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Author:
Herrera Flores, Jorge Alfredo A

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The macroevolution and macroecology of Mesozoic lepidosaurs

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The macroevolution and macroecology of Mesozoic lepidosaurs

Jorge Alfredo Herrera Flores

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Doctor of Philosophy in the Faculty of Science.

University of Bristol, School of Earth Sciences

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Abstract

I studied with the aid of geometric morphometrics and novel phylogenetic comparative methods patterns of macroevolution in Mesozoic lepidosaurs in order to answer some of the intriguing aspects of their early evolution. The results presented here show that: A) The Late Triassic rhynchocephalian *Clevosaurus latidens* was not related to the genus *Clevosaurus* as was previously suggested, and indeed it represents a new genus of an early diverging opisthodontian renamed here as *Fraserosphenodon latidens*. Additionally, parsimony and Bayesian phylogenetic analysis recovered very similar topologies for the phylogeny of Rhynchocephalia, allowing to formally name two higher clades of derived rhynchocephalians: Eusphenodontia and Neosphenodontia. B) Geometric morphometric analysis of rhynchocephalians confirms the high morphological disparity of the group, while evolutionary rates analysis suggests that rhynchocephalian evolution was driven by heterogenous rates. Both, evolutionary rates analysis and geometric morphometrics shows that the modern “Tuatara” has rather low rates and is morphologically average if compared with other rhynchocephalians, which suggests that it is a morphologically conservative species. C) Dental disparity, body size analysis and geometric morphometrics of Mesozoic squamates suggest that small body size, low diversity and low dental disparity seem to have been the ancestral state of the earliest squamates. However, changes in the biota during the Cretaceous Terrestrial Revolution in the Middle/Late Cretaceous triggered changes in the ecosystem that influenced ecological and morphological adaptations in squamates that resulted in their radiation at the end of the Cretaceous. D) Early lepidosaur evolution was driven by heterogeneous rates; nevertheless, when comparing evolutionary rates of rhynchocephalians, squamates and all Lepidosauria, it is possible to appreciate that rhynchocephalian rates of body size evolution were outstandingly high and sustained over a long period of time, which suggests that rhynchocephalian decline may unexpectedly be linked to their high rates of evolution sustained over time. This fits with Simpson’s tachytelic evolution theory that suggests that a lineage with high evolutionary rates is prone to extinction. The thesis shows how modern computational methods can provide answers to long-running debates in comparative macroevolution.

Author’s declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

[redacted]

Jorge Alfredo Herrera Flores

21th of September 2018

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Dedication

A mis padres Rosa María Flores y Lázaro Herrera, de quienes sin su amor y apoyo no me hubiese sido posible llegar hasta aquí. A ustedes les debo todo lo que soy en la vida.

A mí tía Evelia, por su amor, comprensión y cariño.

A mí hermana Soledad, por su apoyo y por cuidar de mis padres en mi ausencia.

A mí querido Gary, por tu apego a la vida y porque pese a tu cansancio y enfermedad esperaste pacientemente mi regreso a casa.

A todas aquellas personas a las que ya no tuve oportunidad de volver a ver.

“El esfuerzo mismo para llegar a las cimas basta para llenar un corazón de hombre. Hay que imaginarse a Sísifo dichoso”

Albert Camus

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Chapter 1

Macroevolution and an overview of Mesozoic lepidosaurs

1.1 Macroevolution and the origin of vertebrate biodiversity

After Charles Darwin (1859) published his book on the origin of the species, the next major advance happened at the beginning of the 20th century when the rediscovery of Mendel´s principles of genetics provided a mechanism for inheritance, and the increase of knowledge of the fossil record led to a complete review of the traditional, gradualistic theory of evolution (Stanley, 1982). The result of the review of traditional evolutionary theory was the development of an amended theory that is currently known as the synthetic theory of evolution, which included as one of its key elements the concept of macroevolution or evolution above the species level (Simpson, 1944; Stanley, 1982). Macroevolution incorporates the study of many different components such as adaptive radiations, rates of speciation and extinction and changes in biodiversity through time (Benton, 2015). In this regard the origin of the biodiversity is one of the most interesting and debated aspects of the study of macroevolution. For example, current vertebrate biodiversity consists of about 60,000 species of which nearly 30,000 are fishes and the other half are tetrapods (Benton, 2010). A study on the origin of current biodiversity by Alfaro et al. (2009) found that about 85 per cent of all living vertebrates are the product of 9 major changes in diversification, of which six are accelerations in diversification rates and the other three are slowdowns. The six accelerations in diversification correspond to six clades: Euteleostei, Ostariophysi, Percomorpha, non-gekkonid squamates, Neoaves and Boreoeutheria (Alfaro, 2009; Benton, 2010). In contrast, the three significant slowdowns in some clades apparently led to what we now know as “living fossils” such as coelacanths, lungfishes, crocodylians and tuatara (Alfaro, 2009; Benton, 2010).

On the other hand, another interesting aspect of the study of macroevolution and the origin of biodiversity is to determine which are the biotic and abiotic factors that drive the diversification of life. So far, different models to explain the history of diversity have been proposed, but two of them are widely discussed: the Red Queen and the Court Jester (Benton, 2009). The Red Queen model was proposed by Van Valen (1973), and it explains that the environment is constantly changing, so in order to survive an organism has also to adapt continuously itself of to the changing environment in order to remain sufficiently adapted to survive (Benton, 2009; 2010). The Court Jester model was proposed by Barnosky (2001), and it mainly focuses on unpredictable changes in the physical environment on a large scale such as climate change, meteorite impacts, changes of ocean chemistry, volcanic eruptions, etc (Benton, 2009; 2010). Both models seem to perfectly explain some of the factors that drive macroevolution in some specific cases, but it is more likely that large-scale evolution is a combination of both, with the Red Queen being the dominating model at local scale or short time scales, while the Court Jester applies on larger temporal scales (Benton, 2009; 2010).

1.2 Modern approaches to the study of macroevolution

After the current theories on macroevolution were well established thanks to the works of evolutionary biologists such as George G. Simpson (1944), many other researchers (e.g. Eldredge, 1971; Eldredge and Gould, 1972; Stanley, 1975) began to provide new ideas as well as actual examples of how macroevolution works. Most of the earliest macroevolutionary studies based on fossil taxa were biased to those lineages that had an exceptionally good fossil record such as horses and some marine invertebrates (e.g. Eldredge, 1971; MacFadden, 1985). Until quite recently, studies on macroevolution with fossil taxa were still quite complicated due to the lack of well organized and updated databases and the absence of efficient analytical approaches to study patterns of evolution (Benton, 2015). However, the study of macroevolution has changed considerably during the last decades, thanks to improvements in the knowledge of the fossil record. The fossil record still represents only a small percentage of all organisms that lived in the past; nevertheless, it is undisputable that the fossil record has been improved considerably for many lineages such as dinosaurs, Mesozoic marine reptiles and earliest mammals among many other vertebrate groups (Brusatte et al. 2008; Grossnickle and Newham, 2016; Stubbs and Benton, 2016). Another improvement in the study of macroevolution is access to large and updated databases of the fossil record, like those provided by the Paleobiology Database, which is a resource established about twenty years ago and that provides to palaeobiologists access to a complete list of occurrences with temporal and geographical data of fossil taxa (Benton, 2015). An additional element that has improved in recent years and has had a positive impact in the study of macroevolution is the considerable increase in the accuracy and precision of the time scales, which help to perform more realistic calculations of changes in evolutionary rates (Benton, 2015).

As mentioned above, improvements to geological time scales and the emergence of large data sources such as the Paleobiology Database have been fundamental for the rise of modern macroevolutionary studies. In addition, novel methods of computational analysis allow palaeobiologists to explore trends in macroevolution with the aid of large and complex datasets. First of all, the study of phylogenetic relationships has improved considerably in recent years. Today there are available new methods to create phylogenies compared with the past when only parsimony analyses were available, but currently it is possible to explore phylogenetic relationships by using other approaches such as Maximum likelihood and Bayesian inference, which allow study of very large datasets that also can include both molecular and morphological characters, or a combination of both (e.g. Simões et al. 2016, 2017a, 2018). Secondly, modern computational geometric morphometrics and studies of disparity have been very helpful to quantify changes in morphology that in the past were very difficult to quantify (Benton, 2015).

These analyses allow palaeobiologists to perform complex statistical protocols to perform multivariate analysis that allow them to visualize ranges of morphological variation and changes in disparity through time (Benton, 2015). Finally, newly developed Phylogenetic comparative methods (PCM) have been crucial for most of the newest macroevolutionary studies (e.g. Brusatte et al. 2008; Sakamoto et al. 2016; Cantalapiedra et al. 2017). These innovative methods help to correct phylogenetic bias, and also to explore evolutionary changes across the trees such as diversification shifts, models of evolution and evolutionary rates (Benton, 2015).

1.3 Early lepidosaur origins

The Lepidosauria is a group of reptiles with a very long evolutionary history, and it is considered as one of the most successful groups of vertebrates. Lepidosaurs are currently divided into two subgroups: the Squamata represented by over 10,000 living species and the Rhynchocephalia, only represented by a single living species, *Sphenodon punctatus* from the islands off New Zealand (Jones et al. 2013; Streicher and Wiens, 2017). Knowledge about the biology, ecology, taxonomy and systematics of extant lepidosaurs is outstanding, but in contrast details about their early origin have been unknown for a long time. Until recently, the oldest known lepidosaur remains were two incomplete dentaries from the Middle Triassic of Vellberg, Germany which were apparently related to the basal rhynchocephalian *Diphydontosaurus* (Jones et al. 2013). The discovery of the Vellberg specimens was very important to the understanding of the early origin of the group, because they were used to calibrate the molecular clock which estimated their origin in the Early/Middle Triassic (Jones et al. 2013). More recently, a complete re-examination of the basal diapsid *Megachirella wachtleri* from the Middle Triassic of Italy reassessed this taxon as the earliest "lizard" and in consequence the oldest known lepidosaur (Simões et al. 2018). The same study also included a molecular clock analysis that estimated the time of divergence of lepidosaurs as Middle Permian, about 269 Myr ago (Simões et al. 2018). This unusually early date is controversial and depends on aspects of the choice of outgroups and the methodology used to estimate timing of origin of clades. With different methods, a younger, Early Triassic date might be calculated.

1.4 Mesozoic lepidosaur fossil record

The lepidosaur fossil record has been notably improved during the last four decades increasing considerably our knowledge about their evolutionary history. With regard to early diverging taxa, it is clear that the fossil record of basal rhynchocephalians is reasonably good. Currently, there are about a dozen recognized genera of basal rhynchocephalians, including the Early Jurassic *Gephyrosaurus* from the United Kingdom (Evans, 1980; Whiteside and Duffin, 2017) the most basal taxon according to most recent phylogenetic studies (e.g. Apesteguía et al. 2014; Hsiou et al. 2015; Herrera-Flores et al. 2018). Other important basal taxa include the genus *Diphydontosaurus*, possibly from the Middle Triassic of Germany (Jones et al. 2013) and certainly from the Late Triassic of England, Italy and the United States (Whiteside, 1986; Renesto, 1995; Heckert, 2004); *Penegephyrosaurus* and *Pelecymala* from the Late Triassic of England (Fraser, 1986; Whiteside and Duffin, 2017; Herrera-Flores et al. 2018); *Planocephalosaurus* from the Late Triassic of England and the United States (Fraser, 1982; Heckert, 2004); *Whitakersaurus* from the Late Triassic of the United States (Heckert et al. 2008); *Deltadectes* from the Late Triassic of Switzerland (Whiteside et al. 2017); *Rebbanasaurus* and *Godavarisaurus* from the Middle Jurassic of India (Evans et al. 2001) and *Sphenocondor* from the Middle Jurassic of Argentina (Apesteguía et al. 2012).

The fossil record of derived rhynchocephalians is also notably good, especially for Jurassic taxa, but the group shows a considerably decrease in their diversity after the Early Cretaceous. Among derived rhynchocephalians, clevosaurs are some of the most common taxa. Clevosaurs are a group of derived carnivorous/omnivorous taxa that lived between the Late Triassic and the Early Jurassic and were divided into three genera (Hsiou et al. 2015). The most basal clevosaur is *Polysphenodon* from the late Triassic of Germany, followed by *Brachyrhinodon* from the Late Triassic of the United Kingdom and

Clevosaurus from the Late Triassic and Early Jurassic of many different localities in Belgium, Brazil, Canada, China, Great Britain, Mexico and South Africa (Fraser, 1988; Fraser and Benton, 1989; Wu, 1994; Sues et al. 1994; Duffin, 1995; Sues and Reisz, 1995; Säilä, 2005; Bonaparte and Sues, 2006; Reynoso and Cruz, 2014; Hsiou et al. 2015; Klein et al. 2015; Herrera-Flores et al. 2018). Other important records of derived rhynchocephalians are those from the exceptionally preserved Middle and Late Jurassic limestones of France and Germany that include taxa such as *Homoeosaurus* (Cocude-Michel, 1963), the semi-aquatic sapheosaurs that include three genera: *Kallimodon*, *Piocormus* and *Sapheosaurus* (Cocude-Michel, 1963, 1967), as well as the highly derived marine pleurosaurs with three genera, *Palaeopleurosaurus*, *Pleurosaurus* and *Vadasaurus* (Dupret, 2004; Bever and Norell, 2017).

The Sphenodontidae, the family to which the extant *Sphenodon punctatus* belongs, is represented by Early Jurassic taxa such as *Zapatadon*, *Sphenovipera* and *Cynosphenodon* (Reynoso, 1996, 2005; Reynoso and Clark, 1998), and some Late Jurassic taxa such as *Theretairus* and *Oenosaurus* (Simpson, 1936; Rauhut et al. 2012) as well as the Early Cretaceous *Derasmosaurus* (Barbera and Macuglia, 1988). On the other hand, the Opisthodontia is a very important group of derived and highly specialized herbivores with a very long geological record (Martínez et al. 2013; Apesteguía et al. 2014; Herrera-Flores, 2018). Late Triassic opisthodontians include genera such as *Fraserosphenodon* and *Sphenotitan* (Martínez et al. 2013; Herrera-Flores et al. 2018); Jurassic taxa include *Opisthias* and *Eilenodon* (Rasmussen and Callison, 1981), while Early Cretaceous taxa include *Toxolophosaurus* and *Priosphenodon minumus* (Throckmorton et al. 1981; Apesteguía and Carballido, 2014). Late Cretaceous opisthodontians include some of the latest Mesozoic records of rhynchocephalians such as *Priosphenodon avelasi* and *Kawasphenodon expectatus* (Apesteguía and Novas, 2003; Apesteguía, 2005). Paleogene opisthodontians include the only known record of an Early Cenozoic rhynchocephalian represented by the early Palaeocene *Kawasphenodon peligrensis* (Apesteguía et al. 2014).

The fossil record of early diverging squamates is quite poor. For many years no stem squamates were known from the Triassic or Early Jurassic (Evans, 2003). Many taxa that were originally described as basal Triassic squamates were subsequently reassessed to other reptilian groups or in some particular cases, their stratigraphic ranges were corrected. Some examples of taxa misinterpreted as Triassic “lizards” were *Fulengia youngi* (Carroll and Galton, 1977), which was later identified as a hatchling prosauropod dinosaur (Evans and Milner, 1989) or the Early Triassic "lizard" *Colubrifer campi* which was reassessed as a primitive procolophonian (Evans, 2001). More recently, a nearly complete dentary of an acrodont lizard named *Tikiguania estesi* from the Late Triassic of India, was described as the oldest known squamate (Data and Ray, 2006), but a re-examination of the fossil showed that *Tikiguania* is indeed a modern Quaternary or Late Tertiary agamid lizard (Hutchinson et al. 2012).

It was only very recently that the first Triassic "squamate" was recognized. The Middle Triassic *Megachirella wachtleri* was originally described by Renesto and Posenato, (2003) as a basal lepidosauromorph, but a subsequent re-examination and phylogenetic analysis suggested possible lepidosaur affinities (Renesto and Bernardi, 2014). More recently, a new phylogenetic analysis combining morphological and molecular data proposed *Megachirella* as the earliest known squamate (Simões et al. 2018). However, the recognition of *Megachirella* as the oldest "squamate", must be taken carefully, because it is possible that future phylogenetic analysis will challenge its position as the oldest known "squamate", and also it does not change the fact that the fossil record of earliest squamates is still very incomplete with a complete absence of specimens from the Late Triassic to the Early Jurassic. Before *Megachirella,* the oldest known squamate was an acrodont lizard from the Early-Middle Jurassic of India named *Bharatagama rebbanensis* (Evans et al. 2002). Nevertheless, a new phylogenetic analysis suggests that *Bharatagama* is more closely related to rhynchocephalians than to squamates (Conrad, 2018). Another basal "squamate" known by fragments of skull, is the "lizard-like" *Marmoretta oxoniensis*, which was originally described as a lepidosauromorph (Evans, 1991); but a recent phylogenetic analysis recovered it as a basal squamate (Simões et al. 2018).

The earliest purpoted snake is a fragment of dentary of a taxon from the Middle Jurassic of England named *Eophis underwoodi* (Caldwell et al. 2015); other early snakes are *Portugalophis lignites*, *Diablophis gilmorei* and *Parviraptor estesi* known from fragments of dentary and maxilla from the Late Jurassic of Portugal, the United States and England respectively (Caldwell et al. 2015). Fossil squamates from the Middle Jurassic are quite rare, nevertheless, some relevant records of crown lizards are known from the Old Cement Works Quarry in Oxfordshire, England (Evans, 1998), and western Siberia in Russia (Averianov et al. 2016). The records from Oxfordshire, England include three species of scincomorphs: *Saurillodon marmorensis*, *Balnealacerta silvestris*, *Bellairsia gracilis*; some fragments of anguimorphs and gekkotans, as well as the “lizard” of uncertain position *Oxiella tenuis* (Evans, 1998). The fossil record of Late Jurassic taxa is not any better in terms of diversity, but at least some complete skeletons are known. Most records of Late Jurassic (and earliest Cretaceous) lizards are fragments of paramacellodid lizards such as *Becklesius*, *Paramacellodus* and *Pseudosaurillus* from the Morrison Formation of North America, the Guimarota Formation of Portugal and the Purbeck Formation of England (Estes, 1983). Other important records of Late Jurassic lizards are those from the limestones of Solnhofen Formation such as *Ardeosaurus*, *Bavarisaurus*, *Eichstaettisaurus* and the recently described *Schoenesmahl* (Mateer, 1982; Estes, 1983; Evans, 2003; Simões et al. 2017b; Conrad, 2018). Additionally, a large-sized paramacellodid named *Sharovisaurus karatauensis* is known from the Late Jurassic Karabastau Formation of Kazakhstan (Hecht and Hecht, 1984). With regard to the fossil record of Early Cretaceous squamates, it is still poor and fragmentary and little better than that of the Late Jurassic. A relatively good fossil record of Early Cretaceous lizards is known from China, Japan, Mexico, Mongolia, Spain and the United States (Evans, 2003). One of the most interesting Early Cretaceous taxa is the Albian lizard *Huehuecuetzpalli mixtecus* from the Tlayua Formation in Mexico which shows a combination of primitive and derived features that place it as a very basal squamate (Reynoso, 1998).

During the last three decades, many Early Cretaceous lizards have been described from China and Spain based on nearly complete skeletons. The Chinese taxa come from the Yixian Formation and are represented by the lizards *Dalinghosaurus*, *Yabeinosaurus*, *Luishusaurus*, *Xianglong* and dubious taxa such as *Jeholacerta* and *Liaoningolacerta* (Evans and Wang, 2005, 2010, 2012; Li et al. 2007). Lizards from the Early Cretaceous of Spain are mainly known from fossil sites in Las Hoyas and Montsec. Lizards from Las Hoyas belong to the Calizas de la Huérguina Formation and are represented by *Hoyalacerta*, *Jucaraseps*, *Meyasaurus* and *Scandensia* (Evans and Barbadillo, 1996, 1997, 1998, 1999; Bolet and Evans, 2012); while *Meyasaurus* and *Pedrerasaurus* are found in La Pedrera de Rúbies Formation in Montsec (Evans and Barbadillo, 1997; Bolet and Evans, 2010). Relatively large assemblages of lizards are known from the Early Cretaceous of Japan, those assemblages include *Sakurasaurus* from Okurodani and Kuwajima Formations (Evans and Manabe, 1999, 2009); *Asagaolacerta*, *Hakuseps*, *Kaganaias*, *Kuroyuriella*, *Kuwajimalla* and other unnamed taxa from Kuwajima Formation (Evans and Manabe, 2008; Evans and Matsumoto, 2015; Evans et al. 2006). Other relevant Early Cretaceous taxa are the snake-like *Tetrapodophis amplectus* from the Aptian Crato Formation in Brazil, which was originally described as a basal four-legged snake (Martill et al. 2015), but may in fact be a very primitive marine squamate (Paparella et al. 2018).

Middle Cretaceous squamates are noticeably rare; however, specimens beautifully preserved in ambar have been found in Myanmar, these specimens include a gecko *Cretaceogekko burmae*, a possible anguimorph *Barlochersaurus winhtini*, a neonate snake *Xiaophis myanmarensis* and undescribed species of agamids, chamaleonids and lacertoids (Arnold and Poinar, 2008; Daza et al. 2016, 2018; Xing et al. 2018). In contrast to the Triassic, Jurassic, Early or Middle Cretaceous taxa, the fossil record of Late Cretaceous squamates is notably good. Many Cenomanian and Turonian localities have provided several exceptionally preserved specimens of basal snakes and basal marine taxa. Some of the remarkable species from the early Late Cretaceous are the early diverging snakes *Najash rionegrina* from Argentina (Apesteguía and Zaher, 2006), the marine snakes *Pachyrhachis problematicus* and *Haasiophis terrasanctus* from Israel (Lee and Caldwell, 1998; Tchernov et al. 2000) and *Eupodophis descouensi* from Lebanon (Rage and Escuillié, 2000). Also very important are the records of the basal marine squamates *Adriosaurus*, *Coniasaurus*, *Pontosaurus* among many others (Caldwell, 1999; Lee and Caldwell, 2000; Pierce and Caldwell, 2004). The fossil record of Late Cretaceous lizards is outstanding for the Campanian and the Maastrichtian, especially for the Barun Goyot and Djadokta formations in the Gobi Desert of Mongolia that have provided a large number of new genera of lizards closely related to anguimorphs, iguanids, gekkotans and scincomorphs (Borsuk-Bialynicka, 1984, 1985, 1988, 1990, 1996; Gao and Norell, 2000). It also must be noted that the fossil record of lizards is notably good for the Late Cretaceous of the United States and Canada, providing a large number of species closely related to teiids, polyglyphanodontids and anguimorphs (e.g. Gao and Fox, 1996; Nydam, 2002; Longrich et al. 2012). Finally, the fossil record of the mosasaurs is excellent, with their fossils found in all continents and including nearly 100 species, many of them known by complete skulls or skeletons (Polcyn et al. 2014).

1.5 Phylogenetic studies on Mesozoic lepidosaurs

Nowadays, there are a good number of phylogenetic studies on fossil lepidosaurs, but most studies have focused on either the Rhynchocephalia or the Squamata separately. In general, fossil rhynchocephalian relationships are better understood than fossil squamate relationships. Initially, rhynchocephalian relationships were merely hypothesized without performing formal analysis (e.g. Fraser, 1986; Whiteside, 1986). One of the first works that formally included novel computational phylogenetic analysis was Fraser and Benton (1989) that included a parsimony analysis as part of the redescription of two poorly known species of Late Triassic taxa. A few years later, their data matrix was modified and updated by Wu (1994) in order to study the phylogenetic relationships of "three" Chinese species of "*Clevosaurus*". Since then, basically all later studies have used the same data matrix, only modifying the number of taxa or adding more characters (e.g. Sues et al. 1994; Reynoso 1996, 1997, 2000, 2005; Reynoso and Clark 1998; Evans et al. 2001; Apesteguía and Novas 2003; Apesteguía and Carballido, 2014; Apesteguía et al. 2012, 2014; Rauhut et al. 2012; Hsiou et al. 2015). One of the most recent phylogenetic analyses of the Rhynchochephalia is the study of Bever and Norell (2017), which for first time included a Bayesian analysis of the group.

With regard to fossil squamate phylogenetics, Borsuk-Bialynicka (1984) was one of the first authors to include a rudimentary phylogenetic analysis of fossil lizards from the Late Cretaceous of Mongolia. Then the first work that included modern computational analysis of squamates was Estes et al. (1988). Subsequent works on fossil squamates only modified and updated the data matrix of Estes et al. (1988) by progressively incorporating fossil taxa. Evans and Barbadillo (1997, 1998) presented one of the first phylogenetic analyses that included species of Cretaceous lizards from Las Hoyas, Spain. Many later works that described new taxa incorporated the same modified data matrix, like for example Reynoso (1998), who included the stem squamate *Huehuecuetzpalli mixtecus* and Reynoso and Callison (2000), who included the early scincomorph *Tepexisaurus tepexi*. It was not until Conrad (2008) published his work on phylogeny and systematics of the Squamata based on morphology that a very complete phylogeny of fossil and extant squamates was available. After this, his data matrix became the basis for almost every newly published fossil lizard. However, Gauthier et al. (2012) published a new phylogeny of squamates based on a different and larger data matrix than Conrad (2008). The two major datasets available to study fossil and extant squamates were very helpful to understanding the early evolution of squamates, but it was noticeable that the phylogenetic position of some species of fossil lizards changed considerably depending on which data matrix was used, and also there were some discrepancies among the relationships of squamate higher clades.

More recently Reeder et al. (2015) presented a new data matrix that combined molecular and morphological data of living taxa, but also incorporated a few fossils. Nevertheless, Conrad (2018) published an improved version of his previous data matrix that included a considerable increase in fossil taxa and number of characters, but unfortunately only a few comments about the changes in the phylogenetic relationships of squamates were given. Then, Simões et al. (2018) published the latest data matrix of fossil squamates, which also includes a large number of rhynchocephalians and basal diapsid as outgroups. The novelty of the new squamate phylogeny of Simões et al. (2018) is that their work found the Middle Triassic *Megachirella wachtleri* as the oldest squamate as well as the Middle Jurassic *Marmoretta oxoniensis* as a stem squamate. It is important to note that the phylogenetic work of Simões et al. (2018) also implies important changes in the position of some higher clades, such as Gekkota, which appears as the sister group of all other squamates, instead of Iguania as was shown by most previous analysis.

1.6 Macroevolutionary studies on Mesozoic lepidosaurs

Studies on exploring patterns of evolution with the aid of novel computational techniques have been widely applied during the last decade to many groups of early tetrapods such as dinosaurs, pterosaurs and early mammals (e.g. Brusatte et al. 2008; Butler et al. 2009; Grossnickle and Polly, 2013). However, very few studies have focused on studying lepidosaur macroevolution, and most of those studies have mainly studied the Rhynchocephalia and the Squamata separately. Jones (2008) studied cranial disparity in *Sphenodon* and the Rhynchocephalia by using geometric morphometric analysis; his results showed that there is a greater variation in the rhynchocephalian skull than was believed, and that skull shape can be directly related to feeding strategies. Another interesting macroevolutionary study on the Rhynchocephalia is Meloro and Jones (2012) who analyzed dental and cranial disparity using geometric morphometric and comparative phylogenetic methods; their results demonstrated that skull shape evolved rapidly in the group, much faster than skull size and tooth number.

Macroevolutionary studies on fossil squamates are also quite scarce. Longrich et al. (2012), studied changes in squamate diversity caused by the K-Pg mass extinction event. Their results suggested that the Chicxulub asteroid impact had more severe consequences on squamate diversity than was previously believed, and in consequence the changes in the ecosystem caused the extinction of several lizard groups. Polcyn et al. (2014) compared taxonomic diversity and morphological disparity in mosasaurs with sea levels, temperature and other external factors that might have influenced the rapid evolution of this group during the Late Cretaceous. Their results showed that mosasaur evolution was mainly influenced by tectonically controlled sea levels that also controlled ocean stratification and abundance of food; they found that mosasaur extinction was mainly provoked by the asteroid impact that produced big changes in the biota that directly affected the food chain. One of the latest macroevolutionary studies on squamates is Da Silva et al. (2018) who studied the ecological origin of snakes with the aid of geometric morphometrics and phylogenetic comparative methods including several specimens of fossil and extant snakes as well as some lizards. Their results demonstrate that the ancestor of snakes seems to have been a terrestrial but not fossorial organism, while the most recent common ancestor of crown snakes was indeed adapted to fossoriality. Finally, the only macroevolutionary study that has studied the entire Lepidosauria is the overview of Mesozoic-Paleogene diversity by Cleary et al. (2018). They collected global occurrences of fossil lepidosaurs from the Triassic to the Paleogene, and with the aid of multivariate analysis documented their distribution through time. Their results suggest that from the Triassic to the Late Cretaceous lepidosaurs had apparently low richness which could have been directly affected by biases in the sampling and quality of the fossil record; also they show that lepidosaur diversity increased considerably by the Late Cretaceous and declined again after the K-Pg boundary, rising again and remaining relatively high during the Paleogene.

As explained above, there are a limited number of macroevolutionary studies on fossil lepidosaurs, and there are still many aspectcs about their early origin and evolution to be investigated. In the present work, I studied patterns of evolution in Mesozoic lepidosaurs using many different approaches, such as geometric morphometrics, dental disparity and analyses of rates of evolutionary change based on discrete morphological characters and body size. This work is divided into four research chapters. The second chapter is about the redescription and phylogeny of a poorly known Triassic rhynchocephalian, but chapters three to five are completely focused on the study of macroevolution. Chapter three is a macroevolutionary study on changes in morphospace through time and evolutionary rates of the Rhynchocephalia. Chapter four is a study of dental disparity, body size evolution and geometric morphometrics of Mesozoic squamates. Chapter five is a study of rates of evolutionary change of the entire Lepidosauria using modern phylogenetic comparative methods. Some of the questions that the present work seeks to answer is to use novel statistical analysis look for a testable definition of what a “living fossil” is, also to explore if the controversial species *C. latidens* represent a distinguishable taxon from *Clevosaurus* as has been previously suggested, as well as to investigate new theories about the causes of the massive radiation of squamates in the Late Cretaceous and to apply modern phylogenetic comparative analysis to examine some alternate explanations to the notorious decline of rhynchocephalians by the end of the Mesozoic. I expect that my work would contribute to the understanding of the early evolution of one of the most successful and fascinating groups of tetrapods.

Chapter 2

Taxonomic reassessment of *Clevosaurus latidens* Fraser, 1993 (Lepidosauria, Rhynchocephalia) and rhynchocephalian phylogeny based on parsimony and Bayesian inference.

A version of this chapter has been published in *Journal of Paleontology*, in collaboration with Thomas L. Stubbs, Armin Elsler and Michael J. Benton. https://doi.org/10.1017/jpa.2017.136. M. J. Benton, T. L. Stubbs and A. Elsler provided general supervision as well as training in the use of phylogenetic methods. I collected the data and carried out all analyses and wrote the MS and final paper. Therefore, we agree an estimate that the chapter represents 80% of my own independent work.

2.1 Introduction

The Rhynchocephalia is an ancient group of reptiles that originated in the early Mesozoic. Currently this group has low diversity, being represented by a single species, the famous "living fossil" *Sphenodon punctatus* from New Zealand (Jones et al. 2013; Cree, 2014; Herrera-Flores et al. 2017). In contrast to their current low diversity, Mesozoic rhynchocephalians were diverse, showing varied morphologies and a wide geographical distribution (Jones, 2006a, 2009; Rauhut et al. 2012; Martínez et al. 2013; Herrera-Flores et al. 2017). Among the earliest rhynchocephalians, species of the genus *Clevosaurus* were the most diverse and widely distributed in the early Mesozoic. *Clevosaurus hudsoni* Swinton, 1939, was the first described species of the genus; it was named after F. G. Hudson, who discovered the fossil remains at Cromhall Quarry, England (Fraser, 1988). Since the description of *C. hudsoni*, nine species of *Clevosaurus* have been erected (*C. bairdi, C. brasiliensis, C. convallis, C. latidens, C. minor, C. mcgilli, C. petilus, C. sectumsemper* and *C. wangi*), and new records have been reported from localities in Belgium, Brazil, Canada, China, Great Britain, Mexico and South Africa (Fraser, 1988, 1993; Wu, 1994; Sues et al., 1994; Duffin, 1995; Sues and Reisz, 1995; Säilä, 2005; Bonaparte and Sues, 2006; Reynoso and Cruz, 2014; Klein et al. 2015).

The anatomy of *Clevosaurus* is well known and the monograph of Fraser (1988) offers a very thorough review of the general morphology of this genus. It is recognized that the genus *Clevosaurus* is highly diverse, but the taxonomic validity of some *Clevosaurus* species has been questioned (Jones, 2006a). Hsiou et al. (2015) presented a review of *C. brasiliensis* that included a phylogenetic analysis of almost all known *Clevosaurus* species. Their study demonstrated that some species may not be valid taxa or perhaps not directly referable to this genus. One of these conflicting taxa is *C. latidens*, a species described by Fraser (1993) from the Late Triassic fissure deposits of Cromhall Quarry, England. The uncertain taxonomic affinity of *C. latidens* and its dubious relationships with *Clevosaurus* have been noted in many previous studies (Jones, 2006a, 2009; Martínez et al. 2013; Hsiou et al. 2015; Klein et al. 2015), and some phylogenetic analyses even suggested a closer relationship with opisthodontians, but no taxonomic revision of this taxon has been carried out.

For a long time, the relationships among rhynchocephalians were poorly known, and most taxa were assessed by overall morphological similarities. The first phylogenetic analysis of the group was performed by Fraser and Benton (1989), followed by many different analyses, including newly described or redescribed taxa (e.g. Wu, 1994; Reynoso, 1996, 1997; Reynoso and Clark, 1998; Reynoso, 2000; Apesteguía and Novas, 2003; Reynoso, 2005; Rauhut et al. 2012; Martínez et al. 2013; Apesteguía and Carballido, 2014; Apesteguía et al. 2012, 2014; Cau et al. 2014; Hsiou et al. 2015). So far, all phylogenetic studies of the Rhynchocephalia have only used parsimony analysis, recovering a few distinct clades. More recently, Bayesian inference methods have been employed for phylogenetic analyses based on morphological characters (e.g. Parry et al. 2016; Wright, 2017), and a recent study suggests that Bayesian methods outperform parsimony for morphological data (O'Reilly et al. 2016; Puttick et al. 2017), recovering more accurate, but less precise results.

To clarify the doubtful taxonomic affinity of *C. latidens*, I reexamined the type specimens and other material described by Fraser (1993). I updated the character matrix of a recent phylogenetic analysis of the Rhynchocephalia (Hsiou et al. 2015), recoded morphological characters for *C. latidens* and performed both parsimony and Bayesian analyses. My results confirm that *C. latidens* is not related to *Clevosaurus*, but represents a new genus. My phylogenetic analyses recover similar topologies using both parsimony and Bayesian approaches. I employ the new phylogeny to propose formal names for two higher clades within Rhynchocephalia.

2.2 Material and methods

I reexamined the type material and other material described by Fraser (1993) as *C. latidens*. All specimens of *C. latidens* consist of fragments of dentary, maxilla and premaxilla, which are housed in the collections of the Virginia Museum of Natural History and the University of Aberdeen. For anatomical comparisons, I reviewed several specimens of *Clevosaurus* from the paleontological collections of the University of Bristol and the University Museum of Zoology in Cambridge.

To explore the phylogenetic relationships of rhynchocephalians and the position of *C. latidens*, I used the largest and most up-to-date data matrix of Rhynchocephalia (Hsiou et al. 2015). I decided to use Hsiou et al. (2015) data matrix for this work instead of other matrices, including those used in other chapters of this thesis (see chapter 3), because it was published before the beginning of this work, and time after I had finished and wrote the results of the rate analysis of the next chapter using an older data matrix. Additionally, Hsiou´s et al. (2015) data matrix includes almost all known species of *Clevosaurus,* in contrast to previous matrices that merely included *C. hudsoni*. I added three taxa: *C. sectumsemper*, *Derasmosaurus pietraroiae* and *Priosphenodon minimus,* and recoded some characters for *C. latidens* and *Pelecymala robustus,* after examination of the type specimens. The new matrix comprises 47 operational taxonomic units scored for 74 characters. I rooted the trees with the lepidosauromorph *Sophineta cracoviensis*. Two squamates, the Late Jurassic–Early Cretaceous *Eichstaettisaurus* and the extant *Pristidactylus,* were also used as outgroups.

The revised taxon-character data matrix was analyzed using both equally weighted maximum parsimony and Bayesian inference. Parsimony analysis was performed in TNT v. 1.5 (Goloboff et al. 2008; Goloboff and Catalano, 2016), first using the “New Technology” search options. The initial tree search used multiple replications with sectorial searches, four rounds of tree fusing, ten rounds of drifting and 200 ratcheting iterations. Following this, the generated most parsimonious trees (MPTs) were analyzed using traditional tree bisection and reconnection branch swapping. All recovered MPTs were then summarized in a 50% majority rule consensus tree, and clade robustness was assessed with Bremer decay indices (Bremer, 1994). Bayesian inference trees were estimated using MrBayes v. 3.2 (Huelsenbeck and Ronquist, 2001; Ronquist et al. 2012). The standard Mk model (Lewis, 2001) with gamma distribution priors for site rate variation was specified. The analysis was performed with four runs of four chains, run for 10^8 generations, sampling parameters every 1000 generations. The first 25% of sampled trees were discarded as burn-in. Convergence was assessed based on effective sample size (ESS) values >200. Results from the Bayesian analysis were summarized using a 50% majority consensus tree, revealing clades that have posterior probability values of ≥ 50%. The data matrix and other supplementary material are included in the “Appendix”.

Repositories and institutional abbreviations.—AUP, University of Aberdeen Paleontology Collection; VMNH, Virginia Museum of Natural History.

2.3 Systematic palaeontology

Superorder Lepidosauria Haeckel, 1866

Order Rhynchocephalia Günther, 1867
Suborder Sphenodontia Williston, 1925
Infraorder Eusphenodontia new infraorder
Neosphenodontia new clade
Opisthodontia Apesteguía and Novas, 2003
Genus *Fraserosphenodon* new genus
Fraserosphenodon latidens Fraser, 1993 new combination

1986 aff. *Pelecymala* Fraser, p. 176, pl. 20, Figs. 8-9.
1988 *Clevosaurus* sp Fraser, p. 163, Fig. 43.
1993 *Clevosaurus latidens* Fraser, p.137, Fig. 2.

Holotype.—VMNH 524, maxillary fragment (Fig. 2.1).

Additional specimens.—VMNH 525–528; AUP 11191-11192.

Differential diagnosis.— *Fraserosphenodon latidens* differs from other opisthodontians by the following unique combination of features. Maxillary teeth with relatively short crown with transversely broadened posterolabial flanges without grooved facets on the labial surface (closely packed teeth, interiorly decreasing in size, with long anterolateral flanges in *Sphenotitan* and scale-shaped, closely packed teeth with both lateral and medial flanges in *Priosphenodon*). Dentary with three generations of teeth. Front of dentary with two successional teeth of rounded shape followed by a series of six or seven very small rounded hatchling teeth (lacking hatchling teeth in *Opisthias*, *Priosphenodon*, *Sphenotitan* and *Toxolophosaurus*). Additional teeth in dentary transversely broadened with a distinct triangular shape in labial view and a rounded and bulbous shape in occlusal view (square-based teeth in *Kawasphenodon* and *Opisthias*; transversally expanded teeth in occlusal view in *Eilenodon*, *Priosphenodon*, *Sphenotitan* and *Toxolophosaurus*). Meckelian channel closed (wide and open in other opisthodontians).

Etymology.—The genus epithet is in honor of the British palaeontologist Nicholas “Nick” Fraser, for his outstanding contributions to the knowledge of the British Triassic fauna, especially for his exceptional work on early rhynchocephalians.

Occurrence.—Cromhall Quarry, Avon, England. Site 5A of Late Triassic fissure deposit.

Remarks.—All *Fraserosphenodon* specimens are quite fragmentary, but its tooth morphology, based on wide and robust teeth for grinding, clearly differs from the characteristic tooth shape for cutting and slicing of the genus *Clevosaurus*, and, indeed, is evidently more similar to that of opisthodontians.

The systematic paleontology section of Fraser's original work referred to the holotype of *F. latidens* (VMNH 524) as a dentary fragment (Fraser, 1993), but the description of this element treated it as a maxillary fragment. My review of VMNH 524 confirms that it is a fragment of the posterior part of the left maxilla (Fig. 2.1). This element includes five well preserved and complete teeth. The maxillary teeth have a relatively short crown with transversely broadened posterolabial flanges without grooved facets on the labial surface and a heavily worn occlusal surface.

I agree with Fraser (1993) that paratype specimen VMNH 525 is a dentary fragment which possibly belongs to the right dentary (Fig. 2.1). This element has three teeth which are also transversally broadened. In labial view all teeth appear distinctly triangular. Only the second and third teeth are heavily worn, and the wear is especially pronounced on the third tooth. In occlusal view, the teeth of VMNH 525 appear round with a bulbous swelling developed medially on each tooth, as was described by Fraser (1993) for specimen VMNH 543. The overall shape of both VMNH 525 and VMNH 543 is also quite similar. Note that Fraser (1993) did not mention specimen VMNH 543 in the systematic paleontology section of his paper, and there is also no specimen in the VMNH collection assigned to *Fraserosphenodon* (*C. latidens*) with that catalog number. It might be that specimen VMNH 543 illustrated and described by Fraser (1993, Fig. 2 C-E) is indeed specimen VMNH 525.

Paratypes VMNH 526-528 are maxillary fragments (Fig. 2.1). Specimens VMNH 526 and 528 (Fig. 2.1) belong to the distal part of the left maxilla, while VMNH 527 (Fig. 2.1) belongs to the mesialmost part of the right maxilla. VMNH 526 and 528 include a series of four complete teeth, which are heavily worn on the occlusal surface, and have a morphology comparable to that of the holotype. The crowns of VMNH 528 are a little higher than in the other specimens (Fig. 2.1). VMNH 527 includes six complete teeth and a very small fragment of a broken tooth in the distal part of the element (Fig. 2.1). The mesialmost tooth of this specimen is very small and rounded; the following tooth is also very small and with a semioval shape. The third to sixth teeth are all transversely broadened, with a rectangular triangle shape in labial view and a heavily worn occlusal surface. Paratype VMNH 529, a maxillary fragment according to Fraser (1993), could not be located within the VMNH collection.

The heavily worn occlusal teeth surfaces in all type specimens suggest that they might belong to adult individuals (Fig. 2.1). A recent study of ontogenetic variation of the dentary in rhynchocephalians (Romo de Vivar-Martínez and Bento-Soares, 2015) demonstrates that the occlusal surface of teeth shows high wear in mature specimens.

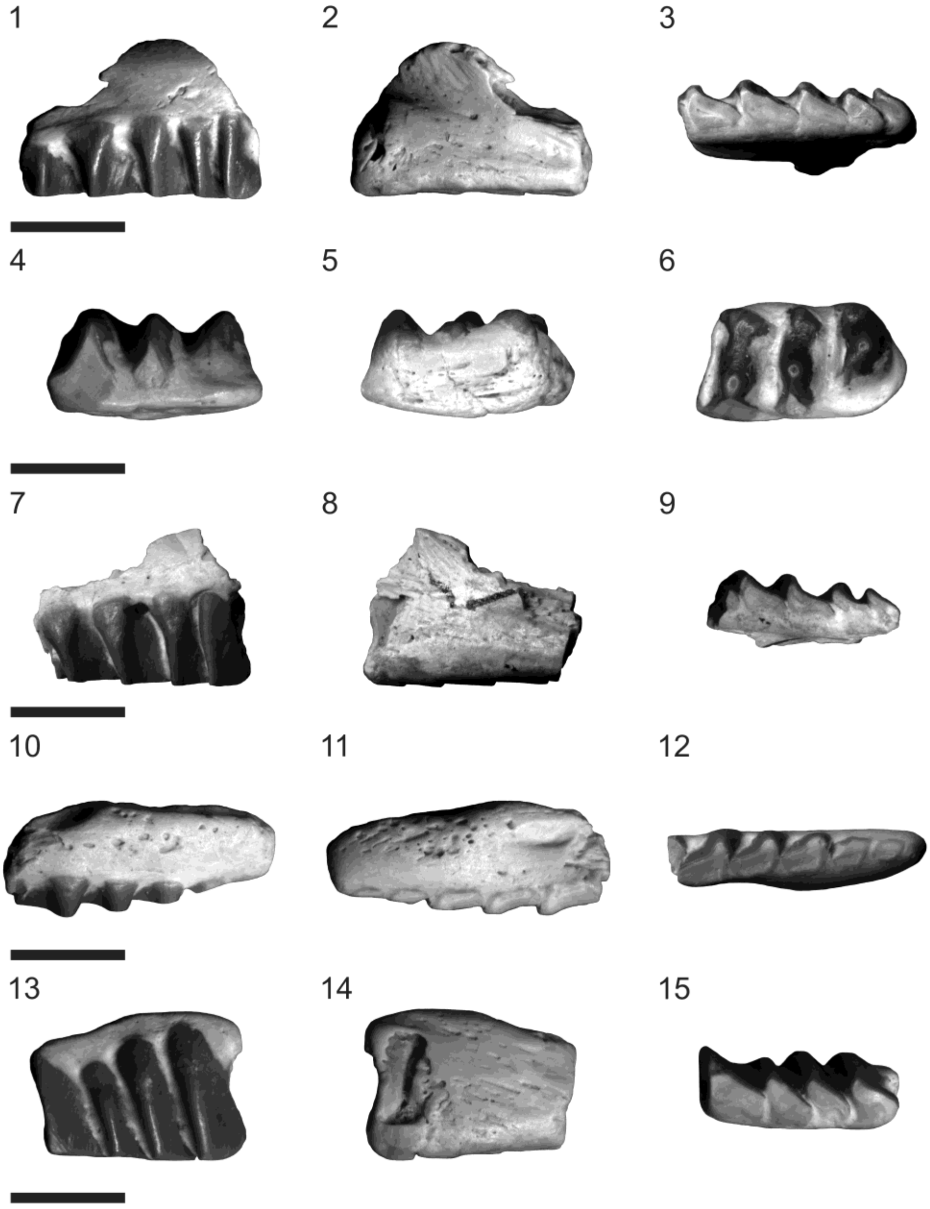

Fig 2.1. *Fraserosphenodon latidens* comb. nov. (1-3) VMNH-524, holotype, left maxilla; (4-6) VMNH-525, paratype, right dentary; (7-9) VMNH-526, paratype, left maxilla; (10-12) VMNH-527, paratype, right maxilla; (13-15) VMNH-528, paratype, left maxilla. Scale bars = 5 mm for (1-3), (7-9) and (10-12); 3.5 mm for (4-6) and (13-15). All specimens are shown in labial, lingual and occlusal views.

Additionally, another six specimens from the AUP collection can be referred to *Fraserosphenodon*. However, apart from AUP 11191 and 11192 (premaxilla and dentary, respectively), the other four specimens attributable to *Fraserosphenodon* are all fragmentary maxillary elements. All these maxillary elements were stored in containers with other rhynchocephalian specimens without being labeled individually, making it impossible to associate the specimens with unique catalog numbers. These specimens all clearly exhibit the characteristic transversely broadened tooth morphology without grooved facets on the labial teeth surfaces, with heavy wear on the occlusal surface. The first specimen is a fragment of a right maxilla. It has four heavily worn teeth that include a small rounded tooth between the second and third tooth, which might represent a dental pathology. The second specimen is a fragment of a right maxilla that includes two isolated but complete teeth. The third specimen is a fragment of a right maxilla and includes four teeth. The mesialmost tooth on this specimen is heavily eroded and the tooth enamel of the third tooth is slightly damaged. The fourth specimen is a fragment of the distal end of a left maxilla; it includes two teeth with a very short crown due to the heavy wear of the occlusal surface. Among all rhynchocephalians specimens in the AUP collection, I did not identify any dentary specimens attributable to *Fraserosphenodon* with preserved coronoid process (contra Fraser, 1993).

Specimen AUP 11191, a right premaxilla (Fig. 2.2), was originally identified as *Clevosaurus* sp. by Fraser (1988), and subsequently reassigned to *C. latidens* by Fraser (1993). The nasal process is broken in AUP 11191, but the ventral and dorsal maxillary processes are well preserved. The distal end of the ventral maxillary process has a clearly flattened oval shape; the dorsal maxillary process is relatively long and is angled at about 60^{o} relative to the ventral maxillary process. On the convex dorsal surface of the premaxilla, between the dorsal maxillary process and the nasal process, it is possible to observe the premaxillary fossa, which is semicircular in shape. AUP 11191 exhibits three complete teeth, of which the distalmost tooth is very small, considerably shorter in relation to the other two teeth. In contrast, the two mesialmost teeth are of regular size and partially fused, and both have a rounded semicircular shape with minor signs of wear. The semifused condition of the two mesialmost teeth of AUP 11191 suggests that this specimen is a juvenile: as seen in other derived rhynchocephalians (e.g. *Clevosaurus* and *Sphenodon*) these teeth fuse over time in mature individuals to form the characteristic chisel-like structure seen in late-diverging rhynchocephalians (Robinson, 1973).

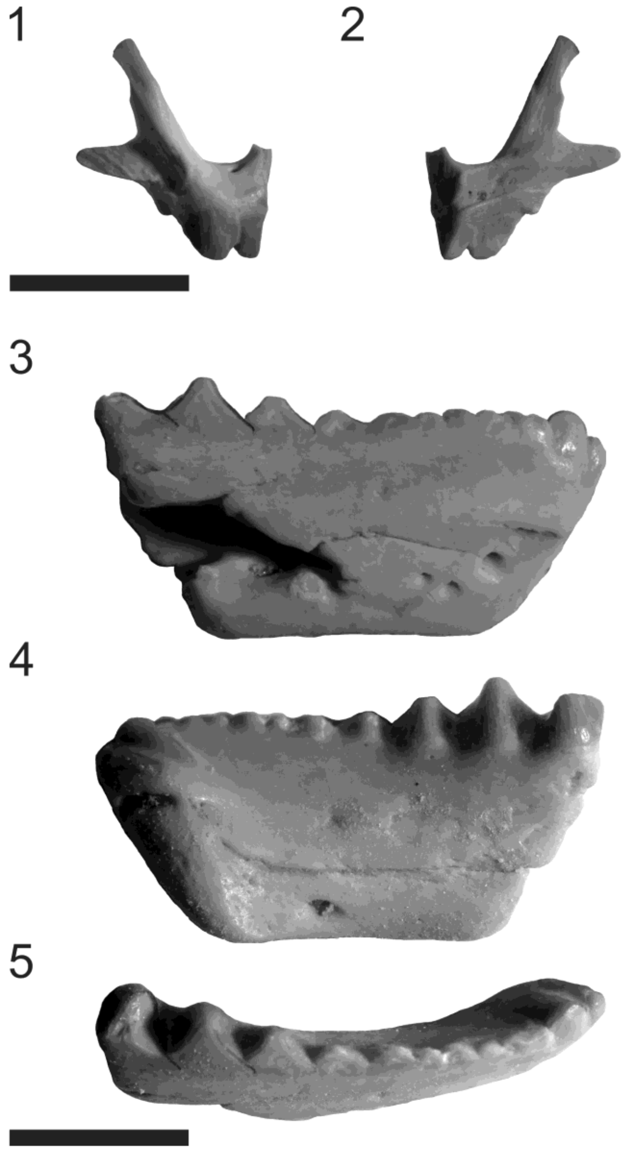

Fig 2.2. *Fraserosphenodon latidens* comb. nov. (1-2) AUP 11191, right premaxilla. Scale bar = 6 mm; (3-5) AUP 11192, right dentary. Scale bar = 3.5 mm. (1-2) shown in labial and lingual views; (3-5) shown in labial, lingual and occlusal views.

Specimen AUP 11192, an anterior fragment of a right dentary (Fig. 2.2), was tentatively assigned to *Pelecymala* by Fraser (1986), but as in the case of AUP 11191, it was later referred to *C. latidens* by Fraser (1993). In the description of AUP 11192, Fraser (1986) noticed that the length of this specimen appeared to be quite similar to that of *C. hudsoni*, but noticeably deeper in height. AUP 11192 has a robust and deep structure, similar to that of opisthodontians (e.g. *Priosphenodon*, *Toxolophosaurus*). The mandibular symphysis in AUP 11192 is quite wide; the Meckelian canal runs along the midline of the jaw. The specimen includes three generations of teeth, but caniniform teeth are lacking. The front of AUP 11192 has two successional teeth of rounded shape similar to those of the premaxilla. These teeth are followed by a series of six to seven small semicircular remnants of hatchling teeth with minor signs of wear on the occlusal surfaces. On the distal end of this element, I find three or four additional teeth that in both labial and lingual view show the same triangular shape as seen in VMNH 525. In occlusal view, the teeth of AUP 11192 show heavy signs of wear and the round and bulbous shape also seen in VMNH 525. This round and bulbous shape is more pronounced in the distalmost additional tooth of AUP 11192. Additionally, AUP 11192 includes three mental foramina of relatively large size (Fig. 2.2), which suggest this specimen comes from a juvenile. The length and height of AUP 11192, as preserved, are 10.5 mm and 5.4 mm respectively.

2.4 Phylogenetic analyses

The parsimony analysis found 7176 MPTs of 265 steps, and the 50% majority rule consensus tree shows good resolution for most clades (Fig. 2.3). The consistency (CI) and retention indices (RI) for the 50% majority rule consensus tree are: CI = 0.38628 and RI = 0.66403. No clade had a Bremer support score greater than 1 (complete statistics and associated files for both phylogenetic analyses can be found in the “Appendix”). Generally, my results agree with other recent studies (Rauhut et al. 2012; Martínez et al. 2013; Apesteguía et al. 2014; Cau et al. 2014; Hsiou et al. 2015). One of the major differences is that our analysis recovers Pleurosauridae as the sister group of Sphenodontidae. The terrestrial *Pamizinsaurus* is the earliest diverging taxon within Sphenodontidae, which includes two major clades. The first clade includes *Ankylosphenodon, Derasmosaurus, Oenosaurus* and *Zapatadon* in a polytomy, while the second clade is well resolved, recovering the Early Jurassic *Cynosphenodon* and the modern *Sphenodon* as successive sister taxa to the clade comprising *Theretairus* and *Sphenovipera*. The strict consensus tree of the second analysis of Cau et al. (2014) also found *Derasmosaurus*, *Oenosaurus* and *Zapatadon* in a similar polytomy, and forming the sister group of the clade comprising *Sphenodon, Cynosphenodon, Sphenovipera, Kawasphenodon* and *Theretairus*. The close relationship of *Sphenovipera* and *Theretairus* has been constantly recovered in previous analyses (e.g. Martínez et al. 2013; Apesteguía et al. 2014; Hsiou et al. 2015).

Within clevosaurs, *Brachyrhinodon* is recovered as the earliest diverging taxon. All *Clevosaurus* species are grouped in a polytomy, which obscures the relationships between the species. The results for clevosaurs are quite similar to those recovered by the strict consensus tree of Hsiou et al. (2015). The only difference is that in their analysis *Polysphenodon* appears as the earliest diverging taxon within Clevosauridae, but all other taxa are recovered in a polytomy. A similar polytomy for clevosaurs was also shown by the strict consensus tree of Rauhut et al. (2012). My results agree with the work of Martínez et al. (2013) and Hsiou et al. (2015) in recovering *F. latidens* as an early diverging opisthodontian. Indeed, I recover *F. latidens* as the earliest diverging taxon within Opisthodontia. This clearly confirms that *F. latidens* is not referable to the genus *Clevosaurus*, and supports the erection of a new opisthodontian genus, as previously suggested (Jones, 2006a, 2009; Martínez et al. 2013; Hsiou et al. 2015; Klein et al. 2015). Within Opisthodontia, the relationships of eilenodontines are quite well resolved; my results only differ from the works of Martínez et al. (2013) and Cau et al. (2014) in finding *Ankylosphenodon* outside Opisthodontia.

Another major difference compared to the previous analyses of Martínez et al. (2013) and Hsiou et al. (2015) is that the Triassic taxon *Pelecymala* is no longer recovered as closely related to Opisthodontia, but is found in a polytomy with early-diverging rhynchocephalians such as *Rebbanasaurus*, the clade *Sphenocondor* and *Godavarisaurus*, and the clade Eusphenodontia.

Overall, the results of the Bayesian analysis (Fig. 2.3) resemble those of the parsimony analysis, but with considerably less resolution. Several large polytomies are recovered, but where clades are resolved, the clade credibility values are often moderately high. The Bayesian 50% majority rule consensus tree also recovers *Pelecymala* in a polytomy with early diverging rhynchocephalians, which confirms that this taxon is not related to opisthodontians as was previously assumed (Martínez et al. 2013; Hsiou et al. 2015). The Bayesian tree does not recover clevosaurs as a monophyletic group; all of them are recovered in a large polytomy that obscures the relationships between the taxa. Relationships among other later diverging rhynchocephalians are unclear; many of them are part of a polytomy that includes *Fraserosphenodon*, but no clevosaurs. This result confirms that *Fraserosphenodon* is not closely related to *Clevosaurus*.

It should be noted that the Bayesian tree recovers a close relationship between the extant *Sphenodon* and the Jurassic *Cynosphenodon*, a close relationship between *Theretairus* and *Sphenovipera*, and pleurosaurs as a monophyletic group. The Bayesian tree does not recover Opisthodontia as a monophyletic group, but completely agrees with the parsimony tree for the interrelationships of eilenodontines, which are quite robust and well resolved.

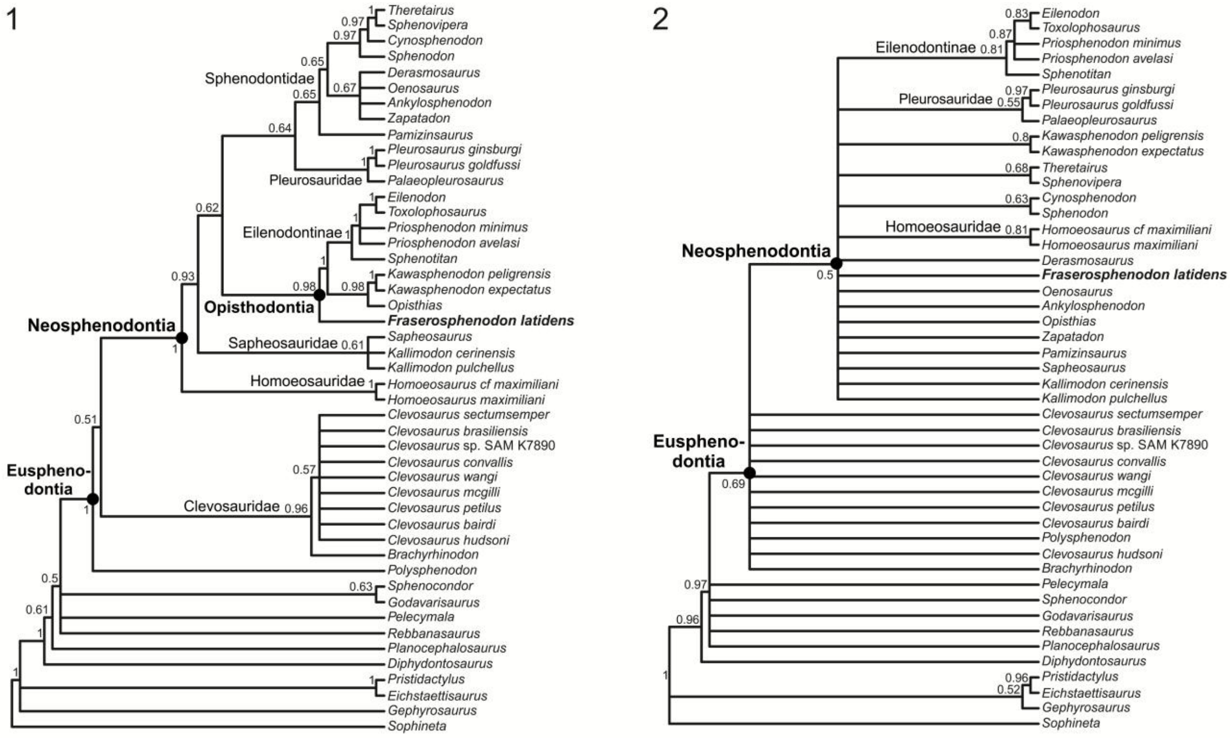

Fig 2.3. Consensus trees recovered from the phylogenetic analyses. (1) Maximum parsimony 50% majority rule consensus tree. The consistency (CI) and retention indices

(RI) for the 50% majority rule consensus tree are: CI = 0.38628 and RI = 0.66403. Node labels denote the proportion of MPTs which recover that node. (2) 50% majority rule consensus tree from the Bayesian-inference analysis, with clade credibility values (decimal proportions) labeled on nodes.

2.5 Discussion

Among Mesozoic rhynchocephalians, clevosaurs were one of the most diverse groups. Clevosaurs are represented by three genera *Polysphenodon*, *Brachyrhinodon* and *Clevosaurus*. The first two genera are monospecific, while *Clevosaurus* has currently nine formally recognized species. The high diversity of the genus *Clevosaurus*, however, is debatable because of the doubtful validity/referral of some of the species, especially those based on poorly preserved or very fragmentary material, such as the three Chinese species (*C. mcgilli*, *C. petilus* and *C. wangi*) or "*C. latidens"* from Great Britain. According to Jones (2006a), the Chinese specimens are too poorly preserved to diagnose them as three distinct species, but clearly all of them belong to *Clevosaurus*. In contrast to the Chinese specimens, the referral of "*C. latidens"* to *Clevosaurus* has been widely questioned (Jones, 2006a, 2009; Martínez et al. 2013; Hsiou et al. 2015; Klein et al. 2015).

Before the description of "*C. latidens"*, specimen AUP 11192, a dentary fragment, was tentatively related to *Pelecymala* based on its transversally wide teeth (Fraser, 1986). When Fraser (1993) formally described "*C. latidens"*, he noted that the tooth morphology of the new "*Clevosaurus*" species was quite similar to that of other taxa with transversely wide teeth such as *Pelecymala robustus* and *Toxolophosaurus cloudi* (Fraser, 1993). Some of the diagnostic characters of the genus *Clevosaurus* based on features of the skull could not be observed in "*C. latidens"* for obvious reasons. However, at least the dentition of "*C. latidens*" did not match that of *Clevosaurus*, which consists of larger, blade-like teeth with lateral flanges. It has been suggested that the tooth morphology of *Clevosaurus* was very specialized for a possible omnivorous or carnivorous diet (Jones 2006b, 2009; Rauhut et al. 2012; Martínez et al. 2013), whereas the dentary and maxillary teeth *"C. latidens"* were more like those of herbivorous taxa. Fraser (1993) also pointed out that the wear facets on teeth of "*C. latidens*" suggested a propalinal movement of the lower jaw, which contrasts with the orthal jaw movement seen in *Clevosaurus*.

Based on dentary, maxillary and premaxillary tooth morphology, as well as the suggested propalinal movement of the lower jaw, my review of "*C. latidens*" specimens confirms that this taxon is not referable to *Clevosaurus*. Our phylogenetic analyses, including both parsimony and Bayesian approaches, confirm its position outside *Clevosaurus*. I rename "*C. latidens*" as *Fraserosphenodon latidens* comb. nov. The parsimony tree (Fig. 2.3) suggests that *F. latidens* is an early diverging opisthodontian, but not closely related to *Pelecymala* as had previously been suggested by Fraser (1986, 1993), Martínez et al. (2013), and Hsiou et al. (2015). When reviewing the type specimens of *Pelecymala* (AUP 11140, 11214-11215), I noticed that the teeth in *Pelecymala* are not transversely broadened as had been described by Fraser (1986), and in contrast their shape is more conical, slightly curved, and labiolingually flattened. The tooth morphology of *Pelecymala* is actually more similar to some of the earliest diverging rhynchocephalians, which is also confirmed by our phylogenetic analyses (Fig. 3). A complete taxonomic redescription of *Pelecymala* appears necessary, but, is beyond the scope of this study. The Bayesian tree (Fig. 2.3) could not recover the exact relationships of *F. latidens*, as this taxon is found in a polytomy that includes many other species. Like the parsimony analysis, however, the Bayesian approach recovers *F. latidens* as a genus that is distinct from *Clevosaurus* and not closely related to clevosaurs. Following the parsimony analysis, we consider *F. latidens* as an early diverging opisthodontian.

The parsimony analysis of Rhynchocephalia showed better resolution than the Bayesian approach. This result is not unexpected, as studies have shown that Bayesian methods are more accurate but less precise than parsimony-based analyses (O'Reilly et al. 2016). There are some minor differences between the internal branches in both trees, but several higher clades are recognized by both phylogenetic methods (Fig. 2.3). Some of these higher clades within Rhynchocephalia have been frequently recovered in other recent phylogenetic analyses, and have been informally named as "crown-sphenodontians", "derived-sphenodontians" and "eupropalinals" (e.g. Apesteguía et al. 2012, 2014; Apesteguía and Carballido, 2014).

I propose formal names for two well supported clades: Eusphenodontia and Neosphenodontia (Fig. 2.3). These two major clades are recovered with relatively high clade credibility values in the Bayesian tree. I define Eusphenodontia as the least inclusive clade containing *Polysphenodon muelleri*, *Clevosaurus hudsoni* and *Sphenodon punctatus*. In the 50% majority rule consensus tree, three unambiguous character transitions are recovered for Eusphenodontia under both ACCTRAN and DELTRAN optimization: wear facets on marginal teeth of the dentary and/or on marginal teeth of the maxilla are clearly visible (character 46: 0 to 1), the premaxillary teeth are merged into a chisel-like structure (character 49: 0 to 1), and the palatine teeth are reduced to a single tooth row with an additional isolated tooth (character 52: 0 to 1). Neosphenodontia is defined as the most inclusive clade containing *Sphenodon punctatus* but not *Clevosaurus hudsoni*. In the 50% majority rule consensus tree, Neosphenodontia is supported by the following six unambiguous character changes that are recovered under both ACCTRAN and DELTRAN optimization: the relative length of the antorbital region increases, reaching one quarter to a third of the complete skull length (character 1: 2 to 1), the posterior edge of the parietal is only slightly incurved inward (character 18: 0 to 1), the parietal foramen is found at the same level or anterior of the anterior border of the supratemporal fenestra (character 19: 0 to 1), the palatine teeth are further reduced to a single lateral row (character 52: 1 to 2), the number of pterygoid tooth rows is reduced to one or none (character 55: 1 to 2), and the ischium is characterised by a prominent process on its posterior border (character 60: 1 to 2). The families Homoeosauridae, Pleurosauridae and Sphenodontidae form in our analyses, as in others, the content of the stem-group Neosphenodontia. Levels of homoplasy in Eusphenodontia and Neosphenodontia are generally high, with individual character consistency indices (CI) often less than 0.5. For both clades, no individual character has a CI of 1 in the 50% majority rule consensus tree (for the complete list of characters, apomorphies and other tree statistics see the “Appendix”). Even if the support values are not high enough especially to the parsimony tree, I am confident enough to name the two new major clades which have been consistently recovered in previous analysis. However, in order to get a more reliable picture and improving the resolution and support values, future analysis should consider the addition of multiple squamate outgroups and not only two taxa as has been frequently used. I consider the formal naming of these higher clades necessary to facilitate future discussion about the phylogenetic relationships of rhynchocephalians.

2.6 Conclusion

This study confirms previous doubts about the referral of “*C. latidens*” to *Clevosaurus*. The recognition of “*C. latidens*” as a new genus now formally named *Fraserosphenodon* emphasizes the high generic diversity of Rhynchocephalia in the Mesozoic, especially among herbivorous taxa. Furthermore, my study demonstrates that the use of Bayesian approaches can be useful to contrast and validate phylogenies that previously were based only on parsimony methods. Bayesian inference exhibits generally lower resolution in some parts of the tree, but a few higher clades are strongly supported and are consistently recovered by both Bayesian and parsimony analyses.

2.7 Appendix

2.7.1 Character list

(1) Antorbital region, length relative to skull length: one-third or more (0); between one-fourth and one-third (1); one fourth or less (2).

(2) Orbit, length relative to skull length: one third or greater (0); less than one third (1).

(3) Supratemporal fenestra, length relative to orbit length: less than 75% (0); 75% or greater (1).

(4) Supratemporal fenestra, length relative to skull length: one-fourth or less (0); more than one-fourth (1).

(5) Lower temporal fenestra, length relative to skull length: one-fourth or less (0) ; more than one-fourth (1).

(6) Maxilla, premaxillary process: elongate (0); reduced (1).

(7) Maxilla, participation in margin of external naris: entering into margin (0); excluded from margin by posterodorsal process of premaxilla (1).

(8) Maxilla, shape of posterior end: tapering posteriorly or very narrow (0); dorsoventrally broad (1).

(9) Lacrimal: present (0); absent (1).

(10) Jugal, shape of dorsal process: broad and short (0); narrow and elongate (1).

(11) Prefrontal and postfrontal, profuse sculpture on bone surface: absent (0); present

(1).

(12) Prefrontal-jugal contact: absent (0); present (1).

(13) Postorbital, marked dorsal ridge and deep ventrolateral concavity: absent (0); present (1).

(14) Frontals, relation: separated (0); fused (1).

(15) Parietals, relation: separated (0); fused (1).

(16) Parietal, width between supratemporal passages relative to interorbital width: broader (0); narrower (1).

(17) Parietal crest: absent (0); present (1).

(18) Parietal, shape of posterior edge: greatly incurved inward (0); slightly incurved inward (1); convex (2).

(19) Parietal foramen, position relative to anterior border of supratemporal fenestra: posterior (0); at the same level or anterior (1).

(20) Lower temporal bar, position: aligned with the maxillary tooth row (0); bowed away beyond the limit of the abductor chamber (1).

(21) Lower temporal bar, posteroventral process of jugal: absent (0); poorly- to moderately-developed, less than half the length of the lower temporal fenestra (1); well-developed, half the length of the lower temporal fenestra or more (2).

(22) Palatine, shape of posterior end: tapers posteriorly (0); widens posteriorly (1).

(23) Pterygoids, anterior contact between bones*: absent (0); small (1); broad (2).

(24) Pterygoids, posterior opening of the interpterygoid vacuity between posteromedial processes: widely open (0); moderately open, as wide as the vacuity (1); almost closed by the posteromedial processes (2).

(25) Pterygoid, central region between three rami: short (0); elongate (1).

(26) Pterygoid, participation in margin of suborbital fenestra: form part of the margin (0); excluded from margin (1).

(27) Quadrate-quadratojugal foramen, relative size: small (0); large (1).

(28) Quadrate-quadratojugal foramen, location: between the quadrate and the quadratojugal (0); entirely within the quadrate (1).

(29) Quadrate-quadratojugal emargination, shape: pronounced (0); reduced (1).

(30) Supratemporal, as a discrete bone: present (0); absent (1).

(31) Inferred jaw motion: orthal (0); propalinal (1).

(32) Degree of propalinality, measured either as palatal tooth row extension or length in which palatines keep parallel to the maxillae: small palatal row, parallel line restricted to the anterior region (0); enlarged, palatines accompanying maxilla half its own length (1); palatines accompanying maxilla by its complete length, 'eupropalinality' (2).

(33) Mandibular symphisis, mentonian process*: absent (0); reduced (1); well-developed and pointed (2); well-developed and rounded (3).

(34) Mandibular symphysis, shape: almost circular, high/length relation near one (0); oval, high/length clearly greater than one (1).

(35) Mandibular symphysis, angle between anterior margin and longitudinal axis of the mandible in lateral view: <120º, symphysis nearly vertical, typically devoid of ventral projections (0); ≥120º, symphysis anterodorsally projected (1).

(36) Mandibular symphysis, symphysial spur: absent (0); well-developed, anterodorsally projected (1); moderately developed (2).

(37) Mandibular foramen, relative size: small (0); large (1).

(38) Glenoid cavity, shape: smooth surface, lacking an anteroposterior central ridge (0); elongate and asymmetrical surface, with a strong anteroposterior central ridge

(1); symmetrical facet with a strong anteroposterior central ridge (2).

(39) Coronoid process, height relative to that of the jaw at the level of the anterior end of the coronoid process: low, weak, less than half the jaw (0); high, equal or more than half the jaw height (1).

(40) Retroarticular process, shape: pronounced (0); reduced, caudally projected (1); reduced, dorsally curved (2).

(41) Dentary, posterior process, relative length: short, not reaching glenoid level (0); elongate, reaching glenoid level (1); elongate, reaching the end of glenoid level (2).

(42) Marginal dental implantation, type: pleurodont (0); degree of posterior acrodonty (1); fully acrodont (2).

(43) Tooth replacement, type: alternate (0); addition at back of jaw (1).

(44) Dentary regionalization with small juvenile teeth (hatchling) in the anterior region of maxilla and dentary: absent, only pleurodont teeth (0); present, with hatchling pleurodont teeth (1); present, with hatchling, successional and additional acrodont teeth (2); absent both in juveniles and adults, only additional acrodont teeth (3).

(45) Dentary, posterior successionals, number in mature individuals: zero (0); one (1); two or more (2).

(46) Marginal teeth, lateral wear facets on dentary and/or medial wear facets on maxilla: absent or smooth (0); present, conspicuous (1).

(47) Marginal teeth, shape of cross section of posterior teeth: nearly circular (0); squared (1); rectangular, wider than long (2).

(48) Premaxillary teeth, number in mature individuals: more than seven (0); seven to four (1); three or less (2).

(49) Premaxillary teeth, general organization in adults: present as discrete teeth (0); merged into a chissel-like structure (1).

(50) Maxillary teeth, posteromedial flanges on posterior teeth: absent or inconspicuous (0); present as small flanges on at least one tooth (1); present as extensive flanges on most teeth (2).

(51) Maxillary teeth, anterolateral flange on posterior teeth: absent (0); present (1).

(52) Palatine teeth, number of tooth rows: two or more (0); a single row plus one isolated tooth (1); a single lateral row (2).

(53) Palatine teeth, flanges: completely absent (0); present at least on a few teeth (1).

(54) Palatine teeth, hypertrophied tooth on anterior region of the palatine bone (stabbing palatine): absent (0); present (1).

(55) Pterygoid teeth, number of tooth rows*: three or more (0); two (1); one or none (2); radial crests (3).

(56) Mandibular teeth, anterolateral flanges: absent (0); present, at least in one tooth (1).

(57) Mandibular teeth, anteromedial flanges: absent (0); present (1).

(58) Mandibular teeth, additionals, enamel ornamentation in adults*: absent (0); present, with numerous fine striae (1); present, with a combination of a few striae and wide grooves (2).

(59) Second sacral vertebra, posterior process: absent (0); present, small (1); present, prominent (2).

(60) Ischium, process on posterior border: absent (0); present as small tubercle (1); present as prominent process (2).

(61) Humerus, length relative to length of presacral column*: <0.12 (0); between 0.12 and 0.21 (1); > 0.21.

(62) Humerus, shape, relation between minimum width of the diaphysis (DW) and maximum length of bone (HL): DW/HL ≤ 0.11 (0); DW/HL > 0.11 (1).

(63) Humerus, shape, relation between minimum width of the diaphysis (DW) and maximum width of distal epiphysis (EW): DW/EW < 0.28 (0); DW/EW between 0.28−0.35 (1), DW/EW > 0.35 (2).

(64) Dentary, proportions (pre-coronoid length/ maximum pre-coronoid height ratio, L/H): gracile, long and low, L/H < 0.18 (0); average, L/H between 0.18−0.28 (1), robust, short and high, L/H > 0.28 (2).

(65) Dentary, successional teeth, maximum concurrent number during ontogeny: six or more (0); three to five (1); two or less (2).

(66) Dentary, anterior successional teeth (not 'caniniform'), number in the adult: two or more clearly discrete teeth (0); one or two poorly distinct (1); none or indistinct (2).

(67) Dentary, successional teeth, striation: present (0); absent (1).

(68) Dentary, posterior successional teeth, lingual groove: absent (0); present (1).

(69) Dentary, hatchling teeth, striation: absent (0); present (1).

(70) Dentary, successional 'caniniform' teeth, shape of basal cross section: nearly circular (0); clearly oval, labio-lingually compressed (1).

(71) Mandibular teeth, additionals, grooves or fossae on labial or lingual sides: absent (0); present (1).

(72) Mandibular teeth, additionals, posterior groove: absent (0); wide and poorly-defined (1); relatively deep and well-defined (2).

(73) Maxilla, facial process, shape of anterior margin relative to main axis of maxilla: low slope, straight or concave (0); high slope, in straight angle (1); high slope, continuous and concave (2); high slope, continuous and convex (3).

(74) Maxilla, facial process, maximum high (FH) with respect to length of maxilla posterior to this point (MPL): FH/MPL < 0.45 (0); FH/MPL between 0.45−0.7 (1); FH/MPL > 0.7 (2).

2.7.2 Data matrix

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xread
74 47
Sophineta
00010000?0??00000?0?0???00??????00?0?????00???????????????????????????0000
Eichstaettisaurus
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Pristidactylus
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Gephyrosaurus
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1
Diphydontosaurus
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Planocephalosaurus
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2]00?1?0010
Rebbanasaurus
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Godavarisaurus
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2]01021??100?????[01]10010100??
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2]??2??????2??1?????????
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Pleurosaurus_ginsburgi
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Brachyrhinodon
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Clevosaurus_hudsoni
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Kallimodon_pulchellus
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Kallimodon_cerinensis
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Pamizinsaurus
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1]??102??2????????12?????????0
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Opisthias
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Toxolophosaurus
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Eilenodon
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Clevosaurus_wangi
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Fraserosphenodon_latidens
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Sphenotitan
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Pelecymala
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Priosphenodon_minimus
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Derasmosaurus
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Clevosaurus_sectumsemper
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;


proc /;
comments 0
;
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2.7.3 PAUP summary

```
Delayed transformation (DELTRAN)
50% MAJ RULE CONCENSUS
Eusphenodontia
Apomorphy lists
\----75 TO +---74
Branch                    Character     Steps     CI   Change
node_75 --> node_74        1            1   0.154  0 --> 2
                           8            1   0.200  0 --> 1
                          14            1   0.500  1 --> 0
                          26            1   0.250  0 --> 1
                          46            1   0.500  0 ==> 1
                          49            1   0.333  0 ==> 1
                          52            1   0.500  0 ==> 1

Neosphenodontia
Apomorphy lists
/----73  TO /---70
Branch                    Character     Steps     CI   Change
node_73 --> node_70        1            1   0.154  2 ==> 1
                          18            1   0.400  0 ==> 1
                          19            1   0.250  0 ==> 1
                          50            1   0.286  1 --> 2
                          52            1   0.500  1 ==> 2
                          55            1   0.429  1 ==> 2
                          60            1   0.500  1 ==> 2

##########################################################################
##########

Accelerated transformation (ACCTRAN)
50% MAJ RULE CONCENSUS
```

Eusphenodontia

```
Apomorphy lists
 \----75 TO  +---74
Branch                     Character     Steps     CI   Change
node_75 --> node_74      35              1   0.200  0 --> 1
                         45              1   0.667  2 --> 0
                         46              1   0.500  0 ==> 1
                         49              1   0.333  0 ==> 1
                         52              1   0.500  0 ==> 1
                         53              1   0.167  1 --> 0
                         66              1   0.667  0 --> 2
                         67              1   0.500  0 --> 1
                         70              1   0.667  1 --> 0
```

Neosphenodontia

```
Apomorphy lists
/----73  TO /---70
Branch                     Character     Steps     CI   Change
node_73 --> node_70      1              1   0.154  2 ==> 1
                         10              1   0.200  1 --> 0
                         13              1   0.500  0 --> 1
                         18              1   0.400  0 ==> 1
                         19              1   0.250  0 ==> 1
                         27              1   0.500  0 --> 1
                         52              1   0.500  1 ==> 2
                         55              1   0.429  1 ==> 2
                         60              1   0.500  1 ==> 2
                         61              1   0.333  1 --> 2
                         65              1   0.667  1 --> 2
```

Chapter 3

Macroevolutionary patterns in Rhynchocephalia: is the tuatara (*Sphenodon punctatus*) a living fossil?

A version of this chapter was published in *Palaeontology*, in collaboration with Thomas L. Stubbs and Michael J. Benton. https://doi.org/10.1111/pala.12284 M. J. Benton and T. L. Stubbs provided general supervision as well as training in the use of methods in R. I collected the data and carried out all analyses and wrote the MS and final paper. Therefore, we agree an estimate that the chapter represents 80% of my own independent work.

3.1 Introduction

The Rhynchocephalia is an ancient group of reptiles that emerged during the Early or Middle Triassic (Jones et al. 2013). They are unusual among the 10,000 species of living reptiles, being ranked at times as an order equivalent to the Crocodilia, Squamata, and Testudines (Pough et al. 2012), but represented today by a single species, *Sphenodon punctatus* (Hay et al. 2010; Jones and Cree, 2012; Cree, 2014). This species is geographically restricted to the islands of New Zealand, and it is best known by its vernacular name ‘Tuatara’. *S. punctatus* was first described by J. E. Gray in 1831, but he misidentified it as an agamid lizard (Sharell, 1966; Robb, 1977; Cree, 2014). A few years later, Günther (1867) noted its similarities with some fossil forms, and in consequence erected the Order Rhynchocephalia, which has long been identified as sister clade to Squamata, the much larger clade comprising lizards and snakes.

Sphenodon punctatus has often been identified as a ‘living fossil’ (Fraser, 1993; Sues et al. 1994; Jones, 2008; Jones et al. 2009; Meloro and Jones, 2012; Cree, 2014) for a variety of reasons: (1) the living form, superficially, seems little different from its distant Mesozoic ancestors; (2) the clade has had a very long duration, but with low diversity and possibly long-lived species and genera; (3) it is the solitary sister clade to the equally ancient Squamata, comprising over 9000 species; (4) there is a long gap in geological time between the modern form and the youngest fossil forms, in the Miocene, Palaeocene, and Cretaceous; and (5) it shows supposedly ‘primitive’ anatomical features such as the closed lower temporal bar.

This view has been disputed because, during the last three decades, many fossil species of rhynchocephalians have been described, so partially rejecting reason (2) above. Several of these newly described species show a wide variety of ecological adaptations, either to terrestrial or marine environments (e.g. *Pamizinsaurus*, *Pleurosaurus*), as well as a diverse array of dietary preferences (Jones, 2008, 2009; Meloro and Jones, 2012; Rauhut et al. 2012; Martínez et al. 2013). These observations contradict the common view of the Rhynchocephalia as a morphologically unchanged group, reason (1) above, and suggest that it had high diversity and morphological disparity through time (Sues et al. 1994; Reynoso, 1997; Reynoso, 2000; Evans et al. 2001; Reynoso, 2005; Jones, 2008; Jones et al. 2009; Apesteguía and Jones, 2012; Cree, 2014). Also, recent work on the extant *Sphenodon* indicates that it is not as conservative as was previously believed (Jones, 2008;

Meloro and Jones, 2012; Cree, 2014), with a presumably secondarily fused lower temporal bar (Whiteside, 1986), thus rejecting reason (5) above. However, the traditional view of the Rhynchocephalia as an unchanged group through time still dominates in textbooks and other sources (e.g. Sharell, 1966; Robb, 1977; Mitchell et al. 2008), despite the lack of clarity over the definition of what is a 'living fossil'. Reseachers may agree on which taxa are 'living fossils' (e.g. Schopf, 1984; Casane and Laurenti, 2013), but there is no testable definition.

The concept of 'living fossils' has been problematic since the term was coined by Charles Darwin (1859), as there is no such identifiable class of organisms, but oft-cited examples do share some or all of the noted features. Note that the phrase 'relict species' encapsulates some characteristics of 'living fossils', referring to a species or a group of species that remains from a large group that is mainly extinct (Grandcolas et al. 2014).

Here, I propose a hypothesis that can be tested by computational morphometric and phylogenetic comparative methods (PCM): 'a living fossil should show both statistically significantly slow rates of morphological evolution and it should be morphologically conservative.' The first measure is assessed with respect to sister taxa and sister clades, and using standard PCM approaches for assessing the statistical significance of evolutionary rates. The second measure of morphological conservatism can be assessed by determining whether the taxon lies close to the early, or geologically earliest, members of its clade or close to the centroid of the hyperdimensional morphospace. The distance of each species from the centroid can be measured, but there is no agreed statistical test to distinguish classes of morphological conservatism, just that the taxon in question is closer to the centroid than other taxa are, perhaps closer to the centroid than the majority of taxa, including fossil forms.

I explore here the morphological disparity of all the Rhynchocephalia, and where the extant *Sphenodon* fits within the clade. Based on a phylogenetic analysis of the whole clade, I identify rates of morphological evolution and changes in morphospace using geometric morphometrics of the lower jaw, and I find evidence that *Sphenodon* evolved slowly, and is morphologically conservative when compared to extinct rhynchocephalians, especially the earliest forms.

3.2 Methods

3.2.1 Phylogeny of Rhynchocephalia

To construct a phylogeny for Rhynchocephalia and explore evolutionary rates, I used the recently published data matrix of 32 taxa and 74 discrete morphological characters from Apesteguía et al. (2014). I ran a Maximum Parsimony analysis with TNT v. 1.1 (Goloboff et al. 2008) following the settings of Apesteguia et al. (2014), and as a result I recovered the same 22 MPTs of 218 steps as they did. All MPTs were reduced to a time-scaled strict consensus tree (Fig. 3.1). The discrete morphological character data matrix and 22 MPTs were used later for evolutionary rates analyses using the methods described below.

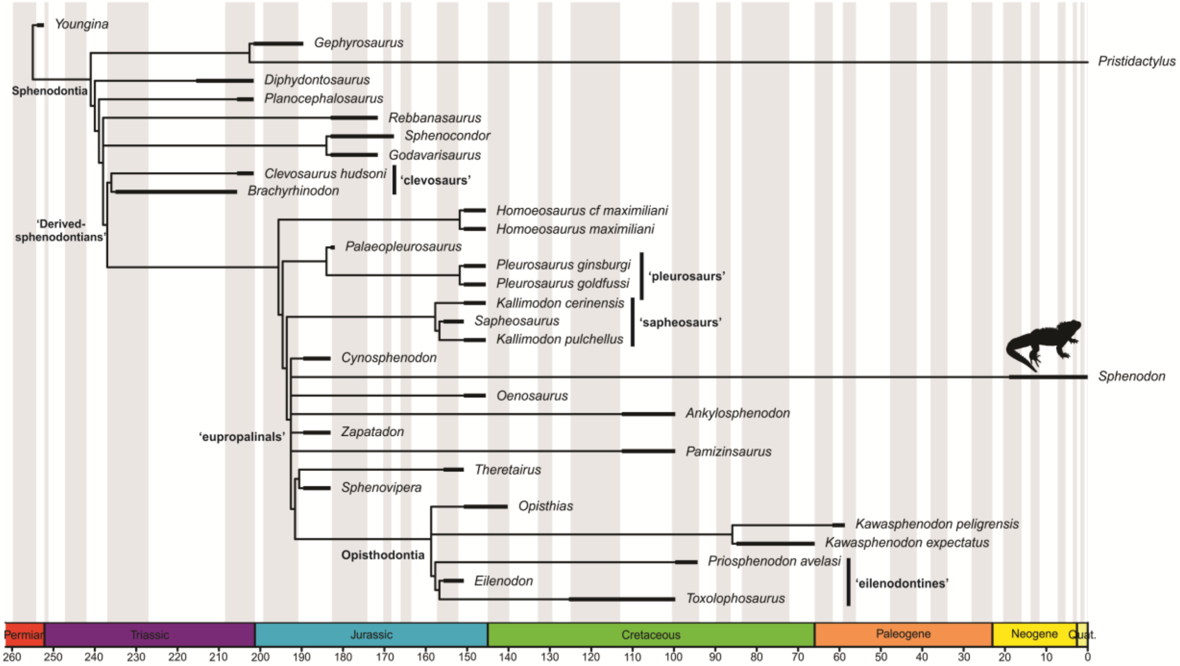


Fig. 3.1. Time-scaled phylogeny of Rhynchocephalia, based on a strict consensus tree of 22 most parsimonious trees. Note that *Youngina* and extant *Pristidactylus* are outgroups to Rhynchocephalia. Abbreviation: Quat., Quaternary.

3.2.2 Evolutionary rates

Rates of morphological evolution were investigated using maximum-likelihood methods, following the protocols of Lloyd et al. (2012), Brusatte et al. (2014) and Wang and Lloyd (2016). I first time-scaled my MPTs, establishing ages for terminal taxa by compiling ages

(FAD, first appearance date and LAD, last appearance date) for each taxon using the Paleobiology Database and the literature, to determine the latest consensus view on the ages of relevant geological formations. Following the work of Brusatte et al. (2014) and Wang and Lloyd (2016), I used two current available methods for determining the dates of nodes and branch durations, the ‘equal’ and ‘minimum branch length’ (mbl) methods. For both methods, I used the settings recommended by Brusatte et al. (2014) and Wang and Lloyd (2016), with a fixed duration of 1 Myr for the ‘minimum branch length’ method and 2 Myr for a root-length of the ‘equal’ method. When dating the trees I used a randomization approach, and performed 100 replicates to incorporate potential uncertainty arising from sampling each terminal taxon’s age randomly from between their first and last appearance dates. This generated 100 time-scaled phylogenies for each of the 22 MPTs, and for both the ‘equal’ and ‘mbl’ methods. Before running the rates analyses I excluded the extant squamate *Pristidactylus*. Using all the time-scaled phylogenies and the discrete morphological character data, I assessed whether rates of morphological evolution were homogeneous, or if particular branches or clades have significantly low or high rates relative to the remainder of the tree (Lloyd et al. 2012). Comparative rates were assessed using Likelihood ratio tests (LRTs) between single rate models (homogenous rates) and two rate models (particular branch has different rates to the rest of the tree). An alpha threshold of 0.01 was used to evaluate significance, with Benjamini-Hochberg false discovery rate correction. Sensitivity tests were performed with *Sphenodon* removed from the tree and character data, to ensure that the long terminal branch associated with *Sphenodon* was not biasing the rates results. All analyses were performed in R (R team, 2015), using the packages paleotree (Bapst, 2012) and Claddis (Lloyd, 2016), and with a modified version of the script of Wang and Lloyd (2016).

To illustrate the evolutionary rates results, I figure one MPT for both the ‘equal’ (MPT 1) and ‘mbl’ (MPT 6) analyses. Pie charts are used to indicate the proportion of significantly high (red) and significantly low (blue) per-branch rates results, based on the 100 dating replications. These trees were selected because they accurately reflect most of the results recovered across all 22 MPTs, and we highlight branches that consistently show the same high/low rates in other MPTs.

3.2.3 Morphospace and disparity analysis

To investigate macroevolutionary trends in Rhynchocephalia, I analyzed changes in morphospace occupation through time, based on variations in dentary shape. We chose to focus on morphological variation in the dentary because it is commonly the best preserved part in fossil rhynchocephalians, which can retain more than 80% of the shape of the complete mandible. Also it has been shown in studies of a broad array of vertebrates that mandibular shape captures information about dietary preferences and so can discriminate major ecomorphological groupings (e.g. Kammerer et al. 2006; Anderson et al. 2011, 2013; Stubbs et al. 2013). Further, mandible shape variation may be measured readily from two-dimensional images. Previous studies have shown that 2D mandibular data are generally very accurate and closely mirror of 3D estimates (Cardini, 2014). I compiled images of dentaries for 30 fossil rhynchocephalians, from the literature, plus pictures from 14 museum specimens of the extant *Sphenodon* to assess variation within this single taxon, and to determine where it falls in comparison with Mesozoic taxa. I did not carry out landmark analysis on skulls or postcranial elements, I had two reasons for focussing on the lower jaw for the landmark study: (a) such studies have been done frequently before by other authors on other vertebrate taxa (both fishes and tetrapods) and the studies have shown good morphometric discrimination between taxa; and (b) the mandible is most frequently preserved and so this maximises the size of the data set; if I had added, say, skull, femur, and humerus for landmark study, the data set of taxa would have been substantially reduced. Additionally, I performed a separate geometric morphometric analysis of all samples of *Sphenodon* to identify the specimen that best represents the average shape of its dentary. All images were uniformly oriented to the same side (right). Seven landmarks and 26 semi-landmarks were set on the dentary images, using the program tpsDig (Rohlf, 2006). In order to consider morphological variation expressed beyond principal components (PC) 1 and 2 (reflecting ~54% of overall shape variation), in my analyses, I also calculated Procrustes distances, derived directly from the Procrustes aligned landmark data. Procrustes distance (the sum of distances between corresponding landmarks from two shapes after superimposition) is the standard distance metric for shape (Zelditch et al. 2012) and is equivalent to utilizing information from all PC axes, not just the first two, or the first five.

After Procrustes superposition to correct for variable sizes of the mandibles and variable orientations of images, the corrected coordinate data from the landmarks were subjected to principal components analysis (PCA) in R (R team, 2015), employing the package geomorph (Adams et al. 2013). Three plots were produced, one to show morphospace occupation through the Mesozoic, one to observe macroevolutionary trends according to different feeding strategies of rhynchocephalians, and another to explore the phylogenetic branching patterns within the morphospace (a phylomorphospace). For the feeding strategies plot, I used the dietary preferences proposed by Jones (2006a, 2009), Rauhut et al. (2012) and Martínez *et al.* (2013) based on rhynchocephalian tooth shape. The phylomorphospace was produced using the R package phytools (Revell, 2012). I randomly selected one dated MPT and cropped the tips missing PC coordinate data. This pruned phylogeny was used to reconstruct ancestral PC coordinate data with maximum likelihood estimation, and the branching pattern was superimposed within the morphospace. As previously mentioned, I included a sample of the extant *Sphenodon* in all plots for comparative purposes. To explore the extent to which *Sphenodon* represents a conservative, or 'average', morphology, we examine Procrustes distances (describing the magnitude of the shape deviation) between each sampled dentary and the Procrustes mean shape of the entire sample (in Morphologika - O'Higgins and Jones, 1999).

To test for statistically significant overlaps in morphospace occupancy between groups of taxa sorted by geological period and by feeding mode, I used our PC coordinate data and performed a one-way NPMANOVA test in PAST (Hammer et al. 2001) using Euclidean distances, 10,000 permutations and Bonferroni-corrected *p*-values. Additionally, morphological disparity for temporal and feeding groups was quantified with the sum of variances metric, calculated using PC coordinate data from the first ten ordination axes (subsuming 91% of overall variation). Confidence intervals associated with calculated disparity values were generated by bootstrapping with 10,000 replications. Disparity calculations were performed in R (R team, 2015).

3.3 Results

3.3.1 Evolutionary rates

Rates analyses using both the 'equal' and 'mbl' methods show similar results overall, with heterogeneous rates found throughout the phylogeny (Fig. 3.2). Both analyses show significantly high rates of character change on basal branches along the ‘backbone’ of the phylogeny, and on the branch leading to ‘derived rhynchocephalians’. These high-rate branches are recovered consistently in most dating replicates, and in most MPTs. Significantly high rates are frequently found on the branch subtending a derived clade formed by *Sphenovipera*, *Theretairus* and the Opisthodontia, although this is not recovered as consistently across dating replicates and in all MPTs (Fig. 3.2). For the extant *Sphenodon*, both methods demonstrated that it has significantly low rates of morphological evolution, which contrasts with the occasionally high and, more often, non-significant rates shown by the branches preceding it, and with its closest relatives, such as the Early Jurassic *Cynosphenodon* (Fig. 3.2). Within the derived rhynchocephalians, the ‘equal’ dated trees also showed higher rates on the internal branches subtending pleurosaurs and eilenodontines (Fig. 3.2A), although these high rates are not seen in the more conservative ‘mbl’ approach (Fig. 3.2B). Another difference between both methods is that for taxa near the base of the tree (*Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*), the ‘mbl’ method found high rates on these terminal branches (Fig. 3.2B), while the ‘equal’ method showed low or non-significant rates (Fig. 3.2A). One interesting case is one of the morphologically specialized species *Pamizinsaurus*, from the Early Cretaceous, which showed low rates of morphological evolution in the ‘mbl’ analyses (Fig. 3.2B). Importantly, all these rates results for extinct taxa are consistent in the sensitivity analyses, when *Sphenodon* is removed.

3.3.2 Morphospace analysis

The morphospace analysis demonstrates that rhynchocephalians experienced important changes in morphospace occupation through time (Fig. 3.3A). Their morphospace in the Triassic was reasonably large, which suggests that the group had an initial burst of high morphological disparity after its origin in the Early or Middle Triassic. On the other hand, Jurassic rhynchocephalians considerably increased their morphospace occupation compared to the Triassic, but also moved into a different morphospace. The PC1-PC2 morphospace plot (Fig. 3A) shows that in the Cretaceous, rhynchocephalians experienced a considerable decrease in morphospace occupation, to about half of the area occupied in the Triassic and a third of that occupied in the Jurassic. The sum of variances disparity metric confirms that Jurassic taxa had the highest disparity, while disparity of Triassic and Cretaceous taxa was subequal and considerably lower (Fig. 3.3A). Results of the

NPMANOVA test only found significant differences in morphospaces between the Triassic and Cretaceous (p = 0.035), and non-significant differences between Triassic and Jurassic taxa. The living *Sphenodon* lies close to the centroid within the morphospace of Triassic taxa and near the zone where morphospaces of Mesozoic taxa overlap.

As expected, the mandibular landmarks provide good discrimination of feeding strategies among rhynchocephalians (Fig. 3.3B). Herbivorous taxa form a tight cluster with a high diversity of species, while insectivorous forms also occupy a relatively tight cluster but with considerably fewer species. The only known durophagous taxon (*Oenosaurus*) occupies a completely different morphospace region to other rhynchocephalians. In the case of omnivorous taxa (which also include carnivores), they show the greatest morphospace occupation, and this slightly overlaps with the herbivorous, insectivorous, and piscivorous morphospaces. For the piscivorous taxa, one of them (*Palaeopleurosaurus*) overlaps with omnivorous taxa, while the other piscivorous taxon (*Pleurosaurus*) occupies distinct morphospace. *Sphenodon*, identified as an omnivore (Sharell, 1966; Robb, 1977; Cree, 2014), falls near the centre of the feeding morphospace plot (Fig. 3.3B). Disparity analyses show that omnivorous taxa had high disparity, while herbivorous and insectivorous had lower disparity. When comparing morphospace occupation through one-way NPMANOVA, only samples of herbivorous-insectivorous (p = 0.005) and herbivorous-omnivorous (p = 0.046) forms were significantly different from each other, while other feeding modes did not show any significant differences among the samples.

The phylomorphospace (Fig. 3.3C) reveals that the shape of the dentary in *Sphenodon* differs from that of its closest relatives. The branch leading to *Sphenodon* traverses PC2 and originates from a cluster of internal nodes and terminal tips also located centrally along PC1. The shape of the dentary in *Sphenodon* is convergent with that in basal forms, such as the ‘clevosaurs’. Some taxa closely related to *Sphenodon* can also trace their branches back to this central cluster from outlying positions in morphospace, such as *Oenosaurus* and *Ankylosphenodon*.

When comparing Procrustes distances between each sampled taxon and the Procrustes mean landmark configuration for all specimens, *Sphenodon* deviates little from the average shape. Of the 31 taxa, *Sphenodon* is the seventh most similar to the average shape. The other forms most similar to the average shape are (in order) *Clevosaurus*, *Opisthias*, *Kallimodon* and *Palaeopleurosaurus*. The most divergent forms are (in order) *Oenosaurus*, *Pleurosaurus*, *Brachyrhinodon*, *Gephyrosaurus*, and *Diphydontosaurus*.

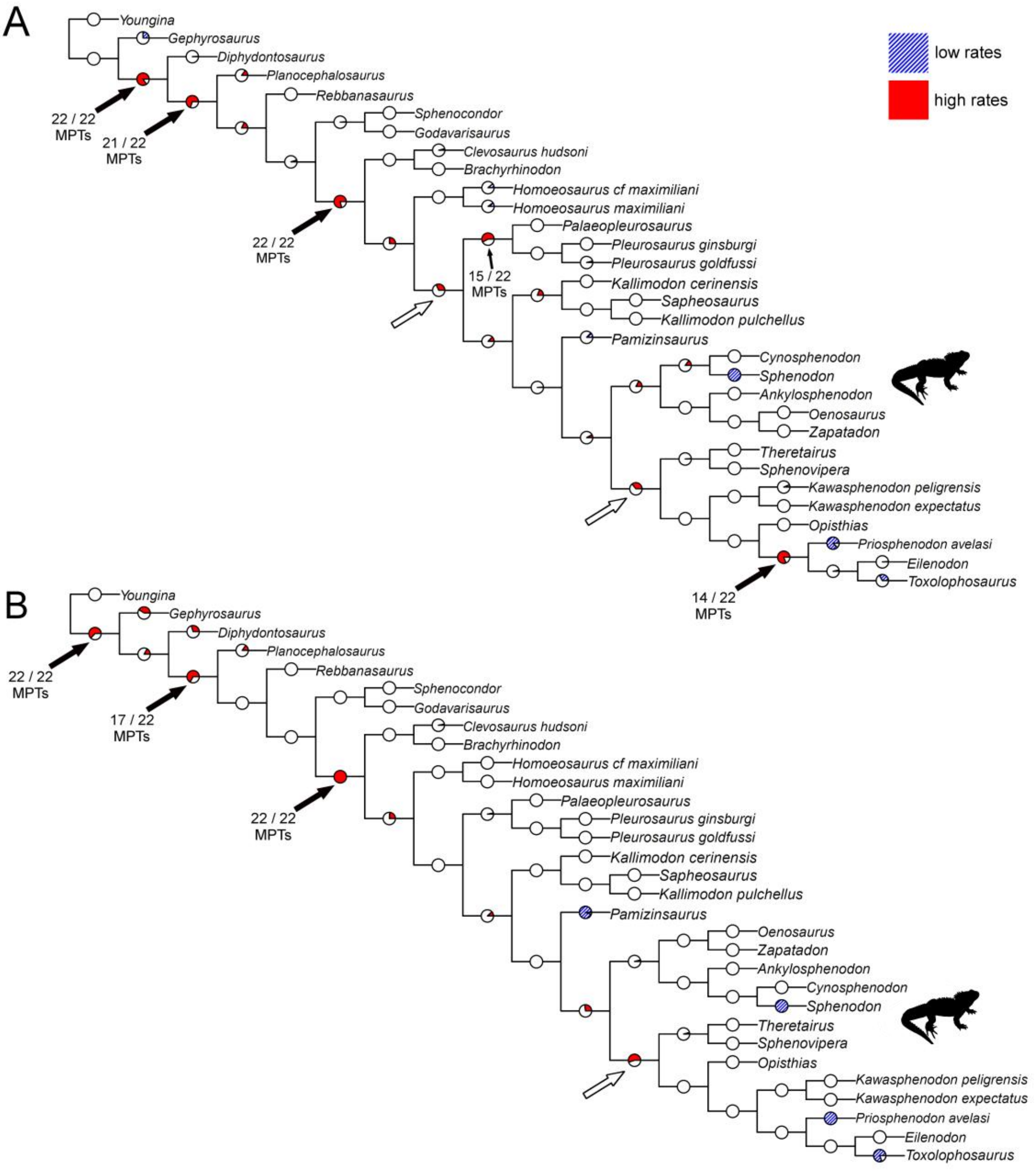


Fig. 3.2. Evolutionary rates analyses of Rhynchocephalia, illustrating results from per-branch likelihood tests using the ‘equal’ (A) and the ‘mbl’ (B) dating methods. One of the 22 most parsimonious trees (MPTs) is illustrated for each analysis. Pie charts on the branches are used to indicate the proportion of significantly high (red), significantly low (blue) and non-significant (white) rates results, based on 100 dating replications. Arrows

denote branches that are consistently found to have significant rates in most MPTs (black arrows) or some MPTs (white arrows). *Sphenodon* illustration by Steven Traver.

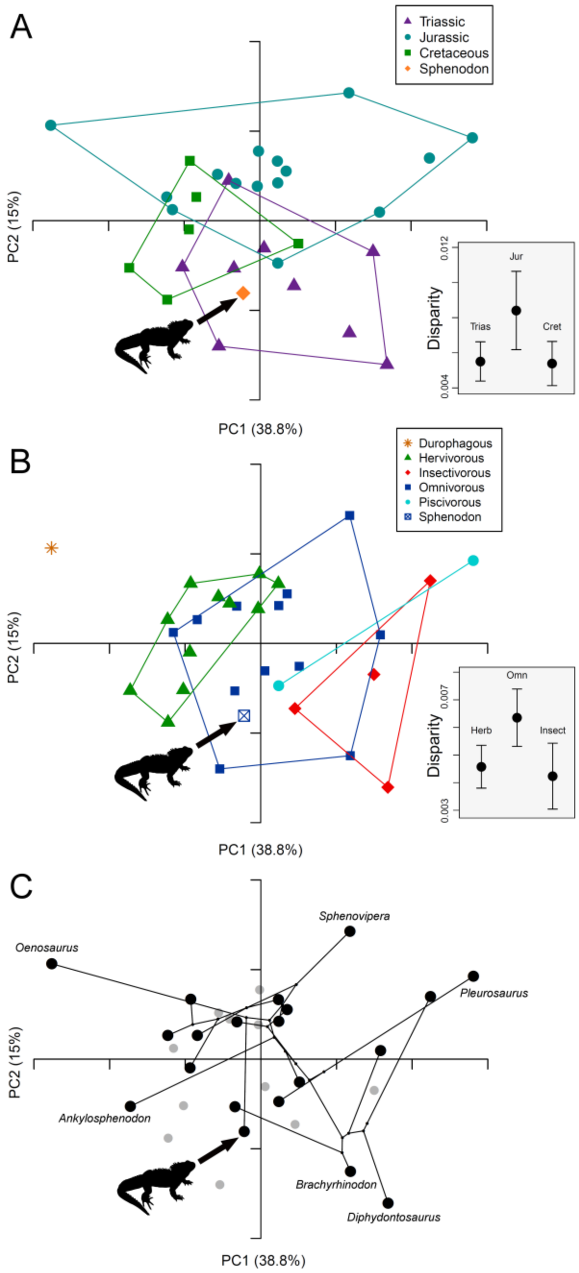


Fig. 3.3. Rhynchocephalian morphospace occupation, based on a geometric morphometric analysis of the dentary. Plots show temporal (A) and dietary (B) groupings, and a phylomorphospace (C). Note that the modern *Sphenodon* lies close to the centre of the morphospace plots. Morphological disparity (sum of variances) plots are included for the temporal (A) and dietary (B) groups. In the phylomorphospace (C), key taxa are named, and only major phylogenetic relationships are shown. Taxa within the morphospace that

were not included in the phylogeny are denoted by grey circles. Error bars are 95% confidence intervals based on 10,000 replications. *Sphenodon* illustration by Steven Traver.

3.4 Discussion

Frequently, the recognition of an extant species as a 'living fossil' is historical, a consequence of the discovery of fossil relatives before the living species, as in the case of the coelacanth *Latimeria* (Casane and Laurenti, 2013). In the case of the tuatara, this species was noted as a living fossil because of its 'almost identical structure' to the Late Jurassic *Homoeosaurus* (Robb, 1977). However, recent studies on *Sphenodon* and some of its fossil relatives have disputed the assumed long-term morphological and molecular stasis of the group (Hay et al. 2008; Jones, 2008; Meloro and Jones, 2012). In Victorian times, only the living form was known, and it was recognized as sister to the highly diverse Squamata (lizards, amphisbaenians and snakes). With increasing knowledge of the fossil record of rhynchocephalians, the morphological similarity between *Sphenodon* and some fossil forms became clear.

These claims became easier to assess with substantial increases in knowledge of fossil rhynchocephalians in the past 30 years (Jones, 2008), and the application of cladistic methodology, following the first phylogenetic analysis of the group (Fraser and Benton, 1989). Recent geometric morphometric works (Jones, 2008; Meloro and Jones, 2012) have refuted the morphological stasis of the Rhynchocephalia by reference to the disparity of skull and tooth shape. My study agrees with Jones (2008) and Meloro and Jones (2012), by showing that the Rhynchocephalia was a diverse group with wide morphological disparity, and not an unchanging group through time, as previously believed. However, I dispute the suggestion by Jones (2008) and Meloro and Jones (2012) that the tuatara is a non-conservative species. My results provide a wider perspective on the position of *Sphenodon* among fossil taxa following a considerable increase in the number of fossil taxa, by using morphological information from the lower jaw and novel macroevolutionary methods to explore rates of morphological evolution over time.

In terms of a numerically testable hypothesis, I suggested earlier that 'a living fossil should show both statistically significantly slow rates of morphological evolution and it should be morphologically conservative.' My study confirms that *Sphenodon* fits both of these criteria and so is a 'living fossil'. First, I found statistically significantly slow rates of morphological evolution in *Sphenodon* (Fig. 3.2). Overall, rates of morphological evolution in rhynchocephalians were heterogeneous (Fig. 3.2A, B), which suggests that the group has had a complex evolutionary history. My study hints that much of the morphological diversity seen in the clade originated through a small number of evolutionary 'bursts', with a mix of high rates on basal and derived branches in the tree (Fig. 3.2). It is unexpected to see 'average' rates of morphological evolution for some highly specialized taxa, such as *Oenosaurus* and *Ankylosphenodon*, as well as low rates for the bizarre *Pamizinsaurus*. However, it is likely that the presence of these unexpected low or average rates in highly specialized taxa is related to the missing data in the cladogram. A clearly example of this is *Pamizinsaurus*, a terrestrial species from the Early Cretaceous that is covered with osteoderms that notably obscure a lot of its taxonomy (Reynoso, 1997).This finding is apparently contradicted by evidence that *Sphenodon* is an advanced taxon based on the presence of derived morphological features (Gorniak et al. 1982; Jones, 2008; Curtis et al. 2010, 2011; Jones et al. 2012). However, recent work (Reynoso, 1996, 2003; Reynoso and Clark, 1998; Reynoso, 2000; Apesteguia and Novas, 2003) suggest that the most closely related species to *Sphenodon* is the Early Jurassic *Cynosphenodon*, a species that showed average rates of morphological change compared to the low rates in *Sphenodon*, according to our analysis. This may indicate that the Sphenodontinae, the clade that comprises *Sphenodon* and *Cynosphenodon*, experienced long-term morphological stasis after the Early Jurassic.

The fact that *Sphenodon* has the highest rate of molecular evolution among living vertebrates (Hay et al. 2008; Subramanian et al. 2008) confirms that rates of molecular and morphological evolution are decoupled (Subramanian et al. 2008). In such comparisons, of course, I cannot comment on rates of change in non-preserved morphology. A problem with our study is that there is such a long time gap between living *Sphenodon* and its Early Jurassic sister taxon, so rates cannot be compared with confidence, and likewise phylogenomic studies can only compare living *Sphenodon* with extant squamates, separated by some 2 x 240 Myr of independent history. The long *Sphenodon* branch is problematic also because it cannot be broken up by intervening branching events, and so any rate calculation is averaged, and likely underestimated.

Second, in terms of morphology, *Sphenodon* passes the test to be called a 'living fossil' because of its conservative position in morphospace (Fig. 3.3). My geometric morphometric study confirms the expanded morphospace of rhynchocephalians in the Triassic and Jurassic, and a decrease in the Cretaceous. The fact that Jurassic rhynchocephalians occupied an almost entirely different morphospace from their Triassic precursors might be a consequence of the Triassic-Jurassic extinction, and dramatic changes in the biota and the ecological position of rhynchocephalians in their ecosystems. The dramatic decrease in morphospace occupied by Cretaceous rhynchocephalians has usually been related to the radiation of squamates (Apesteguía and Novas, 2003; Jones, 2006b; Jones et al. 2009; Meloro and Jones, 2012), but this cannot be confirmed here.

In focusing on lower jaw morphology, I have reduced the sample of morphological characters when compared to studies based on the skull (e.g. Jones, 2008), but I have increased the sample of taxa, and the lower jaw encompasses key information about feeding adaptation (Kammerer et al. 2006; Anderson et al. 2011, 2013; Stubbs et al. 2013). My results differ from those of Jones (2008), who found tight ecomorphological clusters relating to phylogenetic position, such as a cluster of basal taxa (e.g. *Diphydontosaurus*, *Gephyrosaurus*, *Planocephalosaurus*) as well as some derived groups such as clevosaurs. My results show that morphological differences cross-cut phylogeny, with high morphological diversity among basal rhynchocephalians and within the derived genus *Clevosaurus* (Fig. 3.3). Meloro and Jones (2012) suggested that the possible ancestor of *Clevosaurus* must have been '*Sphenodon*-like'. Our results suggest that *Sphenodon* converges with the Triassic species of *Clevosaurus* (*C. hudsoni* and *C. sectumsemper*) close to the centroid of morphospace, and both *Sphenodon* and *Clevosaurus* possess two of the most average mandibular morphologies of all rhynchocephalians. This indicates that at least the morphology of the dentary of modern tuatara seems to be conservative; also it must be considered that my results may be influenced by the fact that most reconstructions of dentaries of fossil rhynchocephalians are based on the dentary of *Sphenodon*.

Tooth shape is also very important for the evolution of feeding modes in rhynchocephalians (Jones, 2009; Meloro and Jones, 2012; Rauhut et al. 2012; Martinez et al. 2013). The most basal taxa (*Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*) are identified as insectivorous because of their piercing teeth, but later species evolved many different tooth shapes reflecting their wide variety of dietary preferences, such as the carnivorous or omnivorous clevosaurs, the omnivorous sphenodontines, the piscivorous pleurosaurs, and the specialized herbivorous eilenodontids (Throckmorton et al. 1981; Rasmussen and Callison, 1981; Jones, 2008; Jones, 2009; Meloro and Jones, 2012; Rauhut et al. 2012; Martinez et al. 2013). One special case of feeding adaptation among rhynchocephalians is the Late Jurassic *Oenosaurus muehlheimensis*, which had a complex crushing dentition for a durophagous diet of molluscs or crabs (Rauhut et al. 2012). Another interesting case of dietary adaptation is the Early Cretaceous *Ankylosphenodon pachyostosus*, which developed continuously growing teeth ankylosed into the lower jaw for an herbivorous diet (Reynoso, 2000).

Throughout their evolutionary history, rhynchocephalians evolved dental and cranial modifications for different ecological niches (Jones, 2008). Current research suggests that rhynchocephalians had at least five dietary preferences (Jones, 2006a, 2009; Rauhut et al. 2012 and Martínez et al. 2013). The morphospaces occupied by rhynchocephalians with these five dietary preferences (Fig. 3.3B) were generally small, except for those with an omnivorous or carnivorous diet, which occupied a wide morphospace area. Evidence of the success of the omnivorous diet is provided by the oldest known survivor of the K-Pg extinction, the early Paleocene *Kawasphenodon peligrensis*, which has been regarded as an omnivore (Apesteguía et al. 2014), as is the extant tuatara (Curtis et al. 2011; Jones et al. 2012; Cree, 2014).

Aspects of the biology of the living tuatara have been noted recently as evidence that it cannot be regarded as a ‘living fossil’. For example, many authors have noted the complexity of the feeding mechanism of *Sphenodon* (Gorniak et al. 1982; Jones, 2008; Curtis et al. 2010, 2011; Jones et al. 2012), and the propalinal movement of the lower jaw has been marked as unique among living amniotes (Gorniak et al. 1982; Jones, 2008; Curtis et al. 2010, 2011; Jones et al. 2012). Another important feature of the tuatara is the presence of a complete lower temporal bar in the skull, which is a derived condition when compared with other fossil rhynchocephalians (Whiteside, 1986; Jones, 2008; Curtis et al. 2011; Jones et al. 2012). Further, studies on the biology of the tuatara have demonstrated that its physiology is quite advanced, because, in contrast to many other living reptiles, the tuatara is well adapted to cold environments (Cree, 2014). Also, the tuatara shows complex behaviour, especially in its interspecific relationship with seabirds (Corkery, 2012; Cree, 2014). In addition, a recent molecular study of the hypervariable regions of mitochondrial DNA of subfossil and extant specimens of the tuatara demonstrated that this species has very high rates of molecular evolution (Hay et al. 2008; Subramanian et al. 2008). Notwithstanding these observations of the uniqueness of *Sphenodon*, my analysis of evolutionary rates and geometric morphometrics suggest not only the dentary of the tuatara is generally morphologically conservative, resembling some of its Mesozoic forebears, but that it actually occupies a position close to the centroid of the hyperdimensional morphospace, as well as in the morphospace bounded by axes PC1 vs. PC2 (Fig. 3.3). Also, *Sphenodon* is recovered as possessing the seventh 'most average' morphology out of the 31 taxa used in this study. One interesting aspect to be considered in the evolution of tuatara is that it is patent that some structures of its body seems to have higher evolutionary rates that drove to the development of innovative structures (e. g. feeding mechanism, lower temporal bar) while at the same time having conservative structures such as the dentary. This contrast between innovative and conservative structures might be related to mosaic evolution, which is an interesting subject that to my knowledge has not been explored in the tuatara and can provide many interesting questions for future work. Even if it fails some of the definitions of 'living fossils', *Sphenodon* is part of a lineage that has been long-enduring and existed at low diversity through hundreds of millions of years, it follows a long time gap with few fossils, and it is a relict, being the survivor of a once more diverse clade and now lone sister to the biodiverse Squamata. I provide a new definition of 'living fossils' here, in terms of both a statistically significantly slow rate of morphological evolution and morphological conservatism. *Sphenodon* shows both characteristics, a slow rate of evolution when compared to the mean for all rhynchocephalians, and a conservative dentary morphology that shows a position close to the centroid in the overall morphospace defined by the extinct members of the clade.

3.5 Appendix

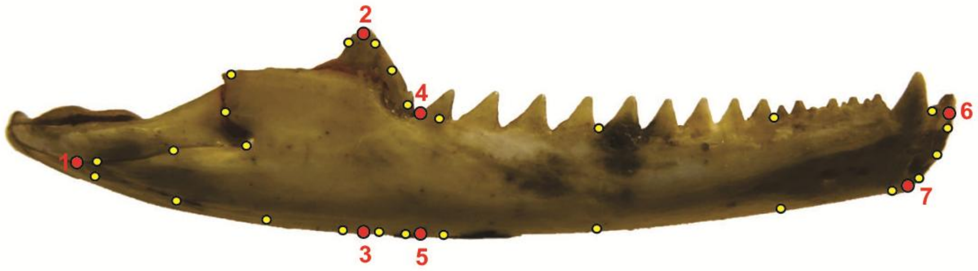
3.5.1 Landmarks and semi-landmarks

A.- List of landmarks

1) The most posterior point of the posterior process of dentary
2) The most dorsal point of coronoid process
3) Ventral point of a vertical line from landmark 2
4) The most posterior point of the most posterior teeth
5) Ventral point of a vertical line from landmark 4
6) The most anterior and superior point of dentary
7) The most antero-ventral point of dentary

B.- Semi-landmarks

26 semi-landmarks were used, all of them are marked as yellow points



Sphenodon punctatus, specimen OUMNH.ZC 700. Picture taken directly from specimen housed at Oxford University Museum of Natural History.

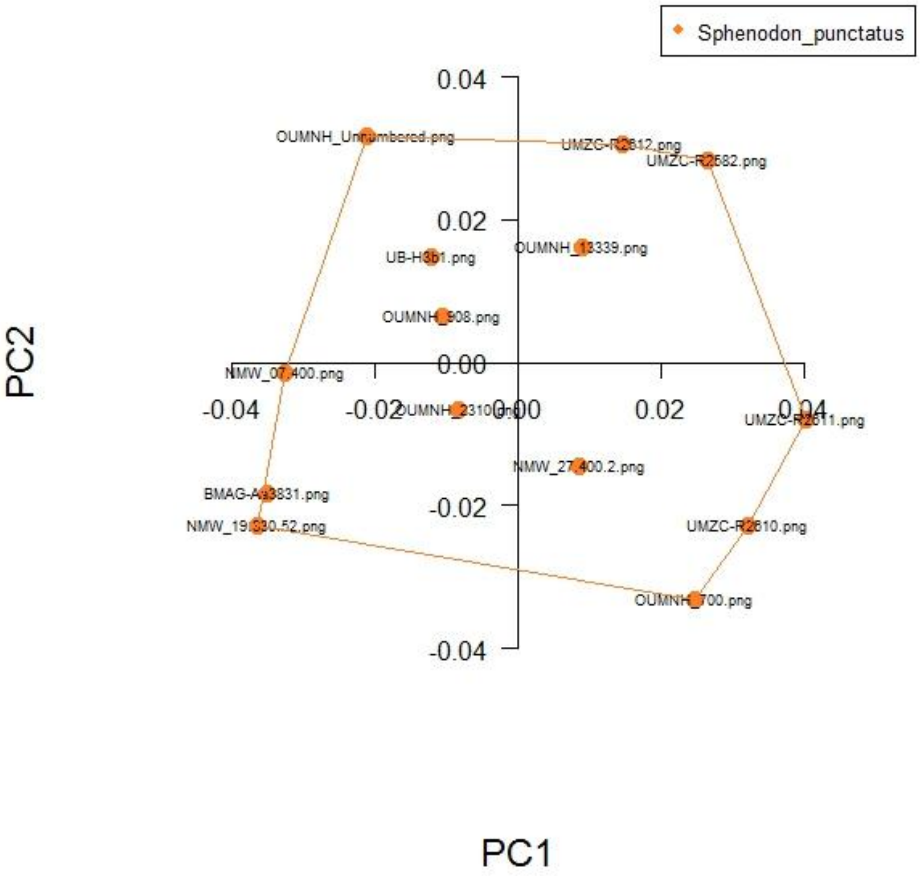
3.5.2 List of specimens

Taxa	**Period**	**Specimen**	**Source of the image**
Brachyrhinodon taylori	Triassic	BMNH R 3559	Fraser & Benton (1989)
Clevosaurus brasilensis	Triassic	UFRGS-PV-0613-T	Romo de Vivar & Soares (2015)
aff. Diphydontosaurus	Triassic	MCSNB 4862	Renesto (1995)
Sphenotitan leyesi	Triassic	Reconstruction	Martínez *et al.* (2013)
Clevosaurus hudsoni	Triassic	Reconstruction	Fraser (1988)
Clevosaurus sectumsemper	Triassic	Reconstruction	Klein *et al.* (2015)
Diphydontosaurus avonis	Triassic	Reconstruction	Whiteside (1986)
Planocephalosaurus robinsonae	Triassic	Reconstruction	Fraser (1982)
Sigmala sigmala	Triassic	Reconstruction	Fraser (1986)
Clevosaurus convallis	Jurassic	Reconstruction	Säilä (2005)
Gephyrosaurus bridensis	Jurassic	Reconstruction	Evans (1980)
aff. Opisthias (Mexico)	Jurassic	Reconstruction	Reynoso & Cruz (2014)
Cynosphenodon huizachalensis	Jurassic	Reconstruction	Reynoso (1996)
Sphenovipera jimmysjoyi	Jurassic	Reconstruction	Reynoso (2005)

Palaeopleurosaurus posidoniae	Jurassic	Reconstruction	Carroll (1985)
Sphenocondor gracilis	Jurassic	Reconstruction	Apesteguia *et al.* (2012)
Opisthias rarus	Jurassic	Reconstruction	Gilmore (1909)
Sapheosaurus	Jurassic	Reconstruction	Cocude-Michel (I963)
aff. Opisthias (Portugal)	Jurassic	Unnumbered specimen	Ortega *et al.* (2009)
Pleurosaurus	Jurassic	1925-I-18	Carroll & Wild (1994)
Eilenodon robustus	Jurassic	Reconstruction	Rasmussen & Callison (1981)
Oenosaurus muehlheimensis	Jurassic	BSPG 2009 I 23	Rauhut *et al.* (2012)
aff. Opisthias (England)	Jurassic	Unnumbered specimen	Evans & Fraser (1992)
Kallimodon	Jurassic	Reconstruction	Cocude-Michel (I963)
Toxolophosaurus cloudi	Cretaceous	Reconstruction	Throckmorton *et al.* (1981)
Ankylosphenodon pachyostosus	Cretaceous	Reconstruction	Gómez-Bonilla (2003)
Pamizinsaurus tlayuaensis	Cretaceous	Reconstruction	Reynoso (1997)
Priosphenodon minimus	Cretaceous	Reconstruction	Apesteguia & Carballido (2014)
Priosphenodon avelasi	Cretaceous	Reconstruction	Apesteguía & Novas (2003)
Kawasphenodon expectatus	Cretaceous	Reconstruction	Apesteguía (2005)
Sphenodon punctatus	Holocene	H3b.1 (OST 111)	Picture taken directly from specimen
Sphenodon punctatus	Holocene	Aa 3831	Picture taken directly from specimen
Sphenodon punctatus	Holocene	NMW.07.400	Picture taken directly from specimen
Sphenodon punctatus	Holocene	NMW.27.400.2	Picture taken directly from specimen
Sphenodon punctatus	Holocene	NMW.19.330.52	Picture taken directly from specimen
Sphenodon punctatus	Holocene	Unnumbered specimen	Picture taken directly from specimen
Sphenodon punctatus	Holocene	OUMNH.ZC-908	Picture taken directly from specimen
*Sphenodon punctatus**	Holocene	OUMNH.ZC-2310	Picture taken directly from specimen
Sphenodon punctatus	Holocene	OUMNH.ZC-13339	Picture taken directly from specimen
Sphenodon punctatus	Holocene	OUMNH.ZC-700	Picture taken directly from specimen
Sphenodon punctatus	Holocene	UMZC R.2610	Picture taken directly from specimen
Sphenodon punctatus	Holocene	UMZC R.2611	Picture taken directly from specimen
Sphenodon punctatus	Holocene	UMZC R.2612	Picture taken directly from specimen
Sphenodon punctatus	Holocene	UMZC R.2582	Picture taken directly from specimen

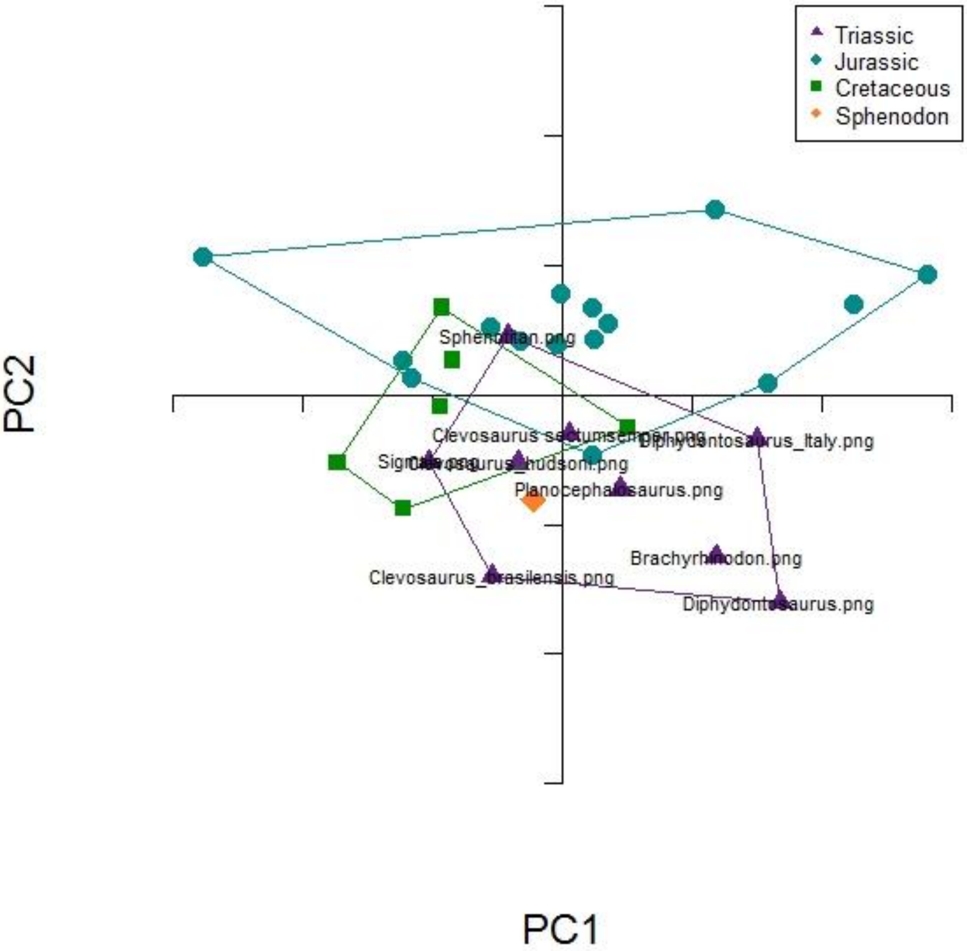
*****This was the specimen included in the geometric morphometric analysis to compare with fossil taxa

3.5.3 Geometric morphometrics of *Sphenodon*

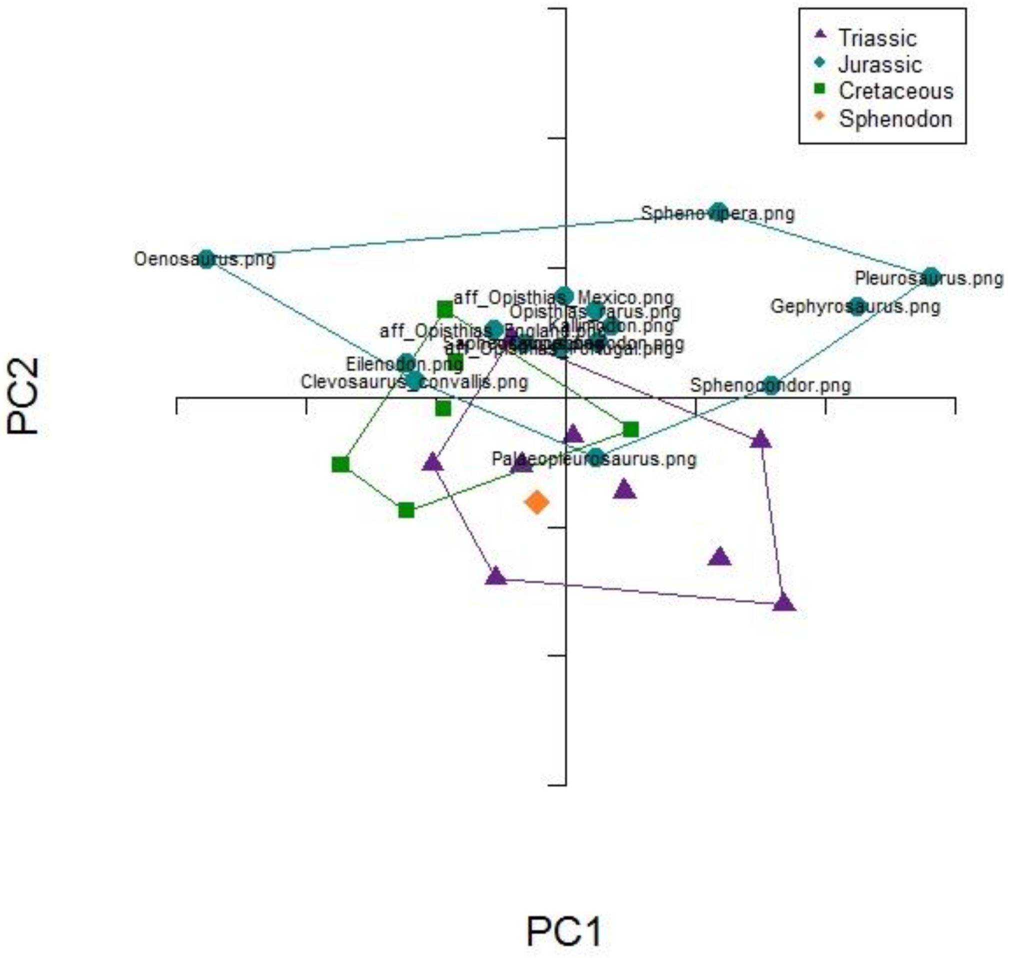


As stated in the methods, I performed a geometric morphometric analysis of the 14 samples of *Sphenodon punctatus* to look for the specimen that best represents the average shape of its dentary. I decided to use specimen OUMNH 2310 from Oxford University Museum of Natural History for the comparison with Mesozoic taxa, because it was the specimen that lies closer to the centre of all samples.

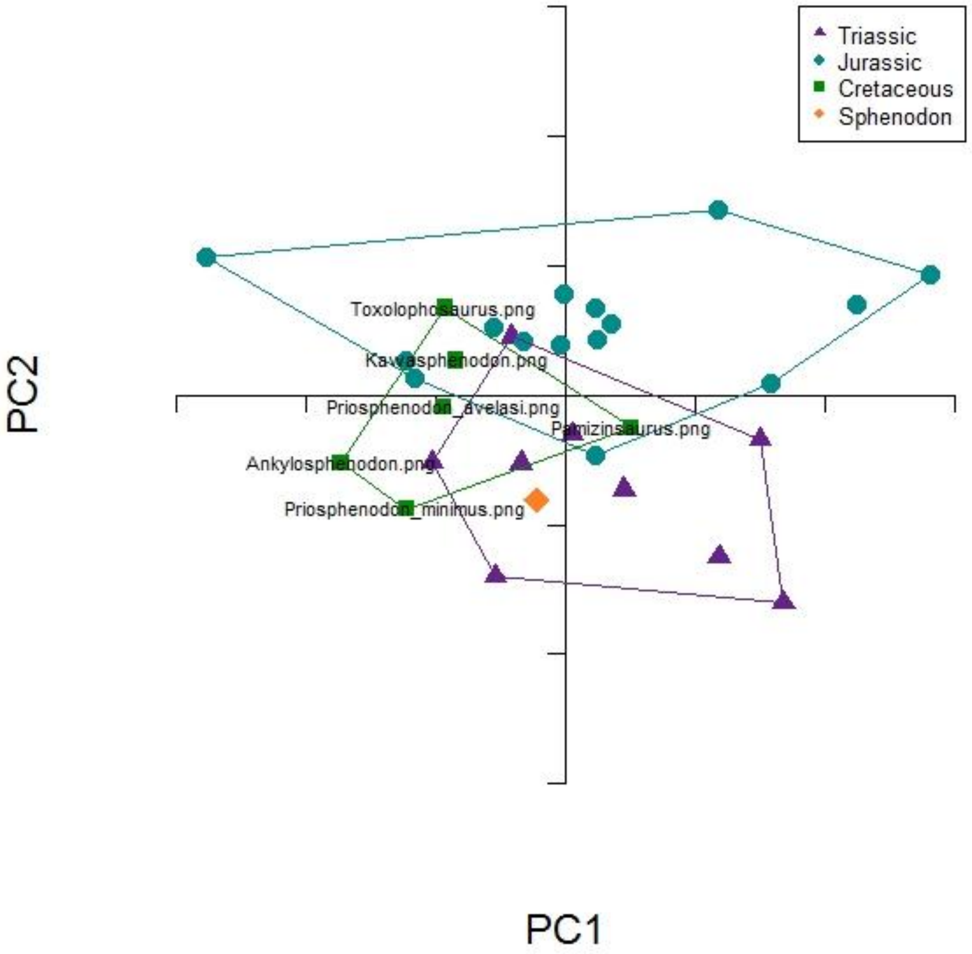
3.5.4 Morphospace through time of the Rhynchocephalia with names on plots



Plot of the morphospace through time of the Rhynchocephalia with names of Triassic taxa used in this study.



Plot of morphospace through time of the Rhynchocephalia with names of Jurassic taxa used in this study.



Plot of morphospace through time of the Rhynchocephalia with names of Cretaceous taxa used in this study.

3.5.5 Results of statistical analyses

3.5.5.1 Results of the NPMANOVA verifying the differences in morphospaces of Mesozoic taxa.

	Triassic	Jurassic	Cretaceous
Triassic	-		
Jurassic	0.07709	-	
Cretaceous	0.0348	0.1608	-

3.5.5.2 Results of the NPMANOVA verifying the differences in morphospaces based on feeding modes.

	Insectivorous	Omnivorous	Piscivorus	Herbivorous
Insectivorous	-			
Omnivorous	0.1368	-		
Piscivorous	1	0.5669	-	
Herbivorous	0.005399	0.0456	0.2298	-

3.5.5.3 Procrustes distances results

Rank order	Taxon/dentary sample	Procrustes chord distances	
1st	Oenosaurus.png	0.181508698	MOST DIFFERENT TO MEAN SHAPE
2nd	Pleurosaurus.png	0.16368134	
3rd	Brachyrhinodon.png	0.124121351	
4th	Gephyrosaurus.png	0.123794596	
5th	Diphydontosaurus.png	0.120763326	
6th	Priosphenodon_minimus.png	0.116463702	
7th	Ankylosphenodon.png	0.115551958	
8th	Sphenovipera.png	0.105402385	
9th	Diphydontosaurus_Italy.png	0.101762592	
10th	Cynosphenodon.png	0.096365208	
11th	Sphenocondor.png	0.09574943	
12th	Eilenodon.png	0.093832817	
13th	Clevosaurus_brasilensis.png	0.093438501	
14th	Kawasphenodon.png	0.085064881	
15th	Sigmala.png	0.083790022	
16th	Priosphenodon_avelasi.png	0.083184498	
17th	Pamizinsaurus.png	0.080687599	
18th	Sphenotitan.png	0.079389306	
19th	Toxolophosaurus.png	0.079274028	
20th	Clevosaurus_convallis.png	0.078229019	

21st	aff_Opisthias_Mexico.png	0.075631829	
22nd	Sapheosaurus.png	0.070644913	
23rd	Planocephalosaurus.png	0.068228506	
24th	Opisthias_rarus.png	0.066947031	
25th	OUMNH_2310.png	0.065918588	Sphenodon
26th	aff_Opisthias_England.png	0.065689537	
27th	Palaeopleurosaurus.png	0.058608643	
28th	Kallimodon.png	0.056571321	
29th	Clevosaurus sectumsemper.png	0.052529975	
30th	aff_Opisthias_Portugal.png	0.04757587	
31st	Clevosaurus_hudsoni.png	0.042837877	MOST SIMILAR TO MEAN SHAPE

3.5.6 Data matrix

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        Diphydontosaurus
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        Planocephalosaurus
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        Rebbanasaurus
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2)?????212200(1 2)01021??100?????(0 1)10010100??
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2)101001020110??0012120012000210211 0?20??022????0000
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	Clevosaurus_hudsoni
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1
	Kallimodon_pulchellus	01110?011?00?0011211112001???10(0
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	Kallimodon_cerinensis	????????????????????1??2010?????(0 1)110?1?(0
1)?1212??(0 1)2120200200022 1??122????00??
	Sapheosaurus		111100?1?0???0011211211001????0(0 1)11021?10(0
1)???01?21?0???2???221??122?????????
	Pamizinsaurus		??????1???0?????????????211??0?0?(1 2)11?1?11?2120?(0
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1)??102??2????????12?????????0
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1)21102112100012??(1 2)2210000011
	Cynosphenodon
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	Opisthias		?????????????????????????????????3111??(0
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	Toxolophosaurus
??????????????????????????????1?31111?0??213012????????112?????222????01??
	Eilenodon
??????????1??????????????????12311112022213012 2?21210?112?????222????0122
	Priosphenodon_avelasi
0110011111111001111101220100011231111202221301221212103112 2(1
2)2??222????0032
	Ankylosphenodon
???1?????1????????????????????1?111?1?111?1?01????0????0?0221??121????0???
	Sphenocondor
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	Sphenovipera
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	Theretairus
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3.5.7 Taxa ages

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"Homoeosaurus_maximiliani",150.8,145.5
"Homoeosaurus_cf_maximiliani",150.8,145.5
"Palaeopleurosaurus",183.0,182.0
"Pleurosaurus_goldfussi",150.8,145.5
"Pleurosaurus_ginsburgi",150.8,145.5
"Brachyrhinodon",235.0,205.6
"Clevosaurus_hudsoni",205.6,201.6
"Kallimodon_pulchellus",150.8,145.5
"Kallimodon_cerinensis",150.8,145.5
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"Pamizinsaurus",112.6,99.7
"Zapatadon",189.6,183.0
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"Cynosphenodon",189.6,183.0
"Opisthias",150.8,140.2
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"Priosphenodon_avelasi",99.7,94.3
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"Ankylosphenodon",112.6,99.7
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"Sphenovipera",189.6,183.0
"Theretairus",155.7,150.8
"Kawasphenodon_expectatus",84.9,66.0
"Kawasphenodon_peligrensis",61.7,58.7
"Oenosaurus",150.8,145.5
```

Chapter 4

Evolutionary radiation and ecomorphological diversification of early squamates

This chapter has not been published. A modified version of this chapter will be prepared for publication with the collaboration of Thomas L. Stubbs and Michael J. Benton.

4.1 Introduction

Extant squamates, represented by lizards, snakes and amphisbaenians, comprise one of the most successful groups of living vertebrates with a huge diversity of over 9,000 living species (Pyron et al. 2013). In contrast to modern taxa, earliest squamates were apparently less diverse during the Mesozoic, until they experienced a big radiation during the Late Cretaceous that substantially increased their diversity and morphological disparity (Evans, 2003). Until very recently, the oldest known squamates were fragmentary remains of snakes from the Middle Jurassic of England (Caldwell et al. 2015) and fragments of lower jaw of an acrodont lizard from the Middle Jurassic of India (Evans et al. 2002), that now are considered to belong to a rhynchocephalian (Conrad, 2018). Until recently, no squamates were known from the Triassic, but *Megachirella wachtleri* from the Middle Triassic of Italy, previously described as a basal lepidosauromorph, has been suggested as the oldest known squamate (Simões et al. 2018).

Previous attempts to characterize squamate biodiversity during the Mesozoic have focused on taxonomic diversity (e.g. Evans, 2003). Recent work has documented changes in lepidosaur diversity from the Mesozoic to the Paleogene, taking into account the biases in the fossil record and environmental influences (Cleary et al. 2018). This work has highlighted low levels of diversity from the Triassic until the Late Cretaceous. But importantly, this research has suggested that exploring the taxonomic diversity of Mesozoic lepidosaurs (including squamates) is hampered by sampling biases, especially the low numbers of localities during many time intervals from which good specimens have been collected. Taxonomic diversity represents one aspect of biodiversity; another important metric is morphological disparity, which is often extrapolated to provide a measure of ecomorphological variety (Brusatte et al. 2008; Stubbs et al. 2013). While sampling biases could influence studies of morphological disparity, there is not such a direct association. For example, an interval with poor sampling and associated with low diversity may still preserve a disparate assemblage of varied forms; it only requires one member of each family, say, to document the total disparity from a locality or age. Very few macroevolutionary studies of Mesozoic squamate disparity have been performed, and these studies have focused on the K-Pg boundary (e.g. Longrich et al. 2012) or on specific groups such as mosasaurs (Polcyn et al. 2014).

Here, I examine the morphological disparity of Mesozoic squamates to test if the expansion of squamate diversity in the Late Cretaceous was associated with increased ecomorphological disparity. The null expectation of Darwinian evolution would be that diversity and disparity would increase and decrease roughly in parallel, on the assumption that speciation is driven by natural selection and adaptation to available resources. I examine three key features. First, I utilize the rich fossil record of squamate dentition to explore dental disparity through time. Further to this, I examine the expansion of body size disparity. Finally, I explore trends of lower jaw morphological disparity based on geometric shape innovation. All metrics agree that the Late Cretaceous represented a time of pronounced phenotypic innovation in Mesozoic squamates.

4.2 Methods

4.2.1 Dental disparity

I compiled a database of dental morphotypes for 205 Mesozoic squamate genera. Generic occurrence records for all squamates ranging from the Late Jurassic to end-Cretaceous were downloaded from the Palaeobiology Database (PBDB; www.paleobiodb.org), accessed via Fossilworks (www.fossilworks.org). Taxa were assigned to dental morphotypes in eight general categories (see Appendix). The dental categories in this study were based on those outlined by Nydam (2002) and were designed to encapsulate the full diversity of dental morphologies present in the squamate fossil record. Taxa showing pronounced heterodonty were assigned two dental morphotypes. Temporal trends in the diversity of dental morphotypes were examined by calculating the relative diversity of each morphotype in 14 geological time bins (Kimmeridgian to Maastrichtian), divided in such a way as to ensure similar durations and adequate sample sizes in each (e.g. Grossnickle and Polly, 2013).

4.2.2 Body size evolution

I studied patterns of body size evolution in Mesozoic squamates by using lower jaw length as a proxy. Lower jaw length is a valuable proxy for body size in fossil squamates because the fossil record of many subgroups is very fragmentary, with a lack of complete skulls and skeletons, and the lower jaw the best preserved element in most species. I consider that using lower jaw as proxy of body size maximizes the size of the data set; because if I had added, skull, femur, and humerus for landmark study, the data set of taxa would have been substantially reduced, especially for snakes. I compiled a database of lower jaw lengths for 108 genera, all for which this could be done, and used the maximum jaw length of the largest known specimen confidently referable to each taxon (see Appendix). Lower jaw lengths were taken directly from specimens, the literature or measured from pictures using ImageJ (Abràmoff et al. 2004). I explored temporal trends of skull-size evolution by plotting $\log_{10}$-transformed lower jaw length against geological time based on the stratigraphic range midpoints of all taxa (e.g. Stubbs and Benton, 2016).

4.2.3 Lower jaw disparity

I studied changes in squamate morphospace occupation through the Mesozoic based on variations of lower jaw shape. Lower jaw shape is a commonly used ecomorphological proxy, because shape innovations are linked to dietary specializations (e.g. Grossnickle and Polly, 2013; Stubbs et al. 2013; Herrera-Flores et al. 2017). I compiled a database of 2D images of lower jaws of 86 genera from the Late Jurassic to the Late Cretaceous, I oriented all images to the same side (right), and seven landmarks and 26 semi-landmarks were set on the lower jaw images (see Appendix), using the program tpsDig (Rohlf, 2006). Before performing our principal components analysis (PCA), I carried out a generalized Procrustes analysis to correct for variable size, positioning and orientations of the specimens. All corrected coordinates then subjected to PCA in R (R team, 2015), using the package Geomorph (Adams et al. 2013). Three primary plots were generated to visualize major shape changes based on principal components 1 and 2, one plot to show changes in morphospace through the Late Jurassic to the Late Cretaceous, and the other two plots to observe macroevolutionary patterns for higher clades (e.g. lizards, snakes, mosasaurs) and dietary guilds in the well-sampled Late Cretaceous squamates. Dietary groups for Late Cretaceous squamates were inferred by tooth shape or by suggested diets provided in the literature (see Appendix).

4.3 Results

4.3.1 Dental disparity

Early squamates, specifically Late Jurassic (Kimmeridgian-Tithonian) taxa, had low dental disparity that was mainly represented by three different morphotypes, and highly dominated by taxa with simple conical teeth (Fig. 4.1a). In the Early Cretaceous, new dental morphotypes appeared, including those with increasing cuspidy, but taxa with conical teeth were still dominant (Fig. 4.1a). In the Cenomanian there was a clear turnover in the dental disparity of squamates. The relative diversity of taxa with conical teeth declined, while taxa with pointed and recurved teeth showed a large increase in relative diversity (Fig. 4.1a). During the Late Cretaceous, there was also increased relative diversity of other rarer and more complex dental morphotypes, including taxa with labiolingually compressed teeth, with increase in cuspidy, and with crushing adaptations (Fig. 4.1a). Overall, trends of dental disparity show a marked shift from a homogeneous assemblage dominated by plesiomorphic conical forms in the Late Jurassic and Early Cretaceous, to a more heterogenous assemblage including more complex forms in the Late Cretaceous.

4.3.2 Body size evolution

During most of early squamate evolution the group was apparently characterized by small body size (Fig. 4.1b). From the Tithonian to the Albian, squamates were represented by taxa of small to moderate body size, with lower jaw lengths less than 100 mm. However, Cenomanian squamates showed a considerable increase in body size ranges, while taxa from the Turonian to Santonian showed stable large body sizes. This is coincident with the diversification of marine mosasaurs. Greatest disparity in lower jaw sizes is seen in the Campanian, where taxa ranged from ~ 10 mm to ~ 1500 mm. Maastrichtian taxa showed a very similar range of body sizes to Campanian taxa.

4.3.3 Lower jaw morphospace trends

Morphological variation in Mesozoic squamate lower jaws is expressed in biplots illustrating principal components 1 and 2 (Fig. 4.2). PC1 represents changes in the elongation of the lower jaw, while PC2 reflects changes in the height of the dentary and coronoid process. In lower jaw morphospace, Late Jurassic squamates formed a relatively wide cluster (Fig. 4.2a). Interestingly, Early Cretaceous taxa had marginally decreased morphospace occupation, largely overlapping Late Jurassic taxa, although some taxa diverged along PC1. Late Cretaceous squamates had expansive morphospace occupation that subsumes the morphospaces of the Late Jurassic and Early Cretaceous taxa, suggesting that squamates at the end of the Cretaceous had a considerably greater disparity than at any point in their earlier history (Fig. 4.2a).

When Late Cretaceous taxa are divided into dietary guilds, some interesting ecological groupings are recovered (Fig. 4.2b). Carnivorous taxa had wide morphospace occupation that overlaps with insectivores and durophages, and completely subsumes the morphospace of piscivores, which formed a tight cluster. Insectivorous taxa also had a wide morphospace with high diversity. Durophages and herbivorous also had a relatively wide morphospace, but herbivorous had considerable higher diversity (Fig. 4.2b).

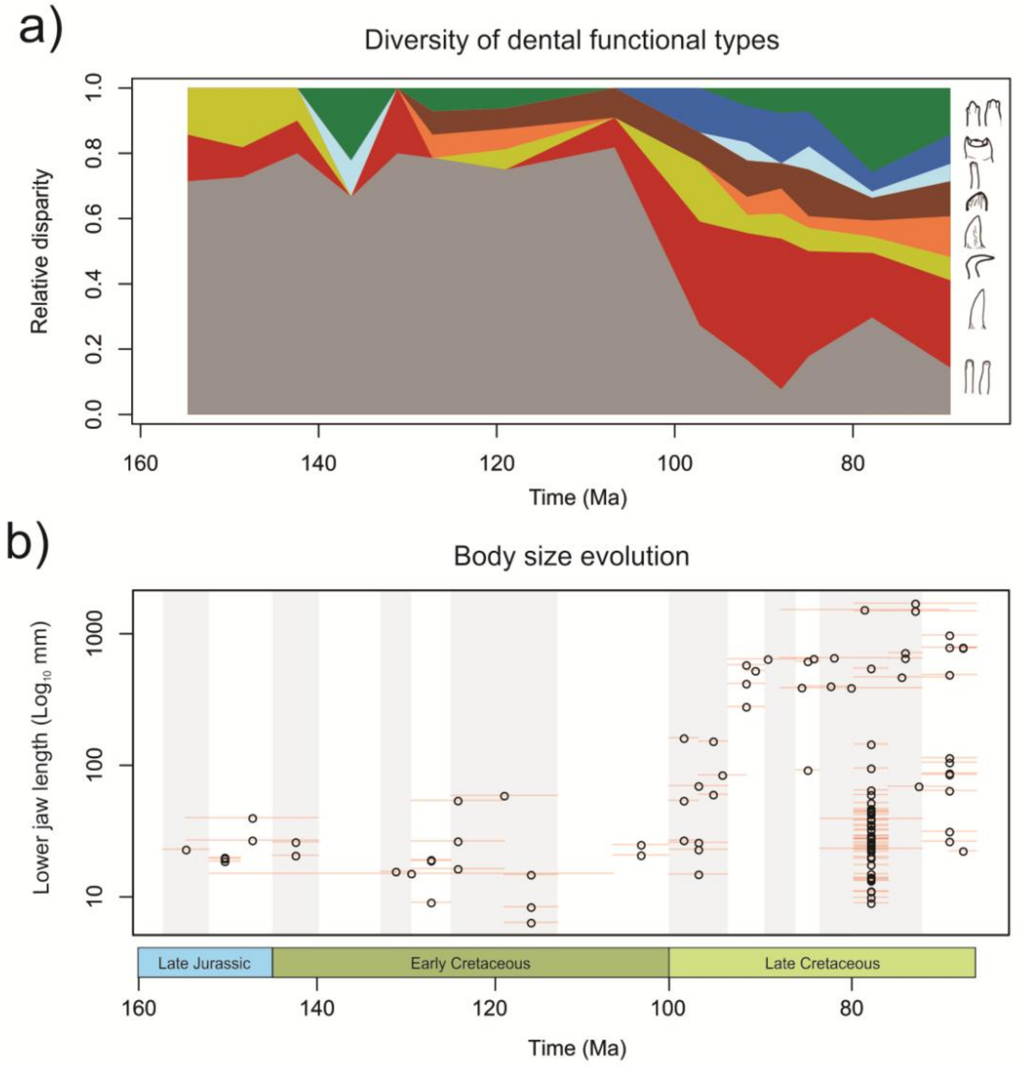


Fig 4.1. a) Dental disparity of squamates trough time. Grey = teeth conical, with small degree of apical facetting/striation; red = compressed, pointed and recurved teeth; yellow = hooked and slender teeth; green = teeth with labiolingual compression and increasing cuspidy, sometimes “leaf-shaped”; brown = teeth enlarged, upright, with greater robustness; orange colour = teeth pointed, triangular and blade-like; navy blue =

transversally-toothed bicuspid; sky blue = teeth with increasing cuspidy without being apically flared nor strongly labiolingually flattened b) Temporal trends of early squamate lower jaw-size evolution.

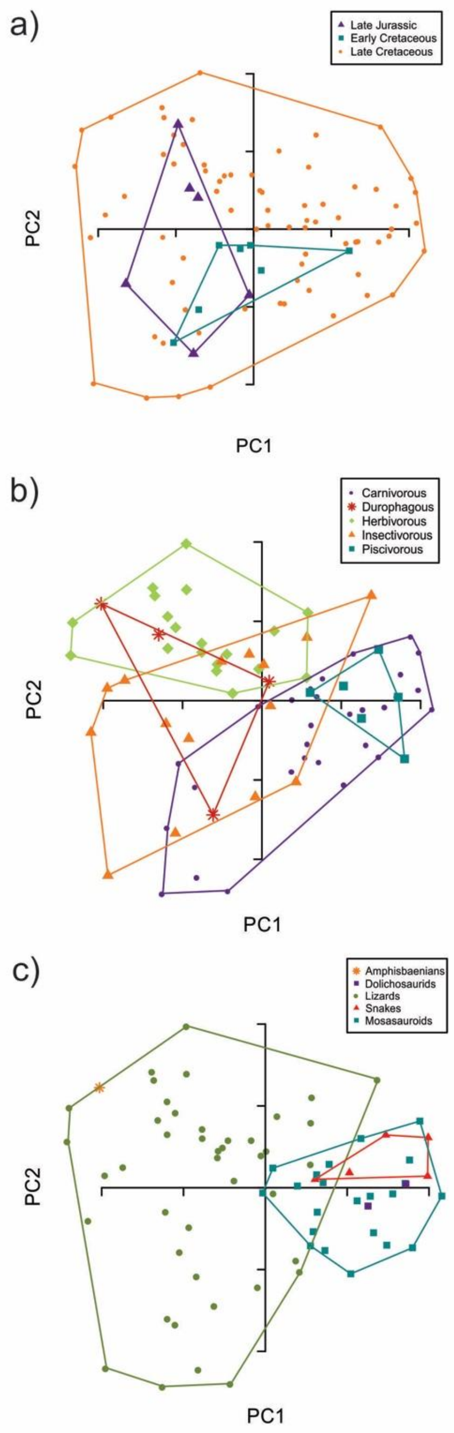


Fig 4.2. Morphospace occupation of Mesozoic squamates from geometric morphometric analysis of the lower jaw. a) Morphospace occupation from the Late Jurassic to the Late

Cretaceous b) Morphospace of Late Cretaceous taxa divided by feeding strategies c) Morphospace of Late Cretaceous taxa divided by body shape.

Lizards show the widest morphospace occupation, extending greatly over both PC1 and PC2. Mosasauroids, dolichosaurs and snakes occupy a distinct area of morphospace restricted to positive PC1 values, with less variation on PC2. This morphotype is represented by elongated lower jaws with a moderate lower jaw height and a relatively high coronoid process. The only Cretaceous taxon possibly referable to a stem amphisbaenian, the “lizard-like” *Slavoia darevskii*, represents a morphological extreme and is positioned at the extremity of PC1, close to lizards with robust jaws such as *Adamisaurus*, *Cherminsaurus* and *Gilmoreteius* (Fig. 4.2c).

4.4 Discussion

Patterns of the rapid diversification of squamates at the end of the Mesozoic have been poorly explored. Some works (e.g. Evans, 2003; Cleary et al. 2018) have analyzed with detail the fossil record of squamates pointing out that there is a possible sampling gap for Jurassic and Early Cretaceous taxa if compared with the apparently high diversity of Late Cretaceous taxa. However, even considering that the limited record of Jurassic-Early Cretaceous taxa was caused by poor sampling and biases in the fossil record and not because they indeed had low diversity, my morphometric analysis of the lower jaw suggest (Fig. 4.2a) that Late Cretaceous squamates had a remarkable radiation in the Late Cretaceous. Samples of Late Jurassic-Early Cretaceous taxa used in my analysis were very limited and it is important to remark that most Jurassic samples come from the same localities and most of them are reconstructions based on different specimens that may not belong to the same species, so result from the morphospaces of Jurassic and Early Cretaceous taxa must be taken with prudence; however my results suggest that Late Cretaceous squamates occupied a huge morphospace. Of course the apparently big radiation of Late Cretaceous squamates must be taken with some reservation, because most of my samples come from localities rich in squamate remains in China, Mongolia and North America. Additionally, the lack of records between the Late Cenomanian and Early Campanian makes it difficult to tell accurately if there was a gradual increase in diversity. On the other hand, the radiation of squamates at the end of the Cretaceous could be directly linked to their rapid adaptation to a greater variety of diets as it is suggested by our plots (Fig. 4.2b, c).

It is important to note that in contrast to squamates, other lepidosaurs such as rhynchocephalians were apparently well adapted to different feeding strategies since the early Mesozoic (Herrera-Flores et al. 2017), but in contrast to rhynchocephalians most squamates ostensibly did not diversify their feeding modes until the Late Cretaceous, as is suggested by my results (Fig. 4.2b). The oldest known “squamate”, the Middle Triassic *M. wachtleri* had very small and conical teeth (Renesto and Bernardi, 2014), that suggest a possible insectivorous diet. Also, other stem squamates such as the Middle Jurassic *Marmoretta oxoniensis* had small and conical teeth, likely for an insectivorous diet (Evans, 1991). This may suggest that the diversification of feeding modes in squamates could have influenced the squamate radiation at the end of the Cretaceous. On the other hand, another key factor that can be directly related to the adaptive radiation of squamates is the adaptation and diversification of their body plan. In spite of the poor fossil record of earliest squamates, taxa such as *M. wachtleri* and *M. oxoniensis* suggest that stem squamates had a standardized lizard-like form (Simões et al. 2018), and other early taxa like *Eophis underwoodi* and *Parviraptor estesi* are too fragmentary and mainly based on cranial material to know if they still retained a lizard-like form or if they had already developed the long body and limb reduction of snakes. However, it is clear that by the end of the Albian and through the Late Cretaceous squamates developed well distinguishable body plans, with the lizard-like shape predominant, followed by the large and long shape with flippers of mosasauroids, the long bodied and limb reduced shape of snakes, and the long-bodied lizard-like shape of the stem amphisbaenians and the dolichosaurs (Fig. 4.2c).

Before the beginning of the Late Cretaceous, squamates had a predominantly small body size with lower jaw lengths well below 100 mm (Fig. 4.1b), and it seems that they had a remarkable increase in their body size ranges until the Cenomanian, which also coincides with the diversification of their feeding strategies around the same age as was discussed above (Fig. 4.2b). In my analysis of body size evolution, we included only taxa since the Late Jurassic (Kimmeridgian), because older taxa with well-preserved lower jaws are almost absent. However, is important to note that two taxa from the Middle Triassic and Middle Jurassic previously known as basal lepidosauromorphs and now suggeted as basal squamates (Simões et al. 2018), had a rather small body size if we consider that the

Triassic *M. wachtleri* had a skull length of about 25 mm (Simões et al. 2018), while the Middle Jurassic *M. oxoniensis* had a skull length of about 23.5 mm according to the reconstruction of Evans (1991: Fig. 1). The apparently standardized small body size of Triassic-Early Cretaceous squamates might have contributed to the poor fossil record of early Mesozoic taxa, due to the commonly difficult preservation of small vertebrates.

The study of tooth disparity of Mesozoic squamates allows us to include a rather larger sample of taxa if compared with our geometric morphometric and body size analyses, but the macroevolutionary patterns were very similar (Fig. 4.1). Taxa from the Late Jurassic to the Early Cretaceous had a relatively low dental disparity, which was widely dominated by a single tooth shape (small and conical teeth). My analysis of dental disparity also supports a shift in squamate morphology and its diversification at the end of the Albian and through the early stages of the Late Cretaceous (Cenomanian-Santonian) that ended with the high diversity and morphological disparity shown by Campanian-Maastrichtian taxa. It must be noted that these changes in dental disparity and ecomorphological adaptations of the body are considered as keys to the diversification and evolutionary success of some early groups of vertebrates, such as is the case of the earliest mammals which also diversified and radiated by the end of the Mesozoic (Luo et al. 2003; Ji et al. 2006; Grossnickle and Polly, 2013). However, even if lower jaw and tooth morphology indicates a diversification of squamates in the Late Cretaceous, it should not be ignored that the fossil record also indicates that there was a notable diversification in body form of Lower Cretaceous taxa. This is clearly noticeable in the specialized morphology of some Lower Cretaceous lizards that were gliders, long bodied swimmers, burrowers, etc. This diversification in body forms is not possible to document if a study is just limited to the analysis of lower jaw, so in order to investigate more about the early diversification of squamates future work should explore relevant information provided by skull and postcranial material that were not taken into account for this study.

Whereas squamates clearly showed an ecological expansion in the Paleocene, following the K-Pg mass extinction 66 Ma (Longrich et al. 2012), the groundwork for their later diversity had been set during the Cretaceous terrestrial revolution (KTR) (Lloyd et al. 2008), when diversification of angiosperms led to huge expansions among key insect groups such as beetles, bugs, bees, ants, and butterflies, and is the root of their current high biodiversity according to most phylogenomic studies (Peters et al. 2017; Zhang et al. 2018). Phylogenomic studies of squamates have been equivocal, with many pointing to the key phase of expansion as following the K-Pg mass extinction (Hsiang et al. 2015), but at least one of the six most species-rich clades of tetrapods, the non-gekkonid lizards tracks its explosive expansion back to the Cretaceous (Alfaro et al. 2009). Further work will be required to assess how much of the modern diversity of squamates can be tracked back to the stimulus of the expansion of opportunities in terrestrial ecosystems during the KTR, 120–80 Ma, and how much to the opportunities created by K-Pg mass extinctions, 66 Ma. This study attempted to contribute to the understanding of the early squamate evolution by using different approaches; however, I consider that it is still difficult to reach any absolute conclusion until an increase in the sampling of Triassic to the Early Cretaceous localities help to decrease the biases in the squamate fossil record. Additionally, something that must be explored is if there are diffreneces about how extant and Mesozoic taxa are shaped, in this regard some preliminary results suggested that fossil and extant taxa might occupy different morphospaces, but more complete analysis are necessary to investigate this topic in detail.

4.5 Appendix

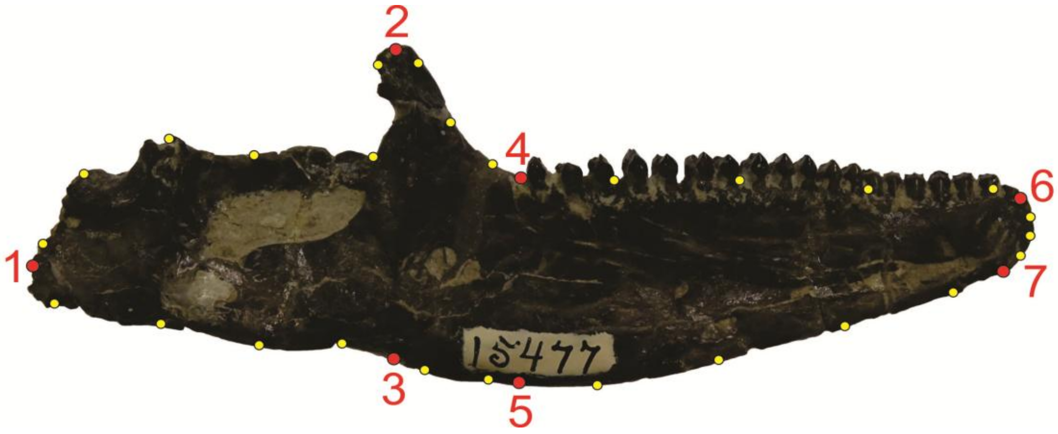
4.5.1 Landmarks and semi-landmarks

A.- List of landmarks

1) The most posterior point of the articular
2) The most dorsal point of coronoid process
3) Ventral point of a vertical line from landmark 2
4) The most posterior point of the most posterior teeth
5) Ventral point of a vertical line from landmark 4
6) The most anterior and superior point of dentary
7) The most antero-ventral point of dentary

B.- Semi-landmarks

26 semi-landmarks were used, all of them are marked as yellow points



Polyglyphanodon sternbergi, specimen USNM 15477. Picture taken directly from specimen housed at Smithsonian Institution.

4.5.2 List of taxa used in the geometric morphometric analysis

Taxa	**Period**	**Epoch**	**Specimen**	**Source**
Bavarisaurus	Jurassic	Upper	Reconstruction	Estes (1983)
Becklesius	Jurassic	Upper	Reconstruction	Estes (1983)
Dorsetisaurus	Jurassic	Upper	Reconstruction	Estes (1983)
Paramacellodus	Jurassic	Upper	Reconstruction	Estes (1983)
Pseudosaurillus	Jurassic	Upper	Reconstruction	Estes (1983)
Schenesmahl	Jurassic	Upper	Reconstruction	Conrad (2018)
Dalinghosaurus	Cretaceous	Lower	IVPP V13281	Evans & Wang (2005)
Huehuecuetzpalli	Cretaceous	Lower	Reconstruction	Estes (1983)
Liushusaurus	Cretaceous	Lower	IVPP V15587A	Evans & Wang (2010)
Norellius	Cretaceous	Lower	Reconstruction	Conrad & Daza (2015)
Pachygenys	Cretaceous	Lower	IGV 294	Keqin & Zhengwu (1999)
Sakurasaurus	Cretaceous	Lower	SBEI 199	Evans & Manabe (2009)
Tepexisaurus	Cretaceous	Lower	IGM 7466	Reynoso & Callison (2000)
Adamisaurus	Cretaceous	Upper	Reconstruction	Alifanov (2000)
Aigialosaurus	Cretaceous	Upper	Reconstruction	Carroll & Debraga (1992)
Aiolosaurus	Cretaceous	Upper	IGM 3/171	Keqin & Norell (2000)
Anchaurosaurus	Cretaceous	Upper	IVPP V10028	Keqin & Lianhai (1995)
Angolasaurus	Cretaceous	Upper	MGUAN-PA 065.	Mateus *et al.* (2012)
Aprisaurus	Cretaceous	Upper	PIN 3142/302	Alifanov (2000)
Bainguis	Cretaceous	Upper	Reconstruction	Borsuk-Bialynicka (1984)
Barungoia	Cretaceous	Upper	PIN 4487/2	Alifanov (2000)
Carusia	Cretaceous	Upper	Reconstruction	Borsuk-Bialynicka (1985)
Chamops	Cretaceous	Upper	Reconstruction	Estes (1983)
Cherminothus	Cretaceous	Upper	Reconstruction	Borsuk-Bialynicka (1984)
Cherminsaurus	Cretaceous	Upper	Reconstruction	Sulimski (1975)
Clidastes	Cretaceous	Upper	Reconstruction	Carroll & Debraga (1992)
Coniasaurus	Cretaceous	Upper	Reconstruction	Caldwell & Cooper (1999)

Ctenomastax	Cretaceous	Upper	IGM 3/62	Keqin & Norell (2000)
Darchansaurus	Cretaceous	Upper	Reconstruction	Sulimski (1975)
Dinilysia	Cretaceous	Upper	Reconstruction	Zaher & Scanferla (2012)
Ectenosaurus	Cretaceous	Upper	FHSM VP-401	Lindgren *et al.* (2011)
Eonatator	Cretaceous	Upper	UPI R 163	Wiman (1920)
Eoxanta	Cretaceous	Upper	Reconstruction	Borsuk-Bialynicka (1988)
Erdenetesaurus	Cretaceous	Upper	Reconstruction	Sulimski (1975)
Eremiasaurus	Cretaceous	Upper	UALVP 51744	Leblanc *et al.* (2012)
Estesia	Cretaceous	Upper	M 3/14	Norell *et al.* (1992)
Eupodophis	Cretaceous	Upper	Reconstruction	Rieppel & Head (2004)
Funiusaurus	Cretaceous	Upper	HGM 41HIII-114	Xu *et al.* (2014)
Gilmoreteius	Cretaceous	Upper	Reconstruction	Sulimski (1975)
Globaura	Cretaceous	Upper	Reconstruction	Borsuk-Bialynicka (1988)
Globidens	Cretaceous	Upper	SDSM 74764	Martin (2007)
Gobekko	Cretaceous	Upper	Reconstruction	Daza *et al.* (2013)
Gobiderma	Cretaceous	Upper	Reconstruction	Conrad *et al.* (2011)
Goronyosaurus	Cretaceous	Upper	Reconstruction	Lingham-Soliar (1991)
Haasiasaurus	Cretaceous	Upper	EJ693	Polcyn *et al.* (1999)
Haasiophis	Cretaceous	Upper	HUJ-Pal.EJ 695	Rieppel *et al.* (2003)
Halisaurus	Cretaceous	Upper	Reconstruction	Bardet *et al.* (2005)
Igua	Cretaceous	Upper	Reconstruction	Borsuk-Bialynicka & Alifanov (1991)
Isodontosaurus	Cretaceous	Upper	Reconstruction	Alifanov (2000)
Konkasaurus	Cretaceous	Upper	Reconstruction	Krause *et al.* (2003)
Latoplatecarpus	Cretaceous	Upper	TMP 84.162.01	Konishi & Caldwell (2011)
Magnuviator	Cretaceous	Upper	Reconstruction	DeMar *et al.* (2017)
Mimeosaurus	Cretaceous	Upper	Reconstruction	Alifanov (2000)
Mosasaurus	Cretaceous	Upper	Reconstruction	Lingham-Soliar (1995)
Myrmecodaptria	Cretaceous	Upper	IGM 3/95	Keqin & Norell (2000)
Pachyrhachis	Cretaceous	Upper	Reconstruction	Caldwell & Lee (1997)
Pannoniasaurus	Cretaceous	Upper	Reconstruction	Makádi *et al.* (2012)
Paraglyphanodon	Cretaceous	Upper	USNM 16580	Gilmore (1943)
Paravaranus	Cretaceous	Upper	MgR-I/67	Borsuk-Bialynicka (1984)
Parmeosaurus	Cretaceous	Upper	IGM 3/139	Keqin & Norell (2000)
Parviderma	Cretaceous	Upper	MgR-I/43	Borsuk-Bialynicka (1984)
Platecarpus	Cretaceous	Upper	Reconstruction	Russell (1967)
Pleurodontagama	Cretaceous	Upper	MgR-III/35	Borsuk-Bialynicka & Moody (1984)
Plioplatecarpus	Cretaceous	Upper	Reconstruction	Holmes (1996)
Plotosaurus	Cretaceous	Upper	Reconstruction	LeBlanc *et al.* (2013)
Polrussia	Cretaceous	Upper	Reconstruction	Alifanov (2000)
Polyglyphanodon	Cretaceous	Upper	USNM No. 15477	Gilmore (1942)
Pontosaurus	Cretaceous	Upper	GBA 1873/4/2	Pierce & Caldwell (2004)
Priscagama	Cretaceous	Upper	ZPAL MgR-III/32	Borsuk-Bialynicka & Moody (1984)
Prognathodon	Cretaceous	Upper	Reconstruction	Russell (1967)
Proplatynotia	Cretaceous	Upper	Reconstruction	Borsuk-Bialynicka (1984)
Prototeius	Cretaceous	Upper	Reconstruction	Denton Jr & O'Neill (1995)

Romeosaurus	Cretaceous	Upper	Reconstruction	Palci *et al.* (2013)
Russellosaurus	Cretaceous	Upper	SMU73056	Polcyn & Bell (2005)
Saichangurvel	Cretaceous	Upper	Reconstruction	Conrad & Norell (2007)
Sanajeh	Cretaceous	Upper	Reconstruction	Wilson *et al.* (2010)
Saniwides	Cretaceous	Upper	MgR-I/72	Borsuk-Bialynicka (1984)
Selmasaurus	Cretaceous	Upper	FHSM VP-13910	Polcyn & Everhart (2008)
Sineoamphisbaena	Cretaceous	Upper	Reconstruction	Wu *et al.* (1996)
Slavoia	Cretaceous	Upper	Reconstruction	Sulimski (1984)
Taniwhasaurus	Cretaceous	Upper	Reconstruction	Novas *et al.* (2002)
Tchingisaurus	Cretaceous	Upper	IGM 3/129	Keqin & Norell (2000)
Temujinia	Cretaceous	Upper	IGM 3/63	Keqin & Norell (2000)
Tianyusaurus	Cretaceous	Upper	Reconstruction	Mo *et al.* (2009)
Tylosaurus	Cretaceous	Upper	Reconstruction	Russell (1967)
Zapsosaurus	Cretaceous	Upper	IGM 3/71	Keqin & Norell (2000)

4.5.3 Feeding modes by taxa

Taxa	**Period**	**Epoch**	**Body form**	**Feeding strategy**
Adamisaurus	Cretaceous	Upper	Lizard	Herbivorous
Aigialosaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Aiolosaurus	Cretaceous	Upper	Lizard	Carnivorous
Anchaurosaurus	Cretaceous	Upper	Lizard	Herbivorous
Angolasaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Aprisaurus	Cretaceous	Upper	Lizard	Herbivorous
Bainguis	Cretaceous	Upper	Lizard	Insectivorous
Barungoia	Cretaceous	Upper	Lizard	Insectivorous
Carusia	Cretaceous	Upper	Lizard	Insectivorous
Chamops	Cretaceous	Upper	Lizard	Herbivorous
Cherminothus	Cretaceous	Upper	Lizard	Carnivorous
Cherminsaurus	Cretaceous	Upper	Lizard	Herbivorous
Clidastes	Cretaceous	Upper	Mosasaur	Carnivorous
Coniasaurus	Cretaceous	Upper	Dolichosaur	Piscivorous
Ctenomastax	Cretaceous	Upper	Lizard	Herbivorous
Darchansaurus	Cretaceous	Upper	Lizard	Herbivorous
Dinilysia	Cretaceous	Upper	Snake	Carnivorous
Ectenosaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Eonatator	Cretaceous	Upper	Mosasaur	Carnivorous
Eoxanta	Cretaceous	Upper	Lizard	Insectivorous
Erdenetesaurus	Cretaceous	Upper	Lizard	Herbivorous
Eremiasaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Estesia	Cretaceous	Upper	Lizard	Carnivorous
Eupodophis	Cretaceous	Upper	Snake	Piscivorous
Funiusaurus	Cretaceous	Upper	Lizard	Herbivorous
Gilmoreteius	Cretaceous	Upper	Lizard	Herbivorous
Globaura	Cretaceous	Upper	Lizard	Insectivorous

Globidens	Cretaceous	Upper	Mosasaur	Durophagous
Gobekko	Cretaceous	Upper	Lizard	Insectivorous
Gobiderma	Cretaceous	Upper	Lizard	Carnivorous
Goronyosaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Haasiasaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Haasiophis	Cretaceous	Upper	Snake	Piscivorous
Halisaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Igua	Cretaceous	Upper	Lizard	Herbivorous
Isodontosaurus	Cretaceous	Upper	Lizard	Durophagous
Konkasaurus	Cretaceous	Upper	Lizard	Durophagous
Latoplatecarpus	Cretaceous	Upper	Mosasaur	Carnivorous
Magnuviator	Cretaceous	Upper	Lizard	Herbivorous
Mimeosaurus	Cretaceous	Upper	Lizard	Insectivorous
Mosasaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Myrmecodaptria	Cretaceous	Upper	Lizard	Insectivorous
Pachyrhachis	Cretaceous	Upper	Snake	Piscivorous
Pannoniasaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Paraglyphanodon	Cretaceous	Upper	Lizard	Herbivorous
Paravaranus	Cretaceous	Upper	Lizard	Insectivorous
Parmeosaurus	Cretaceous	Upper	Lizard	Insectivorous
Parviderma	Cretaceous	Upper	Lizard	Carnivorous
Platecarpus	Cretaceous	Upper	Mosasaur	Carnivorous
Pleurodontagama	Cretaceous	Upper	Lizard	Insectivorous
Plioplatecarpus	Cretaceous	Upper	Mosasaur	Carnivorous
Plotosaurus	Cretaceous	Upper	Mosasaur	Piscivorous
Polrussia	Cretaceous	Upper	Lizard	Insectivorous
Polyglyphanodon	Cretaceous	Upper	Lizard	Herbivorous
Pontosaurus	Cretaceous	Upper	Dolichosaur	Piscivorous
Priscagama	Cretaceous	Upper	Lizard	Insectivorous
Prognathodon	Cretaceous	Upper	Mosasaur	Carnivorous
Proplatynotia	Cretaceous	Upper	Lizard	Carnivorous
Prototeius	Cretaceous	Upper	Lizard	Insectivorous
Romeosaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Russellosaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Saichangurvel	Cretaceous	Upper	Lizard	Herbivorous
Sanajeh	Cretaceous	Upper	Snake	Carnivorous
Saniwides	Cretaceous	Upper	Lizard	Carnivorous
Selmasaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Sineoamphisbaena	Cretaceous	Upper	Lizard	Insectivorous
Slavoia	Cretaceous	Upper	Worm lizard	Durophagous
Taniwhasaurus	Cretaceous	Upper	Mosasaur	Carnivorous
Tchingisaurus	Cretaceous	Upper	Lizard	Herbivorous
Temujinia	Cretaceous	Upper	Lizard	Herbivorous
Tianyusaurus	Cretaceous	Upper	Lizard	Herbivorous
Tylosaurus	Cretaceous	Upper	Mosasaur	Carnivorous

Zapsosaurus	Cretaceous	Upper	Lizard	Herbivorous

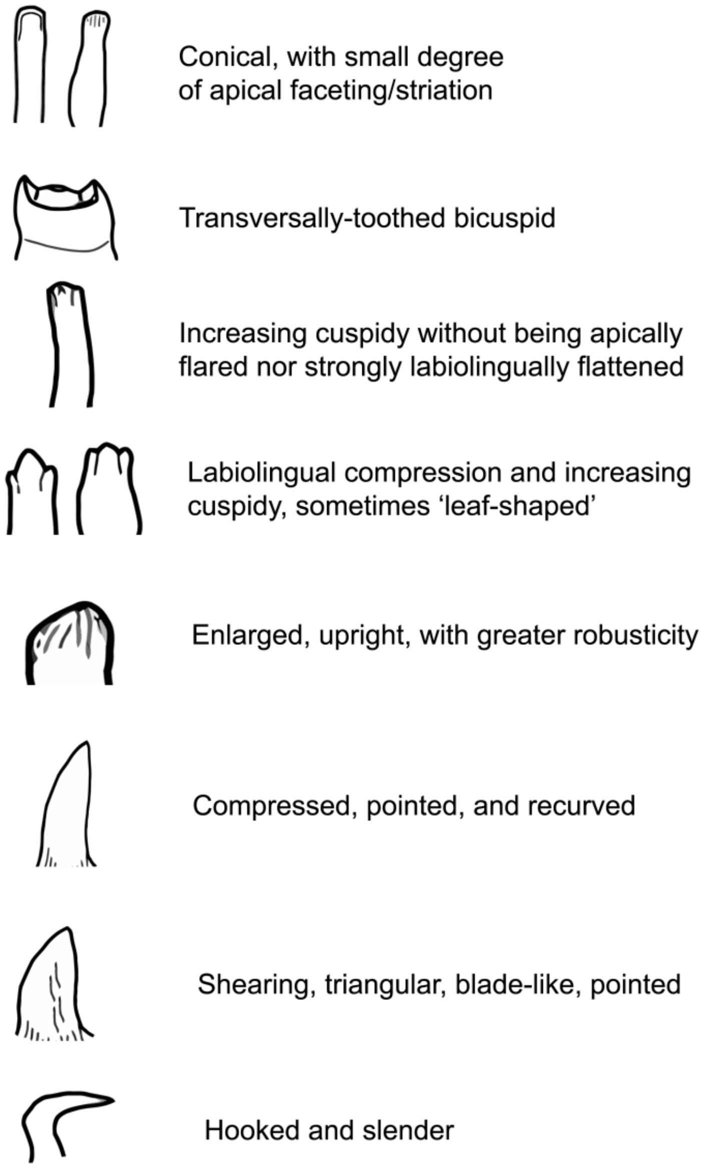
4.5.4 Lower jaw lengths

Taxa	**Period**	**FAD**	**LAD**	**Length (mm)**	**Specimen**
Ardeosaurus	Jurassic	152.1	148.6	19.6	JME-ETT2955
Bavarisaurus	Jurassic	152.1	148.6	19.1	Reconstruction
Schoenesmahl	Jurassic	152.1	148.6	18.7	SNSB-BSPG AS I 563b
Eichstaettisaurus	Jurassic/Cretaceous	152.1	106.75	15.1	MPN 19457
Becklesius	Jurassic	157.3	152.1	23	Reconstruction
Paramacellodus	Jurassic	154.7	139.8	37	Reconstruction
Dorsetisaurus	Jurassic	154.7	139.8	40	Reconstruction
Pseudosaurillus	Jurassic	145.0	139.8	26.2	Reconstruction
Hoyalacerta	Cretaceous	129.4	125.0	9.1	LH 11000
Pedrerasaurus	Cretaceous	129.4	125.0	19.2	MGB 47250
Sakurasaurus	Cretaceous	145.0	139.8	16.7	Reconstruction
Norellius	Cretaceous	132.9	129.4	15.5	Reconstruction
Dalinghosaurus	Cretaceous	129.4	119.0	25.9	IVPP V13281
Meyasaurus	Cretaceous	129.4	125.0	16.8	LH 370
Liushusaurus	Cretaceous	129.4	119.0	16.4	IVPP V15587A
Yabeinosaurus	Cretaceous	129.4	119.0	41	IVPP V13285
Pachygenys	Cretaceous	125.0	113.0	58.7	IGV 294
Tetrapodophis	Cretaceous	119.0	113.0	8.1	BMMS BK 2-2
Olindalacerta	Cretaceous	119.0	113.0	6.5	KMNH VP 400,001
Tijubina	Cretaceous	119.0	113.0	14.8	MPSC-V 010
Huehuecuetzpalli	Cretaceous	106.8	100.5	25	IGM 7389
Tepexisaurus	Cretaceous	106.8	100.5	20.8	IGM 7466
Adriosaurus	Cretaceous	100.5	93.9	26	NHMUK R2867
Aphanizocnemus	Cretaceous	100.5	93.9	23	MSNM V783
Coniasaurus	Cretaceous	100.5	93.9	68.7	Reconstruction
Eupodophis	Cretaceous	100.5	93.9	14.9	MSNM V 4014
Haasiophis	Cretaceous	100.5	97.2	27	HUJ-Pal.EJ 695
Haasiasaurus	Cretaceous	100.5	97.2	161.8	EJ693
Pachyrhachis	Cretaceous	100.5	97.2	50.5	Reconstruction
Pontosaurus	Cretaceous	97.2	93.9	60.2	GBA 1873/4/2
Aigialosaurus	Cretaceous	97.2	93.9	190.4	Reconstruction
Judeasaurus	Cretaceous	97.2	91.85	84.7	HUJI P4000
Tethysaurus	Cretaceous	93.9	89.8	297	MNHN GOU1
Romeosaurus	Cretaceous	93.9	84.95	670	Reconstruction
Russellosaurus	Cretaceous	93.9	89.8	420	SMU 73056
Yaguarasaurus	Cretaceous	93.9	89.8	582	BRV 68
Angolasaurus	Cretaceous	91.85	89.8	526	MGUAN-PA 065
Tylosaurus	Cretaceous	88.05	69.1	720	FHSM VP-2295

Platecarpus	Cretaceous	88.05	75.933	560	YPM 3690
Clidastes	Cretaceous	88.05	72.1	420	Reconstruction
Dinilysia	Cretaceous	86.3	83.6	78.3	MACN-RN 1013
Pannoniasaurus	Cretaceous	86.3	83.6	620	Reconstruction
Selmasaurus	Cretaceous	86.3	84.95	430	FHSM VP-13910
Ectenosaurus	Cretaceous	84.95	83.6	675	FHSM VP-401
Eonatator	Cretaceous	84.95	79.766	401	IGM p881237
Magnuviator	Cretaceous	83.6	72.1	39.4	Reconstruction
Prototeius	Cretaceous	83.6	72.1	23.4	Reconstruction
Adamisaurus	Cretaceous	79.766	75.933	20.2	Reconstruction
Aiolosaurus	Cretaceous	79.766	75.933	35.3	IGM 3/171
Anchaurosaurus	Cretaceous	79.766	75.933	34.1	IVPP V10028
Aprisaurus	Cretaceous	79.766	75.933	45	PIN 3142/302
Bainguis	Cretaceous	79.766	75.933	23	Reconstruction
Barungoia	Cretaceous	79.766	75.933	24.4	PIN 4487/2
Carusia	Cretaceous	79.766	75.933	29.3	ZPAL MgR/III-34
Cherminothus	Cretaceous	79.766	75.933	42.5	Reconstruction
Cherminsaurus	Cretaceous	79.766	75.933	65	MgR-III/24
Ctenomastax	Cretaceous	79.766	75.933	19.5	IGM 3/62
Darchansaurus	Cretaceous	79.766	75.933	60	MgR-III/6
Eoxanta	Cretaceous	79.766	75.933	15	MgR-III/37
Erdenetesaurus	Cretaceous	79.766	75.933	52	Reconstruction
Estesia	Cretaceous	79.766	75.933	143.5	M 3/14
Gilmoreteius	Cretaceous	79.766	75.933	70	MgR-III/18
Globaura	Cretaceous	79.766	75.933	19.7	MgR-III/40
Gobekko	Cretaceous	79.766	75.933	13.3	Reconstruction
Gobiderma	Cretaceous	79.766	75.933	47	MgR-III/64
Gobinatus	Cretaceous	79.766	75.933	34.72	IGM 3/126
Hymenosaurus	Cretaceous	79.766	75.933	11.1	IGM 3/53
Igua	Cretaceous	79.766	75.933	11	MgR-I/60
Isodontosaurus	Cretaceous	79.766	75.933	18	Reconstruction
Latoplatecarpus	Cretaceous	79.766	75.933	548	TMP 84.162.01
Mimeosaurus	Cretaceous	79.766	75.933	18.2	Reconstruction
Myrmecodaptria	Cretaceous	79.766	75.933	22.7	IGM 3/95
Paravaranus	Cretaceous	79.766	75.933	28.2	Reconstruction
Parmeosaurus	Cretaceous	79.766	75.933	29	IGM 3/139
Parviderma	Cretaceous	79.766	75.933	45.5	Reconstruction
Phrynosomimus	Cretaceous	79.766	75.933	14.3	IGM 3/81
Pleurodontagama	Cretaceous	79.766	75.933	27.6	MgR-III/35
Polrussia	Cretaceous	79.766	75.933	10	MgR-I/119
Priscagama	Cretaceous	79.766	75.933	23.6	MgR-III/32
Proplatynotia	Cretaceous	79.766	75.933	39	MgR-I/68
Saichangurvel	Cretaceous	79.766	75.933	28.6	Reconstruction
Saniwides	Cretaceous	79.766	75.933	44	MgR-I/72
Shinisauroides	Cretaceous	79.766	75.933	29.3	ZPAL MgR/I-58

Sineoamphisbaena	Cretaceous	79.766	75.933	13.9	Reconstruction
Slavoia	Cretaceous	79.766	75.933	9.9	Reconstruction
Tchingisaurus	Cretaceous	79.766	75.933	25.4	IGM 3/129
Temujinia	Cretaceous	79.766	75.933	19.2	IGM 3/63
Xihaina	Cretaceous	79.766	75.933	14.1	IVPP V10030
Zapsosaurus	Cretaceous	79.766	75.933	32.2	IGM 3/71
Plioplatecarpus	Cretaceous	79.766	69.05	396	Reconstruction
Mosasaurus	Cretaceous	79.766	66.0	1546	Reconstruction
Prognathodon	Cretaceous	79.766	66.0	867	SDSM 3393
Primitivus	Cretaceous	75.933	69.05	69.5	MPUR NS 161
Taniwhasaurus	Cretaceous	75.933	72.1	729	Reconstruction
Globidens	Cretaceous	75.933	72.1	655	SDSM 74764
Funiusaurus	Cretaceous	72.1	66.0	30.6	HGM 41HIII-114
Paraglyphanodon	Cretaceous	72.1	66.0	26.5	USNM 16580
Plesiotylosaurus	Cretaceous	72.1	66.0	980	LACM 2759
Polyglyphanodon	Cretaceous	72.1	66.0	85.5	USNM No. 15477
Tianyusaurus	Cretaceous	72.1	66.0	54.9	NHMG 8502
Barbatteius	Cretaceous	72.1	66.0	63.3	UBB V.440
Chianghsia	Cretaceous	72.1	66.0	100	NHMG 009318
Halisaurus	Cretaceous	72.1	66.0	710	Reconstruction
Plotosaurus	Cretaceous	72.1	66.0	534	UCMP 32778
Sanajeh	Cretaceous	72.1	66.0	95	Reconstruction
Chamops	Cretaceous	69.05	66.0	22.7	Reconstruction
Eremiasaurus	Cretaceous	69.05	66.0	783	UALVP 51744
Goronyosaurus	Cretaceous	69.05	66.0	792	Reconstruction

4.5.5 Dental morphotypes



Dental categories used in this study are based on those outlined by Nydam (2002).

4.5.6 Dental disparity data

GENUS	PRIMARY_DENTAL_TYPE	SECONDARY_DENTAL_TYPE
Adamisaurus	3_CRUSH	1_CON
Adriosaurus	4_COMP_RECURVE	NA
Aigialosaurus	4_COMP_RECURVE	NA
Aiolosaurus	4_COMP_RECURVE	NA
Altanteius	2_LEAF_CUSPS	NA
Anchaurosaurus	2_LEAF_CUSPS	1_CON
Angolasaurus	4_COMP_RECURVE	NA

Aocnodromeus	1_CON	NA
Aprisaurus	2_LEAF_CUSPS	NA
Apsgnathus	1_CON	NA
Asagaolacerta	8_CUSPID_CON	1_CON
Atokasaurus	1_CON	NA
Bainguis	1_CON	NA
Balnealacerta	1_CON	NA
Barbatteius	8_CUSPID_CON	1_CON
Barungoia	1_CON	NA
Bavarisaurus	1_CON	NA
Becklesius	1_CON	NA
Bellairsia	1_CON	NA
Bharatagama	9_SHEAR_TRIAN	NA
Bicuspidon	10_TRANS_BICUSP	NA
Bothriagenys	1_CON	NA
Brasiliguana	8_CUSPID_CON	1_CON
Carinodens	3_CRUSH	NA
Carusia	1_CON	NA
Catactegenys	1_CON	NA
Cemeterius	9_SHEAR_TRIAN	NA
Chamops	2_LEAF_CUSPS	1_CON
Cherminotus	4_COMP_RECURVE	NA
Cherminsaurus	2_LEAF_CUSPS	1_CON
Chianghsia	4_COMP_RECURVE	NA
Chometokadmon	4_COMP_RECURVE	NA
Chromatogenys	3_CRUSH	1_CON
Clidastes	4_COMP_RECURVE	NA
Cnephasaurus	2_LEAF_CUSPS	NA
Colpodontosaurus	4_COMP_RECURVE	NA
Coniasaurus	3_CRUSH	1_CON
Conicodontosaurus	1_CON	NA
Coniophis	5_HOOKED	NA
Contogenys	1_CON	NA
Ctenomastax	1_CON	NA
Cuencasaurus	1_CON	?
Cyclurasia	2_LEAF_CUSPS	NA
Dakotaseps	1_CON	?
Dalinghosaurus	9_SHEAR_TRIAN	NA
Dallasaurus	4_COMP_RECURVE	NA
Darchansaurus	2_LEAF_CUSPS	1_CON
Desertiguana	2_LEAF_CUSPS	NA
Diablophis	5_HOOKED	NA
Dicothodon	10_TRANS_BICUSP	NA
Dimekodontosaurus	1_CON	NA
Dinilysia	5_HOOKED	NA

Distortodon	10_TRANS_BICUSP	NA
Dollosaurus	9_SHEAR_TRIAN	NA
Dorsetisaurus	4_COMP_RECURVE	NA
Dzhadochtosaurus	1_CON	NA
Ectenosaurus	4_COMP_RECURVE	NA
Eichstaettisaurus	1_CON	NA
Eonatator	4_COMP_RECURVE	NA
Eophis	5_HOOKED	NA
Eoxanta	1_CON	NA
Erdenetesaurus	2_LEAF_CUSPS	NA
Eremiasaurus	9_SHEAR_TRIAN	4_COMP_RECURVE
Estesia	4_COMP_RECURVE	NA
Exostinus	1_CON	NA
Funiusaurus	2_LEAF_CUSPS	NA
Gerontoseps	2_LEAF_CUSPS	NA
Gilmoreteius	2_LEAF_CUSPS	NA
Globaura	1_CON	NA
Globidens	3_CRUSH	NA
Glyptogenys	2_LEAF_CUSPS	NA
Gobekko	1_CON	NA
Gobiderma	4_COMP_RECURVE	NA
Gobinatus	1_CON	?
Goronyosaurus	4_COMP_RECURVE	NA
Gueragama	2_LEAF_CUSPS	NA
Gurvansaurus	1_CON	?
Haasiasaurus	4_COMP_RECURVE	?
Haasiophis	5_HOOKED	?
Hainosaurus	9_SHEAR_TRIAN	NA
Hakuseps	2_LEAF_CUSPS	NA
Halisaurus	4_COMP_RECURVE	NA
Haptosphenus	2_LEAF_CUSPS	NA
Harmodontosaurus	10_TRANS_BICUSP	NA
Hoburogekko	1_CON	NA
Hodzhakulia	1_CON	NA
Hoyalacerta	1_CON	?
Huehuecuetzpalli	1_CON	NA
Igdamanosaurus	3_CRUSH	NA
Igua	2_LEAF_CUSPS	NA
Isodontosaurus	3_CRUSH	?
Jeddaherdan	3_CRUSH	NA
Jucaraseps	1_CON	NA
Judeasaurus	4_COMP_RECURVE	NA
Konkasaurus	3_CRUSH	NA
Kourisodon	4_COMP_RECURVE	?
Kuroyuriella	1_CON	NA

Kuwajimalla	2_LEAF_CUSPS	NA
Labrodioctes	4_COMP_RECURVE	NA
Lamiasaura	1_CON	NA
Latoplatecarpus	4_COMP_RECURVE	NA
Leptochamops	2_LEAF_CUSPS	NA
Liaoningolacerta	1_CON	?
Liushusaurus	1_CON	NA
Lonchisaurus	8_CUSPID_CON	NA
Macrocephalosaurus	2_LEAF_CUSPS	NA
Magnuviator	8_CUSPID_CON	NA
Marmoretta	1_CON	NA
Meyasaurus	1_CON	NA
Mimeosaurus	3_CRUSH	NA
Mimobecklesisaurus	1_CON	NA
Monocnemodon	8_CUSPID_CON	NA
Mosasaurus	9_SHEAR_TRIAN	NA
Myrmecodaptria	1_CON	NA
Norellius	1_CON	NA
Oardasaurus	1_CON	NA
Obamadon	2_LEAF_CUSPS	NA
Odaxosaurus	3_CRUSH	NA
Olindalacerta	1_CON	NA
Orthrioscincus	10_TRANS_BICUSP	NA
Ovoo	5_HOOKED	NA
Oxiella	1_CON	NA
Pachygenys	3_CRUSH	NA
Pachyophis	5_HOOKED	NA
Pachyrhachis	5_HOOKED	NA
Paikasisaurus	1_CON	NA
Palaeosaniwa	4_COMP_RECURVE	NA
Palaeoscincosaurus	3_CRUSH	NA
Pannoniasaurus	4_COMP_RECURVE	NA
Paraderma	5_HOOKED	NA
Paraglyphanodon	10_TRANS_BICUSP	NA
Paramacellodus	1_CON	NA
Parameiva	1_CON	?
Parasaniwa	5_HOOKED	NA
Parasaurillus	1_CON	NA
Paravaranus	1_CON	NA
Pariguana	1_CON	NA
Parmeosaurus	2_LEAF_CUSPS	NA
Parviderma	1_CON	NA
Parviraptor	5_HOOKED	NA
Pedrerasaurus	1_CON	NA
Pelsochamops	3_CRUSH	NA

Penemabuya	1_CON	NA
Peneteius	8_CUSPID_CON	10_TRANS_BICUSP
Phosphorosaurus	4_COMP_RECURVE	?
Phrynosomimus	1_CON	NA
Piramicephalosaurus	2_LEAF_CUSPS	NA
Platecarpus	4_COMP_RECURVE	NA
Plesiotylosaurus	9_SHEAR_TRIAN	NA
Pleurodontagama	1_CON	NA
Plioplatecarpus	4_COMP_RECURVE	NA
Plotosaurus	4_COMP_RECURVE	NA
Pluridens	4_COMP_RECURVE	NA
Polrussia	2_LEAF_CUSPS	NA
Polyglyphanodon	2_LEAF_CUSPS	10_TRANS_BICUSP
Pontosaurus	4_COMP_RECURVE	NA
Portugalophis	5_HOOKED	NA
Primaderma	4_COMP_RECURVE	NA
Primitivus	4_COMP_RECURVE	NA
Priscagama	1_CON	NA
Pristiguana	2_LEAF_CUSPS	NA
Prodenteia	1_CON	?
Prognathodon	9_SHEAR_TRIAN	4_COMP_RECURVE
Proplatynotia	5_HOOKED	NA
Prototeius	1_CON	NA
Pseudosaurillus	1_CON	NA
Ptilotodon	1_CON	NA
Purbicella	1_CON	NA
Pyramicephalosaurus	2_LEAF_CUSPS	NA
Romeosaurus	4_COMP_RECURVE	?
Russellosaurus	4_COMP_RECURVE	?
Saichangurvel	2_LEAF_CUSPS	?
Sakurasaurus	1_CON	?
Sanajeh	5_HOOKED	?
Saniwides	4_COMP_RECURVE	?
Saurillodon	1_CON	?
Saurillus	1_CON	?
Scandensia	2_LEAF_CUSPS	?
Schillerosaurus	1_CON	?
Schoenesmahl	1_CON	?
Selmasaurus	4_COMP_RECURVE	?
Shinisauroides	1_CON	?
Sineoamphisbaena	1_CON	?
Slavoia	3_CRUSH	?
Socognathus	10_TRANS_BICUSP	?
Sphenosiagon	10_TRANS_BICUSP	?
Stypodontosaurus	3_CRUSH	?

Taniwhasaurus	4_COMP_RECURVE	?
Tchingisaurus	2_LEAF_CUSPS	?
Teilhardosaurus	2_LEAF_CUSPS	1_CON
Telmasaurus	4_COMP_RECURVE	?
Temujinia	2_LEAF_CUSPS	?
Tepexisaurus	1_CON	?
Tethysaurus	4_COMP_RECURVE	?
Tetrapodophis	5_HOOKED	?
Tianyusaurus	2_LEAF_CUSPS	NA
Tijubina	1_CON	?
Tripennaculus	2_LEAF_CUSPS	?
Tylosaurus	9_SHEAR_TRIAN	4_COMP_RECURVE
Utahgenys	1_CON	?
Webbsaurus	1_CON	?
Xihaina	2_LEAF_CUSPS	?
Yabeinosaurus	1_CON	?
Yaguarasaurus	4_COMP_RECURVE	?
Zapsosaurus	2_LEAF_CUSPS	?

Chapter 5

Slow and steady wins the race: slow evolutionary rates and the success of squamates

This chapter has not been published. A modified version of this chapter will be prepared for publication with the collaboration of Armin Elsler, Thomas L. Stubbs and Michael J. Benton.

5.1 Introduction

Biodiversity is unevenly distributed across the tree of life (Darwin, 1859; Simpson, 1944). Some clades have incredible species richness and great morphological disparity whilst others are highly conservative. This can be true for sister clades, and perhaps the most striking example of such a dichotomy is in the reptilian Superorder Lepidosauria, today represented by Rhynchocephalia (tuataras) and Squamata (lizards, snakes and amphisbaenians). There are over 10,000 species of living squamates and they have diverse ecologies, morphologies and worldwide distribution. In stark contrast, the Rhynchocephalia are represented by a single species, *Sphenodon punctatus*, which is geographically restricted to the islands of New Zealand (Jones et al. 2013).

The extant diversity of Lepidosauria represents just a snapshot of their long evolutionary history. Lepidosaur origins have been dated to the Early or Middle Triassic (Jones et al. 2013), whilst others propose a Middle Permian origin (Simões et al. 2018), based on projected dates from Middle Triassic “squamate” fossils. During early lepidosaur evolution, the Rhynchocephalia was the more successful and morphologically diverse group and earliest squamates were apparently much less diverse (Evans and Jones, 2010). During the Cretaceous there was a turnover in lepidosaurian diversity; rhynchocephalians declined, but squamates underwent a massive radiation including both morphological and phylogenetic expansion (Evans and Jones, 2010; Cleary et al. 2018). Most of the major squamate clades diversified during the Cretaceous and persisted through the Cretaceous-Paleogene (K-Pg) mass extinction event 66 million years ago (Ma), however, some successful subgroups became extinct, such as the polyglyphanodontian lizards and predatory marine mosasaurs. During the Cenozoic, squamates continued to be important components of terrestrial ecosystems but rhynchocephalians were reduced to some relict species. Currently, there are no deterministic hypotheses that explain the demise of rhynchocephalians and the relative success of squamates. One potentially pivotal factor is rates of trait evolution. In a classic study, George G. Simpson (Simpson, 1944) suggested that lineages with high evolutionary rates (tachytelic) were more prone to extinction, and clades with slow rates (bradytelic) were less susceptible. However, many recent quantitative macroevolutionary analyses have refuted Simpson’s hypothesis. Studies of morphological evolution in dinosaurs (Benson et al. 2014), actinopterygian fish (Rabosky et al. 2013), and crustaceans (Adamowicz et al. 2008), and genome size evolution in plants (Puttick et al. 2015), have shown that the evolutionary success of clades is linked to rapid evolutionary rates and 'evolvability'. In contrast, slow evolutionary rates apparently contributed to the extinction of ichthyosaurs, a once diverse clade of marine reptiles (Fischer et al. 2016). Therefore, it is predicted that phenotypic evolvability, or greater evolutionary versatility, should promote speciation and make clades more persistent on macroevolutionary timescales (Vermeij, 1973; Rabosky et al. 2013).

Here, I present the first large-scale macroevolutionary analysis of rates of morphological evolution in early lepidosaurs using phylogenetic comparative methods. I examine rate heterogeneity of body size evolution, a key trait associated with morphology, ecology and physiology (Stanley, 1973; Schmidt-Nielsen, 1984; Feldman et al. 2016), in Mesozoic and early Paleogene Lepidosauria. I test the hypothesis that squamates show rapid body size evolutionary rates compared to rhynchocephalians. My results demonstrate that the early evolution of lepidosaurs was characterized by heterogeneous rates of body size evolution and, unexpectedly, rhynchocephalians showed significantly higher rates than squamates during the Mesozoic. Rhynchocephalians are characterized by prolonged high rates (tachytelic) making them more susceptible to extinction according to Simpson's classic hypothesis. This result provides a novel explanation for the demise of rhynchocephalians and the success of squamates, which were characterized by comparatively lower evolutionary rates early in their evolutionary history. My findings conflict the prevailing idea that rapid evolutionary rates and 'evolvability' are pivotal to long-term evolutionary success.

5.2 Methods

5.2.1 Phylogeny

An informal supertree of Mesozoic and early Paleogene lepidosaurs was constructed by combining several recent phylogenies for rhynchocephalians and squamates (Appendix). This was necessary because there have been no published phylogenies of all lepidosaurs, and because there are several current but conflicting phylogenies of squamates, and because some extinct lepidosaurs have never been included in a phylogenetic analysis. These taxa were added based on alpha taxonomic opinion (Appendix). In the case of squamates, I build a standardized supertree on squamate relationships according to the latest consensus, but in order to avoid biasing the study to a single topology of the position of squamate higher clades (e.g. Mosasauria + snakes), I produced three supertree frameworks, with different topologies for squamate higher clades, based on the contrasting topologies of Conrad (2008), Gauthier et al. (2012), and Simões et al. (2018). For each supertree we generated a set of 100 trees with polytomies randomly resolved.

5.2.2 Phylogenetic time-scaling

Taxa were dated at a geological stage and substage level (where possible). Age ranges were based on the most recent information available for each taxon. Absolute ages for geological stages were based on the 2017/02 version of the International Chronostratigraphic Chart (Cohen et al. 2013). I time-scaled the trees using the R implementation (Team R, 2013) of the whole tree extended Hedman algorithm (Hedman, 2010; Lloyd et al. 2016) to produce 100 timescaled trees for each topology. I used the "conservative approach" (Hedman, 2010), which ignores taxa that are younger than the preceding outgroup and set the absolute maximum bound t_0 conservatively to the base of the Cambrian (542 Ma) following Lloyd et al. (2016). I used the last appearance dates (LADs) of *Ichthyostega stensioi* (363.33 Ma), *Ymeria denticulata* (358.9 Ma), *Tulerpeton curtum* (358.9 Ma), *Ossirarus kierani* (350.76667 Ma), *Casineria kiddi* (336.16667 Ma), *Palaeomolgophis scoticus* (336.16667 Ma), *Hylonomus lyelli* (315.2 Ma), *Anthracodromeus longipes* (307 Ma), *Petrolacosaurus kansensis* (303.7 Ma), *Orovenator mayorum* (286.8 Ma), *Lanthanolania ivakhnenkoi* (265.1 Ma), *Eunotosaurus africanus* (259.1 Ma), *Weigeltisaurus jaekeli* (256.62 Ma), *Paliguana whitei* (251.2 Ma), and *Sophineta cracoviensis* (247.2 Ma) as outgroup ages. Resolution was set to 10,000. To account for uncertainty in dating I randomly sampled the tip age of each lepidosaur species from a uniform distribution bound by its first and last appearance dates. The current R implementation of the Hedman algorithm (Lloyd et al. 2016) does not allow trees to be scaled that are not fully bifurcating. To visualize the results on a consensus tree including polytomies, I generated an additional timescaled tree for each topology using the minimum branch length (MBL) method with a minimum branch length of 1 Myr (Laurin, 2004) as implemented in the timePaleoPhy function of the R package paleotree (Bapst, 2012).

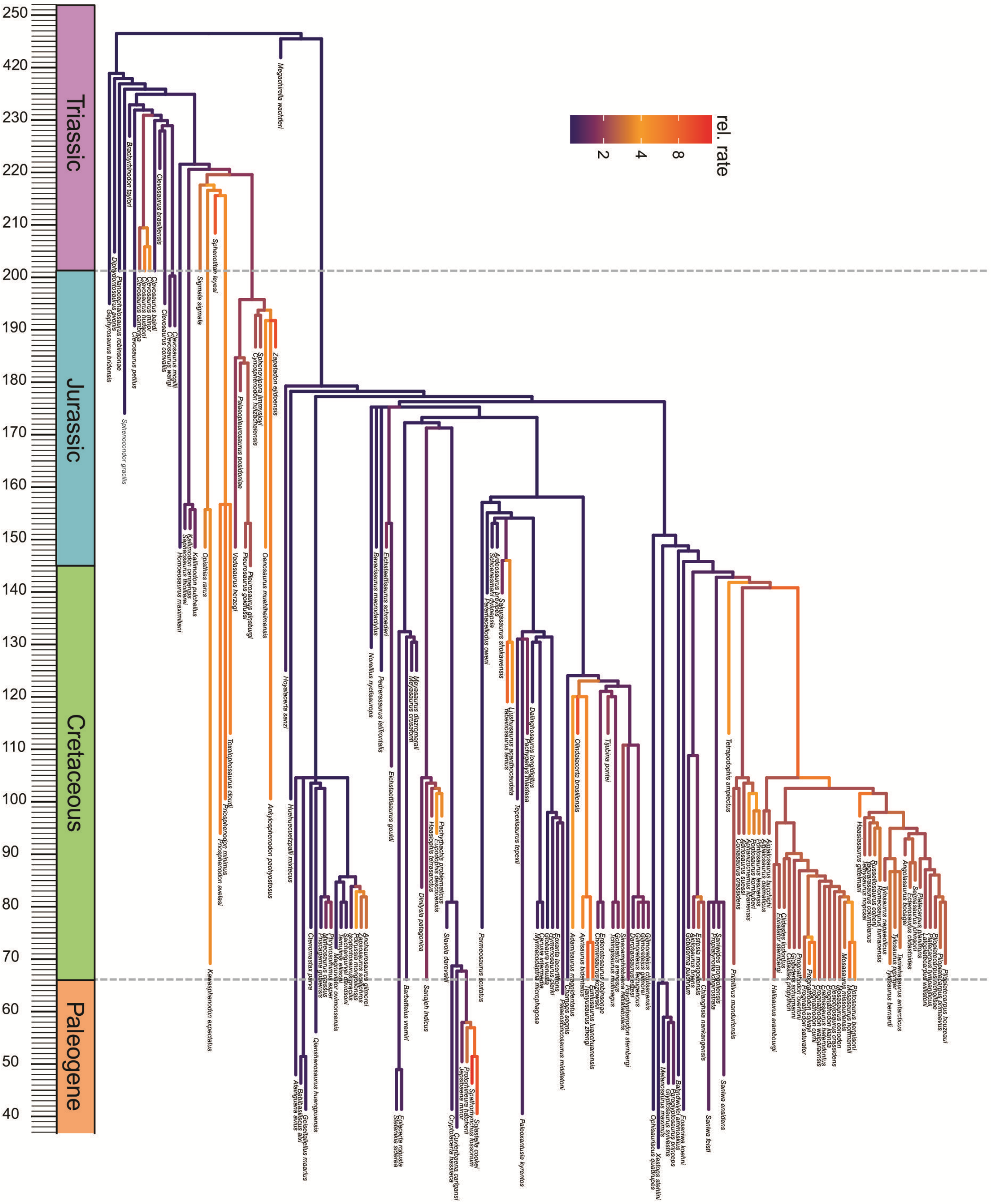


Fig 5.1. Rates of lepidosaurian body size evolution trough time. Colours from purple to red of the time-calibrated informal supertree indicate the increase of evolutionary rates in clades (highest rates orange and red), internal and terminal branches. Relationships

between higher clades of squamates follow the topology of Conrad (2008). For results using the other squamate topologies see Supplementary material.

5.2.3 Proxy for body size

For this study I used body size as proxy for the evolutionary rate analysis, it must be noted that body size has been consistently proved as a reliable proxy for this kind of studies (e. g. Sookias et al. 2012; Ezcurra et al. 2016). On the other hand, the number of complete skulls, skeletons or any other postcranial material is very limited for most early lepidosaurs, especially for taxa with small size such as Mesozoic lizards. Lower jaws are the most complete and best-preserved element in fossil lepidosaurs and were therefore used as proxy for body size. A database with 167 lower jaw lengths was compiled for taxa with complete jaws (Appendix). Lower jaw measurements were taken from the largest specimens available from literature, measured from photographs or directly taken from specimens reviewed by the authors.

5.2.4 Evolutionary rates

I employed BayesTraits V2.0.2 (Venditti et al. 2011) to estimate variable rates models of body size evolution. BayesTraits uses a reversible jump Markov Chain Monte Carlo algorithm (rjMCMC) to detect shifts in the rate of evolution of a continuous trait across a phylogenetic tree. The tree branch lengths are optimized to conform to a Brownian motion model of evolution by rescaling the lengths of branches whose inferred variance of trait evolution deviates from that expected of a homogeneous Brownian motion model. The calculated scalars indicate the amount of acceleration or deceleration relative to the background rate on the branch of interest (Baker et al. 2016). I ran variable rates independent contrast models using the MCMC method with default priors for each timescaled tree. Each tree was run for 120,000,000 iterations and parameters were sampled every 10,000 iterations. 20,000,000 iterations were discarded as burn-in. I calculated the marginal likelihood of the models using the stepping stone sampler (Xie et al. 2011) implemented in BayesTraits. I sampled 1,000 stones and used 100,000 iterations per stone. Convergence was assessed using the R package CODA (Plummer et al. 2006). The smallest effective sample size (ESS) value across all 300 trees was >489. I used the Variable Rates Post Processor (Baker et al. 2016) to extract the final parameters results. Models were compared using a Bayes Factor (BF) test.

Rates results were summarized by calculating a consensus tree for all timescaled trees where the branch lengths had been replaced with the mean rate scalars calculated by BayesTraits. The consensus tree was computed using the R package phytools (Revell, 2012). I calculated the mean branch lengths for each set of trees, ignoring edges that were not present in all trees of a set. I then plotted the (rescaled) branch lengths of the consensus tree onto the MBL tree using ggtree (Yu et al. 2017). Evolutionary rates through time for all trees were calculated using the Variable Rates Post Processor (Baker et al. 2016) with 1,000 time slices per tree and accounting for shared ancestry as implied by phylogeny (Venditti et al. 2011). Mean evolutionary rates through time were calculated for all Lepidosauria and for separate clades (Rhynchocephalia and Squamata). Evolutionary rates were plotted against time using geoscale (Bell, 2015).

Evolutionary rates for Rhynchocephalia and Squamata were directly compared using a two-tailed generalized Wilcoxon test (= Brunner-Munzel Test; Brunner & Munzel, 2000) as implemented in the R package lawstat (Gastwirth et al. 2017). The generalized Wilcoxon test is similar to the commonly applied Mann-Whitney *U* test (Mann & Whitney, 1947) but is better suited to compare groups that have unequal variance and skewed distributions (Neubert & Brunner, 2007; Neuhäuser & Ruxton, 2009; Neuhäuser, 2010). I applied the generalized Wilcoxon test to both the `raw' rates and the mean rates through time accounting for shared ancestry as computed by the Variable Rates Post Processor (Venditti et al. 2011; Baker et al. 2016). For the `raw' rates one rate value corresponds to one branch on one tree, so each branch contributes equally to the resulting rate distribution. For the mean rates through time, which also take into account shared ancestry, a single branch of one tree can produce multiple rate values that contribute to the resulting rate distribution as it is part of several time slices. Longer branches will therefore have a bigger influence on the resulting rate distributions than shorter ones. This approach generated substantially more rate values making it necessary to downsample the distributions of both clades to 40,000 data points due to the associated computational demand. Analyses were repeated for all three different topologies (Appendix).

5.3 Results

My results demonstrate that heterogeneous rates of evolution characterized early lepidosaurian evolution (Fig. 5.1). Results and discussion presented here are based on the supertree incorporating the squamate higher clades topology of Conrad (2008), but patterns of body size evolution were consistent for all three supertree topologies (see Appendix). 99 out of 100 trees exhibit positive evidence for a heterogeneous rate model ($\log(BF)\geq 2$; Raftery, 1996; Meade & Pagel, 2016), 88 out of 100 trees exhibit strong evidence for a heterogeneous rate model ($\log(BF)\geq 5$), and 38 out of 100 trees exhibit very strong evidence for a heterogeneous rate model ($\log(BF)\geq 10$) (Gauthier et al. (2012) topology: 99, 82, 40; Simões et al. (2018) topology: 99, 83, 44). For Rhynchocephalia, early diverging taxa had slow rates of body size evolution. However, evolutionary rates for the diverse neosphenodontians were considerably higher, including sphenodontids, the Opisthodontia, a group of specialized herbivores, and pleurosaurs, a group of fully marine taxa (Fig. 5.1). In squamates, rapid rates of body size evolution are primarily seen in the marine Mosasauroidea and closely related marine Dolichosauridae. High rates are also consistently recovered in polyglyphanodontian scincomorphs, and less consistently in platynotans and Serpentes. All other higher squamate clades are generally characterized by slow evolutionary rates, including the diverse iguanians, gekkotans, and non-polyglyphanodontian scincomorphs (Fig. 5.1).

Temporal evolutionary rate trends show that rhynchocephalians had notably, and consistently, higher rates of body size evolution than squamates and the pooled rates for all lepidosaurs during the Mesozoic (Fig. 5.2). Mean evolutionary rates, from the 100 dated phylogenies, reveal a steady increase in rates of lepidosaurian body size evolution from the Middle Triassic to the Late Jurassic, followed by an abrupt increase in rates during the Late Jurassic and a high plateau in the Early Cretaceous. This trend is mirrored by rhynchocephalians, but the rates were higher for this subclade and the Late Jurassic rate increase and Early Cretaceous plateau are more exaggerated. In contrast, squamate body size evolutionary rates were stable through the Mesozoic and consistently slower, with just two intervals of marked elevated rates during the latest Cretaceous and in the Eocene (Fig. 5.2).

Contrasting evolutionary rate dynamics between all lepidosaurs, rhynchocephalians and squamates are confirmed by examining the distribution of rate parameters for all branches in the 100 dated phylogenies (Fig. 5.3). Density plots for the mean evolutionary rates accounting for shared ancestry show that rhynchocephalians have a long-tail distribution with a greater relative proportion of high rate branches. Conversely, squamates are dominated by slow rate branches and proportionally fewer high rates. As a whole, Lepidosauria shows an intermediate trend between the two constituent subclades. Statistical tests for the phylogenetically corrected evolutionary rates using the two-tailed Generalized Wilcoxon test confirms that rhynchocephalians and squamates had significantly different rates and that generally rhynchocephalians tend to have higher rates than squamates (Table 5.1; see Neuhäuser & Ruxton (2009) for a detailed explanation of the test interpretation).

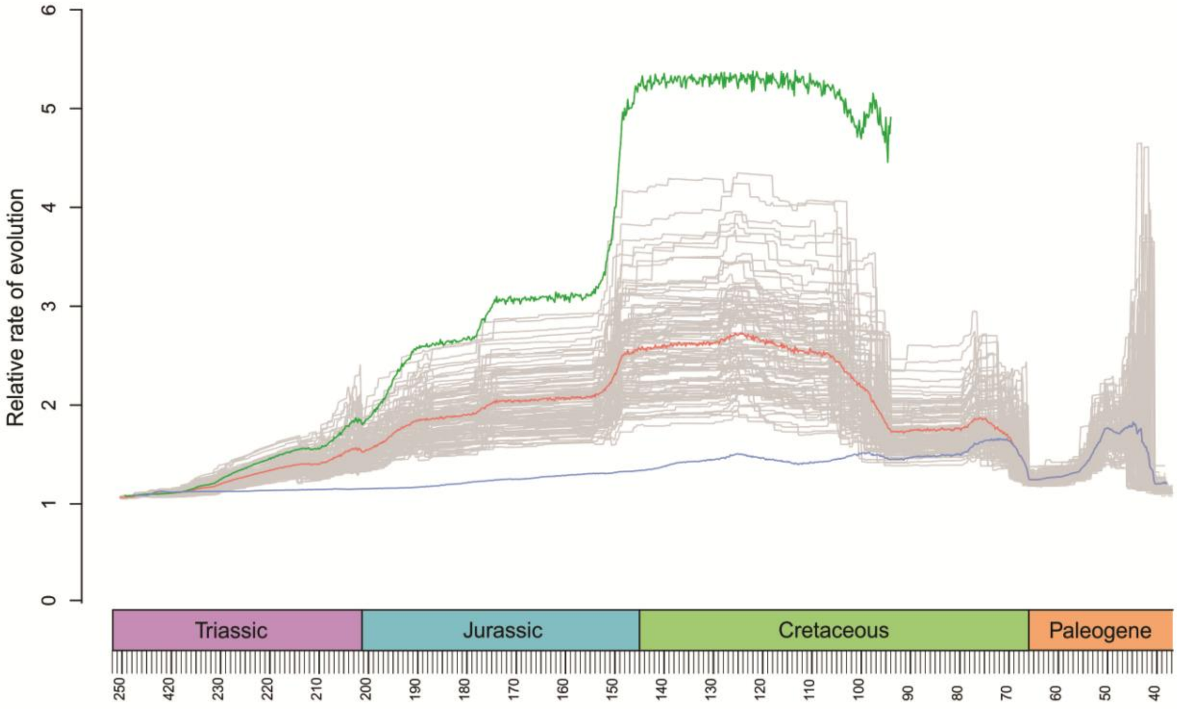


Fig 5.2. Mean time-dependent body size evolutionary rates (accounting for shared ancestry; Venditti et al. 2011) of 100 trees. Red line represents mean rates for the entire Lepidosauria, blue line represents mean rates for the Squamata and green line represents mean rates for the Rhynchocephalia. Grey shaded lines represent Lepidosauria mean rates for each of the 100 trees.

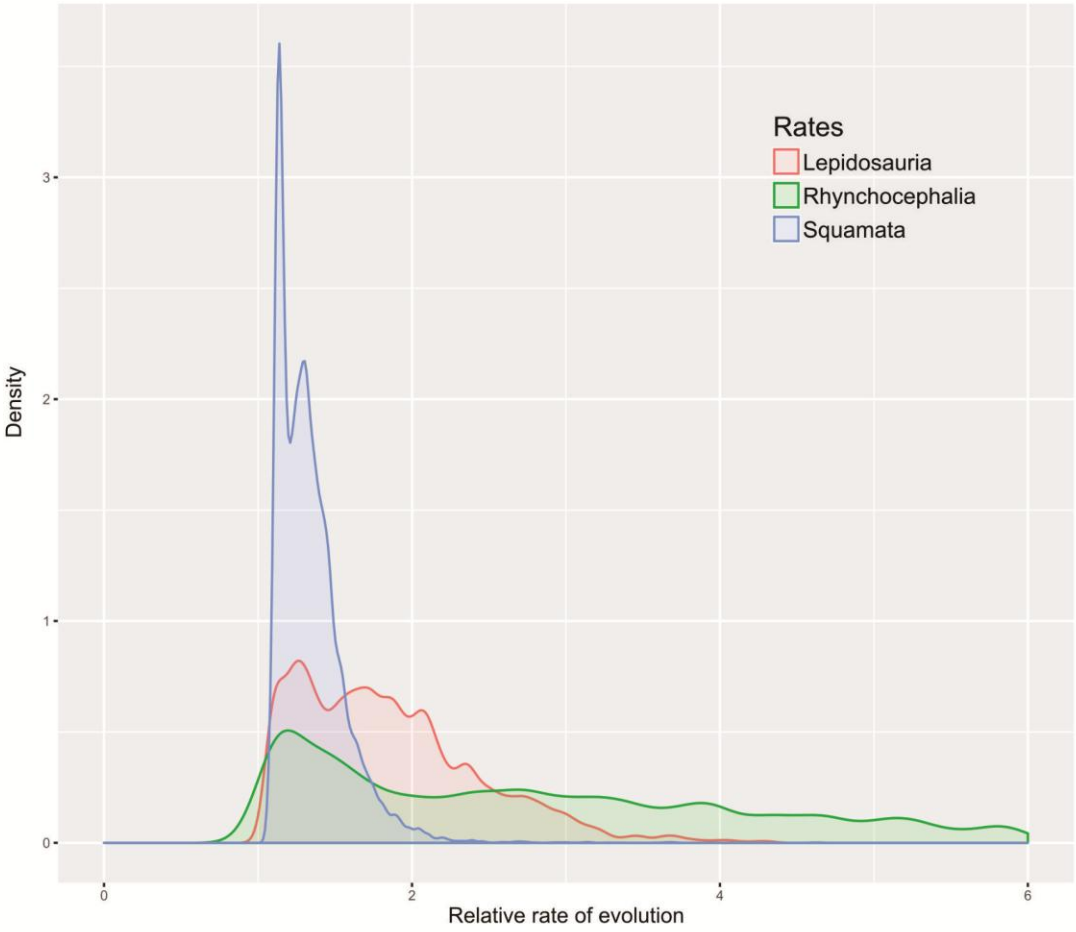


Fig 5.3. Density plot for the mean body size evolutionary rates using the Conrad treeaccounting for shared ancestry as implied by phylogeny for Lepidosauria (red), Rhynchocephalia (green), and Squamata (blue). Rhynchocephalia tend to have higher rates than Squamata. This result is highly significant (see Table 5.1).

Raw rates	**Mean rates accounting for shared ancestry**
Brunner-Munzel Test Statistic = -13.83	Brunner-Munzel Test Statistic = -215.8
df = 9339.1	df = 44765
p-value < 2.2e-16	p-value < 2.2e-16
95 percent confidence interval: 0.4353757 0.4514206	95 percent confidence interval: 0.1571612 0.1633328
Sample estimates: P(X<Y)+.5*P(X=Y) 0.4433981	Sample estimates: P(X<Y)+.5*P(X=Y) 0.160247

Table 5.1. Results of the two-tailed Generalized Wilcoxon Test, comparing the differences in rates for the two major subgroups of the Lepidosauria, Rhynchocephalia (X) and Squamata (Y).

5.4 Discussion

My main result, that extinct rhynchocephalians exhibited significantly faster rates of body size evolution than squamates, is unexpected, and goes against the conventional expectation that rapid evolutionary rates and ‘evolvability’ are key to a clades long-term success (Rabosky et al. 2013). For a long time, the reasons why rhynchocephalians declined dramatically during the late Mesozoic have been unclear, and the imbalance of diversity among the two major lepidosaurian subclades has remained a mystery. Some authors have suggested competition, and posited that the rise of squamates, more specifically lizards, created direct competition for resources between the two groups (Apesteguía and Novas, 2003; Jones, 2006; Jones et al. 2009; Meloro and Jones, 2012). However, no empirical evidence exists. At the very least, such empirical evidence ought to show that the waxing and waning of the two clades occur over the same time interval, but that is not evident: rhynchocephalians declined in diversity in the Early Cretaceous, apparently long before the expansion of squamate diversity.

One of the most relevant aspects of Simpson´s theory is how rates are distributed among lineages, and how even closely related lineages can have completely different rates (Simpson, 1944). In this regard, George G. Simpson´s theories on rates of evolution have only been supported by few empirical examples (e.g. Myers, 1960; McFadden, 1988; Schopf, 1994), but to our knowledge there is no actual example that supports Simpson´s prediction about the extinction of groups with high rates of evolution sustained over long periods of time (Simpson, 1944). I found that among the three different models of distribution of evolutionary rates proposed by Simpson (1944), the tachytelic model seems to fit notably with the fast evolution and subsequent decline of some higher clades of lepidosaurs. Previous studies have suggested the existence of tachytelic evolution in some lineages of extant fishes and bacteria (e.g. Myers, 1960; Woese et al. 1985; Morse et al. 1996), but none of those examples have showed the entire process of Simpson´s tachytelic evolution which suggest that a high rate lineage cannot endure long as such, therefore tachytelic taxa must become horotelic (standard rates), bradytelic (slow rates) or become extinct (Simpson, 1944). The clade Rhynchocephalia was highly successful, but became nearly extinct after the Early Cretaceous (Apesteguía et al. 2014; Herrera-Flores et al. 2017; Cleary et al. 2018). As mentioned above, their decline has been attributed to the rise of lizards, but I believe that the near complete extinction of rhynchocephalians could also have been caused by their sustained high rates of evolution if we consider Simpson´s tachytelic model. It may be true that the radiation of squamates at the end of the Cretaceous contributed to the rhynchocephalian decline by direct competition for resources; but it is important to note that rhynchocephalian decay began early in the Cretaceous, just after they experienced a peak in their morphological disparity in the Late Jurassic and million years before the big radiation of squamates in the Middle/Late Cretaceous. Something important to consider is that there are no records of mid-Late Cretaceous rhynchocephalians and most Late Cretaceous taxa come from the southern continents, so it is possible that this bias in the rhynchocephalian fossil record could have influenced my results. However, this work represents a novel explanation for the rhynchocephalian decline and may explain the survival of only few lineages beyond the K-Pg boundary such as the opisthodontian genus *Kawasphenodon* that survived until the Early Paleocene (Apesteguía et al. 2014) or the well-known extant “tuatara” from New Zealand (*S. punctatus*). Previous evolutionary rate analysis (Herrera-Flores et al. 2017), suggest that the Sphenodontinae, the linage that includes *Sphenodon* and its close relatives, went through an apparently long-term morphological stasis after the Jurassic which also coincides with Simpson´s statement that tachytelic taxa can also become horotelic or bradytelic (Simpson, 1944).

In addition to high rates in Rhynchocephalia, our analyses also identified elevated rates in the Mosasauroidea + Dolichosauridae squamate clade and polyglyphanodontian squamates. These clades, particularly the mosasaurs, were highly successful in the Late Cretaceous but also became extinct at the K-T. However, in contrast to rhynchocephalians, whose decline began long time before the K-Pg boundary (Apesteguía et al. 2014; Herrera-Flores et al. 2017; Cleary et al. 2018), the extinction of mosasaurs and polyglyphanodontians has been directly attributed to the changes in the biota driven by the K-Pg mass extinction event (Longrich et al. 2012; Polcyn et al. 2014). With regard to this, it should not be discarded that the Simpsonian model of change in evolutionary rates may also apply to these squamates clades, because mosasaurs and polyglyphanodontians showed a consistent increase in body size nearly until their extinction at the end of the Cretaceous. Also, those lepidosaur groups that presented small body size or that showed small variation in size may be advantageous because even today large bodied lepidosaurs are very few, while most extant lepidosaurs are represented by small body size. It is possible that Simpson´s tachytelc evolution was an additional force behind the extinction of mosasaurs and polyglyphanodontians, and undoubtedly it is an interesting topic that must be explored along with how Cope´s rule applies to Mezosoic lepidosaurs, but at the moment these topics are beyond the scope of this work.

My work offers a novel and previously unexplored explanation for the decline of rhynchocephalians and suggests that the longevity and ecological dominance of squamates cannot be attributed to rapid evolutionary rates in their early evolutionary history. Simpson´s historical proposal for links between evolutionary rates and long-term persistence and success previously lacked empirical examples using modern computational macroevolutionary techniques, and most other quantitative studies have suggested that rapid evolutionary rates are key to long-term success – I find the opposite was true for Lepidosauria.

5.5 Appendix

5.5.1 Early lepidosaur supertree

The super tree of early lepidosaurs was built in Mesquite (Madison and Madison, 2002) by using for rhynchocephalians the maximum parsimony 50 % majority rule consensus tree of Herrera-Flores et al. (2018: Fig. 3) and combining for early squamates (amphisbaenians, lizards, snakes and mosasaurs) the maximum parsimony strict consensus tree of Conrad (2008: Fig. 54); the maximum parsimony strict consensus tree including only ingroup fossils of Gauthier et al. (2012: Fig. 6); Adams consensus tree of Longrich et al. (2012: Fig. 2); strict consensus tree of Caldwell et al. (2015: Fig. 4b); maximum parsimony strict consensus tree of Martill et al. (2015: Fig. 5); strict consensus tree of the Bayesian analysis of Longrich et al. (2015: Fig. 5); maximum likelihood tree of Simões et al. (2017B: Fig. 1D); and maximum parsimony strict consensus tree of Rio and Mannion (2017: Fig. 10B). After combining and editing the super tree, more taxa were added manually by following other complementary phylogenies and by reviewing the original descriptions of some poorly known species and its possible phylogenetic affinities. In the case of squamates, because of discordances in the relationships among squamate higher clades, we decided to avoid biasing the study to a single topology, so we used for squamates three different topologies based on the three major phylogenetic works on the group (Conrad, 2008; Gauthier et al. 2012; Simões et al. 2018).

Details of all other added taxa are as follow:

Rhynchocephalia

Non-sphenodontian rhynchocephalians

Gephyrosaurus evansae was added as the sister species of *G. bridensis*, while *Penegephyrosaurus curtiscoppi* was added as the sister group of the genus *Gephyrosaurus* according to the qualitative representation of the phylogeny of the Lepidosauria of Whiteside and Duffin (2017: Fig. 9).

Basal rhynchocephalian *Deltadectes elvetica* was added into a polytomy with *Penegephyrosaurus curtiscoppi* because of the suggestion of Whiteside et al. (2017) about that it seems to be closely related to *Gephyrosaurus,* and also because it is one of the only third known genera of non-sphenodontian rhynchocephalians.

Sphenodontians

Whitakersaurus bermani was added into a polytomy with *Diphydontosaurus* and as the sister group of *Planocephalosaurus* and other rhynchocephalians according to the 50% majority rule consensus tree of Jones et al. (2013: Fig. 3).

Paleollanosaurus fraseri was added within the polytomy that includes *Diphydontosaurus* and *Whitakersaurus* based on the similarities in their morphology suggested by Heckert (2004), and the qualitative representation of the phylogeny of the Lepidosauria of Whiteside and Duffin (2017: Fig. 9).

Planocephalosaurus lucasi was added as the sister species of *P. robinsonae* according to the work of Heckert (2004).

Eusphenodontians

The maximum parsimony 50% majority rule consensus tree of the Rhynchocephalia of Herrera-Flores et al. (2018: Fig. 3) shows all *Clevosaurus* species into a polytomy. Here, we added the poorly known *Clevosaurus minor* as the sister species of *C. hudsoni* because of the close relationship between both species suggested by Fraser (1998). *C. sectumsemper* was set as the sister group of the clade of *C. hudsoni* and *C. minor* due to the suggestion of Klein et al. (2015) about that *C. hudsoni* and *C. sectumsemper* are closely related species. Two of the three species of Chinese clevosaurs (*C. wangi* and *C. mcgilli*) were set in the same clade and as a sister group of the clade of *C. convallis* and *C. brasiliensis*. However, it must be noted that Jones (2006) showed that *C. wangi* and *C. mcgilli* may not be valid taxa. *C. bairdi* was set as the sister group of the clades that include *C. wangi*, *C. mcgilli*, *C. convallis* and *C. brasiliensis* because of the apparently close relationship with *C. convallis* and *C. mcgilli* suggested by Sues et al. (1994) and Hsiou et al. (2015). On the other hand, the third species of Chinese *Clevosaurus*, *C. petilus* was set as the sister group of all members of the genus *Clevosaurus* according with the results of the pruned tree of Hsiou et al. (2015: Fig. 5B). Also, it must be pointed out that Jones (2006) showed that *C. petilus* might not belong to the genus *Clevosaurus*, and indeed it could be a different genus as was originally described by Young (1982).

Clevosaurus cambrica was described by Keblee et al. (2018) as closely related to *C. hudsoni* and *C. sectusemper*; therefore it was included into the polytomy that includes *C. sectusemper* and the clade that includes of *C. hudsoni*.

Neosphenodontians

The polytomy within sapheosaurs was resolved by putting together *Kallimodon pulchellus* with the only other known species of the genus *K. cerinensis*. On the other side, we added the poorly known species *Piocormus laticeps* which was added as the sister group of *Sapheosaurus thiollierei* according the suggestions of Cocude-Michel (1963, 1967).

Sigmala sigmala is a taxon that has never been included in a phylogenetic analysis; however it was included as an early diverging opisthodontian based on the suggestions of Fraser (1986) about its morphological similarities with *Opisthias*. Also a direct review of the type specimens made by the first author of this work (J. A. Herrera-Flores) confirms the close relationship of *Sigmala* with the Opisthodontia based on tooth morphology.

Vadasaurus herzogi was added as the sister group of Pleurosauridae (*Palaeopleurosaurus* + *Pleurosaurus*) according to the strict consensus of the maximum parsimony analysis Bever and Norell (2017: Fig. 5a).

Bharatagama rebbanensis was described by Evans et al. (2002) as a primitive acrodont iguanian and possibly the earliest diverging taxon within Iguania; however, this taxon was not included in a phylogenetic analysis. The work of Conrad (2018) included this taxon in a phylogenetic analysis that shows that *Bharatagama* is not related to the Squamata but is closely related to the Rhynchocephalia, specifically with “pleurosaurs”. Therefore we include this taxon in the polytomy that includes the earliest pleurosaur *Vadasaurus*.

Squamates

Lacertilia

Xestops stehlini was originally described as *Paraxestops stehlini* by Hoffstetter (1962), but a posterior review of the genus *Xestops* by Meszoely et al. (1978) considered that *Paraxestops* is a synonym of *Xestops*. So far, only *X. vagans* has been included in phylogenetic analysis (see Conrad, 2008), therefore, here we included *X. stehlini* as the sister species of *X. vagans*.

Three species of the genus *Gilmoreteius* (*G. ferruginous*, *G. gilmorei* and *G. chulsanensis*) were added. According to the work of Keqin and Norel (2000) all *Gilmoreteius* species are clearly distinguishable from each other; however, only *G. chulsanensis* has been included in a phylogenetic analysis (see Simões et al. 2018: Fig. 2), so we placed all the three species into a polytomy.

Eichstaettisaurus gouldi was added as the sister species of *E. schroederi* according to Evans et al. (2004).

Dalinghosaurus longidigitus was added as the outgroup of the clade that includes *Carusia* according to the maximum parsimony analysis of Evans and Wang (2005: Fig. 12A).

Yebeinosaurus tenius was added as a taxon closely related to *Ardeosaurus* according to the maximum parsimony strict consensus tree of Evans et al. (2005: Fig. 17).

Peneteius saueri was added as the sister species of *P. aquilonius* according to the work of Nydam et al. (2007).

Ovoo gurval was added into the politomy that includes other platynotan lizards from Mongolia (e. g. *Saniwa*, *Necrosaurus*) according to the maximum parsimony strict consensus tree of Yi et al. (2013: Fig. 10).

The genus *Dicothodon* and associated species (*D. bajaensis*, *D. cifellii*, *D. moorensis*) were added as a sister taxon of *Polyglyphanodon*, while the genus *Bicuspidon* and associated species (*B. hatzegiensis*, *B. numerosus*, *B. smikros*) were added as the sister group of the Polyglyphanodontini (*Dicothodon* + *Polyglyphanodon*) according to the maximum parsimony strict consensus tree of Nydam et al. (2007: Fig. 5).

Sakurasaurus shokawensis was added as the sister taxon of *Yabeinosaurus* according to the maximum parsimony strict consensus tree of Evans and Manabe (2009: Fig. 10).

Members of the family Contogeniidae (*Contogenys ekalakaensis*, *Palaeosincosaurus middletoni*, *Palaeosincosaurus pharkidodon* and *Utahgenys evansi*) were added into a polytomy with *C. sloani* according to the work of Nydam and Fitzpatrick (2009: Fig. 8). According to the Adams consensus tree of Longrich et al. (2012), *Contogenys* is closely related to *Eoxanta lacertifrons*.

Luishusaurus acanthocaudata was added as a species closely related to *Yabeinosaurus* according to the maximum parsimony strict consensus tree of Evans and Wang (2010: Fig. 11).

Pedrerasaurus latifrontalis from the Early Cretaceous of Spain is apparently related to the Early Cretaceous *Meyasaurus,* but this relationship cannot be confirmed accurately. I added *Pedrerasaurus* into the polytomy that includes *Ardeosaurus*, *Bavarisaurus* and other gekkonomorphs by following the suggestions and Adams consensus tree of Bolet and Evans (2010: Fig. 9).

Hoyalacerta sanzi was added as outgroup of *Huehuecuetzpalli*, Iguania and all other squamates. I regard it as one of the earliest diverging squamate based on the maximum parsimony strict consensus tree of Evans and Wang (2010: Fig. 11) and the recent parsimony analysis of Simões et al. (2017a: Fig. 2) plus the original description of Evans and Barbadillo (1999) who described it as a primitive stem lizard that lies outside crown Squamata. It must be noted that the phylogenetic position of this taxon is quite problematic, it appears to be a wild card taxon whose phylogenetic position constantly changes in different analyses (e.g. Evans and Barbadillo, 1999; Evans and Manabe, 2009; Evans and Wang, 2010; Simões et al. 2015a, 2017a).

Bavarisaurus macrodactylus is a conflictive taxon whose phylogenetic position commonly shifts between stem and crown Squamata. Here, it was added within the polytomy that includes *Ardeosaurus* and *Eichstaettisaurus* based on many phylogenetic studies that show that it seems to be closely related to other Late Jurassic taxa from Bavaria (e.g. Bolet and Evans, 2010: Fig. 8; Evans and Wang, 2010: Fig. 11; Simões et al. 2015a: Fig. 3A).

Chianghsia nankangensis was added as the sister taxon of *Estesia* according to the maximum parsimony strict consensus tree of Mo et al. (2012: Fig. 5).

Jucaraseps grandipes was added as the sister group of the clade that includes *Sakurasaurus* and *Yabeinosaurus* according to the maximum parsimony strict consensus tree of Bolet and Evans (2012: Fig. 4).

Chianghsia nankangensis was added as the sister taxon of *Estesia* according to the maximum parsimony strict consensus tree of Mo et al. (2012: Fig. 5).

Catactagenys solaster, Paracotongenys estesi and *Paleoxantusia kyrentos* all of them considered xantusiid lizards were placed into a polytomy according to the strict consensus and Adams consensus tree of Nydam et al. (2013: Fig. 5).

Desertiguana gobiensis was added as the sister taxon of *Anchaurosaurus* according to the reconstruction of iguanomorph relationships of Alifanov (2013: Fig. 5a).

Funiusaurus luanchuanensis along with other members of the Tuberocephalosaurinae (*Aprisaurus bidentatus*, *Tuberocephalosaurus pompabilis* and *Tianyuasaurus zhengi*) were added as the sister group of the Polyglyphanodontinae. Also *Darchansaurus estesi*, *Cherminsaurus kozlowskii* and *Erdenetesaurus robinsonae* were added to the Polyglyphanodontinae according to the Maximum parsimony strict consensus and 50% majority rule tree of Xu et al. (2014: Fig. 4).

Specimen AMNH FR 21444 included in many previous analyses (e.g. Gauthier et al. 2012; Longrich et al. 2012), was renamed *Norellius nyctisaurops* according to the formal description and naming of the specimen by Conrad and Daza (2015).

Pachygenys adachii was added as the sister species of *P. thlastesa* according to the work of Ikeda et al. (2015).

Babibasiliscus alxi and *Geiseltaliellus maarius* both members of the Corytophaninae were added within Iguania, according to the Adams consensus tree of Conrad (2015: Fig. 6).

Gueragama sulamericana was added as the sister group of the clade that includes *Priscagama*, *Mimeosaurus* and *Phrynosomimus* according to the maximum parsimony strict consensus tree of Simões et al. (2015b: Fig. 3a).

Olindalacerta brasiliensis from the Early Cretaceous of Brazil is apparently related to the family Polyglyphanodontidae; it was added into a polytomy with *Adamisaurus* according to the maximum parsimony strict consensus tree of Simões et al. (2015a: Fig. 3A).

Tijubina pontei was added as the sister group of the clade that includes *Gobinatus* and *Tchingisaurus* according to the maximum parsimony strict consensus tree of Simões et al. (2015a: Fig. 3B).

Asprosaurus bibongriensis was added into a polytomy with *Palaeosaniwa* and other monstersaurs according to the maximum parsimony strict consensus tree of Park et al. (2015: Fig. 9).

Barbatteius vremiri a teiioid lizard was added in a clade with the Early Cretaceous genus *Meyasaurus* which according to the maximum parsimony strict consensus tree of Venczel and Codrea et al. (2015: Fig. 7) is also a teiioid lizard. We added all the four known species of *Meyasaurus* into a polytomy because of the unclear relationship among this genus (Evans and Barbadillo, 1997).

All members that comprise the family Hodzhakuliidae were added to the supertree (*Pachygenys thlastesa, Pachygenys adachii, Hodzhakulia magna, Bagaluus primigenius, Platynotoides altidentatus, Carnoscincus eublepharus).* According to the phylogenetic relationships of the family Hodzhakuliidae of Alifanov (2016), Hodzhakuliidae is closely related to the family Xantusiidae. We added Hodzhakuliidae as the sister group of the clade that includes *Catactagenys* and *Paracontogenys* which are the only Mesozoic taxa referable to Xantusiidae according to Nydam et al. (2013).

Jeddaherdan aleadonta was added as the sister taxon of *Gueragama sulamericana* according to the Bayesian consensus tree of Apesteguía et al. (2016: Fig. 5).

The Early Paleocene *Qianshanosaurus huanpuensis* is an iguanian closely related to the Acrodonta according to the taxonomic review of Dong et al. (2016). This species has never been included in a phylogenetic analysis; however, we included it within the polytomy that includes other stem acrodont lizards such as *Jeddaherdan* and *Gueragama*.

Ardeosarus digitatellus was added into the polytomy that includes *Eichstaettisaurus* and *Norellius* according to the maximum parsimony strict consensus tree of Simões et al. (2016: Fig. 10).

The Late Cretaceous iguanomorph *Magnuviator ovimonsensis* was added as the sister group of the clade that comprises *Saichangurvel* and *Temujinia* following to the maximum parsimony strict consensus tree of DeMar et al. (2017: Fig. 2a).

Late Jurassic squamate *Schoenesmahl dyspepsia* and *Ardeosaurus brevipes* were added as sister taxa according to the work of Conrad (2018).

The Middle Triassic *Megachirella wachtleri* and the Middle Jurassic *Marmoretta oxoniensis* were added as the earliest squamates according to the Bayesian total evidence tree of Simões et al. (2018: Fig. 2)

Amphisbaenians

The Middle Campanian *Slavoia darevskii* was originally found as part of the "Scincomorpha" by Conrad (2008: Fig. 54); however recent morphological and phylogenetic evidence shows that it is more closely related to amphisbaenians. The phylogenetic analysis of Tałanda (2016: Fig. 2) suggest that *S. darevskii* is an early diverging amphisbaenian, therefore we changed the position of this taxon moving it from scincomorpha to the base of amphisbaenians.

The Eocene *Cryptolacerta hassiaca* was originally described as a stem amphisbaenian by Müller et al. (2011: Fig. 3a), however, a posterior phylogenetic analysis found it more related to Lacertidae (Longrich et al. 2015: Fig. 2). The recent work of Tałanda (2016) also shows that the phylogenetic position of *C. hassiaca* is ambiguous by changing between stem Amphisbaenia and Lacertidae (Talanda, 2016: Fig. 2, 3). Tałanda (2016), suggested that *C. hassiaca* may be a lacertid with specialized burrowing adaptations, but unless a new analysis confirm that hypothesis, here we decided to keep it as a stem amphisbaenian.

Solastella cookei was added as the sister group of *Spathorhynchu*s according to the Bayesian analysis of Stocker and Kirk (2016: Fig. 6).

Cuvieribaena carlgansi was found by the maximum parsimony analysis of Čerňanský et al. (2015: Fig. 5) as the sister group of the extant genus *Blanus*. Here, we added *Cuvieribaena* as the sister group of the clade that includes *Blanosaurus* and *Louisamphisbaena* which are the taxa more closely related to *Blanus* according to phylogeny of the Amphisbaenia of Longrich et al. (2015: Fig. 5).

Mosasauria

Aquatic squamates *Coniasaurus crassidens* and *C. gracilodens* were added in a clade that was set as the sister group of *Dolichosaurus longicollis* according to the maximum parsimony majority rule consensus tree of Caldwell (2000: Fig. 13B).

Kaganaias hakusanensis from the Early Cretaceous of Japan is an elongated squamate with apparently aquatic adaptations. The analysis performed by Evans et al. (2006: Fig. 11) showed that its phylogenetic position varies greatly depending on the data matrix used in the analyses. However, it was added into the polytomy that includes other basal aquatic squamates such as *Adriosaurus* and *Dolichosaurus* and as outgroup of the clade that includes *Aphanizocnemus* based on the morphological similarities and the suggestions of Evans et al. (2006).

Adriosaurus microbrachis and *A. skrbinensis* were added into a polytomy with *A. suessi* according to single most parsimonious tree of Caldwell and Palci (2010: Fig. 6).

Acteosaurus tommasinii was added as the sister group of *Aphanizocnemus libanensis* which is also the sister group of *Pontosaurus* according to the single most parsimonious tree of Caldwell and Palci (2010: Fig. 6).

Pontosaurus lesinensis was added as a sister species of *P. kornhuberi* according to Caldwell (2006).

Carsosaurus marchesetti was added as the sister group of *Aigialosaurus* according to the maximum parsimony majority rule consensus tree of Caldwell (2000: Fig. 13B).

Globidens schurmanni described by Martin (2007) was added into the polytomy that includes all other *Globidens* species.

Selmasaurus russelli was added as the sister species of *S. johnsoni* according to the single most parsimonious tree of Polcyn and Everhart (2008: Fig 9).

Eonatator coellensis was added as the sister species of *E. sternbergi* according to the work of Paramo-Fonseca (2013).

Haasiasaurus gittelmani was added as outgroup of *Tethysaurus*, Tylosaurinae and Plioplatecarpinae according to the cladogram of mosasaur genera of Polcyn et al. (2014).

Halisaurus arambourgi was added as the sister species of *H. platyspondylus*, while *H. sternbergi* was renamed as *Eonatator sternbergi* according to the maximum parsimony strict consensus tree of Konishi et al. (2016: Fig. 20). Additionally, two taxa *Phosphorosaurus ortliebi* and *P. ponpetelegans* were added in a clade as the sister group of *E. sternbergi* according to Konishi et al. (2016: Fig. 20).

Five species of *Plioplatecarpus* were added based on the maximum parsimony strict consensus tree and 50% majority rule tree of the phylogeny of the Plioplatercarpinae of Cuthbertson and Holmes (2015: Fig. 20). *P. nichollsae* was added as the sister group of *P. primaevus*; while *P. primaevus* was set as the sister group of the polytomy that includes *P. houzeaui*, *P. marshi* and *P. peckensis*.

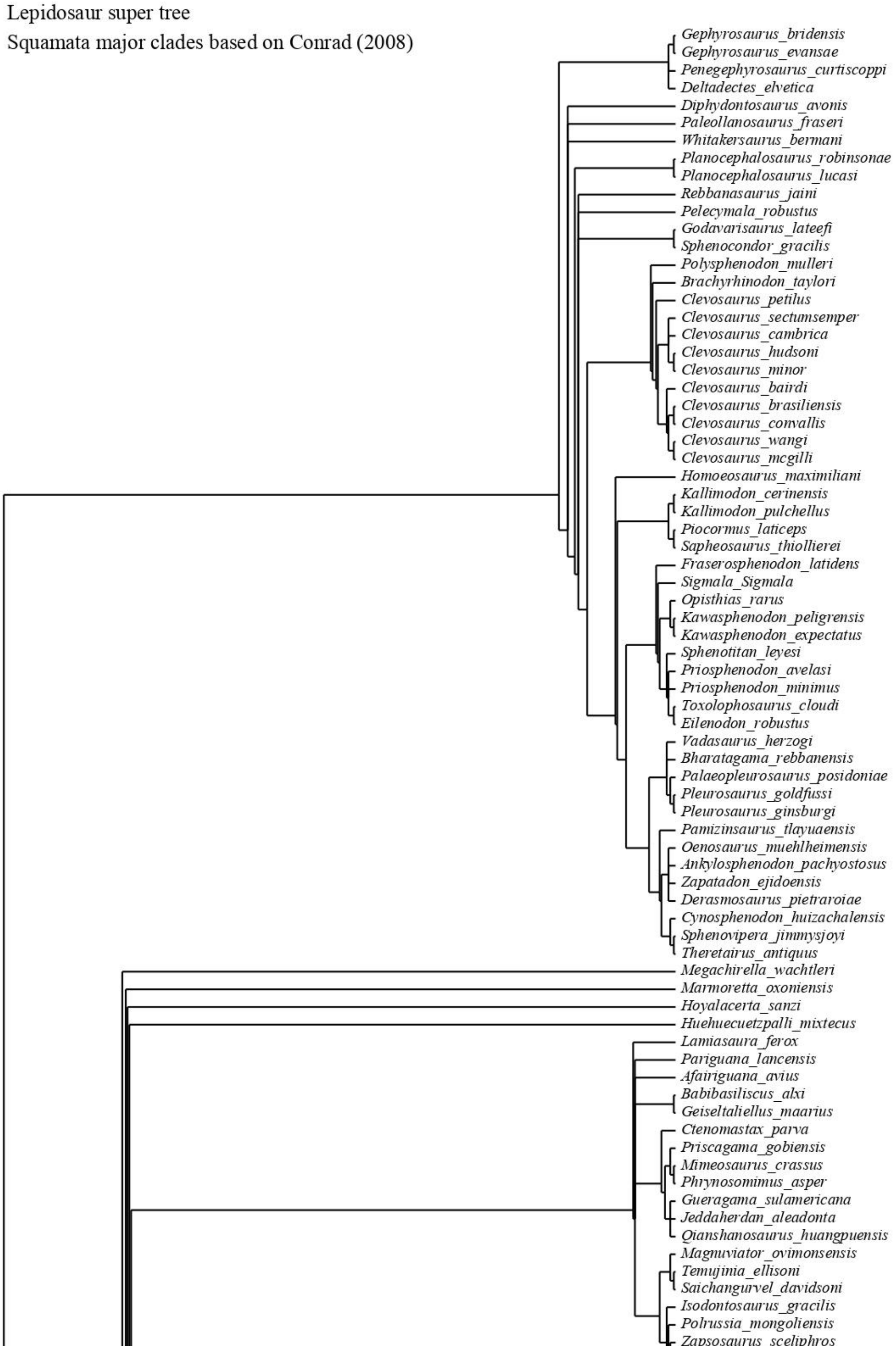
Kaikaifilu hervei was added as the sister group of *Taniwhasaurus* according to the strict consensus tree of the parsimony analysis of Otero et al. (2017: Fig. 12C).

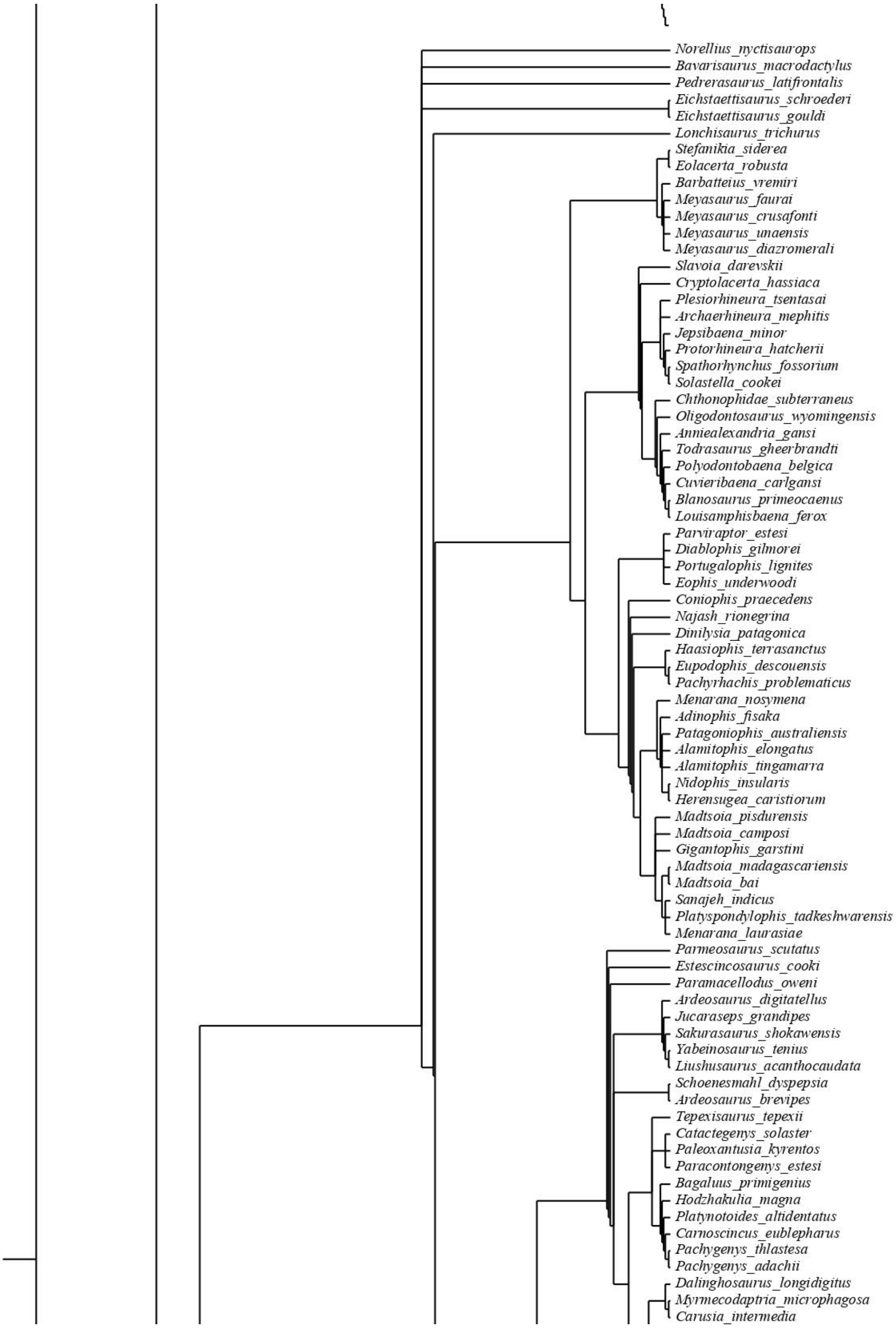
Stefanikia sidereal was added as the sister group of *Eolacerta robusta* according to the maximum parsimony strict consensus tree of Čerňanský and Smith (2017: Fig. 13)

The Early Cretaceous snake-like *Tetrapodophis amplectus* was originally described as a basal snake by Martill et al. (2015); however recent evidence suggests that it is more closely related to basal aquatic squamates. The phylogenetic analysis of Paparella et al. (2018) suggest that *T. amplectus* is a stem non-ophidian pythonomorph, so we changed the position of this taxon by moving it from snakes to the base of Mosasauria (Mosasauroidea + Dolichosauridae).

The Late Cretaceous aquatic squamate *Primitivus manduriensis* was added as a member of the family Dolichosauridae according to the maximum parsimony tree of Paparella et al. (2018: Fig. 10).

Lepidosaur super tree Conrad topology

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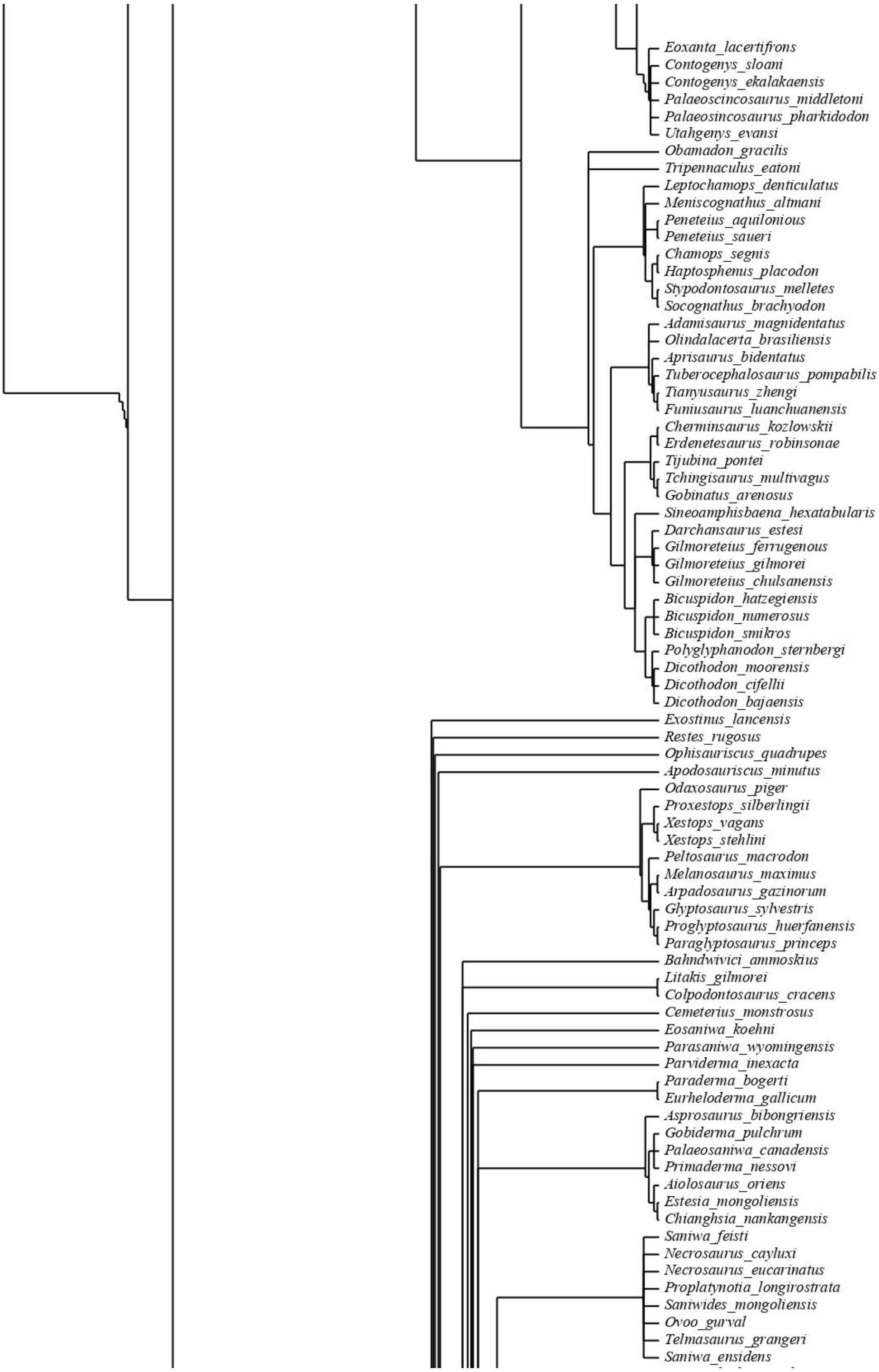
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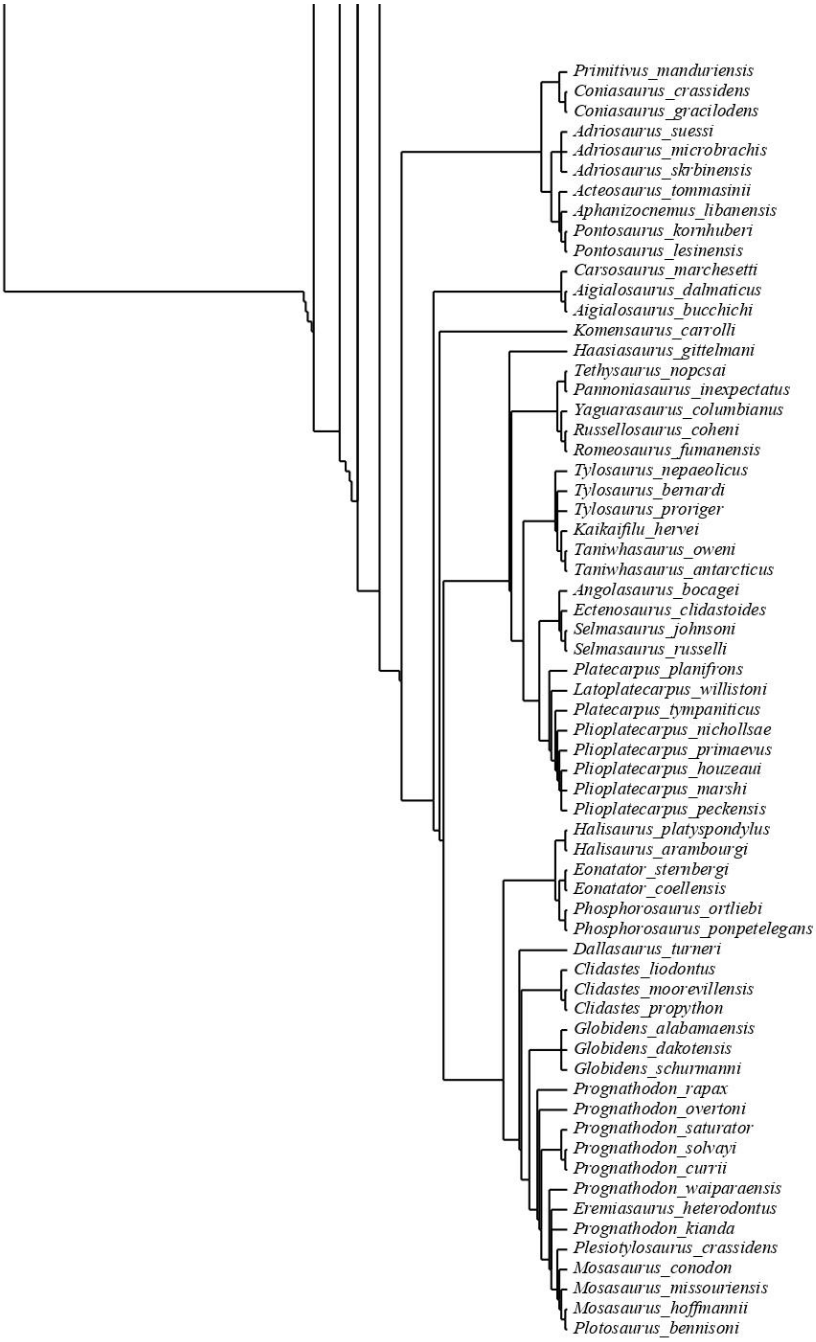
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Prognathodon_kianda
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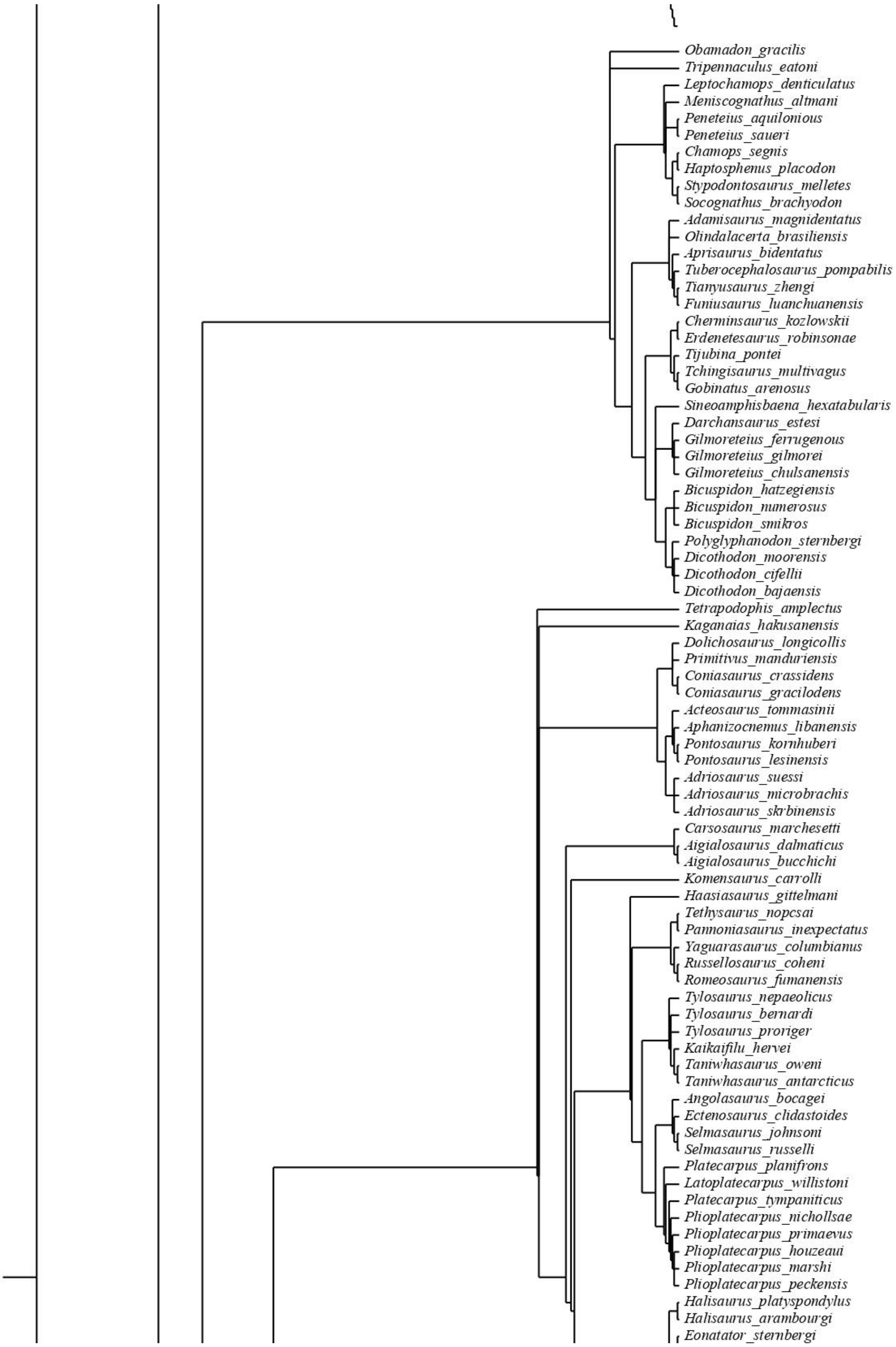
Lepidosaur super tree Gauthier topology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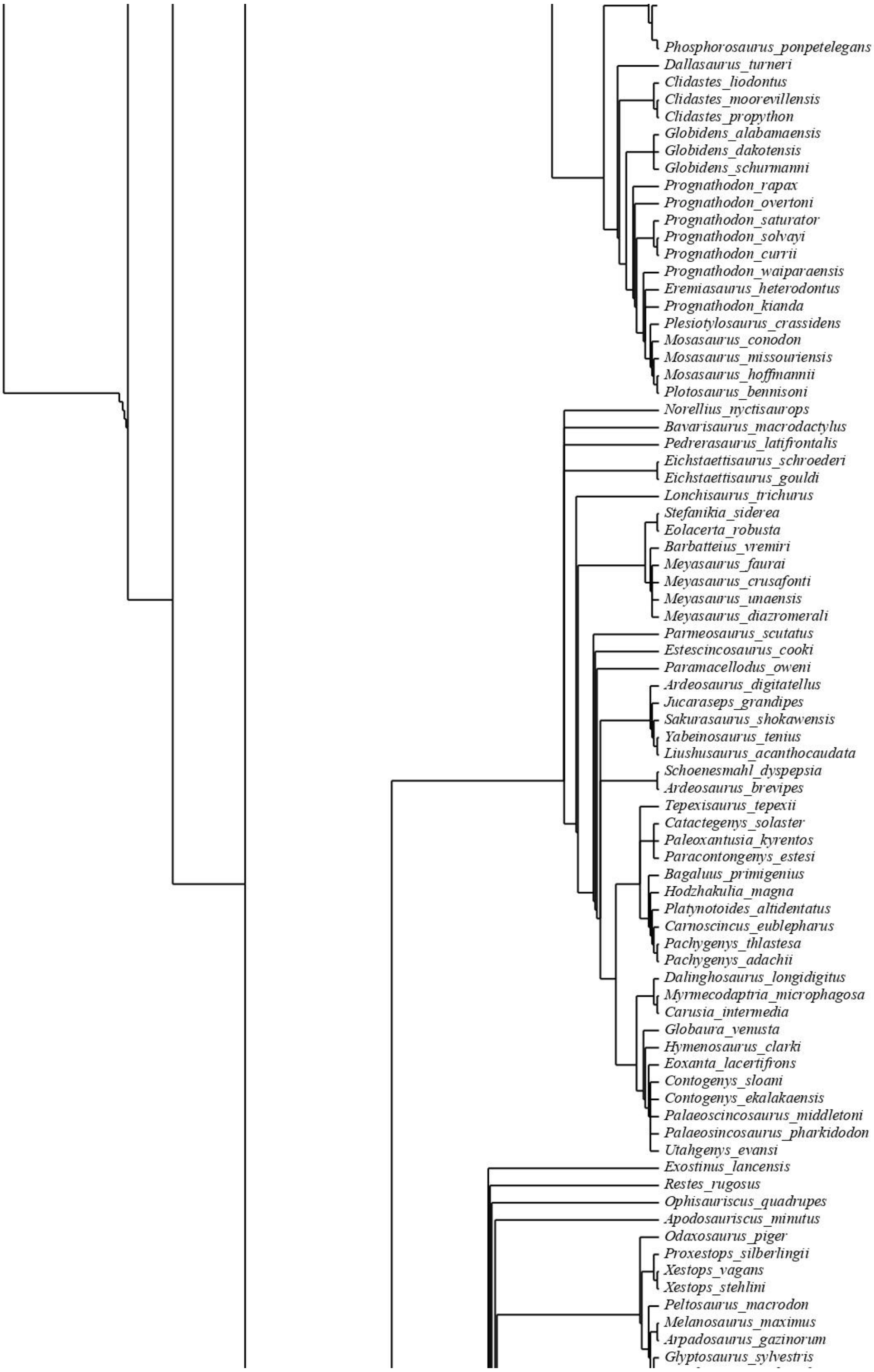
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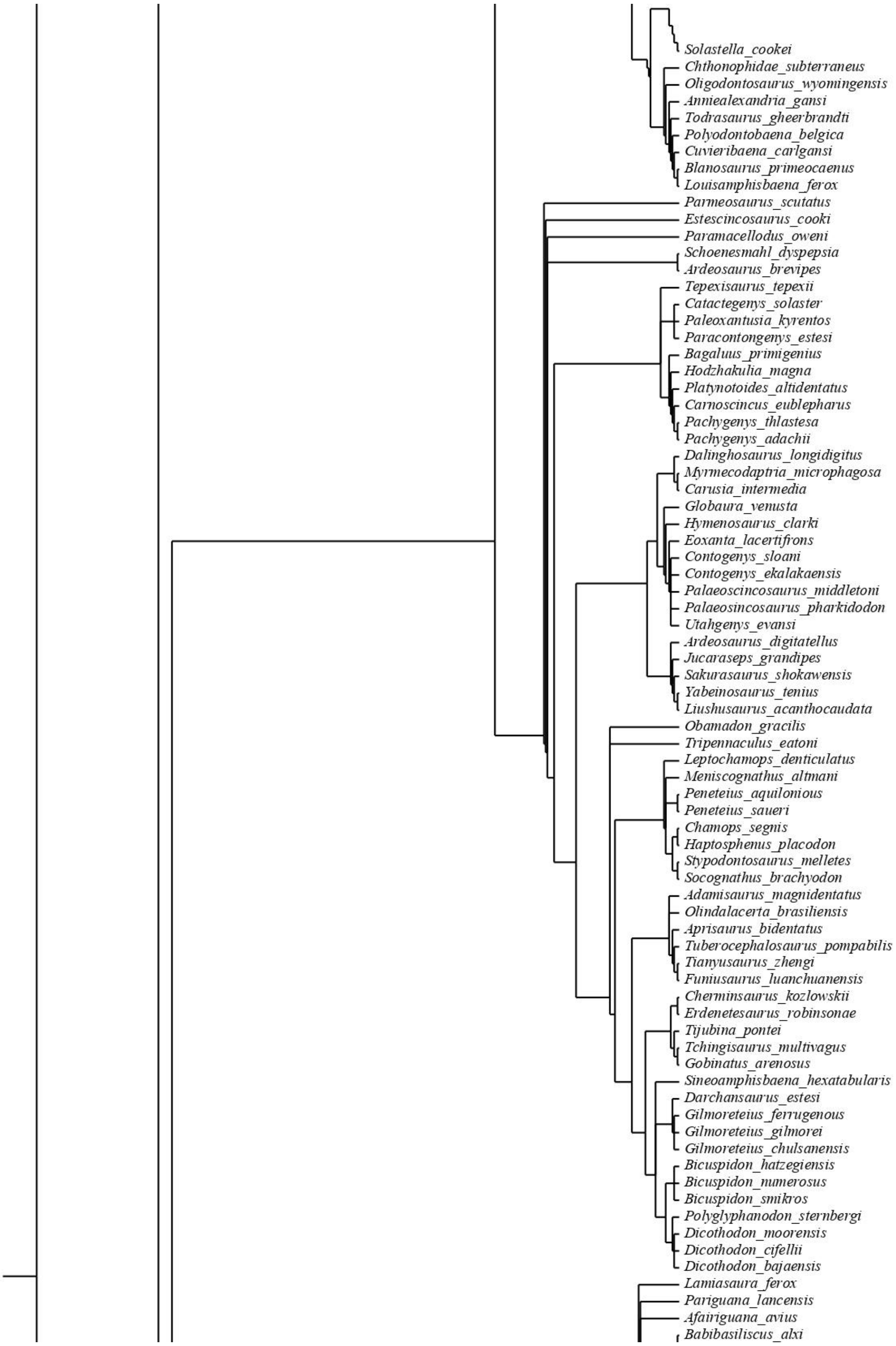
Lepidosaur super tree Simoes topology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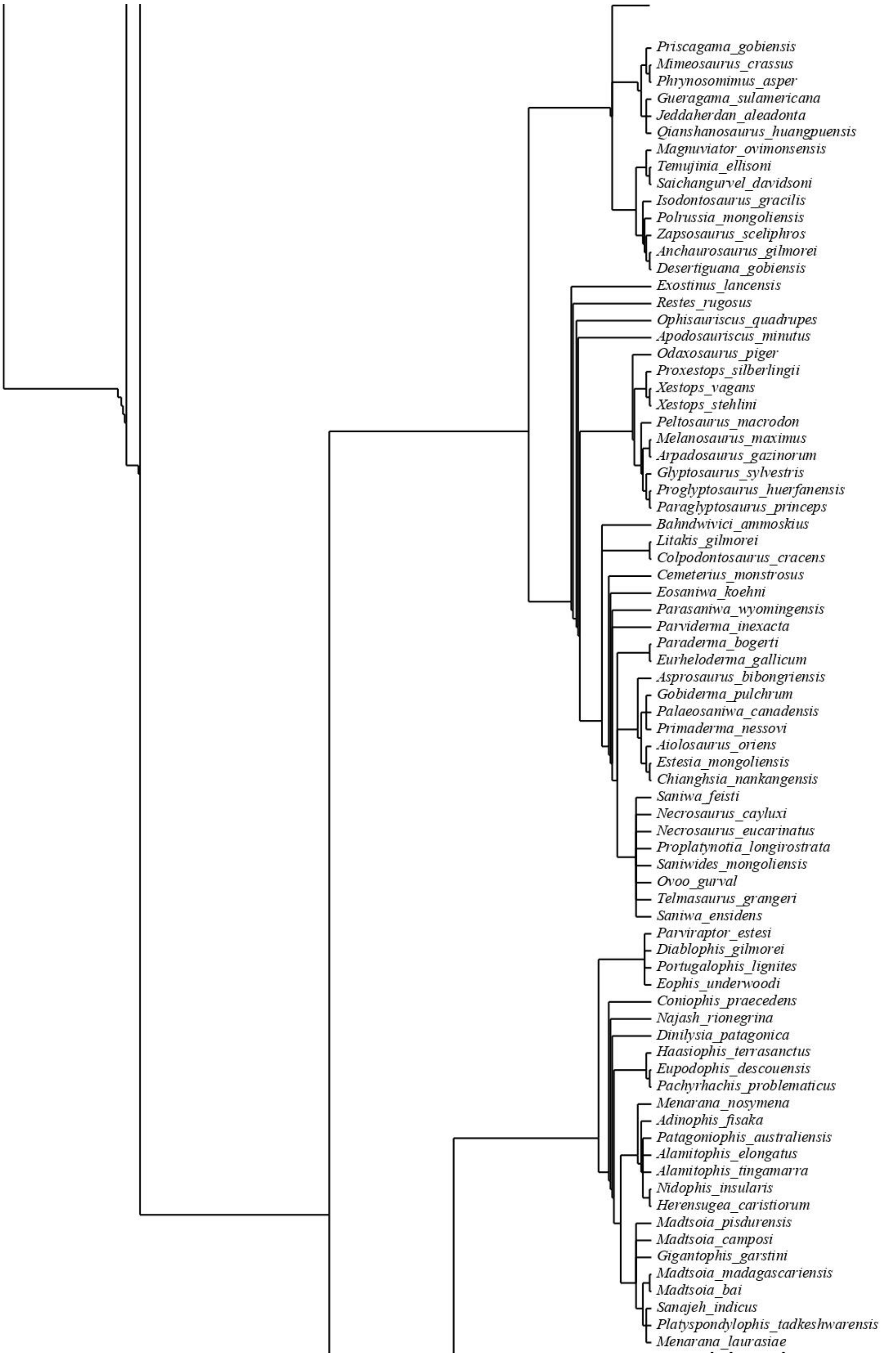
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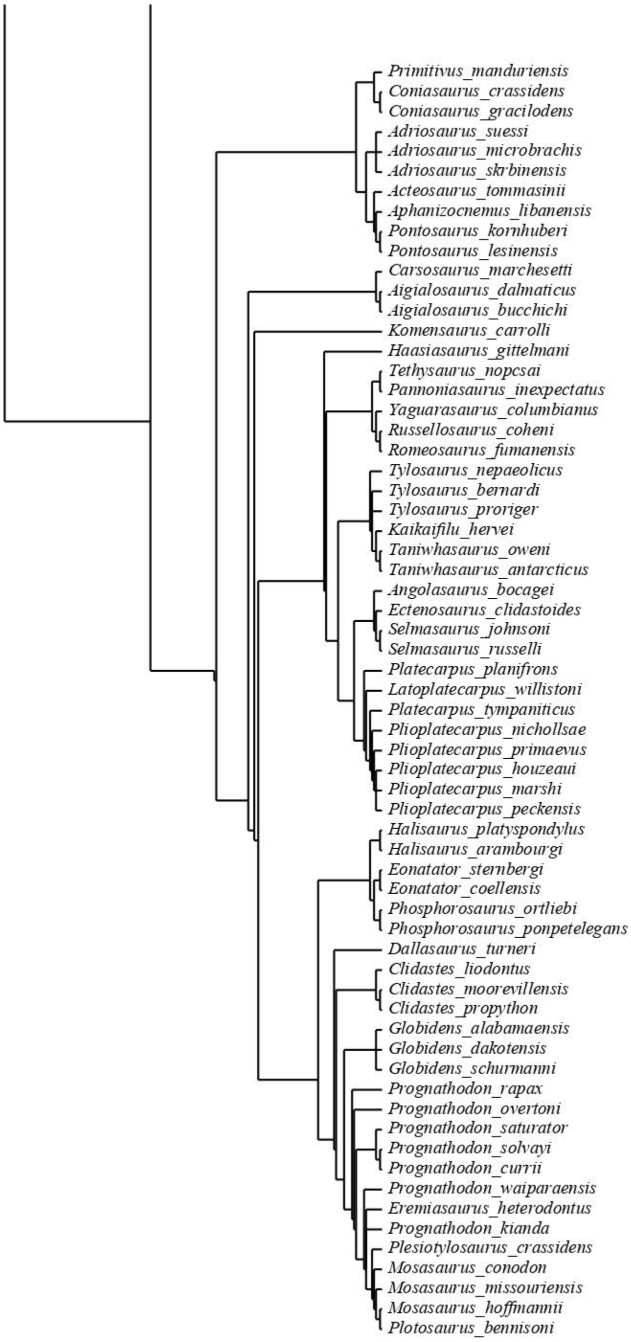
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5.5.2 Body size data

Taxa	**Period**	**FAD**	**LAD**	**Lower_jaw_length**
Huehuecuetzpalli_mixtecus	Cretaceous	106.8	100.5	25.0
Ctenomastax_parva	Cretaceous	79.77	75.93	20.26
Priscagama_gobiensis	Cretaceous	79.77	75.93	23.6
Mimeosaurus_crassus	Cretaceous	79.77	75.93	27.8
Phrynosomimus_asper	Cretaceous	79.77	75.93	13.57
Temujinia_ellisoni	Cretaceous	79.77	75.93	24.51
Saichangurvel_davidsoni	Cretaceous	79.77	75.93	27.82
Isodontosaurus_gracilis	Cretaceous	79.77	75.93	17.57
Zapsosaurus_sceliphros	Cretaceous	79.77	75.93	30.91
Polrussia_mongoliensis	Cretaceous	79.77	75.93	9.0
Tchingisaurus_multivagus	Cretaceous	79.77	75.93	25.4
Gobinatus_arenosus	Cretaceous	79.77	75.93	34.72
Adamisaurus_magnidentatus	Cretaceous	79.77	75.93	32.75
Gilmoreteius_ferrugenous	Cretaceous	79.77	75.93	95.4
Polyglyphanodon_sternbergi	Cretaceous	72.1	66.0	85.5
Sineoamphisbaena_hexatabularis	Cretaceous	79.77	75.93	13.85
Eichstaettisaurus_schroederi	Jurassic	152.1	148.6	8.11
Norellius_nyctisaurops	Cretaceous	132.9	129.4	15.64
Paramacellodus_oweni	Cretaceous	145.0	139.8	27.0
Parmeosaurus_scutatus	Cretaceous	79.77	75.93	26.3
Tepexisaurus_tepexii	Cretaceous	106.8	100.5	20.8
Myrmecodaptria_microphagosa	Cretaceous	79.77	75.93	22.2
Carusia_intermedia	Cretaceous	79.77	75.93	29.3
Globaura_venusta	Cretaceous	79.77	75.93	19.7
Hymenosaurus_clarki	Cretaceous	79.77	75.93	10.8
Eoxanta_lacertifrons	Cretaceous	79.77	75.93	15.0
Gobiderma_pulchrum	Cretaceous	79.77	75.93	47.0
Estesia_mongoliensis	Cretaceous	79.77	75.93	145.3
Aiolosaurus_oriens	Cretaceous	79.77	75.93	35.6
Tetrapodophis_amplectus	Cretaceous	119.0	113.0	8.4
Coniophis_praecedens	Cretaceous	69.05	66.0	-
Najash_rionegrina	Cretaceous	100.5	93.9	-
Dinilysia_patagonica	Cretaceous	86.3	83.6	92.3
Haasiophis_terrasanctus	Cretaceous	100.5	97.2	26.3
Eupodophis_descouensis	Cretaceous	100.5	93.9	14.9
Pachyrhachis_problematicus	Cretaceous	100.5	97.2	54.1
Parviraptor_estesi	Cretaceous	145.0	139.8	-
Diablophis_gilmorei	Jurassic	154.7	148.6	-
Portugalophis_lignites	Jurassic	157.3	152.1	-
Eophis_underwoodi	Jurassic	168.3	166.1	-

Chamops_segnis	Cretaceous	69.05	66.0	22.4
Parasaniwa_wyomingensis	Cretaceous	69.05	66.0	-
Exostinus_lancensis	Cretaceous	69.05	66.0	-
Odaxosaurus_piger	Cretaceous	69.05	66.0	-
Leptochamops_denticulatus	Cretaceous	69.05	66.0	-
Gephyrosaurus_bridensis	Jurassic	201.3	195.1	30.0
Diphydontosaurus_avonis	Triassic	208.5	204.9	15.5
Planocephalosaurus_robinsonae	Triassic	204.9	201.3	20.0
Rebbanasaurus_jaini	Jurassic	182.7	174.1	-
Godavarisaurus_lateefi	Jurassic	182.7	174.1	-
Homoeosaurus_maximiliani	Jurassic	152.1	148.6	23.0
Palaeopleurosaurus_posidoniae	Jurassic	182.7	178.4	61.0
Pleurosaurus_goldfussi	Jurassic	152.1	148.6	96.0
Pleurosaurus_ginsburgi	Jurassic	152.1	145.0	100
Brachyrhinodon_taylori	Triassic	232.0	227.0	30.5
Clevosaurus_hudsoni	Triassic	204.9	201.3	43.0
Kallimodon_cerinensis	Jurassic	154.7	152.1	38.6
Sapheosaurus_thiollierei	Jurassic	154.7	152.1	46.1
Pamizinsaurus_tlayuaensis	Cretaceous	106.8	100.5	14.0
Zapatadon_ejidoensis	Jurassic	190.8	186.8	8.1
Cynosphenodon_huizachalensis	Jurassic	190.8	186.8	29.4
Opisthias_rarus	Jurassic	154.7	148.6	34.5
Toxolophosaurus_cloudi	Cretaceous	125.0	113.0	51.9
Eilenodon_robustus	Jurassic	154.7	148.6	-
Priosphenodon_avelasi	Cretaceous	100.5	93.9	100.0
Ankylosphenodon_pachyostosus	Cretaceous	106.8	100.5	78.4
Sphenocondor_gracilis	Jurassic	178.4	174.1	26.4
Sphenovipera_jimmysjoyi	Jurassic	190.8	186.8	20.5
Theretairus_antiquus	Jurassic	154.7	148.6	-
Kawasphenodon_expectatus	Cretaceous	75.93	69.05	115.0
Oenosaurus_muehlheimensis	Jurassic	152.1	148.6	33.0
Clevosaurus_minor	Triassic	204.9	201.3	23.2
Clevosaurus_sectumsemper	Triassic	208.5	204.9	-
Whitakersaurus_bermani	Triassic	208.5	204.9	-
Polysphenodon_mulleri	Triassic	232.0	220.8	-
Clevosaurus_petilus	Jurassic	199.3	190.8	34.8
Priosphenodon_minimus	Cretaceous	113.0	100.5	19.1
Pelecymala_robustus	Triassic	204.9	201.3	-
Fraserosphenodon_latidens	Triassic	204.9	201.3	-
Sphenotitan_leyesi	Triassic	214.7	208.5	108.2
Clevosaurus_brasiliensis	Triassic	227.0	220.8	27.0
Clevosaurus_convallis	Jurassic	201.3	195.1	20.9
Clevosaurus_bairdi	Jurassic	204.9	201.3	18.5

Clevosaurus_wangi	Jurassic	199.3	190.8	29.4
Clevosaurus_mcgilli	Jurassic	199.3	190.8	20.5
Kallimodon_pulchellus	Jurassic	152.1	148.6	23.8
Derasmosaurus_pietraroiae	Cretaceous	113.0	106.8	-
Bharatagama_rebbanensis	Jurassic	182.7	174.1	-
Eichstaettisaurus_gouldi	Cretaceous	113.0	106.8	15.1
Lamiasaura_ferox	Cretaceous	69.05	66.0	-
Pariguana_lancensis	Cretaceous	69.05	66.0	-
Contogenys_sloani	Cretaceous	69.05	66.0	-
Lonchisaurus_trichurus	Cretaceous	69.05	66.0	-
Estescincosaurus_cooki	Cretaceous	69.05	66.0	-
Paraderma_bogerti	Cretaceous	69.05	66.0	-
Palaeosaniwa_canadensis	Cretaceous	83.6	72.1	-
Cemeterius_monstrosus	Cretaceous	69.05	66.0	-
Litakis_gilmorei	Cretaceous	69.05	66.0	-
Colpodontosaurus_cracens	Cretaceous	69.05	66.0	-
Obamadon_gracilis	Cretaceous	69.05	66.0	-
Tripennaculus_eatoni	Cretaceous	75.93	72.1	-
Peneteius_aquilonious	Cretaceous	69.05	66.0	-
Meniscognathus_altmani	Cretaceous	69.05	66.0	-
Haptosphenus_placodon	Cretaceous	69.05	66.0	-
Stypodontosaurus_melletes	Cretaceous	72.1	66.0	-
Socognathus_brachyodon	Cretaceous	69.05	66.0	-
Gilmoreteius_gilmorei	Cretaceous	79.77	75.93	70.0
Gilmoreteius_chulsanensis	Cretaceous	79.77	75.93	72.0
Adriosaurus_suessi	Cretaceous	100.5	93.9	26
Dolichosaurus_longicollis	Cretaceous	100.5	93.9	-
Pontosaurus_kornhuberi	Cretaceous	97.2	93.9	52
Aigialosaurus_dalmaticus	Cretaceous	97.2	93.9	130
Aigialosaurus_bucchichi	Cretaceous	97.2	93.9	153
Komensaurus_carrolli	Cretaceous	100.5	93.9	-
Halisaurus_platyspondylus	Cretaceous	72.1	66.0	-
Eonatator_sternbergi	Cretaceous	84.95	79.77	356
Dallasaurus_turneri	Cretaceous	93.9	89.8	-
Clidastes_liodontus	Cretaceous	88.05	79.77	388
Clidastes_moorevillensis	Cretaceous	84.95	79.77	-
Clidastes_propython	Cretaceous	84.95	72.1	390
Prognathodon_overtoni	Cretaceous	79.77	72.1	938
Prognathodon_solvayi	Cretaceous	72.1	69.1	660
Prognathodon_currii	Cretaceous	72.1	66.0	1497
Prognathodon_saturator	Cretaceous	69.05	66.0	1185
Prognathodon_waiparaensis	Cretaceous	72.1	66.0	1110
Mosasaurus_conodon	Cretaceous	79.77	66.0	1000

Mosasaurus_hoffmannii	Cretaceous	72.1	66.0	1710
Plotosaurus_bennisoni	Cretaceous	72.1	66.0	791
Mosasaurus_missouriensis	Cretaceous	79.77	72.1	1002
Plesiotylosaurus_crassidens	Cretaceous	72.1	66.0	980
Eremiasaurus_heterodontus	Cretaceous	69.05	66.0	711
Prognathodon_kianda	Cretaceous	72.1	66.0	820
Prognathodon_rapax	Cretaceous	72.1	66.0	-
Globidens_alabamaensis	Cretaceous	83.6	75.93	-
Globidens_dakotensis	Cretaceous	79.77	75.93	-
Tylosaurus_nepaeolicus	Cretaceous	88.05	84.95	828
Tylosaurus_bernardi	Cretaceous	72.1	69.1	1530
Tylosaurus_proriger	Cretaceous	84.95	75.93	1220
Taniwhasaurus_oweni	Cretaceous	83.6	72.1	-
Taniwhasaurus_antarcticus	Cretaceous	75.93	72.1	720
Ectenosaurus_clidastoides	Cretaceous	84.95	83.6	650
Selmasaurus_johnsoni	Cretaceous	86.3	84.95	392
Angolasaurus_bocagei	Cretaceous	91.85	89.8	526
Plioplatecarpus_nichollsae	Cretaceous	79.77	75.93	470
Platecarpus_tympaniticus	Cretaceous	84.95	75.93	559
Latoplatecarpus_willistoni	Cretaceous	79.77	75.93	532
Platecarpus_planifrons	Cretaceous	88.05	83.6	660
Yaguarasaurus_columbianus	Cretaceous	93.9	89.8	582
Russellosaurus_coheni	Cretaceous	93.9	89.8	420
Romeosaurus_fumanensis	Cretaceous	93.9	84.95	645
Tethysaurus_nopcsai	Cretaceous	93.9	89.8	280
Pannoniasaurus_inexpectatus	Cretaceous	86.3	83.6	-
Gephyrosaurus_evansae	Triassic	208.5	201.3	-
Penegephyrosaurus_curtiscoppi	Triassic	208.5	201.3	-
Deltadectes_elvetica	Triassic	208.5	204.9	-
Piocormus_laticeps	Jurassic	152.1	148.6	-
Vadasaurus_herzogi	Jurassic	152.1	148.6	29.2
Halisaurus_arambourgi	Cretaceous	72.1	66.0	490
Phosphorosaurus_ortliebi	Cretaceous	72.1	69.1	-
Phosphorosaurus_ponpetelegans	Cretaceous	72.1	69.1	-
Coniasaurus_crassidens	Cretaceous	100.5	93.9	70
Coniasaurus_gracilodens	Cretaceous	100.5	93.9	-
Adriosaurus_microbrachis	Cretaceous	100.5	93.9	-
Adriosaurus_skrbinensis	Cretaceous	100.5	93.9	-
Pontosaurus_lesinensis	Cretaceous	97.2	93.9	60
Acteosaurus_tommasinii	Cretaceous	100.5	93.9	-
Aphanizocnemus_libanensis	Cretaceous	100.5	93.9	23
Kaikaifilu_hervei	Cretaceous	69.05	66.0	-
Selmasaurus_russelli	Cretaceous	83.6	79.77	-

Plioplatecarpus_primaevus	Cretaceous	79.77	72.1	396
Plioplatecarpus_houzeaui	Cretaceous	72.1	69.05	450
Plioplatecarpus_marshi	Cretaceous	69.05	66	-
Plioplatecarpus_peckensis	Cretaceous	75.93	72.1	-
Carsosaurus_marchesetti	Cretaceous	100.5	93.9	-
Sanajeh_indicus	Cretaceous	72.1	66.0	114.4
Nidophis_insularis	Cretaceous	72.1	66.0	-
Planocephalosaurus_lucasi	Triassic	227.0	220.8	-
Paleollanosaurus_fraseri	Triassic	227.0	220.8	-
Sigmala_Sigmala	Triassic	204.9	201.3	15.0
Ardeosaurus_digitatellus	Jurassic	152.1	148.6	-
Chianghsia_nankangensis	Cretaceous	72.1	66.0	105.5
Eonatator_coellensis	Cretaceous	83.6	72.1	-
Magnuviator_ovimonsensis	Cretaceous	83.6	72.1	39.4
Aprisaurus_bidentatus	Cretaceous	79.77	75.93	45
Tuberocephalosaurus_pompabilis	Cretaceous	79.77	75.93	-
Tianyusaurus_zhengi	Cretaceous	72.1	66.0	87.4
Funiusaurus_luanchuanensis	Cretaceous	72.1	66.0	31.5
Darchansaurus_estesi	Cretaceous	79.77	75.93	60.0
Cherminsaurus_kozlowskii	Cretaceous	79.77	75.93	65.0
Erdenetesaurus_robinsonae	Cretaceous	79.77	75.93	52.0
Gueragama_sulamericana	Cretaceous	93.9	72.1	-
Jeddaherdan_aleadonta	Cretaceous	100.5	89.8	-
Hodzhakulia_magna	Cretaceous	100.5	93.9	-
Bagaluus_primigenius	Cretaceous	119.0	106.8	-
Platynotoides_altidentatus	Cretaceous	119.0	106.8	-
Carnoscincus_eublepharus	Cretaceous	119.0	106.8	-
Pachygenys_thlastesa	Cretaceous	125.0	113.0	59.1
Pachygenys_adachii	Cretaceous	113.0	100.5	-
Asprosaurus_bibongriensis	Cretaceous	83.6	79.77	-
Hoyalacerta_sanzi	Cretaceous	129.4	125.0	9.1
Bavarisaurus_macrodactylus	Jurassic	152.1	148.6	20.0
Dalinghosaurus_longidigitus	Cretaceous	129.4	119.0	26.6
Yabeinosaurus_tenius	Cretaceous	129.4	119.0	54.2
Sakurasaurus_shokawensis	Cretaceous	145.0	139.8	20.7
Liushusaurus_acanthocaudata	Cretaceous	129.4	119.0	15.7
Pedrerasaurus_latifrontalis	Cretaceous	129.4	125.0	18.9
Jucaraseps_grandipes	Cretaceous	129.4	125.0	-
Kaganaias_hakusanensis	Cretaceous	139.8	132.9	-
Catactegenys_solaster	Cretaceous	75.93	72.1	-
Anchaurosaurus_gilmorei	Cretaceous	79.77	75.93	38.3
Desertiguana_gobiensis	Cretaceous	79.77	75.93	-
Barbatteius_vremiri	Cretaceous	72.1	66.0	64.4

Meyasaurus_faurai	Cretaceous	129.4	125.0	-
Meyasaurus_crusafonti	Cretaceous	129.4	125.0	19.2
Meyasaurus_unaensis	Cretaceous	129.4	125.0	-
Meyasaurus_diazromerali	Cretaceous	129.4	125.0	16.6
Olindalacerta_brasiliensis	Cretaceous	119.0	113.0	6.4
Tijubina_pontei	Cretaceous	119.0	113.0	14.4
Peneteius_saueri	Cretaceous	75.93	72.1	-
Dicothodon_moorensis	Cretaceous	106.8	97.2	-
Dicothodon_cifellii	Cretaceous	93.9	89.8	-
Dicothodon_bajaensis	Cretaceous	83.6	72.1	-
Bicuspidon_hatzegiensis	Cretaceous	72.1	66.0	-
Bicuspidon_numerosus	Cretaceous	106.8	97.2	-
Bicuspidon_smikros	Cretaceous	100.5	93.9	-
Schoenesmahl_dyspepsia	Jurassic	152.1	148.6	18.7
Clevosaurus_cambrica	Triassic	204.9	201.3	14.9
Ardeosaurus_brevipes	Jurassic	152.1	148.6	19.6
Globidens_schurmanni	Cretaceous	75.93	72.1	655
Haasiasaurus_gittelmani	Cretaceous	100.5	97.2	159.6
Megachirella_wachtleri	Triassic	244.6	242	25.5
Marmoretta_oxoniensis	Jurassic	167.2	166.1	-
Plesiorhineura_tsentasai	Paleocene	63.3	61.7	-
Archaerhineura_mephitis	Paleocene	61.7	56.8	-
Jepsibaena_minor	Eocene	55.8	50.3	13.2
Spathorhynchus_fossorium	Eocene	50.3	46.2	28.1
Chthonophidae_subterraneus	Paleocene	63.3	61.7	-
Oligodontosaurus_wyomingensis	Paleocene	61.7	56.8	-
Polyodontobaena_belgica	Paleocene	61.6	59.2	-
Blanosaurus_primeocaenus	Eocene	56.0	47.8	-
Louisamphisbaena_ferox	Eocene	41.2	37.8	-
Anniealexandria_gansi	Eocene	55.8	50.3	-
Todrasaurus_gheerbrandti	Paleocene	59.2	56.0	-
Cryptolacerta_hassiaca	Eocene	47.8	41.2	19.2
Paleoxantusia_kyrentos	Eocene	46.2	40.4	17.9
Paracontongenys_estesi	Eocene	46.2	40.4	-
Madtsoia_pisdurensis	Cretaceous	72.1	66.0	-
Madtsoia_camposi	Paleocene	58.7	48.6	-
Gigantophis_garstini	Eocene	37.8	33.9	-
Madtsoia_madagascariensis	Cretaceous	72.1	66.0	-
Madtsoia_bai	Eocene	54.0	48.0	-
Platyspondylophis_tadkeshwarensis	Eocene	56.0	47.8	-
Menarana_laurasiae	Cretaceous	75.93	72.1	
Menarana_nosymena	Cretaceous	72.1	66.0	-
Adinophis_fisaka	Cretaceous	72.1	66.0	-

Patagoniophis_australiensis	Cretaceous	75.93	69.05	-
Alamitophis_elongatus	Cretaceous	75.93	69.05	-
Alamitophis_tingamarra	Eocene	56.0	47.8	-
Herensugea_caristiorum	Cretaceous	75.93	72.1	-
Stefanikia_siderea	Eocene	47.8	41.2	38.5
Eolacerta_robusta	Eocene	47.8	41.2	70.2
Qianshanosaurus_huangpuensis	Paleocene	59.2	56.0	48.5
Cuvieribaena_carlgansi	Eocene	41.2	37.8	11.8
Bahndwivici_ammoskius	Eocene	56.0	47.8	30.3
Babibasiliscus_alxi	Eocene	50.3	46.2	38.6
Afairiguana_avius	Eocene	56.0	47.8	10.5
Protorhineura_hatcherii	Eocene	55.8	50.3	12.3
Geiseltaliellus_maarius	Eocene	47.8	41.2	30.1
Solastella_cookei	Eocene	46.2	40.4	8.3
Eosaniwa_koehni	Eocene	47.8	41.2	48.4
Parviderma_inexacta	Cretaceous	79.77	75.93	-
Saniwa_feisti	Eocene	47.8	41.2	50.0
Necrosaurus_cayluxi	Eocene	37.8	33.9	-
Necrosaurus_eucarinatus	Eocene	47.8	41.2	-
Proplatynotia_longirostrata	Cretaceous	79.77	75.93	39.0
Saniwides_mongoliensis	Cretaceous	79.77	75.93	44.0
Ovoo_gurval	Cretaceous	79.77	75.93	-
Telmasaurus_grangeri	Cretaceous	79.77	75.93	-
Saniwa_ensidens	Eocene	56.0	47.8	68.6
Primaderma_nessovi	Cretaceous	106.8	97.2	-
Eurheloderma_gallicum	Eocene	37.8	33.9	-
Xestops_vagans	Eocene	50.3	46.2	-
Proxestops_silberlingii	Paleocene	63.3	61.7	-
Peltosaurus_macrodon	Eocene	46.2	40.4	-
Melanosaurus_maximus	Eocene	55.8	50.3	78.1
Arpadosaurus_gazinorum	Eocene	55.8	50.3	-
Glyptosaurus_sylvestris	Eocene	50.3	46.2	85.7
Proglyptosaurus_huerfanensis	Eocene	55.8	50.3	-
Paraglyptosaurus_princeps	Eocene	50.3	46.2	125.0
Restes_rugosus	Paleocene	63.3	61.7	-
Ophisauriscus_quadrupes	Eocene	47.8	41.2	23.2
Apodosauriscus_minutus	Eocene	55.8	50.3	-
Kawasphenodon_peligrensis	Paleocene	61.6	59.2	-
Contogenys_ekalakaensis	Paleocene	63.3	61.7	-
Palaeoscincosaurus_middletoni	Paleocene	66.0	63.3	29.7
Palaeosincosaurus_pharkidodon	Cretaceous	75.93	72.1	-
Utahgenys_evansi	Cretaceous	93.9	89.8	-
Xestops_stehlini	Eocene	37.8	33.9	45.6

Slavoia_darevskii	Cretaceous	79.77	75.93	9.9
Primitivus_manduriensis	Cretaceous	75.93	69.05	69.5

Conclusion

The study of the early evolution of lepidosaurs is a difficult task, mainly due to the incompleteness and fragmentary nature of their fossil record. For this reason, I did not say much about diversity through time. The research presented here should contribute to a better understanding of the evolutionary history of the group by trying to provide a response to key questions on lepidosaur macroevolution. To briefly summarize my four research projects, in Chapter 2, I show the importance of the re-evaluation of fossils of poorly known taxa such as *Clevosaurus latidens* whose true taxonomic identity was unknown for over two decades. The re-examination of *C. latidens* allowed me to resolve its uncertain phylogenetic relationships and erect a new genus *Fraserosphenodon*, which confirms the high diversity and morphological disparity among Mesozoic rhynchocephalians. On the other hand, in Chapter 3, I show the importance of combining two different macroevolutionary approaches, namely geometric morphometrics and evolutionary rates analysis, in order to investigate patterns of the early evolution of a very interesting group such as the Rhynchocephalia. Also, I tried to clarify what a “living fossil” is by providing a novel and testable definition. In this regard, my research on the Rhynchocephalia can be controversial because my study found that the extant *Sphenodon* shows the characteristics of a “living fossil” according to our definition (located in morphospace close to the centre based on dentary morphology and very low evolutionary rates), which also is the opposite of what other studies on rhynchocephalians have said about *Sphenodon* which was previously suggested to be a non-conservative species. Hopefully, future work will allow us to test the methods with other taxa considered as “living fossils” to support, improve or discard the testable definition of “living fossils” provided here.

In Chapter 4, I document as others have how squamates had initially small body size, low dental disparity and an apparently low diversity which dramatically changed during the mid /Late Cretaceous when they had a remarkable expansion in dietary preferences and body size ranges presumably triggered by the KTR which provided new sources of food for squamates. Finally, in Chapter 5, with the aid of a supertree of early lepidosaurs and phylogenetic comparative methods I provide a new hypothesis about the dramatic decline and nearly extinction of rhynchocephalians at the end of the Mesozoic. I provide some of the first empirical evidence to support George Simpson´s theories on evolutionary rates, especially his theory that sustained high rates of evolution can lead a lineage to extinction. This represents a new theory about the decline of rhynchocephalians, but it also opens more questions for future research such as if Simpson´s model of rapid evolution and subsequent decline or extinction applies only to the Rhynchocephalia or if it can also apply to other tetrapod groups.

My work tried to cover some key questions about the early evolution of lepidosaurs by using several different novel computational macroevolutionary approaches; however, my work still has limitations. Probably the main limitation on the study of macroevolution of lepidosaurs is the biases in the fossil record, because in contrast to other early tetrapod groups the fossil record for basal taxa in lepidosaurs is quite poor and fragmentary for some groups. This was notable in the difference between the numbers of specimens used in the geometric morphometrics of Mesozoic squamates. In any case, all the methods were applied carefully, taking account of sample sizes in the statistical tests, but it cannot be denied that the gaps in the lepidosaur fossil record may have influenced some results. Fortunately, new discoveries of early diverging lepidosaurs will help to considerably reduce the gaps in their fossil record. Additionally, several new macroevolutionary methods are developed every year which can be applied to large databases like those presented here. So in this respect, I expect that some of the data presented here will be considerably improved in the future to reanalyze them by using the same methods or other novel approaches that help to provide further evidence to support or discard some of the hypotheses produced by my work.

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MACROEVOLUTIONARY PATTERNS IN RHYNCHOCEPHALIA: IS THE TUATARA (*SPHENODON PUNCTATUS*) A LIVING FOSSIL?

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Abstract: The tuatara, *Sphenodon punctatus*, known from 32 small islands around New Zealand, has often been noted as a classic 'living fossil' because of its apparently close resemblance to its Mesozoic forebears and because of a long, low-diversity history. This designation has been disputed because of the wide diversity of Mesozoic forms and because of derived adaptations in living *Sphenodon*. We provide a testable definition for 'living fossils' based on a slow rate of lineage evolution and a morphology close to the centroid of clade morphospace. We show that through their history since the Triassic, rhynchocephalians had heterogeneous rates of morphological evolution and occupied wide morphospaces during the Triassic and Jurassic, and these then declined in the Cretaceous. In particular, we demonstrate that the extant tuatara underwent unusually slow lineage evolution, and is morphologically conservative, being located near the centre of the morphospace for all Rhynchocephalia.

Key words: Rhynchocephalia, Sphenodontia, rates of evolution, living fossils, morphospace.

THE Rhynchocephalia is an ancient group of reptiles that emerged during the Early or Middle Triassic (Jones *et al.* 2013). They are unusual among the 10 000 species of living reptiles, being ranked at times as an order equivalent to the Crocodilia, Squamata and Testudines (Pough *et al.* 2012), but represented today by a single species, *Sphenodon punctatus* (Hay *et al.* 2010; Jones & Cree 2012; Cree 2014). This species is geographically restricted to the islands of New Zealand, and it is best known by its vernacular name 'tuatara'. *S. punctatus* was first described by J. E. Gray in 1831, but he misidentified it as an agamid lizard (Sharell 1966; Robb 1977; Cree 2014). A few years later, Günther (1867) noted its similarities with some fossil forms, and in consequence erected the Order Rhynchocephalia, which has long been identified as sister to Squamata, the much larger clade comprising lizards and snakes.

Sphenodon punctatus has often been identified as a 'living fossil' (Fraser 1993; Sues *et al.* 1994; Jones 2008; Jones *et al.* 2009; Meloro & Jones 2012; Cree 2014) for a variety of reasons: (1) the living form, superficially, seems little different from its distant Mesozoic ancestors; (2) the clade has had a very long duration, but with low diversity and possibly long-lived species and genera; (3) it is the solitary sister clade to the equally ancient Squamata, comprising over 9000 species; (4) there is a long gap in geological time between the modern form and the youngest fossil forms, in the Miocene, Paleocene and Cretaceous; and (5) it shows supposedly 'primitive' anatomical features such as the closed lower temporal bar.

This view has been disputed because, during the last three decades, many fossil species of rhynchocephalians have been described, so partially rejecting reason (2) above. Several of these newly described species show a wide variety of ecological adaptations, either to terrestrial or marine environments (e.g. *Pamizinsaurus*, *Pleurosaurus*), as well as a diverse array of dietary preferences (Jones 2008, 2009; Meloro & Jones 2012; Rauhut *et al.* 2012; Martínez *et al.* 2013). These observations contradict the common view of the Rhynchocephalia as a morphologically unchanged group, reason (1) above, and suggest that it had high diversity and morphological disparity through time (Sues *et al.* 1994; Reynoso 1997, 2000, 2005; Evans *et al.* 2001; Jones 2008; Jones *et al.* 2009; Apesteguía & Jones 2012; Cree 2014). Also, recent work on the extant *Sphenodon* indicates that it is not as conservative as was previously believed (Jones 2008; Meloro & Jones 2012; Cree 2014), with a presumably secondarily fused lower temporal bar (Whiteside 1986), thus rejecting reason (5) above. However, the traditional view of the Rhynchocephalia as an unchanged group through time

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still dominates in textbooks and other sources (e.g. Sharell 1966; Robb 1977; Mitchell *et al.* 2008) despite the lack of clarity over the definition of what a ‘living fossil’ is. Reseachers may agree on which taxa are ‘living fossils’ (e.g. Schopf 1984; Casane & Laurenti 2013), but there is no testable definition.

The concept of ‘living fossils’ has been problematic since the term was coined by Charles Darwin (1859), as there is no such identifiable class of organisms, but oft-cited examples do share some or all of the noted features. Note that the phrase ‘relict species’ encapsulates some characteristics of ‘living fossils’, referring to a species or a group of species that remains from a large group that is mainly extinct (Grandcolas *et al.* 2014).

Here, we propose a hypothesis that can be tested by computational morphometric and phylogenetic comparative methods (PCM): ‘a living fossil should show both statistically significantly slow rates of morphological evolution and it should be morphologically conservative.’ The first measure is assessed with respect to sister taxa and sister clades, and using standard PCM approaches for assessing the statistical significance of evolutionary rates. The second measure of morphological conservatism can be assessed by determining whether the taxon lies close to the early, or geologically earliest, members of its clade or close to the centroid of the hyperdimensional morphospace. The distance of each species from the centroid can be measured, but there is no agreed statistical test to distinguish classes of morphological conservatism, just that the taxon in question is closer to the centroid than other taxa are; perhaps closer to the centroid than the majority of taxa, including fossil forms.

We explore here the morphological disparity of all the Rhynchocephalia, and where the extant *Sphenodon* fits within the clade. Based on a phylogenetic analysis of the whole clade, we identify rates of morphological evolution and changes in morphospace using geometric morphometrics of the lower jaw, and find evidence that *Sphenodon* evolved slowly, and is morphologically conservative when compared to extinct rhynchocephalians, especially the earliest forms.

METHOD

Phylogeny of Rhynchocephalia

To construct a phylogeny for Rhynchocephalia and explore evolutionary rates, we used the recently published data matrix of 74 discrete morphological characters from Apesteguía *et al.* (2014). We ran a maximum parsimony analysis with TNT v. 1.1 (Goloboff *et al.* 2008) following the settings of Apesteguía *et al.* (2014), and as a result we recovered the same 22 MPTs of 218 steps as they did. All MPTs were reduced to a time-scaled strict consensus tree (Fig. 1). The discrete morphological character data matrix

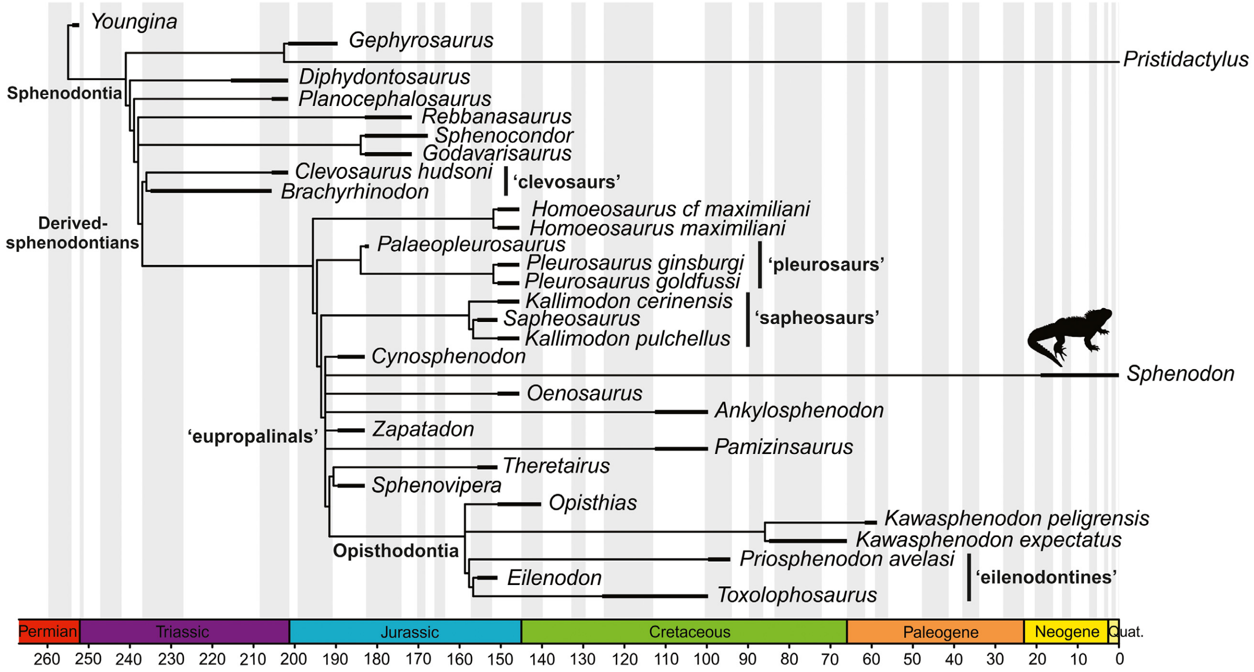

FIG. 1. Time-scaled phylogeny of Rhynchocephalia, based on a strict consensus tree of 22 most parsimonious trees (details in Herrera-Flores *et al.* 2017). Note that *Youngina* and extant *Pristidactylus* are outgroups to Rhynchocephalia. *Abbreviation*: Quat., Quaternary. Colour online.

and 22 MPTs were used later for evolutionary rates analyses using the methods described below.

Evolutionary rates

Rates of morphological evolution were investigated using maximum-likelihood methods, following the protocols of Lloyd *et al.* (2012), Brusatte *et al.* (2014) and Wang & Lloyd (2016). We first time-scaled our MPTs, establishing ages for terminal taxa by compiling ages (FAD, first appearance date and LAD, last appearance date) for each taxon using the Paleobiology Database and the literature, to determine the latest consensus view on the ages of relevant geological formations (https://paleobiodb.org). Following the work of Brusatte *et al.* (2014) and Wang & Lloyd (2016), we used two current available methods for determining the dates of nodes and branch durations, the 'equal' and 'minimum branch length' (mbl) methods. For both methods, we used the settings recommended by Brusatte *et al.* (2014) and Wang & Lloyd (2016), with a fixed duration of 1 myr for the 'minimum branch length' method and 2 myr for a root-length of the 'equal' method. When dating the trees we used a randomization approach, and performed 100 replicates to incorporate potential uncertainty arising from sampling each terminal taxon's age randomly from between their first and last appearance dates. This generated 100 time-scaled phylogenies for each of the 22 MPTs, and for both the 'equal' and 'mbl' methods. Before running the rates analyses we excluded the extant squamate *Pristidactylus*. Using all the time-scaled phylogenies and the discrete morphological character data, we assessed whether rates of morphological evolution were homogeneous, or if particular branches or clades have significantly low or high rates relative to the remainder of the tree (Lloyd *et al.* 2012). Comparative rates were assessed using likelihood ratio tests (LRTs) between single rate models (homogenous rates) and two rate models (particular branch has different rates to the rest of the tree). An alpha threshold of 0.01 was used to evaluate significance, with Benjamini–Hochberg false discovery rate correction. Sensitivity tests were performed with *Sphenodon* removed from the tree and character data, to ensure that the long terminal branch associated with *Sphenodon* was not biasing the rates results. All analyses were performed in R (R Core Team 2015), using the packages `paleotree` (Bapst 2012) and `Claddis` (Lloyd 2016), and with a modified version of the script of Wang & Lloyd (2016).

To illustrate the evolutionary rates results, we figure one MPT for both the 'equal' (MPT 1) and 'mbl' (MPT 6) analyses (Fig. 2). Pie charts are used to indicate the proportion of significantly high and significantly low per-branch rates results, based on the 100 dating replications. These trees were selected because they accurately reflect most of the results recovered across all 22 MPTs, and we highlight branches that consistently show the same high/low rates in other MPTs. All MPTs are individually figured in Herrera-Flores *et al.* (2017).

Morphospace and disparity analysis

To investigate macroevolutionary trends in Rhynchocephalia, we analysed changes in morphospace occupation through time, based on variations in dentary shape. We chose to focus on morphological variation in the dentary because it is commonly the best preserved part in fossil rhynchocephalians, which can retain more than 80% of the shape of the complete mandible. Also it has been shown in studies of a broad array of vertebrates that mandibular shape captures information about dietary preferences and so can discriminate major ecomorphological groupings (e.g. Kammerer *et al.* 2006; Anderson *et al.* 2011, 2013; Stubbs *et al.* 2013). Further, mandible shape variation may be measured readily from two-dimensional images. We compiled images of dentaries for 30 fossil rhynchocephalians from the literature, plus pictures from 14 museum specimens of the extant *Sphenodon* to assess variation within this single taxon, and to determine where it falls in comparison with Mesozoic taxa. We performed a separate geometric morphometric analysis of all samples of *Sphenodon* to identify the specimen that best represents the average shape of its dentary. All images were uniformly oriented to the same side (right). Seven landmarks and 26 semi-landmarks were set on the dentary images (see Herrera-Flores *et al.* 2017), using the program tpsDig (Rohlf 2006).

After Procrustes superposition to correct for variable sizes of the mandibles and variable orientations of images, the corrected coordinate data from the landmarks were subjected to principal components analysis (PCA) in R (R Core Team 2015), employing the package `geomorph` (Adams & Otárola-Castillo 2013). Three plots were produced, one to show morphospace occupation through the Mesozoic, one to observe macroevolutionary trends according to different feeding strategies of rhynchocephalians, and another to explore the phylogenetic branching patterns within the morphospace (a phylomorphospace). For the feeding strategies plot, we used the dietary preferences proposed by Jones (2006*a*, 2009), Rauhut *et al.* (2012) and Martínez *et al.* (2013) based on rhynchocephalian tooth shape. The phylomorphospace was produced using the R package `phytools` (Revell 2012). We randomly selected one dated MPT and cropped the tips that lacked PC coordinate data. This pruned phylogeny was used to reconstruct ancestral PC coordinate data with maximum likelihood estimation, and the branching

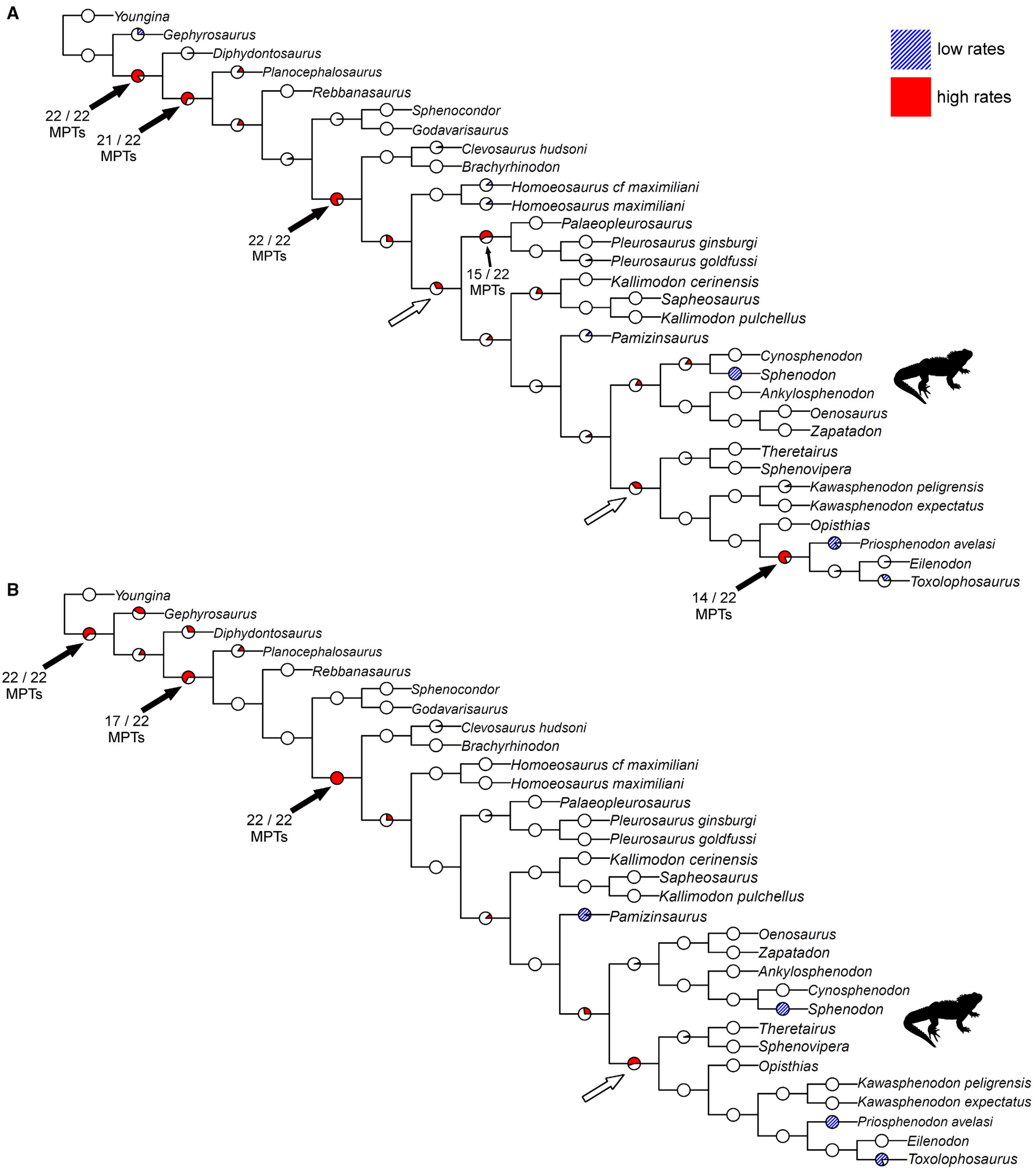

FIG. 2. Evolutionary rates analyses of Rhynchocephalia, illustrating results from per-branch likelihood tests using the 'equal' (A) and the 'mbl' (B) dating methods. One of the 22 most parsimonious trees (MPTs) is illustrated for each analysis. Pie charts on the branches are used to indicate the proportion of significantly high, significantly low and non-significant (white) rates results, based on 100 dating replications. Arrows denote branches that are consistently found to have significant rates in most MPTs (black arrows) or some MPTs (white arrows). For complete results for all MPT trees, see Herrera-Flores *et al.* (2017). *Sphenodon* illustration by Steven Traver. Colour online.

pattern was superimposed within the morphospace. As previously mentioned, we included a sample of the extant *Sphenodon* in all plots for comparative purposes. To explore the extent to which *Sphenodon* represents a conservative, or 'average', morphology, we examined Procrustes distances (describing the magnitude of the shape deviation) between each sampled dentary and the Procrustes mean shape of the entire sample (in `morphologika`; O'Higgins & Jones 1998, 2006).

To test for statistically significant overlaps in morphospace occupancy between groups of taxa sorted by geological period and by feeding mode, we used our PC coordinate data and performed a one-way NPMANOVA test in PAST (Hammer *et al.* 2001) using Euclidean distances, 10 000 permutations and Bonferroni-corrected p-values. Additionally, morphological disparity for temporal and feeding groups was quantified with the sum of variances metric, calculated using PC coordinate data from the first ten ordination axes (subsuming 91% of overall variation). Confidence intervals associated with calculated disparity values were generated by bootstrapping with 10 000 replications. Disparity calculations were performed in R (R Core Team 2015).

RESULTS

Evolutionary rates

Rates analyses using both the 'equal' and 'mbl' methods show similar results overall, with heterogeneous rates found throughout the phylogeny (Fig. 2). Both analyses show significantly high rates of character change on basal branches along the 'backbone' of the phylogeny, and on the branch leading to 'derived rhynchocephalians'. These high-rate branches are recovered consistently in most dating replicates, and in most MPTs. Significantly high rates are frequently found on the branch subtending a derived clade formed by *Sphenovipera*, *Theretairus* and the Opisthodontia, although this is not recovered as consistently across dating replicates and in all MPTs (Fig. 2). For the extant *Sphenodon*, both methods demonstrated that it has significantly low rates of morphological evolution, which contrasts with the occasionally high and, more often, non-significant rates shown by the branches preceding it, and with its closest relatives, such as the Early Jurassic *Cynosphenodon* (Fig. 2). Within the derived rhynchocephalians, the 'equal' dated trees also showed higher rates on the internal branches subtending pleurosaurs and eilenodontines (Fig. 2A), although these high rates are not seen in the more conservative 'mbl' approach (Fig. 2B). Another difference between both methods is that for taxa near the base of the tree (*Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*), the 'mbl' method found high rates on these terminal branches (Fig. 2B), while the 'equal' method showed low or non-significant rates (Fig. 2A). One interesting case is one of the morphologically specialized species *Pamizinsaurus*, from the Early Cretaceous, which showed low rates of morphological evolution in the 'mbl' analyses (Fig. 2B). Importantly, all these rates results for extinct taxa are consistent in the sensitivity analyses, when *Sphenodon* is removed (see supplementary results in Herrera-Flores *et al.* 2017).

Morphospace analysis

The morphospace analysis demonstrates that rhynchocephalians experienced important changes in morphospace occupation through time (Fig. 3A). Their morphospace in the Triassic was reasonably large, which suggests that the group had an initial burst of high morphological disparity after its origin in the Early or Middle Triassic. On the other hand, Jurassic rhynchocephalians considerably increased their morphospace occupation compared to the Triassic, but also moved into a different morphospace. The PC1–PC2 morphospace plot (Fig. 3A) shows that in the Cretaceous, rhynchocephalians experienced a considerable decrease in morphospace occupation, to about half of the area occupied in the Triassic and a third of that occupied in the Jurassic. The sum of variances disparity metric confirms that Jurassic taxa had the highest disparity, while disparity of Triassic and Cretaceous taxa was subequal and considerably lower (Fig. 3A). Results of the NPMANOVA test only found significant differences in morphospaces between the Triassic and Cretaceous ($p = 0.035$), and non-significant differences between Triassic and Jurassic taxa (Herrera-Flores *et al.* 2017, table S1). The living *Sphenodon* lies close to the centroid within the morphospace of Triassic taxa and near the zone where morphospaces of Mesozoic taxa overlap.

As expected, the mandibular landmarks provide good discrimination of feeding strategies among rhynchocephalians (Fig. 3B). Herbivorous taxa form a tight cluster with a high diversity of species, while insectivorous forms also occupy a relatively tight cluster but with considerably fewer species. The only known durophagous taxon (*Oenosaurus*) occupies a completely different morphospace region to other rhynchocephalians. In the case of omnivorous taxa (which also include carnivores), they show the greatest morphospace occupation, and this slightly overlaps with the herbivorous, insectivorous, and piscivorous morphospaces. For the piscivorous taxa, one of them (*Palaeopleurosaurus*) overlaps with omnivorous taxa, while the other piscivorous taxon (*Pleurosaurus*) occupies distinct morphospace. *Sphenodon*, identified as an omnivore (Sharell 1966; Robb 1977; Cree 2014), falls near the centre of the feeding morphospace plot (Fig. 3B). Disparity analyses show that omnivorous taxa had high disparity, while herbivorous and insectivorous had lower disparity. When comparing morphospace occupation through one-way NPMANOVA, only samples of herbivorous–insectivorous (p = 0.005) and herbivorous–omnivorous (p = 0.046) forms were significantly different from each other, while other feeding modes did not show any significant differences among the samples (Herrera-Flores *et al.* 2017, table S2).

The phylomorphospace (Fig. 3C) reveals that the shape of the dentary in *Sphenodon* differs from that of its closest relatives. The branch leading to *Sphenodon* traverses PC2 and originates from a cluster of internal nodes and terminal tips also located centrally along PC1. The shape of the dentary in *Sphenodon* is convergent with that in basal forms, such as the 'clevosaurs'. Some taxa closely related to *Sphenodon* can also trace their branches back to this central cluster from outlying positions in morphospace, such as *Oenosaurus* and *Ankylosphenodon*.

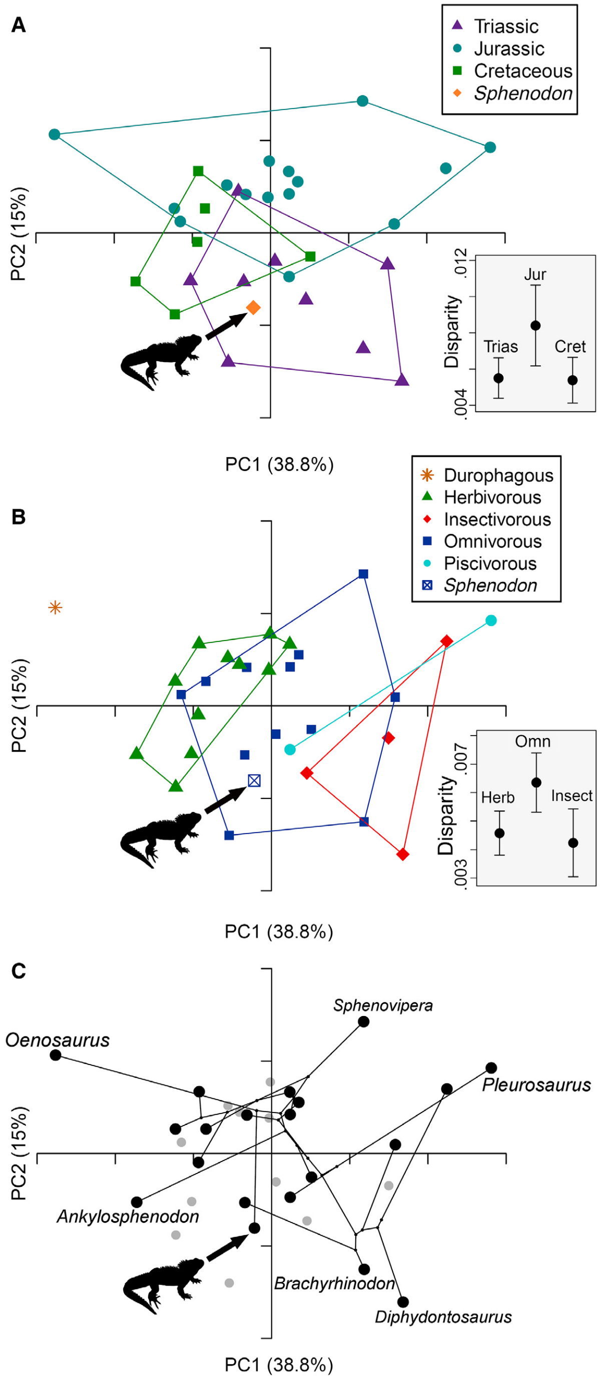

FIG. 3. Rhynchocephalian morphospace occupation, based on a geometric morphometric analysis of the dentary. Plots show temporal (A) and dietary (B) groupings, and a phylomorphospace (C). Note that the modern *Sphenodon* lies close to the centre of the morphospace plots. Morphological disparity (sum of variances) plots are included for the temporal (A) and dietary (B) groups. In the phylomorphospace (C), key taxa are named, and only major phylogenetic relationships are shown. Taxa within the morphospace that were not included in the phylogeny are denoted by grey circles. Error bars are 95% confidence intervals based on 10 000 replications. *Sphenodon* illustration by Steven Traver. For names of taxa in the plots see Herrera-Flores *et al.* (2017). Colour online.

When comparing Procrustes distances between each sampled taxon and the Procrustes mean landmark configuration for all specimens, *Sphenodon* deviates little from the average shape. Of the 31 taxa, *Sphenodon* is the seventh most similar to the average shape. The other forms most similar to the average shape are (in order) *Clevosaurus*, *Opisthias*, *Kallimodon* and *Palaeopleurosaurus*. The most divergent forms are (in order) *Oenosaurus*, *Pleurosaurus*, *Brachyrhinodon*, *Gephyrosaurus* and *Diphydontosaurus* (see full list in Herrera-Flores *et al.* 2017).

DISCUSSION

Frequently, the recognition of an extant species as a 'living fossil' is historical, a consequence of the discovery of fossil relatives before the living species, as in the case of the coelacanth *Latimeria* (Casane & Laurenti 2013). In the case of the tuatara, this species was noted as a living fossil because of its 'almost identical structure' to the Late Jurassic *Homoeosaurus* (Robb 1977). However, recent studies on *Sphenodon* and some of its fossil relatives have disputed the assumed long-term morphological and molecular stasis of the group (Hay *et al.* 2008; Jones 2008; Meloro & Jones 2012). In Victorian times, only the living form was known, and it was recognized as sister to the highly diverse Squamata (lizards, amphisbaenians and snakes). With increasing knowledge of the fossil record of rhynchocephalians, the morphological similarity between *Sphenodon* and some fossil forms became clear.

These claims became easier to assess with substantial increases in knowledge of fossil rhynchocephalians in the past 30 years (Jones 2008), and the application of cladistic methodology, following the first phylogenetic analysis of the group (Fraser & Benton 1989). Recent geometric morphometric works (Jones 2008; Meloro & Jones 2012) have refuted the morphological stasis of the Rhynchocephalia by reference to the disparity of skull and tooth shape. Our study agrees with Jones (2008) and Meloro & Jones (2012), by showing that the Rhynchocephalia was a diverse group with wide morphological disparity, and not an unchanging group through time, as previously believed. However, we dispute the suggestion by Jones (2008) and Meloro & Jones (2012) that the tuatara is a non-conservative species. Our results provide a wider perspective on the position of *Sphenodon* among fossil taxa following a considerable increase in the number of fossil taxa, by using morphological information from the lower jaw and novel macroevolutionary methods to explore rates of morphological evolution over time.

In terms of a numerically testable hypothesis, we suggested earlier that 'a living fossil should show both statistically significantly slow rates of morphological evolution and it should be morphologically conservative.' Our study confirms that *Sphenodon* fits both of these criteria and so is a 'living fossil'.

First, we found statistically significantly slow rates of morphological evolution in *Sphenodon* (Fig. 2). Overall, rates of morphological evolution in rhynchocephalians were heterogeneous (Fig. 2A, B), which suggests that the group has had a complex evolutionary history. Our study hints that much of the morphological diversity seen in the clade originated through a small number of evolutionary 'bursts', with a mix of high rates on basal and derived branches in the tree (Fig. 2). It is unexpected to see 'average' rates of morphological evolution for some highly specialized taxa, such as *Oenosaurus* and *Ankylosphenodon*, as well as low rates for the bizarre *Pamizinsaurus*. This finding is apparently contradicted by evidence that *Sphenodon* is an advanced taxon based on the presence of derived morphological features (Gorniak *et al.* 1982; Jones 2008; Curtis *et al.* 2010, 2011; Jones *et al.* 2012). However, recent work (Reynoso 1996, 2000, 2003; Reynoso & Clark 1998; Apesteguía & Novas 2003) shows that the most closely related species to *Sphenodon* is the Early Jurassic *Cynosphenodon*, a species that showed average rates of morphological change compared to the low rates in *Sphenodon*, according to our analysis. This may indicate that the Sphenodontinae, the clade that comprises *Sphenodon* and *Cynosphenodon*, experienced long-term morphological stasis after the Early Jurassic.

The fact that *Sphenodon* has the highest rate of molecular evolution among living vertebrates (Hay *et al.* 2008; Subramanian *et al.* 2009) confirms that rates of molecular and morphological evolution are decoupled (Subramanian *et al.* 2009). In such comparisons, of course, we cannot comment on rates of change in non-preserved morphology. A problem with our study is that there is such a long time gap between living *Sphenodon* and its Early Jurassic sister taxon, so rates cannot be compared with confidence. Likewise, phylogenomic studies can only compare living *Sphenodon* with extant squamates, separated by some 2 × 240 myr of independent history. The long *Sphenodon* branch is problematic also because it cannot be broken up by intervening branching events, and so any rate calculation is averaged, and probably underestimated.

Second, in terms of morphology, *Sphenodon* passes the test to be called a 'living fossil' because of its conservative position in morphospace (Fig. 3). Our geometric morphometric study confirms the expanded morphospace of rhynchocephalians in the Triassic and Jurassic, and a decrease in the Cretaceous. The fact that Jurassic rhynchocephalians occupied an almost entirely different morphospace from their Triassic precursors might be a consequence of the Triassic–Jurassic extinction, and dramatic changes in the biota and the ecological position of rhynchocephalians in their ecosystems. The dramatic decrease in morphospace occupied by Cretaceous rhynchocephalians has usually been related to the radiation of squamates (Apesteguía & Novas 2003; Jones 2006*b*; Jones *et al.* 2009; Meloro & Jones 2012), but this cannot be confirmed here.

In focusing on lower jaw morphology, we have reduced the sample of morphological characters when compared to studies based on the skull (e.g. Jones, 2008), but we have increased the sample of taxa, and the lower jaw encompasses key information about feeding adaptation (Kammerer *et al.* 2006; Anderson *et al.* 2011, 2013; Stubbs *et al.* 2013). Our results differ from those of Jones (2008), who found tight ecomorphological clusters relating to phylogenetic position, such as a cluster of basal taxa (e.g. *Diphydontosaurus*, *Gephyrosaurus*, *Planocephalosaurus*) as well as some derived groups such as clevosaurs. Our results show that morphological differences cross-cut phylogeny, with high morphological diversity among basal rhynchocephalians and within the derived genus *Clevosaurus* (Fig. 3). Meloro & Jones (2012) suggested that the possible ancestor of *Clevosaurus* must have been '*Sphenodon*-like'. Our results show that *Sphenodon* converges with the Triassic species of *Clevosaurus* (*C. hudsoni* and *C. sectumsemper*) close to the centroid of morphospace, and both *Sphenodon* and *Clevosaurus* possess two of the most average mandibular morphologies of all rhynchocephalians. This indicates that the morphology of the modern tuatara is conservative and it is also an 'average rhynchocephalian'.

Tooth shape is also very important for the evolution of feeding modes in rhynchocephalians (Jones 2009; Meloro & Jones 2012; Rauhut *et al.* 2012; Martínez *et al.* 2013). The most basal taxa (*Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*) are identified as insectivorous because of their piercing teeth, but later species evolved many different tooth shapes reflecting their wide variety of dietary preferences, such as the carnivorous or omnivorous clevosaurs, the omnivorous sphenodontines, the piscivorous pleurosaurs, and the specialized herbivorous eilenodontids (Throckmorton *et al.* 1981; Rasmussen & Callison 1981; Jones 2008, 2009; Meloro & Jones 2012; Rauhut *et al.* 2012; Martínez *et al.* 2013). One special case of feeding adaptation among rhynchocephalians is the Late Jurassic *Oenosaurus muehlheimensis*, which had a complex crushing dentition for a durophagous diet of molluscs or crabs (Rauhut *et al.* 2012). Another interesting case of dietary adaptation is the Early Cretaceous *Ankylosphenodon pachyostosus*, which developed continuously growing teeth ankylosed into the lower jaw for an herbivorous diet (Reynoso 2000).

Throughout their evolutionary history, rhynchocephalians evolved dental and cranial modifications for different ecological niches (Jones 2008). Current research suggests that rhynchocephalians had at least five dietary preferences (Jones 2006*a*, 2009; Rauhut *et al.* 2012; Martínez *et al.* 2013). The morphospaces occupied by rhynchocephalians with these five dietary preferences (Fig. 3B) were generally small, except for those with an omnivorous or carnivorous diet, which occupied a wide morphospace area. Evidence of the success of the omnivorous diet is provided by the oldest known survivor of the K–Pg extinction, the early Paleocene *Kawasphenodon peligrensis*, which has been regarded as an omnivore (Apesteguía *et al.* 2014), as is the extant tuatara (Curtis *et al.* 2011; Jones *et al.* 2012; Cree 2014).

Aspects of the biology of the living tuatara have been noted recently as evidence that it cannot be regarded as a ‘living fossil’. For example, many authors have noted the complexity of the feeding mechanism of *Sphenodon* (Gorniak *et al.* 1982; Jones 2008; Curtis *et al.* 2010, 2011; Jones *et al.* 2012), and the propalinal movement of the lower jaw has been marked as unique among living amniotes (Gorniak *et al.* 1982; Jones 2008; Curtis *et al.* 2010, 2011; Jones *et al.* 2012). Another important feature of the tuatara is the presence of a complete lower temporal bar in the skull, which is a derived condition when compared with other fossil rhynchocephalians (Whiteside 1986; Jones 2008; Curtis *et al.* 2011; Jones *et al.* 2012). Furthermore, studies on the biology of the tuatara have demonstrated that its physiology is quite advanced, because, in contrast to many other living reptiles, the tuatara is well adapted to cold environments (Cree 2014). Also, the tuatara shows complex behaviour, especially in its interspecific relationship with seabirds (Corkery 2012; Cree 2014). In addition, a recent molecular study of the hypervariable regions of mitochondrial DNA of subfossil and extant specimens of the tuatara demonstrated that this species has very high rates of molecular evolution (Hay *et al.* 2008; Subramanian *et al.* 2009).

Notwithstanding these observations of the uniqueness of *Sphenodon*, our analysis of evolutionary rates and geometric morphometrics shows not only that the tuatara is generally morphologically conservative, resembling some of its Mesozoic forebears, but that it actually occupies a position close to the centroid of the hyperdimensional morphospace, as well as in the morphospace bounded by axes PC1 vs PC2 (Fig. 3). Also, *Sphenodon* is recovered as possessing the seventh ‘most average’ morphology out of the 31 taxa used in this study. Even if it fails some of the definitions of ‘living fossil’, *Sphenodon* is part of a lineage that has been long-enduring and existed at low diversity through hundreds of millions of years, it follows a long time gap with few fossils, and it is a relict, being the survivor of a once more diverse clade and now lone sister to the biodiverse Squamata. We provide a new definition of ‘living fossil’ here, in terms of both a statistically significantly slow rate of morphological evolution and morphological conservatism. *Sphenodon* shows both characteristics, a slow rate of evolution when compared to the mean for all rhynchocephalians, and a position close to the centroid in the overall morphospace defined by the extinct members of the clade.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.568jh

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Taxonomic reassessment of *Clevosaurus latidens* Fraser, 1993 (Lepidosauria, Rhynchocephalia) and rhynchocephalian phylogeny based on parsimony and Bayesian inference

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Abstract.—The Late Triassic rhynchocephalian *Clevosaurus latidens* Fraser, 1993 is known from the fissure deposits of Cromhall Quarry, England. Many studies have questioned its referral to the genus *Clevosaurus* Swinton, 1939 and some phylogenetic analyses suggest a close relationship with herbivorous rhynchocephalians. We re-examine the type specimens and referred material of *C. latidens* to elucidate its taxonomic identity. Additionally, we provide new phylogenetic analyses of the Rhynchocephalia using both parsimony and Bayesian approaches. Our taxonomic review and both phylogenetic analyses reveal that *C. latidens* is not referable to *Clevosaurus*, but represents a new genus. We reassess *C. latidens* and provide an amended diagnosis for *Fraserosphenodon* new genus. Both parsimony and Bayesian analyses recover similar topologies and we propose formal names for two higher clades within Rhynchocephalia: Eusphenodontia new infraorder and Neosphenodontia new clade.

UUID: http://zoobank.org/65f29bd1-47e3-4a73-af8c-9181c19319e4

Introduction

The Rhynchocephalia is an ancient group of reptiles that originated in the early Mesozoic. Currently this group has low diversity, being represented by a single species, the famous 'living fossil' *Sphenodon punctatus* (Gray, 1842) from New Zealand (Jones et al., 2013; Cree, 2014; Herrera-Flores et al., 2017). In contrast to their current low diversity, Mesozoic rhynchocephalians were diverse, showing varied morphologies and a wide geographical distribution (Jones, 2006a, 2009; Rauhut et al., 2012; Martínez et al., 2013; Herrera-Flores et al., 2017). Among the earliest rhynchocephalians, species of the genus *Clevosaurus* Swinton, 1939 were the most diverse and widely distributed in the early Mesozoic. *Clevosaurus hudsoni* Swinton, 1939 was the first described species of the genus; it was named after F. G. Hudson, who discovered the fossil remains at Cromhall Quarry, England (Fraser, 1988). Since the description of *C. hudsoni*, nine species of *Clevosaurus* have been erected—*C. bairdi* Sues, Shubin, and Olsen, 1994, *C. brasiliensis* Bonaparte and Sues, 2006, *C. convallis* Säilä, 2005, *C. latidens* Fraser, 1993, *C. mcgilli* Wu, 1994, *C. minor* Fraser, 1988, *C. petilus* Young, 1982, *C. sectumsemper* Klein et al., 2015, and *C. wangi* Wu, 1994—and new records have been reported from localities in Belgium, Brazil, Canada, China, Great Britain, Mexico, and South Africa (Fraser, 1988, 1993; Wu, 1994; Sues et al., 1994; Duffin, 1995; Sues and Reisz, 1995; Säilä, 2005; Bonaparte and Sues, 2006; Reynoso and Cruz, 2014; Klein et al., 2015).

The anatomy of *Clevosaurus* is well known and the monograph of Fraser (1988) offers a very thorough review of the general morphology of this genus. It is recognized that the genus *Clevosaurus* is highly diverse, but the taxonomic validity of some *Clevosaurus* species has been questioned (Jones, 2006a). Hsiou et al. (2015) presented a review of *C. brasiliensis* that included a phylogenetic analysis of almost all known *Clevosaurus* species. Their study demonstrated that some species might not be valid taxa or are perhaps not directly referable to this genus. One of these conflicting taxa is *C. latidens*, a species described by Fraser (1993) from the Late Triassic fissure deposits of Cromhall Quarry, England. The uncertain taxonomic affinity of *C. latidens* and its dubious relationship with *Clevosaurus* have been noted in many previous studies (Jones, 2006a, 2009; Martínez et al., 2013; Hsiou et al., 2015; Klein et al., 2015), and some phylogenetic analyses even suggested a closer relationship with opisthodontians, but no taxonomic revision of this taxon has been carried out.

For a long time, the relationships among rhynchocephalians were poorly known, and most taxa were assessed by overall morphological similarities. The first phylogenetic analysis of the group was performed by Fraser and Benton (1989), followed by many different analyses, including new descriptions or redescriptions of taxa (e.g., Wu, 1994; Reynoso, 1996, 1997, 2000, 2005; Reynoso and Clark, 1998; Apesteguía and Novas, 2003; Rauhut et al., 2012; Martínez et al., 2013; Apesteguía and Carballido, 2014; Apesteguía et al., 2012, 2014; Cau et al., 2014; Hsiou et al., 2015). So far, all phylogenetic studies of the Rhynchocephalia have only used parsimony analysis, recovering a few distinct clades. More recently, Bayesian inference methods have been employed for phylogenetic analyses based on morphological characters (e.g., Parry et al., 2016; Wright, 2017), and recent studies suggest that Bayesian methods outperform parsimony for morphological data (O'Reilly et al., 2016; Puttick et al., 2017), recovering more accurate, but less precise results.

To clarify the doubtful taxonomic affinity of *Clevosaurus latidens*, we re-examined the type specimens and other material described by Fraser (1993). We updated the character matrix of a recent phylogenetic analysis of the Rhynchocephalia (Hsiou et al., 2015), recoded morphological characters for *C. latidens*, and performed both parsimony and Bayesian analyses. Our results confirm that *C. latidens* is not related to *Clevosaurus*, but represents a new genus. Our phylogenetic analyses recover similar topologies using both parsimony and Bayesian approaches. We employ the new phylogeny to propose formal names for two higher clades within Rhynchocephalia.

Material and methods

We re-examined the type material and other material described by Fraser (1993) as *Clevosaurus latidens*. All specimens of *C. latidens* consist of fragments of dentary, maxilla, and premaxilla housed in the collections of the Virginia Museum of Natural History and the University of Aberdeen. For anatomical comparisons, we reviewed several specimens of *Clevosaurus* from the paleontological collections of the University of Bristol and the University Museum of Zoology in Cambridge.

To explore the phylogenetic relationships of rhynchocephalians and the position of *Clevosaurus latidens*, we used the largest and most up-to-date data matrix of Rhynchocephalia (Hsiou et al., 2015). We added three taxa—*C. sectumsemper* Klein et al., 2015, *Derasmosaurus pietraroiae* Barbera and Macuglia, 1988, and *Priosphenodon minimus* Apesteguía and Carballido, 2014—and recoded some characters for *C. latidens* and *Pelecymala robustus* Fraser, 1986 after examination of the type specimens. The new matrix comprises 47 operational taxonomic units scored for 74 characters. We rooted the trees with the lepidosauromorph *Sophineta cracoviensis* Evans and Borsuk-Bialynicka, 2009. Two squamates, the Late Jurassic–Early Cretaceous *Eichstaettisaurus* Kuhn, 1958 and the extant *Pristidactylus* Gray, 1845, were also used as outgroups.

The revised taxon-character data matrix was analyzed using both equally weighted maximum parsimony and Bayesian inference. Parsimony analysis was performed in TNT v. 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016), first using the 'New Technology' search options. The initial tree search used multiple replications with sectorial searches, four rounds of tree fusing, 10 rounds of drifting, and 200 ratcheting iterations. Following this, the generated most parsimonious trees (MPTs) were analyzed using traditional tree bisection and reconnection branch swapping. All recovered MPTs were then summarized in a 50% majority rule consensus tree, and clade robustness was assessed with Bremer decay indices (Bremer, 1994). Bayesian inference trees were estimated using MrBayes v. 3.2 (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2012). The standard Mk model (Lewis, 2001) with gamma distribution priors for site rate variation was specified. The analysis was performed with four runs of four chains, run for 10^8 generations, sampling parameters every 1000 generations. The first 25% of sampled trees were discarded as burn-in. Convergence was assessed based on effective sample size (ESS) values >200. Results from the Bayesian analysis were summarized using a 50% majority consensus tree, revealing clades that have posterior probability values of $\geq$ 50%. The data matrix and analytical scripts are included in the Supplementary Data Set.

Repositories and institutional abbreviations.—AUP = University of Aberdeen Paleontology Collection; BRSUG = Bristol University, School of Earth Sciences Collection; NMS = National Museums Scotland; SAMK = South African Museum; UMZC = University Museum of Zoology, Cambridge; VMNH = Virginia Museum of Natural History.

Systematic paleontology

Superorder Lepidosauria Haeckel, 1866
Order Rhynchocephalia Günther, 1867
Suborder Sphenodontia Williston, 1925
Infraorder Eusphenodontia new infraorder

Remarks.—See Discussion.

Clade Neosphenodontia new clade

Remarks.—See Discussion.

Clade Opisthodontia Apesteguía and Novas, 2003
Genus *Fraserosphenodon* new genus
urn:lsid:zoobank.org:act:6C14E307-718C-47C8-AC8F-C658A048289B

Type species.—*Clevosaurus latidens* Fraser, 1993.

Diagnosis for the genus and only known species.—Moderate-sized rhynchocephalian. Maxillary teeth with relatively short crowns with transversely broadened posterolabial flanges without grooved facets on the labial surface. Robust dentary with a wide mandibular symphysis. Dentary with three generations of teeth. Front of dentary with two rounded successional teeth followed by a series of six or seven very small rounded hatchling teeth. Additional teeth in dentary transversely broadened distinctly triangular in labial view and rounded and bulbous in occlusal view.

Etymology.—The genus epithet is in honor of the British paleontologist Nicholas 'Nick' Fraser, for his outstanding contributions to the knowledge of the British Triassic fauna, especially for his exceptional work on early rhynchocephalians.

Occurrence.—Cromhall Quarry, Avon, England, site 5A of Late Triassic fissure deposit.

Remarks.—All *Fraserosphenodon* specimens are quite fragmentary, but their tooth morphology, based on wide and robust teeth for grinding, clearly differs from the tooth shape for cutting and slicing characteristic of the genus *Clevosaurus*, and, indeed, is more similar to that of opisthodontians.

Fraserosphenodon latidens (Fraser, 1993) new combination
Figures 1–2

1986 aff. *Pelecymala*; Fraser, p. 176, pl. 20, figs. 8, 9.
1988 *Clevosaurus* sp.; Fraser, p. 163, fig. 43.
1993 *Clevosaurus latidens* Fraser, p. 137, fig. 2.

Holotype.—VMNH 524, maxillary fragment (Fig. 1.1–1.3).

Additional specimens.—VMNH 525–528, AUP 11191–11192.

Remarks.—The systematic paleontology section of Fraser's original work referred to the holotype of *Fraserosphenodon latidens* (VMNH 524) as a dentary fragment (Fraser, 1993), but the description of this element treated it as a maxillary fragment. Our review of VMNH 524 confirms that it is a fragment of the posterior part of the left maxilla (Fig. 1.1–1.3). This element includes five well-preserved, complete teeth. The maxillary teeth have relatively short crowns with transversely broadened posterolabial flanges without grooved facets on the labial surface and heavily worn occlusal surfaces.

We agree with Fraser (1993) that paratype specimen VMNH 525 is a dentary fragment that possibly belongs to the right dentary (Fig. 1.4–1.6). This element has three teeth that are also transversely broadened. In labial view, all teeth appear distinctly triangular. Only the second and third teeth are heavily worn, and the wear is especially pronounced on the third tooth. In occlusal view, the teeth of VMNH 525 appear round with a bulbous swelling developed medially on each tooth, as was described by Fraser (1993) for specimen VMNH 543. The overall shape of both VMNH 525 and 543 is also quite similar. Note that Fraser (1993) did not mention specimen VMNH 543 in the systematic paleontology section of his paper, and there is also no specimen in the VMNH collection assigned to *Fraserosphenodon* (*C. latidens*) with that catalog number. It might be that specimen VMNH 543 illustrated and described by Fraser (1993, fig. 2C–E) is indeed specimen VMNH 525.

Paratypes VMNH 526–528 are maxillary fragments (Fig. 1.7–1.15). Specimens VMNH 526 and 528 (Fig. 1.7–1.9, 1.13–1.15) belong to the distal part of the left maxilla, whereas VMNH 527 (Fig. 1.10–1.12) belongs to the mesialmost part of the right maxilla. VMNH 526 and 528 include a series of four complete teeth, which are heavily worn on the occlusal surface, and have a morphology comparable to that of the holotype. The crowns of VMNH 528 are a little higher than in the other specimens (Fig. 1.13–1.15). VMNH 527 includes six complete teeth and a very small fragment of a broken tooth in the distal part of the element (Fig.1.10–1.12). The mesialmost tooth of this specimen is very small and rounded; the following tooth is also very small and of a semioval shape. The third to sixth teeth are all transversely broadened, with a right-angled triangular shape in labial view and a heavily worn occlusal surface. Paratype VMNH 529, a maxillary fragment according to Fraser (1993), could not be located within the VMNH collection.

The heavily worn occlusal tooth surfaces in all type specimens suggest that they might belong to adult individuals (Fig. 1). A recent study of ontogenetic variation of the dentary in rhynchocephalians (Romo de Vivar-Martínez and Bento-Soares, 2015) demonstrates that the occlusal surface of teeth shows high wear in mature specimens.

Additionally, another six specimens from the AUP collection can be referred to *Fraserosphenodon*. However, apart from AUP 11191 and 11192 (premaxilla and dentary, respectively), the other four specimens attributable to *Fraserosphenodon* are all fragmentary maxillary elements. All of these maxillary elements were stored in containers with other rhynchocephalian specimens without being labeled individually, making it impossible to associate the specimens with unique catalog numbers. These specimens all clearly exhibit the characteristic transversely broadened tooth morphology without grooved facets on the labial tooth surfaces, with heavy wear on the occlusal surface. The first specimen is a fragment of a right maxilla. It has four heavily worn teeth that include a small rounded tooth between the second and third tooth, which might represent a dental pathology. The second specimen is a fragment of a right maxilla that includes two isolated but complete teeth. The third specimen is a fragment of a right maxilla and includes four teeth. The mesialmost tooth of this specimen is heavily eroded and the tooth enamel of the third tooth is slightly damaged. The fourth specimen is a fragment of the distal end of a left maxilla; it includes two teeth with very short crowns due to the heavy wear of the occlusal surface. Among all rhynchocephalian specimens in the AUP collection, we did not identify any dentary specimens attributable to *Fraserosphenodon* with preserved coronoid processes (contra Fraser, 1993).

Specimen AUP 11191, a right premaxilla (Fig. 2.1, 2.2), was originally identified as *Clevosaurus* sp. by Fraser (1988) and was subsequently reassigned to *C. latidens* by Fraser (1993). The nasal process is broken in AUP 11191, but the ventral and dorsal maxillary processes are well preserved. The distal end of the ventral maxillary process has a clearly flattened oval shape; the dorsal maxillary process is relatively long and is angled at ~60^{o} relative to the ventral maxillary process. On the convex dorsal surface of the premaxilla, between the dorsal maxillary process and the nasal process, it is possible to observe the premaxillary fossa, which is semicircular in shape. AUP 11191 exhibits three complete teeth, of which the distalmost tooth is very small, considerably shorter in relation to the other two teeth. In contrast, the two mesialmost teeth are of regular size and partially fused, and both have a rounded semicircular shape with minor signs of wear. The semifused condition of the two mesialmost teeth of AUP 11191 suggests that this specimen is a juvenile: as seen in other derived rhynchocephalians (e.g., *Clevosaurus* and *Sphenodon* spp.) these teeth fuse over time in mature individuals to form the characteristic chisel-like structure seen in late-diverging rhynchocephalians (Robinson, 1973).

Specimen AUP 11192, an anterior fragment of a right dentary (Fig. 2.3–2.5), was tentatively assigned to *Pelecymala* Fraser, 1986 by Fraser (1986), but as in the case of AUP 11191, it was later referred to *C. latidens* by Fraser (1993). In the description of AUP 11192, Fraser (1986) noticed that the length of this specimen appeared quite similar to that of *C. hudsoni*, but was noticeably deeper in height. AUP 11192 has a robust and deep structure, similar to that of opisthodontians (e.g., *Priosphenodon* Apesteguía and Novas, 2003, *Toxolophosaurus* Olson, 1960). The mandibular symphysis in AUP 11192 is quite wide; the Meckelian canal runs along the midline of the jaw.

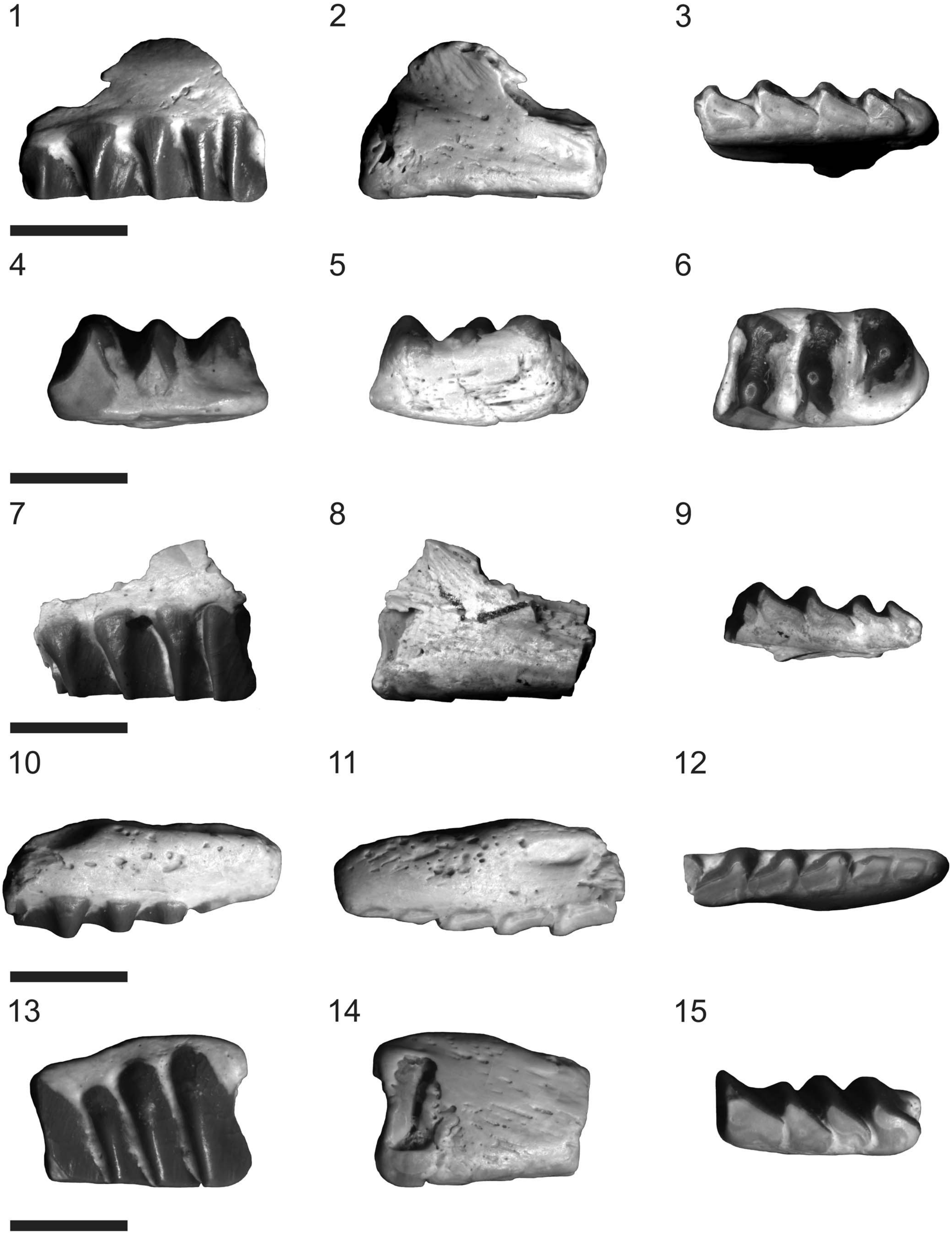

Figure 1. *Fraserosphenodon latidens* n. comb.; all specimens shown in labial, lingual, and occlusal views: (**1–3**) VMNH 524, holotype, left maxilla; (**4-6**) VMNH 525, paratype, right dentary; (**7–9**) VMNH 526, paratype, left maxilla; (**10–12**) VMNH 527, paratype, right maxilla; (**13–15**) VMNH 528, paratype, left maxilla. Scale bars = 5 mm (**1–3**, **7–9**, **10–12**); 3.5 mm (**4–6**, **13–15**).

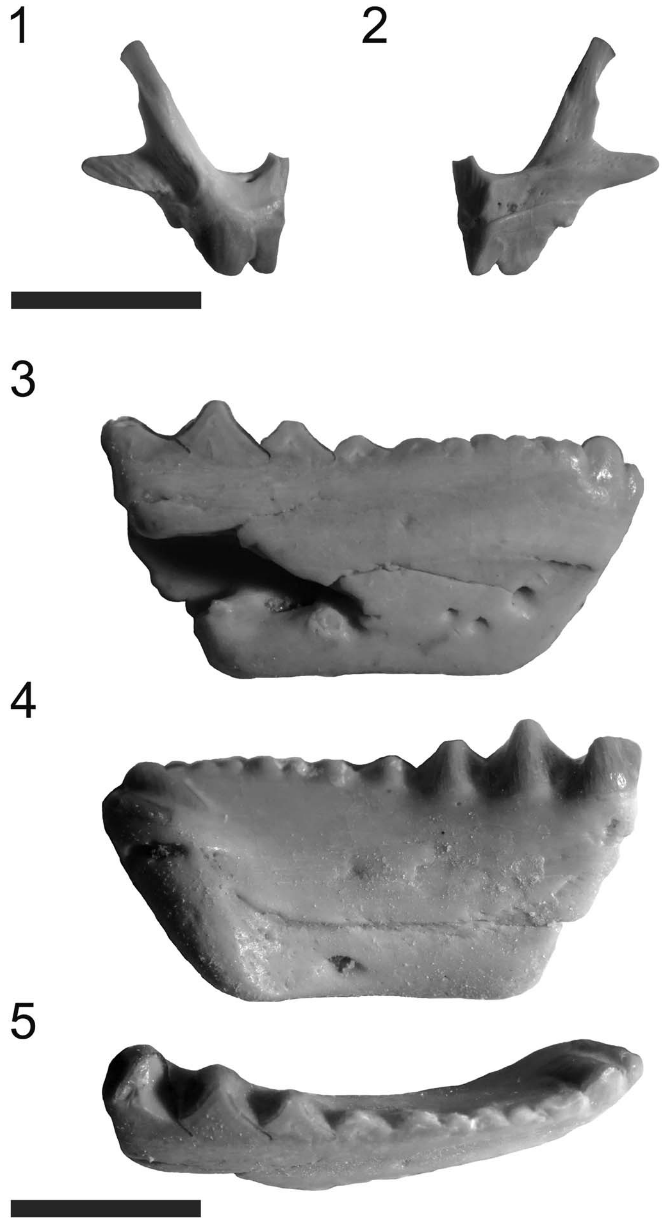

Figure 2. *Fraserosphenodon latidens* n. comb.: (**1, 2**) AUP 11191, right premaxilla, shown in labial (**1**) and lingual (**2**) views; (**3–5**) AUP 11192, right dentary, shown in labial (**3**), lingual (**4**), and occlusal (**5**) views. Scale bars = 6 mm (**1, 2**); 3.5 mm (**3–5**).

The specimen includes three generations of teeth, but caniniform teeth are lacking. The front of AUP 11192 has two rounded successional teeth similar to those of the premaxilla. These teeth are followed by a series of six or seven small semicircular remnants of hatchling teeth with minor signs of wear on the occlusal surfaces. On the distal end of this element, we found three or four additional teeth that in both labial and lingual view show the same triangular shape seen in VMNH 525. In occlusal view, the teeth of AUP 11192 show heavy signs of wear and the round, bulbous shape seen in VMNH 525. This round, bulbous shape is more pronounced in the distalmost additional tooth of AUP 11192. Additionally, AUP 11192 includes three mental foramina of relatively large size (Fig. 2.3), which suggests that this specimen comes from a juvenile. The length and height of AUP 11192, as preserved, are 10.5 mm and 5.4 mm, respectively.

Phylogenetic analyses

The parsimony analysis found 7176 MPTs of 265 steps, and the 50% majority rule consensus tree shows good resolution for most clades (Fig. 3.1). The consistency (CI) and retention indices (RI) for the 50% majority rule consensus tree are 0.38628 and 0.66403, respectively. No clade had a Bremer support score > 1 (complete statistics and associated files for both phylogenetic analyses can be found in the Supplemental Data). Generally, our results agree with those of other recent studies (Rauhut et al., 2012; Martínez et al., 2013; Apesteguía et al., 2014; Cau et al., 2014; Hsiou et al., 2015). One of the major differences is that our analysis recovered Pleurosauridae as the sister group of Sphenodontidae. The terrestrial *Pamizinsaurus* Reynoso, 1997 is the earliest diverging taxon within the Sphenodontidae, which includes two major clades. The first clade includes *Ankylosphenodon* Reynoso, 2000, *Derasmosaurus* Barbera and Macuglia, 1988, *Oenosaurus* Rauhut et al., 2012, and *Zapatadon* Reynoso and Clark, 1998 in a polytomy, whereas the second clade is well resolved, recovering the Early Jurassic *Cynosphenodon* Reynoso, 1996 and the modern *Sphenodon* Gray, 1831 as successive sister taxa to the clade comprising *Theretairus* Simpson, 1926 and *Sphenovipera* Reynoso, 2005. The strict consensus tree of the second analysis of Cau et al. (2014) also found *Derasmosaurus*, *Oenosaurus*, and *Zapatadon* in a similar polytomy, and forming the sister group of the clade comprising *Sphenodon, Cynosphenodon*, *Sphenovipera, Kawasphenodon* Apesteguía, 2005, and *Theretairus*. The close relationship of *Sphenovipera* and *Theretairus* has been constantly recovered in previous analyses (e.g., Martínez et al., 2013; Apesteguía et al., 2014; Hsiou et al., 2015).

Within clevosaurs, *Brachyrhinodon* Huene, 1910 was recovered as the earliest diverging taxon. All *Clevosaurus* species are grouped in a polytomy, which obscures the relationships between the species. The results for clevosaurs are quite similar to those recovered by the strict consensus tree of Hsiou et al. (2015). The only difference is that in their analysis, *Polysphenodon* Jaekel, 1911 appears as the earliest diverging taxon within Clevosauridae, but all other taxa were recovered in a polytomy. A similar polytomy for clevosaurs was also shown in the strict consensus tree of Rauhut et al. (2012). Our results agree with the work of Martínez et al. (2013) and Hsiou et al. (2015) in recovering *Fraserosphenodon latidens* as an early diverging opisthodontian. Indeed, we recovered *F. latidens* as the earliest diverging taxon within Opisthodontia. This clearly confirms that *F. latidens* is not referable to the genus *Clevosaurus*, and supports the erection of a new opisthodontian genus, as previously suggested (Jones, 2006a, 2009; Martínez et al., 2013; Hsiou et al., 2015; Klein et al., 2015). Within Opisthodontia, the relationships of eilenodontines are quite well resolved; our results only differ from the works of Martínez et al. (2013) and Cau et al. (2014) in finding *Ankylosphenodon* outside of Opisthodontia.

Another major difference compared to the previous analyses of Martínez et al. (2013) and Hsiou et al. (2015) is that the Triassic taxon *Pelecymala* was no longer recovered as closely

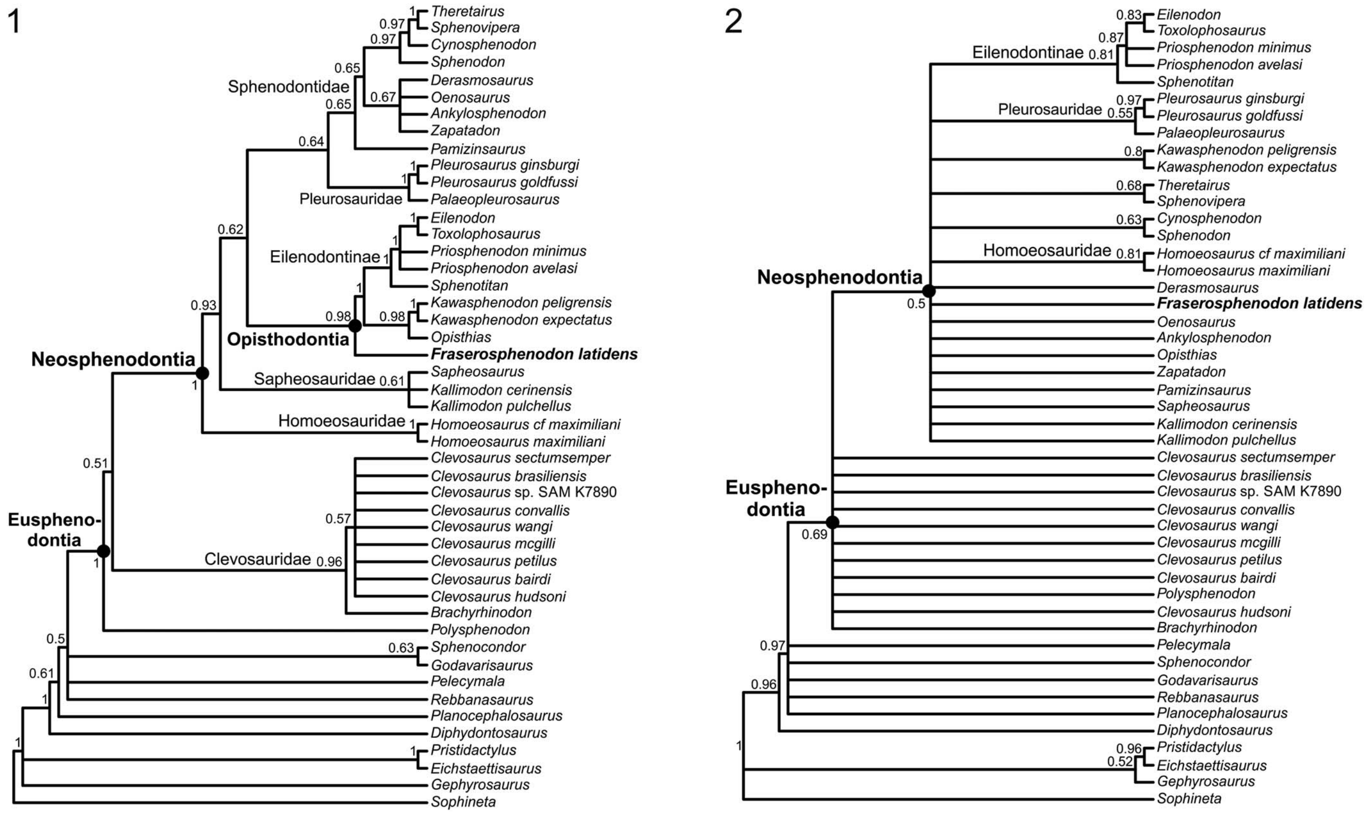

Figure 3. Consensus trees recovered from the phylogenetic analyses: (**1**) maximum parsimony 50% majority rule consensus tree; CI = 0.38628, RI = 0.66403; node labels denote the proportion of MPTs that recover that node; (**2**) 50% majority rule consensus tree from the Bayesian-inference analysis, with clade credibility values (decimal proportions) labeled on the nodes.

related to Opisthodontia, but was found in a polytomy with early-diverging rhynchocephalians such as *Rebbanasaurus* Evans, Prasad, and Manhas, 2001, the clade of *Sphenocondor* Apesteguía, Gomez, and Rougier, 2012 and *Godavarisaurus* Evans, Prasad, and Manhas, 2001, and the clade Eusphenodontia.

Overall, the results of the Bayesian analysis (Fig. 3.2) resemble those of the parsimony analysis, but with considerably less resolution. Several large polytomies were recovered, but where clades are resolved, the clade credibility values are often moderately high. The Bayesian 50% majority rule consensus tree also recovered *Pelecymala* in a polytomy with early diverging rhynchocephalians, which confirms that this taxon is not related to opisthodontians as previously assumed (Martínez et al., 2013; Hsiou et al., 2015). The Bayesian tree did not recover clevosaurs as a monophyletic group; all of them were recovered in a large polytomy that obscures the relationships between the taxa. Relationships among other, later-diverging rhynchocephalians are unclear; many of them are part of a polytomy that includes *Fraserosphenodon*, but no clevosaurs. This result confirms that *Fraserosphenodon* is not closely related to *Clevosaurus*.

It should be noted that the Bayesian tree recovered a close relationship between the extant *Sphenodon* and the Jurassic *Cynosphenodon*, a close relationship between *Theretairus* and *Sphenovipera,* and pleurosaurs as a monophyletic group. The Bayesian tree did not recover Opisthodontia as a monophyletic group, but completely agrees with the parsimony tree for the interrelationships of eilenodontines, which are quite robust and well resolved.

Discussion

Among Mesozoic rhynchocephalians, clevosaurs were one of the most diverse groups. Clevosaurs are represented by three genera: *Polysphenodon*, *Brachyrhinodon*, and *Clevosaurus*. The first two genera are monospecific, whereas *Clevosaurus* currently has nine formally recognized species. The high diversity of the genus *Clevosaurus*, however, is debatable because of the doubtful validity/referral of some of the species, especially those based on poorly preserved or very fragmentary material, such as the three Chinese species (*C. mcgilli*, *C. petilus*, and *C. wangi*) or '*C. latidens*' from Great Britain. According to Jones (2006a), the Chinese specimens are too poorly preserved to diagnose them as three distinct species, but clearly all of them belong to *Clevosaurus*. In contrast to the Chinese specimens, the referral of '*C. latidens*' to *Clevosaurus* has been widely questioned (Jones, 2006a, 2009; Martínez et al., 2013; Hsiou et al., 2015; Klein et al., 2015).

Before the description of '*Clevosaurus latidens*,' specimen AUP 11192, a dentary fragment, was tentatively related to *Pelecymala* based on its transversely wide teeth (Fraser, 1986). When Fraser (1993) formally described '*C. latidens*,' he noted that the tooth morphology of the new '*Clevosaurus*' species was quite similar to that of other taxa with transversely wide teeth such as *P. robustus* and *Toxolophosaurus cloudi* Olson, 1960

(Fraser, 1993). Some of the diagnostic characters of the genus *Clevosaurus* based on features of the skull could not be observed in '*C. latidens*' for obvious reasons. However, at least the dentition of '*C. latidens*' did not match that of *Clevosaurus*, which consists of larger, blade-like teeth with lateral flanges. It has been suggested that the tooth morphology of *Clevosaurus* was very specialized for a possible omnivorous or carnivorous diet (Jones 2006b, 2009; Rauhut et al., 2012; Martínez et al., 2013), whereas the dentary and maxillary teeth '*C. latidens*' were more like those of herbivorous taxa. Fraser (1993) also pointed out that the wear facets on the teeth of '*C. latidens*' suggested a propalinal movement of the lower jaw, which contrasts with the orthal jaw movement seen in *Clevosaurus*.

Based on dentary, maxillary, and premaxillary tooth morphology, as well as the suggested propalinal movement of the lower jaw, our review of '*C. latidens*' specimens confirms that this taxon is not referable to *Clevosaurus*. Our phylogenetic analyses, including both parsimony and Bayesian approaches, confirm its position outside *Clevosaurus*. We rename '*C. latidens*' as *Fraserosphenodon latidens* n. comb. The parsimony tree (Fig. 3.1) suggests that *F. latidens* is an early-diverging opisthodontian, but not closely related to *Pelecymala* as was previously suggested by Fraser (1986, 1993), Martínez et al. (2013), and Hsiou et al. (2015). While reviewing the type specimens of *Pelecymala* (AUP 11140, 11214–11215), we noticed that the teeth of *Pelecymala* are not transversely broadened as had been described by Fraser (1986); in contrast, their shape is more conical, slightly curved, and labiolingually flattened. The tooth morphology of *Pelecymala* is actually more similar to that of some of the earliest diverging rhynchocephalians, which is also confirmed by our phylogenetic analyses (Fig. 3). A complete taxonomic redescription of *Pelecymala* appears necessary, but is beyond the scope of this study. The Bayesian tree (Fig. 3.2) could not recover the exact relationships of *F. latidens*, because this taxon is found in a polytomy that includes many other species. Like the parsimony analysis, however, the Bayesian approach recovered *F. latidens* as a genus distinct from *Clevosaurus* and not closely related to clevosaurs. Following the parsimony analysis, we consider *F. latidens* as an early diverging opisthodontian.

The parsimony analysis of Rhynchocephalia showed better resolution than the Bayesian approach. This result is not unexpected, because studies have shown that Bayesian methods are more accurate but less precise than parsimony-based analyses (O'Reilly et al., 2016). There are some minor differences between the internal branches in both trees, but several higher clades were recognized by both phylogenetic methods (Fig. 3). Some of these higher clades within Rhynchocephalia have been frequently recovered in other recent phylogenetic analyses, and have been informally named as 'crown-sphenodontians,' 'derived-sphenodontians,' or 'eupropalinals' (e.g., Apesteguía et al., 2012, 2014; Apesteguía and Carballido, 2014).

We propose formal names for two well-supported clades: Eusphenodontia and Neosphenodontia (Fig. 3). We define Eusphenodontia as the least inclusive clade containing *Polysphenodon muelleri* Jaekel, 1911, *Clevosaurus hudsoni*, and *Sphenodon punctatus*. In the 50% majority rule consensus tree, three unambiguous character transitions were recovered for Eusphenodontia under both ACCTRAN and DELTRAN optimization: (1) wear facets on marginal teeth of the dentary and/or on marginal teeth of the maxilla are clearly visible (character 46: 0 to 1), (2) the premaxillary teeth are merged into a chisel-like structure (character 49: 0 to 1), and (3) the palatine teeth are reduced to a single tooth row with an additional isolated tooth (character 52: 0 to 1). Neosphenodontia is defined as the most inclusive clade containing *S. punctatus* but not *C. hudsoni*. In the 50% majority rule consensus tree, Neosphenodontia is supported by the following six unambiguous character changes that are recovered under both ACCTRAN and DELTRAN optimization: (1) the relative length of the antorbital region is increased, reaching one-quarter to one-third of the complete skull length (character 1: 2 to 1), (2) the posterior edge of the parietal is only slightly incurved inward (character 18: 0 to 1), (3) the parietal foramen is found at the same level or anterior of the anterior border of the supratemporal fenestra (character 19: 0 to 1), (4) the palatine teeth are further reduced to a single lateral row (character 52: 1 to 2), (5) the number of pterygoid tooth rows is reduced to one or none (character 55: 1 to 2), and (6) the ischium is characterized by a prominent process on its posterior border (character 60: 1 to 2). The families Homoeosauridae, Pleurosauridae, and Sphenodontidae form in our analyses, as in others, the content of the clade Neosphenodontia. Levels of homoplasy in Eusphenodontia and Neosphenodontia are generally high, with individual character consistency indices (CI) often <0.5. For both clades, no individual character has a CI of 1 in the 50% majority rule consensus tree (for the complete list of characters, apomorphies, and other tree statistics, see the Supplemental Data). We consider the formal naming of these higher clades necessary to facilitate future discussion about the phylogenetic relationships of rhynchocephalians.

Conclusion

This study confirms previous doubts about the referral of '*C. latidens*' to *Clevosaurus*. The recognition of '*C. latidens*' belonging to a new genus now formally named *Fraserosphenodon* emphasizes the high generic diversity of Rhynchocephalia in the Mesozoic, especially among herbivorous taxa. Furthermore, our study demonstrates that the use of Bayesian approaches can be useful to contrast and validate phylogenies that were previously based only on parsimony methods. Bayesian inference exhibits generally lower resolution in some parts of the tree, but a few higher clades are strongly supported and are consistently recovered by both Bayesian and parsimony analyses.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9n153

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DISCUSSION

REPLY TO COMMENTS ON: MACROEVOLUTIONARY PATTERNS IN RHYNCHOCEPHALIA: IS THE TUATARA (*SPHENODON PUNCTATUS*) A LIVING FOSSIL?

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WE are interested to see the new analyses and contributions by Vaux *et al.* (2018) concerning *Sphenodon*, and whether it can be called a 'living fossil' or not. We will focus on the part of their paper that is critical of our contribution on rhynchocephalian morphological evolution (Herrera-Flores *et al.* 2017) and comment only briefly on the remainder. We consider first our definition of 'living fossil', and whether such a definition can be meaningful or not, then we consider the specific criticisms offered by Vaux *et al.* (2018) of the analyses in Herrera-Flores *et al.* (2017).

DEFINITION OF 'LIVING FOSSIL'

In their introductory remarks, Vaux *et al.* (2018) do not comment on our definition of 'living fossils' but dilate on the wider sins of other authors. The term 'living fossil' has had a long history, with many definitions and much debate about whether such a term is required or not. Vaux *et al.* (2018) do not like the term, and especially dispute that it can be applied to the New Zealand tuatara, *Sphenodon*. We agree with most of what they say. As we said in our paper (Herrera-Flores *et al.* 2017, p. 320), 'The concept of 'living fossils' has been problematic since the term was coined by Charles Darwin (1859), as there is no such identifiable class of organisms'. Therefore, as we all agree that many definitions hitherto have been inadequate, a core purpose of our paper was to provide a computationally testable definition.

We repeat our definition here (Herrera-Flores *et al.* 2017, p. 320): 'we propose a hypothesis that can be tested by computational morphometrics and phylogenetic comparative methods (PCM): 'a living fossil should show both statistically significantly slow rates of morphological evolution and it should be morphologically conservative.'' We went on to explain how these two features could be measured. We noted that morphological conservatism could be measured by both the distance in morphospace that a specimen or taxon lies from the centroid, or how different the specimen or taxon is from the average shape when using geometric morphometrics. Whether unusually slowly evolving taxa are called 'living fossils' or 'unusually slowly evolving taxa' is a matter of choice. The methods now exist to clarify the 'unusually slowly evolving' end of the spectrum of evolutionary rates in terms of statistically significantly slow rates.

In discussing whether *Sphenodon* is or is not a 'living fossil', Vaux *et al.* (2018) confirm that most previous authors have concurred that it is. Recent research using a quantitative metric unrelated to that in Herrera-Flores *et al.* (2017) has also identified *Sphenodon* as a 'living fossil' (Bennett *et al.* 2018). Vaux *et al.* point out that there is limited fossil evidence of New Zealand rhynchocephalians, and no evidence that the living species, *Sphenodon punctatus*, has had an unusually long duration. There is in fact no fossil evidence that it has had either a short or long duration, and this is probably not exactly relevant as, when using model-based approaches in macroevolution, rates of change are assessed from the sum total of available evidence. Our study was not concerned with *Sphenodon* alone, but with the wider clade Rhynchocephalia, comprising some 30 genera, and against which we assessed whether *Sphenodon* was close to the average morphology, or at the high or low end of calculated evolutionary rates.

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CRITIQUE OF OUR ANALYSIS

Our paper presented two analyses: a study of evolutionary rates within Rhynchocephalia, and a geometric morphospace-disparity analysis. Vaux *et al.* (2018) did not comment on the first of these analyses, which is unfortunate as it addresses many of their concerns, but it is worth referring readers back to our paper, where they can see details of our analyses and results. In the evolutionary rates analyses, we used the data matrix of 74 discrete morphological characters from Apesteguía *et al.* (2014), and found, using PCM approaches, a scatter of significantly fast and slow rates of evolution across the tree; only two taxa showed consistently slow rates of evolution according to different analytical approaches, namely *Sphenodon* and *Priosphenodon*; for *Sphenodon* the slow-rate model was most consistent in all replicate analyses. Further, the consistently slow evolutionary rates shown by *Sphenodon* contrast with average and faster rates shown by the other four taxa within its subclade. The closest sister taxon of living *Sphenodon* is the Early Jurassic genus *Cynosphenodon*.

In commenting on the second analysis, the geometric morphometric study, Vaux *et al.* (2018) mis-characterize it in several ways. First, they stress the role of diet, and state that ‘The authors focused especially on the comparison of morphological variation with inferred diet.’ We did not. Our study was on morphology in an evolutionary sense. Vaux *et al.* (2018) further comment that the phylogeny in our figure 1 ‘indicated that tuatara are equally related to fossil genera that might have eaten plants and insects … bivalves or crabs … and seaweed’. These are interesting comments, but do not in any way affect our result, which was strictly morphospace-based, looking at landmark data on dentary shape.

Vaux *et al.* (2018) go on to give a lengthy, but inaccurate, description of our geometric morphometric morphospace analysis, implying that our purpose was to infer the diet of all the fossil forms with regard to modern *Sphenodon*. This was not what we did. In our plot, we simply labelled taxa by dietary categories previously assigned in the literature (we provided references). We then observed the distribution of the dietary groups in morphospace and related this back to the divergent morphotypes. We made no attempt to statistically link our analysis to diet, and we did not claim to do this; our plot is simply a visualization showing the distribution of dentary shapes and hypothesized diets according to categories established by other authors. Their misunderstanding of our paper is further clarified when they say, ‘Beyond diet estimated from dentary morphology, little consideration was given to other known differences among the rhynchocephalians sampled’. This is true: we made it clear throughout that our study was of disparity among rhynchocephalians living and extinct based on mandible shape. The fact that mandible shape is related to diet is presented, but this is not the core of our argument. Nor did we claim, or attempt, to construct morphospaces that incorporated additional characters of the skull or skeleton.

Vaux *et al.* (2018) then provide discussions of the habitat occupied by modern *Sphenodon*, and the inferred habitats of the fossil forms. None of this discussion has direct relevance to our contribution. We did not claim to factor habitat into our analyses, and we made it clear that our analyses were focused on evolutionary rates in skeletal characters and geometric variation in dentary shape. Vaux *et al.* (2018) conclude this section by saying, ‘Therefore, focusing on a single trait is unlikely to provide a reliable assessment of evolutionary change in general … or estimation of phenotypic stasis’. As readers of our paper will notice, we did not rely on a single trait. Our geometric morphometric analyses concerned dentary shape, and half the paper, which Vaux *et al.* (2018) ignore in their critique, analysed evolutionary rates in 74 skeletal characters that cover a broad range of cranial and postcranial anatomy.

We did not carry out landmark analysis on skulls or postcranial elements, and this would be an additional interesting study for someone to complete in the future. We had two reasons for focusing on the lower jaw for the landmark study: (1) such studies have been done frequently before by other authors on other vertebrate taxa (both fishes and tetrapods) and the studies have shown good morphometric discrimination between taxa; and (2) the mandible is most frequently preserved and so this maximizes the size of the data set; if we had added, say, skull, femur and humerus for landmark study, the data set of taxa would have been substantially reduced. As noted earlier, our first rates study used a data set of 74 characters that *did* include all aspects of skull and skeleton.

In two related comments, Vaux *et al.* (2018) critique our description of *Sphenodon*’s dentary as morphologically ‘average’ and conservative among fossil relatives. They suggest that we did not consider morphological variation expressed beyond principal components (PC) 1 and 2 (reflecting ~54% of overall shape variation). This is not true. In our analyses, we also calculated Procrustes distances, derived directly from the Procrustes aligned landmark data, to determine how close *Sphenodon* was to the average dentary shape for Rhynchocephalia. Procrustes distance (the sum of distances between corresponding landmarks from two shapes after superimposition) is the standard distance metric for shape (Zelditch *et al.* 2012) and is equivalent to utilizing information from all PC axes, not just the first two, or the first five, as suggested by Vaux *et al.* (2018). When we consider these Procrustes distances, *Sphenodon* is recovered as the seventh most similar form to the average shape, out of 31 sampled taxa. We therefore suggested that *Sphenodon* does not have a divergent morphology and could be considered morphologically 'average' or conservative. We also wish to clarify that the dentary of *Sphenodon* is ranked as fourth closest to the centroid of PC1 (the primary axis of variation), not fifth as reported by Vaux *et al.* (2018).

Then, Vaux *et al.* (2018) make two important points that apply to every morphometric study: they urge the need for wide sampling to represent a decent average for the species, and they urge the need for precision and repeatability. In fact, we make these two points ourselves in our Method section, and we describe our strategies. First, Vaux *et al.* (2018) correctly note that there is at best a single mandible specimen for most of the fossil taxa, and so that was all we had. Using single specimens to represent the morphology of extinct species, and in some cases genera, is a common convention in palaeobiological disparity studies (e.g. Brusatte *et al.* 2012; Bhullar *et al.* 2012; Foth *et al.* 2012; Stubbs *et al.* 2013; Grossnickle & Polly 2013; Foth & Joyce 2016). Their first criticism then can only refer to *Sphenodon* for which hundreds of specimens exist in museums. We can answer their first criticism from our Method section (Herrera-Flores *et al.* 2017, p. 321): '[we use our own] pictures from 14 museum specimens of the extant *Sphenodon* to assess variation within this single taxon, and to determine where it falls in comparison with Mesozoic taxa. We performed a separate geometric morphometric analysis of all samples of *Sphenodon* to identify the specimen that best represents the average shape of its dentary.' On the second point, we agree that precision is important, particularly in studies of variation within a single taxon like that presented by Vaux *et al.* (2018), where intraspecific variation will be the source of morphological variation. However, our study encompassed morphological variation across an entire order spanning millions of years. We argue that any minor intraspecific disparity, or variation incorporated by using published reconstructions and photographs of specimens in the literature will not introduce any large-scale bias. Care was taken when selecting what images to use, ensuring all specimens where appropriately orientated and not distorted. This is normal practice in studies such as these.

Vaux *et al.* (2018) go on to discuss the principles of fixed landmarks and semi-landmarks in geometric morphometrics, but we are not clear about their point. We are aware of the differences between fixed landmarks and semi-landmarks, and we have conducted many such studies before and followed standard protocol. It appears that Vaux *et al.* (2018) have misinterpreted our supplementary figure, and we did not fully explain the application of our semi-landmarks and curves. We used seven separate semi-landmarks curves defining the outer margin of the lateral view of the dentary. These curves, and the number of semi-landmark points defining them, were consistently applied across samples. Each of these curves was anchored by the positions of fixed landmarks. During the generalized Procrustes analysis, the semi-landmarks on the curves were allowed to iteratively slide, minimizing the Procrustes distances between each specimen and the average shape (Gunz & Mitteroecker 2013).

Finally, Vaux *et al.* (2018) claim that the phylomorphospace presented in Herrera-Flores *et al.* (2017, fig. 3C) is erroneous. This claim is unfounded. Vaux *et al.* (2018) argue that the branching pattern within the phylomorphospace is a phenogram from dentary shape data, stating that 'the phylogeny (more accurately a phenogram) was derived from the same dentary-shape-variation data used to estimate the principal components.' This is incorrect. The tree topology superimposed in Herrera-Flores *et al.* (2017, fig. 3C) is not a phenogram derived from dentary shape data. As clearly stated in the original paper, figure 3C is a phylomorphospace showing the branching pattern of a phylogenetic tree in dentary shape morphospace. As explicitly described in the Method, this tree was derived from a maximum parsimony analysis using a cladistic character dataset with 74 discrete characters from the whole skeleton. We then projected this topology into the dentary shape morphospace using conventional methods (R package `phytools`; Revell 2012). As before, all our methods are widely used by numerous authors, and we followed established protocols carefully.

CONCLUSION

In summary, we confirm that the following criticisms of Herrera-Flores *et al.* (2017) by Vaux *et al.* (2018) represent misunderstandings or errors by the latter: (1) claims that we tried to infer diet from dentary shape data; (2) that we did not consider morphological variation beyond PC1 and PC2; (3) that semi-landmarks were applied inappropriately; (4) that the phylogeny used in the phylomorphospace was a phenogram from dentary shape data. Comments about using individual specimens, either photographs or reconstructions, to represent taxa in studies of disparity in the fossil record are interesting. However, the practice we applied is common in vertebrate palaeontology and the issue is not specific to our study or detrimental to the results presented in Herrera-Flores *et al.* (2017). We agree with Vaux *et al.* (2018) that care is required when selecting images for geometric morphometric studies.

The tuatara geometric morphometric analyses presented by Vaux *et al.* (2018) offer interesting results about intraspecific variation in the modern and Holocene tuatara, but they present no criticisms nor results that refute the conclusions of Herrera-Flores *et al.* (2017).

Editor. Andrew Smith

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