The Origin and Evolution of Aquatic Adaptations in Cretaceous Squamates

by

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ABSTRACT

Three species of Cretaceous marine squamates are described or redescribed. The first, *Pontosaurus ribaguster* is described from a relatively complete specimen discovered on Hvar Island, Croatia. Preservation of identifiable nektonic teleosts within the gastric cavity (the first identifiable gastric contents described from a dolichosaur) provide strong evidence of a primarily piscivorous diet. The second described species is a new genus and species of plesiopedal mosasauroid, *Portunatasaurus krambergi*, from the Cenomanian-Turonian (U. Cretaceous) of Dugi Otok, Croatia. The specimen preserves an exquisite forelimb showing a unique anatomy that appears to be transitional between *Aigialosaurus* and *Mosasaurus*. The new and unique limb anatomy contributes to a revised scenario of mosasauroid paddle evolution, whereby the abbreviation of the forelimb and the hydrofoil shape of the paddle evolves either earlier in the mosasaur lineage than previously thought, or more times than previously considered. The third description is a reassessment of the lizard *Aphanizocnemus libanensis*. Re-examination suggests that characters cited as supporting varanoid-dolichosaur affinities are misinterpreted, are common to many squamates, or are homoplastic and tightly linked to aquatic adaptation. Available data support the conclusion that *Aphanizocnemus* is not a dolichosaur, a varanoid, nor in fact an anguimorph, but may represent a new form of aquatic scincomorph, a group not previously recognized as having evolved aquatic adaptations. The three descriptions highlight morphological data that has been erroneously used, or were unavailable for, previous studies. A systematic analysis of the Pythonomorpha (inclusive of *Pontosaurus ribaguster* and *Pontosaurus krambergi*¸ and exclusive of *A. libanensis*) shows strong evidence for a monophyletic Aigialosauridae from which the hydropedal mosasauroid condition evolved at least twice. The results also support dolichosaurs as a non-monophyletic assemblage that form successive sister taxa to the derived ophidians. The relationship between mosasauroids (Aigialosauridae) and ophidiomorphs is less conclusive, recovering the ophidiomorph lineage as arising from within the Mosasauroidea, most often as a sister group to the Mosasaurinae. To provide context for their evolutionary history, non-ophidian ophidiomorphs are further investigated through paleobiogeography. Fragmentary discoveries suggest that dolichosaurs originated in the Valanginian (Early Cretaceous) or even the latest Jurassic. Diversity and density peaked in the Cenomanian as a result of a large radiation in the Tethys and Western Interior Seaway. This radiation was likely interrupted by the Cenomanian-Turonian Boundary Event, an extinction event which caused a considerable drop in diversity. Non-ophidian ophidiomorphs persist until the Maastrichtian, while achieving their largest geographical distribution: spanning Europe, North America and South America. Their fossil record indicated that this geographically widespread group inhabited nearshore and offshore marine environments, and made several independent radiations into freshwater environments. Their radiative success was driven by features that were predisposed to functionality in the marine environment. Such ‘preadaptive’ features could explain the propensity of the pythonomorph lineage to invade the water, as evidenced by multiple lineages independently radiating into the marine environment. Fast evolution of aquatically adapted features would subsequently allowed them to colonize the aquatic environment worldwide.

PREFACE

Some of the research conducted for this thesis forms part of an international research collaboration, led by Dr. Michael Caldwell at the University of Alberta, with the Croatian Natural History Museum (Hrvatski prirodoslovni muzej), Zagreb, Croatia. Chapters two and three represent two manuscripts written, figured, and analyzed by M. Campbell Mekarski. M. Caldwell was the supervisory author; *K.* Krizmanić supervised the curation and management of the specimens; and D. Japundžić assisted with the review and interpretation of Croatian literature, assisted with some anatomical interpretation, and prepared the specimen described in Chapter two. Chapters one and four through seven are my original work.

Chapter two of this thesis is in preparation for submission as M. Campbell Mekarski, *D.* Japundžić, K. Krizmanić, and M. Caldwell "A new Cenomanian-Turonian *Pontosaurus* from the Dalmatian Coast, Croatia, and the first described 'dolichosaur' stomach contents" PLoS One. M. Caldwell assisted with manuscript composition and editing; D. Japundžić contributed to geological review and manuscript edits; and K. Krizmanić contributed to manuscript edits.

Chapter three of this thesis is in preparation for submission as M. Campbell Mekarski, D. Japundžić, K. Krizmanić, and M. Caldwell "Description of a new basal mosasauroid with comments on the evolution of the mosasauroid forelimb" Journal of Vertebrate Paleontology. M. Caldwell assisted with manuscript composition, D. Japundžić and K. Krizmanić contributed to manuscript edits.

Chapter seven was originally researched and written for a much more general audience as two parts of the University of Alberta MOOC 'Ancient Marine Reptiles, PALEO 203'. Though all the original writing and the bulk of the background research is all my own, H. Street helped with literature review, and T. Onuczko, M. Caldwell, and H. Street contributed to edits. The included text is all my own original work, and has been greatly edited and supplemented for this thesis from its original format.

The novel taxonomic binomials introduced in chapters two and three are not official under the International Code of Zoological Nomenclature and should not be considered valid at this time.

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This journey has been full of challenges and adventures, both personal and academic, and deep in lessons learned. My heart is full of gratitude to all who shared it with me.

With sincerest thanks,

Michelle

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GENERAL INTRODUCTION TO THESIS

Aquatic adaptation, the change from life on the land to life in the water, is one of the most radical and frequent major evolutionary transitions, yet in many secondary aquatic lineages, little is known about the progression of adaptations leading to an aquatic life. Of the more than 7000 species of extant squamates, only 59 are adapted to life in the aquatic environment: five species of sea kraits, three species of file snakes, 50 species of true sea snakes, and one iguana (Caldwell, 2006). Within these 59 species, there is not a very great diversity of ecological niches, with most being near-shore, tropical reef-dwellers. During the Cretaceous however, terrestrial squamates exhibited a remarkable radiation into ecological roles and aquatic ecosystems around the world. One group in particular–the Pythonomorpha–was responsible for at least three major radiations: the ophidians (including aquatic hind-limbed snakes), the dolichosaurs (elongate, semi-aquatic lizards), and the mosasauroids (including the giant, open-ocean, predatory mosasaurs) (Cope, 1869; Palci and Caldwell, 2010; Caldwell, 2012).

The Pythonomorpha has a long history of study dating back to the early 1800s, when early pioneers of paleontology and comparative anatomy such as Conybeare, Cope, Cuvier, Kornhuber, Kramberger, Mantell, Meyer, and Owen were recognizing and describing these fossils (e.g., Cuvier, 1808; Conybeare, 1822; Mantell, 1829; Owen, 1851; von Meyer, 1860; Cope, 1869; Gorjanovic-Kramberger, 1892; Kornhuber, 1901). Recent decades have seen a renewed interest in this group, resulting in an explosion in the number of species described and revised (e.g., Pierce and Caldwell, 2004; Dutchak and Caldwell, 2009; Palci and Caldwell, 2010; Jiménez-Huidobro et al., 2016; Street and Caldwell, 2016). These studies have prompted questions surrounding the origins and evolutionary trajectories of lineages within the

Pythonomorpha: specifically, regarding independent evolution, coevolution or convergence of specific traits related to their aquatic lifestyle.

The investigation of these questions necessitates a well-resolved phylogeny. Although the taxonomic status of these groups has changed little since their conception, the interfamilial relationships of dolichosaurs, ophidians and mosasauroids—and their relative position among anguimorph and squamate groups—have been modified and debated. As a result, hypotheses surrounding the aquatic adaptations of these Cretaceous marine squamates remain similarly muddled and inconsistent.

To study the remarkable aquatic adaptations observed Cretaceous squamates, the focus must be on the lineages demonstrating terrestrial to aquatic transitions: namely, the dolichosaurs and the basal mosasauroids (the question of aquatic origins of snakes is beyond the scope of this thesis and will not be addressed). These pythonomorph lizards represent an intermediate form between fully terrestrial squamates and the obligate aquatic mosasaurs that later evolved from within the Pythonomorpha. They exhibit a combination of traits ranging from fully terrestrial, to semi and obligitorily aquatic, and are therefore an ideal transitional group in which to study the basal marine adaptations within Cretaceous squamates, and their subsequent evolutionary transformations.

My research investigates whether aquatic adaptations within Cretaceous squamates were convergent or plesiomorphic, compares these traits to other aquatic species, and examines subsequent variation and modification of these adaptations in relation to our understanding of pythonomorph paleoecology. Broader implications of this project include helping to answer the question of whether or not becoming aquatic requires a specific set of characters in order to be successful, thereby increasing our understanding of convergent evolution (the independent evolution of similar features in species from different lineages). To accomplish this, a thorough understanding of the evolution and interrelationships of squamates is necessary. It is therefore essential to derive a new phylogenetic hypothesis that better describes the relationships between these groups. To that end this thesis has two major goals. The first goal will be to describe new species and revisit old interpretations, and use that data to construct a hypothesis of pythonomorph relationships. The second goal will be to better understand the evolution of aquatic traits in Cretaceous squamates based on their phylogenetic and paleobiogeographical context. Thus, chapter one will review literature describing and interpreting pythonomorph lizards and their recent systematic analyses. Chapter two will describe a new species of dolichosaur, and provide evidence that confirms a long standing hypothesis on dolichosaur paleoecology. Chapter three will describe a new genus of aigialosaur and outline a new hypothesis for the evolution of flippers in mosasaurs. Another species, *Aphanizocnemus libanensis*—originally classified as a dolichosaur—is redescribed as a 'scincogekkonomorph' in chapter four, thus removing confounding data from the Pythonomorpha problem. A phylogenetic study is performed in chapter five to clarify relationships between pythonomorph lineages, and revealing support for multiple independent incursions into the marine environment. Chapter six is a paleobiogeographical assessment of dolichosaurs that reveals patterns of origination and radiation, providing context for their evolution and adaption, including evolutionary drivers. Finally, with a clearer understanding of the phylogenetic and biogeographic constraints on aquatic adaptation in Cretaceous squamates, it is possible to discuss specific adaptations within the group. Chapter seven will introduce the problem of aquatic adaptation and some of the solutions evolved by squamates in the context of their evolutionary relationships, answering questions surrounding the ancestral or independent acquisition of certain aquatic traits.

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CHAPTER 1 : A REVIEW OF THE TAXONOMY AND SYSTEMATICS OF PYTHONOMORPH LIZARDS

INTRODUCTION

Lizards and snakes, collectively the Squamata, or scaled reptiles, are generally considered terrestrial as they have few adaptations that would be considered distinctively aquatic. Today, only marine iguanas and sea snakes are considered aquatic squamates. However, Cretaceous rocks of marine origins from around the world have produced fossilized lizards adapted to aquatic life. These fossils represent a dramatic radiation that happened in the mid-Late Cretaceous (~95 million years ago- mya), when a group of squamates—the Pythonomorpha—evolved and underwent a dramatic marine radiation (Bardet et al., 2008). By the time of their extinction at the end of the Cretaceous period (65 mya) they had colonized marine and freshwater environments, evolved into a vastly diverse aquatic group, and had given rise to the mosasaurs - a fully aquatic group of top predators who possessed many of the adaptations distinctive of an aquatic life.

The Pythonomorpha is composed of the Ophidia (including hind-limbed, and legless snakes), the Mosasauridae, and several families of pythonomorph lizards (note that the term 'lizard' is used here and throughout the rest of this manuscript as a short-hand for the paraphyletic assemblage composed of non-ophidian, non-mosasaurid squamates): the Aigialosauridae, the Dolichosauridae, and sometimes, the Coniasauridae. The phylogenetic relationships and composition of the Pythonomorpha, including its location within Squamata, is heavily debated (Calligaris, 1988; Carroll and Debraga, 1992; Caldwell, 2000; Dutchak and Caldwell, 2006; Bardet et al., 2008; Caldwell and Palci, 2010; Palci and Caldwell, 2010;

Gauthier et al., 2012). However, the phylogenetic analysis of Palci and Caldwell (2010) suggests that the ancestors of pythonomorphs were anguimorph lizards that developed features related to skull kinesis, strengthening of the braincase, and aquatic locomotion. Ophidiomorphs (a subset of the Pythonomorpha composed of dolichosaurs and ophidians) are characterized by additional features related to limb reduction, additional skull kinesis, body and neck elongation and a fairly progressive reduction in pectoral girdle elements (Palci and Caldwell, 2010).

The majority of the earliest known pythonomorph lizards originate from the mid-Cretaceous rocks deposited in the Tethys Sea including localities in Croatia and Slovenia (*Adriosaurus, Aigialosaurus, Mesoleptos, Pontosaurus,* e.g., Caldwell, Carroll, and Kaiser, 1995; Cornalia and Chiozza, 1852; Kornhuber, 1893, 1901; Kramberger, 1892; Lee and Caldwell, 2000; Nopcsa, 1908, 1923; Pierce and Caldwell, 2004; von Meyer, 1860), Lebanon (*Aphanizocnemus, Pontosaurus;* Caldwell and Dal Sasso, 2004; Dal Sasso and Pinna, 1997) and Palestine (*Hassiasaurus;* Polcyn, Tchernov, and Jacobs, 1999). A smaller number of species can also be found in more widely separated localities including the Western Interior Seaway (*Dallasaurus*; Bell and Polcyn, 2005), Atlantic shelf (*Vallecillosaurus*; Smith and Buchy, 2008), and Pacific Rim (*Kaganaias*, Evans *et. al*, 2006). Interestingly, most of the fossil record for pythonomorph lizards are articulated, monotypic specimens, though fragmentary material has been found in Australia (Scanlon and Hocknull, 2008), the United States (Liggett et al., 2005; Shimada and Bell, 2006), and Spain (Hontecillas et al., 2015).

The goal of this chapter is to review the literature describing and interpreting pythonomorph lizards from the first descriptions of these animals (Owen, 1842), to the most recent analyses (Simões et al., 2017). This review will provide context for the current understanding of pythonomorph relationships, reveal gaps in knowledge and provide a sense of direction for some of the questions asked throughout this work. Research surrounding the aquatic adaptations of this group will be summarized in Chapter Eight and are not discussed here in Chapter 1.

REVIEW

The study of non-ophidian, non-mosasaurid pythonomorphs has mostly been done in two major surges. The first, from the 1850s to the 1920s was descriptive of new species culminating in a summary by Camp (1923) in his "Classification of the Lizards". After Camp, there was very little published research on dolichosaurs, aigialosaurs and mosasauroids until 1988 (exceptions would include McDowell and Bogert [1954] and Russell [1967]). This year saw the summary of Cretaceous marine lizards by Calligaris (1988) and marked the beginning of what becomes a truly renewed interest in the group. Over the next three decades many publications were released diagnosing, reassessing and analyzing the relationships of the group.

The Ophiosauria (1850-1900)

The earliest work on pythonomorph lizards was done in the mid 19th century with a series of primary descriptions. These included *Coniasaurus crassidens* and *Dolichosaurus longicollis* (Owen, 1850)*,* and *Mesoleptos zendrini* (Cornalia, 1852). The family Dolichosauridae was erected by Gervais (1852) as a monotypic taxon containing only *Dolichosaurus longicollis* (Owen, 1850). Owen (1850) initiated discussion on the broader relationships of the group by proposing that his *Coniasaurus* and *Dolichosaurus* might be marine 'iguanian' lizards.

In the next several decades, while debate raged over the relationships of mosasaurs (e.g., Owen, 1877, and a series of responses between Cope and Baur 1895-1896) several more pythonomorph lizards were introduced into the scientific literature: *Acteosaurus tommasinii* (von Meyer, 1860), *Hydrosaurus* (later *Pontosaurus*) *lesinensis* (Kornhuber, 1873), *Adriosaurus suessi* (Seeley, 1881), *Aigialosaurus dalmaticus*, and *Aigialosaurus novaki* (Kramberger, 1892). It was during this time frame that Cope (1869) first proposed the close relationship of snakes and mosasaurs. He postulated that among squamates, the closest living relatives of mosasaurs were snakes and erected the Pythonomorpha to include these taxa. However, the dolichosaurid and aigialosaurid lizards we now consider part of the Pythonomorpha were not included.

In 1892, Kramberger produced one of the first comprehensive and comparative works on these animals, comparing previously described Cretaceous lizards to his new species: *Aigialosaurus dalmaticus*. This was the work that established the Aigialosauridae, a family he erected to contain *Acteosaurus, Adriosaurus*, *Pontosaurus* (which he had renamed from *Hydrosaurus)*, and *Aigialosaurus-* though he acknowledged that within this family, the first three genera should be subdivided from *Aigialosaurus*. Together with the Dolichosauridae (to which he only assigned *Dolichosaurus*), these two families formed a grouping he called the Ophiosauria- a transitional group between 'lizards' and mosasaurs. *Mesoleptos* was excluded from the Ophiosauria and was instead assigned to the Varanidae.

As it turned out, the name "Ophiosauria" was preoccupied and was shortly thereafter emended to Dolichosauria by Boulenger (1893). In this publication, he also proposed a hypothesis for pythonomorph relationships, regarding the aigialosaurs and dolichosaurs as ancestral to all other lizards, mosasaurs and snakes. Kramberger (1892) acknowledged the transitional nature of the Aigialosauridae, arguing that they were ancestral to dolichosaurs, pythonomorphs (still only including mosasaurs and snakes), and lacertilians. *Carsosaurus marchesetti* (Kornhuber, 1893) was described soon after.

The Classification of Lizards (1901-1923)

Kramberger's 1892 classification was reviewed by Kornhuber (1901) in his description of *Aigialosaurus (=Opetiosaurus) bucchichi*. In his opinion, the members of the Aigialosauridae were sufficiently similar to modern varanids to be placed in the family Varanidae. Instead, he argued that his new species, *O. bucchichi*, was a better example of a transitional form between varanids and pythonomorphs.

Two years later, Nopcsa (1903) once again revised the Cretaceous lizards of the Istrian peninsula. He supported Kramberger's interpretation of Aigialosauridae as a family distinct from the Varanidae, but disagreed on the composition of the family and its placement. He based the classification of the Dolichosauridae on small heads, elongated bodies and necks, and reduced limbs, including *Acteosaurus, Adriosaurus,* and *Pontosaurus* in this family with *Dolichosaurus*. In the large-headed, short-necked Aigialosauridae he placed *Aigialosaurus, Carsosaurus, Opetiosaurus* and *Mesoleptos*. He concluded that the Aigialosauridae and Dolichosauridae shared ancestry with varanids, and assigned both to the Lepidosauria.

During this time, Louis Dollo was writing prolifically on mosasaurs, and in his writings he made several comments regarding aigialosaurs and dolichosaurs, reaching similar conclusions to Nopcsa. Dollo (1903, 1904a, 1904b) considered aigialosaurs true lizards branching off near the Varanidae, and ancestral to the Dolichosauridae and Mosasauridae. Williston (1904) shared this opinion, emphasizing the close relationship of aigialosaurs and dolichosaurs to varanoids. He also praised the striking example of evolution preserved in the transition from terrestrial varanoids, to semi-aquatic aigialosaurs, to aquatic mosasaurs.

Over the next few decades, other anatomists and paleontologists continued to publish on the relationship of these small aquatic lizards and Nopcsa continued to change his interpretations. Nopcsa's (1908) review of fossil reptiles expanded on his ideas that snakes had marine origins and were closely related to dolichosaurs, and further discussed the monophyly of mosasaurs and snakes.

Contrary to Nopcsa and Kornhuber was Féjérváry (1918), who published that similarities between aigialosaurs and mosasaurs were the result of convergence, stating his doubt that such a transformation could have occurred in such a short amount of time (less than ten million years).

Before he died in 1933, Nopcsa published one last paper on fossil lizard relationships (Nopcsa, 1923). In this paper (in which he also described *Eidolosaurus* and *Pachyophis*), he challenged Féjérváry, revised his own earlier classifications, and placed dolichosaurs and aigialosaurs in a closer relationship as sister-subfamilies. He grouped all the above-mentioned lizards into the Dolichosauridae, which he divided into three subfamilies. The Dolichosauinae still included the grouping of *Acteosaurus, Adriosaurus, Pontosaurus* and *Dolichosaurus*, but also included the newly described *Eidolosaurus*. The Aigialosaurinae maintained the *Aigialosaurus-Carsosaurus-Opetiosaurus* grouping, but *Mesoleptos* was removed and placed in a third subfamily: Mesoleptinae. He also discussed similarities in aigialosaur and mosasaur skulls, and between the caudal regions of *Aigialosaurus* and *Pachyophis*. These included: small skulls, a cylindrical body, reduced limbs, many hypapophyses, and the presence of zygosphenes/zygantra. He concluded that the ancestors of mosasaurs could be found within the

Aigialosaurinae, and that snakes were most closely related to dolichosaurs and had a morphologically similar ancestor.

The most lasting classification was made by Camp (1923) in his extensive work “Classification of the Lizards”. Camp (1923) placed the Dolichosauridae, Aigialosauridae and Varanidae inside the Superfamily Varanoidea. He also first classified the Mosasauroidea: a superfamily containing the Mosasauridae and being a sister-superfamily to Varanoidea. Together, the Mosasauroidea and Varanoidea comprised the Platynota. Serpentes was placed outside of the Sauria, as a separate suborder. According to his classification, the Aigialosauridae contained *Aigialosaurus, Opetiosaurus, Carsosaurus* and ?*Mesoleptos* and were defined by fused frontals, pterygoid teeth, reduced limbs and broadened feet. He defined a dolichosaur as having axial elongation, a small skull, thirteen cervical vertebrae, and some aquatic adaptation in the limbs and tail. According to this diagnosis, he included *Acteosaurus, Adriosaurus, Dolichosaurus,* and *Pontosaurus* in the Dolichosauridae.

From Camp to Russell (1954-1967)

Camp’s classification was the generally accepted model of relationships for several decades. In 1954, McDowell and Bogert published a monograph on *Lanthanotus*, in which they placed Lanthanotidae, Dolichosauridae and Aigialosauridae in a polytomy. They also described the mosasaur lineage arising from the Aigialosauridae. Their work laid out each of these groups, their identifying characteristics, and their members. Within the Aigialosauridae was *Aigialosaurus*, *Carsosaurus*, *Opetiosaurus*, ?*Mesoleptos,* and ?*Eidolosaurus* (which they gave a secondary interpretation as a lanthanotid). *Acteosaurus*, *Adriosaurus, Pontosaurus, ?Pachyophis, ?Symoliophis*, and *Dolichosaurus* comprised their Dolichosauridae.

The geologically oldest proposed aigialosaur was described in a very short paper by Kuhn (1958). He described a skull roof fragment found in Late Jurassic deposits from Solnhofen, Germany, and referred it to *Proaigialosaurus hueni*, as it predated any other aigialosaur previously described. The specimen has now unfortunately been lost.

Camp's 1923 classification was revised in 1961, almost four decades after its publication (Camp and Allison, 1961), but the status of Cretaceous marine squamates did not change much excepting that they gained another closely related family, the Helodermatidae.

Russell (1967) published one of the key works in mosasaur paleontology: "The Systematics and Morphology of American Mosasaurs". Though the focus was obviously North American mosasaurs, pythonomorph lizards were also discussed - primarily as an example of what a transitional mosasaur might have been like. Like Camp (1923) the decades following Russell's work produced very little on pythonomorph lizards.

The first cladistic analyses (1988-1993)

Besides the discovery of fragmentary coniasaur material from North America (Bell, Murry, and Osten, 1982), the next major research on pythonomorph lizards commenced with a summary of reptiles from Komen and Lesina (Hvar Island) by Calligaris (1988). Though the publication provides a nice overview of diversity, it does not give any new descriptive details on these lizards (except one new specimen briefly referred to *Opetiosaurus* - now described as *Komensaurus*), or any new hypotheses on relationships (he supported Nopcsa's 1923 phylogeny).

Four years later, Carroll and Debraga (1992) published on the taxonomy and phylogenetic relationships of aigialosaurs. They redescribed *Opetiosaurus bucchichi* and *Aigialosaurus dalmaticus*, and described Calligaris' new specimen. However, instead of giving it a formal taxonomic binomen, they simply referred to it as "the Trieste aigialosaur". The truly notable thing about this publication was that it used a computer generated cladistic analysis to construct cladograms and from there to hypothesize a phylogeny of relationships (the first time this had been done on pythonomorph lizards). Their analysis used fifteen characters and ten terminal clades including Aigialosauridae (which was coded using the three species they had described earlier in their paper). The Aigialosauridae was recovered in a polytomy with *Cherminotus+Saniwa* and *Lanthanotus+Varanus*. Mosasaurs and dolichosaurs were not included.

The same authors published a larger scale version (142 characters, 17 taxa) of this analysis a year later, this time with mosasaurs as the focus (Debraga and Carroll, 1993). Once again, Aigialosauridae was coded as a terminal taxon, prohibiting any comments on the relationships within that family. However, the Aigialosauridae and Mosasauridae were recovered as sister groups forming the Mosasauroidea, which was found in turn to be the sister group of the Varanidae.

The dissertation of Bell (1993) produced another analysis of mosasaur systematics. It is argued that his study gained more traction than Debraga and Carroll's due to better chosen, less redundant characters (Dutchak, 2005). Like Carroll and Debraga (Carroll and Debraga, 1992;

Debraga and Carroll, 1993), the focus was on mosasaurs and only a few small, semi-aquatic forms were chosen. However, unlike earlier analyses, the Aigialosauridae was broken into multiple terminal taxa and therefore tested its monophyly for the first time. The analysis (151 characters, 37 taxa) used *Dallasaurus* (at the time, referred to only as "the Dallas aigialosaur"), *Opetiosaurus*, *Aigialosaurus,* and the Trieste Aigialosaur but did not include any dolichosaurs. When the research was published (Bell, 1997a), it had been edited to 142 characters. This analysis did not recover a monophyletic Aigialosauridae. *A. dalmaticus* and *Komensaurus* (the Trieste Aigialosaur) plotted out with the halisaurines. *Dallasaurus* (the Dallas aigialosaurs) fell into a polytomy with the halisaurine-aigialosaur clade, and the clade containing the rest of the mosasaurs. *O. bucchichi* was located at the base of the tree, as the sister group to all other mosasauroids. In addition, Bell's results did not find support for a sister group relationship between mosasauroids and varanids. It is extremely important to note here that this character set has formed the basis of almost every mosasauroid phylogeny for twenty years, from 1997-2017, and did not get a significant review for almost two decades (e.g., Caldwell and Palci, 2007; Dutchak and Caldwell, 2006, 2009).

Ten years of description and discussion (1995-2005)

Beginning in 1995, and coinciding with the discovery of several new pythonomorph lizards, there was a resurgence in the study of aigialosaurs and dolichosaurs independent of mosasaurids as well as in relation to broader squamate relationships. This began with the redescription of *Carsosaurus marchesetti* (Caldwell et al., 1995) which was focused particularly on describing and comparing the forelimb, and included an analysis of aigialosaur phylogeny using 66 characters and ten taxa. As it was published before Bell (1997), this makes it the first published phylogenetic analysis of aigialosaurs. Unfortunately, the results of the heuristic search produced a polytomy of aigialosaurs (*Aigialosaurus, Carsosaurus, Opetiosaurus* and the Trieste aigialosaur) outside of the Mosasauridae, whereas the strict consensus produced a polytomy of all five taxa. Subsequent tests removing problematic characters gave further support for a monophyletic Aigialosauridae within a monophyletic Mosasauroidea. This paper also referred *Opetiosaurus* to *Aigialosaurus.*

Caldwell (1996) examined mosasauroid limb evolution using a dataset based on Bell's (1993) matrix. Caldwell removed over half of the taxa (37 taxa to 15), and many characters deemed to be phylogenetically uninformative (151 characters to 91). In contradiction to Caldwell et al.'s (1995) earlier findings, the strict consensus yielded a polytomy of aigialosaurs at the base of the Mosasauridae, and the majority rule recovered a paraphyletic Aigialosauridae in a comb on the stem of the Mosasauridae tree.

Several studies in 1997 and 1998 did not focus on pythonomorph lizards in particular, but by including pythonomorphs in analyses of squamate relationships, they nonetheless provided some context on their placement. Lee (1997) provided a novel hypothesis for varanoid and snake affinities by using mostly fossil taxa (10 of 15) in his analysis. This provided strong support for the Pythonomorpha inclusive of mosasaurs and snakes. Lee (1998) expanded on this work and created a larger dataset with more taxa and characters. Once again, mosasauroids and snakes formed a well supported clade—the Pythonomorpha—which nested within the Varanoidea, supporting the close relationship proposed by Carroll and Debraga (1992). Two descriptive papers on legged snakes also supported this relationship (Caldwell and Lee, 1997; Lee and Caldwell, 1998).

The year 1997 also marked the first new ‘dolichosaur’ to be described in many years: *Aphanizocnemus libanensis* (Dal Sasso and Pinna, 1997). The description was accompanied by a small phylogenetic analysis based on Debraga and Carroll (1993). *A. libanensis* formed a polytomy with the Aigialosauridae and the mosasaurid clade (containing four terminal taxa). Interestingly, no other dolichosaurs were included in the analysis. The authors concluded that *Aphanizocnemus* occupied a transitional position between terrestrial varanids and fully aquatic mosasaurs.

The redescription of *Coniasaurus crassidens* (Caldwell and Cooper, 1999) and the description of a new species, *Coniasaurus gracilodens* (Caldwell, 1999a), prompted two further analyses: one smaller analysis focused on the relationships of aigialosaurs, coniasaurs and mosasaurs (Caldwell, 1999a), and the second among the greater Squamata (Caldwell, 1999b). For the first (Caldwell, 1999a), the Bell matrix was once again pared down, this time to 73 characters and 11 taxa (including three aigialosaurs). The results were similar to Caldwell (1996), showing a paraphyletic Aigialosauridae with *Coniasaurus* occupying the sister-position to mosasaurs. Caldwell (1999b) performed an analysis of higher-level squamate phylogeny using the characters and matrix of Estes, DeQuieroz, and Gauthier (1988) which placed coniasaurs and the Mosasauroidea (Aigialosauridae and Mosasauridae) in a clade. The sister group of that clade were the snakes in 12 out of 18 shortest trees supporting the pythonomorph grouping. Unlike Lee (1998), varanids were on the opposite side of the tree. The new hypothesis was that pythonomorphs were not derived varanoids, but basal platynotans, or maybe even basal anguimorphs. This hypothesis was not universally accepted, and was contradicted by Zaher and Rieppel (1999) who questioned treatment of the taxa and characters.

In 1999, Polcyn, Tchernov and Jacobs described *Haasiasaurus gittelmani*, a new basal mosasauroid from Israel. It was originally named as *Haasia gittelmani* and had to be renamed because the generic name was preoccupied (Polcyn et al., 2003). No other new comments on relationships were made.

Completing a redescription of *Adriosaurus suessi*, Lee and Caldwell (2000) also investigated the sister-group relationships of mosasauroids with dolichosaurs, pontosaurs, adriosaurs and snakes. Using a version of Lee's (1998) dataset (updated to 258 characters and 32 taxa), they recovered *Adriosaurus, Aphanizocnemus,* and Dolichosauridae (*Coniasaurus* and *Dolichosaurus*) as successive sister groups to snakes. The sister-group to this dolichosaur-snake clade was the aigialosaur-mosasaur clade (here named Mosasauridae instead of Mosasauroidea), supporting a monophyletic Pythonomorpha. In this analysis, the Pythonomorpha still sat within Varanoidea, as the sister group to Varanidae.

Once again opposing the close relationship of mosasaurs and snakes was Tchernov *et. al.* (2000) and Rieppel and Zaher (2000), who argued that the skull and dentition characteristics uniting these groups were convergent. They did however, support the close relationship of mosasaurs and varanids.

Caldwell (2000) once again modified Bell’s (1993) matrix and his own earlier work (Caldwell, 1996, 1999a) when he performed a cladistic analysis on six genera of mosasaur, three species of aigialosaur, two species of coniasaur and *Dolichosaurus longicollis* (the redescriptive focus of the paper). Using this matrix of twelve taxa and 66 characters, he recovered the Aigialosauridae as a distinct clade (with unresolved internal relationships). Although the strict consensus tree showed a polytomy between mosasaurs, Aigialosauridae, *Dolichosaurus* and the coniasaurs; the majority rules tree found Aigialosauridae and mosasaurs in a clade distinct from the included dolichosaurs: *Dolichosaurus* and *Coniasaurus*.

Lee and Scanlon (2002) further adapted the Caldwell (2000) dataset, reducing the number of characters by ten, and adding *Mesoleptos zendrinii* (which was redescribed in the paper). The results were essentially the same as in Caldwell (2000), except that the newly included *Mesoleptos* was now found to be the closest relative of snakes, followed by *Adriosaurus* and then other dolichosaurs.

A small Moroccan mosasaur described by Bardet, Suberbiola, and Jalil (2003) provided more evidence for the evolution of mosasaurs from within the Aigialosauridae. *Tethysaurus nopcsai* had many features that appeared intermediate between aigialosaurs and more derived mosasaurs, providing a clearer picture of how mosasaurs could have evolved from within the aigialosaur lineage. When included in Caldwell's (2000) dataset, *Tethysaurus* was recovered as the sister group to the derived mosasauroids, with aigialosaurs (*Opetiosaurus, Carsosaurus* and *Aigialosaurs*) forming the sister-group to [*Tethysaurus*[*Halisaurus* and other mosasaurids]].

Following the trend of redescriptions, *Acteosaurus crassicostatus* (Calligaris, 1993) was redescribed in 2004, which resulted in this specimen being referred to *Adriosaurus suessi* (Caldwell and Lee, 2004). *Pontosaurus lesinensis* was also redescribed by Pierce and Caldwell (2004). Analyzing it in a phylogenetic context, they reduced Lee and Caldwell’s (2000) dataset to fifteen taxa and 159 characters. The results were essentially the same: a monophyletic Pythonomorpha, with a monophyletic dolichosaur-snake lineage as the sister group to a monophyletic aigialosaur-mosasaur lineage. *Pontosaurus* fell between [Dolichosauridae, *Aphanizocnemus*] and *Adriosaurus* in the comb leading to the Ophidia. It is interesting to note here that even though this and plenty of other phylogenetic studies assessed the relationships of dolichosaurs in the 1990's and early 2000s, none found any support for a monophyletic Dolichosauridae (sensu Camp, 1923), but instead recovered them as a paraphyletic 'grade' basal to snakes.

Also described in 2004 was *Carentonosaurus mineaui* (Rage and Néraudeau, 2004). It was described as an aigialosaur on the basis of several pachyostotoic vertebrae, a partial rib, and a fragmentary pectoral girdle. It has, due to the partial nature of the specimen, not been used in phylogenetic analysis since.

Vidal and Hedges (2004) used a molecular study to try to disprove the pythonomorph hypothesis, but as mosasaurs can obviously provide no molecular data, their inference is questionable.

Lee (2005) performed an interesting series of phylogenetic analyses whereby he used 248 osteological (based on Lee and Caldwell, 2000), 133 other anatomical, and 18 ecological traits to test the major relationships of extinct and extant squamates. The analysis was run multiple times, using different subsets of characters and taxa, deletion tests, and character weighting. The tests were mostly congruent. The results support the monophyly of the Mosasauroidea (Mosasauridae and Aigialosauridae), and the placement of dolichosaurs as 'stem' snakes, forming successive outgroups after the pythonomorph lineage splits from the mosasauroids. Varanoids formed the outgroup to the Pythonomorpha.

The question of monophyly (2005-present)

Bell and Polcyn's (2005) description of *Dallasaurus turneri* was accompanied by a systematic analysis using the mostly unmodified dataset of Bell (1997), excluding or ignoring changes applied by Caldwell (1996, 1999a, 2000). Once again, the included aigialosaurs were *Aigialosaurus, Dallasaurus, Opetiosaurus,* and the Trieste aigialosaur. This time they also included *Haasiasaurus*. The results of this analysis resolved the polytomy at the base of the tree and showed a paraphyletic Aigialosauridae. *Dallasaurus* and their "Taxon novum YMP" (a taxon that has still not been described as of 2017) plotted out as sister taxa to the mosasaurines, *Haasiasaurus* as the sister taxa to the russellosaurine-halisaurine clade, and *Opetiosaurus* and *Aigialosaurus* as sister taxa to the rest of the mosasauroid lineage. Though a lot of criticisms can be made surrounding their choice of taxa and characters, this paper outlines an extremely important question: that of the monophyletic or polyphyletic nature of derived mosasaurs. Bell and Polcyn argue that paddle-like limbs (previously thought of as a synapomorphy of derived mosasaurs) evolved at least twice within the Mosasauroidea. Their tree topology supports traditional subfamily groupings of mosasaurs suggesting that each mosasaur subfamily could have been a separate aigialosaur radiation, which would therefore make the Mosasauridae polyphyletic.

Later that year, Haber and Polcyn (2005) described *Judeasaurus tchernovi* based on a partial skull. They identified it as a possible dolichosaur, but acknowledged that the material was insufficient to firmly identify it as an aigialosaur or dolichosaur. However, in Polcyn's earlier systematic analysis (Bell and Polcyn, 2005), it plotted out with *Dallasaurus* as the sister taxon to the mosasaurines.

Buchy et al. (2005) contributed significantly to mosasauroid paleobiogeography when their summary of Mexican marine squamates was published. In it they briefly describe several derived mosasaurs (including a holotype specimen), isolated vertebrae assigned to Mosasauroidea, and an articulated partial aigialosaur preserving squamation that would be fully described later (Smith and Buchy, 2008).

Dutchak and Caldwell (2006) used the redescription of *Aigialosaurus dalmaticus* to edit several characters as they had been interpreted by Bell and Polcyn (2005) and perform their own systematic analysis on that data set. Their results showed a polyphyletic 'Aigialosauridae', with *Dallasaurus* at the base of the mosasaurines, *Haasiasaurus*, *Aigialosaurus,* and the Trieste aigialosaur as sequential outgroups at the base of the russelosaurine-halisaurine clade, and *Opetiosaurus* as the sister group to all other mosasauroids.

The year 2006 was an exciting one for pythonomorph researchers, with two nearly complete species being described, both with accompanying systematic analyses. Caldwell (2006) described a second species of *Pontosaurus: P. kornhuberi.* Additionally, he used a highly modified version (77 characters) of Pierce and Caldwell's (2004) matrix to analyze pythonomorph relationships. The results were fairly well supported, with the strict consensus showing *Adriosaurus* as the sister taxon to ophidians; *Pontosaurus* [*P. kornhuberi* and *P. lesinensis*] forming a sister clade to [*Adriosaurus,* ophidians]; and Dolichosauridae and *Aphanizocnemus* falling out basal to the above. The sister clade of all these were the mosasauroids (Mosasauridae and Aigialosauridae).

The second new species was a pythonomorph lizard from Japan (Evans et al., 2006). *Kaganaias hakusanensis* is unique in being from the Pacific, and for being one of the oldest pythonomorph lizards: dating from the Valanginian ⁄ Hauterivian of the Early Cretaceous. In their analyses (based on Lee, 1998; Lee and Caldwell, 2000; and Rieppel and Zaher, 2000), *Kaganaias* plots with dolichosaurs when they are included (Lee and Caldwell, 2000; Rieppel and Zaher, 2000 expanded), and when they are not, it falls out with the amphisbaenians in a sister clade to pythonomorphs (Lee, 1998).

Palci and Caldwell's (2007) description of a new dolichosaur—*Adriosaurus microbrachis*—critically assessed the characters and taxonomic composition of Bell and Polcyn’s (2005) data matrix. This led to a different series of cladograms and therefore different hypotheses regarding the evolution of mosasauroid features. This paper was significant in that it defined Ophidiomorpha for the first time: the clade inclusive of Ophida and the dolichosaurs (including the Dolichosauridae, pontosaurs, adriosaurs, etc). They defined the group as being characterized by (1) elongation of the cervical region (>10 cervical vertebrae); (2) elongation of the dorsal region (>35 precloacal/presacral vertebrae); (3) zygosphenes/zygantra in the precloacal/presacral region; (4) limb reduction or loss, especially in the forelimbs. It excludes – but forms a sister group with - the Mosasauridae and Aigialosauridae (Mosasauroidea). The Pythonomorpha was redefined as the clade containing the Ophidiomorpha and Mosasauroidea. These definitions are the basis of the naming conventions used in this thesis. The authors did not address ingroup relationships of the mosasauroid lineage, but did so for the Ophidiomorpha. They recovered *Adriosaurus* as the sister taxon to the Ophidia, with *Aphanizocnemus* and the Dolichosauridae forming successive sister-groups.

In 2007, after years of being included in phylogenetic analyses, “the Trieste aigialosaur” was finally described and named (Caldwell and Palci, 2007). *Komensaurus carrolli* was identified as a new genus, contrary to the past synonymization of this specimen with

Carsosaurus (Caldwell et al., 1995; Caldwell, 1996). The primary description also inspired a crucial evaluation of Bell and Polcyn's (2005) character list, and a new analysis of the ingroup relationships of Mosasauroidea. A data matrix based on Dutchak and Caldwell's (2006) dataset was revised to include 142 characters and 38 terminal taxa. This analysis supported the polyphyly of mosasaurids, with *Dallasaurus* being the sister group of the mosasaurines, *Carsosaurus* and *Komensaurus* the sister group of the halisaurine-russellosaurine clade, and *Aigialosaurus* as the sister group to all other mosasauroids.

As previously mentioned, another mosasauroid was described the next year. *Vallecillosaurus donrobertoi* preserves the posterior half of a basal mosasauroid from Mexico (Smith and Buchy, 2008). It provided evidence that pythonomorph lizards had achieved intercontinental distribution before the evolution of the mosasaurs. This hypothesis seems to be supported by other finds of isolated vertebrae reported from this time: including possible dolichosaur material from Australia (Scanlon and Hocknull, 2008), France (Houssaye, 2010), Kazakhstan (Averianov, 2001), Kansas (Shimada and Ystesund, 2007), and possibly Patagonia (Albino, 2000).

Conrad (2008) performed a large and very extensive phylogenetic study of squamates. His findings were similar to other, smaller studies on pythonomorph and mosasaur relationships: a Hennigian comb of aigialosaurs leading to the derived mosasaur groups, with the dolichosaurs (*Dolichosaurus, Aphanizocnemus* and *Coniasaurus*) as the sister group. The polyphyly of aigialosaurs was not really tested, as he did not include *Dallasaurus* or *Judeasaurus* which had previously been resolved as basal mosasaurines (Bell and Polcyn, 2005; Caldwell and Palci, 2007; Haber and Polcyn, 2005). He also attempted to resurrect an old, but never properly defined name for the dolichosaur-aigialosaur-mosasaur clade: Mosasauria (March, 1880) which had been mentioned in older literature (mostly in the early 1900s), and generally used interchangeably with Pythonomorpha. Presumably, Conrad (2008) chose not to use the term ‘Pythonomorpha’ as his analysis recovered snakes in a completely different place.

In their redescription of *Aigialosaurus* (here officially renamed from *Opetiosaurus) bucchichi*, Dutchak and Caldwell (2009) once again completed a phylogenetic study based on a heavily modified version of Bell and Polcyn’s 2005 data matrix. Terminal taxa were combined at the generic level where possible in order to focus on larger scale interrelationships of mosasauroids (i.e., not at the specimen or species level). The analysis included five small, semi-aquatic mosasauroids: *Aigialosaurus bucchichi* and *A. dalmaticus*, *Komensaurus, Dallasaurus,* and *Haasiasaurus*. The authors chose not to include *Carsosaurus* due to the low number of characters that could be coded. Though the study provided fairly good resolution within the Mosasauridae, the relationships of the semi-aquatic mosasauroids was less clear. Among trees one step longer than optimum, the hypothesis was that *Aigialosaurs* and *Dallasaurus* form successive outgroups to the Mosasauridae (*Clidastes* and more derived mosasaurs). Outside of this, *Komensaurus, Haasiasaurus* and *Halisaurus* formed a group. Under strict consensus, this relationship broke down into a polytomy among the five genera. The placement of *Halisaurus* was slightly surprising given that it is hydropedal (i.e., aquatically adapted limbs) rather than plesiopedal (i.e., terrestrially adapted limbs) like the rest of the genera within the polytomy. It is also interesting in that it provides a paraphyletic hypothesis for aigialosaurs rather than polyphyletic.

Palci and Caldwell (2010) in their redescription of *Acteosaurus tommasinii* include a cladistic analysis of several marine squamates (including Mosasauridae, Dolichosauridae, Aigialosauridae, pontosaurs, *Adriosaurus*, *Acteosaurus*, *Aphanizocnemus*) and living and fossil snakes. Their trees found no support for a monophyletic Dolichosauridae inclusive of *Pontosaurus.* All of their recovered tree topologies found support for the monophyly of the Ophidiomorpha, inclusive of the Dolichosauridae (*Dolichosaurus, Coniasaurus*), *Pontosaurus*, *Aphanizocnemus*, *Adriosaurus*, *Acteosaurus,* and Ophidia. The Mosasauroidea (Aigialosauridae and Mosasauridae) was recovered as the sister group to Ophidiomorpha, such that the Mosasauroidea and Ophidiomorpha together formed the Pythonomorpha. The authors also described a new species of ophidiomorph lizard this same year: *Adriosaurus skrbinensis* (Caldwell and Palci, 2010). They added this species into their analysis (Palci and Caldwell, 2010), and not surprisingly, obtained the same results. The only difference being that *A. skrbinensis* was found to be the sister group of *A. suessi*.

A treatise by Caldwell (2012) extensively discussed the concept of 'mosasaur' (and their kin, the dolichosaurs and aigialosaurs) as a biologically distinct unit. He concluded that the current usage of the term 'mosasaur' described a particular morphotype of pythonomorphs that were large and had derived flippers, rather than a true biological group (mosasaurs in this sense being polyphyletic). He proposed that "Aigialosauromorpha" or "Aigialosauroidea" would be a more accurate term to describe the lineage of lizards that developed hydropedal limbs in several descendant lineages. A second conclusion was that there was a complete lack of evidence to support the hypothesis that mosasaurs (and their kin) were derived varanoids. In fact, they could not be placed confidently in the Platynota or Varanoidea, but appeared to fit well as basal anguimorphs along with snakes.

Since this time, little new taxonomic data or phylogenetic hypotheses of note has been published on pythonomorph lizards. They continue to be used in squamate and mosasaur phylogenies (e.g., Conrad et al., 2011; Gauthier et al., 2012; Simões et al., 2017), and an isolated teeth and some vertebral material from Spain has been attributed to pythonomorph lizards (Houssaye et al., 2013; Hontecillas et al., 2015). However, lack of new taxa or new hypotheses regarding relationships has somewhat stalled the study of this group.

Summary

The Pythonomorpha has a long history of study dating back to the early 1800s, when early pioneers of paleontology and comparative anatomy such as Conybeare, Cope, Cuvier, Kornhuber, Kramberger, Mantell, Meyer, and Owen were recognising and describing these fossils. Naturally following the alpha taxonomic studies of these species came a series of hypotheses on the relationships of snakes, dolichosaurs and mosasauroids and their broader placement within Squamata. Recent decades have seen a renewed interest in this group, resulting in an explosion in the number of species described and revised. The application of computer generated statistical models have been used to test the relative support for different phylogenetic hypotheses. These studies have generated a huge amount of new anatomical information and phylogenetic hypotheses. However, the lack of consensus among these analyses means that large scale taxonomic revision of the group has not been done, leaving several questions open.

The hypothesized placement of pythonomorph lizards at the base of mosasaur and snake lineages, means that these taxa are extremely important when trying to reconstruct evolutionary relationships and adaptive hypotheses. Major questions surround the origins and evolutionary trajectories of lineages within the Pythonomorpha: such as those regarding the mono- or polyphyly of obligate aquatic mosasaurs, the relationship of snakes among other squamates, and the independent evolution, coevolution, or convergence of specific traits.

The investigation of these questions necessitates a well-resolved phylogeny; however, no phylogenetic study has specifically attempted to resolve the relationships within the whole of the Pythonomorpha. Instead, the focus has generally been to contextualize a single specimen, or to determine the internal relationships of the ophidians, the dolichosaurs, or the mosasauroids. Broader level comparisons have been coincidental, usually due to the choice of outgroups or ingroups. To date, no study has specifically attempted to resolve relationships at the base of the pythonomorph lineage using dolichosaurs and aigialosaurs, which could help to settle some of these outstanding problems. One of the major goals of this thesis is to perform this necessary step, providing the most inclusive hypothesis of basal pythonomorph interrelationships to date.

The questions of where mosasaurs and snakes fit within the Squamata remains a difficult and intensely debated problem (e.g., Martill, Tischlinger, and Longrich, 2015). The close relationship of snakes and mosasaurs remains uncertain and is outside the scope of this work to attempt to resolve. However, due to the possible monpohyly of snakes and other pythonomorphs, it is impossible to completely exclude snakes from the discussion of pythonomorph phylogeny. Indeed, it seems that the snake origins question has been the driving force for many phylogenetic studies including pythonomorph lizards, and it is possible that results from this work may provide evidence for this debate.

The remainder of this chapter will summarize existing data on pythonomorph lizards, and the comparative material used in this thesis.

THE FOSSIL RECORD OF PYTHONOMORPH LIZARDS

Pythonomorph lizards are represented by about 27 species (20 genera) in the fossil record. These are rare finds. Preservational, geographic, and taphonomic biases in this group make biodiversity difficult to assess. This is exemplified by the fact that most of the described species are monotypic and known only from single specimens.

The next section will provide a brief overview of the taxa involved in the Late Cretaceous land-to-sea radiation of squamates. Where possible, I have included relevant notes on the discovery and history of the specimen, and information on stratigraphy, paleoenvironment and paleoecology which are important considerations for understanding adaptations.

Pythonomorpha *incertae sedis*

Isolated material found worldwide has been variously diagnosed as dolichosaur, aigialosaur, or pythonomorph remains. Generally, this is too fragmentary and poorly preserved to be confidently assigned to a genus or even family, though it can contribute to a better spatiotemporal understanding of pythonomorph radiation.

New World pythonomorph grade vertebral remains have been described from the middle Turonian of South Dakota (VonLoh and Bell, 1998), the upper Turonian of Columbia (Páramo-Fonseca, 1994, 1997), the Cenomanian-Turonian of Texas, South Dakota, Colorado, and Kansas (Martin and Stewart, 1977; Bell et al., 1982; Bell and Polcyn, 1996; Cicimurri and Bell, 1996; Shimada and Bell, 2006; Shimada et al., 2006, 2007; Shimada and Ystesund, 2007), the lower Turonian/lower Cenomanian of Mexico (Buchy et al., 2005), and possibly the Campanian-

Maastrichtian of Patagonia (described: Albino, 2000; dolichosaur affinities: Scanlon and Hocknull, 2008).

Tethyan material attributed to pythonomorph lizards comes from at least two instances of isolated teeth and some vertebral material from Upper Cretaceous (Late Campanian-Early Maastrichtian) of Spain (Houssaye et al., 2013; Hontecillas et al., 2015). One specimen, originally described as a snake (Rage and Richter, 1994; Rage and Werner, 1999) has been reinterpreted as a ‘dolichosaur’ (Scanlon and Hocknull, 2008). Several instances of isolated material have been reported from Turonian age deposits in France (Rage, 1989; Bardet et al., 1998a, 2008; Houssaye, 2010), and a single report from a Late Maastrichtian locality (Laurent et al., 2002). Slightly further from the central Tethys region are reports from the Cenomanian-Turonian of Kazakhstan (Averianov, 2001).

A more recent and potentially interesting find was that of a possible dolichosaur from the latest Albian of Queensland, Australia (Scanlon and Hocknull, 2008). This discovery is notable because it represents the first non-marine Gondwanan dolichosaur, found in a fluvial deposit. It is also the oldest (or second-oldest) recorded Australian squamate. The authors compared it most favorably with *Coniasaurus*, but the single vertebra is worn and broken such that it is difficult to assign to a family let alone a genus.

‘Aigialosaurs’ (non-mosasaurid mosasauroids)

The family Aigialosauridae (Kramberger, 1892) was erected for *Aigialosaurus dalmaticus.* Similar lizards from surrounding areas were quickly added, thereby expanding the family (e.g., Carroll and Debraga, 1992; Kornhuber, 1893, 1901, Nopcsa, 1908, 1923). These animals are roughly one to two metres in length, are mostly Cenomanian-Turonian in age, and are found primarily in Tethyan deposits. Their close relationship with mosasaurs has long been understood, as stated by Williston (1904, p. 47): ". . . no more striking examples of evolution presented in all vertebrate paleontology than that of the aquatic mosasaurs of the Upper Cretaceous, through the semiaquatic aigialosaurs of the Lower Cretaceous, from the (hypothetical) terrestrial varanoids of the lowermost Cretaceous or Upper Jura".

The Mosasauroidae (Camp, 1923) indeed shows a remarkably complete sequence of morphologies from near shore reef dwellers to open ocean top predators. The most primitive members of this clade—the 'aigialosaurs'—are small, and retain weight bearing, terrestrial legs (plesiopedal) and hips (plesiopelvic). Aquatic adaptations include a long, laterally flattened tail that likely powered anguilliform swimming. These animals are generally considered to be semi-aquatic, being fully able to move on land or in the water. The larger, later members of this group—the 'mosasaurs'—were obligate aquatic animals suited to open water pursuit (Caldwell, 2012). Their non-weight bearing legs and girdles were optimally adapted for swimming (hydropedal and hydropelvic). In these larger, later forms, the tails shortened relative to their body length and developed vertical, heterocercal flukes.

Recent analyses suggest that the Aigialosauridae may be paraphyletic, with derived mosasaur families originating multiple times from within the group (Caldwell et al., 1995; Bell and Polcyn, 2005; Dutchak and Caldwell, 2006; Caldwell and Palci, 2007). Even so, the term 'aigialosaur' has persisted in the literature, though it has come to refer to a morphotype (Dutchak and Caldwell, 2006): a semi-aquatic lizard possessing some mosasaurid features (especially in the head, e.g., a circular quadrate), but retaining terrestrial, weight-bearing limb and body features. In a similar vein, 'mosasaurs', a polyhyletic group, also represent a morphotype: an obligatorily aquatic animal with aigialosaur-like cranial morphology, and aquatically adapted tails, limbs, and hips (Caldwell, 2012). The need to clean up mosasaur-related nomenclature in light of our new understanding of their relationships is evident.

Below are reviewed species (nine genera) generally considered aigialosaurs.

Aigialosaurus

Synonym—*Opetiosaurus* Kornhuber, 1901 (Caldwell et al., 1995) pg 526

Aigialosaurus bucchichi (Kornhuber, 1901)

Holotype:	BSP 1901/002/0001 - 0005
Referred material:	n/a
Age:	Late Cenomanian
Location:	Hvar Island, Croatia
Data:	Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This impressive specimen was found in a limestone quarry between the villages of Starigrad and Vrboska in Hvar Island, Croatia. It was originally described as the monotypic genus *Opetiosaurus* (Kornhuber, 1901). Several authors suggested that it may be a junior synonym of *Aigialosaurus* (Carroll and Debraga, 1992; Caldwell et al., 1995; Caldwell, 2000; Dutchak and Caldwell, 2006), though other studies disagreed (Bell and Polcyn, 2005;

Polcyn et al., 1999). It was eventually officially reassigned to *Aigialosaurus* (Dutchak and Caldwell, 2009) making *Opetiosaurus* a junior synonym. The fossil preserves most of the skeleton on slab and counter slab. Until recently the two halves were housed at two institutions: an unnumbered postcranial slab at NMW, and the cranial slab and vertebral fragments at GBA. In 2011 the NMW slab was given to the GBA on permanent loan, where it was given a specimen number (0005). In life, the animal would have been between 1-1.5 m long.

Figure 1-1 Holotype of *Aigialosaurs bucchichi* (BSP 1901/002/0001 – 0005). Interpretive drawing from Dutchak and Caldwell 2009.

Aigialosaurus dalmaticus (Kramberger, 1892)

Holotype: BSP 1902II501

Referred material:	n/a
Age:	Late Cenomanian-Early Turonian
Location:	Hvar Island, Croatia
Data:	Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: Like *A. bucchichi*, this specimen was discovered in a limestone quarry between Starigrad and Vrboska. It was the first 'aigialosaur' described in the literature. It is articulated and nearly complete, missing the posterior portion of the tail. It was redescribed by Dutchak and Caldwell (2006), and in later directly compared to *A. bucchichi* (Dutchak and Caldwell, 2009).

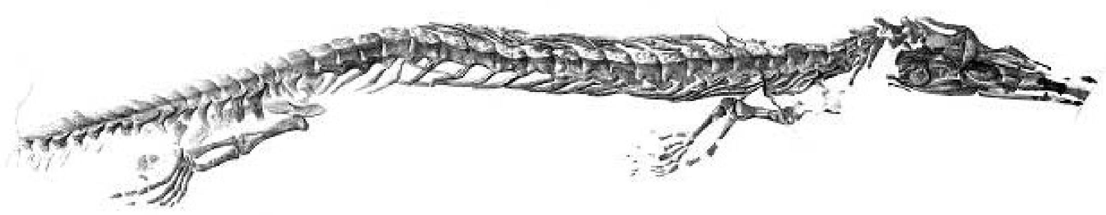

Figure 1-2 Holotype of *Aigialosaurus dalmaticus* (BSP 1902II501). Interpretive drawing from Kramberger 1892.

Aigialosaurus novaki (Kramberger, 1892)

Holotype:	? (missing)
Referred material:	n/a
Age:	Late Cenomanian-Early Turonian

Location: Hvar Island, Croatia

Data: From the literature

Notes: This species was also erected by Kramberger when he described *A. dalmaticus*. It was a segment of 38 articulated caudal vertebrae from the same outcrop as *A. dalmaticus*. It is considered a *nomen dubium* since there are no features differentiating it from any other taxa (Caldwell et al., 1995). The specimen was last seen in Trieste, Italy, but is now considered lost.

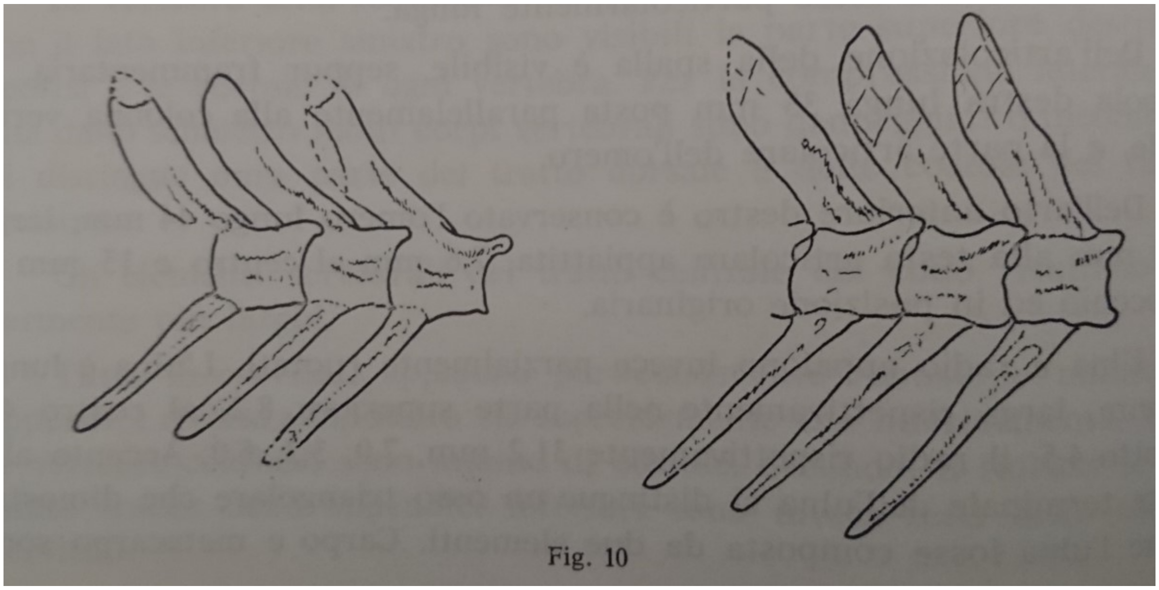

Figure 1-3 Holotype of *Aigialosaurus novaki* (lost specimen). Interpretive drawing from Calligaris 1988.

Carsosaurus

Carsosaurus marchesetti (Kornhuber, 1893)

Holotype: MCSNT 9963

Referred material: n/a

Age: Cenomanian

Location: Komen, Slovenia

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This monotypic specimen is complete except for the skull and neck. In life, it would have been roughly two metres long, making it one of the largest aigialosaurs. It provides proof of viviparity in aigialosaurs, as the specimen represents a gravid female containing at least four embryos, identified by Caldwell and Lee (2001).

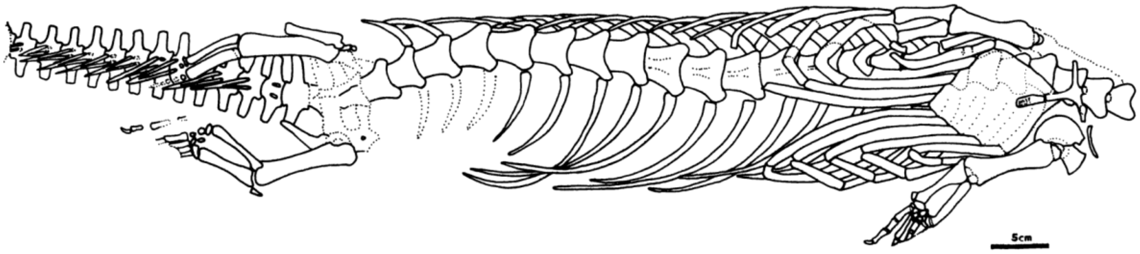

Figure 1-4 Holotype of *Carsosaurus marchesetti* (MCSNT 9963). Interpretive drawing from Caldwell, Carroll and Kaiser, 1995.

Dallasaurus

Dallasaurus turneri (Bell and Polcyn, 2005)

Holotype: TMM 43209-1

Referred material: DMNH 8121-8125, 8127-8141, 8143-8149, 8151-8157, 8161-8180

Age: Middle Turonian

Location: Cedar Hill, Dallas County, Texas, USA

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: The *Dallasaurus* material is fragmentary and mostly disarticulated skull and postcranial elements. Unlike most small Late Cretaceous marine squamates, this animal shows some evidence of hydropelvic anatomy: notably the anteriorly directed superior iliac process (Bell and Polcyn, 2005; Caldwell and Palci, 2007).

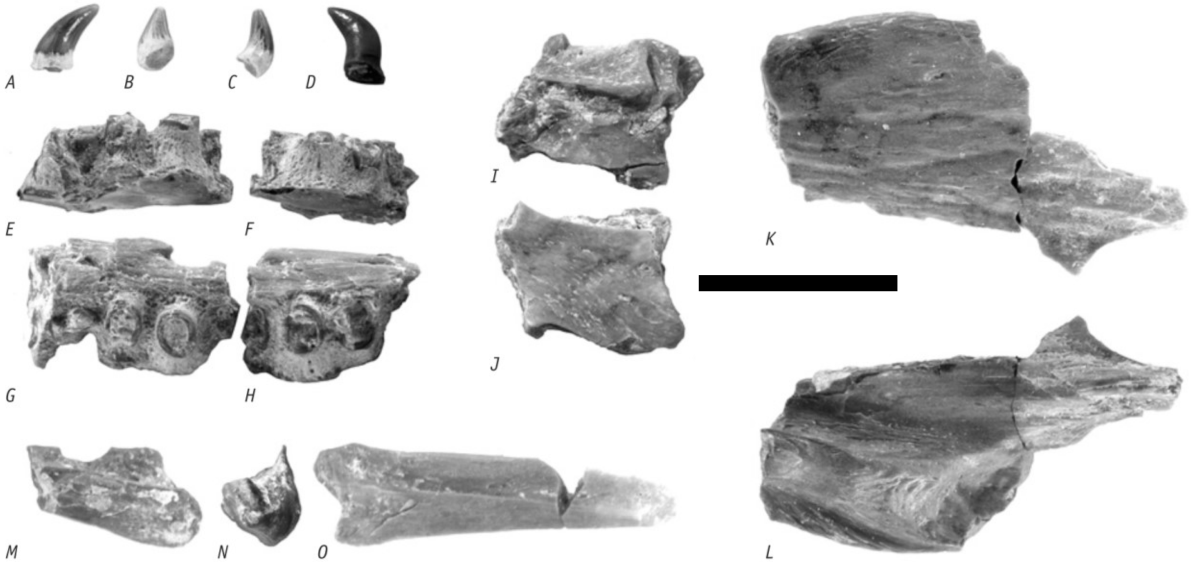

Figure 1-5 Holotype of *Dallasaurus turneri* (TMM 43209-1: cranial elements). Figure adapted from Bell and Polcyn, 2005. A - D – teeth of indeterminate positions illustrating range of tooth morphology; E - H – maxilla fragments in (E, F) medial and (G, H) occlusal view; I, J – parietal fragment in (I) ventral and (J) dorsal view; K, L – medial frontal fragment in (K) dorsal and (L) ventral view; M, N, R – angular in (M) lateral, (N) anterior and (R) medial view; splenial in (O) lateral view; scale bar is 1 cm.

Haasiasaurus

Haasiasaurus gittelmani (Polcyn et al., 1999)

Holotype: HUJ-PAL EJ693

Referred material: HUJ-PAL EJ694, EJ696-698, EJ700, EJ701, EJ703-705

Age: Early Cenomanian

Location: ‘Ein Yabrud, Ramallah, Palestine

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: The partially articulated specimen consists of a mandible, jaw, and body fragments in several blocks. The genus was renamed from *Haasia* in 1999 due to it being a junior homonym (Polcyn et al., 2003).

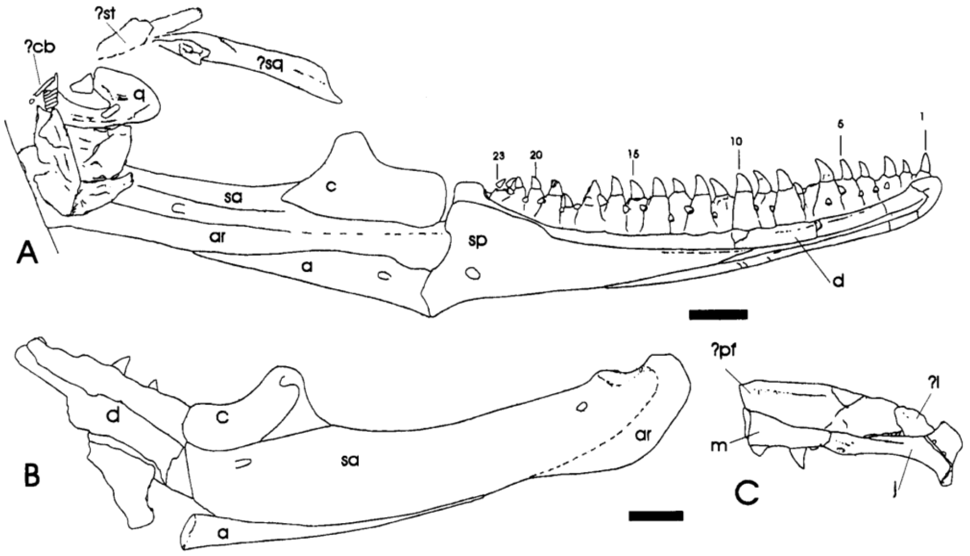

Figure 1-6 Holotype of *Haasiasaurus gittelmani* (HUJ-PAL EJ693: cranial elements). Interpretive drawing from Polcyn, Tchernov and Jacobs, 1999. A, Left mandible and skull elements in medial view; B, left mandible in lateral view; C, lateral view of left maxilla; scale bar is 1 cm.

Judeasaurus

Judeasaurus tchernovi (Haber and Polcyn, 2005)

Holotype:	HUJI P4000
Referred material:	n/a
Age:	Late Cenomanian-Early Turonian
Location:	Unknown locality in the Judean Hills (either Israel or West Bank)
Data:	Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: The incomplete skull that makes up this specimen includes the right maxilla with five anterior teeth, a right jugal, fused frontals and parietals, both postorbitofrontals, supratemporals, squamosals, quadrates and partial mandibles, fragments of cervical vertebrae. It was originally described as a varanoid that was closely related to mosasaurs. In the limited phylogenetic studies it has been included in, it falls near *Dallasaurus*. Bardet and colleagues (2008) describe it as a 'dolichosaur' rather then a mosasauroid.

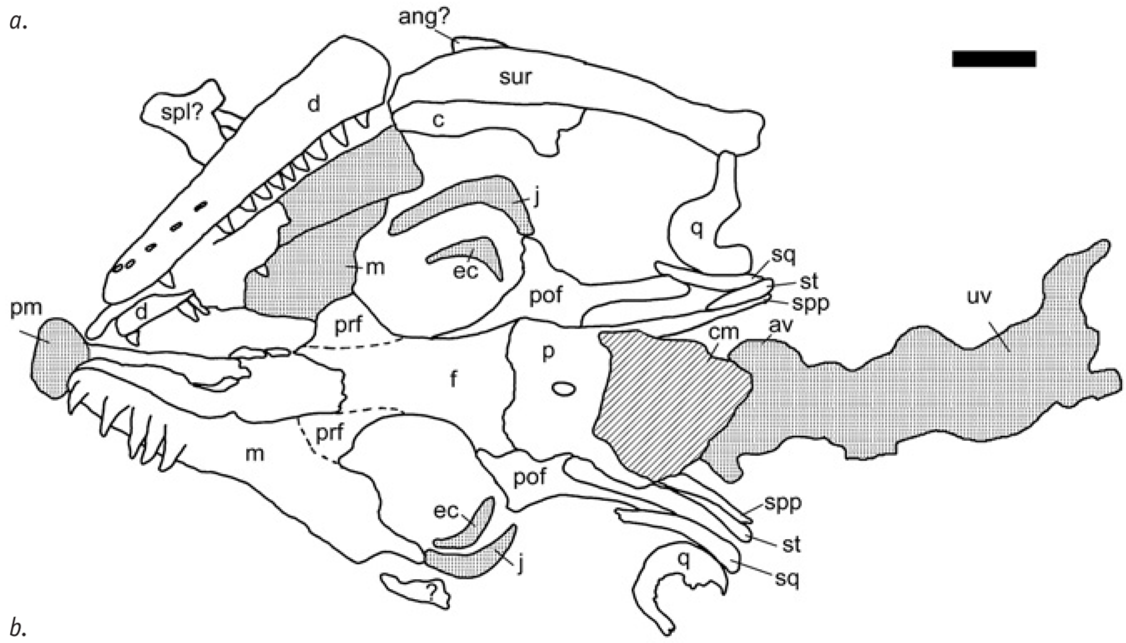

Figure 1-7 Holotype of *Judeasaurus tchernovi* (HUJI P4000: skull and neck). Interpretive drawing from Haber and Polcyn, 2005. Scale bar is 1 cm.

Komensaurus

Komensaurus carrolli (Caldwell and Palci, 2007)

Holotype:	MCSNT 11430 (originally MSCNT 9961), 11431, 11432
Referred material:	n/a
Age:	Late Cenomanian
Location:	Tomačevica, Slovenia
Data:	Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This specimen is broken into three slabs. The largest contains a large portion of the articulated postcranial material, the other two contain disarticulated material: one with cervical and skull fragments, the other with jaw and caudal fragments. This species was originally assigned to *Opetiosaurus* (Calligaris, 1988). It is referred to in the literature as the 'Trieste aigialosaur' in several publications (Carroll and Debraga, 1992; Debraga and Carroll, 1993). It was redescribed by Caldwell and Palci (2007) who erected a new genus for it.

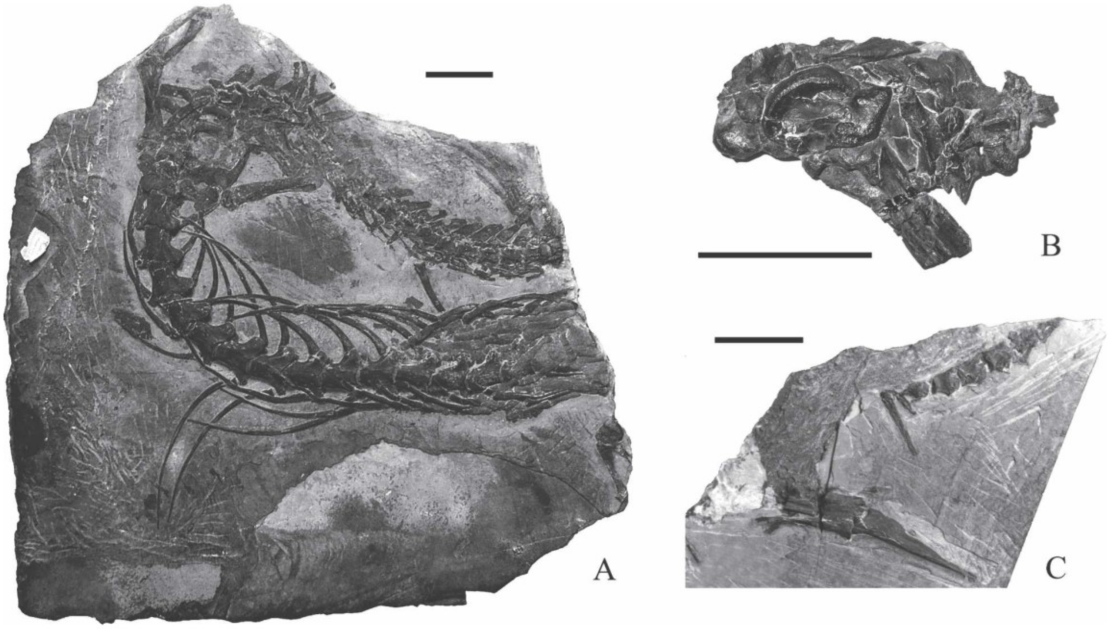

Figure 1-8 Holotype of *Komensaurus carrolli* (MCSNT 11430, 11431, 11432). Photographs from Caldwell and Palci 2007. A, postcranial skeleton; B, cervical vertebrae and skull elements; C, caudal vertebrae and cranial elements; scale bar is 5 cm.

Proaigialosaurus

Proaigialosaurus hueni (Kuhn, 1958)

Holotype: ? (missing)

Referred material: n/a

Age: Late Jurassic

Location: Solnhofen, Bavaria, Germany

Data: From the literature

Notes: This specimen - an impression of the dorsal surface of the skull - is now considered lost. Its last known location was a private unnamed collection. The assignment of this species is contentions. It was originally and briefly described as an aigialosaurid and was accompanied by a sketch. Hoffstetter (1964) thought that it might be a juvenile marine sphenodontian – he suggested *Pleurosaurus* – however, he never saw the specimen in person. Carroll (1988) stated that *Proaigialosaurus* likely belongs to the Aigialosauridae, but later considered it a *nomen dubium*, as the description was insufficient to establish the identity of the genus, and the only known specimen could not be located (Carroll and Debraga, 1992). Its loss is unfortunate, because if an aigialosaur, it would be the oldest record of a mosasauroid worldwide.

Figure 1-9 Holotype of *Proaigialosaurus hueni* (unnumbered). Interpretive drawing based on Kuhn, 1958.

Vallecillosaurus

Vallecillosaurus donrobertoi (Smith and Buchy, 2008)

Holotype: UANL-FCT-R27

Referred material: n/a

Age: Early Turonian

Location: Solnhofen, Bavaria, Germany

Data: From the literature

Notes: Like *Komensaurus*, this specimen is preserved in three slabs: a part and two pieces of counterpart. Together, they preserve the posterior half of the body—including the tail—in articulation. Before it was formally described, it was referred to as the 'Mexico aigialosaur' (Buchy et al., 2005).

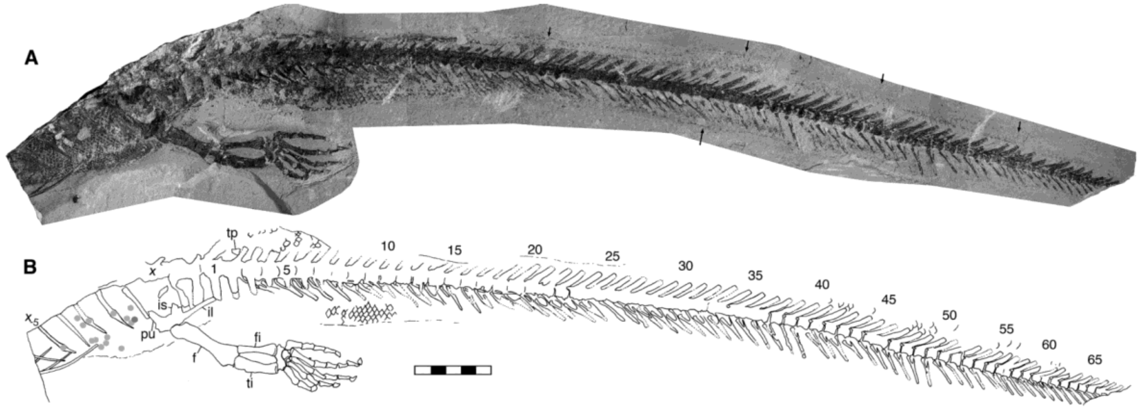

Figure 1-10 Holotype of *Vallecillosaurus donrobertoi* (UANL-FCT-R27). A, photographs, and B, interpretive drawing from Smith and Buchy, 2008. Scale bar is 5 cm.

Unnamed ?mosasauroid

Gen. et sp. nov (Paparella et al., 2015)

Holotype:	MPUR NS 161
Referred material:	n/a
Age:	Upper Campanian-lower Maastrichtian
Location:	Nardò, Lecce, Puglia, Italy
Data:	Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: The specimen, yet to be formally described, is beautifully preserved. It is preserved on a limestone slab articulated and almost complete from the head to the anterior portion of the tail. Notably, it shows exceptional preservation of some soft tissues including muscles and scales. This specimen is particularly interesting because even though it is the youngest mosasauroid yet found, it still retains aquatically adapted morphologies that are considered basal. This indicates that this ecology and body plan were successful throughout the Late Cretaceous, contemporaneous with the larger, fully aquatic mosasaurs.

Figure 1-11 Undescribed, soon-to-be holotype (MPUR NS 161). Photograph by M. Campbell Mekarski.

‘Dolichosaurs’ (non-ophidian ophidiomorphs)

The relationships of ‘dolichosaurids’ with mosasaurs and more broadly, the rest of the squamates, is more uncertain than the aigialosaurs. The Dolichosauridae (within the Dolichosauria) was established to hold *Dolichosaurus* only (Kramberger, 1892) and was considered closely related to the Aigialosauridae. Nopcsa (1903, 1908) enlarged the group, including *Acteosaurus, Adriosaurus* and *Pontosaurus.* He thought that dolichosaurs were more closely related to snakes than mosasaurs and aigialosaurs.

Recent phylogenetic analyses (Caldwell, 2000; Lee and Caldwell, 2000; Palci and Caldwell, 2007, 2010) seem to support Nopcsa’s hypothesis, with ‘dolichosaurs’ forming successive sister groups to ophidians, and aigialosaurs forming the sister group to mosasaurs. According to this interpretation, dolichosaurs are a paraphyletic assemblage: an evolutionary ‘grade’ along the road to snakes. Together with snakes, they form the Ophidiomorpha (Palci and

Caldwell, 2010). Therefore, the correct name for these animals would be non-ophidian ophidiomorphs. I will continue to use the term dolichosaur throughout in reference to this assemblage due to its convenience and historical use.

Dolichosaurs are known mainly from the Cenomanian of Europe and North America. They are fairly small—less than a metre in length—with a long neck, a long tail, and reduced limbs. They are diagnosable by their elongate necks (>10 cervical vertebrae), elongate trunks (>35 presacral vertebrae), zygosphene-zygantra articulations throughout the entire presacral region, and a reduction in forelimb elements. Currently, there are ten described genera.

Acteosaurus

Acteosaurus tommasinii (von Meyer, 1860)

Holotype:	MCSNT 9960
Referred material:	n/a
Age:	Late Cenomanian
Location:	Komen, Slovenia
Data:	Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This articulated specimen is relatively complete from anterior cervical to the ~19th caudal vertebrae. The specimen is very small, and shows notable reduction of the forelimbs. It was initially described by von Meyer (1860) who thought it was closely related to

Dolichosaurus longicollis, but autapomorphic enough to erect a new genus. It was redescribed by Palci and Caldwell (2010).

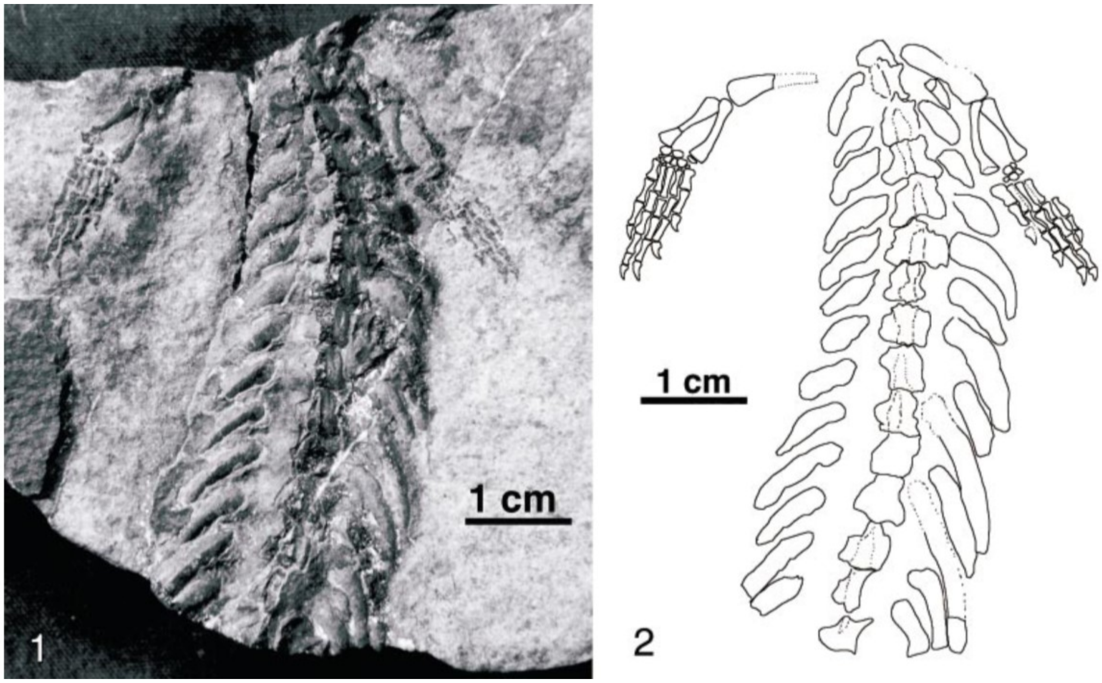

Figure 1-12 Holotype of *Acteosaurus tommasinii* (MCSNT 9960). A, photographs, and B, interpretive drawing from Caldwell and Lee, 2004.

Acteosaurus crassicostatus- Described by Caligaris 1993, reevaluated by Caldwell and Lee (2004) who referred it to *Adriosaurus suessi* (see below).

Adriosaurus

Adriosaurus microbrachis (Palci and Caldwell, 2007)

Holotype:	MCSNT 7792
Referred material:	n/a

Age: Late Cenomanian

Location: Komen, Slovenia

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This specimen is articulated and complete from the posterior cervical to the anterior caudal vertebrae. The specimen is very small, and the majority of the bones have been naturally sheared off, such that most vertebrae are visible as sections through the dorsal plane. This specimen is especially interesting, as it shows extreme reduction of the forelimbs resulting in a complete loss of elements distal to the humerus.

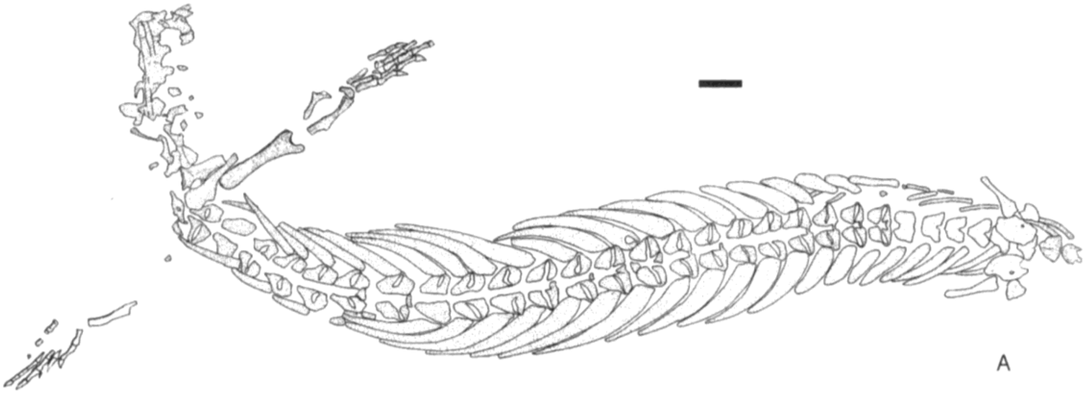

Figure 1-13 Holotype of *Adriosaurus microbrachis* (MCSNT 7792). Interpretive drawing from Palci and Caldwell, 2007. Scale bar is 5 mm.

Adriosaurus skrbinensis (Caldwell and Palci, 2010)

Holotype: SMNH 2158

Referred material: n/a

Age: Late Cenomanian

Location: The village of Skrbina, northwest of Komen, Slovenia

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This fossil is an articulated specimen from posterior half of the skull to the anterior part of the tail. Most of the skull, the preserved limb elements, and some of the caudal and cervical series are preserved as natural moulds. Phosphatic matter in the abdominal region is interpreted as gastric content. The specimen was recovered during the renovation of an old stone house.

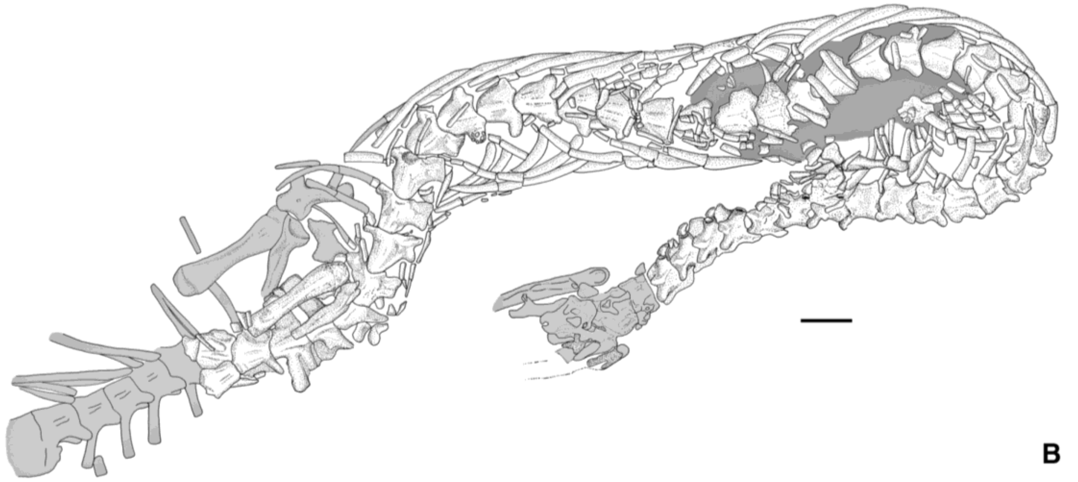

Figure 1-14 Holotype of *Adriosaurus skrbinensis* (SMNH 2158). Interpretive drawing from Caldwell and Palci, 2010. Scale bar is 1 cm.

Adriosaurus suessi (Seeley, 1881)

Holotype: The 'Vienna specimen' NMW unnumbered specimen (missing)

Neotype: BMNH R2867

Referred material: MCSNT 9400

Age: Late Cenomanian

Location: Komen, Slovenia (Vienna specimen and MCSNT 9400); Hvar Island, Croatia (NHM R2867)

Data: Information on holotype from the literature, NHM R2867 was visited, photographed and sketched by M. Campbell Mekarski

Notes: The Vienna holotype was an articulated postcranial skeleton which was stored in the Geological Museum at the University of Vienna. Recent searches for the specimen have not been able to retrieve it, and it is therefore considered lost. A neotype was designated in 2000 by Lee and Caldwell (NHM R2867). The new specimen is a nearly complete and articulated. It was originally identified as *Aigialosaurus* by Nopcsa (1908, 1923), but this was not a robust identification as he grouped all dolichosaur-like forms together without any analysis of characters. The specimen MCSNT 9400 is an articulated section of dorsal vertebrae with shoulder girdle and forelimbs preserved as part and counterpart. It was originally described as a new species by Calligaris, (1993), who named is *Acteosaurus crassicostatus*. The specimen was reevaluated by Caldwell and Lee (2004) who excluded it from *Acteosaurus*, and referred it to *Adriosaurus suessi*, making *Aceteosaurus crassicostatus* a junior synonym of *Adriosaurus suessi.*

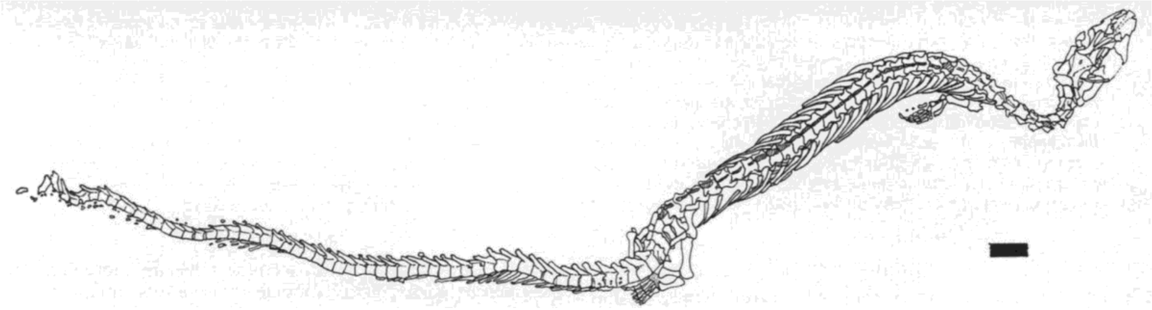

Figure 1-15 Neotype of *Adriosaurus suessi* (BMNH R2867). Interpretive drawing from Lee and Caldwell, 2000. Scale bar is 1 cm.

Adriosaurus sp.

Several specimens have been ascribed to *Adriosaurus*, but not identified or differentiated at a species level.

Specimen:	MCSNT 7749, 7793, 7794, 9400, 11426
Age:	Late Cenomanian
Location:	Komen, Slovenia
Data:	Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: A series of specimens described by Palci (2007) in his PhD thesis have been assigned to the genus *Adriosaurus*. They vary in completeness from a single element to a nearly complete individual. Most are articulated, and several are nearly complete. Unfortunately for some, the preservation is fairly poor, and those that are better preserved are missing key diagnostic features like the skull and limb elements. Some specimens are compared to other *Adriosaurus* fossils in Palci and Caldwell (2007).

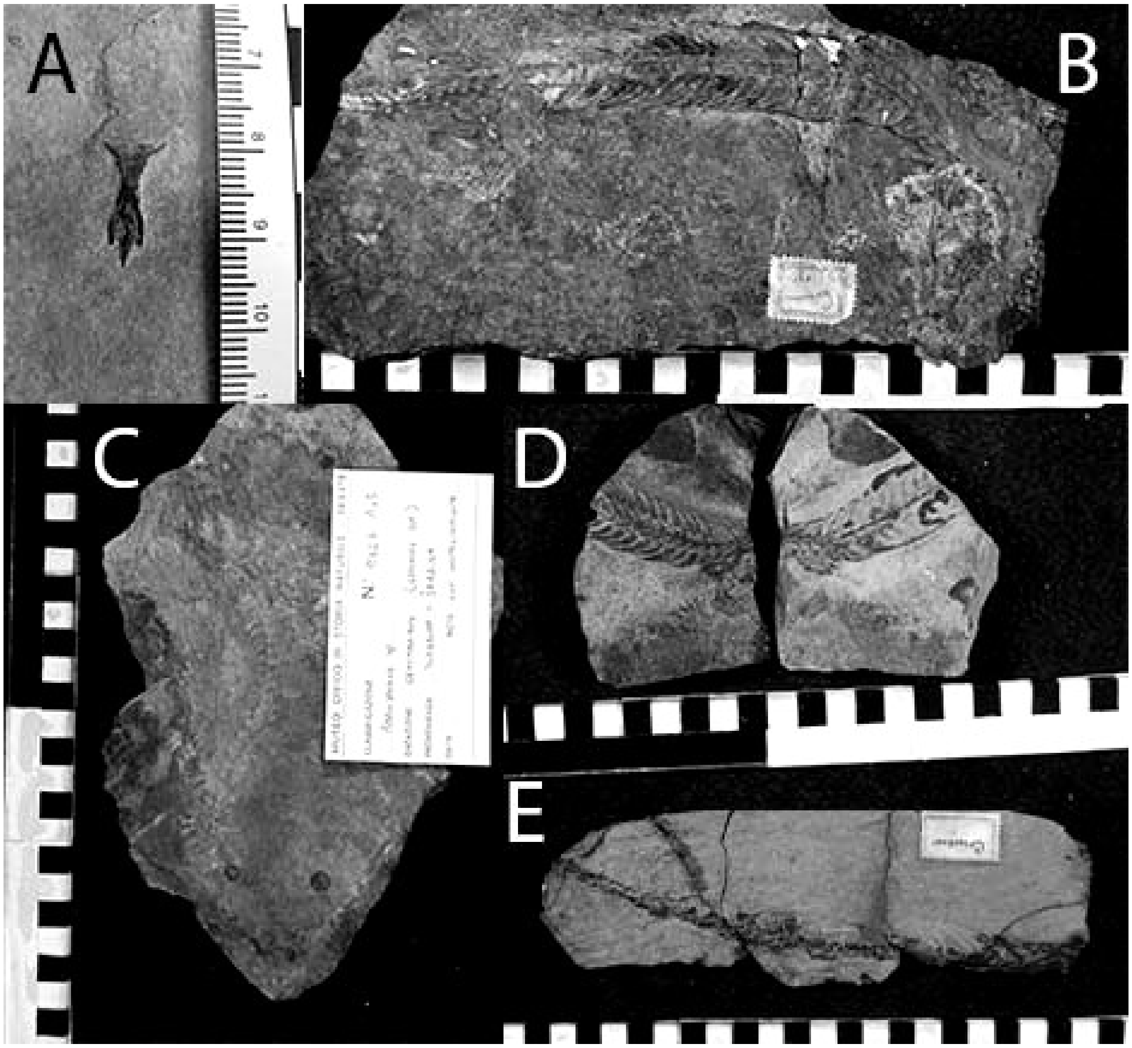

Figure 1-16 Photographs of several *Adriosaurus* fossils. A, MCSNT 7749; B, MCSNT 7793; C, MCSNT; 11426l; D, MCSNT 9400; E, MCSNT 7794.

Aphanizocnemus

Aphanizocnemus libanensis (Dal Sasso and Pinna, 1997)

Holotype: MSNM V783

Referred material: n/a

Age: Middle Cenomanian

Location: En Nammoura, Lebanon

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This tiny specimen is fully complete and articulated from premaxilla to the tip of the tail. The specimen barely measures 30 cm. The skeleton is in generally excellent condition, apart from the skull, which was significantly damaged during preparation. There is speculation that it may represent a juvenile since it shows body ratios and ossification patterns often found in juvenile individuals (Dal Sasso and Pinna, 1997). While certainly aquatic, it is very unique in many of its features, and may not represent an anguimorph at all.

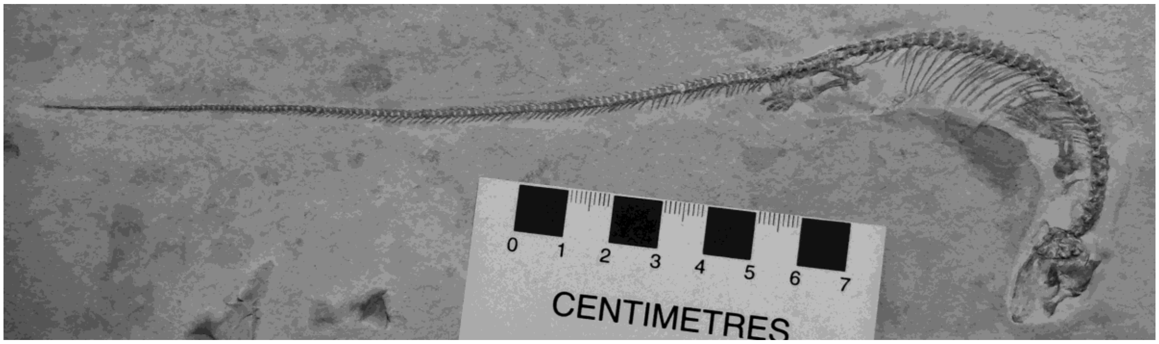

Figure 1-17 Holotype of *Aphanizocnemus libanensis* (MSNM V783). Photograph by M. Campbell Mekarski.

Carentonosaurus

Carentonosaurus mineaui (Rage and Néraudeau, 2004)

Holotype: MNHN IMD 21

Referred material: MNHN IMD 1-59

Age: Late Cenomanian

Location: Charente-Maritime, western France (IMD 21); northern Spain (IMD 1-59)

Data: From the literature

Notes: This specimen is represented by isolated vertebrae, a fragment of the pectoral girdle, and a rib. Further material from Asturias (Northern Spain) was referred to *Carentonosaurus* sp. by Vullo, Bernárdez, and Buscalioni in 2009, and includes more vertebrae, a rib, and a partial jaw. The geology indicates that these animals lived in shallow and fairly warm water on the inner shelf (Rage and Néraudeau, 2004) and/or in coastal lagoons with tidally influenced channels (Vullo et al., 2009).

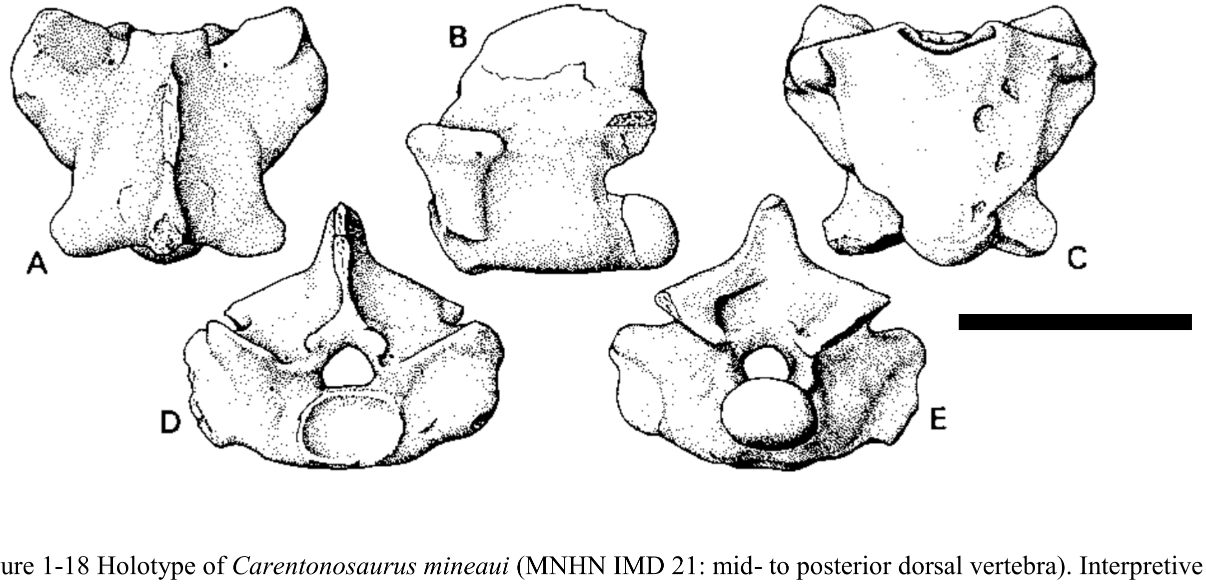

Figure 1-18 Holotype of *Carentonosaurus mineaui* (MNHN IMD 21: mid- to posterior dorsal vertebra). Interpretive drawing from Rage and Néraudeau, 2004; scale bar is 1 cm.

Coniasaurus

Coniasaurus crassidens (Owen, 1850)

Holotype: BMB 007155

Referred material: BMB 007157, 012485.; FSHM VP-13999-14002, 14778; NHM R 1937; SDSM 25896, 34993-35000; SMUSMP 69018-29; TMM 40239-1, 41885-1; WMNM P19913

Age: Cenomanian (and Coniacian?)

Location: Sussex, England; Westfalia, Germany; Texas, South Dakota, Kansas, USA

Data: Data from BMB, NHM, SMUSMP: specimen visit, photos and drawings by M. Campbell Mekarski. Data from FSHM, SDSM, TMM, WMNM: from the literature.

Notes: Numerous fossils have been identified as *C. crassidens* from Southern England (Caldwell and Cooper, 1999), Western Germany (Diedrich, 1997) and the central United States including Texas (Bell et al., 1982; Cicimurri and Bell, 1996; Jacobs et al., 2005a), Kansas (Liggett et al., 2005; Shimada and Ystesund, 2007), Colorado (Shimada et al., 2006), and South Dakota (Bell and Polcyn, 1996; Von Loh and Bell, 1998). The holotype consists of vertebrae and the right ramus of the lower jaw, including several of the characteristically thick teeth. The syntype (BMB 007157) which was also described by Owen (1850), is an articulated length of 12 dorsal vertebrae. These specimens have been discussed and figured several times in the literature (Owen, 1850, 1878; Morris, 1854; Willett, 1871; Woodward and Sherborn, 1890; Crane, 1892), making it the best studied of the pythonomorphs from this time. The other specimens assigned to this species are usually classified based on the characteristic tooth morphology, but several blocks consist of other bones: primarily vertebrae and skull elements. Some of the Texas material (SMUSMP specimens) may be from slightly younger strata from the late Cenomanian – late Turonian. Two specimens from Kansas, tentatively assigned to the species, date from the Coniacian, (Shimada et al., 2007), and Santonian (Shimada and Bell, 2006) and represent the youngest occurrence of this species. An additional report from Saskatchewan, Canada that was tentatively assigned to *Coniasaurus crassidens* would represent the more northern occurrence of the genus in North America (Cumbaa et al., 2006).

Figure 1-19 Holotype of *Coniasaurus crassidens* (BMB 007155). Photograph by M. Campbell Mekarski.

Coniasaurus gracilodens (Caldwell, 1999a)

Holotype: BMNH R44141

Referred material: n/a

Age: early Cenomanian

Location: Sussex, England

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This specimen consists of a block and several isolated elements. The block contains a few articulated vertebrae, rib fragments and a scapulocoracoid. The isolated elements include the frontal, a lacrimal, and a jaw fragment containing teeth. The material was initially figured and identified as *Dolichosaurus longicollis* by Milner (1987 in Owen [1987]), but was not formally described until Caldwell (1999a) who erected a new species for the material.

Figure 1-20 Holotype of *Coniasaurus gracilodens* (BMNH R44141). Photograph by M. Campbell Mekarski.

Coniasaurus sp.

Several specimens have been assigned to *Coniasaurus*, but not identified or differentiated at a species level. The material spans the middle Cenomanian to middle Santonian and originates from the Tethys and Western Interior Seaway. These include an isolated vertebra from the mid-late Cenomanian of Asturias, Spain (Vullo et al., 2009), and a number of reports from the Southern United States (Bell et al., 1982; Bell and Polcyn, 1996; Liggett et al., 2005; Shimada and Bell, 2006; Shimada et al., 2006, 2007; Shimada and Ystesund, 2007). The most interesting of these is material reported from the Late Cenomanian of Texas representing an associated adult and juvenile (M. Polcyn, pers. comm.).

Dolichosaurus

Dolichosaurus longicollis (Owen, 1850)

Holotype:	BMNH R 49002
Referred material:	BMB 008567; BMNH R 32268, R 49907, R 49908
Age:	Cenomanian
Location:	Kent and Sussex, England; Westphalia, Germany
Data:	Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: The holotype specimen preserves the head, forelimbs and dorsal portion of the spine. The other four slabs contain articulated and unarticulated remains of fore- and hindlimbs, and vertebrae from cervical to caudal regions. The only cranial material is in the holotype and it is poorly preserved. These specimens are redescribed together by Caldwell (2000). BMNH R 32268 was found in the same quarry are the holotype. It was originally named *Raphiosaurus sublidens* (Owen, 1842) but was later referred to as *D. longicollis* by (Owen, 1850, 1851, 1878). In Caldwell's redescription (Caldwell, 2000), he notes that the diagnostic characters of *Dolichosaurus* are not comparable to the known osteology of *Coniasaurus*, and therefore could be found to be congeneric based on information from future discoveries. Fragmentary remains attributed to *D. longicollis* have also been reported from Westphalia, Germany (Diedrich, 1997, 1999).

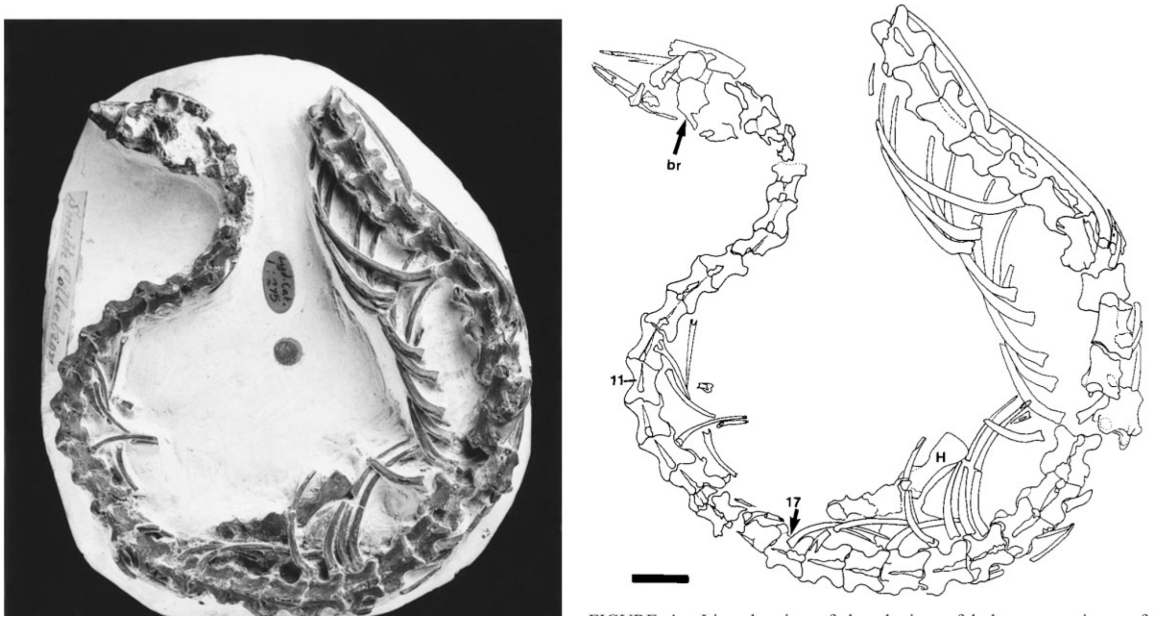

Figure 1-21 Holotype of *Dolichosaurus longicollis* (BMNH R 49002). A, photograph, and B, interpretive drawing from Caldwell, 2000.

Eidolosaurus

Eidolosaurus trauthi (Nopcsa, 1923)

Holotype: GBW 1923/1

Referred material: n/a

Age: middle-late Cenomanian

Location: Komen, Slovenia

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This specimen preserves most of the body (posterior cranial to posterior caudal) as a natural mould. Palci (2007) addressed this specimen in his thesis.

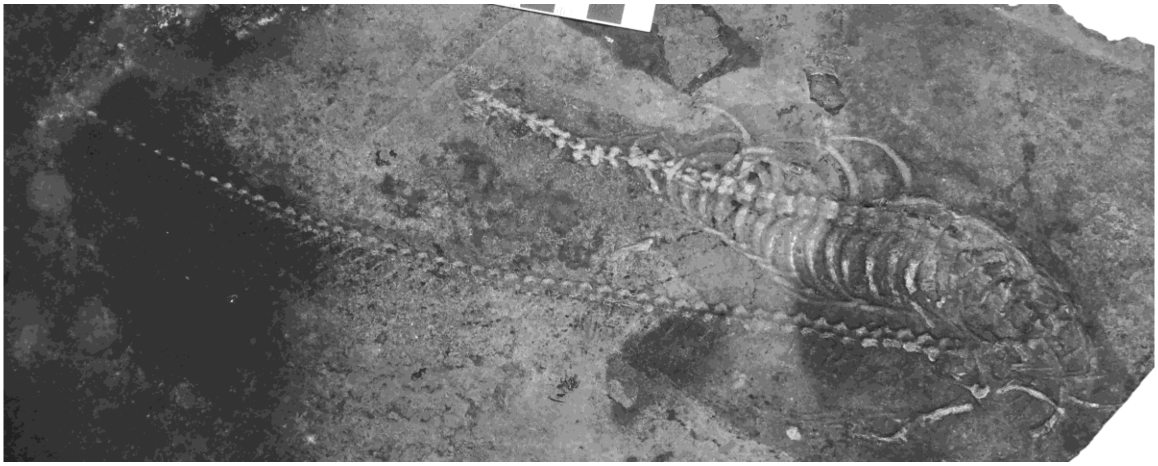

Figure 1-22 Holotype of *Eidolosaurus trauthi* (GBW 1923/1). Photograph by M. Campbell Mekarski

Kaganaias

Kaganaias hakusanensis (Evans et al., 2006)

Holotype: SBEI 1568

Referred material: SBEI 196, 197, 199, 258, 260, 261, 567, 834, 836-838, 845, 1266, 1532, 1793-1796, 1799, 1800, 2007, 2012.

Age: Valanginian-Hauterivian

Location: north-central Honshu, Japan

Data: From the literature

Notes: The holotype of this specimen exists as part and counterpart of a relatively complete, articulated postcranial skeleton including partial hindlimbs. Other material is primarily isolated skull and vertebral elements. The paleoenvironment is fairly unique among the non-ophidian ophidiomorphs; instead of a shallow marine environment, the sediment indicates a freshwater swamp on a floodplain (Isaji et al., 2005) fairly far from the ocean. The stratigraphical position of this animal is also much older than other ophidiomorphs, and is Pacific, not Tethyan. This makes this specimen very informative and significant in this group.

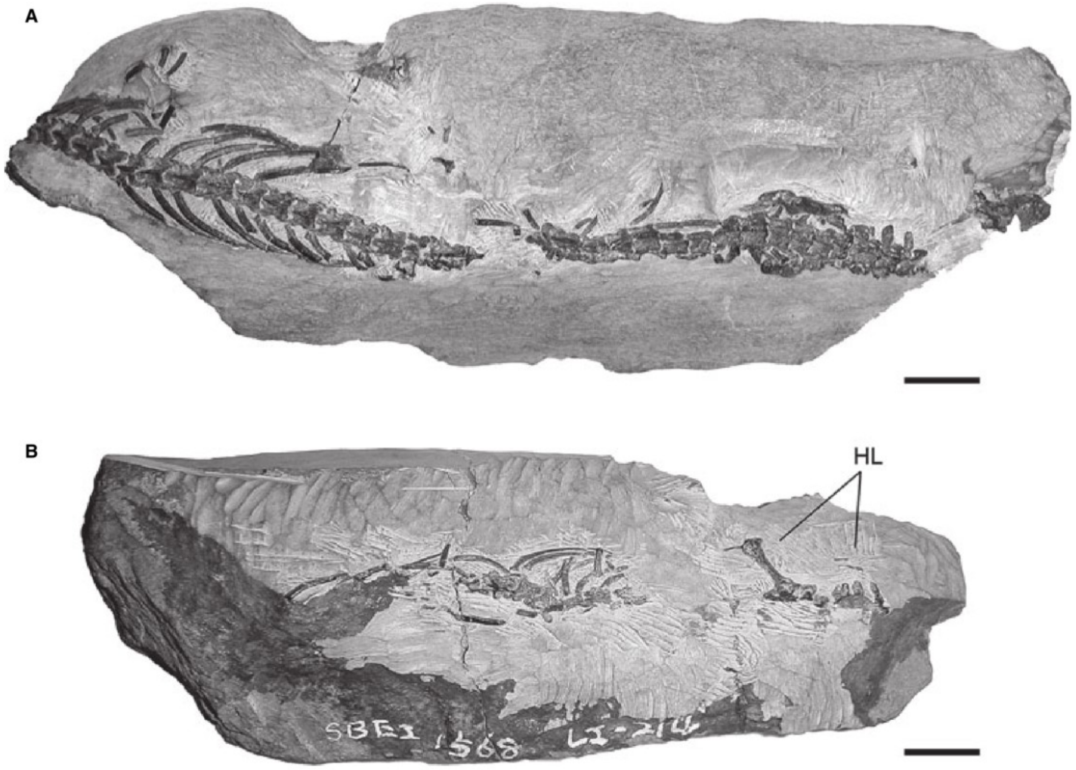

Figure 1-23 Holotype of *Kaganaias hakusanensis* (SBEI 1568). A, slab and B, counterslab with hindlimb, from Evans et al, 2006; scale is 1 cm.

Mesoleptos

Mesoleptos zendrinii (Cornalia, 1852)

Holotype: Unnumbered and lost specimen from Slovenia

Referred material: Unnumbered and lost specimen from Croatia

Age: early Late Cretaceous

Location: Komen, Slovenia (type); Hvar Island, Croatia (lost specimen)

Data: From the literature

Notes: The type specimen was an articulated and nearly complete individual preserving hind limbs and a series of vertebrae from the dorsal to anterior caudal sections. This specimen is now considered lost (Lee and Scanlon, 2002). Another referred specimen from Hvar Island (Kramberger, 1892) – which is also considered lost – was removed from the genus by Lee and Scanlon (2002).

Mesoleptos sp.

Several specimens have been referred to *Mesoleptos* (Calligaris, 1988). Coincidently, all are articulated fossils preserving part of the body without any cranial material.

Specimen: MCSNT 9962

Age: Cenomanian

Location: Komen, Slovenia

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: MCSNT 9962 is once again an articulated partial body, fairly complete from the mid-dorsal to the pelvis but preserves no limbs. It was most recently described by (Palci, 2007) in his thesis.

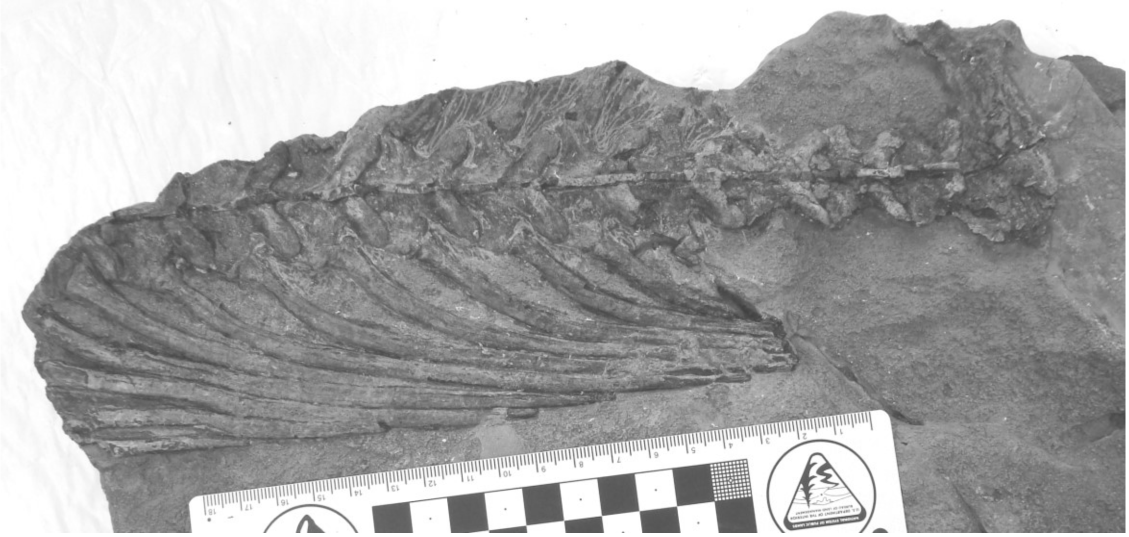

Figure 1-24 *Mesoleptos* sp. (MCSNT 9962). Photograph by M. Campbell Mekarski.

Specimen:	HUJ-PAL EJ699
Age:	early Cenomanian
Location:	‘Ein Yabrud, Palestine
Data:	From the literature

Notes: HUJ-PAL EJ699 (Lee and Scanlon, 2002) is another partial articulated body fossil. It consists of caudal and dorsal vertebrae, a shoulder girdle and partial forelimbs.

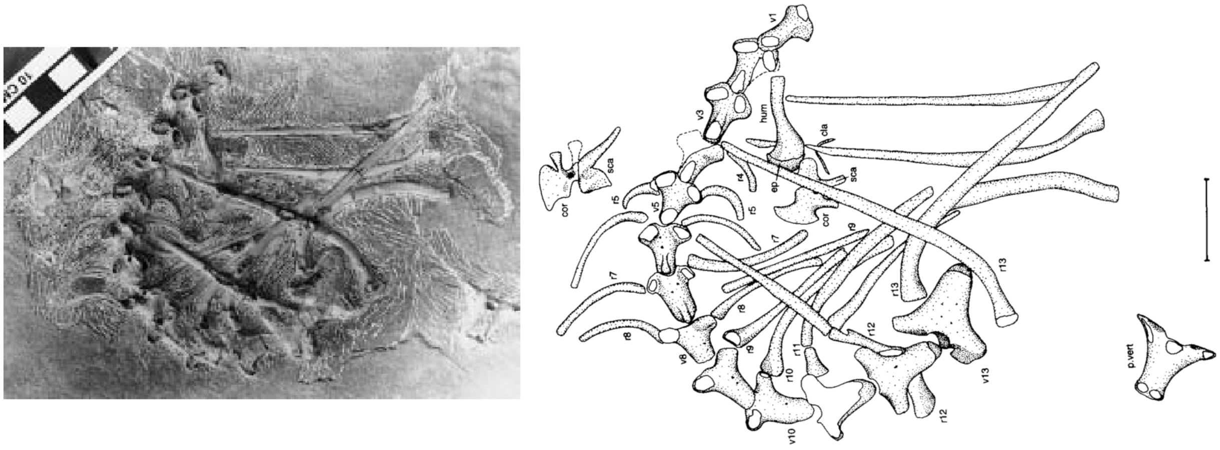

Figure 1-25 *Mesoleptos* sp (HUJ-PAL 699). Photograph interpretive drawing from Lee and Scanlon, 2002; scale is 2 cm.

Pontosaurus

Pontosaurus kornhuberi (Caldwell, 2006)

Holotype: MSNM V3662

Referred material: n/a

Age: Cenomanian

Location: Valley of Al Gabour, near En Nammoura, Lebanon

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This beautifully preserved animal is complete and articulated from the head to the tip of the long tail. It even preserves some soft tissues including scales, tracheal rings and cartilage. It is the most complete pythonomorph lizard described to date.

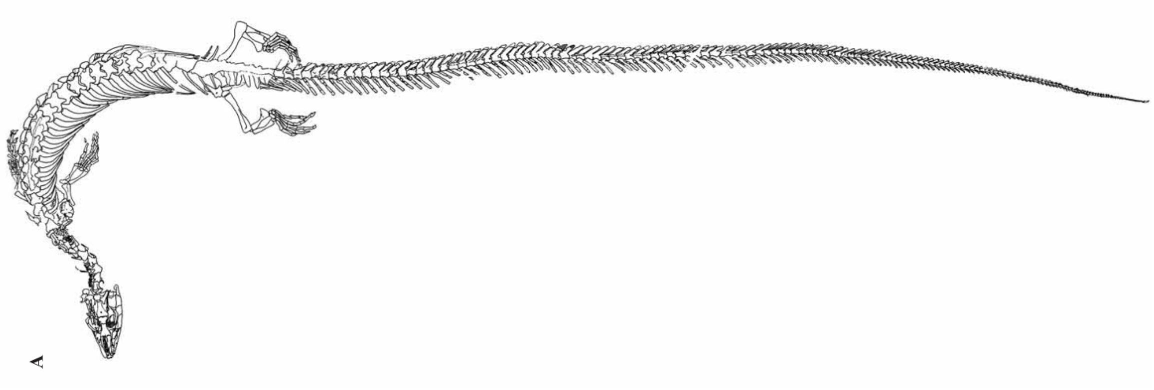

Figure 1-26 Holotype of *Pontosaurus kornhuberi* (MSNM V3662). Interpretive drawing from Caldwell, 2006.

Pontosaurus lesinensis (Kornhuber, 1873; Kramberger, 1892)

Holotype:	GBW 1873/4/1
Referred material:	n/a
Age:	late Cenomanian- early Turonian
Location:	Hvar Island, Croatia
Data:	Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This monotypic specimen is an articulated individual that is complete from the head to the posterior dorsal section. It is fairly rare among Late Cretaceous marine squamates in that the head is fairly well preserved. It was originally described by Kornhuber (1873) who named it *Hydrosaurus* (= *Varanus*). It was later renamed *Pontosaurus* by Kramberger (1892). The specimen was more recently redescribed by Pierce and Caldwell (2004). A second slab (GBW 1873/4/2) was also included in Kornhuber's original description. It is a slightly larger specimen missing the cranial, cervical and posterior caudal material. It was removed from the genus and referred to Dolichosauridae *incertae sedis* by Pierce and Caldwell (2004).

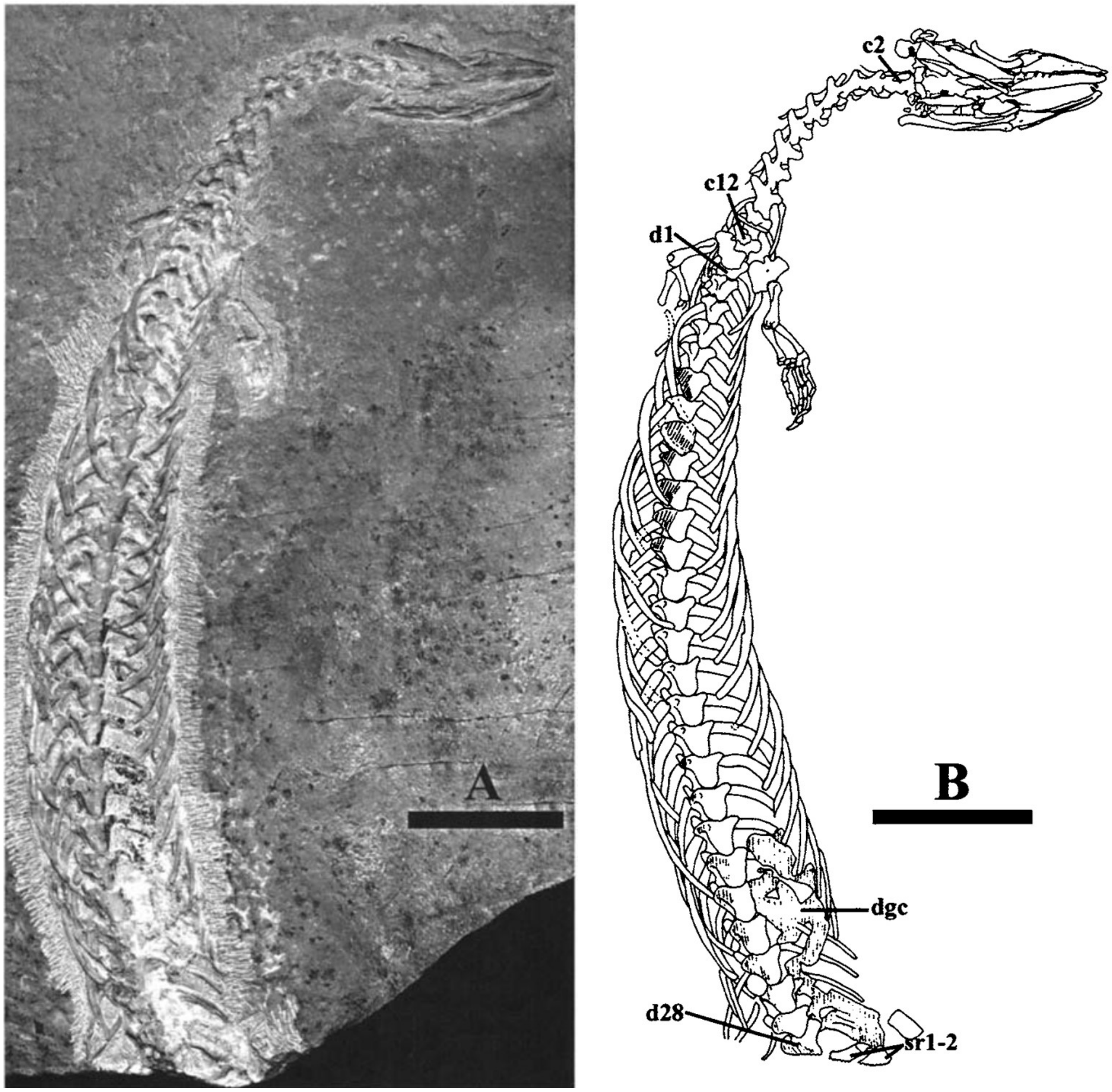

Figure 1-27 Holotype of *Pontosaurus lesinensis* (GBW 1873/4/1). A, photograph and B, interpretive drawing from Pierce and Caldwell, 2004; scale is 5 cm.

Ophidiomorpha incertae sedis

Dolichosaur *incertae sedis* (Kornhuber, 1873; Pierce and Caldwell, 2004)

Specimen: GBW 1873/4/2

Referred material: n/a

Age: Late Cenomanian - Early Turonian

Location: Hvar Island, Croatia

Data: Specimen visit, photos and drawings by M. Campbell Mekarski

Notes: This nicely preserved specimen was originally described by Kornhuber (1873) as *Hydrosaurus lesinensis* along with another specimen. These two specimens were later renamed *Pontosaurus* by Kramberger (1892). In 2004, when Pierce and Caldwell redescribed this material, they removed this specimen from the genus *Pontosaurus* and referred it to Dolichosauridae. They recommend further preparation and a detailed redescription before it can be assigned to a taxon.

Figure 1-28 Dolichosaur *incertae sedis* (GBW 1873/4/2). Photograph by M. Campbell Mekarski.

CONCLUSIONS

To date there has been over 150 years of investigation on Cretaceous marine lizards. These animals are considered closely related and fall into two groups: 1) the aigialosaurs, who are generally accepted to be close relatives of mosasaurs, and 2) the dolichosaurs. The diversity of pythonomorph lizards provides an opportunity to study the transition of terrestrial squamates to marine environments. Such studies however, necessitate well-resolved phylogenies. Unfortunately, there is a high degree of uncertainty surrounding several critical relationships: the position of this group within the Squamata, the relationship of dolichosaurs with snakes, the mono- or paraphyly of the Aigialosauridae, and the subsequent implications for the polyphyly of the Mosasauridae.

In light of the complexity of taxonomic groupings associated with the Pythonomorpha (see Caldwell, 2012), I will for the purposes of this study continue to use the informal terms ‘aigialosaur’ and ‘dolichosaur’ to describe these assemblages even though they may not be monophyletic. The term ‘pythonomorph lizards' will be used when discussing both dolichosaurs and aigialosaurs, without reference to the other clades within the Pythonomorpha (snakes and ‘mosasaurs’).

The questions outlined above emphasize the need for additional data to help resolve some of these problematic relationships. The next two chapters will contribute to this body of information by describing two new species: a new dolichosaur and a new genus of basal mosasauroid (aigialosaur).

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CHAPTER 2 : A NEW CENOMANIAN-TURONIAN *PONTOSAURUS* FROM THE DALMATIAN COAST, CROATIA, AND THE FIRST DESCRIBED ‘DOLICHOSAUR’ STOMACH CONTENTS

ABSTRACT

The Upper Cretaceous limestones from the Dalmatian Coast of Croatia and the Komen Plateau of Eastern Italy and Slovenia have produced a large number of well preserved fossil aquatic marine ophidiomorphs with distinctively long, cylindrical bodies and small reduced limbs. These include *Acetosaurus tommasinii*, *Adriosaurus suessi*, *Adriosaurus skrbinensis*, *Adriosaurus microbrachis*, *Mesoleptos zendrinii*, and *Pontosaurus lesinensis*. In the late 18th century, a fossil lizard was found in Upper Cenomanian platy limestones on Hvar Island, Croatia. It was in the possession of a local collector until 1982 when it was donated to the Croatian Natural History Museum in Zagreb, Croatia. The 36 cm long fossil is well preserved and articulated, missing only the anterior tip of the skull and the greater part of the tail. The new taxon is described and diagnosed by the following features: elongate pontosaur-like skull; unique supraoccipital-parietal articulation, with supraoccipital resting on top of and forming v-shaped suture with parietal; elongate axial skeleton is (12 cervical, 29 dorsal vertebrae); robust, semi-circular ribs; a reduction of the appendicular skeleton, flatter joints, and a broadening of the manus and pes; shorter forelimbs than hindlimbs; considerable dorso-ventral expansion of the caudal region. The new taxon was unequivocally at least partially aquatic: pachyostotic ribs, a laterally compressed tail, and reduced, flattened limbs indicate adaptations for undulatory locomotion. Local sedimentation and associated fauna provide evidence for a productive tropical rudist reef ecosystem on a shallow inner shelf. Preservation of identifiable nektonic teleosts within the

gastric cavity (the first identifiable gastric contents described from a dolichosaur) provide strong evidence of a primarily piscivorous diet. This supports the interpretation of this animal as an ambush predator, able to hide in nooks and crannies, and agile enough to catch fish via tail propelled locomotion in a shallow marine environment.

INTRODUCTION

In 1873, Andreas von Kornhuber, an Austrian naturalist and paleontologist, described a new species of Cretaceous lizard found in the platy limestones on Hvar Island (=Isola di Lesina), Croatia (Kornhuber, 1873). Kornhuber postulated that this small (roughly a metre long), elongate lizard was predominantly aquatic, being a skillful swimmer and agile diver that would chase its prey. He named this lizard *Hydrosaurus lesinensis* based on similarities between this animal and the extant *Hydrosaurus* (=*Varanus*), though he frequently referenced the similarities it shared with snakes. Decades later, Kramberger (1892) determined that this animal shared more similarities with other Cretaceous Tethyan lizards *Acteosaurus* (von Meyer, 1860)*, Adriosaurus* (Seeley, 1881) and *Aigialosaurus* (Kramberger, 1892) than it did with *Varanus*. *Hydrosaurus* was subsequently renamed *Pontosaurus lesinensis* and placed into the newly erected Aigialosauridae with the other Cretaceous lizards (Kramberger, 1892).

In 1903, Nopcsa reevaluated *Pontosaurus* and several other Cretaceous marine lizard, and emended the Dolichosauridae (previously erected as a monotypic family by Gervais—1852—for *Dolichosaurus longicollis*) to include *Dolichosaurus* (Owen, 1850), *Pontosaurus, Acteosaurus,* and *Adriosaurus.* Within the closely related family Aigialosauridae, Nopcsa kept *Aigialosaurus*, but also included *Carsosaurus*, *Mesoleptos* and *Opetiosaurus*. These designations have essentially lasted until today, though their monophyly is no longer unconditionally accepted: dolichosaurs are recovered as a successive series of outgroups to the ophidians or as a sister group to mosasauroids, while aigialosaurs waver between a monophyletic sister group to mosasaurids and a paraphyletic lineage from which mosasaurs arise multiple times (Lee and Caldwell, 1998, 2000, Caldwell, 1999b, 2006; Bell and Polcyn, 2005; Palci and Caldwell, 2010; Caldwell and Palci, 2007; Palci and Caldwell, 2007; Conrad, 2008; Conrad et al., 2011; Gauthier et al., 2012). Even so, these fossil forms are generally accepted to be closely related.

Aigialosaurs and dolichosaurs (and mosasaurs and snakes), are representative of a time in history during which squamates were at their peak in terms of aquatic adaptation. Today, only 59 species of squamates (58 sea snakes, sea kraits and file snakes, and 1 lizard, the marine iguana) are adapted to life in the marine environment. The Late Cretaceous however, was populated by many marine squamate families, occupying near-shore and open ocean habitats in a variety of ecological niches. Currently, there are nine described genera of dolichosaurs (non-ophidian ophidiomorphs) and nine aigialosaurs (non-mosasaurid mosasauroids). The Upper Cretaceous limestones of the Dalmatian Coast of Croatia, and the Komen Plateau of Eastern Italy and Slovenia have been of utmost importance to the study of these two closely related groups as they have produced the majority of its fossil representatives. Among the dolichosaurs, these include *Acetosaurus tommasinii*, *Adriosaurus suessi*, *Adriosaurus skrbinensis, Adriosaurus microbrachis*, *Mesoleptos zendrinii*, and *Pontosaurus lesinensis.* These same rock units have also produced well-preserved basal mosasauroids including *Aigialosaurus dalmaticus, Aigialosaurus bucchichi, Komensaurus carrolli,* and *Carsosaurus marchesetti*.

Pontosaurus is currently represented by two species of which *Pontosaurus lesinensis* is the generic type. As mentioned, it was described by Kornhuber in 1873 as *Hydrosaurus* based on two specimens, and was redesignated by Kramberger in 1892. The specimens were not re-examined in details until 2004. After extensive additional preparation, Pierce and Caldwell redescribed the more complete of the two specimens, and removed the less complete specimen from *Pontosaurus*, treating it as cf. Dolichosauridae. A phylogenetic analysis based on the reprepared and redescribed specimen provided support for a monophyletic Pythonomorpha (Cope, 1869) inclusive of mosasaurs, aigialosaurs, dolichosaurs and snakes. The dolichosaurs formed a paraphyletic 'grade' with *Adriosaurus* and the *Pontosaurus* forming successive sister taxa to the Ophidia.

Caldwell (2006) described a second species of *Pontosaurus*, this one from Lebanon. *Pontosaurus kornhuberi,* Caldwell, 2006, is incredibly well preserved, articulated from head to the tip of the tail, and preserves soft tissues including squamation and elements of the respiratory system. A phylogenetic analysis was conducted based on the dataset of Pierce and Caldwell (2004), and unsurprisingly, similar results were achieved: Aigialosauridae was recovered as the sister group to the Mosasauridae, and the dolichosaurs formed a Hennegian comb with Ophidians at the tip (= the Ophidiomorpha, Palci and Caldwell, 2007). As a result of this and other (see above) studies, the Dolichosauridae—the conventional taxon for *Dolichosaurus, Pontosaurus, Acteosaurus, Adriosaurus* and *Coniasaurus* (Owen, 1850)—should therefore be treated as including only *Dolichosaurus* and *Coniasaurus*, since these tend to show a sister group relationship. The other taxa, if included, would make the family paraphyletic rendering the name taxonomically incorrect. However, I will continue to use the term 'dolichosaur' to refer to the non-ophidian ophidiomorphs.

Here I describe a new species of *Pontosaurus*, reconstruct its paleoenvironment based on sedimentological and micropaleontological characteristics, infer aspects of its paleoecology based on abdominal contents and anatomical features, and present the results of a phylogenetic analysis of ophidiomorph lizards.

Institutional Abbreviations—HPM Croatian Natural History Museum (Hrvatski prirodoslovni muzej), Zagreb, Croatia; **GBA** Geologisches Bundesanstalt Osterrich, Wien, Austria; **MCM**, **DJ**, **KK**, and **MC** refer to authors.

MATERIALS AND METHODS

Discovery and acquisition—Records of the material described in this paper date to the late 18th century. During this time Dalmatian towns were populated with wealthy collectors, who assembled rich collections of natural history objects (Dadić, 1982). Among these were the Fafogna brothers, who obtained the specimen described in this study. The fossil was stored in the Garagnin-Fafogna library in Trogir, Croatia where it was identified and presented as a fossil fish until 1982. At this time, it was transferred to the Department of Geology and Paleontology at the Croation Natural History Museum in Zagreb. In 1987, the fossil was the subject of the graduate work of Dražen Japundžić under the supervision of Drs. Z. Bajraktarević and J. Radovčić

Preparation—The fossil was prepared by DJ in 1987. Before preparation, many of the bones—including the limbs, some vertebrae, and parts of the skull—were covered in matrix. Due to the fragility of the bones, chemical preparation was used instead of removing the matrix mechanically, and followed the techniques of Cooper and Whittington (1965). Formic acid was chosen over hydrochloric or acetic acid so as not to dissolve the calcium phosphate within the bones. A mild solution of 5% formic acid allowed for a slow, controlled dissolution of the limestone. Polyvinyl acetate was applied to exposed bones repeatedly as they were uncovered in order to protect them during the acid preparation. In total, roughly forty hours of preparation was required to prepare the specimen to its current state.

Investigation—Drawings and illustrations were made by MCM, DJ and MC directly from the original specimen using a dissecting microscope and camera lucida attachments. X-rays were commissioned by DJ.

GEOLOGICAL CONTEXT

The fossil discussed here originates from Hvar Island: a Croatian Island in the Adriatic Sea. The exact location of discovery is uncertain, but prolific fossiliferous limestone found between the villages of Stari Grad and Jelsa is the mostly likely origin of the specimen (Kramberger, 1892). Field research suggests a more specific location: a quarry 2.5 km east of Stari Grad, and 500 m north of the road connecting the two villages (Radov*čić*, 1975).

Hvar Island is one in a series of geological structures that form the Adriatic Belt. It is a fragment of a larger, more comprehensive Tethyan Plateau that has since disintegrated through neotectonic movement. Its position and relationship to other geologic units within the Adriatic has generated a great deal of interest over time due to its commercial and paleontological importance.

The fossil-bearing units of Hvar, and analog layers of central Dalmatia (including the Trieste-Komen Plateau of Italy and Slovenia) are a thick carbonate facies of Upper Cretaceous rock that occur layered between dolomite. The limestone is a light, yellowish grey, and is very dense. It is laid down in slabs roughly one to three centimetres thick, with iron oxide stripes at the joints. These rocks have been extensively studied over the past 200 years due to the frequent discovery of attractive fossil vertebrates including a good collection of fish and semi-aquatic reptiles (Kornhuber, 1873). Romer (1966) went so far as to describe it as a classic area of Cretaceous vertebrate study.

Beginning in the late 19th century and continuing to the present, a series of authors described semi-aquatic lizards from Dalmatia and compared them with each other: *Acteosaurus tommasinii* (von Meyer, 1860), *Pontosaurus lesinensis* (Kornhuber, 1873)*, Carsosaurus marchesetti* (Kornhuber, 1893)*, Aigialosaurus (Opetiosaurus) bucchichi* (Kornhuber, 1901)*, Adriosaurus suessi* (Seeley, 1881)*, Aigialosaurus dalmaticus* and *A. novaki* (Gorjanovic-Kramberger, 1892), *Eidolosaurus trauthi* (Nopcsa, 1923)*, Mesoleptos zendrinii* (Cornalia, 1852)*, Komensaurus carrolli* (Caldwell and Palci, 2007)*,* and *Pontosaurus kornhuberi* (Caldwell, 2006). One of the commonalities between these works is the expression of uncertainty in the age of the rock that bears the reptiles.

The fossiliferous “schist” limestone (referred to as “platy limestone” or “fish shales”) contains abundant fish, reptiles, invertebrates and plants (Stur, 1891). Numerous geologists have attempted to date this rock in the last 150 years, and yet the results are still imprecise. Starting in 1873, early researchers were back-and-forth between assigning them to the Upper versus Lower Cretaceous. Kornhuber (1873) argued for Lower Cretaceous based on similarities in fish fauna between Hvar and other localities, Baasani (1879) agreed that the “schist” limestones are Lower Cretaceous in age, while Kramberger (1892) in his description of *Aigialosaurus*, argued for the Upper Cretaceous, and Söhle (1901) again supported Lower Cretaceous. In 1959, Herak conducted an audit of the geological structure of the island to assess groundwater conditions. He concluded that the upper dolomite layer was Upper Cretaceous in age, based partially on the presence of the ostreiform mollusk *Chondrodonta* (Stanton, n.d.). Langer (1961) corroborated these findings with additional molluscan genera and foraminiferans, and proposed a middle to upper Cenomanian age.

In the 1960's and 70's, several teams made broader analyses of Cretaceous and Palaeogene rocks within the Dinarides and the neighbouring coastal isles (Radoičić, 1960; Polšak, 1965; Borović, I., Marinčić, S. & Majcen, 1968; Amšel, 1969; Jelaska, 1973; Tišljar, 1976). This resulted in a better understanding of the fossil deposits, geological composition, paleogeography, and sedimentary correlation with other areas, but still did not provide a more specific date on the Hvar limestones than Upper Cretaceous.

Several papers in the 1970's specifically addressed the invertebrate and fish faunas, comparing their occurrences to better time-calibrated deposits elsewhere. These included two papers by Radovčić (1973, 1975) on the fish of Cretaceous Dalmatia, specifically comparing them with North American deposits. Herak, Marinčić and Polšak (1976) documented the occurrence of a characteristic Cenomanian community of invertebrates including *Ichtyosarcolites bicarinatus, Ichtyosarcolites monocarinatus* (see also Sarı and Özer, 2009)*,* and Turonian invertebrates including *Nerinea olisiponensis,* and *Nerinea requieni.* They concluded that Hvar limestones contained Cenomanian and Turonian parts, but there was no evidence of any delineation between the layers.

Rudist reefs were widespread in the upper Cenomanian, distributed across the Mediterranean Tethys. Rudists were used in several studies on Mediterranean (including

Croatian) geology to subdivide Upper Cretaceous limestones spanning the Cenomanian to Campanian. These studies generally agreed with previous results from invertebrate studies, declaring Cenomanian-Turonian ages (Parona, 1926; Polšak, 1964, 1967; Polšak et al., 1982). *Praeradiolites* rudists were an important index fossil, dating into the Cenomanian/Turonian.

Herak (1983) discussed the problems associated with the origin and tectonics of the Adriatic belt. This led to an elaboration of his ideas in 1985 and 1986, when he reconstructed the tectonics of the Adriatic and Dinaric area, outlining four geotectonic zones. By the 1990's, it was recognised the tectonic movements had resulted in an Upper Cenomanian transgressive trend represented by a set of repeating sequences. Fossiliferous layers containing giant clams, rudist reefs, and rudstones represent ramp/shelf margin; fined grained limestones, microbial mats, and anhydrites represent shallow, hypersaline lagoons or intertidal zones (Radovčić, 1987; Zappaterra, 1990; Vlahović et al., 1994).

Most recent work has focused on examining specific localities and sections on Hvar, enhancing and improving the detail and accuracy of the stratigraphy, paleogeography and tectonics of the Dalmatian Coast (e.g., Radovčić et al., 1983a; Vlahović et al., 2005; Korbar, 2009), and more precisely, the Late Cretaceous of Hvar (Marinčić, 1997; Diedrich et al., 2011). These most recent studies have led to revisions of the geological maps and sections which provide, at last, a firm understanding of the paleoenvironment that the described lizard would have lived in.

Depositional environment—The dense, yellow-grey limestones of Hvar have been the subject of study for almost two hundred years. The result is a relatively refined understanding of the depositional environment that existed during the time of the ophidiomorph lizards, in the Cenomanian and Turonian.

Hvar Island preserves a well-developed carbonate series that spans the upper Cenomanian to lower Turonian across the Adriatic Dinarides (Herak, 1986). The series is characterized by repeating sedimentary sequences signifying multiple shallowing-up sequences composed of rudist-dominated shallow carbonate platform, hypersaline, stagnant lagoons, and intertidal/supratidal strata (Diedrich et al., 2011).

Analysis of oxygen isotopes (Polšak and Leskovšek, 1975) show that the Upper Cretaceous sea ranged from 24-26°C, the temperature of a modern tropical sea. On an open shelf, these conditions would have favored the growth and proliferation of rudist patch reefs, which would have played a key role in the geology of the area—including the differentiation of facies within the carbonate platform. The facies containing abundant rudist fossils is also rich in benthic organisms including mussels, clams, worms, echnoids, oysters (Radovčić, 1975; Radovčić et al., 1983b). The carbonates are granular wakestones-packstones (Tišljar, 1976) composed of shell fragments and fossil detritus. The presence of pelagic elements (notably, cephalopods), indicate a shelf in contact with the open sea. Above these facies layers are usually found a second type of laminae, one characterized by a finer mudstone-wackestone and an absence of fossils. These finer stratifications are linked with localized depressions in the seafloor forming shallow lagoons. In these areas, poor circulation and increased water temperature would cause a decrease in oxygen, and an increase in salt concentration and deposition. These shallow subtidal lagoons had conditions unsuitable to the plethora of benthic organisms of the shelf, explaining the low density of fossils. However, the evaporitic conditions that made these lagoons unsuitable for benthic habitation also made them ideal for the preservation of vertebrates. The low oxygen, high saline environment led to a slow rotting of fish and reptile carcasses, and the higher deposition rate increased their chance of burial. It is these layers that yield the well-preserved reptiles, including the one described herein. Other sparsely preserved organisms of various environmental origin—land plants, crustaceans of the shallow shelf, cephalopods of the deeper shelf—indicate a depositional environment with marine and continental influences, and further support the lagoonal interpretation. A regression of the sea results in the gradual disappearance of the lagoons: becoming first distal intertidal, then middle and upper intertidal, and finally supratidal during the low stand maximum in the late Upper Cenomanian (Diedrich et al., 2011). These widespread sandflats were dominated by biolaminates and preserve extensive dinosaur trackways (Diedrich, 2010). The onset of a new transgression caused by a slowly sinking bottom eventually forms a shallow carbonate platform, initiating a new rudist patch reef system, and completing the cycle. Hundreds of complete and incomplete sequences combine to form a limestone layer hundreds of metres thick. Caused by a sinking sea floor and the deposition of marine carbonate sediment, it records the transgressive trend typical of upper Cenomanian Tethyan sediments (Diedrich et al., 2011).

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811

ANGUIMORPHA Fürbringer, 1900

PYTHONOMORPHA Cope, 1869

Genus *Pontosaurus* Kramberger, 1892

Type Species: *Pontosaurus lesinensis* Kornhuber, 1873

Synonym— *Hydrosaurus lesinensis*

Holotype—GBA 1873/4/2: articulated skeleton including skull, 12 cervical vertebrae, 28 dorsal vertebrae, forelimbs and shoulder girdles, fragmentary hindlimb and pelvic girdle.

Type locality—Hvar Island (=Isola di Lesina), 43° 10' N, 16° 30' E, Croatia; Upper Cenomanian (Upper Cretaceous) platy limestones.

Revised generic diagnosis—Long and slender marine lizard possessing unique supraoccipital-parietal articulation, with supraoccipital resting on top of and forming v-shaped suture with parietal; elongation of all postdentary bones; 10-12 cervical vertebrae; hypapophyses with large unfused peduncles on all cervical vertebrae except the axis; 26-29 dorsal vertebrae; strong, uniform, semicircular ribs curving to the distal point; coracoid without neck (altered from Pierce and Caldwell, 2004).

Pontosaurus ribaguster sp. nov.

(Figs. 1-4)

Diagnosis—A small (~30 cm snout-pelvis), slender lizard with a laterally compressed body; arrowhead-shaped parietal ornamentation around (anterior and lateral) the parietal foramen; elongate neck and body with 41 presacral vertebrae (12 cervical, 29 dorsal); well developed zygosphene-zygantrum articulations; thickened dorsal ribs showing some degree of pachyostosis bent in a semicircle; ribs associated with ultimate dorsal vertebra; at least one pygal vertebra; extremely anteroposteriorly broad neural spines on the anterior caudal vertebrae forming an almost uninterrupted wall of bone; laterally compressed tail with elongate neural spines and haemal arches; reduced pelvic and pectoral girdles; scapula with rectangular posterior process and fenestra; front limbs shorter than rear (humerus:femur = 1:2); elongate preacetabular iliac process.

Remarks— *Pontosaurus ribaguster* shares the following features with other basal ophidiomorphs (e.g., *Dolichosaurus, Adriosaurus, Acteosaurus, Pontosaurus, Coniasaurus*): elongate, cylindrical body with over 25 dorsal vertebrae (29), and 10 or more cervical vertebrae (12); reduced limbs, especially forelimbs (humerus:femur ≈ 1:2); expanded distal end of the fibula; articulated haemal arches; long, narrow neural spines on caudal vertebrae.

Can be differentiated from other ophidiomorph lizards in the following ways: *Acteosaurus* has distally straight ribs with a greater degree of pachyostosis (vs. the gracile, curved ribs of *Pontosaurus ribaguster*); *Adriosaurus* has an M-shaped frontal-parietal suture (in *P. rubaguster* this suture is almost straight), relatively narrower heads on the long bones (humerus, radius, ulna, femur), a broader ilium, and distally straight, very pachyostotic ribs (vs. narrow, consistently curving ribs in *P. ribaguster*); *Carentonosaurus* has wider vertebrae, non-pachyostotic neural spines (pachyostotic in *P. ribaguster*), and smaller postzygapophyses relative to prezygapophysis size; *Coniasaurus* has swollen, bulbous crowns on the posterior dentition (vs. the impressions in HPM 10807 showing uniformly tapering teeth), frontal ala that projects laterally at a much sharper angle, and more gracile, angular vertebrae; *Dolichosaurus* has a smaller head, at least 19 cervical vertebrae (vs. ~12 in *P. ribaguster*), more gracile ribs, and an anterior sacral rib that is much thinner than the posterior sacral rib (vs. in *P. ribaguster* where both are similar in size); *Eidolosaurus* has fewer dorsal vertebrae (23 vs. 29), extremely pachyostotic ribs almost as thick as their corresponding vertebrae are long (vs. only slight pachyostosis in anterior dorsal ribs), non-uniform ribs giving the body a spindle shape (unlike the continuous 'tube' of other non-ophidian ophidiomorphs), and forelimbs only slightly shorter than hindlimbs (vs. a dramatic difference in *P. lesinensis*); *Kaganaias* has fused haemals (vs. articulating), more weakly curved ribs, more than 36 dorsal vertebrae (vs. 29), neural arches that do not project over the following vertebra (vs. overlapping arches in *P. ribaguster*), and neural arches with very little waisting, exhibiting a roughly constant width anteroposteriorly (vs. hourglass shape in *P. ribaguster*); *Mesoleptos* has unusually long, posteriorly tapering trunk vertebrae with a high aspect ratio (more so than other non-ophidian ophidiomorphs), distally straight ribs (vs. distally curving), a sinuous humerus (may be taphonomic), taller neural spines, and fewer dorsal vertebrae (approximately 23 vs 29).

Etymology—This species is named for its ecological role as a swimmer and piscivore shown by the dietary remains preserved in its abdominal cavity. In Croatian (the specimen's country of origin) *riba,* is fish; and *gŭster*, lizard. This name is doubly appropriate given that the specimen was originally interpreted and presented as a fossil fish.

Type Locality and Horizon—Upper Cretaceous (Upper Cenomanian-Turonian) of Hvar Island, Croatia. Between the towns of Stari Grad and Jelsa. Part of the Adriatic-Dinaric Carbonate Platform.

Holotype—HPM 10807, housed in the Hrvatski prirodoslovni muzej (Croatian Natural History Museum – HPM), Zagreb, Croatia. The specimen is encased in a block of platy limestone that preserves the incomplete articulated body of one individual in dorsal view (Figure 1). The skull is preserved posterior to the prefrontals and exposes the posterior right mandible. The postcranium preserves a complete cervical and dorsal series, 20 caudal vertebrae, pelvic and pectoral girdles, and incomplete remains of all four limbs.

OSTEOLOGICAL DESCRIPTION

Overall Impression

The specimen discussed in this paper is preserved in a limestone slab roughly 50 cm long, 20 cm wide and 2.5 cm thick. The specimen is articulated and mostly complete from the skull to the anterior caudal region. The anterior part of the skull and the majority of the tail are missing, cut off at the edges of the limestone slab (Figure 1). The 36 cm specimen is exposed in dorsal view from the cranium to the posterior-dorsal series, where the body twists, exposing the pelvic and caudal regions in left lateral view. The skull was flattened and compressed from the right during fossilization. It is consequently preserved deformed and broken in dorsal view, with the right mandible exposed in lateral view. The postcranial axial skeleton suffered minimal taphonomic damage and is in tight articulation. The pelvic and pectoral girdles are fragmentary and ill-defined, a result of excessive acid preparation. The right forelimb is crushed against the body, and the elements of the manus are broken, dislocated and difficult to interpret. The left forelimb is further from the body and is better articulated than the right; however, most of the manual region appears ‘melted’ together due to acid damage. The left hindlimb is the best preserved of the limbs, though it is still missing most of the tarsal elements. The right hindlimb lies underneath of the body though elements are recognisable emerging from under the base of

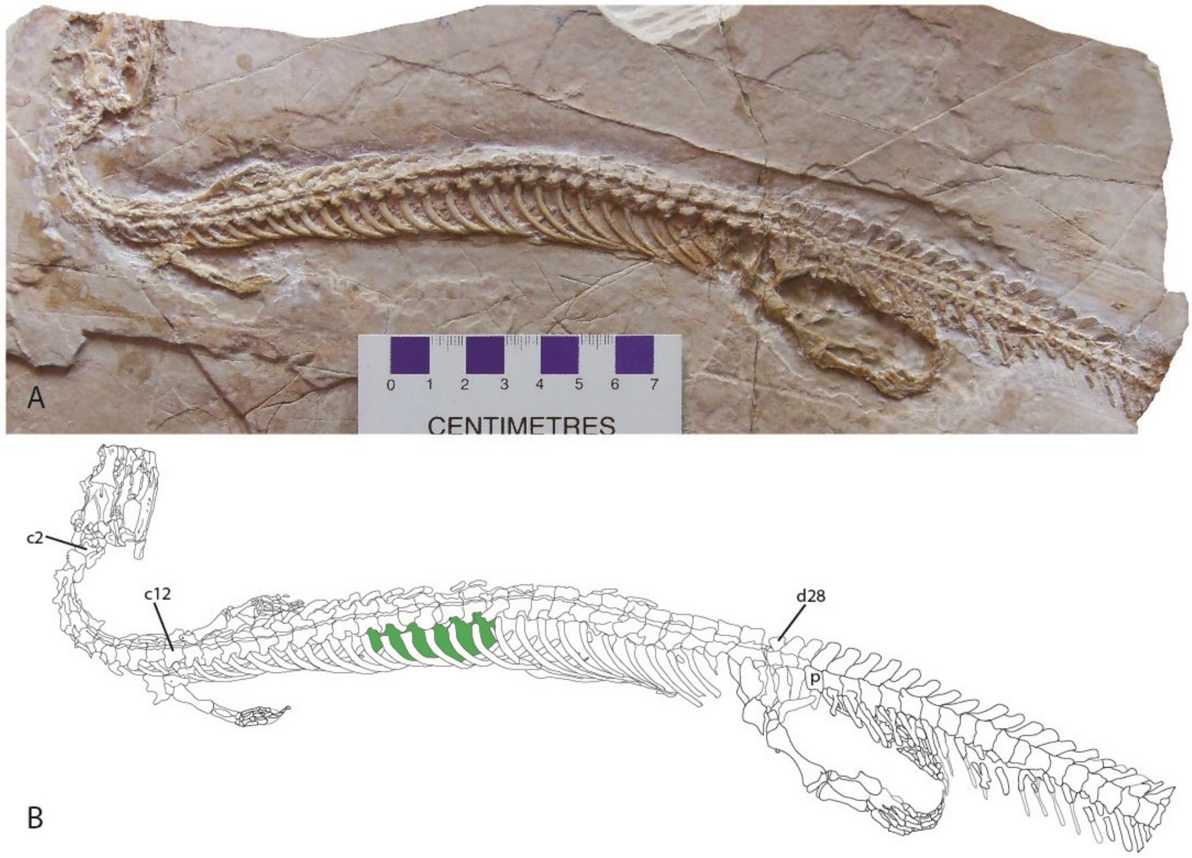

Figure 2-1 The holotype of *Pontosaurus ribaguster* (HPM 10807), housed in the Hrvatski prirodoslovni muzej (Croatian Natural History Museum), Zagreb, Croatia. **A**, photo; **B**, interpretive drawing. **Abbreviations**: **c**, cervical vertebra; **d**, dorsal vertebra; **p**, pygal vertebra. Grey lines in (B) indicate impressions only, shaded areas represent gastric content.

the tail. There are several large cracks through the slab, obscuring the atlas-axis area, and the anterior pelvis.

Skull

As in other dolichosaurs, the skull and jaws are long, smooth and slender (Figure 2). The skull elements remain mostly in articulation, though interpretation of the individual elements is made difficult by the degree of crushing and shattering, obscuring natural edges. Most of the snout is missing, cut off just anterior to the orbits. The head is inclined and embedded in the sediment in

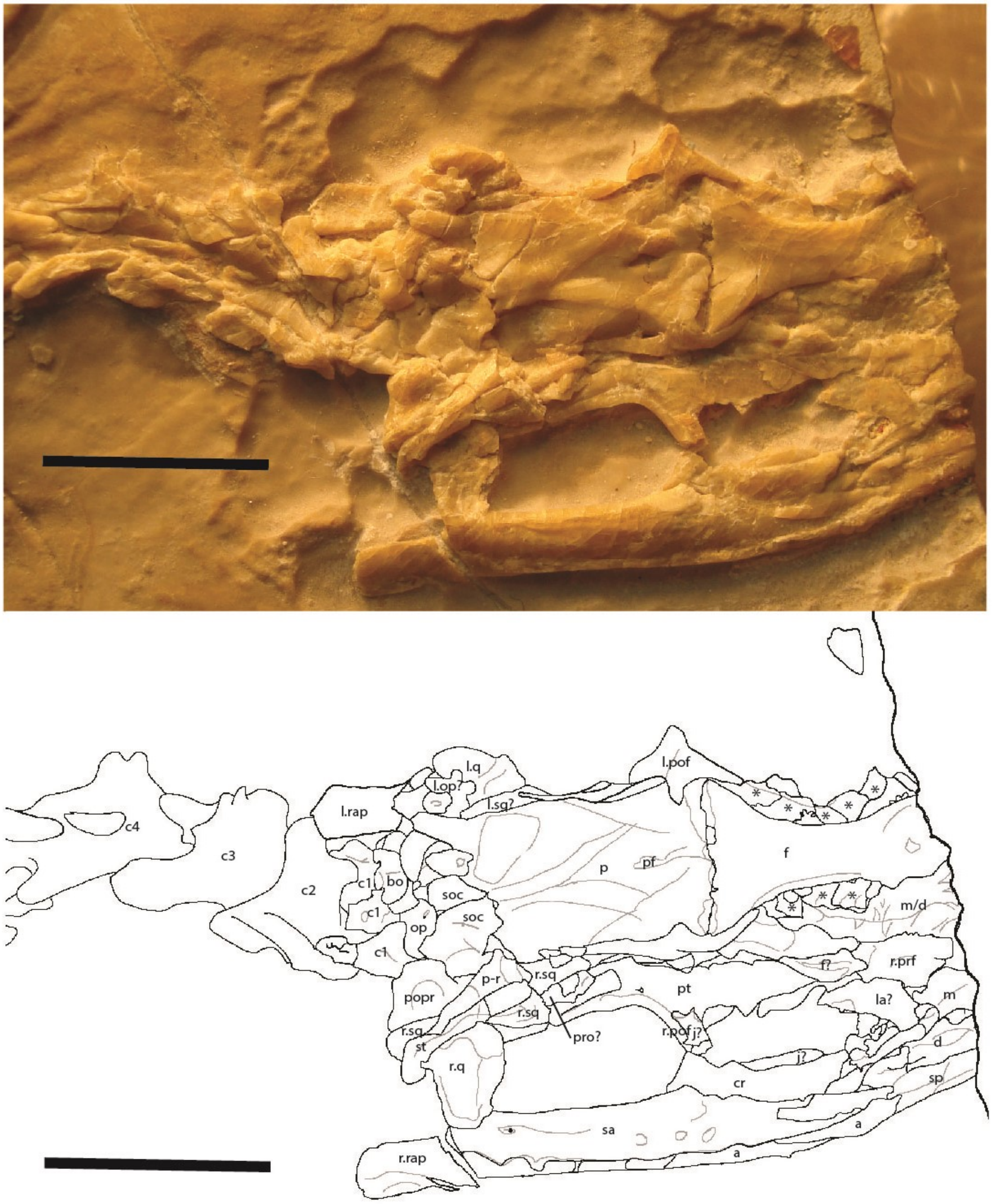

Figure 2-2 Head and anterior cervical vertebrae of *Pontosaurus ribaguster* (HPM 10807). **A**, photograph; **B**, interpretive drawing. **Abbreviations: bo**, basioccipital; **c**, cervical vertebra; **cr**, coranoid; **d**, dentary; **f**, frontal; **j**, jugal; **la**, lacrimal; **m**, maxilla; **op**, opisthotic; **p**, parietal; **p-r**, parietal ramus; **pf**, parietal foramen; **pof**, postorbitofrontal; **popr**, paraoccipital process of the exoccipital-opisthotic; **prf**, prefrontal; **pro**, prootic; **pt**, pterygoid; **q**, quadrate; **rap**, retroarticular process; **sa**, surangular; **soc**, supraoccipital; **sp**, splenial; **sq**, squamosal; **st**, supratemporal Asterisks label possible sclerotic ring fragments. Where two sides are labeled, each abbreviation is preceded by **r.** (right) or **l.** (left). Scale bars equal 1 cm.

such a way that the skull roof is visible in dorsal view, while the right side of the skull and mandible has been rotated dorsolaterally, exposing the lateral aspects. The basicranium is exposed in dorsal view and remains in articulation with the atlas.

Maxilla—The posterior portion of the right maxilla is badly fragmented, although several fragments remain in contact with the prefrontal. A slender posterior process projecting from the deeply notched posterior maxillary margin is overlain by fragments of what is likely the anterior process of the jugal. No teeth are preserved, though a bulbous mass on the ventral border of the maxilla resembles the tooth pedestals described in *Pontosaurus lesinensis* (Pierce and Caldwell, 2004), and would match the position of the posterior end of the tooth row in both *P. kornhuberi* (Caldwell, 2006) and *A. dalmaticus* (Carroll and Debraga, 1992).

Lacrimal—A sub-trapezoidal fragment overlying the maxilla is interpreted as the lacrimal. It is in contact with the maxilla anteriorly and the prefrontal superiorly. It is similar in size and shape to the lacrimal of *Aigialosaurus dalmaticus* (Carroll and Debraga, 1992), including a small dorsoposterior process. The lacrimal would have contributed to the anterior orbital margin between the prefrontal above and the jugal below. It is still in articulation with a fragment of the maxilla anteriorly. The presence of the lacrimal represents a clear difference from snakes, where it is absent (Lee and Caldwell, 1998). A lacrimal was identified in *Pontosaurus lesinensis* by Kornhuber (1873), but Pierce and Caldwell (2004) revised this, identifying it instead as a piece of the prefrontal.

Prefrontal—Fragments of both left and right prefrontals are identifiable in *Pontosaurus ribaguster*, though the right is better preserved. Both elements are broken, cut off by the edge of the limestone slab, but it appears that the element would have been long and tapering posteriorly as in *P. lesinensis* (Pierce and Caldwell, 2004) and other mosasauroids (Debraga and Carroll, 1993). The medial border is fairly flat where it would have articulated with the lateral edge of the frontal, though it has several uneven spines that may have formed an interdigitating suture. Laterally, it articulates with the lacrimal and the maxilla. A small bump on the posterolateral edge is identified as a small supraorbital process.

Jugal—Due to the extreme breakage and flattening of the lateral surface of the skull, the identification of the jugal is problematic. Two pieces are tentatively identified: the first, a very thin and elongate element sitting superior to the coronoid; the second piece, which sits on the lateral surface of lacrimal and/or maxilla, may represent the anterior point of the jugal. If these interpretations are correct, then the jugal would have extended just anterior to the orbit as in mosasauroids (Debraga and Carroll, 1993) and *P. kornhuberi* (Caldwell, 2006).

Frontal—The frontal is almost completely preserved, and is only missing the anterior border and processes. It is long, flat, and approximately the same length as the parietal. As in other 'dolichosaurs', it is hourglass-shaped in dorsal view—expanded anteriorly and posteriorly, and constricted above the orbits. As the prefrontal and postorbitofrontal do not meet, the borders of this constriction would have formed the dorsal margin of the orbits. There also appears to be a slight sagittal crest on the frontal as in *Coniasaurus gracilodens* (Caldwell, 1999a).

The posterior margin of the frontal was slightly shattered as it was forced against the parietal, but in life the margin would have been essentially straight as in *Pontosaurus lesinensis* (Pierce and Caldwell, 2004) with perhaps a slight posterior projection of the lateral edges which would have overlain parietal lappets as in *P. kornhuberi* (Caldwell, 2006). A distinct valley forms a gap between the frontal and parietal. This gap could be taphonomic, or a true anatomical feature indicative of mesokinesis in the skull or delayed dermatocranial ossification (as discussed for *P. kornhuberi*; Caldwell, 2006).

The right anterolateral corner (including the right lateral process) of the frontal may be preserved as a displaced element sitting between the displaced right prefrontal and pterygoid. It preserves a groove running near the lateral surface that could be the bilateral counterpart of the groove visible on the left anterolateral edge of the frontal. However, the interpretation is uncertain: an alternative interpretation for this element is as the palatal ramus of the right pterygoid, due to its contact with the quadrate ramus posteriorly.

Parietal—The parietal is a very wide, rectangular element. Like *Pontosaurus kornhuberi*, the anterolateral projections of the parietal are broadly overlapped by the postorbitofrontal (Caldwell, 2006). The dorsal surface has a broad, flattened ‘crest’ more similar to the condition in *P. kornhuberi* (Caldwell, 2006) than *P. lesinensis* (Pierce and Caldwell, 2004). In contrast, the parietal foramen is more similar in size to *P. lesinensis* than *P. kornhuberi*; it is similar to both species and to mosasauroids in the distance it sits from the frontal-parietal suture (Carroll and Debraga, 1992; Debraga and Carroll, 1993; Pierce and Caldwell, 2004; Caldwell, 2006). Anterior and lateral to the foramen are a pair of anteromedially oriented ridges that originate from the anteriormost point of contact with the prootic and project anteriorly to form an arrowhead-shaped ornamentation around the parietal foramen (in dorsal view). As in *P. kornhuberi*, there is a very broadly expanded decensus parietalis (‘parietal wing’) which rises slightly to meet the anterior margin of the prootic (Caldwell, 2006) and forms the origin of the anteriorly directed ridge bracketing the foramen on the parietal table.

The posterior margin is in broad contact with the supraoccipital, and at the midline, this contact forms an interdigitating w-shaped suture, which is synapomorphic for the genus *Pontosaurus.* The contact between these elements is planar as in snakes; the supraoccipital does not lie beneath the parietal as in lizards. This would have formed an elongate and very flat skull.

The parietal ramus is broken and dislocated on both sides. The right side is more completely preserved and identifiable; it lies laterally displaced from—but in line with—the rear margin of the parietal table medially and the decensus parietalis laterally. The right ramus is still in articulation with the supratemporal and overlies the squamosal and the paroccipital process of the exoccipital-opisthotic.

Postorbitofrontal—The postfrontal and postorbital of *Pontosaurus ribaguster* appear to have fused to form the tetra-radiate postorbitofrontal. Both left and right sides are preserved, though the lateral side and posterior tip of the right postorbitofrontal is damaged, and the posterior ramus of the left postorbitofrontal is broken off the main body of the element; this description is derived from both elements.

The postorbitofrontal is composed of the main body of the element which sits just posterior to the frontal-parietal suture. Branching from this point are four distinct rami. The anterior (frontal) ramus clasps the posterolateral corners of the frontal. This ramus is relatively thin and long, reaching up the frontal halfway between the base, and the beginning of the supraorbital constriction. The medial (parietal) ramus is narrow and short and overlaps the parietal just posterior to the frontal-parietal suture. The lateral (jugal) ramus is short (roughly the same length as the medial ramus) and very broad. Due to damage, the jugal contact cannot be observed. The posterior (squamosal) ramus, preserved on both sides, is extremely long and thin, making up roughly half the anterior-posterior length of the element. Each forms the lateral margin of a supratemporal fenestra, extending posteriorly almost the full length of the parietal table to contact the squamosal at an oblique angle. Overall, the entire configuration and shape is extremely similar to *Pontosaurus kornhuberi* (Caldwell, 2006).

The condition of the postorbitofrontal is particularly interesting in *Pontosaurus ribaguster*. Although fusion between the postorbital and postfrontal is clearly advanced, a groove extending from the lateral margin of the anterior ramus medially to join the margin between the medial and posterior rami clearly indicates the position of the common suture. This makes the anterior and medial rami homologous to the prefrontal, and the lateral and posterior rami homologous to the postfrontal. This could represent an intermediate stage between the more oblique, unfused postorbital and postfrontal of *P. lesinensis*, and the fully fused postorbitofronal of *P. kornhuberi* (Pierce and Caldwell, 2004; Caldwell, 2006). It is important to note that even though fusion appears incomplete, the shape and orientation of the four rami in *P. ribaguster* is almost identical to *P. kornhuberi*, but distinct from *P. lesinensis*, which has less developed lateral and medial rami that are oriented more obliquely. It is important to note here that the presence of the postfrontal/postorbital/postorbitofrontal is variable among squamates, with various families—and genera within those families—possessing different combinations of one, two, or none of these elements (Estes et al., 1988; Caldwell, 2006).

Squamosal— The anterior portions of both squamosals are preserved in articulation with the postorbitofrontals. The postorbitofrontal appears to sit in a groove on the anterio-lateral surface of the squamosal, making it appear that the squamosal is clasping the postorbitofrontal. The rear portion of the squamosal is preserved only on the right side, overlapped by the displaced supratemporal arcade. The squamosal is long and thin and forms the posterolateral border of the supratemporal fenestra. Posteriorly, the squamosal cups the dorsal margin of the quadrate, and in life would have contacted the descending process on the posterior supratemporal. Anteromedially it lies in contact with the prootic and a sub-cylindrical fragment interpreted as part of the epipterygoid. Posteromedially it borders the lateral margin of the paroccipital process of the exoccipital-opisthotic.

Supratemporal—The supratemporal is a small, elongate block of bone that sits lengthwise against the parietal ramus. It extends posteriorly beyond the parietal before expanding slightly to form a club-shaped descending process that articulates with the squamosal and quadrate. The element is also preserved lying over top of the paroccipital process of the exoccipital-opisthotic and may have contacted it in life.

Exoccipital—The braincase suffered the highest degree of breakage of the entire skull, making meaningful interpretation of the braincase elements difficult. Two fragments can be confidently assigned to the exoccipital-opisthotic. The first is the robust paroccipital process. This contacts the supraoccipital dorsomedially, and the squamosal dorsolaterally. The process is a large oval, depressed in the middle, extending to an arcuate point ventrolaterally at the most ventral point of contact with the squamosal (like *P. lesinensis*, Figure 3; Pierce and Caldwell, 2004). The second fragment preserves the exit foramen for cranial nerves X-XII. It articulates dorsally with the supraoccipital, medially with the basioccipital, and laterally with the paroccipital process fragment. Together, these two fragments give a good idea of the shape of the right half of the exoccipital-opisthotic: a hatchet-shaped in posterior view, broadest laterally and narrowing medially, very similar to *Varanus*.

Supraoccipital—The ventral margin of the supraoccipital was rotated dorsally post-mortem, and lies in dorsal view posterior to the parietal. It has a very long broad contact dorsally with the posterior margin of the parietal: a feature unique to pontosaurs among squamates (Caldwell, 2006). The element retains this broad expansion posteriorly forming a deep, rectangular element. The right lateral rotation of the skull in this area means that the posterior margin is obscured by breakage and other bone fragments, and the foramen magnum cannot be located. Posteriorly, it overlaps and underlaps the exoccipital-opisthotic, although crushing and rotation has rendered the exact position of the suture indeterminant.

On the median dorsal surface is a raised t-shaped 'crest' that originates at the parietal suture and narrows posteriorly down the midline of the element. In *P. kornhuberi* (Caldwell, 2006) this area was interpreted to have housed an unossified element which would have overlapped the parietal dorsally. This morphology is evidenced in *P. lesinensis* (Pierce and Caldwell, 2004), which shows a sub-rectangular supraoccipital with a clover-shaped anteromedial shelf overlapping the parietal to form a w-shaped suture, and the 'stem' extending down the midline groove of the supraoccipital. I expect that the same morphology would have existed here, evidenced by the rough texture of the bone in this area (visible under magnification). As discussed in Pierce and Caldwell (2004) and Caldwell (2006), this is a similar configuration to snakes; the only difference being that in snakes the supraoccipital never overlaps the parietal.

Prootic?—An element tentatively identified as the prootic is visible in parallel contact with the squamosal. It has been taphonomically rotated outwards, and in life would have been ventral to this element.

Basioccipital—The basioccipital is preserved as a pair of round tuberosities sitting in contact with fragments of the atlas. The base of the occipital condyle may be visible posteriorly, identified by a narrowing then abrupt widening delineated by a rim.

Quadrate—The right quadrate has been rotated such that it is visible in right lateral view. It remains in articulation with the ramus formed by the squamosal, supratemporal and parietal, which formed the suspensory arcade from which the quadrate would hang. The left quadrate is obscured by the braincase, but the dorsal surface can be identified. As in other pythonomorphs, the quadrate is a backwards C-shape. Though the element is broken in places, it is possible to identify a small, rounded swelling (the remains of the suprastapedial process) posterior to the large, posteriorly extended head, and a well developed tympanic ala. The infrastapedial process most of the suprastapedial process are missing as a result of breakage (indicated by the uneven margins of the element). The quadrate shaft is robust and almost vertical. Ventrally, a large, saddle-shaped ventral condyle (roughly half the length of the maximum anterior-posterior length of the quadrate) articulates broadly with the surangular.

The quadrate is similar in shape to *Pontosaurus lesinensis* and *P. kornhuberi*, but has a larger, more squared off ventral cotyle (Pierce and Caldwell, 2004; Caldwell, 2006); it is also shorter and squatter than the quadrate of *P. lesinensis*. Overall, the quadrate morphology is very similar to other dolichosaus and mosasauroids (Russell, 1967; Carroll and Debraga, 1992).

Pterygoid—The majority of the right pterygoid is visible between the skull roof and the right mandible. The anterior segment—including the entire palatal ramus—is obscured, but the posterior segment is almost completely visible in right lateral view. It is a long, broad element lacking any trace of pterygoid teeth. A small process arising from the midpoint of the dorsal surface bears the articulation for the basipterygoid process of the basisphenoid. The posterior end of the quadrate ramus extends backwards to contact the quadrate underneath the displaced right suspensorial arcade. Ventrally, the robust ectopterygoid process angles anteriorly. A smaller, pointed process anterior to the ectopterygoid process is the likely a part of the articulation with palatine. A long shallow furrow runs lengthwise from the posterior end to the epipterygoid process. Overall, this element is indistinguishable from that of *Pontosaurus lesinensis* (Pierce and Caldwell, 2004). It is also very comparable to the element identified as the postorbitofrontal in *Adriosaurus skrbinensis* (Caldwell and Palci, 2010), which I suspect is a misidentification, and that this element in the latter represents the left pterygoid (pers. obs.).

Ectopterygoid—The ectopterygoids cannot be confidently identified in this specimen. A small, rectangular fragment emerging from between the squamosal and the prootic has been tentatively identified as the ectopterygoid due to its position and its columnar shape.

Sclerotic plates—A collection of small, square elements bordering the supraorbital constriction of the frontal on both left and right sides are interpreted here as sclerotic plates. Based on their size, there would have been roughly twelve of the elements in each ring. Similar squared elements can be observed in the orbit of *P. kornhuberi*, and though they were colorized by Caldwell (2006) in a figure 3 of that publication, they were not identified as such in the text, nor discussed regarding their presence and importance.

Lower jaw

The right mandible, exposed in lateral view, is well preserved from the retroarticular process to the edentulous posterior portion of the dentary. It remains in articulation with the quadrate posteriorly, and lies almost in contact with the right maxilla anteriorly. It appears to have been compressed anterodorsally, as the anterior ends of the surangular and angular appear crushed and overlapping the dentary. The left mandible is under the skull, and only the retroarticular process is visible posterior to the braincase in medial view.

Dentary—Only the posterior, edentulous portion of the right dentary is preserved in lateral view. The rest is missing, cut off at the edge of the limestone slab. The posterior end is overlapped by the maxilla and the splenial. The obscured posterior margin of the dentary means that the presence of an intramandibular joint cannot be determined.

A natural mold of the left dentary and maxilla is visible between the right lateral margin of the frontal and the right prefrontal. Curved, pointed impressions oriented dorsally and ventrally are most likely the impressions of occluding maxillary and dentary teeth. Not much detail can be gleaned from these impressions other than the approximate shape and size of the marginal teeth; they are curved and pointed, and fairly typical of an anguimorph.

Splenial—The posterolateral splenial bulges beneath and posterior to the dentary in lateral view. A small knob-like process is visible dorsally on the splenial-dentary suture, is also observed in *Pontosaurus lesinensis* (pers. obs.). In lateral view, it looks very similar to *P. lesinensis* (Pierce and Caldwell, 2004).

Coronoid—The coronoid is a low, sloping element that sits on the dorsal edge of the surangular. The anterior process is fairly long, but the extent of its contacts with the splenial and dentary are uncertain due to damage in this area. Dorsally, it is slightly concave, and there relatively large posteromedial process extending dorsally from behind the surangular (compared to the smaller coronoid process of *P. lesinensis*; Pierce and Caldwell, 2004).

Angular—The angular is an extremely long, splint of bone that runs below the articular. Anteriorly, it contacts the splenial; in lateral view, it is overlain dorsally by the angular. It is difficult to discern the posterior extent of this element, as several cracks along the ventral margin of the mandible conceal the true posterior margin. The two most probable margins between the retroarticular process and the angular are immediately below the posterior margin of the coronoid (as in *Varanus*) or just posterior to that point (as in *Pontosaurus lesinensis*; Pierce and Caldwell, 2004).

Surangular—Laterally, the surangular is long and robust. It stays dorsoventrally tall throughout its length, narrowing posteriorly far less than in *Pontosaurus lesinensis* (Pierce and Caldwell, 2004). The damage at the anterior end of the surangular means that the shape of the contact with the dentary cannot be determined. Anterodorsally, the element flattens on the dorsolateral surface to create a seat for the coronoid. A small, low coronoid buttress can be observed at the posterior end of this seat. Laterally, in the middle of the element are three circular depressions in a line. A small foramen sits in a longitudinal groove on the posterodorsal surface (also observed in *P. lesinensis*). Posterodorsally, the surangular rises slightly to contact the ventral surface of the quadrate. Laterally, the surangular appears to be the sole contributor to the articular cotyle, to the exclusion of the articular. Though there is a crack through the slab in this area, small portions of the suture are visible anterior to the crack, and posterior to the quadrate contact. Posteriorly, the contact with the articular is obfuscated by a crack in the limestone that runs almost exactly through the suture.

Articular-Prearticular—Damage and cracking throughout the mandible obscures the suture between the articular and prearticular. In *Pontosaurus lesinensis* the elements are fused into one compound bone (Pierce and Caldwell, 2004), a state also observed in mosasauroids

(Russell, 1967; Debraga and Carroll, 1993). Anteriorly, the (pre)articular is extremely narrow, running ventrally to the surangular to contact the angular at the anterior margin. Posterior to the articular cotyle, the articular forms a broad, rectangular retroarticular process which is preserved on both the left and right sides of the skull. The posterior margin is arcuate, and not inflected.

Postcranial skeleton

The postcranial skeleton of *Pontosaurus ribaguster* is articulated, almost complete, missing only the posterior part of the tail (Figure 1). There is some minor breakage and crushing throughout, and some damage resulting from acid preparation, which is most noticeable on the limbs. The vertebrae suffer the most breakage, and are run through with calcite in many places (especially the neck). The anterior half of the skeleton lies in dorsal view, slightly rotated laterally towards the right side. Just anterior to the pelvic girdle, the body is axially rotated to the right, exposing the posterior part of the skeleton in left lateral view. The cervical spine is bent to the right, while the remainder of the skeleton is laid out relatively straight.

Axial skeleton

Sixty-three vertebrae are preserved as relatively complete elements (Figure 1). It is possible to recognise twelve cervical vertebrae inclusive of the atlas-axis complex, 29 dorsal vertebrae, two sacral vertebrae, one pygal vertebra and 19 caudal vertebrae. The cervical and dorsal vertebrae are preserved in dorsal view, the pygal and caudal vertebrae in left lateral view. The dorsal and cervical vertebrae are all articulated to their adjacent ribs.

Cervical region—The cervical series is completely represented, though it is the poorest preserved portion of the axial skeleton. The neural spines have been sheared off, leaving the centra, neural canals, and fragments of transverse processes and zygapophyses. Twelve cervicals are identified, from C1 (preserving the neural arches and intercentrum) to C12, identified as such due to it placement relative to the sternal cartilage, humerus, and pectoral elements, and the morphology of the adjacent ribs. This gives the same cervical count as *Pontosaurus kornhuberi* (=12, Caldwell, 2006), but more than *Pontosaurus lesinensis* (=10/11; Pierce and Caldwell, 2004). A cervical count of ten or greater is diagnostic of the Ophidiomorpha, including pachyophiids (Lee and Caldwell, 1998; Lee et al., 1999) and other dolichosaurs (Caldwell, 2000; Lee and Caldwell, 2000; Palci and Caldwell, 2010).

Like *P. lesinensis, P. kornhuberi*, and *Acteosaurus* the cervical vertebrae increase caudally in width and length, but the change is minimal. The atlas (C1) is only recognized from the left and right neural arches, the rest is obscured within the crushed fragments of the back of the skull. Pre- and post-zygapophyses are variably present, but are in general better preserved on the right side. The prezygapophyses are straight and narrow, while the postzygapophyses are shorter, and appear more squared off and robust. The close articulation of the vertebrae and orientation of preservation means that the presence of zygosphenes and zygantra is impossible to determine. Synapophyses are visible from the third cervical onwards, but cannot be identified on C1 or C2. Hypapophyses are visible in lateral view on the C4 and C5. Posterior to this, these processes are hidden: initially covered by the cervical ribs, then the entire vertebral column rotates so that the vertebrae are only visible in dorsal view.

Remnants of cervical ribs can be seen on the left side beginning at C5 and C8 on the right, though in life the first cervical ribs were probably located more anteriorly. The cervical ribs on C5-7 are straight, splint-like and tiny: less than half the length of the associated centrum. The ribs associated with C8-10 are much more robust, longer—at least the length of the centrum—and curved. An abrupt increase in size is again noticeable in the ribs of C11 and C12. The heads on ribs C10-12 are anteriorly expanded, unicapitate, and show an anterior-dorsal ridge running lengthwise along the rib shaft.

Dorsal region—The dorsal region is made up of 29 vertebrae, for a total presacral count of 41 vertebrae. This is the similar to most other dolichosaurs with reliable dorsal counts including *P. lesinensis* (28 dorsals, 40 presacrals; Pierce and Caldwell, 2004), *P. kornhuberi* (26 dorsals, 38 presacrals; Caldwell, 2006), *Adriosaurus suessi* (29 dorsals; Lee and Caldwell, 2000), *Adriosaurus microbrachis* (28 dorsals; Palci and Caldwell, 2007), and *Acteosaurus* (27 dorsals; Palci and Caldwell, 2010). *Mesoleptos* (Cornalia, 1852) and *Eidolosaurus* (Nopcsa, 1923) were both described as having 23 dorsal vertebrae, and *Dolichosaurus longicollis* at least 32 (Caldwell, 2000), all well outside this range. Like the other two *Pontosaurus* species and other dolichosaurs, the vertebrae increase in size posteriorly until the last few vertebrae before the pelvis, where the vertebrae show a decrease in size and robustness that corresponds to a decrease in rib length and thickness. In *P. lesinensis*, this transition happens around the 25th of 28 dorsals, in *P. kornhuberi* the 22nd of 26, and in *P. ribaguster* around the 24th of 29. The posterior-most dorsal vertebrae also appear to be more tightly articulated than the anterior series, though this could be an artifact of taphonomy, resulting from torsion of the body.

The butterfly-shaped neural arches common to dolichosaurs are well preserved. The pre-zygopophyses project anterolaterally at slightly less than 45° to the sagittal plane. The smaller, triangular post-zygopophyses project laterally. The facets do appear to incline above the horizontal to face ventrolaterally. Zygosphene-zygantra articulations are present throughout the dorsal column, and are most visible around D10-D14. The neural spines are broken off, though their bases are easily identified along the column, and in some places their remains can be seen projecting over the subsequent vertebral centra as in *Adriosaurus skrbinensis* (Caldwell and Palci, 2010). The neural spines are thick and robust (more so than in *Carentonosaurus mineaui*; Rage and Néraudeau, 2004), and appear pachyostotic. Overall, the vertebrae are broad (wider than long), robust, and rounded, indicating some degree of pachyostosis. Pachyostosis can also be observed in *Carentonosaurus mineaui* (Rage and Néradeau, 2004), *Adriosaurus suessi* (Seeley, 1881), *Mesoleptos zendrini* (Cornalia and Chiozza, 1852), and pachyophiid snakes.

All dorsal vertebrae support ribs that articulate with the anteriorly positioned synapophyses (as in other ophidiomorphs; Pierce and Caldwell, 2004). The right ribs are partially visible until about dorsal vertebra 15. Posterior to this, the animal is rolled enough that only the left ribs are visible. Rib tips visible between the rib cage on the left side (especially around D21-24) show the true length of the ribs (five-six vertebral lengths), which almost meet the opposing rib. In profile, the ribs appear slightly flattened dorsoventrally. Where they articulate with the vertebrae, the ribs have slightly expanded heads, broader than seen on the cervical ribs. Farther from the zygapophyses, they get rounder, before narrowing to a point distally. The dorsal ribs protrude almost laterally from the midline before bending ventrally and posteriorly to form a rough semicircle which is unlike the relatively straight ribs of *Acteosaurus tommasinii* (Palci and Caldwell, 2010), or the distally straight ribs of *Mesoleptos zendrinii* (Lee and Scanlon, 2002) and *Adriosaurus suessi* (Seeley, 1881). This results in a deep and laterally compressed body profile that was likely vertically oval in cross section. This is also in contrast to *Acteosaurus* (Calligaris, 1993; Palci and Caldwell, 2010) and *Adriosaurus* (Seeley, 1881; Palci and Caldwell, 2007; Caldwell and Palci, 2010) who have heavily pachyostotic vertebrae and ribs along their length. The anterior ribs are extremely robust and may represent a pachyostotic adaptation to a coastal aquatic lifestyle as seen in *Aigialosaurus bucchichi* (Dutchak and Caldwell, 2009). This is in stark contrast to the slender ribs of *Dolichosaurus longicollis* (Caldwell, 2000).

The last nine ribs (D21-D29) are markedly thinner than the more anterior ribs as in *Kaganaias hakusanensis* (Evans et al., 2006), and the final three ribs appear distinctly shorter than the rest, they are damaged, making their precise length difficult to determine. Relatively short ribs associated with the last three vertebrae is also observed in *Pontosaurus kornhuberi* (Caldwell, 2006): a condition noted by Kornhuber (1901) who described them as 'dorsolumbar' ribs. This pattern of gradually increasing and then abruptly decreased pachyostosis along the dorsal series varies in precise location among species, but is also seen in *Aigialosaurus bucchichi* (Dutchak and Caldwell, 2009), *P. kornhuberi* (Caldwell, 2006), *P. lesinensis* (Pierce and Caldwell, 2004), *Dolichosaurus longicollis* (Caldwell, 2000), and *K. hakusanensis* (Evans et al., 2006).

Sacral region—The left pelvic region clearly shows both sacral vertebrae with their respective sacral ribs in articulation with the ilium. The sacral vertebrae are noticeably smaller than the preceding dorsal vertebrae. The transverse processes are hugely expanded, almost as wide as their associated vertebrae are long, a situation also observed in *Adriosaurus skrbinensis* (Caldwell and Palci, 2010). The sacral ribs are in contact along the distal half of their length, with the second curving forward slightly to meet the first. The shape of the first is more bulbous distally, the second is more subrectangular. The first rib appears to have a distal 'shoulder', where it abruptly narrows to articulate with the ilium. The neural spines are short, stout, and round; the first in particular, appears almost semicircular in lateral view. Comparisons between the sacral vertebrae of *Pontosaurus ribaguster*, and that of *P. lesinensis* and *P. kornhuberi* are difficult due to the poor preservation of the sacral region in all three specimens, though all are interpreted as having two sacral vertebrae (Pierce and Caldwell, 2004; Caldwell, 2006).

An alternative hypothesis would be an interpretation more similar to that seen in *Pontosaurus kornhuberi* (Caldwell, 2006). It is possible that the crack that obliterates the pelvis of *P. ribaguster* runs through the first sacral, rather than the 29th dorsal, and that the plate-like bone fragments anterior to what I have identified as the first transverse process are the first sacral 'rib' aligned with the second sacral transverse process. According to this interpretation, the element I identified as the second sacral vertebrae would be a pygal in contact with the ilium (as in *P. kornhuberi*). This would give the animal a dorsal count of 28, a sacral count of two, and a pygal count of two.

Pygal region— Immediately posterior to the second sacral vertebra is a vertebra in contact with the ilium but not articulated with it. This is interpreted as a pygal vertebra as it does not possess haemal arches. As in *Acteosaurus*, the vertebra is slightly shorter anteroposteriorly than the posterior dorsals and anterior caudals (Palci and Caldwell, 2010). It resembles the two pygals of *Pontosaurus kornhuberi* (Caldwell, 2006) in having reduced neural spines, longer centra relative to the sacrals, and a distally narrowed transverse process. Unlike *P. kornhuberi* however, the transverse process is directed anteriorly.

Caudal region— *Pontosaurus ribaguster* preserves the remains of 19 caudal vertebrae in left lateral view. The whole tail appears laterally compressed (as in *P. kornhuberi*; Caldwell, 2006), and very tall as a result of elongate haemal and neural spines. As in other dolichosaurs, the vertebral centra are longer than tall, and do not contribute much to this compression; this is another feature distinguishing them from mosasauroids (Russell, 1967). The zygapophyses remain quite robust and large—especially the prezygapophyses—throughout the preserved portion of the tail. This is very similar to the situation in *Acteosaurus* (Palci and Caldwell, 2010). The vertebrae show a minimal decrease in size from the first to last, indicating that the tail would have been very long, probably contributing to at least half of the total body length. For comparison, *P. kornhuberi* has a complete tail numbering 163 vertebrae; 63% of its body length (Caldwell, 2006).

The first caudal shows the remains of enlarged transverse processes that are noticeably different in shape and orientation from the remainder of the caudal vertebrae. The first seems to project anteriorly, and the second laterally. This is a similar observation to that made by Caldwell (2006) in his description of *Pontosaurus kornhuberi*, who describes an anteriorly directed 'j'-shaped process in dorsal view. He suggests that these might be lymphapophyses: modified transverse processes that support lymph node clusters superior to the cloaca. Alternatively (or additionally), it could represent the insertion for the *m. caudofemoralis*, a muscle integral to tail-driven locomotion. The transverse processes on the remainder of the caudal vertebrae are broken off, but their bases are dorsoventrally thin and axially quite long, stretching almost the entire length of the centra.

The first caudal vertebra also shows a unique neural spine morphology compared to the rest of the caudal region. It is much broader, is more squared off at the corners, and projects more dorsally than the remainder of the neural spines. This gives the appearance of an almost continuous surface of bone laterally, with very few spaces. This seems consistent with a laterally compressed tail and a robust area of attachment for large caudal muscles. The remainder of the neural spines are thinner (anteroposteriorly), and project more posteriorly (about 40° off the horizontal) similar to the anterior caudals of *Pontosaurus kornhuberi*. However, the posterior neural spines of *P. ribaguster* are not as broad as *P. kornhuberi*, leaving larger spaces between them. The neural spines show a shelf roughly halfway up the anterior margin.

The haemapophyses are positioned posteriorly on the centrum, such that the haemal arches contact the anterior margin of the following vertebra. Like *Pontosaurus kornhuberi*, the haemals of *P. ribaguster* do not fuse to the haemapophyses (Caldwell, 2006). The haemals themselves fuse roughly halfway down their length, forming a true haemal arch, which extends ventrally into a haemal spine. They are about twice as long as the neural spines. It is possible that the depth of the tail would have been at least twice that indicated by the osteology based on the soft tissue preservation in *P. kornhuberi* (Caldwell, 2006).

Appendicular skeleton

The appendicular skeleton is mostly present, but not well preserved. Both right and left forelimbs lie beside the trunk in relatively natural position on their respective sides (Figure 3). The left limb is better preserved than the right, with most the carpal elements and phalanges preserved in place. The right limb suffered more severe damage and is rotated about the longitudinal axis of the humerus resulting in the dislocation and breakage of the more distal elements. The radius and ulna are crossed, and the bones of the manus are scattered. The left and right coracoids are visible, as is the left scapula. Some cartilage associated with the sternum and pectoral girdle is also preserved. The pro- and epipodials are the same length and together make up about half the total length of the forelimb (similar to the condition in *Pontosaurus lesinensis* and *P. kornhuberi*; Pierce and Caldwell, 2004; Caldwell, 2006). The hindlimb elements are figured in Figure 4. The left hindlimb lies away from the body and is mostly present, except for the metatarsal elements and most of the fibula. Except for the distal phalanges, the right hindlimb lies underneath the body. However, epipodial elements can be identified between the ribs, and most of the tarsals are exposed. The right pelvis is completely obscured by the body, but the left pelvis is mostly complete and exposed. Unfortunately, a break in the limestone block passes straight through the anterior pelvic region, obscuring many details.

The front legs are about half the length of the back legs, which makes them proportionally shorter than in *P. kornhuberi*. The front limbs are slightly shorter than the length of the head, which is similar to the condition in *P. lesinensis*. The femur is longer than the tibia/fibula, and the combined length of these elements is roughly equivalent to the length of the pes. Thus, *P. ribaguster* follows the trends in pontosaur limb evolution outlined by Caldwell (2006): 1) reduction in limbs relative to body size; 2) reduction of the forelimb relative to the hindlimb; and 3) reduction of the pro- and epipodial elements relative to the manus and pes.

Pectoral girdle—Though the degree of breakage and crushing makes interpretation difficult, it does appear that the scapula and coracoid are unfused as in most aigialosaurs (Carroll and Debraga, 1992), *Coniasaurus gracilodens* (Caldwell, 1999a), *Dolichosaurus longicollis* (Caldwell, 2000) and *Acteosaurus tommasinii* (Palci and Caldwell, 2010). This is contrary to the interpretation of *P. lesinensis* (Pierce and Caldwell, 2004); the condition in *P. kornhuberi* could not be determined (Caldwell, 2006). None of the scapulae or coracoids is complete and therefore the relative sizes of the two elements is uncertain, though they do appear to be reduced as in *P. lesinensis* (Pierce and Caldwell, 2004). Unusually, there is a foramen visible on both left and right scapula near the glenoid rim, a feature also present in *Carentonosaurus mineaui* (Rage and Néraudeau, 2004) but absent in other dolichosaurs. The scapular blade (visible on the left side) is

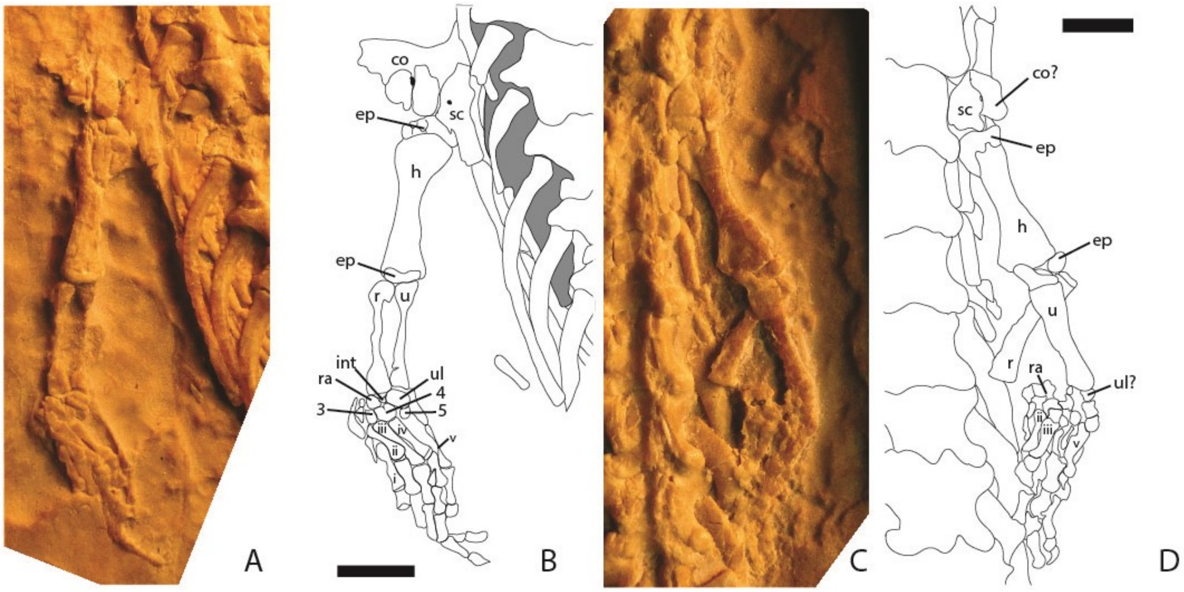

Figure 2-3 Forelimbs and pectoral region of *Pontosaurus ribaguster* (HPM 10807). **A**, photograph of left forelimb and girdle; **B**, interpretive drawing of A; **C**, photograph of right forelimb and girdle; **D**, interpretive drawing of C. Shaded areas represent cartilaginous remains. **Abbreviations**: **co**, coracoid; **ep**, epiphysis; **h**, humerus; **int**, intermedium; **r**, radius; **ra**, radiale; **sc**, scapula; **u**, ulna; **ul**, ulnare, **2-5**, distal carpals; **i-v**, metacarpals. Scale bars equal 5 mm.

quite long, and projects posteriorly. The coracoid margin is broken bilaterally, but is slightly more complete on the right side. It appears to be roughly fan-shaped as in *Coniasaurus* and *Haasiasaurus* (Caldwell, 1999a; Polcyn et al., 1999). A coracoid foramen is identifiable on the left side, though the presence of an anterior emargination cannot be confirmed. I cannot reasonably identify any clavicle or interclavicles.

Cartilage preserved anterior and medial to the coracoid on the right side is interpreted as the supracoracoid cartilage. Fragments of the sternal cartilage are also visible between the dorsal ribs 1-4 on the left side, along with fragments of probable bronchial cartilages.

Overall, the pectoral girdle is relatively small and gracile, corresponding to the reduction of the forelimbs.

Humerus—Both left and right humeri are preserved in dorsal view. The right humerus suffered less breakage and better preserves anatomical details. The humerus is expanded at both ends, constricted at mid-shaft, and small (roughly two vertebrae long), typical of a dolichosaur. Thick epiphyses are present on both proximal and distal heads. Proximally, the lateral tubercle is quite large, and there is a crest for the attachment of the deltoid muscle. Distally, as in *Pontosaurus lesinensis* and *P. kornhuberi*, the capitulum and trochlea appear flattened and reduced. The distal epiphysis bears a bulbous expansion over the capitulum that articulates with the radius.

Radius and ulna—The epipodials are not well preserved on either side: on the right, they appear dissolved away mid-shaft, leaving only fragments of the distal and proximal ends; the left side is more complete, but the manus has been flipped over, dislocating and crossing the ulna over the radius. The left forelimb—still in articulation, though medially crushed—shows that the radius and ulna are in close proximity proximally where they articulate with the humerus. Distally, they were most likely divergent, as evidenced by the position of the right carpal elements, resulting in a wide antebrachial space as in *Pontosaurus kornhuberi* (Caldwell, 2006). This is common to most mosasauroids (Russell, 1967; Caldwell et al., 1995) and dolichosaurs (e.g., *Adriosaurus suessi,* Lee and Caldwell, 2000) and contributed to the formation of a wide, flat forearm.

The radius is simple and rod-like, with a squared off proximal end, and an expanded, flat distal end. Medially, it is concave, and laterally it is fairly straight. Overall, it is extremely similar in shape to *Pontosaurus kornhuberi* (Caldwell, 2006).

The ulna is broader than the radius, but a similar length. It is thickened proximally and distally, and is constricted along the shaft. The proximal expansion is greater, and it is possible to identify the remains of the olecranon process on the proximal end of the left ulna curving around the humerus, very similar in shape to *Adriosaurus skrbinensis* (Caldwell and Palci, 2010). The distal epiphysis is well developed and articulates with the ulnare.

Carpals—The crushed and dislocated nature of the right manus prohibits meaningful interpretation, but the majority of the left wrist is better preserved. There are four carpal elements preserved in each of the proximal and distal rows. The ulnare, intermedium, proximal centrale, and radiale make up the proximal row, and distal carpals two through five are in the distal row. There is no identifiable pisiform element, which is not unexpected given the poor preservation of the fifth digit. The ulnare is large and laterally contacts a small intermedium, which is in turn contacting a large centrale. Small fragments of the radiale are preserved lateral to the centrale. The remnants of the radiale are one of the few identifiable carpal elements in the right limb, and based on this, the radiale was quite large and sub rectangular. Below these four elements are carpals two through five. The third and fourth are still in articulation with their respective metacarpals, while metacarpals two and five have been taphonomically disturbed. Like other dolichosaurs, carpal four is the largest, followed by carpals three, five and two. Overall the carpal morphology of all three *Pontosaurus* species is similar (Pierce and Caldwell, 2004; Caldwell, 2006): flattened and distally enlarged, which may have prevented wrist mobility, especially pronation.

Metacarpals—Though it is possible to tentatively identify metacarpals in the right manus, it is the left manus that best preserves them. All five are present. However, the first and fifth are mostly broken away, leaving fragments and impressions. The third metacarpal is the longest (roughly the length of the pro- and epipodials combined), followed by the fourth, and second. The first and fifth appear shorter than the rest, but their exact lengths are uncertain. The three preserved metacarpals are elongate and straight, expanded at the ends, and constricted midshaft. Metacarpals two, three and four articulate with their respective distal carpals, and it appears that metacarpal five may have articulated with distal carpal five and the ulnare, but this could be taphonomic displacement.

Phalanges—The phalanges are mostly preserved, with the distal ends of digit one, two, four, and five preserved as natural moulds. The phalangeal formula appears to be 2-3-4-5-3, which is primitive for lepidosaurs (Carroll, 1988). Like other dolichosaurs (*Pontosaurus lesinensis,* Pierce and Caldwell, 2004; *Pontosaurus kornhuberi*, Caldwell, 2006; *Adriosaurus,* Palci, 2007), the longest digit is the fourth, then the third, second, fifth and first. The length of the digits relative to each other is essentially the same length as to the other *Pontosaurus* species (pers. obs.). The phalanges are hourglass-shaped and typical of other dolichosaurs. The small terminal unguals are poorly preserved, but appear claw-like and pointed, with a well-developed ventral tubercle.

Pelvic girdle—Only the left half of the pelvic girdle is exposed in the specimen, the right being presumably hidden under the body. Only the ilium is well preserved. The other elements are obscured by a break in the limestone slab, which passes through the first sacral vertebrae, the ischium, and the pubis (Figure 4).

The ilium is extremely elongate through the posterior superior iliac crest, which articulates with the two sacral ribs and contacts the pygal vertebra. Anteriorly, the element expands to meet the ischium and pubis before narrowing and hooking ventrally into the preacetabular iliac process, which is much more elongate than seen in *Acteosaurus tommasinii* (Palci and Caldwell, 2010) or *Adriosaurus suessi* (Lee and Caldwell, 2000). Like *Pontosaurus kornhuberi* (Caldwell, 2006) and *Dolichosaurus longicollis* (Caldwell, 2000). A small anterodorsal process is visible just above the acetabular depression.

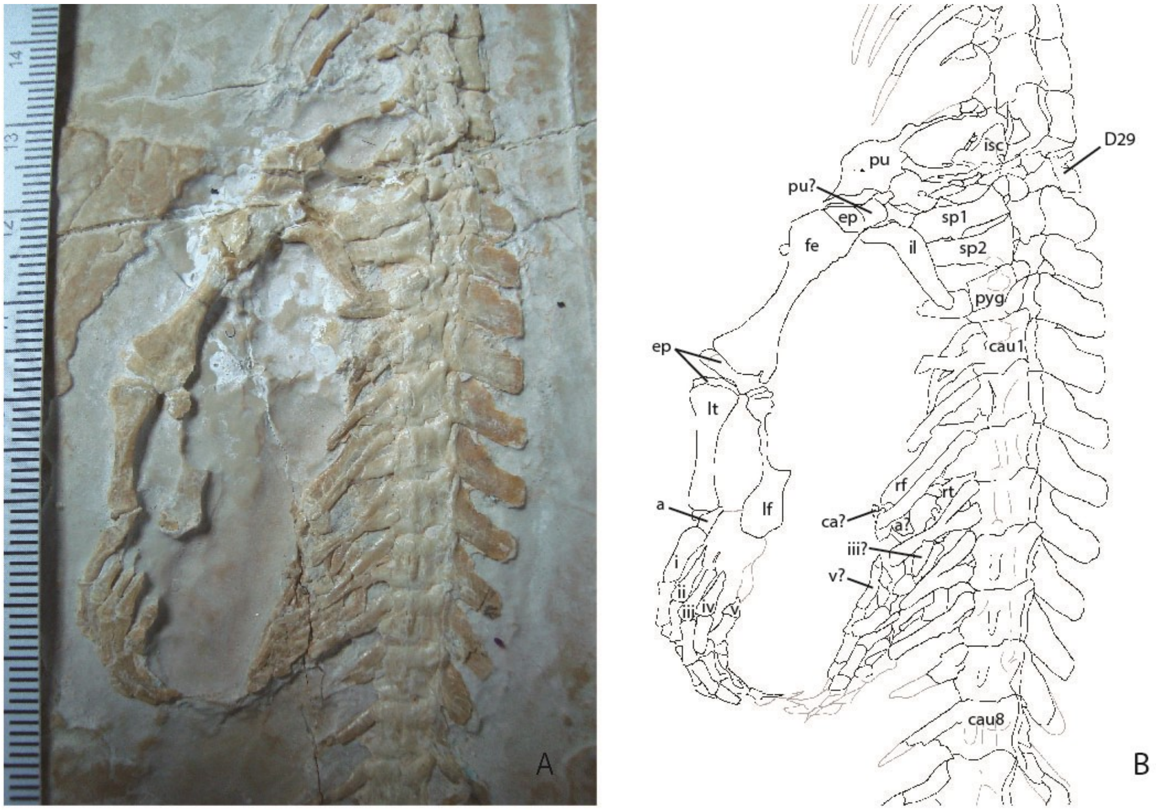

Figure 2-4 Hindlimbs and pelvic region of *Pontosaurus ribaguster* (HPM 10807). **A**, photograph showing left and right hindlimbs, pelvic region, posterior dorsal and anterior caudal vertebrae; **B**, interpretive drawing of (A). Grey lines indicate impressions. **Abbreviations**: **a**, astragalus; **ca**, calcaneum; **cau**, caudal vertebra; **ep**, epiphysis; **fe**, femur; **il**, ilium; **ics**, ischium; **lf**, left fibula; **lt**, left tibia; **pu**, pubis; **pyg** pygal vertebra; **rf**, right fibula; **rt**, right tibia; **sp**, sacral process; **i-v**, metatarsals 1 to 5.

The large, robust pubis is broken, but the general hatchet-shape typical of dolichosaurs is visible. The proximal head of the element is mostly present, preserving the pubic foramen and the anterior pubic process. The medially-directed shaft is mostly broken away, and only a sliver remains.

The poorly preserved ischium is split through the middle, with pieces separated and missing. It appears to be shorter than the pubis, and curved along its anterior margin for the thyroid fenestra as in *Acteosaurus tommasinii* (Palci and Caldwell, 2010) and *Adriosaurus skrbinensis* (Caldwell and Palci, 2010). It also has a posteriorly directed groove midshaft as in *Pontosaurus kornhuberi* (Caldwell, 2006). Otherwise, not much detail can be ascertained.

Femur—The femur is the longest appendicular bone at 24 mm (roughly four vertebral lengths). It is almost twice the length of the epipodials, and twice the length of the humerus. Like the other appendicular long bones, it is proximally and distally expanded, and constricted midshaft. Proximally, and especially distally, the ends are also flattened dorsoventrally. A large, semicircular epiphysis caps the proximal end of the femur where it articulates with the acetabulum. A well-developed trochanter is visible on the proximal head. Distally, another epiphysis caps the femur, this one with rounded condyles for the articulation of the tibia and fibula. Like *P. kornhuberi*, the shaft bears a long proximal-distal crest, distal to which is a long fossa. This has been interpreted as the insertion of the *m. caudofemoralis* (Caldwell, 2006).

Tibia and fibula—The tibia is roughly half the length of the femur and slightly shorter than the fibula, which itself is approximately the length of the ilium. The tibia is preserved mostly intact, while the fibula is missing most the proximal half. Proximally, both are capped with thick epiphyses. Distally, the two elements are divergent, creating a wide and flattened limb. The tibia is proximally expanded, and slender along the rest of its length. It is much more gracile than the fibula. It has a long crest running longitudinally. The fibula, though broken, shows the opposite condition to the tibia, being more expanded distally than proximally. This condition can be observed in *Pontosaurus kornhuberi* (Caldwell, 2006), *Acteosaurus tommasinii* (Palci and Caldwell, 2010) and *Adriosaurus suessi* (Lee and Caldwell, 2000). Both elements are fairly straight along their outer edges, and concave on their inner margins creating an enlarged antebranchial space. The distal end of the fibula narrows at just proximal to the distal articular surface forming a 'bulb'-shaped distal end. It is unclear whether this shape is anatomical, or taphonomic.

Tarsals—Two mesopodial elements are preserved in the left pes, and several fragments in the right. An unknown element preserved in the left pes resting against the distal end of the tibia is of a similar shape, size, and position to another unknown element identified in *Pontosaurus kornhuberi* (Caldwell, 2006), and could represent a distal epiphysis of the tibia. The second tarsal element is interpreted as the astragalus. In the right pes, several small elements can be seen between the ribs. Most of these are unidentifiable, though the large element distal to the fibula is likely the calcaneum (fibulare).

Metatarsals—The metatarsals are all represented on the right pes, though only the first is complete. Remains of the left metatarsals are also preserved under the body, though they are broken, dislocated, and difficult to differentiate. As in the manus, the middle three are longer than the first and fifth, with metatarsal three being the longest. These relative sizes are the same as *Acteosaurus tommasinii* (Palci and Caldwell, 2010). All appear hourglass-shaped with proximal and distal expansions. Metatarsal I is the only complete element, and like *A. tommasinii,* the proximal end is square, while the distal end is rounded. The first metatarsal is unique compared to the other four in being expanded along the length, making it more robust than the other four. This is an aquatically derived feature associated with the thick leading edge of a hydrofoil, and is seen in a number of other secondarily aquatic amniote groups (e.g., ichthyosaurs, pleasiosaurs). Epiphyses are visible on several metatarsal elements.

Phalanges—The phalanges are relatively well preserved considering the poor preservation of the meso- and metapodium. The phalangeal formula appears to be 2-3-4-5-3, though the count is not certain since several phalangeal elements are crushed against their neighbours and/or preserved as vague impressions. The fifth digit is particularly ambiguous, and may have four phalangeal elements. Unfortunately, neither pes is preserved well enough to make this distinction, as both could be interpreted as having either three or four phalanges in the fifth digit.

The phalanges of the pes are constricted midshaft, with proximal and distal expansions bearing two distinct condyles for articulation with their preceding and subsequent element. The terminal unguals are—like the manus—small, claw-like, and hooked with a sharp tip and distinct ventral tubercles for ligamentous attachment.

Gastric contents

Preserved high in the abdominal cavity, well in front of the pelvis, are a number of disarticulated elements identified as gastric contents (Figure 1). They lie within the body cavity between the tenth and seventeenth dorsal vertebrae. The remains are tightly packed, and appear to occupy the entire body cavity, indicating that they are gastric rather than colonic contents, as colonic contents would be constrained to a narrower, more longitudinal space (as in the well delineated colonic remains of *Platecarpus tympaniticus*, LACM 128319; Lindgren et al., 2010).

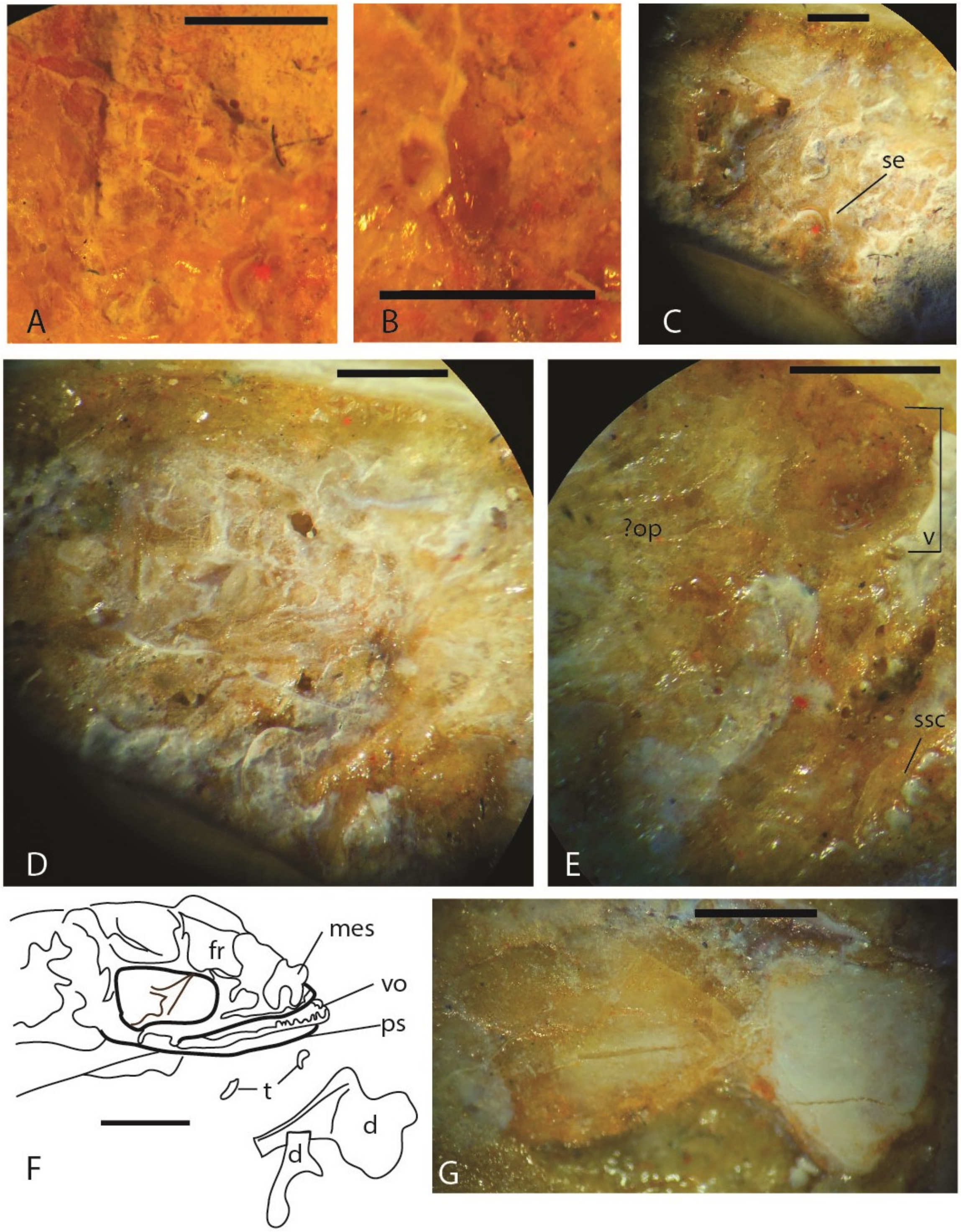

Figure 2-5 Abdominal contents of *Pontosaurus ribaguster* (HPM 10807). **A**, a grouping of cycloid scales from a teleost fish; **B**, teleost tooth; **C**, unidentified bony element with spiny process; **D**, skull and dentary elements from teleost fish; **E**, vertebrae, and dercetid scale; **F**, interpretive drawing of D; **G**, *Eurypholis* scale located in posterior dorsal region. **Abbreviations**: **d**, dentary; **fr**, frontal; **mes**, mesethmoid; **op**, operculum; **ps**, parasphenoid; **ssc**, serrated scutes; **t**, tooth; **v**, vertebra; **vo**, vomer (with teeth). Scale bars equal 1 mm.

They occupy the same space as the gastric contents reported in *Adriosaurus skrbinensis*, which lie between the tenth and eighteenth dorsal vertebrae (of 30; Caldwell and Palci, 2010).

Scattered among unidentifiable, partially digested scraps are several elements that can be confidently ascribed to teleost fishes. They include cycloid scales (Figure 5a), several peg-shaped teeth (Figure 5b, d, f), and vertebrae and an opercular element (Figure 5e). Certain remains indicate the presence of at least three separate fish. The first is a nearly complete, articulated skull roughly 5 mm long (Figure 5d, f). The skull is well enough preserved that is possible to identify the maxilla, vomer, frontals, parasphenoid, and mesethmoid. Unfortunately, it is impossible to confidently classify it beyond Teleostei.

Lunate scutes with serrations on their posterior, concave margins (Fig 5e) are comparable to the flank scutes of dercetid fishes (order Aulopiformes, suborder Enchodontoidei), and would correspond to a fish approximately 10 cm long (Bieńkowska-Wasiluk et al., 2015, Figure 5j, k). Figure 5g shows a pair of triangular, shield-shaped scales, one of which shows a long canal for sensory structures running down the midline. These are diagnostic of *Eurypholis*, a dercetid fish known the Cenomanian-Turonian of the Tethys (Woodward, 1901; Gallo et al., 2005). These eponymous broad, shield-shaped scales lay on the dorsal portion of the torso, just posterior to the head. The 2 mm long scales represent a fish approximately 5-6 cm in length. It is important to note that the *Eurypholis* scales are not found within the stomach area that all the other remains are in, but are found between the 25th and 26th dorsal ribs. This could indicate preservation within the colon, or could be unassociated with the lizard, and deposited posthumously.

PHYLOGENETIC ANALYSIS

The specimen is clearly a squamate, as it possesses the following squamate synapomorphies identified by Estes et al. (1988): single-headed ribs, transverse fronto-parietal suture, and fused parietals. The elongate body and laterally compressed tail are distinguishing features which are rare among squamates, found only in the Pythonomorpha. The pachyostotic ribs, elongate neck, and considerably smaller forelimbs compared to hindlimbs are synapomorphies of the Ophidiomorpha (Caldwell and Palci, 2010). The well developed forelimbs and length of the neck mean that among ophidiomorphs, the specimen can be classified as a 'dolichosaur' grade animal rather than a true ophidian. *Pontosaurus ribaguster* is considered to be a basal ophidiomorph because it exhibits axial elongation and limb reduction (especially in the forelimb). Like other *Pontosaurus* species, it has a diagnostic W-shaped parietal-supraoccipital suture. The vertebral count also more closely matches that of *P. kornhuberi* and *P. lesinensis* than any other ophidiomorph lizard.

In order to test this anatomy-based phylogenetic placement summarized above, *Pontosaurus ribaguster* was included in a phylogenetic analysis of dolichosaur grade ophidiomorphs that is based on a modified version of the Simões et al. (2017) dataset. Historically, phylogenetic analyses for dolichosaurs have been derived from Lee (1998). The Simões et al. (2017) dataset was chosen because it was created to identify relationships specifically within the Pythonomorpha, rather than the Squamata as a whole. A dataset designed specifically to address interrelationships among the ophidiomorph lizards would be ideal in this case, but is beyond the scope of this study.

In addition to *Pontosaurus ribaguster*, thirteen species of ophidiomorph lizard were included in the analysis: *Acteosaurus tommasinii,* three species of *Adriosaurus* (*A. suessi, A. skrbinensis, A. microbrachis*), *Coniasaurus crassidens* and *C. gracilodens*, *Dolichosaurus longicollis*, *Eidolosaurus trauthi*, *Kaganaias hakusanensis*, *Mesoleptos zendrinii*, and the two previously reported pontosaurs (*P. kornhuberi* and *P. lesinensis*). These thirteen species were coded according to Simões' (2017) dataset of 131 osteological characters (see character list, Appendix 1). Character codings were based on direct examination of the material. After coding, 60 characters were found to be variant. The final matrix used is in Appendix 2.

The data was analysed using the heuristic search algorithm (traditional search with tree bisection reconnection swapping algorithm) and New Technology Search (sectorial search, drift, and tree fusing algorithms) in TNT (Goloboff et al., 2008a), employing 1000 random sequence additions. All characters were analyzed unordered and without character weighting. For determining character polarity, the hypothetical outgroup of Simões' (et al.,2017; based on Bell, 1997) was used. The degree of support for each grouping was ascertained through bootstrapping and jackknifing, calculated in TNT. Results are visualized in Figure 6.

In the parsimony analysis, both heuristic and new technology searches recovered 6 optimal trees, each with a length of 78 (similarity = 0.91). The strict consensus tree (which was the same for both search methods) is shown in Figure 6a with bootstrap and jackknife supports.

The same data was also tested using model-based methods. Maximum likelihood analysis (MK substitution model, gamma distribution, ascertainment bias correction) was performed using W-IQ-TREE (Trifinopoulos et al., 2016). Branch support was then established using approximate likelihood ratio supports and bootstrap values. The strict consensus tree is displayed

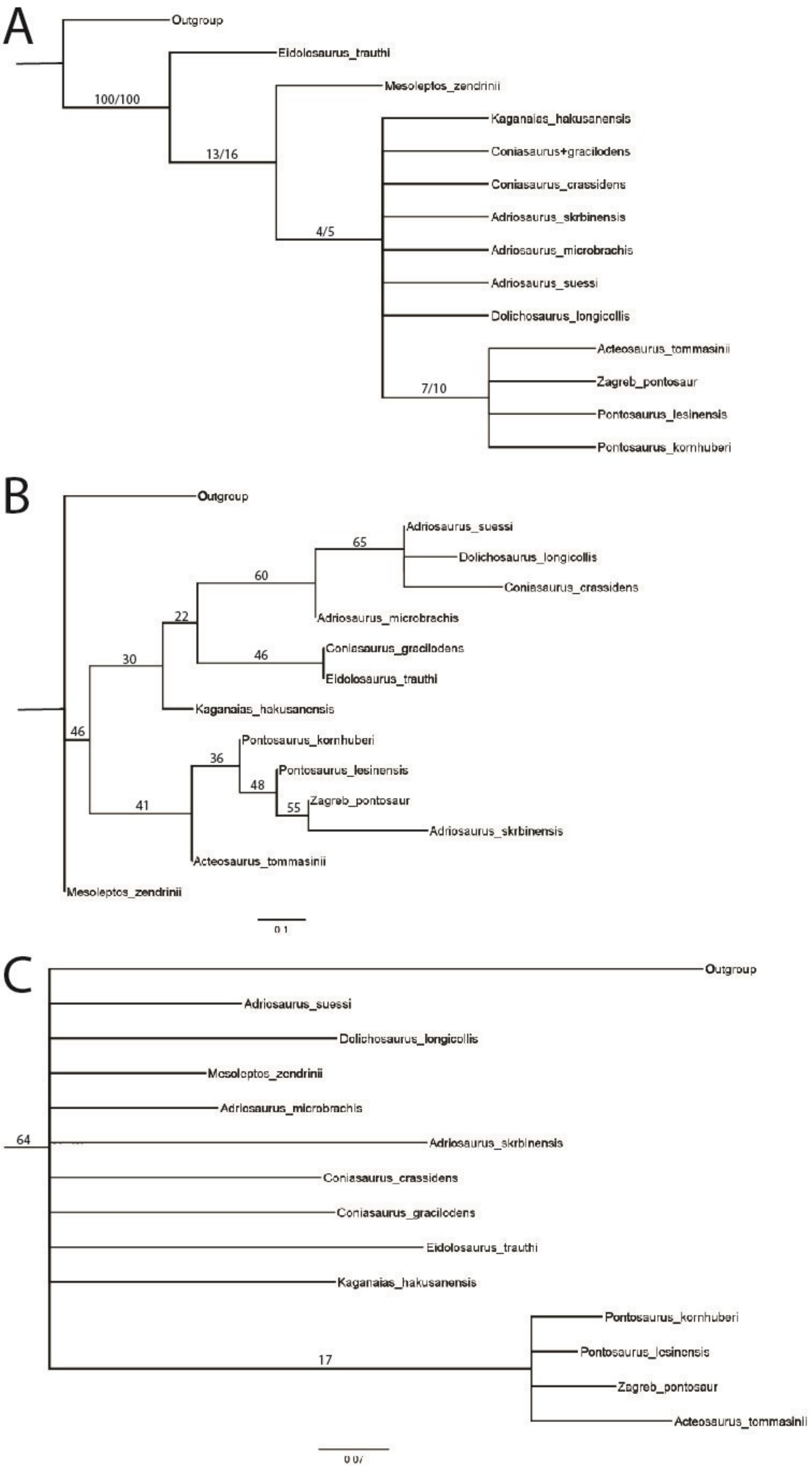
A
Outgroup
Eidolosaurus_trauthi
100/100
Mesoleptos_zendrinii
13/16
Kaganaias_hakusanensis
Coniasaurus+gracilodens
Coniasaurus_crassidens
Adriosaurus_skrbinensis
4/5
Adriosaurus_microbrachis
Adriosaurus_suessi
Dolichosaurus_longicollis
Acteosaurus_tommasinii
Zagreb_pontosaur
7/10
Pontosaurus_lesinensis
Pontosaurus_kornhuberi
B
Outgroup
Adriosaurus_suessi
65
Dolichosaurus_longicollis
60
Coniasaurus_crassidens
Adriosaurus_microbrachis
22
Coniasaurus_gracilodens
46
30
Eidolosaurus_trauthi
Kaganaias_hakusanensis
46
Pontosaurus_kornhuberi
36
Pontosaurus_lesinensis
48
55
Zagreb_pontosaur
41
Adriosaurus_skrbinensis
Acteosaurus_tommasinii
Mesoleptos_zendrinii
0.1
C
Outgroup
Adriosaurus_suessi
Dolichosaurus_longicollis
Mesoleptos_zendrinii
Adriosaurus_microbrachis
64
Adriosaurus_skrbinensis
Coniasaurus_crassidens
Coniasaurus_gracilodens
Eidolosaurus_trauthi
Kaganaias_hakusanensis
Pontosaurus_kornhuberi
Pontosaurus_lesinensis
17
Zagreb_pontosaur
Acteosaurus_tommasinii
0.07

Figure 2-6 Phylogenetic analysis of dolichosaur relationships using different methods. **A**, unweighted maximum parsimony, strict consensus of six most parsimonious trees (78 steps each): values above branches indicate bootstrap values and jackknife values. **B**, maximum likelihood: branches proportional to their length, values above branches indicate bootstrap values, scale bar represents branch length. **C**, Bayesian clade credibility tree drawn from 8912 posterior trees: branches are proportional to their length, values above branches indicate clade probabilities, scale bar represents branch length. *Pontosaurus ribaguster* is here named the 'Zagreb pontosaur'.

in Figure 6b. Bayesian analysis (gamma rates, 8 categories, 10000000 generations, burn in fraction 0.25, temperature = 0.01) was performed using MrBayes (Ronquist et al., 2011), the clade credibility tree (consensus tree) is shown in Figure 6c.

The basic topologies of the trees show similar patterns. In both parsimony and model based methods, the three pontosaurs are grouped together with *Acteosaurus*. However, the maximum likelihood tree recovers *Adriosaurus skrbinensis* in this pontosaur clade, and removes *Actersaurus* to sistergroup status of this clade.. The Bayesian and parsimony trees show a four-way polytomy within the pontosaur clade (three *Pontosaurus* species and *Acteosaurus*). Outside of this clade is a polytomy with most of the other dolichosaurs. Parsimony and maximum likelihood retrieve *Mesoleptos* and *Kaganaias* as basal to the other dolichosaurs, though maximum likelihood recovers it as basal to the dolichosaur lineage that excludes *Pontosaurus* and *Acteosaurus*.

The results of the maximum likelihood analysis show the most difference from the other methods. The three *Pontosaurus* species are grouping in a monophyletic clade as in the other methods, but as mentioned, *Adriosaurus skrbinensis* is also recovered in this clade. *Acteosaurus* falls out as the sister taxon to the pontosaur clade. A large sister clade to the pontosaur-acteosaur group contains a nested set of taxa not grouped according to their genus: *Adriosaurus suessi*, *Dolichosaurus longicollis*, and *Coniasaurus crassidens* form a polytomy with *Adriosaurs* *microbrachis* as their sister taxon. Basal to this group of four are *Coniasaurus gracilodens* and *Eidolosaurus trauthi*, recovered as sister taxa. At the base of the 'other dolichosaur' clade is *Kaganaias hakusanensis*, and at the very base of the tree, below the split between the pontosaur and 'other dolichosaur' lineages, is *Mesoleptos zendrinii*.

All analyses imply that the three pontosaur species form a monophyletic clade. *Acteosaurus* appears to be either a sister taxon to *Pontosaurus,* or a pontosaur itself. The diagnostic features of *Pontosaurus* include a cervical count of 10-12 (*Acteosaurus* has at least 10), a dorsal count of 26-29 (*Acteosaurus* has 27), hypapophyses with large unfused peduncles on C2-C10 (not visible in *Acteosaurus*), and a unique supraoccipital-parietal suture (elements lost in *Acteosaurus*). This suggests the possibility that *Acteosaurus* and *Pontosaurus* are congeneric. If so, *Acteosaurus,* von Meyer, 1860, has priority, rendering *Pontosaurus*, Kornhuber, 1873, a subjective junior synonym. However, at minimum, the existence of fused cervical peduncles in *Acteosaurus* should be established before such a taxomomic amendment was made.

Interpretation of the relationships of the other dolichosaurs included in the analysis is problematic. Few species are as completely preserved as the three *Pontosaurus* species. Most are missing cranial material and are embedded in limestone slabs, allowing observation of only one side of the specimen. Even in this reduced dataset, *Mesoleptos* can only be scored for 23% of characters, *Eidolosaurus* for 25%, and *Acteosaurus* for 32%. The three *Pontosaurus* species have among the best representation of material, at 75%, 72%, and 57% (for *P. kornhuberi*, *P. lesinensis*, and *P. ribaguster*, respectively). The large amounts of missing information suggest that the topology of the tree cannot be very robust or well supported, a view confirmed by the low bootstrap values. The large polytomies suggest that positioning of most dolichosaurs is not well supported, as they are able to fit into many places with little loss of parsimony. The exception to this is *Acteosaurus* and the three *Pontosaurus* species, whose grouping is the only relatively well-supported result of these tests.

DISCUSSION

The genus *Pontosaurus*

In terms of novelty, articulation, completeness, and retention of identifiable stomach contents, HPM 10807 represents an extremely important addition to the understanding of pontosaurs and dolichosaurs. Consequently, this description of the specimen furthers our understanding of the anatomy, systematics, and ecology of the genus *Pontosaurus*.

The three pontosaurs are distinguishable from each other in several ways: the postorbital/postfrontal is fused into the postorbitofrontal in *P. ribaguster* and *P. kornhuberi*, but is unfused in *P. lesinensis*; the parietal has a midline ridge in *P. kornhuberi* and *P. ribaguster*; the parietal foramen is large in *P. ribaguster* and *P. lesinensis,* small in *P. kornhuberi*; there are 10/11 cervical vertebrae in *P. lesinensis*, 12 in *P. kornhuberi* and *P. ribaguster*; *P. lesinensis* has 28 dorsal vertebrae, *P. ribaguster* 29, and *P. kornhuberi* 26; *P. kornhuberi* is interpreted as having two pygals, *P. ribaguster* as one; *P. ribaguster* has longer haemal arches than *P. kornhuberi*. Qualitative evaluation can therefore clearly distinguish between *P. ribaguster* and the other two species.

All three *Pontosaurus* species are from Cenomanian-aged, Tethyan deposits: *P. kornhuberi* from the Cenomanian of Lebanon, *P. lesinensis* and *P. ribaguster* from the upper

Cenomanian deposits of Hvar Island, Croatia. These lizards, like other dolichosaurs, are elongate in neck and body, with laterally compressed tails making up at least half their body length (based on the caudal morphology of *P. kornhuberi*), reduced appendicular elements with flattened joints, shorter forelimbs than hindlimbs, and pointed, slender skulls. Specifically, the genus *Pontosaurus* can be diagnosed according to vertebral counts, the curvature and uniformity of the ribs, the absence of a coracoid neck, and a unique skull articulation with the supraoccipital resting on top of and forming a v-shaped suture with the parietal (see revised diagnosis, above).

Phylogenetic analyses support the monophyletic grouping of the pontosaurs, with the possible exception of *Acteosaurus*, which—depending on the analysis—falls within the pontosaur lineage, or as a sister taxon to it. Unfortunately, *Acteosaurus* lacks a skull, preventing direct comparison of diagnostic features, though the postcranial material is very similar to the three *Pontosaurus* specimens. I refrain from commenting on other phylogenetic hypotheses about the interrelationships of ophidiomorph lizards until there is more character information because: (1) only three dolichosaurs have 50% character codings in this reduced, variable character only, dataset, (2) we currently lack a dataset targeted at assessing ophidiomorph lizards, and (3) this is beyond the scope of the study. As far as phylogenetic hypotheses within the pontosaur lineage, we currently lack new characters that would reliably differentiate them. Nevertheless, qualitatively, *P. ribaguster* seems most like *P. kornhuberi¸* rather than its contemporary Hvar lizard, *P. lesinensis*.

Piscivory in *Pontosaurus ribaguster*

Pontosaurus ribaguster preserves the second record of dolichosaur stomach contents, and the first instance where it was possible to identify prey. The only other record of gastric contents in a dolichosaur comes from *Adriosaurus skrbinensis,* which preserved a phosphatic mass interpreted as partially digested gastric contents. It was hypothesized that the source of the phosphatic material was the bones of small fish, but a lack of distinguishable bony elements prohibited robust conclusions (Caldwell and Palci, 2010). It is therefore impossible to make dietary comparisons with other dolichosaurs. However, there is a reasonably good record of gastric contents in Cretaceous marine anguimorphs: primarily from mosasaurids, which appear to have been almost entirely macrophagous. Examples include a *Prognathodon overtoni* specimen containing fragmentary elements of a sea turtle, a megalopid fish, a small undetermined fish, and an ammonite (Konishi et al., 2011). A *Mosasaurus missouriensis* specimen from the same quarry was found with a large (roughly one metre long) aulopiform fish with a punctured skull and truncated centra (Konishi et al., 2014). *Tylosaurus proriger* has been recorded with preserved stomach contents consisting of mosasaur, fish, shark and bird fragments (Bjork, 1981; Massare, 1987). Fish found in the digestive tracts of *Platecarpus tympaniticus* (1.2 m long fish; Lindgren et al., 2010) and *Plotosaurus bennisoni* (small fish; Russell, 1967; Massare, 1987) appear to have been swallowed whole. It seems that large mosasaurs were generally opportunistic, able to consume any manner of prey that they came upon. Certain specialists did exist (e.g., *Globidens* being durophagous; Martin, 2007). In any case, these large, pelagic mosasaurs are probably poor analogues for the small, gracile dolichosaurs.

A better analogue for *Pontosaurus* might be modern sea snakes and sea kraits. These ophidians are elongate and slender, and occupy primarily shallow marine environments including reefs. As ophidians, these animals employ particularly mobile jaws to swallow large fish whole without the risk of asphyxiation (Greene, 1997). As in all ophidiomorphs, the tips of the dentaries in *Pontosaurus kornhuberi* (see Caldwell, 2006) are not tightly sutured together at the mandibular symphysis; if this joint was ligamentous, it is very probable that it permitted abduction of the dentary tips away from each other. If the intramandibular joint could indeed form a kink or outward bend as has been suggested (Lee et al., 1999), the gape could have been increased, as in snakes, to permit the swallowing of large prey items. A slender, gracile skull implies a lack of large biting muscles, and pointed, curving teeth suggest a piercing tooth morphology. Together, these morphologies suggest that *Pontosaurus* swallowed soft-bodied prey whole. Lack of puncture marks or gouges on the gastric contents (including a complete teleost skull) of *P. ribagster* support this conclusion, indicating that macrophagy (tearing apart of large prey items) was likely not employed by the animal. Instead, *P. ribaguster* (and other ophidiomorph lizards) likely used its elongate head and neck with its small, pointed teeth to hunt reef fish; first piercing them on their pointed, curved teeth, before swallowing them whole.

Paleobiology

Previous hypotheses on the paleobiology of ophidiomorph lizards used their anatomy (small limbs, rigid body, pachyostotic ribs, reduced girdles, expanded areas for attachment of basal caudal musculature (spinalis, longissimus), elongate and laterally flattened tail) to suggest the dolichosaurs had a reduced capacity for terrestrial locomotion, but they were likely strong and agile swimmers capable of powerful bursts of speed. Their locomotor anatomy (in addition to their large heads, long necks, and pointed teeth) and the sedimentary conditions of the rocks in which they are found (rudist reef, shallow marine lagoon), were used in the past to infer a shallow marine, ambush predation niche for *Coniasaurus, Pontosauus, Dolichosaurus*, and *Adriosaurus* (Caldwell, 1999a, 2000, 2006; Lee and Caldwell, 2000; Pierce and Caldwell, 2004;

Caldwell and Palci, 2010). These animals were hypothesized to have relatively low manoeuverability and speed, relying on their slender frame to hide within crevices and narrow spaces formed by rocky shores and reefs in order to ambush small fish and other soft bodied prey like the marine snakes of today (Greene, 1997). It is uncertain what the degree of connection to land would have been: whether these animals rested daily on a rocky shore, whether they left the oceans annually to breed, or whether they were fully aquatic and viviparous as in other extinct aquatic reptiles including eosauropterygians (Cheng et al., 2004; O'Keefe and Chiappe, 2011), ichthyosaurs (Maxwell and Caldwell, 2003; Dal Sasso and Pinna, 2006; Motani et al., 2014a), mosasauroids (Caldwell and Lee, 2001), and basal marine archosauromorphs (Liu et al., 2017).

Overall, the anatomy of *P. ribaguster* supports the general hypothesis of dolichosaur paleobiology (see above). The number, size and morphology of the vertebrae, the shape of the ribs, and the shape and dimensions of the apophysis suggest that *Pontosaurus ribaguster* had a long, slender neck and an elongated and cylindrical body supported by strong and uniform ribs. The base of the tail (pygals and anterior caudals) had broad transverse processes, neural spines and haemal arches, which likely provided an expanded surface for the insertion for an enlarged caudal musculature, important in tail driven locomotion. Though the complete tail of *P. ribaguster* is not preserved, the anterior portion is similar to the caudal anatomy of *P. kornhuberi*, which is exquisitely preserved: 168 caudal vertebrae making up 68% of the total body length. The vertebrae have long, projecting upper and lower spinous processes, creating a tall, laterally compressed tail which likely had well-developed musculature along its length. This is characteristic of an animal adapted to axial swimming. Fragile and reduced appendicular elements (long bones, clavicle, interclavicle, pubis) indicate a weakening of the trunk-extremities connection resulting from the reduced reliance on the extremities to provide the thrust-generating role in locomotion. Strengthening of the joints and more robust bones in the manus and pes is characteristic of stiffer, more flipper-like podial elements, more useful for steering than for supporting body weight. The main driving force in swimming would have been derived from the body and the characteristic, oar-like tail, while the limbs would have aided movements.

As observed in *Pontosaurus kornhuberi*, the well-developed posterior superior iliac crest would have provided a broad proximal attachment site for the femoral extenders. As discussed by Caldwell (2006), this could represent a functional focus on limb flexion associated with the synergistic flexion of the caudofemoralis, whereby a flexion of the adductor musculature attached to the posterior iliac crest could have contributed to the contraction (powerstroke) of the caudofemoralis, driving a powerful tail stroke. Passive retraction of the femur would have recharged the elastic energy of the muscles prior to the next contraction. Caldwell (2006) suggests that this anatomy is suggestive of a strong, rapid powerstroke that would have produced a large boost of speed suited to ambush predation.

The limbs—which are similar in morphology front to back, while exhibiting negative allometry—are extremely reduced, flattened and expanded distally, and show elongation of the digits to form a flipper-like shape. Their limbs appear to have been too small to have generated any significant force either on land, or in the water. The flattening and distal expansion of the limbs likely prevented the pronation of the wrist, further limiting the ability to walk efficiently on land, but providing the stiffness required to steer effectively in water. The expansion of the first metacarpal and first metatarsal suggest the potential of the limbs as effective hydrofoils—decreasing anterior-posterior drag, and maximizing steering potential. When not being used to steer, they were likely held against posteriorly against the body (Debraga and Carroll, 1993; Lee et al., 1999). The more rapid reduction of the forelimb relative to the hindlimb has no obvious adaptive advantage, but is a common feature shared with early snakes (Caldwell and Lee, 1997; Lee and Caldwell, 1998).

Pontosaurus ribaguster also demonstrates a small degree of pachyostosis in the trunk region- particularly to the anterior thoracic ribs. This anatomical condition is a thickening of periosteal bone caused by increased osteogenesis in the periosteum. This adaptation helps achieve neutral buoyancy in shallow diving tetrapods by counteracting the buoyancy produced by air in the lungs (Bardet et al., 2008; de Buffrénil et al., 2010; Houssaye et al., 2011; Houssaye, 2013a). It implies that a significant amount of time was spent underwater, presumably hunting and foraging for food.

The discovery of fish remains within the gastric space of *P. ribaguster* corroborates the dolichosaur paleobiology hypothesis, providing extremely strong evidence for a primarily piscivorous diet. Identifiable teleost remains in the gastric space of *P. rigabuster* are associated with fish 5-10 cm long—16-33% of the body length (without the tail)—which is easily within the size range of prey that modern aquatic ophidians are able to swallow whole (King, 2002), supporting a feeding style where *P. ribaguster* shallows relatively small piscivorous prey whole rather than tearing large fish into smaller pieces.

Reef-type sedimentation and oxygen isotopes in the limestone reveals that in the Upper Cretaceous, the area that this lizard inhabited was a tropical rudist reef on a shallow shelf ranging in temperature from 24-26°C (Polšak & Leskovšek, 1975), and bordered by anoxic lagoons which preserved carcasses for fossilization (Radovčić, 1975, Radovčić, Tišljar, Jelaska, 1983). The diagnostic teleost scales in the abdominal cavity of *P. ribguster* are both from dercetid fishes, with two scales being referable to *Eurypholis*, a Cretaceous (including the Cenomanian

Tethys) marine fish from lagoonal or restricted shallow subtidal sediments (Forey et al., 2003), which is in agreement with the sedimentological conclusions. Sympatric fossil remains of gastropods, bivalves, teleosts, cephalopods, crustaceans, and other marine lizards suggest that a rich and diverse ecosystem supported abundant life.

Together, these lines of evidence (morphological, sedimentological, gastrointestinal) substantiates the hypothesis that pontosaurs hunted in warm, shallow marine waters, using agility to ambush small reef-dwelling fish. Since all dolichosaurs so far described have been assigned to this particular niche, this raises the questions of resource partitioning, particularly among the Cenomanian dolichosaurs of Istria and Dalmatia. *Adriosaurus* and *Acteosaurus* are the smallest of the Adriatic dolichosaurs, with 14 cm and 16 cm trunks, respectively. *Eidolosaurus* records a 21 cm trunk length, the three *Pontosaurus* species measure 30-36 cm, and *Mesoleptos* likely measured roughly 40 cm from pectoral to pelvic girdle (all measurements are pers. obs.). Ophidiomorph lizards shared the mid-late Cenomanian shallow marine environments of the Tethys with another group of marine anguimorphs: the aigialosaurs. In the Adriatic region alone were *Aigialosaurus* (trunk length 30-50 cm depending on species), *Komensaurus* (trunk length ~50 cm), and *Carsosaurus*, who with a trunk length of roughly 75 cm was the largest of the Adriatic aigialosaurs. Even though all these animals are small (<1 m), their body sizes are fairly evenly spread across this range, with very little overlap. It is necessary to point out that since most of these species are monotypic, I am basing these sizes off of a single individual, which may not be representative of the adult size range.

The close spatiotemporal relationships of these marine pythonomorph lizards suggest that these taxa were able to partition resources within shared habitats. These animals must have partitioned either their environment, their feeding habits, or their prey. Unfortunately, the morphology of their teeth (which would provide some indication of prey preference) is not well represented, with tooth morphology being unknown for many species. The teeth that are preserved are the teeth of generalists, being small, sharp, conical, and slightly recurved (Massare, 1987). A closer investigation into the tooth morphology of these animals might provide better insight into their paleoecology.

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CHAPTER 3 : DESCRIPTION OF A NEW BASAL MOSASAUROID WITH COMMENTS ON THE EVOLUTION OF THE MOSASAUROID FORELIMB

ABSTRACT

A new genus and species of plesiopedal mosasauroid, *Portunatasaurus krambergeri*, from the Cenomanian-Turonian (U. Cretaceous) of Croatia is described. An articulated skeleton, representing an animal roughly a metre long was found in 2008 on the island of Dugi Otok. The specimen is articulated, in approximate life position, and is well represented from the anterior cervical series to the pelvis. Preserved elements include cervical and dorsal vertebrae, rib fragments, pelvic fragments, and an exquisitely preserved right forelimb. The taxon possesses plesiomorphic characters such as terrestrial limbs and an elongate body similar to basal mosasauroids such as *Aigialosaurus* or *Komensaurus*, but also shares derived characteristics with mosasaurine mosasaurids such *Mosasaurus*. The articulated hand shows a unique anatomy that appears to be transitional between *Aigialosaurus* and *Mosasaurus*, including ten ossified carpal elements (as in aigialosaurs), intermediately reduced pro- and epipodials, and a broad, flattened first metacarpal (as in mosasaurines). The new and unique limb anatomy contributes to a revised scenario of mosasauroid paddle evolution, whereby the abbreviation of the forelimb and the hydrofoil shape of the paddle evolves either earlier in the mosasaur lineage than previously thought, or more times than previously considered. The presence of this new genus, the third and geologically youngest species of aigialosaur from Croatia, suggests an unrealized diversity and ecological importance of this family within the shallow Tethys Sea.

INTRODUCTION

The invasion of the marine environment by a secondarily aquatic group, and the concomitant evolution of aquatic adaptations, is widespread in nature. In the Mesozoic alone, it can be observed in many major diapsid groups including protorosaurs, crocodilians, phytosaurs, ichthyosaurs, plesiosaurs, choristoderes, and pleurosaurs (Carroll, 1997). Squamates underwent their most dramatic period of marine radiation during the mid-Late Cretaceous, when three clades of small, terrestrial squamates radiated into aquatic environments: snakes, dolichosaurs and mosasauroids.

Mosasauroids are classically divided into the primitive small to medium-sized aigialosaurs (Aigialosauridae: Kramberger, 1892) and the massive derived mosasaurs (Mosasauridae: Gervais, 1852) (Romer, 1956; Russell, 1967; Carroll and Debraga, 1992; Bell, 1993, 1997a; Bell and Polcyn, 2005; Caldwell, 2012). Mosasaurs are well adapted for the marine environment with propulsive tails, flippers, and modified skulls for specialized feeding. Aigialosaurs are closely related to mosasaurs and are generally considered to be semi-aquatic, having weight bearing limbs and an elongate, laterally compressed tail. Derived mosasaurs appear in the Coniacian and reached a cosmopolitan distribution by the Santonian-Campanian (Russell, 1967). Aigialosaurs are more restricted temporally and geographically; to date, they have only been found in Cenomanian and Turonian deposits of the Tethys (*Aigialosaurus, Carentonosaurus, Carsosaurus, Komensaurus, Haasiasaurus*; e.g., Gorjanovic-Kramberger, 1892; Kornhuber, 1893, 1901; Polcyn et al., 1999; Rage and Néraudeau, 2004; Caldwell and Palci, 2007), Western Interior Seaway (*Dallasaurus*; Bell and Polcyn, 2005) and Atlantic shelf (*Vallecillosaurus*; Smith and Buchy, 2008). One additional possible occurrence comes from the Upper Jurassic Solnhofen Limestone of Bavaria: *Proaigialosaurus huenei* (Kuhn, 1958). The description of this species is based on a single skull fragment (now lost), and is inadequate to determine family-level placement.

The diversity of basal and derived mosasauroids across the Tethyan platform provides an opportunity to study the transition of terrestrial squamates to marine environments. These studies necessitate well-resolved phylogenies; however, due to the paucity of known material, much of which is incomplete and described over a century ago, relationships in this group remain unresolved. For instance, the monophyly of the Mosasauroidea, its relationships with other probable anguimorph groups (including snakes and dolichosaurs) and its placement within the greater squamate tree are all contentious topics with divergent hypotheses (see Dutchak, 2005; Bardet et al., 2008; Caldwell and Palci, 2010; Caldwell, 2012; Gauthier et al., 2012). Recent efforts to redescribe some of these specimens (e.g., Caldwell et al., 1995; Dutchak and Caldwell, 2006, 2009) have revealed that they are characterized by various combinations of plesiomorphic and derived characters. This emphasizes the importance of new specimens as valuable sources of information regarding marine squamate diversity, evolution, and aquatic radiation.

Here, we will present the description of a new genus of ancient marine squamate from Cenomanian-Turonian (Upper Cretaceous) age limestone found on the Croatian coast. The well-articulated specimen consists of a worn impression and a few remaining bones. Although incomplete, the specimen includes important features of the vertebrae and forelimb that place it within the mosasauroid lineage. Importantly, it also possesses some unique morphological features of the manus and vertebral column that can be used to differentiate it at the genus level. We will provide a detailed description and diagnosis of this new genus and provide interpretations of its biology in the evolutionary context of the mosasauroid paddle.

Institutional Abbreviations—CNHM Croatian Natural History Museum (Hrvatski prirodoslovni muzej), Zagreb, Croatia; **GBA** Geologisches Bundesanstalt Osterrich, Wien, Austria; **MCSNT** Museum Civico Naturale di Trieste, Trieste, Italy; **UALVP** University of Alberta Vertebrate Paleontology Laboratory; **MCM**, **DJ**, **KK**, and **MC** refer to authors.

MATERIALS AND METHODS

The specimen was removed in 2011 using a portable rock saw. It was transported in 2012 to the University of Alberta in Edmonton, Alberta, Canada for preparation. Drawings and illustrations were made by MCM and MC directly from the original specimen by eye, or using a dissecting microscope and camera lucida attachments. Photographs were taken by the authors at the time of discovery (DJ: 2008), several months after discovery (DJ and MC: 2009), at the time of excavation (DJ and MC: 2011), and before and after preparation (MCM and MC: 2012, 2013 and 2014).

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811

ANGUIMORPHA Fürbringer, 1900

PYTHONOMORPHA Cope, 1869

MOSASAUROIDEA Camp, 1923

AIGIALOSAURIDAE Kramberger, 1892

PORTUNATASAURUS gen. nov.

Type species—*Portunatasaurus krambergeri*, sp. nov.

Diagnosis—As for type and only species.

Etymology—After the island of Dugi Otok, Croatia, where the holotype was found (Figure 1). The Latin name for Dugi Otok is 'Portunata', while 'saurus', in Latin means lizard.

PORTUNATASAURUS KRAMBERGERI, sp. nov.

(Figs. 2–4)

Diagnosis—Plesiopedal mosasauroid roughly one metre in length, differing from all other basal mosasauroids in following combination of characteristics: elongate neck (roughly 10 cervical vertebrae), and trunk (18 dorsal vertebrae); humerus robust and elongate (roughly equal in length to two anterior dorsal vertebrae) and roughly three times longer than distally wide; medial notch in distal end of humerus; proximal and distal articular facets capped by thick unfused ossified epiphyseal cartilage; distally expanded and flattened radius and ulna; differentiated from all other described aigialosaurs in having expanded and robust first metacarpal, and different number of cervical and dorsal vertebrae; differs from *Vallecillosaurus donrobertoi* and *Carsosaurus marchesettii* in possessing ultimate rib pair on final dorsal vertebra; has fewer short posterior presacral ribs than *V. donrobertoi*, *A. dalmaticus*, and *C. marchesettii*; humerus is more robust than in *C. marchesettii* or any *Aigialosaurus* species; possesses intermedium; and, radius wider distally than proximally, differentiating it from *Komensaurus carrolli*.

Etymology— Specific name in honor of Dr. Dragutin Gorjanović-Kramberger: great Croatian geologist, paleontologist and paleoanthropologist, university professor and director of the Geological and Palaeontological Department of the National Museum in Zagreb, in recognition of his contribution to the study of Late Cretaceous Adriatic marine lizards and for scientific achievements in the field of vertebrate paleontology in Croatia and worldwide.

Type Locality and Horizon—Dugi Otok, 44.05° N, 14.99° E, Croatia; Cenomanian-Turonian (Upper Cretaceous) platy limestones (Fuček et al., 1991). Part of the Adriatic-Dinaric Carbonate Platform (Fig. 1). Microfossil assemblages corroborate dating and indicate an open shelf basin.

Holotype—CNHM 10808, housed in the Hrvatski prirodoslovni muzej (Croatian Natural History Museum – CNHM), Zagreb, Croatia. The specimen is encased in a large block of platy limestone that preserves the incomplete articulated body of one individual in ventral view (Fig. 2). Preserved elements include most of the cervical and dorsal vertebrae, the right forelimb, and fragments of the pelvic girdle, pectoral girdle, and ribs. Impressions of cervical and dorsal ribs, and skull are also preserved.

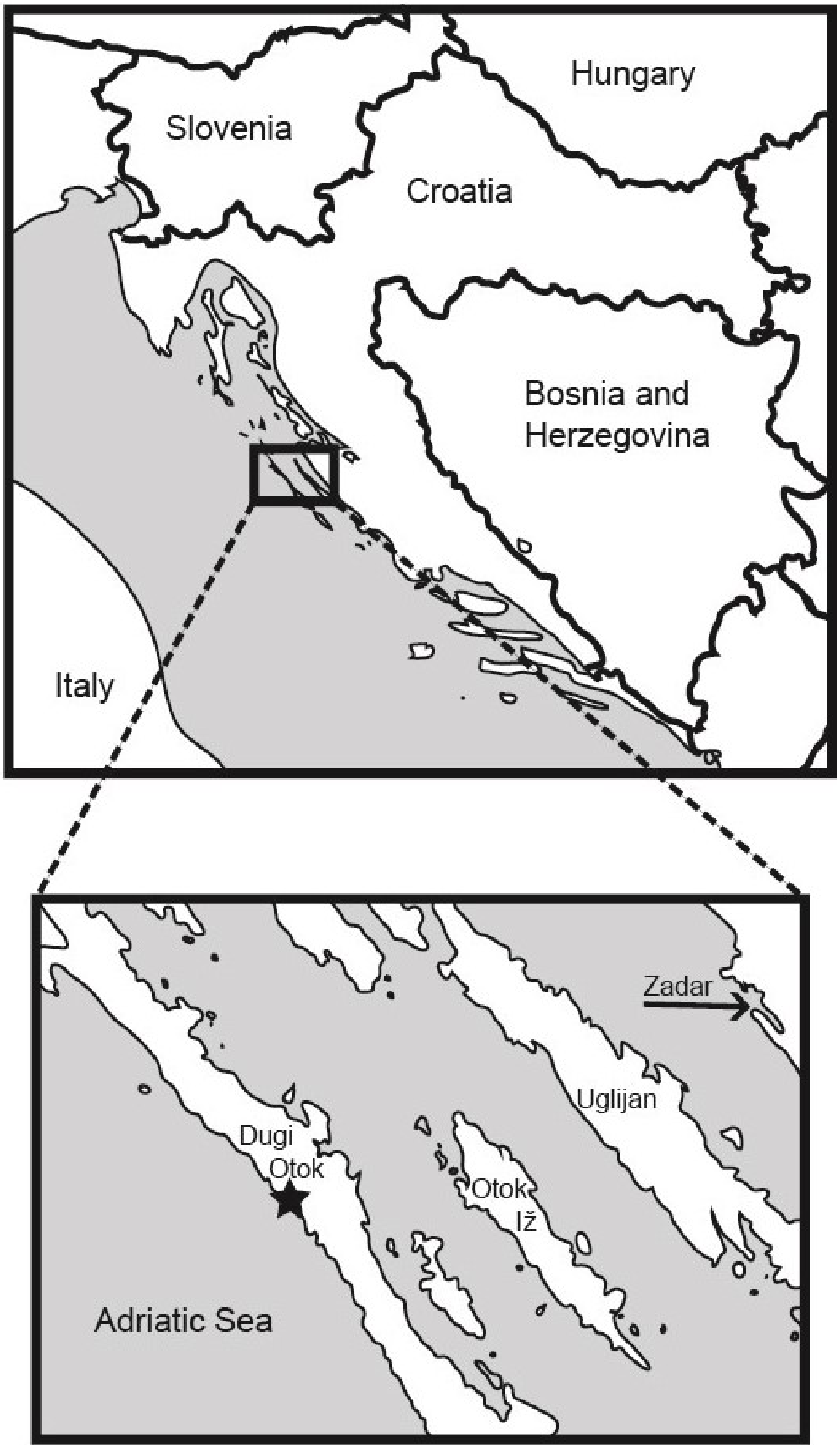

Figure 3-1 Map of Western Croatia showing the location of the island Dugi Otok (Long Island). Star indicates specimen's locality.

OSTEOLOGICAL DESCRIPTION

State of preservation

CNHM 10808 is preserved either as bony fossil material or impressions of the bone from the skull to the base of the tail (Fig. 2). The skeleton lies in ventral view, slightly rolled to the right, and is in near perfect articulation in a natural position. The vertebral column (and corresponding ribs) from the third cervical to roughly the third caudal are preserved in whole, in part, or as impressions. The right forelimb, and fragments of the pelvis and pectoral girdle are preserved. The hind limbs, and most of the caudal region are lost. The impression of the left forelimb is distinguishable in oblique lighting, and the cranium appears preserved in ventral-lateral view as a weathered impression.

At the time of its discovery in 2008 by biologist and underwater researcher Donat Petricoli, the fossilized skeleton was mostly complete from the second or third cervical to the third caudal vertebra. At this time, the preserved section of the vertebral series was nearly complete (Fig. 2B). Several ribs were preserved in articulation with the vertebrae. The entirety of the right forelimb was articulated, and several elements of the shoulder girdle, pelvic girdle, and skull could still be identified. There was even preservation of some cartilaginous elements including the sternal cartilage and tracheal rings. Much of this data is now lost and preserved only as photographs.

Unfortunately, after three years of weathering on the sea cliffs (due to improper field processing and drawn out permit approvals), the specimen now consists of a worn impression and a few remaining bones (Fig. 2D). Most the cervical and dorsal vertebrae have been reduced to shattered fragments and their associated ribs are mostly preserved as molds. Of

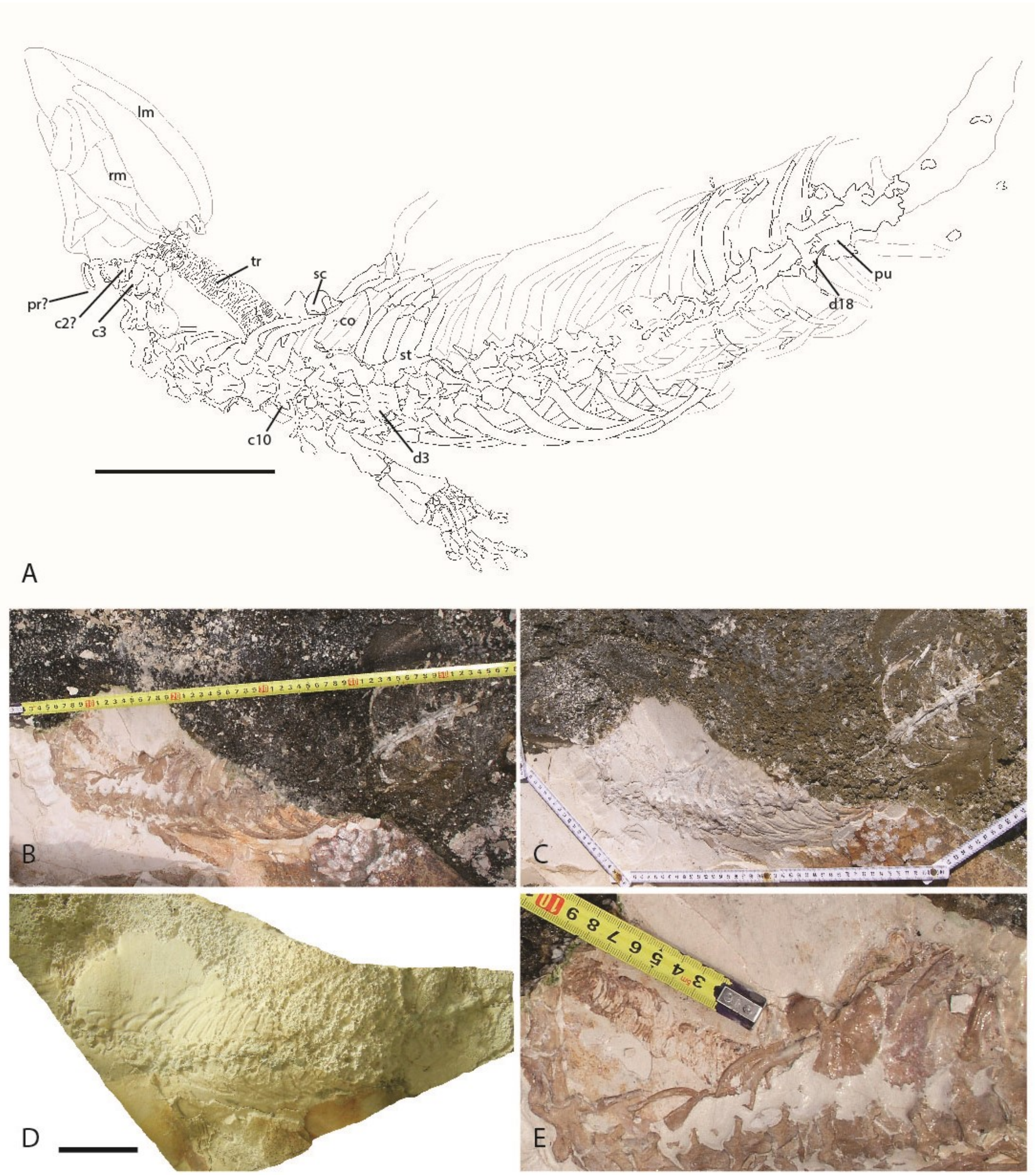

Figure 3-2 The holotype of *Portunatasaurus krambergeri*, CNHM 10808, housed in the Hrvatski prirodoslovni muzej (Croatian Natural History Museum), Zagreb, Croatia. **A**, composite interpretive outline showing the most complete skeleton able to be reconstructed using combined data from photos dating back to 2008; **B**, photograph taken June 2008, shortly after discovery; **C**, photograph taken October 2008; **D**, photograph of specimen as currently preserved; **E**, detail of (B), showing tracheal rings, scapula, coracoid, and sternal cartilage. Grey lines in (A) indicate impressions only. **Abbreviations**: **c**, cervical vertebra; **co**, coracoid; **d**, dorsal vertebra; **lm**, left mandible; **pr**, parietal ramus; **pu**, pubis; **rm**, right mandible; **sc**, scapula; **st**, sternal cartilage; **tr**, tracheal rings. Scale bars equal 10 cm.

the bones that remain, many are split, and are only seen internally. Impressions from the cervical and most of the dorsal ribs are present, as is the impression of the pectoral girdle and skull. The right forelimb was exposed during preparation, and is preserved in exquisite detail in medial view.

For the purposes of this description, we will use the maximum amount of data available to us, including photographs and notes taken in 2008, 2009 and 2011 before the fossil was recovered.

Skull

The skull (Fig. 2A–D) is represented only as a badly weathered natural mould visible in oblique lighting, which reveals little other than approximate size. Details are impossible to make out due to the heavy encrustation and subsequent scaring of the rock by barnacles. The impression indicates that the skull was about 14 cm long and would have been exposed in ventral view. It is possible to make out the right and left mandibles (Fig. 2A), and what is likely an impression of the right side of the brain case and the right maxilla. The impression is missing the tip of the snout. A single squared off bony element bearing two longitudinal grooves located at what we interpret as the posterior-lateral corner of the skull roof is interpreted as a part of the parietal ramus (Fig. 2A). At the time of discovery, this fragment appeared to have a posterior tuberosity, which would describe a posterior portion of the parietal ramus similar in shape to *Aigialosaurus bucchichi* (Dutchak and Caldwell, 2009). Other interpretations for this element include a fragment of cervical vertebra or perhaps a squamosal. Photographs from 2008 and

2009 show other bone fragments around the posterior edge of the cranial impressions. However, the worn and broken nature of these elements makes them impossible to identify.

Photographs from 2008 show the remains of tracheal rings exiting the posterior of the skull between the two mandibles and exposed on the left side of the cervical vertebrae (Fig. 2A, D). They continue in a straight line, not following the curve of the neck, to disappear adjacent to C9. Proportionally, they are similar in diameter to the tracheal rings preserved in *Pontosaurus kornhuberi* (Caldwell, 2006).

Axial skeleton

Thirty-one vertebrae are variously preserved as impressions, bone shards or relatively complete elements (Figs. 2, 3). There are eight cervical vertebrae preserved (none of which can be identified as C1 or C2), eighteen dorsal vertebrae and five caudal vertebrae, which are all preserved in ventral view (Fig. 2**).**

Cervical region—The cervical series, exposed in ventral view, is well preserved in the original images of the specimen from 2009 (Fig. 2B). In its present state, after weathering, extraction and preparation, these elements can only be recognised as fragments of broken bone and worn impressions with little diagnostic detail (Fig 2C).

There are eight preserved cervicals in *Portunatasaurus krambergeri.* The anterior-most preserved cervical is most likely C3, and sits just posterior to the skull impression. We interpret this element as C3 and not the atlas or axis due to the lack of an intercentrum, and its equivalent size to the next vertebrae. The fragments visible anterior and to the left side of the C3 are

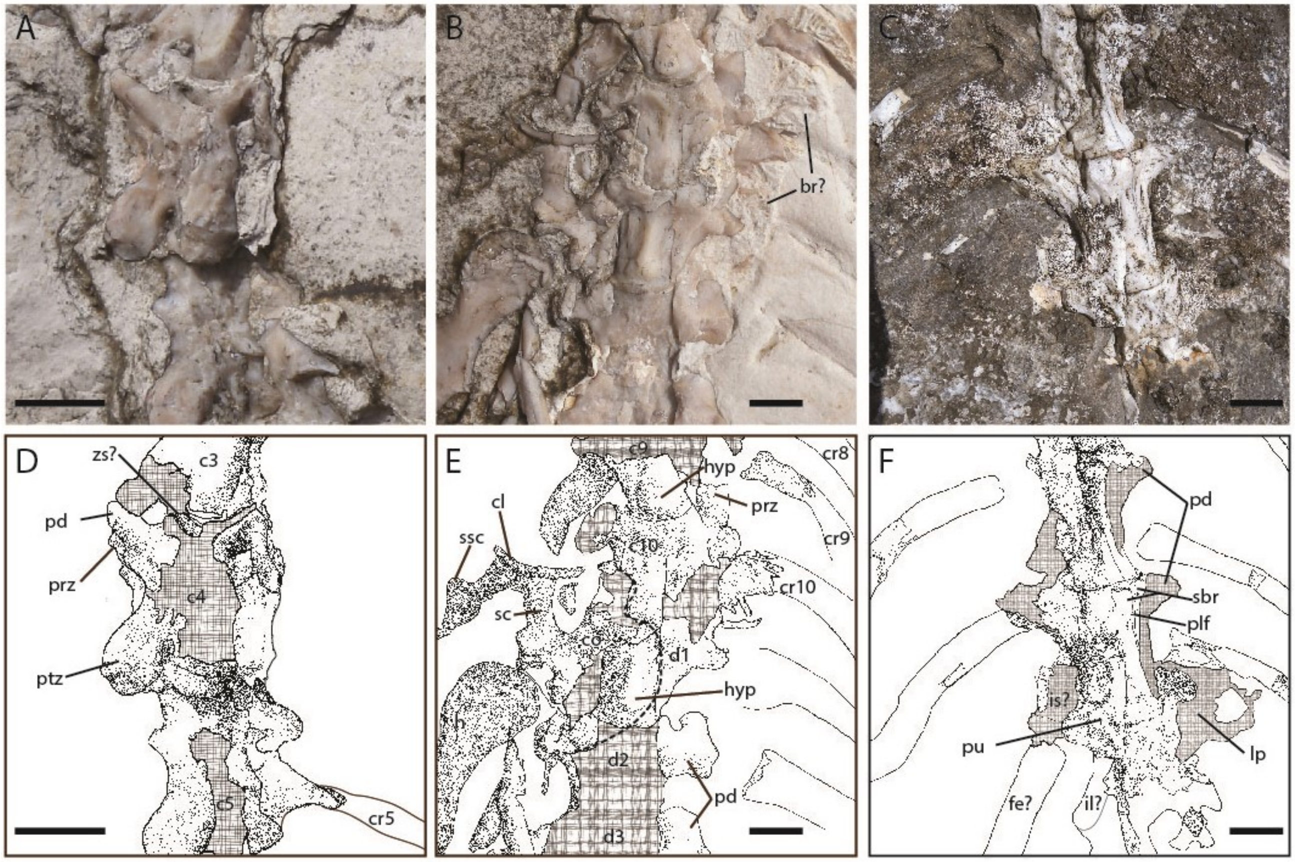

Figure 3-3 Anterior cervical, cervical-dorsal transition, and posterior dorsal vertebrae of *Portunatasaurus krambergeri* (CNHM 10808). **A**, photo of anterior cervicals 3rd to 5th; **B**, photo of posterior cervical (9th and 10th) and anterior dorsal (1st to 3rd) vertebrae, and pectoral girdle; **C**, photo of posterior dorsal vertebrae (17th and 18th) and remains of first few postsacral vertebrae; **D**, interpretive drawing of (A); **E**, interpretive drawing of (B); F, interpretive drawing of (C). Hatched areas in drawings indicate where bone surface has been broken away and bone is visible internally only. Areas with outlines but without stippling indicate areas where all bone has been stripped away, leaving only impressions. Dashed line indicates the outline of the coracoid element as it laid over the vertebral column. **Abbreviations**: **br**, bronchial rings; **c**, cervical vertebra; **cl**, clavicle; **co**, coracoid; **cr**, cervical rib; **d**, dorsal vertebra; **fe**, femur; **h**, humerus; **hyp**, hypapophyses or hypopophyseal element; **il**, ilium; **is**, ischium; **lp**, left pelvis; **pd**, paradiapophyses; **plf**, **paralymphatic fossae; prz**, prezygapophysis; **ptz**, postzygapophysis; **pu**, pubis; **sbr**, subcentral ridges; **sc**, scapula; **ssc**, suprascapular cartilage; **zs**, zygosphene. Scale bars equal 1 cm.

interpreted as the posterior part of C2. C1 is presumably lost within the eroded remains that form the posterior-most portion of the skull and anterior-most portion of the neck. The remainder of the cervical vertebrae curve towards the pectoral girdle. The preserved right scapula and clavicle locates the transition between cervical and dorsal vertebrae between the eighth and ninth preserved vertebra. Thus, the number of cervicals is most likely ten. This would give it a greater number of cervical vertebrae to other mosasauroids such as *Aigialosaurus dalmaticus* and *A. bucchichi* with 7–9 cervicals (Dutchak and Caldwell, 2006, 2009); and an unnumbered *Carsosaurus* specimen (MCSNT) that preserves seven cervical vertebrae not including the atlas-axis complex, making the cervical count at least nine. It is also comparable to dolichosaurs such as *Pontosaurus kornhuberi* with 10 cervicals (Caldwell, 2006); *P. lesinensis* with 12 cervicals (Pierce and Caldwell, 2004); and *Acteosaurus tommasinii* with at least 10 (Palci and Caldwell, 2010).

The second vertebra (C4) is among the best preserved (Fig. 3A, D), and shows that the vertebrae are indeed procoelous, as the condyle is ventrally exposed by post-mortem displacement of the following centrum. Worn hypapophyses are visible on several of the cervical vertebrae that have their ventral surface preserved (best seen on C9, Fig. 3B, E). No trace of peduncles/intercentra can be seen. Carroll and Debraga (1992) and Dutchak and Caldwell (2009) noted that for *Aigialosaurus bucchichi*, there are no obvious hypapophyses on the cervicals. However, upon examination of the type specimen, we identified several hypapophyses and articulated peduncles on the last four cervicals of *A. bucchichi,* the hypapophyses of which are similar in shape (sub-triangular) and placement (posterior end of the centrum) to those in *Portunatasaurus*. This arrangement is also comparable to *Komensaurus carrolli* (Caldwell and Palci, 2007) and *Haasiasaurus gittelmani* (Polcyn et al., 1999). The size and shape of the hypopophyses are different between preserved vertebrae seven and eight (identified as C9 and C10) and nine (identified as D1), further supporting the interpretation of a cervical to dorsal transition in this region.

The pre- and postzygapophyses are best preserved on C4 and are generally obscured beyond C6. The prezygapophyses are straight and narrow, and project at roughly 45° from the centrum. The postzygapophyses project more dorsally, are much more inflated and robust, and have smooth rounded ends. The close articulation of the vertebrae and the degree of wear and breakage means that the presence of zygosphenes and zygantra is impossible to determine along most of the column. The only potentially discernable zygosphene is a protrusion preserved on C4 (Fig. 3A, D). Relatively large and robust paradiapophyseal processes can be seen along most of the cervical section but the margins are sheared and broken which prohibits further interpretation.

Impressions or remnants of cervical ribs can be seen on the left side beginning at C5. *Aigialosaurus bucchichi* (Dutchak and Caldwell, 2009) shows cervical ribs on the last four cervical vertebrae, and *Dallasaurus turneri* (Bell and Polcyn, 2005) shows rib articulations on what is probably cervical three or four. However, in both cases, since the anterior cervical series is incomplete, the number of cervical ribs is uncertain. The impression of CNHM 10808's first cervical rib is a small and splint-like shape with minimal curvature. The ribs associated with C6 and C7 are larger and show a gentle curve at the distal end. The ribs of C8–10 show an increase in size and robustness compared to C6 and C7. The rib head can be seen well preserved on C5 and C8–10 (Fig. 3A, B, D, E) in the 2009 photos. These are anteriorly expanded, unicapitate, and show a ventral depression in the capitulum immediately distal to the attachment. The concavity is bordered by a narrow, sharp, anterior edge and a broader, blunter posterior edge. Overall, the ribs are similar to other anguimorphs.

Unlike dolichosaurs (e.g., *Pontosaurus lesinensis*: Pierce and Caldwell, 2004; *Acteosaurus tommasinii*: Palci and Caldwell, 2010) the cervical vertebrae increase in width and length only minimally as they progress caudally. Additionally, unlike the typical mosasauroid (and lizard) condition of having cervicals much smaller than dorsals, the posterior cervicals of *P. krambergeri* are roughly the same size as the anterior dorsals (though both are markedly smaller than the posterior dorsals, a condition also seen in *Haasiasaurus*; Polcyn, Tchernov and Jacobs, 1999). Although the vertebrae are similar in morphology, there is an increase in size between the last cervical and first dorsal ribs.

Dorsal Region—The positions of the scapula and 'pelvic bone' suggest a dorsal count of 18 (Fig. 2). This falls within the range with other mosasauroids such as *Aigialosaurus bucchichi* (18–19; Dutchak and Caldwell, 2009), but is less than *Komensaurus carrolli* (roughly 21; Caldwell and Palci, 2007), *Carsosaurus marchesetti* (21, pers. obs), and *A. dalmaticus* (roughly 21; Dutchak and Caldwell, 2006). The eleventh to fourteenth vertebrae are indistinct and suffer from the greatest amount of exposure, weathering, and subsequent barnacle encrustation. Reliable counts are made possible by the nearly complete series of rib impressions on the left side of the body. This gives a total of 28 presacral vertebrae, less than that of *Dallasaurus turneri* which has at minimum 31 presacral vertebrae, and likely at least 34 (Bell and Polcyn, 2005). Several dorsal vertebrae (e.g., D1, Fig. 3B, D) are slightly displaced, clearly exposing their procoelous condition.

Moving caudally along the dorsal column, the vertebral centra become proportionally longer and narrower, and overall, the vertebrae become larger. The degree of weathering obscures details of most dorsal vertebrae (though 2008 photographs show that they were well preserved upon initial exposure). The first and last dorsal vertebrae remain the best preserved. The proximal placement of the synapophyses gives a T-shaped ventral profile to the vertebrae; a similar shape can be observed in other aigialosaurs (e.g., Kornhuber 1893, Polcyn et al. 1999), dolichosaurs (e.g., Pierce and Caldwell, 2004), mosasaurs (Bell and Polcyn, 2005) and snakes. The vertebrae do not appear to be pachyostotic as in *Carentonosaurus mineaui* (Rage and Néraudeau, 2004), *Adriosaurus suessi* (Seeley, 1881), *Mesoleptos zendrini* (Cornalia, 1852), or pachyophiid snakes.

The first dorsal vertebra (Fig. 3B, E) has what appears to be a non-peduncle-bearing, hypapophyseal element. It is not uncommon to have such a structure here; it can be seen in other lizards such as geckos (first 8 verts), *Varanus* (first 9 verts; Romer, 1956) and *Mosasaurus conodon* (H. Street pers.comm, 2017). Also visible on the left side of this vertebra is a short precondylar constriction. There are no subcentral foramina.

Though the centrum is sheared off, D2 and D3 (Fig. 3B, E) preserve the left paradiapophyses quite well. They are positioned quite anteriorly, project laterally, and are almost saddle shaped in ventral view. They are very large and robust, taking up over half the length of the centrum. The sheared surfaces allow an internal view of these vertebrae, exposing a very high internal density possibly indicating pachy- or osteosclerosis, both adaptations for buoyancy and trim control in shallow water swimmers (Houssaye, 2013b).

The last few dorsal vertebrae (Fig. 3C, F) have rolled slightly towards the left exposing more of the right lateral side. They are better preserved than the mid-dorsal series and show features not identifiable or visible elsewhere. The margins of the centra are clearly visible and show that the ventral margins are subparallel, tapering slightly towards the rear. The curvature of the condyle and constriction of the centrum are reduced, making the centra appear spool-shaped in ventral view. Mosasaurs and aigialosaurs show a similar transition in centrum morphology. In aigialosaurs, this transition begins in the caudal series, and in mosasaurs this change occurs in the anterior dorsals (Caldwell, 1996). In *Portunatasaurus,* the condition appears to be intermediate, transitioning in the mid- to rear dorsal area. It has been proposed that this shift—which corresponds to a reorientation of the articular facets—is an adaptation to anguilliform locomotion in swimming animals (Russell, 1967; Carroll and Debraga, 1992).

The last dorsal vertebrae (Fig. 3C, F) show several features not visible along the rest of the column. The transverse processes project anterolaterally from each vertebra at an angle of about 45° to the length of the centrum. They are narrow and triangular, and are restricted to the anterior quarter of the centrum. On the left side, well-developed paralymphatic fossae are clearly visible, although like the anterior-most dorsal vertebra, subcentral foramina cannot be identified. As in *Carsosaurus marchesettii* (Kornhuber 1893), *Haasiasaurus gittelmani* (Polcyn, Tchernov and Jacobs, 1999), *Aigialosaurus bucchichi* (Dutchak and Caldwell, 2009) and *Komensaurus carrolli* (Caldwell and Palci, 2007), there is a groove running down the ventral surface of the centrum, bordered by a raised edge (the subcentral ridges). On the anterior-most portion of the centrum, these ridges swell into a pair of mounds that sit ventral to the cotylar ridge.

The ribs (Fig. 2) on the right side of the animal are mostly broken and overlapping, making it difficult to count and identify them. Due to the slight lateral rotation of the body, the medial portions of the left ribs are laid almost flat on the slab, though they are preserved only as impressions and bone fragments. Photographs from 2008 show the well preserved ribs, providing additional anatomical details (Fig. 2B). Like *Carsosaurus marchesetti* (Kornhuber 1893) and *Aigialosaurus bucchichi* (Dutchak and Caldwell, 2009), *Portunatasaurus krambergeri* retains a high number of elongate trunk ribs, which is a condition plesiomorphic for squamates (Hoffstetter and Gasc, 1969). Following the pattern shown by the vertebrae, the ribs become larger posteriorly. Extreme weathering makes the eleventh to fourteenth rib sets difficult to assess, but at D15, the ribs are drastically reduced in size. The ribs continue to decrease in length and thickness posteriorly, with the final, shortest, slenderest dorsal rib articulating with the final dorsal vertebra (D18) as in *A. bucchichi* (Dutchak and Caldwell, 2009).

The ribs branch off the centra in a downward arch and then bend inwards medially. This curvature, with the shape and length of the ribs (up to five vertebral lengths) indicate a deep body profile which supports our interpretation that the animal was semi-aquatic, swimming with lateral body undulations. The anterior ribs are extremely robust and may represent a pachyototic adaptation to a coastal aquatic lifestyle as seen in *A. bucchichi* (Dutchak and Caldwell, 2009). In contrast, the rib impressions of the last three presacrals are more slender and do not show any notable degree of pachyostosis. This pattern of gradually increasing and then abruptly decreased pachyostosis in the lumbar region varies slightly in precise location among species, but is also seen in *Aigialosaurus bucchichi* (Dutchak and Cadlwell, 2009), *Pontosaurus kornhuberi* (Caldwell, 2006), *P. lesinensis* (Pierce and Caldwell, 2004), *Dolichosaurus longicollis* (Caldwell, 2000), and *Kaganaias hakusanensis* (Evans et al., 2006) and was noted by Kornhuber (1901) who described them as 'dorsolumbar' ribs.

Sacral and Caudal Regions—The most posterior bone fragments and indistinct impressions on the slab are presumably the remains of two sacral and the first few caudal vertebrae. They are almost completely missing and/or worn away, and have no diagnosable characteristics to note. The impression of a short, straight bone on the left side of the first sacral vertebrae may be a sacral rib, though I interpret this impression as the ilium due to the slender nature of the element.

Appendicular skeleton

The best-preserved portion of this specimen is the distal portion of the right forelimb, which was discovered during preparation (thus saved from destruction) and is preserved in exquisite detail. The humerus and portions of the ulna can be best observed in photos taken in 2008, shortly after the time of discovery. The pectoral girdle is incompletely preserved, though the earliest photos show that the left shoulder girdle was mostly complete upon excavation. The pelvic girdle is indistinct, and its morphology can only be partially interpreted.

Pectoral girdle—At the time of its discovery, *Portunatasaurus krambergeri* had a relatively complete left shoulder girdle (Fig. 2B, E), and a well-represented right pectoral girdle, with fragments of the scapula, coracoid, clavicle, and cartilaginous elements (Figs. 3B, E and 4D). All elements are relatively close to life position, with the right scapula suffering some rotation towards the head on the median plane. Presently, most of these elements are still identifiable.

The clavicle is long and very slender. It is broken into two pieces near the vertebral column; the larger, lateral piece narrows to a point dosolaterally, and the smaller piece closest to the midline shows that the medial end of the element is squared off as seen in *Carsosaurus marchesetti* (Caldwell et al., 1995).

The right scapula is broken and contains many unnatural edges; however, most of the element remains. The left scapula has been lost since discovery. Between the remains of the right scapula, and images of the left, it is possible to reconstruct its shape and size. Like *Carsosaurus marchesetti* (Caldwell et al., 1995), *Carentonosaurus mineaui* (Rage and Néradeau, 2004), and *Halisaurus sternbergi* (Wiman, 1920), it was hatchet-shaped, and less than half the size of the coracoid. The anterior portion of the ‘hatchet’ was less elongate than the posterior portion, which embraced the glenoid fossa. The right coracoid is preserved as an impression and as shattered fragments overlying C10, D1 and D2, but is missing the medial border. The left coracoid is preserved only in photographs. Overall the shape is cresentic and almost semi-circular. The position and presence of a short, notch-like anterior (primary) emargination can be seen in the preserved part of the right coracoid, and photographs of the left confirm this. The portion of the right coracoid that contained the coracoid foramen is missing, though it is visible close to the glenoid fossa on the left. Overall, the shape, size and emargination of the coracoid element are similar to other mosasauroids (e.g., Russell, 1967; Caldwell, 1999; Caldwell et al., 1995; Polcyn, Tchernov and Jacobs, 1999), especially that of *Halisaurus sternbergi* (Wiman, 1920) and *Clidastes liodontus* (Russell, 1967).

The scapula and coracoid are not coossified as in *Aigialosaurus bucchichi* (Durchak and Caldwell, 2009), and *Pontosaurus lesinensis* (Pierce and Caldwell, 2004), but are preserved as two distinct elements like most aigialosaurs (Carroll and DeBraga, 1992), *Coniasaurus gracilodens* (Caldwell, 1999a), and *Dolichosurus longicollis* (Caldwell, 2000).

The posterio-laterally facing glenoid fossa is identifiable, and is still in association with the head of the humerus. The glenoid fossa is dominated by the coracoid, which contributes about half of the socket, whereas the scapula makes up about a third. Medial to the glenoid, the coracoid narrows, forming a neck separating the glenoid fossa from the coracoid body. The scapulacoracoid fenestra is deep and quite wide, and like the glenoid fossa, has a greater contribution from the coracoid than from the scapula. This is consistent with other large- and small-bodied mosasauroids.

Preserved medial to the right scapula, and lying in contact with the clavicle is a boot shaped element that we identify as a piece of suprascapular cartilage. The placement of this element is consistent with the scapula's direction of rotation, and its position in contact with the scapula and clavicle support this interpretation. Though it is no longer preserved, 2008 photographs show the presence of the left sternal cartilage. Large, shield-shaped, and almost complete (missing the posterior apex), it would have articulated with four or five costosternal cartilages as in *Carsosaurus marchesetti* (Caldwell et al., 1995).

In its current state, there are fragments of organic material scattered across the left pectoral area, most noticeable in the area between the anterior dorsal ribs (Figs. 3B, 4A). This can be best interpreted as bronchial rings as seen in *Pontosaurus kornhuberi* in a similar location and state of preservation (Caldwell, 2006). Other interpretations include pectoral cartilage fragments, soft tissue preservation, or unassociated organic material.

Forelimb—The long bones of the forelimb were well preserved and mostly complete at the time of discovery, but in the current state there are few bony remains (Fig. 2, 4). The humerus is observed only as a natural mould. It is short, stocky, and shaped like a peanut: slightly constricted at mid-shaft and bulbous at both ends. In the 2008 photos, features such as the capitellum, trochlear groove, and coronoid fossa are visible (Fig. 4A). As in *Dallasaurus turneri* (Bell and Polcyn, 2005), remains of ossified epiphyses are visible on both proximal and distal heads; epiphyseal sutures are distinctly visible on both caps. Proximally, there is a domed glenoid condyle and what is probably a large postglenoid process. Moving distally, a crest for deltoid attachment is identifiable and the ectepicondylar and entepicondylar foramina appear to be absent. Distally, both the ectepicondyle and entepicondyle are well developed, and between

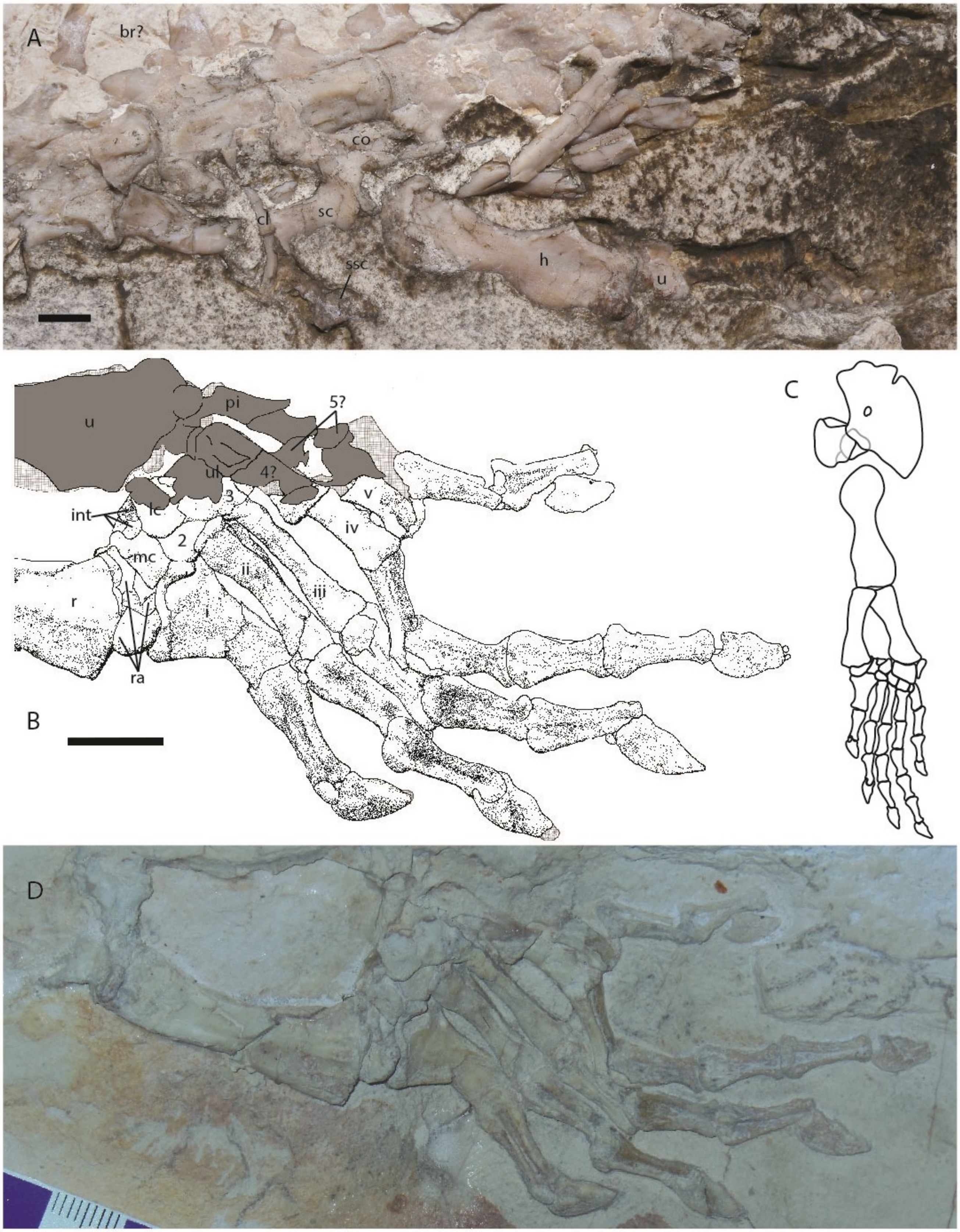
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Figure 3-4 Right forelimb and pectoral region of *Portunatasaurus krambergeri* (CNHM 10808). **A**, 2009 photograph of upper right forelimb showing girdle fragments, humerus and ulnar impression (an interpretive drawing of this region can be seen in Fig 3F); **B**, interpretive drawing of (D); **C**, author's reconstruction of right forelimb; **D**, 2012 photograph of right manus after preparation. Hatched areas in drawings indicate where bone surface has been broken away and bone is visible internally or as an impression. Grey areas without stippling indicate elements preserved in 2009 but not preserved in present state. **Abbreviations**: **br**, bronchial rings; **cl**, clavicle; **co**, coracoid; **h**, humerus; **int**, intermedium; **lc**, lateral centrale; **mc**, medial centrale; **pi**, pisiform; **r**, radius; **ra**, radiale; **sc**, scapula; **ssc**, suprascapular cartilage; **u**, ulna; **ul**, ulnare, **2-5**, distal carpals; **i-v**, metacarpals. Scale bars equal 1 cm.

those condyles, the radial facet and the ulnar facet meet at a greater than 90° angle. A medial notch separates the rounded radial condyle and well developed trochlea, similar to other mosasaurines such as *Plotosaurus* (Russell, 1967). Compared to other dolichosaurids, the overall shape of the humerus is relatively much larger and stockier than *Pontosaurus kornhuberi* (Caldwell, 2006) and *Acteosaurus tommasinii* (Palci and Caldwell, 2010). It is similar in relative length to *Adriosaurus suessi* (Seeley, 1881), *Carsosaurus marcheretti* (Caldwell et al., 1995) and *Aigialosaurus bucchichi* (Dutchak and Caldwell, 2009), but is a much broader and more robust element. Morphologically, it is intermediate between *A. bucchichi* and *Halisaurus sternbergi* (Wiman, 1920).

The ulna was incomplete at the time of discovery, with only fragments (including the proximal end) remaining in a well-defined natural mould (Fig. 4A). The radius—like the hand—was revealed during preparation (Fig. 4B, D). The radius and ulna are roughly three quarters the length of the humerus, with the ulna being slightly larger than the radius (like the condition in *Carsosaurus* and *Komensaurus*). Both elements are more robust than other aigialosaurs. Like dolichosaurs (e.g., *Pontosaurus kornhuberi*, Caldwell, 2006; and *Adriosaurus*, Lee and Caldwell, 2000) and most mosasauroids (e.g., *Carsosaurus marchesetti,* Caldwell et al., 1995; *Komensaurus carrolli,* Caldwell and Palci, 2007), the elements are in close contact proximally where they meet the humerus, and diverge distally where they attach to the wrist. They are separated on the distal border of the antebrachial space by three carpal elements. In between, the medial curves of the radius and ulna outline a much rounder antebranchial space than seen in aigialosaurs, though not quite as round as in *Clidastes*.

In *Portunatasaurus krambergeri*, the radius is sub rectangular: quite straight on the outside edge and curved on its antebrachial margin. Unlike *Komensaurus carrolli* (Caldwell and Palci, 2007), it is wider distally than proximally, though it is similar in that the shaft is bent slightly. The ulna is similarly shaped: thickened and squared off proximally, slightly constricted at mid-shaft, and expanded distally (though not to the extent of the proximal end). Like *Komensaurus carrolli* (Caldwell and Palci, 2007), both radius and ulna have unfused calcified epiphyses on both ends, with the distal ulnar epiphysis being particularly extensive.

Manus—The hand of *Portunatasaurus krambergeri* is the most complete of any small-bodied mosasauroid yet discovered. Most mesopodial and metapodial elements are preserved in articulation, and suffer only minor taphonomic damage. All phalanges and unguals are preserved, and cartilaginous elements can be identified in some places. Digit five has suffering the most damage and dislocation.

This specimen preserves several carpal elements in articulation with varying degrees of breakage that make it difficult to identify anatomical boundaries in some places. In total, we interpret ten carpal elements (Fig. 4**),** more than has been identified in any other mosasauroid except for *Carsosaurus marchesetti* (Caldwell et al., 1995). These are identified as the radiale, lateral centrale, intermedium, medial centrale, ulnare, pisiform, and distal carpals two through five. This configuration resembles that of extant anguimorphs, in which all carpal bones are ossified, and is distinct from all derived mosasaurs, in which at least somecarpal elements remain unossified (Caldwell et al., 1995; Caldwell, 1996). It also indicates that this animal was an adult and not a juvenile.

The radiale is broken, but the pieces remain in life position. Like *Pontosaurus kornhuberi* (Caldwell, 2006), this asymmetrical element is shaped like an apostrophe: expanded laterally, tapering medially, and cupping the medio-distal articular surface of the radius. The lateral and medial margins are both enlarged and rounded into distinct lobes, the medial being much smaller and contributing to the margin of the antebrachial space. The medial centrale—which also contributes to the antebrachial space—is blocky and articulates with the radiale, intermedium, lateral centrale and distal carpal two. The medial centrale and the slightly larger lateral centrale surround the intermedium, and are the only two elements in articulation with it. The intermedium is a very tiny element as is the condition in most aigialosaurs (Caldwell, 1996) except *Komensaurus carrolli* (Caldwell and Palci, 2007). It is broken into several pieces, and it is unclear if all the fragments in this area belong to the intermedium. The lateral centrale and ulnare are only partially preserved, though it is clear that the ulnare is the largest carpal element and most likely sub-rectangular and sitting in articulation with distal carpals three, four and five. In the 2009 photos, it is possible to identify large pieces of this partially preserved blocky element. The pisiform can be identified as an elongate, broken and misplaced element in 2009 photos, and is missing in the current state. This is consistent with other mosasauroids (e.g., *Plotosaurus,* Camp, 1951; *Carsosaurus,* Kornhuber, 1893) who generally have more elongate pisiform elements than dolichosaurs. It is impossible to tell the natural shape of most of the distal carpals, as they have been variously lost, broken or crushed together. However, as in *Carsosaurus* and

Komensaurus, the largest distal carpel element was the fourth, followed by the third, second and finally the smallest: the fifth.

The first four metacarpals are well preserved, with the fourth being broken and dislocated, and the fifth being present but incomplete. As in other pythonomorphs, the first and fifth metacarpals are shorter and more robust than the more elongate medial elements. Metacarpal II and III are the longest and III is the most slender. Metacarpal IV and V are broken and disarticulated, and their length is uncertain, though the fifth appears quite short (as in *Aigialosaurus bucchichi*, Dutchak and Caldwell, 2009). The first metacarpal articulates with the radiale, while the remaining metacarpals articulate with their respective distal carpals (as in *Pontosaurus kornhuberi,* Caldwell, 2006; *A. bucchichi*, Dutchak and Caldwell, 2009; and *Carsosaurus marchesetti,* Caldwell et al., 1995). Metacarpal II, III and IV are hourglass shaped and generally aigialosaur-like. The first metacarpal is unique among compared pythonomorphs. It is extremely wide and robust compared to the others, which is a common mosasauroid feature, but not to this degree of expansion (Caldwell, 1996). The best anatomical match for this element is to mosasaurine mosasaurs. It is extremely broadly expanded compared to the other metacarpal elements, and possesses an anteroproximal overhanging crest (Bell, 1997a). The metacarpals all show epiphyseal plates at their proximal ends, and expanded squared off distal ends.

Every phalangeal element is present, mostly complete, and well preserved. Digits one through four are in close articulation, and digit five has been slightly displaced. The phalanges are elongate and terminate in rounded unguals. Each phalanx is proximally expanded and bulbous, and shows a high degree of distal tapering before flaring out into a distal condyle with two condylar heads where it articulates with the next phalangeal element. The terminal unguals are claw-like and very slightly curved, not hooked as seen in *Pontosaurus kornhuberi* (Caldwell, 2006). They are similar to—though more elongate than—the ungual of *Dallasaurus turneri* (Bell and Polcyn, 2005), and are overall similar to *Komensaurus carrolli* (Caldwell and Palci, 2007) and *Haasiasaurus gittelmani* (Polcyn et al., 1999). Well-defined proximal and ventral tubercles for ligamentous attachment are easily visible. Like other aigialosaurs and terrestrial anguimorphs, *P. krambergeri* has a claw-like ungual on digit five. This is unlike the condition seen in the more derived mosasaurs. Also like other basal mosasauroids and dolichosaurs, the phalangeal formula is 2-3-4-5-3 (e.g., Caldwell, 1996; Dutchak and Caldwell, 2009; Palci and Caldwell, 2010), which is primitive for all lepidosauromorphs (Carroll, 1988).

One unexplained feature of the digits is the deep grooves aligned on the lateral side of each phalanx and ungual. These are deep, uniform, and lie in perfect alignment with proximal and distal phalanges in the same digit. This could be the result of taphonomic deformation causing the bone to collapse inwards into the hollow cavity, but the grooves do not align with the plane of the sedimentary layers. Instead, the grooves are anatomically in the same position on the lateral side of each phalange and face different directions relative to the sediment layers depending on the independent rotation of each digit. Additionally, there is no evidence of cracking around the phalangeal grooves, unlike the rest of the carpal elements which were taphonomically broken and displaced. The grooves more likely represent anatomical features, possibly housing tendons or ligaments for some specialized role in aquatic locomotion. We have also identified this potentially synapomorphic feature on *Haasiasaurus gittelmani* (Polcyn et al., 1999) and *Aigialosaurus bucchichi* (Dutchak and Caldwell, 2009), adding support to this interpretation.

Pelvic girdle—The pelvic girdle (Fig. 3C, F) is indistinct and its organization can only be partly interpreted. One element can be identified in the 2009 photo as the right pubis (identified based on its hatchet-like morphology similar to *Vallecillosaurus donrobertoi*: Smith and Buchy, 2008), and is in articulation with another element that might be the ischium. Posterior to these elements in an impression which may represent the ilium (oriented posteriorly, not anteriorly as in mosasaurs: Debraga and Carroll, 1993), and another more lateral impression which may represent the femur. The left side pelvic elements are vaguely identified as molds. None of these elements can be adequately described.

DISCUSSION

Relationships

Portunatasaurus krambergeri represents a new genus and species that preserves important new anatomy previously unknown for basal mosasauroids. However, phylogenetically informative data on the cranial anatomy remains non-existent, and as current data matrices are cranial-centric, such an analysis would bias and perturb phylogenetic inferences (Roure et al., 2012) and would have a higher likelihood of misplacing the incomplete taxon based on homoplastic characters (Wiens, 2001): notably in this case, the limbs. In addition, a phylogenetic analysis focusing on all Cretaceous semi-aquatic squamates has not been attempted, and the work required to construct a set of informative and relevant characters for this group is beyond the scope of this paper. Consequently, we present instead a qualitative character assessment of *Portunatasaurus*.

The animal presented is accepted to be a squamate, showing synapomorphies including procoelous vertebrae, single headed ribs, cervical intercentra forming prominent hypapophyses, loss of the entepicondylar foramen (humerus), enlarged distal epiphysis of the ulna, loss of gastralia, and probably, an anterior coracoid emargination (Estes et al., 1988).

Most recent cladistic analyses of squamates recognise two major clades: Iguania and Scleroglossa (e.g., Estes et al., 1988; Evans and Barbadillo, 1997; Lee, 1998, 2005; Lee and Caldwell, 2000; Vidal and Hedges, 2004; Conrad, 2008). Though *Portunatasaurus. krambergeri'*s lack of skull complicates classification, no known iguanian shows a long-bodied morphology. Overall, the postcranial skeleton of *Portunatasaurus* shows only minor differences from those of known basal mosasauroids. The high number of presacral vertebrae (greater than 26) is a synapomorphy for the Anguimorpha, though this is also a feature of several other long-bodied squamate taxa (see Palci and Caldwell, 2010 for discussion). Additionally, though the cervical intercentra are not preserved, the placement of the hypapophyses indicates that they were sutured to posterior part of preceding centrum. *P. krambergeri* is confidently placed within the Pythonomorpha (Cope, 1869) based on the synapomorphies listed by Lee (1997) and Lee (1998), including circular condyles and loss of axial epiphyses. Following Palci and Caldwell (2007, 2010), the Pythonomorpha is split into two major groups: the Mosasauroidea (Camp, 1923; Bell, 1997a; Lee, 1998; Caldwell, 1999b) and the Ophidiomorpha (Palci and Caldwell, 2007). Ophidiomorphs (including dolichosaurs and snakes) are characterized by reduction of the limbs and extreme elongation of the neck (ten or more cervical vertebrae) and trunk (greater than 35 thoracic vertebrae). With well developed front limbs, and cervical and thoracic counts of (probably) ten and eighteen respectively, the placement of *Portunatasaurus* within the Ophidiomorpha can be ruled out.

The Mosasauroidea is node-defined as the most recent common ancestor of the Aigialosauridae (Kramberger, 1892) and Mosasauridae (Gervais, 1852), and all its descendants

(DeQueiroz and Gauthier, 1992). Synapomorphies shared by this group that are assessable in *Portunatasaurus* include: posteriorly facing vertebral condyles, cervical intercentra not sutured or fused to preceding centrum, and probably, transverse process on posterior cervicals situated on middle of lateral surface of centra (Lee, 1997). Mosasauroids are also unified by the presence of axial elongation in the cervical, dorsal and caudal regions, the presence of zygosphenes/zygantra in the presacral region, and some degree of limb reduction. The aigialosaurs (Kramberger, 1892) are currently understood as small bodied basal mosasauroids (less than two metres) from the Late Cretaceous (Caldwell, 2012). Unfortunately, the missing cranial and caudal regions mean that many of the Aigialosauridae synapomorphies laid out by Carroll and DeBraga (1992) cannot be identified on *Portunatasaurus*. However, *P. krambergeri* and other aigialosaurs lack some derived features possessed by some mosasaurids, such as a reduction in ossified carpal elements, a posterior facing glenoid, a phalangeal formula greater than 2-3-4-5-3, unclawed unguals, and an expansion of opposite ilial processes (deBraga and Carroll, 1993; I. Paparella, pers. comm., 2017). In terms of overall similarity, *Portunatasaurus* most closely resembles *Carsosaurus marchesetti* (Kornhuber, 1893). Therefore, of the two families within the Mosasauroidea, *Portunatasaurus* is ruled out of the Mosasauridae.

In summary, using increasingly exclusive sets of diagnostic features, it is possible to diagnose *Portunatasaurus* as an ‘aigialosaurian’ form of basal mosasauroid. We surmise that *P. krambergeri* constitutes a more derived grade of aigialosaur occupying a similar placement to *Dallasaurus* due to the anatomies it shares with this animal (humerus and vertebral shape) and with mosasaurines (an expanded first metacarpal and a medial notch on the humerus). We do not consider *P. krambergeri* to be a juvenile because of the high degree of ossification observed in the carpals and the epiphyses. With the caveat that it cannot be directly compared to *Judeasaurus* *tchernovi* due to lack of comparable features, *Portunatasaurus* is considered different from all previously described mosasauroids and requires a new name. There is no cause to assign it to any known aigialosaur genus, and so we establish a new binomen: *Portunatasaurus krambergeri*.

Aquatic adaptations in mosasauroids

The anatomical features of *Portunatasaurus krambergeri* contribute to a growing body of evidence that helps explain the origin of the larger, more derived Mosasauridae and their rise to dominance during the Late Cretaceous. Current evidence suggests that mosasaurids evolved from more basal mosasauroids from the Upper Cenomanian through to the Turonian. By the end of the Turonian, most mosasauroid subfamilies are recognizable from fossils found in North and South America, Europe, and Africa (Halisaurinae, Plioplaticarpinae, Tethysaurinae, Tylosaurinae, Yaguarasaurinae; deBraga and Carroll, 1997), suggesting that mosasaurs rapidly radiated across the northern Atlantic and southward along the Gondwanan coasts. *Portunatasaurus krambergeri* falls within the critical time period when small-bodied mosasauroids were becoming less prevalent, and the larger mosasaurs were transitioning into the niche of top oceanic predators. Though mosasauroid records from the Cenomanian-Turonian span four continents and five mosasaur sub-families, the number of specimens is low, as most are monotypic. As such, the discovery of a new genus of basal mosasauroid from this transitional time provides further evidence that the rise of the large-bodied mosasaurs originated in the Tethys.

The record of mosasauroids from this time is particularly interesting in that it spans the evolution of aquatic locomotor morphologies in mosasaurs. Aigialosaurs are plesiopelvic and plesiopedal: possessing facultatively terrestrial, weight bearing girdles and limbs. Derived mosasaurs are hydropedal and hydropelvic: obligatorily aquatic, possessing paddle-shaped limbs, and incapable of carrying their own weight on land (Bell and Polcyn, 2005; Caldwell and Palci, 2007). Whether these transitions happened once, or evolved multiple times is a subject of debate within the literature (e.g., Bell and Polcyn, 2005; Caldwell and Palci, 2007; Dutchak and Caldwell, 2009), with up to six independent evolutionary occurrences being proposed (Dutchak and Caldwell, 2009). Plesiopelvic taxa tend to fall out basal to hydropelvic taxa within mosasauroid phylogenies (Bell, 1993; Dutchak and Caldwell, 2009; Reeder et al., 2015). Therefore, as discussed by Dutchak and Caldwell (2009), a better understanding of the distribution of plesiopedal and hydropedal taxa within the mosasauroid tree would contribute to a reconstruction of limb evolution within the group.

Figure 5 shows a hypothetical scenario of forelimb evolution from terrestrial ancestors to mosasaurine mosasaurs. On the left, *Varanus* represents a typical terrestrial anguimorph forelimb. The forelimb of *Aigialosaurus* is similar (as previously noted; e.g., de Braga and Carroll, 1993; Dutchak and Caldwell, 2009). The hand is still narrow, the fingers elongate, the wrist bent, the carpals still present and ossified, and the pro- and epipodials contributing to over half the length of the limb. Differences include a reduction in relative limb sized caused by a broadening and shortening of the long bones and an increased separation between the distal ends of the radius and ulna, widening the antebrachial space. The unguals are also straighter and blunter than the hooked, claw-like unguals of *Varanus*. This initial transition matches the first stage described by Camp (1942), who was the first to propose the stages of evolution for the mosasauroid flipper. Both forms are classified as plesiopedal (Bell and Polcyn, 2005) and plesiopelvic (Caldwell and Palci, 2007), and are overall plesiomorphic to the limbed-anguimorph

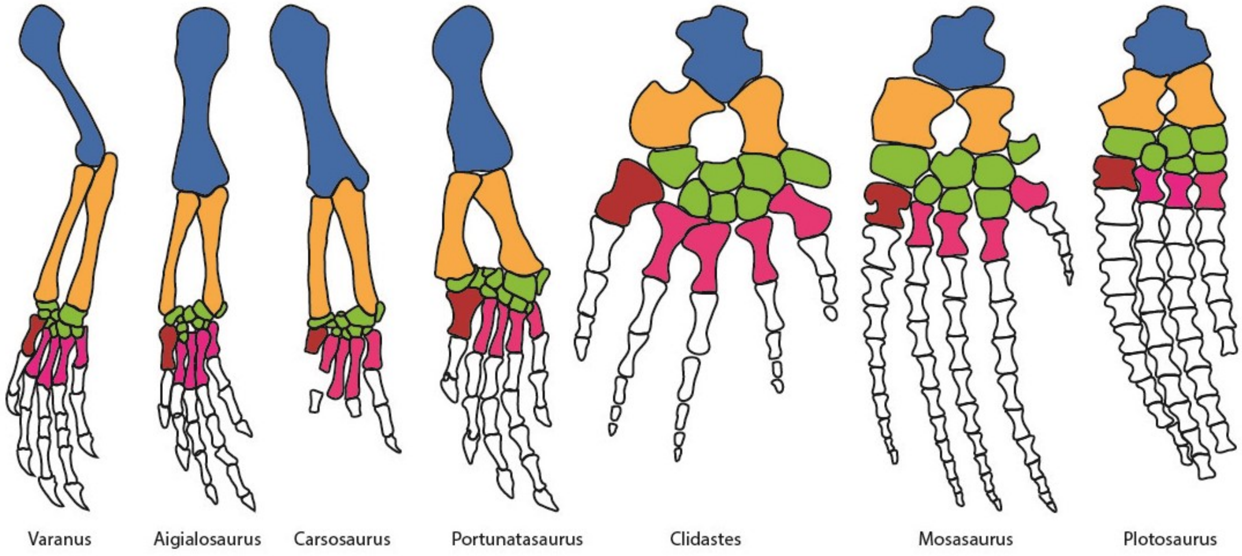

Figure 3-5 Forelimbs of *Portunatasaurus*; a terrestrial squamate (*Varanus*); two aigialosaurs (*Aigialosaurus* and *Carsosaurus*); and two mosasaurines (*Mosasaurus* and *Plotosaurus)*. Sources: Varanus albigularis after University of Alberta Museum of Zoology 947, *Aigialosaurus bucchichi* after GBA 1901/002/0005; *Carsosaurus marchesetti* after MCSNT unnumbered; *Portunatasaurus krambergeri* after CNHM 10808; *Clidastes* sp. after Carroll (1997); *Mosasaurus conodon* after Russell (1967); *Plotosaurus bennisoni* after Camp (1942). Color key: blue, humerus; orange, radius and ulna; green, carpal elements; pink, metacarpals; red, first metacarpal.

condition. Key evolutionary changes in the group at this stage were most conspicuous in the skull and caudal region (de Braga and Carroll, 1997).

The transition from an *Aigialosaurus*-grade animal to a doubly larger, *Carsosaurus*-grade animal is marked by further increases in the robustness and decrease in relative length of the pro- and epipodial elements, now also observed in the phalanges. The expansion of the radiale and migration of some carpal elements also represent a straightening of the wrist. This is consistent with Camp’s (1942) second stage of mosasaur flipper evolution, though he describes it in the context of *Clidastes*, *Platecarpus* and other early mosasaurs.

In *Portunatasaurus* we see a progression of Camp’s second stage: an elongated pisiform, straightened wrist, and a considerably decreased aspect ratio in the humerus, radius and ulna. All three arm elements are much broader relative to their length, and the contribution of the arm bones relative to the length of the entire limb is diminished, constituting roughly half of the length, and indicating a more aquatic lifestyle (Caldwell et al., 1995; Caldwell, 1996). The distal end of the humerus is flattened, which would have resulted in a stiffer, less mobile elbow. The phalanges show more expansion on their articular facets making them more bulbous on each end. The metacarpals are shortened relative to the length of the fingers, and the first metacarpal is greatly expanded. The expanded base of the first digit could support the leading edge of a hydrofoil shaped flipper, though no soft tissues have been found to support this hypothesis. The mesopodials are also beginning to expand and broaden, causing an enlargement and rounding of the antebranchial space: a trend that continues in the subsequent stage. Additionally, *P. krambergeri* presents several limb characters previously considered synapomorphies for the Mosasaurinae: a mosasaur subfamily present in North America by the Coniacian, and cosmopolitan by the Campanian (Russell, 1967). These include a medial notch in the humerus, expanded articulation surfaces on the distal ends of the radius and ulna, and a broadly expanded first metacarpal. It is possible that these features represent a shared ancestry between *P. krambergeri* and the family Mosasaurinae, supporting the multiple origin hypothesis for mosasaurs proposed by Bell and Polcyn (2005).

The most striking difference in the limb transition from *Portunatasaurus* to *Clidastes* is once again a major decrease in the relative contribution of the arm bones to the limb length. This is caused by a major change in the aspect ratio of humerus, radius and ulna, which in *Clidastes* are roughly as long as they are wide. The preaxial border of the radius is enlarged, and is thought to be the attachment point for a ligament running the length of the paddle (deBraga and Carroll, 1993). There is a reduction in the number of ossified mesopodials (from ten to seven; see also

Caldwell, 1996), and an increase in the number of phalanges (hyperphalangy). The unguals also show a major shift in morphology, looking shorter, blunter, and more tapered. The rest of the animal also showed new aquatic adaptations after this evolutionary stage including an increase in body size and hydropelvic girdles.

The third and fourth stage of limb evolution described by Camp (1942) is shown in derived, fully aquatic mosasaurs such as *Mosasaurus* and *Plotosaurus*. Large body size and the presence of flippers and caudal fins typify these stages. The upper limb elements become broader than long (now contributing to less than half the length of the limb), the phalanges continue to shorten and broaden even as they increase in number and their articulations become planar, the digits become adpressed, and the pisiform enlarges and rotates outwards. Until now, this was the first stage in which an enlarged first metacarpal could be observed. In the most derived cases (*Plotosaurus*), the flipper elongates, each digit is almost in contact with its neighbour, and the fifth digit is reduced.

According to this updated, more comprehensive scenario of mosasauroid evolution, the stages of adaptation are as follows: 1) facultatively-aquatic aigialosaur-grade animals develop elongate bodies, mosasaur-like skulls, laterally compressed tails, vertebrae that facilitate lateral undulation, and reduced limbs; 2) *Carsosaurus*-grade animals roughly double in body size from the previous grade, further reduce limb length, increase the robustness of limb elements, and widen and straighten to wrist; 3) *Portunatasaurus*-like animals show a transition from the plesiopedal to hydropedal condition, with a substantial reduction in the aspect ratio of the limbs, an expansion in the articular facets on most limb bones, further broadening and flattening of the wrist, and an expanded first metacarpal suggesting a hydrofoil-shaped flipper which would have increased the locomotor capacity; 4) in small mosasaurs like *Clidastes*, the body size increases though the body is less elongate, the limbs bones are as wide as long, the wrist is less mobile due to the expanded carpals, the number of ossified carpal elements decreases, the rotated pisiform increases the surface area of the palm, the manus and pes are overall more flipper-like, and the girdles are no longer weight bearing making these animals obligatorily aquatic; 5) in *Mosasaurus*-like animals, the body size reaches its maximum, the flippers show hyperphalangy and a well-developed hydrofoil shape, the fifth digit is reduced, and the tail bears a heterocercal caudal fin; 6) the final stages of mosasaur evolution seen in animals like *Plotosaurus* show rounded and tile-like limb bones with flexible articulations, adpressed digits, and the loss of additional ossified carpals and the fifth digit.

As in other marine tetrapods (ichthyosaurs, pleurosaurs, sauropterygians), radically different constraints on support and locomotion drive the drastic changes in limb anatomy. Water is the main selection force in the evolution of the lineage, and the rate of evolution reflects the strength of this selective pressure. Within the relatively uniform marine environment, optimizing locomotor efficiency, buoyancy, and resistance were selected for regardless of niche. This resulted in strong directional evolution. In the case of the mosasaurine limb, this trend can be summarized as a gradual abbreviation of limbs and a change in their shape to enhance stabilization and manoeuvering.

In an environment of such strong and uniform selection, it is plausible that multiple closely related lineages would converge upon phenetically similar forms. We agree with Bell and Polcyn (2005) that hydropedal limbs could be homoplastic across the mosasauroid tree. *Portunatasaurus krambergeri* provides additional evidence by demonstrating possible mosasaurine features (though they are minor), and its clear differences from other aigialosaurs and basal mosasaurs. Until now, *Dallasaurus* and *Tethysaurus* provided the best examples of mosasauroid limbs less hydropedal than derived mosasaurs and less plesiopedal than other aigialosaurs. It was argued that the conclusions of Bell and Polcyn (2005) may have relied too strongly on incomplete knowledge of the limbs in these more transitional taxa (Caldwell and Palci, 2007). *P. krambergeri* fills these gaps, therefore lending support to this theory. Unfortunately, the incomplete preservation of the pelvic girdle does not allow for similar inferences regarding the transition for plesio- to hydropelvic morphologies.

Paleobiology

The limestone layer that *Portunatasaurus krambergeri* was recovered from is interpreted as a marine patch reef – lagoon environment located in the southern European Tethys Sea deposited on the then Adriatic Carbonate Platform (Zappaterra, 1990; Vlahović et al., 2005). Fossils found above, below, and in the same layers as *P. krambergeri* include terrestrial plants, rudist biostromes, teleost fishes, ammoniates, corals, bivalves, and other marine invertebrates.

The number, size and morphology of the vertebrae, and the shape of the ribs, suggest that this new specimen had a long and slender neck, and an elongated and cylindrical body characteristic of an animal adapted to anguilliform swimming. The limbs and girdles are fully ossified, and evidence of extensive cartilage indicate a pectoral girdle very like *Carsosaurus marchesetti*, which was proposed to have increased the range of motion of the forelimb (Caldwell et al., 1995). The reduction of the upper limb bone elements, together with the increased size and robustness of the mesopodial elements in the manus, and the expansion of the leading edge (first metacarpal and digit) suggest a stiffer, flipper-like forelimb, more useful for swimming and steering in the water, than for supporting body weight on land. The large suprascapular cartilage is similar to other anguimorphs including aigialosaurs, mosasaurs and varanoids, and may be a synapomorphy for the suborder (Caldwell et al., 1995). Based on the anatomy of its closest relatives, the tail, though unpreserved, would likely have been the prime propulsive organ for locomotion.

It is reasonable to conclude that *P. krambergeri* lived in or along coastal environments, as well as out on the open platform in the widespread Tethyan patch reef-lagoon environments stretching across the European Tethys to North Africa (Föllmi and Delamette, 1991; Gušić and Jelaska, 1993). Its osteology suggests at least a semi-aquatic lifestyle, likely to a greater degree than *Aigialosaurus*. However, its proximity to subaerial exposures of reef mounds, islands, and perhaps even continental coastal margins, coupled with the robustness of the shoulder girdle and manus, give no reason to assume that *P. krambergeri* was obligatorily aquatic.

CONCLUSIONS

Mosasaur evolution was driven largely by a single selective force: effective aquatic locomotion. This powerful selection pressure resulted in a relatively fast (approximately fifteen million years) change from plesiopedal, plesiopelvic aigialosaurs to hydropedal, hydropelvic mosasaurs. *Portunatasaurus krambergeri* is an important new source of information on the aquatic adaptation and evolution of early mosasauroids, as it represents an intermediate adaptive stage between these two endpoints. Qualitative analysis indicates that *P. krambergeri* is an aigialosaur more derived than the genera *Aigialosaurus*, *Dallasaurus*, *Carsosaurus*, or *Komensaurus*. *P. krambergeri* presents novel and important information: possessing an intermediate morphology between aigialosaur-grade plesiopedal mosasauroids and mosasaurine-grade hydropedal mosasauroids. These transitional features include size, body length, girdle shape, location of transition of centrum shape, as well as numerous features of the forelimb.

Early mosasauroids are small bodied, with plesiopedal features: elongate pro- and epipodials (constituting more than one-half of total limb length); minimal expansion of humeral, radial, ulnar and phalangeal epiphyses and articulation surfaces; long, slender phalanges with uniaxial articulations; small and closely articulated pisiforms; and small, angular mesopodials. Large-bodied, derived mosasaurs have limbs adapted for aquatic environments: shortened pro- and epipodials elements as broad or broader than long and contributing to less than half the length of the limb; expanded carpal elements including a large, projecting pisiform; a thickened first digit, especially in the metacarpal; expanded articulations on distal and proximal ends of pro- epi- meso- and metapodials; planer articulations on shortened phalanges; and shortened and blunted unguals. The morphology of the limb suggests that *P. krambergeri* is functionally between aigialosaurs and mosasaurs in terms of its locomotor capabilities.

Unfortunately, as noted by Caldwell and Palci (2007) and Dutchak and Caldwell (2009), the instability of the mosasauroid tree topology (Bell, 1997a; Caldwell, 2000; Bell and Polcyn, 2005; Dutchak and Caldwell, 2009; Gauthier et al., 2012; Polcyn et al., 2014; Reeder et al., 2015) makes an evolutionary comparison of aquatically adaptive features between mosasaur taxa problematic. It is imperative that mosasauroid relationships are better resolved in order to generate more robust hypotheses surrounding the aquatic adaptation of mosasaurs and their concurrent diversification.

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CHAPTER 4 : REASSESSMENT OF THE UPPER CRETACEOUS MARINE LIZARD *APHANIZOCNEMUS LIBANENSIS,* DAL SASSO AND PINNA 1997 – TO BE OR NOT TO BE A DOLICHOSAUR?

ABSTRACT

Aphanizocnemus libanensis is a small monotypic lizard from platy limestones deposited in patch reef lagoons stretching across the Tethyan platform from North Africa to Europe (Cenomanian; Upper Cretaceous). The sole specimen is articulated and nearly complete, though the skull was destroyed during collection. The original description placed the taxon within the Varanoidea as a member of the aquatic Dolichosauridae based primarily on features related to axial elongation and limb reduction. Features unique to the taxon include a short facial region, a slender and elongate body, reduced limbs especially posteriorly, and a unique tibia. Here, I redescribe *Aphanizocnemus libanensis*, and review the diagnosis of Dal Sasso and Pinna (1997). Re-examination suggests that characters cited as supporting varanoid-dolichosaur affinities are misinterpreted, i.e., an intramandibular joint, a character diagnostic of pythonomorphs (the group including the Dolichosauridae, Serpentes and the Mosasauria), is actually a break in the dentary associated with the considerable damage to the skull. Other anatomical features (i.e., the unfused, simple girdles; the reduced, flattened limbs; the shorter hind limb; and the poorly ossified tarsus), while present in dolichosaurs, are common to many squamates, and are likely homoplastic and tightly linked to aquatic adaptation. The hallmark feature of the specimen is the strongly regressed tibia, which is short and flat, with unclear articular surfaces. Limb reduction is a characteristic of the Pythonomorpha, but it is also common to numerous families within Squamata, including the Scincomorpha. The available data support the conclusion that

Aphanizocnemus is not a dolichosaur, a varanoid, nor in fact an anguimorph, but may represent a new form of aquatic scincomorph, a group not previously recognized as having evolved aquatic adaptations.

INTRODUCTION

In the Cenomanian and Turonian, the Tethys Sea was an epicentre of aquatic adaptation among squamates (Bardet et al., 2008). In this shallow, epicontinental seaway, one group of squamates gave rise to multiple aquatically derived lineages. The Pythonomorpha (Cope, 1869) is a diverse group of lizards that evolved a variety of aquatically adapted morphologies and radiated into aquatic environments around the globe during the Late Cretaceous (Lee and Caldwell, 2000; Caldwell, 2006; Bardet et al., 2008; Caldwell and Palci, 2010). Ranging in size from half a metre to almost 20 metres long (Caldwell and Palci, 2010; Jimenez-Huidobro and Caldwell, 2016), they spanned the globe and habited a range of freshwater and marine ecosystems, from shorelines, estuaries, shallow seas, rivers, and the open ocean (Holmes et al., 1999; Averianov, 2001; Bardet et al., 2008).

Though the precise relationships within the Pythonomorpha are incompletely resolved (see Chapter 5; Caldwell and Lee, 1997; Lee and Caldwell, 1998, 2000; Zaher and Rieppel, 1999; Caldwell, 2000, 2003; Rage and Escuillié, 2000; Rieppel and Zaher, 2000; Tchernov et al., 2000; Pierce and Caldwell, 2004; Vidal and Hedges, 2004; Dutchak and Caldwell, 2006; Caldwell and Palci, 2007, 2010; Conrad, 2008; Martill et al., 2015; Reeder et al., 2015; Caldwell et al., 2015) at least four morphological groupings can be recognized: the mosasaurs, the aigialosaurs, the dolichosaurs, and the ophidians. The mosasaurs were the largest, most aquatically derived members of the Pythonomorpha (possessing flippers, flukes, and a hydrodynamic body plan), and are the only group to reach a truly cosmopolitan distribution (Caldwell, 2012). Their monophyly is questionable, with recent hypotheses suggesting at least two lineages evolving a 'mosasaur' morphotype (Bell and Polcyn, 2005; Haber and Polcyn, 2005; Dutchak and Caldwell, 2006; Caldwell and Palci, 2007; Simões et al., 2017). Examples of the derived, hydropedal morphotype include *Mosasaurus, Prognathodon, Platecarpus*, and *Tylosaurus* (Lindgren et al., 2010; Konishi et al., 2011; Jiménez-Huidobro et al., 2016; Street and Caldwell, 2016). Aigialosaurs (plesiopedal mosasauroids) are considered basal to the derived mosasaurs. They are medium sized (1-3m), short-necked, limbed lizards with laterally compressed tails for swimming. They include *Komensaurus, Aigialosaurus, Carsosaurus, Haasiasaurus,* and *Portunatasaurus* (Gorjanovic-Kramberger, 1892; Kornhuber, 1893; Caldwell et al., 1995; Caldwell and Lee, 2001; Haber and Polcyn, 2005; Dutchak and Caldwell, 2006, 2009; Caldwell and Palci, 2007; Chapter 3). The dolichosaurs are small (<1m), axially elongate, with reduced limbs, and are often pachyostotic. They have a close but uncertain relationship to derived ophidians (see Chapter 5; Lee and Caldwell, 2000; Caldwell and Palci, 2010; Palci and Caldwell, 2010), and include genera such as *Pontosaurus, Adriosaurus, Coniasaurus,* and *Acteosaurus*(Owen, 1850; von Meyer, 1860; Kornhuber, 1873; Seeley, 1881; Gorjanovic-Kramberger, 1892; Bell and Polcyn, 1996; Caldwell, 1999a; Caldwell and Cooper, 1999; Lee and Caldwell, 2000; Pierce and Caldwell, 2004; Palci and Caldwell, 2007, 2010). The early marine snakes, the pachyophiids, are often preserved with reduced limbs, and include *Pachyrachis, Pachyophis, Haasiophis*, and *Eupodophis* (Lee and Caldwell, 1998; Lee et al., 1999; Rage and Escuillié, 2000; Tchernov et al., 2000).

Aphanizocnemus libanensis (Dal Sasso and Pinna, 1997; Figure 1) was described from the Upper Cretaceous of Lebanon (Middle Cenomanian, roughly 95 Ma). It was assigned to the Dolichosauridae, within the Varanoidea. It was diagnosed based on the uniquely shaped parietals (broad and almost square parietal table), a short facial region, rear limbs shorter than the front limbs, the flat tibia without articular facets, the lack of a fibula. The skull structure, and some unusual proportions in the postcranial skeleton raised some doubts about the maturity of this individual, and the authors acknowledge that it could represent a juvenile. The principal problem regarding the diagnosis of this specimen was the poor preservation and subsequent misidentification of elements supporting a varanoid-dolichosaur affinity. Additionally, many of the morphological similarities to dolichosaurs can be interpreted as homoplastic characteristics linked to aquatic adaptation.

Aphanizocnemus has been used to support the phylogenetic position of dolichosaurs in several phylogenetic analyses (Lee and Caldwell, 2000; Rieppel and Zaher, 2000b; Pierce and Caldwell, 2004; Palci and Caldwell, 2007; Rieppel et al., 2007; Conrad, 2008; Caldwell and Palci, 2010). Considering the ongoing debate surrounding the evolution and phylogenetic relationships of mosasaurs, aigialosaurs, dolichosaurs, and snakes (see above), a reassessment of the type specimen is imperative. Here, I will here redescribe and rediagnose *Aphanizocnemus libanensis,* Dal Sasso and Pinna, 1997, which is represented by a single specimen from Lebanon, and is curated at the Museo Civico di Storia Naturale in Milano, Italy (MSNM V783).

GEOLOGICAL CONTEXT

The precise locality where *Aphanizocnemus* was found is unknown; however, it was most likely recovered from the 'Fish Beds' of the Sannine Formation, Lebanon (Dal Sasso and Pinna, 1997). Several Sannine outcrops in Lebanon have produced squamate remains: Nammoura, Hakel, and Hadjula. Al Nammoura (or En Nammoura) is a is mid-Cenomanian Lagerstätten located in Garbour Valley in the north of Lebanon that produced the holotypes of *Pontosaurus kornhuberi* (Dal Sasso and Renesto, 1999; Caldwell and Dal Sasso, 2004; Caldwell, 2006) and the hind-limbed snake *Eupodophis* (=*Podophis*) *descouensi* (Rage and Escuillié, 2000). The Sannine Formation was laid down in a low energy, shallow carbonate platform thought to represent a system of lagoons, rudist patch reefs, and small islands (Dal Sasso and Pinna, 1997; Dalla Vecchia et al., 2002). The appropriately named "fish beds" produce mainly teleosts and crustaceans, but also bivavles, plants, and rare tetrapods including turtles, lizards, and limbed snakes (Dal Sasso and Renesto, 1999; Dalla Vecchia et al., 2002). Dalla Vecchia et al. (2002) proposed that this locality was laid down in an anoxic, possibly hypersaline lagoon, allowing the stunning preservation of soft tissues.

Lithologically, the specimen is preserved in a greyish yellow, compact limestone with fine, parallel laminations and flint lenticular inclusions. Based on the color and the flint lenticular inclusions of the slab, *Aphanizocnemus* is thought to originate from the Hakel outcrop (Dal Sasso and Pinna, 1997). Hakel (or Hâqel) is associated with a small basin on the outer margin of the continental shelf, is the same age or slightly younger than the Nammoura and Hadjula outcrops (Dalla Vecchia et al., 2002), and has also produced *Eupodophis descouensi* (Rieppel and Head, 2004).

SYSTEMATIC PALEONTOLOGY

LEPIDOSAURIA Haeckel, 1866

SQUAMATA Oppel, 1811

APHANIZOCNEMUS Dal Sasso and Pinna, 1997

Type species—*Aphanizocnemus libanensis*

Revised generic diagnosis—As for type and only species

Aphanizocnemus libanensis Dal Sasso and Pinna, 1997

(Figs. 1-4)

Revised diagnosis—A small (286 mm total length) lizard characterized by small size; short facial region; expanded parietals that envelop cranial vault; an increased number of presacral vertebrae (35); an elongate tail (141 vertebrae) with low, posteriorly directed haemal and neural processes; reduced girdles- especially the pelvic girdle; planar pubes shaped like frying pans; rear limbs shorter than forelimbs; a reduced, block-like tibia; and short limbs relative to foot size (manus and pes <50% total limb length).

Holotype— MSNM V783, curated by the Museo di Storia Naturale di Milano. The specimen is articulated and nearly complete, and is visible in right dorso-lateral view impressed into a limestone slab.

Type Locality and Horizon—Upper Cretaceous (Mid-Cenomanian) of Lebanon (most likely Sannine Formation, Hakel outcrop).

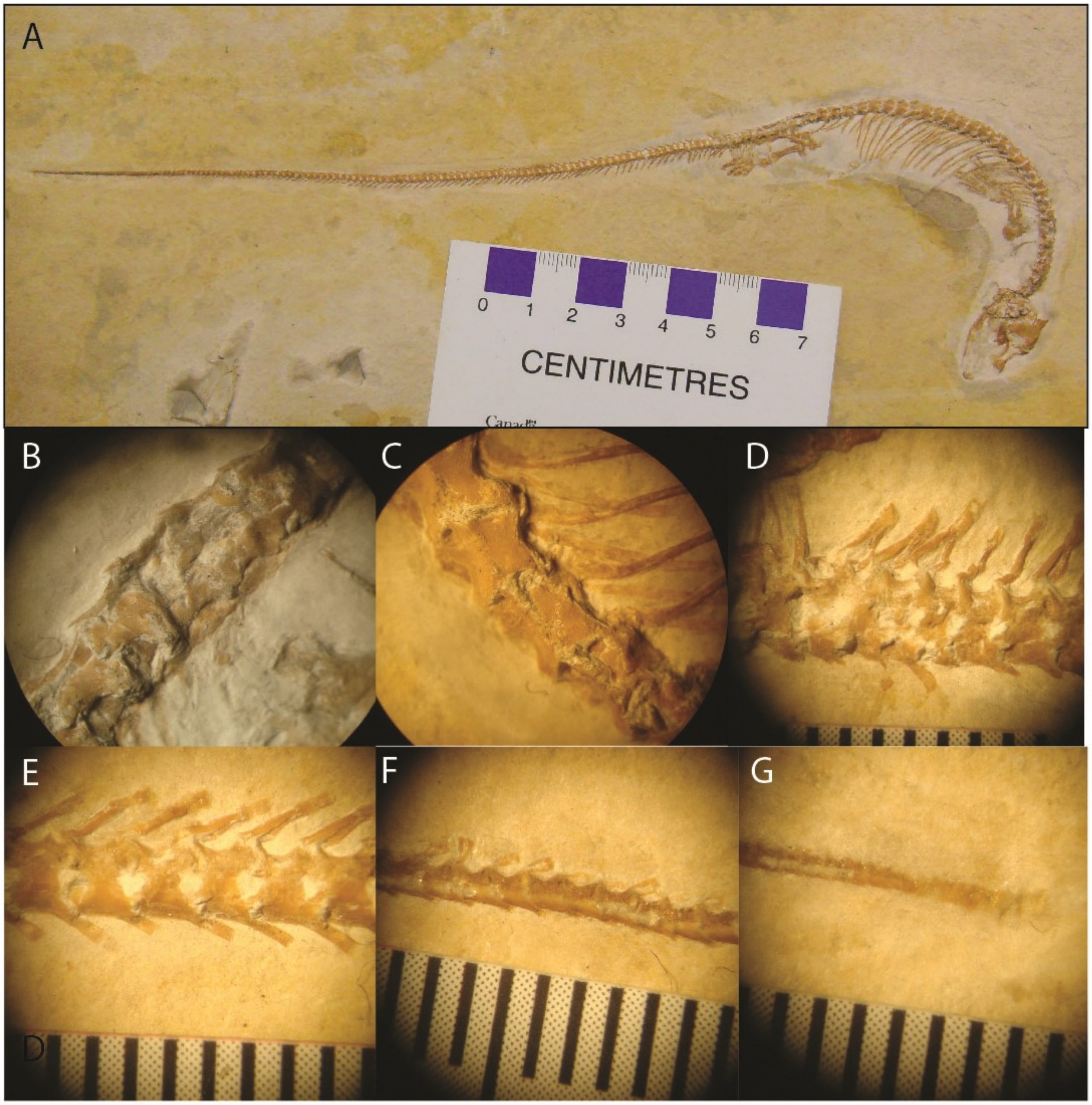

Figure 4-1 The holotype of *Aphanizocnemus libanensis* (MSNM V783). **A**, photograph; **B**, detail of cervical vertebrae; **C**, detail of dorsal vertebrae; **D**, detail of anterior caudal vertebrae; **E**, detail of mid-caudal vertebrae; **F**, detail of posterior caudal vertebrae; **G**, detail of caudal tip.

OSTEOLOGICAL DESCRIPTION

Overall Impression

Aphanizocnemus libanensis is represented by an articulated and relatively complete specimen preserved in dorso-lateral view on a limestone slab. Overall, the 286 mm specimen is well preserved, but the head has been severely damaged such that many elements are beyond identification. Rotation along the vertebral axis resulted in different views along the length of the fossil. Flattening of the skull during fossilization has exposed the dorsal and right lateral surfaces, with the cervical series also being preserved in right lateral view. Rotation through the dorsal series result in the pectoral region being visible in dorso-lateral view, the abdominal region in dorsal view, and the pelvic region in lateral view. The caudal region is exposed completely in right lateral view. Both forelimbs and hindlimbs are visible, though the left forelimb is partially obscured behind the ribcage, and the left hindlimb is overlain by anterior caudal vertebrae.

Skull

The skull is the worst preserved region of the specimen, with many of the bones making up the snout and cheek being missing, and the temporal region and brain case being crushed beyond meaningful identification or interpretation (Figure 2). The best-preserved regions of the cranium are the skull roof and the right mandible. Overall, the small skull (roughly 22 mm) is fairly elongate, roughly four times as long as it is broad, with a short snout and large orbits.

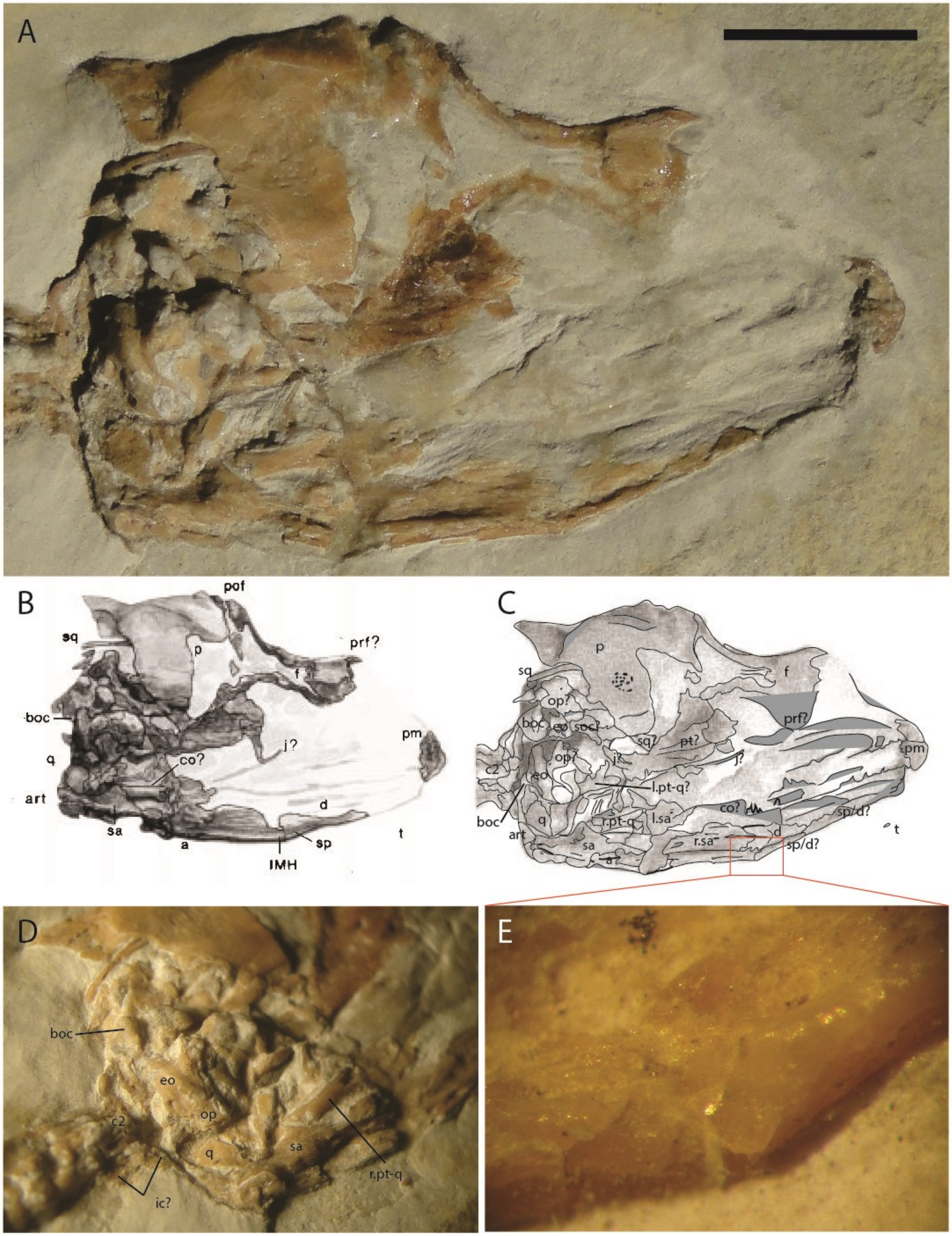
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Figure 4-2 Head and anterior cervical vertebrae of *Aphanizocnemus libanensis* (MSNM V783). **A**, photograph; **B**, interpretive drawing from Dal Sasso and Pinna (1997); **C**, reinterpreted drawing; **D**, detail of the back of the skull from a posteriolateral view with oblique lighting; **E**, detail of right mandible, showing the break interpreted as the IMH in Dal Sasso and Pinna (1997). **Abbreviations: a**, angular; **art**, articular; **boc**, basioccipital; **c**, cervical vertebra; **co**, coronoid; **d**, dentary; **eo**, exoccipital; **f**, frontal; **ic**, intercentra; **j**, jugal; **p**, parietal; **pm**, premaxilla; **pof**, postorbitofrontal; **prf**, prefrontal; **pt**, pterygoid; **pt-q**; quadrate process of the pterygoid; **q**, quadrate; **sa**, surangular; **soc**, supraoccipital; **sp**, splenial; **sq**, squamosal; **t**, tooth. Where two sides are labeled, each abbreviation is preceded by **r.** (right) or **l.** (left). Scale bars equal 5 mm.

The majority of the snout region is missing, and only the anterior tip of the premaxilla remains in dorsal view. The premaxilla appears to be fused, but a central break could be interpreted as the margin between paired premaxillae. The left side shows a distinct embayment between the lateral processes and the ascending nasal process for the anterior border of the nares. The maxillae are completely missing, with the right being preserved as a vague impression. This serves only to confirm the anatomical position of the premaxilla and therefore the length of the skull (22 mm).

The frontal-parietal complex are the best preserved elements of the skull. The frontal is a single element, hourglass shaped in dorsal view, and slightly broader posteriorly than anteriorly. At its narrowest point it is roughly half the width of the frontoparietal suture. The anterior border most has a broad embayment for articulation with the nasals. The posterior margin of the frontal forms a gently undulating fronto-parietal suture with a slight posterior projection on the lateral edges. On the left side of the frontal, the suture for the postfrontal/postorbitofrontal is visible. The anterior-most tip of the left postfrontal/postorbitofrontal is the only portion preserved, extending roughly halfway down the frontal. The parietal is roughly the same length as the frontal. It is massive, single fused element, that covers the entire cranial vault. The parietal is almost square, narrowing only slightly in the posterior third. Ornamentation includes several small depressions in a circular pattern in the middle of the parietal roof, and a broad ridge crossing the left anterolateral corner of the parietal. Neither a parietal foramen nor can the impression of one can be identified, but given the damage, I cannot be certain that it was absent. The posterior border is shattered away, but the left posterior wing preserves a lip where it would have articulated with the squamosal and supratemporal. The left squamosal is disarticulated from the parietal, and sits medial to it. It is long, slender and bends posteriorly where it would cup the quadrate.

Inferior to right posterior corner of the frontal is a jumble of flattened bones that may represent pterygoids, the right postorbital, and/or the anterior right squamosal. Anterior to this is a thin, curved impression which may represent the maxillary process of the jugal. Posterior to the mass, a thin splint of bone in line with a thin, anteriorly directed impression is identified as the postorbital ramus of the jugal. Posterior and inferior to this is a y-shaped element that could be part of the left supratemporal arcade or the quadrate ramus of the pterygoid (identified as the coronoid by Dal Sasso and Pinna, 1997).

The braincase is completely shattered, with few discernable elements (Figure 2D). A relatively broad flat element posterior to the largest parietal fragment is interpreted as another parietal fragment, though it could be the supraoccipital. Instead I identify a piece just ventral to this as the supraoccipital due to the raised ridge it bears. The basioccipital is recognisable due to the bulbous tuberosities at the posterior of the skull, at the apex of the cervical series. Dorsal to this is a fragment of bone preserving a large foramen, identified as the exit foramen for cranial nerves X-XII which makes this a piece of the exoccipital-opisthotic. Lateral to this is another fragment of what is likely the exoccipital, specifically the basioccipital process. The right fragments of the basioccipital and the opisthotic appear to have their natural suture preserved. Medially, these two elements separate, creating the opening for the foramen magnum.

The right quadrate is identifiable by its size, robustness, and location. It is not the element identified as the quadrate by Dal Sasso and Pinna (Figure 2B), which is the exoccipital. The quadrate is in articulation with the surangular, just posterior to the broken piece of the quadrate process of the pterygoid. The quadrate is tall, with a thin, posterolaterally directed conch. The cephalic condyle is broken away. It is uncertain whether the bone fragment anterior to this element represents the anterior half of the same quadrate, making the quadrate ovoid rather than columnar.

Lower jaw

The right mandible, exposed in lateral view, is well preserved enough to identify most of the component elements, though not their extent or complete shape. Due to breakage, it is impossible to tell whether the surangular, prearticular, and articular are separate elements, or if they have fused to form the compound bone. They will be identified as separate elements for ease of description.

Anteriorly, only impressions remain from the dentary, including several impressions of teeth. The posteroventral portion of the dentary remains, in articulation with a short splint of a splenial.

Along the central ventral margin of the mandible is are two long, splint like bones between which Dal Sasso and Pinna (1997) identified an intramandibular joint (Figure 1B), but under closer inspection is merely the result of breakage (Figure 1E). Dorsal to this, the right surangular is preserved as two pieces connected by a continuous impression. The posterior piece preserves the surangular foramen. The element would have been dorsoventrally tall, narrowing posteriorly. The left surangular is preserved in lingual view just posterior and dorsal to the right. It preserves the anterior inferior dental foramen, is contiguous with an impression running anteriorly, and is still in articulation with a fragment of the left coronoid.

The articular is split anteroposteriorly from the surangular by an unidentified bony mass. Posterior to this, it is relatively well preserved, and it is possible to identify the mandibular fossa and the large, triangular articular facet. Posterodorsally, the surangular rises slightly to contact the ventral surface of the quadrate. Laterally, the surangular appears to be the sole contributor to the articular cotyle, to the exclusion of the articular. Posterior to the quadrate articulation, the elements have been slightly disarticulated, revealing the articulation between surangular and the articular. The articular flares posteriorly to form the retroarticular process, which remains partially obscured by the limestone.

A single isolated tooth is preserved just below the anterior snout. It is very small, slightly bent, and fairly uniform in width until the pointed tip.

Axial skeleton

Aphanizocnemus libanensis has 35 presacral, 2 sacral, and 141 caudal vertebrae. All are relatively well preserved, articulated, and visible in dorsal or lateral view. The vertebrae are procoelous, seem large in proportion to their associated ribs, and have notably low neural spines along the entire spine (Figure 1B-G).

The atlas-axis complex is obfuscated by the crushing of the skull making a precise cervical count impossible. If my interpretation of the occipital is correct, then it is likely that the first completely preserved vertebra is the second cervical (axis) based on positioning. This first vertebrae also appears to have two intercentra, which would support the identification of this element as the axis (Figure 2D). However, quality of preservation makes this uncertain, and it is possible that vertebra represents the third cervical.

Besides the uncertain identification of the axis-atlas complex, the cervical series is completely represented, though it is the poorest preserved portion of the axial skeleton. Overall, the cervical vertebrae are slightly shorter than the dorsal vertebrae. They do not exhibit pachyostosis, and instead show clearly defined process (Figure 1B). Pre- and post-zygapophyses are variably worn, but are clearly present. The close articulation of the vertebrae and orientation of preservation means that the presence of zygosphenes and zygantra is impossible to determine. Hypapophyses are visible ventral to cervical vertebrae, and one appears to have been displaced below the fourth cervical.

Remnants of rib heads are visible from the seventh cervical vertebrae onwards, but it is unclear how far anteriorly they begin. A transverse process with what appears to be a posteriorly facing articular facets can be identified on the fourth cervical vertebrae. Impressions from ribs are visible below the eighth vertebrae. These impressions do not preserve much detail, though they do indicate shorter ribs than in the dorsal region. Therefore the first vertebra with long ribs is the ninth, which likely represent the first sternal rib.

Dal Sasso and Pinna (1997) identified the eleventh vertebrae as the last cervical (Figure 3A). I disagree with this interpretation based on the changing lengths of the ribs anterior to this region (see above), and the positioning of the pectoral girdle. Impressions below the ninth vertebrae show elements too robust to be ribs that likely represent cartilaginous shoulder elements. According to this, I identify the ninth vertebrae as the first dorsal, giving a cervical count of eight. The long ribs originating from the tenth vertebra (as long as the rest of the dorsal ribs) supports this interpretation.

The dorsal region (Figure 1C) is therefore comprises 27 vertebrae which are roughly equal in size along their length. The dorsal vertebrae are notable in their pronounced, hook-shaped pre- and postzygapophyses, which are largest in the mid-dorsal region. The neural spines are low and thin, and run the length of the vertebrae. Zygosphene-zygantral articulations are present throughout the column, and are angled almost straight anteriorly. A distinctive lumbar region is present as of the 20th dorsal vertebrae. At this point, the vertebrae become longer, and slenderer, with more acutely angled pre- and postzygapophyses. At this point the ribs begin to reduce in size, and are completely absent in the last two dorsal vertebrae.

All dorsal vertebrae support ribs that articulate with the anteriorly positioned synapophyses. The right ribs are visible in full, the left are obscured behind the vertebral column and the right ribs. The ribs are overall very narrow and straight, grooved posterolaterally, and sweep backwards rather than curve down and in to form the slender abdominal cavity. Instead of narrowing to a point, the tips of the ribs expand and broaden distally into an oar-shape. This is especially noticeable on the anterior ribs, just posterior to the forelimbs.

The sacral region is made of two unfused vertebrae (Figure 4), easily identified by the broad sacral ribs. Neither contacts the ilium, as the pelvis has been displaced ventrally from the body. The sacral vertebrae appear to be smaller than the preceding dorsal vertebrae. The sacral ribs do not contact, even though the first angles posteriorly, and the second slightly anteriorly. Both appear roughly rectangular. Though the sacral vertebrae have been slightly crushed, it is possible to tell that the neural spines are extremely short, barely rising above the level of the vertebrae.

Immediately posterior to the second sacral is a vertebrae in contact with the ilium that lacks a haemal arch. This is interpreted as a pygal vertebra. It is roughly the same size as the sacral vertebrae, and slightly larger than the first few caudal vertebrae. It appears to have an anteriorly directed transverse process.

The caudal region (Figure 1D-G) is extremely long, representing about 60% of the animal's total length (or roughly 150% of the snout-vent length). The tail would have been quite slender, as the centrum make up half of the dorso-ventral height. I counted 141 vertebrae, though the poor preservation of the tip makes this number tentative. The first few caudal vertebrae (Figure 1D) have well developed transverse process which gradually decrease in size until by the 25th caudal, they are unidentifiable. Concurrently, the neural spines become longer and the vertebrae shorter. The neural spines in this region are thin, extremely inclined caudally (except dorsal to the pes), and are expanded distally. The haemal arches are roughly twice the length of the neural spines, and project almost perpendicularly from the posterior margin of the centra. They fuse roughly halfway along their length, forming a true haemal arch, which extends ventrally into a spatula-shaped haemal spine. The centra are taller than long, and still possess robust zygapophyses.

Around the 25th caudal, the morphology of the caudal vertebrae changes again (Figure 1E). The vertebral centra are almost completely smooth, lacking any transverse processes. The haemal arches abruptly change their orientation, and instead of projecting almost ventrally (as in the anterior portion of the tail), they sweep posteriorly at an angle more similar to the neural arches. Instead of having a spatula-shaped haemal spine, the distal tip is now rectangular. The pre- and postzygapophyses have also moved, and are now positioned more ventrally.

The last third of the tail has very small, tightly articulated vertebrae (Figure 1F). The haemal arches and neural spines are shorter relative to the length of their centra, and are angled almost parallel to the long axis of the tail, such that they lie almost touching the following vertebra. In the case of the haemals, this loss of length is caused by the loss of the haemal spine, as the haemals fuse into an arch very distally. The very tip of the tail is worn away (Figure 1G), but the vertebrae do not appear to fuse. Haemal arches cannot be identified on the last ten vertebrae, though the zygapophyses are still identifiable as tiny nubs.

Pectoral girdle and forelimbs

The left and right forelimbs and shoulder girdles lie pressed together ventral to the vertebral column (Figure 3). Most of the osseous elements are present, however, neither the sternum, interclavicle, nor any cartilaginous elements have been preserved indicating that they were non-calcified elements. Impressions connecting the girdles to the vertebral column may represent some of these elements, but the impression is to vague to be interpreted.

Long, thin, curved impressions anterior to the pectoral girdles likely represent the clavicle(s). The right shoulder girdle is almost completely preserved, though the elements are somewhat worn, and the left is either missing or obscured underneath the right. The scapula and coracoid are approximately the same size and appear to be fused into a single scapulocoracoid element. The anterior margin of the scapula has a long emargination that would border the scapular fenestra. The scapulocoracoid fenestra is deep and narrow. The coracoid is fan shaped,

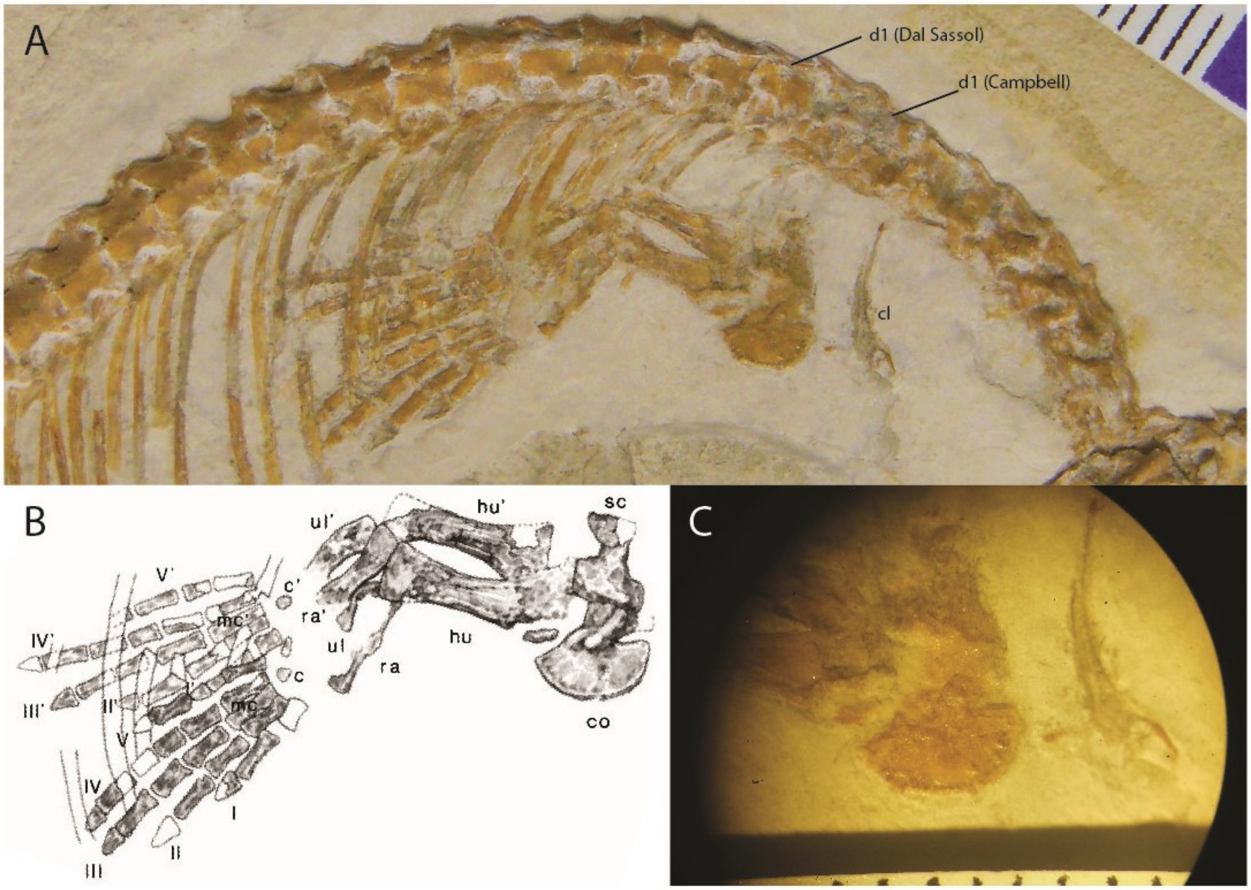

Figure 4-3 Forelimbs and pectoral region of *Aphanizocnemus libanensis* (MSNM V783). **A**, photograph; **B**, interpretive drawing from Dal Sasso and Pinna (1997); **C**, detail of girdle elements. **Abbreviations**: **c**, carpals; **cl**, clavicle; **co**, coracoid; **d**, dorsal vertebra; **hu**, humerus; **mc**, metacarpals; **ra**, radius; **sc**, scapula; **ul**, ulna; **I-V**, first to fifth digit.

almost semicircular, and has rugose ornamentation around the border. Dal Sasso and Pinna (1997) could not identify a supracoracoid foramen, but it is present at the apex of the scapulocoracoid fenestra. The glenoid fossa is clearly visible posterior to the two elements, as the humerus has been slightly displaced from the fossa. Overall, the pectoral girdle is small (roughly three vertebral lengths), but not greatly reduced relative to the length of the forelimbs.

The front and back legs are the same length, which is also equivalent to the length of the head (roughly eight vertebrae in length). Within the forelimbs, the pro- and epipodial elements are also roughly equivalent in size. The phalangeal elements are extremely developed, such that the manus is half the length of the entire forelimb.

Both left and right humeri are both preserved, with the right overlying the left. They are very robust bones with more expanded distally than proximally. The articular heads are very simple, almost columnar, with very little accessory ridges or tubercles. Bulbous remains at the proximal and distal ends of both humeri represent the epiphyses, not the humerus (contra Dal Sasso and Pinna, 1997). A prominent deltopectoral crest is visible proximally on the right humerus, and the humeral crest on the left.

The radius and ulna are incompletely preserved and provide little anatomical detail. The radius appears thinner than the ulna, dorsoventrally flattened, and weakly curved. The ulna curves medially, and like the radius, appears dorsoventrally flattened. The olecranon process is identifiable, but reduced. The forelimbs—still in articulation, though crushed—shows that the radius and ulna are in close proximity proximally where they articulate with the humerus, and distally where they contact the carpal elements, resulting in a relatively narrow antebranchial space.

All of the carpal elements except one are missing. The single remaining capral is from the right manus. Due to its position, it likely originated from the distal row. Dal Sasso and Pinna (1997) identified it as the fourth carpal, which is possible given its position, and its relative likelihood of preservation (being the largest and most robust of the carpal elements).

The metacarpals are reasonably well preserved and easily identified. They are robust, and almost rectangular, rather than the more typical hourglass shape. The longest element is the third.

The phalanages are notable in their size and robustness. Like the metacarpals, they are subrectangular rather than hourglass-shaped. The phalangeal formula is 2-3-4-5-3. The longest digit is the fourth, then the third, second, fifth and first. The last phalanx before the ungual is longer than the phalanges preceding it. The terminal unguals are broader at the base than phalanges they are attached to, which is partially due to a well developed ventral tubercle. The ungual tips are straight, not hooked, and with blunt tips (could be a result of taphonomy).

Pelvic girdle and hindlimbs

Like the forelimbs, both hindlimb and the pelvis are preserved ventral to the vertebral column, with the right leg clearly exposed, and the left obscured behind the tail (Figure 4). The pelvis is composed of fused paired ilia, ischia, and pubes, is smaller than pectoral girdle (two vertebral lengths as opposed to three), and more reduced.

The elongate, blade-like ilium is visible in lateral view. It rises posterodorsally through the posterior superior iliac crest, which articulates with the two sacral ribs. Anteriorly, it contacts the pubis and ischium to participate in the dorsal portion of the acetabulum. A small bump on the dorsal margin is interpreted as the preacetabular iliac process.

The pubes are planar, frying-pan-shaped elements, broad and round posteriorly, with a rectangular anterior process. The right pubis is preserved in ventral view, the left pubis is in dorsal view, and shows the pubic foramen in line with the medial edge of the acetabulum.

The right ischium is mostly visible, having been rotated ventrally, while the left is mostly covered with the remainder of the pelvis and sacral ribs. It is roughly equal in size to the pubis,

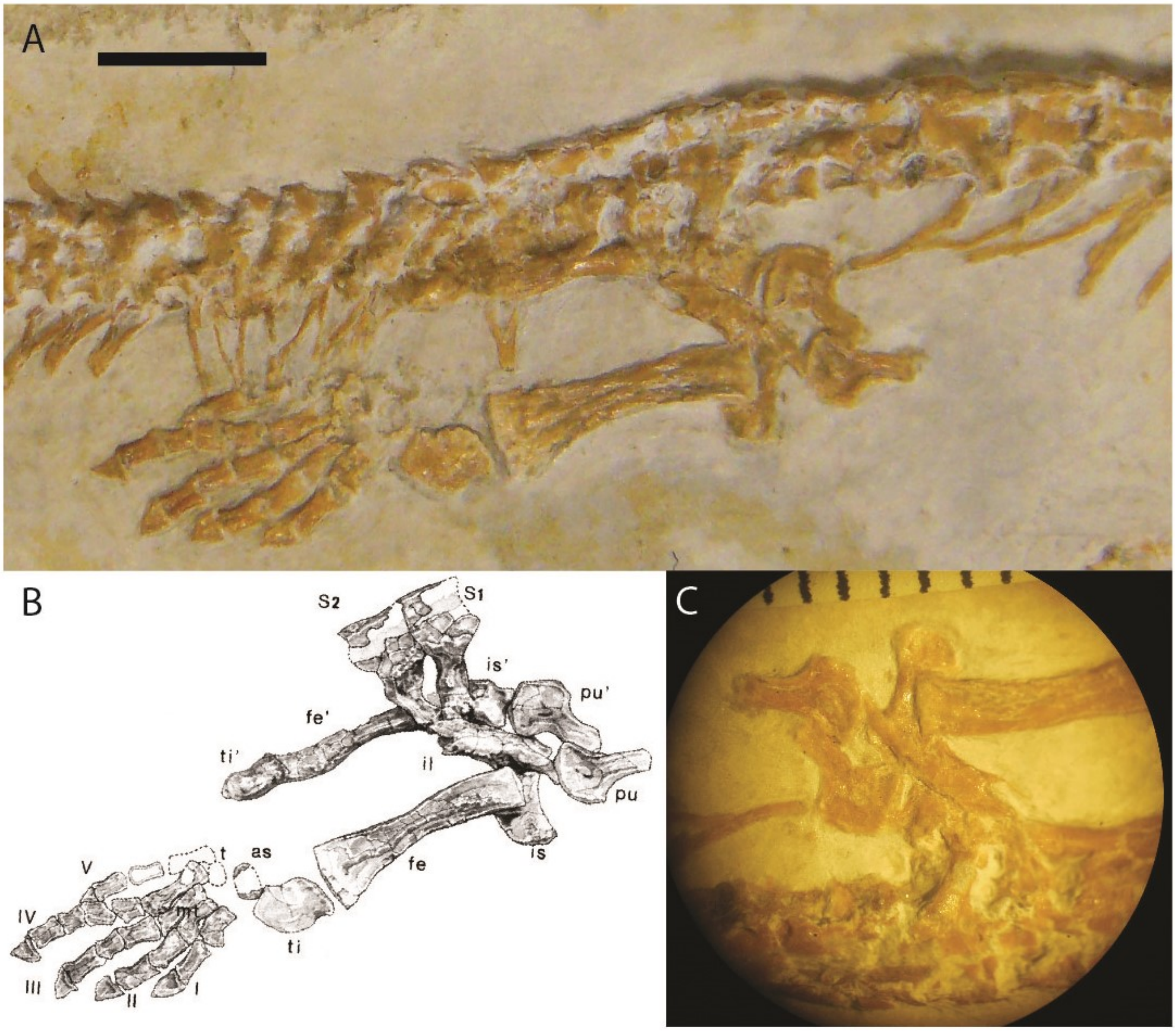

Figure 4-4 Hindlimbs and pelvic region of *Aphanizocnemus libanensis* (MSNM V783). **A**, photograph; **B**, interpretive drawing from Dal Sasso and Pinna (1997); **C**, detail of girdle elements. **Abbreviations**: **as**, astragalus; **fe**, femur; **fi**, fibula; **il**, ilium; **is**, ischium; **mt**, metatarsals; **pu**, pubis; **s**, sacral vertebrae; **t**, tarsal 4; **ti**, tibia; **I-V**, first to fifth digit. Scale bar equals 5 mm.

broadening toward the medial synphasis. It is smoothly convex along the ventral margin, and concave along the anterior margin, reaching a point at the apex which points anteriorly towards the pubis. Rugose ornamentation along the anteroventral border indicates the presence of a well developed proishiadic cartilage.

The femurs are both preserved: the right completely visible in anterodorsal view, and the left half hidden beneath the vertebral column. The dorsal margin is almost flat, while the ventral margin is gently concave. There is very little constriction midshaft, making the element subrectangular, except for the distal end which is expanded and flattened dorsoventrally. The articular surfaces are very simple, and lack epiphyses. A long, proximal-distal groove runs almost the full length of the femur.

The tibia is extremely unusual. Instead of the usual long bone constricted midshaft and expanded at the ends, it is thick, blocky, and very short. It is 40% the length of the femur, almost completely flattened, and with very weak articular surfaces. A slight hook on the anterior lateral corner is the only trace of a midshaft constriction. The anteromedial border bears a strong ridge, and the lateral margin is sinusoidal, forming a large bump midway between the humerus and astragalus. Dal Sasso and Pinna (1997) suggest that the tibia has been rotated medially, and in life position anteromedial crest would have articulated with the femur, accentuating the knee, and causing the limb to bend medially. There is no trace of the fibula.

The tibia and fibula would have articulated with the oval astragalus, which is the only tarsal element preserved (very fragmentally). The outline of another tarsal element—likely the fourth tarsal—is preserved proximal to the fourth digit. The tarsal elements were likely very reduced, as the space between the epipodials and metapodials is quite short. The first four metatarsals are well preserved, and the fifth is represented by a clear outline. The fourth metatarsal is the longest, the first and fifth are the shortest. The first metatarsal is L-shaped, and thicker than the rest. The second also has a strange shape, with the distal half abruptly widening at a shelf midshaft.

The phalanges are well preserved considering the poor preservation of the meso- and metapodium. The pedal phalangeal formula is the same as the manual: 2-3-4-5-3. Like the manual phalanges, the pedal phalanges are rectangular and blocky, barely constricted midshaft. They are also very robust, some being almost as wide as long. The penultimate phalanges are once again more developed than the preceeding phalanges. The unguals are much stockier than in the manus, being very broad and flat, with an low and elongate ventral tubercle.

DISCUSSION: What Aphanizocnemus is not

The specimen was originally described as a new species within the family Dolichosauridae, within the superfamily Varanoidea, and the infraorder Aguimorpha. Dal Sasso and Pinna interpreted it as closely related to the small, elongate, aquatic dolichosaurs (e.g., *Adriosaurus, Acteosaurus, Pontosaurus, Eidolosaurus;* von Meyer, 1860; Kornhuber, 1873; Seeley, 1881; Nopcsa, 1923) based on its aquatically derived features, axial elongation, and dimensional similarities (in particular cranial and appendicular ratios). It was considered a distinct genus due to its more pronounced aquatic adaptation- especially the reduction of the hindlimbs. However, the specimen presented is very distinct from the dolichosaurs that it was compared to, it does not display features characteristic of a varanoid lizard, and many morphologies raise doubts that it is even an anguimorph.

Dolichosauridae

The Dolichosauridae (Gervais, 1852) is a group of small, Late Cretaceous squamates. Though the Dolichosauridae was established for a monophyletic group, current hypotheses state that dolichosaurs are polyphyletic: a series of successive outgroups to the Ophidia, and most accurately described as non-ophidian ophidiomorphs (e.g., Lee and Caldwell, 2000; Lee and Scanlon, 2002; Caldwell, 2006; Palci and Caldwell, 2010).

The Ophidiomorpha is characterized by features mainly related to body elongation, limb reduction, and skull kinesis (Palci and Caldwell, 2010). Most characteristic is the elongation of the neck which, uniquely among squamates, increases in the number of vertebrae to ten or more. Dal Sasso and Pinna (1997) interpreted the neck to have 10-11 cervical vertebrae, though they do not discuss how they delineated the dorsal from the cervical region. Based on rib lengths and the location of the shoulder girdle, I interpret the neck to be eight vertebrae long, and therefore not synapomorphic with ophidiomorphs. As a result of the shorter, less elongate body, *Aphanizocnemus* also has a much larger head relative to its body (21% total body length) than dolichosaurs (average 14%; Dal Sasso and Pinna, 1997).

Ophidiomorpha synapomorphies relating to skull kinesis include a mobile, non-sutural premaxilla-maxilla contact (Palci and Caldwell, 2010). Though the maxilla is absent in *Aphanizocnemus*, the premaxilla is broad and robust, with a dorso-lateral facet suggesting a non-mobile suture. The presence of the intramandibular joint (IMJ) is a feature diagnostic to the Pythonomorpha (Cope, 1869), the group containing mosasauroids and ophidiomorphs. Dal Sasso and Pinna (1997) interpreted *Aphanizocnemus* as having an IMJ. Since the IMJ is associated with kinesis of the lower jaw, the joint (between the angular and splenial) is always directly below the joint between the surangular and dentary. This allows outward bending of the jaw to increase gape size (Lee et al., 1999). The mandible preserved in *Aphanizocnemus* shows that the joint between the dentary and surangular is not above the 'IMJ' (Figure 1a, c). Close inspection shows that the 'IMJ' probably does not represent a natural margin, but a break (Figure 1e).

Both *Aphanizocnemus* and ophidiomorphs express limb reduction, however ophidiomorphs generally express a greater reduction in the forelimbs relative to their hindlimbs (Caldwell, 2006; Palci and Caldwell, 2010). Contrarily, *Aphanizocnemus* shows a greater degree of limb reduction in the rear limbs. Limb reduction is strongly associated with aquatic adaptation (Carroll, 1985), and is therefore poor support for taxonomic closeness.

Further support that *Aphanizocnemus* does not represent a dolichosaur comes from the quadrate, which was misidentified by Dal Sasso and Pinna (1997). The quadrate in *Aphanizocnemus* is not rounded and conch-like (typical of pythonomorphs), but is flatter and more ovoid.

The skull roof of *Aphanizocnemus* is also decidedly non-dolichosaur-like. The parietal of dolichosaurs is far longer than it is wide, and narrows considerably posterior to the frontal-parietal suture, before widening posteriorly. It also has a median ridge with descending sides, and long thin parietal rami. The parietal of *Aphanizocnemus* is almost square, nearly flat, and has short, broad parietal rami. Though not preserved, the frontals indicate that the nasals were wide and rounded, unlike the splint-like condition of dolichosaurs.

Finally, the vertebrae are well preserved in *Aphanizocnemus*, clearly showing features that are not dolichosaur-like. The neural arches of dolichosaurs are wide and expanded into a butterfly shape. The neural arches observed in the specimen are more squared, with hook-shaped pre- and postzygapophyses that project pre- and postaxially, rather than obliquely. The caudal vertebrae, which are longer than tall in dolichosaurs (Russell, 1967) show the opposite condition in *Aphanizocnemus*. Furthermore, if Dal Sasso and Pinna's (1997) interpretation of *Aphanizocnemus* as a dolichosaur more derived than all other genera described, then we would expect it to show pachyostosis. Houssaye (2013) expressed confusion at the lack of pachyostosis in *Aphanizocnemus* given its presumed relationship to dolichosaurs and habitat on a shallow carbonate platform. All known pachyophiids (limbed marine snakes) and the more derived dolichosaurs (*Adriosaurus,* Seeley, 1881; *Pontosaurus*, Kornhuber, 1873) all share this trait (Palci and Caldwell, 2010), yet the vertebrae and ribs of *Aphanizocnemus* are more gracile than most dolichosaurs.

Varanoidea

According to Rieppel et al. (2007), varanoid platynotans possess three unambiguous synapomorphies. Two are not able to be assessed in *Aphanizocnemus,* but the third provides the most immediate evidence that *Aphanizocnemus* is not a varanoid: varanoids have paired frontals, while *Aphanizocnemus* clearly has one fused frontal element.

Of the varanoid synapomorphies listed by Caldwell (1999b), *Aphanizocnemus* does not have strongly oblique condyle-cotyle orientations (it is almost perfectly horizontal, and is clearly visible in lateral view in the cervical and caudal vertebrae) nor a reduced articulation of dentary-postdentary bones.

Of the unambiguous Pan-Varanoidea synapomorphies listed by Gauthier et al. (2012), *Aphanizocnemus* does not have a maxillary tooth row ending anterior to midorbit (impressions go to the midorbit).

The caudal vertebrae also bear some specific morphologies not found in other varanids. As discussed by Dal Sasso and Pinna (1997), the reduced and vertically inclined transverse processes in the anterior caudal region, and the absent transverse processes posteriorly, is not seen in varanoids. Similarly, the neural spines and chevrons are posteriorly inclined in *Aphanizocnemus,* and perpendicular to the vertebral axis in varanoids.

Additionally, the single tooth preserved is very tiny and peg-like, not at all like the large, recurved teeth of varanoids.

Anguimorpha

According to Estes et al. (1988), 26 or more presacral vertebrae is a synapomorphy of the Anguimorpha, but the presence of this many vertebrae can also be seen in other long-bodied squamates, such as the Amphisbaenidae, Dibamidae, Pygopodidae, Scincidae, and Gymnophthalmidae. However, the absence of several synapomorphies indicates that it does not fall within the Anguimorpha.

Comparing *Aphanizocnemus* against the anguimorph synapomorphies identified by Conrad (2008) and Conrad et al. (2010) is problematic, because most of these features cannot be identified on the specimen due to poor preservation. The one that can be observed is the anterior presacral ribs lacking distal expansion, which is not the case in *Aphanizocnemus*, whose anterior ribs are quite expanded distally.

DISCUSSION: What Aphanizocnemus is

Though the unique anatomy and poor preservation of *Aphanizocnemus libanensis* makes interpretation difficult. Dal Sasso and Pinna (1997) note that the small size, parietal shape, short face, and lack of ossification in some appendicular elements led O. Rieppel to suggest that *Aphanizocnemus* was an immature animal. Though possible that the individual represents a juvenile, I interpret the lack of ossification in the limbs as an aquatic adaptation. The well ossified axial skeleton (including the tip of the tail and the spinous processes), epiphyses, and skull would support this (Anderson Maisano, n.d.).

Squamate

For all of its peculiarities, *Aphanizocnemus libanensis* is unequivocally a squamate. Of the synapomorphies observed by Estes et al. (1988), the following can be observed on MSNM V783: transverse frontoparietal suture, single headed ribs, cervical interventra forming prominent hypapophyses, lack of entepicondylar foramen in humerus, lack of gastralia, procelous vertebrae, fused parietal, dorsal intercentra lost, and an anterior coracoid emargination. The phalangeal formula of 2-3-4-5-3 also supports the assignment, as this is the typical and primitive condition for squamates (Greer, 1991).

Scleroglossa

Within the Squamata, *Aphanizocnemus* is a better fit with the Scleroglossa (scincomorphs, gekkotans, snakes, amphisbaenians, anguimorphs; note that molecular phylogenies recover a different relationship, see Townsend et al., 2004; Vidal and Hedges, 2009) than the Iguania. Though none of the unambiguous scleroglossan synapomorphies identified by Gauthier et al. (2012) are assessable in *Aphanizocnemus*, the high vertebral count, flat cranial vault, low snout, and slender ptetygoids share more affinity with scleroglossans than iguanians (Romer, 1956; Estes et al., 1988). Unfortunately, the record of Mesozoic, non-pythonomorph, scleroglossan lizards with a relatively complete skeleton is rare making comparisons between contemporaneous taxa problematic. The best comparisons include the following species.

Scandensia ciervensis (early Cretaceous, Las Hoyas, Spain; Evans and Barbadillo, 1998) is interpreted as a stem squamate. It is similarly long-bodied and short faced. It differs from *Aphanizocnemus* in that its vertebrae are quite elongate; the limbs are well developed, long, and extremely gracile; it has fewer presacral vertebrae (25/26 vs 35 in *Aphanizocnemus*); a parallel-sided frontal (vs hourglass-shaped in *Aphanizocnemus*); and a more lightly built parietal.

Hoyalacerta sanzi is another stem squamate from the lower Cretaceous of Las Hoyas, Spain (Evans and Barbadillo, 1999). Though described as having reduced limbs, they are still much longer, more gracile, and overall more suited for terrestrial locomotion than the limbs of *Aphanizocnemus*. The parietal is broad, but not so much as *Aphanizocnemus*, and the mandibular elements are more gracile. Though fewer in number (28-29 presacrals vs 35-36 in *Aphanizocnemus*), the vertebrae are extremely similar in shape, and like *Aphanizocnemus*, have long low neural ridges rather than spines. The ribs are also comparable, being very thin, distally expanded in the anterior dorsal series, and grooved.

Eichstaettisaurus (Kuhn, 1958) compares very favorably with *Aphanizocnemus*. This gekkonomorph genus is represented by two species, one from the late Jurassic (*E. schroederi;*

Solnhofen, Germany; Broili, 1938) and the other from the Early Cretaceous (*E. gouldi;* Southern Italy; Evans et al., 2004). Both *Eichstaettisaurus* and *Aphanizocnemus* possess blunt snouts, wide and square parietals, short parietal rami, fused and hourglass-shaped frontals, zygosphene articulations, loss of pubic tubercle, and penultimate phalanages being longer than the preceding one. However, the parietals in *Eichstaettisaurus* are paired, and the limbs and girdles very disparate.

One of the best comparisons is the Early Cretaceous, Las Hoyas lizard *Jucaraceps grandipes* (scincogekkonomorph; Bolet and Evans, 2012). This small (< 6 cm) lizard is very similar to *Aphanizocnemus* in profile, with a short head, small limbs, an elongate body, and a very long, skinny tail. The frontal-parietal complex is almost identical to *Aphanizocnemus*, except for the pairing of the frontals. The teeth are the same size relative to the skull, the premaxilla is the same shape, and the mandibular elements are similarly proportioned and shaped. Axially, the presacral count is similar (at least 31 in *Jucaraceps*, 35-36 in *Aphanizocnemus*; 8 cervical vertebrae in both), and both lizards have low neural ridges, and slender, almost straight ribs. The primary differences lie in the limbs. The limb bones, which are gracile elongate in *Jucaraceps*, are thick and short in *Aphanizocnemus*. In *Jucaraceps,* the phalanges are long and delicate, especially compared to the broad, flattened phalanges of *Aphanizocnemus*.

Pedrerasaurus is a scincogekkonomorph from the Early Cretaceous of Catalonia, Spain (Bolet and Evans, 2010). Like *Aphanizocnemus*, the cranial material is badly crushed, but some details are comparable. The head is overall similar in shape and proportions. Both the parietals and frontals are extremely similar in shape, though the frontals are interpreted as paired in *Pedrerasaurus* (based on an impression). The hockey-stick squamosals and tall, columnar quadrates are also similar. Postcranially, the vertebrae and ribs are similar in their outline and proportions (they are preserved as impressions in *Pedrerasaurus*). Both ilia are long and rod like, and though shaped differently, both pubes are flattened elemtents with a short symphysial process. The major differences lie in the limbs, which are elongate and fairly unremarkable in *Pedrerasaurus*, compared to the reduced, autapomorphic limbs of *Aphanizocnemus*.

Liushusaurus acanthocaudata (Evans and Wang, 2010) is a scincogekkonomorph known from the early Cretaceous of China, and is represented by several specimens varying in size and ontogenetic development. The skull is extremely like *Aphanizocnemus*: square parietal, the shape of the frontal (paired in *Liushusaurus*) and premaxilla, the size of the orbits and teeth, the squamosal, and the quadrate morphology. Like the other lizards discussed, the primary differences are in the limbs, which are typical of a terrestrial lizard. The girdles however, are remarkably similar considering the different ecology. The scapulocoracoid is very similarly shaped, the ilium and ischium are almost identical, and even the pubes are similar (though much more angular in *Liushusaurus*. Additionally, like *Aphanizocnemus* and *Eichstaettisaurus,* the penultimate phalanages are longer than the preceding ones.

Scincogekkonomorphs

As discussed above, the most comparable species to *Aphanizocnemus* are those classified within the Scincogekkonomorpha. Scincogekkonomorpha is most recently defined as all taxa sharing a more recent common ancestor with *Gekko gecko* and *Scincus scincus* than with *Iguana iguana* (Conrad, 2008). Certain features used to support the relationship of *Aphanizocnemus* and ophidiomorphs (zygosphenes/zygantra, limb reduction, presacral elongation) are also common features within the basal members of this group (Greer and Wadsworth, 2003; Conrad, 2008; Bolet and Evans, 2012). Unfortunately, the five synapomorphies of this clade recognised by Conrad (2008) are unable to be assessed in *Aphanizocnemus* due to the poor preservation of the skull. Though these synapomorphies cannot be recognised, the favorable comparison with other basal scincogekkonomorphs leaves me comfortable with my interpretation.

With this classification comes two provisos. First, that the anatomy of *Aphanizocnemus* is incompletely known, limiting a complete analysis of features which may be taxonomically important. Second, that the relationships within the Squamata is unresolved (e.g., see Conrad, 2008; Vidal and Hedges, 2009; Gauthier et al., 2012), with relationships at the base of the Squamate tree (where these lizards are recovered) being particularly unreliable. Future analyses may change tree topologies and therefore the classification of these early squamates.

CONCLUSIONS

Aphanizocnemus is a small, aquatic lizard that represents one of several aquatic radiations within the Squamata in the Mesozoic. Its slender, elongate body is reminiscent of dolichosaurs, aigialosaurs, and many small, living scincids. Though originally described as a dolichosaur, several of the characteristics used to make this diagnosis were misinterpreted, or represent homoplastic features that result from aquatic adaptation. My new interpretation supports the assignment of *Aphanizocnemus* to the basal Scincogekkonomorpha, along with other basal squamates including *Jucaraceps, Liushusaurus,* and *Pedrerasaurus*. This is consistent with the frequent occurrence of axial elongation and limb reduction within this group.

The functional anatomy of *Aphanizocnemus*, and the geological context of the limestone that it is preserved in, strongly indicate that this animal was aquatic, and specialized for calm, shallow waters (Dal Sasso and Pinna, 1997). Such a lifestyle has not been documented in basal scincogekkonomorphs, and therefore *Aphanizocnemus* represents a novel adaptive radiation within this group. Previously, the record of Mesozoic marine radiation in squamates was restricted primarily to the Pythonomorpha, but *Aphanizocnemus* demonstrates that the conditions that prompted this radiation affected the Squamata more broadly. Future material may demonstrate additional squamate lineages that were also a part of this dramatic Cretaceous radiation.

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CHAPTER 5 : AN EXAMINATION OF PYTHONOMORPH INTERRELATIONSHIPS USING NEW INFORMATION FROM *PORTUNATASAURUS KRAMBERGI* AND *PONTOSAURUS RIBAGUSTER* (SQUAMATA: PYTHONOMORPHA)

ABSTRACT

During the Cretaceous, terrestrial squamates exhibited a remarkable series of radiations into the waterways of the world. One group of particular interest–the Pythonomorpha–was responsible for at least three major marine radiations: the ophidians (including aquatic hind-limbed snakes), the dolichosaurs (elongate, semi-aquatic lizards), and the mosasauroids (including the giant, open-ocean, predatory mosasaurs). The Pythonomorpha has a long history of study dating back to the early 1800s, when early pioneers of paleontology and comparative anatomy such as Conybeare, Cope, Cuvier, Kornhuber, Kramberger, Mantell, Meyer, and Owen were recognising and describing these fossils. Recent decades have seen a renewed interest in this group, resulting in an explosion in the number of species described and revised. These studies have prompted questions surrounding the origins and evolutionary trajectories of lineages within the Pythonomorpha: specifically regarding the independent evolution, coevolution, or convergence of specific traits. The investigation of these questions necessitates a well-resolved phylogeny; however, no phylogenetic study has specifically attempted to resolve the relationships within the whole of the Pythonomorpha. Instead, the focus has generally been to contextualize a single specimen, or to determine the internal relationships of the ophidians, the dolichosaurs, or the mosasauroids. Broader level comparisons have been coincidental, usually due to the choice of outgroups or ingroups. This study is the first to focus on the relationships at the base of the Pythonomorph lineage using a comprehensive selection of basal members. Parsimony- and

model-based methods show strong support for multiple independent incursions into the marine environment. This indicates that many of the traits uniting all or most of this group (axial elongation, limb reduction, the development of paddles and flippers) were independent acquisitions showing similar–though slightly different–solutions to the problem of aquatic adaptation. Most notably, these results correspond with stratigraphic and anatomical evidence which support the hypothesis that mosasaurs are a polyphyletic group representing at least two independent incursions into the water.

INTRODUCTION

The Pythonomorpha has a long history of study dating back to the early 1800s, when early pioneers of paleontology and comparative anatomy such as Conybeare (1822), Cope (1869), Cuvier (1808), Kornhuber (1873, 1901), Kramberger (1892), Mantell (1829, 1851), von Meyer (1860), and Owen (1840, 1842, 1850, 1851, 1878) were recognising and describing these fossils. Recent decades have seen a renewed interest in this group, resulting in an explosion in the number of species described and revised (e.g., Caldwell, 1999a, 2006; Bell and Polcyn, 2005; Houssaye and Bardet, 2013; Palci et al., 2013a; Konishi et al., 2015; Street and Caldwell, 2016). These studies have prompted questions surrounding the origins and evolutionary trajectories of lineages within the Pythonomorpha: specifically regarding independent evolution, coevolution or convergence of specific traits. The investigation of these questions necessitates a well-resolved phylogeny; however, no phylogenetic study has specifically attempted to resolve the relationships within the whole of the Pythonomorpha. Instead, the focus has generally been to contextualize a single specimen, or to determine the internal relationships of the ophidians, the dolichosaurs, or the mosasauroids. Broader level comparisons have been coincidental, usually due to the choice of outgroups or ingroups. This study is the first to focus on the relationships at the base of the pythonomorph lineage using a comprehensive selection of basal members. The goal is to resolve pythonomorph relationships at the base of the group, where the most ambiguity lies.

Uncertainty in the story of Pythonomorph evolution can be boiled down to three key questions: 1) the relationship of aigialosaurs and mosasaurs (mosasauroids); 2) the relationship of dolichosaurs and snakes (ophidiomorphs); and 3) the relationship of ophidiomorphs and mosasauroids (Pythonomorpha). The aim of this study is to produce testable hypotheses concerning these questions.

Question 1, mosasauroids—The term Mosasauroidea was formally established by Camp (1923) to include only the derived mosasaurs, but in more recent literature, the term is used to describe both plesiopedal ('aigialosaurs') and hydropedal ('mosasaurs') forms. On the other hand, the Aigialosauridae (Kramberger, 1892) was conceived for *Acteosaurus, Adriosaurus, Pontosaurus,* and *Aigialosaurus*. Today, in addition to several more recently discovered species, only the last of these genera is considered an aigialosaur, with the rest being referred to the Dolichosauridae/Ophidiomorpha. The terms Mosasauroidea and Aigialosauridae are problematic because of the question of monophyly. Several studies have questioned the monophyly of the aigialosaurs with respect to mosasaurs and ophidiomorphs (e.g., Caldwell et al., 1995; Bell, 1997; Lee, 1998; Caldwell, 1999a; Lee and Caldwell, 2000; Caldwell, 2012), and some more recent studies have postulated a more specific hypothesis: that multiple independent lineages of mosasaurs evolved the derived mosasaurid body plan from within the aigialosaur group (Caldwell et al., 1995; Bell, 1997; Haber and Polcyn, 2005; Polcyn and Bell, 2005; Caldwell and Palci, 2007; Dutchak and Caldwell, 2009; Caldwell, 2012; Palci et al., 2013).

In broad terms, there are two distinct mosasaur morphoytpes, referred to here as the mosasaurine mosasaurs and the non-mosasaurine mosasaurs, who consistently differ in certain features (e.g., brow ridges, paddle morphology). Observations of aigialosaur species have shown that aspects of these two subsets of features can also be observed in plesiopedal forms. The central thesis in this study is that derived mosasaurs will be recovered as polyphyletic, separated into two or possibly three lineages (see Caldwell, 2012). Further, each of the mosasaur lineages will have a collection of aigialosaurs at their base. This means that the Aigialosauridae is indeed monophyletic as the varied clades of 'mosasaurs' are in fact nothing more than independent radiations within the several aigialosaur clades. Therefore, the collection of small bodied, plesiopedal squamates colloquially referred to as aigialosaurs is nothing but a paraphyletic assemblage, better expressed as a morphotype.

Question 2, ophidiomorphs—The close relationship between mosasaurs and snakes has been discussed almost since the first mosasaur was discovered. The association was first proposed by Cope (1869), who erected the Pythonomorpha to include these taxa. Kramberger (1892) went on to describe how the Pythonomorpha (mosasaurs and snakes) arose from the Dolichosauria (=Ophiosauria: dolichosaurs and aigialosaurs). Nopcsa (1908, 1923) was the first to propose that dolichosaurs were more closely related to snakes than mosasaurs and aigialosaurs. However, even early on the relationships of snakes within squamates was highly debated, with other researchers arguing that snakes were not close relatives of the aigialosaurs, dolichosaurs, and mosasaurs (Féjérváry, 1918; Camp, 1923; Bellairs and Underwood, 1951). The debate has only intensified with the advent of computed cladistics. Some phylogenetic analyses (Lee, 1997, 1998, Lee and Caldwell, 1998, 2000; Caldwell, 2000; Lee and Scanlon, 2002; Pierce and Caldwell, 2004; Palci and Caldwell, 2007, 2010; Pyron et al., 2013; Reeder et al., 2015) support Nopcsa's dolichosaur-snake hypothesis, while other analyses support the relationships of snakes with amphisbaenids and dibamids, exclusive of the dolichosaurs (e.g., Estes et al., 1988; Zaher and Rieppel, 1999; Rieppel and Zaher, 2000; Vidal and Hedges, 2004, 2009).

The studies that find dolichosaurs and snakes to be close relatives do not find them to be sister groups. Instead, 'dolichosaurs' are usually recovered as paraphyletic: a series of successive sister groups to ophidians. According to this interpretation, dolichosaurs are a paraphyletic assemblage: an evolutionary 'grade' along the road to snakes. The morphology of dolichosaurs certainly suggests this, as they seem to display more or less 'watered-down' versions of ophidian morphologies. My hypotheses for this study are that the ophidians will be recovered as a monophyletic group derived from a dolichosaur lineage, such that the base of the Ophidia will be formed by a series of dolichosaurs or (more likely) dolichosaur families.

Question 3, pythonomorphs—The final major question is the relationship of ophidiomorphs and mosasauroids, specifically where these lineages diverged. The general consensus seems to be that the Pythonomorpha is split into two major lineages: the Mosasauroidea and the Ophidiomorpha (Nopcsa, 1923; Lee, 1997, 2005b, Caldwell, 1999a, 2000, 2006; Lee and Caldwell, 2000; Lee and Scanlon, 2002; Pierce and Caldwell, 2004; Evans et al., 2006; Palci and Caldwell, 2010, 2007). It is only in older literature that other hypotheses can be found. Dollo (1903, 1923) suggested that dolichosaurs and mosasaurs were more closely related than aigialosaurs; and Kramberger (1892) advocated that the closest relationships between the four pythonomorph clades were between dolichosaurs and aigialosaurs, and between mosasaurs and snakes.

Following the bulk of the literature, and also based on personal observations of similarity, I predict that my results will show a Pythonomorpha split into two major clades: the ophidiomorphs (dolichosaurs and ophidians) and the mosasauroids (aigialosaurs and mosasaurs).

MATERIALS AND METHODS

Characters—The character list was based on Simões et al. (2017) that analyzed a series of different phylogenetic methods applied to mosasauroid interrelationships. This in turn was derived in sequence from Jimenez-Huidobro & Caldwell (2016), Palci et al. (2013), Leblanc, Caldwell, & Bardet (2012), Caldwell & Palci (2007), Bell & Polcyn (2005), and Bell (1997). This matrix originally constituted 131 unordered, multistate morphological characters and 44 taxa. Character constructions were not altered, and I did not add or remove any characters. Character definitions are in Appendix I, and the complete data matrix is found in Appendix III along with recoded characters.

Outgroup—Following Bell (1997; and subsequent iterations), the outgroup is an artificial theoretical outgroup taxon based on several species of *Varanus*, and is not coded from any real taxonomic unit. Besides *Varanus* and this hypothetical varanid, the only other outgroup to the Mosasauroidea that has any precedent are the dolichosaurs (Simões et al., 2017). This obviously does not work for the present study, as dolichosaurs are part of the ingroup analysis. Choosing any other outgroup would have been controversial due to the uncertain placement of mosasauroids, dolichosaurs, and snakes within the Squamata. Not only are these groups inconsistently found to be monophyletic, their placement within the Squamata also has them fall within Varanoidea (e.g., Lee, 1997, 2005a; Lee and Caldwell, 2000), as stem anguimorphs (e.g., Caldwell et al., 1995; Caldwell, 1999b; Lee, 2005b), or outside of Scleroglossa (e.g, Gauthier et al., 2012). While we acknowledge the problems associated with using a not-real outgroup (e.g., *a priori* assumptions on polarity; Nixon and Carpenter, 1993; Simões et al., 2017), it was retained in this study for the sake of comparison and consistency.

Ingroup—The ingroup was greatly altered from Simões et al. (2017) by including all known species of pythonomorph lizards (dolichosaurs and aigialosaurs) and five basal ophidians, to total 66 taxa. The composition of the ingroup changed according to the test being performed, therefore, the ingroup composition of each test is described below.

When composing this study, I briefly considered removing all the limb and girdle characters that are considered aquatic adaptations to see if this changes the topology of the cladograms. This approach was tried in a diapsid phylogeny by Motani et al. (2014) and by Chen et al. (2014). They found that including aquatic characters could cause the formation of an aquatic 'super-clade'. When the 'aquatic characters' were removed, the individual marine reptile clades were still recovered, but their interrelationships changed. The major problem here is the *a priori* judgement by the authors about which traits are homoplastic and carry no phylogenetic signal. My solution to this problem is to simply create a dataset that is essentially aquatic, removing the terrestrial component.

Analyses

For some time, parsimony based methods have been the standard of phylogenetic inference among paleontologists. Parsimony under implied weighting has become more used over recent years as it has been demonstrated to better handle datasets with high degrees of homoplasy, such as in lineages boasting multiple aquatic adaptations (Goloboff et al., 2008b). However, simulations indicate that parsimony based methods are outperformed by model based methods in obtaining the correct tree with molecular datasets (Saitou and Imanishi, 1989; Kuhner and Felsenstein, 1994), and more recently with morphological datasets (Wright and Hillis, 2014; O'Reilly et al., 2016).

Bayesian has recently been demonstrated to outperform maximum parsimony, even with coding gaps and ambiguity, and especially when evolutionary rates are variable (Wright and Hillis, 2014; O'Reilly et al., 2016).

Following the suggestions of Simões et al., (2017) I decided to run two parsimony-based analyses, and two model-based analyses. Parsimony results will be more comparable to past studies, while model-based methods could arguably present stronger support for topological relationships. A variety of models can help account for the disparity caused by different branch lengths and evolutionary rates, and taking the results of four different analyses into account can serve as an additional test of confidence in the results.

Unweighted maximum parsimony (UP)—The data was analysed using the Heuristic search algorithm (traditional search with tree bisection reconnection (TBR) swapping algorithm; 100 replicates x 100 iterations), New Technology Search algorithm (1000 rounds 'sectorial search', 1000 rounds 'drift', and 1000 rounds 'tree fusing' algorithms), and implicit enumeration (if number of taxa was less than twenty) algorithm in TNT (Goloboff et al., 2008a), adding 1000 Wagner trees from random sequence additions. In all cases, the most parsimonious trees were the same length regardless of the search algorithm. In most cases, the strict consensus tree topology was the same, and where different, the only changes were a more poorly resolved tree with a larger polytomies. The degree of support for each grouping was ascertained through Bremer supports and bootstrapping, calculated in TNT. Trees were exported to Mesquite v. 3.2 for analyses (Maddison and Maddison, 2017), and then to FigTree v. 1.4.3 for reformatting (Rambaut and Drummond, 2016a).

Maximum parsimony with implied weighting (IWP)—Parsimony analyses following the parameters outlined above was also performed under the implied weighting algorithm (Goloboff et al., 2008b) using the default function (K = 3.0) and swapping algorithm (TBR; 100 replicates x 100 iterations). Again, trees were exported to Mesquite v. 3.2 for analyses (Maddison and Maddison, 2017), and then to FigTree v. 1.4.3 for reformatting (Rambaut and Drummond, 2016a).

Maximum likelihood (ML)— Maximum likelihood analysis (MK substitution model, gamma distribution with eight categories, ascertainment bias correction) was performed using IQtree (Nguyen et al., 2015; Trifinopoulos et al., 2016) following the parameters of Simões et al. (2017). Branch support was established using approximate likelihood ratio supports and bootstrap values (1000 replicates; Minh et al., 2013). Trees were reformatted in FigTree v.1.4.3 (Rambaut and Drummond, 2016a).

Bayesian inference (BI)— Bayesian analyses (Mk model, invariable gamma rates, 8 categories, variable rates, burn in fraction 0.25) were performed using MrBayes v. 3.2.5

(Ronquist et al., 2011) following the suggestions of Simões et al. (2017). Each analysis ran for ten million generations. The temperature was independently determined for each analysis using preliminary runs in order to obtain optimal chain mixing values (0.4-0.8). To assess the spread of each run, I checked the potential scale reduction factors, and used Tracer v. 1.6 (Rambaut et al., 2014) to make sure that the effective sample size for each parameter was at least 200 and that the run reached a stationary phase. The maximum credibility tree was found using TreeAnnotator v. 2.4.3 (Rambaut and Drummond, 2016b) from the product of all posterior probabilities, and formatted using FigTree v.1.4.3 (Rambaut and Drummond, 2016a).

RESULTS AND DISCUSSION

Two preliminary tests were applied to the complete dataset in order to remove problematic taxa. The 'good dataset' was then subjected to four tests using different subsets of taxa: the first was the complete 'good' dataset, the second included ophidians in the analysis, the third included only taxa with relatively well preserved cranial material, and the fourth contained only pythonomorph lizards.

Preliminary results 1: All taxa

Rationale—Before I performed any modifications on the data, I preformed a preliminary analysis using the Simões et al. (2017) dataset, including all species of aigialosaurs and dolichosaurs currently described in the literature. This included all 44 taxa included in the original dataset (seven of which are pythonomorph lizards), and the addition of twenty-two more aigialosaur and dolichosaur taxa. Since the goal of this run was to act as a preliminary 'check' for the data, and provide context for the remainder of the tests, only one analysis was run: a parsimony analysis using a New Technology Search algorithm since the number of taxa was greater than 50.

Results—The heuristic search of 66 taxa (37 mosasaurs, 23 pythonomorph lizards, five ophidians, a hypothetical outgroup) and 131 characters retrieved 5772 optimal trees with a length of 652 steps (Figure 1A). The consistency index (CI) was 0.2530 and the retention index (RI) was 0.6327. At the base of the tree, *Carsosaurus, Haasiasaurus*, and (*Aigialosaurus bucchichi* and *Aigialosaurus dalmaticus*) fall in a polytomy with the rest of the Pythonomorpha. Within this clade, the remainder of the taxa are split into two groups, a russelosaurine clade with *Coniasaurus crassidens,* and *Komensaurus* at the base, and a mosasaurine-ophidiomorph clade. Within in this second clade, four groups of ophidiomorphs form successive outgroups to the mosasaurines. The first is a pontosaur clade containing the three *Pontosaurus* species, *Acteosaurus*, and *Adriosaurus skrbinensis.* The second clade in the 'comb' is the *Adriosaurus* clade containing *Adriosaurus suessi, A. microbrachis, Dolichosaurus, Mesoleptos, Coniasaurus gracilodens,* and *Kaganaias*. The third, is *Eidolosaurus* and *Portunatasaurus* and the fourth is *Vallecillosaurus* (interpreted as an aigialosaur, even though it is falling within the 'dolichosaur comb'). The fifth is *Judeasaurus, Carentonosaurus,* and the ophidians, and finally, *Dallasaurus* and the rest of the mosasaurines.

Discussion— The arrangement of the mosasaur clades within the tree is essentially the same as that seen in Simões et al. (2017), which is expected given that the same dataset is used. The 'aigialosaurs' are as expected, scattered across the tree at the base of the major mosasaur lineages, and at the base of the Pythonomorpha. The interesting results concern the ophidiomorphs. Preliminary results recover dolichosaurs and ophidians in a series of clades that

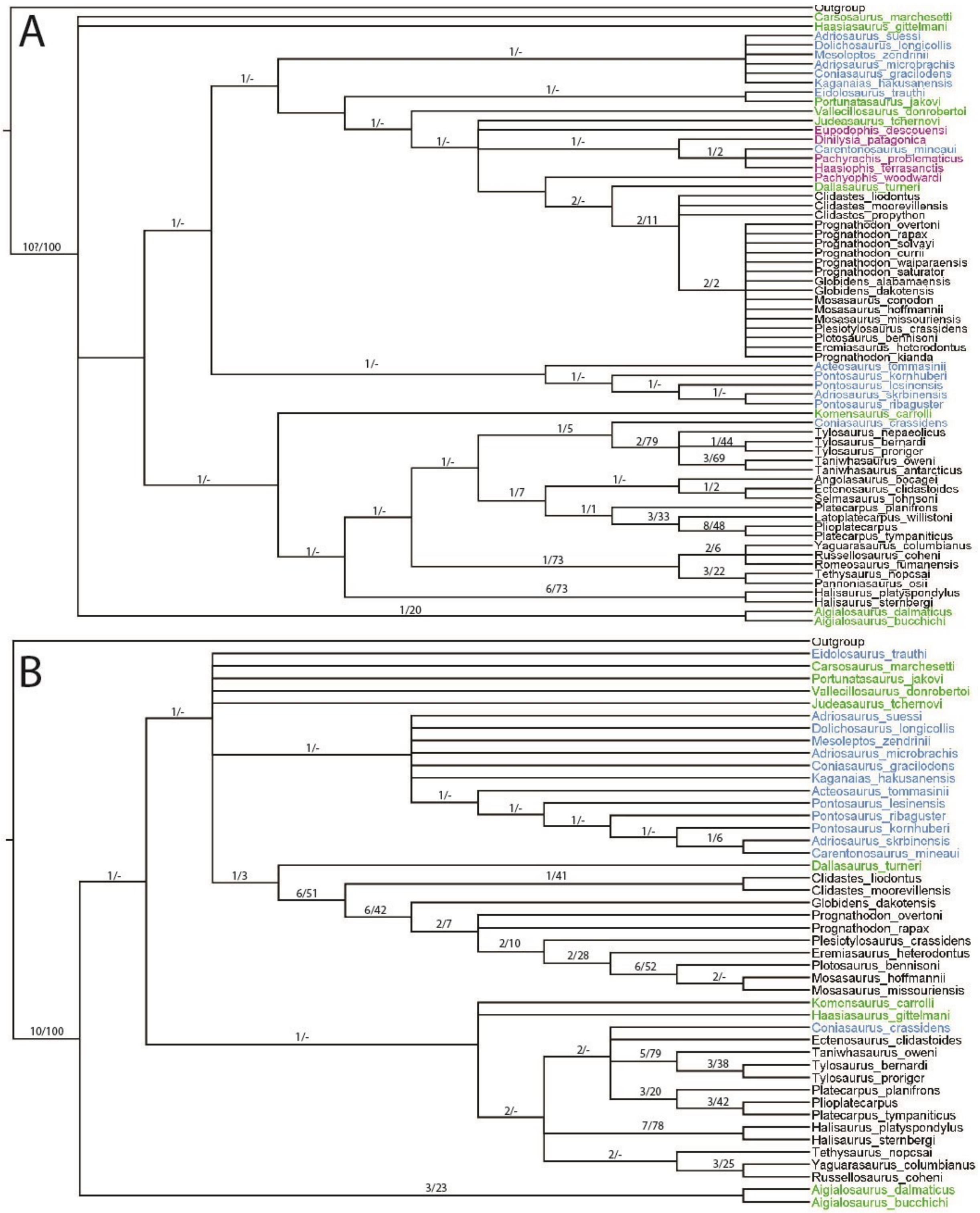

Figure 5-1 Preliminary results showing strict consensus using a modified version of the matrix from Simoes et al. (2017). **A**. Strict consensus of 5772 MPTs (66 taxa) CI = 0.2530, RI = 0.6327; **B**. Strict consensus of 39 MPTs (46 taxa), CI = 0.3519, RI = 0.6678. Bremer decay values and bootstrap support of 1000 replicates is given for each node, no value is given where neither value could be obtained. Green text indicated aigialosaurs, blue indicates dolichosaurs, and pink indicates ophidians.

form successive outgroups to the mosasaurines. This result (ophidiomorphs within the aigialosaur-mosasaur clade) has not been obtained in any published phylogeny. However, besides the nodes joining the hydropedal mosasauroids, the results are generally poorly supported.

Preliminary results 2: Cut derived taxa

Rationale—It has been demonstrated that too many derived taxa can reduce resolution at the base of the tree (Puttick et al., 2017). Since the base of the tree (i.e., the relationships between mosasaurs, dolichosaurs, aigialosaurs, and snakes) is our primary interest, we removed the ophidians and some derived mosasaur taxa from the analysis such that the total taxa was comprised of at least 50% pythonomorph lizards. I selectively removed species to maintain a phylogenetically diverse assemblage. The species removed were: *Clidastes propython, Prognathodon currii, Prognathodon waiparaensis, Prognathodon saturator*, *Prognathodon kianda, Prognathodon solvayi, Globidens alabemensis, Mosasaurus conodon, Tylosaurus nepaeolicus, Latoplatecarpus willistoni, Taniwhasaurus antarcticus, Romeosaurus fumanensis, Pannoniosaurus osii, Selmasaurus johnsoni, Angolasaurus bocagei,* and the 5 snake species. This resulted in a total of 46 taxa (22 mosasaurs, 23 pythonomorph lizards, a hypothetical outgroup).

Results—The heuristic search of 46 taxa and 131 characters retrieved 39 optimal trees with a length of 437 steps (Figure 1B). In this result, the two *Aigialosaurus* species were recovered as the outgroup to the rest of the Pythonomorpha, and the remainder of the ingroup was split into two major clades. *Komensaurus* and *Haasiasaurus* were recovered at the base of the non-mosasaurine mosasaur lineage, and *Coniasaurus crassidens* plotted out with the tylosaurines. The second major clade is comprises the mosasaurines and the dolichosaurs. At the base of this lineage are several aigialosaurs—*Carsosaurus*, *Portunatasaurus*, *Vallecillosaurus*, and *Judeasaurus*—in a polytomy with a large dolichosaur clade (containing all coded dolichosaurs except *C. crassidens* and *Eidolosaurus*), and the mosasaurines (with *Dallasaurus* being the most basal member).

Discussion—Once again, the placement of the aigialosaurs and the major split of the mosasaurs into two clades matches my hypotheses. The majority of the dolichosaurs form a monophyletic group, which is as expected, but their position as a possible sister group to the mosasaurine lineage is surprising. It is possible that these results are being influenced by the lack of overlapping data (i.e., many pythonomorph fossils being either a body, a head, or a couple isolated elements), especially given the poor support.

Test 1: A ‘good’ dataset

Rationale—Using the results from the second round of preliminary analyses, I used the prune tree feature of TNT to identify taxa that were causing a lack of resolution in the 10-step-suboptimal (71896 trees) and optimal (39 trees) runs. This analysis identified that at least two nodes could be gained by removing *Judeasaurus, Kaganaias, Carentonosaurus, Coniasaurus crassidens*, and *Coniasaurus gracilodens*, whose incomplete codings were causing uncertainty. To keep the proportion of pythonomorph lizards greater than 50%, five more mosasaur taxa from were also removed (eliminated based on most incomplete material): *Globidens dakotensis,*

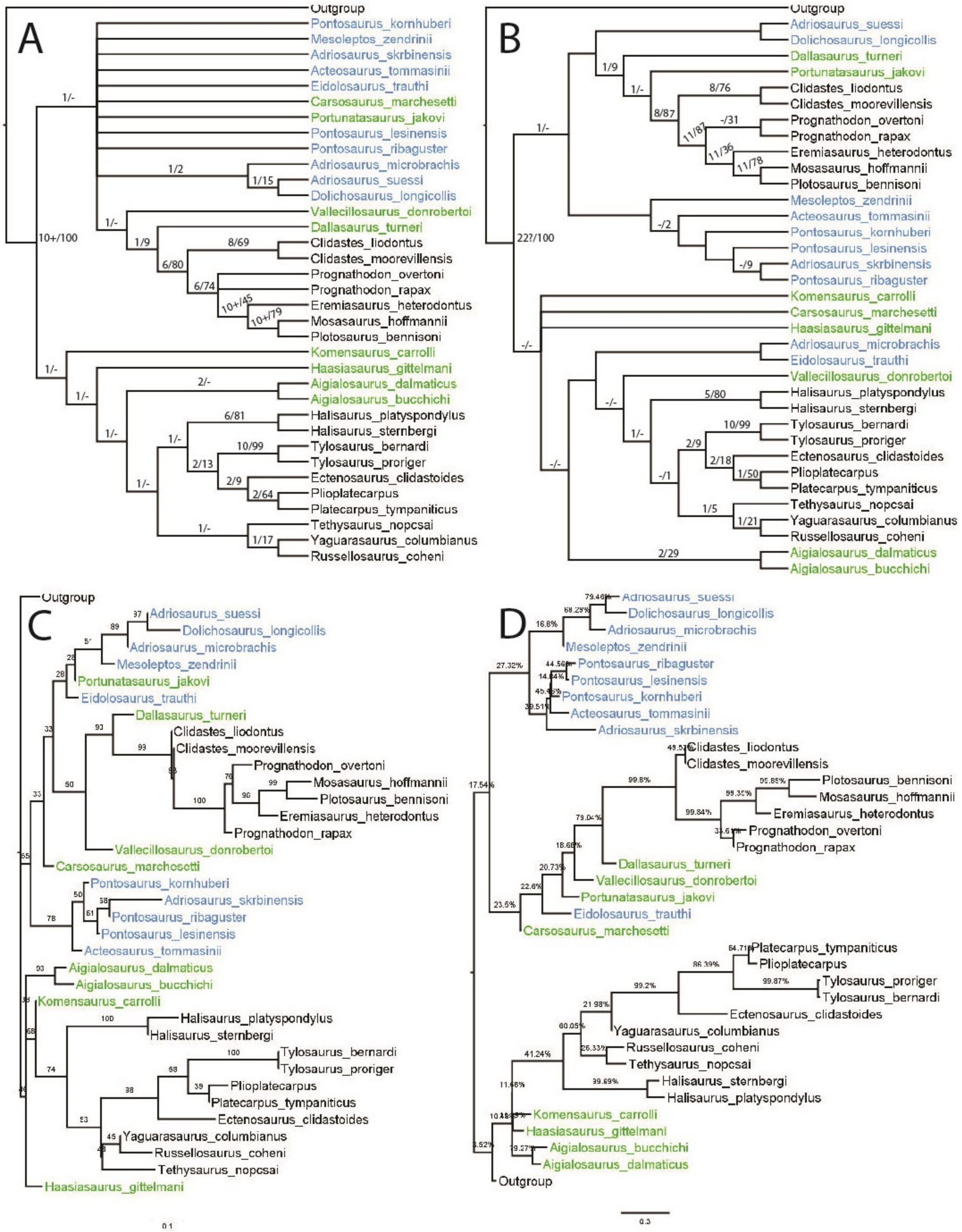
A
Outgroup
Pontosaurus_kornhuberi
Mesoleptos_zendrinii
Adriosaurus_skrbinensis
Acteosaurus_tommasinii
Eidolosaurus_trauthi
Carsosaurus_marchesetti
Portunatasaurus_jakovi
Pontosaurus_lesinensis
Pontosaurus_ribaguster
Adriosaurus_microbrachis
Adriosaurus_suessi
Dolichosaurus_longicollis
Vallecillosaurus_donrobertoi
Dallasaurus_turneri
Clidastes_liodontus
Clidastes_moorevillensis
Prognathodon_overtoni
Prognathodon_rapax
Eremiasaurus_heterodontus
Mosasaurus_hoffmannii
Plotosaurus_bennisoni
Komensaurus_carrolli
Haasiasaurus_gittelmani
Aigialosaurus_dalmaticus
Aigialosaurus_bucchichi
Halisaurus_platyspondylus
Halisaurus_sternbergi
Tylosaurus_bernardi
Tylosaurus_proriger
Ectenosaurus_clidastoides
Plioplatecarpus
Platecarpus_tympaniticus
Tethysaurus_nopcsai
Yaguarasaurus_columbianus
Russellosaurus_coheni
1/-
1/2
1/15
1/-
1/9
8/69
6/80
6/74
10+/45
10+/79
10+/100
1/-
1/-
2/-
1/-
6/81
1/-
10/99
2/13
2/9
2/64
1/-
1/-
1/17
B
Outgroup
Adriosaurus_suessi
Dolichosaurus_longicollis
Dallasaurus_turneri
Portunatasaurus_jakovi
Clidastes_liodontus
Clidastes_moorevillensis
Prognathodon_overtoni
Prognathodon_rapax
Eremiasaurus_heterodontus
Mosasaurus_hoffmannii
Plotosaurus_bennisoni
Mesoleptos_zendrinii
Acteosaurus_tommasinii
Pontosaurus_kornhuberi
Pontosaurus_lesinensis
Adriosaurus_skrbinensis
Pontosaurus_ribaguster
Komensaurus_carrolli
Carsosaurus_marchesetti
Haasiasaurus_gittelmani
Adriosaurus_microbrachis
Eidolosaurus_trauthi
Vallecillosaurus_donrobertoi
Halisaurus_platyspondylus
Halisaurus_sternbergi
Tylosaurus_bernardi
Tylosaurus_proriger
Ectenosaurus_clidastoides
Plioplatecarpus
Platecarpus_tympaniticus
Tethysaurus_nopcsai
Yaguarasaurus_columbianus
Russellosaurus_coheni
Aigialosaurus_dalmaticus
Aigialosaurus_bucchichi
1/9
1/-
8/76
8/87
-/31
11/87
11/36
11/78
1/-
-/2
-/9
22?/100
-/-
-/-
-/-
5/80
1/-
10/99
2/9
2/18
1/50
-/1
1/5
1/21
2/29
C
Outgroup
Adriosaurus_suessi
Dolichosaurus_longicollis
Adriosaurus_microbrachis
Mesoleptos_zendrinii
Portunatasaurus_jakovi
Eidolosaurus_trauthi
Dallasaurus_turneri
Clidastes_liodontus
Clidastes_moorevillensis
Prognathodon_overtoni
Mosasaurus_hoffmannii
Plotosaurus_bennisoni
Eremiasaurus_heterodontus
Prognathodon_rapax
Vallecillosaurus_donrobertoi
Carsosaurus_marchesetti
Pontosaurus_kornhuberi
Adriosaurus_skrbinensis
Pontosaurus_ribaguster
Pontosaurus_lesinensis
Acteosaurus_tommasinii
Aigialosaurus_dalmaticus
Aigialosaurus_bucchichi
Komensaurus_carrolli
Halisaurus_platyspondylus
Halisaurus_sternbergi
Tylosaurus_bernardi
Tylosaurus_proriger
Plioplatecarpus
Platecarpus_tympaniticus
Ectenosaurus_clidastoides
Yaguarasaurus_columbianus
Russellosaurus_coheni
Tethysaurus_nopcsai
Haasiasaurus_gittelmani
97
89
51
28
28
33
93
99
93
76
99
96
100
50
33
65
50
58
61
78
93
39
68
100
74
58
100
39
98
53
45
48
46
0.1
D
Adriosaurus_suessi
Dolichosaurus_longicollis
Adriosaurus_microbrachis
Mesoleptos_zendrinii
Pontosaurus_ribaguster
Pontosaurus_lesinensis
Pontosaurus_kornhuberi
Acteosaurus_tommasinii
Adriosaurus_skrbinensis
Clidastes_liodontus
Clidastes_moorevillensis
Plotosaurus_bennisoni
Mosasaurus_hoffmannii
Eremiasaurus_heterodontus
Prognathodon_overtoni
Prognathodon_rapax
Dallasaurus_turneri
Vallecillosaurus_donrobertoi
Portunatasaurus_jakovi
Eidolosaurus_trauthi
Carsosaurus_marchesetti
Platecarpus_tympaniticus
Plioplatecarpus
Tylosaurus_proriger
Tylosaurus_bernardi
Ectenosaurus_clidastoides
Yaguarasaurus_columbianus
Russellosaurus_coheni
Tethysaurus_nopcsai
Halisaurus_sternbergi
Halisaurus_platyspondylus
Komensaurus_carrolli
Haasiasaurus_gittelmani
Aigialosaurus_bucchichi
Aigialosaurus_dalmaticus
Outgroup
79.46%
68.29%
16.8%
27.32%
44.56%
14.24%
45.45%
39.51%
49.57%
99.8%
95.85%
99.35%
99.84%
33.61%
79.04%
18.66%
20.73%
22.6%
23.5%
17.54%
64.71%
86.39%
99.87%
99.2%
21.98%
60.05%
26.33%
41.24%
99.69%
11.68%
19.27%
8.52%
0.3

Figure 5-2 Phylogenetic analysis of Test 1 ‘A good dataset’ using different methods. **A**. UP: Strict consensus of 42 trees from traditional search (CI = 0.3881; RI = 0.6401) and 42 trees from new technology search (CI = 0.3881; RI = 0.6401); 388 steps each; Bremer decay values and bootstrap support of 1000 replicates is given for each node, no value is given where neither value could be obtained. **B**. IWP: Strict consensus of 3 trees (CI = 0.4148; RI = 0.6779; score = 40.36); 388 steps; Bremer decay values and bootstrap support of 1000 replicates is given for each node. **C**. ML tree; branches proportional to length (scale bar represents branch length); values above branches indicate bootstrap support. **D**. BI maximum clade credibility tree from 10,001 posterior trees; branches are proportional to their length (scale bar represent branch length); values above branches give clade probabilities. Green text indicated aigialosaurs, and blue indicates dolichosaurs.

Mosasaurus missouriensis, Plesiotylosaurus crassidens, Taniwhasaurus oweni, and *Platecarpus planifrons*.

Results—The UP analysis (Figure 2A) shows the pythonomorphs divided into two clades: a mosasaurine-dolichosaur clade, and a non-mosasaurine mosasaur clade. *Carsosaurus, Portunatasaurus,* and all of the dolichosaurs included in the analysis are in a polytomy with the mosasaurine clade. The only pythonomorph lizards grouped together in this polytomy are *Adrisaurus suessi, Adriosaurus microbrachis,* and *Dolichosaurus longicollis*. The largest clade within the polytomy is the mosasaurine lineage, which has *Vallecillosaurus* and *Dallasaurus* as successive outgroups at the base of a well resolved mosasaurine clade (Street and Caldwell, 2016; Simões et al., 2017). The non-mosasaurine mosasaur clade is also well resolved and as expected, with a series of aigialosaurs at the base. The sister clade are the two *Aigialosaurus* species. *Haasiasaurus* and *Komensaurus* form successive sister groups beyond this.

Under IWP the tree topology changes quite a bit (Figure 2B). Once again, the tree is split into two major clades: a clade containing mosasaurines, and a second containing non-mosasaurine mosasaurs. The mosasaurines again form a monophyletic lineage, this time with *Portunatasaurus* and *Dallasaurus* as the nearest successive sister taxa. Basal to this is a small clade comprised of *Adriosaurus suessi* and *Dolichosaurus longicollis* (*Adriosaurus microbrachis* is not contained within this clade). Once again, the majority of the dolichosaurs plot at the base of the mosasaurine lineage, but are this time contained within a monophyletic clade containing the three *Pontosaurus* species, *Acteosaurus, Adriosaurus skrbinensis*, and *Mesoleptos* (the basal-most member). On the non-mosasaurine side of the tree, *Haasiasaurus, Komensaurus,* and then *Aigialosaurus* are once again at the base of the non-mosasaurine mosasaur clade. It is *Vallecillosaurus* (previously on the mosasaurine side of the tree) who plots out as the closest sister taxon to the non-mosasaurine mosasaurs, then a small dolichosaur clade containing *Adriosaurus microbrachis* and *Eidolosaurus trauthi*, then the *Aigialosaurus* clade, and finally *Komensaurus, Haasiasaurus,* and *Carsosaurus* (also on the other side of the tree in the unweighted analysis) in a polytomy at the base.

The ML tree shows the same topology as the UP analyses, but with more resolution (Figure 2C). *Dallasaurus* and then *Vallecillosaurus* are the successive sister taxa to the mosasaurines. Outside of this, the dolichosaurs are resolved into several groups. Most closely related to *Vallecillosaurus, Dallasaurus,* and the mosasaurines is a dolichosaur group comprised of [[[[*Dolichosaurus longicollis* and *Adriosaurus suessi*] *Adriosaurus microbrachis*] *Mesoleptos*] *Portunatasaurus*] and finally *Eidolosaurus*. *Carsosaurus* falls out basal to this dolichosaur-mosasaurine group, and basal to that is a pontosaur group of *Acteosaurus, Adriosaurus skrbinensis,* and the three *Pontosaurus* species. The non-mosasaurine side of the tree once again has *Komensaurus, Haasiasaurus* and *Aigialosaurus* at the base, but in a different order. In the ML tree, *Komensaurus* is the closest sister taxon to the non-mosasaurine mosasaurs, as opposed to the furthest, then the *Aigialosaurus* group, and finally *Haasiasaurus* as the most basal taxon on this side of the tree.

The maximum posterior credibility tree from the BI analysis shows similar results to the IW and ML analyses, except that the dolichosaurs are all (except one) collected within a monophyletic group (Figure 2D). The two major divisions in the tree are 1) the non-mosasaurine mosasaur lineage, with *Komensaurus, Haasiasaurus,* and the *Aigialosaurus* group forming the most successive outgroups; and 2) the mosasaurine-dolicosaur group. This second group is divided into a dolichosaur lineage and a mosasaurine lineages. The mosasaurines form a monophyletic group, with *Dallasaurus, Vallecillosaurus, Portunatasaurus, Eidolosaurus,* and *Carsosaurus* forming the least-to-most basal succession of outgroups. The dolichosaurs (except for *Eidolosaurus*) are all contained within a monophyletic group split into two lineages. The adriosaur lineage is formed by *Mesoleptos* [*Adriosaurus microbrachis* [*Adriosuarus suessi,* and *Dolichosaurus longicollis*]]. The pontosaur lineage by *Adriosaurus skrbinensis* [*Acteosaurus tommasinii* [*Pontosaurus kornhuberi* [*P. lesinensis* and *P. ribaguster*]]].

Discussion—The results of the first test all tell roughly the same story, a Pythonomorpha split into two principal groups, the first containing mosasaurines and ophidiomorphs, and the second containing the non-mosasaurine mosasaurs. Both hydropedal mosasaur lineages stem from a series of aigialosaurs that form the basal-most branches of the tree. As in the preliminary tests, the results match my hypotheses in all but one way: the position of the ophidiomorphs. While I predicted that the split between the mosasauroids and ophidiomorphs would happen at the base of the Pythonomorpha, the ophidiomorphs are forming one, or two adjacent groups at the base of the lineage leading to the mosasaurines.

The plesiopedal mosasauroids ('aigialosaurs'), as per my hypothesis, do not form a monophyletic group, but instead form the basal branches of the mosasaurine and non-mosasaurine mosasaur lineages. *Aigialosaurus, Haasiasaurus,* and *Komensaurus* consistently plot out as basal to the non-mosasaurine mosasaurs, while *Dallasaurus, Vallecillosaurus,* and *Portunatasaurus* stay on the mosasaurine side of the tree. *Dallasaurus* is consistently recovered as the sister group to the mosasaurines, and the placement of *Portunatasaurus* is unsurprising given the similarity of its forelimbs to derived mosasaurines (Chapter 3).

The non-ophidian ophidiomorphs appear to form two distinct, and relatively well supported groups. The first is a pontosaur group, comprised of the three *Pontosaurus* species, *Acteosaurus,* and possibly *Adriosaurus skrbinensis*. The second is a dolichosaur/adriosaur group, formed by *Adriosaurus suessi, A. microbrachis*, and *Dolichosaurus longicollis. Mesoleptos* jumps between these two groups, but always plots out basally.

The placement of the Ophidiomorpha within the Mosasauroidea (plesiopedal and hydropedal mosasauroids) has seldom been reported before. Dollo (1903, 1904a, 1904b) considered aigialosaurs true lizards branching off near the Varanidae, and ancestral to the Dolichosauridae and Mosasauridae, which would match the topology presented here. McDowell and Bogert (1954) predicted that the Lanthanotidae, Dolichosauridae and Aigialosauridae (including mosasaurids) were sister-families, which doesn't specifically predict, nor contradict the results of my first test.

Test 2: Snakes

Rationale—The only major group of pythonomorphs not represented in the analyses thus far are the ophidians. To truly complete a robust analysis of pythonomorph interrelationships, they need to be included. So, five basal ophidians were included in the analysis: *Pachyophis woodwardi*, *Eupodophis descouensi, Dinilysia patagonica, Pachyrachis problematicus,* and

Haasiophis terrasanctus. *Adriosaurus skrbinensis* was removed from the analysis, as post-analysis pruning tests from test 1 (above) indicated that it was causing a two node loss of resolution. To maintain the 50% pythonomorph lizard ratio, I removed six derived mosasaur taxa with the most missing data, three mosasaurines and three non-mosasaurines: *Plioplatecarpus, Prognathodon rapax, Yaguarasaurus colombianus, Eremiasaurus heterodontus, Russellosaurus coheni,* and *Halisaurus platyspondylus.*

Results—The UP analyses were not very successful, as they produced a basal polytomy, of which five branches represented clades (Figure 3A). One clade contained all six mosasaurines. The second contained the non-mosasaurine mosasaurs, but without *Halisaurus* and *Tethysaurus*, which plotted together in the first test. The final three clades were aigialosaur and dolichosar clades all consistently recovered in the first test: the two *Aigialosaurus* species; the pontosaur clade (*Acteosaurus* and the three *Pontosaurus* species); and the adriosaur-dolichosaur clade (containing only *Dolichosaurus* and *Adriosaurus suessi*). None of the ophidians plotted together, each contributing its own branch to the polytomy at the base of the tree.

In contrast, the consensus tree from IWP was fully resolved (one optimal tree, length 388, score: 39.95; Figure 3B). The topology is identical to the implied weighting results from the first test, except for the addition of snakes, and *Vallecillosaurus* moved from the base of the russelosaurine clade to the base of the mosasaurine clade. Surprisingly, the five ophidians are spread across the tree. On the russellosaurine side of the tree, [[*Haasiophis*, *Pachyrachis*] and *Dinilysia*] form a clade that falls out as the sister group to *Tethysaurus*. On the mosasaurine side, *Eupodophis* is the third in a series of successive outgroups to the mosasaurines (outside of

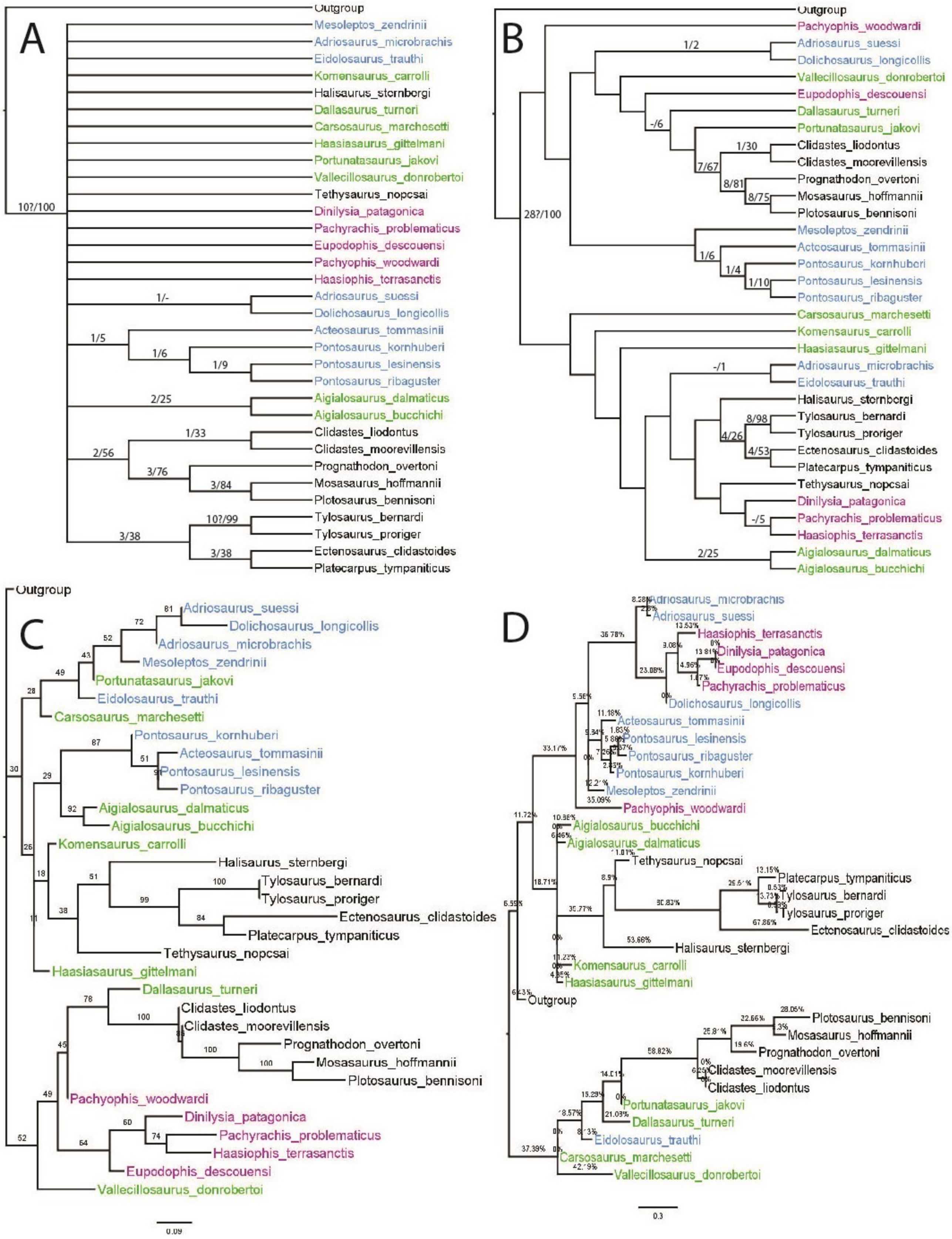
A
Outgroup
Mesoleptos_zendrinii
Adriosaurus_microbrachis
Eidolosaurus_trauthi
Komensaurus_carrolli
Halisaurus_sternbergi
Dallasaurus_turneri
Carsosaurus_marchesetti
Haasiasaurus_gittelmani
Portunatasaurus_jakovi
Vallecillosaurus_donrobertoi
Tethysaurus_nopcsai
10?/100
Dinilysia_patagonica
Pachyrachis_problematicus
Eupodophis_descouensi
Pachyophis_woodwardi
Haasiophis_terrasanctis
1/-
Adriosaurus_suessi
Dolichosaurus_longicollis
1/5
Acteosaurus_tommasinii
1/6
Pontosaurus_kornhuberi
1/9
Pontosaurus_lesinensis
Pontosaurus_ribaguster
2/25
Aigialosaurus_dalmaticus
Aigialosaurus_bucchichi
1/33
Clidastes_liodontus
2/56
Clidastes_moorevillensis
3/76
Prognathodon_overtoni
3/84
Mosasaurus_hoffmannii
Plotosaurus_bennisoni
10?/99
Tylosaurus_bernardi
3/38
Tylosaurus_proriger
3/38
Ectenosaurus_clidastoides
Platecarpus_tympaniticus
B
Outgroup
Pachyophis_woodwardi
1/2
Adriosaurus_suessi
Dolichosaurus_longicollis
Vallecillosaurus_donrobertoi
Eupodophis_descouensi
Dallasaurus_turneri
-/6
Portunatasaurus_jakovi
1/30
Clidastes_liodontus
7/67
Clidastes_moorevillensis
Prognathodon_overtoni
8/81
Mosasaurus_hoffmannii
8/75
Plotosaurus_bennisoni
28?/100
Mesoleptos_zendrinii
Acteosaurus_tommasinii
1/6
Pontosaurus_kornhuberi
1/4
Pontosaurus_lesinensis
1/10
Pontosaurus_ribaguster
Carsosaurus_marchesetti
Komensaurus_carrolli
Haasiasaurus_gittelmani
-/1
Adriosaurus_microbrachis
Eidolosaurus_trauthi
Halisaurus_sternbergi
8/98
Tylosaurus_bernardi
4/26
Tylosaurus_proriger
4/53
Ectenosaurus_clidastoides
Platecarpus_tympaniticus
Tethysaurus_nopcsai
Dinilysia_patagonica
-/5
Pachyrachis_problematicus
Haasiophis_terrasanctis
2/25
Aigialosaurus_dalmaticus
Aigialosaurus_bucchichi
C
Outgroup
81
Adriosaurus_suessi
72
Dolichosaurus_longicollis
52
Adriosaurus_microbrachis
43
Mesoleptos_zendrinii
49
Portunatasaurus_jakovi
28
Eidolosaurus_trauthi
Carsosaurus_marchesetti
Pontosaurus_kornhuberi
87
51
Acteosaurus_tommasinii
9
Pontosaurus_lesinensis
29
Pontosaurus_ribaguster
30
92
Aigialosaurus_dalmaticus
Aigialosaurus_bucchichi
26
Komensaurus_carrolli
18
Halisaurus_sternbergi
51
100
Tylosaurus_bernardi
Tylosaurus_proriger
38
99
84
Ectenosaurus_clidastoides
11
Platecarpus_tympaniticus
Tethysaurus_nopcsai
Haasiasaurus_gittelmani
78
Dallasaurus_turneri
100
Clidastes_liodontus
Clidastes_moorevillensis
85
46
100
Prognathodon_overtoni
100
Mosasaurus_hoffmannii
Plotosaurus_bennisoni
49
Pachyophis_woodwardi
60
Dinilysia_patagonica
74
Pachyrachis_problematicus
52
64
Haasiophis_terrasanctis
Eupodophis_descouensi
Vallecillosaurus_donrobertoi
0.09
D
8.28%
Adriosaurus_microbrachis
Adriosaurus_suessi
13.53%
Haasiophis_terrasanctis
36.78%
9.08%
0%
13.81%
Dinilysia_patagonica
4.96%
Eupodophis_descouensi
23.08%
1.87%
Pachyrachis_problematicus
0%
Dolichosaurus_longicollis
5.56%
11.18%
Acteosaurus_tommasinii
9.34%
1.83%
Pontosaurus_lesinensis
0%
Pontosaurus_ribaguster
2.35%
Pontosaurus_kornhuberi
Mesoleptos_zendrinii
35.09%
Pachyophis_woodwardi
33.17%
11.72%
10.86%
Aigialosaurus_bucchichi
0%
6.46%
Aigialosaurus_dalmaticus
11.01%
Tethysaurus_nopcsai
18.71%
8.9%
13.15%
Platecarpus_tympaniticus
0.53%
Tylosaurus_bernardi
13.73%
Tylosaurus_proriger
6.59%
35.77%
80.83%
67.86%
Ectenosaurus_clidastoides
0%
53.66%
Halisaurus_sternbergi
11.23%
Komensaurus_carrolli
0%
4.35%
Haasiasaurus_gittelmani
Outgroup
28.05%
Plotosaurus_bennisoni
32.66%
Mosasaurus_hoffmannii
25.81%
19.6%
Prognathodon_overtoni
58.82%
0%
Clidastes_moorevillensis
0%
Clidastes_liodontus
14.01%
0%
Portunatasaurus_jakovi
15.29%
21.03%
Dallasaurus_turneri
18.57%
0%
Eidolosaurus_trauthi
37.39%
0%
Carsosaurus_marchesetti
42.19%
Vallecillosaurus_donrobertoi
0.3

Figure 5-3 Phylogenetic analysis of Test 2 ‘Snakes’ using different methods. **A**. UP: Strict consensus of 39 trees from traditional search (CI = 0.3285; RI = 0.4648) and 78 trees from new technology search (CI = 0.3272; RI = 0.4613); 383 steps each; Bremer decay values and bootstrap support of 1000 replicates is given for each node, no value is given where neither value could be obtained. **B**. IWP: single optimal tree (CI = 0.4124; RI = 0.6268; score = 39.95); 383 steps; Bremer decay values and bootstrap support of 1000 replicates is given for each node. **C**. ML tree; branches proportional to length (scale bar represents branch length); values above branches indicate bootstrap support. **D**. BI maximum clade credibility tree from 10,001 posterior trees; branches are proportional to their length (scale bar represent branch length); values above branches give clade probabilities. Green text indicated aigialosaurs, blue indicates dolichosaurs, and pink indicates ophidians.

Portunatasaurus and *Dallasaurus*), while *Pachyophis* is the basal-most member on the mosasaurine half of the tree.

In the ML tree, the inclusion of snakes does not greatly affect the topology of the tree (Figure 3C). Most of the groups remain unaffected, but the position of the two large dolichosaur groups relative to the two mosasaur groups completely changes. The mosasaurine group (with *Dallasaurus*) remains, but the dolichosaur sister group is replaced with *Pachyophis* and a snake group: *Eupodophis* [*Dinilysia* [*Pachyrachis, Haasiophis*]]. On the other side of the tree are the non-mosasaurine mosasaurs, most of the aigialosaurs, and all the dolichosaurs. At the base of this super-group is the larger dolichosaur group with a couple of aigialosaurs included: *Carsosaurus* [*Eidolosaurus* [*Portunatasaurus* [*Mesoleptos* [*Adriosaurus microbrachis* [*Adriosaurus suessi* and *Dolichosaurus*]]]]]. Next is the second pythonomorph lizard group, containing the pontosaurs (*Acteosaurus* and the three *Pontosaurus* species) in a sister group relationship with the two *Aigialosaurus* species, and then *Haasiasaurus*, and *Komensaurus* as sister groups to the non-mosasaurine mosasaurs.

The BI tree recovers almost the same topology as the BI tree from Test 1, with the large exception of the dolichosaur group now being the sister group to the non-mosasaurine mosasaur lineage rather than the mosasaurine lineage (Figure 3D). The distribution of aigialosaurs remains unaltered except for movement up or down their respective Hennigian combs. Four of the ophidians (all except *Pachyophis*) form a monophyletic group within the adriosaur lineage, as the sister group to *Dolichosaurus*. *Pachyophis* falls out as the basal-most member of the dolichosaur group.

Discussion—The results of this test were associated with a number of problems. Pruning tests performed on the results of the UP and IWP tests both indicated that the addition of the snake taxa (in particular *Eupodophis* and *Pachyophis*) were decreasing the resolution and confidence of the tree topology. The ML test had to be run without ascertainment bias correction due to the number of taxa with <50% missing data. This is likely the reason for the loss in resolution in the UP results. The tree topology did not change relative to the first test in the IWP, but the position of all ophidiomorph taxa was contradictory between ML and BI results.

Considering this, it is reassuring that the results among the plesiopedal and hydropedal mosasauroids did not change. They were still split into a mosasaurine and non-mosasaurine group, and the plesiopedal ‘aigialosaurs’ were split between these two lineages in the same pattern as the first test, matching my original predictions.

The position of ophidiomorph taxa become less confident, with inconsistent groupings and relationships between the four analyses. Most of the ophidiomorphs (and all of the ophidians) fall into a polytomy in the UP analysis, with the exception of the pontosaurs, which still group together, and an *Adriosaurus suessi-Dolichosaurus longicollis* sister group. In the IWP, the ophidiomorph lizards plot at the base of the mosasaurine lineage (as in test 1), though the ophidians (except *Eupodophis* and *Pachyophis*, whose placement is questionable) nest deeply within the non-mosasaurine mosasaurs. In the MP, the ophidiomorph lizards and ophidians once again plot on opposite sides of the tree, but have switched the mosasaur lineage they are associated with. The BI tree is the only result that recovers all ophidiomorphs in a monophyletic group (except *Eidolosaurus*, which remains on the opposite side of the tree). Poor bootstrap values, and a complete lack of Bremer support do not lend much confidence to the placement of the ophidians within the parsimony analyses, nor do the clade probabilities in the BI tree. The only relatively good support values for a monophyletic Ophidia are in the ML tree.

The position of ophidians nested within the Mosasauroidea is an evolutionary hypothesis that is not well supported within the literature. Kramberger (1892) proposed that mosasaurs and snakes were more closely related to each other than to the Dolichosauria (dolichosaurs and aigialosaurs), which our results partially support (except for the placement of the non-mosasaurine mosasaurs). However, since the introduction of cladistic analyses, the sister-group relationship of mosasaurs and snakes (to the exclusion of pythonomorph lizards) has never been supported.

Overall, it seems that the results of this test cannot be confidently interpreted, at least in terms of the relationships of ophidians relative to the rest of the Pythonomorpha. This is hardly surprising given the inconsistent placement of ophidians relative to the rest of the Squamata in the literature. Their unusual and derived morphology, and the poor and partial preservation of the basal taxa continue to obscure attempts to ascertain their phylogeny. More complete specimens and/or a less biased dataset might help to clarify these relationships in future.

Test 3: Test 1 with heads

Rationale—Cranial characters can been argued to be more phylogenetically informative on higher level relationships than postcranial characters as there are more of them on a finer scale of morphological observation, and they appear to change more rapidly than do postcranial characters. In addition—or perhaps resultantly—cranial characters make up 61% of the dataset (80/131 characters). Therefore, for my third test I wanted to use only taxa that were preserved with a head and could therefore be coded for some cranial characters. I cut all taxa with less than 25% of cranial characters coded from the dataset used in test 1 (not 2 because of the problems discussed above). Using these criteria, I removed: *Carsosaurus, Portunatasaurus, Vallecillosaurus, Mesoleptos, Eidolosaurus, Acteosaurus, Adriosaurus microbrachis, Dolichosaurus longicollis* (has cranial elements preserved, but only two cranial characters coded-3.9%), *Adriosaurus skrbinensis* (previously recommended to be removed based on pruning results, and only 9 cranial characters coded-17.6%), *Komensaurus* (only 10 cranial characters coded-19.6%), and *Dallasaurus* (19 cranial characters-23%). The mosasaur taxa removed to maintain the ratio were the species removed in test two, in addition to *Tylosaurus bernardi, Clidastes liodontus, Ectenosaurus clidastoides,* and *Plotosaurus bennisoni*.

Results—All analyses in this test produced roughly the same topology (Figure 4). Two major groups were formed: one, containing the dolichosaurs, aigialosaurs, *Halisaurus* and *Tethysaurus*, and the other containing the rest of the derived mosasaurs. In all cases, the mosasaurines [*Clidastes moorevillensis* [*Mosasaurus hoffmannii, Prognathodon overtone*]] formed a sister group with the tylosaurs [*Tylosaurus proriger, Platecarpus tympaniticus*]. In one case (UP, Figure 4A) *Adriosaurus suessi* plotted out as the basal member of this derived mosasaur group. The second group (the 'basal' group) always contained an *Aigialosaurus* lineage (containing *A. dalmaticus* and *A. bucchichi*), and a *Pontosaurus* lineage (containing *P. kornhuberi, P. lesinensis,* and *P. ribaguster*). In most cases (UP, ML, BI; Figure 4A, C, D), *Halisaurus* and *Tethysaurus* plotted out as the basal members of this group. The IWP results find these two species to be deeply nested within the clade (Figure 4B). *Halisaurus* and *Adriosaurus suessi* form the sister group to the pontosaurs, and *Tethysaurus* is the sister taxon to the *Aigialosaur* lineage. *Haasiasaurus* shows the most movement around the tree depending on

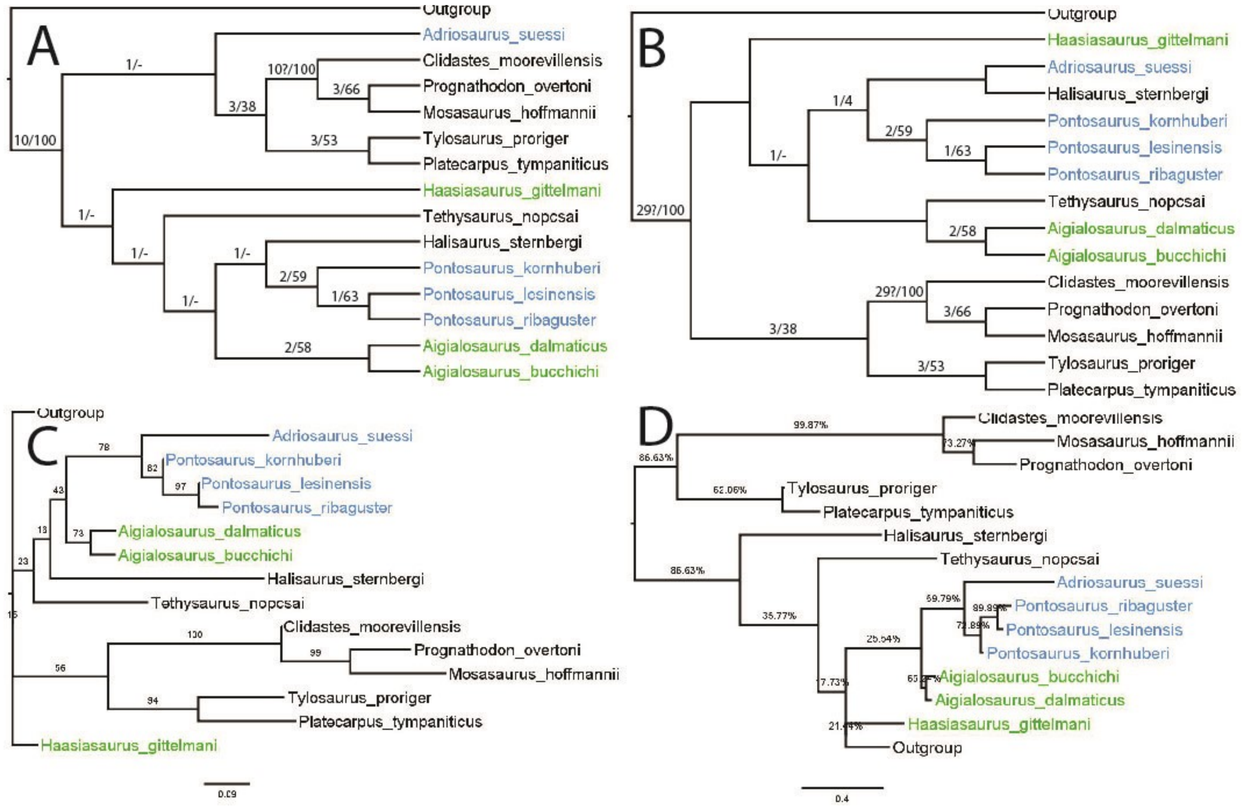

Figure 5-4 Phylogenetic analysis of Test 3 'Heads' using different methods. **A**. UP: single optimal tree from traditional, new technology, and implicit enumeration searches (CI = 0.5894; RI = 0.6029); 263 steps each; Bremer decay values and bootstrap support of 1000 replicates is given for each node, no value is given where neither value could be obtained. **B**. IWP: single optimal tree (CI = 0.5871; RI = 0.5993; score = 23.65); 263 steps; Bremer decay values and bootstrap support of 1000 replicates is given for each node. **C**. ML tree; branches proportional to length (scale bar represents branch length); values above branches indicate bootstrap support. **D**. BI maximum clade credibility tree from 10,001 posterior trees; branches are proportional to their length (scale bar represent branch length); values above branches give clade probabilities. Green text indicated aigialosaurs, and blue indicates dolichosaurs.

which analysis was run. In the UP and IWP, it was the most basal taxon in the 'basal' lineage, below *Tethysaurus* and *Halisaurus*; whereas in the BI analysis it was below all other pythonomorph lizards, but more derived than these two mosasaurs. In the ML analysis, it was right at the base of the tree, in a polytomy with the outgroup and the group containing all other ingroup taxa.

Discussion—The whole point of this particular test was an attempt to resolve some of the uncertainty that was theoretically caused by more fragmentary specimens: in particular, those missing cranial data. As a result, the average completeness of pythonomorph lizards in this analysis is much higher. In terms of the pythonomorph lizards cut from this test, I do not feel that I am losing much information regarding the placement relative to other taxa, as some (e.g., *Dallasaurus*) have been consistent in their placement, while others (e.g., *Carsosaurus*) have jumped all over the tree. This goal of this test is to more confidently resolve the relationships between the major mosasaur lineages, the plesiopedal mosasauroids, and the ophidiomorphs. To some degree, this goal was achieved, as indicated by complete resolution of every tree, and the higher Bootstrap, Bremer, and clade probability values. However, the topology of these trees is surprising. In all four cases, there are two major groups. The first contains the hydropedal mosasaurs *Clidastes, Prognathodon, Mosasaurus, Tylosaurus,* and *Platecarpus*. The second contains the plesiopedal mosasauroids, the dolichosaurs (except *Adriosaurus* in UP), *Halisaurus,* and *Tethysaurus*. Within this second, 'variety' group, the pontosaurs and the two *Aigialosaurus* species maintain their own lineages, which *Halisaurus* and *Tethysaurus* remain basal to (UP, ML, BI) or nested within (IWP). *Haasiasaurus* is usually basal-most in this clade (UP, IWP) but also plots out in a polytomy with the outgroup (ML), or in a more derived position than *Halisaurus* and *Tethysaurus*.

The removal of *Tethysaurus* and *Halisaurus* from the derived mosasaur lineage is unexpected, but not unreasonable given their basal nature (Bardet et al., 2003). This study is not the first to recover these taxa closer to the pythonomorph lizards than to the more derived mosasaurs. Bell (1997) and Dutchak and Caldwell (2009) both recovered a sister group relationship between russellosaurs and mosasaurines, with a polytomy of aigialosaurs and halisaurines recovered basally.

Test 4: Pythonomorph 'lizards' only

Rationale—In order to test whether the relationships between the pythonomorph lizards hold up without the influence of any derived taxa, I decided to run the test two dataset using only the aigialosaurs and dolichosaurs. This left me with a dataset of 18 taxa: the outgroup, nine dolichosaurs, and eight aigialosaurs.

Results—As in the first two tests, the unweighted parsimony analyses resulted in a large polytomy of pythonomorph lizards with only a couple of resolved clades (Figure 5A). In this case, only two clades were recovered: an *Aigialosaurus* clade (with the two *Aigialosaurus* species), and an *Adriosaurus* clade (containing *A. microbrachis, A. suessi,* and *Dolichosaurus*).

The results from the ML and IWP analyses (Figure 5B, C) show almost the same results, which (if the non-comparable species were removed) is a tree topology similar to the ML and BI results from the first, second and third tests, and the IWP results from the first and third test. These trees all show dolichosaurs divided into two major sister groups: 1) a pontosaur group containing the three *Pontosaurus* species and *Acteosaurus*, and 2) an adriosaur group containing *Adriosaurus suessi* and *A. microbrachis*, *Dolichosaurus*. *Mesoleptos* and *Eidolosaurus* do move around, but they generally are recovered as basal members of the adriosaur lineage. Among all of these similar trees, aigialosaurs fail to form a monophyletic group, and instead are recovered as the basal members of the dolichosaur (and mosasaur) lineages. In the ML and IWP analyses of

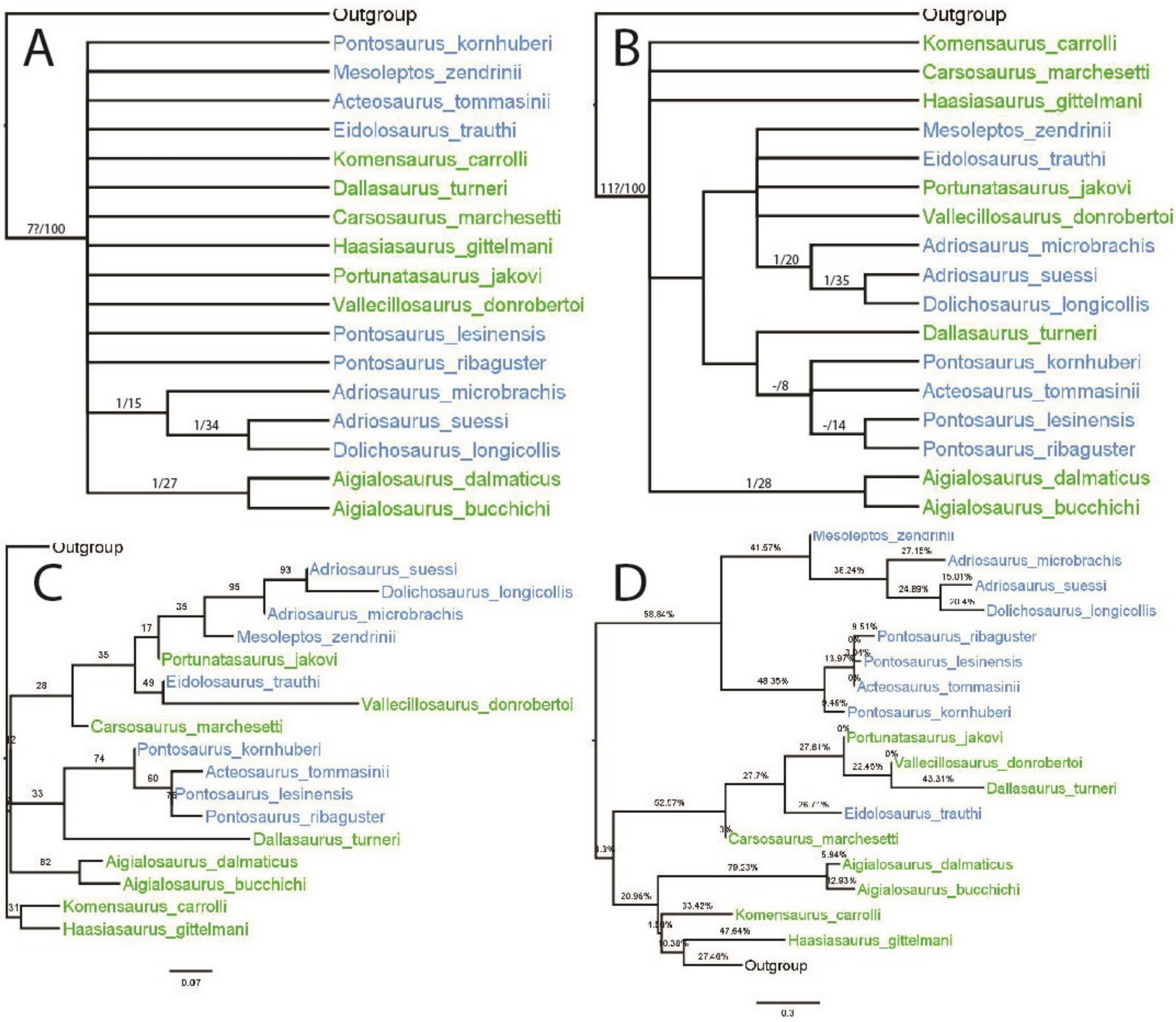

Figure 5-5 Phylogenetic analysis of Test 4 ‘Pythonomorph Lizards’ using different methods. **A**. UP: Strict consensus of 140 trees from implicit enumeration (CI = 0.6320; RI = 0.3947) and 1377 trees from traditional and new technology searches (CI = 0.5563; RI = 0.1710); 103 steps each; Bremer decay values and bootstrap support of 1000 replicates is given for each node, no value is given where neither value could be obtained. **B**. IWP: strict consensus of 35 optimal trees (CI = 0.7453; RI = 0.6447; score = 5.10); 2103 steps; Bremer decay values and bootstrap support of 1000 replicates is given for each node. **C**. ML tree; branches proportional to length (scale bar represents branch length); values above branches indicate bootstrap support. **D**. BI maximum clade credibility tree from 10,001 posterior trees; branches are proportional to their length (scale bar represent branch length); values above branches give clade probabilities. Green text indicated aigialosaurs, and blue indicates dolichosaurs.

test four (and most other tests and analyses), *Portunatasaurus* and *Vallecillosaurus* are recovered as basal members of the adriosaur lineage, mixed up with *Eidolosaurus* and *Mesoleptos*. *Carsosaurus* also often joins this comb of species, but its position is more variable across the different tests and analyses. In other tests, *Dallasaurus* consistently plots at the base of the mosasaurine group, but in the absence of the mosasaurines in test four, it is recovered as the sister taxon to the pontosaur group. Basal to the junction of the pontosaur and adriosaur lineages are the aigialosaurs *Komensaurus, Haasiasaurus,* and *Aigialosaurus*, with the *Aigialosaurus* pair being recovered as more derived than the other two species in the ML analysis.

The BI results maintain the two dolichosaur groups (*Mesoleptos* remains a basal taxon within the adriosaur group) as sister groups, but without any of the aigialosaurs (Figure 5D). All of the aigialosaurs (and *Eidolosaurus*) are contained within their own monophyletic group. Within the aigialosaur group, there are two lineages: one containing *Carsosaurus* [*Eidolosaurus* [*Portunatasaurus* [*Vallecillosaurus* and *Dallasaurus*]]], and the second containing [[*Aigialosaurus bucchichi* and *A. dalmaticus*][*Komensaurus* [the outgroup and *Haasiasaurus*]]].

Discussion—Unsurprisingly (due to the partial nature of the fossils), the results of this analysis are not strongly supported, and UP gives very little information at all. The most strongly supported groups are, obviously, the ones that have been repeatedly showing up throughout all of the tests and analyses: the pontosaur group (*Pontosaurus* and *Acteosaurus*) and the adriosaur group (*Adriosaurus suessi, A. microbrachis, Dolichosaurus,* and perhaps *Mesoleptos*). Though more poorly supported, the 'mosasaurine aigialosaurs' (*Dallasaurus, Vallecillosaurus, Portunatasaurus*) and the 'non-mosasaurine aigialosaurs' (*Komensaurus, Haasiasaurus, Aigialosaurus*) tend to plot together as well. The 'non-mosasaurine aigialosaurs' plot out at the base of the tree, while the 'mosasaurine aigialosaurs' either form a sister group to them (BI), or intersperse among the ophidiomorphs (IWP, ML)- which makes sense considering their tendency to plot with the mosasaurine lineage in previous tests.

The trees show two hypotheses of the relationship between mosasauroid lizards and ophidiomorph lizards. In IWP and ML, the ophidiomorphs are split into two groups, each with mosasauroids at the base, in addition to mosasauroids at the base of the tree. This would suggest a mosasauroid lineage from which ophidiomorphs evolved at least twice, a hypothesis that I cannot find any direct support for in the literature, though several authors do propose that dolichosaurs may arise from an aigialosaur or aigialosaur-like lineage (Kramberger, 1892; Dollo, 1903, 1904a). In contrast, the BI shows ophidiomorphs and mosasauroids each in their own distinct group (except for *Eidolosaurus*), implying a common ancestor, but separate evolutionary trajectories. The BI results follow my original hypothesis, and is the more popular hypothesis in the literature (e.g., Nopcsa, 1923; Lee and Scanlon, 2002; Pierce and Caldwell, 2004; Lee, 2005a; Caldwell, 2006; Evans et al., 2006; Palci and Caldwell, 2007, 2010). Indeed, the BI tree in this final test is the only result to support my hypothesis of divergent Pythonomorpha containing separate ophidiomorph and mosasauroid lineages.

CONCLUSIONS

The tree topologies derived from the four tests all show slightly different results. Nonetheless, their combined information helps to build an evolutionary scenario with some relatively well-supported components.

Concerning mosasauroids—The results strongly support my hypothesis that the hydropedal condition evolved twice in mosasaurs: once at the base of the mosasaurine lineage, and once at the base of the russellosaur-halisaur-tethysaur lineage. The results strongly suggest that the plesiopedal ‘aigialosaurs’ are a paraphyletic assemblage (to the exclusion of derived mosasaurs, and potentially ophidiomorphs), and that ‘aigialosaurus’ and derived mosasaurs together comprise the monophyletic Aigialosauridae. This result is supported even when derived mosasaurs were excluded. ‘Aigialosaurs’ (plesiopedal mosasauroids) appear in various combinations forming successive sister taxa to both the mosasaurine and non-mosasaurine mosasaurs. *Dallasaurus, Vallecillosaurus* and *Portunatasaurus* are consistently recovered as basal members of the mosasaurine lineage (with *Dallasaurus* being the most derived), whilst *Komensaurus* and *Haasiasaurus* are almost always recovered as basal members of the non-mosasaurine mosasaur lineage. *Aigialosaurus bucchichi* and *A. dalmaticus* seem to represent either basal members of the non-mosasaurine lineage, or the entire Mosasauroidea. The halisaurines¸ which are sometimes found outside of the two major mosasaur lineages (Bell, 1997a; Dutchak and Caldwell, 2009; Simões et al., 2017), are generally recovered as the basal-most hydropedal members within the non-mosasaurine lineage. The position of *Eidolosaurus* and *Carsosaurus* is inconsistent, and more conclusions regarding their relationships must wait further study.

Together, the above results create a problem for the ‘Aigialosauridae’. Either, the family has to be restricted to contain only the two described *Aigialosaurus* species (per Bell and Polcyn, 2005), or it has to be expanded to include all plesiopedal and hydropedal mosasauroids (per Caldwell, 2012). Consequently, these results also pose a problem for the Mosasauridae as currently understood (see Caldwell [2012] for a detailed review of the problem). The trees produced here support many of the clades proposed by Bell (1993, 1997) including the

Mosasaurinae and the Russellosaurinae. However, the Mosasauridae as a monophyletic group is not supported.

Concerning ophidiomorphs—Within the Ophidiomorpha, some of the ophidiomorph lizards were recovered in two relatively well supported groups. The first includes *Adriosaurus suessi, Adriosaurus microbrachis*, and *Dolichosaurus longicollis*, and possibly *Mesoleptos zendrinii*. I would suggest that this group be the bearer of the name Dolichosauridae, since the family as defined appears to be polyphyletic (to the exclusion of ophidians). The second well supported group of ophidiomorph lizards are the pontosaurs, containing *Pontosaurus lesinensis, P. kornhuberi, P. ribaguster,* and *Acteosaurus crassicostatus*.

The relationship of ophidiomorph lizards and snakes cannot be confidently discussed based on the results of this study, as the ophidians formed a monophyletic group originating from within the dolichosaurs (as expected), formed a group originating from within the non-mosasaurine mosasaurs (unexpected), or from within the mosasaurines (also unexpected). I suspect that the placement of ophidians in our study may result from the dataset, which was constructed to study the relationships of derived mosasaurs, and would therefore be lacking in characters able to differentiate between mosasauroids and ophidians. Adding more derived ophidians such that there is an even distribution of ophidiomorphs and mosasauroids could also help support an independent lineage of ophidiomorphs. Unfortunately, the uncertain results from this study do not help to confidently answer the question of ophidiomorph origins or monophyly.

Concerning pythonomorphs—The most surprising result from this study, both in terms of consistency and novelty, is the position of the ophidiomorphs relative to the mosasauroids. As discussed, ophidiomorphs have been proposed to be closely related to mosasauroids (e.g., Lee, 1997; Caldwell, 1999b; Lee and Scanlon, 2002; Pierce and Caldwell, 2004; Palci and Caldwell, 2010; Gauthier et al., 2012; Reeder et al., 2015), or from a completely different branch of the squamate tree (Camp, 1923; Carroll, 1988; Evans and Wang, 2005; Conrad, 2008), but have never been proposed as members of the Mosasauroidea. Yet, contrary to prior studies, and to my original hypothesis, most of the results from this study support the Ophidiomorpha (dolichosaurs and ophidians) arising from within the Mosasauroidea, most often as a sister group to the mosasaurine lineage. These results most closely resemble the hypothesis of Kramberger (1892) who discussed the transitional nature of the aigialosaurs, arguing that they were ancestral to dolichosaurs, and that both groups were transitional between lizards and pythonomorphs (which he defined as the group containing mosasaurs and snakes).

Though I am not yet ready to support the 'ophidiomorphs are actually mosasauroids' hypothesis, the results of these analyses, and the unique features shared by these two lineages (e.g., axial elongation, skull kinesis) continue to support their close relationship.

Concerning the future—Although this study provides a clearer picture of basal pythonomorph taxa, their interrelationships remain problematic due to the large amount of missing data for many of these specimens. Better specimens, 3D imaging of specimens preserved in slabs, a better sampling of ophidians, and a dataset tailored to this specific question would likely help elucidate some of the more problematic relationships described herein. Regardless, this study highlights the importance of including pythonomorph lizards in phylogenetic analyses of snakes and mosasaurs, due to their close, and possibly nested, relationships.

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CHAPTER 6 : SPATIOTEMPORAL DISTRIBUTIONS OF NON-OPHIDIAN OPHIDIOMORPHS

ABSTRACT

Non-ophidian ophidiomorphs, informally referred to as ‘dolichosaurs’ are small-bodied aquatic lizards that lived in shallow seaways, rivers and reef environments during the Late Cretaceous. Preservational, geographic, and taphonomic biases in this group make trends in biodiversity difficult to assess. This is exemplified by the fact that the majority of the described species are monotypic and known only from single specimens, imparting very little information on morphological or spatial variation. Fortunately, recent finds have dramatically altered traditional views of the stratigraphic distribution and global range of the dolichosaurs. Here is presented a revision of the spatial and temporal distributions of non-ophidian ophidiomorph lizards (‘dolichosaurs’) from Cretaceous sediments worldwide. Fragmentary discoveries suggest that the fossil record of dolichosaurs begins in the Valanginian (Early Cretaceous) or even the latest Jurassic. This is followed by a dense Cenomanian record from Tethyan and British deposits, and rarer specimens from North America. Though there is a significant drop in the number of specimens recorded from the Turonian-Maastrichtian, these rare occurrences represent the largest geographical distribution of dolichosaurids: spanning Europe, North America and South America. These occurrences show a much more temporally diverse pattern than previously indicated. The geographic and temporal distributions shown here reveal patterns that are critical to the understanding of the evolution and aquatic radiation of ophidiomorphs and other aquatic squamates.

INTRODUCTION

The early Late Cretaceous is undoubtedly one of the most interesting periods in the evolution of squamates. Primarily terrestrial throughout their evolutionary history, the Squamata underwent a unique and spectacular aquatic radiation into the marine realm. The core of this radiation was accomplished by two groups: the Mosasauroidea (aigialosaurs and mosasaurs) and the Ophidiomorpha (dolichosaurs and snakes).

Mosasauroids were a diverse group of aquatic squamates that lived during the Late Cretaceous (late Cenomanian, 95 million years ago [mya] to the Cretaceous-Paleogene boundary, 66 mya). Their fossil record spans the globe, and can be found on all major landmasses. The group is composed of derived mosasaurs: fully aquatic, open ocean top predators with flippers and fins; and aigialosaurs: small (less than two metres), shallow water piscivores with weight bearing hips and limbs (Caldwell, 2012).

The Ophidiomorpha was first proposed by Palci and Caldwell (2010) as the clade containing the Ophidia (including pachyophiids and limbed snakes) and 'dolichosaur' grade animals including: *Acteosaurus* (von Meyer, 1860), *Adriosaurus* (Seeley, 1881), *Coniasaurus* and *Dolichosaurus* (Owen, 1850), *Eidolosaurus* (Nopcsa, 1923), *Mesoleptos* (Cornalia, 1852), and *Pontosaurus* (Kornhuber, 1873). The relationships of 'dolichosaurids' with snakes, mosasauroids, and more broadly, the rest of the squamates, is contested. The Dolichosauridae was established for the genus *Dolichosaurus* by Kramberger (1892) and was considered closely related to the Aigialosauridae. Nopcsa (1903, 1908) enlarged the group, including *Acteosaurus*, *Adriosaurus* and *Pontosaurus*. Nopcsa (1908, 1923) was the first to propose that dolichosaurs were more closely related to snakes than mosasaurs and aigialosaurs. From the start, this hypothesis was contentious, supported by some (e.g., McDowell and Bogert, 1954) but rejected by others (e.g., Féjérváry, 1918; Camp, 1923). The advent of computer generated cladistic analyses in the 1980's intensified the debate on the relationship of snakes and dolichosaurs. Some recent phylogenetic analyses (Caldwell, 2000; Lee and Caldwell, 2000; Lee and Scanlon, 2002; Pierce and Caldwell, 2004; Palci and Caldwell, 2007, 2010) support Nopcsa's dolichosaur-snake hypothesis. However, instead of finding the Dolichosauridae and the Ophidia to be sister groups, these analyses instead recover 'dolichosaurs' as successive sister groups to ophidians. According to this interpretation, dolichosaurs are a paraphyletic assemblage: an evolutionary 'grade' along the road to snakes. These studies also generally find a sister group relationship between ophidiomorphs and mosasauroids, forming the monophyletic Pythonomorpha (Cope, 1869; Lee, 1997; Caldwell, 1999a). This is far from a universal view, with other analyses supporting the relationships of snakes with amphisbaenids and dibamids, exclusive of the dolichosaurs (Zaher and Rieppel, 1999; Rieppel and Zaher, 2000b). However, as this study is concerned with temporal and spatial distributions, and not phylogenetic relationships, the general conclusions drawn will rely on the phylogenetic hypothesis of Palci and Caldwell (2010).

Previously, knowledge of non-ophidian ophidiomorphs consisted primarily of Cenomanian finds from the Tethys, though there are productive localities from the Turonian of Europe, and the Cenomanian-Turonian of the Western Interior Seaway. A much smaller number of more spatially diverse discoveries (including Asia, Australia, and South America) come from sediments as old as the Hauterivian, and as young as the Maastrichtian. This indicates that our understanding of the evolution of this group needs to be re-evaluated, as they show a much more temporally and spatially diverse pattern than previously indicated.

Much of this bias comes from the incompleteness of the fossil and stratigraphic record, as well as sampling bias due to taphonomy and historical importance: e.g., commercially quarried Adriatic limestone, and a culture of collecting 'curios' in 18th and 19th century Europe increased chances of discovery in western and southern Europe (Dadić, 1982). However, it is evident that some combination of preservational, geographic, geological, taphonomic, and depositional biases contributes to the spotty record of dolichosaurs worldwide. This is exemplified by the fact that many of the described species are monotypic and known only from single specimens. Records of these animals consist of articulated specimens on limestone slabs, or isolated elements (usually vertebrae). Non-deposition, high-energy and/or biologically active environments, erosion of major rock units, and the small size of the animals themselves diminish the likelihood of preservation and discovery, and causes underestimations of diversity and abundance (Brown et al., 2013; Cleary et al., 2015).

Despite these factors, recent finds have dramatically altered traditional views of the stratigraphic distribution and global range of the dolichosaurs. Despite a limited sampling, understanding the occurrence of this group through space and time is critical to the study of the evolution and adaption of both dolichosaurs and snakes.

DEFINITIONS

'Dolichosaurs'—Several phylogenetic analyses have found dolichosaurs to form a Hennigian Comb as successive sister taxa to snakes (Lee and Caldwell, 2000; Pierce and Caldwell, 2004; Caldwell and Palci, 2010; Palci and Caldwell, 2010, Chapter 5). Therefore, the term 'dolichosaur' will be used in this study to refer to non-ophidian ophidiomorphs (elongate, limbed—but limb-reduced—Cretaceous marine squamates) as the term is well understood even though it does not include snakes. In a similar fashion, the term ‘aigialosaur’ will be used in this study to refer to non-mosasaurid (plesiopedal and plesiopelvic) mosasauroids.

SPATIOTEMPORAL DISTRIBUTION OF DOLICHOSAURS

Dolichosaur fossils have recently been reported from well beyond the range that they were historically thought to be restricted to. These records range from articulated specimens to isolated elements (primarily teeth and vertebrae). The isolated elements more difficult to reliably assign to a genus or family, which is unfortunate, given that most originate from outside the Mediterranean Tethys and often represent the only possible record of a dolichosaur from their locality. Uncertainty is expressed where each report is discussed.

The present study brings the current understanding of the distribution of non-ophidian ophidiomorphs up to date, identifies patterns in their distribution, and attempts to explain these patterns and distributions.

Hauterivian (Lower Cretaceous); Figure 1A

Japan—The geologically oldest proposed dolichosaur is *Kaganaias hakusanensis*, described from the Kuwajima Formation (Tetori Group) of central Honshu, Japan (Evans et al., 2006). The Kuwajima Formation has been variously dated from the Neocomian (Early Cretaceous, 146-130 mya), though an late Hauterivian age is best supported by biostratigraphy and zircon fission-track dating (see Evans et al, 2006 for discussion). The formation alternates between beds of fine-grained sandstones, mudstones, and coarse sandstones (Isaji et al., 2005).

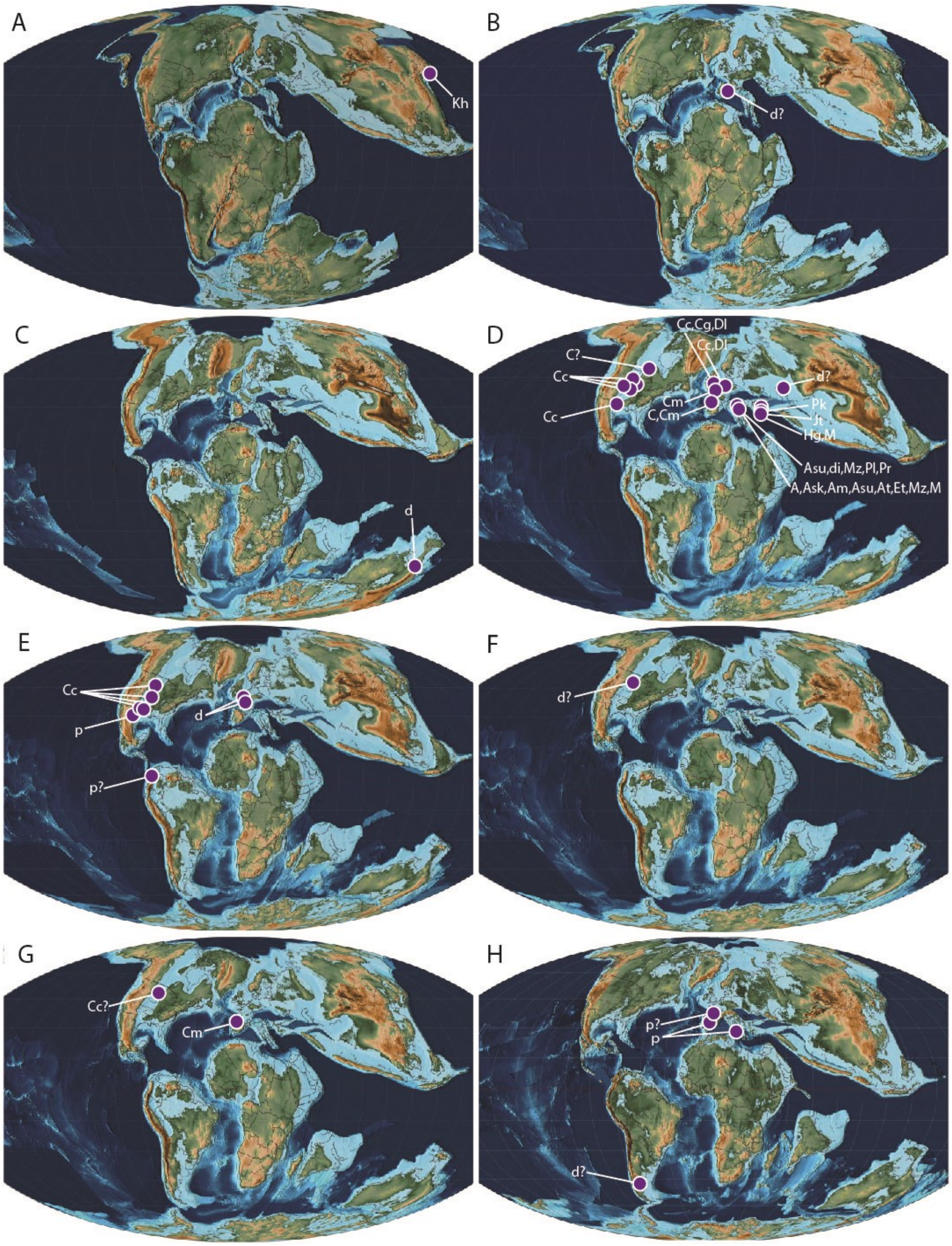

Figure 6-1 Paleogeographic distributions of dolichosaurs during the Late Cretaceous. **A**, Hauterivian (132.9-129.4 My); **B**, Barremian (129.4-125.0 My); **C**, Albian (113.0-100.5 My); **D**, Cenomanian (100.5-93.9 My); **E**, Turonian (93.9-89.8 Ma); **F**, Coniacian (89.8-86.3 Ma); **G**, Santonian (86.3-83.6 Ma); **H**, Campanian/Maastrichtian (83.6-66.0 My). **Abbreviations**: **A**, *Adriosaurus sp.*; **Am**, *Adriosaurus microbrachis*; **Ask**, *Adriosaurus skrbinensis*; **Asu**, *Adriosaurus suessi*; **At**, *Acteosaurus tommasinii*; **C**, *Coniasaurus sp.*; **Cc**, *Coniasaurus crassidens*; **Cg**, *Coniasaurus gracilodens*; **Cm**, *Carentonosaurus mineaui*; **d**, dolichosaur; **Dl**, *Dolichosaurus longicollis*; **Et**, *Eidolosaurus trauthi*; **Hg**, *Haasiasaurus gittelmani*; **Jt**, *Judeasaurus tchernovi*; **Kh**, *Kaganaias hakusanensis*; **M**, *Mesoleptos* sp.; **Mz**, *Mesoleptos zendrinii*; **Pk**, *Pontosaurus kornhuberi*; **Pl**, *Pontosaurus lesinensis*; **Pr**, *Pontosaurus ribaguster*; **p**, pythonomorph lizard. (because of their proximity, all the localities in France, and the USA are not shown). Paleogeographic reconstructions based on Scotese (2014).

The coarse sandstone layers are found with pebbles, gravels and driftwood, and are interpreted to be channel deposits. The fine sandstones and mudstones are the fossil bearing units, containing *in situ* tree trunks, and interpreted as inter-channel deposits. These layers are dominated by three facies (Isaji et al., 2005): one representing a peat marsh, one a shallow freshwater lake, and the third a subaerial swamp. The fossil lizards originate from two facies: one containing freshwater aquatic invertebrates, fish, turtles, and choristoderes which is interpreted as a freshwater lake; the second with lower concentrations of freshwater aquatic invertebrates, fish, turtles, and choristoderes, and dominated by terrestrial fauna (lizards, mammals, dinosaurs). The latter depositional environment would have been at least 100 km from the sea, and is interpreted as a vegetated freshwater swamp that was subject to flooding such as could be found on a delta plain or river floodplain.

Barremian (Lower Cretaceous); Figure 1B

Spain—The next oldest record attributed to a dolichosaur comes from the Barremian of Spain. These isolated vertebrae were initially described as a snake (Rage and Richter, 1994), but additional data on Cretaceous squamates caused the original authors to rescind this referral (Rage and Werner, 1999). It has since been suggested that it is more likely a dolichosaur (Scanlon and Hocknull, 2008). The vertebrae were recovered from the famous Las Hoyas locality (Cuenca Province, Castilla-La Mancha) of eastern Spain: a fossil lagerstätte of the La Huérguina Formation preserving a freshwater lacustrine environment (Buscalioni and Fregenal-Martinez, 2010). This rich lithographic limestone locality produces plants, invertebrates, and complete, fully articulated vertebrates including birds, dinosaurs, pterosaurs, amphibians, turtles, crocodiles, and lizards (Sanz et al., 1988; Evans and Barbadillo, 1997, 1999; Ortego et al., 1999; Bolet and Evans, 2012). The locality is interpreted as a seasonal subtropical wetland ecosystem (Buscalioni and Fregenal-Martinez, 2010).

Albian (Lower Cretaceous); Figure 1C

Australia—A single, incomplete vertebra identified as a dolichosaur (*incertae sedis*) comes from the latest Albian of Queensland, Australia (Scanlon and Hocknull, 2008). The specimen originates from the Winton Formation, considered to be latest Albian in age. The fossiliferous, silty claystone associated with this find has produced extensive fossil remains including plants, insects, molluscs, lungfish, turtles, crocodilians, pterosaurs, and dinosaurs. The formation is an extensive fluvial sequence composed of several fossiliferous horizons. The larger elements associated with the dolichosaur remains include bones that have been reworked and transported, indicating an active system at the time of the dolichosaur's deposition (Exon and Senior, 1976; Scanlon and Hocknull, 2008).

Cenomanian (Upper Cretaceous); Figure 1D

By far the highest concentrations of discovered dolichosaurs are Cenomanian in origin. All originate from two seaways: the majority from the Tethys (northern and southern margins), and the remainder from the Western Interior Seaway.

In the Late Cretaceous, a transgressive phase of the Tethys Sea covered much of Europe (including Western Europe, the Mediterranean region, and Eastern Europe), the Middle East, and northeastern Africa. The flooded continental margins formed widespread shallow seas dotted with islands. This supported the development of extensive patch-reefs, lagoons, and barrier reefs. In Western Europe, from Ireland to Germany, the warmer waters of the Tethys mixed with the cooler waters of the Atlantic in the Anglo-Paris Basin, forming a temperate zone. This caused the deposition of chalks and marls, rather than the limestones that dominate the rest of the Tethyan region.

The Western Interior Seaway was an inland sea that split the western from the eastern side of North America, and stretched from the Arctic Ocean to the Gulf of Mexico. It was formed by the subduction and convergence of the Farallon and North American plates. This caused a basin to form down the center of the continent which was subsequently flooded from the north and south beginning in the Barremian-Middle Albian. The two arms connected in the Late Albian, and the seaway persisted until the Mid-Maastrichtian, close to the end of the Cretaceous (Hattin, 1982; Kauffman and Caldwell, 1993).

Tethys: Anglo Paris Basin

England—In the early to late Cenomanian, much of England (which sat in the Anglo-Paris Basin) was submerged under the Tethys and the Northern Atlantic. This basin formed a broad continental shelf under a shallow sea. The depositional environment produced the Lower Chalk: massive soft chalk deposits interspersed with thinner marl and harder, lithified chalk layers. The soft chalks represent deeper water settings, while the harder chalks and marls are thought to have formed in a shallower environment nearer to shore. The fossils of the chalk are diverse and well studied. A variety of invertebrate (bivalves, cephalopods, arthropods, sponges, bryozoans, echinoderms) and vertebrate (teleost fishes, sharks, sauropterygians, ichthyopterygians, dinosaurs, and pterosaurs) remains show a relatively complete picture of the ecosystem (Owen, 1842, 1850, 1878). Dolichosaur fossils are rarer, and are found only in Lower Chalk outcrops in Sussex and Kent (southeast of England). *Coniasaurus crassidens* and *Dolichosaurus longicollis* are both represented by multiple fragmentary remains spanning the Chalk Marl Formation (lower-middle Cenomanian) and the Grey Chalk Formation (Upper Cenomanian), to the Plenus Marl Horizon (upper Cenomanian) (Owen, 1850, 1851, 1878). This indicates that both species occupied shallow water environments in England spanning the Cenomanian. *Coniasaurus gracilodens* is represented by a single specimen from the Zig Zag Chalk Formation (Lower Cenomanian) of Sussex (Caldwell, 1999a).

Germany—Like England, Cenomanian Germany sat in the Anglo-Paris Basin, covered by a shallow sea. It is therefore unsurprising that similar taxa make up the fossil fauna. Fragmentary *Coniasaurus crassidens* and *Dolichosaurus longicollis* have been found in Halle/Westphalia in northwest Germany (Diedrich, 1997, 1999) in the Blackcoloured Formation in the Puzosia Event (upper Cenomanian). The Puzosia Event is an ammonite scour trough system corresponding to the Plenus Marl of England and represents an offshore marine environment on a deep (150-200 m), flat shelf (Diedrich, 1999).

Tethys: Adriatic region

Slovenia—In the late Cretaceous, the Adriatic region was a massive shallow marine carbonate platform that supported rudist and coral reefs. For many centuries, the yellowish-grey limestone has been quarried for building material, which produced huge numbers of fossil plants, invertebrates, fish, and—more rarely—lizards (Stur, 1891). Komen (or Comen) is located on the Istrian Peninsula. It is one of the richest sites for Late Cretaceous shallow marine squamates, producing both dolichosaurs and basal mosasauroids. Though most of the outcrops that produced these lizards can no longer be located, the fish and lizard bearing beds around Komen have been dated to the middle to late Cenomanian (Parona, 1926; Langer, 1961; Polšak et al., 1982; Fuček et al., 1990; Jurkovšek and Kolar-Jurkovšek, 2007).

The Komen limestones are dark grey and thinly laminated mudstone to wackestone. They contain abundant invertebrates, fish, plants, rudists, and squamates, and represent a very shallow, highly restricted shore comprised of lagoons separated by rudist reefs (Cavin and Kolar-Jurkovšek, 2000; Jurkovšek and Kolar-Jurkovšek, 2007).

Besides the Lower Chalk of England, the Komen beds produced the first described dolichosaurs: *Mesoleptos zendrinii* (Cornalia, 1852)*, Acteosaurus tommasinii* (von Meyer, 1860), *Adriosaurus suessi* (Seeley, 1881), *Eidolosaurus trauthi* (Nopcsa, 1923), *Adriosaurus microbrachis* (Palci and Caldwell, 2007), and *Adriosaurus skrbinensis* (Caldwell and Palci, 2010). The same beds have also produced the basal mosasauroids *Carsosaurus marchesetti* (Kornhuber, 1893) and *Komensaurus carrolli* (Caldwell and Palci, 2007). The volume of specimens and species from the same locality (likely the Pivor Formation) indicate an unprecedented concentration of small marine squamates sharing this region.

Croatia—Roughly 300 km south of Komen, on the Dalmatian Coast of Croatia, is the Island of Hvar (Isola di Lesina). On the north side of this island, between the towns of Stari Grad and Jelsa is an outcrop of late Cenomanian carbonates spanning the late Cenomanian to early Turonian which is the most likely origin of a myriad of shallow marine squamates (Herak, 1959;

Langer, 1961; Herak et al., 1976). Like the fossils from Komen, the dolichosaurs and aigialosaurs discovered here are among the first described representatives of their respective families. *Adriosaurus suessi* (Seeley, 1881), *Pontosaurus lesinensis* (Kornhuber, 1873; Kramberger, 1892), *Mesoleptos zendrinii* (Cornalia, 1852), a newly described species of *Pontosaurus* (Campbell Mekarski and Caldwell, in prep), and several indeterminate dolichosaur remains comprise the described dolichosaur fanua. Among the basal mosasauroids, the monotypic holotypes of *Aigialosaurus dalmaticus, Aigialosaurus bucchichi,* and *Aigialosaurus novaki* originate from Hvar (Kramberger, 1892; Kornhuber, 1901), as well as a new genus of aigialosaur (Campbell Mekarski and Caldwell, in prep). Interestingly, Hvar has produced the single known specimen of *P. lesinensis, Pontosaurus* sp. nov*., A. dalmaticus, A. bucchichi, A. novaki*, and Hvar mosasauroid gen. et. sp. nov, indicating a different ecosystem structure than the paleoenvironment at Komen even though the fossiliferous layers containing the lizards are also dated to the late Cenomanian (Starigrad Formation; Marinčić, 1997; Diedrich et al., 2011). The depositional setting at Hvar was a highly restricted shallow marine environment, most likely in very shallow lagoons surrounded by rudist reefs on an inner platform close to the shore (Radovčić et al., 1983b; Fuček et al., 1990; Diedrich et al., 2011).

Tethys: Eastern Reaches

Kazakhstan—Far to the east of Komen and Hvar is Kazakhstan, which in the Cenomanian also lay on the norther border of the Tethys. A single isolated vertebra was described from the upper mid-Cenomanian upper phosphatic horizon of the Mangyshlak Plateau (Averianov, 2001). The indeterminate dolichosaur is associated with a diverse assemblage of sharks, cephalopods, gastropods, echinoderms, and bivalves. The depositional environment was shallow marine with terrestrial input and can be correlated to the Anglo-Paris Basin (Gale et al., 1999).

Tethys: middle eastern region

Lebanon—The ‘Fish Beds’ of the Sannine Formation, Lebanon are the origin of several taxa of Cenomanian small marine squamates. The Sannine Formation was laid down in a low energy, shallow carbonate platform thought to represent a system of lagoons, rudist patch reefs, and small islands (Dal Sasso and Pinna, 1997; Dalla Vecchia et al., 2002). The appropriately named “fish beds” produce mainly teleosts and crustaceans, but also bivavles, plants, and rare tetrapods including turtles, lizards, and limbed snakes (Dal Sasso and Renesto, 1999; Dalla Vecchia et al., 2002). Several Sannine outcrops in Lebanon have produced squamate remains: Nammoura, Hakel, and Hadjula. Al Nammoura (or En Nammoura) is a mid-Cenomanian Lagerstätten located in the Garbour Valley in the north of Lebanon that produced the holotype of *Pontosaurus kornhuberi* (Dal Sasso and Renesto, 1999; Caldwell and Dal Sasso, 2004; Caldwell, 2006). This specimen is the most complete pythonomorph lizard described to date, preserving the entire skeleton, scalation, and cartilage. This same locality also produced the holotype of the hind-limbed snake *Eupodophis* (=*Podophis*) *descouensi* (Rage and Escuillié, 2000). Dalla Vecchia et al. (2002) proposed that this locality developed in an anoxic, possibly hypersaline lagoon, leading to the stunning preservation of soft tissues. It is dated to the latest middle Cenomanian based on foraminiferan biostratigraphy, the same age or slightly older than the locality at Hakel and Hadjula (Dalla Vecchia et al., 2002). Hakel (or Hâqel) is associated with a small basin on the outer margin of the continental shelf, and has also produced four specimens of *Eupodophis descouensi* (Rieppel and Head, 2004).

Aphanizocnemus libanensis and another undescribed taxon are small marine squamates of uncertain affinities (see Chapter 4) from the lower-middle Cenomanian of Lebanon (Dal Sasso and Pinna, 1997; Dal Sasso and Renesto, 1999). The exact locality of its discovery is uncertain, but it is almost certainly from one of the three Sannine outcrops mentioned above.

Palestine—The ‘Ain Yabrud (or ‘Ein Jabrud) locality of Palestine is an early to middle Cenomanian outcrop that has produced several small marine squamates. These include the hind-limbed snakes *Pachyrachis* and *Haasiophis* (Caldwell and Lee, 1997; Tchernov et al., 2000), and the pythonomorph lizard *Haasiasaurus* (=*Haasia*) *gittelmani* (Polcyn et al., 1999, 2003). *Haasiasaurus* was described as a mosasauroid, but may represent a more basal pythonomorph lineage (see Chapter 5). An articulated specimen of *Mesoleptos* can also be attributed to this locality (Lee and Scanlon, 2002). The locality is alternatively assigned to the Amminidav Formation (Chalifa, 1985, 1989) or the Bet-Meir Formation (Lee and Caldwell, 1998; Lee and Scanlon, 2002), of the latest early Cenomanian. The depositional environment of ‘Ain Yabrud is a low energy, shallow marine platform interpreted as a bay close to a river mouth or an inter-reef lagoon similar to the depositional environment in Al Nammoura, Hvar, and Komen (Lee and Caldwell, 1998; Polcyn et al., 1999; Jacobs et al., 2005b). The fossiliferous interval preserves terrestrial plants, squamates, turtles, teleost fishes, elasmobranchs, ammonites, bivalves, crustaceans, and echinoderms- often including soft tissue structures (Polcyn et al., 1999)

Israel—The Judean Hills near Jerusalem have produced another basal pythonomorph lizard of uncertain affinities: *Judeasaurus tchernovi* (Haber and Polcyn, 2005). The most likely origin of this specimen is the mid-Cenomanian Kefar Sha'ul Formation, part of the Judea Group. The depositional environment was a restricted basin with input from the open ocean (Haber and Polcyn, 2005).

Atlantic margin

France—Southwest of the Anglo-Paris basin, lying roughly on the border of the Cenomanian Atlantic Ocean and the Tethys Seaway, is the Aquitaine Basin. This basin currently occupies the south west quadrant of modern France, and in the Cenomanian, was overtaken by the transgression of the Atlantic Ocean. Deposits from this the western edge of the Aquitaine Basin have produced isolated material (mostly vertebrae) of *Carentonosaurus mineaui,* an ophidiomorph lizard of uncertain affinities (Rage and Néraudeau, 2004). The specimens come from at least two localities in Western France: the lower upper Cenomanian of Île Madame (Charente Maritime), the upper Cenomanian of La Couronne (Charente), and possibly other locations including the lower Cenomanian of Les Renardières (Charente Maritime), the basal upper Cenomanian of Roullet-Saint-Estèphe (Charente), and the upper Cenomanian of Douce Amie (Sarthe). The specimens from Île Madame come from two units, both Cenomanian in age: the majority from the 'Dm' unit, a silty limestone corresponding to a deeper marine environment, and the rest from the 'C4ms' unit, a silty unit indicative of very shallow, high-energy marine environment (Rage and Néraudeau, 2004; Csiki-Sava et al., 2015). Nearby localities in the same Cenomanian deposits have also produced specimens referred to *Simoliophis rochebrunei*, a hind-limbed snake (Bardet et al., 2008).

Spain—The La Cabaña Formation (middle?–late Cenomanian) of Asturias, Spain is a microsite that preserves vertebrate remains of a shallow coastal platform and lagoon with continental input (Vullo et al., 2009). The vertebrate fauna includes fish, turtles, crocodilians, plesiosaurs, dinosaurs, pterosaurs, and marine squamates. The mixture of terrestrial and marine fauna is believed to result from a transgressive lag likely containing reworked remains from older middle Cenomanian deposits (Vullo et al., 2009; Csiki-Sava et al., 2015). The assemblage of La Cabaña compares favorably to that of Charentes (France), which was also part of the Bay of Biscay (Csiki-Sava et al., 2015). Vullo et al. (2009) suggest that the Bay formed an area of endemism during the mid-Cretaceous. Among the endemic taxa supporting this hypothesis is the marine squamate *Carentonosaurus* (Rage and Néraudeau, 2004). *Carentonosaurus* is the most abundant tetrapod taxon in Charentes and Asturias, but isolated *Coniasaurus*-like vertebra and *Simoliophis*-like vertebra have also been identified (Vullo et al., 2009).

Western Interior Seaway

The Western Interior Sea was a continental flooding of the foreland basin which runs longitudinally down the center of North America. The basin, which was caused by the uplift of the Rocky Mountains to the west, was inundated from the north by the Arctic Ocean, and from the south by the Atlantic/Tethys. The high sea levels resulted from a period of globally high temperatures in the Late Cretaceous. Little to no polar ice, and higher rates of sea floor spreading caused a sea level that was much higher than it was today. This period lasted from the late Albian (approx. 100 mya) to the late Maastrichtian (approx. 66 mya) and was marked by three major transgressive/regressive events (Kauffman and Caldwell, 1993; Robinson Roberts and

Kirschbaum, 1995). This shallow epicontinental seaway, along with the Tethys Sea, has the densest concentration of Cretaceous small marine squamates, though most of the occurrences in the Western Interior are assigned to a single genus: *Coniasaurus*.

United States—Several Cenomanian formations from the southern United States have produced disarticulated and incomplete remains of the dolichosaur *Coniasaurus*. The Eagle Ford Shale Formation, Greenhorn Formation, Graneros Shale Formation, and Lake Waco Formation all represent shallow, marine environments with fragmentary *Coniasaurus* remains.

The Eagle Ford is the only formation in the Western Interior that has so far produced more than one type of small marine squamate: the dolichosaur *Coniasaurus crassidens* (Bell et al., 1982; Jacobs et al., 2005a) and the basal mosasauroid *Dallasaurus turneri* (Bell and Polcyn, 2005). The Formation spans the early Cenomanian to the latest Turonian, and contacts the Coniacian Austin Chalk. The only Cenomanian marine squamate represented is *Coniasaurus,* which is found in the Tarrant and Britton Members of Texas (Bell et al., 1982; Jacobs et al., 2005a). The paleoenvironment was shallow, low-energy marine in association with a river delta (Kauffman and Caldwell, 1993; Denne et al., 2016).

The Greenhorn Formation is extensively exposed throughout the central states: Wyoming, South Dakota, Colorado, Nebraska, Kansas, and New Mexico. The Formation spans the mid Cenomanian to mid Turonian (Von Loh and Bell, 1998). The higher beds yield derived marine squamates (mosasaurs), while the lower beds (Orman Lake Member) produce *Coniasaurus* until just below the Cenomanian-Turonian boundary in Kansas (Liggett et al., 2005), Colorado (Shimada et al., 2006), and South Dakota (Von Loh and Bell, 1998). Like the Eagle Ford, the depositional environment is shallow, low-energy marine (Von Loh and Bell, 1998). The abundance of *Coniasaurus* material from this Formation is particularly notable; for example, Shimada et al. (2006) recovered almost 400 isolated teeth from a deposit in southeastern Colorado.

The middle-Cenomanian Graneros Shale Formation contacts the base of the Greenhorn Formation in Kansas. The depositional environment was both shallower, and higher energy than the Greenhorn Formation. *Coniasaurus* remains (including teeth and a partial maxilla) have been found here, but only at the top of the formation, at the contact between the Graneros Shale and Greenhorn (Liggett et al., 2005).

Unlike the previous formations bearing *Coniasaurus* fossils, the Lake Waco Formation of Texas is higher energy, with consistent current action. The Bluebonnet Member had a depositional environment that was shallower, likely a foreshore or bar with abundant plant fossils likely representing marsh-growing reeds (Silver, 1963).

Canada—Cumbaa et al. (2006), in a description of a Cenomanian bonebed fauna from Saskatchewan, Canada, report fragmentary vertebral and dental elements that they tentatively identify as *?Coniasaurus crassidens*. The locality at the Pasquia Hills is a middle Cenomanian deposit on the northernmost upland of the Manitoba Escarpment, part of the Belle Fourche Member of the Ashville Formation (Cumbaa et al., 2006). If these remains do represent a coniasaur, it would be the first and only occurrence from Canada. However, Shimada and Ystesund (2007) express their doubt that the specimens represent a dolichosaur, citing personal communications with the original authors.

Turonian (Upper Cretaceous); Figure 1E

Though the Turonian is nowhere near as rich in dolichosaur species or density as the Cenomanian, it does reflect a wider geographical distribution (Europe, North America, and South America). The drop in diversity could be attributed to sampling bias, or to an extinction event: the Cenomanian-Turonian Boundary Event (CTBE), which caused significant biotic and geologic changes between these two time periods (Lamolda et al., 1994; Caldwell and Cooper, 1999).

Other marine squamates achieve a broader diversity and distribution during this time. Limbed snakes, which were exclusively known from Northern and Southern margins of the Mediterranean Tethys, became known intercontinentally in the Turonian (Gardner and Cefelli, 1999; Rage and Werner, 1999; Caldwell and Albino, 2001). Mosasauroids, also exclusively known from Europe in the Cenomanian, increase in size and distribution and by the mid-Turonian could be found in Africa, Europe, and North and South America (Von Loh and Bell, 1998; Bardet et al., 2003, 2008; Buchy et al., 2005; Schulp et al., 2008; Smith and Buchy, 2008; Longrich, 2016).

Colombia—The Villeta Formation near Yaguará, Colombia is a late Turonian deposit of laminated limestones with well preserved vertebrate remains. The majority comprised fish, but marine squamates include indeterminate ‘varanoid’ and ‘pythonomorph lizard remains, and the basal mosasauroid *Yaguarasaurus colombuanus* (Páramo-Fonseca, 1994, 1997). The Turonian of Colombia represented a maximal transgression flooding the plains of Colombia to the Andes. The depositional environment at Yaguará was shallow, low-energy marine with anoxic conditions, thus explaining the good state of preservation.

Mexico—The early Turonian limestones at Vallecillo, northeast Mexico are part of the Agua Neuva Formation (Buchy et al., 2005). The formation does not typically produce macrofossils, except near Vallecillo, which corresponds to a low-energy, outer shelf environment with localized anoxic episodes. These restricted preservational conditions allowed a diverse vertebrate fauna—including turtles, fishes, sauropterygians, and squamates—to be preserved complete and often with soft tissue impressions and gastric contents. This is the state of preservation of *Vallecillosaurus donrobertoi* (Smith and Buchy, 2008). Though this animal is described as an aigialosaur, the designation is based on caudal neural spine length. Otherwise, the incompleteness of the specimen (pelvis, hind limbs, and anterior caudals) and the lack of diagnostic elements allow that this specimen could be an aigialosaur or a dolichosaur.

United States—Several formations in the United States preserve Turonian-aged *Coniasaurus* material. These include some formations that span the Cenomanian-Turonian, indicating a long history of *Coniasaurus* occupation in the Western Interior Basin.

The Boquillas Formation (upper middle Turonian, southeastern Texas) is produced *Coniasaurus* material, as well as indeterminate Mosasauroidea and Russellosaurina material. The Ernst Member, which preserves the fossil lizards, was deposited on the shallow open shelf (Cicimurri and Bell, 1996)

As mentioned above, the Eagle Ford (spanning the early Cenomanian to latest Turonian of Texas) is the only formation in the Western Interior to produce more than one small marine squamate: the dolichosaur *Coniasaurus crassidens* (Bell et al., 1982; Jacobs et al., 2005a) and the basal mosasauroid *Dallasaurus turneri* (Bell and Polcyn, 2005). Unlike the Cenomanian members, which produced only *Coniasaurus,* the Turonian Kamp Ranch Member has produced

Coniasaurus and *Russellosaurus* (Bell et al., 1982; Jacobs et al., 2005a; Polcyn and Bell, 2005). At the top of the Formation is the Arcadia Park Member, which contacts the Austin Chalk (Coniacian). *Coniasaurus* specimens have also been recovered from this member (Bell et al., 1982; Jacobs et al., 2005a, 2005b) which is also the source of the mosasauroid *Dallasaurus* (Bell and Polcyn, 2005). Like the Britton Member, the Arcadia Member was deposited on a shallow marine shelf in association with a freshwater delta (Denne et al., 2016).

The Carlile Shale (which overlies the Greenhorn Formation; Shimada and Bell, 2006) of South Dakota and Kansas has also yielded isolated *Coniasaurus* remains (Bell and Polcyn, 1996; Shimada and Ystesund, 2007). The Turner Sandy Member of South Dakota (Bell and Polcyn, 1996), and the Fairport Chalk Member of Kansas (Everhart and Darnell, 2004; Shimada and Ystesund, 2007) are the source of the coniasaur material. The Shales were deposited in a very shallow marine environment close to the shoreline, and are Upper Turonian in age.

France— An isolated vertebra of an indeterminate "dolichosaurid" was described by Rage in 1989. The vertebra originates from Sainte-Maure, Touraine, in western France. It is derived from the Saumur Tuffeau, dated to the middle Turonian, and representing outer to inner shelf environments (Rage, 1989; Bardet et al., 1998b). Isolated aigialosaurid and mosasaurid vertebrae have also been found in these deposits (Bardet et al., 1998b).

A set of 25 isolated vertebrae were discovered in a quarry south of Le Paluau, Indre-et-Loire, western France corresponding to the stratigraphical unit 'Falun de Continvoir': a shallow marine environment of late Turonian age (Houssaye, 2010). The unique shape of the vertebrae was used to suggest that these disarticulated elements may represent a new pythonomorph taxon, though due to a lack of clearly distinctive characters, the taxon was not named (Houssaye, 2010). The different size classes recovered suggest that several individuals are represented.

Coniacian (Upper Cretaceous); Figure 1F

United States—Shimada et al. (2007) described what appears to be an unusually large dolichosaurid tooth similar in anatomy to *Coniasaurus crassidens.* The find originates from an upper Coniacian unit in the Smoky Hill Chalk Member of the Niobrara Chalk Formation in Trego County, Kansas. Due to the isolated nature of the tooth, it is impossible to tell if it is indeed a dolichosaur, but if it is, it would represent the largest dolichosaur described (based on tooth scaling; Shimada et al., 2007). It would also represent the only Coniacian record of dolichosaurs worldwide.

Santonian (Upper Cretaceous); Figure 1G

United States—The Coniacian-aged *Coniasaurus* discovery of Shimada et al. (2007) is not the youngest reported *Coniasaurus.* Another occurrence was described by Shimada and Bell (2006) from the same Member and Formation: the Smoky Hill Member of the Niobrara Chalk. A single isolated vertebra diagnosed as *Coniasaurus* sp. was recovered from layers established as middle Santonian in age. Mentioned above, the Smoky Hill Member represents the Coniacian-Campanian shallow carbonate platform flooded by the Western Interior Sea (Shimada and Bell, 2006). Unlike most other *Coniasaurus*-bearing units, the Formation was deposited a few hundred kilometres from shore. It was inhabited by other marine squamates including: *Clidastes,* *Platecarpus*, and *Tylosaurus* (Everhart, 2005; Shimada et al., 2007; Jimenez-Huidobro et al., 2016).

Spain—A collection of 10 isolated vertebrae and 16 teeth was discovered in the Calvero de la Higuera complex, near the village of Pinilla del Valle, northwest of Madrid, Spain (Hontecillas et al., 2015). The complex is a series of cave deposits known for Pleistocene mammals and hominids located. The 26 specimens originate from karstic structures formed from Santonian aged marine marls, sandstones, and dolomites. During the Quaternary, the area was karstified, and eventually infilled with fluvial sediments and with sediments formed during the degradation of the karst structures (Peréz-González et al., 2010). It is these reworked Quaternary sediments which produce both Cretaceous and Quaternary vertebrate remains, including the squamate material described. The material was assigned to *Carentonosaurus mineaui*, and based on the age of the parent rock, is dated to the Santonian (Hontecillas et al., 2015). This significantly extends the range of this genus, which was previously only known from the Cenomanian.

Campanian-Maastrichtian (Upper Cretaceous); Figure 1H

Argentina—Albino (2000) reported on an isolated vertebrae from the La Colonia Formation (Campanian-Maastrichtian) of Argentina. The deposit was suggested to be an estuary, coastal plain, or tidal flat, since marine, fluvial, and terrestrial taxa are all present. Among these was a single vertebrae that Albino (2000) assigned ‘Serpentes incertae sedis”. However, this assignment has since been questioned, with Scanlon and Hocknull (2008) comparing it more favorably to a dolichosaur.

Spain—The “Lo Hueco” site of Cuenca, central Spain is a late Campanian-early Maastrichtian site has a diverse vertebrate fauna including turtle, crocodiles, and dinosaurs. The site is located in the upper part of the ‘‘Margas, Arcillas y Yesos de Villalba de la Sierra’’ Formation, and likely represents a muddy flood plain near the coast, crossed by sandy delta channels, and subjected to both brackish and fresh water influence (Barroso-Barcenilla et al., 2009; Csiki-Sava et al., 2015). Two isolated vertebrae were identified as a novel type of pythonomorph lizard, though the taxon was left unnamed due to the minimal amount of represented material (Houssaye et al., 2013).

France—Another isolated vertebra was described from the late Maastrichtian Cassagnau locality (Auzas Marls Formation) of Haute-Garonne, south-west France (Laurent et al., 2002). The authors mention that the undescribed form is known from Campanian and early Maastrichtian localities in Southern France, in addition to the late Maastrichtian locality described in the paper. It is incomplete, and as mentioned by (Houssaye et al. (2013), it cannot be determined whether it represents a pythonomorph or not.

Italy—A newly reported pythonomorph lizard was reported by Paparella et al. (2015). Originating from late Campanian/early Maastrichtian deposits in Apulia, Italy, the specimen has yet to be formally described. Therefore, its precise placement within the Pythonomorpha remains uncertain.

DISCUSSION

Oceanographic context

The radiation of aquatic squamates is obviously very closely tied to the seaways and oceans they were colonizing. The beginning of the Cretaceous (~145 mya) is roughly 55 million years after the break up of Pangea, and about 35 my after Gondwana started to separate. The continents were still relatively close together (or attached), global sea levels were relatively low, and the Atlantic was only just maturing into an ocean and beginning to form between South America and southern Africa (Haq et al., 1988; Polcyn et al., 1999; Blakey, 2008; Bardet et al., 2014; Scotese, 2014; Csiki-Sava et al., 2015). The earliest Cretaceous represented a greenhouse period, with high global CO_2 concentrations and ocean temperatures exceeding 30°C in the tropics (Littler et al., 2011). Cold sea-surface temperatures and a global anoxic event dominated the Aptian-early Albian, until increased oceanic crust production and hydrothermal activity through the Albian-early Turonian drove a long-term warming trend caused by CO_2, and a global eustatic sea level rise (Haq et al., 1988; Clarke and Jenkyns, 1999; Davey and Jenkyns, 1999; Leckie et al., 2002; Jenkyns et al., 2012; Csiki-Sava et al., 2015). The resulting changes in ocean circulation, oceanic stratification, and nutrient partitioning lead to a reorganization of planktonic communities that subsequently caused widespread carbonate deposition in the Late Cretaceous (Leckie et al., 2002). These conditions drove the development of extensive foraminiferan chalk deposits in temperate waters (e.g., the Anglo-Paris Basin and the Western Interior Sea) and of extensive rudistid carbonate platforms in more tropical waters (e.g., Caribbean Tethys and Mediterranean Tethys) (Fuček et al., 1991; Davey and Jenkyns, 1999).

By the mid-Cretaceous, the separation of Gondwana was nearly complete. The rapid spreading of the seafloor and the fragmentation of the continents resulted in shallow epicontinental seas bordering many of the major landmasses that acted as corridors between larger water bodies such as the Tethys, Atlantic, and Pacific (see Bardet et al., 2014; Csiki-Sava et al., 2015 for discussion). In Europe, the complex tectonics created a very dynamic archipelago within the Tethys, unlike any other ecosystem of the time. Blocks of continental crust moving into the spreading area of the Tethys created a series of moving and fluctuating islands that altered population dynamics and geological features in their wake (Csiki-Sava et al., 2015). This unique region formed the basis of many unique faunas, and was arguably the driving force behind many distinctive radiations (Bardet et al., 2008; Bardet, 2012; Csiki-Sava et al., 2015).

Reconstruction of Cenomanian current patterns show a circumglobal current flowed westward through the Tethys Seaway and across the Atlantic, forming the ‘SuperTethys’ (Föllmi and Delamette, 1991; Caldwell and Cooper, 1999). This current is thought to be the primary method of dispersal of certain invertebrate taxa. For example, bivalves go through a planktonic stage, during which time their larvae are free floating and subject to dispersal along ocean currents. Rudist bivalves are known from the Lower Cretaceous (Berriasian-Valanginian) of the European Tethys, but are not recorded in the Caribbean region of the SuperTethys until the Barremian (Johnson and Kauffman, 1990). This dispersal is thought to have been a result of the westward prevailing current carrying the rudist larvae across the Atlantic. This current is one of the factors believed to have facilitated the explosive radiation of rudist reefs that replaced coral-algal paleocommunities during the Barremian-Cenomanian (Johnson and Kauffman, 1990). In addition to rudist-dominated communities being ubiquitous throughout the SuperTethys, invertebrate faunas from the mid-Cretaceous of Australia and New Zealand have also been shown to correspond to European faunas, implying an unrestricted migration route between these two ecosystems during or before the Cenomanian (Stilwell and Henderson, 2002).

The mid-Turonian represents a maximum transgression, with the highest water levels of any time during the Cretaceous (Haq et al., 1988; Davey and Jenkyns, 1999). After the mid-Turonian, mid-Cretaceous sea levels and temperatures drop (Clarke and Jenkyns, 1999; Jenkyns et al., 2004). Even though cyclic transgressions continued throughout the Late Cretaceous (early Turonian, early Coniacian, middle Santonian, late Campanian; (Hancock and Kauffman, 1979), an overall trend towards lower sea levels. This period also represents the closing of the Tethys: the center of dolichosaur diversity and evolution. As the Atlantic spread and Africa rotated, several microcontinents (Central Turkey, Western Iran, Apulia) drifted northward, and the Tethys subducted (Polcyn et al., 1999; Blakey, 2008). The eventual result was the closing of the Tethys, the formation of the Alps, and the assimilation of southern Europe into the European content. Thus, lower sea levels, tectonic activity, fewer carbonate shelves, and lower sea surface temperatures likely negatively influenced the evolution and dispersion of dolichosaurs during the latest Cretaceous and could have been a key factor in their extinction.

Paleoenvironment

Dolichosaurs, though widespread across the world (on every continent except Africa and Antarctica), were primarily distributed within a paleolatitudinal belt between 25ºN and 50ºN. Within this belt, three major seaways have produced the majority of dolichosaur records: the southern Western Interior Sea, the northern Tethys, and the eastern margin of the Atlantic where it meets the Tethys. No dolichosaur remains have been found north of this paleolatitudinal belt, though there are several possible occurrences south of it including isolated remains from Colombia (~5ºN), Argentina (~40ºS), and Australia (~45ºS).

Within these areas, dolichosaurs are found in a range of depositional environments. They can be found in freshwater and marine deposits, though the vast majority are marine. Within epicontinental marine environments, they have been found in deposits representing tidal flats, lagoons, swamps, reefs, deltas, basins, and the open shelf. Their paleoenvironments were generally warm, but still ranged from the more temperate chalks of England to the more tropical limestones from southern Europe (Polšak and Leskovšek, 1975). Assuming that the depositional environments reflect ecological occurrence, this indicates a wide range of ecological niches within relatively shallow, warm water. This is in agreement with hypothesized paleobiological niche of dolichosaurs as shallow, warm water, marine ambush predators (Caldwell, 1999a, 2000, 2006; Lee and Caldwell, 2000; Pierce and Caldwell, 2004; Caldwell and Palci, 2010). Optimal preservation seems to have taken place not on the reefs themselves, but in intra-reef lagoons with localized anoxic conditions (Radovčić et al., 1983a; Diedrich et al., 2011).

It has been suggested, that like similarly sized modern marine reptiles, dolichosaurs may have been subject to thermophysiological constraints (due to small body size) that limited their habitats to water between 20 and 30C (Jacobs et al., 2005b). Thus, the warm waters of the mid-Cretaceous (late Albian-early Campanian), which are estimated to have reached 20C in the Arctic (Jenkyns et al., 2004) and 35C equatorially (Norris et al., 2002), would have provided little barrier to migration, even into high latitudes.

Of all the dolichosaurs, fossils attributed to *Coniasaurus* have the best record, providing a unique opportunity to see habitat variation within the genus. In the Western Interior Sea, *Coniasaurus*-bearing rocks were deposited in waters ranging from 20-30ºC, which corresponds well to the temperature range inhabited by modern aquatic squamates: sea snakes and the marine iguana (Jacobs et al., 2005a). Most of the *Coniasaurus* material originates from beds that represent near shore deposits. However, the Kansas deposits, including the Fairport Chalk (Shimada and Ystesund, 2007), the basal Greenhorn Limestone (Liggett et al., 2005), and the Niobrara Chalk (Shimada and Bell, 2006) are all offshore deposits, representing environments hundreds of kilometres from the nearest coastline. It is important to note that the fragmentary quality of most *Coniasaurus* fossils make it uncertain whether they are indeed congeneric, but their distribution within different biomes in the Western Interior Sea raise the possibility of niche partitioning.

In comparison to other Cretaceous marine squamates, dolichosaurs occupy a broader range paleoenvironments then limbed snakes, who exclusively occupied the carbonate platforms of the Mediterranean Tethys, especially the more tropical southern margin (Rage and Escuillié, 2003; Bardet et al., 2008). Spatially, dolichosaurs are less diverse than mosasauroids. Though the smaller aigialosaurs were mostly restricted to the Tethys and Western Interior Seaway, derived mosasaurids were cosmopolitan in distribution, with a diverse range of habitats including open ocean, near shore, and even freshwater environments (Bardet et al., 2008; Makádi et al., 2012).

Origin, radiation, extinction

Robust hypotheses on the origin of dolichosaurs have been precluded by the poor fossil record in the Early Cretaceous. Three records (an articulated specimen and two isolated vertebrae) from three distant localities on three continents (Japan, Spain, and Australia) have justifiably prohibited much spatiotemporal analysis. These early occurrences are equally confounding because all three come from freshwater deposits, while all Cenomanian-Campanian dolichosaurs originate from marine beds. Two models have been proposed to explain this: a Tethyan origin, or a Western Pacific origin, though the possibility of multiple independent lineages must also be addressed.

Tethyan origin—Early pythonomorph diversity is highest in the Western Tethys (southern Europe and the Middle East; Bardet et al., 2008). Therefore, the most parsimonious explanation is that this area was the area of origin for all pythonomorphs, including dolichosaurs. Shallow carbonate shelves bordering southern Laurasia and eastern Gondwana from the Berriasian to the Barremain (Lower Cretaceous) would have provided an easy route by which small pythonomorph lizards, adapted to shallow marine environments, could have spread to Japan and Australia. These shallow epicontinental shelves kept the animals comfortably within their tropical to temperate belt, and likely provided very little obstruction to dispersal. Once established on coastlines bordering the Pacific, independent populations could have adapted to freshwater environments several times, eventually colonizing the widely distant river and lake deposits. High sea surface temperatures in the Southern Hemisphere in the late Albian could explain the presence of a dolichosaur in Australia, at the highest latitudinal occurrence of any platynotan during the mid-Cretaceous (Jacobs et al., 2005a; Scanlon and Hocknull, 2008). A native dolichosaur population remaining within the Tethys would have formed the basis of the explosive radiation in the Cenomanian.

The origin and distribution of other marine tetrapods support this hypothesis. A similar model has been proposed for mosasauroids. Prior to the Turonian, mosasauroids (aigialosaurs) are exclusively found in Tethyan deposits from the Mediterranean and the Middle East

(Kramberger, 1892; Kornhuber, 1893, 1901; Polcyn et al., 1999; Dutchak and Caldwell, 2006, 2009; Caldwell and Palci, 2007). After an initial westward dispersal to the Western Interior, they quickly developed more specialized adaptations to the marine environment, dispersed globally, and by the mid-Turonian could be found in the Western Interior, the Atlantic, the Tethys, and possibly the Pacific; and by the end of the Turonian, they were essentially cosmopolitan (Bardet et al., 2003, 2008, 2014; Kear et al., 2005; Houssaye and Bardet, 2013). Since aigialosaurs are here interpreted to have had similar paleoecological niches as dolichosaurs, it stands to reason that their distribution would have followed a similar route. Ophidians are also though to have originated in or around the southern Tethys (African platform), which is also the location of their first major radiation (Rage and Werner, 1999). Like dolichosaurs, ophidians are interpreted as having originated in the Early Cretaceous, radiated to North America in the mid-Cretaceous, and established themselves in South America before the Cretaceous-Tertiary boundary (Gardner and Cefelli, 1999; Rage and Werner, 1999).

The absence of dolichosaur material in Tethyan deposits prior to the Cenomanian is the primary challenge to this model. The lack of pythonomorph lizards in the early Cretaceous could be simply explained by a sampling bias caused by the limited exposure of certain ages (Csiki-Sava et al., 2015).

Western Pacific origin—The alternative to the Tethyan origin model, is that of a Western Pacific origin. Evans et al., (2006) hypothesized that the ancestral pythonomorph lizards initially colonized freshwater, before adapting to brackish and finally marine environments. They suggest that *Kaganaias* could represent an early, freshwater stage of that transition, implying that the high concentration of Cenomanian Tethyan dolichosaurs represents a lineage already well established and adapted to the marine environment, having successfully radiated and migrated from their freshwater origins.

Following an initial invasion of the marine environment somewhere along the Western Pacific margin, a rapid radiation in the upper Early Cretaceous would have had basal dolichosaurs expanding their range westwards to the Tethys, or eastwards across North America and into Europe while making multiple independent freshwater reinvasions in Australia and Spain. The North American radiation would have likely happened later, in the early Late Cretaceous. Several terrestrial groups—including squamates (e.g., Nydam et al., 2007)—may have followed this migration pattern in the Late Cretaceous, indicating that such a model is certainly within the realm of possibility (see Csiki-Sava et al., 2015 for discussion).

Late Cretaceous radiations and extinctions—As of the Cenomanian, the distribution pattern of dolichosaurs appears relatively straightforward. In the early to mid Cenomanian, a rapid radiation and diversification within the European Tethys is reflected in the diversity of the fossil record. A parallel radiation likely had *Coniasaurus*-like forms expanding their range westward across the Tethys, crossing the northern margin of the narrow Atlantic, and radiating throughout the interior of North America during the maximum Cretaceous transgression (Jacobs et al., 2005a). The speed of their migration was such that by the middle Cenomanian, they were well established up and down the Western Interior Seaway. The speed and route of their migration closely matches that of the rudist bivalves, that spread westward through the SuperTethys during the Barremian-Cenomanian (Johnson and Kauffman, 1990; Caldwell and Cooper, 1999). Although the bivalve larvae would have floated on prevailing currents, it is more likely that the actively swimming dolichosaurs followed either the southern coastline of the Atlantic along western Africa to South America, or the northern coastline through the Baltics and along eastern North America (Caldwell and Cooper, 1999). The migration pattern also compares well with that proposed for the Turonian distribution of russellosaurines and aigialosaurs (Bell, 1997b; Bardet et al., 2008; Kear et al., 2013).

Interestingly, after the Cenomanian, there is no record of dolichosaurs in Asia or Australasia, both of which had pre-Cenomanian records. Several hypotheses exist to explain this: first, that these tentative, fragmentary records are not dolichosaurs at all. Second, it is possible that dolichosaur populations did exist on these continents, but have not been found due to sampling bias and their relative rarity. Finally, that these animals suffered from the mass-extinction event association with the end of the Cenomanian, the Cenomanian-Turonian boundary event (CTBE; Lamolda et al., 1994). The CTBE was a short (~250ka) global oceanic anoxic event possibly linked to rapid oceanic plateau formation and/or increased rates of ridge crest volcanism (Lamolda et al., 1994; Kerr, 1998; Davey and Jenkyns, 1999; Leckie et al., 2002; Wan et al., 2003; Turgeon and Creaser, 2008). The event lead to an extensive faunal turnover, especially in the marine realm where it caused the extinction of roughly 27% of marine invertebrates (Turgeon and Creaser, 2008), and an estimated 90% of benthic foraminiferans, and 50-70% of planktonic foraminiferans (Wang et al., 2001). These invertebrate extinctions were particularly important since these taxa were the builders of the carbonate platforms that formed the basis of the dolichosaurs' ecosystems. The CTBE, which restructured marine ecosystems globally, could easily have affected dolichosaur ecosystems and thus populations, causing an extinction or near-extinction of dolichosaurs outside of their population centres: the Tethys and the Western Interior. The radiation of mosasauroids in the Tethys during the Turonian (Bardet et al., 2008; Kear et al., 2013) likely exacerbated the situation, possibly putting competition and predation pressures on any surviving dolichosaur populations.

More surprisingly is the absence of any dolichosaurs in the Eastern Tethys after the CTBE, which had been the center of known dolichosaur diversity in the Cenomanian. This absence is likely an artefact of collection bias combined with the rarity of these fossils. However, it is also possible that the Eastern European dolichosaurs suffered extinction associated with the CTBE. The combination of the CTBE and the Turonian radiation of mosasauroids could explain why from the Turonian-Santonian, the only records of dolichosaurs are from the Eastern Atlantic Margin/Western Tethys and the Americas.

The Turonian through to the Santonian has a sparse though consistent record of dolichosaurs from the Western Interior and Western Tethys indicating that though these animals persisted, they generally remained a small part of the fauna in their established biogeographic centres. A peak transgression or maximum flooding during the mid-Turonian (Davey and Jenkyns, 1999) could have facilitated a possible South American radiation represented by two occurrences from South America. This first, indeterminate pythonomorph remains from Columbia in the Turonian hint at the possibility of a southward migration starting from the Western Interior, moving down along the island system that was Central America, to the shallow epicontinental sea the covered much of the northern half of South America in the mid-Turonian. A second possible occurrence, a single vertebra from Argentina, would imply the continuation of the southward radiation, which reached the southern coast of South America by the Campanian-Maastrichtian.

A recently discovered pythonomorph lizard from Apulia, Italy in the Campanian-Maastrichtian implies that even though the diversity of these animals decreased into the late Cretaceous, they continued to persist among the more diverse lineages of aquatic reptiles including mosasaurs and sauropterygians.

The Maastrichtian finds of Italy and France (above) are the youngest records of non-ophidian ophidiomorphs, implicating the End Cretaceous Mass Extinction as the event that caused the extinction of this group.

Species distributions and endemism—The internal relationship of dolichosaurs are not well resolved, therefore it is difficult to discuss the distribution patterns of separate lineages. However, some interesting patterns do emerge surrounding some distinct paleocommunities.

In the late Cenomanian of Europe, four distinct dolichosaur communities appear to exist. The most diverse is in the Adriatic region, with multiple genera from Slovenia and Croatia (Calligaris, 1988; Bardet et al., 2008). A second, Middle Eastern fauna appears to have some unique species such as *Judeasaurus* and *Haasiasaursu*, but also appears to have some crossover with the Adriatic region, as both faunas have produced *Mesoleptos* and *Pontosaurus* fossils. The Anglo-Paris basin has produced abundant fragmentary *Coniasaurus* and *Dolichosaurus* fossils originating from the Northern Tethys margin, but which do not appear in the southern or eastern Tethys. Finally, *Carentonosaurus* seems to be endemic to the Bay of Biscany/Charentes region at the Eastern margin of the Atlantic. The spatial distribution of these marine lizards must have been impacted by their paleoenvironment and paleoclimate. Climatically, it seems that *Coniasaurus* and *Dolichosaurus* must have been adapted to the more temperate climate of the Northern Tethys margin, while the Middle Eastern and Adriatic faunas were better suited for warmer, more tropical areas on the southern Tethys. Environmentally, *Carentonosaurus* seems to have been the only dolichosaur adapted to the Atlantic coastal terrigenous landscape of the Bay of Biscay. The broad carbonate platforms of the Adriatic and Middle East supported the highest diversity, while the cooler chalk deposits of the Anglo-Paris basin was intermediate.

In the Turonian-Santonian, the only record of dolichosaurs in Europe is from France and Spain, suggesting the possibility that the endemic lineage specific to the Central Atlantic eastern margin may have continued to thrive in this area whilst their counterparts in other areas of Europe suffered extinction or near-extinction during the CTBE.

The Mediterranean Tethys, despite being continuous with the Northern and Western Tethys regions, and the Atlantic ocean, seem to display a unique fauna (Bardet et al., 2014). This indicates that even though migration was theoretically possible, other biological or ecological boundaries must have existed to enforce this local endemism.

Among all known dolichosaurs, specimens attributed to *Coniasaurus* are the most spatially diverse and numerous. *Coniasaurus crassidens* is recognised from the Cenomanian Chalk of England, spanning the early to late Cenomanian. Fossils with similar vertebrae and characteristically swollen teeth are also found in late Cenomanian deposits in Germany, and late Cenomanian to Santonian rocks from Kansas, Colorado, South Dakota, and Texas (see above for specific localities and references). These occurrences are all temperate waters, no *Coniasaurus* fossils have been found from warmer, tropical deposits which indicates a cooler environmental tolerance for this genus. The fossil record indicates an early Cenomanian origin for the genus, which likely spread to the Western Interior following the prevailing westward current of the SuperTethys throughout the Cenomanian (Caldwell and Cooper, 1999). *Coniasaurus* fossils have not been recovered from European deposits younger than the CTBE, implying that the European lineage may have been driven to extinction by this event. However, numerous Turonian records in the Western Interior indicate an established lineage that may have persisted to at least the Santonian (based on fragmentary remains from the Coniacian and Santonian of Kansas). A single indeterminate Columbian record in the Turonian hints that the North American lineage even radiated after the boundary event, migrating and establishing new populations in South America. The tentatively assigned dolichosaur vertebra from the Campanian-Maastrichtian of Argentina may attest to the continued evolution and radiation of the North American *Coniasaurus* lineage.

Overall, the fossil record of dolichosaurs shows a high degree of endemism. This is surprising, as no known physical barriers would have obstructed their potential migration. And yet, dolichosaurs are not the only group that show a surprising amount of characteristic localized faunas. An interesting correlation exists between the multiple endemic populations of dolichosaurs and that Late Cretaceous pan-chelonioids, certain Tethyan mosasaurs, and the latest Cretaceous plesiosaurs, who all—despite a suite of marine dispersal routes—showed a high degree of endemism even though they were distributed worldwide in shallow marine environments (Hirayama, 1997; Vincent et al., 2011; Bardet, 2012; Kear et al., 2013; Bardet et al., 2014). It is possible that this is related to island biogeography, and that these populations were specialized to the particular ecology surrounding an island or island system, leading to geographic separation and speciation. Alternatively, their isolated populations could be a response to habitat fragmentation and insulated environments caused by the high tectonic activity of the Tethys. We can only assume that strong ecological constraints such as environmental preferences or dietary specializations dictated such separation across multiple marine reptile groups. This alludes to the danger posed to dolichosaurs by the CTBE: if these faunas were so specialized to a particular corner of the Tethys, then their disappearance could have been caused by changes to, or the loss of, their particularly specialized and unique habitats.

Summary

Previously thought to be limited in space and time to the Tethys and Western Interior Seaway of the mid-Cretaceous, dolichosaurs are now understood to have a more complex history story than previously reported. Current knowledge of dolichosaurs indicates a large diversity of species, despite the low number of identifiable specimens. In some areas (Mediterranean regions), dolichosaurs are preserved primarily as articulated skeletons, while in others (western Europe, North America) fragmentary remains provide little diagnostic information. Though biogeographic patterns and processes remain obscured by several varieties of bias in the fossil record, some general patterns are clear. Early pythonomorph diversity is highest in the Western Tethys and this is the likely area of origin of ophidiomorphs, including dolichosaurs. A radiation in the upper Early Cretaceous likely had early dolichosaurs expanding their range across the Tethys and making multiple independent freshwater incursions in areas as far away as Japan and Australia. The North American radiation likely happened later, in the early Late Cretaceous. An extinction event at the end of the Cenomanian may have caused the extinction or near-extinction of most dolichosaur lineages, save for an eastern Atlantic fauna, and the North American fauna. These lineages persisted and radiated in the Late Cretaceous, eventually going extinct at the Cretaceous-Tertiary boundary. We expect that future discoveries—especially in areas with tentative and fragmentary dolichosaur remains—will provide new data about the evolutionary and paleogeographical history of pythonomorph lizards. Understanding the occurrence of this group through space and time is critical to the study of their evolution and adaption, including evolutionary drivers and their aquatic radiation.

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CHAPTER 7 : DENSITY OF WATER AS A DRIVER FOR THE HIGH INCIDENCE OF CONVERGENCE BETWEEN AQUATIC SQUAMATES AND OTHER SECONDARILY AQUATIC TETRAPODS

ABSTRACT

When unrelated organisms are subjected to similar selection pressures, they often evolve similar traits in response. This phenomenon is called convergence. Since the physical constraints associated with the aquatic environment are extremely different than those on land, they provide powerful selection pressures on animals that secondarily enter the water from terrestrial environments. It is for this reason that amniotes occupying the marine environment arguably show a higher degree of convergence than observed in any other niche. As these groups became increasingly aquatic, they all had to adapt to the same challenges and limitations in a medium with vastly different physical properties than air. One of the most fundamental differences, and one that requires major adaptations to deal with, is density. Sea water is approximately 800 times as dense as air. Functionally, this causes massive differences in the way an animal lives, including how it moves, eats, and senses its surroundings. Because the density difference between air and water is so profound, the selective pressure it imposes is great. The means the most physically optimal solutions to the density problem are under massive selection pressures and therefore have a greater chance of being converged upon. Using the example of Cretaceous squamates I will discuss how the density of water impacts the ecology and physiology of secondarily aquatic organisms, leading to an overwhelming degree of convergence between several independent lineages of marine amniotes across time.

INTRODUCTION

Throughout the course of evolutionary history, many groups of terrestrial amniotes have made the transition to the aquatic environment. These groups include pinnipeds, cetaceans, sauropterygians, ichthyopterygians, mosasauroids, testudines, crocodylomorphs, and many other groups from across the amniote tree. These different groups of marine amniotes may look very different from each other, but each had to overcome the same problem when they transitioned from land to water. Amniotes are adapted for life on land: the amniotic membrane prevents desiccation of the embryo, which effectively allowed early amniotes to reproduce out of the water for the first time in their evolutionary history. Separated from the water, amniotes continued to evolve adaptations for a life on land. When these highly evolved and adapted lineages returned to the water, they had to once again adapt anatomically and behaviorally to a life in the water. As each of these groups became increasingly aquatic, they all had to secondarily adapt to the same challenges and limitations in a medium much denser than air. This is the aquatic problem.

Extant secondarily aquatic tetrapods summons to mind images of crocodilomorphs, such as alligators and crocodiles; marine mammals such as whales, sea lions, and manatees; or birds such as penguins and ducks. Squamates are not the most classic example of secondary aquatic adaptation, but many are adapted to an aquatic life. Of the more than 7000 species of living squamates, 59 are adapted for a fully to partially aquatic life, one species of iguana, 50 species of true sea snakes, 5 species of sea kraits, and 3 species of file snakes.

While these living squamates show many unique and interesting adaptations for life in a marine environment, the true peak of squamate evolution in aquatic environments happened during the Cretaceous. At this time several lineages independently made the transition to an aquatic lifestyle. This adaptive radiation was dominated by the Pythonomorpha, i.e., the dolichosaurs, aigialosaurs, mosasaurs, and early snakes. However, at least one other squamate lineage adapted to life in the sea (see Chapter 4), and it is likely that the true diversity of the Cretaceous squamate aquatic radiation is as yet unrealized.

This study will review some of the remarkable adaptations that squamates evolved to overcome the aquatic problem, and how they evolved into some of the top predators of the Mesozoic oceans.

DISCUSSION

The aquatic problem (secondarily adapting to a life in the water) is not just a single problem that needs to be overcome. The aquatic problem comprises several parts, all of which need to be addressed in order to survive and thrive. These include adaptations for movement (propulsion, stability, drag), buoyancy, homeostasis (thermoregulation, ion balance), sensation (sight, sound, smell), feeding, and reproduction. In this next section, I will discuss adaptations exhibited by Cretaceous marine squamates to overcome each of these adaptive hurdles.

Squamate paleontologists are fortunate in that there is an extraordinary sequence of well-preserved material spanning the 30-35 million year history of mosasauroids. This sequence shows a steady pattern of adaptation, from a terrestrial lizard anatomy to a highly specialized marine predator with a suite of adaptations to meet locomotor, feeding and homeostatic needs. Many of these adaptations are very similar to other aquatic amniote lineages, displaying excellent examples of convergent evolution.

Movement

Though most animals are capable of swimming across the surface of water, the three dimensional nature of the aquatic environment means that massive changes are required to locomote effectively enough to hunt and avoid predation within the water.

Thrust—Rather than deriving thrust and momentum from pushing off the ground (as in terrestrial limbed tetrapods), secondarily aquatic tetrapods must generate thrust by pushing against the water itself. Aquatic squamates primarily derive their propulsive force through axial locomotion: using their bodies and tails to generate the thrust that results in movement. Extant sea snakes and plesiopedal pythonomorphs have evolved an elongate, flattened, paddle-like tail that increases the amount of thrust their tails generate as they undulate in an anguilliform motion (Caldwell, 2002).

Basal pythonomorphs, such as dolichosaurs and aigialosaurs, were almost certainly anguilliform swimmers. Their long slender bodies, flexible vertebral columns, and elongate (>50% total body length), laterally flattened tails are the same features seen in extant anguilliform swimmers such as sea snakes. These features are convergent with other fossil taxa such as thalattosaurs and pachypleurosaurs (Carroll, 1985).

Originally, it was thought that derived mosasaurs were also anguilliform swimmers, with their entire bodies moving in a sinusoidal motion like snakes or eels (Lingham-Soliar, 1991; Everhart, 2005). The absence of fossil evidence suggesting other forms of locomotion, such as a caudal fin, was used to support those conclusions.

However, some recent studies of the structure of mosasaur vertebrae (Lindgren et al., 2007, 2010) challeneged this hypothesis, and in 2013 a *Prognathodon* was described that preserved caudal soft tissue (Lindgren et al., 2013). The tail shows a bilobed, heterocercal caudal fluke supported by connective tissue, where the longer, lower lobe is supported by vertebrae, while a blade of cartilage supported the shorter upper lobe. This tail morphology is convergent with the crescent-shaped flukes of ichthyosaurs, metriorhynchid crocodyliforms and whales (Lindgren et al., 2013). This shows that the derived mosasauroids were carangiform swimmers, undulating only the rear portion of their bodies, similar to the way alligators, some lamnid sharks, and cod swim, which provides enhanced locomotor efficiency (Thomson and Simanek, 1977; Lauder, 2000).

Although relatively shorter than in the more basal forms, the muscular tail of derived mosasaurs was still 42-52% of their body length. The tail was laterally flattened, and with the lobed heterocercal tail, this resulted in a higher surface area to push against the water. The base of the mosasaur tail would have been relatively inflexible, and would have provided a stable anchor for strong musculature.

Evolutionarily, as mosasauroids became more derived, the vertebral column lost its flexibility, making the body stiffer (Caldwell, 2002). The caudal or tail region became more specialized, and over time, a downward kink developed in the caudal vertebrae, a cartilaginous blade developed on the top of the bend. The change in morphology in the tail and appendages reflects a progressive shift from lagoonal dwellers to near shore paddlers to trans-oceanic animals capable of high speed attacks. These patterns of evolution are similar to those observed in the marine crocodiles, ichthyopterygians, sauropterygians, and cetaceans (Carroll, 1985; Debraga and Carroll, 1993; Nakajima et al., 2014; Scheyer et al., 2014).

Drag—The high density of water also contributes to the problem of drag. Drag resists the movement of bodies through any medium and is increased by both higher density and viscosity. The high density of the water causes inertial drag. As a body moves through water it disturbs the water molecules, forcing the water to flow around it. Once the body has passed through the water, it leaves an empty space where the body used to be. Water enters this space, creating turbulence and a suction force that pulls on the object that created it. This is inertial drag. To minimize inertial drag, a body should be shaped so that it disturbs the water as little as possible as it passes through, a phenomenon called streamlining. The optimal shape to accomplish this is a spindle or torpedo shape, pointed anteriorly and posteriorly, exposing a small amount of surface area in the direction of movement (Lovvorn et al., 2001). This body plan, roughly 5.5 times as long as wide, is referred to as fusiform. The loss of hind limbs and external ears are further adaptations that contribute to a streamlined shape.

The second type of drag is called viscous drag. Viscous drag is due to the higher viscosity of water. A highly viscous material resists flow, which causes a lot more friction as it moves over a surface and slows an animal down. To decrease viscous drag, the surface needs to be as smooth and frictionless as possible. Mosasauroid scales are well known from numerous fossils (Everhart, 2005; Smith and Buchy, 2008; Lindgren et al., 2009; Konishi et al., 2012), some of which are exceptionally well preserved. They had small, diamond-shaped, overlapping scales, and some had a raised ridge down the center. These small ridges may actually have acted like shark skin, reducing the amount of viscous drag by maintaining a thin layer of water around the animal (Dean and Bhushan, 2010; Palmer and Young, 2015). The ridges in the scales would trap water against the body. That way, as the mosasaur moved, friction would be generated between water and water instead of between water and the animal's body, generating much less drag.

Stability—The three-dimensional nature of an open water life requires active swimmers to be able to stabilize their bodies against the drag forces that cause roll, pitch, and yaw. At slow speeds, the force of drag is minimized, and secondarily aquatic squamates can easily control their direction using small corrections from non-specialized forelimbs (i.e., dolichosaurs, aigialosaurs, *Aphanizocnemus*). As the animal evolves to become faster within the water, the drag forces proportionally increase. In squamates this is solved by evolving flippers. A stiffer, higher surface area flipper directs more water more forcefully than a terrestrially adapted limb, allowing the animal to counteract drag forces and change their direction. Some large-footed aigialosaurs and dolichosaurs have been suggested to have had webbing between their digits for this purpose (e.g., Lee and Caldwell, 2000; Palci and Caldwell, 2010, Chapter 3). In later genera, such as *Plotosaurus*, the thicker digits were arranged tightly together to form a stiff, wing-like flipper, somewhat resembling ichthyosaur and plesiosaur flippers (Lindgren et al., 2009). In still other genera, such as *Tylosaurus*, the flippers were less ossified, more cartilaginous, and highly flexible (Caldwell, 1996). During active locomotion, the flippers were most likely held close to the body to reduce drag while the tail powered the animal through the water and were only extended to help steer when a change of direction was needed.

Among other amniote lineages, even the most derived and specialized flippers are not sufficient for counteracting roll, which is why the dorsal fin evolves. In extant teleosts, chondrichthyans, and tetrapods, the fast swimming species are the ones with the largest dorsal fins, to stabilize their bodies against the drag forces that cause unwanted changes in direction that they are exposed to at high speeds (Carroll, 1985). No mosasaur has ever been recovered with evidence of a dorsal fin. Either, the large flippers (Lindgren et al., 2009) were sufficient to provide necessary stability, or such a feature still awaits discovery (see Russell, 1967; Lindgren et al., 2007).

Buoyancy

Air breathing creates another problem for an aquatic amniote - buoyancy. Most amniotes are positively buoyant. For an animal actively hunting in the water column, this means a lot of excess energy spent trying to constantly swim down. Being neutrally buoyant is far more efficient, and the massive energy savings it brings mean that it is one of the first skeletal changes associated with aquatic adaptation that is seen in many aquatic squamates. This is because more common ways for aquatic amniotes to increase the density of the body is to increase the mass of the skeleton, which can be done by pachyostosis and osteosclerosis (Houssaye, 2013a, 2013b).

Pachyostosis is the condition where the bones get thicker and more massive. These thick bones have a much higher mass than those of terrestrial animals, thus increasing an animal's density and achieving neutral buoyancy. This feature is common to many ophidiomorphs (*Carentonosaurus, Adriosaurus, Pontosaurus,* pachyophiid snakes), and possibly some Aigialosaurs (*Aigialosaurus, Haasiasaurus, Carsosaurus, Komensaurus*) (Houssaye, 2013b). In the fossil record, this feature is convergent in choristoderes, mesosaurs, and ophidiomorphs (Houssaye and Bardet, 2012; Nakajima et al., 2014; Houssaye et al., 2015).

Osteosclerosis is where the bones stay the same size, but get much denser through the deposition of minerals in the inner cavities. This is also a feature that is fairly common to basal pythonomorohs (e.g., *Komensaurus, Haasiasaurus, Pontosaurus, Acteosaurus*).

Homeostasis

Osmoregulation—Maintain an osmotic (salt and water) balance within the body requires specific adaptations in an environment made up of nothing but salt water. Every time these animals eat underwater, a large amount of salt is absorbed by the body. Even though salt is an essential mineral for their bodies, the concentrations in saltwater are too high for most terrestrial animals to process and excrete, causing dehydration and death. Thus, secondarily marine amniotes must evolve adaptations that enable them to safely process the extra salt they ingest.

Most modern marine amniotes (sea turtles, marine iguanas, saltwater crocodiles, penguins, and some seabirds) have independently evolved a special salt gland in their heads which concentrate salt from the blood so that it can be expelled passively.

The marine iguana has salt glands above their eyes that are connected to their nostrils, and they forcibly remove the salt from their salt glands by sneezing.

Fossil evidence for a soft tissue structure such as a salt gland is rare, but has been recorded. *Geosaurus* is a marine thalattosuchian, a fully aquatic lineage of crocodylomorph from the Jurassic and Cretaceous. One *Geosaurus* specimen preserves natural casts of a lobed structure within the orbits, and these structures are the right shape and in the right position to represent the salt glands (Fernández and Gasparini, 2007). Personal communication with H. Street (2016) and observation of mosasaur skulls supports the presence of a similar structure in mosasaurines.

Thermoregulation—Compared to air, water is an extremely good heat conductor. It move conducts heat roughly 24 times as fast, which means that marine amniotes need adaptations to thermoregulate if they need to maintain a body temperature above that of the ambient water. It is for this reason that all extant aquatic squamates are all tropical in distribution. However, Cretaceous squamate fossils from the Antarctic indicate that some lineages of derived mosasaurs were able to tolerate colder water temperatures. Since these animals were active predators (Konishi et al., 2014), their metabolism must have been functioning at a high enough temperature for their muscles to be capable of pursuit and capture, indicting thermoregulatory capabilities.

Since mosasaurs must be able to maintain a certain temperature within their muscles, then they must have either been gigantothermic (big enough that their surface area to volume ratio limited heat loss) or at least partially endothermic (producing their own heat). Isotope research favors the latter, with mosasaur isotope values falling between that of a poikilothermic fish and endothermic pelagic seabirds (Bernard et al., 2010; Harrell et al., 2016).

Sensation

The density of water affects light and sound much differently than air. This often results in a change in the senses that aquatic amniotes rely on in the water.

Sight— The properties of water affect how light behaves in three main ways. First, the greater density of the water causes light to bend less than it would in air, making things seem closer than they are. Second, light gets absorbed by water molecules and scattered by suspended particles. This means that light doesn't travel as far as it does in air, resulting in a restricted visual range. Finally, water acts like a light filter, stripping away greater portions of the visible spectrum of light with increasing depth. Warm colors like red and orange barely penetrate the water at all, while greens and blues penetrate deepest. Only 50% of light is able to penetrate to 10 metres, only 12.5% by 30 metres, and by 200 metres, there is total darkness.

Though not as proportionately large as ichthyosaurs, mosasaurs still had fairly large eyes that were probably useful for seeing in dimly lit waters. Like ichthyosaurs, mosasaurs had sclerotic rings (Russell, 1967), which support the eyeball and change its shape in order to focus the eye. The large eyes faced laterally from the head, giving the mosasaur a wide range of vision, but would have prevented binocular vision and limited depth perception (except for *Phosphorosaurus ponpetelegans*; Konishi et al., 2015).

In addition to adaptations to help them see, mosasaurs also developed adaptations to prevent being seen in water. Some exceptionally well preserved specimes of mosasaur squamation preserve some of their pigment, showing bands of dark and light shading over their bodies (Lindgren et al., 2010, 2014). Similar patterns in modern animals such as tiger sharks help to break up the light hitting the animal, making them harder to see and therefore better ambush predators.

Sound—Hearing underwater, unlike sight, functions better than it does on land. Sound travels more efficiently through higher density mediums, traveling much farther, and up to 5 times faster in seawater than in air. On land, sound vibrations strike the amniote eardrum through an air-filled, outer ear canal. But when a typical terrestrial animal is submerged, water fills the ear canal, decreasing the ability to hear. Underwater, it is much more common to pick up the vibrations caused by sound through the skull bones, a phenomenon called bone conduction.

There is evidence that Cretaceous squamates improved upon this type of sound conduction with adaptations to the middle ear. The evolution of large bony plates derived from the extracolumella in the ears of mosasaurs (e.g., as in *Platecarpus tympaniticus;* Konishi et al., 2012) facilitates the detection of sounds using bone conduction. The hard, cone shaped bony formation is derived from the extracolumella, and sat within the quadrate, where the eardrum is located in their terrestrial relatives. This cone shaped plate would have picked up sound in the water, focused it, and directed it towards the inner ear far more effectively than the skull bones. The plates transmit sound to the inner ear with less distortion and also allow the animal to detect the direction that the sound came from. This is convergent with cetaceans, who develop a conch-like tympanic bone.

CONCLUSION:

Mosasaurs evolved relatively quickly from small shore-dwelling lizards into the dominant marine predators of Earth's oceans. Their adaptations to life in the ocean included major modifications to the axial skeleton and limbs, including a long body and tail with a heterocercal fin, and strong flippers in a variety of shapes. Mosasaurs also had small scales covering their body that decreased drag and may have had shading that made them hard to see. With acute senses of hearing and sight, not much would have escaped these supremely well adapted predators, the undisputed rulers of the late Cretaceous seas.

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GENERAL CONCLUSION TO THESIS

To date, 150 years of study on Cretaceous marine squamates (Chapter 1) has resulted in the hypothesis that dolichosaurs, aigialosaurs, mosasaurs, and ophidians are closely related, and united within the Pythonomorpha. However, the interrelationships among these fossil assemblages remained untested. This thesis represents the first critical review of the anatomy, phylogeny, and paleoecology of Pythonomorpha as a whole. Previous studies have addressed subsets of the Pythonomorpha, but none have performed a rigorous analysis of all these lineages together.

My description of the dolichosaur *Pontosaurus ribaguster* (Chapter 2) expands the current knowledge of dolichosaur diversity. Identifiable nektonic teleost remains in the abdominal cavity provide strong evidence for a pisciverous diet in dolichosaurs.

My description of the new basal mosasauroid *Portunatasaurus krambergi* (Chapter 3) represents an unrealized diversity of small pythonomorph lizards in the Turonian. The forelimb preserves an intermediate anatomy between terrestrial anguimorphs and derived mosasaurs. It suggests that the 'mosasaurine' paddle evolved earlier in the lineage than previously thought.

The reassessment of *Aphanizocnemus libanensis* (Chapter 4) removes this problematic and confounding taxa from the Dolichosauridae, Varanoidea, and Anguimorpha. It is reassigned to the Scincogekkonomorpha, and represents the first aquatic taxon for the group.

Using the new data from chapters two and three, and removing the confounding presences of *Aphaniocnemus,* I performed my own analysis of pythonomorph interrelationships (Chapter 5). Results support that the Aigialosauridae (inclusive of derived 'mosasaurs') is a monophyletic lineage from within which the hydropedal condition evolved at least twice. The results show weaker support for dolichosaurs as a non-monophyletic group that form successive sister taxa to snakes. The relationship between mosasauroids (Aigialosauridae) and ophidiomorphs is less conclusive, recovering the ophidiomorph lineage as arising from within the Mosasauroidea, most often as a sister group to the Mosasaurinae.

A review of in the paleogeographic distributions of non-ophidian ophidiomorphs (Chapter 6) shows that they were a geographically widespread, and temporally long-lived group of lizards. Two hypotheses Early Cretaceous origins include a Tethyan or Pacific origin. A large radiation resulted in peak diversity in the Cenomanian, which was curbed by an extinction event at the Cenomanian-Turonian boundary. During the latest Cretaceous, dolichosaurs persisted in Europe and North America, and may have expanded their range to South America by the end of the Cretaceous, before the Cretaceous-Paleogene event caused their extinction.

My review of aquatic adaptations in Cretaceous squamates (Chapter 7) demonstrates that the high selective pressure of the aquatic environment resulted in aquatically derived features that are extremely convergent among the sister lineages of the Pythonomorpha, and with other aquatic amniote groups. Though the ecological roles and habitats of pythonomorphs was varied (reef, shallow marine shelf, delta, river, open ocean), all of these animals were well adapted to the environment, and possessed a suite of aquatic adaptations modified to their particular habitats and niches.

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APPENDIX 1: CHACTER LIST

Description of characters used in phylogenetic analysis. All characters are treated as unordered and without weight assumptions. The numbers in brackets refer to character number as listed by Simões (et al., 2017).

See edits to character 93, and 94 (**bolded**).

(1) Premaxilla predental rostrum I: total lack of a bony rostrum (0); or presence of any predental rostrum (1). In lateral profile, the anterior end of the premaxilla either exhibits some bony anterior projection above the dental margin, or the bone recedes posterodorsally from the dental margin. State 1 produces a relatively taller lateral profile with an obvious 'bow' or 'prow.'

(2) Premaxilla predental rostrum II: rostrum very short and obtuse (0); or distinctly protruding (1); or very large and inflated (2). In *Clidastes* a short, acute, protruding rostrum (state 1) produces a 'V'-shaped dorsal profile and, as far as is known, is peculiar to that genus. An alternative condition, described as 'U'- shaped, includes those taxa whose rostral conditions span the whole range of states of characters 1 and 2. Hence, the descriptive character is abandoned in favor of a more informative structure-based series.

(3) Premaxilla shape: bone broadly arcuate anteriorly (0); or relatively narrowly arcuate or acute anteriorly (1). In virtually all lizards the premaxilla is a very widely arcuate and lightly constructed element, and the base of the internarial process is quite narrow as in Aigialosaurus bucchichi. All other mosasaurids have a very narrowed premaxilla with the teeth forming a tight curve and the internarial process being proportionally wider (state 1). *Tethysaurus* was recoded

as having state 0.

(4) Premaxilla internarial bar width: narrow, distinctly less than half of the maximum width of the rostrum in dorsal view (0); or wide, being barely narrower than the rostrum (1). *Aigialosaurus* was recoded as having state 0.

(5) Premaxilla internarial bar base shape: triangular (0); or rectangular (1). A vertical cross-section through the junction of the internarial bar and the dentigerous rostrum produces an inverted triangle in most taxa. But in state 1, this cross-section is transversely rectangular because the broad ventral surface of the bar is planar.

(6) Premaxilla internarial bar dorsal keel: absent (0); or present (1). In state 1 a ridge rises above the level of a normally smoothly continuous transverse arch formed by the bones of the anterior muzzle.

(7) Premaxilla internarial bar venter: with entrance for the fifth cranial nerve close to rostrum (0); or far removed from rostrum (1). The conduit that marks the path of the fifth cranial nerve from the maxilla into the premaxilla is expressed as a ventrolateral foramen within the premaxillo-maxillary sutural surface at the junction of the internarial bar and the dentigerous rostrum. State 1 includes a long shallow groove on the ventral surface of the bar. Anteriorly, this groove becomes a tunnel entering the bone at an extremely shallow angle, but disappearing below the surface at least 1 cm behind the rostrum.

(8) Frontal shape in front of the orbits: sides sinusoidal (0); or bone nearly triangular and sides relatively straight (1). In state 1, the area above the orbits is expanded and an isosceles triangle is formed by the rectilinear sides. In certain taxa, a slight concavity is seen above the orbits, but anterior and posterior to this, there is no indication of a sinusoidal or recurved edge.

(9) Frontal width: element broad and short (0); intermediate dimensions (1); or long and narrow (2). Mosasauroid frontals can be separated into a group that generally has a maximum length to maximum width ratio greater than 2:1 (state 2), between 1.5:1 and 2:1 (state 1), or equal to or less than 1.5:1 (state 0).

(10) Frontal narial emargination: frontal not invaded by posterior end of nares (0); or distinct embayment present (1). In some mosasauroids, the posterior ends of the nares are concomitant with the anterior terminus of the frontal-prefrontal suture and, therefore, there is no marginal invasion of the frontal by the opening. However, in other mosasauroids this suture begins anterior and lateral to the posterior ends of the nares, causing a short emargination into the frontal.

(11) Frontal midline dorsal keel: absent (0); or low, fairly inconspicuous (1); or high, thin, and well-developed (2).

(12) Frontal ala shape: sharply acuminate (0); or more broadly pointed or rounded (1). In state 0, the anterolateral edge of the ala is smoothly concave, thus helping to form the sharply pointed or rounded and laterally oriented posterior corners. In some forms the anterolateral edge of the ala may be concave, but the tip is not sharp and directed laterally.

(13) Frontal olfactory canal embrasure: canal not embraced ventrally by descending processes (0); or canal almost or completely enclosed below (1). In state 1, very short descending processes from the sides of the olfactory canal surround and almost, or totally, enclose the olfactory nerve.

(14) Frontal posteroventral midline: tabular boss immediately anterior to the frontal-parietal suture absent (0); or present (1). A triangular boss with a flattened ventral surface at the posterior end of the olfactory canal is represented by state 1.

(15) Frontal-parietal suture: apposing surfaces with low interlocking ridges (0); or with overlapping flanges (1). In state 0, an oblique ridge on the anterior sutural surface of the parietal intercalates between a single median posterior and a single lateral posterior ridge from the frontal. In state 1, these ridges are protracted into strongly overlapping flanges. The dorsal trace of the suture can be quite complex with a portion of the parietal embraced by the posterior extension of these frontal flanges.

(16) Frontal-parietal suture overlap orientation: suture with oblique median frontal and parietal ridges contributing to overlap (0); or with all three ridges almost horizontal (1). In state 0, the median ridge from the frontal and the single parietal ridge are oriented at a distinct angle to the upper skull surface while the outer, or lateral, frontal ridge appears to be nearly horizontal. In *Tylosaurus nepaeolicus* and T. *proriger* (state 1), the obliquity of the intercalating ridges is reclined almost to the horizontal, greatly extending the amount of lateral overlap.

(17) Frontal invasion of parietal I: lateral sutural flange of frontal posteriorly extended (0); or median frontal sutural flange posteriorly extended (1); or both extended (2); or suture straight (3). In all mosasaurines the oblique median frontal sutural ridge extends onto the dorsal surface of the parietal table and embraces a portion of the anterior table within a tightly crescentic midline embayment. In *Plioplatecarpus* and *Platecarpus*, the lateral oblique sutural ridge from the frontal is greatly protracted posteriorly to cause a large, anteriorly convex embayment in the dorsal frontal-parietal suture. In this case the entire posterolateral corner of the frontal is extended backwards to embrace the anterolateral portion of the parietal table on both sides. Consequently, the parietal foramen is very widely embraced laterally and the oblique anterior sutural ridge of the parietal occupies a position inside the embayment within the frontal. *Dallasaurus* was recoded as ?.

(18) Frontal medial invasion of parietal II: if present, posteriorly extended median sutural flange short (0); or long (1). The median oblique sutural flange is either short, not reaching back to the parietal foramen (state 0), or tightly embraces the foramen while extending backwards to a position even with or beyond its posterior edge (state 1).

(19) Parietal length: dorsal surface relatively short with epaxial musculature insertion posterior, between suspensorial rami only (0); or dorsal surface elongate, with epaxial musculature insertion dorsal as well as posterior (1).

(20) Parietal table shape: generally rectangular to trapezoidal, with sides converging, but not meeting (0); or triangular, with sides contacting in front of suspensorial rami (1); or triangular table with posterior portion forming parasagittal crest or ridge (2).

(21) Parietal foramen size: relatively small (0); or large (1). If the foramen is smaller than or equal to the area of the stapedial pit, it is considered small. If the foramen is significantly larger or if the distance across the foramen is more than half the distance between it and the nearest edge of the parietal table, the derived state is achieved.

(22) Parietal foramen position I: foramen generally nearer to center of parietal table, well away from frontal-parietal suture (0); or close to or barely touching suture (1); or huge foramen straddling suture and deeply invading frontal (2). Generally in state 1, the distance from the foramen to the suture is about equal to or less than one foramen's length.

(23) Parietal foramen ventral opening: opening is level with main ventral surface (0); or opening surrounded by a rounded, elongate ridge (1).

(24) Parietal posterior shelf: presence of a distinct horizontal shelf projecting posteriorly from

between the suspensorial rami (0); or shelf absent (1). In some mosasauroids, a somewhat crescent-shaped shelf (in dorsal view) lies at the posterior end of the bone medial to, and below, the origination of the suspensorial rami.

(25) Parietal suspensorial ramus compression: greatest width vertical or oblique (0); or greatest width horizontal (1). In *Tylosaurus*, the anterior edge of the ramus begins very low on the lateral wall of the descending process, leading to formation of a proximoventral sulcus, but the straps are horizontal distally.

(26) Parietal union with supratemoral: suspensorial ramus from parietal overlaps supratemporal without interdigitation (0); or forked distal ramus sandwiches proximal end of supratemporal (1).

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

(28) Prefrontal contact with postorbitofrontal: no contact at edge of frontal (0); of elements in contact there (1). State 1 is usually described as the frontal being emarginated above the orbits. Often this character can be evaluated by examining the ventral surface of the frontal where depressions outline the limits of the sutures for the two ventral elements.

(29) Prefrontal-postorbitofrontal overlap: prefrontal overlapped ventrally by postorbitofrontal (0); or prefrontal overlapped laterally (1). Postorbitofrontal ventral overlap of the prefrontal is extreme in Platecarpus tympaniticus and

Plioplatecarpus, such that there is even a thin flange of the frontal interjected between the prefrontal above and the postorbitofrontal below. In *T. proriger*, the postorbitofrontal sends a long narrow process forward to fit into a lateral groove on the prefrontal. In *Plesiotylosaurus*, the overlap is relatively short and more oblique, and there is no groove on the prefrontal.

(30) Postorbitofrontal shape: narrow (0); or wide (1). In *Clidastes* and the *Globidensini*, the lateral extent of the element is almost equal to half of the width of the frontal and the outline of the bone is basically squared.

(31) Postorbitofrontal transverse dorsal ridge: absent (0); or present (1). In state 1, an inconspicuous, low, and narrowly rounded ridge traces from the anterolateral corner of the parietal suture across the top of the element to disappear behind the origin of the jugal process.

(32) Maxilla tooth number: 20–24 (0); or 17–19 (1); or 15–16 (2); 12–14 (3).

(33) Maxillo-premaxillary suture posterior terminus: suture ends above a point that is anterior to or level with the midline of the fourth maxillary tooth (0); or between the fourth and ninth teeth (1); or level with or posterior to the ninth tooth (2). These somewhat arbitrary divisions of the character states are meant to describe in more concrete terms those sutures that terminate far anteriorly, those that terminate less anteriorly, and those that terminate near the midlength of the maxilla, respectively.

(34) Maxilla posterodorsal process: recurved wing of maxilla dorsolaterally overlaps a portion of the anterior end of the prefrontal (0); or process absent (1).

(35) Maxilla posterodorsal extent: recurved wing of maxilla prevents emargination of prefrontal on dorsolateral edge of external naris (0); or does not (1).

(36) Jugal posteroventral angle: angle very obtuse or curvilinear (0); or slightly obtuse, near 120° (1); or 90° (2). *Aigialosaurus* was recoded as having state 1, *Russellosaurus* and *Tethysaurus* were recoded as having state 2.

(37) Jugal posteroventral process: absent (0); or present (1).

(38) Ectopterygoid contact with maxilla: present (0); or absent (1).

(39) Pterygoid tooth row elevation: teeth arise from robust, transversely flattened, main shaft of pterygoid (0); or teeth arise from thin pronounced vertical ridge (1). In state 0, the teeth emanate from the relatively planar surface of the thick, slightly dorsoventrally compressed main shaft of the pterygoid. In state 1, a tall, thin dentigerous ridge emanates ventrally from a horizontal flange that forms the base of the quadratic ramus and the ectopterygoid process, thus causing the main shaft to be trough-shaped. Although the outgroup we selected (*Varanus*) does not possess pterygoid teeth we decided to code the primitive condition as state 0 because that is the condition observed in fossil varanoids like *Ovoo gurval* and basal anguimorphs like *Ophisaurus apodus*.

(40) Pterygoid tooth size: anterior teeth significantly smaller than marginal teeth (0); or anterior teeth large, approaching size of marginal teeth (1). As per the argument discussed for character 40 we coded the outgroup as having state 0.

(41) Quadrate suprastapedial process length: process short, ends at a level well above midheight (0); or of moderate length, ending very near midheight (1); or long, distinctly below midheight (2); suprastapedial process absent (3). *Russellosaurus* was recoded as having state 2.

(42) Quadrate suprastapedial process constriction: distinct dorsal constriction (0); or virtually no dorsal constriction (1). Lack of constriction results in an essentially parallel-sided process in posterodorsal view, but can also include the tapering form characteristic of some *Tylosaurus*.

(43) Quadrate suprastapedial ridge: if present, ridge on ventromedial edge of suprastapedial process indistinct, straight and/or narrow (0); or ridge wide, broadly rounded, and curving

downward, especially above stapedial pit (1).

(44) Quadrate suprastapedial process fusion: no fusion present (0); or process fused to, or in extensive contact with, elaborated process from below (1). A posterior rugose area may be inflated and broadened mediolaterally to partially enclose the ventral end of a broad and elongate suprastapedial process as in *Halisaurus*. In *Globidens*, *Prognathodon*, and *Plesiotylosaurus*, the process is fused ventrally to a narrow pedunculate medial extension of the tympanic rim. A similar condition is present in *Ectenosaurus*, except that the tympanic rim is not medially extended and has a short projection that overlaps a portion of the suprastapedial process posteriorly.

(45) Quadrate stapedial pit shape: pit broadly oval to almost circular (0); or relatively narrowly oval (1); or extremely elongate with a constricted middle (2). In state 0, the length to width ratio is less than 1.8:1; in state 1 it ranges from 1.8:1 to 2.4:1; and in state 2, it is greater than 2.4:1.

(46) Quadrate posteroventral ascending tympanic rim condition: ascending ridge small or absent (0); or a high, elongate triangular crest (1); or a crest extremely produced laterally (2). In state 1, this extended rim causes a fairly deep sulcus in the ventral portion of the intratympanic cavity. In *Plioplatecarpus*, the entire lower tympanic rim and ala are expanded into a large conch (state 2), which tremendously increases the depth of the intratympanic cavity.

(47) Quadrate ala thickness: ala thin (0); or thick (1). In state 0, the bone in the central area of the ala is only about 1 mm thick in medium-sized specimens and that area is usually badly crushed or completely destroyed. Alternatively, the ala extends from the main shaft with only minor thinning, providing a great deal of strength to the entire bone. *Tethysaurus* was recoded as having state 0.

(48) Quadrate conch: ala and main shaft encompassing a deeply bowled area (0); or alar concavity shallow (1). A relatively deeper sulcus in the anterior part of the intratympanic cavity and more definition to the ala and the main shaft are features of state 0. *Tethysaurus* was recoded as having state 0.

(49) Basisphenoid pterygoid process shape: process relatively narrow with articular surface facing mostly anterolaterally (0); or somewhat thinner, more fan- shaped with a posterior extension of the articular surface causing a more lateral orientation (1).

(50) Quadrate ala groove: absent (0); or long, distinct, and deep groove present in anterolateral edge of ala (1); or groove along dorsal margin of quadrate ala (2).

(51) Quadrate median ridge: single thin, high ridge, dorsal to ventral (0); or ridge low and rounded with divergent ventral ridges (1).

(52) Quadrate anterior ventral condyle modification: no upward deflection of anterior edge of condyle (0); or distinct deflection present (1). A relatively narrow bump in the otherwise horizontal trace of the anterior articular edge is also supertended by a sulcus on the anteroventral face of the bone.

(53) Quadrate ventral condyle: condyle saddle-shaped, concave in anteroposterior view (0); or gently domed, convex in any view (1).

(54) Basioccipital tubera size: short (0); or long (1). Long tubera are typically parallel-sided in posterior profile and protrude ventrolaterally at exactly 45° from horizontal. Short tubera have relatively large bases that taper distally, and emanate more horizontally.

(55) Basioccipital tubera shape: tubera not anteroposteriorly elongate (0); or anteroposteriorly

elongate with rugose ventrolateral surfaces (1).

(56) Basioccipital canal: absent (0); or present as a pair separated by a median septum (1); or present as a single bilobate canal (2).

(57) Dentary tooth number: 20–24 (0); 17–19 (1); 15–16 (2); 14 (3); 13 (4); 12 (5). It is easy to assume this character is correlated with the number of maxillary teeth, except that is not the case in *Ectenosaurus clidastoides*, which has 16 or 17 maxillary teeth and only 13 dentary teeth.

(58) Dentary anterior projection: projection of bone anterior to first tooth present (0); or absent (1).

(59) Dentary anterior projection length: short (0); or long (1). In state 1, the projection of bone anterior to the first tooth is at least the length of a complete tooth space. *Russellosaurus* was recoded as not applicable.

(60) Dentary medial parapet: parapet positioned at base of tooth roots (0); or elevated and strap-like, enclosing about half of height of tooth attachment in shallow channel (1), or strap equal in height to lateral wall of bone (2). States 1 and 2 are possible sequential stages of modification from a classically pleurodont dentition to the typical mosasaur ‘sub-thecodont’ dentition. *Tethysaurus* was recoded as ?.

(61) Splenial-angular articulation shape: splenial articulation in posterior view almost circular (0); or laterally compressed (1).

(62) Splenial-angular articular surface: essentially smooth concavoconvex surfaces (0); or distinct horizontal tongues and grooves present (1).

(63) Coronoid shape: coronoid with slight dorsal curvature, posterior wing not widely fan-shaped

(0); or very concave above, posterior wing greatly expanded (1). *Ectenosaurus* was recoded as having state 0.

(64) Coronoid posteromedial process: small but present (0); or absent (1). *Russellosaurus* was recoded as having state 0, *Ectenosaurus* was recoded as having state 1.

(65) Coronoid medial wing: does not reach angular (0); or contacts angular (1). *Aigialosaurus* was recoded as ?.

(66) Coronoid posterior wing: without medial crescentic pit (0); or with distinct excavation (1). In state 1, there is a posteriorly open, ‘C’-shaped excavation in the medial side of the posterior wing of this element. *Dallasaurus* was recoded as ?.

(67) Surangular coronoid buttress: low, thick, about parallel to lower edge of mandible (0); or high, thin, rapidly rising anteriorly (1). A rounded dorsal edge of the surangular remains almost parallel to the ventral edge as it approaches the posterior end of the coronoid, meeting the latter element near its posteroventral edge in state 0. In state 1, the dorsal edge rises and thins anteriorly until meeting the posterior edge of the coronoid near its apex, producing a triangular posterior mandible in lateral aspect.

(68) Surangular-articular suture position: behind the condyle in lateral view (0); or at middle of glenoid on lateral edge (1); anterior to condyle (2). In state 1, there is usually an interdigitation in the dorsal part of the suture. *Aigialosaurus dalmaticus* was rescored as 2.

(69) Surangular-articular lateral suture trace: suture descends and angles or curves anteriorly (0); or is virtually straight throughout its length (1). In state 1, the suture trails from the glenoid posteriorly about halfway along the dorsolateral margin of the retroarticular process, then

abruptly turns anteriorly off the edge and strikes in a straight line for the posterior end of the angular.

(70) Articular retroarticular process inflection: moderate inflection, less than 60º (0); or extreme inflection, almost 90º (1).

(71) Articular retroarticular process innervation foramina: no large foramina on lateral face of retroarticular process (0); or one to three large foramina present (1).

(72) Tooth surface I: teeth finely striate medially (0); or not medially striate (1). In "Russellosaurinae," medial tooth striations are very fine and groups of tightly spaced striae are usually set apart by facets, leading to a fasciculate appearance. *Angolasaurus* was recoded as ?, *Aigialosaurus* was recoded as having state 1.

(73) Tooth surface II: teeth not coarsely textured (0); or very coarsely ornamented with bumps and ridges (1). In both species of *Globidens* and in *Prognathodon overtoni*, the coarse surface texture is extreme, consisting of thick pustules, and vermiform or anastomosing ridges. Teeth in *P. rapax* are smooth over the majority of their surface, but usually a few widely scattered, large, very long, sharp-crested vermiform ridges are present.

(74) Tooth facets: absent (0); or present (1). *Halisaurus* teeth are smoothly rounded except for the inconspicuous carinae. *Clidastes* is described in numerous places as having smooth unfaceted teeth, but many immature individuals and some larger specimens have teeth with three distinct facets on the medial faces. Adult *Tylosaurus* proriger has indistinct facets. *Mosasaurus* has taken this characteristic to the extreme. *Russellosaurus*, *Tethysaurus*, *Angolasaurus*, *Ectenosaurus*, *Platecarpus* (*P. planifrons* and *P. tympaniticus*), and *Plioplatecarpus* have been recoded as having state 0.

(75) Tooth fluting: absent (0); or present (1). In *Ectenosaurus*, and some *Platecarpus planifrons*, several broadly rounded vertical ridges alternate with shallow, round-bottomed grooves completely around the teeth. *Tethysaurus* was recoded as having both states 0 and 1, because grooves can be observed in larger specimens. *Angolasaurus* was recoded as having state 1.

(76) Tooth inflation: crowns of posterior marginal teeth conical, tapering throughout (0); or crowns of posterior marginal teeth swollen near the tip or above the base (1).The rear teeth of *Globidens* and *Prognathodon overtoni* are distinctly fatter than other mosasauroid teeth, but those of *P. rapax* are also swollen immediately distal to the base.

(77) Tooth carinae I: absent (0); or present but extremely weak (1); or strong and elevated (2). *Halisaurus* exhibits the minimal expression of this character (state 1) in that its marginal teeth are almost perfectly round in cross-section; the carinae are extremely thin and barely stand above the surface of the teeth.

(78) Tooth carinae serration: absent (0); or present (1).

(79) Tooth replacement mode: replacement teeth form in shallow excavations (0); or in subdental crypts (1). All mosasauroids that can be evaluated have an ‘anguimorph’ type of tooth replacement, which is to have interdental positioning of replacement teeth and resorption pits associated with each. *Angolasaurus* was recoded as ?.

(80) Atlas neural arch: notch in anterior border (0); or no notch in anterior border (1). *Dallasaurus* was recoded as ?.

(81) Atlas synapophysis: extremely reduced (0); or large and elongate (1). In state 1, a robust synapophysis extends well posteroventral to the medial articular surface for the atlas centrum,

and it may be pedunculate (*Clidastes*) or with a ventral ‘skirt’ that gives it a triangular shape (*Mosasaurus*). A very small triangular synapophysis barely, if at all, extends posterior to the medial articular edge in state 0.

(82) Zygosphenes and zygantra: absent (0); or present (1). This character assesses only the presence of zygosphenes and zygantra, not their relative development. Nonfunctional and functional are considered as present. Although the outgroup we selected (*Varanus*) does not possess zygosphene and zygantra we decided to code the primitive condition as present because these structures can be observed in primitive varanoids like *Saniwa*.

(83) Zygosphene and zygantra number: present on many vertebrae (0); or present on only a few (1). As per the argument discussed for character 84 we coded the outgroup as having state 0.

(84) Hypapophyses: last hypapophysis occurs on or anterior to seventh vertebra (0); or on eight or posteriorly (1).

(85) Synapophysis height: facets for rib articulations tall and narrow on posterior cervicals and anterior trunk vertebrae (0); or facets ovoid, shorter than the centrum height on those vertebrae (1).

(86) Synapophysis length: synapophyses of middle trunk vertebrae not laterally elongate (0); or distinctly laterally elongate (1). The lateral extension of the synapophyses from the middle of the trunk is as much as 70–80% of the length of the same vertebra is represented by state 1.

(87) Synapophysis ventral extension: synapophyses extend barely or not at all below ventral margin of cervical centra (0); or some extend far below ventral margin of centrum (1). In state 1, two or more anterior cervical vertebrae have rib articulations that dip well below the centrum,

causing a very deeply concave ventral margin in anterior profile.

(88) Vertebral condyle inclination: condyles of trunk vertebrae inclined (0); or condyles vertical (1).

(89) Vertebral condyle shape I: condyles of anterior-most trunk vertebrae extremely dorsoventrally depressed (0); or essentially equidimensional (1). In state 0, posterior height: width ratios of anterior trunk vertebrae are close to 2:1. In state 1, they are between to 4:3 and 1:1.

(90) Vertebral condyle shape II: condyles of posterior trunk vertebrae not higher than wide (0); or slightly compressed (1). In state 1, the posterior condylar aspect reveals outlines that appear to be higher than wide and even perhaps slightly subrectangular, due to the slight emargination for the dorsal nerve cord.

(91) Vertebral synapophysis dorsal ridge: sharp ridge absent on posterior trunk synapophyses (0); or with a sharp-edged and anteriorly precipitous ridge connecting distal synapophysis with prezygapophysis (1). In state 0, the ridge in question, if present, may be incomplete or it may be rounded across the crest with the anterior and posterior sides about equally sloping.

(92) Vertebral length proportions: cervical vertebrae distinctly shorter than longest vertebrae (0); or almost equal or are the longest (1).

(93) Presacral vertebrae number I: relatively few, **38** [changed from ‘32’] or less (0); or numerous, 39 or more (1). Here, presacral vertebrae are considered to be all those anterior to the first bearing an elongate transverse process.

(94) Presacral vertebrae number II: if **fewer than 32** [changed from ‘if few’], then 28 or 29 (0);

30 or 31 (1).

(95) Sacral vertebrae number: two (0); or less than two (1). Numerous well preserved specimens of derived mosasauroids have failed to show any direct contact of the pelvic girdle with vertebrae in the sacral area. Certainly, no transverse processes bear any type of concave facet for the ilium, and so it is generally assumed that a ligamentous contact was established with only one transverse process. Depending on one's perspective, it could be said that derived mosasauroids have either no or one sacral vertebra.

(96) Caudal dorsal expansion: neural spines of tail all uniformly shortened posteriorly (0); or several spines dorsally elongated behind middle of tail (1). *Dallasaurus* was recoded as ?.

(97) Haemal arch length: haemal arches about equal in length to neural arch of same vertebra (0); or length about 1.5 times greater than neural arch length (1). This ratio may be as great as 1.2:1 in state 0. Comparison is most accurate in the middle of the tail and is consistent even on those vertebrae in which the neural spines are also elongated.

(98) Haemal arch articulation: arches articulating (0); or arches fused to centra (1).

(99) Tail curvature: no structural downturn of tail (0); or tail with curved posterior portion (1).

(100) Body proportions: head and trunk shorter than or about equal to tail length (0); or head and trunk longer than tail (1).

(101) Scapula/coracoid size: both bones about equal (0); or scapula about half the size of coracoid (1). *Dallasaurus* was recoded as ?.

(102) Scapula width: no anteroposterior widening (0); or distinct fan-shaped widening (1); or extreme widening (2). In state 0, the anterior and posterior edges of the scapula encompass less

than one quarter of the arc of a circle, but in state 1, the arc is increased to approximately one third. In state 2, the distal margin encompasses almost a half-circle and the anterior and posterior borders are of almost equal length.

(103) Scapula dorsal convexity: if scapula widened, dorsal margin very convex (0); or broadly convex (1). In state 0, the anteroposterior dimension is almost the same as the proximodistal dimension. In state 1, the anteroposterior dimension is much larger.

(104) Scapula posterior emargination: posterior border of bone gently concave (0); or deeply concave (1). In state 1, there is a deeply arcuate emargination on the posterior scapular border, just dorsal to the glenoid. It is immediately bounded dorsally by a corner, which begins a straight-edged segment that continues to the dorsal margin.

(105) Scapula-coracoid suture: unfused scapula-coracoid contact has interdigitate suture anteriorly (0); or apposing surfaces without interdigitation (1). *Dallasaurus* was recoded as ?.

(106) Coracoid neck elongation: neck rapidly tapering from medial corners to a relatively broad base (0); or neck gradually tapering to a relatively narrow base (1); coracoid neck absent (2). In state 1, this character describes an outline of the bone, which is nearly symmetrical and gracefully fan-shaped, with gently concave, nearly equidistant sides.

(107) Coracoid anterior emargination: present (0); or absent (1).

(108) Humerus length: humerus distinctly elongate, about three or more times longer than distal width (0); or greatly shortened, about 1.5 to 2 times longer than distal width (1); or length and distal width virtually equal (2); or distal width slightly greater than length (3).

(109) Humerus postglenoid process: absent or very small (0); or distinctly enlarged (1).

(110) Humerus glenoid condyle: if present, condyle gently domed and elongate, ovoid in proximal view (0); or condyle saddle-shaped, subtriangular in proximal view and depressed (1); or condyle highly domed or protuberant and short ovoid to almost round in proximal view (2). In some taxa, the condylar surfaces of the limbs were finished in thick cartilage and there was no bony surface of the condyle to be preserved. This condition is scored as not represented. In some taxa, the glenoid condyle extends more proximally than does the postglenoid process (state 2), and it is not ovoid as state 0. *Dallasaurus* was recoded as having state 0.

(111) Humerus deltopectoral crest: crest undivided (0); or split into two separate insertional areas (1). In state 1, the deltoid crest occupies an anterolateral or anterior position confluent with the glenoid condyle, while the pectoral crest occupies a medial or anteromedial area that may or may not be confluent with the glenoid condyle. The deltoid crest is often quite short, broad, and indistinct, being easily erased by degradational taphonomic processes.

(112) Humerus pectoral crest: located anteriorly (0); or medially (1). In state 1, the pectoral crest is located near the middle of the flexor (or medial) side on the proximal end of the bone.

(113) Humerus ectepicondylar groove: groove or foramen present on distolateral edge (0); or absent (1).

(114) Humerus ectepicondyle: absent (0); or present as a prominence (1). A radial tuberosity is reduced in size in *Prognathodon*, but very elongated in *Plesiotylosaurus*. *Tethysaurus* was recoded as having state 0.

(115) Humerus entepicondyle: absent (0); or present as a prominence (1). The ulnar tuberosity protrudes posteriorly and medially from the posterodistal corner of the bone immediately proximal to the ulnar facet, causing a substantial dilation of the posterodistal corner of the

humerus. *Tethysaurus* was recoded as having state 0.

(116) Radius shape: radius not expanded anterodistally (0); or slightly expanded (1); or broadly expanded (2).

(117) Ulna contact with centrale: broad ulnare prevents contact (0); or ulna contacts centrale (1). In state 1, the ulnare is omitted from the border of the antebrachial foramen. There is usually a well-developed faceted articulation between the ulna and the centrale (or intermedium, as used by Russell, 1967).

(118) Radiale size: large and broad (0); or small to absent (1).

(119) Carpal reduction: carpals number six or more (0); or five or less (1).

(120) Pisiform: present (0); or absent (1).

(121) Metacarpal I expansion: spindle-shaped, elongate (0); or broadly expanded (1). The broad expansion is also associated with an anteroproximal overhanging crest in every case observed.

(122) Phalanx shape: phalanges elongate, spindle-shaped (0); or blocky, hourglass-shaped (1). *Mosasaurus* and *Plotosaurus* have phalanges that are slightly compressed and anteroposteriorly expanded on both ends. *Dallasaurus* was recoded as ?.

(123) Ilium crest: crest blade-like, articulates with sacral ribs (0); or elongate, cylindrical, does not articulate with sacral ribs (1).

(124) Ilium acetabular area: arcuate ridge supertending acetabulum (0); or acetabulum set into broad, short ‘V’-shaped notch (1). The primitive ilium has the acetabulum impressed on the lateral wall of the bone, with a long narrow crest anterodorsally as the only surrounding

topographic feature. In state 1, the acetabular area is set into a short, broadly ‘V’-shaped depression that tapers dorsally. The lateral walls of the ilium are therefore distinctly higher than the rim of the acetabulum.

(125) Pubic tubercle condition: tubercle an elongate protuberance located closer to the midlength of the shaft (0); or a thin semicircular crest-like blade located close to the acetabulum (1).

(126) Ischiadic tubercle size: elongate (0); or short (1). In state 0, the tubercle is as long as the shaft of the ischium is wide, but it is only a short narrow spur in state 1.

(127) Astragalus: notched emargination for the crural foramen, without pedunculate fibular articulation (0); or without notch, pedunculate fibular articulation present (1). For state 0, the tibia and fibula are of equal length about the crural foramen and the astragalus contacts both to about the same degree. The form of the latter element is symmetrical and subcircular with a sharp proximal notch. In state 1, the outline of the element is basically reniform and the tibial articulation is on the same line as the crural emargination. The fibula is also shortened and its contact with the astragalus is narrow.

(128) Appendicular epiphyses: formed from ossified cartilage (0); or from thick unossified cartilage (1); or epiphyses missing or extremely thin (2). Ends of the limb bones show distinct vascularization and rugose surfaces indicating an apparently thick non-vascularized, unossified cartilage cap. Extremely smooth articular surfaces suggest the epiphyses were excessively thin or perhaps even lost.

(129) Hyperphalangy: absent (0); or present (1). Hyperphalangy is defined as presence of one or more extra phalanges as compared to the primitive amniote formula of 2-3-4-5-3.

(130) Posterior thoracic vertebra: not markedly longer than anterior thoracic vertebrae (0); or are markedly longer (1).

(131) Ectopterygoid process of pterygoid: distal portion of process not offset anterolaterally and/or lacking longitudinal grooves and ridges (0); distal portion of process is offset anterolaterally and bears longitudinal grooves and ridges (1).

APPENDIX 2: CHAPTER 2 DATA MATRIX

Character-taxon matrix used for phylogenetic analysis. Matrix composed of 66 taxa and 131 characters. ? = missing data;-= inapplicable.

Recoded Characters indicated below matrix.

Outgroup

0?000000?00??00???00000??000?00?0?00?000???0??00?0000000?000??0000000?0?0000?000
?000?000?00?0?00?00000-?000000000000000000000?0000

Adriosaurus_suessi

0-00???10101??0000??00?0??10?0???00??0????????????????????????????0?0????????????1?1
?0????011-010000??????010??????1????1000???100?

Dolichosaurus_longicollis

??00??????????????????10110
0000011-0??00?10-?0011???????1??????0????2?0?

Pontosaurus_kornhuberi

0-0010101101??0-3-0000?11?10-10?01-10????????010?0?0?????1-???????0??00?0100???101
0100????011-00000000-01200?????010?0??00001?1000?

Mesoleptos_zendrinii

???10110?

0??00??0??0??00-010000?00???????????????0?0?

Adriosaurus_microbrachis

???10??00

0???11-0?10??10-0100001?0100--111-0??101100?

Adriosaurus_skrbinensis

??????????????????0011???????10???????????????????????????????0??????00????????????1?1

00???11-0?10???0-011?001?1?000??????0010?000?

Acteosaurus_tommasinii

???10?00?

0??001-0?00??10-0?2000?00?0101?0??000001000?

Coniasaurus_crassidens

???????????????????????????????1100?????????????????????0?1??0010?0????0100121???10?0

000000??????????????10????????????????????????

Eidolosaurus_trauthi

??0100?00

????00-011?00???????0?1???011?????00010?001?

Carentonosaurus_mineaui

???10?010

10001?????0??00-01????????????????????????0?

Aigialosaurus_dalmaticus

?????0?12100??0-3-0000?11000-10??0010???3---?011?0???000?????00???02001?0000???10??
?000???01000????????????0????0000000000001?1000?

Aigialosaurus_bucchichi

0-0??1?12?00??0-3-0000?11000-10???-100001?00?0010000100031-0?00?00110??000000-
?1???0?00????10??0000?010000100-???000000000????1??00

Komensaurus_carrolli

??20?0?000?0???????????????0000????????????1???0
?01??00?0?00???????????????0000?000?0011?000?

Halisaurus_platyspondylus

10100000211000003?10101?0?00???11-???1?20010000?0001???????101?000100010000101
??0?????00????????1?????????????????????????1?????00

Halisaurus_sternbergi

0-100?00210000003?0010100000???021-???0020?1?000?0?01??0?1?1101?0?0100010?00100?
10??00100??0011101011111001001000010111001111?010?

Dallasaurus_turneri

???????0??0???1??0????????????????????0??????????????????00010??0?1????101002?0?11??0
0111110?????1???0-0???01000000????????0???0?1?

Clidastes_liodontus

111000?020010?10101001111?10?1021002??1010?0000000010100{1 2}0021?10001000?1010

020101100000110101?111101011000021010111210001010001211?

Clidastes_moorevillensis

1110000020010010101001111?10?1021?020?1010?00010000101002002101000100001010020

10110000011?101?1111??011000021010111210001010001211?

Carsosaurus_marchesetti

???1???00

????00?0?10??10-0001000001000000000001??001?

Haasiasaurus_gittelmani

??11?02?00????????00001010000000000000001?0??10

000001000000?0???11100100?000000000000000???000?

Portunatasaurus_jakovi

???1?00

????000?????10-0?000??001001100010?????001?

Vallecillosaurus_donrobertoi

???

???????01100??????????????????????01?0?000??

Judeasaurus_tchernovi

0-0????02??0??100-?000??1????10????20???0000??110???0????1-???1???0??00100000-???1?

??

Clidastes_propython

111000?12001001010100111??10?1021?0???1010?00010000101001002101?101000010100201
0110000011?10???1?1??????00021010111210?0???????2?10

Prognathodon_overtoni

101000?10011001011100l?11111?10300120011101l0110?00101003002101011100101100121
1????0?0?110?11-?111110111001212101l1??0???010000211?

Prognathodon_rapax

101000?100010010111001111?11?1?31?020?1110?1011000011100?1-21010???000011001211
0110?00011110?????1??01?0011212101112100010?????2?1?

Prognathodon_solvayi

0-00000100010010101011111110?0030?110?1110010100?00111?141-2?010101?00000101211
0?10001011?10????????01?01??????????????????????????

Prognathodon_currii

1000????0111??????10???11?11?0030?120??1???????0????1???51-????????000??100?20???
???

Prognathodon_waiparaensis

1010000??????????????????????????21?111??10110?0010???3???101????????00{0 1}01211
??0

Prognathodon_saturator

???00??10?11001011101l1???10000????20?111?01011000010l??3??2101??010010110012110
?10?01011110????01??0??????????????2???????????????

Globidens_alabamaensis

???????10?1110101?????????10?10?1?????1010?111?0??010???????1010?1100001100110101 1

??0?011??0????????????0??21010111????????????2?1?

Globidens_dakotensis

1110?0?10111??10101001?11?11?10310020?1010?10110?0{0 1}10100???????????????1100

1101011?00?011?10?????????????????????????????????????10

Mosasaurus_conodon

???1??2101????00001010021101110

01011011?????1???1?001031110111?1???????????2?1?

Mosasaurus_hoffmannii

111001?00011??10111002111?1100031??21?1000?00101?110110030021010?11011010100211

01110110110?1??11111?02100113111011121000111000 12110

Mosasaurus_missouriensis

111001?10011??10111001?11?11?003001???1000?00100?1{0 1}0110?3002?01011101101010

02?1011?0000110111?1??11?01??00?????????2100?11?????2?1?

Plesiotylosaurus_crassidens

11101??10?11??10111001111?1110031?1??01100?10110?0?1011?2002111011100??10100211

?????00011?10????????0110011312101112100010?????2???

Plotosaurus_bennisoni

101001?10101??10111011?11111?0011002001000?001000110110?101?1?1???10110000012??

010?10?011??11???1?1?0210011311101112100011??1??211?

Tylosaurus_nepaeolicus

121111?001010111??1001?11001100300021100 11?02111100100 1?4012100000000000010021

1100??00010101????00?????????200010001011100???????00

Tylosaurus_bernardi

121111?001110?11??1001?11001100310?21??0????20001001001?401?1000000000000100211

100?00001010101100010110110120001000?011100????0?100

Taniwhasaurus_oweni

121111?00?21??11????01????011003?0?21??011?02000?0010???301???00?0?????0111?2??10

0????01010?????00??1???????????????????????????0?

Taniwhasaurus_antarcticus

121111?00?210?11??1001?11?01100?0??21???11?02000?0010????01?1000?00?0??0111021??

0??????1?1??????00??????????????????????????????0?

Tylosaurus_proriger

1211111001110?11??1001?11001100310021000 11?0200010010010401210000000000000010021

1100?00001010101100010110110120001000101110010?001100

Yaguarasaurus_columbianus

0-10?0?02000???0201200?11000?0?3001111??210020011000000013001???????????00?00100?

?1??0?

Eremiasaurus_heterodontus

101001?10111??101?10?1?11?11?01300020?111??1??0??1?111??20021010??1011?10{0 1}0

121?01??0100110?0??11111001?01???10???????????01??01??1?

Prognathodon_kianda

101001??00?1??1?1?10?1?11??0???30??2111?10?10110000101??20021?10001000010001201???0

Russellosaurus_coheni

101??0002000111020120001100 0?0120?121100210020011200000121-1100000001001000001 00??1

Romeosaurus_fumanensis

??????????????????????????1????20??21?1021002011?2011???2001??00000100?10000100?????01101??0?????????0-11??00?00?00???????????????1

Ectenosaurus_clidastoides

11100010200111102011100 01?00?0111011100010012101110??00230020001000000100010201001001001???0????????010110021???0012010100?????1110

Plioplatecarpus

???????0011100100-1113011?01000?0??1100021100200?0{0 1}1100251-21101000000100000201??0??000110000????0??010110020?110012011100?????1?00

Platecarpus_planifrons

1010000001011?100-1110?11?00??13000?100021001000?0{0 1}110015002100100000010001 02011010000011??0????????010110020?1100?2011100?????1?00

Platecarpus_tympaniticus

0-100000011111100-1111011?01001300011?002110110010{0 1}1100251-211010000001000 00201100100001100000100010010110020??1?012011100101101100

Latoplatecarpus_willistoni

0-1000?00120111?0-111{1 2}0?1?01001300021?0021001200101110025 1-2110100000100010 2011110001011??0?????0???2111?????????????????????????0

Selmasaurus_johnsoni

101000?100011110201200011?01-01?0??21?0011011100?000101151-21111000000100010201 1010000011000???????????????????????????????????????

Angolasaurus_bocagei

101??0?01?11???0??1100?1??00?0?30????1??21000100100010015 1-21?010001001?00102? 1??1???0?

Tethysaurus_nopcsai

0-00?0?02110??10201200?11000-0?00??21??0010020001?20000111-?10010001000000{0 1} 00-0??10?111000???????0??1110?00?????000???????000?????0

Pannoniasaurus_osii 0-00?0??????????????????????0???????????01002000??200???01-20010?00??000001020???10? 1110000???0??0?????01???0???000??????00???????

Pontosaurus_lesinensis

0-00?0?01101??0?3-1010?11110-10??1-200??0??0?01000?0?????1-???00000?00?101001??1 0??1?01???011-0?????10-0?200???00010?00000?????0000

Dinilysia_patagonica

???????0000?1?1?1010---10000-102?01??0??3-?0??10?0?0?0?14????00??0--??????????10101
000110011-??????---------------------????????01

Pachyrachis_problematicus

0-00?0?10001??0?1012---000010002001??0013-?0?011?0?11???400?2010000—100000010011
101000100011-1??0?1---------------------?000?12?00

Eupodophis_descouensi

??3--0?001?0?0?00?41-2??????0--??????0?????10?0
00110001-101001---------------------?10-112?1?

Pachyophis_woodwardi

??0002???????????100?0?????10???
????001-??????---------------------???????0??

Haasiophis_terrasanctis

0-00?0?12001??1?2010---00000-0000?1??0013-?0??111?00010?01-1?000010--10000000-
011101?0????011-1100?1---------------------01???1200?

Pontosaurus_ribaguster

???????01?11??0?3-1010?11?10-100????????0??0?010?0?0??????????00??0??00????0????
0???00????011-0?10??10-012000??10010?00?0000???000?

Coniasaurus_gracilodens

???????0011110003-?????????0-??301-???00???????????????????????????????100010-1??1

??????11??????????10-0101????????????????????????

Kaganaias_hakusanensis

?????????????????????????????????0??????0000?00000000??????????????????100000-

???10?1010100?1-0?11???????????????????????00?10???0?

Changes to coding based on personal observation of specimens:

Character 16:

- *Pontosaurus kornhuberi* - → ?

Character 19:

- *Pontosaurus kornhuberi* 0 → 1

Character 68:

- *Pontosaurus kornhuberi* ? → 1

Character 69:

- *Pontosaurus kornhuberi* ? → 0

Character 74:

- *Dallasaurus* 0 → 1
- *Prognathodon waiparensus* 0 → 0/1
- *Prognathodon solvayi* ? → 1
- *Eremiasaurus* 0 → 0/1

Character 80:

- *Pontosaurus kornhuberi* 1 → 0

Character 101:

- *Pontosaurus kornhuberi* 0 → 1

Character 105:

- *Haasiasaurus gittelmani* ? → 0

Character 107:

- *Aigialosaurus bucchichi* 0 → 1
- *Pontosaurus kornhuberi* ? → 0

Character 114:

- *Pontosaurus kornhuberi* 1 → 0

Character 118:

- *Haasiasaurus gittelmani* 1 → 0

Character 119:

- *Haasiasaurus gittelmani* 1 → 0

Character 120:

- *Haasiasaurus gittelmani* 1 → 0

Character 130:

- *Haasiasaurus gittelmani* ? → 0

APPENDIX 3: CHAPTER 5 DATA MATRIX

Character-taxon matrix used for phylogenetic analysis. Matrix composed of 66 taxa and 131 characters. ? = missing data;-= inapplicable.

Recoded Characters indicated below matrix.

Outgroup

0?000000?00??00???00000??000?00?0?00?000???0??00?0000000?000??0000000?0?0000?000
?000?000?00?0?00?00000-?0000000000000000000000?0000

Adriosaurus_suessi

0-00???10101??0000??00?0??10?0???00??0?????????????????????????????0?0????????????1?1
?0????011-010000??????010???????1????1000???100?

Dolichosaurus_longicollis

???00??????????????????10110
0000011-0??00?10-?0011???????1??????0????2?0?

Pontosaurus_kornhuberi

0-0010101101??0-3-0000?11?10-10?01-10????????010?0?0?????1-???????0??00?0100???101
0100????011-00000000-01200?????010?0??00001?1000?

Mesoleptos_zendrinii

???10110?

0??00??0??0??00-010000?00???????????????0?0?

Adriosaurus_microbrachis

???10??00

0???11-0?10??10-0100001?0100--111-0??101100?

Adriosaurus_skrbinensis

??????????????????0011???????10???????????????????????????????0??????00????????????1?1

00???11-0?10???0-011?001?1?000??????0010?000?

Acteosaurus_tommasinii

???10?00?

0??001-0?00??10-0?2000?00?0101?0??000001000?

Coniasaurus_crassidens

???????????????????????????????1100?????????????????????0?1??0010?0????0100121???10?0

000000??????????????10????????????????????????

Eidolosaurus_trauthi

??0100?00

????00-011?00???????0?1???011?????00010?001?

Carentonosaurus_mineaui

???10?010

10001?????0??00-01????????????????????????0?

Aigialosaurus_dalmaticus

?????0?12100??0-3-0000?11000-10??0010???3---?011?0???000?????00???02001?0000???10??
?000???01000????????????0????0000000000001?1000?

Aigialosaurus_bucchichi

0-0??1?12?00??0-3-0000?11000-10???-100001?00?0010000100031-0?00?00110??000000-
?1???0?00????10??0000?010000100-???000000000????1??00

Komensaurus_carrolli

??20?0?000?0????????????????0000???????????1???0
?01??00?0?00???????????????0000?000?0011?000?

Halisaurus_platyspondylus

10100000211000003?10101?0?00????11-???1?20010000?0001???????101?000100010000101
??0?????00????????1?????????????????????????1?????00

Halisaurus_sternbergi

0-100?00210000003?0010100000???021-???0020?1?000?0?01??0?1?1101?0?0100010?00100?
10??00100??0011101011111100100100001011100 1111?010?

Dallasaurus_turneri

???????0??0???1??0????????????????????0?????????????????00010??0?1????101002?0?11??0
0111110?????1???0-0???01000000????????0???0?1?

Clidastes_liodontus

111000?020010?10101001111?10?1021002??1010?0000000010100{1 2}0021?10001000?1010
020101100000110101?111101011000021010111210001010001211?

Clidastes_moorevillensis

1110000020010010101001111?10?1021?020?1010?00010000101002002101000100001010020
10110000011?101?1111??011000021010111210001010001211?

Carsosaurus_marchesetti

???1???00
????00?0?10??10-0001000001000000000001??001?

Haasiasaurus_gittelmani

???????????????????????????????????????11?02?00????????0000101000000000000001?0??10
000001000000?0???11100100?000000000000000???000?

Portunatasaurus_jakovi

???1?00
????000??????10-0?000??001001100010?????001?

Vallecillosaurus_donrobertoi

???
???????01100??????????????????????01?0?000??

Judeasaurus_tchernovi

0-0????02??0??100-?000??1????10????20???0000??110???0????1-???1???0??00100000-???1?
??

Clidastes_propython

111000?12001001010100111??10?1021?0???1010?00010000101001002101?1010000101002010110000011?10???1?1??????00021010111210?0???????2?10

Prognathodon_overtoni

101000?100110010111001?11111?1030012001110110110?00101003002101011100101100121 1????0?0?110?11-?1111101110012121011 1??0???010000211?

Prognathodon_rapax

101000?10001001011100111 1?11?1?31?020?1110?1011000011100?1-21010???0000110012110110?00011110?????1??01?00112121011121000 10?????2?1?

Prognathodon_solvayi

0-0000010001001010101111111 0?0030?110?1110010100?00111?141-2?010101?000001012110?10001011?10????????01?01??????????????????????????

Prognathodon_currii

1000????0111??????10???11?11?0030?120??1???????0????1???51-????????000??100?20???

Prognathodon_waiparaensis

1010000?????????????????????????21?111??10110?0010???3???101????????00{0 1}01211??0

Prognathodon_saturator

???00??10?1100101110111???10000????20?111?010110000101??3??2101??010010110012110?10?01011110????01??0??????????????2???????????????

Globidens_alabamaensis

??????10?1110101?????????10?10?1?????1010?111?0??010???????1010?11000011001101011
??0?011??0????????????0??21010111????????????2?1?

Globidens_dakotensis

1110?0?10111??10101001?11?11?10310020?1010?10110?0{0 1}10100???????????????1100
1101011?00?011?10?????????????????????????????????????10

Mosasaurus_conodon

??1??2101????00001010021101110
01011011?????1???1?001031110111?1??????????2?1?

Mosasaurus_hoffmannii

111001?00011??10111002111?1100031??21?1000?00101?110110030021010?11011010100211
01110110110?1??11111?0210011311101112100011100012110

Mosasaurus_missouriensis

111001?10011??10111001?11?11?003001???1000?00100?1{0 1}0110?3002?01011101101010
02?1011?0000110111?1??11?01??00?????????2100?11?????2?1?

Plesiotylosaurus_crassidens

11101??10?11??10111001111?1110031?1??01100?10110?0?1011?2002111011100??10100211
?????00011?10????????0110011312101112100010?????2???

Plotosaurus_bennisoni

101001?10101??10111011?11111?0011002001000?001000110110?101?1?1???10110000012??
010?10?011??11???1?1?0210011311101112100011??1??211?

Tylosaurus_nepaeolicus

121111?001010111??1001?11001100300021100 11?021111001001?40121000000000000010021
1100??00010101????00?????????200010001011100???????00

Tylosaurus_bernardi

121111?001110?11??1001?1100110031 0?21??0????20001001001?401?10000000000000100211
100?00001010101100010110110120001000?011100????0?100

Taniwhasaurus_oweni

121111?00?21??11????01????011003?0?21??011?02000?0010???301???00?0?????0111?2??10
0????01010?????00??1????????????????????????????0?

Taniwhasaurus_antarcticus

121111?00?210?11??1001?11?01100?0??21???11?02000?0010???01?1000?00?0??011102 1??
0??????1?1??????00???????????????????????????????0?

Tylosaurus_proriger

12111110011 10?11??1001?110011003100210001 1?020001001001040121000000000000010021
1100?000010101011000101101101200010001011 10010?001100

Yaguarasaurus_columbianus

0-10?0?02000???0201200?11000?0?3001111??21002001100000013001???????????00?00100?
?1???0?

Eremiasaurus_heterodontus

101001?10111??101?10?1?11?11?01300020?111??1??0??1?111??20021010??1011?10{0 1}0
121?01??0100110?0??11111001?01???10???????????01??01??1?

Prognathodon_kianda

101001??00?1??1?1?10?1?11??0???30??2111?10?10110000101??20021?10001000010001201?

??0

Russellosaurus_coheni

101??00020001110201200011000?0120?121100210020011200000121-110000000100100000

100???1

Romeosaurus_fumanensis

?????????????????????????1????20??21?1021002011?2011???2001??00000100?10000100???

??01101??0?????????0-11??00?00?00???????????????1

Ectenosaurus_clidastoides

1110001020011110201110001?00?0111011100010012101110??00230020001000000010001020

1001001001???0????????010110021???0012010100?????1110

Plioplatecarpus

???????0011100100-1113011?01000?0??1100021100200?0{0 1}1100251-211010000001000

00201??0??000110000????0??010110020?110012011100?????1?00

Platecarpus_planifrons

1010000001011?100-1110?11?00??13000?100021001000?0{0 1}110015002100100000010001

02011010000011??0????????010110020?1100?2011100?????1?00

Platecarpus_tympaniticus

0-100000011111100-1111011?01001300011?002110110010{0 1}1100251-211010000001000
00201100100001100000100010010110020??1?012011100101101100

Latoplatecarpus_willistoni

0-1000?00120111?0-111{1 2}0?1?01001300021?00210012001011100251-2110100000100010
2011110001011??0?????0???2111?????????????????????????0

Selmasaurus_johnsoni

101000?100011110201200011?01-01?0??21?0011011100?000101151-2111100000100010201
1010000011000???????????????????????????????????????

Angolasaurus_bocagei

101??0?01?11???0??1100?1??00?0?30????1??2100010010001001 51-21?010001001?00102?
1??1??0?

Tethysaurus_nopcsai

0-00?0?02110??10201200?11000-0?00??21??0010020001?20000111-?10010001000000{0 1}
00-0??10?111000???????0??1110?00????000???????000?????0

Pannoniasaurus_osii 0-
00?0???????????????????????0??????????01002000??200???01-20010?00??000001020???10?
1110000???0??0?????01???0???000???????00???????

Pontosaurus_lesinensis

0-00?0?01101??0?3-1010?11110-10??1-200??0??0?01000?0?????1-???00000?00?101001??1
0??1?01???011-0?????10-0?200???00010?00000?????0000

Dinilysia_patagonica

???????0000?1?1?1010---10000-102?01??0??3-?0??10?0?0?0?14????00??0--??????????10101
000110011-??????---------------------????????01

Pachyrachis_problematicus

0-00?0?10001??0?1012---000010002001??0013-?0?011?0?11???400?2010000—100000010011
101000100011-1??0?1---------------------?000?12?00

Eupodophis_descouensi

??????????????????????????????????????3--0?001?0?0?00?41-2??????0--??????0?????10?0
00110001-101001---------------------?10-112?1?

Pachyophis_woodwardi

??0002???????????100?0?????10???
????001-??????---------------------???????0??

Haasiophis_terrasanctis

0-00?0?12001??1?2010---00000-0000?1??0013-?0??111?00010?01-1?000010--10000000-
011101?0????011-1100?1---------------------01???1200?

Pontosaurus_ribaguster

???????01?11??0?3-1010?11?10-100????????0??0?010?0?0??????????00??0??00????0????
0???00????011-0?10??10-012000??10010?00?0000???000?

Coniasaurus_gracilodens

???????0011110003-?????????0-??301-???00???????????????????????????????100010-1??1

??????11??????????10-0101????????????????????????

Kaganaias_hakusanensis

?????????????????????????????????0??????0000?00000000??????????????????100000-

???10?1010100?1-0?11???????????????????????00?10???0?

Changes to coding:

Character 16:

- *Pontosaurus kornhuberi* - → ?

Character 19:

- *Pontosaurus kornhuberi* 0 → 1

Character 68:

- *Pontosaurus kornhuberi* ? → 1

Character 69:

- *Pontosaurus kornhuberi* ? → 0

Character 74:

- *Dallasaurus* 0 → 1
- *Prognathodon waiparensus* 0 → 0/1
- *Prognathodon solvayi* ? → 1
- *Eremiasaurus* 0 → 0/1

Character 80:

- *Pontosaurus kornhuberi* 1 → 0

Character 101:

- *Pontosaurus kornhuberi* 0 → 1

Character 105:

- *Haasiasaurus gittelmani* ? → 0

Character 107:

- *Aigialosaurus bucchichi* 0 → 1
- *Pontosaurus kornhuberi* ? → 0

Character 114:

- *Pontosaurus kornhuberi* 1 → 0

Character 118:

- *Haasiasaurus gittelmani* 1 → 0

Character 119:

- *Haasiasaurus gittelmani* 1 → 0

Character 120:

- *Haasiasaurus gittelmani* 1 → 0

Character 130:

- *Haasiasaurus gittelmani* ? → 0