o grupo como proximamente relacionado ao clado Varanoidea, rejeitando hipóteses de proximidade com serpentes ou numa posição mais basal dentro de Squamata. Espera-se que os resultados provenientes desta tese contribuam consideravelmente para o conhecimento deste incrível grupo.

**Palavras-chave:** Dolichosauridae; Cretáceo Superior; Mar Interior Ocidental; Anatomia pós-craniana; Varanoidea.

## Table of contents

Acknowledgements .....	v
Abstract .....	vii
Resumo .....	viii
General Introduction .....	13
The clade Mosasauria .....	14
Basal mosasaurians: dolichosaurs .....	15
Basal mosasauroids: “aigialosaurs” .....	20
The family Mosasauridae .....	22
The enigmatic relationships of mosasaurians within Squamata.....	24
The importance of gathering new data for improving our understanding of the mosasaurian evolution.....	25
Thesis organization .....	27
References .....	27
Chapter 1 - A new and exquisitely preserved fossil marine lizard with embryos.....	37
Abstract .....	37
Resumo .....	38
1.1. Introduction .....	39
1.2. Material and methods .....	40
1.3. Results .....	41
1.3.1. Systematic Paleontology .....	41
1.3.2. Paleobiogeographic and geochronological settings .....	42
1.3.3. Ontogeny of cranial elements.....	44
1.3.4. Phylogenetic relationships of the dolichosaurids .....	44
1.4. Discussion .....	45
1.4.1. Paleobiology of <i>Coniasaurus</i> .....	45
1.4.2. Niche partitioning between adults and juveniles.....	46
1.4.3. The role of viviparity in mosasaurian evolution .....	47
References .....	47
Supplementary Text .....	53
Description of DMNH-1601 adult remains.....	53
List of characters .....	63
Character codings .....	68
References .....	68
Chapter 2 – New remains of North American coniasaurs (Squamata: Mosasauria) from the Upper Cretaceous of Texas and a revision of the genus <i>Coniasaurus</i> .....	72
Abstract .....	72

Resumo.....	73
2.1. Introduction .....	74
2.2. Methods.....	76
2.2.1. Institutional abbreviations .....	76
2.2.2. Specimens analyzed .....	76
2.2.3. Geological settings and localities .....	79
2.3. Results: description of specimens .....	84
2.3.1. Egyptian Way specimens .....	85
2.3.2. DFW Airport specimens.....	88
2.3.3. Lowes Farm specimens .....	93
2.3.4. 1382 locality specimens .....	93
2.3.5. New Locality specimen.....	94
2.3.6. Texas Memorial Museum specimens .....	94
2.3.7. Redescription of Bell <i>et al.</i> (1982) coniasaur cranial remains .....	95
2.4. Discussion .....	97
2.4.1. A revision of the genus <i>Coniasaurus</i> .....	97
2.4.2. The reliability of phylogenetic characters and the quality of fossil specimens ...	103
2.5. Final considerations.....	105
References .....	105
Chapter 3 - Patterns of tooth attachment and implantation in <i>Coniasaurus</i> (Squamata, Mosasauria) based on high-resolution CT data.....	114
Abstract .....	114
Resumo.....	115
3.1. Introduction .....	116
3.2. Methods.....	118
3.3. Results .....	118
3.4. Discussion .....	119
3.4.1. Homologies and homoplasies regarding mosasaurian tooth attachment patterns	119
3.4.2. Limitations of CT-based histology.....	120
3.5. Final considerations.....	121
References .....	121
Chapter 4 - Ontogenetic trends in <i>Coniasaurus</i> (Squamata, Mosasauria) and its implications to the paleobiology and evolution of basal mosasaurians .....	125
Abstract .....	125
Resumo.....	126
4.1. Introduction .....	127
4.2. Methods.....	127
4.3. Description of specimens and anatomical comparisons.....	128

4.3.1. Cranial remains .....	128
4.3.2. Axial remains .....	131
4.3.3. Appendicular remains .....	134
4.4. Discussion .....	134
4.4.1. How many embryos did <i>Coniasaurus</i> bear? .....	134
4.4.2. Changes in lifestyles through development .....	135
4.4.3. Systematic considerations .....	136
4.5. Final considerations.....	137
References .....	138
Chapter 5 - Evolution of the postcranial skeleton in basal mosasaurians (Squamata, Mosasauria).....	142
Abstract .....	142
Resumo.....	143
5.1. Introduction .....	144
5.2. Methods.....	145
5.2.1. Institutional Abbreviations .....	145
5.2.2. Specimens analyzed .....	145
5.2.3. Measurements.....	145
5.2.4. CT Data .....	145
5.3. Anatomical comparisons .....	146
5.3.1. Axial skeleton.....	146
5.3.2. Appendicular skeleton.....	152
5.4. Discussion .....	161
5.4.1. Presacral count characters .....	161
5.4.2. The postcranial skeleton among distinct basal mosasaurian lineages.....	162
5.4.3. Postcranial characters and the dolichosaur / mosasaurian relationships .....	168
5.5. Final considerations.....	170
References .....	170
Chapter 6 – A phylogenetic analysis of Mosasauria (Squamata) supports the hypothesis of varanoid affinities for the clade.....	176
Abstract .....	176
Resumo.....	177
6.1 Introduction .....	178
6.2 Material and Methods.....	179
6.2.1. Dataset selection and modifications .....	179
6.2.2. Dataset analysis .....	180
6.3 Results .....	181
6.4 Discussion .....	183

6.4.1. Mosasaurians as anguimorph lizards.....	183
6.4.2. Mosasauria as a monophyletic group .....	184
6.4.3. Dolichosauridae as a monophyletic group .....	185
6.4.4. Issues within Mosasauroidae.....	186
6.4.5. Taxonomic sampling tests .....	188
6.4.6. The importance of comprehensive taxonomic sampling regarding fossil taxa....	189
6.5 Final considerations.....	191
References .....	192
Appendix 1 - List of characters added to matrix .....	195
Appendix 2 – Taxon and character matrix .....	196
Appendix 3 - List of apomorphies.....	216
General Conclusions .....	223
General References .....	225

## **General Introduction**

Fossils of the remarkable mosasaurs, the largest lizards that have ever lived on Earth, have been captivating scientists' interests from centuries now. Some of the first documented records of mosasaur findings date back to the 18<sup>th</sup> century, when many bones were recovered by Dr. Johann Leonard Hoffmann near the city of Maastricht, Netherlands (Pieters *et al.*, 2012). In particular, one specimen, a very large mosasaur skull, was already famous during the late 18<sup>th</sup> - early 19<sup>th</sup> centuries: the commonly known, at that time, "*Le Grand Animal des Maastricht*", initially considered as a crocodile and later a sperm whale (Caldwell, 2012). By 1794 Maastricht was under the siege of French armies, which confiscated the "petrified crocodile" and sent it to the Muséum national d'Histoire naturelle (MNHN) in Paris, where it stays up to modern days (Pieters *et al.*, 2012). In Paris, it was studied by the famous naturalist Georges Cuvier (1808), who firstly provided a detailed analysis of the specimen and concluded that the "*Grand Animal de Maastricht*" was rather related to monitor lizards. However, it took years until the specimen was formally named during the 1820's: *Mosasaurus hoffmanni*, namely the "lizard of Meuse river" and honoring Dr. Hoffmann (Caldwell, 2012). All these facts happened during the very beginning of Paleontology as a modern science, even before the name "dinosaur" was coined by Owen (1841), so the name "mosasaur" is even older than the name "dinosaur".

Mosasaur remains were very rare in Europe during the 19<sup>th</sup> century, but many new specimens started to be found in North America later that century, leading Marsh (1879) to propose the name Mosasauria for a new suborder of lacertilians which would encompass all these taxa of aquatic lizards. Mosasaurian remains were also studied by a series of other famous and very important naturalists and paleontologists during the late 19<sup>th</sup> - early 20<sup>th</sup> centuries, such as Owen (1877), Cope (1869), Osborn (1899), Camp (1923) and Nopcsa (1923), helping to define Paleontology as a science. Since Cuvier (1808) firstly proposed lizard affinities for mosasaurs, no other author has found contrary evidence to that. However, the relationships of mosasaurians with other squamates are still an open question up to modern days, whose details will be discussed below. Finding new evidence that help to answer the question "what kind of lizard is a mosasaurian?" is one of the main goals of this thesis.

## The clade Mosasauria

Mosasaurians were a group of extinct aquatic lizards well nested within Squamata, although their exact phylogenetic relationships with other squamates is still a matter of intense debate (Carroll *and* DeBraga, 1992; Bell, 1997; Lee, 1998; Caldwell, 1999a; Zaher *and* Rieppel, 1999; Rieppel *and* Zaher, 2000a; Conrad, 2008; Gauthier *et al.*, 2012; Reeder *et al.*, 2015). They were essentially marine reptiles, yet two non-marine records are known: the amphibious wetland dolichosaur *Kaganaias hakusanensis* (Evans *et al.*, 2006) and the freshwater mosasaurid *Pannoniasaurus inexpectatus* (Makádi *et al.*, 2012). Mosasaurian irradiation started approximately at the beginning of the Late Cretaceous, during the Cenomanian/Turonian stages (~100-90Ma), and went through the Cretaceous up to the end of the Maastrichtian stage (~65Ma) (Russell, 1967; DeBraga *and* Carroll, 1993; Polcyn *et al.*, 2014), when they became extinct probably due to the catastrophic consequences related to the K/T mass extinction events (Gallagher *et al.*, 2012). However, two records of basal mosasaurians are remarkable for being dated as Early Cretaceous: an isolated vertebra of a putative coniasaur from the Albian of Australia (~112-100Ma) (Scanlon *and* Hocknull, 2008) and the dolichosaur *Kaganaias hakusanensis* from the Valanginian/Hauterivian of Japan (~140-130Ma) (Evans *et al.*, 2006).

Mosasaurian lizards presented a great morphological and paleobiological diversity with a worldwide distribution during the Late Cretaceous, as their fossils were recovered from sediments in all continents (Bell, 1997; Carvalho *and* Azevedo, 1998; Bardet *et al.*, 2005; Martin *and* Fernández, 2007; Scanlon *and* Hocknull, 2008; Páramo-Fonseca, 2011; Konichi *et al.*, 2012). Some of them were large marine forms, as the Mosasaurinae *Mosasaurus hoffmanni* with 17,5m long (Lingham-Soliar, 1995) and the Tylosaurinae *Hainosaurus bernardi* with 13m long (Lindgren, 2005). Mosasauria is a clade formed by three traditionally recognized groups: the basal forms commonly referred to as dolichosaurs (basal mosasaurians), formed by small to medium-sized animals with long necks and reduced forelimbs; “aigialosaurs” (basal mosasauroids), a likely paraphyletic assemblage of mosasauroids which presents slightly modified swimming tails but plesiomorphic, facultatively terrestrial, limbs (plesiopedal *sensu* Bell and Polcyn, 2005); and the monophyletic family Mosasauridae, which includes some members with highly derived, fully aquatic tail and limbs (hydropedal). Despite being a possible paraphyletic assemblage, the name dolichosaur is popular in the literature and therefore will be sometimes used in this thesis for avoiding nomenclature confusion. Dolichosaurs are usually found as the basalmost group, being the sister-group of mosasauroids (clade Mosasauroidea) (Conrad, 2008; Conrad *et al.*, 2011; Gauthier *et al.*, 2012), although some

authors consider at least some dolichosaurs to be more related to snakes than to mosasaurs (Lee, 1998; Lee *and* Caldwell, 2000; Caldwell *and* Palci, 2010). Within Mosasauoidea, basal mosasauroids (formerly referred as “aigialosaurs”) are the sister-group of the Mosasauridae family, popularly known as mosasaurs (Polcyn *and* Bell, 1994; Rieppel *and* Zaher, 2000a; Dutchak, 2005; Conrad, 2008; Caldwell *and* Palci, 2010; Gauthier *et al.*, 2012). Characters joining Mosasauria as a monophyletic clade include, among others, the presence of an intramandibular joint, a modified pleurodont dentition and the cervical intercentrae position (Polcyn *and* Bell, 1994; Zaher *and* Rieppel, 1999; Rieppel *and* Zaher, 2000a; Conrad 2008, Conrad *et al.*, 2011; Gauthier *et al.*, 2012; Reeder *et al.*, 2015).

### **Basal mosasaurians: dolichosaurs**

Dolichosaurs were relatively small and long-bodied marine squamates closely related to mosasauroids (Conrad, 2008; Gauthier *et al.*, 2012; Reeder *et al.*, 2015). Characters typically found in the group include the presence of an elongated body, usually presenting more than 10 cervical and 26 dorsal vertebrae, very reduced forelimbs in relation to hindlimbs and the presence of zygosphenes-zygantrum accessory articulation (Caldwell, 2000; Pierce *and* Caldwell, 2004; Evans *et al.*, 2006; Conrad, 2008; Caldwell *and* Palci, 2010). Dolichosaur fossils are found mainly in Cenomanian-Turonian marine sediments of North America and Eurasia (Caldwell, 1999b; Lee *and* Scanlon, 2002; Haber *and* Polcyn, 2005; Jacobs *et al.*, 2005; Bell *et al.*, 2013). Although some dolichosaurs were recently described or redescribed (Lee *and* Caldwell, 2000; Pierce *and* Caldwell, 2004; Haber *and* Polcyn, 2005; Evans *et al.*, 2006; Palci *and* Caldwell, 2010), some aspects of their anatomy are still poorly understood, and this may have led researchers to reach distinct systematic conclusions regarding the relationships of the group within Squamata (i.e. Lee, 1998; Lee *and* Caldwell, 2000; Caldwell *and* Palci, 2010 contra DeBraga *and* Carroll, 1993; Rieppel *and* Zaher, 2000a; Conrad, 2008). 17 dolichosaur taxa have been described in the literature, but as *Acteosaurus crassicosatus* is probably a junior synonym of *Adriosaurus suessi* (Caldwell *and* Lee, 2004) and *Introrsisaurus pollicidens* was described in the basis of a single shed tooth from a totally different geological context (Jurassic outcrop; Seiffert, 1973), it is possible to recognize 15 valid dolichosaur taxa up to now (Table 1).

**Table 1 – List of valid dolichosaur taxa described and named in the literature.**

<b>Taxon</b>	<b>Reference</b>	<b>Holotype</b>	<b>Age and locality of the holotype</b>
<i>Acteosaurus tommasinii</i>	Von Meyer (1860). Redescribed by Palci and Caldwell (2010)	MCSNT 9960: articulated postcranial skeleton.	Upper Cenomanian of Slovenia
<i>Adriosaurus microbrachis</i>	Palci and Caldwell (2007)	MCSNT 7792: articulated mid-portion of the trunk with limbs	Upper Cenomanian of Slovenia
<i>Adriosaurus skrbiniensis</i>	Caldwell and Palci (2010)	SMNH 2158: articulated posterior portion of the skull, hindlimbs and axial series up to anteriormost caudals	Upper Cenomanian of Slovenia
<i>Adriosaurus suessi</i>	Seeley (1881). Redescribed by Lee and Caldwell (2000).	Unnumbered specimen at NMW: articulated posteriormost portion of the trunk, hindlimbs and tail	Upper Cenomanian of Slovenia
<i>Aphanizocnemus libanensis</i>	Dal Sasso and Pinna (1997)	MSNM V783: nearly complete individual, missing only anteriormost portion of the skull	Middle Cenomanian of Lebanon
<i>Coniasaurus crassidens</i>	Owen (1850). Redescribed by Caldwell and Cooper (1999)	BMB 007155: a left maxilla and 14 disassociated dorsal vertebrae	Lower to Middle Cenomanian of England

<i>Coniasaurus gracilodens</i>	Caldwell (1999)	BMNH R44141: partially preserved skull, four dorsal vertebrae and a scapulocoracoid complex	Lower Cenomanian of England
<i>Dolichosaurus longicollis</i>	Owen (1850). Redescribed by Caldwell (2000).	BMNH R 49002: partially preserved skull, cervical and axial series	Lower Cenomanian of England
<i>Eidolosaurus trauthi</i>	Nopcsa (1923)	GBA 1923-001-0001: a natural mold comprising partially preserved skull and limbs and a complete axial series	“Neocomian” of “Istria, Dalmatia” (more precise information is lacking; Irene Zorn, pers. comm.)
<i>Judeasaurus tchernovi</i>	Haber and Polcyn (2005)	HUJI P4000: partially preserved skull and fragments of cervical vertebrae	Upper Cenomanian-Lower Turonian of Israel
<i>Kaganiaias hakusanensis</i>	Evans <i>et al.</i> (2006)	SBEI 1568: articulated and partially preserved axial skeleton with hindlimbs	Berriasian-Hauterivian of Japan
<i>Mesoleptos zendrinii</i>	Cornalia and Chiozza (1852). New specimen reported by Lee and Scanlon (2002)	Unnumbered specimen at MCSNM (lost?): partially preserved axial series and fragments of a hindlimb	Upper Cenomanian of Slovenia
<i>Pontosaurus kornhuberi</i>	Caldwell (2006)	MSNM V3662: complete individual	Cenomanian of Lebanon

		with soft tissues preserved on a slab	
<i>Pontosaurus lesinensis</i>	Kornhuber (1873). Redescribed by Pierce and Caldwell (2004)	GBA 1873/4/2: nearly complete skull and axial series up to sacral level. Forelimbs preserved	Upper Cenomanian of Croatia
<i>Primitivus manduriensis</i>	Paparella <i>et al.</i> (2018)	MPUR NS 161: nearly complete skeleton, missing small portions of the tail and skull	Upper Campanian – Lower Maastrichtian of Italy

*Acteosaurus* was a genus composed by two species: *Acteosaurus tommasinii* von Meyer, 1860 and *Acteosaurus crassicostatus* Calligaris, 1993, but the later is probably a junior synonym of *Adriosaurus suessi* (Caldwell and Lee, 2004). It was recovered from Upper Cenomanian sediments of Slovenia, and it is a non-pachyostotic dolichosaur characterized by a very peculiar vertebral morphology of the dorsal vertebrae, which are constricted posteriorly rather than in the middle of the elements (Palci and Caldwell, 2010).

*Adriosaurus* is a pachyostotic dolichosaur genus composed by three species: *Adriosaurus suessi* Seeley, 1881, *Adriosaurus microbrachis* Palci and Caldwell, 2007 and *Adriosaurus skrbinsensis* Caldwell and Palci, 2010. As *Acteosaurus*, they were all recovered from Upper Cenomanian rocks of Komen, Slovenia (Lee and Caldwell, 2000; Palci and Caldwell, 2007; Caldwell and Palci, 2010). Morphology of its skull, pectoral girdles and pelvis have been used to support the hypothesis of dolichosaurs being closely related to snakes (Lee and Caldwell, 2000; Caldwell and Palci, 2010). *A. microbrachis* have been described as possessing a very unusual vestigial forelimb, with only a reduced humerus present (Palci and Caldwell, 2007).

*Aphanizocnemus libanensis* Dal Sasso and Pinna, 1997 is the only species of the genus, recovered from Middle Cenomanian rocks of Lebanon. It was described as a dolichosaur, but recently restudied by Mekarski (2017) and considered to be not even an anguimorph, but instead a scincogekkonomorph. One of its more conspicuous character is the presence of a very reduced, square-shaped, tibia (Dal Sasso and Pinna, 1997).

*Coniasaurus* is a genus of dolichosaur represented by two distinct species: *Coniasaurus crassidens* Owen, 1850 and *Coniasaurus gracilodens* Caldwell, 1999. It is often found to be closely related to *Dolichosaurus longicollis* Owen, 1850, forming the family Dolichosauridae (Caldwell, 2000; Palci and Caldwell, 2010). However, the lack of more complete *Coniasaurus* postcranial remains and *Dolichosaurus* cranial remains have prevented a proper comparison so far. *Coniasaurus* and *Dolichosaurus* had a wide distribution during the Upper Cretaceous (Cenomanian to Santonian), with specimens being recovered from rocks of USA (Bell *et al.*, 1982; Bell, 1993; Shimada and Bell, 2006; Shimada and Ystesund, 2007; Shimada *et al.*, 2007; Nagrodski *et al.*, 2012), England (Owen, 1850; Caldwell and Cooper, 1999; Caldwell, 1999b) and Germany (Diedrich, 1997). Most conspicuous character of *Coniasaurus* is the highly heterodont dentition the taxon bears, with anteriormost teeth being conical and recurved and posteriormost swollen and bulbous (Owen, 1850; Caldwell and Cooper, 1999).

*Eidolosaurus trauthi* Nopcsa, 1923 is the only species of the genus and it was not redescribed recently. Holotype is composed by a mold of a relatively complete animal, from the posterior part of the skull to the tip of the tail. Geological information is scarce, and Nopcsa (1923) only referred to specimen as recovered from “Neocomian” rocks of “Istria, Dalmatia”.

*Judeasaurus tchernovi* Haber and Polcyn, 2005 is the single species of the genus, recovered from Upper Cenomanian – Lower Turonian rocks of Israel. Holotype is composed by well-preserved portions of the skull and anteriormost cervical vertebrae. *Judeasaurus* present a unique suite of characters seem both in terrestrial varanoid lizards and in mosasaurian lizards (Haber and Polcyn, 2005).

*Kaganaias hakusanensis* Evans *et al.*, 2006 is the only species of the genus and it was found in a Berriasian-Hauterivian outcrop of Japan. The single known specimen is composed by an articulated middle portion of the axial skeleton (mostly presenting dorsal vertebrae) and portions of the limbs (Evans *et al.*, 2006). It is the only valid mosasaurian taxa described for the Lower Cretaceous so far.

*Mesoleptos zendrinii* Cornalia and Chiozza, 1852 is the only species of the genus, known only by postcranial remains. Holotype was recovered from Upper Cretaceous rocks of Komen, Slovenia, but additional referred specimens were found in Lower Cenomanian rocks of Israel as well (Lee and Scanlon, 2002). It was originally described as closely related to dolichosaurs (Cornalia and Chiozza, 1852; Nopcsa, 1923), but Lee and Scanlon (2002) found *Mesoleptos* as the sister-group of their Ophidia.

*Pontosaurus* is a genus composed by two species: *Pontosaurus lesinensis* Kornhuber, 1873 and *Pontosaurus kornhuberi* Caldwell, 2006. Former was recovered from Upper Cenomanian-Upper Turonian rocks of Hvar Island, Croatia, while the latter from Middle Cenomanian rocks of Lebanon (Pierce and Caldwell, 2004; Caldwell, 2006). Both include some of the most complete and better preserved dolichosaurs: *P. lesinensis* is composed by a complete skull, an axial series going through the first sacral ribs and the forelimbs (Pierce and Caldwell, 2004), while *P. kornhuberi* is virtually complete, from the anterior end of the snout to the posterior end of the tail (Caldwell, 2006).

*Primitivus manduriensis* Paparella *et al.*, 2018 is the most recent described dolichosaur, being recovered surprisingly from Upper Campanian-Lower Maastrichtian rocks of Puglia, Italy, which make it the only dolichosaur described from the latest Upper Cretaceous. Holotype is composed by a relatively complete (missing mostly the posteriormost portion of the tail) and poorly preserved specimen. It is also one of the few dolichosaurs with impressions of soft tissues. A phylogenetic analysis recovered *P. manduriensis* within Dolichosauridae and closely related to both *Pontosaurus lesinensis* and *Dolichosaurus longicollis* (Paparella *et al.*, 2018).

### **Basal mosasauroids: “aigialosaurs”**

Basal mosasauroids form a grade of semi-aquatic marine squamates, closely related to the family Mosasauridae, that is sometimes referred to as “aigialosaurs” in the literature (Bell, 1997; Caldwell, 1999a; Polcyn *and* Bell, 2005; Conrad *et al.*, 2011). They are known from Upper Cretaceous rocks of Europe, Asia and North America (Carroll *and* DeBraga, 1992; Polcyn *et al.*, 1999; Dutchak, 2005; Dutchak *and* Caldwell, 2009). A monophyletic Mosasauroidea clade (“aigialosaurs” plus Mosasauridae) is supported by characters as the presence of a strongly curved suprapedial process of the quadrate, expanded tooth bases, lateral compression and dorsoventral deepening of the tail and a scapula shorter than the coracoid (Bell, 1997; Conrad, 2008; Conrad *et al.*, 2011). Russell (1967), in his landmark study on the evolution of mosasaurs, also considered “aigialosaurs” to be the ancestors of mosasaurids, even before the first cladistic analyses of mosasaurs. McDowell *and* Bogert (1954) once considered the living lizard *Lanthanotus borneensis* to be a relict “aigialosaur”, but subsequent works rejected this hypothesis (Russell, 1967; Rieppel, 1980; Estes *et al.*, 1988; Carroll *and* DeBraga, 1992).

*Aigialosaurus dalmaticus* Kramberger, 1892 was discovered in Upper Cenomanian – Lower Turonian rocks of Hvar Island, Croatia, and it was redescribed by Dutchak and Caldwell

(2006). Holotype comprises a relative complete individual, lacking only the anteriormost tip of the snout and most of the tail. A second species of the genus, *Aigialosaurus novaki*, has also been described by Kramberger (1892) in the basis of 38 caudal vertebrae, but these were found to be undistinguishable from the caudal vertebrae of *Opetiosaurus buccichi* by Carroll and DeBraga (1992). The genus *Opetiosaurus* was suggested to be a synonym of *Aigialosaurus* (Dutchak and Caldwell, 2009), but a recent phylogenetic study have suggested that they may not be the same (Madzia and Cau, 2017).

*Carentonosaurus mineaui* Rage and Néraudeau, 2004 is a non-mososaurid mosasauroid from the Upper Cenomanian of the Madame Island, France. Holotype is a single mid- or posterior dorsal vertebra (MHNH, IMD 21), but 49 additional vertebrae were referred to the taxon (Rage and Néraudeau, 2004). It was a pachyostotic animal, probably associated with shallow marine environments (Houssaye *et al.*, 2008).

*Carsosaurus marchesetti* Kornhuber, 1893 has a single known specimen, composed by articulated remains of the axial (posterior cervicals to anterior caudals) and appendicular skeletons. It was collected from Cenomanian-Turonian rocks of Komen, Slovenia, and presents one of the better preserved basal mosasauroid appendicular skeleton (Caldwell, 1995). *C. marchesetti* holotype also present preserved remains of four embryonic individuals in the trunk region, being the first reported live-bearing mosasauroid (Caldwell and Lee, 2001).

*Haasiasaurus gittelmani* Polcyn *et al.*, 1999 is a basal mosasauroid from the Lower Cenomanian of Israel, although a later study found it to be nested within Mosasauridae (Bell and Polcyn, 2005). Its generic name was firstly described as *Haasia*, but as this name was preoccupied it was later corrected to *Haasiasaurus* (Polcyn *et al.*, 2003). Holotype is composed by a block containing a left mandible, quadrate and other skull fragments, but referred specimens to this taxon also include another skull and several axial remains (Polcyn *et al.*, 1999).

*Komensaurus carrolli* Caldwell and Palci, 2007 is a basal mosasauroid from the Upper Cenomanian of Komen, Slovenia. It was for a long time referred in the literature as the “Trieste aigialosaur” until the formal description of Caldwell and Palci (2007), and the holotype includes portions of the skull, axial and appendicular skeletons.

*Opetiosaurus buccichi* Kornhuber, 1901 was suggested to belong to the genus *Aigialosaurus* as *A. buccichi* (Dutchak and Caldwell, 2009), but some studies do not find support for this hypothesis (Madzia and Cau, 2017). The holotype was found in Upper Cenomanian rocks of the Hvar Island, Croatia, and it is composed by a relative complete

specimen with most of the postcranial skeleton and portions of the skull (Dutchak and Caldwell, 2009).

*Proaigialosaurus huenei* Kuhn, 1958 was described in the basis of a skull fragment from the Upper Jurassic of Solnhofen, Germany, but as the holotype is lost (Carroll and DeBraga, 1992; Dutchak, 2005), based on a fragmentary material from a very distinct geological context, it is not considered a valid basal mosasauroid taxon here.

*Vallecillosaurus donrobertoi* Smith and Buchy, 2008 is the only basal mosasauroid described from outside Europe so far. Its remains have been recovered from Lower Turonian rocks of Nuevo León State, Mexico. Initially, holotype was composed by a plate containing a posterior half of the axial skeleton (including hindlimbs) and two additional tail portions, but a later work was able to find additional holotype slabs containing the trunk region (even the sternal ribs and costal cartilages) and forelimbs (Buchy and Smith, 2011). It is also one of the few basal mosasauroids bearing impressions of soft tissues (Smith and Buchy, 2008).

*Walteria jeffersonensis* Mehl, 1931 was described as a putative “aigialosaur” trackway from the Lower Cretaceous of Colorado (USA), but Lockley *et al.* (1992) considered the record as dubious because Mehl (1931) only presented line drawings of the specimen and the original specimen was not found.

### **The family Mosasauridae**

If by one hand dolichosaurs and “aigialosaurs” are currently represented by respectively 15 and 7 valid species, on the other Mosasauridae is by far the most diverse group of the clade, with more than 70 species described to date. Within Mosasauridae three distinct subfamilies are traditionally recognized: Mosasaurinae, Tylosaurinae and Plioplatecarpinae (Russell, 1967; DeBraga and Carroll, 1993; Bell, 1997), which have a cosmopolitan distribution during most of the Late Cretaceous (Polcyn *et al.*, 2014). Recent works have proposed three more basal divisions for mosasaurids: Halisaurinae (Bardet *et al.*, 2005), Tethysaurinae (Makádi *et al.*, 2012) and Yaguarasaurinae (Palci *et al.*, 2013).

Mosasaurinae is the most diverse subfamily of mosasaurs and includes the first mosasaur taxon to be named, *Mosasaurus hoffmanni* (Street and Caldwell, 2016). *M. hoffmanni* is also the possible largest mosasaur known, with size estimations reaching up to 17,5m long (Lingham-Soliar, 1995). The evolution of the tail in Mosasaurinae shows modifications in the anatomy of the caudal vertebrae, suggesting a progressive shift from nearshore dwellers to pelagic cruisers (Lindgren *et al.*, 2011). Taxonomic composition of many mosasaurine genera

are unresolved, since taxa as *Clidastes*, *Prognathodon* and *Mosasaurus* are often found to be paraphyletic (Bell, 1997; Bell and Polcyn, 2005; Simões *et al.*, 2017). *Dallasaurus turneri*, formerly referred in the literature as the “Dallas aigialosaur” was actually found to be one of the basalmost members of the Mosasaurinae, even retaining plesiomorphic limbs capable of walk on land which implies on multiple “flipper” limbs acquired through mosasaur evolution (Bell and Polcyn, 2005).

Tylosaurinae is a mosasaurid clade that also includes some gigantic taxa, such as *Tylosaurus* and *Hainosaurus* (Jimenez-Huidobro, 2016), and it is characterized, among other characters, by a projection of the premaxilla anterior to the teeth, the premaxillary rostrum (Russell, 1967; Bell, 1997). Like mosasaurines, tylosaurines were top predators during the Late Cretaceous, and the analysis of gut contents have shown that these animals included fish, birds, turtles, plesiosaurs and even other mosasaurs in their diet (Everhart, 2004). They were abundant from the Coniacian through the Campanian but become likely replaced by mosasaurines during the Maastrichtian (Polcyn *et al.*, 2014).

Plioplatecarpinae includes medium-sized mosasaurs well represented in the fossil record, especially in North America, encompassing seven distinct genera (Konishi and Caldwell, 2011). Russell (1967) included in his Plioplatecarpinae the genera *Prognathodon* and *Plesiotylosaurus*, but more recent phylogenetic work recovered the genera within Mosasaurinae (Bell, 1997; Bell and Polcyn, 2005; Caldwell and Palci, 2007). At least some plioplatecarpines seem to have possessed a high maneuverability, making these mosasaurs agile predators (Cuthbertson *et al.*, 2015). Like mosasaurines, the taxonomy of plioplatecarpines is still unresolved, because genera such as *Platecarpus* and *Plioplatecarpus* may be para or polyphyletic (Bell, 1997; Bell and Polcyn, 2005; Polcyn and Everhart, 2008; Konishi and Caldwell, 2011).

Halisaurinae was erected to encompass the genera *Halisaurus* and *Eonatathor* in the basis of cranial and appendicular characters (Bardet *et al.*, 2005), although more recently taxa such as *Phosphorosaurus* and *Pluridens* were added (Polcyn *et al.*, 2012; Longrich, 2016). This subfamily is usually recovered as the sister-group of Natantia, a clade including the more derived Mosasaurinae, Tylosaurinae and Plioplatecarpinae taxa (Bardet *et al.*, 2005; Polcyn *et al.*, 2014).

Tethysaurinae and Yaguarasaurinae are the less diverse subfamilies of Mosasauridae, being currently represented by two and four species, respectively (Makádi *et al.*, 2012; Palci *et*

*al.*, 2013; Simões *et al.*, 2017), although some works do not agree with these assemblages (e.g. Polcyn *et al.*, 2014).

### **The enigmatic relationships of mosasauroidea within Squamata**

Despite mosasauroidea being known by a vast fossil record, there is still little consensus about their phylogenetic relationships within Squamata. The debate around the systematic position of mosasauroidea dates back to the 19th century. Cuvier (1808) firstly provided a detailed analysis of those remains, concluding that the "Grand Animal de Maastricht" was rather related to monitor lizards, a conclusion followed by subsequent studies (Mantell, 1829; Goldfuss, 1844; Owen, 1850). Cope (1869) was the first author to suggest a close relationship between mosasauroidea and snakes, forming a group he named Pythonomorpha. Cope's hypothesis triggered an intense debate in the scientific community through the next few decades, with some authors in favor of a mosasauroidea-varanoid affinity (e.g. Owen, 1877; Marsh, 1879; Baur, 1890; Williston, 1904; Nopcsa, 1923), others in favor of a mosasauroidea-snake affinity (e.g. Boulenger, 1891; Cope, 1895) and a third group suggesting a distinct subdivision for mosasauroidea within lacertilians (e.g. Osborn, 1899; Fejérváry, 1918). Camp (1923), in his landmark study on the relationships of lizards, comprehensively reviewed the mosasauroidea systematics debate, adding precise arguments to many anatomical questions and concluding that mosasauroidea were really varanoid-like lizards. His conclusion was followed by most authors through the next decades (McDowell and Bogert, 1954; Russell, 1967; Rieppel, 1980; Borsuk-Bialynicka, 1984; Carroll and DeBraga, 1992), and the former debate basically ended with Camp's conclusive review.

With the popularization of Cladistics, fresh start was given in the 1990's on the issue of mosasauroidea affinities. Estes *et al.* (1988) provided the first cladistic analysis of squamates, but did not include any fossil taxa in their matrix. Carroll and DeBraga (1992) published the first cladistic analysis to include aigialosaurs, obtaining a result that placed aigialosaurs as varanoids in a polytomy with the clades (*Lanthanotus* + *Varanus*) and (*Cherminotus* + *Saniwa*). Later, DeBraga and Carroll (1993), added mosasauroidea and recovered aigialosaurs as their sister-group, forming the clade Mosasauroidea, and Varanidae as the sister-group of Mosasauroidea. The same conclusion was reached in later studies (Polcyn and Bell, 1994; Bell, 1997). However, Caldwell *et al.* (1995) and Lee (1997a, b) challenged the varanoid affinities of mosasauroidea and proposed a close relationship between mosasauroidea and snakes, re-heating the long-standing debate first triggered by Cope and Owen. A series of studies followed, using a cladistic approach to analyze new morphological evidence at hand (Lee, 1998; Caldwell, 1999a; Lee and

Caldwell, 2000; Caldwell *et al.*, 2003). These studies were revised by Zaher and Rieppel (Zaher, 1998; Zaher *and* Rieppel, 1999; Rieppel *and* Zaher, 2000a, b; Rieppel *and* Zaher, 2001), who rejected the hypothesis of a close relationship between mosasaurs and snakes and an aquatic origin for snakes, concluding that the anatomical similarities between snakes and mosasaurs were not homologous. More recent works also were not able to reach a consensus regarding mosasaurian systematics, concluding that mosasaurs are either derived varanoids (Conrad, 2008; Wiens *et al.*, 2010; Conrad *et al.*, 2011), are nested within Pythonomorpha (Caldwell *and* Palci, 2010; Palci *et al.*, 2013. Paparella *et al.*, 2018) or lie outside of Anguimorpha (Gauthier *et al.*, 2012; Reeder *et al.*, 2015). The frequently heterogeneous sampling and the low representativeness of mosasaurian diversity in squamate phylogenetic analyses can be seen as the two main factors who perpetrate the lack of a consensus on the systematics of the group. On the other hand, many new basal mosasaurian and mosasauroid taxa were recently described (i.e. Bell *and* Polcyn, 2005; Caldwell *and* Palci, 2007; Smith *and* Buchy, 2008; Caldwell *and* Palci, 2010; Makádi *et al.*, 2012; Campbell *et al.*, 2016; Paparella *et al.*, 2018), making possible to include a wider sampling and new anatomical data into novel studies.

Some of the most divergent aspects in the scientific community regarding the systematics of mosasaurs include their pattern of tooth implantation, replacement and histology (Lee, 1997a; Zaher *and* Rieppel, 1999; Caldwell *et al.*, 2003; Rieppel *and* Kearney, 2005; Caldwell, 2007; Luan *et al.*, 2009; Liu *et al.*, 2016), the presence of an intramandibular joint in the mandible (Caldwell *and* Lee, 1997b; Rieppel *and* Zaher, 2000a) and the braincase morphology (Lee *and* Caldwell, 1998; Rieppel *and* Zaher, 2000b). Recently, Caldwell (2012) also questioned traditional characters used to link mosasaurs and varanoids, as the posteriorly retracted nares, the Meckel's canal anatomy and the number of presacral vertebrae. Most of these discussions, especially regarding the anatomy of the dentition, were based mainly on more derived taxa (Mosasauridae) and, for this reason, the study of these patterns in dolichosaurs stands as an essential step to better understand the early evolution of those features in the group.

### **The importance of gathering new data for improving our understanding of the mosasaurian evolution**

The debate around the origins and phylogenetic relationships of dolichosaurs, mosasaurs, varanoids and snakes during the past three decades was based primarily on redescrptions of previously known fossil specimens (e.g. Caldwell *and* Cooper, 1999; Lee *and* Caldwell, 2000; Pierce *and* Caldwell, 2004; Palci *and* Caldwell, 2010), reinterpretations of key

anatomical features (e.g. Caldwell and Lee, 1997; Caldwell and Lee, 1998; Rieppel and Zaher, 2000a, b; Polcyn *et al.*, 2005; Caldwell, 2012) and anatomical comparisons of relatively derived taxa (e.g. Zaher and Rieppel, 1999; Caldwell *et al.*, 2003; Luan *et al.*, 2009; Liu *et al.*, 2016). However, describing new and nicely preserved specimens, generating the most reliable morphological data as possible (i.e. CT-Scan data) and including wider taxonomical samplings in phylogenetic studies, especially basal forms, are crucial steps for better understanding the evolution of mosasaurian lizards as a whole.

Recently, Simões *et al.* (2016) questioned the quality of characters present in very large phylogenetic matrices, regarding specifically the relationships of squamate reptiles. The authors concluded that nearly one-third of the characters present in these matrices should be recoded or even excluded from analyses due to fails in tests of similarity (Patterson, 1982), conjunction (Patterson, 1982; Freudestein, 2005), independency of characters (e.g. Farris, 1983; de Pinna, 1991; Kluge, 2003; Sereno, 2007) and the distinction between characters and character states (Hennig, 1966). Laing *et al.* (2017) criticized the argument of Simões *et al.* (2016) of simply deleting “problematic” characters, arguing that the presence of larger matrices in the literature is inevitable and necessary for the development of systematics, since the availability of morphological data will only increase over time. In this thesis I follow the opinion of Laing *et al.* (2012). In addition, although the quality of character construction is indeed important in phylogenetic reconstructions, this thesis also address on the problem of relying character codings based on poorly preserved specimens and/or based on interpretative drawings present in the literature, since it seems to be the case in some of the matrices (e.g. Conrad, 2008; Conrad *et al.*, 2011; Gauthier *et al.*, 2012). Whenever possible, authors should personally study the specimens included in their analysis or use a very reliable source of morphological information, such as a large number of high-quality photos and CT-Scan files.

This contribution greatly improves the debate on the evolution of basal mosasaurians by: 1) Providing new morphological data on *Coniasaurus* anatomy by describing dozens of new specimens, based on the CT-Scan of nearly 400 hundred bones of Texas coniasaurs, and making this data available for future research; 2) Updating the taxonomic diversity of North American coniasaurs by describing a new species from the Cenomanian of Texas and providing a taxonomic revision of the genus; 3) Reporting the first evidence of viviparity in a dolichosaur lizard; 4) Describing the ontogenetic variation of a dolichosaur for the first time in the literature; 5) Describing the patterns of tooth attachment and implantation in a dolichosaur for the first time; 6) Comparing in detail the anatomy of the postcranial skeleton among the most of the

dolichosaur taxa, finding new diagnostic characters for some main lineages; and 7) Testing the phylogenetic relationships of the clade Mosasauria within Squamata by gathering the new morphological data provided by this work and adding it into the morphological matrix of Gauthier *et al.* (2012). The results obtained here strongly support the hypothesis of mosasaurians being anguimorph lizards, closely related to varanoids, instead of being related to snakes or lying outside of Scleroglossa, as discussed in detail by the next chapters.

### **Thesis organization**

This thesis is subdivided into six distinct chapters, each one covering a distinct aspect of the dolichosaurian anatomy, development, paleobiology and phylogenetic relationships. Chapter 1 is formatted to be submitted for a high-profile journal with a broader audience (such as Nature / Science), while subsequent chapters are formatted for submission in high impact but more specific journals (such as PlosOne, Zoological Journal of the Linnean Society, Journal of Vertebrate Paleontology, etc). Chapter 1 describes a new *Coniasaurus* species, the first dolichosaur formally described for North America, as well as the first viviparity record in a basal mosasaurian. Additional North American coniasaur remains are described in Chapter 2, and a taxonomic revision of the genus is provided. In Chapter 3 patterns of tooth attachment and implantation and firstly described for a dolichosaur taxon using CT data. Chapter 4 describes ontogenetic trends in *Coniasaurus*, using embryonic, juvenile and adult specimens for morphological comparisons. The postcranial anatomy of dolichosaurs is extensively discussed in Chapter 5, finding new diagnostic characters for some lineages and discussing the systematic implications of using “presacral vertebrae count” characters in phylogenetic analyses. Finally, Chapter 6 gather the new morphological data provided by the former chapters and applies it to the morphological dataset provided by Gauthier *et al.* (2012), expanding the taxonomical sampling of basal mosasaurians, mosasauroids an plesiopedal mosasaurs, finding consistent evidence to support the hypothesis of mosasaurians being closely related to varanoid lizards.

### **References**

- Augusta, B.G.; Polcyn, M.J.; Zaher, H.; Jacobs, L.L. 2016. A gravid coniasaur (*Coniasaurus sp.*) from the Upper Cretaceous of Texas and the development of dolichosaurs. In: 5TH TRIENNIAL MOSASAUR MEETING - A GLOBAL PERSPECTIVE ON MESOZOIC

- MARINE AMNIOTES, 2016, Uppsala. **Program and Abstracts**. Uppsala: Uppsala University. p. 2-3.
- Bardet, N.; Suberbiola, X.P.; Iarochene, M.; Bouya, B.; Amaghaz, M. 2005. A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halosaurinae (Squamata: Mosasauridae). **Zoological Journal of the Linnean Society** 143: 447-472.
- Bardet, N.; Suberbiola, X.P.; Jalil, N.E. 2003. A new mosasauroid (Squamata) from the Late Cretaceous (Turonian) of Morocco. **Comptes Rendus de l'Académie des Sciences** 2(8): 607-616.
- Baur, G.H.C.L. 1890. On the characters and systematic position of the large sea-lizards, Mosasauridae. **Science** 405: 262-262.
- Bell, B.A.; Murry, P.A.; Osten, L.W. 1982. *Coniasaurus* Owen, 1850 from North America. **Journal of Paleontology** 56(2): 520-524.
- Bell, G.L. 1993. **A Phylogenetic Revision of Mosasauroida (Squamata)**. Unpublished Ph.D. thesis, University of Texas at Austin, Austin, 293 p.
- Bell, G.L. 1997. A phylogenetic revision of North American and Adriatic Mosasauroida. In: Callaway, J.M.; Nicholls, E.L.(eds.). **Ancient Marine Reptiles**. Academic Press. 293–332.
- Bell, G.L.; Barnes, K.R.; Polcyn, M.J. 2013. Late Cretaceous mosasauroids (Reptilia, Squamata) of the Big Bend region in Texas, USA. **Earth and Environmental Science Transactions of the Royal Society of Edinburgh** 103: 1-11.
- Bell, G.L.; Polcyn, M.J. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). **Netherlands Journal of Geosciences** 84 (3): 177-194.
- Borsuk-Bialynicka, M. 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. **Palaeontologia Polonica** 46: 5-105.
- Boulenger, G. 1891. Notes on the osteology of *Heloderma horridum* and *H. suspectum* with remarks on the systematic position of the Helodermatidae and the vertebrae of the Lacertilia. **Proceedings of the Zoological Society of London** 1891: 109-118.
- Caldwell, M.W. 1995. The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroids and varanoids. **Journal of Vertebrate Paleontology** 15(3): 516-531.

- Caldwell, M.W. 1999a. Squamate phylogeny and the relationships of snakes and mosasauroids. **Zoological Journal of the Linnean Society** 125: 115-147.
- Caldwell, M.W. 1999b. Description and phylogenetic relationships of a new species of *Coniasaurus* Owen, 1850 (Squamata). **Journal of Vertebrate Paleontology** 19(3): 438-455.
- Caldwell, M.W. 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in Squamates. **Journal of Vertebrate Paleontology** 20(4): 720-735
- Caldwell, M.W. 2007. Ontogeny, anatomy and attachment of the dentition in mosasaurs (Mosasauridae: Squamata). **Zoological Journal of the Linnean Society** 149: 687-700.
- Caldwell, M.W. 2012. A challenge to categories: What, if anything, is a mosasaur?. **Bulletin de la Société Géologique de France** 183(1): 7-34.
- Caldwell, M.W.; Budney, L.A.; Lamoureux, D.O. 2003. Histology of tooth attachment tissues in the Late Cretaceous mosasaurid *Platecarpus*. **Journal of Vertebrate Paleontology** 23 (3): 622-630.
- Caldwell, M.W.; Cooper, J.A. 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the Lower Chalk (Cretaceous; Cenomanian) of SE England. **Zoological Journal of the Linnean Society** 127: 423-452.
- Caldwell, M.W.; Lee, M.S.Y. 1997. A snake with legs from the marine Cretaceous of the Middle East. **Nature** 386: 705-709.
- Caldwell, M.W.; Lee, M.S.Y. 2001. Live birth in Cretaceous marine lizards (mosasauroids). **Proceedings of the Royal Society: Biological Sciences** 268: 2397-2401.
- Caldwell, M.W.; Palci, A. 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) of Slovenia with a review of mosasauroid phylogeny and evolution. **Journal of Vertebrate Paleontology** 27(4): 863-883.
- Caldwell, M.W.; Palci, A. 2010. A new species of marine ophidiomorph lizard, *Adriosaurus skrbiniensis*, from the Upper Cretaceous of Slovenia. **Journal of Vertebrate Paleontology** 30(3): 747-755.
- Camp, C.L. 1923. Classification of the lizards. **Bulletin of the American Museum of Natural History** 48: 289-481.
- Campbell, M.; Japundzic, D.; Krizmanic, K.; Caldwell, M.W. 2016. A new genus of Tethyan dolichosaurid from the Turonian of Croatia. In: 5TH TRIENNIAL MOSASAUR MEETING

- A GLOBAL PERSPECTIVE ON MESOZOIC MARINE AMNIOTES, 2016, Uppsala.  
**Program and Abstracts.** Uppsala: Uppsala University. p. 5-6.

- Carroll, R.L.; Debraga, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. **Journal of Vertebrate Paleontology** 12(1): 66-86.
- Carvalho, L.B.; Azevedo, S.A.K. 1998. Proposta taxonômica para os répteis marinhos (Lepidosauria, Mosasauridae) do Neocretáceo da Bacia Pernambuco-Paraíba, Nordeste do Brasil. **Boletim do Museu Nacional** 43: 1-14.
- Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. **Bulletin of the American Museum of Natural History**, 310: 1-182.
- Conrad, J.L.; Ast, J.C.; Montanari, S.; Norell, M.A. 2011. A combined evidence phylogenetic analysis of Anguimorpha (Reptilia: Squamata). **Cladistics** 27: 230-277.
- Cope, E.D. 1869. On the reptilian orders Pythonomorpha and Streptosauria. **Proceedings of the Boston Society of Natural History** 12: 250-261.
- Cope, E.D. 1895. Reply to Dr. Baur's critique of my paper on the paroccipital bone of the scaled reptiles and the systematic position of the Pythonomorpha. **American Naturalist** 29: 1003-1005.
- Cuthbertson, R.S.; Maddin, H.C.; Holmes, R.B.; Anderson, J.S. 2015. The braincase and endosseous labyrinth of *Plioplatecarpus peckensis* (Mosasauridae, Plioplatecarpinae), with functional implications for locomotor behavior. **The Anatomical Record** 298: 1597-1611.
- Cuvier, G.C.F. 1808. Sur le grand animal fossile des carrières de Maestricht. **Annales du Muséum National d'Histoire Naturelle** 12: 145-176.
- DeBraga, M.; Carroll, 1993. The origin of mosasaurs as a model of macroevolutionary patterns and processes. **Evolutionary Biology** 27: 245-322.
- Diedrich, C. 1997. Ein dentale von *Coniosaurus crassidens* Owen (Varanoidea) aus dem Ober-Cenoman von Halle/Westf. (NW-Deutschland). **Geologie und Paläontologie in Westfalen** 47: 43-51.
- Dutchak, A.R. 2005. A review of the taxonomy and systematic of aigialosaurs. **Netherlands Journal of Geosciences** 84(3): 221-229.
- Dutchak, A.R.; Caldwell, M.W. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. **Journal of Vertebrate Paleontology** 29(2): 437-452.

- Estes, R.; de Queiroz, K.; Gauthier, J. 1988. Phylogenetic relationships within Squamata. In: Estes, R.; Pregill, G. (eds). **Phylogenetic relationships of the lizard families**. Stanford, Stanford University Press, p. 119-282.
- Evans, S.E.; Manabe, M.; Noro, M.; Isajis, S.; Yamaguchi, M. 2006. A longbodied lizard from the Lower Cretaceous of Japan. **Paleontology** 49(6): 1143-1165.
- Everhart, M.J. 2004. Plesiosaurs as the food of mosasaurs; new data on the stomach contents of a *Tylosaurus proriger* (Squamata; Mosasauridae) from the Niobrara Formation of Western Kansas. **The Mosasaur** 7: 41-46.
- Fejérváry, G.J. 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. **Annales Historico-Naturales Musei Nationalis Hungarici** 16: 341-467.
- Field, D.J.; LeBlanc, A.; Gau, A.; Behlke, A.D. 2015. Pelagic neonatal fossils support viviparity and precocial life history of Cretaceous mosasaurs. **Palaeontology** 2015: 1-7.
- Gallagher, W.B.; Miller, K.G.; Sherrell, R.M.; Browning, J.V.; Field, M.P.; Olsson, R.K.; Sugarman, P.J.; Tuorto, S.; Wahyudi, H. 2012. On the last mosasaurs: Late Maastrichtian mosasaurs and the Cretaceous-Paleogene boundary in New Jersey. **Bulletin de la Société Géologique de France** 183(2): 145-150.
- Gauthier, J.A.; Kearney, M.; Maisano, J.A.; Rieppel, O.; Behlke, A.D.B. 2012. Assembling the Squamate tree of life: perspectives from the phenotype and the fossil record. **Bulletin of the Peabody Museum of Natural History** 53(1): 3-308.
- Goldfuss, A. 1844. The skull structure of the *Mosasaurus*, explained by means of a description of a new species of this genus. **Transactions of the Kansas Academy of Science** 116: 27-46.
- Golobof, P.; Farris, J.; Nixon, K. 2003. **T.N.T.: Tree Analysis Using New Technology**. Software and Documentation freely available by the authors and by the Hennig Society. Available in: <[www.zmuc.dk/public/phylogeny](http://www.zmuc.dk/public/phylogeny)>. Access in: 23/07/2016.
- Haber, A.; Polcyn, M.J. 2005. A new marine varanoid from the Cenomanian of the Middle East. **Netherlands Journal of Geosciences** 84(3): 247-255.
- Jacobs, L.L.; Polcyn, M.J.; Taylor, L.H.; Ferguson, K. 2005. Sea-surface temperatures and palaeoenvironments of dolichosaurs and early mosasaurs. **Netherlands Journal of Geosciences** 84(3): 269-281.
- Konishi, T.; Caldwell, M.W. 2011. Two new Plioplatecarpinae (Squamata, Mosasauridae) genera from the Upper Cretaceous of North America, and a global phylogenetic analysis of plioplatecarpines. **Journal of Vertebrate Paleontology** 31(4): 754-783.

- Konishi, T.; Tanimoto, M.; Utsunomiya, S.; Sato, M.; Watanabe, K. 2012. A large Mosasaurinae (Squamata: Mosasauridae) from the Latest Cretaceous of Osaka Prefecture (SW Japan). **Paleontological Research** 16(2): 79-87.
- Lee, M.S.Y. 1997a. On snake-like dentition in mosasaurian lizards. **Journal of Natural History** 31: 303-314.
- Lee, M.S.Y. 1997b. The phylogeny of varanoid lizards and the affinities of snakes. **Philosophical Transactions of the Royal Society of London B: Biological Sciences** 352: 53-91.
- Lee, M.S.Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. **Biological Journal of the Linnean Society** 65: 369-453.
- Lee, M.S.Y.; Caldwell, M.W. 1998. Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. **Philosophical Transactions of the Royal Society of London B: Biological Sciences** 353: 1521-1552.
- Lee, M.S.Y.; Caldwell, M.W. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. **Journal of Paleontology** 74(5): 915-937.
- Lee, M.S.Y.; Scanlon, J.D. 2002. The Cretaceous marine squamate *Mesoleptos* and the origin of snakes. **Bulletin of the Natural History Museum London (Zoology Series)** 68: 131-142.
- Lindgren, J. 2005. The first record of *Hainosaurus* (Reptilia: Mosasauridae) from Sweden. **Journal of Paleontology** 79(6): 1157-1165.
- Lindgren, J.; Polcyn, M.J.; Young, B.A. 2011. Landlubbers to leviathans: evolution of swimming in mosasaurine mosasaurs. **Paleobiology** 37: 445-469.
- 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 B: Biological Sciences** 347: 155-172.
- Liu, M.; Reed, D.A.; Cecchini, G.M.; Lu, X.; Ganjawalla, K.; Gonzales, C.S.; Monahan, R.; Luan, X.; Diekwisch, T.G.H. 2016. Varanoid tooth eruption and implantation in a Late Cretaceous mosasaur. **Frontiers in Physiology** 7: 1-9.
- Luan, X.; Walker, C.; Dangaria, S.; Ito, Y. Druzinsky, R.; Jarosius, K.; Lesot, H; Rieppel, O. 2009. The mosasaur tooth attachment apparatus as paradigm for the evolution of the gnathostome periodontium. **Evolution and Development** 11(3): 247-259.

- Makádi, L.; Caldwell, M.W.; Ösi, A 2012. The first freshwater mosasauroid (Upper Cretaceous, Hungary) and a new clade of basal mosasauroids. **PLoS ONE** 7 (12): e51781. doi:10.1371/journal.pone.0051781.
- Mantell, G. 1829. A tabular arrangement of the organic remains of the county of Sussex. **Transactions of the Geological Society of London** 3: 201-216.
- Marsh, O.C. 1879. New characters of mosasauroid reptiles. **American Journal of Science** 19(3): 83-87.
- Martin, J.E.; Fernández, M. 2007. The synonymy of the Late Cretaceous mosasaur (Squamata) genus *Lakumasaurus* from Antarctica with *Taniwhasaurus* from New Zealand and its bearing upon faunal similarity within the Weddellian Province. **Geological Journal** 42: 203-211.
- McDowell, S.B.; Bogert, C.M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. **Bulletin of the American Museum of Natural History** 105: 1-142.
- Nagrodski, M.; Shimada, K.; Schumacher, B.A. 2012. Marine vertebrates from the Hartland Shale (Upper Cretaceous: Upper Cenomanian) in southeastern Colorado, USA. **Cretaceous Research** 37: 78-88.
- Nopcsa, F.B. 1923. *Eidolosaurus* und *Pachyophis*: Zwei neue Neocom-Reptilien. **Palaeontographica** 65: 99-154.
- Osborn, H.F. 1899. A complete mosasaur skeleton, osseous and cartilaginous. **Bulletin of the American Museum of Natural History** 1: 167-188.
- Owen, R. 1841. **Report on British fossil reptiles, part II**. Report for the British Association for the Advancement of Science, Plymouth: 60-294.
- Owen, R. 1850. Description of the fossil reptiles of the Chalk Formation. *In*: Dixon, F. (Ed), **The geology and fossils of the Tertiary and Cretaceous Formations of Sussex**. London, Longman, Brown, Green, and Longman. p. 378-404.
- Owen, R. 1877. On the rank and affinities of the reptilian class of Mosasauridae, Gervais. Geological Society of London, **Quarterly Journal** 33: 682-719.
- Palci, A.; Caldwell, M.W. 2010. Redescription of *Acteosaurus tommasinii* von Meyer, 1860, and a discussion of evolutionary trends within the clade Ophidiomorpha. **Journal of Vertebrate Paleontology** 30(1): 94-108.

- Palci, A.; Caldwell, M.W.; Papazzoni, C.A. 2013. A new genus and subfamily of mosasaurs from the Upper Cretaceous of Northern Italy. **Journal of Vertebrate Paleontology** 33(3): 599-612.
- Paparella, I.; Palci, A.; Nicosia, U.; Caldwell, M.W. 2018. A new fossil marine lizard with soft tissues from the Late Cretaceous of southern Italy. **Royal Society Open Science** 5(6): doi 172411.
- Páramo-Fonseca, M.E. 2011. Mosasauroids from Colombia. **Bulletin de la Société Géologique de France** 182(2): 103-109.
- Pierce, S.; Caldwell, M.W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur, *Pontosaurus lesinensis* (Kornhuber, 1873). **Journal of Vertebrate Paleontology** 24: 376-389.
- Pieters, F. F., Rompen, P. G., Jagt, J. W., and Bardet, N. (2012). A new look at Faujas de Saint-Fond's fantastic story on the provenance and acquisition of the type specimen of *Mosasaurus hoffmanni* Mantell, 1829. **Bulletin de la Société géologique de France** 183(1): 55-65.
- Polcyn, M.J.; Bell, G.L. 1994. *Coniasaurus crassidens* and its bearing on varanoid-mosasauroid relationships. **Journal of Vertebrate Paleontology**, Supplemental 14: 42A.
- Polcyn, M.J.; Bell, G.L. 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(3): 321-333.
- Polcyn, M.J.; Tchernov, E.; Jacobs, L.L. 1999. The Cretaceous biogeography of the Eastern Mediterranean with a description of a new basal mosasauroid from 'Ein Yabrud, Israel. In: SECOND GONDWANAN DINOSAUR SYMPOSIUM. **Proceedings of the Second Gondwanan Dinosaur Symposium**. National Science Museum Monographs 15, Tokyo, Japan. p. 259-290.
- Polcyn, M.J.; Jacobs, L.L.; Araújo, R.; Schulp, A.S.; Mateus, O. 2014. Physical drivers of mosasaur evolution. **Palaeogeography, Palaeoclimatology, Palaeoecology** 400: 17-27.
- Reeder, T.W.; Townsend, T.M.; Mulcahy, D.G.; Noonan, B.P.; Wood, P.L.Jr.; Sites, J.W.Jr.; Wiens, J.J. 2015. Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny and Reveal Unexpected Placements for Fossil Taxa. **PLoS ONE** 10(3): e0118199.doi:10.1371/journal.pone.0118199.
- Rieppel, O.; Kearney, M. 2005. Tooth replacement in the Late Cretaceous mosasaur *Clidastes*. **Journal of Herpetology** 39(4): 688-692.

- Rieppel, O.; Zaher, H. 2000a. The intramandibular joint in squamates and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. **Fieldiana (Geology), New Series** 43: 1-69.
- Rieppel, O.; Zaher, H. 2000b. The braincases of mosasaurs and *Varanus*, and the relationships of snakes. **Zoological Journal of the Linnean Society** 129: 489-514.
- Rieppel, O.; Zaher, H. 2001. Re-building the bridge between mosasaurs and snakes. **Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen** 221(1): 111-132.
- Rieppel, O. 1980. **The phylogeny of anguimorph lizards**. Birkhauser Verlag, Basel, 86 p.
- Russell, D.A. 1967. Systematics and morphology of American mosasaurs. **Bulletin of the Peabody Museum of Natural History** 23: 1-241.
- Scanlon, J.D.; Hocknull, S.A. 2008. A dolichosaurid lizard from the latest Albian (mid-Cretaceous) Winton Formation, Queensland, Australia. **Transactions of the Kansas Academy of Science (Fort Hays Studies Special Issue - Proceedings of the Second Mosasaur Meeting)**: 131-136.
- Shimada, K.; Bell, G.L. 2006. *Coniasaurus* Owen, 1850 (Reptilia: Squamata), from the Upper Cretaceous Niobrara Chalk of Western Kansas. **Journal of Paleontology** 80(3): 589-593.
- Shimada, K.; Everhart, M.J.; Ewell, K. 2007. A unique reptilian (large dolichosaurid lizard?) tooth from the Upper Cretaceous Niobrara Chalk of western Kansas. **Transactions of the Kansas Academy of Science** 110(3/4): 213-219.
- Shimada, K.; Ystesund, T.K. 2007. A dolichosaurid lizard, *Coniasaurus* cf. *crassidens*, from the Upper Cretaceous Carlile Shale in Russell County, Kansas. **Transactions of the Kansas Academy of Science** 110(3/4): 236-242.
- Smith, K.T.; Buchy, M.L. 2008. A new aigialosaur (Squamata: Anguimorpha) with soft tissues remains from the Upper Cretaceous of Nuevo León, Mexico. **Journal of Vertebrate Paleontology** 28(1): 85-94.
- Street, H.P.; Caldwell, M.W. 2016. Rediagnosis and redescription of *Mosasaurus hoffmannii* (Squamata: Mosasauridae) and an assessment of species assigned to the genus *Mosasaurus*. **Geological Magazine**: 1-37. doi:10.1017/S0016756816000236.
- Wiens, J.J.; Kuczynski, C.A.; Townsend, T.; Reeder, T.W.; Mulcahy, D.G.; Sites, J.W.Jr. 2010. Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. **Systematic Biology** 59(6): 674-688.

- Williston, S.W. 1904. The relationships and habits of the mosasaurs. **The Journal of Geology** 12(1): 43-51.
- Zaher, H.; Rieppel, O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. **American Museum Novitates** 3271: 1-19.
- Zaher, H. 1998. The phylogenetic position of *Pachyrhachis* within snakes (Squamata, Lepidosauria). **Journal of Vertebrate Paleontology** 18: 1-3.

## **Chapter 1 - A new and exquisitely preserved fossil marine lizard with embryos**

### **Abstract**

Mosasaurians were a group of aquatic or semi-aquatic Late Cretaceous lizards whose phylogenetic relationships within Squamata forms one of the most complex and intensely debated topic in the systematics of group. One of the main issues in assessing mosasaurian phylogenetic relationships is that although the fossil record of derived forms is plenty, less is known regarding their basalmost radiation, the commonly referred dolichosaurs. Here a new species of dolichosaur, *Coniasaurus* sp. nov., is reported from the Upper Cenomanian of Texas in the basis of exquisitely preserved remains of one gravid female and several embryos. The new species is the first dolichosaur formally described for North America, shedding light into the earliest mosasaurian colonization of the Western Interior Seaway. Analysis of tooth morphology reveals that its dentition sharply changed through ontogeny, suggesting adults and juveniles to occupy distinct ecomorphospaces. Limb and caudal vertebrae morphology strongly suggest that *Coniasaurus* was more adapted for aquatic locomotion than other dolichosaurs, which may explain why it is the only dolichosaur found in North America. Viviparity is described for the first time in a dolichosaur and may have had an important role since the earliest steps of the mosasaurian evolution.

## Resumo

Mosassaurianos foram um grupo de lagartos aquáticos ou semiaquáticos que viveram durante o Cretáceo Tardio. Suas relações filogenéticas dentro de Squamata formam um dos problemas mais complexos e intensamente debatido na Sistemática do grupo. Um dos principais problemas ao tentar recuperar a história filogenética do grupo é que embora o registro fóssil de formas derivadas seja substancial, muito menos é conhecido em relação à sua irradiação mais basal, cujos membros são popularmente conhecidos como dolicossauros. Neste trabalho é reportada uma nova espécie de dolicossauro, *Coniasaurus* sp. nov., do Cenomaniano Superior do Texas (EUA), com base em restos extraordinariamente preservados de uma fêmea grávida e vários embriões. Esta nova espécie é o primeiro registro de um dolicossauro formalmente descrito para a América do Norte, elucidando pontos importantes sobre as primeiras colonizações do Mar Interior Ocidental pelos mosassaurianos. A análise da morfologia dentária revelou que sua dentição mudava consideravelmente durante a ontogenia, sugerindo que adultos e juvenis ocupavam ecomorfoespaços distintos. A anatomia da cauda e dos membros também sugere que *Coniasaurus* estava mais adaptado para a locomoção aquática do que outros dolicossauros, o que pode ajudar a explicar por quê ele é o único dolicossauro encontrado em rochas norte-americanas. Pela primeira vez na literatura a viviparidade é descrita para um dolicossauro, mostrando que ela pode ter desempenhado um importante papel durante o início da evolução dos mosassaurianos.

## 1.1. Introduction

Mosasauria is a clade of extinct aquatic or semi-aquatic lizards, essentially marine, with a global distribution during the Late Cretaceous (Jacobs *et al.*, 2005a; Jacobs *et al.*, 2005b). Although well nested within Squamata, the exact phylogenetic relationships of mosasaurians with other squamates is still an unresolved question (Bell, 1997; Lee, 1998; Zaher and Rieppel, 1999; Conrad, 2008; Caldwell and Palci, 2010; Gauthier *et al.*, 2012). Three groups are traditionally recognized within Mosasauria: the plesiopedal dolichosaurs and “aigialosaurs” (basal mosasauroids) and the family Mosasauridae (Bell, 1997; Conrad, 2008; Caldwell and Palci, 2010; Gauthier *et al.*, 2012). Dolichosaurs are often found as the basalmost mosasaurian arrangement, sister-group of Mosasauroida (basal mosasauroids + Mosasauridae) (Bell, 1997; Conrad, 2008; Gauthier *et al.*, 2012; Polcyn and Bell, 1994; Rieppel *et al.*, 2007), but some authors consider at least some dolichosaurs to be more related to snakes than to mosasaurs (Lee, 1998; Lee and Caldwell, 2000; Caldwell and Palci, 2010). Dolichosaurs are found mainly in Laurasian rocks, especially in eastern Europe and Middle East (Nopcsa, 1923; Lee and Caldwell, 2000; Lee and Scanlon, 2002; Haber and Polcyn, 2005; Caldwell, 2006; Palci and Caldwell, 2007), England (Owen, 1850; Caldwell, 1999; Caldwell and Cooper, 1999; Caldwell, 2000) and USA (Bell *et al.*, 1982; Bell and Polcyn, 1996; VonLoh and Bell, 1998; Everhart and Darnell, 2004; Shimada *et al.*, 2007; Nagrodski *et al.*, 2012). Dolichosauridae is a family that was initially erected by Gervais (1852) to encompass only the British dolichosaurs described by Owen in 1850 (*Coniasaurus crassidens* and *Dolichosaurus longicollis*). It had some taxa added in later works (Nopcsa, 1923; Camp, 1923), but more recently it has been used again including only the British dolichosaur genera, as originally conceived (Rieppel *et al.*, 2007; Caldwell and Cooper, 1999).

An interesting shift in the dolichosaurian taxonomic diversity can be noticed when comparing the fossil record longitudinal variation. In eastern portions of what was becoming the North Atlantic (nowadays Eastern Europe and Middle East) this fauna was occupied by distinct species of adriosauroids, pontosauroids, acteosauroids, eidolosauroids, mesoleptos and judeosauroids, all possessing generalist dentitions (Nopcsa, 1923; Lee and Caldwell, 2000; Lee and Scanlon, 2002; Haber and Polcyn, 2005; Caldwell, 2006; Palci and Caldwell, 2007). On the other hand, in more central and western portions of the North Atlantic the dominant taxa were the dolichosaurids, especially the heterodont coniasauroids which are the only known dolichosaurs to colonize the Western Interior Seaway (Owen, 1850; Bell *et al.*, 1982; Caldwell, 1999; Caldwell and Cooper, 1999; Caldwell, 2000). Dolichosaur fossils are most frequently found in plates

(Lee and Caldwell, 2000; Haber and Polcyn, 2005; Caldwell, 2006), thus preventing a proper tridimensional evaluation of their anatomy. The absence of more complete tridimensionally preserved dolichosaurs contribute to the high number of missing data in phylogenetic analyses including these lizards, which may contribute to the lack of consensus regarding their phylogenetic relationships. Although the diversity of the derived mosasaurids in the USA is plenty (Bell, 1997; Russel, 1967; Polcyn *et al.*, 2014), only a few isolated dolichosaur remains have been reported for the Western Interior Seaway (Bell *et al.*, 1982; Bell and Polcyn, 1996; VonLoh and Bell, 1998; Everhart and Darnell, 2004; Liggett *et al.*, 2005; Shimada and Bell, 2006; Shimada *et al.*, 2007; Nagrodski *et al.*, 2012;). Every North American dolichosaur remain have been assigned either to *Coniasaurus crassidens* (Bell *et al.*, 1982; VonLoh and Bell, 1998; Everhart and Darnell, 2004; Shimada and Ystesund, 2007; Nagrodski *et al.*, 2012) or to *Coniasaurus* sp. (Bell and Polcyn, 1996; Liggett *et al.*, 2005; Shimada and Bell, 2006; Shimada *et al.*, 2007), and no endemic dolichosaur taxon has been described for North America so far.

This work description of what is now the most complete coniasaur specimen known adds substantial anatomical data to the taxon. One of the most conspicuous character of *Coniasaurus* is its highly heterodont dentition, which was suggested as having crushing and cutting functions, allowing the animal to fed on a range of small invertebrates and fishes (Caldwell and Cooper, 1999). The new species described here encompass fossil remains of one adult female and at least two embryos. Viviparity has been reported in mosasaurians only in the mosasaurid *Clidastes* (Field *et al.*, 2015) and in the basal mosasauroid *Carsosaurus* (Caldwell and Lee, 2001), so this contribution also represents the first record of viviparity in dolichosaurs. Anatomical comparisons of adults and embryos reveals that the dental morphology sharply changed through *Coniasaurus* ontogenetic development, suggesting that adults and juveniles occupied distinct ecomorphospaces. Coniasaur appendicular and axial anatomy suggests that it was more adapted to aquatic locomotion than other dolichosaurs, which may explain why it is the only dolichosaur found in North American rocks.

## 1.2. Material and methods

Here are described disarticulated but associated bones of the specimen DMNH-1601, which was found in siderite concretions. Elements were isolated by screen washing, and then CT-scanned at the University of Texas High-Resolution X-ray CT Facility, using a FeinFocus microfocal X-ray source operating at 170 kV and 0.19 mA. CT-resolutions ranged from 24.9  $\mu\text{m}$  for adult bones to 9.67  $\mu\text{m}$  for embryonic remains. Phylogenetic relationships of

dolichosaurids were tested by performing a parsimony analysis in the software TNT 1.5 (Goloboff and Catalano, 2016), using a dataset of 70 morphological characters coded for 13 taxa. Characters were left unordered and a heuristic search with 100 replications, saving 1000 trees by replication, was performed. Retention (Farris, 1989) and Consistency (Kluge and Farris, 1969) indexes were calculated with the “stats.run” script, while Bremer support values with the “bremer.run” script, both available at: <http://phylo.wikidot.com/tntwiki>. Bootstrapping (Felsenstein, 1985) was performed with the standard (sample with replacement) option and 5000 replicates. Living varanoids were chosen as successive outgroups, since they are often found closely related to mosasaurians in the literature (Bell, 1997; Zaher and Rieppel, 1999; Gauthier *et al.*, 2012; Rieppel *et al.*, 2007; see also Chapter 6 of this thesis) (but for alternative views see Lee, 1998; Caldwell and Palci, 2010; Gauthier *et al.*, 2012). Morphological matrix and codings, as well as detailed descriptions, are given by Supplementary Text.

### **1.3. Results**

#### **1.3.1. Systematic Paleontology**

##### **Order Squamata Opper, 1811**

##### **Suborder Mosasauria Conrad, 2008**

##### **Family Dolichosauridae Gervais, 1852**

##### **Genus *Coniasaurus* Owen, 1850**

##### **Type species *Coniasaurus crassidens* Owen, 1850**

##### ***Coniasaurus* sp. nov.**

**Holotype:** DMNH-1601, comprising associated and disarticulated remains from a gravid adult female (Figure 1.1 A-J) and several embryos (Figure 1.1 K-Q). This specimen is housed at the Perot Museum of Natural History, Dallas, USA.

**Type locality, horizon and age:** Lewisville Lake Spillway, SMU locality 518, Dallas County (Texas). Eagle Ford Group, Upper Britton Formation, *Sciponoceras gracile* ammonite Zone, Upper Cenomanian (~94.4Ma).

**Diagnosis:** Heterodont coniasaur-like dentition, with labial sulcus present but lacking a lingual shelf. Upper jaw dentition composed of 4 premaxillary and nearly 15 maxillary teeth. Presence of premaxillary medial egg tooth in embryos. Parietal with distinctive crest tapering posteriorly, with converging lateral surfaces. Pineal foramen ellipsoid, open in dorsal surface and enclosed by bone in ventral surface. Interprezygapophyseal lamina only slightly notched, less curved, and sometimes presenting a medial ridge projecting anteriorly. Cervical pre- and

postzygapophyseal articulation angled (30°-45°). Cervical peduncles unfused with hypapophyses in juveniles and fused in adults. Postzygoprezygapophyseal lamina (PPRL) and posterior centrosynapophyseal lamina (PCYL) well developed, forming a conspicuous sulcus in lateral surface of the dorsal vertebrae neural arches. Sacrals fused, with the first being broader than the second one. Femoral distal epiphysis triangular shaped, with a medial tubercle dividing well developed distinct facets for both the tibia and the fibula.

**Comments:** a complete description of the adult *Coniasaurus* sp. nov. anatomy is given by supplementary text. Embryonic remains are described in Chapter 4 of this thesis.

### 1.3.2. Paleobiogeographic and geochronological settings

The mid-Cretaceous was a time of major changes in Earth's ecosystems. High sea-levels (Haq, 2014) reorganized the arrangement of land and sea, and high global temperatures prevailed, with the Cretaceous Thermal Maximum occurring in the Cenomanian and Turonian (O'Brien *et al.*, 2017). These high temperatures, along with creation of new habitat through inundation (Figure 1.2), and the reorganization of ecological niches through mid-Cretaceous extinctions, may have played a role in the invasion of the seas by many squamate groups during this time (Polcyn *et al.*, 2014), amongst those the dolichosaurs. Dolichosaurs had a broad geographic distribution in the mid-Cretaceous (Figure 1.2A) ranging from the Near East to the Western Interior Seaway and occupying a number of different settings (Jacobs *et al.*, 2005b; Bardet *et al.*, 2008; Ifrim *et al.*, 2008).

The distribution of dolichosaurs is restricted to the northern hemisphere, with one exception discussed below (Scanlon and Hocknull, 2008). Most taxonomic diversity is concentrated in the Anglo-Paris Basin and the remnants of the Apulian plate, now emplaced in the Adriatic region (Nopcsa, 1923; Lee and Caldwell, 2000; Pierce and Caldwell, 2004; Caldwell, 2006; Caldwell and Palci, 2010; Palci and Caldwell, 2007; 2010). In addition to those from the Anglo-Paris, Diedrich (1997) reported dolichosaurs from what is now Germany, and represent the most northern occurrences on Laurasia. Other Gondwanan specimens have been found in the Middle and Near East (Dal Sasso and Pinna, 1997; Dalla Vecchia and Venturini, 1999; Averianov, 2001; Haber and Polcyn, 2005).

Caldwell and Cooper (1999) speculated a westerly overwater dispersal route to North America for dolichosaurs, following prevailing surface currents inferred from the dispersal and westerly migration of invertebrate groups; however, it is as likely they moved along the southern margins of the Tethys-Atlantic-Gulf where they maintained close proximity to shore. Since the equatorial gateway between Africa and South America was not completed until the

Late Turonian (Jacobs *et al.*, work in progress), it is reasonable to assume that emergent features linked Africa and South America in the Early Cenomanian or at least the overwater dispersal route was short. Additionally, ocean circulation simulations suggest predominantly westerly currents may have aided dispersal along the southern margin, though some simulations do indicate clockwise gyre or easterly currents along the northern margin (Hay, 2009).

Most reports of dolichosaurs are from the Cenomanian and Turonian; however, a few reports from North America are worth mentioning. Shimada and Bell (2006) reported a vertebra from the Middle Santonian (~85Ma) and Shimada *et al.* (2007) a purported dolichosaur tooth from the Upper Coniacian of Kansas. The vertebra reported by Shimada and Bell (2006) is indeed a dolichosaur; however, there is a gap of about 5 million years from the youngest known specimens from Texas. All other specimens recovered from Kansas are contemporaneous with the Texas specimens. Shimada and Bell (2006) discussed a number of possibilities to explain such an unexpected occurrence, hundreds of kilometers from the paleoshoreline; however, none of those included the obvious ones. Namely, the specimen was collected elsewhere and erroneously cataloged or that it was transported to the reported locality in recent times, possibly by accident, hitching a ride in the field gear of an unsuspecting prospector. In any event, it will be interesting to see if additional specimens show up in the middle Santonian of Kansas in the future. The tooth reported by Shimada *et al.* (2007) is probably not a lizard because the ankylosis is restricted to a well-defined circular base and falls in a single plane and does not reflect the typical pleurodont implantation seen in lizards, including dolichosaurs. In pleurodont implantation, the tooth is ankylosed at both the base and the medial wall of the dentary. The uniformly ventral and circular base of attachment of the reported tooth is reminiscent of that in some fishes in which the tooth is cemented to the surface of the jaw. Cumba *et al.* (2006) reported ? *cf.* *Coniasaurus* from the Cenomanian of Saskatchewan, Canada; however, examination of their figure rules out referral to *Coniasaurus* but instead suggests it is likely a teiid or a skinkid. There are two occurrences in the Pacific (Evans *et al.*, 2006; Scanlon and Hocknull, 2008). Evans *et al.* (2006) reported a long bodied platynotan squamate from the Lower Cretaceous (Berriasian–Hauterivian; ~ 129.4 Ma) of Japan. The specimen reported by Evans, does have a number of characters that suggest dolichosaurid affinities; however, it was not possible to study the specimen during this thesis development, and therefore resist inclusion here. The specimen reported by Scanlon and Hocknull (2008), appears to be a varanoid but shares no derived features with dolichosaurs and is not further considered here.

### 1.3.3. Ontogeny of cranial elements

Comparable embryonic cranial remains of *Coniasaurus* sp. nov. include two frontal fragments and several jaw sections. Jaw sections are mostly fragmentary, but seven elements can be unequivocally assigned to specific bones: two maxillae (one left and one right) and five dentaries (three left and one right). Two of the left dentaries pieces cannot be overlapped, and as two frontal fragments were also found among embryonic remains at least two individuals were present in the mother's belly. The number of embryos carried by females could be higher than this, since the number reported for the basal mosasauroid *Carsosaurus* is at least four (Caldwell and Lee, 2001).

Adult and embryonic frontal fragments are crushed dorsoventrally. The main distinction in their morphology is that the grooves on the cristae cranii are more conspicuous in embryos than in the adult (Figure 1.3). As these grooves receive the cartilaginous solium suprasetale, the more evident grooves in embryos reflect the more cartilaginous composition of the skull. Antermost portions of the embryonic frontals are not preserved, so the frontoparietal suture cannot be morphologically assessed. There is significant change in the tooth shape across ontogeny (Figure 1.4). Adult dentition is typically coniasaur-like, with antermost teeth being less robust, more conical and more recurved than posteriormost elements. An anterodorsally oriented carinae is present in every crown, but it is more conspicuous on posteriormost teeth. On the other hand, antermost embryonic teeth are nearly straight, almost not recurved at all. The anterodorsal carinae in embryos is much more vertical, and a conspicuous and pointed apex is present in every tooth, either anteriorly or posteriorly located. This pointed apex suggests a more piercing function, rather than crushing or cutting functions more likely present in adult coniasaurs. Although the mode of tooth implantation is the same despite the ontogenetic stage, the orientation of the teeth regarding the tooth-bearing elements (TBE) changes. In the adult, tooth crowns are inserted vertically in the TBEs, regardless their location on the element. In embryos, teeth are inserted more diagonally (Figure 1.4), which may also be related to distinct functions of the dentition. Labial sulcus on the crowns, an autapomorphy of the genus *Coniasaurus*, are already present in the embryos, but slightly less conspicuous and more laterally located rather than more anteriorly located in adults.

### 1.3.4. Phylogenetic relationships of the dolichosaurids

A single most parsimonious tree was recovered in the basis of 113 steps, presenting a consistency and retention indexes of respectively 0,72 and 0,75. Although not the scope of the present phylogenetic analysis, this contribution recovered a monophyletic dolichosaur

assemblage as the sister-group of Mosasauroida (Figure 1.5), as in Paparella *et al.* (2018) and *contra* the results found in most of the previous works (e.g. Conrad, 2008; Caldwell and Palci, 2010; Lee and Caldwell, 2000). This clade was recovered in the basis of three characters: presence of zygantum-zygosphene articulation (character 38); well-developed pedestals in caudal vertebrae (character 52); and reduced forelimbs (character 57). Mosasauria was also recovered as a monophyletic clade in the basis of 19 characters. However, one of the most interesting results of this analysis was the recovery of *Dolichosaurus* within *Coniasaurus* genus. Caldwell (Caldwell, 2000) firstly proposed the hypothesis of *Dolichosaurus* and *Coniasaurus* potentially belonging to the same genus, but as the holotype of *Coniasaurus* sp. nov. is the first known coniasaur specimen preserving both cranial and postcranial remains, this hypothesis remained untested up to now. Here a monophyletic *Coniasaurus* genus, inclusive of *Dolichosaurus longicollis*, was recovered based on four characters: marked heterodonty (character 1); orientation of tooth crowns (character 4); presence of constriction right before vertebral condyle (character 37); and a “T-shaped” dorsal vertebrae centra (character 44). *Dolichosaurus longicollis* was recovered as the sister group of *Coniasaurus* sp. nov. due to two characters: the presence of a lateral carving on each side of the centrum (character 45); and posterior base of neural spine very large (character 46). These results support the hypothesis of *Dolichosaurus* and *Coniasaurus* actually belonging to the same genus.

## 1.4. Discussion

### 1.4.1. Paleobiology of *Coniasaurus*

Three anatomical regions of *Coniasaurus* sp. nov. shed light into the aquatic adaptations of *Coniasaurus*: forelimbs, hindlimbs and vertebrae. Forelimb is particularly reduced in coniasaurs and other dolichosaurs in general, but the deltopectoral crest in coniasaurs is intriguingly well developed (observable in both holotypes of *Coniasaurus* sp. nov. and *C. longicollis*). This is suggestive of a small but strong arm, which could have helped in the maneuverability of the animal during the aquatic locomotion. Moreover, it could also have helped in the terrestrial locomotion, for grasping during reproduction or for clinging to floating mats of kelp, a hypothesis firstly suggested by Bell and Polcyn (Bell and Polcyn, 1996). At the same time, *Coniasaurus* sp. nov. retained plesio-pedal limbs, as revealed by the morphology of its limbs and digits, being a clear example of an animal with intermediate features between a terrestrial lizard and a totally aquatic animal. In *Coniasaurus* sp. nov., the distal part of the femur retains a unique morphology among dolichosaurs, with well-developed distinct facets for

both the tibia and the fibula, separated by a medial tubercle. This arrangement makes the femoral distal end to be roughly triangular in lateral view (Figure 1.6). A similar morphology of the femur is also noticeable in other Mesozoic aquatic reptiles, such as mosasaurs (Russel, 1967), ichthyosauriforms (Motani *et al.*, 2014), elasmosaurs (Kubo *et al.*, 2012), pliosaurs (Smith and Vincent, 2010) and marine snakes (Lee and Caldwell. 1998). The occurrence of a similar femoral distal morphology among many distinct marine reptile radiations suggest this condition to be closely related to aquatic locomotion.

*Coniasaurus* possessed a very deep tail, with long haemal arches projecting posteroventrally. Figure 1.6C shows a *Coniasaurus* sp. nov. caudal vertebra with most of the haemal arch preserved. In this specimen, haemal arch is approximately 13,1mm long, while the height of the caudal vertebra at its midpoint (from the ventral part of the centrum up to the dorsal part of the neural arch, without considering the neural spine) is nearly 7mm, giving a haemal arch / vertebral height ratio of 1,87. For instance, in other dolichosaurs this same ratio has a maximum value of nearly 1,57 in *Aphanizocnemus*, 1,55 in *Acteosaurus*, and 1,65 in *Adriosaurus*. However, this ratio in *Coniasaurus* is still far from that of mosasauroids as the value of nearly 3,45 found in *Opetiosaurus*. At the same time, postsacral vertebrae in *Coniasaurus* can only be divided into two distinct regions: pygal and caudal, while in more derived mosasaurs they can be divided into three distinct units: pygal, intermediate caudal and terminal caudal (Lindgren *et al.*, 2011).

Both limbs and caudal morphology suggest a higher capability of aquatic locomotion in *Coniasaurus* than in other dolichosaurs. Considering that the Western Interior Seaway was far from the lands that nowadays form European landmasses during the Late Cretaceous, a higher capability of *Coniasaurus* to move in the aquatic environment may explain why it is the only dolichosaur taxon found in North America so far.

#### **1.4.2. Niche partitioning between adults and juveniles**

Morphology of the dentition is quite distinct between the adult and the embryos. Such ontogenetic differences in skull and dentition morphologies is expected when there is a dietary shift from juveniles to adults, as it is the case, for instance, in *Caiman* (Monteiro *et al.*, 1997). Other reptiles maintain the same overall morphology of the dentition, suggesting niche partitioning between animals in distinct ontogenetic stages (Augusta, 2013). Adult dentition is formed by anteriormost teeth more conical and recurved, and posteriormost elements being straighter and more robust, with a putative crushing and cutting functions. Morphologic of the adult dentition suggest a diet based on moderately hard-bodied invertebrates and fishes, which

matches the associated fauna of the Eagle Ford Group in Texas (Moreman, 1942). In juveniles, teeth are more gracile and bear a very pointing apex, suggesting a more piercing function. These differences support the interpretation of juveniles feeding at soft-bodied invertebrates and adults hunting crustaceans and fishes.

### **1.4.3. The role of viviparity in mosasaurian evolution**

Viviparity in Mosasauria have been previously reported for the Mosasauroidae clade, including the basal mosasauroid *Carsosaurus marchesetti* (Caldwell and Lee, 2001) and the mosasaurine *Clidastes* (Field *et al.*, 2015). However, this condition has never been previously described for a dolichosaur lizard. *Coniasaurus* sp. nov. holotype provide a unique evidence of viviparity among basal mosasaurians by preserving remains of an adult female and several embryos. Some of the embryo bones are even attached to the adult elements by remains of the rock matrix. This first record of viviparity in a dolichosaur squamate, suggesting that this condition may have evolved earlier in the common ancestor of dolichosaurids and mosasauroids, and may even have been present in their terrestrial ancestor. Viviparity has been traditionally considered as an aquatic adaptation, and although recent study questioned this view (Motani *et al.*, 2014) the record of viviparity is vast among extinct marine reptiles (Field *et al.*, 2015; Caldwell and Lee, 2001; Motani *et al.*, 2014). Giving birth to living juveniles may have somewhat helped the dispersion and evolution of these animals through the marine environment, allowing *Coniasaurus* to colonize at the same time regions as far to the East as the British landmasses and as far to the West as the Southern portions of the Western Interior Seaway.

## **References**

- Augusta, B.G. 2013. **Revisão sistemática e ontogenética dos materiais cranianos atribuídos ao gênero *Mariliasuchus* (Crocodyliformes, Notosuchia) e suas implicações taxonômicas e paleobiológicas.** Master in Science dissertation, Universidade de São Paulo, 303 p.
- Averianov, A.O. 2001. The first find of a dolichosaur (Squamata, Dolichosauridae) in Central Asia. **Paleontological Journal** 35(5): 525-527.
- Bardet, N.; Houssaye, A.; Rage, J.C.; Pereda Suberbiola, X. 2008. The Cenomanian-Turonian (late Cretaceous) radiation of marine squamates (Reptilia): the role of the Mediterranean Tethys. **Bulletin de la Société géologique de France** 179(6): 605-622.

Bell, B.A.; Murry, P.A.; Osten, L.W. 1982. *Coniasaurus* Owen, 1850 from North America. **Journal of Paleontology** 56(2): 520-524.

Bell, G.L. 1997. A phylogenetic revision of North American and Adriatic Mosasauroida. In: Callaway, J.M.; Nicholls, E.L.(eds.). **Ancient Marine Reptiles**. Academic Press. 293–332.

Bell, G.L.; Polcyn, M.J. 1996. Distribution of the lizard, *Coniasaurus*, in the Western Interior Cretaceous Seaway and its paleoecological implications. **Geological Society of America, Rocky Mountain Section, Abstracts with Programs** 28: 2.

Bell, G.L.; Polcyn, M.J. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). **Netherlands Journal of Geosciences** 84 (3): 177-194.

Caldwell, M.W. 1999. Description and phylogenetic relationships of a new species of *Coniasaurus* Owen, 1850 (Squamata). **Journal of Vertebrate Paleontology** 19(3): 438-455.

Caldwell, M.W. 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in Squamates. **Journal of Vertebrate Paleontology** 20(4): 720-735.

Caldwell, M.W. 2006. A New Species of "*Pontosaurus*"(Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a Phylogenetic Analysis of Pythonomorpha. **Società Italiana di Scienze Naturali**: 1-44.

Caldwell, M.W.; Cooper, J.A. 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the Lower Chalk (Cretaceous; Cenomanian) of SE England. **Zoological Journal of the Linnean Society** 127: 423-452.

Caldwell, M.W.; Lee, M.S.Y. 2001. Live birth in Cretaceous marine lizards (mosasauroids). **Proceedings of the Royal Society: Biological Sciences** 268: 2397-2401.

Caldwell, M.W.; Palci, A. 2010. A new species of marine ophidiomorph lizard, *Adriosaurus skrbinsensis*, from the Upper Cretaceous of Slovenia. **Journal of Vertebrate Paleontology** 30(3): 747-755.

Camp, C.L. 1923. Classification of the lizards. **Bulletin of the American Museum of Natural History** 48: 289-481.

Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. **Bulletin of the American Museum of Natural History**, 310: 1-182.

Cumba, S.L.; Schröder-Adams, C.; Day, R.G.; Phillips, A.J. 2006. Cenomanian bonebed faunas from the northeastern margin, Western Interior Seaway, Canada. **Bulletin of New Mexico Museum of Natural History and Science** 35: 139-155.

Dal Sasso, C.; Pinna, G. 1997. *Aphanizocnemus libanensis* n. gen. n. sp, a new dolichosaur (Reptilia, Varanoidea) from the Upper Cretaceous of Lebanon. **Paleontologia Lombarda** 7: 1-31.

Dalla Vecchia, F.M.; Venturini, S. 1999. The Middle Cenomanian Lagerstätte of Al Nammoura (Kesrouâne Caza, N. Lebanon). **Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"** 20: 75-78.

Diedrich, C. 1997. Ein dentale von *Coniosaurus crassidens* Owen (Varanoidea) aus dem Ober-Cenoman von Halle/Westf. (NW-Deutschland). **Geologie und Paläontologie in Westfalen** 47: 43-51.

Evans, S.E.; Manabe, M.; Noro, M.; Isajis, S.; Yamaguchi, M. 2006. A longbodied lizard from the Lower Cretaceous of Japan. **Paleontology** 49(6): 1143-1165.

Everhart, M.J.; Darnell, M.K. 2004. Occurrence of *Ptychodus mammillaris* (Elasmobranchii) in the Fairport Chalk Member of the Carlile Shale (Upper Cretaceous) of Ellis County, Kansas. **Transactions of the Kansas Academy of Science** 107(3): 126-130.

Field, D.J.; LeBlanc, A.; Gau, A.; Behlke, A.D. 2015. Pelagic neonatal fossils support viviparity and precocial life history of Cretaceous mosasaurs. **Palaeontology** 2015: 1-7.

Gallagher, W.B.; Miller, K.G.; Sherrell, R.M.; Browning, J.V.; Field, M.P.; Olsson, R.K.; Sugarman, P.J.; Tuorto, S.; Wahyudi, H. 2012. On the last mosasaurs: Late Maastrichtian mosasaurs and the Cretaceous-Paleogene boundary in New Jersey. **Bulletin de la Société Géologique de France** 183(2): 145-150.

Gauthier, J.A.; Kearney, M.; Maisano, J.A.; Rieppel, O.; Behlke, A.D.B. 2012. Assembling the Squamate tree of life: perspectives from the phenotype and the fossil record. **Bulletin of the Peabody Museum of Natural History** 53(1): 3-308.

Gervais, P. 1852. **Zoologie et Paleontologie Françaises (Animaux Vertébrés)**. Paris, Arthus Bertrand, 274 p.

Goloboff, P.A.; Catalano, S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. **Cladistics** 32(3): 221-238.

Haber, A.; Polcyn, M.J. 2005. A new marine varanoid from the Cenomanian of the Middle East. **Netherlands Journal of Geosciences** 84(3): 247-255.

Haq, B.U., 2014. Cretaceous eustasy revisited. **Global and Planetary Change** 113: 44-58.

Hay, W.W. 2009. Cretaceous oceans and ocean modeling. **SEPM Special Publication** 91: 243-271.

Ifrim, C.; Buchy, M.C.; Smith, K.T.; Giersch, S.; Everhart, M.J. 2008. Paleoenvironment and preliminary description of early Turonian (Late Cretaceous) aquatic squamates from Vallecillo, North-eastern Mexico. In **Proceedings of the Second Mosasaur Meeting**: x1-x16.

Jacobs, L.L.; Ferguson, K.; Polcyn, M.J.; Rennison, C. 2005a. Cretaceous d13C stratigraphy and the age of dolichosaurs and early mosasaurs. **Netherlands Journal of Geosciences** 84(3): 257-268.

Jacobs, L.L.; Polcyn, M.J.; Taylor, L.H.; Ferguson, K. 2005b. Sea-surface temperatures and palaeoenvironments of dolichosaurs and early mosasaurs. **Netherlands Journal of Geosciences** 84(3): 269-281.

Kubo, T.; Mitchell, M.T.; Henderson, D.M. 2012. *Albertonectes vanderveldei*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. **Journal of Vertebrate Paleontology** 32(3): 557-572.

Lee, M.S.Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. **Biological Journal of the Linnean Society** 65: 369-453.

Lee, M.S.Y.; Caldwell, M.W. 1998. Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. **Philosophical Transactions of the Royal Society of London B: Biological Sciences** 353: 1521-1552.

Lee, M.S.Y.; Caldwell, M.W. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. **Journal of Paleontology** 74(5): 915-937.

Lee, M.S.Y.; Scanlon, J.D. 2002. The Cretaceous marine squamate *Mesoleptos* and the origin of snakes. **Bulletin of the Natural History Museum London (Zoology Series)** 68: 131-142.

Liggett, G.A.; Shimada, K.; Bennett, S.C.; Schumacher, B.A. 2005. Cenomanian (Late Cretaceous) reptiles from northwestern Russell County, Kansas. **PaleoBios** 25(2): 9-17.

Lindgren, J.; Polcyn, M.J.; Young, B.A. 2011. Landlubbers to leviathans: evolution of swimming in mosasaurine mosasaurs. **Paleobiology** 37: 445-469.

Monteiro, L.R.; Cavalcanti, M.J.; Sommer, H.J.S. 1997. Comparative ontogenetic shape changes in the skull of Caiman species (Crocodylia, Alligatoridae). **Journal of Morphology** 231(1): 53-62.

Moreman, W. L. 1942. Paleontology of the Eagle Ford Group of north and central Texas. **Journal of Paleontology** 16(2): 192-220.

Motani, R.; Jiang, D.Y.; Tintori, A.; Rieppel, O.; Chen, G.B. 2014. Terrestrial origin of viviparity in Mesozoic marine reptiles indicated by Early Triassic embryonic fossils. **PLoS one** 9(2): e88640.

Nagrodski, M.; Shimada, K.; Schumacher, B.A. 2012. Marine vertebrates from the Hartland Shale (Upper Cretaceous: Upper Cenomanian) in southeastern Colorado, USA. **Cretaceous Research** 37: 78-88.

Nopcsa, F.B. 1923. *Eidolosaurus* und *Pachyophis*: Zwei neue Neocom-Reptilien. **Palaeontographica** 65: 99-154.

O'Brien, C.L.; Robinson, S.A.; Pancost, R.D.; Damste, J.S.S.; Schouten, S.; Lunt, D.J.; Alsenz, H.; Bornemann, A.; Bottini, C.; Brassell, S.C.; Farnsworth, A. 2017. Cretaceous sea-surface temperature evolution: Constraints from TEX86 and planktonic foraminiferal oxygen isotopes. **Earth-science reviews** 172: 224-247.

Owen, R. 1850. Description of the fossil reptiles of the Chalk Formation. *In*: Dixon, F. (Ed), **The geology and fossils of the Tertiary and Cretaceous Formations of Sussex**. London, Longman, Brown, Green, and Longman. p. 378-404.

Palci, A.; Caldwell, M.W. 2007. Vestigial forelimbs and axial elongation in a 95 million-year-old non-snake squamate. **Journal of Vertebrate Paleontology** 27(1): 1-7.

Palci, A.; Caldwell, M.W. 2010. Redescription of *Acteosaurus tommasinii* von Meyer, 1860, and a discussion of evolutionary trends within the clade Ophidiomorpha. **Journal of Vertebrate Paleontology** 30(1): 94-108.

Paparella, I.; Palci, A.; Nicosia, U.; Caldwell, M. W. 2018. A new fossil marine lizard with soft tissues from the Late Cretaceous of southern Italy. **Royal Society Open Science** 5(6): 172411.

Pierce, S.; Caldwell, M.W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur, *Pontosaurus lesinensis* (Kornhuber, 1873). **Journal of Vertebrate Paleontology** 24: 376-389.

Polcyn, M.J.; Bell, G.L. 1994. *Coniasaurus crassidens* and its bearing on varanoid-mosasauroid relationships. **Journal of Vertebrate Paleontology**, Supplemental 14: 42A.

Polcyn, M.J.; Jacobs, L.L.; Araújo, R.; Schulp, A.S.; Mateus, O. 2014. Physical drivers of mosasaur evolution. **Palaeogeography, Palaeoclimatology, Palaeoecology** 400: 17-27.

Rieppel, O.; Conrad, J.L.; Maisano, J.A. 2007. New morphological data for *Eosaniwa koehni* Haubold, 1977 and a revised phylogenetic analysis. **Journal of Paleontology** 81(4): 760-769.

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

Scanlon, J.D.; Hocknull, S.A. 2008. A dolichosaurid lizard from the latest Albian (mid-Cretaceous) Winton Formation, Queensland, Australia. **Transactions of the Kansas Academy of Science (Fort Hays Studies Special Issue - Proceedings of the Second Mosasaur Meeting)**: 131-136.

Shimada, K.; Bell, G.L. 2006. *Coniasaurus* Owen, 1850 (Reptilia: Squamata), from the Upper Cretaceous Niobrara Chalk of Western Kansas. **Journal of Paleontology** 80(3): 589-593.

Shimada, K.; Everhart, M.J.; Ewell, K. 2007. A unique reptilian (large dolichosaurid lizard?) tooth from the Upper Cretaceous Niobrara Chalk of western Kansas. **Transactions of the Kansas Academy of Science** 110(3/4): 213-219.

Shimada, K.; Ystesund, T.K. 2007. A dolichosaurid lizard, *Coniasaurus* cf. *crassidens*, from the Upper Cretaceous Carlile Shale in Russell County, Kansas. **Transactions of the Kansas Academy of Science** 110(3/4): 236-242.

Smith, A.S.; Vincent, P. 2010. A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany. **Palaeontology** 53(5): 1049-1063.

VonLoh, J.P.; Bell, G.L. 1998. Fossil reptiles from the Late Cretaceous Greenhorn Formation (Late Cenomanian-Middle Turonian) of the Black Hills region, South Dakota. **Dakoterra** 5: 29-38.

Zaher, H.; Rieppel, O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. **American Museum Novitates** 3271: 1-19.

## Supplementary Text

### Description of DMNH-1601 adult remains

DMNH-1601 represents the most complete coniasaur specimen ever found, including remains from a gravid adult female and several embryos. Adult remains comprise a fragmented frontal, partial parietal, right quadrate, left dentary, fragmentary remains of the mandible, fragmentary tooth bearing elements, 3 cervical, 35 dorsal, 2 sacral and 29 caudal vertebrae, many isolated ribs, humerus, femur, tibia, fibula, four phalanges and one ungual. As for the embryos, the preserved elements in this specimen include a premaxilla, fragmentary frontals, isolated tooth bearing elements, many cervical, dorsal and caudal vertebrae and some unidentified fragmented bones, but these will be described in a forthcoming contribution. The degree of preservation in this specimen is remarkable, as it is tridimensional and lacks higher levels of taphonomical distortion.

### Cranial skeleton

*Frontal.* The frontal of this specimen is crushed and fragmentary, comprising a posterior left portion of the bone (Figure S1). Frontal bone is a single element as in other mosasaurians and many squamates, already fused even in embryos, and distinguished from the paired frontals in snakes (Cundall and Irish, 2008). Lee and Caldwell (2000) identified the presence of paired frontals in the dolichosaur *Adriosaurus*, but a reexamination of the specimen NHMUK-R2867 revealed that it is actually broken, and not unfused. Laterally, frontal gently bends to form the medial wall of the orbit. None articulation of the frontal with other bones (parietal, postorbitofrontal, prefrontal and nasal) is visible due to fragmentation. As for the subolfactory processes, only the left one is better preserved, with the right element being severely crushed. However, as the crushing axis appears to be dorsoventral, both elements seems to be in their natural position, showing that they do not contacted each other ventrally nor bended medially as in the embryos (Augusta *et al.*, in prep.) and allowing a wider space for the subolfactory tract. Subolfactory processes also does not contact each other ventrally in *Coniasaurus gracilodens* (Caldwell, 1999), mosasauroids (pers. obs.), *Lanthanothus borneensis* (McDowell and Bogert, 1954) and *Shinisaurus crocodilurus* (Conrad, 2004), *contra* the condition found in *Varanus* (Bahl, 1937; pers. obs.) and *Heloderma suspectum* (pers. obs.). In ventral view it is possible to note that the dorsal wall of the frontal projects laterally over the cristae cranii. The cristae expand posterolaterally, and the groove to receive the cartilaginous solium suprasetale is only barely visible in this specimen.

*Parietal.* This bone adds new morphological information to the genus since it is only the second parietal known for *Coniasaurus* and the parietal of *C. gracilodens* holotype (Caldwell, 1999) is severally broken. As the frontal, the parietal is a single fused element (Figure S2). In DMNH-1601 it comprises mostly the anterior portion of the bone, with the left frontal tab entirely preserved. Supratemporal processes are lacking. Dorsally, a large and ellipsoid pineal foramen is present, totally encompassed by the parietal. Morphologically, this ellipsoid foramen differs from the teardrop shaped foramen seen in some dolichosaurs (i.e. *Adriosaurus suessi*, *Pontosaurus kornhuberi*). Ventrally, the pineal foramen is totally enclosed by bone. The anteriormost portion of the parietal is broken at the right anterolateral projection, but the left one is well preserved. It is possible to note that the frontoparietal suture formed a straight line in dorsal view as in modern varanids, *Coniasaurus gracilodens* (Caldwell, 1999) and *Pontosaurus lesinensis* (Pierce and Caldwell, 2004), differing from the "wavy" shape of the suture found in some dolichosaurs, as the "M-shape" of *Judeasaurus* (Haber and Polcyn, 2005) or the "W-shape" of *Pontosaurus kornhuberi* (Caldwell, 2006). Frontoparietal suture is also considerably interdigitated, as seen in anterior view (Figure S2-A), approaching the condition found in more derived mosasauroids (Russell, 1967; Bell and Polcyn, 2005). It bears several grooves and ridges that change their orientation based on their position: they are obliquely oriented at more lateral regions and dorsoventrally oriented at more medial regions. The anterolateral process of the parietal bears a dorsoventrally flat and medially elongated surface for the articulation with the postorbitofrontal, so the latter can clasp the parietal posteriorly and the frontal anteriorly. In lateral view, a concave surface in the mid-portion of the parietal (the medial wall of the supratemporal fossa) probably served as an area of attachment for the *m. pseudotemporalis superficialis* (mPstS). The dorsalmost portion of the parietal narrows towards its posterior end, forming a conspicuous crest (Figure S2-D) that is present also in other mosasaurians (Russell, 1967; Pierce and Caldwell, 2004; Caldwell, 2006). The posteriormost portion of this crest is roughly triangular, with converging lateral surfaces, a condition apparently autapomorphic for *Coniasaurus* sp. nov.

*Dentary.* A partial middle portion of the left dentary is preserved in DMNH-1601. It is a massive bone with eight crowns preserved in natural position (Figure S3). Both the anterior and posteriormost portions are missing. No mental foramina are visible in the lateral wall of the dentary. Dolichosaur remains are usually preserved in slabs, thus preventing a proper morphological comparison of DMNH-1601 with other taxa in three dimensions. In mosasaurs the dentary is an anteriorly tapering bone, with robustness in variable degrees (Russell, 1967), while in coniasaurs (DMNH-1601 included) it is a somewhat straight bone with not much

difference between anterior and posterior height. This morphology approaches more the condition found in other dolichosaurs such as *Coniasaurus longicollis* (former *Dolichosaurus longicollis*; see illustrations in Caldwell, 2000) and *Judeasaurus* (Haber and Polcyn, 2005) than more advanced mosasauroids. Ventrally, the dentary is straight, and not curved, as in modern lizards. A dental shelf projects medially to support the tooth bases, being especially conspicuous in the more posterior region. It bends anteriorly, raising the height of the anteriormost crowns to the same level that the posteriormost, enclosing a curved Meckel's groove. In anterior view it is possible to note that the bone is uniformly rounded ventrally, from the lateral wall just above the teeth crowns to the medial dental shelf. Ventrally, the element is broken and reveals a large Meckel's groove, running along the entire bone length. In medial view the Meckel's groove bends both anteriorly and posteriorly, just like *Coniasaurus crassidens* (specimen NHMUK R 3421; Caldwell and Cooper, 1999).

*Dentition.* The dentition is heterodont with fully pleurodont mode of tooth implantation (*sensu* Zaher and Rieppel, 1999), similar to modern varanoids and lacking the autapomorphic condition of more derived mosasauroids in having an extended bony base (Polcyn *et al.*, 1999; Zaher and Rieppel, 1999) (Figure S3). Neither resorption pits nor replacement teeth are present. Anteriormost teeth are less robust and bear more recurved apices than posteriormost, and crowns become larger towards the end of tooth row. Teeth present a labial sulcus that is characteristic of *Coniasaurus* (Caldwell and Cooper, 1999), although in DMNH-1601 this sulcus is only barely visible, and it is more mesially oriented rather than more laterally oriented as in NHMUK-R 3421 (Caldwell and Cooper, 1999). Crown ornamentation is subtle, with only fine longitudinal striations across the entire crown, and neither resorption pits nor teeth in replacement position are visible in this specimen. Also, *Coniasaurus crassidens* possess a dentition bearing a marked labial tooth shelf (Caldwell and Cooper, 1999), absent in DMNH-1601. The tip of the crowns is angled at approximately 45°, forming an anterodorsal oriented keel. This keel lacks the crenulations in the carenae seem in *C. crassidens*, but this may be due to a more advanced stage of wear, since many embryos do possess crenulations. Largest crowns are present in the middle-to-posterior part of the dentary.

### **Axial skeleton**

*Cervical vertebrae.* Three incomplete cervical vertebrae are preserved in DMNH-1601 (Figure S4). No remains of either the atlas nor the axis are preserved. Size of the vertebrae and the proportions of both the hypapophyses and the synapophyses suggest that the elements preserved here are probably reminiscent of a more anterior (Figure S4 A-F), an intermediate

(Figure S4 G-L) and a more posterior (Figure S4 M-R) cervical vertebrae, although the exact position of each element cannot be confidently asserted. Just one of them, the more posterior one, has a partially preserved neural arch. Hypapophyses are present in all the elements, and in the two posteriormost a fused intercentrum is also preserved. Cervical elements get relatively shorter and more robust towards the posterior region of the body, and the hypapophyses become gradually a thinner and smaller process. Centrum is conspicuously compressed dorsoventrally, and a marked constriction lies just before the condyle. Pre- and postzygapophyseal articulation became more angled posteriorly, from a contact of nearly 30° in the more anterior to approximately 45° in the more posterior element, being more angled than in other dolichosaurs. Synapophyses are uniformly bended lateroventrally, and many scars are strongly marked just anterior and posterior to them, at the region which received muscle attachments (*Mm. intertransversari* of Russell, 1967). The area for the rib articulation is larger in posteriormost vertebrae, reflecting a bigger rib size towards the pectoral girdle. Interprezygapophyseal lamina (TPRL of Tschopp (2016)) forming the zygosphenes is only visible at the posteriormost element, where it is a somewhat convex projection with a medioanteriorly oriented tip, but its exact shape cannot be evaluated since the lamina is broken. In the same element it is possible to note that the postzygoprezygapophyseal lamina (PPRL) is deeply carved, forming a somewhat "U" line in dorsal view (Figure S4-P). Posterior centrosynapophyseal lamina (PCYL) is moderately developed, originating a sulcus between it and the PPRL in lateral view (Figure S4 C, I and O). None of the European specimens assigned to *Coniasaurus* possess preserved cervical vertebrae. On the other hand, one specimen assigned to *Dolichosaurus longicollis* (*C. longicollis* according to the present contribution) has 17 cervicals preserved (NHMUK-R49002). Two main differences between *Coniasaurus* sp. nov. and *C. longicollis* cervical vertebrae are noticeable. Firstly, the intercentrum / hypapophysis contact is fused in the former and unfused in the latter. However, this feature is ontogenetic related, since embryonic remains of *Coniasaurus* sp. nov. have unfused intercentrae. Secondly, the angle of pre- and postzygapophyseal articulation between the taxa is also slightly different: more angled upwards in *Coniasaurus* sp. nov. and more horizontal in *C. longicollis*, although the precise orientation of this articulation in *C. longicollis* cannot be measured accurately because in the specimen the axial skeleton is still articulated and immersed in the rock matrix.

*Dorsal vertebrae.* *Coniasaurus* sp. nov. possessed at least 32 dorsal vertebrae, evidencing that the genus *Coniasaurus* owns the longest presacral series among dolichosaurs. There is no sign of pachyostosis, contrary to what is found in the dolichosaurs *Adriosaurus* (Lee and Caldwell, 2000; Caldwell and Lee, 2004; Caldwell and Palci, 2010), *Acteosaurus* (Palci

and Caldwell, 2010) and *Pontosaurus* (Caldwell, 2006). Dorsal vertebrae are averagely longer than cervical and caudal vertebrae. Zygosphenes and zygantra articulations are present throughout the entire dorsal series, and the TPRL forming the zygosphenes is only slightly notched (Figure S5-D), contrary to British coniasaurs and dolichosaurs where the lamina is more U-shaped. In some of the DMNH-1601 dorsal vertebrae zygosphenes a medial tubercle projects anteriorly, originating a tripartite lamina (Figure S5-D). The morphology of the zygosphene-zygantral articulation is quite distinct from that of snakes, in which the TPRL is straight. Neural spine is considerably tall, with both prespinal (PRSL) and postspinal (POSL) laminae projecting dorsally to constitute a rectangular neural spine in lateral view. Neural spine reaches its maximum measurable height in a mid-dorsal vertebra which is almost as tall (14,1 mm) as long (14,9 mm). The size of the neural spines highlights how deep was the body of *Coniasaurus* sp. nov., not only in the caudal region but through the whole body. Although in European specimens the neural arch is usually broken and thus cannot be confidently measured, in *Coniasaurus* sp. nov. it really appears taller than in other taxa of the genus. Neural arches bear greatly developed pre- and postzygapophyses, with the first being considerably larger than the second. In dorsal view, the prezygapophyses widens anterolaterally and forms a rectangular projection which receives the postzygapophyses in a nearly horizontal articulation, markedly distinct from the angled contact between those elements in the cervical vertebrae. Separation between the prezygapophyses and the zygosphenes is given by a conspicuous notch, especially visible in anterior view. Postzygapophyses project posterolaterally, separating from the prezygapophyses a "U" PPRL line in dorsal view. From the postzygapophyses a centropostzygapophyseal lamina (CPOL) arises anteromedially to meet the basis of the neural spine. In posterior view, this forms a wide canal to receive the spinal cord ventrally and the zygosphenes of the next vertebra dorsolaterally. Just below the postzygapophysis a synapophysis projects laterally to receive the rib articulation. Anteriorly to the synapophysis a PCYL is more developed than in cervical vertebrae, originating a slightly more conspicuous carving in the lateral surface of the neural arch, between the PCYL and the PPRL. Centrum is more straight ventrally, not as much curved as in other anguimorphs. It is also uniformly compressed dorsoventrally through the entire dorsal series and possess a gradually more conspicuous ventral sulcus towards the caudal region. The same sulcus is also present in *Eidolosaurus* and in more derived mosasauroids (pers. obs.). Dorsal vertebrae of *Coniasaurus* sp. nov. differs from British dolichosaurids by possessing a less curved TPRL in dorsal view and a straighter ventral surface of the centrum. It is also quite distinctive from *Adriosaurus*, *Acteosaurus* and *Pontosaurus* dorsal vertebrae by lacking any degree of pachyostosis.

*Sacral vertebrae.* Two fused vertebrae were recovered associated with other remains of DMNH-1601 and are herein interpreted as the sacrals (Figure S6). The first sacral is broader and slightly shorter than the second one, as in *Adriosaurus* (Lee and Caldwell, 2000) and *Aphanizocnemus* (Dal Sasso and Pinna, 1997). Similar to *C. longicollis*, the length of the sacral centrum is considerably less than the average dorsal vertebra length, but DMNH-1601 differs from *C. longicollis* by having fused sacral vertebrae. The elements are completely fused at all contacting regions: neural arches, pre- and postzygapophyses articulation and vertebral centra (Figure S6-D and H). No signal of abnormal bone growth, such as osteophytes, spondylitis or bony masses, are present, so it is assumed here that the fusion of the sacrals is a natural co-ossification, as in *Lanthanothus* (Rieppel, 1980) and some species of *Varanus* (pers. obs.), and not a paleopathology. However, this individual is a gravid female and the fusion of the elements may also reflect some kind of sexual dimorphism. Unfortunately, there is a high degree of bone damage in this element, preventing the description of many important sacral features. All the areas for articulation with the sacral ribs are broken, but it is possible to note two large areas at each side of the fused vertebrae which received large sacral ribs. Fusion of the sacral ribs remains unclear since these elements were not preserved. Ventrally a deep sulcus runs along both elements, and the exact point where the first sacral ends and the second one begins is indistinguishable due to the complete fusion of the elements. The PPRL also forms a "U" line in dorsal view, but contrary to what happens in dorsal and cervical vertebrae the "U" is oriented anterolaterally, and not posterolaterally. Mosasaurs do not possess "true" sacral vertebrae once the ilium lacks any contact with the axial skeleton, even in the earlier radiations (Russell, 1967; Bell and Polcyn, 2005; Lindgren *et al.*, 2011), and thus prevent an unequivocal comparison between homologous regions between them and *Coniasaurus*.

*Pygal vertebra.* At least one pygal was present in *Coniasaurus* sp. nov. axial skeleton (Figure S7). It is partially preserved, comprehending the vertebral centrum, neural arch and fragmentary transverse processes. Pygal centrum is slightly longer than sacral centrum but shorter than the average dorsal centrum. Ventrally, the centrum is noticeably concave due to projections of both transverse processes. Condyle and cotyle are considerably less dorsoventrally compressed than those of sacral and presacral vertebrae. Transverse processes are nearly half of the centrum length at the proximal portion, and the total size of them cannot be measured due to bone breakage. They are ovoid in cross section, similar to the condition of *Dallasaurus* (Bell and Polcyn, 2005). Transverse processes projects ventrolaterally and are formed by the union of the centroprezygapophyseal lamina (CPRL) anterodorsally with the anterior centrosynapophyseal lamina (ACYL) anteroventrally and the posterior

centrosynapophyseal lamina (PCYL) posteriorly. In anterior view, the contact between the CPRL and the ACYL forms a sulcus noticeable in the left transverse process. Laterally, the projection of both transverse processes originates a deep sulcus in the neural arch that is even more conspicuous than in dorsal vertebrae. The PPRL is more widely open being, in dorsal view, more "(" shaped than "U" shaped. Neural arch is really tall, forming a large posterior channel to receive large zygosphenes from the first caudal vertebra. Both the neural spine and the zygosphenes are broken, thus preventing the description of their morphology. Regarding the zygapophyses, only the left postzygapophysis is preserved, revealing an angle of articulation with either the second pygal of the first caudal of nearly 45°.

*Caudal vertebrae.* There are 30 caudal vertebrae presenting transverse processes and haemapophyses. In mosasaurs, the caudal region can be divided into three distinct regions: pygal, intermediate caudal and terminal caudal, based on the presence or absence of either transverse processes and haemal arches (Lindgren *et al.*, 2011). The condition present here is that only two regions are clearly distinguishable: pygal and caudal, which is closer to the condition found in living anguimorphs, although the tail of *Coniasaurus* sp. nov. was considerably deeper. Through the entire caudal series, the position of the transverse processes is conservative: within the anterior half of the centrum lateral wall (Figure S8). The centrum is always longer than taller, contrary to taller than longer centra found in more derived mosasaurs (Russell, 1967). Caudal vertebrae of *Coniasaurus* sp. nov. were probably more lightly build elements than dorsal vertebrae, which explains why they present a much higher degree of damage. None of them are completely preserved, and just one, still immersed in the rock matrix, preserves the entire length of the haemal arches. That element, in particular, highlights how deep was *Coniasaurus* sp. nov. tail, since the haemal arches are approximately three times longer than centrum height (13,1mm against 7mm of the centrum + the neural arch at its midpoint). Haemal arches articulate posterodorsally with well-developed haemapophyses. These are long ridges that run laterally across the entire ventral surface of the vertebral centrum, forming a deep sulcus in the middle of the centrum. Haemapophyses project posteroventrally to receive the dorsal portion of each haemal arch lamina. Caudal centrum is also more rounded and less compressed dorsoventrally, as it is in the only preserved pygal vertebra and contrary to what is found in presacral elements. Between the transverse process and the PPRL there is also a marked carving in the lateral wall of the neural arch. Neural arches are rarely well preserved among the caudal vertebrae. However, in those which they are present it is possible to note that the neural spine is much more posteriorly, recumbent oriented than in presacral vertebrae, strikingly distinctive from the rectangular neural spine of dorsal elements. PPRL gets

progressively more widely open in dorsal view towards the tail end, closer to the condition found in the pygal rather than the "U" shaped in presacral vertebrae. Zygosphenes are only clearly observable in some of the preserved caudal vertebrae, seeming to be less developed than in presacral elements. Pre- and postzygapophyseal articulation present a similar angled condition found in cervical vertebra, with laminae touching each other at a nearly 45° contact.

*Ribs.* Dozens of rib fragments were preserved in association with DMNH-1601. Two main morphotypes can be distinguished within the many preserved rib fragments: 1) Elements that are larger, more robust and dorsoventrally compressed (Figure S9), bearing strong costal grooves and sub rectangular in cross section; and 2) Elements that are more gracile, rounded in cross section. Morphotype 1 probably encompass trunk ribs, and morphotype 2 cervical ribs. The articular head of the ribs follow the overall shape of the element, being more oval, larger and dorsoventrally compressed in the trunk elements and more rounded and gracile in the cervical elements.

### **Appendicular skeleton**

*Humerus.* Humerus is strikingly similar to that of *C. longicollis* holotype, bearing in both specimens a well-developed deltopectoral crest, a shaft twisted and a tubercle in the mid-portion of the bone (Figure S10). This is a robust bone, being expanded both proximally and distally, lacking the characteristic hourglass or even rectangular shape seen in more derived mosasauroids (Russell, 1967). Overall, the humerus of DMNH-1601 is striking similar to that of the *C. longicollis* holotype, highlighted by 3 morphological features: the presence of a well-developed deltopectoral crest, the rotation of the shaft and the presence of a tubercle in the mid-portion of the bone (Figure S10-A). The relatively well developed deltopectoral crest, occupying an area of nearly 50% of the shaft length, appear to be a modification for aquatic propulsion, since this feature is also present in more derived mosasauroids (Russel, 1967). In the mid-portion of the humerus shaft a noticeable twist rotate the proximal region, matching the exact condition found in *C. longicollis* humerus. This rotation is significantly stronger than in modern varanoids, and this condition is also not present in any other dolichosaur or mosasauroid so far known. A conspicuous crest marks this rotation in the shaft (Figure S10). In the middle portion of the shaft, right dorsally after this crest, a small tubercle is projecting both in *Coniasaurus* sp. nov. and *C. longicollis* holotypes. Proximal head is strongly compressed lateromedially in proximal view, bearing a long anteroposterior articular surface to contact the glenoid fossa. Unfortunately, pectoral girdle elements are absent, preventing more accurate

reconstructions of limb musculature. Medial tubercle is much less developed, as in modern varanoids, being represented by a small and rounded tuberosity. Humerus shaft is narrower than both epiphyses but still more robust than in modern terrestrial lizards. Ectepicondyle is more developed and larger than entepicondyle. Just proximally to ectepicondyle there are two small tuberosities in the ventrolateral surface of the shaft (Figure S10-B). As in *Lanthanothus*, the entepicondylar foramen is represented only by a notch in the anteroventral surface of the bone (Rieppel, 1980). Ectepicondylar foramen also appears to be absent. Absence of both foramina was also reported for the dolichosaurs *C. longicollis* (Caldwell, 2000) and *Pontosaurus kornhuberi* (Caldwell, 2006).

*Femur*. DMNH-1601 has preserved both a proximal and a distal portions of the femur (Figure S11). The proximal portion present well developed both an articular head and an internal trochanter. Articular head is anteroposteriorly compressed in proximal view, and the bone gently slopes towards the trochanter outer surface. There are strong muscle scars for the *m. iliofemoralis* near the internal trochanter. Medial wall of the proximal part is slightly concave, visible mainly in anterior and posterior views. Most of the femur's shaft is lost in the specimen. As the shaft is broken, it is possible to notice that the cross section of the element is more subtriangular towards the proximal end and more circular, oval shaped towards the distal end. Distal epiphysis is ossified (against the unossified condition of some dolichosaur specimens; i.e. Palci and Caldwell, 2007; Caldwell and Palci, 2010) subtriangular in shape, and present well-developed and noticeable articular surfaces for the zeugopod elements. A bony tubercle in the middle of the ventralmost portion of the femur separates the articular surfaces for the tibia and the fibula by projecting ventrolaterally. Dorsally to this tubercle, a medial crest rises toward the shaft, separating the distal part of the femur in two distinct regions. This configuration is unique among dolichosaurs, but often found in other aquatic reptiles such as mosasaurs (Russell, 1967), ichthyosauriforms (Motani *et al.*, 2014), elasmosaurs (Kubo *et al.*, 2012), pliosaurs (Smith and Vincent, 2010) and marine snakes (Lee and Caldwell, 1998), suggesting a high correlation of this trait with aquatic habits.

*Tibia*. This element is also only preserved in DMNH-1601 among every coniasaur specimen, being a more robust and shorter bone than in extant lizards (Figure S12). The tibia is subequal in length to the humerus. As in other terrestrial squamates, the tibia of *Coniasaurus* is strongly expanded proximally and forms a nearly triangular articular surface to receive the femur. A marked cnemial crest descends lateroventrally up to the medial portion of the bone. From that point, the width of the element remains nearly the same towards the distal end, up to the surface which will articulate with the tarsal bones. Just above the distal end, in its anterior

edge, a tuberosity projects anteriorly, forming a structure similar to the ridges of some living varanoids tibiae (Rieppel, 1980), although much more ventrally located. The general morphology of the tibia is very similar to that of extant varanoids and extinct dolichosaurs such as *Acteosaurus* and *Adriosaurus* (Lee and Caldwell, 2000; Palci and Caldwell, 2010;), but differs from *Aphanizocnemus*, which bears a highly reduced and flat tibia (Dal Sasso and Pinna, 1997), and *Pontosaurus kornhuberi*, which possess a narrower and more gracile element (Caldwell, 2006).

*Fibula.* Two associated small fragments (Figure S13) are herein interpreted as the proximal and distal portions of the fibula. One of the elements is larger than the other, so the possibility of both representing the same portion (distal or proximal) of a left and a right elements is unlikely. In addition, they are much smaller and less robust than the tibia, presenting none characteristic feature nor match the expected size for the forelimb zeugopods. This set of features suggest that the elements really belonged to the fibula. In squamates, the fibula is usually more expanded distally than proximally, so the larger fragment is interpreted here as a distal portion and the smaller one the proximal. Proximal fragment is strongly flattened near the shaft, being expanded only very close to the articular head. Laterally, a weakly developed crest runs towards the shaft, being broken at its mid-point. This crest is connected with the articular head by a diagonally oriented process. The distal portion of the fibula is more heavily built, being subtriangular in cross section. A lateral crest is also present in this fragment, being here more developed and robust, although is unclear whether it formed a continuous projection with the proximal crest. Beneath the crest an articular surface, obliquely oriented, probably received the astragalus or the calcaneum.

*Metatarsal element.* A single metapodium element was found among DMNH-1601 remains (Figure S14). This bone is approximately half the size of the humerus and a quarter the size of the femur, presenting a very expanded proximal end, which matches the proportional size and shape of both the first and fifth metatarsals in basal mosasaurians. Contrary to what is found in most squamates, the fifth metatarsal is not hooked in basal mosasaurians, with the only exception being the recently described *Primitivus manduriensis* (Paparella *et al.*, 2018). Therefore, it is not clear whether the DMNH-1601 metapodium represents the first or the fifth element.

*Phalanges.* Two complete phalanges and one distal phalangeal portion are preserved in DMNH-1601 (Figure S15). Unfortunately, as these are isolated elements, the total phalangeal formula cannot be evaluated. Overall morphology is similar between the three bones. Distal phalangeal tips are rounded and notched on each side, while the proximal portion has an "U"

shaped articular surface to receive the precedent phalanx or metacarpal/metatarsal element. Joint surfaces are well developed, which has been suggested to be related with active use in land locomotion (Evans *et al.*, 2006). Phalangeal ventral surface bears a medial sulcus, as in some modern lizards (Figure S15-B). In *Aphanizocnemus libanensis*, phalanges from the pes are considerable shorter than those from the manus (Dal Sasso and Pinna, 1997). If *Coniasaurus* presented the same condition, the phalanges described here are likely manus, not pes, elements.

*Ungual.* A single unguis is preserved in DMNH-1601. It is curved and pointed as in other squamates (Figure S16), dark brown in color, and subtriangular in shape in distal view. Unguis is dorsoventrally flattened and very elongated, matching the expected morphology for a plesiomorphic squamate. Its distal portion is covered with a dark layer of tissue and it is bifurcated at its very tip. In medial and lateral views, the articular surface of the proximal portion is "C" shaped.

### **List of characters**

The following list of characters was built using morphological characters from Estes *et al.* (1988), Rieppel and Zaher (2000), Bell and Polcyn (2005), Conrad (2008), Palci and Caldwell (2010) and Gauthier *et al.* (2012). Character and/or states that were modified, such as deleting irrelevant states, inversion of polarization due to differences in the outgroups or characters that were slightly changed are described as "Modified from...". Characters that were new or extensively modified were labeled stating this and figured on the second volume of this thesis.

1. Dentition, "coniasaur-like" heterodonty: (0) absent; (1) present, with posteriormost teeth being significantly distinct in shape and proportions from the anteriormost teeth and bearing an anterodorsally oriented carena. New or extensively modified character (Figure S17).

2. Dentition, presence of a conspicuous groove on the anterolateral surface of the crown: (0) absent; (1) present. New or extensively modified character (Figure S18).

3. Dentition, bases of marginal teeth: (0) smooth, dentine and enamel not infolded; (1) dentine and enamel infolded into pulp cavity ("plicidentine"), resulting in longitudinal grooves externally at base of teeth. Gauthier *et al.* (2012).

4. Dentition, marginal teeth: (0) all vertical; (1) all recurved; (2) anterior teeth recurved and posterior teeth vertical. Gauthier *et al.* (2012).

5. Dentition, expanded bases on marginal teeth: (0) absent; (1) present, main shafts of teeth somewhat separated. Conrad (2008).

6. Maxilla, tooth number: (0) 12 or less; (1) 13 or more. Modified from Bell and Polcyn (2005).
7. Maxilla, facial process height: (0) tall, to skull roof; (1) reduced. Modified from Gauthier *et al.* (2012).
8. Maxilla, narial margin rises at: (0) high angle; (1) low angle. Gauthier *et al.* (2012).
9. Maxilla, facial process apical surface faces: (0) laterally; (1) dorsolaterally. Modified from Gauthier *et al.* (2012).
10. Nasal-prefrontal suture: (0) present; (1) absent. Estes *et al.* (1988).
11. Nasals, size: (0) large; (1) greatly reduced or absent. Palci and Caldwell (2010).
12. Frontals, fusion: (0) paired; (1) fused. Estes *et al.* (1988).
13. Frontal, anterior constricted neck: (0) present; (1) absent. Modified from Conrad (2008).
14. Frontal, subolfactory processes: (0) absent; (1) arch beneath brain but do not contact; (2) arch beneath brain to articulate on ventral midline. Modified from Gauthier *et al.* (2012).
15. Frontal, invaded by external nares: (0) absent; (1) present. Conrad (2008).
16. Frontal, proportional size: (0) short; (1) elongated. New or extensively modified character (Figure S19).
17. Frontoparietal suture, dorsal view: (0) W-shaped; (1) transverse. Modified from Conrad (2008).
18. Parietal, width of dorsal aspect of parietal table: (0) very large anteriorly and posteriorly; (1) gradually tapers posteriorly; (2) very thin posteriorly. New or extensively modified character (Figure S20).
19. Prefrontal, posterior extent along orbital margin: (0) extends to midorbit; (1) terminates in anterior half of orbit. Modified from Gauthier *et al.* (2012).
20. Postfrontal/postorbital, forking of medial surface: (0) present; (1) absent. Modified from Rieppel and Zaher (2000).
21. Jugal, extension: (0) does not extend anteriorly past orbit; (1) extends anteriorly past orbit. Palci and Caldwell (2010).
22. Jugal, posteroventral process: (0) present; (1) absent. Conrad (2008).
23. Quadrate, shape: (0) bowed more or less, but not in both lateral and posterior views; (1) massive, and strongly bowed anteriorly in lateral view and laterally in posterior view, throughout length, and with prominent ventrally-directed suprastapedial process forming cavum tympani. Gauthier *et al.* (2012).
24. Quadrate, suprastapedial process: (0) short; (1) long. Bell and Polcyn (2005).

25. Quadrate, infrastapedial process: (0) absent; (1) present, but weakly developed; (2) present and well developed. Modified from Bell and Polcyn (2005).

26. Supraoccipital, contact with parietal: (0) does not contact, unossified gap persists between the two elements; (1) sutural contact with parietal, entire anterodorsal edge of supraoccipital contacts parietal. Modified from Palci and Caldwell (2010).

27. Mandible, symphysis: (0) present; (1) absent. Rieppel and Zaher (2000).

28. Mandible, Meckel's canal opening: (0) opens medially for most of length; (1) opens ventrally anterior to anterior inferior alveolar foramen. Gauthier *et al.* (2012).

29. Mandible, splenial-angular articulation: (0) splenial overlaps angular; (1) with ball on angular fitting into socket on splenial. Modified from Gauthier *et al.* (2012).

30. Dentary, shape of long axis: (0) ventrally convex; (1) ventrally straight. Conrad (2008).

31. Dentary, size of posteriormost mental foramen: (0) same size as others; (1) enlarged relative to others. Gauthier *et al.* (2012).

32. Angular, anterior separation from coronoid: (0) angular broadly separated from coronoid; (1) angular taller anteriorly, closely approaching coronoid. Modified from Gauthier *et al.* (2012).

33. Retroarticular process size: (0) short, process shorter than articular cotyle; (1) long, process over 2 times longer than articular cotyle. Modified from Palci and Caldwell (2010).

34. Body shape: (0) round, ribs smoothly curved; (1) laterally compressed, middle and distal regions of ribs straight. Palci and Caldwell (2010).

35. Vertebrae, presacral number increase: (0) 32 presacrals or fewer; (1) 33–40; (2) 41 or more. Modified from Gauthier *et al.* (2012).

36. Vertebrae, neural spines: (0) short and broad; (1) tall and narrow. Modified from Conrad (2008).

37. Vertebrae, precondylar constriction: (0) absent; (1) present. Modified from Estes *et al.* (1988).

38. Zygosphene-zygantrum accessory intervertebral articulations: (0) absent; (1) present. Modified from Gauthier *et al.* (2012).

39. Vertebrae, pachyostosis of mid-dorsals: (0) absent; (1) present. Gauthier *et al.* (2012).

40. Cervical vertebrae, number: (0) six or fewer; (1) seven; (2) eight or more. Gauthier *et al.* (2012).

41. Cervical vertebrae, pedicle: (0) absent; (1) projecting ventrally with discrete fore and aft margins. Gauthier *et al.* (2012).

42. Cervical vertebrae, intercentrum fusion: (0) All fused to preceding centrum; (1) At least some are sutured to preceding centrum; (2) not sutured or fused to preceding centrum. Palci and Caldwell (2010).

43. Cervical ribs: (0) widens distally, at least in last cervical; (1) tapers distally. Gauthier *et al.* (2012).

44. Dorsal vertebrae, shape: (0) “V” shaped, with lateral sides converging towards condyle; (1) “T” shaped, with abrupt expansion anteriorly; (2) “Box” shaped, with lateral sides running nearly parallel. New or extensively modified character (Figure S21).

45. Dorsal vertebrae, presence of a lateral “carving” in the lateral aspect of the vertebrae, between the centrum and the neural arch: (0) absent; (1) present. New or extensively modified character (Figure S22).

46. Dorsal vertebrae, width of posterior base of the neural spine: (0) equal or subequal to the anterior base; (1) posterior base larger than anterior one. New or extensively modified character (Figure S23).

47. Dorsal vertebrae, number: (0) 25 or less; (1) between 26 and 30; (2) 31 or more. New or extensively modified character.

48. Sacral vertebrae, fusion: (0) absent; (1) present. New or extensively modified character (Figure S24).

49. Caudal vertebrae, deepness: (0) regular; (1) very deep, forming a strong sculling organ. New or extensively modified character (Figure S25).

50. Caudal vertebrae, neural spines of posterior elements: (0) projecting dorsally or posterodorsally; (1) projecting almost horizontally, highly inclined posteriorly. Palci and Caldwell (2010).

51. Caudal vertebrae, zygapophyses and transverse processes: (0) well developed, zygapophyses extending more one-fourth the length of centrum; (1) reduced, creating greater flexibility of the trunk and tail. Conrad (2008).

52. Caudal vertebrae, pedestals for chevrons: (0) bulges; (1) well-developed, expressed as relatively deep and discrete pedestals. Rieppel and Zaher (2000).

53. Caudal vertebrae, haemal arch (intercentrum) position: (0) mainly contacting pedicles on preceding centrum but still bordering condyle; (1) well forward of condyle on preceding centrum. Modified from Gauthier *et al.* (2012).

54. Scapulocoracoid: (0) large; (1) reduced. Modified from Gauthier *et al.* (2012).

55. Coracoid, anterior (primary) coracoid emargination: (0) present; (1) absent. Modified from Estes *et al.* (1988).

56. Scapula, size relative to the coracoid: (0) scapula subequal to, or larger than the coracoid; (1) scapula smaller than the coracoid. Modified from Conrad (2008).

57. Forelimbs, proportional size in relation to the hindlimbs (humerus length/femur length): (0) nearly 1; (1) between 0,85 and 0,65; (2) 0,6 or less. New or extensively modified character.

58. Humerus, deltopectoral crest proportional size: (0) larger length of the crest measuring less than 50% of the humerus shaft length; (1) larger length of the crest measuring 50% or more of the humerus shaft length. New or extensively modified character (Figure S26).

59. Humerus, deltopectoral crest relative position: (0) located anteriorly; (1) located medially. Bell and Polcyn (2005).

60. Humerus, shaft twisted: (0) absent; (1) present. New or extensively modified character (Figure S26).

61. Humerus, distinct tubercle in the mid-point of the shaft: (0) absent; (1) present. New or extensively modified character (Figure S26).

62. Humerus, ectepicondylar foramen: (0) present; (1) absent. Estes *et al.* (1988).

63. Ilium, tubercle: (0) present; (1) absent. Gauthier *et al.* (2012).

64. Femur, shape: (0) curved in dorsoventral plane; (1) not curved in dorsoventral plane. Gauthier *et al.* (2012).

65. Femur, internal trochanter: (0) well developed as a prominent, distinct head; (1) poorly developed or absent. Estes *et al.* (1988).

66. Tibia, notching of distal epiphysis: (0) notch not present, epiphysis gently convex for astragalocalcaneal articulation; (1) distinct notch present, fitting onto a ridge on the astragalocalcaneum. Estes *et al.* (1988).

67. Fibula, posterodistal process of fibula: (0) weakly developed to absent; (1) strongly developed, triangular process extends posteriorly beyond calcaneum. Palci and Caldwell (2010).

68. Astragalus and calcaneum: (0) co-ossified; (1) separate. Palci and Caldwell (2010).

69. Fifth metatarsal: hooked (0); not hooked (1). Palci and Caldwell (2010).

70. Biogeography: (0) East Asia and Australia; (1) North America/ Central America; (2) Europe/western Asia. Modified from Conrad (2008).



- Caldwell, M.W.; Cooper, J.A. 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the Lower Chalk (Cretaceous; Cenomanian) of SE England. **Zoological Journal of the Linnean Society** 127: 423-452.
- Caldwell, M.W.; Lee, M.S.Y. 2004. Reevaluation of the Cretaceous marine lizard *Acteosaurus crassicostatus* Calligaris, 1993. **Journal of Paleontology** 78(3): 617-619.
- Caldwell, M.W.; Palci, A. 2010. A new species of marine ophidiomorph lizard, *Adriosaurus skrbiniensis*, from the Upper Cretaceous of Slovenia. **Journal of Vertebrate Paleontology** 30(3): 747-755.
- Caldwell, M.W. 1999. Description and phylogenetic relationships of a new species of *Coniasaurus* Owen, 1850 (Squamata). **Journal of Vertebrate Paleontology** 19(3): 438-455.
- Caldwell, M.W. 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in Squamates. **Journal of Vertebrate Paleontology** 20(4): 720-735
- Caldwell, M.W. 2006. A New Species of "Pontosaurus" (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a Phylogenetic Analysis of Pythonomorpha. **Società Italiana di Scienze Naturali**: 1-44.
- Conrad, J.L. 2004. Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). **Zoological Journal of the Linnean Society** 141(3): 399-434.
- Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. **Bulletin of the American Museum of Natural History**, 310: 1-182.
- Cundall, D.; Irish, F. (2008). The snake skull. *Biology of the Reptilia*, 20, 349-692.
- Dal Sasso, C.; Pinna, G. 1997. *Aphanizocnemus libanensis* n. gen. n. sp, a new dolichosaur (Reptilia, Varanoidea) from the Upper Cretaceous of Lebanon. **Paleontologia Lombarda** 7: 1-31.
- Dutchak, A.R. 2005. A review of the taxonomy and systematic of aigialosaurs. **Netherlands Journal of Geosciences** 84(3): 221-229.
- Estes, R.; de Queiroz, K.; Gauthier, J. 1988. Phylogenetic relationships within Squamata. In: Estes, R.; Pregill, G. (eds). **Phylogenetic relationships of the lizard families**. Stanford, Stanford University Press, p. 119-282.
- Evans, S.E.; Manabe, M.; Noro, M.; Isajis, S.; Yamaguchi, M. 2006. A longbodied lizard from the Lower Cretaceous of Japan. **Paleontology** 49(6): 1143-1165.
- Gauthier, J.A.; Kearney, M.; Maisano, J.A.; Rieppel, O.; Behlke, A.D.B. 2012. Assembling the Squamate tree of life: perspectives from the phenotype and the fossil record. **Bulletin of the Peabody Museum of Natural History** 53(1): 3-308.

- Haber, A.; Polcyn, M.J. 2005. A new marine varanoid from the Cenomanian of the Middle East. **Netherlands Journal of Geosciences** 84(3): 247-255.
- Kubo, T.; Mitchell, M.T.; Henderson, D.M. 2012. *Albertonectes vanderveldei*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. **Journal of Vertebrate Paleontology** 32(3): 557-572.
- Lee, M.S.Y.; Caldwell, M.W. 1998. Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. **Philosophical Transactions of the Royal Society of London B: Biological Sciences** 353: 1521-1552.
- Lee, M.S.Y.; Caldwell, M.W. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. **Journal of Paleontology** 74(5): 915-937.
- Lindgren, J.; Polcyn, M.J.; Young, B.A. 2011. Landlubbers to leviathans: evolution of swimming in mosasaurine mosasaurs. **Paleobiology** 37: 445–469.
- McDowell, S.B.; Bogert, C.M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. **Bulletin of the American Museum of Natural History** 105: 1-142.
- Motani, R.; Jiang, D.Y.; Tintori, A.; Rieppel, O.; Chen, G.B. 2014. Terrestrial origin of viviparity in Mesozoic marine reptiles indicated by Early Triassic embryonic fossils. **PloS one** 9(2): e88640.
- Palci, A.; Caldwell, M.W. 2007. Vestigial forelimbs and axial elongation in a 95 million-year-old non-snake squamate. **Journal of Vertebrate Paleontology** 27(1): 1-7.
- Palci, A.; Caldwell, M.W. 2010. Redescription of *Acteosaurus tommasinii* von Meyer, 1860, and a discussion of evolutionary trends within the clade Ophidiomorpha. **Journal of Vertebrate Paleontology** 30(1): 94-108.
- Paparella, I.; Palci, A.; Nicosia, U.; Caldwell, M.W. 2018. A new fossil marine lizard with soft tissues from the Late Cretaceous of southern Italy. **Royal Society Open Science** 5(6): doi 172411.
- Pierce, S.; Caldwell, M.W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur, *Pontosaurus lesinensis* (Kornhuber, 1873). **Journal of Vertebrate Paleontology** 24: 376-389.
- Polcyn, M.J.; Tchernov, E.; Jacobs, L.L. 1999. The Cretaceous biogeography of the Eastern Mediterranean with a description of a new basal mosasauroid from 'Ein Yabrud, Israel. In: SECOND GONDWANAN DINOSAUR SYMPOSIUM. **Proceedings of the Second Gondwanan Dinosaur Symposium**. National Science Museum Monographs 15, Tokyo, Japan. p. 259-290.

- Rieppel, O.; Zaher, H. 2000. The intramandibular joint in squamates and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. **Fieldiana (Geology), New Series** 43: 1-69.
- Rieppel, O. 1980. **The phylogeny of anguimorph lizards**. Birkhauser Verlag, Basel, 86 p.
- Russell, D.A. 1967. Systematics and morphology of American mosasaurs. **Bulletin of the Peabody Museum of Natural History** 23: 1-241.
- Smith, A.S.; Vincent, P. 2010. A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany. **Palaeontology** 53(5): 1049-1063.
- Street, H.P.; Caldwell, M.W. 2016. Rediagnosis and redescription of *Mosasaurus hoffmannii* (Squamata: Mosasauridae) and an assessment of species assigned to the genus *Mosasaurus*. **Geological Magazine**: 1-37. doi:10.1017/S0016756816000236.
- Tschopp, E. 2016. Nomenclature of Vertebral Laminae in Lizards, with Comments on Ontogenetic and Serial Variation in Lacertini (Squamata, Lacertidae). **PloS one** 11(2): e0149445.
- Zaher, H.; Rieppel, O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. **American Museum Novitates** 3271: 1-19.

**Chapter 2 – New remains of North American coniasaurs**  
**(Squamata: Mosasauria) from the Upper Cretaceous of Texas and**  
**a revision of the genus *Coniasaurus***

**Abstract**

Coniasaurs were long-bodied plesioipedal squamates closely related to the more derived clade Mosasauroidae. They are key taxa to understand the evolution of the Mosasauria, since several specimens are known from both British and North American Upper Cretaceous rocks. Two coniasaur species are currently known in the literature: *Coniasaurus crassidens* Owen 1850 and *Coniasaurus gracilodens* Caldwell, 1999, and a third one, *Coniasaurus* sp. nov., was described in the first Chapter of this thesis. Here additional remains of coniasaurs from the Upper Cretaceous of Texas were describe, adding new morphological information to the anatomy of the genus. Coniasaur remains were compared to British coniasaurs and dolichosaurs, and the results gathered here support the hypothesis that the genus *Dolichosaurus* is a junior synonym of *Coniasaurus*. The new composition of the genus *Coniasaurus* proposed here comprises now four distinct species. At least two of these were present in the Western Interior Seaway during the early Late Cretaceous. The data gathered by this contribution provide plenty of new anatomical information regarding the cranial, axial and appendicular skeletons of *Coniasaurus* from 53 distinct specimens. *Coniasaurus* is established here as the most reliable dolichosaur to use for coding phylogenetic characters because it is known from several tridimensionally well preserved specimens with a very low degree of taphonomical distortion, contrary to most of the other dolichosaur lizards.

**Keywords:** Dolichosauridae; Mosasauria; Late Cretaceous; Western Interior Seaway.

## Resumo

Os coniaçauros são lagartos plesiopedaís alongados proxímamente relacionados ao clado Mosasauróidea. Eles são um componente chave para a compreensão da evolução de Mosasauria como um todo, já que diversos espécimes de coniaçauros foram encontrados em rochas do Cretáceo Superior na América do Norte e na Grã-Bretanha. Duas espécies de coniaçauros foram descritas na literatura: *Coniasaurus crassidens* Owen 1850 e *Coniasaurus gracilodens* Caldwell, 1999, e uma terceira, *Coniasaurus* sp. nov., foi descrita no primeiro capítulo desta tese. Neste trabalho são descritos novos espécimes de coniaçauro do Cretáceo Superior do Texas, adicionando novas informações morfológicas sobre a anatomia do gênero. Estes espécimes foram comparados com aqueles encontrados na Inglaterra, e o resultado desta análise suporta a hipótese do gênero *Dolichosaurus* ser um sinônimo júnior do gênero *Coniasaurus*. A nova composição do gênero *Coniasaurus* proposta aqui inclui quatro espécies distintas, e pelo menos duas destas estavam presentes no Mar Interior Ocidental da América do Norte durante o início do Cretáceo Tardio. Os dados gerados aqui fornecem importantes informações anatômicas referentes aos esqueletos craniano, axial e apendicular de *Coniasaurus* com base em 53 espécimes distintos. *Coniasaurus* é estabelecido aqui como o dolicoçauro mais confiável para ser codificado em análises filogenéticas por ser conhecido por diversos espécimes tridimensionalmente preservados que apresentam um grau de distorção tafonômica relativamente baixo quando comparados à maioria dos outros espécimes de dolicoçauros.

**Palavras-chave:** Dolichosauridae; Mosasauria; Cretáceo Tardio; Mar Interior Ocidental.

## 2.1. Introduction

Dolichosaurs were relatively small and long-bodied marine squamates, interpreted mostly often as lizards closely related to mosasauroids (Conrad, 2008; Gauthier *et al.*, 2012; Reeder *et al.*, 2015), although some authors consider at least some dolichosaurs to be more related to snakes than to mosasaurs (Lee, 1998; Lee and Caldwell, 2000; Caldwell and Palci, 2010). The characters joining dolichosaurs and mosasauroids as a monophyletic Mosasauria include, among others, the presence of an intramandibular joint, a modified pleurodont dentition and the cervical intercentrae position (Polcyn and Bell, 1994; Zaher and Rieppel, 1999; Rieppel and Zaher, 2000a; Conrad 2008, Conrad *et al.*, 2011; Gauthier *et al.*, 2012; Reeder *et al.*, 2015). Dolichosaur fossil remains are reported for Cenomanian-Coniacian marine sediments of North America and Eurasia (Caldwell, 1999b; Lee and Scanlon, 2002; Haber and Polcyn, 2005; Jacobs *et al.*, 2005; Bell *et al.*, 2013). These lizards were characterized by the elongation of the body (especially the neck and the tail), by possessing reduced limbs and by the fusion of the cervical intercentrae with the posterior part of the preceding pleurocentrum (Nopcsa, 1923; Caldwell, 2000; Conrad, 2008). They can be considered key fossil taxa for Anguimorpha systematics due to their importance on understanding the evolution of Mosasauria, Varanoidea and snakes.

Among all the described dolichosaur species, *Coniasaurus* is by far the taxon with more specimens reported so far. Only in Texas, the fossil record of *Coniasaurus* is considerably vast and its geochronological distribution ranges from the Middle Cenomanian to the Coniacian, in a time interval of nearly 11 Ma (Jacobs *et al.*, 2005). Nevertheless, the majority of the described coniasaur specimens encompass very incomplete individuals. Owen (1850) described both *Coniasaurus crassidens* and *Dolichosaurus longicollis* in the same contribution, the first based on a left maxilla (originally interpreted as the right dentary) and 14 associated dorsal vertebrae and the later based on some very fragmentary and poorly preserved skull remains and some nicely preserved postcranial remains. Bell *et al.* (1982) described the first record of the genus in North America, including some disarticulated and associated skull and vertebral remains of *Coniasaurus crassidens* from Texas. A left maxilla with six teeth was reported by Bell (1993) as the first occurrence of *Coniasaurus* from the Upper Cretaceous of South Dakota, although its exactly stratigraphic relationships could not be recovered at that time. Bell and Polcyn (1996) and Cicimurri and Bell (1996) reported the occurrence of *Coniasaurus* remains (cranial, axial and shed teeth) from Texas, South Dakota and Kansas, expanding the known geographic distribution of the genus through the Western Interior Seaway. Diedrich (1997) described a

fragmentary dentary with the typical coniasaur teeth morphology from Germany. VonLoh and Bell (1998) reported the presence of *Coniasaurus* remains from South Dakota in the basis of a fragmentary maxilla with six teeth, three cervical vertebrae, one dorsal vertebra, one caudal vertebra and ten isolated shed teeth. Caldwell and Cooper (1999) redescribed the type and referred materials of *Coniasaurus crassidens* from UK, and Caldwell (1999) described a new species within the genus: *Coniasaurus gracilodens*. Caldwell (2000) redescribed the holotype and referred specimens of *Dolichosaurus longicollis* and raised the hypothesis that *Coniasaurus* and *Dolichosaurus* could be synonymized in the basis of more complete specimens description, since *Coniasaurus* was diagnosed primarily from cranial characters and *Dolichosaurus* primarily from postcranial features. Everhart and Darnell (2004) reported the occurrence of the shark *Ptychodus mammillaris* from the Carlile Shale of Kansas but cited in their introduction (page 1) that the University of Kansas also housed two coniasaur vertebrae. Liggett *et al.* (2005) described remains of *Coniasaurus* cf. *C. crassidens* from Kansas, including a partial left maxilla, two dorsal vertebrae, one caudal vertebra and four isolated shed teeth. Shimada and Bell (2006) reported the occurrence of one coniasaur vertebra from Kansas. Shimada and Ystesund (2007) and Shimada *et al.* (2007) described respectively two isolated vertebrae and one shed tooth referred to *Coniasaurus* but looking at the illustrations these materials apparently do not possess unequivocal coniasaur diagnostic features. Scanlon and Hocknull (2008) described an isolated trunk vertebra from Australia and tentatively referred it to *Coniasaurus*, but the specimen apparently lacks any coniasaur true diagnostic feature. Nagrodski *et al.* (2012) reported the occurrence of 18 coniasaur teeth from Colorado, but figured only one, so it is unclear whether this is a confidently record of *Coniasaurus* or not.

In this contribution several remains of *Coniasaurus* from the Upper Cretaceous (Cenomanian-Turonian) of Texas are described, based on 53 specimens. Coniasaur remains published earlier during the 80's (Bell *et al.*, 1982) were also redescribed. The new data gathered here shed light into the anatomy of previously unknown coniasaur bones, including the ilium, surangular and pterygoid. The description of these well-preserved specimens allowed us to compare in detail the anatomy of North American coniasaurs with that of UK specimens, supporting the hypothesis that *Dolichosaurus* and *Coniasaurus* actually belong to the same genus (Caldwell, 2000; Chapter 1 of this thesis), the later having taxonomic priority. At least two coniasaur species, maybe three, lived in the Western Interior Seaway during the early Late Cretaceous, the Westernmost record of the taxon. North American coniasaurs constitute one of the most important and reliable sources of anatomical information regarding the morphology of dolichosaurs, since they are known from several tridimensionally well preserved specimens,

and so their inclusion in phylogenetic studies investigating the evolution of basal mosasaurians should be priority.

## 2.2. Methods

Here are described coniasaur remains recovered from six distinct localities. Specimens were assigned to the genus *Coniasaurus* by possessing diagnostic dentition and vertebral characters (for an emended diagnosis of the genus, see item 2.3.). Nomenclatural references follow Bahl (1937), Oelrich (1956), Romer (1956) and Russell (1967) for cranial and postcranial skeletons, Smith and Dodson (2003) for the dentition and Tschopp (2016) for the vertebral laminae.

### 2.2.1. Institutional abbreviations

**BMB**, Booth Museum of Natural History, Brighton, England; **DMNH**, Perot Museum of Nature and Science, Dallas, USA; **MZSP**, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **NHMUK**, Natural History Museum, London, England; **SMU**, Southern Methodist University, Dallas, USA; **TMM**, Texas Memorial Museum, Austin, USA.

### 2.2.2. Specimens analyzed

53 North American coniasaur specimens were analyzed in this work (Table 1). Most complete and better-preserved specimens were CT-Scanned at the University of Texas High-Resolution X-ray Computed Tomography Facility, with resolution ranging from 19 $\mu$ m to 25 $\mu$ m, in order to better illustrate their morphology and evaluate internal structures. Each specimen bringing new morphological data on *Coniasaurus* anatomy are described in detail below. Detailed comparisons were also performed with the following British dolichosaurids: *Coniasaurus crassidens* (BMB 007155, BMB 007157, BMB 012485, NHMUK R1937, NHMUK R23421, NHMUK R25790, NHMUK R62), *Coniasaurus gracilodens* (NHMUK R 44141) and *Dolichosaurus longicollis* (BMB 0085687, NHMUK R32268, NHMUK R49902, NHMUK R49907, NHMUK R49908).

**Table 1 - List of North American specimens analyzed in this work.**

<b>Specimen Number</b>	<b>Institution</b>	<b>Locality</b>	<b>Identification</b>
DMNH-1601	DMNH	Lewisville Lake Spillway	Holotype of <i>Coniasaurus</i> sp. nov., composed by an adult gravid female preserving fragmented frontal, partial parietal, right quadrate, left dentary, fragmentary remains of the mandible, fragmentary tooth bearing elements, 3 cervical, 35 dorsal, 2 sacral and 29 caudal vertebrae, many isolated ribs, humerus, femur, tibia, fibula, four phalanges and one ungual and several embryonic remains.
SMU-69018	SMU	DFW Airport	Nearly complete left pterygoid
SMU-69019	SMU	DFW Airport	Fragmented left dentary
SMU-69020	SMU	DFW Airport	Six associated jaw sections, including four dentary and two maxillary fragments
SMU-69021	SMU	DFW Airport	Fragmented right maxilla
SMU-69022	SMU	DFW Airport	One isolated dorsal vertebra
SMU-69023	SMU	DFW Airport	Fragment of a right maxilla
SMU-69024	SMU	DFW Airport	Four cervical and one dorsal vertebra
SMU-69025	SMU	DFW Airport	Two caudal vertebrae
SMU-69026	SMU	DFW Airport	One isolated cervical vertebra
SMU-69027	SMU	DFW Airport	Fragmented left dentary
SMU-69028	SMU	DFW Airport	Four cervical, twelve dorsal, two caudal and several unidentifiable vertebrae
SMU-69029	SMU	DFW Airport	One cervical and thirteen dorsal vertebrae
SMU-72396	SMU	Egyptian Way	Specimen comprising associated remains of a prefrontal, 2 cervical, 25 dorsal, 1 pygal, 6 caudal and 3 indeterminate vertebrae, several isolated ribs and one partial ilium
SMU-72398	SMU	Egyptian Way	Fragmented left dentary with four tooth crowns
SMU-72399	SMU	Egyptian Way	Fragmented left maxilla with three tooth crowns

SMU-72400	SMU	Egyptian Way	Two associated dorsal vertebrae
SMU-72401	SMU	Egyptian Way	Two articulated dorsal vertebrae
SMU-72403	SMU	Egyptian Way	Twelve associated (articulated or not) dorsal, two caudal and one indeterminate vertebra
SMU-72404	SMU	Egyptian Way	One isolated cervical vertebra
SMU-72406	SMU	Egyptian Way	One isolated dorsal vertebra
SMU-72407	SMU	Egyptian Way	One isolated cervical vertebra
SMU-72408	SMU	Egyptian Way	Six associated dorsal vertebrae and one caudal vertebra
SMU-72409	SMU	Egyptian Way	Associated remains of one cervical and three dorsal vertebrae
SMU-72382	SMU	DFW Airport	Right surangular
SMU-72383	SMU	DFW Airport	Jaw fragment with one tooth crown (juvenile)
SMU-72384	SMU	DFW Airport	Fragmented left maxilla with three tooth crowns
SMU-72385	SMU	DFW Airport	Fragmented left dentary with eight tooth crowns
SMU-72386	SMU	DFW Airport	Anterior portion of the left dentary with seven tooth crowns
SMU-72387	SMU	DFW Airport	Left maxilla with nine tooth crowns (still in the rock matrix)
SMU-72388	SMU	DFW Airport	Right dentary with fifteen tooth crowns (still in the rock matrix)
SMU-72389	SMU	DFW Airport	Anterior part of the frontal
SMU-72390	SMU	DFW Airport	Fragments of one left maxilla and several jaw sections

SMU-72391	SMU	DFW Airport	Fragments of one left maxilla and several jaw sections
SMU-72392	SMU	DFW Airport	Fragmented left dentary with nine tooth crowns
SMU-72393	SMU	DFW Airport	Fragmented left maxilla with three tooth crowns
SMU-72394	SMU	DFW Airport	Fragmented jaw section with eight tooth crowns (still in the rock matrix)
SMU-72395	SMU	DFW Airport	Fragmented frontal (still in the rock matrix)
SMU-72425	SMU	DFW Airport	Fragmented midportion of a frontal bone
SMU unnumbered	SMU	DFW Airport	2 dorsal vertebrae
SMU unnumbered	SMU	DFW Airport	Approximately 30 vertebral remains
SMU-72397	SMU	Lowes Farm	Seven isolated dorsal vertebrae, four of them still articulated
SMU-72419	SMU	Lowes Farm	One isolated dorsal vertebra
SMU-76276	SMU	Lowes Farm	Right dentary with 16 tooth crowns
SMU-72411	SMU	1382	Fragmented frontal
SMU-72422	SMU	1382	Two isolated dorsal vertebrae
SMU-72424	SMU	1382	Two isolated dorsal vertebrae
SMU-72416	SMU	New locality	Isolated humerus
SMU unnumbered	SMU	Taco Bell	Three fragmentary dorsal vertebrae
TMM 40305-1	TMM	Bouldin Creek	Nearly complete left maxilla of <i>C. crassidens</i>
TMM 41935-1	TMM	Arrowhead Drive	Two articulated dorsal vertebrae
TMM 41935-2	TMM	Arrowhead Drive	Three associated dorsal vertebrae
TMM 42562-24	TMM	Abbot Labs	One dorsal vertebra still immersed in the rock matrix
TMM 42562-39	TMM	Abbot Labs	One isolated dorsal vertebra

### 2.2.3. Geological settings and localities

*Coniasaurus* remains are found in Middle Cenomanian through Late Turonian aged sediments in north and central Texas (Figure 2.1). Most of these specimens have been collected with good stratigraphic control and age determination based on biostratigraphy and

geochemical dating methods (e.g. Walaszczyk and Cobban, 2006; Gradstein *et al.*, 2012). Sediments of this age were deposited during the Late Cretaceous high-stand (Haq, 2014), the Cretaceous Thermal Maximum (O'Brien *et al.*, 2017) and the completion of the Western Interior Seaway.

Two units of formational or supraformational status are broadly recognized in central and north Texas (Adkins and Lozo, 1951; Donovan *et al.*, 2015); the Woodbine and the Eagle Ford Shales. In north Texas, transitional facies composed of sandy clay and thin limestones and known as the Tarrant, rests on an angular unconformity on typical shelf-strandplain deposits of the Lewisville member of the Woodbine Formation and underlies typical dark marine shales of the Eagle Ford. The Tarrant has been variably placed at the top of the Woodbine as part of the Lewisville Member (Stephenson, 1953a, b) or as a basal unit of the Eagle Ford (Moreman, 1942; Brown and Pierce, 1962; Norton, 1965; Powell, 1968). Stephenson (1953b) biostratigraphically correlated the top of the Pepper Shale in the Waco area to the top of the Lewisville Member of the Woodbine in North Texas. Both the Pepper Shale and Tarrant mark the earliest occurrences of *Coniasaurus* in North America, so for purpose of this contribution Stephenson (1953b) will be followed and include the Tarrant in the Woodbine but maintain use of Tarrant in recognition of its distinct facies.

Figure 2.2 provides a generalized view of the geology and the stratigraphic position of *Coniasaurus* bearing localities in the North Texas area which are discussed in the following paragraphs.

The Tarrant in the Dallas area is about 5.5 meters thick, and falls within the *Conlinoceras tarrantense* ammonite Zone which is 95.73Ma  $\pm$  .61Ma (Kennedy, 1988; see also Cobban *et al.*, 2006; Slatterly *et al.*, 2015; Jacobs *et al.*, 2005). The Lowes Farm and Egyptian Way localities are in the Tarrant and composed of buff muds and shales with thin limestones (Figure 2.2). Myers (2010) reported a new ornithocheirid pterosaur from the Lowes Farm locality. Fish teeth are common and isolated teeth of ?brachauchenian plesiosaurs and fragmentary turtles elements are found occasionally at both localities, and at the Egyptian Way locality, an un-identified non-*Coniasaurus* squamate parietal was also recovered (Michael Polcyn, personal communication). Both of these localities have produced semi-articulated material. Just below the Tarrant, in typical Lewisville Member sandstones, the pholidosaurid crocodile, *Terminonaris* was reported by Adams *et al.* (2011).

Overlying the Woodbine (Tarrant inclusive), the Eagle Ford in north Texas ranges from ~139 meters in the north part of Dallas County to ~116 meters in the south (fide Kennedy, 1988 and subtracting thickness of Tarrant). The Eagle Ford thins significantly south of Dallas, and is

about 57 meters at Waco and less than 10 meters at Austin (Adkins and Lozo, 1951). In the Dallas area, The Eagle Ford is divided into the Britton (overlying the Tarrant) and Arcadia Park (overlying the Britton) with a prominent thin limestone layer, the Kamp Ranch Limestone, falling 2.5 meters above the base of the Arcadia Park (Kennedy, 1988).

Four distinct depositional sequences, identified in South Texas, were correlated across Texas by Donovan *et al.*, 2015. In their scheme the Britton Formation in the Dallas area is subdivided into a Lower and Upper Britton correlating to the entirety of the Lower Eagle Ford (LEF) and Lower Member of the Upper Eagle Ford (UEF) respectively. The Arcadia Park (Kamp Ranch inclusive) is correlated with the Upper Member of the UEF. At the Mobil Research Borehole in the Dallas area, the bottom 7.6 meters of the Britton falls within the Lower Member of the LEF and is largely bentonite poor, whereas the next ~21 meters fall within the bentonite rich Upper Member of the LEF (Donovan *et al.*, 2015).

The lowest occurrences of *Coniasaurus* in the Britton are those recovered by SMU field parties during the construction of Braniff Airlines Terminal 2W in the early 1970s (now Terminal B) and described along with other material by Bell *et al.* (1982). This locality is very low in the Lower Britton and likely falls in the bentonite poor layers, based on the proportional transect distance to the underlying contact with the Woodbine and overlying contact with the Austin Chalk measured approximately east-west. More recently other *Coniasaurus* material was recovered a bit higher in the section from the bentonite rich zone, also at the Dallas-Fort Worth International Airport locality (South Fork of Hackberry Creek DFW). Disarticulated *Coniasaurus* elements are found with inoceramid prisms, fragmentary inoceramids and other invertebrates, and abraded fish-bone and teeth in cemented shale lenses within a non-cemented grey shale, just below a pair of prominent bentonite beds. Specimens were recovered by acid preparation of these limestone lenses. This locality lies approximately 6 Km northeast of the angular unconformity at the base of Tarrant reported by Adams and Carr (2010). The locality is estimated to be around the top of the lower third of the Eagle Ford, based on the proportional transect distance measurement method used above. The bentonites are currently undated, and ammonites are not known from the locality; however, correlations of Donovan *et al.* (2015) place the Lower Britton bentonite-rich beds in the Dallas area in the Upper Member of the Lower Eagle Ford Fm. which is the lower part of the Upper Cenomanian in age (approximately 94.5-95.5Ma). The South Fork of Hackberry Creek DFW locality also yielded a relatively complete plesiosaur specimen, missing the head. It was erroneously identified as *Polytychodon*, mounted and resided at the Braniff Airlines terminal for many years. Recently this material was

returned to SMU and has been re-prepared and preliminary analysis indicates it is a large leptocleidid and not a pliosaur.

Higher in the section in the section, the Upper Britton (sensu Donovan *et al.*, 2015) falls mainly within the Cenomanian *Sciponoceras gracile* ammonite Zone ~94.4Ma (Joo and Sageman, 2014). The upper part of the *S. gracile* Zone in the Dallas area preserves red weathering fossiliferous concretions (Kennedy, 1988) and the Lewisville Lake Spillway locality is found at this horizon. The locality produces a rich *S. gracile* Zone invertebrate fauna, occasional fish teeth and body fossils, an association of plesiosaur phalanges (Michael Polcyn, personal communication), and the most complete *Coniasaurus* specimen known to date; a gravid female reported in the Chapter 1 of this thesis. The published record from the locality includes the first North American toothed pteranodontoid pterosaur (Myers, 2015) and a study of decapod crustaceans based on several thousand specimens collected at the locality, including a new species (Bishop and Brannen, 1992; Bishop *et al.*, 1992).

The Taco Bell Locality is located stratigraphically above the Lewisville Lake Spillway locality but below Kamp Ranch Limestone. The fossils are preserved as isolated elements in buff colored shale with thin carbonates and no concretions. Assuming an eastward dip of 60ft per mile as in Dallas County (Roberts, 1953) and given the localities close proximity to the Kamp Ranch contact (0.85 miles to the east) this would put this locality at about 15-16 meters below the Kamp Ranch. Thus, it is likely well within the *S. gracile* Zone, which extends to an unconformity lying below the *Pseudaspidoceras flexuosum* Zone fauna that falls 2.5 meters below the Kamp Ranch Limestone according to Kennedy (1988). The only other fauna at the locality are numerous isolated fish teeth.

The remainder of the *Coniasaurus* specimens from the Dallas area described here come from the Arcadia Park which falls in the Upper Member of the Upper Eagle Ford Fm. of Donovan *et al.* (2015). The Eagle Ford Drive #2 locality (The 1382 locality) temporarily exposed large areas of Kamp Ranch and overlying Arcadia Park during housing construction. *Coniasaurus* fossils are found as isolated elements from within and immediately above the Kamp Ranch but no *Coniasaurus* fossils were recovered yet from below it. *Collignonoceras woollgari regulare* is found in abundance in the Kamp Ranch Limestone. This lowest Middle Turonian ammonite Zone is between about 92.1Ma and 92.9Ma in age (Joo and Sageman, 2014). It's not clear how far above the Kamp Ranch *C. woollgari* extends; however, Kennedy (1988) reports the *Prionocyclus hyatti* Zone, *Hoplitoides sandovalensis* Subzone fauna about 10 meters above the Kamp Ranch and the *Prionocyclus hyatti* Zone, *Coilopoceras springeri* Subzone about 19 meters above the Kamp Ranch. *P. hyatti* is present high in the section with

*Prionocyclus cf. mocombi* noted about one meter below the contact with the overlying unconformity.

The so-called "New Locality" produced an isolated humerus (SMU-72416). The locality is about 1.2 Km east of Kamp Ranch outcrops and assuming an eastward dip of 60ft per mile as in Dallas County (Roberts, 1953), the locality is about 14 meters above the Kamp Ranch and probably falls in the the *Prionocyclus hyatti* Zone, *Coilopoceras springeri* Subzone.

The top of the Eagle Ford and the Eagle Ford-Austin Chalk transition in the north Texas area is complicated and variable over short distances. In the Dallas area Eagle Ford-Austin Chalk transition is unconformable and marked by a phosphatic layer, grading into about 2.5 meters of "calcarinitic chalk, blue / grey, slightly marly" with "grains of black phosphate throughout (Hancock and Walaszczyk, 2004). North of Dallas this phosphatic zone is gone and the Austin Chalk rests conformably on the Eagle Ford at Choctaw Creek (Smith 1981), preserving the Upper Turonian at least in that area. Though not described here, isolated vertebrae and teeth of *Coniasaurus* have been collected in the Prosper Texas area, west of Smith's (1981) Choctaw Creek locality. Given the thickness of the section in this area and the ages reported by Smith (1981) these may be the Upper Turonian in age and thus the youngest specimens known in north Texas.

Figure 2.3 provides a generalized view of the geology and the stratigraphic position of *Coniasaurus* bearing localities in the central Texas area, discussed in the following paragraphs. Adkins and Lozo (1951) and Kennedy and Cobban (1990) are followed for ammonite and inoceramid biostratigraphy and Joo and Sageman (2014) for refined dating of ammonite Zones. *Coniasaurus* specimens in the collection of the Vertebrate Paleontology Laboratory (VPL) at the University of Texas at Austin, were found in a number of localities in central Texas. Two isolated vertebrae (TMM 42562-24 and TMM 42562-39) from the Abbot Labs locality (TMM locality 42562), two articulated dorsal vertebrae (TMM 41935-1) and three associated dorsal vertebrae (TMM 41935-2) from the Arrowhead Drive locality (TMM locality 41935), and a nearly complete left maxilla (TMM 40305-1) from Bouldin Creek locality (TMM locality 40305) are described herein.

The Arrowhead Drive specimens are from the Bluebonnet member of the Lake Waco Formation. Adkins and Lozo (1951) report the bulk of the Bluebonnet member belongs to the Middle Cenomanian *Acanthoceras amphibolum* Zone or about 95.7Ma (Joo and Sageman, 2014).

The Abbott Labs locality record in the files of the VPL at the University of Texas at Austin does not give any geological context but of the fishes listed in the associated fauna, the

co-occurrence of *Ptychodus anonymus* (Cenomanian-Turonian) *Ptychodus decurrens* (Albian-Cenomanian) and *Cretoxyrhina mantelli* (Cenomanian-Coniacian), suggest an undifferentiated Cenomanian age. The locality probably lies within the Pepper or Lake Waco Formations.

The Bouldin Creek locality record provides no geological context or associated fauna and thus the specimen may come from any of the units in Figure 2.3 falling between the Buda and the Austin Chalk.

### **2.3. Results: description of specimens**

#### **Systematic Paleontology**

#### **Order Squamata Opper, 1811**

#### **Suborder Mosasauria Marsh, 1880**

#### **Family Dolichosauridae Gervais, 1852**

#### **Genus *Coniasaurus* Owen, 1850**

#### **Type species *Coniasaurus crassidens* Owen, 1850**

**Generic emended diagnosis:** small and very elongated plesio-pedal marine squamate, bearing a characteristic heterodont dentition. Dentition composed by anteriormost teeth conical, pointed and recumbent and posteriormost teeth swollen. Carinae anterodorsally oriented in the more posterior teeth. Ornamentation of the crown composed mainly by fine and faint longitudinal striations. Subtle constriction present between tooth base and crown. Dentition composed by 19-22 teeth (4 premaxillary and 15-18 maxillary). Very elongated neck, with up to 19 cervicals. Non-pachyostotic dorsal vertebrae with a large neural spine running across the entire neural arch and ventrally nearly straight. Dorsal vertebrae centrum slightly constricted dorsoventrally and presenting a subtle constriction between the centrum and the condyle, with an almost horizontal pre- and postzygapophyseal articulation. More than 30 dorsal vertebrae. Humerus and femur conspicuously twisted, rotated near its proximal half, and presenting a medial tubercle. Deltopectoral crest well developed (nearly 50% of humerus size). Iliac blade strongly oriented vertically.

**Comments:** *Coniasaurus* and *Dolichosaurus*, the two traditional members of the family Dolichosauridae, are closely related taxa whose diagnoses were based respectively on cranial and postcranial remains (Caldwell, 1999; Caldwell and Cooper, 1999; Caldwell, 2000), but the lack of either more complete postcranial remains for *Coniasaurus* and more complete cranial remains for *Dolichosaurus* prevented a proper comparison between the taxa up to the present. Both phylogenetic (Chapter 1) and compared anatomy results support the hypothesis of

*Dolichosaurus* being a junior synonym of *Coniasaurus* (see item 2.4.1. for a more detailed discussion). The new composition of the family Dolichosauridae proposed here is: *Coniasaurus crassidens* Owen, 1850; *Coniasaurus longicollis* (Owen, 1850); *Coniasaurus gracilodens* Caldwell, 1999; and *Coniasaurus* sp. nov. (Chapter 1). Because the utility of a monogeneric family is questionable, future works could also propose a more inclusive Dolichosauridae assemblage, as it was done in the description of the dolichosaur *Primitivus* (Paparella *et al.*, 2018).

### 2.3.1. Egyptian Way specimens

Egyptian way locality has yielded several coniasaur remains, including three cranial, 70 axial and one appendicular remains (Table 1). Elements from this locality are usually preserved in a light beige-yellow color. SMU-72396 is the most complete, comprising a long axial series, one cranial (prefrontal) and one appendicular (ilium) remains. This specimen appears to correspond to a subadult, as the intercentrae is not fused to the cervical hypapophyses and this condition appears to be related to earlier ontogenetic stages (Augusta *et al.*, 2016). Since SMU-72396 is the most complete and certainly comprises the same individual, it will be the only one described here in detail.

SMU-72396 is a nicely preserved specimen, with a long axial series preserved. Dorsal vertebrae present in the specimen has the diagnostic features that match with a *Coniasaurus* identification: 1) Non-pachyostotic dorsal vertebrae with a large neural spine running across the entire neural arch and ventrally nearly straight; 2) Dorsal vertebrae centrum slightly constricted dorsoventrally and presenting a subtle constriction between the centrum and the condyle, with an almost horizontal pre- and postzygapophyseal articulation. Also, in dorsal series it is not complete and the specimen likely had more than 30 dorsals, which reinforces a *Coniasaurus* identification. The presence of a hypapophyses with unfused peduncles suggest that this is a subadult specimen (Augusta *et al.*, 2016), an interpretation supported also by the intense vascularization observable in some vertebral elements. The occurrence of pre- and postzygapophyseal articulations angled in the cervical vertebrae and nearly horizontal in the dorsal elements and an interprezygapophyseal lamina only slightly notched suggest affinities of this specimen with *Coniasaurus* sp. nov. On the other hand, differences in the sacral and pygal vertebrae argues against this assessment. The lack of comparable cranial remains in this specimen also difficult its proper specific identification. A conservative approach will be taken here, so this specimen will not be assigned to any coniasaur species.

*Cervical vertebrae.* Two cervical vertebrae are preserved in this specimen (Figure 2.4). The small size of the hypapophyses and the large size of the synapophyses suggest that they were more posterior elements. One of them, the more posterior one, is exquisitely preserved and preserves a nearly intact neural arch, lacking only the region nearby the right zygosphenic projection. This is the better-preserved cervical vertebra of all known coniasaur specimens, since neither DMNH-1601 possess a complete cervical element. In lateral view it is possible to note that the neural spine forms an ascending process, rising posterodorsally at a nearly 30° angle. This condition is very different from that of dorsal vertebrae, in which the neural spine forms a rectangular projection that rises dorsally from the entire extension of the neural arch. Zygosphenes are well developed and faces zygantra ventrolaterally. The intercentrum is not fused to the hypapophyses, and this is an indicative of an early developmental stage (Augusta *et al.*, 2016). Pre- and postzygapophyseal articulation are angled, but in a lesser degree than that of DMNH-1601. This may be related to the relative position of each cervical vertebrae along the axial series. In other aspects, such as the constriction of the centrum and the condyle, the development of vertebral laminae and the morphology of the synapophyses, these elements here are identical to those of *Coniasaurus* sp. nov.

*Dorsal vertebrae.* 25 dorsal vertebrae are preserved in SMU-72396 (Figure 2.5), the longest axial series from an unequivocal single coniasaur individual after the holotype of *Coniasaurus* sp. nov. The size of the largest dorsal elements here are considerably smaller than the larger DMNH-1601 elements, matching what would be expected for a subadult individual. Some of the dorsal vertebrae preserved in this specimen are broken in the middle of the neural spine, a condition that resemble the "dorsal notch" of the neural arch proposed by Caldwell and Cooper as a *Coniasaurus* distinguish feature. However, a closer look at this clearly reveal that this "notch" was produced by a taphonomical breakage, not a biological process (see the discussion, item 2.4.1., for more details on this topic). Two main differences between the dorsal vertebrae of *Coniasaurus* sp. nov. and SMU-72396 are noticeable, both regarding the absence of a sulcus. Firstly, in *Coniasaurus* sp. nov. the postzygoprezygapophyseal lamina (PPRL) and the posterior centrosynapophyseal lamina (PCYL) are well developed, forming a conspicuous sulcus in lateral view of the vertebrae, while in SMU-72396 this sulcus is not apparent. Secondly, the ventral sulcus observable in more posterior elements in *Coniasaurus* sp. nov. is also not visible here. However, these differences may be ontogenetic related, since SMU-72396 is probably a subadult. No signal of pachyostosis is observable in any of the dorsal vertebrae.

*Sacral vertebrae and sacral ribs.* Two sacral vertebrae and two fragmentary sacral ribs were recovered in association with the other elements of SMU-72396 (Figure 2.6). These

elements are considerably different from those of *Coniasaurus* sp. nov., but as this individual probably represents a subadult it is unclear now whether these differences are truly anatomical distinctions or are ontogenetic related features. The sacral vertebrae in SMU-72396 are closely associated but not fused as in DMNH-1601. Ventrally, the contact between the condyle and the cotyle appears to be strongly immobile, while the pre- and postzygapophyseal articulation were angled at nearly 45°, also contributing to prevent movement. In *Coniasaurus* sp. nov., the first sacral is broader and slightly shorter, while in SMU-72396 the first sacral is only slightly broader laterally but is subequal in length with the second element. Zygosphenes were present in both elements, facing the zygantrum ventrolaterally. Neural spines are broken but do appear to have being very tall as in the dorsal vertebrae. Sacral ribs are represented by two fragments that match exactly the size for the rib attachment on the sacral vertebrae. They are nearly twice the width of trunk ribs, being proximally very flattened elements. Distally, the sacral ribs probably enlarged dorsoventrally to contact the ilium.

*Pygal vertebrae.* SMU-72396 preserves one vertebral element that is interpreted here as a pygal vertebra (Figure 2.7). It has a shortened centrum (relatively shorter and wider than dorsal elements) and possess two extensive lateral projections that are possibly broken transverse processes. Ventrally, the centrum is concave, as in *Coniasaurus* sp. nov. Prezygapophyses are projecting dorsolaterally at nearly 30°, revealing an angled articulation that was also present in *Coniasaurus* sp. nov. However, some differences are also noticeable when comparing this element with the one preserved in the *Coniasaurus* sp. nov. holotype: 1) The centrum is more dorsoventrally compressed in SMU-72396 and more concave ventrally in DMNH-1601; 2) Transverse processes are more robust and projects more ventrally in DMNH-1601. An intense vascularization is noticeable through the entire neural arch of the bone, supporting the interpretation of the individual as at an immature stage of development.

*Caudal vertebrae.* Six caudal vertebrae are preserved in SMU-72396 (Figure 2.8). They are severally damaged; therefore, it is hard to accurately classify their position along the tail. Haemapophyses and transverse processes are present in all five elements. One of them, the largest and probably the anteriormost one, preserves most of the neural arch, a condition that it is also not found among DMNH-1601 caudal vertebrae. The neural spine projects mainly posterodorsally, overlapping the proceeding neural arch. Pre- and postzygapophyseal articulation is deeply inclined, nearly 45°. This may have diminished the individual vertebral mobility, so the anterior portion of the tail could have acted as a rigid propulsion organ. A zygosphene lamina can be seen in this element and it is relatively well developed, so at least in the anteriormost caudal vertebrae *Coniasaurus* possessed well developed zygosphene-zygantra

articulations. Morphology of the caudal centrum appears to be identical to that of *Coniasaurus* sp. nov.

*Ribs.* 25 rib fragments were collected associated with this specimen. In general terms, their morphology does not differ from the one present in DMNH-1601, by being sub rectangular in cross section, flattened, bearing strong costals grooves and an oval articular head.

*Ilium.* A partially preserved ilium was found in association with vertebral remains of the specimen SMU-72396 and is the only girdle element preserved in any of the coniasaur specimens described here. Ilium is broken at the beginning of the iliac blade but preserves its entire articulation surface for both the pubis and ischium (Figure 2.9). Even lacking most of the iliac blade, it is possible to note that this projection would not be strongly bended horizontally as in terrestrial varanoids (Rieppel, 1980), but instead would be slightly curved and more vertically oriented than in other dolichosaurs, approaching the condition found in basal mosasauroids (except *Kaganaias hakusanensis* which possessed a horizontal iliac blade; Evans *et al.*, 2006). This distinct blade orientation is probably related to the aquatic lifestyle of coniasaurs, as other marine reptiles (i.e. mosasauroids, nothosaurs, plesiosaurs and ichthyosaurs) also possessed more vertically/diagonally oriented iliac blades. In addition, modifications at the pelvic girdle morphology in aquatic reptiles have also been suggested to be related to viviparity (Cheng *et al.*, 2004). The acetabular region of the ilium is very reduced compared to other mosasaurians, being roughly triangular in shape, and this small size is in accordance with the small and laterally compressed femur's head. Dorsally to the acetabulum there is no signal of a *spina preacetabuli*; in modern varanoids, both *Lanthanotus* and *Heloderma* lack this structure, but *Varanus* possess a very developed one (Rieppel, 1980). Among dolichosaurs, *Adriosaurus skrbinsensis* have a small anterodorsal process of the ilium, just above the acetabular fossa (Caldwell and Palci, 2010), that could be homologous to the *spina preacetabuli*. The medial wall of the ilium presents a deep groove (Figure 2.9), probably for muscle attachment.

### **2.3.2. DFW Airport specimens**

In the DFW airport locality a total of 13 cranial and 32 axial coniasaur remains were recovered (Table 1). Fossil materials from this location are generally slightly more fragmentary than in other previous localities, thus preventing the precise identification of many vertebral remains. As the postcranial remains from the DFW airport locality are in general badly preserved and do not add new anatomical information, only the cranial remains found at this locality will be described.

*Jaw sections.* Several jaw sections were recovered from the DFW locality. As the elements were isolated and sometimes were very fragmentary, they were identified either as maxillae or dentaries fragments on the presence of identifiable medial sulcus or Meckel's groove portions. Longer preserved bones were more easily identified by the overall shape, even when they were still immersed in the rock matrix. Remains that could not be addressed to a maxilla nor a dentary are cited on Table 1 but will not be described here.

*Maxilla and maxillary dentition.* Five undoubtedly maxillary remains were found at this locality. All of them present the unequivocal *Coniasaurus* teeth morphology: heterodont dentition, carinae anterodorsally oriented and anteriormost teeth being more conical and elongate against posteriormost being more bulbous and robust. SMU-72384 comprises a small fragment of a left maxilla mid-portion with three preserved tooth crowns (Figure 2.10). The two anteriormost preserved teeth are broken near their tips, while the posteriormost is more complete. The enamel layer is missing on the labial surface of the crowns, widely exposing the dentin. Interesting, no labial sulcus is visible in this specimen, which suggests that this sulcus is built entirely by enamel wrinkles, without any dentin participation. On the other hand, the lingual surface of the posteriormost tooth is better preserved and show no signal of a lingual shelf, thus indicating that this specimen regards *Coniasaurus* sp. nov. and not *C. crassidens*. A relatively large sulcus is present in the dorsal surface of the bone. This sulcus is believed to have accommodated both the palatine artery and vein, which respectively supplies and drains the lateral aspect of the palate, medial to the tooth row (Porter and Witmer, 2015). Within this sulcus, in medial view, there is a foramen of unknown relationships, since it appears too small to have accommodated a branch of the maxillary artery. Anteriorly, the path of the maxillary artery bifurcates into a more dorsal and a more ventral passages. In dorsal view it is possible to notice that the lateral wall of the maxilla bends anteromedially to cover this sulcus and maybe contact another bone (septomaxilla?). Two foramina are preserved in lateral view of the maxilla, being the lateral exits of the trigeminal nerve's maxillary ramus.

SMU-72387 is a nearly complete left maxilla from a juvenile/subadult individual, bearing nine tooth crowns preserved in their original position. This element is still immersed in the rock matrix, and because of that only its lateral side is visible. The lateral wall of the maxilla is relatively low, lacking a well-developed ascending process as in *C. gracilodens*. Moreover, this maxilla also differs from that of *C. crassidens* holotype by being relatively shorter, bearing nearly 15 alveoli, the same number as in *C. gracilodens*. On the other hand, the teeth morphology present in this specimen is clearly different from *C. gracilodens* and possess the typical well developed heterodonty of *C. crassidens* and *Coniasaurus* sp. nov. As this maxilla

possess these "intermediate" characters, it is reasonable to suppose that it belonged to *Coniasaurus* sp. nov. and that the extreme elongation of the maxilla, with a very low ascending process and room for 18 alveoli, is an autapomorphy for *C. crassidens*. The narial margin of SMU-72387 rises at a low angle, gradually tapering anteriorly. The premaxillary process, besides ventrally broken, appears to have been toothless and served as an articular surface for the premaxilla. As the bone is lacking its posterior end, it is not possible to evaluate the shape and extension of the maxilla suborbital ramus. Laterally four foramina for the maxillary branch of the fifth nerve are preserved just above the teeth level.

The last three maxillary elements are more fragmentary. SMU-72390 comprises, besides several unidentified jaw sections, a fragmentary left maxilla from a juvenile. It has four preserved tooth crowns in position and one preserved foramen in the lateral surface of the bone just above the anteriormost tooth. As SMU-72384, there is an anterodorsally bending over the medial sulcus. Just posterior to this bending of the maxillary lateral wall there is a smaller sulcus, followed by a foramen in its anterior end, which may have carried some vascular branch of an artery or vein. Interesting, within this smaller sulcus there is a very tiny foramen facing medially in a relative position very similar to that foramen of unknown relationships present in SMU-72384. SMU-72391 also comprises several unidentified jaw sections and a fragmentary left maxilla, although here the element is relatively bigger and possibly regards a subadult/young adult animal. Two teeth are completely preserved in natural position and two more preserves only their broken bases (Figure 2.10). A large and deep medial sulcus runs dorsally. Laterally, two foramina for the V nerve are present. The internal path for the maxillary artery bifurcates anteriorly, changing from a wider opening posteriorly to a double passage anteriorly. SMU-72393 is a small and fragmentary remain of a left maxilla. It has three teeth preserved in medial view and two others empty alveoli visible. A large medial sulcus is present dorsally. Judging by the size of the dental elements this bone probably belonged to a subadult individual, since the teeth are noticeable larger than SMU-72387 and smaller than SMU-72384. The lateral side of the bone is not visible since it is covered by paraffin for protection of the element.

*Frontal.* Three fragmentary frontal bones are preserved among the DFW specimens. SMU-72389 is the most complete, comprising nearly 50% of the whole bone (Figure 2.11). The element is broken both anteriorly and posterolaterally, lacking well preserved parietal processes. Ventrally, however, the element is well preserved, and the subolfactory processes are clearly visible with no signal of taphonomical distortion. As in *C. gracilodens* and *Coniasaurus* sp. nov., the subolfactory processes do not meet ventrally at the frontal midline.

Besides this bone being nearly the same size and overall presenting a similar morphology as that of *C. gracilodens* holotype, the subolfactory processes are quite distinct: in the DFW specimen they are much narrower and show no signal of a ventral groove to receive the solium suprasedale, only ventrolaterally scars. This may indicate that SMU-72389 was not a *C. gracilodens*. The only facet for articulation observable in this specimen is the posterolateral facet for the postorbitofrontal, visible especially in the left side. SMU-72395 is a posterior fragment of a frontal still immersed in the rock matrix with overall morphology very similar to that of SMU-72389. However, the posterolateral and the posteriormost regions are better preserved here, revealing a nearly straight frontoparietal suture. In addition, long, tapering anteriorly, facets for the frontal process of the postorbitofrontal are present in each side of the bone, from the frontoparietal suture to the level where the subolfactory processes start to run parallel. SMU-72425 is a juvenile fragmentary midportion of a frontal. Besides being a tiny bone in general proportions, the grooves for the solium suprasedale in the posteroventral portions of the subolfactory processes are conspicuous, a typical condition found in immature coniasaur specimens (Augusta *et al.*, 2016). Because of that, the subolfactory processes are proportionally larger lateromedially. No articular facet is visible, since most of the preserved bone comprises the middle portion of the frontal.

*Dentary and dentary dentition.* Four fragmentary dentaries were recovered from the DFW airport locality. The presence of a Meckel's groove and a straight ventral surface were the main characters used to distinct dentary fragments from other isolate jaw sections. SMU-72385 is a left mid-to-posterior fragmented dentary with eight preserved teeth and a broken base of a ninth tooth (Figure 2.12). This specimen probably belonged to a juvenile/subadult individual due to its small proportions, but it does present the typical *C. crassidens* tooth morphology: enlarged posterior teeth, with well-developed labial sulcus, crenulated and anterodorsally oriented carinae and a lingual shelf present in some teeth. This indicate that at least two species of *Coniasaurus* were present in the Western Interior Seaway during the early Late Cretaceous: *Coniasaurus* sp. nov. and *C. crassidens*. Most of the medial surface of the bone is broken, including the dental shelf, revealing the narrow Meckel's groove running just above the teeth. The ventral surface is completely straight, contrary to most extant lizards in which it is curved, and the lateral surface bear just one small foramen at the level of the third preserved tooth. SMU-72386 represents a fragmentary right dentary (Figure 2.12) and presents the exact same proportions and teeth morphology of SMU-72385, so both specimens may have belonged to the same individual. It has eight teeth preserved in natural position (two of them with broken tips) and four additional empty alveoli. Laterally there are two preserved foramina above the

first and the second tooth crowns. Meckel's groove is exposed due to bone breakage and runs ventromedially along the entire element.

SMU-72388 comprises a nearly complete but poorly preserved right dentary, lacking only its anteriormost portion. The element is immersed into the rock matrix but is possible to notice the presence of 15 crowns and room for more four, which fits with a total number of 19 dentary teeth expected for *Coniasaurus* sp. nov. since only the anterior tip of the bone is missing. Teeth also lacks the lingual shelf on the crowns, an additional support for the relation of this specimen with *Coniasaurus* sp. nov. Meckel's groove is bended in medial view, running ventrally on the middle of the bone, anterodorsally on its anterior end and posterodorsally on the posterior end, the same pattern found in *C. crassidens* (Caldwell and Cooper, 1999). The lateral surface is not exposed on the other side of the rock since the material is too fragile. SMU-72392 is a left dentary with 10 teeth, the posteriormost being broken at the middle, and room for additional two. The posterodorsal inclination of the Meckel's groove indicate that the bone represents the mid-to-posterior part of the original dentary. Lingual shelves are visible in some teeth, thus indicating a *C. crassidens* identification. As in other DFW airport dentaries, the dental shelf is severally damaged.

*Surangular.* In all the specimens described here, the surangular is only represented by SMU-72382 (Figure 2.13). It corresponds to the left element and comprises the anterior portion of the bone, lacking its posteriormost area. Overall, the bone is sub-rectangular in shape, with a dorsal crest in its mid-portion near the sutural articulation with the coronoid. A conspicuous canal is visible in medial view, corresponding to Oelrich's (1956) mandibular foramen. This canal is believed to have conducted the mandibular ramus of the trigeminal nerve, the *chorda tympani* division of the facial nerve's hyomandibular ramus, the mandibular artery and the tracheal vein, as well as bearing part of the Meckel's cartilage (Bahl, 1937; Oelrich, 1956; Russell, 1967; Porter and Witmer, 2015). Just dorsal to the mandibular foramen, in anterior view, there is another foramen that probably represents the internal path for the anterior surangular foramen. In lateral view, a strong ridge for attachment of the adductor musculature of the mandible is not present as it is in more derived mosasauroids (i.e. *Russellosaurus*; Polcyn and Bell, 2005). Unfortunately, surangular participation on glenoid facet and the contact with articular, prearticular and angular cannot be evaluated due to the lack of the posteriormost portion of the bone.

### 2.3.3. Lowes Farm specimens

Three coniasaur specimens were recovered from the Lowes Farm locality, including one dentary and eight dorsal vertebrae (Table 1). These remains are preserved in a white / light grey color for the vertebrae and in a light orange color for the dentary. Below is the description of the dentary bone.

*Dentary and dentary dentition.* A nearly complete dentary, SMU-76276, lacking only its more posterior and ventral portions, was found at the Lowes Farm locality (Figure 2.14). This specimen is still immersed in the rock matrix and thus only the lateral surface of the bone is exposed. Sixteen teeth are preserved in natural position, but there appears to be room for at least eighteen. Teeth morphology is quite remarkable in this specimen: heterodonty is lesser developed than in other coniasaur remains found in North America. Antermost teeth are more conical and elongated, and posteriormost are more swollen, but the differentiation is subtler. In the mesial surface of the posteriormost crowns there is a carina anterodorsally oriented, but at a lower angle than in *C. crassidens* or *Coniasaurus* sp. nov. Longitudinal striations run across the entire crown surface. These aspects suggest affinities of this specimen with the taxon *Coniasaurus gracilodens*, described by Caldwell (1999) in the basis of a single specimen. However, the holotype of *C. gracilodens* lacks the dentary, thus preventing a proper comparison between the specimens. Because of that, it is not possible to assign SMU-76276 to *C. gracilodens*, only to *Coniasaurus* sp. As the lateral surface of the bone is severely eroded, the exact number of foramina cannot be evaluated. Ventrally, the bone is straight and only bends dorsally at its very anterior end.

### 2.3.4. 1382 locality specimens

In the 1382 locality were recovered only one cranial and four axial coniasaur remains (Table 1). Fossil materials from this location present higher degrees of damage, probably because of taphonomical forces during deposition and/or fossilization. Coniasaur remains were found in association with another marine squamate commonly found in Texas: *Dallasaurus turneri* (Bell and Polcyn, 2005).

### 2.3.5. New Locality specimen

The new locality has yielded a single coniasaur bone: SMU-72416, an isolated right humerus (Figure 2.15). It is well preserved, although eroded near the epiphyses, and present all the diagnostic characters expected for a coniasaur humerus: it is small, presenting a conspicuous twisted shaft and possess a well-developed deltopectoral crest, occupying nearly 50% of the whole humeral length. It is also quite distinctive from the other marine squamate often found in this region: *Dallasaurus turneri* (Bell and Polcyn, 2005). This element is slightly smaller than the DMNH-1601 humerus: 13,7mm against 17,2mm from the holotype of *Coniasaurus* sp. nov., although as the epiphyses are broken the element may have been somewhat bigger (but probably no more than 15mm at all). The proximal head of SMU-72416, on the other hand, is wider and more robust lateromedially than that of *Coniasaurus* sp. nov. As the humeri of *Coniasaurus* sp. nov. and *D. longicollis* are striking similar, and the element is unknown in *C. crassidens* and *C. gracilodens*, it is not possible to identify this element at the species level. Both entepicondylar and ectepicondylar foramen are absent in this specimen too, as in other dolichosaurs.

### 2.3.6. Texas Memorial Museum specimens

In addition to the coniasaur specimens from the SMU and the Perot Museum of Natural History and Sciences paleontological collections described in this paper, coniasaur remains present at the Texas Memorial Museum (TMM) collection (summarized in Table 1) will also be described. One of the specimens, TMM 40305-1, is especially relevant because it represents an unequivocal *Coniasaurus crassidens* maxilla. Therefore, it confirms the presence of at least two coniasaur taxa in the Western Interior Seaway during the early Late Cretaceous.

*Maxilla.* TMM 40305-1 comprises a nearly complete maxilla that is quite identical to that of *C. crassidens* holotype (Figure 2.16). The bone is still embedded in the rock matrix, but as it is partially prepared both the lateral and part of the medial surfaces are exposed. The anteriormost end of the bone is missing. The maxilla is a very elongated bone, with a very low ascending process. Seven foramina for the maxillary branch of the V nerve pierce the lateral wall of the maxilla, and an additional one could have been present in the anteriormost end of the element, matching the same number described for *C. crassidens* (7-8; Caldwell and Cooper, 1999; pg. 434). Two articular facets are visible in the posterior end of the bone: one running laterally and one dorsolaterally. The first is only partially exposed and has an elongated, tapering anteriorly facet to receive the suborbital process of the jugal. The second appears to be entirely exposed, being an elongated facet that tappers both anterodorsally and posteroventrally

to receive a ventral process of the lacrimal. Articulations with other bones are not observable because the bone is not entirely prepared. 13 tooth crowns are preserved in locus, but only in the preserved portion there are room for at least three more, totalizing 16 in the preserved portion and maybe 18 for the whole element. 18 teeth are also the same number described for *C. crassidens* (Caldwell and Cooper, 1999; pg. 436). Unfortunately, tooth crowns appear to be really worn and, as most of them they are medially covered by the rock matrix, their morphology cannot be completely evaluated. In general terms, anteriormost teeth are more conical and elongated, while posteriormost are swollen, as in all coniasaurs. The presence and morphology of others dentition features, such as the carinae and the lingual shelves, cannot be confirmed or properly described.

### **2.3.7. Redescription of Bell *et al.* (1982) coniasaur cranial remains**

In 1982, Bell and colleagues reported the first occurrence of *Coniasaurus* out of Europe. Besides being a landmark work, the description and illustration of the referred specimens were more superficial. As one of the goals of the present study is to summarize the occurrence of all coniasaur specimens from Texas, it is worthy to redescribe cranial remains originally described in that contribution, including new illustrations and anatomical information. A list of that specimens is provided by Table 1.

*Maxilla.* Four maxillary remains were reported by Bell *et al.* (1982). They all are representative of right maxillae. SMU-69020 includes two maxillary fragments that possess very distinct teeth sizes, so they cannot be interpreted as coming from the same individual (Figure 2.17 A-D). Both SMU-69021 (Figure 2.17 E and F) and SMU-69023 (Figure 2.17 G and H) include a middle maxillary fragment with five teeth preserved in natural position. These elements do not differ in any morphological feature from that maxillae already described here by possessing large medial sulcus, a path for the maxillary artery that bifurcates anteriorly and a projection of the bone that bends anterodorsally to partially cover the medial sulcus.

*Pterygoid.* Bell *et al.* (1982) reported a coniasaur pterygoid recovered from the DFW locality. Although *Coniasaurus* is by far the most common squamate found at that locality, it is important to be careful before assign an isolated pterygoid to the genus. The lack of the pterygoid among all coniasaur holotypes and referred specimens prevents any morphological comparison. However, as this material was originally described by Bell *et al.* (1982), was found in the same locality where many coniasaur bones were recovered and possess an overall morphology that is consistent to what would be expected for a coniasaur, it will be redescribed

here. Caldwell (1999) reported the occurrence of pterygoid fragments for *C. gracilodens*, but those are too fragmentary for a proper morphological comparison. Only the discovery of more complete specimens in the future will either confirm or reject the assignment of this pterygoid to *Coniasaurus*.

SMU-69028 comprises a nearly complete left pterygoid (Figure 2.18). Five teeth are preserved in natural position within a relative short row, and fragments of a sixth are also preserved anteriorly. Among living anguimorphs, the pterygoid is toothed in some anguids, *Shinisaurus*, *Heloderma* and *Lanthanothus*, and toothless in other anguids, *Xenosaurus* and *Varanus* (Evans, 2008). Pterygoid is also toothed in all the mosasaurian grades: dolichosaurs (e.g. *Coniasaurus gracilodens*; Caldwell, 1999), basal mosasauroids (e.g. *Opetiosaurus bucchichi*, Dutchak and Caldwell, 2009) and mosasaurids (Russell, 1967). Pterygoid dentition is homodont, with the crows being relatively swollen lateromedially similarly to *Coniasaurus* most posterior marginal teeth. Tooth row extends posteriorly up to the midpoint of the ectopterygoid process, while in some mosasaurs it goes further posteriorly (Russell, 1967). Anteriorly, the palatine process of the pterygoid is broken, lacking its anteriormost end, but the preserved portion shows that this process was relatively large lateromedially, as in varanoids (Evans, 2008) and contrary to the narrower process found in *Shinisaurus* (Conrad, 2004). Two long and narrow facets can be seen both dorsally and ventrally in this process and served as a clasping articulation to receive the palatine. Laterally to the tooth row a short and broad ectopterygoid process projects in a right angle, contrary to modern anguimorphs which have ectopterygoid processes projecting anterolaterally (Evans, 2008) but similar to the condition found in most mosasaurs (Russell, 1967). The angle and relative position of the ectopterygoid process suggest that the ectopterygoid bone was much more posteriorly placed than in modern anguimorphs, matching the condition found in *Judeasaurus* (Haber and Polcyn, 2005). The dorsolateral end of the ectopterygoid process bends ventromedially to touch the ventral part of the bone, similarly to what happens in *Clidastes* (Russell, 1967). There is a sulcus in the dorsal surface of this process that probably served as an articular facet for the ectopterygoid. Unfortunately, the lateroventral region of the process is damaged and thus it is not possible to confirm if the ectopterygoid clasped or not the pterygoid. Dorsally, crests of the palatine and the ectopterygoid processes converges medially and, between these, a foramen pierces the bone. A similar foramen is present in some species of mosasaurs but absent in others (see Figure 22 of Russell, 1967). The quadrate ramus of the pterygoid is a very elongated process that runs posterolaterally to contact the quadrate bone. It is a thin and lateromedially compressed

projection that resembles more the morphology found in *Varanus* and *Heloderma* than the "feather shape" of mosasaurs (Russell, 1967).

*Dentary*. Six dentary fragments were reported by Bell *et al.* (1982), including five remains of left dentaries and one that cannot be undoubtedly assigned as either left or right element. SMU-69019 is the most complete of those, bearing a nicely preserved anterior portion of the dentary (Figure 2.19 A and B). Eight teeth and two additional alveoli are preserved in natural position, although some of them are still covered by rock matrix. A lingual shelf is visible on posteriormost crowns, with matches for *C. crassidens* affinities. Interesting, the anteriormost end of the bone is preserved, revealing a complete absence of a bony mandibular symphysis. In coniasaurs, the mandibular rami were only connected by intramandibular ligaments, the same condition found in more derived mosasaurs (Russell, 1967). Meckel's groove is only barely exposed medioventrally, bending anterodorsally near the anterior end of the dentary. It is a very thin path that ends in a circular opening. Two foramina are visible, only in the anteriormost portion of the dentary lateral surface. SMU-69020 (four elements, Figure 2.19 C and D) and SMU-69027 (one element, Figure 2.19 E and F) comprises fragments in variable degrees of preservation that do not provide any new information regarding *Coniasaurus* dentary morphology.

## 2.4. Discussion

### 2.4.1. A revision of the genus *Coniasaurus*

In their redescription of *Coniasaurus crassidens*, Caldwell and Cooper (1999) erected 19 characters for the revised diagnosis of the genus *Coniasaurus*. Caldwell (1999) described a new species of *Coniasaurus* (*C. gracilodens*) and updated the emended generic diagnosis of the previous work by including 11 revised diagnostic characters to encompass both species within the same taxonomic unit. However, some of that characters are actually simplesiomorphies, shared with either other dolichosaurs or living varanoids, or simply does not apply for the new composition of the genus *Coniasaurus* presented here. Each of them will be discussed below. For an emended diagnosis of other *Coniasaurus* species, see item 2.3.

**1) Snout elongate anterior to orbits, similar to aigialosaurs and mosasaurs (excluded):** the snout elongation is characteristic for many anguimorphs, including dolichosaurs, mosasauroids and living varanoids. Therefore, it is an uninformative character for a generic diagnosis;

**2) Maxilla with fifteen to eighteen dental alveoli (modified):** this character was just re-written to fit the number for the whole dentition, since in DMNH-1601 embryos there is a premaxilla preserved;

**3) Long premaxillary contact with maxilla (excluded):** dolichosaurian premaxilla-maxilla contact was rather short. Caldwell (1999) even stated that in his work, on page 443: “The contact of the maxilla with the premaxilla was presumably quite short and involved the maxillary margin just anterior to the premaxillary process (...)”, so his inclusion of this character in *Coniasaurus* generic diagnosis may have been a typo;

**4) External narial opening long and posteriorly positioned on maxilla (excluded):** the retraction of the nares it is also a characteristic feature of many varanoids, including mosasauroians. Although there are some critics regarding whether this is or not a shared homology between varanoids and mosasauroians (Caldwell, 2012), this character is widely present in many other taxa and thus cannot be used to identify *Coniasaurus* alone;

**5) Anterior maxillary teeth elongated, pointed and recurved (modified):** the set of diagnostic characters regarding the dentition was reduced for avoiding redundancy. The morphology of upper jaw teeth usually matches the morphology of lower jaw elements, so the decision here was to unify the description of the dentition regardless individual crowns belonged to the maxilla or the dentary. Likewise, many squamate taxa present anterior maxillary teeth elongated, pointed and recurved, so this character was also redescribed for encompass coniasaur-like dentition as a whole;

**6) Posterior maxillary teeth swollen or may be bulbous tipped (modified - see character 5);**

**7) Splenial elongate, narrow anteriorly, and broadly exposed in medial view (excluded):** this is another character not unique to *Coniasaurus*. Living *Varanus* also present splenials with the same features as described above (pers. obs.);

**8) Inferior alveolar foramen enclosed by dorsal ossifications of splenial (excluded):** unfortunately, good dentaries preserved in medial view are only present in *Coniasaurus*, therefore preventing a proper comparison among other dolichosaurs. However, in mosasauroians at least the anterior inferior alveolar foramen is also entirely enclosed by the splenial (Russell, 1967), while both are in some anguimorphs, such as *Varanus salvator* (Conrad, 2004);

**9) Meckel's groove closed along length of dentary (excluded):** same case as above, with mosasauroians also presenting a Meckel's groove closed for most of its length;

**10) Anterior dentary teeth not as swollen/bulbous as posterior teeth (modified - see character 5);**

**11) More posterior teeth may be swollen and bulbous, with labial sulcus, posteriorly directed apex, and narrow lingual shelf (*C. crassidens*), or may be slightly thickened but still conical (*C. gracilodens*) (modified):** this character actually regards a range of dentition morphology that varies within the genus. The presence of a labial sulcus in marginal teeth is a synapomorphy shared by *C. crassidens* and *Coniasaurus* sp. nov. Narrow lingual shelves are present only in *C. crassidens*, while the less conspicuous heterodonty is a diagnostic character for *C. gracilodens*.

Morphological comparisons between the holotypes and referred specimens of *Coniasaurus* sp. nov., *C. crassidens*, *C. gracilodens* and *D. longicollis* showed that all these taxa shared a lot of characters, including both plesiomorphies and apomorphies. When considering only the synapomorphies present in the new emended *Coniasaurus* generic diagnosis provided here, *Coniasaurus* sp. nov. shares seven characters with *C. crassidens*, seven with *C. gracilodens* and six with *D. longicollis*. In addition, the revision of the specific diagnosis for each of those dolichosaurid taxa revealed that *Coniasaurus* sp. nov. has 11, *C. crassidens* has 2, *C. gracilodens* has 4 and *D. longicollis* has 2 unequivocal diagnostic characters. This character distribution among dolichosaurids shows that each taxon is basically equally distinct from each other in morphological terms, making it hard to justify that *Dolichosaurus* and *Coniasaurus* are distinct genera within Dolichosauridae, supporting the hypothesis of *Dolichosaurus* being a junior synonym of *Coniasaurus*. Both taxa were both described in the same contribution (Owen, 1850), but according to the Article 24.2.2. of the International Code of Zoological Nomenclature: "If two or more names, different or identical, and based on the same or different types, or two or more nomenclatural acts, are published on the same date in the same or different works, the precedence of the names or acts is fixed by the First Reviser unless Article 24.1 applies." (International Commission on Zoological Nomenclature, 2000). Before this thesis, *Coniasaurus* was known from two distinct species and *Dolichosaurus* from just one. In addition, there have been much more specimens referred to *Coniasaurus* than to *Dolichosaurus* in the literature, and the taxon name also appeared first in Owen's contribution. This background supported the decision of giving preference to *Coniasaurus* over *Dolichosaurus*. As *D. longicollis* still have two diagnostic features, one being comparable with *C. gracilodens* (absence of scapulocoracoid fenestra) and the other not being comparable with any other coniasaur (total number of cervicals), the proposition here is to keep the validity of the species, but within the genus *Coniasaurus*: *C. longicollis*. The discovery of future and more complete specimens of the taxon should clarify whether or not it actually belongs to a distinct coniasaur species or it should be classified into either *C. crassidens*, *C.*

*gracilodens* or *Coniasaurus* sp. nov. On the other hand, the family Dolichosauridae is still valid according to the Article 40 of the International Code of Zoological Nomenclature: "**Article 40. Synonymy of the type genus.** 40.1. **Validity of family-group names not affected.** When the name of a type genus of a nominal family-group taxon is considered to be a junior synonym of the name of another nominal genus, the family-group name is not to be replaced on that account alone." (International Commission on Zoological Nomenclature, 2000).

Many of the diagnostic characters given for *C. crassidens*, *C. gracilodens* and *C. longicollis* on the literature (Caldwell and Cooper, 1999; Caldwell, 1999, 2000) are actually shared plesiomorphies or does not apply for one or more taxa within the genus in the new composition presented here, so an emended and reduced diagnosis will be provided below for each coniasaur taxa based on really unique features of their anatomy, followed by a discussion of whether or not each previous diagnostic character was excluded.

#### ***Coniasaurus crassidens* Owen, 1850**

**Emended diagnosis:** heterodont dentition with labial sulcus and prominent lingual shelf on the posteriormost marginal teeth. Extreme elongation of maxilla, with a very low ascending process and room for nearly 18 alveoli.

**Discussion:** the revised diagnosis presented by Caldwell and Cooper included five specific diagnostic characters for *C. crassidens* as follows: **1) Characterized by heterodont maxillary tooth characters (excluded):** this is a diagnostic character for the genus *Coniasaurus*, not for *C. crassidens*; **2) Anterior-most maxillary tooth gracile, recurved, and bears long lateral groove beginning at or near gum-line and extending to tip (excluded):** same as character 1; **3) Posterior maxillary and mandibular teeth bulbous and lingually expanded (excluded):** same as character 1; **4) Fine crenulations on anterodorsal carina of tooth crown (excluded):** the presence of crenulations along the anterodorsally oriented carinae seems to be related to the wear degree of the crown, since in DMNH-1601 the embryos do possess these crenulations and the adult does not, and the main surface exposed to worn effects during occlusion was probably the carina; **5) Crown with deep sulcus on anterolateral (labial) face, posteriorly directed apex, and broad lingual shelf (modified):** the presence of the labial sulcus in marginal teeth is a character shared by *C. crassidens* and *Coniasaurus* sp. nov., while the broad lingual shelf really appears to be autapomorphic for *C. crassidens*, since neither the adult nor the embryos of *Coniasaurus* sp. nov. present this condition.

In addition, in Caldwell and Cooper (1999) generic emended diagnosis for *Coniasaurus*, they proposed the occurrence of a notch in the middle of neural arch, especially visible in lateral

view, to be a diagnostic feature of *Coniasaurus*. After reevaluating the British specimens of *Coniasaurus* it appears for us that this dorsal "notch" in the neural spine is a taphonomical breakage, not a biological feature. In many North American coniasaurs the neural spine is also broken at its midpoint. A closer view at these specimens revealed that the neural spine thickens both anteriorly and posteriorly (only posteriorly in *Coniasaurus* sp. nov. and *C. longicollis*), toward either close to the interprezygapophyseal lamina or the medial point between the postzygapophyses. This thickening of the neural spine at both its anterior and posterior ends probably let the midpoint of the spine to be more fragile and, thus, more likely to break during taphonomical processes, leading to the false impression of a real "notch".

### ***Coniasaurus gracilodens* Caldwell, 1999**

**Emended diagnosis:** coniasaur with less marked heterodonty, lacking lateral grooves and well developed carinae in the crowns. Maxillary ascending process high and strongly arched medially. Small, shield-shaped septomaxilla. Postzygapophyseal foramina present in dorsal vertebrae.

**Discussion:** the diagnosis presented by Caldwell (1999) presented 12 specific diagnostic characters for *C. crassidens* as follows: **1) Extremely elongate fused frontals (excluded):** elongation of the frontals is a widespread feature among anguimorphs, so this character is not considered here as a good diagnostic feature; **2) Prefrontal and postfrontal widely separated above orbit (excluded):** the dorsal separation of the prefrontal and postfrontal is also a widespread character for anguimorphs, including the dolichosaur *Pontosaurus*, with exception of *Lanthanothus* and *Heloderma* that possess a very close relationship between these bones; **3) Elongate vomeropalatine bones (excluded):** simplesiomorphy for *Coniasaurus* related to the elongation of the snout; **4) Small, shield-shaped septomaxilla (maintained):** although the bone identified by Caldwell (1999) as the septomaxilla do not looks like a mosasauroid septomaxilla (pers. obs.), no other dolichosaur have this bone preserved. Therefore, the option was to keep this character in the diagnosis until new specimens are found and proper morphological comparisons can be done; **5) Maxilla with low, medially overarched ascending process (modified):** actually, the ascending process of *C. gracilodens* is quite high when compared to *C. crassidens*, being more similar to the condition found in extant varanoids. However, the arching of the ascending process, although also present in other squamates, seems to be more developed here, and was maintained as an autapomorphic condition for *C. gracilodens*; **6) Narial emargination begins at second maxillary tooth (excluded):** it also begins near the second maxillary tooth in *Shinisaurus* (Conrad, 2004) and *Lanthanothus*

(McDowell and Bogert, 1954). In *Varanus*, the emargination starts between the third and fourth maxillary teeth (pers. obs.). In other dolichosaurs and basal mosasauroids it is not possible to confidently evaluate this condition; **7) Lateral wall of maxilla tall (excluded)**: similar to character 5, the tall wall of the maxilla approaches more the condition found in extant varanids and, because of that, is here considered a plesiomorphy; **8) Medial shelf wide and runs full length of maxilla (excluded)**: this character is also hard to assess because few basal mosasaurians have good, complete maxillae preserved in medial view. However, *Judeasaurus tchernovi* has, and in the taxon the shelf also runs through the entire maxilla (Haber and Polcyn, 2005; pers. obs.); **9) Teeth with numerous fine vertical striae (modified)**: fine longitudinal striations are present in all *Coniasaurus* specimens with teeth well preserved, so this character is included as a generic diagnostic feature for the genus; **10) Posterior maxillary teeth thick and conical, but not bulbous, and lack labial sulcus as seen in *Coniasaurus crassidens* (maintained)**: although this character regards the lack of a condition, it is a useful character to separate coniasaur species and it was kept; **11) Maxilla robust and shorter than *C. crassidens* (excluded)**: although *Coniasaurus* sp. nov. does not possess a maxilla preserved, many other North American coniasaur specimens do, and actually the extreme elongation of the maxilla may be an autapomorphy of *C. crassidens*, with *C. gracilodens* and *Coniasaurus* sp. nov. sharing a shorter plesiomorphic maxilla; **12) Approximately fifteen dental alveoli, as compared to eighteen in *C. crassidens* (excluded)**: same as character 11. Other North American coniasaur specimens appears to possess nearly 15 maxillary alveoli, and they rather possess a more *Coniasaurus* sp. nov. than a *C. gracilodens* dentition, so the number of 15 maxillary alveoli appears to be plesiomorphic for *Coniasaurus*.

### *Coniasaurus longicollis* Owen, 1850

**Emended diagnosis:** very elongated neck with at least 19 cervical vertebrae. Scapulocoracoid fenestra absent.

**Discussion:** the revised diagnosis presented by Caldwell (2000) presented eight generic and specific diagnostic characters for *Dolichosaurus longicollis* as follows: **1) At least nineteen cervical vertebrae with large posteriorly placed hypapophyses and unfused peduncles (modified)**: the cervical series is only complete in the holotype of *C. longicollis* and it is thus incomparable with other coniasaur specimens. Conservatively, the cervical number was maintained as an autapomorphic and diagnostic character of *C. longicollis*, although the discover of more complete specimens in the future may reveal that this feature is present also

in other coniasaur taxa. The second part of this diagnostic character is uninformative: hypapophyses are posteriorly placed in all dolichosaurs, the fusion of the peduncle is ontogenetic related (Augusta *et al.*, 2016) and the size of the latter is related to the position of the element along the cervical series.; **2) At least thirty-two trunk vertebrae (excluded)**: the large number of dorsal vertebrae is a synapomorphy for the genus *Coniasaurus*, since *Coniasaurus* sp. nov. also possessed at least 32 dorsal vertebrae; **3) Long, slightly curved ribs, body laterally compressed (excluded)**: the lateral body compression is a condition widespread among dolichosaurs; **4) Scapulocoracoid fenestra absent (maintained)**: the only coniasaur specimen presenting the scapula and the coracoid is the holotype of *C. gracilodens*, which do possess a scapulocoracoid fenestra, so up to now this character appears to be autapomorphic for *C. longicollis*; **5) Forelimb shorter and less robust than hindlimb (excluded)**: this feature is also a character shared by all dolichosaurs; **6) Humerus subequal in length to two anterior dorsal vertebrae (modified)**: this condition is shared with *Coniasaurus* sp. nov. and is here considered as a diagnostic feature of the genus, in which the ratio between humerus length and two anterior dorsal vertebrae is less than one. In the holotype of *C. longicollis* this ratio is nearly 0,94, while in *Coniasaurus* sp. nov. is 0,92. The same ratio is nearly 1,05 for *Adriosaurus suessi*, 1,02 for *Pontosaurus lesinensis* and 1,28 for *Eidolosaurus*. Although the reduction of the forelimb is a common feature among dolichosaurs, in coniasaurs it appears to be more pronounced; **7) Ectepicondylar foramen absent (excluded)**: this condition is shared with *Coniasaurus* sp. nov., *Pontosaurus* and *Adriosaurus*; **8) At least one pygal vertebra (excluded)**: *Coniasaurus* sp. nov. possess at least one unequivocal pygal vertebra too. *Pontosaurus* and *Adriosaurus* also possess at least one, maybe two, pygal vertebrae.

#### 2.4.2. The reliability of phylogenetic characters and the quality of fossil specimens

Recently, some authors have questioned the character construction present in larger squamate matrices (e.g. Caldwell, 2012; Simões *et al.*, 2017). Although the concern on the conceptualization and quality of a character is indeed important, there is also another important concern to be aware that has not been discussed recently in the literature regarding mosasaurians and related squamates: the quality of fossil specimens. This is an issue especially in the cases where authors rely the codification of characters for some fossil taxa on the description and illustrations present in the literature, as appears to be the case, for instance, in Conrad (2008) and Gauthier *et al.* (2012) morphological matrices. When analyzing character scorings in these matrices, especially in *Coniasaurus*, *Dolichosaurus*, *Adriosaurus*, *Pontosaurus*,

*Aphanizocnemus* and *Eidolosaurus*, it is clear that many of the conditions coded for these taxa were simply not observable in the specimens.

A clear example in this topic is provided by the *Adriosaurus suessi* specimen NHMUK-R2867, redescribed by Lee and Caldwell (2000). Even though this is a nearly complete specimen, the preservation of the material is very poor. A reanalysis of this specimen has revealed that many of the characters described and illustrated by the authors, especially regarding the skull anatomy, are simply not visible. Figure 2.20 illustrates better the question by comparing a recent photograph of this specimen skull with the illustration provided by Lee and Caldwell (2000). In their discussion, the cited authors recovered four characters supporting the clade formed by *Adriosaurus* + Ophidia (Lee and Caldwell, 2000; pgs. 924, 925): 1) Premaxilla-maxilla contact mobile; 2) Frontals paired; 3) Postorbitofrontal ventral process large; 4) Supratemporal superficial. However, none of these characters are clearly observable in the specimen due to preservational issues. Although the premaxilla-maxilla mobile contact was probably present because it is a condition found in other mosasaurians, the breakages and erosion of the bony surfaces considerably affect the adequate assessment of the *Adriosaurus* skull morphology. In particular, the posterior part of the skull is simply an indistinguishable bony mass, thus preventing any consistent interpretation of skull bones posterior to the frontal. There appears to be a mediolateral line of breakage through the skull at the orbits level, what probably led the frontal bone to break during taphonomical processes (Figure 2.20). Thus, I disagree with the interpretation of Lee and Caldwell (2000) that the frontals are paired. The anterior part of the bone appears to be the better-preserved part of the whole skull, revealing two important features: a triradiate morphology anteriorly and the fusion of the elements into a single bone. These patterns match more the condition found in other anguimorphs and are very similar to those of *Coniasaurus gracilodens* frontal (Caldwell, 1999). At the same time, they are completely different from that of snakes. This fact highlights how important is to rely the codification of characters on nicely preserved specimens, regardless how complete they are, and how poorly preserved specimens can potentially lead to mistakes during phylogenetic reconstructions.

It is important clarify that what is being suggested here it is not the exclusion of fossil specimens from phylogenetic analysis, as they are very important to reconstruct phylogenetic relationships (Gauthier *et al.*, 1988; Donoghue *et al.*, 1989; Wiens and Collins, 2004). Instead, the suggestion is that authors should be careful when codifying characters based purely on the literature, particularly when the specimens are poorly preserved. Whenever possible, looking at the fossil materials personally will be always the best way to precisely codify a character in

poorly preserved fossil specimens. In addition, CT-Scan approaches are possibly the best way to clarify distinct interpretations regarding the same fossil specimen (e.g. Polcyn *et al.*, 2005), and should therefore be applied more often in Paleontology to shed light on the morphology of key specimens. With the new data generated from this thesis, *Coniasaurus* arises as the most reliable dolichosaur lizard to use in phylogenetic analyses of the group, since it is known now from several well-preserved tridimensional bones, allowing proper comparisons and codings for many characters that are currently being coded as missing in most dolichosaurs.

## 2.5. Final considerations

This contribution provided plenty of new anatomical data for *Coniasaurus* based on dozens of new described specimens. The new anatomical data allowed a comprehensive review of the genus *Coniasaurus*, pointing to more precise diagnostic characters for each taxon of the genus. *Coniasaurus* is now composed by four species: *C. crassidens*, *C. longicollis*, *C. gracilodens* and *Coniasaurus* sp. nov. which possess, respectively, 2, 2, 4 and 11 diagnostic characters. A discussion of fossil specimens' overall quality also recognizes *Coniasaurus* as the most reliable dolichosaur for character codings in phylogenetic analysis, since it has better preserved tridimensional bones than any other basal mosasaurian.

## References

- Adams, R.L.; Carr, J.P. 2010. Regional depositional systems of the Woodbine, Eagle Ford, and Tuscaloosa of the US Gulf Coast. **Gulf Coast Association of Geological Societies Transactions** 60: 3-27.
- Adams, T.L.; Polcyn, M.J.; Mateus, O.; Winkler, D.A.; Jacobs, L.L. 2011. First occurrence of the long-snouted crocodyliform *Terminonaris* (Pholidosauridae) from the Woodbine Formation (Cenomanian) of Texas. **Journal of Vertebrate Paleontology** 31(3): 712-716.
- Adkins, W. S.; Lozo, F. E. 1951. Stratigraphy of the Woodbine and Eagle Ford, Waco area, Texas. East Texas Geological Society.
- Augusta, B.G.; Polcyn, M.J.; Zaher, H.; Jacobs, L.L. 2016. A gravid coniasaur (*Coniasaurus* sp.) from the Upper Cretaceous of Texas and the development of dolichosaurs. In: 5TH TRIENNIAL MOSASAUR MEETING - A GLOBAL PERSPECTIVE ON MESOZOIC MARINE AMNIOTES, 2016, Uppsala. **Program and Abstracts**. Uppsala: Uppsala University. p. 2-3.

- Bahl, K.N. 1937. Skull of *Varanus* monitor (Linn.). **Records of the Indian Museum** 39: 133-174.
- Bell, B.A.; Murry, P.A.; Osten, L.W. 1982. *Coniasaurus* Owen, 1850 from North America. **Journal of Paleontology** 56(2): 520-524.
- Bell, G.L. 1993. The first record of *Coniasaurus* (Squamata) from South Dakota. **Proceedings of South Dakota Academy of Science** 72: 333.
- Bell, G.L.; Polcyn, M.J. 1996. Distribution of the lizard, *Coniasaurus*, in the Western Interior Cretaceous Seaway and its paleoecological implications. **Geological Society of America, Rocky Mountain Section, Abstracts with Programs** 28: 2.
- Bell, G.L.; Polcyn, M.J. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). **Netherlands Journal of Geosciences** 84 (3): 177-194.
- Bell, G.L.; Barnes, K.R.; Polcyn, M.J. 2013. Late Cretaceous mosasauroids (Reptilia, Squamata) of the Big Bend region in Texas, USA. **Earth and Environmental Science Transactions of the Royal Society of Edinburgh** 103: 1-11.
- Bishop, G.A.; Brannen, N.A.; Hill, L.E.; Meyer, J.P.; Pike, A.J.; Sampson, C. 1992a. The Britton Notopocorystes assemblage: an Eagle Ford decapod assemblage from the Cretaceous of north-central Texas. **Gulf Coast Association of Geological Societies Transactions** 42: 413-424.
- Bishop, G.A.; Brannen, N.A. 1992b. *Homolopsis pikeae*, new species (Decapoda), a crab from the Cretaceous of Texas. **Journal of Crustacean Biology** 12(2): 317-323.
- Boettcher, R. 1990. New Information on the Reproductive Biology of Ichthyosaurs (Reptilia). **Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaeontologie)** 164: 1-51.
- Brown, C.W.; Pierce, R.L. 1962. Palynologic correlations in Cretaceous Eagle Ford Group, northeast Texas. **AAPG Bulletin** 46(12): 2133-2147.
- Caldwell, M.W. 1999. Description and phylogenetic relationships of a new species of *Coniasaurus* Owen, 1850 (Squamata). **Journal of Vertebrate Paleontology** 19(3): 438-455.
- Caldwell, M.W. 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in Squamates. **Journal of Vertebrate Paleontology** 20(4): 720-735.

- Caldwell, M.W. 2006. A New Species of "Pontosaurus" (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a Phylogenetic Analysis of Pythonomorpha. **Società Italiana di Scienze Naturali**: 1-44.
- Caldwell, M.W. 2012. A challenge to categories: What, if anything, is a mosasaur?. **Bulletin de la Société Géologique de France** 183(1): 7-34.
- Caldwell, M.W.; Cooper, J.A. 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the Lower Chalk (Cretaceous; Cenomanian) of SE England. **Zoological Journal of the Linnean Society** 127: 423-452.
- Caldwell, M.W.; Lee, M.S.Y. 2001. Live birth in Cretaceous marine lizards (mosasauroids). **Proceedings of the Royal Society: Biological Sciences** 268: 2397-2401.
- Caldwell, M.W.; Lee, M.S.Y. 2004. Reevaluation of the Cretaceous marine lizard *Acteosaurus crassicostatus* Calligaris, 1993. **Journal of Paleontology** 78(3): 617-619.
- Caldwell, M.W.; Palci, A. 2010. A new species of marine ophidiomorph lizard, *Adriosaurus skrbiniensis*, from the Upper Cretaceous of Slovenia. **Journal of Vertebrate Paleontology** 30(3): 747-755.
- Camp, C.L. 1923. Classification of the lizards. **Bulletin of the American Museum of Natural History** 48: 289-481.
- Cheng Y.N.; Wu, X.C.; Ji, Q. 2004. Triassic marine reptiles gave birth to live young. **Nature** 432: 383-386.
- Cicimurri, D.J.; Bell, G.L. 1996. Vertebrate fauna of the Boquillas Formation of Brester County, Texas: a preliminary report. **Journal of Vertebrate Paleontology** 16: 28A.
- Cobban, W.A.; Walaszczyk, I.; Obradovich, J.D.; McKinney, K.C. 2006. A USGS zonal table for the Upper Cretaceous middle Cenomanian-Maastrichtian of the Western Interior of the United States based on ammonites, inoceramids, and radiometric ages: **U.S. Geological Survey Open-File Report** 2006-1250: 46 p.
- Conrad, J.L. 2004. Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). **Zoological Journal of the Linnean Society** 141(3): 399-434.
- Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. **Bulletin of the American Museum of Natural History**, 310: 1-182.
- Conrad, J.L.; Ast, J.C.; Montanari, S.; Norell, M.A. 2011. A combined evidence phylogenetic analysis of Anguimorpha (Reptilia: Squamata). **Cladistics** 27: 230-277.

- Dal Sasso, C.; Pinna, G. 1996. *Besanosaurus leptorhynchus* n. gen. n. sp., a new shastasaurid ichthyosaur from the Middle Triassic of Besano (Lombardy, N. Italy). **Paleontologia Lombarda** 4: 3-23.
- Dal Sasso, C.; Pinna, G. 1997. *Aphanizocnemus libanensis* n. gen. n. sp, a new dolichosaur (Reptilia, Varanoidea) from the Upper Cretaceous of Lebanon. **Paleontologia Lombarda** 7: 1-31.
- Diedrich, C. 1997. Ein dentale von *Coniosaurus crassidens* Owen (Varanoidea) aus dem Ober-Cenoman von Halle/Westf. (NW-Deutschland). **Geologie und Paläontologie in Westfalen** 47: 43-51.
- Donoghue, M.J.; Doyle, J A.; Gauthier, J.; Kluge, A.G.; Rowe, T. 1989. The importance of fossils in phylogeny reconstruction. **Annual Review of Ecology and Systematics** 20(1): 431-460.
- Donovan, A.D.; Gardner, R.D.; Pramudito, A.; Staerker, T.S.; Wehner, M.; Corbett, M.J.; Lundquist, J.J.; Romero A.M.; Henry, L.C.; Rotzien, J.R.; Boling, K.S. 2015. Chronostratigraphic relationships of the Woodbine and Eagle Ford Groups across Texas. **GCAGS Journal** 4: 67-87.
- Dutchak, A.R.; Caldwell, M.W. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. **Journal of Vertebrate Paleontology** 29(2): 437-452.
- Evans, S. E. 2008. The skull of lizards and tuatara. **Biology of the Reptilia** 20: 1-347.
- Evans, S.E.; Manabe, M.; Noro, M.; Isajis, S.; Yamaguchi, M. 2006. A longbodied lizard from the Lower Cretaceous of Japan. **Paleontology** 49(6): 1143-1165.
- Everhart, M.J.; Darnell, M.K. 2004. Occurrence of *Ptychodus mammillaris* (Elasmobranchii) in the Fairport Chalk Member of the Carlile Shale (Upper Cretaceous) of Ellis County, Kansas. **Transactions of the Kansas Academy of Science** 107(3): 126-130.
- Field, D.J.; LeBlanc, A.; Gau, A.; Behlke, A.D. 2015. Pelagic neonatal fossils support viviparity and precocial life history of Cretaceous mosasaurs. **Palaeontology** 2015: 1-7.
- Gauthier, J.A.; Kearney, M.; Maisano, J.A.; Rieppel, O.; Behlke, A.D.B. 2012. Assembling the Squamate tree of life: perspectives from the phenotype and the fossil record. **Bulletin of the Peabody Museum of Natural History** 53(1): 3-308.
- Gauthier, J.A.; Kluge, A.G.; Rowe, T. 1988. Amniote phylogeny and the importance of fossils. **Cladistics** 4(2): 105-209.

- Gervais, P. 1852. **Zoologie et Paleontologie Françaises (Animaux Vertébrés)**. Paris, Arthus Bertrand, 274 p.
- Golobof, P.; Farris, J.; Nixon, K. 2003. T.N.T.: Tree Analysis Using New Technology. Software and documentarion made avaulable by the authors and the Hennig Society at [www.zmuc.dk/public/phylogeny](http://www.zmuc.dk/public/phylogeny).
- Gradstein, F.M.; Ogg, J.G.; Schmitz, M.; Ogg, G. 2012. The Geologic Time Scale 2012: Boston, Elsevier, 1144 p., doi:10.1016/B978-0-444-59425-9.00004-4.
- Haber, A.; Polcyn, M.J. 2005. A new marine varanoid from the Cenomanian of the Middle East. **Netherlands Journal of Geosciences** 84(3): 247-255.
- Hancock, J.M.; Walaszczyk, I., 2004. Mid-Turonian to Coniacian changes of sea level around Dallas, Texas. **Cretaceous Research** 25(4): 459-471.
- Haq, B.U. 2014. Cretaceous eustasy revisited. **Global and Planetary Change** 113: 44-58.
- Houssaye, A. 2013. Palaeoecological and morphofunctional interpretation of bone mass increase: an example in Late Cretaceous shallow marine squamates. **Biological Reviews** 88(1): 117-139.
- International Comission on Zoological Nomenclature. 2000. **International Code of Zoological Nomenclature** (4ed). London, The International Trust for Zoological Nomenclature.
- Jacobs, L.L.; Polcyn, M.J.; Taylor, L.H.; Ferguson, K. 2005. Sea-surface temperatures and palaeoenvironments of dolichosaurs and early mosasaurs. **Netherlands Journal of Geosciences** 84(3): 269-281.
- Joo, Y.J.; Sageman, B.B. 2014. Cenomanian to Campanian carbon isotope chemostratigraphy from the Western Interior Basin, USA. **Journal of Sedimentary Research** 84(7): 529-542.
- Kennedy, W.J. 1988. Late Cenomarian and Turonian ammonite faunas from north-east and central Texas. **Special Papers in Palaeontology**.
- Kennedy, W.J.; Cobban, W.A. 1990. Cenomanian ammonite faunas from the Woodbine Formation and lower part of the Eagle Ford Group, Texas. **Palaeontology** 33(1): 75-154.
- Kubo, T.; Mitchell, M.T.; Henderson, D.M. 2012. *Albertonectes vanderveldei*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. **Journal of Vertebrate Paleontology** 32(3): 557-572.
- Lee, M.S.Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. **Biological Journal of the Linnean Society** 65: 369-453.

- Lee, M.S.Y.; Caldwell, M.W. 1998. Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. **Philosophical Transactions of the Royal Society of London B: Biological Sciences** 353: 1521-1552.
- Lee, M.S.Y.; Caldwell, M.W. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. **Journal of Paleontology** 74(5): 915-937.
- Lee, M.S.Y.; Scanlon, J.D. 2002. The Cretaceous marine squamate *Mesoleptos* and the origin of snakes. **Bulletin of the Natural History Museum London (Zoology Series)** 68: 131-142.
- Liggett, G.A.; Shimada, K.; Bennett, S.C.; Schumacher, B.A. 2005. Cenomanian (Late Cretaceous) reptiles from northwestern Russell County, Kansas. **PaleoBios** 25(2): 9-17.
- Lindgren, J.; Polcyn, M.J.; Young, B.A. 2011. Landlubbers to leviathans: evolution of swimming in mosasaurine mosasaurs. **Paleobiology** 37: 445–469.
- McDowell, S.B.; Bogert, C.M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. **Bulletin of the American Museum of Natural History** 105: 1-142.
- Moreman, W.L., 1942. Paleontology of the Eagle Ford Group of north and central Texas. **Journal of Paleontology**: 192-220.
- Motani, R.; Jiang, D.Y.; Tintori, A.; Rieppel, O.; Chen, G.B. 2014. Terrestrial origin of viviparity in Mesozoic marine reptiles indicated by Early Triassic embryonic fossils. **PloS one** 9(2): e88640.
- Myers, T.S. 2010. A new ornithocheirid pterosaur from the Upper Cretaceous (Cenomanian–Turonian) Eagle Ford Group of Texas. **Journal of Vertebrate Paleontology** 30(1): 280-287.
- Myers, T.S., 2015. First North American occurrence of the toothed pteranodontoid pterosaur *Cimoliopterus*. **Journal of Vertebrate Paleontology** 35(6): e1014904.
- Nagrodski, M.; Shimada, K.; Schumacher, B.A. 2012. Marine vertebrates from the Hartland Shale (Upper Cretaceous: Upper Cenomanian) in southeastern Colorado, USA. **Cretaceous Research** 37: 78-88.
- Nopcsa, F.B. 1923. *Eidolosaurus* und *Pachyophis*: Zwei neue Neocom-Reptilien. **Palaeontographica** 65: 99-154.
- Norton, G. H. (1965). Surface geology of Dallas County. **The geology of Dallas County: The Dallas Geological Society**: 40-125.

- O'Brien, C.L.; Robinson, S.A.; Pancost, R.D.; Damste, J.S.S.; Schouten, S.; Lunt, D.J.; Alsenz, H.; Bornemann, A.; Bottini, C.; Brassell, S.C.; Farnsworth, A. 2017. Cretaceous sea-surface temperature evolution: Constraints from TEX86 and planktonic foraminiferal oxygen isotopes. **Earth-science reviews** 172: 224-247.
- Oelrich, T.M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). **University of Michigan Museum of Zoology Miscellaneous Publications** 94: 1–122.
- Owen, R. 1850. Description of the fossil reptiles of the Chalk Formation. *In*: Dixon, F. (Ed), **The geology and fossils of the Tertiary and Cretaceous Formations of Sussex**. London, Longman, Brown, Green, and Longman. p. 378-404.
- O'Keefe, F.R.; Chiappe, L M. 2011. Viviparity and K-selected life history in a Mesozoic marine plesiosaur (Reptilia, Sauropterygia). **Science** 333(6044): 870-873.
- Palci, A.; Caldwell, M.W. 2007. Vestigial forelimbs and axial elongation in a 95 million-year-old non-snake squamate. **Journal of Vertebrate Paleontology** 27(1): 1-7.
- Palci, A.; Caldwell, M.W. 2010. Redescription of *Acteosaurus tommasinii* von Meyer, 1860, and a discussion of evolutionary trends within the clade Ophidiomorpha. **Journal of Vertebrate Paleontology** 30(1): 94-108.
- Pierce, S.; Caldwell, M.W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur, *Pontosaurus lesinensis* (Kornhuber, 1873). **Journal of Vertebrate Paleontology** 24: 376-389.
- Polcyn, M.J.; Bell, G.L. 1994. *Coniasaurus crassidens* and its bearing on varanoid-mosasauroid relationships. **Journal of Vertebrate Paleontology**, Supplemental 14: 42A.
- Polcyn, M.J.; Bell, G.L. 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(3): 321-333.
- Polcyn, M.J.; Jacobs, L.L.; Haber, A. 2005. A morphological model and CT assessment of the skull of *Pachyrhachis problematicus* (Squamata, Serpentes), a 98 million year old snake with legs from the Middle East. **Palaeontologia Electronica** 8(1): 1-24.
- Polcyn, M.J.; Tchernov, E.; Jacobs, L.L. 1999. The Cretaceous biogeography of the Eastern Mediterranean with a description of a new basal mosasauroid from 'Ein Yabrud, Israel. *In*: SECOND GONDWANAN DINOSAUR SYMPOSIUM. **Proceedings of the Second Gondwanan Dinosaur Symposium**. National Science Museum Monographs 15, Tokyo, Japan. p. 259-290.

- Porter, W.R.; Witmer, L.M. 2015. Vascular patterns in iguanas and other squamates: Blood vessels and sites of thermal exchange. **PloS one** 10(10): e0139215.
- Powell, J.D. 1968. Woodbine-Eagle Ford transition, Tarrant Member. Fieldtrip Guidebook, South-Central Section, Stratigraphy of the Woodbine Formation, Tarrant County, Texas. **Geological Society of America, Boulder**: 27-43.
- Reeder, T.W.; Townsend, T.M.; Mulcahy, D.G.; Noonan, B.P.; Wood, P.L.Jr.; Sites, J.W.Jr.; Wiens, J.J. 2015. Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny and Reveal Unexpected Placements for Fossil Taxa. **PLoS ONE** 10(3): e0118199.doi:10.1371/journal.pone.0118199.
- Rieppel, O. 1980. **The phylogeny of anguimorph lizards**. Birkhauser Verlag, Basel, 86 p.
- Rieppel, O.; Conrad, J.L.; Maisano, J.A. 2007. New morphological data for *Eosaniwa koehni* Haubold, 1977 and a revised phylogenetic analysis. **Journal of Paleontology** 81(4): 760-769.
- Rieppel, O.; Zaher, H. 2000. The intramandibular joint in squamates and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. **Fieldiana (Geology), New Series** 43: 1-69.
- Roberts, C.N. 1953. Geology of the Dallas Quadrangle, Dallas County, Texas". **Field and Laboratory** 21: 21-33.
- Romer, A.S. 1956. **Osteology of the reptiles**. Chicago, University of Chicago Press, 772 p.
- Russell, D.A. 1967. Systematics and morphology of American mosasaurs. **Bulletin of the Peabody Museum of Natural History** 23: 1-241.
- Scanlon, J.D.; Hocknull, S.A. 2008. A dolichosaurid lizard from the latest Albian (mid-Cretaceous) Winton Formation, Queensland, Australia. **Transactions of the Kansas Academy of Science (Fort Hays Studies Special Issue - Proceedings of the Second Mosasaur Meeting)**: 131-136.
- Seiffert, J. 1973. Upper Jurassic lizards from central Portugal. **Memórias do Serviço Geológico de Portugal (Nova Série)** 22: 1-85.
- Shimada, K.; Bell, G.L. 2006. *Coniasaurus* Owen, 1850 (Reptilia: Squamata), from the Upper Cretaceous Niobrara Chalk of Western Kansas. **Journal of Paleontology** 80(3): 589-593.
- Shimada, K.; Everhart, M.J.; Ewell, K. 2007. A unique reptilian (large dolichosaurid lizard?) tooth from the Upper Cretaceous Niobrara Chalk of western Kansas. **Transactions of the Kansas Academy of Science** 110(3/4): 213-219.

- Shimada, K.; Ystesund, T.K. 2007. A dolichosaurid lizard, *Coniasaurus* cf. *crassidens*, from the Upper Cretaceous Carlile Shale in Russell County, Kansas. **Transactions of the Kansas Academy of Science** 110(3/4): 236-242.
- Simões, T.R.; Caldwell, M.W.; Palci, A.; Nydam, R.L. 2017. Giant taxon-character matrices: quality of character constructions remains critical regardless of size. **Cladistics** 33(2): 198-219.
- Slattery, J.S.; Cobban, W.A.; McKinney, K.C.; Harries, P.J.; Sandness, A.L. 2015. Early Cretaceous to Paleocene paleogeography of the Western Interior Seaway: the interaction of eustasy and tectonism. **Wyoming Geological Association Guidebook**: 22-60.
- Smith, C.C. 1981. Calcareous nannoplankton and stratigraphy of late Turonian, Coniacian, and early Santonian age of the Eagle Ford and Austin groups of Texas. **USGS** 1075: 1-98.
- Smith, J.B.; Dodson, P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. **Journal of Vertebrate paleontology** 23(1): 1-12.
- Smith, A.S.; Vincent, P. 2010. A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany. **Palaeontology** 53(5): 1049-1063.
- Stephenson, R. 1953a. Large invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. **US Geological Survey Professional Paper** 242: 1-8.
- Stephenson, L.W. 1953b. Mollusks from the Pepper shale member of the Woodbine formation, McLennan County, Texas: **US Geological Survey Professional Paper** 243: 57-67.
- Tschopp, E. 2016. Nomenclature of Vertebral Laminae in Lizards, with Comments on Ontogenetic and Serial Variation in Lacertini (Squamata, Lacertidae). **PloS one** 11(2): e0149445.
- VonLoh, J.P.; Bell, G.L. 1998. Fossil reptiles from the Late Cretaceous Greenhorn Formation (Late Cenomanian-Middle Turonian) of the Black Hills region, South Dakota. **Dakoterra** 5: 29-38.
- Wiens, J.J.; Collins, T. 2004. The role of morphological data in phylogeny reconstruction. **Systematic Biology** 53(4): 653-661.
- Zaher, H.; Rieppel, O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. **American Museum Novitates** 3271: 1-19.

## **Chapter 3 - Patterns of tooth attachment and implantation in *Coniasaurus* (Squamata, Mosasauria) based on high-resolution CT data**

### **Abstract**

There is a long-standing debate around the putative homologies between mosasaurian and snake dentitions. Two main hypotheses arise in the literature: that both groups present homologous characters and can be interpreted as thecondonts; or that features of the dentition in each group evolved independently, and both clades present a modified pleurodont dentition. Although many studies in this topic have been published so far, none of them evaluated tooth attachment conditions present in basal mosasaurians (dolichosaurs), a key group to understand character transformation and distribution. Several *Coniasaurus* jaw sections were CT-scanned, using resolutions of up to 6 $\mu$ m, which allowed the identification of at least two distinct tissues involved in tooth attachment: cementum and alveolar bone. Reduced attachment size, a thin cementum layer, the lack of a basal plate and the presence of subtle dentin infoldings suggest coniasaur tooth attachment as presenting a plesiomorphic, varanoid condition, *contra* the interpretation of being snake-like. CT-based histology can be very useful by being a non-destructive method, allowing the inclusion of many specimens in a histological study, but limitations of the technique prevent the proper assessment of many tissue features.

**Keywords:** Histology; Dolichosauridae; Cementum; Alveolar Bone; Thecodonty; Pleurodonty.

## Resumo

Existe um grande debate sobre a possível presença de homologias entre as dentições de serpentes e mosassaurianos. Duas hipóteses principais aparecem na literatura: a de que ambos os grupos apresentam características homólogas que permitem sua identificação como tecodontes; e a de que caracteres na dentição de cada grupo evoluíram independentemente, culminando na interpretação dos táxons apresentando uma dentição pleurodonte modificada. Embora muitos estudos na área foram publicados nos últimos anos, nenhum deles avaliou os padrões de fixação dentária presentes nos mosassaurianos basais (dolicossauros), um grupo chave para o entendimento dos padrões de transformação e distribuição destes caracteres. Diversos fragmentos mandibulares e maxilares de *Coniasaurus* foram tomografados, usando resoluções de até 6µm, o que permitiu a identificação de pelo menos dois tecidos envolvidos na fixação dentária: cimento e osso alveolar. A presença de uma área de fixação reduzida, uma fina camada de cimento, sutis invaginações da dentina e a ausência de uma lâmina basal sugerem que *Coniasaurus* apresentava uma dentição plesiomórfica, similar à dos lagartos varanóides, e diferente da dentição presente nas serpentes. Técnicas de histologia baseadas em tomografia computadorizada podem ser muito úteis por serem um método não-destrutivo, permitindo a inclusão de vários espécimes num dado estudo, mas as limitações da técnica previnem uma avaliação apropriada de diversas características dos tecidos.

**Palavras-chave:** Histologia; Dolichosauridae; Cimento; Osso Alveolar; Tecodontia; Pleurodontia.

### 3.1. Introduction

Dentition characters have long been used in the literature for either support or reject the hypothesis of mosasaurs being closely related to snakes. First use of dentition characters to establish these systematic relationships dates back to the XIX century. Cope (1869) firstly proposed the order Pythonomorpha to encompass mosasaurs and snakes, listing 20 diagnostic characters, three of them being related to dentition or jaw anatomy: the absence of “fangs”, the absence of a mandibular symphysis and the presence of an intramandibular joint. In 1878, Cope argues in favor of Pythonomorpha’s validity against criticism from Richard Owen (1877), including tooth attachment, implantation and replacement characters. Most of the subsequent works rejected Cope’s Pythonomorpha assemblage, either suggesting varanoid affinities for mosasaurs (Owen, 1877; Marsh, 1880; Baur, 1890; Williston, 1904; Nopcsa, 1923; Camp, 1923; McDowell and Bogert, 1954; Russell, 1967; Rieppel, 1980; Borsuk-Bialynicka, 1984; Carroll and DeBraga, 1992) or a distinct subdivision for mosasaurs within lacertilians (i.e. Osborn, 1899; Fejérváry, 1918). However, Caldwell *et al.* (1995) and Lee (1997a, b) challenged the varanoid affinities of mosasaurs and proposed a close relationship between mosasaurs and snakes, re-heating the long-standing debate firstly triggered by Cope and Owen. In particular, Lee (1997) used two dental characters to support the hypothesis of snake-like dentition in mosasaurs: the recumbent position of replacement teeth and the presence of a thecodont mode of tooth implantation. Zaher and Rieppel (1999) provided a wide revision of tooth replacement and implantation among squamates, concluding that thecodonty was absent in Squamata and that the recumbent position in mosasaurian replacement teeth was the result of postmortem displacement. They also found that the distribution of resorption pits (extensive necrosis at the base of functional teeth) was uninformative regarding the relationships between mosasaur and snakes, rejecting the hypothesis of homology between the dentition in these taxa.

Contributions examining mosasaur dental characters up to the end of the 20<sup>th</sup> century were based mostly on overall macromorphology until Caldwell *et al.* (2003) provided the first histological investigation of mosasauroid tooth attachment, examining thin sections of a *Platecarpus* right dentary. Caldwell *et al.* (2003) found in *Platecarpus* the attachment tissues (such as periodontal ligaments and cementum) traditionally used to diagnose thecodonty, as well as interdental ridges (which they called mesial and distal socket walls) separating successive teeth, concluding that thecodonty was indeed present in mosasauroids. Rieppel and Kearney (2005) analyzed thin sections of *Clidastes* dentaries, corroborating Caldwell *et al.* (2003) findings of ridges separating successive teeth are present in mosasauroids and

alethinophidian snakes but remembering that this condition was absent in scolecophidian snakes and unknown in more basal mosasauroids. The authors also concluded that replacement teeth developed in a vertical position in *Clidastes*, suggesting that a nearly horizontal mode of tooth replacement was autapomorphic for snakes. In 2006, Budney and colleagues studied the tooth attachment histology in the Cretaceous snake *Dinilysia patagonica*, finding alveolar bone in the taxon and concluding that tissues usually associated with thecodonty might be broadly distributed within Squamata. Caldwell (2007) described tooth ontogeny, anatomy and attachment in three mosasaurid genera: *Mosasaurus*, *Platecarpus* and *Prognathodon*. He supported the view that mosasaurids do possess thecodonty, but his findings also agreed with Zaher and Rieppel (1999) and Rieppel and Kearney (2005) in which mosasaurs do not possess horizontally replacement of the teeth in any point of their tooth ontogeny. Caldwell (2007) concluded that mosasaurs are highly autapomorphic in most features of their dental anatomy, including a unique “zig-zag” movement path for the replacement teeth.

In the last decade researchers continued to investigate patterns of tooth attachment, development and replacement in mosasaurs and related squamates. Luan *et al.* (2009) found four distinct mineralized tissues anchoring teeth to the jaw in the halisaurine mosasaur *Halisaurus sternbergi*: acellular cementum, trabecular cellular cementum, mineralized periodontal ligament and interdental ridges, but no alveolar bone was observed in their work. Because of the patterns of tooth attachment and the lack of alveolar bone, Luan *et al.* (2009) suggested that mosasaurs bear interdental ridges and not true sockets, concluding that mosasaur attachment might be an early step in the evolution of thecodonty, but it is not true thecodonty. Maxwell *et al.* (2011) described the histology of dental tissues in *Varanus*, founding vascularized cementum and alveolar bone and supporting the hypothesis that major tooth germ tissues are present in all amniotes. The authors also concluded that cementum, in *Varanus*, is not involved in tooth attachment, and hypothesized that the osteocementum found in derived mosasaurs may had evolved from a similar varanoid-like vascularized cementum. Liu *et al.* (2016) found mosasaurs to bear varanoid mode of tooth implantation and replacement, presenting resorption pits, inclined position of tooth replacement (which was not the result of postmortem displacement) and pseudothecodonty mode of tooth implantation. These results were challenged by LeBlanc *et al.* (2017), which proposed that attachment tissues in mosasaurs were indeed homologous to those of snakes and crocodylians.

If on one hand there was intensive research regarding the patterns of tooth attachment, implantation and replacement in mosasaurs, varanoids and snakes through the past two decades, on the other hand all these works included only mosasaurids and not basal forms in their

comparisons. The lack of data in more basal members of the group prevented the understanding of the dental characters evolution from a primitive condition to a more derived one. Here is provided the first description of the tooth implantation histology in a basal mosasaurian (*sensu* Conrad, 2008): the dolichosaur *Coniasaurus*. Dolichosaurs are usually interpreted as either stem mosasauroids (e.g. Conrad, 2008; Gauthier *et al.*, 2012; Reeder *et al.*, 2015) or stem pythonomorphs (e.g. Lee, 1998; Lee and Caldwell, 2000; Caldwell and Palci, 2010), so understanding dentition patterns in dolichosaurs can clarify whether these patterns are the result of evolutionary convergence or homology among distinct anguimorph lineages.

### 3.2. Methods

22 jaw sections, including eight dentaries, five maxillae and nine undetermined jaw sections, were micro CT-scanned at the University of Texas High-Resolution X-ray CT Facility, using a FeinFocus microfocal X-ray source operating at 170 kV and 0.19 mA. CT-resolutions ranged from 24.9  $\mu\text{m}$  for adult bones to 9.67  $\mu\text{m}$  for embryonic remains. Four of these, including two dentaries and two maxillae (SMU-72390, SMU-72391, SMU-72398 and SMU-72399), were also CT-scanned using a higher resolution (6  $\mu\text{m}$ ) in a Scanco Medical MicroCT 35, in the Texas A&M College of Dentistry at Dallas, operating with similar parameters.

### 3.3. Results

Attachment site for marginal teeth is very shallow in dolichosaurs, much more like those of varanoid lizards (Caldwell *et al.*, 2003) than those of mosasauroids or snakes (Fig. 3.1). There are no interdental ridges separating successive teeth as in derived mosasauroids. A basal plate ankylosing the lingual base of the tooth is also absent, and lingually the element touches the tooth-bearing element only in its sloping lingual surface (Fig. 3.2A and C). These two characters support the classification of the dolichosaurian tooth attachment as fully pleurodont *sensu* Zaher and Rieppel (1999), the exact same pattern found in varanoid lizards. Two additional characters are also different in *Coniasaurus* than in mosasauroids. Firstly, only a thin layer of cementum covers the lingual margin of the teeth (Fig. 3.2), *contra* the conspicuously thick layer found in Mosasauroidea. Secondly, resorption pits are completely absent. Nearly a hundred dolichosaur jaw sections were analyzed, and resorption pits were not observed in any single specimen. From a topological view, dolichosaurs present a mode of tooth attachment and implantation nearly indistinguishable from that of varanoid lizards. Replacement teeth were not

found in any specimen as well, suggesting that they were supported only by soft tissues. Therefore, the position of replacement teeth in relation to marginal teeth cannot be assessed.

Two distinct attachment tissues can be recognized in the CT data. Firstly, a thin and very compact layer covers tooth lingual base and a small portion of the labial surface of the teeth, ankylosing the element to the tooth-bearing bone (Fig. 3.2A and C). This compact tissue is here interpreted as the cementum, although the exact type of cementum (acellular, cellular, etc) cannot be assessed. Cementum present a labial thickness that varies from nearly 50 $\mu$ m to 200 $\mu$ m. Just below the tooth, a more vascularized tissue, rich in osteons, is present, and it is here interpreted as the alveolar bone. Alveolar bone is present both below the tooth element and in between teeth (Fig. 3.2B and D). No trace of periodontal ligaments could be found among the CT data. The distinction of enamel and dentin, as well as the micromorphology of enamel crystallites, also could not be evaluated using only CT data.

Curiously, cross sections of some *Coniasaurus* jaw sections revealed an infolding structure of the dentin near the basalmost portion of the tooth base (Fig. 3.3). These were not present in distalmost portions of the base, only at their proximalmost region. Evident well-developed infoldings of the dentin is one of the features characterizing varanoid plicidentine (Kearney and Rieppel, 2006; Maxwell *et al.*, 2011). Although the exact definition of plicidentine can be more restrictive or broader in the literature (Maxwell *et al.*, 2011), a less complex pattern of dentin infolding may have preceded the varanoid highly infolded plicidentine. Therefore, *Coniasaurus* dentin might represent an intermediate step between a not infolded dentin at all and the complex infolded varanoid plicidentine.

### **3.4. Discussion**

#### **3.4.1. Homologies and homoplasies regarding mosasaurian tooth attachment patterns**

Overall, the anatomy and histology of tooth attachment in *Coniasaurus* is much more similar to those of varanoid lizards than to those of derived mosasauroids and/or snakes. The shallow attachment site, the lack of basal plates and interdental ridges and the thin cementum layer support the interpretation of the coniasaur tooth attachment patterns as plesiomorphic. This conclusion as an important significance concerning the evolution of tooth attachment in anguimorphan lizards. Two main hypotheses are present in the literature regarding the homology of mosasauroid and snake dentitions: 1) They present a homologous and synapomorphic mode of tooth implantation, which could be identified as true thecodonty

(Cope, 1869; Lee, 1997; Caldwell *et al.*, 2003; Caldwell, 2007; LeBlanc *et al.*, 2017); or 2) Mosasauroid and snakes present distinct modes of tooth implantation, and therefore similarities between them are the result of homoplasies (Zaher and Rieppel, 1999; Rieppel and Kearney, 2005; Luan *et al.*, 2009; Liu *et al.*, 2016). As most of the literature so far was including only more derived taxa, this analysis of tooth attachment patterns in a basal mosasaurian is very relevant for understanding character transformation through the evolution of Mosasauria.

Coniasaurs and other basal mosasaurians are usually interpreted either as stem mosasauroids (e.g. Rieppel and Zaher, 2000; Conrad, 2008; Wiens *et al.*, 2010; Conrad *et al.*, 2011; Gauthier *et al.*, 2012) or stem ophidiomorphs (e.g. Lee, 1998; Lee and Caldwell, 2000; Caldwell and Palci, 2010; Paparella *et al.*, 2018). As coniasaurs present a plesiomorphic mode of tooth attachment, fully pleurodont (*sensu* Zaher and Rieppel, 1999) as in varanoids and some other terrestrial lizards, even if mosasaurs and snakes are found to be true “thecodonts” in the feature, this feature must be interpreted as evolutionary convergence because of parsimony. In addition, scolecophidian snakes also do not present a “thecodont” mode of tooth implantation, only alethinophidian does (Zaher and Rieppel, 1999), supporting the hypothesis of derived mosasauroids and snakes dentition not being homologous. The lack of a basal plate, present in snakes (Zaher and Rieppel, 1999), and the presence of subtle but present dentin infoldings at the base of the teeth also approach coniasaur dentition closer to that of varanoids than to that of mosasauroids, and the inclusion of these features as characters in phylogenetic analysis may influence the systematic position of mosasaurians within Squamata.

### **3.4.2. Limitations of CT-based histology**

In this work several dentition patterns were identified, such as the presence of cementum and alveolar bone, the lack of a basal plate and the presence of dentin infoldings, in *Coniasaurus* using a non-destructive method (CT scanning). However, important questions remained unanswered by not performing traditional histology sections: what is the proportion of cellular and acellular cementum? Are there periodontal ligaments in *Coniasaurus*? What is the composition of the cementum layer in the taxon? Even using very high resolutions (6 $\mu$ m), many details of the tissues could not be evaluated. Therefore, CT data can be view as a complementary, not substitute, method for histological studies. The non-destructive nature of the scanning can help at including a wider sampling of specimens, while the destructive traditional histology methods can perform more detailed analyses of the tissues.

### 3.5. Final considerations

The results obtained here support Zaher and Rieppel (1999) conclusions that similarities in tooth implantation between derived snakes and mosasauroids evolved independently from standard pleurodony and cannot be used as an evidence to support the monophyly hypothesis of Pythonomorpha. In fact, the overall patterns of tooth attachment and implantation in *Coniasaurus* are much closer to those found in varanoid lizards than to those present in mosasauroids or snakes. CT-based histology is an important non-destructive method for evaluating these patterns in a wide range of specimens, but limitations in the technique prevent the substitution of traditional histological sections.

### References

- Baur, G.H.C.L. 1890. On the characters and systematic position of the large sea-lizards, Mosasauridae. **Science** 405: 262-262.
- Borsuk-Bialynicka, M. 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. **Palaeontologia Polonica** 46: 5-105.
- Caldwell, M.W. 2007. Ontogeny, anatomy and attachment of the dentition in mosasaurs (Mosasauridae: Squamata). **Zoological Journal of the Linnean Society** 149: 687-700.
- Caldwell, M.W.; Budney, L.A.; Lamoureux, D.O. 2003. Histology of tooth attachment tissues in the Late Cretaceous mosasaurid Platecarpus. **Journal of Vertebrate Paleontology** 23 (3): 622-630.
- Caldwell, M.W.; Carroll, R.L.; Kaiser, H. 1995. The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroids and varanoids. **Journal of Vertebrate Paleontology** 15(3): 516-531.
- Caldwell, M.W.; Palci, A. 2010. A new species of marine ophidiomorph lizard, *Adriosaurus skrbinsensis*, from the Upper Cretaceous of Slovenia. **Journal of Vertebrate Paleontology** 30(3): 747-755.
- Camp, C.L. 1923. Classification of the lizards. **Bulletin of the American Museum of Natural History** 48: 289-481.
- Carroll, R.L.; Debraga, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. **Journal of Vertebrate Paleontology** 12(1): 66-86.
- Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. **Bulletin of the American Museum of Natural History**, 310: 1-182.

- Conrad, J.L.; Ast, J.C.; Montanari, S.; Norell, M.A. 2011. A combined evidence phylogenetic analysis of Anguimorpha (Reptilia: Squamata). **Cladistics** 27: 230-277.
- Cope, E. D. 1878. Check-list of North American Batrachia and Reptilia: With a Systematic List of the Higher Groups, and an Essay on Geographical Distribution; Based on the Specimens Contained in the US National Museum (Vol. 1). **US Government Printing Office**: 115 p.
- Cope, E.D. 1869. On the reptilian orders Pythonomorpha and Streptosauria. **Proceedings of the Boston Society of Natural History** 12: 250-261.
- Fejérváry, G.J. 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. **Annales Historico-Naturales Musei Nationalis Hungarici** 16: 341-467.
- Gauthier, J.A.; Kearney, M.; Maisano, J.A.; Rieppel, O.; Behlke, A.D.B. 2012. Assembling the Squamate tree of life: perspectives from the phenotype and the fossil record. **Bulletin of the Peabody Museum of Natural History** 53(1): 3-308.
- Kearney, M.; Rieppel, O. 2006. An investigation into the occurrence of plicidentine in the teeth of squamate reptiles. **Copeia** 2006(3): 337-350.
- LeBlanc, A.R.; Lamoureux, D.O.; Caldwell, M.W. 2017. Mosasaurs and snakes have a periodontal ligament: timing and extent of calcification, not tissue complexity, determines tooth attachment mode in reptiles. **Journal of anatomy** 231(6): 869-885.
- Lee, M.S.Y. 1997a. On snake-like dentition in mosasaurian lizards. **Journal of Natural History** 31: 303-314.
- Lee, M.S.Y. 1997b. The phylogeny of varanoid lizards and the affinities of snakes. **Philosophical Transactions of the Royal Society of London B: Biological Sciences** 352: 53-91.
- Lee, M.S.Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. **Biological Journal of the Linnean Society** 65: 369-453.
- Lee, M.S.Y.; Caldwell, M.W. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. **Journal of Paleontology** 74(5): 915-937.
- Liu, M.; Reed, D.A.; Cecchini, G.M.; Lu, X.; Ganjawalla, K.; Gonzales, C.S.; Monahan, R.; Luan, X.; Diekwisch, T.G.H. 2016. Varanoid tooth eruption and implantation in a Late Cretaceous mosasaur. **Frontiers in Physiology** 7: 1-9.
- Luan, X.; Walker, C.; Dangaria, S.; Ito, Y. Druzinsky, R.; Jarosius, K.; Lesot, H; Rieppel, O. 2009. The mosasaur tooth attachment apparatus as paradigm for the evolution of the gnathostome periodontium. **Evolution & Development** 11(3): 247-259.

- Marsh, O.C. 1880. New characters of mosasauroid reptiles. **American Journal of Science** 19(3): 83-87.
- Maxwell, E.E.; Caldwell, M.W.; Lamoureux, D.O.; Budney, L.A. 2011. Histology of tooth attachment tissues and plicidentine in *Varanus* (Reptilia: Squamata), and a discussion of the evolution of amniote tooth attachment. **Journal of Morphology** 272(10): 1170-1181.
- McDowell, S.B.; Bogert, C.M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. **Bulletin of the American Museum of Natural History** 105: 1-142.
- Nopcsa, F.B. 1923. *Eidolosaurus* und *Pachyophis*: Zwei neue Neocom-Reptilien. **Palaeontographica** 65: 99-154.
- Osborn, H.F. 1899. A complete mosasaur skeleton, osseous and cartilaginous. **Bulletin of the American Museum of Natural History** 1: 167-188.
- Owen, R. 1877. On the rank and affinities of the reptilian class of Mosasauridae, Gervais. Geological Society of London, **Quarterly Journal** 33: 682-719.
- Paparella, I.; Palci, A.; Nicosia, U.; Caldwell, M.W. 2018. A new fossil marine lizard with soft tissues from the Late Cretaceous of southern Italy. **Royal Society Open Science** 5(6): doi 172411.
- Reeder, T.W.; Townsend, T.M.; Mulcahy, D.G.; Noonan, B.P.; Wood, P.L.Jr.; Sites, J.W.Jr.; Wiens, J.J. 2015. Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny and Reveal Unexpected Placements for Fossil Taxa. **PLoS ONE** 10(3): e0118199.doi:10.1371/journal.pone.0118199.
- Rieppel, O. 1980. **The phylogeny of anguimorph lizards**. Birkhauser Verlag, Basel, 86 p.
- Rieppel, O.; Kearney, M. 2005. Tooth replacement in the Late Cretaceous mosasaur *Clidastes*. **Journal of Herpetology** 39(4): 688-692.
- Rieppel, O.; Zaher, H. 2000a. The intramandibular joint in squamates and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. **Fieldiana (Geology), New Series** 43: 1-69.
- Russell, D.A. 1967. Systematics and morphology of American mosasaurs. **Bulletin of the Peabody Museum of Natural History** 23: 1-241.
- Wiens, J.J.; Kuczynski, C.A.; Townsend, T.; Reeder, T.W.; Mulcahy, D.G.; Sites, J.W.Jr. 2010. Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. **Systematic Biology** 59(6): 674-688.

Williston, S.W. 1904. The relationships and habits of the mosasaurs. **The Journal of Geology** 12(1): 43-51.

Zaher, H.; Rieppel, O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. **American Museum Novitates** 3271: 1-19.

**Chapter 4 - Ontogenetic trends in *Coniasaurus* (Squamata, Mosasauria) and its implications to the paleobiology and evolution of basal mosasaurians**

**Abstract**

Use of ontogenetic data is fundamental in systematics for establishing hypothesis of homology, character polarization and cladogram rooting, but the lack of embryonic and juvenile remains in Paleontology make this use much more limited among fossil taxa. Here embryonic remains of the dolichosaur *Coniasaurus* sp. nov. from the early Late Cretaceous of Texas, are described. Embryonic remains were compared to adult and subadult remains from nearby localities, and ontogenetic trends were observed. Some of the remains represent the first occurrence of specific bones for the genus *Coniasaurus*, such as the premaxilla and the quadrate. A single medial premaxillary tooth may represent an egg tooth, also present in some viviparous squamates. Coniasaurs bore at least two, maybe three, embryos during pregnancy. Sharp changes in dental and postcranial anatomy through development indicate possible dietary and locomotion shifts, respectively. Four characters were found to be ontogenetic related and may support character polarization, while eight characters were found to be not ontogenetic related, and therefore are considered here as strongly correlated with phylogenetic constraints. This is only the third record of viviparity in the clade Mosasauria, first among dolichosaurs, and highlight the importance of this trait during the mosasaurian evolution.

**Keywords:** Dolichosauridae; Mosasauria; Cretaceous; Ontogeny; Systematics.

## Resumo

O uso de dados ontogenéticos em sistemática é fundamental para estabelecer hipóteses de homologia, polarização de caracteres e enraizamento de cladogramas, mas a relativa ausência de espécimes embriológicos e juvenis em Paleontologia torna estes usos limitados quando se trata de táxons fósseis. Neste trabalho são descritos espécimes embriológicos do dolicossauro *Coniasaurus* sp. nov., provenientes do Cretáceo tardio do Texas (EUA). Os espécimes foram comparados com outros referentes à adultos e sub-adultos encontrados na mesma região, e então as tendências ontogenéticas foram comparadas. Alguns dos restos embriológicos descritos aqui representam as primeiras ocorrências de certos ossos em *Coniasaurus*, como a pré-maxila e o quadrado. Um único dente medial na pré-maxila pode representar um dente de ovo, que também está presente em alguns outros lagartos vivíparos. Os coniazauros retinham pelo menos dois, talvez três, embriões durante a gestação. Mudanças drásticas na anatomia dentária e pós-craniana ao longo do desenvolvimento indicam possíveis mudanças de hábitos de vida relacionadas à alimentação e à locomoção. Quatro caracteres morfológicos foram relacionados aqui à ontogenia, fornecendo suporte às hipóteses de polarização destes caracteres presentes na literatura. Por outro lado, oito caracteres não foram considerados como relacionados ao desenvolvimento e, portanto, são interpretados aqui como caracteres relacionados à evolução do grupo, tendo uma boa utilidade em análises filogenéticas. Este é apenas o terceiro registro de viviparidade dentro do clado Mosasauria, o primeiro dentre os dolicossauros, e evidencia a importância desta característica na evolução do grupo.

**Palavras-chave:** Dolichosauridae; Mosasauria; Cretáceo; Ontogenia; Sistemática.

## 4.1. Introduction

Ontogenetic data has a fundamental role in systematic studies of animals, being widely used for establishing homology hypothesis between structures (Nelson, 1978; Roth, 1984) and for character ordination, polarization and cladogram rooting (Rieppel, 1988; de Pinna, 1994; Mabee, 2000; Bryant, 2001), although some authors do question the reliability of ontogeny for character polarization (Mabee and Humphries, 1993). In addition, knowing ontogenetic parameters is also crucial for interpreting fossil taxa taxonomy and paleobiology (e.g. Rashid *et al.*, 2018). Fossil record of viviparity among marine Mesozoic reptiles is relatively common (e.g. Boetcher, 1990; Renesto *et al.*, 2003; Cheng *et al.*, 2004; O’Keefe and Chiappe, 2011; Motani *et al.*, 2014), but in mosasaurian lizards it has been reported previously only twice: once for the basal mosasauroid *Carsosaurus* (Caldwell and Lee, 2001) and once for the mosasaurid *Clidastes* (Field *et al.*, 2015). Although viviparity is traditionally considered an aquatic adaptation, especially in larger marine reptiles which could not walk on land, Motani *et al.* (2014) challenged this view by pointing that it may be present in terrestrial ancestors of aquatic Mesozoic reptiles, and not necessarily constrained by the aquatic lifestyles.

As the occurrence of fossilized juveniles and embryonic remains is quite rare in Paleontology, it makes the few records very relevant. Here embryonic remains associated with an adult female (specimen DMNH-1601; see Chapter 1) of the dolichosaur *Coniasaurus* sp. nov., from the early Late Cretaceous of Texas, are described. These were compared to subadult and adult coniasaur remains from nearby localities, and the paleobiologic and systematic implications of the highlighted ontogenetic trends were discussed. The presence of viviparity in the basalmost mosasaurian radiation, the commonly referred “dolichosaurs”, does support Motani *et al.* (2014) view in which terrestrial ancestors of mosasaurian lizards were likely viviparous animals.

## 4.2. Methods

Embryonic specimens were recovered by screen washing the sediments bearing DMNH-1601 associated materials. Nearly 300 embryonic remains were recovered, although mostly considerably fragmented. These were compared with both the adult DMNH-1601 and additional coniasaur remains from other localities. Ontogenetic stages of isolated elements were evaluated considering a series of conditions, such as relative size, degree of internal vascularization and degrees of long bone terminal fusions. The later, however, was taken carefully into account, since the terminal fusions greatly vary along the distinct Squamate

clades, and no terminal fusion universally coincides to sexual or skeletal mature size (Maisano, 2002).

### 4.3. Description of specimens and anatomical comparisons

#### 4.3.1. Cranial remains

*Premaxilla.* A single premaxilla was found only within embryonic remains of DMNH-1601 (Fig. 4.1). As premaxilla was an unknown bone up to now for *Coniasaurus*, its morphology with any other adult specimen of the same genus cannot be compared. In the embryo, the premaxilla is a 2mm long bone, broken at the middle of the narial bar. The element is already fused in coniasaur embryos, matching the same ontogenetic condition found in most squamates (Estes *et al.*, 1988), but differing from lizards as *Lanthanotus* which have paired narial bars even in juvenile specimens (Rieppel, 1992). Narial bar is considerably broader than in other dolichosaurs, such as *Pontosaurus* (Pierce and Caldwell, 2004; Caldwell, 2006; Fig. 4.1F), and the bar lateral edges run parallel to each other (Fig. 4.1A). Ventrally, five alveoli are present in the anteriormost edge of the bone, two in each side and a single element in the anteroventral premaxillary edge (Fig. 4.1B), which may be an egg tooth. If the middle element is indeed an egg tooth, *Coniasaurus* bears the same number of alveoli present in mosasaurs: two in each side (Russell, 1967). Maxillary processes are very reduced, like *Varanus*, but articulation with maxilla was loosely. *Pontosaurus* maxillary processes (Fig. 4.1F) are longer than this specimen, but it is unclear whether these differences are ontogenetic or phylogenetically related. No ethmoidal foramen is visible in the specimen. Ventrally, an elongated process runs from just after the medial tooth to the broken end of the bone (Fig. 4.1B), making the narial bar subtriangular in cross-section.

*Frontals.* DMNH-1601 has three frontal fragments preserved, one belonging to the adult specimen and two embryonic remains (Fig. 4.2). These were compared to NHMUK-R44141, the holotype of *C. gracilodens*, which bears a completely preserved frontal (Fig. 4.2-IV). Frontal is fused early in *Coniasaurus* development, during embryonic stages of development (Fig. 4.2-I and II), the expected condition for most squamates (Estes *et al.*, 1988). Both embryonic frontals are crushed just above the subolfactory processes (Fig. 4.2A), which may reflect a lesser degree of ossification in these stages. Possibly the most evident ontogenetic trend in coniasaur frontal is the presence of more conspicuous ventral grooves in the posteriormost portion of the subolfactory processes (Fig. 4.2B). These grooves receive the cartilaginous *solium suprasedale* in lizards (Oelrich, 1956), and the presence of conspicuous

grooves in embryos reveals a more cartilaginous composition of the skull due to earlier stages of development. Subolfactory processes are well developed but never touch each other ventrally (Fig. 4.2C), neither in adults nor in embryos, as in the varanoids *Saniwa* (Gauthier *et al.*, 2012), *Lanthanotus* (McDowell and Bogert, 1954) and *Shinisaurus crocodilurus* (Conrad, 2004) and in mosasauroids. Frontal is only moderately constricted in the interorbital region, both in embryos and adults (Fig. 4.2A). Posteriormost region is broken in every *Coniasaurus* sp. nov. frontals, so the frontoparietal suture shape and interdigitation pattern cannot be assessed. *Coniasaur* frontal is more similar in shape to those of varanoids by being constricted at mid-orbit than those of mosasaurs, which are solid and nearly triangular plates (Russell, 1967). The two embryonic frontal fragments are from nearly the same anatomical region, indicating the presence of at least two individuals in the female's womb.

*Quadrate*. A single distal portion of an embryonic right quadrate is the first record of the bone for *Coniasaurus* (Fig. 4.3). Mandibular condyle is well developed, bending both medially and laterally, and forming a somewhat inverted saddle (Fig. 4.3A and B), very similar to *Shinisaurus* (Conrad, 2004). Anteromedially there is a small and concave facet for articulation with the quadrate ramus of the pterygoid (Fig. 4.3A). Laterally, a large posterior crest arises just above the mandibular condyle (Fig. 4.3B). In cross section, the posterior crest is laterally convex (Fig. 4.3C). The element is broken at both medial and tympanic crests. A quadrate foramen pierces the bone medially and laterally (Fig. 4.3A and B), running slightly obliquely through the bone as in *Shinisaurus* (Conrad, 2004). Foramen is tiny sized as in most squamates (Gauthier *et al.*, 2012). Mosasauroids quadrates are considerably wide lateromedially (Russell, 1967), while *Coniasaurus* quadrate is more compressed (Fig. 4.3D and E). No sign of both suprastapedial and infrastapedial processes were preserved, thus preventing an assessment of their development.

*Maxillae*. Two maxillary fragments were found among DMNH-1601 remains, all belonging to embryos. None adult maxilla was recovered in this specimen. Two subadult maxillary remains from the Egyptian Way locality and four adult remains from the DFW Airport locality (see Chapter 2 for a description of each locality) were also included for anatomical comparisons. As the maxillary remains were very fragmentary, morphological comparisons are limited to some portions of the bone. Fig. 4.4 depicts three maxillary fragments (one embryonic, one juvenile and one adult) from nearly the same anatomical region (mid-to-posterior portion of the bone). Two maxillary foramina are visible in both the adult and subadult specimens, while the juvenile bears only an anterior edge of one large foramen in the lateral side of the bone (Fig. 4.4B). One main ontogenetic trend is clearly visible in Fig. 4.4: the

development of a larger medial sulcus in the dorsal surface of the maxilla (Fig. 4.4C), which is very small in embryos and considerably larger in subadult and adult specimens. This sulcus probably receives the palatine artery and vein (Porter and Witmer, 2015), so an increase in size probably reflects a higher blood supply capacity in later stages. Maxillary dental shelf is very thin and narrow in every ontogenetic stage, as in living varanoid lizards.

*Dentaries.* For evaluating dentary ontogeny, fragments from five embryos and one adult of DMNH-1601, two subadult individuals from the Egyptian Way locality and three additional adult specimens from the DFW Airport locality were included. Two of the embryonic dentary fragments are from the same side and from the same anatomical region, indicating they belonged to distinct individuals. Dentaries are in general less fragmentary than maxillary elements, allowing better morphological comparisons. Mental foramina are proportionally larger in embryos than in adults and subadults (Fig. 4.5B). Dentary is ventrally straight, as in other mosasauroids (character 357 of Gauthier *et al.*, 2012), in any stage of development. As in the maxilla, dentary dental shelves are thin and narrow (Fig. 4.5A). Meckel's groove is ventromedially exposed in every stage, the same condition found in other dolichosaurs (e.g. Caldwell and Cooper, 1999). One embryonic specimen preserves the anteriormost region of the dentary, revealing a very small symphyseal area (Fig. 4.5A-I).

*Dentition.* *Coniasaurus* bears a heterodont dentition with three distinct tooth morphotypes: 1) Anteriormost elements, which are more conical, backwards recurved and presenting a tapering apex; 2) Middle elements, presenting an intermediate morphology between anteriormost and posteriormost elements; and 3) Posteriormost elements, which are more robust and swollen and present a keeled carena in both mesial and distal surfaces, *contra* the former elements in which a carena is present only in the mesial surface (Fig. 4.6). Although these morphotypes can be differentiated from each other, it is hard to provide a precise count of each type alongside *Coniasaurus* dentition because morphotypes gradually changes from anterior to posterior elements, and no specimen with a complete dentition is known. Ontogenetically the most conspicuous change in *Coniasaurus* dentition is the loss of very sharp and pointing apex present in embryos and absent in subadults and adults, reflecting a possible change in feeding habits (see Discussion). In addition, teeth got more robust through development, which is particularly noticeable in dorsal view (Fig. 4.6C): embryonic teeth are always considerably more constricted labiolingually than the same elements in adults and subadults. Much less differences are perceptible when comparing subadults and adult specimens. In particular, subadults appear to have had sharper keels in both mesial and distal carina, but this may also reflect a more advanced degree of enamel wear. There are no

differences in tooth attachment patterns through ontogeny; every stage presents a very shallow attachment site for marginal teeth, resembling a varanoid mode of tooth implantation (see Chapter 3). The dentition is fully pleurodont *sensu* Zaher and Rieppel (1999). No resorption pits nor basal plates were observed in any studied specimen. Curiously, one of the embryonic specimens bears what appears to be a replacement tooth in a wrong position, in which one crown is considerably smaller and morphologically distinct from the others (Fig. 4.4-I). The presence of a failure in tooth shedding may indicate that tooth replacement started even in embryonic stages.

### 4.3.2. Axial remains

*Cervical vertebrae.* Six embryonic (Fig. 4.7-I) and three adult (Fig. 4.7-III) cervical vertebrae from DMNH-1601, as well as two elements from SMU-72396 (Fig. 4.7-II) and one isolated cervical vertebra from the DFW locality (SMU-69026; Fig. 4.7-IV) were compared. Fused intercentra in hypapophyses are present only in the adult DMNH-1601, not being present in embryonic *Coniasaurus* sp. nov., in juvenile SMU-72396 and in the larger specimen SMU-69026. Absence of intercentra fusion in SMU-69026, a specimen similar in size with the adult DMNH-1601, indicates either that this specimen had not completed skeletal maturity, even considering its relatively large size, or that intercentra fusion is indeed an autapomorphy of *Coniasaurus* sp. nov., with SMU-69026 belonging to a distinct taxon. The latter is considered to be true here. Dorsoventral compression of the vertebral centrum is a noticeable ontogenetic trend, especially in posterior view (Fig. 4.7E), with condyles and cotyles being more rounded in embryos and juveniles and more dorsoventrally compressed in adults. A conspicuous constriction just before the condyle is observed in juveniles and adults, but absent in embryos, which may be due to incompleteness of ossification processes. Synapophyses are closer to the vertebral centrum in embryos and juveniles than in adults (Fig. 4.7E), and also less robust. In ventral view (Fig. 4.7B), it is possible to notice a trend in the shape of the centrum, being more “Y” shaped in embryos and more “T” shaped in adults.

*Dorsal vertebrae.* Ontogenetic trends were assessed by comparing six embryonic (Fig. 4.8-I) and 32 adult (Fig. 4.8-II) dorsal vertebrae from DMNH-1601, 25 from SMU-72396 (Fig. 4.8-III) and one from the DFW locality (SMU-69022; Fig. 4.8-IV). Some ontogenetic trends are observable regarding the centrum morphology. Firstly, it gets proportionally more elongate and laterally thinner (Fig. 4.8B). Secondly, there is a conspicuous curvature in the ventral surface of the centrum, especially visible in lateral view (Fig. 4.8C), a feature that disappears already in juveniles. A constriction right before the condyle, not visible in embryonic cervicals,

is noticeable in dorsal elements, but only slightly marked (Fig. 4.8B). In embryos, the centrum is somewhat constricted at its mid-portion, with both the cotyle and the condyle being laterally larger than the middle of the centrum, while in juvenile and adults the centrum presents the same thickness in any part of it. A deep sulcus in the lateral surface of the centrum, formed by the development of postzygoprezygapophyseal lamina (PPRL) and the posterior centrosynapophyseal lamina (PCYL), is present only in the adult DMNH-1601, supporting the interpretation of this feature being an autapomorphy of *Coniasaurus* sp. nov. and SMU-69022 belonging to a distinct coniasaur taxon (Fig. 4.8C). Dorsal centra also gets more compressed dorsoventrally through ontogeny, as in cervicals, although in the Fig. 4.8-IV the selected specimen is slightly taphonomically distorted, being compressed laterally and giving a more rounded aspect to the condyle and cotyle. The angle of zygosphene-zygantrum articulation (Fig. 4.8E) seems consistent through ontogeny, being lateroventrally oriented in juveniles and adults (unfortunately, this feature is not visible in embryos). An evident posterior thickness of the neural spine base, a synapomorphy shared by *Coniasaurus* sp. nov. and *C. longicollis* (Chapter 2 of this thesis), is present in the adult DMNH-1601 and the juvenile SMU-72396, but not observable in embryonic remains (neural arches were rarely preserved in these specimens) and not present in SMU-69022, which indicates that this specimen belong to a distinct taxon other than *Coniasaurus* sp. nov. and *C. longicollis*.

*Sacral vertebrae.* Sacrals were preserved only in the adult DMNH-1601 (Fig. 4.9-II) and in the juvenile SMU-72396 (Fig. 4.9-I). *Coniasaurus* bears two sacral vertebrae as in other dolichosaurs (Chapter 2 of this thesis), but these are fused only in DMNH-1601, being an autapomorphy of *Coniasaurus* sp. nov. Fusion of sacral vertebrae is probably absent in embryos, since other fused elements of the adult are unfused in embryos (e.g. hypapophyses with intercentrum and diapophysis with haemal arches), but no undisputed sacral vertebrae was found among embryonic remains. First sacral is relatively smaller than second one in DMNH-1601, but subequal in size in SMU-72396 (Fig. 4.9A). As in other vertebral elements, sacral centrum is more dorsoventrally compressed in the adult than in the juvenile. Sacral vertebrae size is smaller than the average dorsal vertebrae size for both specimens, a condition shared by every coniasaur taxa (e.g. Caldwell, 2000). Although broken in both specimens, sacral region receiving sacral ribs seems to be larger in the second element than in the first one either in adult and juvenile forms.

*Pygal vertebrae.* Three pygal vertebrae were preserved embryonic remains of DMNH-1601 (Fig. 4.10-I), and only one in both SMU-72396 (Fig. 4.10-II) and in the adult DMNH-1601 (Fig. 4.10-III). If only one pygal was indeed present in *Coniasaurus* axial series, the

presence of three embryonic pygals would indicate that at least three individuals were developing inside the female. Curiously, centrum morphology of the pygal develop opposite ontogenetic trends than other presacral vertebrae. Presacral centra gets more dorsoventrally compressed through ontogeny, but pygal centrum becomes more rounded, taller dorsoventrally (Fig. 4.10E) in the adult, while more compressed in embryos and in the juvenile (although crushed in the later; Fig. 4.10-II). Transverse processes go through major ontogenetic changes in pygal elements. Firstly, they are only thin projections, needle shaped, in embryos, becoming anteroposteriorly larger but still dorsoventrally compressed in juveniles and conspicuously more robust elements in the adult (Fig. 4.10C). Secondly, orientation of the processes also changes through development: they are more laterally oriented in immature specimens and more ventrolaterally oriented in the adult (Fig. 4.10D). As in dorsal vertebrae, the centrum is also more curved ventrally in lateral profile in embryos and straighter in juveniles and adults (Fig. 4.10C). An anterior transverse process sulcus is visible only in the adult specimen, but was probably absent in juveniles and embryos since in these the processes were much more compressed dorsoventrally (Fig. 4.10D). Pre- and postzygapophyseal articulation appears to become slightly more ventrally oriented in adults than in juveniles (Fig. 4.10E).

*Caudal vertebrae.* Specimen DMNH-1601 was represented by eight embryonic (Fig. 4.11-I) and 24 adult (Fig. 4.11-III) caudal vertebrae. These were compared to five juvenile elements (specimen SMU-72396; Fig. 4.11-II) and to an additional adult caudal vertebra from the DFW locality (specimen SMU-69025; Fig. 4.11-IV). There are considerable changes in caudal morphology regarding the element placement (more anterior, middle or more posterior) in tail, so for anatomical comparisons mid-caudals of the different specimens were chosen. As in pygal vertebrae, there is an ontogenetic trend towards the anteroposterior growth of the transverse process (Fig. 4.11C), which basically doubles its size. Ventrally, diapophyses proportionally longer and more robust, with a ventral sulcus in the middle of the centrum becoming more conspicuous (Fig. 4.11B). Haemal arches are fused to diapophyses in the adult DMNH-1601, but only in this specimen. As it is the case for the intercentra fusion in cervical elements, it is possible that the fusion of these vertebral elements is an autapomorphy of *Coniasaurus* sp. nov., since they were observed only in the adult DMNH-1601. Changes in centrum morphology, either getting more compressed as in presacral vertebrae or more rounded as in pygal elements, is not observed in caudal vertebrae (Fig. 4.11E). Another difference from other vertebral elements is the lateral compression of the centrum, which is present only in embryonic remains of dorsal elements (Fig. 4.8B) but present in every ontogenetic stage of caudal vertebrae. Haemal arches are posteriorly placed in every ontogenetic stage (Fig. 4.11C),

even in embryos, suggesting this feature to be phylogenetically rather than ontogenetically related.

### 4.3.3. Appendicular remains

*Humerus*. Three specimens were used to compare ontogenetic trends in coniasaur humerus: an embryonic humerus attached to an adult dorsal vertebra from DMNH-1601 (Fig. 4.12-I), a juvenile isolated element from the New Locality (Fig. 4.12-II) and the humerus from the adult DMNH-1601 specimen (Fig. 4.12-III). Because the embryonic element is still attached to adult bone, only the lateral portion of the bone is visible. Characteristic twist in the humerus shaft is already present in earlier ontogenetic stages, but the shaft does get more twisted in the adult. On the other hand, the conspicuous tubercle in the shaft mid-portion only appears in adult forms (both in DMNH-1601 and *C. longicollis*; see Chapter 2). Deltopectoral crest becomes slightly more elongated and thinner through development, which may be an adaptation for higher swimming distances. Epiphyses are not completely ossified in earlier stages, a condition expected for juvenile squamates, although the absence of epiphyseal fusion cannot be taken as an undisputed evidence of sexual maturity (Maisano, 2002). A tuberosity just above the ectepicondyle is also present solely in the adult (Fig. 4.12B). In proximal view it is possible to notice that the area for the articulation with the glenoid fossa is more developed in the juvenile than in the adult (Fig. 4.12E), suggesting differences in movement limitations. Ectepicondylar foramen is absent even in earlier stages, suggesting this character to be more phylogenetic than ontogenetic related.

## 4.4. Discussion

### 4.4.1. How many embryos did *Coniasaurus* bear?

DMNH-1601 is a holotype bearing associated but disarticulated remains of an adult female and several embryos. The exact number of embryonic individuals, however, cannot be assessed without error because of bone disarticulation. Morphological evidences indicate the presence of at least two, maybe three, embryos.

Embryonic jaw sections are mostly fragmentary within DMNH-1601, but at least two dentaries certainly represent two distinct individuals (Fig. 4.13A and B). These elements are fragments of anteriormost regions of left dentaries, and thus could not have belonged to the same individual. The same is valid for the frontals (Fig. 4.2), were the two embryonic remains are from nearly the same anatomical region. However, three embryonic pygal vertebrae were

found among DMNH-1601 remains, which may indicate the presence of three embryos. Derived mosasaurs acquired multiple pygals through the evolution of swimming in the clade, with some mosasaurines such as *Plotosaurus* presenting more than 30 pygals (Lindgren *et al.*, 2011). On the other hand, semi-aquatic dolichosaurs presented a much lower count, closer to that of living squamates. Two pygals were reported for *Adriosaurus* (Lee and Caldwell, 2000) and *Pontosaurus* (Caldwell, 2006), and only one for *Dolichosaurus* (Caldwell, 2000) and *Kaganaias* (Evans *et al.*, 2006). As *Adriosaurus* and *Pontosaurus* axial skeletons are preserved mostly in dorsal view, and as *Dolichosaurus* was found to be nested within the genus *Coniasaurus* as a distinct species (see Chapters 1 and 2), a number of just one pygal seems reasonable. If *Coniasaurus* indeed possessed only one pygal in his vertebral count, then at least three embryonic individuals were carried by females at the same time. This number could be greater, since the semi-aquatic and basal mosasauroid *Carsosaurus* beared at least four embryos (Caldwell and Lee, 2001).

#### 4.4.2. Changes in lifestyles through development

Some of the noted *Coniasaurus* ontogenetic trends seems to be related to changes in lifestyles. Dietary shifts through development were likely present in the taxon especially when analyzing the ontogeny of tooth morphology (Fig. 4.6). Embryos are already heterodont, but they possess more gracile dental elements, with crowns being more mediolaterally compressed and bearing a conspicuous needle-shaped apex (Fig. 4.6-I). Subadults and adults, on the other hand, beared more robust elements, without a piercing apex and presenting a more developed anterodorsally oriented carena (Fig. 4.6-II and III). Adult crowns are also more swollen, especially in posteriormost elements (Fig. 4.6C). Massare (1987) divided marine Mesozoic reptiles into distinct ecological “guilds” based on tooth morphology. According to that division, coniasaur neonates (based on embryonic tooth morphology) can be classified into the piercing guild, especially because their needle-shaped crown apex. Subadults and adults were more likely to have belonged to the crunching guild, what could indicate that neonates fed on soft-bodied invertebrates while adults fed on thin-shelled invertebrates, such as crustaceans. Paleofauna of the Eagle Ford Group does support *Coniasaurus* dietary habits including crustaceans, as these are common findings among fossil invertebrates of the region (Moreman, 1927).

In addition, ontogeny also supports changes in the relative swimming capability of neonates and adults. Transverse processes of both pygal and caudal elements get proportionally more developed in subadults in relation to embryos, and even more in adults in relation to

subadults (Fig. 4.10C). Transverse processes received massive epaxial musculature in mosasaurs (Russell, 1967), so the more developed processes in adults indicate proportionally stronger tails, allowing better swimming capabilities. Neural spines and haemal arches are mostly broken in the studied specimens, so detailed comparisons of the tail musculature height cannot be done. Two additional ontogenetic trends of the humerus may also be related to locomotion constraints. Firstly, deltopectoral crest became relatively longer and more laterally oriented in adults (Fig. 4.12A). Secondly, the area for the articulation with the glenoid fossa is relatively larger in juveniles than in adults (Fig. 4.12E). Deltopectoral crest serves as a basis for musculature insertion (Russell, 1967), so the larger crests in adults indicate proportionally larger musculature. The larger area for articulation with the glenoid fossa in juveniles indicates differences in movement limitation, so the humerus morphology also supports adult and juveniles having distinct swimming capabilities. Even considering that dolichosaurs had tiny forelimbs, these may have had some function in maneuverability.

#### 4.4.3. Systematic considerations

Ontogenetic trends in *Coniasaurus* may also have systematic implications for the evolution of the genus and for character distribution and polarization in squamate matrices as well. Firstly, a putative egg tooth is present in the embryonic premaxilla. Viviparous squamate embryos and neonates can retain a non-functional egg tooth, which is reabsorbed faster than in oviparous animals (Ananeva and Orlov, 2013; Griffith *et al.*, 2015). In the latter group, egg tooth is usually oriented anterodorsally for helping to break the egg, but in viviparous lizards it is posteroventrally oriented. In both groups the egg tooth is larger than the marginal teeth (Ananeva and Orlov, 2013), so it is possible that the medial premaxillary tooth represents not an egg tooth but instead a functional marginal tooth, as in some varanoids (Gauthier *et al.*, 2012; character 413). In general, the presence or absence of an egg tooth is uninformative for phylogenetic purposes (Griffith *et al.*, 2015), but it is reported here as a relevant anatomical information. Viviparity is also shown to be present in three distinct mosasaurian radiations: basal mosasaurians (dolichosaurs; this work), basal mosasauroids (Caldwell and Lee, 2001) and mosasaurids (Field *et al.*, 2015). Therefore, it seems reasonable to suppose that it was present really early in mosasaurian evolution, maybe as early as in their terrestrial ancestors, as it was hypothesized by Motani *et al.* (2014).

Some characters used in phylogenetic analyses were observable here to be ontogenetic related. Although ontogenetic trends may not be reliable parameters for character polarization (Mabee and Humphries, 1993), they may serve as additional support for polarization in addition

to outgroup comparisons. Character 437 of Gauthier *et al.* (2012) regards the absence (state 0) or presence (state 1) of swollen teeth. In taxa with a considerably variation of tooth morphology through development, such as *Coniasaurus*, tooth crowns do get more swollen in later stages (Fig. 4.6C), supporting the polarization of the character. However, tooth characters are very plastic in reptiles, and in fossil specimens of unknown developmental stages codification may reflect ontogeny. Cervical intercentrum is unfused in embryos and fused in adult hypapophyses (character 243 of Conrad, 2008), so polarization may be unfused (state 0) → fused (state 1). Two new characters found in previous Chapters of this thesis may also have their polarization “tested”, both agreeing with former codifications. First, ventral shape of dorsal vertebra does changes from more “V” shaped centrum (state 0) in embryos to more “T” shaped (state 1) in adults (Fig. 4.8B). Second, sacrals are unfused (state 0) in subadults and fused (state 1) in adults (Fig. 4.9), although sacral fusion may be an autapomorphy of *Coniasaurus* sp. nov.

On the other hand, some characters were found to be not ontogenetic related, being constant in embryos/juveniles and adults. Therefore, they are considered here as being phylogenetically more informative. Tooth crown height is constant through development (Fig. 4.5; character 416 of Gauthier *et al.*, 2012). Frontal is already fused in embryos, highlighting this fusion as occurring early in coniasaur development as in most squamates (Estes *et al.*, 1988). Cervical and caudal intercentrum position (characters 461 and 475, respectively, of Gauthier *et al.*, 2012) is constant through ontogeny (Figs. 7C and 11C). The posterior thickness of neural spine bases, a character found to unite *Coniasaurus* sp. nov. and *C. longicollis* in a monophyletic assemblage (see Chapter 2), was found in both embryos and adults. Ectepicondylar foramen (character 530 of Gauthier *et al.*, 2012) is absent either in juveniles and adults (Fig. 4.12). Zygosphene-zygantrum articulation angle (character 468 of Gauthier *et al.*, 2012) is constant through ontogeny, always being lateroventrally oriented (Fig. 4.8E). Consistent states through ontogeny for every one of these characters support the interpretation of these characters being phylogenetically, and not ontogenetically, related, highlighting their importance in squamate phylogenetic studies.

#### **4.5. Final considerations**

This contribution describes for the first time embryological remains in a dolichosaur lizard, highlighting important trends through its development. An analysis of isolated dentaries, frontals and pygal vertebrae reveals the presence of at least two, maybe three, embryos within the gravid female during pregnancy. Four characters were found to be ontogenetically related,

helping to test hypothesis of character polarization: presence of swollen teeth, fusion of cervical intercentra, shape of the ventral surface of the centrum and the fusion of sacral vertebrae. On the other hand, seven characters were found as being not ontogenetically related, and therefore phylogenetically more informative: tooth crown proportional height, frontal fusion, intercentrum position in cervical and caudal vertebrae, posterior thickness of neural spine bases, absence of humeral ectepicondylar foramen, and zygosphenes-zygantrum articulation angle. Changes in cranial and appendicular anatomy through development suggest adults and juveniles to occupy distinct ecomorphospaces, which would have helped them having no niche partitioning.

## References

- Anan'eva, N. B.; Orlov, N. L. 2013. Egg teeth of squamate reptiles and their phylogenetic significance. **Biology Bulletin** 40(7): 600-605.
- Boettcher, R. 1990. New Information on the Reproductive Biology of Ichthyosaurs (Reptilia). **Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaeontologie)** 164: 1–51.
- Bryant, H.N.; Wagner, G. 2001. Character polarity and the rooting of cladograms. *The character concept in evolutionary biology*, 319-337.
- Caldwell, M.W.; Cooper, J.A. 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the Lower Chalk (Cretaceous; Cenomanian) of SE England. **Zoological Journal of the Linnean Society** 127: 423-452.
- Caldwell, M.W.; Lee, M.S.Y. 2001. Live birth in Cretaceous marine lizards (mosasauroids). **Proceedings of the Royal Society: Biological Sciences** 268: 2397-2401.
- Caldwell, M.W. 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in Squamates. **Journal of Vertebrate Paleontology** 20(4): 720-735
- Caldwell, M.W. 2006. A New Species of "Pontosaurus" (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a Phylogenetic Analysis of Pythonomorpha. **Società Italiana di Scienze Naturali**: 1-44.
- Cheng Y.N.; Wu, X.C.; Ji, Q. 2004. Triassic marine reptiles gave birth to live young. **Nature** 432: 383–386.

- Conrad, J.L. 2004. Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). **Zoological Journal of the Linnean Society** 141(3): 399-434.
- Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. **Bulletin of the American Museum of Natural History**, 310: 1-182.
- de Pinna, M.C.C. 1994. Ontogeny, rooting, and polarity. In: Scotland, R.W.; Siebert, D.J.; Williams, D.M. **Models in phylogeny reconstruction**. Systematics Association Special Volume (52). Oxford, Clarendon Press. p. 157-157.
- Estes, R.; de Queiroz, K.; Gauthier, J. 1988. Phylogenetic relationships within Squamata. In: Estes, R.; Pregill, G. (eds). **Phylogenetic relationships of the lizard families**. Stanford, Stanford University Press, p. 119-282.
- Evans, S.E.; Manabe, M.; Noro, M.; Isajis, S.; Yamaguchi, M. 2006. A longbodied lizard from the Lower Cretaceous of Japan. **Paleontology** 49(6): 1143-1165.
- Field, D.J.; LeBlanc, A.; Gau, A.; Behlke, A.D. 2015. Pelagic neonatal fossils support viviparity and precocial life history of Cretaceous mosasaurs. **Palaeontology** 2015: 1-7.
- Gauthier, J.A.; Kearney, M.; Maisano, J.A.; Rieppel, O.; Behlke, A.D.B. 2012. Assembling the Squamate tree of life: perspectives from the phenotype and the fossil record. **Bulletin of the Peabody Museum of Natural History** 53(1): 3-308.
- Griffith, O.W.; Blackburn, D.G.; Brandley, M.C.; Van Dyke, J.U.; Whittington, C.M.; Thompson, M.B. 2015. Ancestral state reconstructions require biological evidence to test evolutionary hypotheses: a case study examining the evolution of reproductive mode in squamate reptiles. **Journal of Experimental Zoology Part B: Molecular and Developmental Evolution** 324(6): 493-503.
- Lee, M.S.Y.; Caldwell, M.W. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. **Journal of Paleontology** 74(5): 915-937.
- Lindgren, J.; Polcyn, M.J.; Young, B.A. 2011. Landlubbers to leviathans: evolution of swimming in mosasaurine mosasaurs. **Paleobiology** 37: 445-469.
- Mabee, P.M.; Humphries, J. 1993. Coding polymorphic data: examples from allozymes and ontogeny. **Systematic Biology** 42(2): 166-181.
- Mabee, P.M. 2000. The usefulness of ontogeny in interpreting morphological characters. **Phylogenetic analysis of morphological data**: 84-114.
- Maisano, J.A. 2002. Terminal fusions of skeletal elements as indicators of maturity in squamates. **Journal of Vertebrate Paleontology** 22(2): 268-275.

- Massare, J. A. (1987). Tooth morphology and prey preference of Mesozoic marine reptiles. **Journal of Vertebrate Paleontology** 7(2): 121-137.
- McDowell, S.B.; Bogert, C.M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. **Bulletin of the American Museum of Natural History** 105: 1-142.
- Moreman, W.L. 1927. Fossil zones of the Eagle Ford of north Texas. **Journal of Paleontology**: 89-101.
- Motani, R.; Jiang, D.Y.; Tintori, A.; Rieppel, O.; Chen, G.B. 2014. Terrestrial origin of viviparity in Mesozoic marine reptiles indicated by Early Triassic embryonic fossils. **PloS one** 9(2): e88640.
- Nelson, G. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. **Systematic Zoology** 27(3): 324-345.
- O'Keefe, F.R.; Chiappe, L.M. 2011. Viviparity and K-selected life history in a Mesozoic marine plesiosaur (Reptilia, Sauropterygia). **Science** 333(6044): 870-873.
- Oelrich, T.M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). **University of Michigan Museum of Zoology Miscellaneous Publications** 94: 1-122.
- Pierce, S.; Caldwell, M.W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur, *Pontosaurus lesinensis* (Kornhuber, 1873). **Journal of Vertebrate Paleontology** 24: 376-389.
- Porter, W.R.; Witmer, L.M. 2015. Vascular patterns in iguanas and other squamates: Blood vessels and sites of thermal exchange. **PloS one** 10(10): e0139215.
- Rashid, D.J.; Surya, K.; Chiappe, L.M.; Carroll, N.; Garrett, K.L.; Varghese, B.; Balilleul, A.; O'Connor, J.K.; Chapman, S.C.; Horner, J.R. 2018. Avian tail ontogeny, pygostyle formation, and interpretation of juvenile Mesozoic specimens. **Scientific reports** 8(1): 9014.
- Renesto, S.; Lombardo, C.; Tintori, A.; Danini, G. 2003. Nothosaurid embryos from the Middle Triassic of northern Italy: an insight into the viviparity of nothosaurs?. **Journal of Vertebrate Paleontology** 23(4): 957-960.
- Rieppel, O. 1988. **Fundamentals of comparative biology**. Boston, Birkhauser Verlag: 202 p.
- Rieppel, O. 1992. The skeleton of a juvenile *Lanthanotus* (Varanoidea). **Amphibia-Reptilia** 13(1): 27-34.
- Roth, V.L. 1988. The biological basis of homology. **Ontogeny and systematics**: 1-26.

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

Zaher, H.; Rieppel, O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. **American Museum Novitates** 3271: 1-19.

## **Chapter 5 - Evolution of the postcranial skeleton in basal mosasaurians (Squamata, Mosasauria)**

### **Abstract**

Basal mosasaurians, commonly referred to as “dolichosaurs”, are a group of extinct aquatic squamates most commonly found in Cenomanian-Turonian rocks of North America and Europe. Some postcranial features usually found among the group include the presence of an elongated neck, reduced forelimbs and accessory zygankrum-zygosphenes articulations. While some of these were used in phylogenetic analyses to support the Pythonomorpha hypothesis (i.e. a monophyletic assemblage including dolichosaurs, mosasauroids and snakes), a global analysis of the postcranial anatomy of dolichosaurs have not been performed so far. Here, the postcranial anatomy of dolichosaurs were extensively compared, allowing the identification of important insights regarding its evolution. Presacral count characters are concluded to not be adequate for phylogenetic purposes and should be replaced by cervical and dorsal counts. Pubic morphology and cervical extension in dolichosaur do not support the Pythonomorpha hypothesis. New postcranial diagnostic characters were identified for some dolichosaur lineages. *Aphanizocnemus*, *Eidolosaurus* and *Primitivus* seem to lack some important dolichosaur features and may therefore be found outside Mosasauria in phylogenetic analyses including a broader taxonomical sampling. Postcranial characters supporting either hypotheses of mosasaurians as varanoids or pythonomorphs are discussed, evidencing the importance of detailed anatomic studies including basalmost radiations for better understanding character distribution.

**Keywords:** Dolichosauridae; Cretaceous; Systematics; Axial regionalization.

## Resumo

Mosassaurianos basais, comumente chamados de “dolicossauros”, são um grupo de lagartos aquáticos extintos encontrados mais frequentemente em rochas do Cenomaniano-Turoniano da América do Norte e Europa. Alguns caracteres pós-cranianos que caracterizam o grupo incluem a presença de um pescoço alongado, membros dianteiros reduzidos e articulações acessórias nas vértebras (zigósfeno e ziganthro). Embora alguns caracteres pós-cranianos tenham sido utilizados em análises filogenéticas para dar suporte à hipótese Pythonomorpha (isto é, o agrupamento monofilético que inclui dolicossauros, mosassauróides e serpentes), uma análise global da anatomia pós-craniana dos dolicossauros ainda não foi realizada. Nesta contribuição, a anatomia do esqueleto pós-craniano dos dolicossauros foi extensivamente comparada, permitindo a identificação de tendências sobre sua evolução. Os caracteres morfológicos chamados de “contagem de vértebras pré-sacrais” foram considerados aqui como inadequados para fins de reconstruções filogenéticas, e deveriam ser substituídos por caracteres que levem em consideração o número de vértebras cervicais e dorsais independentemente. A morfologia do púbis e a contagem de vértebras cervicais não favorece a hipótese Pythonomorpha, ao contrário do que apontaram estudos anteriores. Novos caracteres diagnósticos do esqueleto pós-craniano foram identificados para algumas linhagens de dolicossauros. *Aphanizocnemus*, *Eidolosaurus* e *Primitivus* aparentam não possuir algumas das características diagnósticas dos dolicossauros e, portanto, podem representar linhagens não-relacionadas ao clado Mosasauria em análises incluindo uma maior amostragem taxonômica. Caracteres fornecendo suporte tanto para a hipótese dos mosassauros serem relacionados aos varanóides como às serpentes são discutidos, evidenciando a importância de estudos anatômicos detalhados que incluam as radiações mais basais de um grupo para melhor compreender a distribuição de caracteres.

**Palavras-chave:** Dolichosauridae; Cretáceo; Sistemática; Regionalização axial.

## 5.1. Introduction

Dolichosaurs are a group of semi-aquatic lizards whose monophyly and phylogenetic relationships are intensely debated in the scientific community (Carroll and DeBraga, 1992; Bell, 1997; Lee, 1998; Caldwell, 1999a; Zaher and Rieppel, 1999; Rieppel and Zaher, 2000a; Conrad, 2008; Gauthier *et al.*, 2012; Reeder *et al.*, 2015). Sixteen species of dolichosaurs are currently recognized (including those listed at the General Introduction of this thesis and the new *Coniasaurus* sp. nov. described in Chapter 1), ranging from rocks of Japan in the East to the Eastern portions of the North American Western Interior Seaway in the West, and from the Berriasian-Hauterivian in the Lower Cretaceous to the Campanian-Maastrichtian in the Upper Cretaceous, although the vast majority of dolichosaurs were described from Cenomanian-Turonian rocks (Owen, 1850; Nopcsa, 1923; Dal Sasso and Pinna, 1997; Caldwell, 1999; Lee and Caldwell, 2000; Lee and Scanlon, 2002; Pierce and Caldwell, 2004; Haber and Polcyn, 2005; Caldwell, 2006; Evans *et al.*, 2006; Palci and Caldwell, 2007; Caldwell and Palci, 2010; Palci and Caldwell, 2010; Paparella *et al.*, 2018; Chapter 1 of this thesis). Phylogenetic analyses of mosasaurian lizards (dolichosaurs and mosasauroids) are still inconclusive regarding their relationships within Squamata, with three main hypothesis arising: 1) Mosasauria is a monophyletic clade closely related to varanoid lizards (e.g. Rieppel and Zaher, 2000; Conrad, 2008; Wiens *et al.*, 2010; Conrad *et al.*, 2011); 2) Mosasauria is a monophyletic clade in a more basal position within Squamata, being the sister-group of Scleroglossa (Gauthier *et al.*, 2012); 3) Mosasauria is a paraphyletic assemblage, with dolichosaurs being more closely related to snakes than to mosasauroids (e.g. Lee, 1998; Lee and Caldwell, 2000; Caldwell and Palci, 2010; Paparella *et al.*, 2018).

As the skull of many dolichosaur specimens is crushed and badly damaged, many postcranial features are commonly associated to the group and used for assigning specimens as dolichosaurs. These include the presence of an elongated neck, with at least 10 cervical vertebrae, reduced limbs and the presence of accessory zygantrum-zygosphene vertebral articulation (e.g. Dal Sasso and Pinna, 1997; Caldwell, 2000; Palci and Caldwell, 2007; Caldwell and Palci, 2010). However, an extensive survey of the dolichosaur postcranial skeleton, including as much specimens as possible, have not been made so far. This is a crucial line of research, since many postcranial characters were used to either support or reject phylogenetic hypothesis regarding dolichosaur affinities. A discussion of each postcranial character used to support the hypothesis of mosasaurians being more closely related to varanoids or to snakes is provided in the end of the work. Hypothesis of mosasaurians as the

sister-group of *Scleroglossa* was entirely supported by cranial characters in Gauthier *et al.* (2012), and therefore was not tested here.

## 5.2. Methods

### 5.2.1. Institutional Abbreviations

**BMB**, Booth Museum of Natural History, Brighton, England; **DMNH**, Perot Museum of Nature and Science, Dallas, USA; **GBA**, Geological Survey of Austria; **MCSNT**, Museo Civico di Storia Naturale di Trieste; **MSNM**, Museo di Storia Naturale di Milano; **MZSP**, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **NHMUK**, Natural History Museum, London, England; **SMU**, Southern Methodist University, Dallas, USA;

### 5.2.2. Specimens analyzed

In addition to the coniasaur specimens already cited in the Chapter 2 of this thesis, 14 basal mosasaurians and basal mosasauroids specimens, housed in European collections, were personally studied. These were: *Acteosaurus tommasinii* (MCSNT 9960), *Adriosaurus microbrachis* (MCSNT 7792), *Adriosaurus suessi* (NHMUK PR 2867; MCSNT 9400), *Adriosaurus* sp. (MCSNT 7793; MCSNT 11426), *Aphanizocnemus libanensis* (MSNM V783), *Carsosaurus marchesetti* (MCSNT unnumbered), *Eidolosaurus trauthi* (GBA 1923/001/0001), *Komensaurus carrolli* (MCSNT 11430-2), *Mesoleptos zendrinii* (MCSNT 9962), *Opetiosaurus buccichi* (GBA 1901/002/0001-0005), *Pontosaurus kornhuberi* (MSNM V3662) and *Pontosaurus lesinensis* (GBA 1873/004/0001-0002).

### 5.2.3. Measurements

Measurements were taken using a digital caliper three times for each structure. Whenever both limbs were preserved in a specimen, both were measured and then an average number was calculated.

### 5.2.4. CT Data

CT images used in this work were taken according to the methodology already cited in the Chapter 1 of this thesis.

### 5.3. Anatomical comparisons

#### 5.3.1. Axial skeleton

*Vertebral formula.* There is a considerable variation in mosasaurian vertebral counts regarding distinct modules (cervical, dorsal, pygal, etc.; see Table 1), but some common patterns can be noticed. Cervical count appears to bear a strong phylogenetic signal than dorsal count. Overall, dolichosaurs present the highest cervical count: 10 or more (10 in most taxa, 11 in *Pontosaurus lesinensis* and *Eidolosaurus trauthi* and 19 in *Coniasaurus longicollis*), followed by *Lanthanotus* and *Varanus* with 9, *Heloderma*, *Shinisaurus* and *Plotosaurus* with 8, basal mosasauroids with 7 or 8 and most mosasaurids with 7. Dorsal vertebrae count vary more within clades: it is higher than 30 in the dolichosaurs *Coniasaurus* (32) and *Kaganaias* (36) and in the mosasaurids *Mosasaurus* (38) and *Plotosaurus* (35); between 26 and 30 in the dolichosaurs *Acteosaurus* (27), *Adriosaurus* (28-30), *Aphanizocnemus* (26) and *Pontosaurus* (26-29) and in the living varanoids *Heloderma* (26-28), *Lanthanotus* (26) and in some *Varanus* species (26); and below 26 in the dolichosaurs *Eidolosaurus* (23) and *Primitivus* (22), in basal mosasauroids (18-21), in the mosasaurids *Halisaurus* (24), *Ectenosaurus* (22), *Platecarpus* (22) and *Tylosaurus* (23) and in most *Varanus* species (18-25). The distinct variation patterns among cervical and dorsal series cast doubts on the quality of characters regarding only “presacral counts”, since these are clearly distinct evolutionary modules (see item 5.4.1. on the Discussion). Sacral number is consistent (2) for every taxon preserving them. Pygal counts, on the other hand, present some slight variation in basal members of the Mosasauria, and varies a lot within crown Mosasauridae. Only 1 is present in most dolichosaurs, living anguimorphs and in the basal mosasauroids *Carsosaurus* and *Valecillosaurus*. 2 pygals are reported for the dolichosaurs *Adriosaurus suessi* and *Pontosaurus kornhuberi*, 3 for the basal mosasaurid *Dallasaurus*, 4 in the basal mosasauroid *Aigialosaurus* and in the mosasaurid *Halisaurus* and 5 to 30 in other mosasaurids. Complete caudal series are lacking for most fossil taxa, thus preventing a proper comparison between caudal counts.

**Table 1 – Vertebral formula in some anguimorph lizards. Abbreviations: Ce = cervical vertebrae; Do = dorsal vertebrae; PC = presacral count; Sa = sacral vertebrae; Py = pygal vertebrae; Cd = caudal vertebrae other than pygals.**

Taxon	Clade	Ce	Do	PC	Sa	Py	Cd	References
<i>Acteosaurus tommasinii</i>	Basal mosasaurian (dolichosaur)	10	27	37	2	?	?	Palci and Caldwell (2010); pers. obs.
<i>Adriosaurus microbrachis</i>	Basal mosasaurian (dolichosaur)	?	28	?	?	?	?	Caldwell and Lee (2004); pers. obs.
<i>Adriosaurus skrbiniensis</i>	Basal mosasaurian (dolichosaur)	10	30	40	2	?	?	Caldwell and Palci (2010)
<i>Adriosaurus suessi</i>	Basal mosasaurian (dolichosaur)	10	29	39	2	2	?	Lee and Caldwell (2000); pers. obs.
<i>Aphanizocnemus libanensis</i>	Basal mosasaurian (dolichosaur)	8-10	26-28	36	2	1	141	Dal Sasso and Pinna (1997); Mekarski (2017); pers. obs.
<i>Coniasaurus</i> sp. nov.	Basal mosasaurian (dolichosaur)	?	32	?	2	1	?	Chapter 1 of this thesis
<i>Coniasaurus longicollis</i>	Basal mosasaurian (dolichosaur)	19	32	51	2	1	?	Caldwell (2000); pers. obs.
<i>Eidolosaurus trauthi</i>	Basal mosasaurian (dolichosaur)	11	23	34	2	1	?	Nopcsa (1923); pers. obs.
<i>Kaganaias hakusanensis</i>	Basal mosasaurian (dolichosaur)	?	36	?	2	1	?	Evans <i>et al.</i> (2006)
<i>Pontosaurus kornhuberi</i>	Basal mosasaurian (dolichosaur)	10	26	36	2	2	163	Caldwell (2006); pers. obs.

<i>Pontosaurus lesinensis</i>	Basal mosasaurian (dolichosaur)	11	29	40	2	?	?	Pierce and Caldwell (2004); pers. obs.
<i>Primitivus manduriensis</i>	Basal mosasaurian (dolichosaur)	10	22	32	2	?	?	Paparella <i>et al.</i> (2018)
<i>Aigialosaurus dalmaticus</i>	Basal mosasauroid (“aigialosaur”)	7-8	19-20	27	2	4	?	Dutchak and Caldwell (2006)
<i>Carsosaurus marchesetti</i>	Basal mosasauroid (“aigialosaur”)	?	21	?	?	1	?	Caldwell and Lee (2001); pers. obs.
<i>Opetiosaurus buccichi</i>	Basal mosasauroid (“aigialosaur”)	7-8	18-19	26	2	?	?	Dutchak and Caldwell (2009); pers. obs.
<i>Vallecillosaurus donrobertoi</i>	Basal mosasauroid (“aigialosaur”)	?	19	?	2	1	?	Smith and Buchy (2008); Buchy and Smith (2011)
<i>Halisaurus sternbergii</i>	Mosasauridae: Halosaurinae	7	24	31	-	4	?	Bardet and Superbiola (2005)
<i>Dallasaurus turneri</i>	Mosasauridae: Mosasaurinae	?	?	34	-	3	70	Bell and Polcyn (2005); Lindgren <i>et al.</i> (2011)
<i>Mosasaurus</i>	Mosasauridae: Mosasaurinae	7	38	45	-	8	75	Russell (1967)
<i>Plotosaurus bennisoni</i>	Mosasauridae: Mosasaurinae	8	35	43	-	30	60	Lindgren <i>et al.</i> (2007, 2011)
<i>Ectenosaurus</i>	Mosasauridae: Plioplatecarpinae	7	22	29	-	?	?	Russell (1967)
<i>Platecarpus</i>	Mosasauridae: Plioplatecarpinae	7	22	29	-	5	91-96	Russell (1967)

<i>Tylosaurus</i>	Mososauridae: Tylosaurinae	7	22- 23	29- 30	-	6-7	90- 112	Russell (1967)
<i>Heloderma</i>	Anguimorpha: Helodermatidae	8	26- 28	34- 36	2	1	27	Boulenger (1891); McDowell and Bogert (1954); Hoffstetter and Gasc (1969)
<i>Lanthanotus</i>	Anguimorpha: Lanthanotidae	9	26	35	2	1	68- 63	McDowell and Bogert (1954); Rieppel (1980)
<i>Shinisaurus</i>	Anguimorpha: Shinisauridae	8	18- 19	26- 27	2	0-1	nearly 40	McDowell and Bogert (1954); Conrad (2006)
<i>Varanus</i>	Anguimorpha: Varanidae	9	18- 26	27- 35	2	1	?	McDowell and Bogert (1954); Hoffstetter and Gasc (1969); Burnell <i>et al.</i> (2012); Cieri (2018)

*Cervical vertebrae.* The atlas and axis are both preserved in *Adriosaurus suessi* (Lee and Caldwell, 2000), *Pontosaurus lesinensis* (Pierce and Caldwell, 2004), *Pontosaurus kornhuberi* (Caldwell, 2006) and in *Eidolosaurus trauthi* as molds (Nopcsa, 1923). As most dolichosaur specimens are preserved in plates, it is very hard to properly describe the atlas and the axis once a tridimensional view of the elements is not possible. Atlas is always anteroposteriorly compressed in dolichosaurs as in most squamates, being represented by a thin and curved element (Figure 5.1A). Axis, as in more derived mosasaurs (Russell, 1967) is a much more robust element, very similar in size to the anterior cervical elements. Cervical elements other than the atlas and the axis vary in number, with dolichosaurs presenting the longest cervical count of all mosasaurians. It is important to state which definition of “cervical vertebrae” is being used here though. The most widely used definition of cervical vertebrae in squamate systematics is the one given by Hoffstetter and Gasc (1969): all those elements preceding the one bearing the first rib united to the sternum. However, sternum is often not preserved in fossil specimens and because of it this definition of cervical vertebrae cannot be

applied for many extinct taxa. In this work vertebral elements bearing hypapophyses and short ribs are considered as cervicals. Although the complex atlas and axis is preserved only in a few taxa, other cervical remains are known for most dolichosaurs. A feature shared by all dolichosaurs is the elongation of the neck, with every taxon described so far presenting at least 10 cervical elements (11 in *Pontosaurus lesinensis* and *Eidolosaurus trauthi*, and 19 in *Coniasaurus longicollis*), while living anguimorphs always present a number below 10 (Hoffstetter and Gasc, 1969) and mosasauroids between 7 and 8 (Russell, 1967; Dutchak and Caldwell, 2009; Lindgren *et al.*, 2011). Cervical hypapophyses in dolichosaurs always present large peduncles, which is unfused in most taxa and fused in adult *Coniasaurus* sp. nov. (an autapomorphy of the taxon; see Chapter 1) as showed in Figure 5.1. As most specimens are preserved in slabs, features such as the angle of the pre- and postzygapophyses articulation cannot be assessed. Future studies providing CT data of known specimens may pave the way for proper morphological comparisons.

*Dorsal vertebrae.* Dorsal elements are by far the most common postcranial element preserved among dolichosaur remains. This vertebral module bears the highest variation in mosasaurian lizards. While cervical count seems to be strongly phylogenetically related (dolichosaurs universally presenting 10 or more and mosasauroids typically 7), dorsal counts appears to be more functionally than phylogenetically constrained. Another possible hypothesis is that there is a lot of homoplasy in mosasaurian dorsal formula. Living anguimorphs usually present between 26 and 28 dorsal elements (McDowell and Bogert, 1954; Hoffstetter and Gasc, 1969; Rieppel, 1980; Conrad, 2006), although some *Varanus* species have 25 or less elements (Cieri, 2018). In mosasaurians, this count is: below 26 in two dolichosaurs (*Eidolosaurus* and *Primitivus*), in basal mosasauroids (18-19 in *Opetiosaurus*, 19 in *Vallecillosaurus*, 19-20 in *Aigialosaurus* and 21 in *Carsosaurus*; Caldwell and Lee, 2001; Dutchak and Caldwell, 2006; Smith and Buchy, 2008; Dutchak and Caldwell, 2009; Buchy and Smith, 2011) and in halisaurine, plioplatecarpine and tylosaurine mosasaurs (Russell, 1967); between 26 and 30 in most dolichosaurs (26 in *Aphanizocnemus*, 26-29 in *Pontosaurus*, 27 in *Acteosaurus* and 28-30 in *Adriosaurus*; Dal Sasso and Pinna, 1997; Lee and Caldwell, 2000; Pierce and Caldwell, 2004; Caldwell, 2006; Palci and Caldwell, 2010); and higher than 30 in two dolichosaur genera (*Coniasaurus* with at least 32 and *Kaganaias* with at least 36; Caldwell, 2000; Evans *et al.*, 2006; Chapter 1 of this work) and in mosasaurine mosasaurs (Russell, 1967). Pachyostosis is variably present in dolichosaurs: *Adriosaurus*, *Eidolosaurus*, *Pontosaurus* and *Primitivus* do possess at least some degree of this feature, while *Acteosaurus*, *Aphanizocnemus*, *Coniasaurus*

and *Kaganaias* do not bear any trace of it. Zygosphenes are present in every dolichosaur taxa, and although they are lacking in living varanoids, some extinct varanoid taxa do present a “zygosphene-like” structure (Smith *et al.*, 2008). Shape of zygosphenes vary among taxa, with most dolichosaurs presenting a straight lamina in dorsal view, and coniasaurs presenting a more recurved lamina. Neural spines are very large and tall, running through the entire neural arch, in *Coniasaurus*, and usually broken in other taxa, but *Kaganaias* appears to have had a relatively lower neural spine (Evans *et al.*, 2006). Neural arches are usually lateromedially larger in their anteriormost portion, but in *Adriosaurus* they are slightly larger at their posteriormost portion (Figure 5.2B). Ventrally, dorsal centrum has a somewhat “V” shape in most dolichosaurs, while it is more “T” shaped in *Coniasaurus*, basal mosasauroids and in the basal mosasaurid *Dallasaurus* (pers. obs.; Figure 5.2). Most mosasaurids present a “box-shaped” centrum. Zygapophyses preserves a similar size through the vertebral column, a primitive condition that differs from the one found in more derived mosasaurs in which zygapophyses of more posterior elements are relatively smaller (Russell, 1967).

*Sacral vertebrae.* Sacrals, as in most squamates, are always represented by two elements that are slightly shorter than the average dorsal vertebrae. Size of sacral elements in relation to each other varies a lot, even at intrageneric level, and thus bear few or no phylogenetical sign at all among mosasaurian lizards. For instance, the first sacral element is lateromedially larger than the second one (the most common condition in sacrum-bearing lizards; Hoffstetter and Gasc, 1969) in *Adriosaurus suessi*, *Aphanizocnemus libanensis* and *Coniasaurus* sp. nov., while the opposite is true for *Adriosaurus skrbiniensis*, *Kaganaias hakusanensis* and *Coniasaurus longicollis* (Figure 5.3). Sacral ribs are stout and robust elements, dorsoventrally compressed, as in varanoid lizards. The sacral region of *Coniasaurus* sp. nov. is striking similar to the one of *Heloderma*, with fused elements and recurved contact between pre- and postzygapophyses (Figure 5.3A and C). However, in *Heloderma* the sacral ribs are also fused, while in *Coniasaurus longicollis* they are not (Figure 5.3B).

*Pygal vertebrae.* The first caudal elements bearing transverse processes but no synapophyses nor peduncles for haemal arches are considered here as pygal vertebrae. In basal mosasaurians the number of pygals is usually low, being just 1 in the dolichosaurs *Aphanizocnemus*, *Coniasaurus*, *Eidolosaurus* and *Kaganaias* and in the basal mosasauroids *Carsosaurus* and *Vallecillosaurus*, and 2 in the dolichosaurs *Adriosaurus* and *Pontosaurus*. The count is 3 in the basal mosasaurid *Dallasaurus* and 4 in the basal mosasauroid *Aigialosaurus* and in the halisaurine *Halisaurus*. In more derived mosasaurids the number of pygals starts to greatly increase: 5 in *Platecarpus*, 6 or 7 in *Tylosaurus*, 8 in *Mosasaurus* and 30 in *Plotosaurus*

(Russell, 1967; Lindgren *et al.*, 2011). Pygals are the same size or slightly shorter than sacrals in dolichosaurs. Pygal transverse processes is ovoid both in *Coniasaurus* (Chapter 1 of this thesis) and *Dallasaurus* (Bell and Polcyn, 2005).

*Other caudal vertebrae.* Lindgren *et al.* (2011) classified caudal vertebrae into three distinct categories: pygal (bearing transverse processes but no chevrons), intermediate caudals (bearing transverse processes and chevrons) and terminal caudals (bearing chevrons only). However, this classification cannot be adequately assessed in dolichosaurs because most specimens are preserved in slabs (thus their tridimensional morphology cannot be viewed) and tridimensionally preserved specimens, like North American coniasaurs, are not complete. Therefore, only two caudal “categories” are considered here: pygal and “other caudals”. Relatively complete caudal series are only present in *Aphanizocnemus libanensis* (bearing 141 elements), *Pontosaurus kornhuberi* (bearing 163 elements) and *Adriosaurus suessi* (bearing at least 65 elements). Caudal centrum in dolichosaurs is always slightly longer than taller, contrary to the opposite condition found in derived mosasaurids (Russell, 1967). Dolichosaurs presented a haemal arch / vertebral height (measured from the ventral part of the centrum to the dorsal part of the neural arch, without considering the neural spine) of nearly 1,55 in *Aphanizocnemus* and *Acteosaurus*, 1,65 in *Adriosaurus* and a considerably higher ratio of 1,87 in *Coniasaurus* (Chapter 1 of this thesis). This ratio evidence distinct muscle attachment areas which may be linked to distinct aquatic swimming capabilities. Although the ratio is higher in coniasaurs, it is considerably less than in mosasauroids (3,45 in *Opetiosaurus* and higher in more derived mosasaurids).

*Ribs.* Two categories of ribs are present in dolichosaurs: anteriormost elements, more gracile and rounded in cross section (cervical ribs) and posteriormost elements, larger, more robust and bearing costal grooves (trunk ribs). Number of cervical ribs varies according to the number of cervical vertebrae. Trunk ribs can be pachyostotic in taxa presenting this condition (e.g. *Adriosaurus* and *Pontosaurus*). Dolichosaurs presenting pachyostosis also present ribs that are closer to dorsal vertebrae, giving a laterally compressed body aspect, which may be related to distinct lifestyles than those not presenting these features (e.g. *Acteosaurus* and *Coniasaurus*).

### **5.3.2. Appendicular skeleton**

*Digits and phalangeal formula.* Every basal mosasaurian and basal mosasauroid with one or both manus preserved present the squamate plesiomorphic 2-3-4-5-3 phalangeal formula (Dal Sasso and Pinna, 1997; Polcyn *et al.*, 1999; Caldwell and Lee, 2004; Pierce and Caldwell,

2004; Caldwell, 2006; Dutchak and Caldwell, 2006; Caldwell and Palci, 2007; Dutchak and Caldwell, 2009; Buchy and Smith, 2011; Paparella *et al.*, 2018). A manus formula of ?-3-3-4-? was reported for *Adriosaurus suessi* (Lee and Caldwell, 2000), but the specimen is poorly preserved and lacks some phalanges, therefore this number cannot be confidently assessed (Figure 5.4). Regarding the pes, the plesiomorphic squamate formula is 2-3-4-5-4 (Gauthier *et al.*, 2012), which is present in the dolichosaurs *Adriosaurus microbrachis* (Palci and Caldwell, 2007) and *Primitivus manduriensis* (Paparella *et al.*, 2018), and in the basal mosasauroids *Haasiasaurus gittelmani* (Polcyn *et al.*, 1999) and *Vallecillosaurus donrobertoi* (Smith and Buchy, 2008). However, a reduction of one element in the fifth digit, giving a pes phalangeal formula of 2-3-4-5-3, is observed in the dolichosaurs *Acteosaurus tommasinii* (Palci and Caldwell, 2010), *Aphanizocnemus libanensis* (Dal Sasso and Pinna, 1997) and *Pontosaurus kornhuberi* (Caldwell, 2006), and in the basal mosasauroid *Opetiosaurus buccichi* (Dutchak and Caldwell, 2009). In derived mosasaurids, limbs evolved to paddle-like structures for specialized aquatic locomotion, which lead digits to acquire two main differences in relation to more basal members of the Mosasauria: 1) hyperphalangy in both manus and pes; and 2) lost of ungual phalanges (present uniformly in basal mosasaurians and mosasauroids) (Russell, 1967).

*Scapula and coracoid.* These bones are fused elements in the dolichosaurs *Aphanizocnemus*, *Pontosaurus lesinensis* (maybe in *P. kornhuberi* as well) and in the basal mosasauroid *Opetiosaurus* (Dal Sasso and Pinna, 1997; Pierce and Caldwell, 2004; Caldwell, 2006; Dutchak and Caldwell, 2009) and unfused elements in the dolichosaurs *Acteosaurus*, *Adriosaurus*, *Coniasaurus* and *Primitivus*, in the basal mosasauroids *Carsosaurus* and *Haasiasaurus* and in mosasaurs (Russell, 1967; Caldwell, 1999; Polcyn *et al.*, 1999; Caldwell, 2000; Caldwell and Lee, 2001; Bell and Polcyn, 2005; Palci and Caldwell, 2007, 2010; Paparella *et al.*, 2018). Size of the elements in relation to each other also varies within Mosasauria. Coracoid is much larger than the scapula in the dolichosaurs *Adriosaurus microbrachis*, *Aphanizocnemus*, *Coniasaurus*, *Pontosaurus* and *Primitivus* (Dal Sasso and Pinna, 1997; Caldwell, 1999, 2000; Pierce and Caldwell, 2004; Caldwell, 2006; Palci and Caldwell, 2007; Paparella *et al.*, 2018), in the basal mosasauroids *Opetiosaurus* and *Haasiasaurus* (Polcyn *et al.*, 1999; Dutchak and Caldwell, 2009) and in some mosasaurs such as *Tylosaurus* (Russell, 1967), and the scapula is nearly the same size as the coracoid in the dolichosaur *Adriosaurus skrbiniensis* (Palci and Caldwell, 2007) and in most mosasaurids (Russell, 1967). One synapomorphy of Squamata recognized by Estes *et al.* (1988) is the anterior emargination of the coracoid, which is present in most members of the Mosasauria but

lost in the dolichosaurs *Coniasaurus* and *Primitivus* (Caldwell, 1999, 2000; Paparella *et al.*, 2018). A single coracoid foramen is present in most basal mosasaurian lizards (*Carsosaurus marchesetti* had two; Caldwell *et al.*, 1995). The scapula is emarginated, forming a margin for the scapulocoracoid fenestra, in the dolichosaurs *Aphanizocnemus* and *Coniasaurus gracilodens* (Dal Sasso and Pinna, 1997; Caldwell, 1999), in the basal mosasauroid *Opetiosaurus* (Dutchak and Caldwell, 2009) and in mosasaurids (Russell, 1967), while not emarginated in *Coniasaurus longicollis* and *Pontosaurus lesinensis* (Caldwell, 2000; Pierce and Caldwell, 2004). A feature distinguishing more derived mosasaur from basal forms is the suture between the scapula and the coracoid, which is interdigitated in most mosasaurids (Russell, 1967). This feature is probably only weakly developed in *Dallasaurus* (Bell and Polcyn, 2005) and not present at all in basal forms.

*Clavicle and interclavicle.* Clavicles and interclavicles are absent in many dolichosaurs, but it is unclear whether these were not present in the skeleton or are absent due to preservational biases. Taxa presenting fragmentary clavicles include *Adriosaurus skrbiniensis*, *Aphanizocnemus*, *Mesoleptos* and *Pontosaurus*. Among these, the clavicle is a more robust element, expanded proximally, in *Aphanizocnemus* and *Pontosaurus*, (Dal Sasso and Pinna, 1997; Caldwell, 2006) while in *Adriosaurus* and *Mesoleptos* it is a very thin, strap-like, structure (Lee and Scanlon, 2002; Caldwell and Palci, 2010), closer in shape to that of basal mosasauroids (Caldwell *et al.*, 1995). Interclavicle is absent in every dolichosaur taxa but *Pontosaurus*, in which it is a thin and flat bar, close in shape to the interclavicles of mosasaurine mosasaurs (Russell, 1967; Pierce and Caldwell, 2004; Caldwell, 2006).

*Sternum.* A calcified sternum is present in the dolichosaur *Coniasaurus longicollis* (Caldwell, 2000), in the basal mosasauroid *Carsosaurus* (Caldwell *et al.*, 1995) and probably in mosasaurs, although this structure is rarely preserved in mosasaurs: for instance, only two mosasaurine specimens had this structure preserved: *Clidastes propython* and *Mosasaurus missouriensis* (Russell, 1967; Konishi *et al.*, 2014). Sternum was solely cartilaginous in every other dolichosaur, being partially preserved as cartilage fragments in *Pontosaurus* and *Primitivus* (Caldwell, 2006; Paparella *et al.*, 2018). In the basal mosasauroid *Vallecillosaurus* it was also preserved as a fragment of the original cartilage (Buchy and Smith, 2011).

*Humerus.* Typically, dolichosaurs present a very reduced forelimb in relation to the hindlimb. This is especially noticeable when comparing the ratio between the humerus and the femur (Table 2). Most dolichosaurs present values for this ratio that ranges from 0,4 to 0,6, with most ranging from 0,5 to 0,58. Only three taxa have very distinct values: *Eidolosaurus trauthi* (0,7), *Aphanizocnemus libanensis* (0,76) and *Primitivus manduriensis* (0,8). The only basal

mosasauroid preserving both humerus and femur analyzed in this work is *Carsosaurus marchesetti*, which presents a humerus subequal in size to the femur (ratio of 0,92) like more derived mosasaurs. *Adriosaurus microbrachis* was described presenting a very unusual vestigial humerus and lacking more distal forelimb elements (Palci and Caldwell, 2007). Although the morphology of the humerus is indeed distinct from other dolichosaurs, by having a very reduced distal end (Figure 5.5A and B), the absence of epipodial, mesopodial and metapodial elements can be taphonomically and not biologically related. Coniasaurs present a set of unique, synapomorphic humeral characters in relation to other dolichosaurs: 1) very large deltopectoral crests; 2) shaft conspicuously twisted; and 3) noticeable crest and tubercle in the mid-portion of the shaft (Figure 5.5C; see also Chapter 2). In other dolichosaurs, the humerus is usually a short element presenting a constriction in the middle of the shaft, with both proximal and distal ends expanded (*Adriosaurus microbrachis* is an exception by presenting an expansion only in the proximal head). Ectepicondylar and entepicondylar foramina are always absent in dolichosaurs. Deltopectoral crest can be square-shaped, like in adriosaurs (Figure 5.5A and B), or more rounded, like in coniasaurs (Figure 5.5C). In basal mosasauroids, the humerus is similar in shape to that of dolichosaurs but lacks the conspicuous reduction in size seen in most dolichosaurs. On the other hand, derived mosasaurs present a very distinctive humerus due to specialization for aquatic locomotion, being a massive, hourglass-shaped bone, very expanded proximally and distally and with a large area for articulation with the glenoid fossa (Russell, 1967).

**Table 2 – Humerus / femur ratio in basal mosasaurians. Measurements are given in millimeters. Sources marked as “this work” indicate specimens that were personally measured by the first author.**

Taxon	Humerus length	Femur length	Hum/Fem ratio	Source
<i>Acteosaurus tommasinii</i>	6,55	13,9	0,47	This work
<i>Adriosaurus microbrachis</i>	6,4	12,3	0,52	This work
<i>Adriosaurus skrbinensis</i>	?	?	0,4	Caldwell and Palci (2010)
<i>Adriosaurus suessi</i>	5,8	9,9	0,58	This work

Undescribed <i>Adriosaurus</i> specimen (MCSNT 11426)	6,3	11,3	0,56	This work
<i>Aphanizocnemus libanensis</i>	5,8	7,6	0,76	This work; Dal Sasso and Pinna (1997)
<i>Coniasaurus</i> sp. nov.	17,6	35,4	0,5	This work
<i>Eidolosaurus trauthi</i>	13,9	19,8	0,7	This work
<i>Pontosaurus kornhuberi</i>	16,5	33	0,5	Caldwell (2006)
<i>Primitivus manduriensis</i>	34,74	43,23	0,8	Paparella <i>et al.</i> (2018)
<i>Carsosaurus marchesetti</i>	80	86,6	0,92	This work

*Radius* and *ulna*. In contrast to terrestrial lizards, in mosasaurians the radius and the ulna are always distally divergent elements, an adaptation usually interpreted as related to aquatic locomotion (Russell, 1967; Pierce and Caldwell, 2004; Paparella *et al.*, 2018). Ulna is usually larger than the radius, except in *Acteosaurus tommasinii* and *Adriosaurus suessi* where the opposite is true (Lee and Caldwell, 2000; Palci and Caldwell, 2010). Typically, the radius is more expanded distally while the ulna is more expanded proximally, as seen in *Acteosaurus*, *Aphanizocnemus*, *Pontosaurus*, *Carsosaurus*, *Platecarpus*, *Clidastes*, *Tylosaurus*, and in living anguimorphs with legs (Russell, 1967; Caldwell *et al.*, 1995; Dal Sasso and Pinna, 1997; Pierce and Caldwell, 2004; Caldwell, 2006; Conrad, 2006; Palci and Caldwell, 2010), but in *Adriosaurus skrbiniensis*, *Primitivus* and *Opetiosaurus* both are more expanded proximally (Dutchak and Caldwell, 2009; Caldwell and Palci, 2010; Paparella *et al.*, 2018) and in *Adriosaurus suessi*, *Plotosaurus* and *Ectenosaurus* they are more expanded distally (Russell, 1967; Lee and Caldwell, 2000). Distal end of the radius can be rounded, as in *Acteosaurus* (Palci and Caldwell, 2010), or square, as in *Adriosaurus* (Caldwell and Lee, 2004; Caldwell and Palci, 2010), while distal end of the ulna is always squarer.

*Carpal and metacarpal elements*. These elements are only known in articulated specimens, usually preserved in slabs, and therefore are unknown in taxa like *Coniasaurus*. Composition of the mesopodium is consistent regarding the distal row, always presenting carpals two to five. However, the same is not true for the proximal row, which can be composed by three, four, five or six elements. *Adriosaurus* present a proximal row formed by three elements: a radiale, an intermedium and an ulnare (Caldwell and Lee, 2004). Taxa presenting four elements also varies in presence / absence of the same: *Pontosaurus* has radiale, medial

centrale, intermedium and ulnare (Caldwell, 2006); *Primitivus* and the basal mosasauroid *Vallecillosaurus* present radiale, lateral centrale, ulnare and pisiform (Buchy and Smith, 2011; Paparella *et al.*, 2018); and mosasaurine mosasaurs usually have radiale, intermedium, ulnare and pisiform elements (Russell, 1967). The basal mosasauroids *Komensaurus* and *Carsosaurus* bears the highest count for the proximal carpal row with, respectively, five and six elements: *Komensaurus* has radiale, lateral centrale, medial centrale. ulnare and pisiform (Caldwell and Palci, 2007); and *Carsosaurus* has radiale, lateral centrale, medial centrale. intermedium, ulnare and pisiform (Caldwell *et al.*, 1995). In mosasaurians, the largest proximal carpal element is usually the ulnare, as seen in the dolichosaur *Adriosaurus*, in the basal mosasauroids *Vallecillosaurus* and *Carsosaurus* and in most derived mosasaurs (Russell, 1967; Caldwell *et al.*, 1995; Lee and Caldwell, 2000; Buchy and Smith, 2011), although in *Pontosaurus*, *Primitivus* and in some mosasaurines the radiale and the ulnare are nearly subequal in size (Russell, 1967; Caldwell, 2006; Paparella *et al.*, 2018). The intermedium is relatively small in basal mosasaurians (Caldwell, 2006). Metacarpal morphology is consistent through the evolution of the group, with metacarpals one and five being hourglass-shaped rather than rod-like. First metacarpal is conspicuously broader, and the third is the longest element (Russell, 1967; Caldwell *et al.*, 1995; Dal Sasso and Pinna, 1997; Polcyn *et al.*, 1999; Caldwell and Lee, 2004; Caldwell, 2006; Caldwell and Palci, 2007; Buchy and Smith, 2011; Paparella *et al.*, 2018).

*Pubis.* A hatchet-like pubis, proximally expanded, is characteristic for every basal mosasaurian preserving this bone. It is slightly more cross-shaped in *Adriosaurus skrbiniensis* than in other dolichosaurs (Caldwell and Palci, 2010), with distinctive anterior and posterior ends near the pubis head. This morphology is very distinct, for instance, to those snakes bearing pelvic elements, in which the pubis is not much expanded proximally, and it is distally recurved (Figure 5.6B and C; Lee and Caldwell, 1998; Houssaye *et al.*, 2011). *Adriosaurus suessi* has a very damaged pubis due to poorly preservation of the specimen, but an undescribed adriosaur from the Museo Civico di Storia Naturale di Trieste, MCSNT-11426, has a nicely preserved pubis (Figure 5.6A). Anteriorly, a pubic process or tubercle rises opposite to the ischium, which can be more developed and conspicuous as in *Acteosaurus*, *Adriosaurus*, *Eidolosaurus*, *Pontosaurus*, *Komensaurus*, *Vallecillosaurus* and some *Clidastes* species (Nopcsa, 1923; Russell, 1967; Caldwell, 2006; Caldwell and Palci, 2007; Smith and Buchy, 2008; Caldwell and Palci, 2010; Palci and Caldwell, 2010), or less developed and subtle as in *Aphanizocnemus*, *Primitivus*, *Mosasaurus* and *Tylosaurus* (Russell, 1967; Dal Sasso and Pinna, 1997; Paparella *et al.*, 2018). Distally, the pubis narrows to form a rod-like structure, ending in

a square-shape terminal. A pubic obturator foramen is apparently absent in the dolichosaurs *Acteosaurus* and *Adriosaurus microbrachis* (Palci and Caldwell, 2007; 2010), and present as a large opening in *Adriosaurus* sp. (Figure 5.6A), *Adriosaurus skrbinensis*, *Aphanizocnemus*, *Pontosaurus kornhuberi* and in mosasauroids (Russell, 1967; Dal Sasso and Pinna, 1997; Bell and Polcyn, 2005; Caldwell, 2006; Caldwell and Palci, 2007; 2010).

*Ischium*. This element is slightly shorter than the pubis, nearly 80% of the later length, in the dolichosaurs *Acteosaurus*, *Adriosaurus*, *Pontosaurus*, *Primitivus* and in the mosasaur *Platecarpus* (Russell, 1967; Caldwell, 2006; Caldwell and Palci, 2010; Palci and Caldwell, 2010; Paparella *et al.*, 2018), while it is nearly the same size of the pubis in the dolichosaur *Aphanizocnemus*, *Komensaurus*, *Mosasaurus*, *Tylosaurus* and living anguimorphs (Russell, 1967; Dal Sasso and Pinna, 1997; Conrad, 2006; Caldwell and Palci, 2007). For most mosasaurians, the ischium is an anteriorly concave and posteriorly convex bone, as seen in the dolichosaurs *Acteosaurus*, *Adriosaurus*, *Aphanizocnemus*, *Eidolosaurus* and *Pontosaurus*, in the basal mosasauroid *Komensaurus* and in the mosasaur *Tylosaurus* (Nopcsa, 1923; Russell, 1967; Dal Sasso and Pinna, 1997; Caldwell, 2006; Caldwell and Palci, 2007; 2010; Palci and Caldwell, 2010). This shape is also seen in the living anguimorphs *Lanthanotus* and *Shinisaurus* (Rieppel, 1980; Conrad, 2006). However, the dolichosaur *Primitivus*, some species of the living *Varanus* and the mosasaurs *Mosasaurus* and *Platecarpus* present an ischium that is both anteriorly and posteriorly concave, hourglass-shaped (Russell, 1967; Dal Sasso and Pinna, 1997; Paparella *et al.*, 2018). A strong and marked posterior ischiadic tubercle is seen in every mosasaurian with this bone preserved. A variation in bone arrangement that may be connected to aquatic lifestyles is the anterior rotation of the ischium, seen in mosasaurians preserving pelvic bones near their original articulation position (e.g. Russell, 1967; Dal Sasso and Pinna, 1997; Caldwell and Palci, 2007; 2010). This arrangement gives the thyroid fenestra an elliptical shape, *contra* the circular shape seen in living anguimorphs.

*Ilium*. Every basal mosasaurian has an ilium with a long, posteriorly tapering, iliac blade, forming a rod-like structure. Most of taxa, such as the dolichosaurs *Acteosaurus*, *Adriosaurus suessi*, *Aphanizocnemus* and *Coniasaurus* and the basal mosasauroids *Aigialosaurus* and *Komensaurus* present a more vertically oriented iliac blade, in contrast to the more horizontally oriented blade seen in living lizards (Dal Sasso and Pinna, 1997; Caldwell, 2000; Lee and Caldwell, 2000; Dutchak and Caldwell, 2006; Palci and Caldwell, 2007; 2010; Chapter 1 of this thesis). In *Coniasaurus*, especially in *C. longicollis* (Figure 5.3B), the iliac blade is strongly vertically oriented, much more similar to what is seen in mosasauroids (Russell, 1967; Bell and Polcyn, 2005). Lee and Caldwell (2000) appears to have misinterpreted

the ilium in *Adriosaurus suessi*, as seen in their figure 5 (Figure 5.7 of this work). In this specimen (NHMUK-R2867), the ilium actually covers the acetabular region of the pubis (Figure 5.7C). *A. suessi* had a very mosasaurian-like ilium, with a tapering and recurved posterior ramus. An anterior iliac process, present in *Varanus*, is absent in mosasaurian lizards, but may be present as a reduced tubercle in *Adriosaurus suessi* (Figure 5.7C). Dutchak and Caldwell (2006) interpreted the ilium of *Aigialosaurus dalmaticus* as presenting a very unusual, autapomorphic, anterior iliac process, but it is more likely that the interpretation of Carroll and DeBraga (1992), in which that bone represents part of the ilium and part of the pubis, is true. In figure 5 of Dutchak and Caldwell (2006) is even possible to notice a possible obturator foramen, which would match the identification of the anteriormost element as part of the pubis. The ilium of *Aphanizocnemus* differs from the element in other dolichosaurs by being heavily built, in contrast to the most common rod-like shape (Dal Sasso and Pinna, 1997).

*Femur.* Distal end of the femur is usually larger than proximal end, as seen in most mosasaurians (Nopcsa, 1923; Russell, 1967; Dal Sasso and Pinna, 1997; Caldwell, 2000; Lee and Caldwell, 2000; Caldwell, 2006; Dutchak and Caldwell, 2006; Palci and Caldwell, 2007; Smith and Buchy, 2008; Palci and Caldwell, 2010; Paparella *et al.*, 2018; Chapter 1 of this thesis), although they can be subequal in size, as in *Adriosaurus skrbiniensis*, *Komensaurus* and *Kaganaias* (Evans *et al.*, 2006; Caldwell and Palci, 2007; 2010). Femoral shaft is always constricted at its mid-length in mosasaurian lizards. Usually, femoral epiphyses are unossified in dolichosaurs, but they are ossified in *Coniasaurus* sp. nov. (Chapter 1 of this thesis). *Coniasaurus* sp. nov. has also some femoral features mostly seen in mosasaurids, as a triangular-shaped distal end (which may be present in *Primitivus* and *Vallecillosaurus* as well; Smith and Buchy, 2008; Paparella *et al.*, 2018) with a prominent tubercle separating the articular surfaces for the tibia and the fibula. However, it also presents a well-developed femoral head and internal trochanter, as in basal mosasauroids *Komensaurus* and *Vallecillosaurus* (Caldwell and Palci, 2007; Smith and Buchy, 2008) and in living varanoids. *Coniasaurus* sp. nov. has not a complete femur preserved, but one specimen assigned to *C. longicollis* (BMB 008567; Caldwell, 2000) has a complete element that present a unique bending in its shaft (Figure 5.8). Curiously, this element also bears a conspicuous crest and a tubercle at its mid-portion, really resembling the humerus synapomorphies for the genus (Chapter 2 of this thesis). It may be true that both humerus and femur share synapomorphic characters for *Coniasaurus*, including a twisted shaft, a conspicuous crest running longitudinally and a tubercle lying at the middle of the element.

*Tibia and fibula.* As in other squamates, the tibia is always more expanded proximally and the fibula more expanded distally in basal mosasaurians. In derived mosasaurids, however, the tibia is usually also more expanded distally than proximally (Russell, 1967). Tibia and fibula are also divergent elements as the radius and the ulna. Distal margin of the tibia may present a notch, as seen in *Adriosaurus*, *Coniasaurus* and *Komensaurus* (pers. obs.; Figure 5.9), which is also present in living varanoids (Gauthier *et al.*, 2012) but absent in mosasaurids and in the dolichosaurs *Acteosaurus* and *Primitivus* (Palci and Caldwell, 2010; Paparella *et al.*, 2018). Typically, the tibia is the larger element, as in *Acteosaurus*, *Adriosaurus*, *Coniasaurus*, *Primitivus*, *Vallecillosaurus* and mosasaurids (Russell, 1967; Lee and Caldwell, 2000; Smith and Buchy, 2008; Caldwell and Palci, 2010; Palci and Caldwell, 2010; Paparella *et al.*, 2018; Chapter 1 of this thesis), but both elements can be roughly the same size, as in the basal mosasauroids *Aigialosaurus* and *Komensaurus* (Dutchak and Caldwell, 2006; Palci and Caldwell, 2007), or the fibula can be a larger element as seen in *Pontosaurus* (Caldwell, 2006). *Aphanizocnemus libanensis* present a unique tibial morphology by having an extremely reduced, square-shaped element (Dal Sasso and Pinna, 1997).

*Tarsal and metatarsal elements.* Only two specimens of dolichosaur present a relatively well preserved and complete tarsus: the holotypes of *Pontosaurus kornhuberi* (Caldwell, 2006) and *Primitivus manduriensis* (Paparella *et al.*, 2018). This restricts the anatomical comparisons of the tarsal composition and morphology among basal mosasaurians. In *Primitivus*, as in mosasauroids, the proximal tarsal row is composed by the calcaneum and the astragalus (Paparella *et al.*, 2018), while in *Pontosaurus* there is also an extra and unidentified element (Caldwell, 2006). Among mosasaurian lizards, the astragalus is usually larger than the calcaneum, being a separate, not fused, element with an “U” shape. The only known two exceptions are the basal mosasauroids *Haasiasaurus* and *Vallecillosaurus*, where both elements are fused into a single astragalocalcaneum as in modern squamates (Polcyn *et al.*, 1999; Smith and Buchy, 2008). *Primitivus* present a more plesiomorphic tarsal distal row, bearing one centrale element and distal tarsals one to four (Paparella *et al.*, 2018). *Pontosaurus*, *Haasiasaurus* and *Vallecillosaurus* have only distal tarsals three and four (Polcyn *et al.*, 1999; Caldwell, 2006; Smith and Buchy, 2008), while mosasaurids bear only the fourth element (Russell, 1967; Caldwell, 1996). Regarding the pes metapodium, the first and the fifth metatarsals are always shorter and stouter than the second, third and fourth elements. There is some variation regarding the most elongate metatarsal: this is the third one in the dolichosaurs *Acteosaurus* and *Pontosaurus* and in the basal mosasauroid *Vallecillosaurus* (Caldwell, 2006; Smith and Buchy, 2008; Palci and Caldwell, 2010), the fourth in the dolichosaurs

*Aphanizocnemus* and *Primitivus* and in the basal mosasauroid *Haasiasaurus* (Dal Sasso and Pinna, 1997; Polcyn *et al.*, 1999; Paparella *et al.*, 2018) and both third and fourth appears to be subequal in length in the dolichosaur *Adriosaurus suessi* and in the basal mosasauroid *Opetiosaurus* (Lee and Caldwell, 2000; Dutchak and Caldwell, 2009). Contrary to the condition found in most squamates, the fifth metatarsal is not hooked in most mosasaurians, with the only known exceptions being the dolichosaur *Primitivus* and the basal mosasauroids *Haasiasaurus* and *Vallecillosaurus* (Polcyn *et al.*, 1999; Smith and Buchy, 2008; Paparella *et al.*, 2018).

## 5.4. Discussion

### 5.4.1. Presacral count characters

One of the postcranial characters supporting the Pythonomorpha hypothesis is the “hypapophyses/hypapophyseal peduncles extending to the 10th presacral/precloacal vertebra or beyond (i.e., 10 or more cervical vertebrae” (character 102 of Palci and Caldwell, 2010; character 97 of Paparella *et al.*, 2018), which implies that snakes do have an elongated neck with a high cervical count. However, developmental studies do support the interpretation of snakes bearing a short, instead of a long, neck (Gomez *et al.*, 2008; Woltering, 2012). In addition, most squamates morphological matrices available in the literature uses one or more characters named “number of presacral vertebrae” (e.g. character 236 of Conrad, 2008; character 101 of Palci and Caldwell, 2010; characters 454-458 of Gauthier *et al.*, 2012). However, presacral vertebrae count is measuring two distinct modules: cervical and dorsal elements. For instance, if we compare taxa such as *Primitivus* and *Halisaurus*, they both present very similar presacral counts: 32 and 31 respectively (Table 1), and so they would probably receive the same state coding in a presacral vertebrae number character. However, despite having similar presacral counts, they present distinct cervical and dorsal counts: *Primitivus* has 10 cervicals and 22 dorsals against only 7 cervicals and 24 dorsals in *Halisaurus*. The same is valid for other taxa with similar presacral counts.

Vertebral numbers can bear strong phylogenetical sign for some clades, with distinct patterns appearing really early in the evolution of distinct lineages (Müller *et al.*, 2009). Vertebral number is defined through ontogeny by a process called segmentation clock, which rhythmically forms the precursors of the vertebrae: the somites (Dequéant and Pourquié, 2008). In extremely elongated animals, such as snakes, an increased speed of the segmentation clock during early development lead to the formation of a higher number of relatively smaller somites,

which will greatly increase the final vertebral number seen in the clade (Gomez *et al.*, 2008). In addition, the action of distinct *Hox* genes expressions along the body axis turns different somite regions into distinct vertebral modules (e.g. cervical, dorsal, sacral, etc), making vertebral column very regionalized (Müller *et al.*, 2009). Consequently, there are genetic, ontogenetic and phylogenetic reasons for considering each vertebral module as an independent evolutionary module and therefore distinct phylogenetic characters. In limbless taxa it may be hard to assess distinct vertebral regions instead of “presacral number” of vertebrae, but developmental studies do show distinct vertebral regionalization among these. For instance, Gomez *et al.* (2018) found the corn snake (*Pantherophis guttatus*) to bear 3 cervical, 219 thoracic, 4 cloacal and 70 caudal vertebrae. Whenever a taxon cannot be properly assessed regarding the cervical/dorsal (or thoracic) vertebral number, it should be coded as “missing” for these characters.

In mosasaurians, the cervical module seems to be more conservative than the dorsal one, as seen in Table 1. Dolichosaurs consistently present 10 or more cervicals, while the number of dorsals vary from as low as 22 to as high as 36 (Evans *et al.*, 2006; Paparella *et al.*, 2018). Within Mosasauroidea, there are consistently 7 cervical vertebrae (the eighth cervical described for *Plotosaurus* may have been misinterpreted; Michael Polcyn, pers. comm.), while the number of dorsals is usually lower than 25, with only some mosasaurines presenting more than 30 dorsal vertebrae. The elongation of the neck (10 or more cervicals) also appears in some taxa from other aquatic amniote lineages, such as Mesosauridae (Modesto, 1999), Ichthyopterygia (Dal Sasso and Pinna, 1996), Thallatosauriformes (Liu and Rieppel, 2005), Sauropterygia (Rieppel, 2000) and Plesiosauria (Druckenmiller and Russel, 2008), and therefore may be also linked to an aquatic lifestyle.

#### **5.4.2. The postcranial skeleton among distinct basal mosasaurian lineages**

Basal mosasaurians typically share the following postcranial features: 1) Elongated neck, with at least 10 cervical vertebrae; 2) Elongated trunk with at least 26 dorsal vertebrae; 3) Very reduced forelimbs in relation to the hindlimb (humerus/femur ration below 0,65); 4) Presence of zygantrum-zygosphene articulation; and 5) Well-developed pedestals for haemal arches in caudal vertebrae. Three taxa, *Aphanizocnemus libanensis*, *Eidolosaurus trauthi* and *Primitivus manduriensis* present also some features that are very distinct from other dolichosaurs, and thus may represent a unique basal mosasaurian lineage or even a non-

mosasaurian lineage of aquatic lizards. Each of the main basal mosasaurian lineages (i.e., the dolichosaur genera discussed so far) will be discussed below regarding their postcranial skeleton, focusing especially on diagnostic characters.

#### 5.4.2.1. *Adriosaurus*

*Adriosaurus* is a genus composed by three described species: *A. suessi* (Seeley, 1881; Lee and Caldwell, 2000), *A. microbrachis* (Palci and Caldwell, 2007) and *A. skrbinensis* (Caldwell and Palci, 2010). The most recent diagnosis of the genus *Adriosaurus* is the one provided by Caldwell and Palci (2010), which includes the following 12 diagnostic features:

- 1) **Small marine squamate with elongate neck, body, and tail:** shared by all dolichosaurs;
- 2) **10 cervical vertebrae:** shared with most dolichosaurs;
- 3) **28–30 dorsal vertebrae:** shared with *Pontosaurus lesinensis*;
- 4) **At least 65 caudal vertebrae:** probably shared by all dolichosaurs, but hard to assess since only a few present relatively complete caudal series;
- 5) **Zygosphenes/zygantra present in presacral region:** shared by all dolichosaurs;
- 6) **Tail deep, laterally compressed:** shared by all dolichosaurs;
- 7) **Limbs reduced in size:** shared by all dolichosaurs;
- 8) **Forelimbs much shorter than hind limbs:** shared by all dolichosaurs;
- 9) **Strongly expanded distal end of fibula:** shared with *Acteosaurus* and *Pontosaurus*;
- 10) **Laterally compressed trunk region:** shared with *Acteosaurus* and *Pontosaurus*;
- 11) **Pachyostotic dorsal vertebrae and ribs:** shared with *Pontosaurus*;
- 12) **Neural arches on dorsal vertebrae anteroposteriorly short and broad, only slightly constricted at midlength:** this is a consequence of pachyostosis, which “inflates” the vertebrae and diminish the constriction degree. Therefore, it is also shared with the pachyostotic *Pontosaurus*.

As seen, none of the *Adriosaurus* diagnostic characters currently provided by the literature can distinguish its postcranial skeleton from that of *Pontosaurus*, and only one from

*Pontosaurus* (fusion of the scapula and the coracoid into a single element; see item 5.4.2.7.) is lacking in *Adriosaurus*. It is also very similar to the postcranial skeleton of *Acteosaurus* in a lesser degree. However, the results of this work were able to add five new diagnostic characters regarding *Adriosaurus* postcranial anatomy:

- 1) **Neural arches that are larger posteriorly than anteriorly** (Figure 5.2B);
- 2) **Square-shaped deltopectoral crest in humerus** (Figure 5.5A and B);
- 3) **Rounded distal end of the radius;**
- 4) **Proximal carpal row formed by three elements: a radiale, an intermedium and an ulnare** (only observable in *A. suessi* though);
- 5) **Ulnare is the largest carpal element** (also only visible in *A. suessi*);

#### 5.4.2.2. *Acteosaurus*

*Acteosaurus* was a genus composed by two species: *A. tommasinii* (von Meyer, 1860; Palci and Caldwell, 2010) and *A. crassicostatus* (Calligaris, 1993), but the later was suggested to belong to *Adriosaurus suessi* by Caldwell and Lee (2004). The most recent diagnosis given for the genus and only valid species was provided by Palci and Caldwell (2010):

- 1) **Neural arches in dorsal region not mediolaterally constricted at mid-length but instead further posteriorly (just anterior to small postzygapophyses):** unique character;
- 2) **Postzygapophyses in dorsal region small and subtriangular in dorsal view:** unique character, but appears to be taphonomically related;
- 3) **Absence of pachyostosis on both vertebrae and ribs:** shared by every other non-pachyostotic dolichosaur (e.g. *Aphanizocnemus*, *Coniasaurus* and *Kaganaias*);
- 4) **Relatively shorter and more gracile forelimbs differentiate this taxon from *Adriosaurus suessi* (in which femur/mdv = 3.3–3.6 and humerus/mdv = 1.6–2.2):** shares similar values with those of *Adriosaurus* (see Table 2), with *Adriosaurus skrbiniensis* showing an even more gracile forelimb.

Anatomical comparisons from this work were not able to find new postcranial diagnostic features for *Acteosaurus*. Having only one unquestionable diagnostic feature calls

into question the maintenance of *Acteosaurus* as a distinct genus and not a species of *Adriosaurus* or *Pontosaurus*. Unfortunately, there is only one acteosaur specimen currently known, so new findings in the future should clarify the diagnosis and relationships of the taxon.

#### 5.4.2.3. *Coniasaurus*

*Coniasaurus* is now one of the better known dolichosaur so far, with currently four species recognized: *C. crassidens* (Owen, 1850; Caldwell and Cooper, 1999), *C. (Dolichosaurus) longicollis* (Owen, 1850; Caldwell, 2000; Chapter 1 of this thesis), *C. gracilodens* (Caldwell, 1999) and *Coniasaurus* sp. nov. (Chapter 1 of this thesis). The most recent diagnosis of the genus is the one provided by the Chapter 2 of this thesis, which includes the following seven postcranial characters:

- 1) **Very elongated neck, with up to 19 cervicals;**
- 2) **Non-pachyostotic dorsal vertebrae with a large neural spine running across the entire neural arch and ventrally nearly straight;**
- 3) **Dorsal vertebrae centrum slightly constricted dorsoventrally and presenting a subtle constriction between the centrum and the condyle, with an almost horizontal pre- and postzygapophyseal articulation;**
- 4) **More than 30 dorsal vertebrae;**
- 5) **Humerus and femur conspicuously twisted, rotated near its proximal half, and presenting a medial tubercle;**
- 6) **Humeral deltopectoral crest well developed (nearly 50% of humerus size);**
- 7) **Iliac blade strongly oriented vertically.**

#### 5.4.2.4. *Kaganais*

*Kaganais hakusanensis* is the single species of the genus, and it was described from rocks of the “Neocomian” of Japan by Evans *et al.* (2006). The most recent diagnosis for the taxon is the one provided by the same work, which follows:

- 1) **A small (c. 300 mm snout–pelvis length) gracile lizard with a bilaterally compressed body:** shared with *Adriosaurus* and *Pontosaurus*;

- 2) **An elongated trunk with at least 36–46 dorsal vertebrae bearing deep lateral recesses, low roughened neural spines and well-developed zygosphenozygantral articulations in which the zygosphene faces ventrolaterally:** unique character;
- 3) **Thickened ribs with dorsal and ventral tubercles:** unique character;
- 4) **A sacrum in which the second sacral rib is broader than the first:** shared with *Adriosaurus skrbinenesi* and *Coniasaurus longicollis*;
- 5) **A single pygal vertebra, haemal arches that are fused to pedicles on the caudal vertebrae:** shared with *Coniasaurus* sp. nov.;
- 6) **A long slender ilium:** shared by all mosasaurians;
- 7) **Hindlimbs that were small in relation to trunk length, with a straight robust femur:** shared by all dolichosaurs.

As *Kaganaias* is a taxon known by a single species, from a complete different geological and stratigraphic context than other dolichosaurs, phylogenetic analyses with broader taxonomic sampling may find it occupying a distinct position within Anguimorpha, maybe even outside Mosasauria.

#### 5.4.2.5. *Mesoleptos*

*Mesoleptos zendrinii* is a taxon originally described by Cornalia and Chiozza (1852), with a new assigned specimen described by Lee and Scanlon (2002). There is no described diagnosis for *Mesoleptos* available in the literature, and thus the phylogenetic relationships of the genus are still controversial. It has been suggested to bear affinities with dolichosaurs by Cornalia and Chiozza (1852) and Nopcsa (1923) and with snakes, as the sister-group of Serpentes, by Lee and Scanlon (2002). *Mesoleptos* holotype may be lost (Calligaris, 1988; Lee and Scanlon, 2002), and therefore the lack of anatomical information prevents proper morphological comparisons.

#### 5.4.2.6 *Pontosaurus*

*Pontosaurus* is a genus of dolichosaur composed by two species: *P. lesinensis* (Kornhuber, 1873; Pierce and Caldwell, 2004) and *P. kornhuberi* (Caldwell, 2006), although a

third species is cited in Mekarski (2017) but not published so far. The most recent diagnosis provided for the genus is the one found in Caldwell (2006), which includes four postcranial characters:

- 1) **10-12 cervical vertebrae:** shared by most dolichosaurs (and actually the cervical count considered here for *P. lesinensis* is 11 instead of 12);
- 2) **Hypapophyses with large, unfused peduncles on C2-C10:** shared by most dolichosaurs;
- 3) **26-28 dorsal vertebrae:** shared with *Acteosaurus*, *Adriosaurus microbrachis* and *Aphanizocnemus*;
- 4) **Fused scapulocoracoid with primary coracoid emargination:** shared with *Aphanizocnemus*.

As seen above, there are no diagnostic feature for *Pontosaurus* postcranial skeleton currently available in the literature, but the morphological comparisons here allowed the identification of two new potential diagnostic characters for *Pontosaurus*, which follows:

- 1) **Presence of interclavicle:** present in *P. lesinensis* and *P. kornhuberi*. Although taphonomical constraints may influence the preservation of the interclavicle in other dolichosaurs, this bone is up to now only known in *Pontosaurus*;
- 2) **Fibula larger than the tibia:** hindlimbs are only known in *P. kornhuberi*, but as this feature appear only in this taxon and in no other known dolichosaur it is considered here as a diagnostic character for the genus until new specimens clarify the character distribution;

#### 5.4.2.7. *Aphanizocnemus*, *Eidolosaurus* and *Primitivus*

Three taxa originally identified as related to dolichosaurs caught the attention during the morphological comparisons: *Aphanizocnemus* (Dal Sasso and Pinna, 1997), *Eidolosaurus* (Nopcsa, 1923) and *Primitivus* (Paparella *et al.*, 2018). Only the later was not personally analyzed for this work. From the five postcranial characters typically related to dolichosaurs pointed here, *Eidolosaurus* and *Primitivus* lack the second (at least 26 dorsal vertebrae) and the third (very reduced forelimbs), while *Aphanizocnemus* lack the third and may lack the first as well (Mekarski, 2017, identified eight instead of ten cervical vertebrae). Characters four (zygantrum-zygosphene articulation) and five (well-developed pedestals for haemal arches in

caudal vertebrae), although typical for dolichosaurs, also appears in other squamate lineages, so basically the only postcranial character uniting these taxa to the dolichosaurs is the elongated neck. While *Aphanizocnemus* may not have a very elongated neck, as stated by Mekarski (2017), both *Eidolosaurus* and *Primitivus* are very poorly preserved: *Eidolosaurus* is just a cast, and *Primitivus* is badly damaged. Therefore, the precise identification of the vertebral counts in these taxa is problematic. In phylogenetic analyses with a broader taxonomic sampling, it would not be a surprise to find these taxa occupying a very basal position within Mosasauria or even falling anywhere else among squamates. For instance, Mekarski (2017) suggested *Aphanizocnemus* to bear closer relationships to scincogekkonomorphs. A CT-Scan analysis of these specimens would greatly contribute to our anatomic and systematic knowledge of the same, since it would allow a much better evaluation of their morphology.

### 5.4.3. Postcranial characters and the dolichosaur / mosasaurian relationships

#### 5.4.3.1. The Varanoidea hypothesis

The most recent phylogenetic analysis recovering mosasaurians as closely related to varanoid lizards is the one provided by Conrad *et al.* (2011), which include four postcranial characters supporting it. Each of these is discussed below:

- 1) **Reduced zygapophyses and transverse processes, adding flexibility to the trunk and tail** (character 250, state 1): not valid. What is different in basal mosasaurians is actually the angle of pre- and postzygapophyses articulation, which is more horizontal for better flexibility. Transverse processes are still quite large in basal forms, and reduced in more derived mosasauroids;
- 2) **Straight (rather than angulated) clavicle** (character 261, state 0): may not be valid. *Aphanizocnemus* and *Pontosaurus* present a clearly recurved clavicle, and although the first may not be a dolichosaur, the later certainly is;
- 3) **Absence of an anterior (primary) coracoid fenestra** (character 262, state 0): not valid. Actually, only *Coniasaurus* and *Primitivus* lack this fenestra, the other dolichosaurs with the pelvic girdle do present it;
- 4) **Astragalus and calcaneum separate (unfused)** (character 292, state 0): valid, but reversed in *Haasiasaurus* and *Vallecillosaurus* (Polcyn *et al.*, 1999; Smith and Buchy, 2008).

#### 5.4.3.2. The Pythonomorpha hypothesis

The most recent phylogenetic analysis recovering mosasaurians as pythonomorphs is the one provided by Paparella *et al.* (2018), which include six postcranial characters supporting it as follows:

- 1) **Presence of zygosphenes and zygantra** (character 96, state 1): may be valid, but many other squamate lineages also present it. In a broader taxonomic sampling this character may not be optimized to support the Pythonomorpha hypothesis;
- 2) **Ribs beginning of the third or more anterior cervical vertebra** (character 103, state 0): not valid because character is weakly constructed. This appears to be a character that highly varies within squamates. For instance, cervical ribs start on C4 in *Lanthanotus*, C5 in *Varanus* and *Shinisaurus* present rudimentary cervical ribs on C3 (Rieppel, 1980; Conrad, 2006);
- 3) **Pelvis small** (character 116, state 1): not valid because character is weakly constructed. Every lineage presenting axial elongation and limb reduction, such as limbless lizards, will present reduction of pelvis as well, so in broader taxonomic sampling this character also may not be optimized to support the Pythonomorpha hypothesis;
- 4) **Distal end of tibia convex for astragalocalcaneal articulation** (character 120, state 1): not valid. Among taxa where this character is visible, there is a notch in the distal end of the tibia in *Adriosaurus*, *Aphanizocnemus* and the basal mosasauroids *Komensaurus* (Figure 5.9), while it is convex in *Acteosaurus* and *Primitivus*, so by parsimony this character is more probably to be coded as notched than convex for basal mosasaurians, even more if *Primitivus* falls outside of Mosasauria. In addition, when including a broader taxonomic sampling the primitive state will be convex and the derived state notched, which would probably optimize the character to unite mosasaurians to varanoid lizards that also present the same notch.
- 5) **Astragalus and calcaneum separated, not fused** (character 121, state 1): same as in Conrad *et al.* (2011) work: character valid, but reversed in *Haasiasaurus* and *Vallecillosaurus* (Polcyn *et al.*, 1999; Smith and Buchy, 2008).
- 6) **Epiphyses on skull and axial skeleton absent** (character 126, state 1): may be valid, but character seems weakly constructed. This character is probably

ontogenetic and ecomorphologically related, appearing in juvenile and in derived aquatic lineages.

### 5.5. Final considerations

Although testing the phylogenetic relationships of mosasaurians within squamates was beyond the scope of this Chapter, the results of this chapter highlight how important is to provide broader morphological comparisons when analyzing character distribution within a clade. Either hypothesis of mosasaurians as varanoids or pythonomorphs include characters that are not valid or are weakly constructed when analyzing most of the basal forms, evidencing how careful codification must be in order to better recover evolutionary histories.

Recognition of new diagnostic characters for adriosaur and pontosaur improves our knowledge on these important dolichosaur lineages. In addition, a careful analysis of *Aphanizocnemus*, *Eidolosaurus* and *Primitivus* suggest that these may not be related to mosasaurians but instead to other squamate lineages. A phylogenetic analysis with a broad taxonomic sampling, including the new data provided by this survey, is required for testing the affinities of these taxa.

### References

- Bardet, N.; Suberbiola, X.P.; Iarochene, M.; Bouya, B.; Amaghaz, M. 2005. A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halisaurinae (Squamata: Mosasauridae). **Zoological Journal of the Linnean Society** 143: 447-472.
- Bell, G.L. 1997. A phylogenetic revision of North American and Adriatic Mosasauroida. In: Callaway, J.M.; Nicholls, E.L.(eds.). **Ancient Marine Reptiles**. Academic Press. 293–332.
- Bell, G.L.; Polcyn, M.J. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). **Netherlands Journal of Geosciences** 84 (3): 177-194.
- Boulenger, G. 1891. Notes on the osteology of *Heloderma horridum* and *H. suspectum* with remarks on the systematic position of the Helodermatidae and the vertebrae of the Lacertilia. **Proceedings of the Zoological Society of London** 1891: 109-118.
- Buchy, M.C.; Smith, K.T. 2011. New portions of the holotype of *Vallecillosaurus donrobertoi* (Squamata, Mosasauroida) from the early Turonian (Upper Cretaceous) of Mexico. *In:*

- Calvo, J.; Porfiri, J.D.; González Riga, B.; Dos Santos, D. 2011. **Paleontología y dinosaurios desde América Latina**. Mendoza, Ediunc: 296 p.
- Burnell, A.; Collins, S.; Young, B.A. 2012. Vertebral morphometrics in *Varanus*. **Bulletin de la Société Géologique de France** 183(2): 151-158.
- Caldwell, M.W.; Carroll, R.L.; Kaiser, H. 1995. The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroids and varanoids. **Journal of Vertebrate Paleontology** 15(3): 516-531.
- Caldwell, M.W. 1996. Ontogeny and phylogeny of the mesopodial skeleton in mosasauroid reptiles. **Zoological Journal of the Linnean Society** 116(4): 407-436.
- Caldwell, M.W. 1999. Description and phylogenetic relationships of a new species of *Coniasaurus* Owen, 1850 (Squamata). **Journal of Vertebrate Paleontology** 19(3): 438-455.
- Caldwell, M.W. 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in Squamates. **Journal of Vertebrate Paleontology** 20(4): 720-735
- Caldwell, M.W. 2006. A New Species of "Pontosaurus" (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a Phylogenetic Analysis of Pythonomorpha. **Società Italiana di Scienze Naturali**: 1-44.
- Caldwell, M.W.; Cooper, J.A. 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the Lower Chalk (Cretaceous; Cenomanian) of SE England. **Zoological Journal of the Linnean Society** 127: 423-452.
- Caldwell, M.W.; Lee, M.S.Y. 2001. Live birth in Cretaceous marine lizards (mosasauroids). **Proceedings of the Royal Society: Biological Sciences** 268: 2397-2401.
- Caldwell, M.W.; Lee, M.S.Y. 2004. Reevaluation of the Cretaceous marine lizard *Acteosaurus crassicostatus* Calligaris, 1993. **Journal of Paleontology** 78(3): 617-619.
- Caldwell, M.W.; Palci, A. 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) of Slovenia with a review of mosasauroid phylogeny and evolution. **Journal of Vertebrate Paleontology** 27(4): 863-883.
- Caldwell, M.W.; Palci, A. 2010. A new species of marine ophidiomorph lizard, *Adriosaurus skrbiniensis*, from the Upper Cretaceous of Slovenia. **Journal of Vertebrate Paleontology** 30(3): 747-755.
- Calligaris, R. 1988. I rettili fossili degli "Strati calcarei ittiolitici di comeno" e dell'isola di Lesina. **Atti Museo Civico di Storia Naturale di Trieste** 41: 85-125.
- Calligaris, R. 1993. *Acteosaurus crassicostatus* nuova specie di Dolichosauridae negli Strati Calcarei Ittiolitici di Comeno. **Atti Museo Civico di Storia Naturale di Trieste** 45:29-34.

- Carroll, R.L.; Debraga, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. **Journal of Vertebrate Paleontology** 12(1): 66-86.
- Cieri, R.L. 2018. The axial anatomy of monitor lizards (Varanidae). **Journal of Anatomy**: 1-8. doi: 10.1111/joa.12872.
- Conrad, J.L. 2006. Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). **Journal of Morphology** 267(7): 759-775.
- Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. **Bulletin of the American Museum of Natural History**, 310: 1-182.
- Conrad, J.L.; Ast, J.C.; Montanari, S.; Norell, M.A. 2011. A combined evidence phylogenetic analysis of Anguimorpha (Reptilia: Squamata). **Cladistics** 27: 230-277.
- Cornalia, E.; Chiozza, L. 1852. Cenni geologici sull' Istria. **Giornale dell' I. R. Istituto Lombardo** 3: 1-35.
- Dal Sasso C, Pinna G. 1996. *Besanosaurus leptorhynchus* n. gen. n. sp., a new shastasaurid ichthyosaur from the middle Triassic of Besano (Lombardy, N. Italy). **Paleontologia Lombarda** 4:3-23.
- Dal Sasso, C.; Pinna, G. 1997. *Aphanizocnemus libanensis* n. gen. n. sp, a new dolichosaur (Reptilia, Varanoidea) from the Upper Cretaceous of Lebanon. **Paleontologia Lombarda** 7: 1-31.
- Dequéant, M.L.; Pourquié, O. 2008. Segmental patterning of the vertebrate embryonic axis. **Nature Reviews Genetics** 9(5): 370-382.
- Druckenmiller P.S., Russel A.P. 2008. A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews, 1922. **Zootaxa** 1863, 1-120.
- Dutchak, A.R.; Caldwell, M.W. 2006. Redescription of *Aigialosaurus dalmaticus* KRAMBERGER, 1892, a Cenomanian mosasauroid lizard from Hvar Island, Croatia. **Canadian Journal of Earth Science** 43(12): 1821-1834.
- Dutchak, A.R.; Caldwell, M.W. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. **Journal of Vertebrate Paleontology** 29(2): 437-452.
- Evans, S.E.; Manabe, M.; Noro, M.; Isajis, S.; Yamaguchi, M. 2006. A longbodied lizard from the Lower Cretaceous of Japan. **Paleontology** 49(6): 1143-1165.
- Gauthier, J.A.; Kearney, M.; Maisano, J.A.; Rieppel, O.; Behlke, A.D.B. 2012. Assembling the Squamate tree of life: perspectives from the phenotype and the fossil record. **Bulletin of the Peabody Museum of Natural History** 53(1): 3-308.

- Gomez, C.; Özbudak, E.M.; Wunderlich, J.; Baumann, D.; Lewis, J.; Pourquié, O. 2008. Control of segment number in vertebrate embryos. **Nature** 454(7202): 335-339.
- Haber, A.; Polcyn, M.J. 2005. A new marine varanoid from the Cenomanian of the Middle East. **Netherlands Journal of Geosciences** 84(3): 247-255.
- Hoffstetter, R.; Gasc, J.P. 1969. Vertebrae and ribs of modern reptiles. **Biology of the Reptilia** 1(5): 201-310.
- Houssaye, A.; Xu, F.; Helfen, L.; De Buffrénil, V.; Baumbach, T.; Tafforeau, P. 2011. Three-dimensional pelvis and limb anatomy of the Cenomanian hind-limbed snake *Eupodophis descouensi* (Squamata, Ophidia) revealed by synchrotron-radiation computed laminography. **Journal of Vertebrate Paleontology** 31(1): 2-7.
- Konishi, T.; Newbrey, M.G.; Caldwell, M.W. 2014. A small, exquisitely preserved specimen of *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the upper Campanian of the Bearpaw Formation, western Canada, and the first stomach contents for the genus. **Journal of Vertebrate Paleontology** 34(4), 802-819.
- Kornhuber, A. 1873. Über einen neuen fossilen saurier aus Lesina. **Herausgegeben von der k. k. geologischen Reichsanstalt Wien** 5(4): 75-90.
- Lee, M.S.Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. **Biological Journal of the Linnean Society** 65: 369-453.
- Lee, M.S.Y.; Caldwell, M.W. 1998. Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. **Philosophical Transactions of the Royal Society of London B: Biological Sciences** 353: 1521-1552.
- Lee, M.S.Y.; Caldwell, M.W. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. **Journal of Paleontology** 74(5): 915-937.
- Lee, M.S.Y.; Scanlon, J.D. 2002. The Cretaceous marine squamate *Mesoleptos* and the origin of snakes. **Bulletin of the Natural History Museum London (Zoology Series)** 68: 131-142.
- Lindgren, J.; Jagt, J.W.; Caldwell, M.W. 2007. A fishy mosasaur: the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. **Lethaia** 40(2): 153-160.
- Lindgren, J.; Polcyn, M.J.; Young, B.A. 2011. Landlubbers to leviathans: evolution of swimming in mosasaurine mosasaurs. **Paleobiology** 37: 445-469.
- Liu J, Rieppel O. 2005. Restudy of *Anshunsaurus huangguoshuensis* (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou, China. **Amer Mus Novit** 488:1- 34.

- McDowell, S.B.; Bogert, C.M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. **Bulletin of the American Museum of Natural History** 105: 1-142.
- Mekarski, M.M. 2017. **The Origin and Evolution of Aquatic Adaptations in Cretaceous Squamates**. Unpublished Ph.D. thesis, University of Alberta, 467 p.
- Modesto SP. 1999. Observations on the structure of the Early Permian reptile *Stereosternum tumidum* Cope. **Pal afr** 35: 7–19.
- Müller, J.; Scheyer, T.M.; Head, J.J.; Barrett, P.M.; Werneburg, I.; Ericson, P.G.; Pol, D.; Sánchez-Villagra, M.R. 2010. Homeotic effects, somitogenesis and the evolution of vertebral numbers in recent and fossil amniotes. **Proceedings of the National Academy of Sciences** 107(5): 2118-2123.
- Nopcsa, F.B. 1923. *Eidolosaurus* und *Pachyophis*: Zwei neue Neocom-Reptilien. **Palaeontographica** 65: 99-154.
- Owen, R. 1850. Description of the fossil reptiles of the Chalk Formation. In: Dixon, F. (Ed), **The geology and fossils of the Tertiary and Cretaceous Formations of Sussex**. London, Longman, Brown, Green, and Longman. p. 378-404.
- Palci, A.; Caldwell, M.W. 2007. Vestigial forelimbs and axial elongation in a 95 million-year-old non-snake squamate. **Journal of Vertebrate Paleontology** 27(1): 1-7.
- Palci, A.; Caldwell, M.W. 2010. Redescription of *Acteosaurus tommasinii* von Meyer, 1860, and a discussion of evolutionary trends within the clade Ophidiomorpha. **Journal of Vertebrate Paleontology** 30(1): 94-108.
- Paparella, I.; Palci, A.; Nicosia, U.; Caldwell, M.W. 2018. A new fossil marine lizard with soft tissues from the Late Cretaceous of southern Italy. **Royal Society Open Science** 5(6): doi 172411.
- Pierce, S.; Caldwell, M.W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur, *Pontosaurus lesinensis* (Kornhuber, 1873). **Journal of Vertebrate Paleontology** 24: 376-389.
- Polcyn, M.J.; Tchernov, E.; Jacobs, L.L. 1999. The Cretaceous biogeography of the Eastern Mediterranean with a description of a new basal mosasauroid from 'Ein Yabrud, Israel. In: SECOND GONDWANAN DINOSAUR SYMPOSIUM. **Proceedings of the Second Gondwanan Dinosaur Symposium**. National Science Museum Monographs 15, Tokyo, Japan. p. 259-290.
- Reeder, T.W.; Townsend, T.M.; Mulcahy, D.G.; Noonan, B.P.; Wood, P.L.Jr.; Sites, J.W.Jr.; Wiens, J.J. 2015. Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny

- and Reveal Unexpected Placements for Fossil Taxa. **PLoS ONE** 10(3): e0118199. doi:10.1371/journal.pone.0118199.
- Rieppel O. 2000. Sauropterygia I - Placodontia, Pachypleurosauria, Nothosauroida, Pistosauroida. In: Handbuch der Paläoherpetologie 12A:1-134.
- Rieppel, O. 1980. **The phylogeny of anguimorph lizards**. Birkhauser Verlag, Basel, 86 p.
- Rieppel, O.; Zaher, H. 2000. The intramandibular joint in squamates and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. **Fieldiana (Geology), New Series** 43: 1-69.
- Russell, D.A. 1967. Systematics and morphology of American mosasaurs. **Bulletin of the Peabody Museum of Natural History** 23: 1-241.
- Seeley, H.G. 1881. On remains of a small lizard from the Neocomian rocks of Comen, near Trieste, preserved in the Geological Museum of the University of Vienna. **Quarterly Journal of the Geological Society of London** 37: 52–56.
- Smith, K.T.; Buchy, M.L. 2008. A new aigialosaur (Squamata: Anguimorpha) with soft tissues remains from the Upper Cretaceous of Nuevo León, Mexico. **Journal of Vertebrate Paleontology** 28(1): 85-94.
- Smith, Krister T., Bhart-Anjan S. Bhullar, and Patricia A. Holroyd. 2008. "Earliest African record of the Varanus stem-clade (Squamata: Varanidae) from the early Oligocene of Egypt." **Journal of Vertebrate Paleontology** 28.3: 909-913.
- Von Meyer, H. 1860. *Acteosaurus tommasinii* aus dem schwarzen Kreide-Schiefer von Comen am Karste. **Palaeontographica** 7: 223–231.
- Wiens, J.J.; Kuczynski, C.A.; Townsend, T.; Reeder, T.W.; Mulcahy, D.G.; Sites, J.W.Jr. 2010. Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. **Systematic Biology** 59(6): 674-688.
- Woltering, M.J. 2012. From lizard to snake; behind the evolution of an extreme body plan. **Current genomics** 13(4): 289-299.
- Zaher, H.; Rieppel, O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. **American Museum Novitates** 3271: 1-19.

## **Chapter 6 – A phylogenetic analysis of Mosasauria (Squamata)** **supports the hypothesis of varanoid affinities for the clade**

### **Abstract**

Phylogenetic relationships of the clade Mosasauria compose one of the most debated topics in the systematics of Squamata. Three main hypotheses are present in the literature: 1) Mosasaurians are closely related to varanoid lizards; 2) Mosasaurians are closely related to snakes; 3) Mosasaurians occupy a more basal position within Squamata, as the sister-group of Scleroglossa. Although the phylogenetic relationships of the group are controversial, only a few works have provided comprehensive taxonomic samplings of basal mosasaurians in global matrices of Squamata. Here, a phylogenetic analysis combined the largest taxonomic sampling of basal mosasaurians ever tested (75% of the dolichosaurs and 70% of the “aigialosaurs”) into the largest original morphological matrix of squamates available in the literature. Results strongly supported the interpretation of mosasaurians as anguimorph lizards, being the sister-group of Varanoidea. A monophyletic clade of dolichosaurs were also found, with the intriguing *Aphanizocnemus* nesting within the group as the basalmost member of the clade. *Primitivus* and *Eidolosaurus* were found in the base of Mosasauria, being the sister-group of all other mosasaurians. 6 out of 8 taxonomic inclusion/exclusion tests recovered mosasaurians or closely related to or nested within Varanoidea, except for the 2 tests encompassing only crown mosasaurids, highlighting the importance of including an adequate taxonomic sampling of basal forms when testing the phylogenetic relationships of an extinct clade.

**Keywords:** Dolichosauridae; Mosasauroidae; Varanoidea; Cretaceous; Phylogeny.

## Resumo

As relações filogenéticas do clado Mosasauria compõe um dos tópicos mais intensamente debatidos na sistemática de Squamata. Três hipóteses principais estão presentes na literatura: 1) Mosassaurianos são proximamente relacionados aos lagartos varanóides; 2) Mosassaurianos são proximamente relacionados às serpentes; 3) Mosassaurianos ocupam uma posição mais basal dentro de Squamata, sendo o grupo-irmão de Scleroglossa. Embora as relações filogenéticas do grupo formem um tema controverso, apenas uma pequena parcela dos trabalhos incluiu uma ampla amostragem de mosassaurianos basais em matrizes globais de Squamata. Neste trabalho, uma análise filogenética combinou a maior amostragem de mosassaurianos basais já testada (75% dos doliocossauros e 70% dos “aigialossauros”) dentro da maior e mais ampla matriz morfológica original de Squamata presente na literatura. Os resultados obtidos aqui fornecem suporte à hipótese dos mosassaurianos como lagartos anguimorfos, sendo recuperados como o grupo-irmão de Varanoidea. Um clado monofilético de doliocossauros também foi recuperado, com o intrigante *Aphanizocnemus* recuperado como o membro mais basal do grupo. *Primitivus* e *Eidolosaurus* foram recuperados na base de Mosasauria, sendo o grupo-irmão de todos os outros mosassaurianos. 6 de 8 testes taxonômicos e inclusão/exclusão de táxons recuperaram os mosassaurianos ou como proximamente relacionados ou como caindo dentro de Varanoidea, com exceção dos 2 testes incluindo apenas os mosassaurídeos mais derivados. Estes resultados demonstram a importância de incluir uma amostragem taxonômica adequada de formas basais ao testar hipóteses de relacionamento filogenético para um dado clado extinto.

**Palavras-chave:** Dolichosauridae; Mosasauroidae; Varanoidea; Cretáceo; Filogenia.

## 6.1 Introduction

Mosasauria is a clade formed by aquatic and semi-aquatic, especially marine, squamates that lived during the Late Cretaceous (Russell, 1967; Conrad, 2008; Caldwell and Palci, 2010; Gauthier *et al.*, 2012; Polcyn *et al.*, 2014). Known by dozens of species and hundreds of specimens, the diversity of Mosasauria can be broadly divided into three major radiations: basal mosasaurians (commonly referred to as “dolichosaurs”), the sister-group of a less inclusive Mosasauroida clade; basal mosasauroids (commonly referred to as “aigialosaurs”), the sister-group of the monophyletic Mosasauridae; and the family Mosasauridae, formed by four major subfamilies: Mosasaurinae, Plioplatecarpinae, Tylosaurinae and Halisaurinae (Russell, 1967; Carroll and DeBraga, 1992; Bell, 1997; Rieppel and Zaher, 2000; Bardet *et al.*, 2005; Bell and Polcyn, 2005; Conrad, 2008; Caldwell and Palci, 2010; Conrad *et al.*, 2011; Gauthier *et al.*, 2012), although some authors consider other additional arrangements such as Tethysaurinae (Makádi *et al.*, 2012) and Yaguarasaurinae (Palci *et al.*, 2013) as well.

Despite known by a relatively vast fossil record, there is little consensus regarding the affinities of the group within Squamata (see the General Introduction of this thesis for an extensive historic background of the controversy concerning mosasaurian phylogenetic relationships). Studies who recover mosasaurians as varanoid-like lizards usually are based on characters as retraction of external nares, supratemporal morphology, ventral aspect of the dentary, palate anatomy, etc (e.g. DeBraga and Carroll, 1993; Conrad, 2008; Conrad *et al.*, 2011), while characters as the presence of zygosphenes and zygantra, splenial-angular articulation, tooth attachment and implantation and the lack of ossification between the astragalus and calcaneum are usually used as supporting the hypothesis of mosasaurians being closely related to snakes (e.g. Lee, 1997; Palci and Caldwell, 2010; Paparella *et al.*, 2018). The recent global squamate analysis provided by Gauthier *et al.* (2012) shed even more controversy on the systematic position of the group, by recovering the clade in a much more basal position within Squamata, as the sister-group of Scleroglossa. Gauthier *et al.* (2012) results were supported by characters as the width of the frontoparietal suture, the lack of a dorsal process of the ectopterygoid and the absence of an iliac tubercle.

Most of the squamate phylogenies published so far include only a small sample of mosasaurian taxa, continuing to perpetrate the lack of a consensus regarding the systematics of the group. The only broad squamate phylogenetic analyses including a larger sample of mosasaurians are those provided by Conrad (2008) and Conrad *et al.* (2011), which recovers the clade within a Varanoidea assemblage. Therefore, one of the main objectives of this

contribution is to include a wide Mosasauria sample in a large squamate matrix, hoping to find new evidence that helps shedding light into the origin and evolution of mosasaurian lizards.

## 6.2 Material and Methods

### 6.2.1. Dataset selection and modifications

Gauthier *et al.* (2012) morphological matrix was chosen for evaluating the phylogenetic relationships of mosasaurians within Squamata, since it is the most complete squamate morphological dataset available in the literature, both in number of characters and taxonomic sample size. 19 new Mosasauria taxa were included in the dataset, one was rescored (*Aigialosaurus dalmaticus*) and two originally generic terminals (*Adriosaurus* and *Pontosaurus*) were each divided into two terminals of specific level. These additions represented a total sample size of 26 taxa of mosasaurians, representing 21 additional taxa than the original work of Gauthier *et al.* (2012). Taxa added represented mainly basal forms (dolichosaurs and “aigialosaurs”) and plesiopedal mosasaurs (*sensu* Bell and Polcyn, 2005), although the four hydropedal mosasaurs originally included in Gauthier *et al.* (2012) dataset were maintained. Taxonomic sample included 11 dolichosaur species (*Acteosaurus tommasinii*, *Adriosaurus suessi*, *Adriosaurus skrbinensis*, *Aphanizocnemus libanensis*, *Coniasaurus* sp. nov., *Coniasaurus longicollis*, *Eidolosaurus trauthi*, *Judeasaurus tchernovi*, *Pontosaurus kornhuberi*, *Pontosaurus lesinensis* and *Primitivus manduriensis*), 5 basal mosasauroids (*Aigialosaurus dalmaticus*, *Carsosaurus marchesetti*, *Haasiasaurus gittelmani*, *Komensaurus carrolli* and *Opetiosaurus buccichi*) and 10 mosasaurids (*Dallasaurus turneri*, *Eonatathor collensis*, *Eonatathor sternbergi*, *Tethysaurus nopcsai*, *Russellosaurus coheni*, *Pannoniasaurus inexpectatus*, *Clidastes*, *Platecarpus*, *Plotosaurus* and *Tylosaurus*). Most taxa were coded on the basis of personal examination of the specimens, high-resolution photographs and CT-data available on either MZUSP or SMU collections, with the exception of *Adriosaurus skrbinensis*, *Primitivus manduriensis*, *Aigialosaurus dalmaticus* and *Pannoniasaurus inexpectatus* which were coded based on the descriptions available in the literature, and *Clidastes*, *Platecarpus*, *Plotosaurus* and *Tylosaurus*, which were already coded in the original dataset. *Adriosaurus*, *Pontosaurus* and *Aigialosaurus* were rescored based on personal analysis of the specimens, correcting a series of errors that were present on the original dataset provided by Gauthier *et al.* (2012). Unpublished data on new specimens and CT-data of known specimens regarding *Dallasaurus turneri* and *Tethysaurus nopcsai* were provided by Michael Polcyn (work in progress) and helped to score a lot of characters not available before in mosasaurians, especially

regarding the palate and the septomaxilla. A rigorous, conservative codification approach was followed, scoring only the clearly visible characters.

Minor modifications were performed in the matrix, in order to better describe character distribution and avoid redundancy. Five characters were deleted: 454-458, as they regard the presacral vertebral counts, which is problematic because these characters actually deal with at least two distinct modules (dorsal and cervical; see Chapter 5 for a more detailed discussion on this issue). One character of Gauthier *et al.* (2012) was modified for encompassing one additional state: “460. Cervical vertebrae, number: (0) six or fewer; (1) seven; (2) eight; (3) nine; (4) ten or more. Source: Chapter 5 [ordered]”. In order to facilitate the discussion, Gauthier *et al.* (2012) characters will be referred here specifically as GX[Y], where X is the number of the character in the original work and Y is the state number. New characters derived from this thesis will be referred to as NX[Y], characters from Bell (1997) as BX[Y] and characters from Conrad (2008) as CX[Y].

Fourteen additional characters, ten provided by this thesis and four from the literature, were added for covering more aspects of the mosasaurian anatomical variation and are listed on Appendix 1. The final version of the matrix, encompassing 211 taxa, 619 characters, and respective character codings is presented by Appendix 2.

### **6.2.2. Dataset analysis**

Phylogenetic analysis was performed with the version 1.5 of TNT (Goloboff and Catalano, 2016). As traditional and exhaustive search methods are problematic when handling with very large datasets, with more than 200 taxa (Goloboff, 2002), an heuristic search using the “New Technology” tool of TNT was performed with the command “xmult = consense 5;”, which runs a combined analysis of up to seven distinct algorithms: Wagner, SPR, TBR, Ratchet, Sectorial searches, Tree-fusing and Tree-drifting (Goloboff, 1999; Nixon, 1999; Goloboff and Farris, 2001) until the strict consensus of the most parsimonious trees (MPTs) stabilize for five times. The use of combined algorithms allows the software to find minimum length and MPTs quicker and more efficiently in larger datasets than using each method alone or using traditional search methods (Goloboff, 2002). After finding an initial set of MPTs, an additional search, aiming to find the entire set of MPTs, was performed with the command “bb;”, starting to perform TBR branch-swapping until every possible MPT is found, sometimes reaching the memory limitation of the T.N.T. (100.000 trees). However, stopping at 100.000 trees and not finding every possible MPT is not a problem, since saving a good number of trees (at least 20.000 or 30.000) already gives a reliable strict consensus (Zaher and Pol, 2017). The strict

consensus of all the MPTs was calculated later with the command “nelsen;”. After the initial results, the iterative positional congruence (reduced) – IterPCR – protocol (Pol and Escapa, 2009) was followed for recognizing problematic taxa. This protocol identifies unstable taxa and/or branches and ignore their position in the strict consensus, allowing a better resolution of the more stable taxa and branches, and is particularly useful in datasets with lots of fossil taxa and missing data. Retention (Farris, 1989) and Consistency (Kluge and Farris, 1969) indexes, were calculated with the “stats.run” script, freely available at: <http://phylo.wikidot.com/tntwiki>. Bremer support (Bremer, 1994) was calculated by saving 5000 suboptimal trees for each interval of additional steps (1, 3, 5, 7 and 9), and then calculating the values with the function Trees → Bremer Supports on T.N.T. Bootstrapping (Felsenstein, 1985) was performed with the standard (sample with replacement) option and 2000 replicates. A list of synapomorphies for each relevant taxa and clade is provided by Appendix 3.

Phylogenetic tests were posteriorly performed in order to verify the influence of specific mosasaurian groups into the placement of the clade within Squamata. Tests were made by including and/or excluding four sets of traditionally recognized mosasaurian groups: dolichosaurs, “aigialosaurs” (basal mosasaurians), mosasaurids and hydropedal mosasaurs. The same protocol for finding all possible MPTs (up to the limit of 100.000 provided by T.N.T.) was followed.

### 6.3 Results

100.000 most parsimonious trees were recovered, reaching the memory limitation of the T.N.T., with a length of 5286 steps (CI: 0,185; RI: 0,793), representing 144 less steps than the original results of Gauthier *et al.* (2012), even after adding 19 new fossil taxa and a considerably amount of missing data to the dataset. The strict consensus of the MPTs is depicted by Figure 6.1. Although the in-group relationships of basal mosasaurians and some basal mosasauroids were not resolved in this first analysis, one remarkable result arises from it: the consistent recovery of Mosasauria within Anguimorpha, as the sister-group of Varanoidea. This arrangement is significantly distinct from that found by Gauthier *et al.* (2012), which recovered Mosasauria in a much more basal position within Squamata, as the sister-group of Scleroglossa. In addition, *Shinisaurus* is found to be in a more derived position within Anguimorpha, being the sister-group of the clade formed by Varanoidea + Mosasauria, and not the sister-group of Xenosauridae as in the results of Gauthier *et al.* (2012). The results presented here approach more the topologies found in Rieppel and Zaher (2000), Rieppel *et al.* (2007), Conrad (2008),

Wiens *et al.* (2010), Conrad *et al.* (2011) and Yi and Norell (2013), although in this work Mosasauria was recovered as the sister-group of Varanoidea, and not lying within varanoids (*sensu* the phylogenetic definition of Varanoidea given by Conrad (2008): *Heloderma*, *Lanthanotus*, *Varanus*, and all descendants of their last common ancestor).

Since the relationships between dolichosaurs and some basal mosasauroids were not resolved, resulting in a big basal polytomy within Mosasauria (Figure 6.1), the IterPCR protocol was followed for identifying unstable taxa. Two taxa were recognized as unstable and were removed from the analysis: the dolichosaur *Judeasaurus tchernovi* and the mosasauroid *Pannoniasaurus inexpectatus*. Both are probably unstable due to “soft polytomies” (lack of data supporting clades; Maddison, 1989). *Judeasaurus* is only known by a single skull preserved in ventral view (Haber and Polcyn, 2005), and therefore it cannot be scored for many important cranial and postcranial characters that defines mosasaurian clades nor be compared to other dolichosaurs, since no other specimen has the skull preserved in ventral view. *Pannoniasaurus* was described on the basis of isolated bones from dozens of individuals (Makádi *et al.*, 2012), which may represent a problem for phylogenetic analyses since they may represent individuals from different ages, sex and even species. A second analysis, removing *Judeasaurus* and *Pannoniasaurus* from the dataset, was run, also recovering 100.000 trees with a length of 5285 steps (Figure 6.2). Although internal nodes of Mosasauria in general found little Bremer and Bootstrap supports, two key nodes were recovered on the basis of relatively good supports: Mosasauria as a monophyletic group (5/91) and the clade formed by Mosasauria + Varanoidea (5/50) (Figure 6.2). In this analysis, the originally described dolichosaurs *Primitivus* and *Eidolosaurus* were found to constitute the sister-group of all other mosasaurians. A monophyletic Dolichosauridae clade was found, as in Evans *et al.* (2006) and Paparella *et al.* (2018) and *contra* most phylogenetic analysis including a larger sample of dolichosaurs (e.g. Lee and Caldwell, 2000; Conrad, 2008; Palci and Caldwell, 2010; Conrad *et al.*, 2011). *Aphanizocnemus* was found to be the sister-group of all other dolichosaurs. The basal mosasauroids *Haasiasaurus* and *Carsosaurus* were found to be more closely related to dolichosaurs than to other mosasauroids, but this is likely an artifact related to the incompleteness of the specimens (see item 6.4.2. below for more details). Mosasauroidea was also found as a monophyletic assemblage, but the relationships of basal forms (“aigialosaurs”) and plesiopedal mosasaurids were largely unresolved (Figure 6.2). When running the analysis with characters completely unordered, mosasaurians were still recovered as closely related to varanoids, but nesting in a polytomy between them, varanids, *Heloderma*, *Gobiderma*, *Estesia* and *Aiolosaurus* (Figure 6.3). In-group relationships were also mostly unresolved, resulting in

a polytomy between mosasauroids, “acteosaurines” (see item 6.4.3. for a more detailed discussion on dolichosaur lineages), “coniasaurines” and other mosasaurians.

## 6.4 Discussion

### 6.4.1. Mosasaurians as anguimorph lizards

The Anguimorpha clade recovered here is supported by 14 unambiguous synapomorphies, from which mosasaurians could be coded for nine of them, having seven present: 1) Anterior ethmoidal foramina exiting via premaxilla body (G7[2]; present in mosasauroids and reversed to [0] in dolichosaurs); 2) Presence of long and converging vomer ventral ridges (G222[1]; visible only in *Tethysaurus*); 3) Long and slender palatine process clasping in a groove on dorsal surface of vomer (G234[2]; visible only in *Tethysaurus*); 4) Neck elongation, presenting at least seven cervical vertebrae (G460[1]; dolichosaurs consistently present 10 or more cervicals [4] and basal mosasauroids eight [2]); 5) Cervical intercentrum located at posterior end of preceding centrum (G461[1]; present in every mosasaurian); 6) Caudal haemal arch contacting pedicles on preceding centrum but still bordering condyle (G475[2]; present in most mosasaurians, although some of them show the condition [3]); 7) Clavicle not presenting any notch or fenestra (G500[0]; only visible in *Carsosaurus*).

Mosasaurians nested within Anguimorpha is the most common result found in the literature, but their exact relationships with other members of the clade is highly debated. Works favoring a close relationship with snakes (the Pythonomorpha hypothesis; e.g. Lee, 1998; Lee and Caldwell, 2000; Palci and Caldwell, 2010; Paparella *et al.*, 2018) usually reach this result based on characters related to limb reduction, tooth implantation and replacement, intramandibular joint and the presence of zygantara-zygosphenes accessory articulations. On the other hand, characters as the origin of jaw musculatures on parietal, narial retraction, expanded basis of marginal teeth and the lack of fusion between the articular-prearticular complex and the surangular supports the interpretation of mosasaurians either closely related to (Conrad, 2008) or nested within Varanoidea (e.g. DeBraga and Carroll, 1993; Rieppel and Zaher, 2000; Rieppel *et al.*, 2007; Conrad *et al.*, 2011; Yi and Norell, 2013). This analysis recovered Mosasauria not within Varanoidea, but nesting as the sister-group of the later. 14 unambiguous synapomorphies are supporting this hypothesis: 1) Palatal shelf of premaxilla bifid posteriorly (G2[1]; only visible in derived mosasaurids); 2) Nasal anterior width less than anterior frontal width (G18[2]); 3) Narial margin of maxilla arising at low angle (G118[1]); 4) Maxilla posterior process ending on anterior half of orbit (G124[1]); 5) Jugal overlapping the most posterior

maxillary tooth (G143[1]); 6) Main portion of vomer rod-like (G214[1]); 7) Splenial not extending posteriorly to the end of the coronoid apex (G376[1]); 8) Posterior mylohyoid foramen located anterior to coronoid apex (G385[2]); 9) Dorsal and ventral margins of the coronoid dentary process parallel sided (G395[1]); 10) Prearticular and surangular not fused (G401[1]); 11) Bases of marginal teeth expanded (G426[1]; reversed to [0] in dolichosaurs, xenosaurs and anguids); 12) Cervical intercentrum shorter than pedicle (G464[1]); 13) Symphyseal process of pubis expanded distally (G513[0]); 14) Dermal skull bone lightly rugose (G572[1]).

#### 6.4.2. Mosasauria as a monophyletic group

Total group Mosasauria was recovered here as a monophyletic assemblage on the basis of eight synapomorphies: 1) Internasal process of maxilla reaching more than half way to frontal between nasals (G10[1]); 2) Fusion of the frontals (G36[1]); 3) “Pythonomorph” quadrate (G186[1]); 4) Olecranon process on proximal epiphysis of ulna reduced or absent (G532[1]); 5) Internal trochanter of femur poorly developed or absent (G550[1]; reversed to 0 in *Coniasaurus* and some basal mosasauroids); 6) Haemal arches on caudal vertebrae elongated, forming a sculling organ (N612[1]; changed to 2 in hydropedal mosasaurs); 7) Reduction of forelimbs in relation to hindlimbs (N613[1]; changed to 2 in more derived dolichosaurs and reversed to 0 in hydropedal mosasaurs); 8) Radius and ulna diverging distally (N619[1]). While a monophyletic mosasaurian assemblage (dolichosaurs + mosasauroids) is usually recovered in the literature (e.g. Polcyn and Bell, 1994; Bardet *et al.*, 2003; Conrad, 2008; Wiens *et al.*, 2010; Conrad *et al.*, 2011; Gauthier *et al.*, 2012; Yi and Norell, 2013; Reeder *et al.*, 2015), works favoring the Pythonomorpha hypothesis tend to find dolichosaurs as more closely related to snakes than to mosasauroids (e.g. Lee and Caldwell, 2000; Lee and Scanlon, 2002; Pierce and Caldwell, 2004; Palci and Caldwell, 2007; Caldwell and Palci, 2010; Palci *et al.*, 2013). An exception to this scenario is the recent contribution of Paparella *et al.* (2018) describing the dolichosaur *Primitivus*. In their work, a monophyletic Mosasauria clade was recovered as the sister-group of snakes, but with a monophyletic assemblage of dolichosaurs more closely related to mosasauroids than to snakes.

In this work, however, *Primitivus* was not found within the dolichosaurian assemblage, but together with *Eidolosaurus* forming a clade that is the sister-group of all other mosasaurians. They are separated from the rest of the group by not presenting the following five unambiguous synapomorphies: 1) Supratemporal shorter than squamosal-parietal contact (G167[1]; 0 in *Primitivus* and unknown in *Eidolosaurus*); 2) Ilium blade strongly inclined vertically (G522[1];

0 in *Primitivus*, unknown in *Eidolosaurus* and changed to 2 in hydropedal mosasaurs); 3) Carpal intermedium small (G535[1]; changed to 2 in *Primitivus*); 4) Astragalus and calcaneum separated elements (G561[2]; 1 in *Primitivus*, unknown in *Eidolosaurus* and 0 in *Haasiasaurus*); 5) Phalangeal count reduction in pes, reducing digit V to three phalanges (G566[4]; 0 *Primitivus* and unknown in *Eidolosaurus*). Unfortunately, *Eidolosaurus* could not be scored for any of these characters because the large amount of missing data in the holotype (it is represented only by a single cast of an individual without cranial remains preserved). Nevertheless, an important result of this analysis was to find both *Primitivus* and *Eidolosaurus*, originally described as dolichosaurs (Nopcsa, 1923; Paparella *et al.*, 2018), in the base of the mosasaurian clade, and not within Dolichosauridae.

### 6.4.3. Dolichosauridae as a monophyletic group

Although most phylogenetic analyses with a large sample size of dolichosaurs found the group to be paraphyletic (e.g. Lee and Caldwell, 2000; Conrad, 2008; Palci and Caldwell, 2010; Conrad *et al.*, 2011), here a monophyletic clade of dolichosaurs was found, and will be referred here to as Dolichosauridae. A more inclusive definition of the family also deals with the issue of the family being monogeneric after the synonym of *Dolichosaurus* with *Coniasaurus* (see Chapter 2 for a more detailed discussion). Evans *et al.* (2006) and Paparella *et al.* (2018) also found a monophyletic clade of dolichosaurs, although in the later *Primitivus* was nested within dolichosaurs. The Dolichosauridae family considered here is the clade formed by *Aphanizocnemus*, *Coniasaurus* and the lineage of pachyostotic dolichosaurs (*Acteosaurus*, *Adriosaurus* and *Pontosaurus*), and it is joined by the presence of one single unambiguous character: dorsal vertebrae number between 25 and 30 (N608[2]; changed to 3 in the more elongated *Coniasaurus*). Although the basal mosasauroids *Haasiasaurus* and *Carsosaurus* were found closely related to dolichosaurs than to other mosasauroids, this result is probably related to missing data regarding these two taxa, since from the four synapomorphies of mosasauroids found in this work both could not be scored for three of them. The inclusion of more characters in the future should resolve this position. *Aphanizocnemus* was recently proposed to be a “scincogekkonomorph” lizard instead of a dolichosaur (Mekarski, 2017), but here it was still recovered within Dolichosauridae.

Dolichosaurs exclusive of *Aphanizocnemus* are joined by the extreme reduction of forelimbs (N613[2]). This clade recovers two distinct lineages of dolichosaurs: “coniasaurines”, joined by six unambiguous synapomorphies: 1) Well-developed femoral internal trochanter

(G550[0]); 2) Increased dorsal vertebrae number, with more than 30 elements (N608[3]); 3) Posterior enlargement of the neural spine base (N609[1]); 4) Presence of a lateral “carving” on dorsal vertebrae (N610[1]); 5) Enlarged deltopectoral crest on humerus (N615[1]); 6) Humeral shaft twisted (N618[1]); and “acteosaurines”, joined by three unambiguous synapomorphies: 1 and 2) Presence of pachyostosis on mid-dorsal vertebrae and ribs (G469[1] and G478[1]); 3) Reduced scapulocoracoid (G488[1]). In some trees, an increase from one to two pygal vertebrae (N611[2]) also supports the clade. Novelty results recovered here evidence the presence of two main lineages of dolichosaurs, distinct both in geographic distribution and paleobiology. “Coniasaurines” were very elongated lizards, with probably higher swimming capabilities (see Chapter 1 for a more detailed discussion on this topic), that ranged from Southern portions of the Artic Sea to Southeastern portions of the Western Interior Seaway (coniasaur records reported from Germany in Diedrich, 1997 and Australia in Scanlon and Hocknull, 2008 are too fragmentary for a reliable taxonomic identification, and therefore are ignored here). “Acteosaurines” were slightly shorter and pachyostotic animals which paleobiogeographical distribution restricted to portions of the North Atlantic (on what is nowadays Europe around the Adriatic Sea).

#### 6.4.4. Issues within Mosasauroida

The Mosasauroida clade recovered here (inclusive of *Opetiosaurus*, *Komensaurus* and *Aigialosaurus* but exclusive of *Haasiasaurus* and *Carsosaurus*) was joined by four synapomorphies (one unambiguous, N607, and three ambiguous): 1) Postorbital with process extending lateral to tapering apex of jugal (G83[3]; unknown in *Haasiasaurus* and *Carsosaurus*); 2) Large supraorbital process of prefrontal (B29[1]; unknown in *Haasiasaurus* and *Carsosaurus*); 3) Quadrate ala thick (B51[1]; absent in *Haasiasaurus* and unknown in *Carsosaurus*); 4) Presence of at least 3 pygal vertebrae (N611[3]; absent in *Carsosaurus* and unknown in *Haasiasaurus*). Three basal mosasauroids, *Opetiosaurus*, *Komensaurus* and *Aigialosaurus*, were found in a polytomy with the Mosasauridae branch, and therefore it is not possible to state whether each one of these are more related to each other or to the mosasaurid branch. The “mosaic” anatomy of “aigialosaurs”, presenting intermediate characters between dolichosaurs, varanoids and mosasaurs, and the lack of more and better-preserved specimens, may be two important factors behind the poor resolution of these animals in this analysis.

Mosasauridae was found as a monophyletic group, as it is commonly found in the literature (e.g. DeBraga and Carroll, 1993; Bell, 1997; Lee and Caldwell, 2000; Polcyn and

Bell, 2005; Makádi *et al.*, 2012 Simões *et al.*, 2017), on the basis of three unambiguous synapomorphies: 1) Femur not curved in dorsoventral plane (G549[1]); 2) Humerus hourglass shaped (C275[1]); 3) Enlarged deltopectoral crest on humerus (N615[1]). However, this analysis was not able to resolve the relationships between the basalmost members of the family, resulting in a polytomy between *Russellosaurus*, *Tethysaurus*, *Dallasaurus*, *Eonatathor* and the clade formed by hydropedal mosasaurs (Figure 6.2). In this analysis, hydropedal mosasaurs were separated from other mosasaurs on the basis of ten unambiguous synapomorphies: 1) Frontal broadly overlapping prefrontal dorsally (G50[1]); 2) Postorbital overlapping squamosal in V shaped contact (G78[3]); 3) Parietal posterior overgrown, covering nuchal fossa (G94[2]); 4) Supratemporal longer than squamosal-parietal contact (G167[0]); 5) Presence of coronoid eminence (G386[0]); 6) Ilium blade anteriorly oriented (G522[2]); 7) Epiphyses on long bones absent (G527[1]); 8 and 9) Hyperphalangy on manus and pes (G544[1] and G567[1]); 10) Forelimbs subequal in size to hindlimbs (N613[0]). The hydropedal clade of mosasaurs found here is divided internally into two main lineages: Mosasaurinae (*Clidastes* + *Plotosaurus*) and a clade formed by *Tylosaurus* and *Platecarpus*. Mosasaurines are joined by five unambiguous synapomorphies: 1) Basipterygoid process short (G333[1]); 2) Vidian canal caudal opening within basisphenoid (G337[0]); 3) Surangular dorsal margin rises steeply anterodorsally to coronoid (G400[1]); 4) Increased dorsal vertebrae number, with more than 30 elements (N608[3]); 5) Well-developed postglenoid process on humerus (B122[1]), while *Tylosaurus* and *Platecarpus* are joined by two unambiguous synapomorphies: 1) Postorbital nearly excludes squamosal from upper temporal fenestra (G77[1]); 2) Quadrate ala thin (B51[0]).

Although finding a monophyletic Mosasauridae, this analysis was not able to resolve the relationships between plesiopterygians. Therefore, hypotheses as *Dallasaurus* as a mosasaurine (Bell and Polcyn, 2005), *Russellosaurus* closely related to *Tethysaurus* and both to the clade formed by tylosaurines and plioplatecarpines (Polcyn and Bell, 2005), and *Eonatathor* as the sister of all other mosasaurids (Polcyn *et al.*, 2014) could not be tested. This result is not entirely surprising, since the taxonomic sampling of mosasaurids taken here is very low (nearly 15% of the known species, against 75% of the dolichosaurs and 70% of the “aigialosaurs”). In the future, increasing taxonomic sampling of mosasaurids and adding new characters will probably resolve this basal polytomy in the clade.

### 6.4.5. Taxonomic sampling tests

#### 6.4.5.1. Only dolichosaurs

Including only dolichosaurs on the matrix changed the position of mosasaurians from sister-group of varanoids to be nested within Varanoidea, being more closely related to varanids than to monstersaurs (Figure 6.4). In-group relationships of this expanded Varanidae remained unresolved at the base, with a polytomy between *Lanthanotus*, *Aiolosaurus*, (*Saniwa* + *Varanus*) and dolichosaurs. In-group relationships of dolichosaurs also remained largely unresolved, resulting in a polytomy between *Aphanizocnemus*, (*Primitivus* + *Eidolosaurus*), *Coniasaurus* and “acteosaurines”.

#### 6.4.5.2. Only basal mosasauroids

When only “aigialosaurs” were included in the matrix, the same result as the “only dolichosaurs test” was obtained: mosasaurians nesting within Varanidae (Figure 6.5). The only exception is that *Aiolosaurus* was excluded from this clade in the test. In-group relationships were unresolved, forming a polytomy between *Saniwa*, *Lanthanotus*, *Varanus* and basal mosasauroids. In-group relationships between “aigialosaurs”, on the other hand, were totally resolved, with *Haasiasaurus* and *Carsosaurus* being successively found as the sister taxa of all other basal mosasauroids, and *Aigialosaurus* the sister of (*Opetiosaurus* + *Komensaurus*).

#### 6.4.5.3. Only mosasaurids

With a mosasaurid-only taxonomic sampling the result was very distinct from the other tests. The group was still found among anguimorphs, but this time more closely related to the “fossorial group” of Gauthier *et al.* (2012) than to varanoids (Figure 6.6), and these two as the sister-group of varanoids. Within Mosasauria, two clades were recovered: one formed by hydropedal mosasaurs and the other formed by more primitive, plesiopedal, forms.

#### 6.4.5.4. Only hydropedal mosasaurids

Having only *Tylosaurus*, *Platecarpus*, *Plotosaurus* and *Clidastes* on the analysis resulted in the same topology as the former test, with mosasaurids being more closely related to the “fossorial group” than to varanoids (Figure 6.7).

#### 6.4.5.5. No dolichosaurs

Removing dolichosaurs, having only mosasauroids, in the dataset resulted in mosasaurians again nesting within Anguimorpha as the sister-group of varanoids (Figure 6.8). Not surprisingly, “aigialosaurs” formed a paraphyletic assemblage, with *Carsosaurus* being the sister of all other mosasauroids, followed by *Haasiasaurus* being the sister of all the reminiscent mosasauroids, and by a polytomy between *Opetiosaurus*, *Komensaurus* and *Aigialosaurus* as the sister of Mosasauridae.

#### 6.4.5.6. No basal mosasauroids

By excluding “aigialosaurs” from the analysis, but keeping dolichosaurs and mosasaurids, a very similar result to the complete dataset was obtained (Figure 6.9). Mosasauria was recovered as the sister-group of Varanoidea, with *Primitivus* and *Eidolosaurus* being the sister of all other mosasaurians. Within that clade, a polytomy between *Aphanizocnemus*, dolichosaurids (“coniasaurines” + “acteosaurines”) and mosasaurids was found.

#### 6.4.5.7. No mosasaurids

When no mosasaurids were included in the dataset, mosasaurians were again found to be nested within Varanidae, with an unresolved polytomy between *Saniwa*, *Lanthanotus*, *Varanus* and mosasaurians (Figure 6.10). Within Mosasauria, a large polytomy was found between all dolichosaurs and “aigialosaurs”, with the only clades recovered being “coniasaurines”, “acteosaurines” and the clade formed by *Primitivus* and *Eidolosaurus*.

#### 6.4.5.8. No hydropedal mosasaurs

Without only the hydropedal mosasaurs, mosasaurians were again recovered within Varanidae, but this time as the sister-group of *Saniwa* among all other varanids (Figure 6.11). Within the clade, Dolichosauridae and Mosasauroidae lineages were recovered, nesting in a polytomy between the two of them and *Haasiasaurus*, *Carsosaurus*, *Primitivus* and *Eidolosaurus*.

### 6.4.6. The importance of comprehensive taxonomic sampling regarding fossil taxa

Gauthier *et al.* (2012) found mosasaurians to be nested not only outside of Anguimorpha, but outside of Scleroglossa as well. In their work, they found 24 synapomorphies of crown Scleroglossa, from which mosasaurians could be scored for only 3 of them. However,

after raising the taxonomic sampling in this analysis for including a higher number of dolichosaurs, “aigialosaurs” and plesiopedal mosasaurs, the presence of Scleroglossan synapomorphies in Mosasauria could be better evaluated. Firstly, this analysis confirmed the presence of nine of them: 1) Reduction of the nasal supranarial process (G22[1]; in mosasaurians, the entire nasal bone is greatly reduced); 2) Fusion of the frontals (G36[1]); 3) Base of squamosal temporal ramus lying against the parietal (G162[1]; present in every plesiopedal mosasaurian that could be scored for this character); 4) Absence of squamosal ascending process (G165[1]; present in every plesiopedal mosasaurian that could be scored for this character); 5) Septomaxilla dorsally expanded (G200[1]; only visible in *Tethysaurus* and thanks to CT data availability); 6) Pterygoid separation being broad at base and somewhat narrow anteriorly (G258[2]; only visible in *Tethysaurus* and thanks to CT data availability); 7) Ectopterygoid posterior process being a small lateral knob structure (G283[1]; only visible in *Russellosaurus*); 8) Splenial anteriorly extending to nearly two-thirds of the mandible length (G375[2]; visible in *Pontosaurus lesinensis* and *Haasiasaurus*, and also visible in NHMUK-R3421, a cf. *Coniasaurus crassidens* left mandible which was not scored in this analysis); 9) Presence of a small carpal intermedium (G535[1]; visible in *Adriosaurus suessi*, *Pontosaurus* and *Carsosaurus*). Secondly, from the six Scleroglossan synapomorphies certainly not present in mosasaurians, five of them were also reversed in at least some anguimorphs: 1) Temporal muscles originating dorsally on parietal (G90[0]; also reversed in the clade formed by Lanthanotidae + Varanidae); 2) Prearticular and surangular unfused (G401[0]; also reversed in *Heloderma* and some fossil varanoids); 3) Clavicle being a simple rod-like element (G502[0]; also reversed in *Varanus salvator* and *Shinisaurus*); 4) Interclavicle anterior process length / interclavicle length being less than 0.20 (G508[0]; also reversed in *Xenosaurus* and *Shinisaurus*); 5) Absence of an enlarged distal epiphysis of ulna that is nearly hemispherical (G533[0]; also reversed in *Xenosaurus*). Thirdly, the remaining nine scleroglossan characters could not be scored for the basal forms due to lack of preservation or because they are soft tissue characters. Therefore, this analysis found more evidence to support the hypothesis of mosasaurian as scleroglossan lizards than the contrary.

Although Gauthier *et al.* (2012) stated that their reduced mosasaurian taxonomic sampling were not a big issue when recovering the phylogenetic relationships of the clade within Squamata (p. 52), here was found robust evidence that shows the opposite scenario. The inclusion of more basal forms of mosasaurians, including dolichosaurs and plesiopedal mosasauroids, seemed to play an essential role in recovering the clade within Scleroglossa and within Anguimorpha. Many characters that could not be scored for the basal mosasaurians

originally present in Gauthier *et al.* (2012) dataset (*Adriosaurus*, *Pontosaurus* and *Aigialosaurus*) were scored here thanks to the inclusion of new taxa, especially *Coniasaurus*, *Carsosaurus*, *Haasiasaurus*, *Tethysaurus* and *Russellosaurus*. Furthermore, during the reanalysis of the original codification some characters were found to bear miscodifications for *Adriosaurus*, *Pontosaurus* and *Aigialosaurus* (i.e. *Adriosaurus* was scored with the state 3 in the character 460, which originally has only states 0, 1 and 2). The amount of new data provided by this analysis, gathered by the inclusion of additional basal mosasaurians and plesiopedal mosasauroids, inclusion of new characters and by performing scoring correction on basal forms already present in the original dataset can be seen as the main factor that is changing the position of mosasaurians from stem-Scleroglossa to well-nested within Anguimorpha, as the sister-group of Varanoidea.

In addition, phylogenetic tests performed here highlighted the sensibility of the dataset to the exclusion of basal mosasaurians. In 6 of 8 tests, mosasaurians were not recovered as the sister-group or nested within Varanoidea in only 2 of them: when only derived mosasaurids were included and dolichosaurs and “aigialosaurs” were excluded (Figures 6 and 7). Therefore, the original mosasaurian taxonomic sampling of Gauthier *et al.* (2012), including only two dolichosaurs, one “aigialosaur” and four highly derived hydropedal mosasauroids, cannot be understood as an adequate sample for testing the phylogenetic relationships of the group within Squamata.

## 6.5 Final considerations

This analysis provided a consistent test of the mosasaurian phylogenetic relationships within Squamata by including the largest sample of basal forms ever tested so far (75% of the dolichosaurs and 70% of the “aigialosaurs”, as well as five plesiopedal mosasaurids) into the largest original morphological matrix available in the literature (Gauthier *et al.*, 2012). Mosasauria was found not only within Scleroglossa, but also within Anguimorpha, as the sister-group of Varanoidea.

*Primitivus* and *Eidolosaurus*, originally described as dolichosaurs, were found to form a clade that is the sister-group of all other mosasaurians, and not nested within Dolichosauridae. *Aphanizocnemus* was found as the sister of all other dolichosaurs (“coniasaurines” and “acteosaurines”). The relationships of basal mosasauroids (“aigialosaurs”) remained largely unresolved, with *Haasiasaurus* and *Carsosaurus* being more closely related to dolichosaurs than to mosasauroids, and *Opetiosaurus*, *Komensaurus* and *Aigialosaurus* nesting within

Mosasauroidea in a polytomy between each other and Mosasauridae. Tests of inclusion and exclusion of taxa showed that in 6 out of 8 tests mosasaurians were still recovered or as the sister or within Varanoidea. In only two, when excluding dolichosaurs and basal mosasauroids, mosasaurians were recovered as more closely related to the “fossorial group” of Gauthier *et al.* (2012) than to varanoid lizards, highlighting the importance of a comprehensive taxonomic sampling of basal forms when evaluating the phylogenetic relationships of a given clade.

## References

- Bardet, N.; Suberbiola, X.P.; Iarochene, M.; Bouya, B.; Amaghaz, M. 2005. A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halisaurinae (Squamata: Mosasauridae). **Zoological Journal of the Linnean Society** 143: 447-472.
- Bardet, N.; Suberbiola, X.P.; Jalil, N.E. 2003. A new mosasauroid (Squamata) from the Late Cretaceous (Turonian) of Morocco. **Comptes Rendus de l'Académie des Sciences** 2(8): 607-616.
- Bell, G.L.; Polcyn, M.J. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). **Netherlands Journal of Geosciences** 84 (3): 177-194.
- Bell, G.L. 1997. A phylogenetic revision of North American and Adriatic Mosasauroidea. In: Callaway, J.M.; Nicholls, E.L.(eds.). **Ancient Marine Reptiles**. Academic Press. 293–332.
- Bremer, K. R. 1994. Branch support and tree stability. **Cladistics** 10(3): 295-304.
- Caldwell, M.W.; Palci, A. 2010. A new species of marine ophiomorph lizard, *Adriosaurus skrbiniensis*, from the Upper Cretaceous of Slovenia. **Journal of Vertebrate Paleontology** 30(3): 747-755.
- Carroll, R.L.; Debraga, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. **Journal of Vertebrate Paleontology** 12(1): 66-86.
- Conrad, J.L.; Ast, J.C.; Montanari, S.; Norell, M.A. 2011. A combined evidence phylogenetic analysis of Anguimorpha (Reptilia: Squamata). **Cladistics** 27: 230-277.
- Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. **Bulletin of the American Museum of Natural History**, 310: 1-182.
- de Braga, M.; Carroll, 1993. The origin of mosasaurs as a model of macroevolutionary patterns and processes. **Evolutionary Biology** 27: 245-322.

- Diedrich, C. 1997. Ein dentale von *Coniosaurus crassidens* Owen (Varanoidea) aus dem Ober-Cenoman von Halle/Westf. (NW-Deutschland). **Geologie und Paläontologie in Westfalen** 47: 43-51.
- Evans, S.E.; Manabe, M.; Noro, M.; Isajis, S.; Yamaguchi, M. 2006. A longbodied lizard from the Lower Cretaceous of Japan. **Paleontology** 49(6): 1143-1165.
- Farris, J. S. 1989. The retention index and the rescaled consistency index. **Cladistics** 5(4): 417-419.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. **Evolution** 39(4): 783-791.
- Gauthier, J.A.; Kearney, M.; Maisano, J.A.; Rieppel, O.; Behlke, A.D.B. 2012. Assembling the Squamate tree of life: perspectives from the phenotype and the fossil record. **Bulletin of the Peabody Museum of Natural History** 53(1): 3-308.
- Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. **Cladistics** 15(4): 415-428.
- Goloboff, P.A. 2002. Techniques for analyzing large data sets. In **Techniques in molecular systematics and evolution** (eds DeSalle, R.; Giribet, G.; Wheeler, W.), pp. 70-79. Basel: Birkhäuser Verlag.
- Goloboff, P.A.; Catalano, S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. **Cladistics** 32(3): 221-238.
- Goloboff, P.A.; Farris, J.S. 2001. Methods for quick consensus estimation. **Cladistics** 17(1): S26-S34.
- Haber, A.; Polcyn, M.J. 2005. A new marine varanoid from the Cenomanian of the Middle East. **Netherlands Journal of Geosciences** 84(3): 247-255.
- Kluge, A.G.; Farris, J.S. 1969. Quantitative phyletics and the evolution of anurans. **Systematic Biology** 18(1): 1-32.
- Lee, M.S.Y. 1997a. On snake-like dentition in mosasaurian lizards. **Journal of Natural History** 31: 303-314.
- Lee, M.S.Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. **Biological Journal of the Linnean Society** 65: 369-453.
- Lee, M.S.Y.; Caldwell, M.W. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. **Journal of Paleontology** 74(5): 915-937.
- Lee, M.S.Y.; Scanlon, J.D. 2002. The Cretaceous marine squamate *Mesoleptos* and the origin of snakes. **Bulletin of the Natural History Museum London (Zoology Series)** 68: 131-142.

- Maddison, W. 1989. Reconstructing character evolution on polytomous cladograms. **Cladistics** 5(4): 365-377.
- Makádi, L.; Caldwell, M.W.; Ösi, A 2012. The first freshwater mosasauroid (Upper Cretaceous, Hungary) and a new clade of basal mosasauroids. **PLoS ONE** 7 (12): e51781. doi:10.1371/journal.pone.0051781.
- Nixon, K.C. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. **Cladistics** 15: 407-414.
- Palci, A.; Caldwell, M.W. 2007. Vestigial forelimbs and axial elongation in a 95 million-year-old non-snake squamate. **Journal of Vertebrate Paleontology** 27(1): 1-7.
- Palci, A.; Caldwell, M.W. 2010. Redescription of *Acteosaurus tommasinii* von Meyer, 1860, and a discussion of evolutionary trends within the clade Ophidiomorpha. **Journal of Vertebrate Paleontology** 30(1): 94-108.
- Palci, A.; Caldwell, M.W.; Papazzoni, C.A. 2013. A new genus and subfamily of mosasaurs from the Upper Cretaceous of Northern Italy. **Journal of Vertebrate Paleontology** 33(3): 599-612.
- Paparella, I.; Palci, A.; Nicosia, U.; Caldwell, M.W. 2018. A new fossil marine lizard with soft tissues from the Late Cretaceous of southern Italy. **Royal Society Open Science** 5(6): doi 172411.
- Pierce, S.; Caldwell, M.W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur, *Pontosaurus lesinensis* (Kornhuber, 1873). **Journal of Vertebrate Paleontology** 24: 376-389.
- Pol, D.; Escapa, I.H. 2009. Unstable taxa in cladistic analysis: identification and the assessment of relevant characters. **Cladistics** 25(5): 515-527.
- Polcyn, M.J.; Bell, G.L. 1994. *Coniasaurus crassidens* and its bearing on varanoid-mosasauroid relationships. **Journal of Vertebrate Paleontology**, Supplemental 14: 42A.
- Polcyn, M.J.; Bell, G.L. 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(3): 321-333.
- Polcyn, M.J.; Jacobs, L.L.; Araújo, R.; Schulp, A.S.; Mateus, O. 2014. Physical drivers of mosasaur evolution. **Palaeogeography, Palaeoclimatology, Palaeoecology** 400: 17-27.
- Reeder, T.W.; Townsend, T.M.; Mulcahy, D.G.; Noonan, B.P.; Wood, P.L.Jr.; Sites, J.W.Jr.; Wiens, J.J. 2015. Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny and Reveal Unexpected Placements for Fossil Taxa. **PLoS ONE** 10(3): e0118199. doi:10.1371/journal.pone.0118199.

- Rieppel, O.; Zaher, H. 2000a. The intramandibular joint in squamates and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. **Fieldiana (Geology), New Series** 43: 1-69.
- Rieppel, O.; Conrad, J.L.; Maisano, J.A. 2007. New morphological data for *Eosaniwa koehni* Haubold, 1977 and a revised phylogenetic analysis. **Journal of Paleontology** 81(4): 760-769.
- Russell, D.A. 1967. Systematics and morphology of American mosasaurs. **Bulletin of the Peabody Museum of Natural History** 23: 1-241.
- Scanlon, J.D.; Hocknull, S.A. 2008. A dolichosaurid lizard from the latest Albian (mid-Cretaceous) Winton Formation, Queensland, Australia. **Transactions of the Kansas Academy of Science (Fort Hays Studies Special Issue - Proceedings of the Second Mosasaur Meeting)**: 131-136.
- Simões, T.R.; Caldwell, M.W.; Palci, A.; Nydam, R.L. 2017. Giant taxon-character matrices: quality of character constructions remains critical regardless of size. **Cladistics** 33(2): 198-219.
- Wiens, J.J.; Kuczynski, C.A.; Townsend, T.; Reeder, T.W.; Mulcahy, D.G.; Sites, J.W.Jr. 2010. Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. **Systematic Biology** 59(6): 674-688.
- Yi, H.Y.; Norell, M.A. 2013. New materials of *Estesia mongoliensis* (Squamata: Anguimorpha) and the evolution of venom grooves in lizards. **American Museum Novitates** (3767), 1-31.
- Zaher, H.; Pol, D. 2017. **Tutorial para uso das funções básicas do programa T.N.T. no curso “Origem e evolução dos amniotas”**. Universidade de São Paulo, 59 p.

### Appendix 1 - List of characters added to matrix

606. Prefrontal, supraorbital process: (0) process absent, or present as a very small rounded knob; (1) distinct to large, triangular or rounded, overhanging wing. Source: Bell (1997).

607. Quadrate, thickness of quadrate ala: (0) thin; (1) thick. Source: Bell (1997).

608. Dorsal vertebrae, number of elements: (0) 18 or less; (1) Between 19 and 24; (2) Between 25 and 30; (3) Between 31 and 50; (4) Between 51 and 100; (5) 101 or more. Source: Chapters 1 and 5 [ordered].





























?0111??1102??0?0000?1?????01??010000110??0?001000000000?????0?011000011000??00?0?????????????????30311?0?1?0??00  
0??0?????????0??0000?0000?00?100?????????  
?????????????????500?????????

Anomochilus leonardi

1100?0110110000010111?100010001000002311000121??01010013?0001????1????????????????????10000?01000011?1??2?  
2?000?1?020000100?2000010201?0011????????????????1????1?????0????1130000220?111210001100021111010100021120101?  
000010?0000010041?0100003?00?1?131000000?1?001??00000??220?0?1?????0001101000??11?0000?01111?0010012??11?010  
00020121211111101?000?0?000010?13?0?101200010?200?210011?000000000??02000111000111?00?0000????????????????30311  
??1?0?0000??0??????0??????????????????????0????0??01?????1????????????????????1????????????????????0000?0000?00?11  
0??????????????????0??500?????????

Anilius scytale

1100??0110110000010111?100010001000002311000301??01010023?0001????1????????????????????100001?01000001?1??2?  
2?000?1?123000000?2000010201?0021????????????????1?????00000?0000?11130000210011121001110002111310101?0020020101  
?000010?030001004200100003?00?01131000000?01000100100?10??2?200001?????0001101000??11?0010??01111?1100012??11?00  
10000201212111011101?00?02?1000?1????1?1?0?000100?00?211011?01?????010?2200222100011101?100001?0?0?1??????3031  
1?1013030000??001?????02?????????1????1?????0?1??0?1??0??0100??1????????????????????0000?0000?00??  
11024????????1?0??101??100500?0??????

Cylindrophis ruffus

1100??011011000001011????0010001000002311000121??0101003?0001????00?31?010?????1?0?100001??1000001?1?20  
??000?1??123000000??000110201?0011????????????????1?????002010?0000??113000020101?12100111000211131010100020120101  
?00?010?030001004200100003?00?01131000000?01000100011010??2?200001?????0001101000??11?0000?01011010?0012??11?00  
01100201212111011101?000?1?000010?11?1011012000000200?211011?01?????0??2200022100011101?000001??0??01??????303  
11?1013030000??001?????02?????????1????1?????0?1??0?1??0??0100??1????????????????????0000?0000?00??  
??11024????????1?04?110??1100500?0??????

Uropeltis melanogaster

1000001100110000010111?110010001000002311000122??01010013?0001????1????????????????????100001??200002??1?2??  
2?00??1?023000000??000011201?0011????????????????1????1????????????11300002400111210001100021110101000?021120001?0  
00?10?0?00100?1?0100033000?1?131000000?1?00100100000??2?200001?????2001?0?000??11?0?0?011011?0000012??12??0??0  
?020121211111101?000?1?000010?11?011012000100200?010011?01?????0??1000021110011101?00001??0??01??????30311?1  
013030000??001?????02?????????1????1?????0?1??0?1??0??0100??1????????????????????0000?0000?00??110?  
?????????????1??????500?????????

Xenopeltis unicolor

1100??011011000002011????0010?0?1000?2310000221??01010013?0001????10????????????????100001?01000011?1??2?  
?000?2????3000000?00?2102?1?0011????????????????1?????002030?010??1113012020001113100111001211101101?0020120?02?  
0?010?03?0?0100420010110??0?02131100001?02000101011010??2?20111?????0002201000??11?0010?01101211000012??10?0000  
0002012101110?1101?0??0?00010?0?1000?1?2?????2110?1?0000?00000?200?4441100101101?100001??0??01??????30311?  
1013030000??001?????02?????????1????1?????1????1??1?????1????????????????????1????????????????????0000?0000?00??11  
024??0?001?04?110??0??500?????????

Loxocemus bicolor

1100??011011000002011????0010?010000?2311000211??01010013?0001????00?31?110?????0?31?100001??2000011?1?20?  
2?000?2??23000000??0000102?1?0011????????????????1?????002030?010??111301402000111310011100121110110100020120?02?  
00?010?030?0100420010110??0?02131100001?02000101011010??2?200211?????0002201000??11?0010?01101211000011??10?001  
010020121011111101?000?0?000010?11?0?101?020100200?211011?00000000010?22001321100111101?100001??0??01??????3031  
1?101303000021?001?????02?????????1????1?????0?1??0?1??0??01?????1????????????????????0010?0000?00??  
11024????????1?04?110??0??500?????????

Xenophidion acanthognathus

1100??001?11000002011????0010?0101?0?2?11000321??0?010012?0001????1????????????????????100?01??200002??1?1?2?  
?000?2??23000010??0000102?1?0011????????????????1?????002030?010??0113002020?00113100111001211121?100?0020120?02?  
0?010?03000100420010110??0?02131100101?02000101011010??2?200001?????0002201000??11?0000?01101100?00012??11?00?0  
110?0121011111101?0?0?0?00010?11?101100?02?2??0?2100?1?0000?0000??2300032110011101?1000001?00?01??????30311?  
1013030000??001?????02?????????1????1?????1????1????1?????1????????????????????1????????????????????0000?0000?00??11  
0?????????????????????500?????????

Casarea\_dussumieri

1100??001011000002011????0010?0?2200?2310000311??01010012?0101????00?31?010?????0?4?0?100101??1000011?1?10?  
2?000?2??23000010??0000102?1?0011????????????????1?????0010300010??01130020201011131001110022111011101?0020120?02?  
00?010?0??0000420010110??00?01131100101?02000101011010??2?200101?????0002201000??11?0000?0101201000012??10?000  
010020121011111101?000?0?000010?11?101101?1?010?100?211011?000000000??23000321100111101?10000??0?0?1??????0??  
??11????000??001?????02?????????1????1?????1????1????1?????1????????????????????1????????????????????0000?0000?00??1  
10??????????????????0??500?????????

Haasiophis terrasanctus

??000??10????002111????001?0010?000?1????????????????022?0??1????000?3?0010??0?????0?1?0001?0?00000111?00??0  
??11?12300?00??00?0?0?1?0011????????????????1?????0020?0?0000?011300?0?????????1????????????????????0????????10?  
?????1??20??????????02131?0100?0200?101??0100?2?201??1?????0?011000?????????0?????1??100??1??1??0?0?????????0?  
1?111?1?0?00??0010?1?0001?0?0101?0100?1??1?01?????0?0?2?00?331100111??1?100?0?????????????????13?1??130??2?1?10  
1?????0?????????1?????1?????0?11?01?01001??1?????????????????011?????10111?01??0??0000?0000?0?????????????????  
??????????5??????????

Eupodophis descouensis

11200??10?00?0????1????????????????0?????0?1????????????????000?10010??0??4?1????0????????????????0??0??  
1?????0?0000?????02?????1????????????????1?????00?????0100??1130?0?????????01????????????10?????00?0?????????0??0??  
?1?420??11?????????1?1????00?0?????1?1?0?0?????0?????????0????????????????????0?????1?10?????????1????1?????????????1?????  
????????????0????????????????????1?????????0?????0003?1?0?11?????00?0?????????????????313?101313?????001?????0??  
?????????1?????1?????????0??01001??1?????????????????011?????1?????????????????000000?????????????????????????50  
0?????????

Pachyrhachis problematicus

1?00??1?????????11?????????????0?000?????????????????0?2?0?1????000?310010??000?4?1?1?0001??0000011?000??0?  
??11?1300?00??20?0?2?1?0011????????????????1?????0020?1?0100??1130?40?00?0?????????????????????????????????0??













*Aphanizocnemus libanensis:*

All trees:

Char. 100: 0 --&gt; 1

Char. 516: 1 --&gt; 0

Char. 618: 1 --&gt; 0

*Coniasaurus* sp. nov.:

All trees:

No autapomorphies:

*Coniasaurus longicollis:*

All trees:

No autapomorphies:

*Eidolosaurus trauthi:*

All trees:

No autapomorphies:

*Pontosaurus kornhuberi:*

All trees:

No autapomorphies:

*Pontosaurus lesinensis:*

Some trees:

Char. 92: 0 --&gt; 1

Char. 526: 1 --&gt; 0

*Primitivus manduriensis:*

All trees:

No autapomorphies:

*Aigialosaurus dalmaticus:*

All trees:

Char. 544: 1 --&gt; 0

*Carsosaurus marchesetti:*

All trees:

Char. 489: 1 --&gt; 0

Char. 544: 1 --&gt; 0

Some trees:

Char. 526: 1 --&gt; 0

Char. 527: 0 --&gt; 1

*Haasiasaurus gittelmani:*

All trees:

Char. 524: 1 --&gt; 0

Some trees:

Char. 555: 2 --&gt; 0

*Komensaurus carrolli:*

All trees:

No autapomorphies:

*Opetiosaurus buccichi:*

All trees:

No autapomorphies:

*Dallasaurus turneri:*

All trees:

Char. 615: 0 --&gt; 1

*Eonatathor coellensis:*

Some trees: Char. 578: 1 --> 3  
 Char. 457: 1 --> 2

*Eonatathor sternbergi:*

Some trees:  
 Char. 393: 1 --> 0

*Tethysaurus nopcsai:*

Some trees:  
 Char. 48: 0 --> 1  
 Char. 266: 0 --> 1  
 Char. 393: 1 --> 0  
 Char. 469: 2 --> 3

*Russellosaurus coheni:*

Some trees:  
 Char. 48: 0 --> 1

*Clidastes:*

All trees:  
 Char. 48: 0 --> 1  
 Char. 428: 0 --> 1

*Platecarpus:*

All trees:  
 Char. 92: 0 --> 1  
 Char. 312: 0 --> 1  
 Char. 420: 2 --> 3  
 Char. 421: 1 --> 0  
 Char. 422: 0 --> 1  
 Char. 472: 0 --> 1

Char. 578: 1 --> 3

*Plotosaurus:*

All trees:  
 Char. 292: 0 --> 1  
 Char. 355: 0 --> 1  
 Char. 391: 2 --> 1  
 Char. 421: 1 --> 2  
 Char. 422: 0 --> 1  
 Char. 462: 3 --> 0  
 Char. 534: 0 --> 1

*Tylosaurus:*

All trees:  
 Char. 142: 0 --> 1  
 Char. 462: 3 --> 0  
 Char. 469: 2 --> 3  
 Char. 489: 1 --> 0

**Anguimorpha:**

All trees:  
 Char. 6: 1 --> 2  
 Char. 57: 1 --> 2  
 Char. 137: 0 --> 1  
 Char. 177: 0 --> 1  
 Char. 221: 0 --> 1  
 Char. 233: 0 --> 2  
 Char. 339: 0 --> 1  
 Char. 445: 0 --> 1  
 Char. 454: 0 --> 1  
 Char. 455: 0 --> 1

Char. 469: 01 --> 2

Char. 494: 2 --> 0

Char. 583: 0 --> 1

Char. 597: 0 --> 1

Some trees:

Char. 231: 0 --> 1

**Shinisaurus + Varanoidea + Mosasauria**

+ “**Fossorial group**”:

All trees:

Char. 89: 2 --> 0

Char. 128: 0 --> 1

Char. 267: 0 --> 1

Char. 327: 0 --> 12

Char. 343: 0 --> 1

Char. 347: 0 --> 1

Char. 348: 0 --> 1

Char. 367: 0 --> 1

Char. 419: 3 --> 2

Char. 420: 3 --> 2

Char. 426: 0 --> 1

Char. 524: 0 --> 1

Char. 529: 1 --> 2

Char. 555: 0 --> 1

**Varanoids + Mosasauria + “Fossorial group”:**

All trees:

Char. 37: 0 --> 1

Char. 215: 0 --> 1

Char. 293: 0 --> 1

Char. 348: 1 --> 23

Char. 359: 2 --> 01

Char. 374: 23 --> 1

Char. 387: 1 --> 0

Char. 417: 0 --> 1

Char. 480: 2 --> 1

Char. 498: 1 --> 0

Some trees:

Char. 492: 01 --> 1

**Varanoidea + Mosasauria:**

All trees:

Char. 1: 0 --> 1

Char. 17: 0 --> 12

Char. 117: 0 --> 1

Char. 123: 0 --> 1

Char. 142: 0 --> 1

Char. 213: 0 --> 1

Char. 375: 0 --> 1

Char. 384: 0 --> 2

Char. 394: 0 --> 1

Char. 400: 1 --> 0

Char. 425: 0 --> 1

Char. 458: 0 --> 1

Char. 507: 1 --> 0

Char. 566: 2 --> 1

**Varanoidea:**

All trees:

Char. 203: 0 --> 1

Char. 254: 1 --> 0

Char. 279: 0 --> 1  
 Char. 324: 0 --> 1  
 Char. 343: 1 --> 0  
 Char. 356: 0 --> 1  
 Char. 370: 0 --> 1  
 Char. 372: 0 --> 1  
 Char. 378: 0 --> 1  
 Char. 415: 0 --> 2  
 Char. 417: 1 --> 2  
 Char. 424: 0 --> 1  
 Char. 496: 0 --> 1  
 Char. 524: 1 --> 0

**Mosasauria:**

All trees:

Char. 9: 0 --> 1  
 Char. 185: 0 --> 1  
 Char. 526: 0 --> 1  
 Char. 544: 0 --> 1  
 Char. 611: 0 --> 1  
 Char. 612: 0 --> 1  
 Char. 618: 0 --> 1

Some trees:

Char. 35: 0 --> 1

*Primitivus + Eidolosaurus:*

All trees:

Char. 463: 0 --> 1

**Mosasauria** exclusive of *Primitivus + Eidolosaurus*:

All trees:

Char. 166: 0 --> 1  
 Char. 516: 0 --> 1  
 Char. 529: 2 --> 1  
 Char. 555: 1 --> 2  
 Char. 560: 0 --> 4

Some trees:

Char. 611: 1 --> 2

*Haasiasaurus + Carsosaurus +*

**Dolichosauridae:**

Some trees:

Char. 374: 1 --> 2  
 Char. 420: 2 --> 3  
 Char. 469: 2 --> 3

**Dolichosauridae:**

All trees:

Char. 607: 1 --> 2

Some trees:

Char. 611: 2 --> 1

**Dolichosauridae** exclusive of

*Aphanizocnemus:*

All trees:

Char. 612: 1 --> 2

**“Coniasaurines”:**

All trees:

Char. 544: 1 --> 0  
 Char. 607: 2 --> 3

Char. 608: 0 --> 1

Char. 609: 0 --> 1

Char. 614: 0 --> 1

Char. 617: 0 --> 1

**“Acteosaurines”:**

All trees:

Char. 463: 0 --> 1

Char. 472: 0 --> 1

Char. 482: 0 --> 1

Some trees:

Char. 610: 1 --> 2

**Mosasauroidea:**

All trees:

Char. 606: 0 --> 1

Some trees:

Char. 82: 2 --> 3

Char. 605: 0 --> 1

Char. 610: 1 --> 3

**Mososauridae:**

All trees:

Char. 543: 0 --> 1

Char. 613: 0 --> 1

Char. 614: 0 --> 1

Some trees:

Char. 55: 1 --> 2

Char. 385: 0 --> 1

Char. 454: 2 --> 1

Char. 482: 0 --> 1

Char. 524: 1 --> 0

**“Hydropedal mosasaurids”:**

All trees:

Char. 49: 0 --> 1

Char. 77: 1 --> 3

Char. 93: 1 --> 2

Char. 166: 1 --> 0

Char. 354: 1 --> 0

Char. 385: 1 --> 0

Char. 516: 1 --> 2

Char. 521: 0 --> 1

Char. 538: 0 --> 1

Char. 612: 1 --> 0

Some trees:

Char. 86: 0 --> 1

Char. 128: 1 --> 2

Char. 144: 2 --> 0

Char. 177: 1 --> 0

Char. 240: 2 --> 1

Char. 257: 2 --> 0

Char. 310: 0 --> 1

Char. 381: 0 --> 1

Char. 392: 1 --> 0

Char. 417: 1 --> 2

Char. 458: 1 --> 0

Char. 518: 0 --> 1

**Russellosaurina** (*Tylosaurus* +  
*Platecarpus*):

All trees:

Char. 76: 0 --> 1

Char. 606: 1 --> 0

**Mososaurinae** (*Plotosaurus* + *Clidastes*):

All trees:

Char. 332: 0 --> 1

Char. 336: 1 --> 0

Char. 399: 0 --> 1

Char. 607: 1 --> 3

Char. 615: 0 --> 1

## **General Conclusions**

The six chapters developed in this thesis adds substantial data to the knowledge of the basal mosasaurian anatomy, ontogeny, diversity and phylogenetic relationships of the group within Squamata. Right now, the phylogenetic position of mosasaurians within squamates is still an open question in the systematics of Squamata, and most works including these lizards in global phylogenetic analyses comprise a very limited taxonomical sampling of basal forms. The main goal of the present thesis was to review the morphology of the dolichosaurs, and to later test the relationships of Mosasauria in a broader squamate context. Our results strongly support the interpretation of mosasaurians being closely related to varanoid lizards. Overall contribution of each chapter to the present thesis is given below.

Chapter 1 describes a new species of *Coniasaurus* from the North Texas, the most complete coniasaur specimen ever found. Exquisitely preserved remains encompass an adult female and several embryos, representing the first record of viviparity for a dolichosaur lizard. A phylogenetic analysis recovered a *Coniasaurus* genus inclusive of *Dolichosaurus longicollis*, suggesting *Coniasaurus* and *Dolichosaurus* to be synonyms. Although still presenting plesiomorphic limbs, *Coniasaurus* also bears modifications in the humerus, femur and caudal vertebrae that suggest better swimming skills than other dolichosaurs, which may explain why it is the only dolichosaur found in North American rocks.

Chapter 2 describes in detail the anatomy of several additional coniasaur specimens from the North Texas, concluding that *Coniasaurus* and *Dolichosaurus* were indeed synonyms and giving name preference to the former. It also provides a taxonomic revision of the genus *Coniasaurus*, which is found to bear 4 taxa: *Coniasaurus crassidens* Owen, 1850, *Coniasaurus (Dolichosaurus) longicollis* Owen, 1850, *Coniasaurus gracilodens* Caldwell, 1999 and *Coniasaurus* sp. nov. (Chapter 1 of this thesis). New diagnoses for each species are given by this chapter. As many previously unknown coniasaur bones were described, the chapter contributed with a lot of new anatomical information for the genus. *Coniasaurus* is suggested to be the most reliable dolichosaur taxon to be used in phylogenetic analyses, as it is known by several well-preserved specimens in three dimensions.

In Chapter 3 the patterns of tooth attachment and implantation were described for the first time in a dolichosaur lizard. Dentition characters are some of the most commonly used characters used to support the Pythonomorpha hypothesis (mosasaurians and snakes being

closely related), and our results strongly contradicts this interpretation. The very shallow attachment site for marginal teeth, lack of interdental ridges separating successive teeth, lack of basal plates and the presence of poorly developed dentin infoldings are some of the characters which evidence dental characters of *Coniasaurus* to be more closely related to those of varanoids than to those of snakes. These results suggest that the similarities between snakes and derived mosasaurids dentitions are the result of homoplasies, and not homologies.

Embryonic remains of *Coniasaurus* sp. nov. were described in Chapter 4, and the main ontogenetic trends were compared through different specimens in distinct ontogenetic stages. Embryonic remains and ontogenetic series are quite rare in the fossil record, especially regarding mosasaurian lizards, so North American coniasaurs provided a unique opportunity to evaluate the ontogenetic development in Mosasauria. *Coniasaurus* bore at least two, maybe three, embryos during pregnancy. Changes in lifestyle through development were observed, mainly regarding swimming skills and dietary habits. Some of the ontogenetic trends also provided tests for the polarization of some characters used in the literature.

Compared anatomy of the dolichosaurian postcranial skeleton is given by Chapter 5. New diagnostic characters for each dolichosaur genus were provided, and previous diagnoses available in the literature were also revised. A discussion about the utility of “presacral count” characters was given, suggesting authors to replace these characters for specific vertebral modules (cervical, dorsal, etc) counts in phylogenetic analyses. Finally, postcranial characters used to support a closer relationship of mosasaurians to either varanoids or snakes were discussed in the light of the new data brought by this chapter.

Chapter 6 compiled the new data gathered by each previous chapter in a global squamate morphological matrix, including 211 taxa (encompassing the largest sample of basal mosasaurians ever tested) and 619 characters. Results of this chapter recovered Mosasauria as the sister-group of Varanoidea, with monophyletic Dolichosauridae and Mosasauridae and a paraphyletic assemblage of basal mosasauroids (“aigialosaurs”). *Primitivus* and *Eidolosaurus* were found to form a clade that is the sister-group of all other mosasaurians. Eight inclusion / exclusion taxonomic tests were performed, and in only two of them (both removing basal forms) the mosasaurians were not recovered as closely related to varanoids, highlighting the importance of comprehensive taxonomical samplings in phylogenetic analyses.

## General References

- Adams, R.L.; Carr, J.P. 2010. Regional depositional systems of the Woodbine, Eagle Ford, and Tuscaloosa of the US Gulf Coast. **Gulf Coast Association of Geological Societies Transactions** 60: 3-27.
- Adams, T.L.; Polcyn, M.J.; Mateus, O.; Winkler, D.A.; Jacobs, L.L. 2011. First occurrence of the long-snouted crocodyliform *Terminonaris* (Pholidosauridae) from the Woodbine Formation (Cenomanian) of Texas. **Journal of Vertebrate Paleontology** 31(3): 712-716.
- Adkins, W. S.; Lozo, F. E. (1951). Stratigraphy of the Woodbine and Eagle Ford, Waco area, Texas. East Texas Geological Society.
- Anan'eva, N. B.; Orlov, N. L. 2013. Egg teeth of squamate reptiles and their phylogenetic significance. **Biology Bulletin** 40(7): 600-605.
- Augusta, B.G. 2013. **Revisão sistemática e ontogenética dos materiais cranianos atribuídos ao gênero Mariliasuchus (Crocodyliformes, Notosuchia) e suas implicações taxonômicas e paleobiológicas**. Master in Science dissertation, Universidade de São Paulo, 303 p.
- Augusta, B.G.; Polcyn, M.J.; Zaher, H.; Jacobs, L.L. 2016. A gravid coniasaur (*Coniasaurus sp.*) from the Upper Cretaceous of Texas and the development of dolichosaurs. In: 5TH TRIENNIAL MOSASAUR MEETING - A GLOBAL PERSPECTIVE ON MESOZOIC MARINE AMNIOTES, 2016, Uppsala. **Program and Abstracts**. Uppsala: Uppsala University. p. 2-3.
- Averianov, A.O. 2001. The first find of a dolichosaur (Squamata, Dolichosauridae) in Central Asia. **Paleontological Journal** 35(5): 525-527.
- Bahl, K.N. 1937. Skull of *Varanus* monitor (Linn.). **Records of the Indian Museum** 39: 133-174.
- Bardet, N.; Houssaye, A.; Rage, J.C.; Pereda Suberbiola, X. 2008. The Cenomanian-Turonian (late Cretaceous) radiation of marine squamates (Reptilia): the role of the Mediterranean Tethys. **Bulletin de la Société géologique de France** 179(6): 605-622.
- Bardet, N.; Suberbiola, X.P.; Iarochene, M.; Bouya, B.; Amaghaz, M. 2005. A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halisaurinae (Squamata: Mosasauridae). **Zoological Journal of the Linnean Society** 143: 447-472.
- Bardet, N.; Suberbiola, X.P.; Jalil, N.E. 2003. A new mosasauroid (Squamata) from the Late Cretaceous (Turonian) of Morocco. **Comptes Rendus de l'Académie des Sciences** 2(8): 607-616.

- Baur, G.H.C.L. 1890. On the characters and systematic position of the large sea-lizards, Mosasauridae. **Science** 405: 262-262.
- Bell, B.A.; Murry, P.A.; Osten, L.W. 1982. *Coniasaurus* Owen, 1850 from North America. **Journal of Paleontology** 56(2): 520-524.
- Bell, G.L. 1993. **A Phylogenetic Revision of Mosasauroida (Squamata)**. Unpublished Ph.D. thesis, University of Texas at Austin, Austin, 293 p.
- Bell, G.L. 1993. The first record of *Coniasaurus* (Squamata) from South Dakota. **Proceedings of South Dakota Academy of Science** 72: 333.
- Bell, G.L. 1997. A phylogenetic revision of North American and Adriatic Mosasauroida. In: Callaway, J.M.; Nicholls, E.L.(eds.). **Ancient Marine Reptiles**. Academic Press. 293–332.
- Bell, G.L.; Barnes, K.R.; Polcyn, M.J. 2013. Late Cretaceous mosasauroids (Reptilia, Squamata) of the Big Bend region in Texas, USA. **Earth and Environmental Science Transactions of the Royal Society of Edinburgh** 103: 1-11.
- Bell, G.L.; Polcyn, M.J. 1996. Distribution of the lizard, *Coniasaurus*, in the Western Interior Cretaceous Seaway and its paleoecological implications. **Geological Society of America, Rocky Mountain Section, Abstracts with Programs** 28: 2.
- Bell, G.L.; Polcyn, M.J. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). **Netherlands Journal of Geosciences** 84 (3): 177-194.
- Bishop, G.A.; Brannen, N.A.; Hill, L.E.; Meyer, J.P.; Pike, A.J.; Sampson, C. 1992a. The Britton Notopocorystes assemblage: an Eagle Ford decapod assemblage from the Cretaceous of north-central Texas. **Gulf Coast Association of Geological Societies Transactions** 42: 413-424.
- Bishop, G.A.; Brannen, N.A. 1992b. *Homolopsis pikeae*, new species (Decapoda), a crab from the Cretaceous of Texas. **Journal of Crustacean Biology** 12(2): 317-323.
- Boettcher, R. 1990. New Information on the Reproductive Biology of Ichthyosaurs (Reptilia). **Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaeontologie)** 164: 1–51.
- Borsuk-Bialynicka, M. 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. **Palaeontologia Polonica** 46: 5-105.
- Boulenger, G. 1891. Notes on the osteology of *Heloderma horridum* and *H. suspectum* with remarks on the systematic position of the Helodermatidae and the vertebrae of the Lacertilia. **Proceedings of the Zoological Society of London** 1891: 109-118.
- Bremer, K. R. 1994. Branch support and tree stability. **Cladistics** 10(3): 295-304.

- Brown, C.W.; Pierce, R.L. 1962. Palynologic correlations in Cretaceous Eagle Ford Group, northeast Texas. **AAPG Bulletin** 46(12): 2133-2147.
- Buchy, M.C.; Smith, K.T. 2011. New portions of the holotype of *Vallecillosaurus donrobertoi* (Squamata, Mosasauridae) from the early Turonian (Upper Cretaceous) of Mexico. *In: Calvo, J.; Porfiri, J.D.; González Riga, B.; Dos Santos, D. 2011. Paleontología y dinosaurios desde América Latina*. Mendoza, Ediunc: 296 p.
- Burnell, A.; Collins, S.; Young, B.A. 2012. Vertebral morphometrics in Varanus. **Bulletin de la Société Géologique de France** 183(2): 151-158.
- Caldwell, M.W. 1996. Ontogeny and phylogeny of the mesopodial skeleton in mosasauroid reptiles. **Zoological Journal of the Linnean Society** 116(4): 407-436.
- Caldwell, M.W. 1999. Description and phylogenetic relationships of a new species of *Coniasaurus* Owen, 1850 (Squamata). **Journal of Vertebrate Paleontology** 19(3): 438-455.
- Caldwell, M.W. 1999a. Squamate phylogeny and the relationships of snakes and mosasauroids. **Zoological Journal of the Linnean Society** 125: 115-147.
- Caldwell, M.W. 1999b. Description and phylogenetic relationships of a new species of *Coniasaurus* Owen, 1850 (Squamata). **Journal of Vertebrate Paleontology** 19(3): 438-455.
- Caldwell, M.W. 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in Squamates. **Journal of Vertebrate Paleontology** 20(4): 720-735
- Caldwell, M.W. 2006. A New Species of "Pontosaurus" (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a Phylogenetic Analysis of Pythonomorpha. **Società Italiana di Scienze Naturali**: 1-44.
- Caldwell, M.W. 2007. Ontogeny, anatomy and attachment of the dentition in mosasaurs (Mosasauridae: Squamata). **Zoological Journal of the Linnean Society** 149: 687-700.
- Caldwell, M.W. 2012. A challenge to categories: What, if anything, is a mosasaur?. **Bulletin de la Société Géologique de France** 183(1): 7-34.
- Caldwell, M.W.; Budney, L.A.; Lamoureux, D.O. 2003. Histology of tooth attachment tissues in the Late Cretaceous mosasaurid *Platecarpus*. **Journal of Vertebrate Paleontology** 23 (3): 622-630.
- Caldwell, M.W.; Carroll, R.L.; Kaiser, H. 1995. The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroids and varanoids. **Journal of Vertebrate Paleontology** 15(3): 516-531.

- Caldwell, M.W.; Cooper, J.A. 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the Lower Chalk (Cretaceous; Cenomanian) of SE England. **Zoological Journal of the Linnean Society** 127: 423-452.
- Caldwell, M.W.; Lee, M.S.Y. 1997. A snake with legs from the marine Cretaceous of the Middle East. **Nature** 386: 705-709.
- Caldwell, M.W.; Lee, M.S.Y. 2001. Live birth in Cretaceous marine lizards (mosasauroids). **Proceedings of the Royal Society: Biological Sciences** 268: 2397-2401.
- Caldwell, M.W.; Lee, M.S.Y. 2004. Reevaluation of the Cretaceous marine lizard *Acteosaurus crassicostatus* Calligaris, 1993. **Journal of Paleontology** 78(3): 617-619.
- Caldwell, M.W.; Palci, A. 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) of Slovenia with a review of mosasauroid phylogeny and evolution. **Journal of Vertebrate Paleontology** 27(4): 863-883.
- Caldwell, M.W.; Palci, A. 2010. A new species of marine ophidiomorph lizard, *Adriosaurus skrbiniensis*, from the Upper Cretaceous of Slovenia. **Journal of Vertebrate Paleontology** 30(3): 747-755.
- Calligaris, R. 1988. I rettili fossili degli "Strati calcarei ittiolitici di comeno" e dell'isola di Lesina. **Atti Museo Civico di Storia Naturale di Trieste** 41: 85-125.
- Calligaris, R. 1993. *Acteosaurus crassicostatus* nuova specie di Dolichosauridae negli Strati Calcarei Ittiolitici di Comeno. **Atti Museo Civico di Storia Naturale di Trieste** 45:29-34.
- Camp, C.L. 1923. Classification of the lizards. **Bulletin of the American Museum of Natural History** 48: 289-481.
- Campbell, M.; Japundzic, D.; Krizmanic, K.; Caldwell, M.W. 2016. A new genus of Tethyan dolichosaurid from the Turonian of Croatia. In: 5TH TRIENNIAL MOSASAUR MEETING - A GLOBAL PERSPECTIVE ON MESOZOIC MARINE AMNIOTES, 2016, Uppsala. **Program and Abstracts**. Uppsala: Uppsala University. p. 5-6.
- Carroll, R.L.; Debraga, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. **Journal of Vertebrate Paleontology** 12(1): 66-86.
- Carvalho, L.B.; Azevedo, S.A.K. 1998. Proposta taxonômica para os répteis marinhos (Lepidosauria, Mosasauridae) do Neocretáceo da Bacia Pernambuco-Paraíba, Nordeste do Brasil. **Boletim do Museu Nacional** 43: 1-14.
- Cheng Y.N.; Wu, X.C.; Ji, Q. 2004. Triassic marine reptiles gave birth to live young. **Nature** 432: 383-386.
- Cicimurri, D.J.; Bell, G.L. 1996. Vertebrate fauna of the Boquillas Formation of Brester County, Texas: a preliminary report. **Journal of Vertebrate Paleontology** 16: 28A.

- Cieri, R.L. 2018. The axial anatomy of monitor lizards (Varanidae). **Journal of Anatomy**: 1-8.  
doi: 10.1111/joa.12872.
- Cobban, W.A.; Walaszczyk, I.; Obradovich, J.D.; McKinney, K.C. 2006. A USGS zonal table for the Upper Cretaceous middle Cenomanian-Maastrichtian of the Western Interior of the United States based on ammonites, inoceramids, and radiometric ages: **U.S. Geological Survey Open-File Report 2006-1250**: 46 p.
- Conrad, J.L. 2004. Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). **Zoological Journal of the Linnean Society** 141(3): 399-434.
- Conrad, J.L. 2006. Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). **Journal of Morphology** 267(7): 759-775.
- Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. **Bulletin of the American Museum of Natural History**, 310: 1-182.
- Conrad, J.L.; Ast, J.C.; Montanari, S.; Norell, M.A. 2011. A combined evidence phylogenetic analysis of Anguimorpha (Reptilia: Squamata). **Cladistics** 27: 230-277.
- Cornalia, E.; Chiozza, L. 1852. Cenni geologici sull' Istria. **Giornale dell' I. R. Istituto Lombardo** 3: 1-35.
- Cope, E. D. 1878. Check-list of North American Batrachia and Reptilia: With a Systematic List of the Higher Groups, and an Essay on Geographical Distribution; Based on the Specimens Contained in the US National Museum (Vol. 1). **US Government Printing Office**: 115 p.
- Cope, E.D. 1869. On the reptilian orders Pythonomorpha and Streptosauria. **Proceedings of the Boston Society of Natural History** 12: 250-261.
- Cope, E.D. 1895. Reply to Dr. Baur's critique of my paper on the paroccipital bone of the scaled reptiles and the systematic position of the Pythonomorpha. **American Naturalist** 29: 1003-1005.
- Cundall, D., and Irish, F. (2008). The snake skull. *Biology of the Reptilia*, 20, 349-692.
- Cuthbertson, R.S.; Maddin, H.C.; Holmes, R.B.; Anderson, J.S. 2015. The braincase and endosseous labyrinth of *Plioplatecarpus peckensis* (Mosasauridae, Plioplatecarpinae), with functional implications for locomotor behavior. **The Anatomical Record** 298: 1597-1611.
- Cuvier, G.C.F. 1808. Sur le grand animal fossile des carrières de Maestricht. **Annales du Muséum National d'Histoire Naturelle** 12: 145-176.
- Dal Sasso, C.; Pinna, G. 1996. *Besanosaurus leptorhynchus* n. gen. n. sp., a new shastasaurid ichthyosaur from the Middle Triassic of Besano (Lombardy, N. Italy). **Paleontologia Lombarda** 4: 3-23.

- Dal Sasso, C.; Pinna, G. 1997. *Aphanizocnemus libanensis* n. gen. n. sp, a new dolichosaur (Reptilia, Varanoidea) from the Upper Cretaceous of Lebanon. **Paleontologia Lombarda** 7: 1-31.
- Dalla Vecchia, F.M.; Venturini, S. 1999. The Middle Cenomanian Lagerstätte of Al Nammoura (Kesrouâne Caza, N. Lebanon). **Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"** 20: 75-78.
- de Braga, M.; Carroll, 1993. The origin of mosasaurs as a model of macroevolutionary patterns and processes. **Evolutionary Biology** 27: 245-322.
- de Pinna, M.C.C. 1994. Ontogeny, rooting, and polarity. In: Scotland, R.W.; Siebert, D.J.; Williams, D.M. **Models in phylogeny reconstruction**. Systematics Association Special Volume (52). Oxford, Claredon Press. p. 157-157.
- Dequéant, M.L.; Pourquié, O. 2008. Segmental patterning of the vertebrate embryonic axis. **Nature Reviews Genetics** 9(5): 370-382.
- Diedrich, C. 1997. Ein dentale von *Coniosaurus crassidens* Owen (Varanoidea) aus dem Ober-Cenoman von Halle/Westf. (NW-Deutschland). **Geologie und Paläontologie in Westfalen** 47: 43-51.
- Donoghue, M.J.; Doyle, J A.; Gauthier, J.; Kluge, A.G.; Rowe, T. 1989. The importance of fossils in phylogeny reconstruction. **Annual Review of Ecology and Systematics** 20(1): 431-460.
- Donovan, A.D.; Gardner, R.D.; Pramudito, A.; Staerker, T.S.; Wehner, M.; Corbett, M.J.; Lundquist, J.J.; Romero A.M.; Henry, L.C.; Rotzien, J.R.; Boling, K.S. 2015. Chronostratigraphic relationships of the Woodbine and Eagle Ford Groups across Texas. **GCAGS Journal** 4: 67-87.
- Druckenmiller P.S., Russel A.P. 2008. A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews, 1922. **Zootaxa** 1863, 1-120.
- Dutchak, A.R. 2005. A review of the taxonomy and systematic of aigialosaurs. **Netherlands Journal of Geosciences** 84(3): 221-229.
- Dutchak, A.R.; Caldwell, M.W. 2006. Redescription of *Aigialosaurus dalmaticus* KRAMBERGER, 1892, a Cenomanian mosasauroid lizard from Hvar Island, Croatia. **Canadian Journal of Earth Science** 43(12): 1821-1834.
- Dutchak, A.R.; Caldwell, M.W. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. **Journal of Vertebrate Paleontology** 29(2): 437-452.

- Estes, R.; de Queiroz, K.; Gauthier, J. 1988. Phylogenetic relationships within Squamata. In: Estes, R.; Pregill, G. (eds). **Phylogenetic relationships of the lizard families**. Stanford, Stanford University Press, p. 119-282.
- Evans, S. E. 2008. The skull of lizards and tuatara. **Biology of the Reptilia** 20: 1-347.
- Evans, S.E.; Manabe, M.; Noro, M.; Isajis, S.; Yamaguchi, M. 2006. A longbodied lizard from the Lower Cretaceous of Japan. **Paleontology** 49(6): 1143-1165.
- Everhart, M.J. 2004. Plesiosaurs as the food of mosasaurs; new data on the stomach contents of a *Tylosaurus proriger* (Squamata; Mosasauridae) from the Niobrara Formation of Western Kansas. **The Mosasaur** 7: 41-46.
- Everhart, M.J.; Darnell, M.K. 2004. Occurrence of *Ptychodus mammillaris* (Elasmobranchii) in the Fairport Chalk Member of the Carlile Shale (Upper Cretaceous) of Ellis County, Kansas. **Transactions of the Kansas Academy of Science** 107(3): 126-130.
- Farris, J. S. 1989. The retention index and the rescaled consistency index. **Cladistics** 5(4): 417-419.
- Fejérváry, G.J. 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. **Annales Historico-Naturales Musei Nationalis Hungarici** 16: 341-467.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. **Evolution** 39(4): 783-791.
- Field, D.J.; LeBlanc, A.; Gau, A.; Behlke, A.D. 2015. Pelagic neonatal fossils support viviparity and precocial life history of Cretaceous mosasaurs. **Palaeontology** 2015: 1-7.
- Gallagher, W.B.; Miller, K.G.; Sherrell, R.M.; Browning, J.V.; Field, M.P.; Olsson, R.K.; Sugarman, P.J.; Tuorto, S.; Wahyudi, H. 2012. On the last mosasaurs: Late Maastrichtian mosasaurs and the Cretaceous-Paleogene boundary in New Jersey. **Bulletin de la Société Géologique de France** 183(2): 145-150.
- Gauthier, J.A.; Kearney, M.; Maisano, J.A.; Rieppel, O.; Behlke, A.D.B. 2012. Assembling the Squamate tree of life: perspectives from the phenotype and the fossil record. **Bulletin of the Peabody Museum of Natural History** 53(1): 3-308.
- Gauthier, J.A.; Kluge, A.G.; Rowe, T. 1988. Amniote phylogeny and the importance of fossils. **Cladistics** 4(2): 105-209.
- Gervais, P. 1852. **Zoologie et Paleontologie Françaises (Animaux Vertébrés)**. Paris, Arthus Bertrand, 274 p.
- Goldfuss, A. 1844. The skull structure of the *Mosasaurus*, explained by means of a description of a new species of this genus. **Transactions of the Kansas Academy of Science** 116: 27-46.

- Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. **Cladistics** 15(4): 415-428.
- Goloboff, P.A. 2002. Techniques for analyzing large data sets. In **Techniques in molecular systematics and evolution** (eds DeSalle, R.; Giribet, G.; Wheeler, W.), pp. 70-79. Basel: Birkhäuser Verlag.
- Goloboff, P.A.; Catalano, S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. **Cladistics** 32(3): 221-238.
- Goloboff, P.A.; Farris, J.S. 2001. Methods for quick consensus estimation. **Cladistics** 17(1): S26-S34.
- Goloboff, P.; Farris, J.; Nixon, K. 2003. **T.N.T.: Tree Analysis Using New Technology**. Software and Documentation freely available by the authors and by the Hennig Society. Available in: <[www.zmuc.dk/public/phylogeny](http://www.zmuc.dk/public/phylogeny)>. Access in: 23/07/2016.
- Gomez, C.; Özbudak, E.M.; Wunderlich, J.; Baumann, D.; Lewis, J.; Pourquié, O. 2008. Control of segment number in vertebrate embryos. **Nature** 454(7202): 335-339.
- Gradstein, F.M.; Ogg, J.G.; Schmitz, M.; Ogg, G. 2012. The Geologic Time Scale 2012: Boston, Elsevier, 1144 p., doi:10.1016/B978-0-444-59425-9.00004-4.
- Griffith, O.W.; Blackburn, D.G.; Brandley, M.C.; Van Dyke, J.U.; Whittington, C.M.; Thompson, M.B. 2015. Ancestral state reconstructions require biological evidence to test evolutionary hypotheses: a case study examining the evolution of reproductive mode in squamate reptiles. **Journal of Experimental Zoology Part B: Molecular and Developmental Evolution** 324(6): 493-503.
- Haber, A.; Polcyn, M.J. 2005. A new marine varanoid from the Cenomanian of the Middle East. **Netherlands Journal of Geosciences** 84(3): 247-255.
- Hancock, J.M.; Walaszczyk, I., 2004. Mid-Turonian to Coniacian changes of sea level around Dallas, Texas. **Cretaceous Research** 25(4): 459-471.
- Haq, B.U. 2014. Cretaceous eustasy revisited. **Global and Planetary Change** 113: 44-58.
- Hay, W.W. 2009. Cretaceous oceans and ocean modeling. **SEPM Special Publication** 91: 243-271.
- Hoffstetter, R.; Gasc, J.P. 1969. Vertebrae and ribs of modern reptiles. **Biology of the Reptilia** 1(5): 201-310.
- Houssaye, A. 2013. Palaeoecological and morphofunctional interpretation of bone mass increase: an example in Late Cretaceous shallow marine squamates. **Biological Reviews** 88(1): 117-139.

- Houssaye, A.; Xu, F.; Helfen, L.; De Buffr enil, V.; Baumbach, T.; Tafforeau, P. 2011. Three-dimensional pelvis and limb anatomy of the Cenomanian hind-limbed snake *Eupodophis descouensi* (Squamata, Ophidia) revealed by synchrotron-radiation computed laminography. **Journal of Vertebrate Paleontology** 31(1): 2-7.
- Ifrim, C.; Buchy, M.C.; Smith, K.T.; Giersch, S.; Everhart, M.J. 2008. Paleoenvironment and preliminary description of early Turonian (Late Cretaceous) aquatic squamates from Vallecillo, North-eastern Mexico. In **Proceedings of the Second Mosasaur Meeting**: x1-x16.
- International Commission on Zoological Nomenclature. 2000. **International Code of Zoological Nomenclature** (4ed). London, The International Trust for Zoological Nomenclature.
- Jacobs, L.L.; Ferguson, K.; Polcyn, M.J.; Rennison, C. 2005. Cretaceous  $\delta^{13}C$  stratigraphy and the age of dolichosaurs and early mosasaurs. **Netherlands Journal of Geosciences** 84(3): 257-268.
- Jacobs, L.L.; Polcyn, M.J.; Taylor, L.H.; Ferguson, K. 2005. Sea-surface temperatures and palaeoenvironments of dolichosaurs and early mosasaurs. **Netherlands Journal of Geosciences** 84(3): 269-281.
- Joo, Y.J.; Sageman, B.B. 2014. Cenomanian to Campanian carbon isotope chemostratigraphy from the Western Interior Basin, USA. **Journal of Sedimentary Research** 84(7): 529-542.
- Kearney, M.; Rieppel, O. 2006. An investigation into the occurrence of plicidentine in the teeth of squamate reptiles. **Copeia** 2006(3): 337-350.
- Kennedy, W.J. 1988. Late Cenomanian and Turonian ammonite faunas from north-east and central Texas. **Special Papers in Palaeontology**.
- Kennedy, W.J.; Cobban, W.A. 1990. Cenomanian ammonite faunas from the Woodbine Formation and lower part of the Eagle Ford Group, Texas. **Palaeontology** 33(1): 75-154.
- Kluge, A.G.; Farris, J.S. 1969. Quantitative phyletics and the evolution of anurans. **Systematic Biology** 18(1): 1-32.
- Konishi, T.; Caldwell, M.W. 2011. Two new Plioplatecarpinae (Squamata, Mosasauridae) genera from the Upper Cretaceous of North America, and a global phylogenetic analysis of plioplatecarpines. **Journal of Vertebrate Paleontology** 31(4): 754-783.
- Konishi, T.; Tanimoto, M.; Utsunomiya, S.; Sato, M.; Watanabe, K. 2012. A large Mosasaurinae (Squamata: Mosasauridae) from the Latest Cretaceous of Osaka Prefecture (SW Japan). **Paleontological Research** 16(2): 79-87.
- Konishi, T.; Newbrey, M.G.; Caldwell, M.W. 2014. A small, exquisitely preserved specimen of *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the upper Campanian of the

- Bearpaw Formation, western Canada, and the first stomach contents for the genus. **Journal of Vertebrate Paleontology** 34(4): 802-819.
- Kornhuber, A. 1873. Über einen neuen fossilen saurier aus Lesina. **Herausgegeben von der k. k. geologischen Reichsanstalt Wien** 5(4): 75-90.
- Kubo, T.; Mitchell, M.T.; Henderson, D.M. 2012. *Albertonectes vanderveldei*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. **Journal of Vertebrate Paleontology** 32(3): 557-572.
- LeBlanc, A.R.; Lamoureux, D.O.; Caldwell, M.W. 2017. Mosasaurs and snakes have a periodontal ligament: timing and extent of calcification, not tissue complexity, determines tooth attachment mode in reptiles. **Journal of anatomy** 231(6): 869-885.
- Lee, M.S.Y. 1997a. On snake-like dentition in mosasaurian lizards. **Journal of Natural History** 31: 303-314.
- Lee, M.S.Y. 1997b. The phylogeny of varanoid lizards and the affinities of snakes. **Philosophical Transactions of the Royal Society of London B: Biological Sciences** 352: 53-91.
- Lee, M.S.Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. **Biological Journal of the Linnean Society** 65: 369-453.
- Lee, M.S.Y.; Caldwell, M.W. 1998. Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. **Philosophical Transactions of the Royal Society of London B: Biological Sciences** 353: 1521-1552.
- Lee, M.S.Y.; Caldwell, M.W. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. **Journal of Paleontology** 74(5): 915-937.
- Lee, M.S.Y.; Scanlon, J.D. 2002. The Cretaceous marine squamate *Mesoleptos* and the origin of snakes. **Bulletin of the Natural History Museum London (Zoology Series)** 68: 131-142.
- Liggett, G.A.; Shimada, K.; Bennett, S.C.; Schumacher, B.A. 2005. Cenomanian (Late Cretaceous) reptiles from northwestern Russell County, Kansas. **PaleoBios** 25(2): 9-17.
- Lindgren, J. 2005. The first record of *Hainosaurus* (Reptilia: Mosasauridae) from Sweden. **Journal of Paleontology** 79(6): 1157-1165.
- Lindgren, J.; Jagt, J.W.; Caldwell, M.W. 2007. A fishy mosasaur: the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. **Lethaia** 40(2): 153-160.
- Lindgren, J.; Polcyn, M.J.; Young, B.A. 2011. Landlubbers to leviathans: evolution of swimming in mosasaurine mosasaurs. **Paleobiology** 37: 445-469.
- 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 B: Biological Sciences** 347: 155-172.
- Liu J, Rieppel O. 2005. Restudy of *Anshunsaurus huangguoshuensis* (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou, China. **Amer Mus Novit** 488:1– 34.
- Liu, M.; Reed, D.A.; Cecchini, G.M.; Lu, X.; Ganjawalla, K.; Gonzales, C.S.; Monahan, R.; Luan, X.; Diekwisch, T.G.H. 2016. Varanoid tooth eruption and implantation in a Late Cretaceous mosasaur. **Frontiers in Physiology** 7: 1-9.
- Luan, X.; Walker, C.; Dangaria, S.; Ito, Y. Druzinsky, R.; Jarosius, K.; Lesot, H; Rieppel, O. 2009. The mosasaur tooth attachment apparatus as paradigm for the evolution of the gnathostome periodontium. **Evolution & Development** 11(3): 247-259.
- Mabee, P.M.; Humphries, J. 1993. Coding polymorphic data: examples from allozymes and ontogeny. **Systematic Biology** 42(2): 166-181.
- Mabee, P.M. 2000. The usefulness of ontogeny in interpreting morphological characters. **Phylogenetic analysis of morphological data**: 84-114.
- Maddison, W. 1989. Reconstructing character evolution on polytomous cladograms. **Cladistics** 5(4): 365-377.
- Maisano, J.A. 2002. Terminal fusions of skeletal elements as indicators of maturity in squamates. **Journal of Vertebrate Paleontology** 22(2): 268-275.
- Makádi, L.; Caldwell, M.W.; Ösi, A 2012. The first freshwater mosasauroid (Upper Cretaceous, Hungary) and a new clade of basal mosasauroids. **PLoS ONE** 7 (12): e51781. doi:10.1371/journal.pone.0051781.
- Mantell, G. 1829. A tabular arrangement of the organic remains of the county of Sussex. **Transactions of the Geological Society of London** 3: 201-216.
- Marsh, O.C. 1880. New characters of mosasauroid reptiles. **American Journal of Science** 19(3): 83-87.
- Martin, J.E.; Fernández, M. 2007. The synonymy of the Late Cretaceous mosasaur (Squamata) genus *Lakumasaurus* from Antarctica with *Taniwhasaurus* from New Zealand and its bearing upon faunal similarity within the Weddellian Province. **Geological Journal** 42: 203-211.
- Massare, J. A. (1987). Tooth morphology and prey preference of Mesozoic marine reptiles. **Journal of Vertebrate Paleontology** 7(2): 121-137.

- Maxwell, E.E.; Caldwell, M.W.; Lamoureux, D.O.; Budney, L.A. 2011. Histology of tooth attachment tissues and plicidentine in *Varanus* (Reptilia: Squamata), and a discussion of the evolution of amniote tooth attachment. **Journal of Morphology** 272(10): 1170-1181.
- McDowell, S.B.; Bogert, C.M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. **Bulletin of the American Museum of Natural History** 105: 1-142.
- Mekarski, M.M. 2017. **The Origin and Evolution of Aquatic Adaptations in Cretaceous Squamates**. Unpublished Ph.D. thesis, University of Alberta, 467 p.
- Modesto SP. 1999. Observations on the structure of the Early Permian reptile *Stereosternum tumidum* Cope. **Pal afr** 35: 7–19.
- Moreman, W.L. 1927. Fossil zones of the Eagle Ford of north Texas. **Journal of Paleontology**: 89-101.
- Moreman, W.L., 1942. Paleontology of the Eagle Ford Group of north and central Texas. **Journal of Paleontology**: 192-220.
- Motani, R.; Jiang, D.Y.; Tintori, A.; Rieppel, O.; Chen, G.B. 2014. Terrestrial origin of viviparity in Mesozoic marine reptiles indicated by Early Triassic embryonic fossils. **PloS one** 9(2): e88640.
- Müller, J.; Scheyer, T.M.; Head, J.J.; Barrett, P.M.; Werneburg, I.; Ericson, P.G.; Pol, D.; Sánchez-Villagra, M.R. 2010. Homeotic effects, somitogenesis and the evolution of vertebral numbers in recent and fossil amniotes. **Proceedings of the National Academy of Sciences** 107(5): 2118-2123.
- Myers, T.S. 2010. A new ornithocheirid pterosaur from the Upper Cretaceous (Cenomanian–Turonian) Eagle Ford Group of Texas. **Journal of Vertebrate Paleontology** 30(1): 280-287.
- Myers, T.S., 2015. First North American occurrence of the toothed pteranodontoid pterosaur *Cimoliopterus*. **Journal of Vertebrate Paleontology** 35(6): e1014904.
- Nagrodski, M.; Shimada, K.; Schumacher, B.A. 2012. Marine vertebrates from the Hartland Shale (Upper Cretaceous: Upper Cenomanian) in southeastern Colorado, USA. **Cretaceous Research** 37: 78-88.
- Nelson, G. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. **Systematic Zoology** 27(3): 324-345.
- Nixon, K.C. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. **Cladistics** 15: 407-414.

- Nopcsa, F.B. 1923. *Eidolosaurus* und *Pachyophis*: Zwei neue Neocom-Reptilien. **Palaeontographica** 65: 99-154.
- Norton, G. H. (1965). Surface geology of Dallas County. **The geology of Dallas County: The Dallas Geological Society**: 40-125.
- O'Brien, C.L.; Robinson, S.A.; Pancost, R.D.; Damste, J.S.S.; Schouten, S.; Lunt, D.J.; Alsenz, H.; Bornemann, A.; Bottini, C.; Brassell, S.C.; Farnsworth, A. 2017. Cretaceous sea-surface temperature evolution: Constraints from TEX86 and planktonic foraminiferal oxygen isotopes. **Earth-science reviews** 172: 224-247.
- O'Keefe, F.R.; Chiappe, L. M. 2011. Viviparity and K-selected life history in a Mesozoic marine plesiosaur (Reptilia, Sauropterygia). **Science** 333(6044): 870-873.
- Oelrich, T.M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). **University of Michigan Museum of Zoology Miscellaneous Publications** 94: 1–122.
- Osborn, H.F. 1899. A complete mosasaur skeleton, osseous and cartilaginous. **Bulletin of the American Museum of Natural History** 1: 167-188.
- Owen, R. 1841. **Report on British fossil reptiles, part II**. Report for the British Association for the Advancement of Science, Plymouth: 60-294.
- Owen, R. 1850. Description of the fossil reptiles of the Chalk Formation. *In*: Dixon, F. (Ed), **The geology and fossils of the Tertiary and Cretaceous Formations of Sussex**. London, Longman, Brown, Green, and Longman. p. 378-404.
- Owen, R. 1877. On the rank and affinities of the reptilian class of Mosasauridae, Gervais. Geological Society of London, **Quarterly Journal** 33: 682-719.
- Palci, A.; Caldwell, M.W. 2007. Vestigial forelimbs and axial elongation in a 95 million-year-old non-snake squamate. **Journal of Vertebrate Paleontology** 27(1): 1-7.
- Palci, A.; Caldwell, M.W. 2010. Redescription of *Acteosaurus tommasinii* von Meyer, 1860, and a discussion of evolutionary trends within the clade Ophidiomorpha. **Journal of Vertebrate Paleontology** 30(1): 94-108.
- Palci, A.; Caldwell, M.W.; Papazzoni, C.A. 2013. A new genus and subfamily of mosasaurs from the Upper Cretaceous of Northern Italy. **Journal of Vertebrate Paleontology** 33(3): 599-612.
- Paparella, I.; Palci, A.; Nicosia, U.; Caldwell, M.W. 2018. A new fossil marine lizard with soft tissues from the Late Cretaceous of southern Italy. **Royal Society Open Science** 5(6): doi 172411.
- Páramo-Fonseca, M.E. 2011. Mosasauroids from Colombia. **Bulletin de la Société Géologique de France** 182(2): 103-109.

- Pierce, S.; Caldwell, M.W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur, *Pontosaurus lesinensis* (Kornhuber, 1873). **Journal of Vertebrate Paleontology** 24: 376-389.
- Pieters, F. F., Rompen, P. G., Jagt, J. W.; Bardet, N. (2012). A new look at Faujas de Saint-Fond's fantastic story on the provenance and acquisition of the type specimen of *Mosasaurus hoffmanni* Mantell, 1829. **Bulletin de la Société géologique de France** 183(1): 55-65.
- Pol, D.; Escapa, I.H. 2009. Unstable taxa in cladistic analysis: identification and the assessment of relevant characters. **Cladistics** 25(5): 515-527.
- Polcyn, M.J.; Bell, G.L. 1994. *Coniasaurus crassidens* and its bearing on varanoid-mosasauroid relationships. **Journal of Vertebrate Paleontology**, Supplemental 14: 42A.
- Polcyn, M.J.; Bell, G.L. 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(3): 321-333.
- Polcyn, M.J.; Jacobs, L.L.; Araújo, R.; Schulp, A.S.; Mateus, O. 2014. Physical drivers of mosasaur evolution. **Palaeogeography, Palaeoclimatology, Palaeoecology** 400: 17-27.
- Polcyn, M.J.; Jacobs, L.L.; Haber, A. 2005. A morphological model and CT assessment of the skull of *Pachyrhachis problematicus* (Squamata, Serpentes), a 98 million year old snake with legs from the Middle East. **Palaeontologia Electronica** 8(1): 1-24.
- Polcyn, M.J.; Tchernov, E.; Jacobs, L.L. 1999. The Cretaceous biogeography of the Eastern Mediterranean with a description of a new basal mosasauroid from 'Ein Yabrud, Israel. In: SECOND GONDWANAN DINOSAUR SYMPOSIUM. **Proceedings of the Second Gondwanan Dinosaur Symposium**. National Science Museum Monographs 15, Tokyo, Japan. p. 259-290.
- Porter, W.R.; Witmer, L.M. 2015. Vascular patterns in iguanas and other squamates: Blood vessels and sites of thermal exchange. **PloS one** 10(10): e0139215.
- Powell, J.D. 1968. Woodbine-Eagle Ford transition, Tarrant Member. Fieldtrip Guidebook, South-Central Section, Stratigraphy of the Woodbine Formation, Tarrant County, Texas. **Geological Society of America, Boulder**: 27-43.
- Rashid, D.J.; Surya, K.; Chiappe, L.M.; Carroll, N.; Garrett, K.L.; Varghese, B.; Balilleul, A.; O'Connor, J.K.; Chapman, S.C.; Horner, J.R. 2018. Avian tail ontogeny, pygostyle formation, and interpretation of juvenile Mesozoic specimens. **Scientific reports** 8(1): 9014.
- Reeder, T.W.; Townsend, T.M.; Mulcahy, D.G.; Noonan, B.P.; Wood, P.L.Jr.; Sites, J.W.Jr.; Wiens, J.J. 2015. Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny

- and Reveal Unexpected Placements for Fossil Taxa. **PLoS ONE** 10(3): e0118199.doi:10.1371/journal.pone.0118199.
- Renesto, S.; Lombardo, C.; Tintori, A.; Danini, G. 2003. Nothosaurid embryos from the Middle Triassic of northern Italy: an insight into the viviparity of nothosaurs?. **Journal of Vertebrate Paleontology** 23(4): 957-960.
- Rieppel, O. 1988. **Fundamentals of comparative biology**. Boston, Birkhauser Verlag: 202 p.
- Rieppel, O. 1992. The skeleton of a juvenile *Lanthanotus* (Varanoidea). **Amphibia-Reptilia** 13(1): 27-34.
- Rieppel O. 2000. Sauropterygia I - Placodontia, Pachypleuroosauria, Nothosauroida, Pistosauroida. In: *Handbuch der Paläoherpetologie* 12A:1-134.
- Rieppel, O. 1980. **The phylogeny of anguimorph lizards**. Birkhauser Verlag, Basel, 86 p.
- Rieppel, O.; Conrad, J.L.; Maisano, J.A. 2007. New morphological data for *Eosaniwa koehni* Haubold, 1977 and a revised phylogenetic analysis. **Journal of Paleontology** 81(4): 760-769.
- Rieppel, O.; Kearney, M. 2005. Tooth replacement in the Late Cretaceous mosasaur *Clidastes*. **Journal of Herpetology** 39(4): 688-692.
- Rieppel, O.; Zaher, H. 2000a. The intramandibular joint in squamates and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. **Fieldiana (Geology), New Series** 43: 1-69.
- Rieppel, O.; Zaher, H. 2000b. The braincases of mosasaurs and *Varanus*, and the relationships of snakes. **Zoological Journal of the Linnean Society** 129: 489-514.
- Rieppel, O.; Zaher, H. 2001. Re-building the bridge between mosasaurs and snakes. **Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen** 221(1): 111-132.
- Roberts, C.N. 1953. Geology of the Dallas Quadrangle, Dallas County, Texas". **Field and Laboratory** 21: 21-33.
- Romer, A.S. 1956. **Osteology of the reptiles**. Chicago, University of Chicago Press, 772 p.
- Roth, V.L. 1988. The biological basis of homology. **Ontogeny and systematics**: 1-26.
- Russell, D.A. 1967. Systematics and morphology of American mosasaurs. **Bulletin of the Peabody Museum of Natural History** 23: 1-241.
- Scanlon, J.D.; Hocknull, S.A. 2008. A dolichosaurid lizard from the latest Albian (mid-Cretaceous) Winton Formation, Queensland, Australia. **Transactions of the Kansas Academy of Science (Fort Hays Studies Special Issue - Proceedings of the Second Mosasaur Meeting)**: 131-136.

- Seeley, H.G. 1881. On remains of a small lizard from the Neocomian rocks of Comen, near Trieste, preserved in the Geological Museum of the University of Vienna. **Quarterly Journal of the Geological Society of London** 37: 52–56.
- Seiffert, J. 1973. Upper Jurassic lizards from central Portugal. **Memórias do Serviço Geológico de Portugal (Nova Série)** 22: 1–85.
- Shimada, K.; Bell, G.L. 2006. *Coniasaurus* Owen, 1850 (Reptilia: Squamata), from the Upper Cretaceous Niobrara Chalk of Western Kansas. **Journal of Paleontology** 80(3): 589-593.
- Shimada, K.; Everhart, M.J.; Ewell, K. 2007. A unique reptilian (large dolichosaurid lizard?) tooth from the Upper Cretaceous Niobrara Chalk of western Kansas. **Transactions of the Kansas Academy of Science** 110(3/4): 213-219.
- Shimada, K.; Ystesund, T.K. 2007. A dolichosaurid lizard, *Coniasaurus* cf. *crassidens*, from the Upper Cretaceous Carlile Shale in Russell County, Kansas. **Transactions of the Kansas Academy of Science** 110(3/4): 236-242.
- Simões, T.R.; Caldwell, M.W.; Palci, A.; Nydam, R.L. 2017. Giant taxon-character matrices: quality of character constructions remains critical regardless of size. **Cladistics** 33(2): 198-219.
- Slattery, J.S.; Cobban, W.A.; McKinney, K.C.; Harries, P.J.; Sandness, A.L. 2015. Early Cretaceous to Paleocene paleogeography of the Western Interior Seaway: the interaction of eustasy and tectonism. **Wyoming Geological Association Guidebook**: 22-60.
- Smith, A.S.; Vincent, P. 2010. A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany. **Palaeontology** 53(5): 1049-1063.
- Smith, C.C. 1981. Calcareous nannoplankton and stratigraphy of late Turonian, Coniacian, and early Santonian age of the Eagle Ford and Austin groups of Texas. **USGS** 1075: 1-98.
- Smith, J.B.; Dodson, P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. **Journal of Vertebrate paleontology** 23(1): 1-12.
- Smith, K.T.; Buchy, M.L. 2008. A new aigialosaur (Squamata: Anguimorpha) with soft tissues remains from the Upper Cretaceous of Nuevo León, Mexico. **Journal of Vertebrate Paleontology** 28(1): 85-94.
- Smith, K.T.; Bhullar S.B.; Holroyd, P.A. 2008. Earliest African record of the Varanus stem-clade (Squamata: Varanidae) from the early Oligocene of Egypt. **Journal of Vertebrate Paleontology** 28.3: 909-913.
- Stephenson, R. 1953a. Large invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. **US Geological Survey Professional Paper** 242: 1-8.

- Stephenson, L.W. 1953b. Mollusks from the Pepper shale member of the Woodbine formation, McLennan County, Texas: **US Geological Survey Professional Paper** 243: 57-67.
- Street, H.P.; Caldwell, M.W. 2016. Rediagnosis and redescription of *Mosasaurus hoffmannii* (Squamata: Mosasauridae) and an assessment of species assigned to the genus *Mosasaurus*. **Geological Magazine**: 1-37. doi:10.1017/S0016756816000236.
- Tschopp, E. 2016. Nomenclature of Vertebral Laminae in Lizards, with Comments on Ontogenetic and Serial Variation in Lacertini (Squamata, Lacertidae). **PloS one** 11(2): e0149445.
- Von Meyer, H. 1860. *Acteosaurus tommasinii* aus dem schwarzen Kreide-Schiefer von Comen am Karste. **Palaeontographica** 7: 223–231.
- VonLoh, J.P.; Bell, G.L. 1998. Fossil reptiles from the Late Cretaceous Greenhorn Formation (Late Cenomanian-Middle Turonian) of the Black Hills region, South Dakota. **Dakoterra** 5: 29-38.
- Wiens, J.J.; Collins, T. 2004. The role of morphological data in phylogeny reconstruction. **Systematic Biology** 53(4): 653-661.
- Wiens, J.J.; Kuczynski, C.A.; Townsend, T.; Reeder, T.W.; Mulcahy, D.G.; Sites, J.W.Jr. 2010. Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. **Systematic Biology** 59(6): 674-688.
- Williston, S.W. 1904. The relationships and habits of the mosasaurs. **The Journal of Geology** 12(1): 43-51.
- Woltering, M.J. 2012. From lizard to snake; behind the evolution of an extreme body plan. **Current genomics** 13(4): 289-299.
- Zaher, H. 1998. The phylogenetic position of *Pachyrhachis* within snakes (Squamata, Lepidosauria). **Journal of Vertebrate Paleontology** 18: 1–3.
- Zaher, H.; Rieppel, O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. **American Museum Novitates** 3271: 1-19.