The Evolution and Phylogeny of Early Amniotes

David P. Ford

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Department of Earth Sciences
and Jesus College,
University of Oxford

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Supervised by Prof. Roger B. J. Benson

Declaration

The contents of this thesis are all my own work, except where otherwise stated. The views and opinions expressed herein are mine and not necessarily those of any other person or body unless so attributed.

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David P. Ford

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Abstract

ABSTRACT

Amniotes are a monophyletic group that first arose around 320 million years ago and soon diverged into the two crown-group clades, Synapsida and Sauropsida.

One of the principle differences in morphology between these clades is in temporal fenestration, a feature fundamental to amniote classification for over a century. Recent work questions the emphasis on this feature in amniote systematics, and it is clear that patterns of temporal fenestration among early amniotes are more variable than is implicit in the current system of coding. I propose a series of new characters designed to replace the currently used characters. I conclude that my new coding can play a role in resolving the phylogeny of early amniotes.

I redescribe *Orovenator mayorum* from the lower Permian, using high-resolution μCT. I find similarities with varanopids, a group typically assigned to Synapsida. I include *Orovenator* in a phylogenetic analysis to differentiate between early diapsids and synapsids, and find a monophyletic clade of *Orovenator* + varanopids, raising questions about whether this clade belongs to Synapsida or Sauropsida.

I present the results of a new phylogenetic analysis of early amniotes using 286 discrete characters and 60 taxa, using both parsimony and Bayesian inference. My results suggest that varanopids and *Orovenator mayorum* form a monophyletic group positioned within Sauropsida, challenging the traditional view of varanopids as early synapsids.

I also find a sister group relationship between neodiapsids and parareptiles, with Captorhinidae positioned stem-ward to this group within Sauropsida. This topology conflicts with the conventional hypothesis of Eureptilia. Additional parsimony analyses were run with topological constraints, to compare tree lengths of alternative hypotheses and apply statistical tests.

My results have implications for hypotheses concerning the transition between 'pelycosaur'-grade synapsids of the early Permian and therapsid-grade synapsids of the middle Permian, and on patterns of evolution of temporal fenestration in early amniotes.

Extended Abstract

EXTENDED ABSTRACT

Amniotes comprise all mammals and reptiles, accounting for almost four fifths of all land vertebrate diversity. They share the ability to produce an amniotic egg, defined by a series of extraembryonic membranes, which serve to protect and nourish the embryo during development. Amniotes are a monophyletic group that first arose around 320 million years ago in the Carboniferous period, and soon diverged into the two crown-group clades, Synapsida, total-group mammals, and Sauropsida, total-group reptiles. The transition from a physiological reliance on wet conditions to a fully terrestrial ecology required changes in modes of respiration and locomotion, freeing early amniotes from the bauplan of non-amniote tetrapods, leading to morphological disparity that we can observe in the fossil record.

The early diverging groups of amniotes retained many plesiomorphic features, with few diagnostic anatomical differences between them. One of the principle differences in morphology was the number of openings or fenestrae that evolved in the temporal region of the skull; one in synapsids and two in diapsids, a group of derived sauropsids. Although this feature has been fundamental to amniote classification for over a century, recent work has begun to question the relevance of temporal fenestration, as it is currently coded for, in amniote systematics. It is now widely accepted that patterns of temporal fenestration are highly variable in early amniotes, and fenestrae have been lost, regained or highly modified in all lineages. Parareptiles, a group traditionally

considered as early diverging sauropsids in which temporal fenestrae were absent, are now recognised as possessing a wide-range of temporal openings, which may even be a synapomorphy of the group.

Much of the new data on parareptiles and other early amniotes has not yet been considered in the wider context of early amniote evolution. Recent phylogenetic research has focused on resolving intra-clade affiliations rather than the interrelationships of major taxonomic groups. The relative incompleteness of existing phylogenetic character lists for early amniotes can only be remedied by detailed cross-clade assessment. One of the aims of my thesis is to compile a new character-taxon matrix, specifically designed to perform a broad-based phylogenetic analysis of early amniotes.

In this thesis, I also explore the efficacy of temporal fenestration as a character in early amniote systematics. I will show that patterns of temporal fenestration among early amniotes are more variable than is implicit in the current system of coding, and that coding for the presence or absence of a 'lower' temporal opening fails basic tests of homology. I propose a series of new characters, which takes into account my observations of variation and similarity in temporal fenestration across a wide range of early amniotes. I include these new characters into my new character-taxon matrix, and compare the results against the same dataset with the traditional presence/absence coding. I conclude that my new coding, based on detailed observations of temporal morphology, can play a role in resolving the phylogeny of early amniotes.

One of the earliest known diapsids, *Orovenator mayorum* from the lower Permian of Oklahoma, is redescribed using high-resolution μCT, revealing remarkable details of the skull anatomy. My findings are relevant to both palaeoecology (suggesting burrowing and nocturnality) and phylogeny. My research on *Orovenator* reveals a number of anatomical similarities with varanopids, a group typically assigned to Synapsida. *Orovenator* and other sauropsids share at least 16 character states with varanopids, many of which were not recognised by previous studies. These include a rounded

subnarial shelf of the premaxilla, a posterodorsal extension of the external naris, the asymmetrical bifurcation of the anterior vomer, and a prominent dorsomedial shelf of the surangular. This exceptional degree of similarity between *Orovenator* and varanopids questions our current understanding of relationships among early amniotes. I test this by including *Orovenator* in a phylogenetic data matrix used in an earlier study to differentiate between early diapsids and synapsids, and find a monophyletic clade of *Orovenator* + varanopids, within Diapsida. I therefore propose that *Orovenator* forms a clade with varanopids; raising questions about whether this clade belongs to Synapsida or Sauropsida.

Finally, I present the results of phylogenetic analyses of my new character-taxon matrix of early amniotes, which is one of the largest and most comprehensive to date. My character list of 286 discrete characters was assembled by undertaking a comprehensive review of key phylogenetic studies on stem- and early crown-group amniotes, and was augmented by new characters based on my examination of *Orovenator mayorum*. Since my objective was not to resolve the in-group relationships of early amniote subclades, but to resolve the relationships among higher taxonomic groups, my taxon sample of 60 taxa was focused on the basal chronologically early members of each clade. Phylogenetic analysis was performed using both maximum parsimony and Bayesian inference. Both methods were used in order to present a fully comprehensive series of results.

My results confirm my initial hypothesis that varanopids and *Orovenator mayorum* form a monophyletic group. I also find this group to be positioned within Sauropsida, challenging the traditional view of varanopids as 'pelycosaur'-grade early synapsids, which was established over 75 years ago. I also find a sister group relationship between neodiapsids and parareptiles, with Captorhinidae positioned stem-ward to this group within the total-group reptiles (Sauropsida). This topology conflicts with the conventional hypothesis of captorhinids as the sister taxon to diapsids within Eurep-

tilia. I also find an unexpected degree of uncertainty over the affinities of caseasaurs as synapsids, stem-amniotes or stem-reptiles. A series of additional parsimony analyses were run, which included topological constraints, to compare tree lengths of alternative phylogenetic hypotheses. Pairwise Templeton tests were used to statistically compare the topologically-constrained analyses to the most parsimonious trees.

My results have implications for hypotheses concerning the transition between 'pelycosaur'-grade synapsids of the early Permian and therapsid-grade synapsids of the middle Permian, and on patterns of evolution of temporal fenestration in early amniotes.

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The past eight years have been a long and sometimes overwhelming journey for me. At times stressful and frustrating, at others joyful and up-lifting. Higher education as a full-time endeavour for anyone of a certain age is not for the faint-hearted, but if approached with enthusiasm, discipline and, above all, a strong determination to succeed, it can become, and indeed has proven to be, the most rewarding and enthralling period of my life. Any undertaking of this nature is never a solo effort. There have been many people who have shared this journey with me. None, apart from one, have been with me all the way, but each has had a part to play, some more than others, and now, as I write the last few paragraphs of my final efforts as a student, I take a few moments to say thank you.

When I finally hung up my 'business' boots in 2009, I had a vague idea of applying to UCL to read for a M.Sci in Palaeobiology. I realised quite quickly that A-levels in French and English (1977 vintage) weren't going to cut it as entry level qualifications, and I needed an academic reference. David Norman, whom I'd known since the mid-1990's during my occasional forays into palaeontology as a layman, kindly offered to supply the reference (it turned out that David was to be my doctoral 'grandfather'). If I recall, it ended something like;"although I can't vouch for David's academic capabilities, if hard work and enthusiasm are anything to go by, he should do well". I also had some marvellously supportive tutors at UCL, who took a chance on me. Thank

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I'd given some thought about applying to Oxford. In December, 2013, I met Roger Benson. My wife, Jan, and I had a couple of beers with him in the Eagle and Child. We talked about some research ideas I had on Permian diapsids, and he passed Jan's 'first impressions' test, always a good sign. This still left me with the task of getting into the Oxford NERC-DTP studentship, which somehow I managed to do. So for the past four years Roger has been my supervisor, and I don't honestly think I could have had a better one. I know he takes his responsibility to his students very seriously, and is truly outstanding in responding to manuscript drafts. But beyond this, Roger allowed me the freedom to express my own ideas and concepts. When I needed him, he was always there to give advice. When I didn't, my work and my time were my responsibility. He has taught me how to write objectively about my research, how to plan the narrative of a paper, how not to use insane words like 'runs' and 'approaches' and 'lateromedial' in descriptive anatomy. He taught me to be a better researcher than I ever thought I could be. I was proud to have him as co-author on my first paper. Thank you Roger, for all of your help and guidance.

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Earlier I mentioned that only one person had been with me since the beginning of my journey. Not just my academic journey, but my journey through life. This year my wife, Jan, and I will celebrate our 35th wedding anniversary. During the past eight years her support and love, patience and understanding have been the bedrock of all my efforts. At times I have been selfish, irritating, annoying, depressed, sick and hospitalised, yet Jan has always been there for me, to make sure I recover and keep on track. To you, my dearest Burnie, this whole work is dedicated.

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Institutional Abbreviations

INSTITUTIONAL ABBREVIATIONS

AM, Albany Museum, Grahamstown, South Africa; BMRP, Burpee Museum of Natural History, Rockford, Illinois; BP, Evolutionary Studies Institute, University of Witwatersrand, Johannesburg, South Africa; FMNH, Field Museum of Natural History, Chicago, USA; KUVP, University of Kansas Natural History Museum, Lawrence, USA; MCSNM Museo Civico di Storia Naturale, Milan, Italy; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; NHMUK, Natural History Museum, London, UK; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, USA; ROM, Royal Ontario Museum, Toronto; YPM, Yale Peabody Museum of Natural History, New Haven, USA.

Chapter 1

An Introduction to Early Amniotes

The history of life on Earth has been punctuated by major macroevolutionary transitions. These have included the origin of oxygenic photosynthesis, the prokaryotic/eukaryotic division, the Cambrian 'explosion' of animal phyla and the invasion of land by plants, invertebrates and vertebrates. Amniotes were the only group of vertebrates to make a complete transition to land, freed from their dependence on wet and humid environments via a series of evolutionary innovations related to gas exchange, reproduction, and various other functions that supported a fully-terrestrial life history (Ritter 1995, Sumida 1997, Reisz 1997, Janis and Keller 2001).

Amniotes are defined by the presence of characteristic extraembryonic membranes that allow development of embryos in air on land. The systematic definition of crown-group Amniota, which has remained basically unchanged since first erected by Haeckel (1866), is the most recent common ancestor of synapsids, the crown-group mammals, and sauropsids, the crown-group reptiles (which includes all lizards, snakes, turtles, crocodiles and birds). Amniotes first appear in the fossil record in the late Bashkirian of the Carboniferous, around 318 million years ago (Ma), (Carroll 1964, Benton *et al.* 2015), and probably diverged into the two crown-group clades quite early in their history.

Throughout this thesis, I use the term 'early amniotes' to refer to those groups within the amniote crown-group that had appeared by the late Carboniferous, and were to dominate terrestrial faunas for most of the Permian; 'pelycosaur'- grade synapsids, captorhinids, 'protorothyridids', parareptiles, and early diapsids outside of their crown-group (Sauria).

During the last few decades, relatively few researchers have proposed large-scale systematic hypotheses on early amniotes (Romer and Price 1940, Benton 1985, Gauthier

et al. 1988a and 1988b, Laurin and Reisz 1995, deBraga and Rieppel 1997), although the origins of mammals and reptiles can only be truly understood when placed in the context of early amniote evolution.

In this thesis, I focus on the initial stages of amniote evolution. I present a detailed examination of the cranial anatomy of an early sauropsid, and discuss the implications of this study for amniote interrelationships. I review the morphology of temporal fenestration in early amniotes, one of the fundamental characters of amniote systematics, and propose a new approach to its characterisation in phylogenetic analyses. Finally, I present a new phylogeny of early amniotes, and propose a series of evolutionary hypotheses based on the results.

In this chapter, I will consider the basic questions that underpin this thesis. What are amniotes? What are the morphological traits that distinguish them from non-amniotes? Who are their closest relatives? I will then provide a brief history of the research and various hypotheses that have lead to our current understanding of early amniote phylogeny. Finally, I will summarise the aims of my thesis in respect to the subsequent research chapters.

1.1 What are Amniotes?

Any extant animal whose embryo develops within a suite of extraembryonic membranes, the amnion, chorion and allantois, is an amniote (Parker and Haswell 1940). This applies to both *in utero* development in viviparous species such as therian mammals and many squamates, and to *in ovo* development in oviparous species, including monotreme mammals and most reptiles (Pyron and Burbrink 2014).

In an amniote egg, the embryo is enclosed in a fluid-filled amnion, while nutrients and proteins are stored in the albumen and yolk sac. Oxygen diffuses through the porous eggshell and is absorbed into the blood vessels lining the chorioallantoic membrane, and CO_2 is like-wise expelled. Nitrogenous waste is stored in the allantois. The evolution of chorioallantoic gas exchange was one factor that enabled both reproduction on land and an eventual increase in egg size (Szarski 1968), whilst other studies suggest that a fibrous shell membrane, similar to those of extant oviparous reptiles, was equally important to the evolution of the amniote egg (Packard and Seymour 1997). Whilst we can infer that the characteristic membranes were present in all extinct members of the amniote crown-group, it is difficult to determine where they appeared on the stem-lineage.

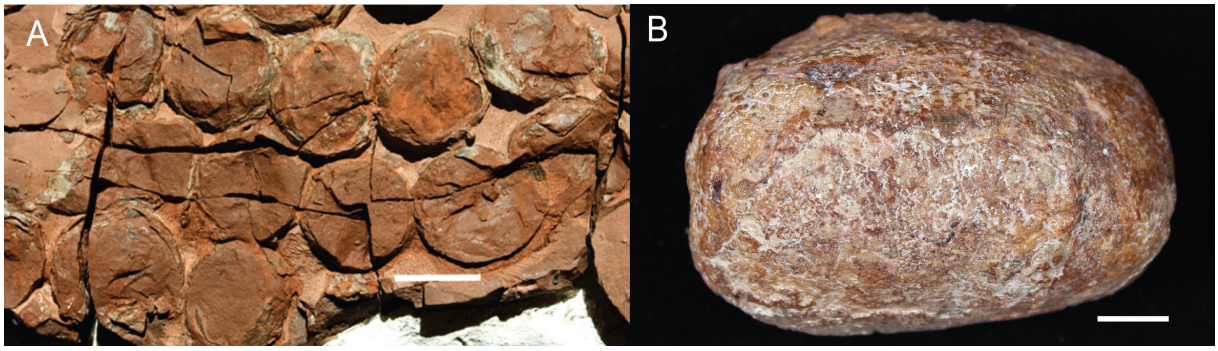


Figure 1: A, fossilised eggs from the Upper Elliot Formation of South Africa (from Reisz *et al.* 2012). Scale bar=5cm. B, putative fossilised egg from Permo-Carboniferous of Texas (Romer and Price 1939). Scale bar=1cm. (Photo by author).

Although evidence for amniotic eggs are not altogether absent from the fossil record, they are not known with any degree of certainty during the earliest history of amniotes. Currently, the earliest fossil amniote nesting sites are from the Upper Elliot Formation of South Africa (Fig.1A). They contain embryos of the sauropodomorph dinosaur *Massospondylus* (Reisz *et al.* 2012). The Upper Elliot Formation is Lower Jurassic (Hettangian - Sinemurian) in age (McPhee *et al.* 2017). The earliest evidence of mineralised egg shell is associated with neonate specimens of the basal sauropodomorph *Mussaurus patagonicus* from the Upper Triassic of Argentina (Bonaparte and Vince 1979), giving an earliest possible date of these fossils of 208.5 Ma, around 110 million years after the appearance of the earliest crown-group amniote. Romer and Price (1939) described a specimen from the Permo-Carboniferous redbeds of Texas (around 299 Ma), which they considered was the oldest vertebrate egg (Fig.1B). Hirsch (1979) questioned this interpretation, concluding that the outer layer (hypothesised as an eggshell by Romer and Price, 1939) was not calcareous, although the high phosphorus content in the outer layers suggested an organic origin, perhaps representing a 'soft, parchment-like organic shell layer' (Hirsch 1979:1083). Even if Carboniferous eggs were known, identifying them to particular species or even groups might not be possible, and therefore the main tool available to palaeontologists for identifying early members of the amniote crown-group is phylogenetic analysis of skeletal character states.

1.2 Amniote characteristics

The transition to a fully terrestrial life-style has led to the acquisition of several skeletal traits, which we can use to identify fossil amniotes. Many of these traits are correlated with changes in locomotion and feeding mechanics, such as the evolution of the as-

tragalus and the distinctive transverse flange of the pterygoid. Others are linked to the loss of anamniote features, such as palatal fangs or the sensory grooves of the lateral line of the skull, which are present in osteolepiform fishes and temnospondyl anamniotes (Klembara 1996). Although reproductive traits provide a definition of amniotes, reproduction might be less important than various other biological functions in allowing amniotes to be truly terrestrial animals. Reproduction is a periodic and infrequent activity, whereas functions like feeding, breathing and locomotion are constant requirements and all have their own challenges on land compared to in water.

1.2.1 Gas exchange

Janis and Keller (2001) proposed a series of morphological correlates that imply changes to modes of ventilation, gas exchange and feeding behaviour in stem-amniotes compared to other early tetrapods. Extant amphibians that possess lungs use buccal pumping to acquire most of their O_2 and rely principally on the cutaneous loss of CO_2. Buccal pumping is a method of aspiration where air in the buccal cavity is pumped under positive pressure into the lung or gas bladder. In extant amphibians this is usually achieved by elevating the floor of the mouth and tongue, whilst closing the nostrils and glottis (Brainerd and Owerkowicz 2006).

Consequently, in order to maximise the volume in the buccal cavity, non-amniote tetrapod heads, in general, are transversely broad and dorsoventrally narrow (Fig 2D,E,F). The physical requirements of efficient buccal pumping constrain the head morphology to this general shape. This can be observed in many early tetrapods, including temnospondyls (members of the lissamphibian stem-group), and is likely to represent the primitive condition for tetrapods.

Buccal pumpers also have few cervical vertebrae. Extant amphibians lack a distinct trachea, and instead possess a short, broad larygeotracheal chamber (Janis and Keller 2001), since increasing the distance and narrowing the pathway between the buccal cavity and the lungs would reduce the efficiency of buccal pumping. Most amniotes have long necks, with five or more cervical vertebrae that accommodate a trachea. The atlas/axis complex in amniotes is consequently strengthened, with the atlas pleurocentrum and axial intercentrum sutured or fused (Lee and Spenser 1997).

Most living amphibians, and most likely also early tetrapods, rely on cutaneous gas exchange. Only a minority of their O_2 requirement is gained this way, but most of their CO_2 loss is via the skin (Janis and Keller 2001). CO_2 is much more soluble in water than in air, and extant amphibians need to maintain a moist skin surface to maximise CO_2 loss, as much as to counter the effects of water loss.

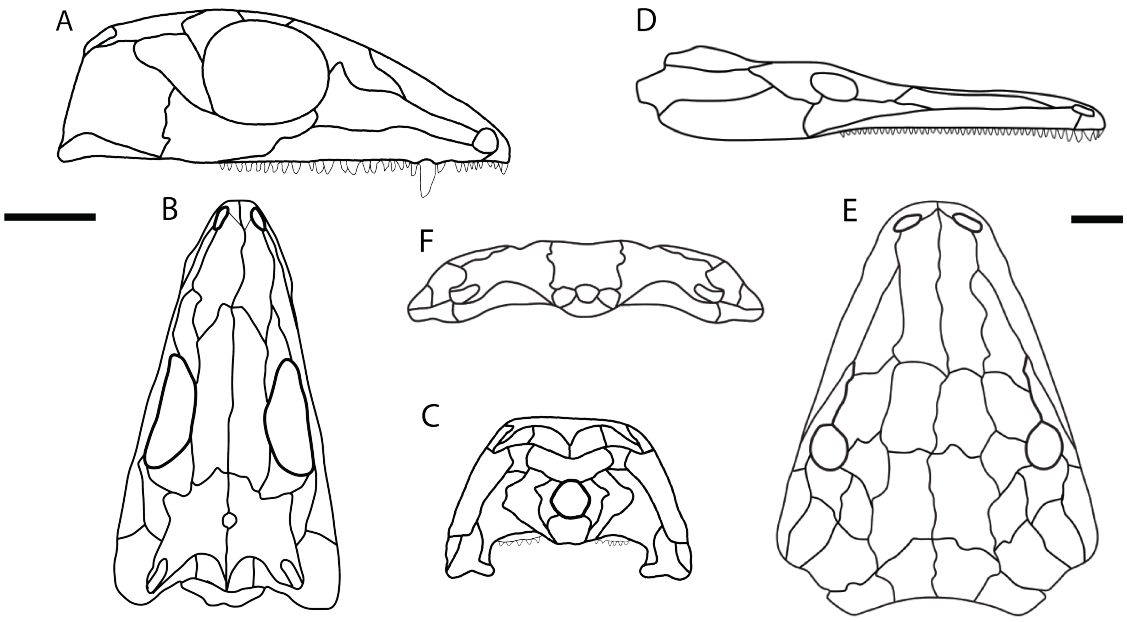


Figure 2: Permian amniote and temnospondyl skulls in lateral (A, D), dorsal (B, E) and posterior (C, F) view. A, B and C, the early amniote *Protorothyris archeri* (from Clark and Carroll 1973). Scale bar =1cm. D, E and F, the temnospondyl *Saharastega moradiensis* (from Damiani *et al.* 2006). Scale bar=5cm

In air, O_2 is much more abundant than water, and CO_2 much less soluble. Amniotes expel very little CO_2 cutaneously, and their skin does not need to be highly permeable. Indeed, extant amniotes have keratinised and relatively impermeable skins, reducing water loss. In order for amniotes to expel sufficient amounts of CO_2, ventilation rates via exhalation need to be a lot higher to avoid the effects of respiratory acidosis (Janis and Keller 2001). Amniotes achieve this by costal respiration, where the ribs possess a degree of mobility at the junction with the vertebral column, and muscles acting on the ribs create differential pressure in the thoracic cavity, drawing air into the lungs. Amniotes have evolved long, curved ribs, with mobile proximal articulation. Costal lung ventilation in amniotes freed the head from the morphological constraints of buccal pumping, allowing smaller, deeper, and narrower skulls, and longer necks (Fig. 2A,B,C).

1.2.2 Jaw musculature and feeding mechanics

The shift from buccal pumping to costal ventilation also freed the amniote head, and the tongue, to adapt to different feeding styles (Brainerd and Owerkowicz 2006). Changes to skull morphology allowed reconfiguration of the jaw musculature, and this led to a diversification of feeding modes. In many anamniotes, the skull tends to be flat with

dorsally positioned orbits (Fig.2). If major jaw-closing muscles had originated on the dermal skull roof immediately above the point of insertion on the mandible, they would have been too short to act effectively on jaw mechanics (Frazetta 1968). Therefore, for example in temnospondyl skulls, the jaw musculature originates on the skull roof anterior and medial to the area of insertion on the mandible, such that in a closed position they ran almost horizontally between the skull roof and mandible (Frazetta 1968). Olson (1961) suggested that this tangential attachment was important in raising and closing the jaws, but less effective when the jaws approached occlusion, since the muscle fibres were unable to shorten further.

In stem- and early crown-group amniotes the skulls became more vertically developed and the orbits placed laterally. This increase in height allowed placement of the jaw musculature directly above the insertion areas on the mandible, producing a strong jaw-closing mechanism (Frazetta 1968). Olson (1961) suggested these two types of muscle arrangement were essential to a diversification of feeding mechanics in tetrapods. The kinetic inertial system, where the adductor muscles are almost horizontal on jaw closure, is expressed by a rapid closing of the lower and upper jaw. The jaws, once closed, exert no further force, and this mechanism involves only vertical movement. This system is found in early tetrapods, e.g. the temnospondyl *Eryops*, mainly involving the posterior adductor muscles (Olson 1961).

The second system, the static pressure system (Olson 1961), exerts pressure once the jaws have closed, and can have vertical, lateral and possibly propalinial movement. Carroll (1969b) noted the distinctive amniote feature of a broad pterygoid flange of the palate, often posteroventrally inclined, for the origin of the pterygoideus muscle, suggesting this flange was indicative of a differentiation of the adductor musculature and the static system. The pterygoideus muscle increased the manipulative ability of the jaw, and improved the processing of capture prey or plant material (Iordansky 2010). It is absent in all extant fish, frogs and salamanders (Iordansky 2010).

Janis and Keller (2001) suggested that the evolution of static pressure was key to the mechanical processing of plant material, and therefore the development of herbivory in tetrapods. Herbivory is observed to have been present only in amniotes and crownward stem-group amniotes, e.g. diadectomorphs (Hotton *et al.* 1997, Sues and Reisz 1998, Modesto *et al.* 2014, Liu and Bever 2015).

The kinetic inertial system of rapid jaw closure served mainly to entrap prey without applying static pressure. Many anamniotes and some stem-amniotes (e.g. *Seymouria*, Klembara *et al.* 2005b; temnospondyls, Milner and Sequeira 2011) have large and often recurved teeth on the vomers, palatine and pterygoid (palatal fangs), which

were used to stab and retain prey in the absence of static pressure. This feature is absent in amniotes. The marginal dentition of temnospondyls, gephyrostegids and seymouriamorphs retain infolded labyrinthine enamel to strengthen the teeth against the rapid closure of the jaws, suggestive of inertial jaw mechanics (Janis and Keller 2001), and is a feature also lost in crown-group amniotes and diadectomorphs (Laurin and Reisz 1997). Some sphenacodontian synapsids are known to have infolded dentine (plicidentine) at the base of some teeth, but this is believed to be associated with the increase of attachment area for teeth with shallow roots (Brink *et al.* 2014).

1.2.3 Locomotion

The terrestrialisation of stem- and crown-group amniotes led to changes in the structure of the limbs and podials, as well as the strengthening of posture. The evolution of the proximal tarsus (astragalus and calcaneum) is a good example of this. The origin of the astragalus was considered an important diagnostic feature of amniotes in early cladistic studies (Gauthier *et al.* 1988, Laurin and Reisz 1995). Rieppel (1993) suggested the astragalus was a neomorph, resulting from developmental re-patterning, and could not be considered as homologous with the various elements of the anamniote tarsus. This was based on the observation that the ossification of the astragalus in extant reptiles does not involve the fusion of multiple ossification centres (Fabrezi *et al.* 2007). However, more recent studies on captorhinids (O'Keefe *et al.* 2006), the early 'protorothyridid' *Hylonomus* (Meyer and Anderson 2013) and the basal parareptile *Mesosaurus* (Piñeiro *et al.* 2016) have conclusively shown that, in sauropsids at least, the astragalus was formed by the fusion of the intermedium, tibiale, and two centrali (C3 and C4) from the primitive anamniote tarsus (the four-centre hypothesis of O'Keefe *et al.* 2006).

Interestingly, partial fusion of some of these elements is present in stem-amniotes (*Proterogyrinus*, Holmes 1984; *Gephyrostegus*, Carroll 1970) and the microsaur *Tuditanus* (Carroll and Baird 1968). O'Keefe *et al.* (2006) further suggested that the single ossification of the astragalus found in extant reptiles probably arose in the diapsid lineage. The presence of a single ossification of astragalus in the late Permian diapsid *Hovasaurus* (Currie 1981, Carroll 1997) indicates that this probably occurred earlier than the emergence of crown-group reptiles.

Another important aspect of terrestrial adaptation was the postural control of the trunk during locomotion. The epaxial musculature of vertebrates lies dorsal to the vertebral column. In extant amphibians the epaxial muscles are undifferentiated, providing a unilateral and single-phased action for the lateral bending of the trunk (Ritter

1995). This lateral flexibility is necessary for swimming in the larval stage of extant amphibians. Conversely, birds and mammals have a bilateral, two-phased activation pattern of the epaxial muscles, resulting in synchronous postural support of the limbs (Ritter 1995). The 'exaptation' of the epaxial musculature from locomotory to postural control may be related to the functional role of the rib cage. Janis and Keller (2001) suggested that only with the loss of the larval stage, and the differentiation of the epaxial muscles, could the ribcage be freed from its usual task of trunk posture in adult anamniotes and used in costal ventilation (Janis and Keller 2001)

Sumida (1997) reviewed fossils across a spectrum of anamniotes and early amniotes, focusing on the axial and appendicular skeleton. This study was based on the premise that the increasingly terrestrial adaptation of stem-amniotes required functional changes to locomotor features. He noted a number of skeletal change to the limbs of stem- and early crown-group amniotes, including a well-developed internal trochanter of the proximal femur, fusing of the atlantal and axial vertebrae to support the neck and head, a larger olecranon process of the ulna and an increase in tibial length compared to the femur.

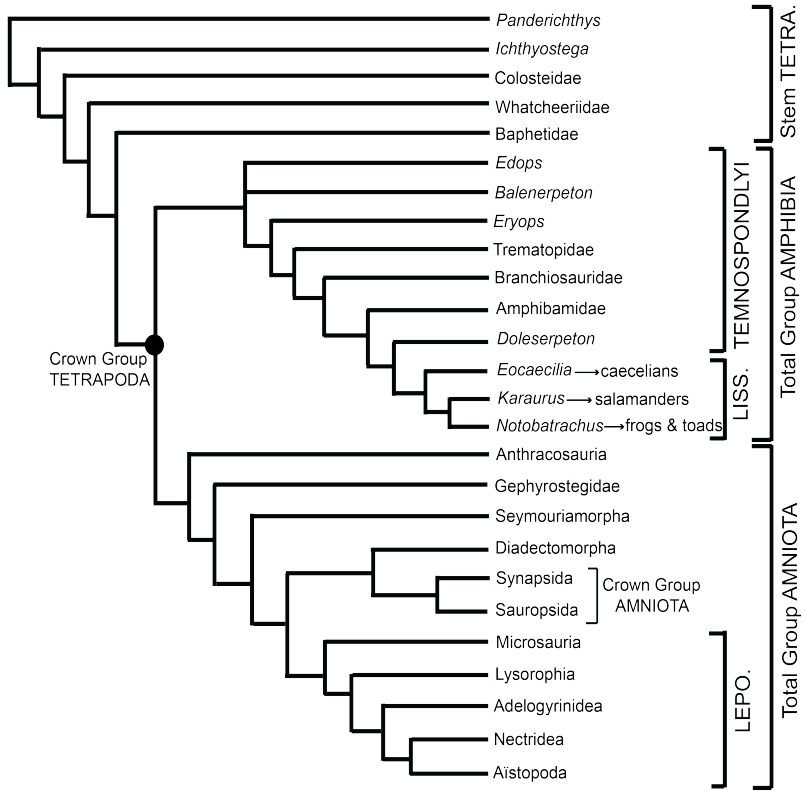


Figure 3: Early tetrapod phylogeny according to the temnospondyl hypothesis of lissamphibians origins. Modified from Ruta and Coates (2007). *Abbreviations*: LEPO=Lepospondyli; LISS=Lissamphibia; TETRA=Tetrapoda.

1.3 Amniote interrelationships with other tetrapods

1.3.1 Diadectomorpha

Diadectomorphs are considered by most studies to be the monophyletic sister taxon to crown-amniotes (Gauthier *et al.* 1988, Benton 1991, Laurin and Reisz 1995, Ruta *et al.* 2003, Pyron 2011). This group consists of *Limnoscelis*, *Tseajaia* and several diadectids, and ranges from the Upper Pennsylvanian to the late Permian (Liu and Bever 2015). Diadectomorphs share a number of common features with crown-group amniotes, including the loss of the lateral line of the skull, reduction or absence of the temporal notch, the tabular and postparietal restricted to the occiput, the presence of a well-developed transverse flange of the pterygoid with a row of large teeth on the posterior rim and at least two pairs of sacral ribs (Lee and Spenser 1997).

Based on several similarities of the temporal and occipital region, Berman *et al.* (1992) and Berman (2000) suggested that diadectomorphs were the sister group of 'pelycosaur'-grade synapsids, within the crown-group Amniota. This hypothesis was disputed by Kissel and Reisz (2004) and Reisz (2007), on the basis that the three characters suggested by Berman *et al.* (1992) as uniting synapsids and diadectomorphs were 'problematic'. Nevertheless, further analysis by Berman (2013) continues to recover diadectids as sister taxon to synapsids.

1.3.2 Lepospondyli

The sister taxon to Diadectomorpha + Amniota is the Lepospondyli (Fig.3), a monophyletic clade of small-bodied anamniotes comprised of five groups (nectridians, adelogyrinids, aïstopods, lysorophians and microsaurs), from the Carboniferous and early Permian (Anderson 2007). Their sister group relationship with diadectomorphs and amniotes is well established in phylogenetic studies of early tetrapods (Laurin 1996, Laurin and Reisz 1997, Ruta *et al.* 2003, Vallin and Laurin 2004, Ruta and Coates 2007, Pyron 2011). Lepospondyls are relevant to on-going debates about the origins of living amphibians, the Lissamphibia (frogs, salamanders and caecilians),

If Lissamphibians, or caecilians alone, are nested within lepospondyls, as proposed by several studies (Laurin and Reisz 1997, Vallin and Laurin 2004, Anderson *et al.* 2008, Pyron 2011), then lepospondyls are not included in the amniote stem-lineage. The other hypothesis, in which lissamphibians are nested within temnospondyls (Ruta *et al.* 2003, Ruta and Coates 2007), results in a more inclusive stem-lineage for amniotes, including seymouriamorphs, *Gephyrostegus* and anthracosaurs (Fig.3).

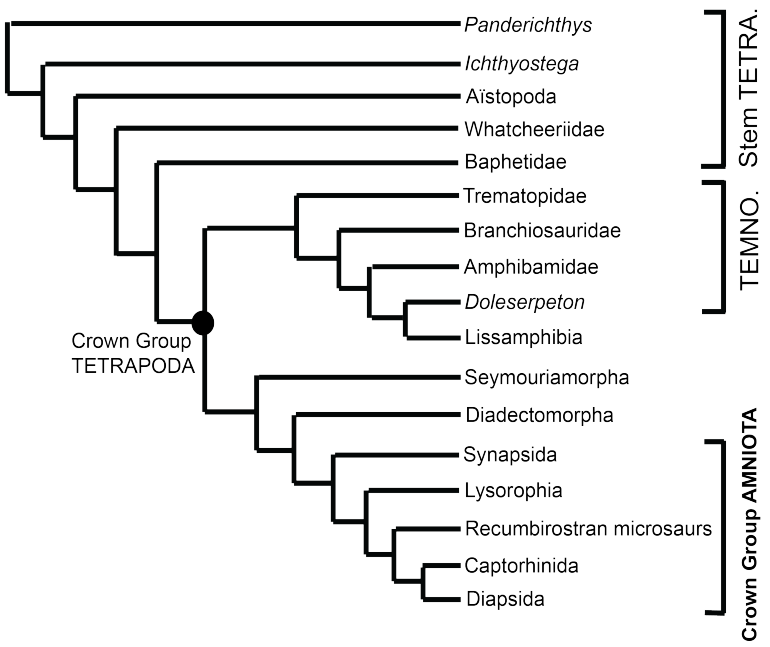


Figure 4: Early tetrapod phylogeny based on the polyphyly of lepospondyls (aïstopods, lysorophians and recumbirostran microsaurs). Modified from Pardo *et al.* (2018). *Abbreviations*: TEMNO= Temnospondyli; TETRA= Tetrapoda.

Recently, Pardo *et al.* (2017) proposed a new hypothesis on lepospondyl interrelationships, where recumbirostran microsaurs and lysorophians, formally two subgroups of lepospondyls, are recovered within the crown-group Amniota, as sister to captorhinids and diapsids, and aïstopoda in a much more basal position, effectively making lepospondyls a polyphyletic group (Fig.4).

1.3.3 Seymouriamorpha and *Gephyrostegus*

Seymouria, from the early Permian of south-western North America and Germany, is often used as an outgroup in phylogenetic analyses of early amniotes (Laurin and Reisz 1995, deBraga and Rieppel 1997, Laurin and Piñeiro 2017, MacDougall *et al.* 2018). A few features of this taxon are shared with amniotes, such as the suture between the neural arch and centrum and reduced intercentra (Clack 2012), but the skull displays primitive anamniote traits, like the deeply embayed otic notch and palatal fangs (Klembara *et al.* 2005a). Fossils of larval and metamorphic individuals of *Discosauriscus*, a seymouriamorph from the early Permian, confirm the amphibian-like life history of this group (Klembara 1997). *Gephyrostegus*, from the late Carboniferous of the Czech Republic, has been recovered a sister taxon to seymouriamorphs in several analyses, often nested between the most basal stem-amniote, anthracosaurs, and seymouriamorphs

(Clack and Finney 2005, Ruta and Coates 2007, Klembara *et al.* 2014).

1.4 A brief history of early amniote systematics

What we now consider to be the earliest known amniote, *Hylonomus lyelli*, was also the first of the early amniotes to be named (Dawson 1860). Dawson recognised three new species of *Hylonomus* (*H. lyelli*, *H. aciedentatus* and *H. wymani*), only one of which, *H. lyelli*, remains valid. Initially, Dawson considered *Hylonomus* as reptilian, closer to lizards in morphology than to amphibians. However, Cope (1868) assigned the taxon to the non-amniote group, Microsauria Dawson, 1863 and in later work Dawson agreed with this assignment (Dawson 1882). A revision of the Microsauria by Romer (1950) suggested Dawson may have been right in his first assessment, and this was later confirmed by Carroll (1964). This process of re-assignment was typical of early amniote systematics for much of the following century.

During the late 19th and early 20th century, new fossil evidence was readily assimilated into a growing mosaic of vertebrate interrelationships that ranged from Carboniferous amphibians to extant reptiles and mammals. Palaeontologists regularly raised new orders, sub-orders and families to account for the increasingly diverse hypotheses and morphologies of the newly discovered taxa.

1.4.1 North America and South Africa, late 19th to early 20th century

The discoveries of early amniotes in the late 19th and early 20th century were mostly restricted to specific groups, 'pelycosaurs' from the Permo-carboniferous strata of southwest North America (*Ophiacodon*, *Dimetrodon*, *Edaphosaurus*, *Clepsydrops*, *Sphenacodon* and *Haptodus*) and parareptiles from the Permian of South Africa and Brazil (*Mesosaurus*, *Stereosternum*, *Pareiasaurus*, *Procolophon*, *Eunotosaurus*), as well as some isolated taxa from North America (*Bolosaurus* and *Captorhinus*). Not surprisingly, many of these new taxa were considered to be closely related. Cope named Pelycosauria Cope, 1878, as a suborder of Rhynchocephalia Gunther, 1867, to include the families Clepsydropidae Cope, 1878 (*Clepsydrops*, *Dimetrodon*) and Bolosauridae Cope, 1878 (*Bolosaurus*, *Diadectes*). Two years later, Cope (1880) replaced Rhynchocephalia with the order Theromorpha Cope, 1878, to include the two suborders Pelycosauria (which included Theriodontia Owen, 1876) and Anomodontia Owen, 1876. Both Theromorpha and Anomodontia are today recognised as therapsids.

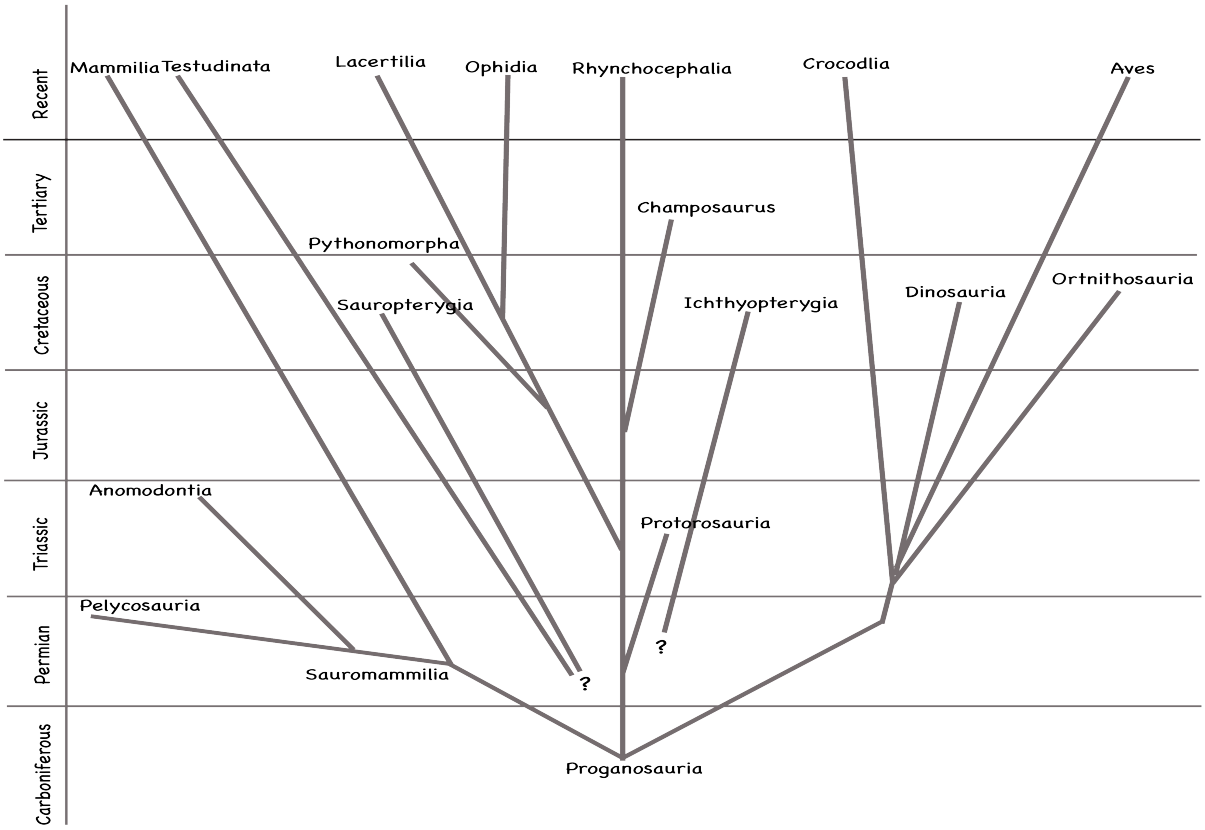


Figure 5: A time-calibrated sketch of amniote interrelationships. Modified from Baur (1887)

Baur (1887) disagreed with Cope's hypothesis that Theromorpha were the ancestors of all reptiles (including Pelycosauria, and therefore all mammals). Baur thought that Theromorpha were much too specialized to be the *de facto* ancestor of mammals, and possibly even reptiles, suggesting that a common ancestor of both Theromorpha and Rhynchocephalia existed in the Carboniferous. For this new basal group, he named the new order Proganosauria Baur, 1887, to include the newly described taxon, *Stereosternum* (a mesosaur). In the same paper, Baur also produced one of the first attempts at a structured, time-calibrated amniote phylogeny (Fig.5).

Cope named a new division of Pelycosauria, the suborder Cotylosauria Cope 1880, with only one family, the Diadectidae Cope, 1880. Later, he revised Cotylosauria to include the families Pareiasauria Seeley, 1888, Pariotichidae Cope, 1883 (captorhinids) and Diadectidae. Throughout the 1890's a succession of papers from Seeley (1892, 1895a, 1895b), Zittel (1895), Haeckel (1895), and Baur and Case (1897) juggled with the relative taxonomic positions of Pelycosauria, Theriodontia, Pareiasauridae Lydekker 1889, Procolophonia Seeley, 1888 and Rhynchocephalia, often switching from ordinal to subordinal level and vice versa.

Eventually, a new systematic classification was proposed by Osborn (1903), for the division of reptiles into two sub-classes, Synapsida Osborn, 1903 and Diapsida Osborn, 1903, based on the number of arches in the temporal region of the skull (Fig.6). This hypothesis, as Osborn noted, was based on several previous studies, and was similar to the approach of Broom (1901). Osborn included the orders Cotylosauria and Anomodontia in Synapsida, whilst in the Diapsida he placed Rhynchocephalia, Proganosauria, Pelycosauria, Procolophonia and Protorosauria Huxley, 1871 (an archosauromorph group).

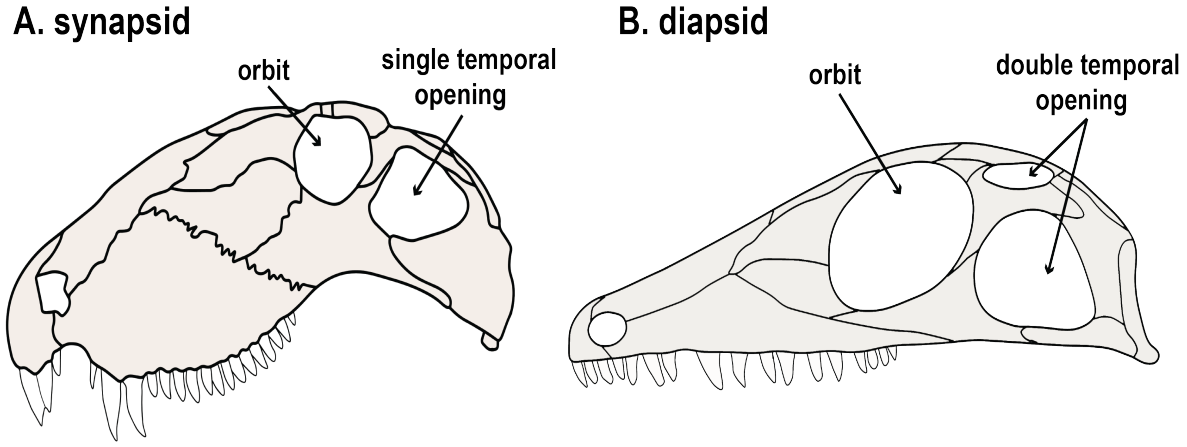


Figure 6: Skulls showing temporal openings in left lateral view. A, the synapsid 'pelycosaur' *Dimetrodon*; B, the diapsid *Youngina*

The first systematic revision of Pelycosauria was published by Case (1907), maintaining its subordinal position within Rhynchocephalia, and describing pelycosaurs as 'primitive Diapsidan reptiles', which included the families Poliosauridea Case 1907 (ophiacodontids), Clepsydropidae Cope, 1878 (sphenacodontids), Naosaurinae Case, 1907 and Edaphosauridae Cope, 1882 (both containing taxa now considered to be edaphosaurids).

Williston (1908), reviewing Cotylosauria Cope 1878, noted that 'the name Cotylosauria must accompany the Diadectidae wherever the family is placed', based on rules of nomenclature (Williston 1908:140). Two years later, Williston (1911) proposed a systematic revision of North American Permian vertebrates, and abandoned Pelycosauria Cope, 1878 in favour of Theromorpha Cope 1878, which included sphenacodontids, ophiacodontids and caseids (based on his recent description of *Casea broilii*). He expanded Cotylosauria to include diadectids, limnoscelids, seymouriamorphs and captorhinids. In the same year, Case (1911) published his revision of Cotylosauria, which included the suborders Diadectosauria Case, 1911, to include the genus *Bolosaurus*, Pareiasauria Lydekker 1889, to include the families Captorhinidae Case 1911 and Sey-

mouridae Williston, 1911, and Procolophonia Seeley 1888.

Williston (1910) described *Araeoscelis* from the lower Permian of Texas, noting its similarities with squamates, but mostly its affinities with *Kalidiosaurus* from Germany (Credner 1889), with which he eventually established the family Kalidiosauridae Williston, 1912. Later Vaughn (1955) revised this to the infraorder Araeoscelidia Williston, 1913, and placed it within the order Cotylosauria, fast becoming a catch-all for non-pelycosaurian taxa. Williston (1915) also described *Mycterosaurus* from the early Permian of Texas, recognising its similarity with *Dimetrodon*, and provisionally placing it in the Poliosauridae (ophiacodontids), along side another taxon, *Varanops*, in the sub-order Pelycosauria, which he had abandoned just a few years earlier. Williston's organisation of the Pelycosauria was now taking a more familiar shape; Sphenacodontidae Marsh 1878, to include *Clepsydrops*, *Sphenacodon* and *Dimetrodon*, Ophiacodontidae Nopsca, 1923 to include *Ophiacodon*, Poliosauridae Case, 1907 to include *Varanosaurus*, *Varanops*, *Mycterosaurus*, Edaphosauridae Cope 1882 to include *Edaphosaurus* and Caseidae Williston,1911 to include *Casea*.

Goodrich (1916) attempted to summarise the work of Cope and Baur (1887), in light of Osborn's reclassification (Osborn 1903). He placed a group he named Protosauria Goodrich, 1916, as a central group at the base a two-way split between the single fenestrated mammal line, which he named Theropsida Goodrich, 1916, and the double fenestrated reptile line leading to birds, the Sauropsida Huxley, 1864 (Fig.7). In the Protosauria he placed Cotylosauria, Pareiasauria and Procolophonia together with the stem-group amniotes Microsauria (a prescient view, perhaps, given the recent paper by Pardo *et al.* 2017).

Watson (1917) produced a classification of pre-Jurassic tetrapods that included the super-order Cotylosauria and named the new orders Seymouriamorpha Watson 1917 and Diadectomorpha Watson, 1917, to include pareiasaurs and procolophonids and Captorhinomorpha Watson, 1917 to include captorhinids and limnoscelids. The sister group to the cotylosaur super-order was Anomodontia Owen, 1876, which included the order Caseasauria Williston, 1912, quite separate from the order Pelycosauria, and various orders of therapsids. This was the first time that caseids had been considered as a separate group to pelycosaurs.

Williston's monumental work 'The Osteology of the Reptiles', although published posthumously (Williston 1925), resulted from his research in the early part of the century. Based principally of the concept of temporal fenestration consolidated by Osborn, he named the new subclasses Anapsida Williston, 1917 (to include the orders Cotylosauria, Eunotosauria Watson 1917 and Testudinata Oppel, 1811) and Parapsida

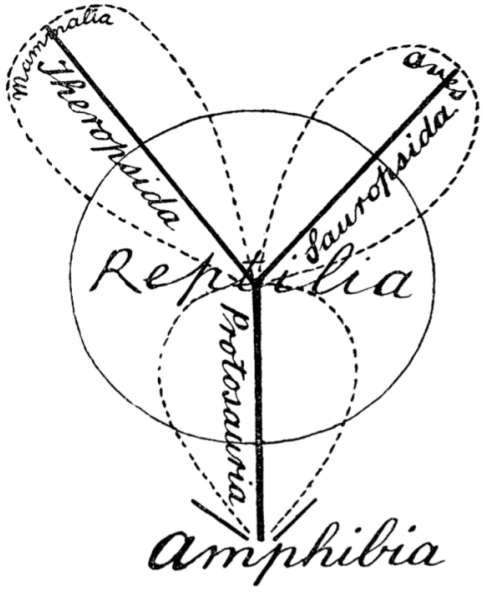


Figure 7: Sketch showing the dichotomy of the main amniote groups, Theropsida (mammal-line) and Sauropsida (bird-line) from the basal amniote stem (Protosauria). Reproduced from Goodrich (1916)

Williston, 1825 (to include Proganosauria Baur, 1887 and Protorosauria Huxley, 1871). He maintained Diapsida Osborn, 1903, to include Eosuchia Broom, 1914. He also maintained Synapsida Osborn, 1903, to include Pelycosauria Cope, 1878 and Therapsida Broom, 1905.

1.4.2 Africa and Madagascar, 1910 to 1940

In the early 19th century to the late 1930's, many new Permian taxa were discovered and described by Robert Broom. His work on the 'mammal-like reptiles' of the Permian Karoo led to a reclassification of Anomodontia Owen, 1876 into four separate orders, Deinocephalia Seeley, 1894, Therocephalia Broom, 1903, Anomodontia and Cynodontia Owen, 1861, which together he named Therapsida Broom, 1905. In 1907 he published a short description of *Heleosaurus* as an early diapsid reptile. Later, he described a new fossil skull from the upper Permian of South Africa, *Youngina capensis* (Broom 1914). In the same paper, Broom named a new diapsid suborder, Eosuchia Broom, 1914, which included the family Younginidae Broom, 1914, to which both *Youngina* and *Heleosaurus* were assigned.

Broom continued his Karoo discoveries with *Elliotsmithia* (1937), which he assigned to the Pelycosauria as a close relative of *Mycterosaurus*, and *Owenetta* (1939), placing this taxon in the Cotylosauria, within the suborder Procolophonia. Broom also described *Millerina* (= *Milleretta*) *rubidgei* (1939), which he found unable to classify

with the groups that existed at that time, despite the good condition of the skull. He believed it might require an order of its own, representing a possible ancestor of all other reptiles outside the Cotylosauria (the basal group of mainly anapsid reptiles). This is probably the first indication of a sauropsid order quite separate from captorhinids and eosuchian diapsids.

Although from the lower Triassic of the Karoo, *Prolacerta broomi* (Parrington 1935) was also an important discovery from this prolific period in South African palaeontology. Parrington thought this taxon to be transitional from the eosuchian (as exemplified by *Youngina*) to squamate lineage. Its archosaurian affinities were later discussed by Gow (1975).

Expeditions of the Muséum national d'Histoire naturelle, Paris, to Madagascar in the early 1920's discovered *Hovasaurus*, which Piveteau (1926) originally recognised as a mesosaur, and therefore assigned to Proganosauria Baur, 1887, mainly due to ample evidence of an aquatic life style. He also recovered specimens of *Tangasaurus*, which Haughton (1924) had discovered in the late Permian Karoo beds of Tanganyika (Tanzania), and tentatively assigned to Diapsida, along with *Youngina*. Haughton (1930) later combined these taxa into the family Tangasauridae Houghton, 1924.

1.4.3 Russia, 1938 to 1956

The middle Permian Mesen River basin deposits of Russia have yielded a remarkable series of fossils, many of which were first described by Ivan Efremov. *Nycteroleter ineptus* (Efremov 1938) was the first to be named and placed in the family Procolophonidae Lydekker 1889, still considered to be a suborder of Cotylosauria Cope, 1878. *Bashkyroleter baskyricus* (1940), *Nyctiphuretus acudens* (1938) and *Rhipaeosaurus tricuspidens* (1940) followed, and were placed into the same family. Efremov (1938) also described *Mesenosaurus*, and assigned it to Pelycosauria, although subsequent discoveries led to this taxon being described as the oldest archosaur by Ivakhnenko (1978), and later still as a varanopid by Reisz and Berman (2001). The discovery of *Ennatosaurus* (Efremov 1956) was important, since it represented, and still does, the youngest caseid known, and Efremov's brief description, expanded upon by Olson (1962), recognised it as such.

1.4.4 North America, 1937 to 1956

The late 1930's was also a productive period for North American early amniote discoveries. Stovall (1937) described a giant caseid from Oklahoma, *Cotylorhynchus*. Two specimens of a small, gracile tetrapod from the late Carboniferous of Kansas were described

by Lane (1945). The first, *Petrolacosaurus*, was assigned to Pelycosauria, the second, *Podargosaurus*, was considered to be closely related to Williston's *Araeoscelis*. Peabody (1952) noted that both taxa were synonymous, and recognised *Petrolacosaurus* as a basal eosuchian, which stood 'so close to the primary dichotomy of reptilian radiation that they retain the basic plan of a primitive cotylosaur' (Peabody 1952:37). Both Watson (1954) and Vaughn (1955) tentatively placed *Petrolacosaurus* within Theropsida Goodrich, 1916, although Vaughn did consider it might be related to *Araeoscelis*, a view Tatarinov (1964) expanded upon by placing both taxa into the order Araeoscelidia Williston, 1913. Stovall, Price and Romer (1966), in a paper principally concerned with postcranial material of the caseid *Cotylorhynchus*, thought it probable that *Petrolacosaurus* was a primitive edaphosaurid, stating that the unproven diapsid nature of the temporal region did not allow the assignment of this taxon to Eosuchia, noting further that 'the time of appearance of *Petrolacosaurus* is one at which an eosuchian is hardly to be expected' (Stovall, Price and Romer 1966:29). New specimens allowed Reisz (1981) to confirm the diapsid nature of the upper temporal region, vindicating Peabody's initial diagnosis.

Romer (1937) published a short paper on several new pelycosaur taxa, hoping to discuss them in greater detail in a review of the group, which was nearing completion. These taxa included *Eothyris* and *Aerosaurus greenleeorum*, which he considered a small sphenacodontid. Also in 1937, Price described two new cotylosaurs from the Permian of Texas, which he named *Romeria* and *Protorothyris*, and created two new families Romeriidae Price, 1937 and Protorothyrididae Price, 1937, within Captorhinomorpha Watson, 1917.

The Review of the Pelycosauria (Romer and Price 1940) was a seminal work on early amniote systematics, underpinning much of our current understanding of early synapsid phylogeny. It divided the order Pelycosauria Cope, 1978, into three suborders, Ophiacodontia Romer and Price, 1940 to include the new family Eothyrididae Romer and Price, 1940, Sphenacodontia Romer and Price, 1940 to include the new family Varanopsidae Romer and Price, 1940, and Edaphosauria Cope 1882, to include the family Caseidae Williston, 1911 and the genus *Mycterosaurus* in the family Nitosauridae Romer and Price, 1940. The hypothetical relationships with Therapsida Broom, 1905 was also presented as closely aligned to sphenacodontid origins (Fig.8).

Olson (1947) reviewed the cotylosaurian family Diadectidae, noting that the inclusion of both captorhinomorphs and diadectomorphs in the same order Cotylosauria was untenable since he found both to be on different branches of reptile evolution, despite the anapsid condition of captorhinids. He therefore proposed a division of basal

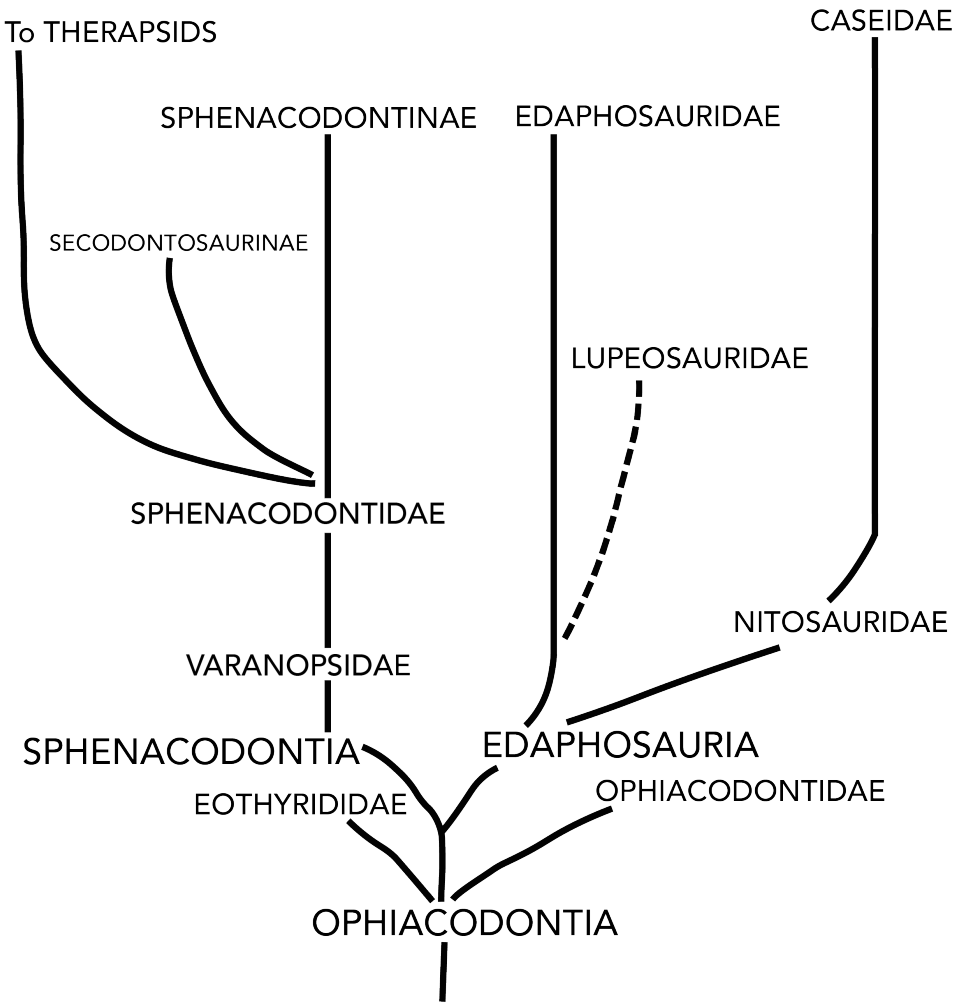


Figure 8: Sketch of the interrelationships of the Pelycosauria. Modified from Romer and Price (1940)

reptiles into two groups, the subclass Parareptilia Olson, 1947, with orders Diadecta Olson, 1947 to include procolophonids and pareiasaurs and Chelonia Latreille 1800, plus the subclass Eureptilia Olson, 1947, with the infraclasses Captorhina Olson, 1947, Synapsida Osborn, 1903, Parapsida Williston, 1925, Euryapsida Colbert, 1945 and Diapsida Osborn, 1903. Olson's concept of parareptile and eureptile clades was largely disregarded for the next 40 years until the advent of the cladistic age, when these terms were revisited.

In 1956 Romer published his influential Osteology of the Reptiles (Romer 1956). He included three 'sauropsid' subclasses, Anapsida Williston, 1917, Lepidosauria Haeckel, 1866 and Archosauria Cope 1869. Under Anapsida, he placed the orders Cotylosauria Cope, 1878 (the only non-sauropsid order) and Chelonia and under Lepidosauria, the orders Eosuchia Broom, 1905, Rhynchocephalia Gunther, 1867 and Squamata Oppel,

1811 . In Cotylosauria Cope, 1878 he placed seymouriamorpha Watson, 1917, Diadectomorpha Watson, 1917 (including procolophonids and pareiasaurs) and Captorhinomorpha Watson, 1917 (including captorhinids, romeriids and limnoscelids). Millerettids and younginiforms he included in the Eosuchia.

1.4.5 Early cladistic analysis, 1950 to 1986

The theory of phylogenetic systematics, first proposed by Hennig (1950, English translation 1966), transformed systematic research in palaeontology. Heaton and Reisz (1986) applied this method in their review of the relationships of captorhinomorph reptiles, which only consisted of captorhinids, including *Romeria*, and 'protorothyridids', after the reassignment of limnoscelids to Diadectomorpha (Heaton 1980). They concluded that 'protorothyridids' were more closely related to diapsids than captorhinids, and that Captorhinomorpha Williston, 1917, should be abandoned as a formal term.

A large-scale phylogenetic analysis of diapsid reptiles by Benton (1985) established the monophyly of Romer's two main reptile stems, the Lepidosauria and Archosauria. He also recovered the late Carboniferous diapsid *Petrolacosaurus* stemward to the lepidosaur/archosaur dichotomy, and named a new clade, Neodiapsida, which included all diapsid reptiles except *Petrolacosaurus*, effectively abandoning the use of Eosuchia Broom, 1905. One of the practical difficulties of Hennigs' method of phylogenetic analysis was the computational restriction on the size and complexity of the dataset. This problem was resolved by an almost exponential increase in computer processing capabilities during the 1980's, launching a new era of computer-assisted phylogenetic analysis.

1.4.6 Post-cladistic systematics

The first study of amniote phylogeny to use computer programs designed to assist parsimony analysis was Gauthier *et al.* (1988b) (Fig. 9A). This analysis proposed fundamental divisions in amniote interrelationships that are still recognised today, including the monophyly of a group that is now recognised as Parareptilia Olson, 1947, although Gauthier *et al.* (1988b) only tentatively recognised this unexpected clade, which united taxa with the anapsid condition of the temporal region from the Cotylosauria with mesosaurs and millerettids.

Laurin and Reisz (1995), in their re-evaluation of amniote phylogeny, recovered a similar tree topology to Gauthier *et al.* (1988), except for the position of testudines and the genus *Mesosaurus* (Fig.9B). Testudines (or Testudinata) are placed as a sister

taxon to captorhinids in Gauthier *et al.* (1988), but are recovered as crown-group parareptiles in Laurin and Reisz (1995). *Mesosaurus* is recovered as a basal parareptile in Gauthier *et al.* (1988), and as a basal sauropsid in Laurin and Reisz (1995). The phylogenetic positions of both testudines and *Mesosaurus* remain the focus of debate in the present day (see chapter 4 for more discussion on both these issues). Laurin and Reisz (1995) also applied the nomen Eureptilia Olson, 1947, to the monophyletic sister clade of parareptiles, which included captorhinids, romeriids (=‘protorothyridids’) and diapsids.

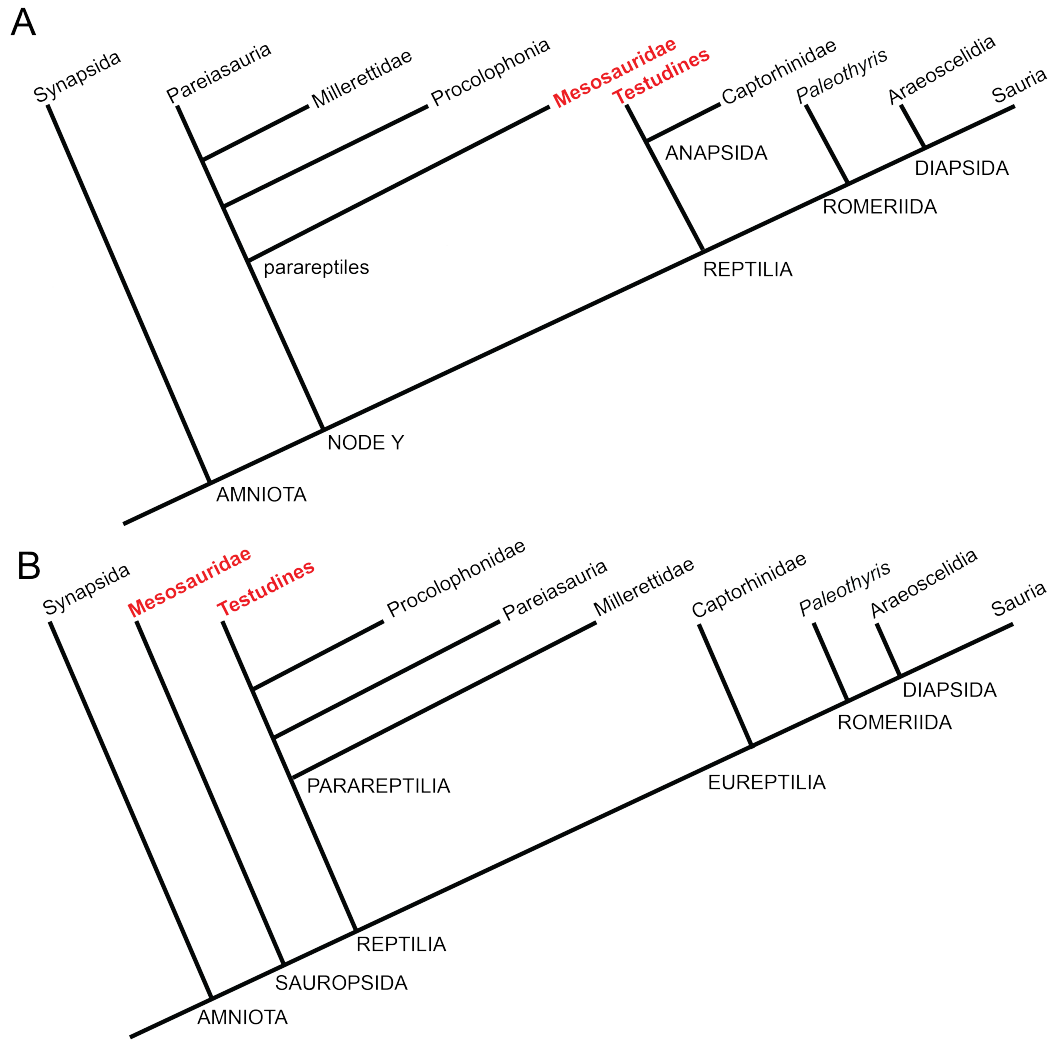


Figure 9: Cladograms of amniote phylogeny. A, from Gauthier *et al.* (1988). B, from Laurin and Reisz (1995). Mesosauridae and Testudines are shown in red to highlight the alternate hypotheses

The broad consensus of early amniote phylogeny has changed little from these early analyses, although most researchers now accept the diapsid origin of turtles. Since the beginning of the 21st century, the majority of phylogenetic analyses of early amniotes

has focused on the fine-tuning of intra-group relationships, resolving many outstanding questions of early amniote phylogeny. The position of 'protorothyridids' has been found to be paraphyletic in respect to diapsids (Müller and Reisz 2006), the interrelationships of synapsid taxa have been thoroughly explored (Benson 2012, Reisz and Fröbisch 2014, Brocklehurst *et al.* 2016), and the phylogeny of the Parareptilia and Captorhinidae is well documented (MacDougall *et al.* 2017, 2018, Modesto *et al.* 2018).

Perhaps, the most significant change to early amniote phylogenetic studies has been the introduction of molecular analyses, which has been used to establish turtles as an extant sister group of archosaurs, and to reject the hypothesis of the sister taxon relationship of birds and mammals, i.e. Haematothermia Owen, 1866. Probabilistic methods, such as Bayesian inference, have been used in tandem with, or sometimes in place of, parsimony in several morphological phylogenetic studies (Müller and Reisz 2006, Tsuji *et al.* 2012, Sobral *et al.* 2015, Bever *et al.* 2015, Modesto *et al.* 2015, Brocklehurst *et al.* 2016). New Bayesian models now use morphological clocks to estimate absolute divergence times in fossil-only or fossil and extant operational terminal unit (total evidence) datasets (Simões *et al.* 2018).

Despite many decades of post-cladistic systematic research, new hypotheses continue to challenge our understanding of vertebrate phylogeny. Recent work by Pardo *et al.* (2017) (see 1.3.2 above) has suggested that some microsaur groups, traditionally considered lepospondyl amphibians, may be sister to eureptiles within Amniota. The Permian amniote *Eunotosaurus*, long believed to be a parareptile, may be a diapsid (Bever *et al.* 2015). Both these hypotheses have benefitted from novel anatomical data revealed by μCT analysis of previously-described fossil specimens.

1.5 Aims of the thesis

Developments in computational phylogenetics methods, and the introduction of new probabilistic models for fossil data, are important advances in systematic research. However, the character-taxon matrix remains the fundamental unit on which any hypothesis is based. Good practise of character choice, with the appropriate observations of primary similarity (as conjectures of homology), remains a key issue. However, reviewing characters, or proposing new ones, is often limited due to the condition of the fossil specimens. The use of μCT techniques has revolutionised this aspect of phylogenetic studies. One of the aims of my thesis is to explore this method of augmenting character data, and to see what effect novel anatomical observation has on phylogenetic analysis.

In chapter two of my thesis, I present a detailed a re-examination, using μCT data, of two specimens of the earliest known neodiapsid *Orovenator mayorum* from the Cisuralian of Oklahoma (Reisz *et al.* 2011). My results reveal new anatomical data, which I have applied to an existing character-taxon matrix. The results are discussed, and observations are made in respect to paleoecology and palaeobiology of this extraordinary taxon. I also present my preliminary conclusion of the interrelationships of *Orovenator* with other early amniotes.

Temporal fenestration in early amniotes is fundamental to their systematics, as the preceding paragraphs have shown. Although many studies have questioned the underlying relevance of this system (Romer 1956, deBraga and Rieppel 1997, MacDougall *et al.* 2014), no studies have yet attempted a systematic review of the comparative anatomy of temporal fenestrae in early amniotes.

In chapter three of my thesis I undertake such a review, and suggest a new method for the characterisation of temporal fenestration that maximises observations of primary homology.

Computer-assisted phylogenetic analyses allow for the use of large datasets to establish hypotheses on the interrelationships of a comprehensive range of taxa. Few large-scale analyses of early amniotes have been attempted in the last decade, with most analyses focusing on resolving within-group relationships. The principle aim of this thesis is to produce a new dataset, compiled from a wide range of early amniotes, to review the traditional hypotheses of early amniote phylogeny.

In chapter 4 of my thesis I present the results of one of the largest phylogenetic analyses of early amniotes to date, using a novel dataset and incorporating important new data from the results of the analysis detailed in chapter 2. In this study, I have applied the new method of characterisation of temporal fenestration derived from chapter 3, and used maximum parsimony and two Bayesian probabilistic models.

Chapter 2

A redescription of *Orovenator mayorum* (Sauropsida: Diapsida) using high-resolution μCT, and its consequences for early amniote phylogeny

Authors note: This chapter has been published as Ford and Benson (2018) in the journal *Papers in Palaeontology* (see references for full citation). RBJB contributed to this paper with structural advice and editing of the original draft manuscript. All other data collection, analysis, figures and writing of the draft manuscript was performed by DPF.

2.1 Introduction

Amniota comprise all mammals and reptiles (including birds). Today they are a major component of global ecosystems, accounting for almost four fifths of land vertebrate diversity, yet much about their origin and early divergences remains obscure. Amniotes first appear in the fossil record in the upper Carboniferous, with the earliest taxa known from the Pennsylvanian coal measures of Joggins, Nova Scotia (Carroll 1964). Fossils from this locality provide evidence that the mammal/reptile divergence had already occurred by the late Bashkirian (319-318 Ma) (Benton *et al.* 2015), as members of both the mammalian total-group (Synapsida) and reptilian total-group (Sauropsida) are already present (Reisz and Müller 2004; Müller and Reisz 2005a). The recent discoveries of the oldest caseid (Reisz and Fröbisch 2014) and parareptile

(Modesto *et al.* 2015) in the upper Pennsylvanian (Gzhelian 304-299 Ma) confirm that the basal amniote dichotomy was well established by that time, and all major clades of early synapsids (caseasaurs, varanopids, edaphosaurids, ophiacodontids and sphenacodontians) and early sauropsids (parareptiles, captorhinids and diapsids) had emerged.

Early synapsids, characterised by a single, lateral, temporal fenestra, were both abundant and diverse in the early Permian (Reisz 2014; Angielczyk and Kammerer 2018). Sauropsids were somewhat less common, and principally represented by early-diverging clades: the parareptiles and captorhinids (MacDougall *et al.* 2017a, b). By contrast diapsids, representing the sauropsid group that includes all extant reptiles and birds and typically possessing two temporal fenestrae, are rare in early Permian deposits. Few diapsids of this age have been reported, other than the highly plesiomorphic araeoscelidians (Vaughn 1955; Reisz 1981; deBraga and Reisz 1995). In fact, apart from an isolated parietal (Carroll 1968), *Orovenator mayorum* from the Dolese Quarry, Richards Spur, Oklahoma, is the only non-araeoscelidian diapsid reported so far from the lower Permian (Reisz *et al.* 2011a). The Dolese Quarry has yielded a unique assemblage of early Permian terrestrial vertebrates from claystone fissures deposited in Lower Ordovician limestone (Reisz *et al.* 2015). Recent taphonomic analysis of the fossils and associated matrix has confirmed a karstic environment of cave systems preserved in an upland locality (MacDougall *et al.* 2017b). The radiometric (U-Pb) dating of speleothems from the cave systems has defined the absolute age of these deposits at 289 ±0.68 m (Woodhead *et al.* 2010), equivalent to the early Artinskian (Cohen *et al.* 2013; ICS 2018).

Taxonomic classifications of early amniotes have been closely associated with patterns of temporal fenestration, and osteological differences were otherwise limited between the earliest synapsids and sauropsids (Reisz 1972). Patterns of temporal fenestration have largely prevailed as a key character in the systematic classification of amniotes since Osborn (1903), and are consistent with seminal studies on cladistic hypotheses (e.g. Gauthier *et al.* 1988; Laurin and Reisz 1995; deBraga and Rieppel 1997). Nevertheless, researchers have noted a high degree of variability of temporal fenestration amongst early amniotes, even within closely related groups (e.g. parareptiles; Cisneros *et al.* 2004; Tsuji *et al.* 2010). This apparent plasticity in temporal fenestration is further exemplified by the secondary loss of the lower temporal fenestra amongst araeoscelidian diapsids (Reisz *et al.* 1984) and the complete loss of temporal fenestration leading to the 'anapsid' condition of total-group turtles (Bever *et al.* 2015). Furthermore, recent studies have questioned the efficacy of characters based on tem-

poral fenestration in performing broad-based phylogenetic analyses of early amniotes (MacDougall and Reisz 2014).

The presence of diapsid-like temporal fenestration in *Orovenator* was noted by Reisz *et al.* (2011a). *Orovenator* was consequently recovered as the earliest known neodiapsid, the sister group to the araeoscelidian diapsids, based on analysis of a sauropsid-focused data matrix (Reisz *et al.* 2011a). Subsequent phylogenetic analyses have therefore assumed diapsid affinities and examined the relationships of *Orovenator* relative to other sauropsids, with synapsids included only as a single, composite outgroup (Chen *et al.* 2014; Bever *et al.* 2015) or omitted entirely (Pritchard and Nesbitt 2017).

Here, I use micro-computed tomography (μCT) to investigate the anatomy of *Orovenator*. This approach has revealed remarkable detail of the cranial osteology of *Orovenator*, including the first complete three-dimensional visualisation of an early diapsid septomaxilla, the medial surface of the antorbital region and the structure of the nasolacrimal canal, a complete reconstruction of the palate and the pathways of major arteries in the basicranium and maxilla. Several anatomical features also provide evidence of the palaeoecology of *Orovenator*, indicating nocturnality and burrowing behaviour. I also use three-dimensional modelling to present a reconstruction of the skull of *Orovenator* based on the scan data of the holotype and referred specimen.

Orovenator shares various character states with araeoscelidians such as *Petrolacosaurus kansensis* (Reisz 1981). However, I also report a series of morphological features shared with varanopids, a group that is typically assigned to Synapsida. Several such features, including the anterodorsal process of the surangular and posterolateral extension of the external naris, have been noted by earlier studies (Reisz *et al.* 2011a). Although similarities have hitherto been documented between varanopids and early diapsids (Reisz and Modesto 2007; Reisz *et al.* 2010), the present study demonstrates that the similarities are more numerous and detailed than previously recognised, calling into question the phylogenetic distinctness of varanopids from early diapsids. To explore these similarities further, I score *Orovenator* into an existing phylogenetic data matrix designed to recognise affinities between diapsids and varanopids (Reisz *et al.* 2010). This analysis finds varanopids in a clade with *Orovenator*, among early diapsids, implying homoplasy between diapsid- and synapsid-like temporal fenestration. However, it is also clear that much relevant variation in anatomical character states has not been included together in existing phylogenetic data matrices for early amniotes. I therefore suggest that the paradigm of Varanopidae as a clade within Synapsida, and not Sauropsida, should be subject to further scrutiny.

2.2 Material and method

Orovenator mayorum is represented by two specimens, OMNH 74606 (holotype) and OMNH 74607 (referred specimen), held in the collection of the Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma. The holotype is here considered to be a juvenile, since it is approximately 33% smaller and lacks the dermal sculpturing of the referred specimen.

Both specimens were scanned in a single field resulting in 1901 slices and a voxel size of 17.8 μm at the University of Texas High-Resolution CT Facility in Austin, Texas using the North Star Imaging ACTIS scanner, with 2048 x 2048 Perkin Elmer flat-panel detector and 0.72 mm aluminium filter. The beam was set to 160 kV, and 0.2 mA. The holotype of the varanopid *Mycterosaurus longiceps* (FMNH-UC 692) was scanned at the μCT facilities in the University of Chicago, Department of Organismal Biology and Anatomy, using the GE scanner with a 0.5 mm copper filter. The resolution achieved was 30.3 μm (135 kV, 0.2 mA), with 3071 slices. All specimens were digitally segmented using Mimics Materialise v.18.0 x64 (http://biomedical.materialise.com/mimics).
High-resolution models produced in Mimics were exported as .ply files, then imported into Blender (https:// www.blender.org) and rendered as two-dimensional images for the figures used in the present study. All reconstructions of the skull of *Orovenator* were carried out in Blender using the available elements of both OMNH 74606 and 74607. Composite reconstructions of the skull were made by downscaling elements from OMNH 74607 by 33% of natural size. Mirror imaging or duplication from both specimens was used to replace some elements.

2.3 SYSTEMATIC PALAEONTOLOGY

AMNIOTA Haeckel, 1866
SAUROPSIDA Huxley, 1864
DIAPSIDA Osborn, 1903
NEODIAPSIDA Benton, 1985

Genus *Orovenator* Reisz *et al.*, 2011a
Type species. *Orovenator mayorum* Reisz *et al.*, 2011a

Material. OMNH 74606 (holotype), a partial skull including premaxillae, septomaxillae, maxillae, left lacrimal, left prefrontal, left nasal, right jugal, vomers, palatines, pterygoids, ectopterygoids, parabasisphenoid, right epipterygoid, left quadrate, partial stapes and scleral plates. OMNH 74707 (referred specimen), a partial skull including frontals, prefrontals, right parietal, lacrimal, pterygoid, palatine, partial supratemporal, partial atlas/ axis and third cervical and an isolated caudal. The referred specimen is assigned to the same species as the holotype based on the distinctive morphology of the lacrimal (Reisz *et al.* 2011a).

Locality and horizon. Dolese Brothers Limestone Quarry, Richards Spur, Comanche County, Oklahoma, USA. Clay-stone fissure fills dated to 289 ± 0.68 Ma (Woodhead *et al.* 2010) in the Ordovician Arbuckle Limestone. Earliest Artinskian of the Cisuralian (early Permian).

Revised diagnosis. Small diapsid reptile (estimated adult skull length 45mm) distinguished by a rounded transition of the dorsal and lateral surfaces of the subnarial bar of the premaxilla*, a moderate anterodorsal inclination of the anterior surface of the premaxillae (rostral process)*, an elongate external naris, a transversely curved lacrimal that forms an antorbital ridge on the snout (autapomorphy), a buttress and crest on the medial surface of the maxilla dorsal to the 9th alveolus*, a parietal that extends anteriorly along the midline as far as the anteriormost point of the postfrontal, mediolaterally narrow suborbital fenestrae*, an elongate dentary that extends posteriorly to a point directly ventral to the inferred midpoint of the lateral temporal fenestra, and a surangular that forms a dorsal shelf above the adductor fossa and anteriorly forms a trough receiving the posterodorsal process of the coronoid (modified from Reisz *et al.* 2011a, with additions annotated*).

2.4 Description

2.4.1 The skull

Most bones of the skull and mandible are at least partially preserved in either OMNH 74606 (Fig.1) or OMNH 74607 (Fig.2). The occipital region, postorbital, squamosal, articular and most of the braincase are not preserved. Despite this, the approximate disposition of some of the missing bones can be deduced from the articular facets on the adjacent bones.

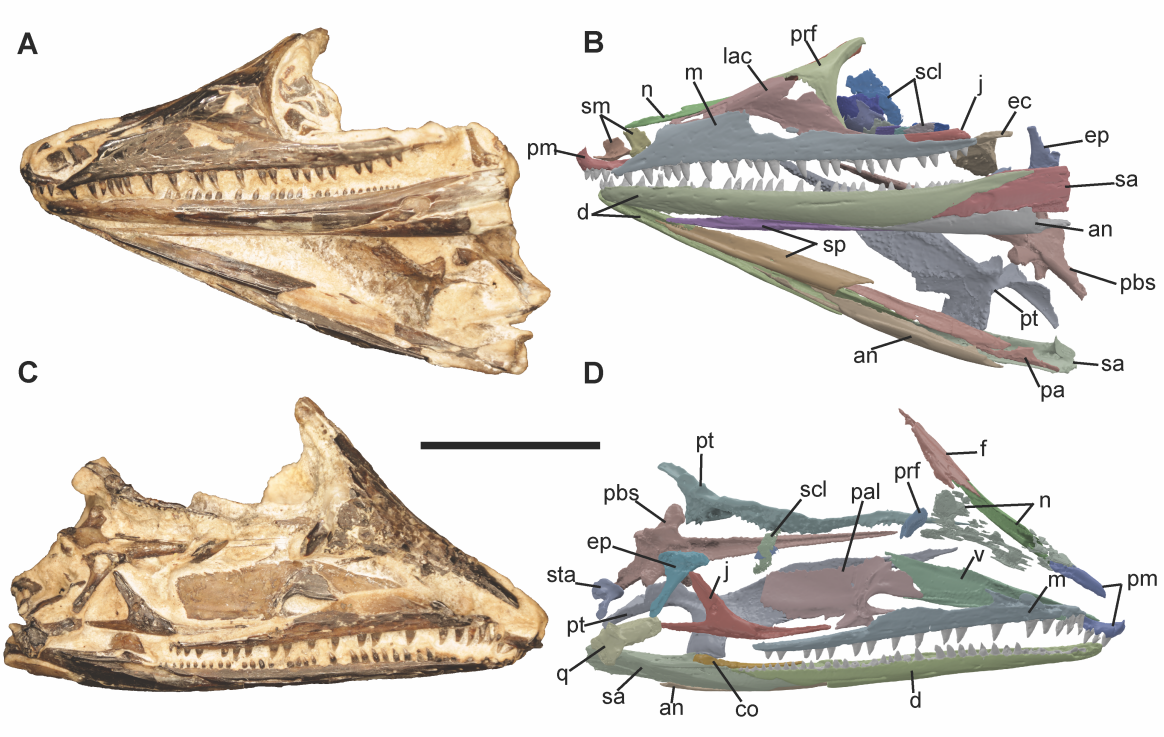


Figure 1: *Orovenator mayorum* (holotype OMNH 74606). A, left lateral view; B, segmented elements from μCT scan of specimen in left lateral view; C, right lateral view; D, segmented elements from μCT scan of specimen in right lateral view. *Abbreviations*: an, angular; co, coronoid; d, dentary; ec, ectopterygoid; ep, epipterygoid; f, frontal; j, jugal; lac, lacrimal; m, maxilla; n, nasal; pa, prearticular; pal, palatine; pbs, parabasisphenoid; pm, premaxilla; prf, prefrontal; pt, pterygoid; q, quadrate; sa, surangular; scl, scleral plates; sm, septomaxilla; sp, splenial; sta, stapes; v, vomer. Scale bar represents 1cm.

2.4.1.1 Snout

The dorsal surface of the snout is mediolaterally broad, and almost flat. This is accentuated by the dorsal exposure of the prefrontals and lacrimals (Fig.3C). The snout of *Orovenator* is proportionately long, with the antorbital region approximately double the length of the postorbital region. The mediolateral width and dorsoventral height of the snout attenuate anteriorly, resulting in a rather wedge-shaped appearance. The anterior end of the snout, constituted by the premaxilla and anterior part of the maxilla, is inflected anteroventrally from the level of the 5th maxillary alveolus (Fig.3A). The external nares are elongate, ovoid openings that face anterolaterally and are enclosed principally by the premaxilla and maxilla. The lacrimal and nasal only make a small contribution to the posterior margin of the external naris (Fig.3B). The rostral process of the premaxilla is moderately procumbent.

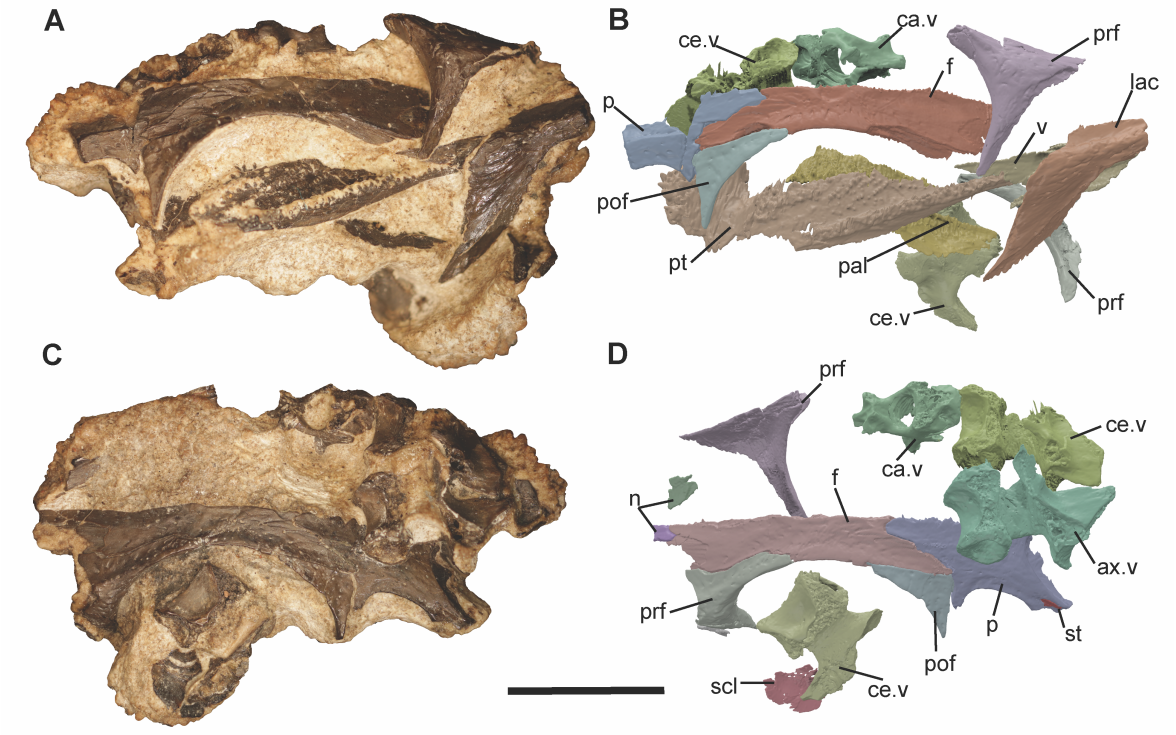


Figure 2: *Orovenator mayorum* (referred specimen OMNH 74607). A, right lateral view; B, segmented elements from μCT scan of specimen in right lateral view; C, left lateral view; D, segmented elements from μCT scan of specimen in left lateral view. *Abbreviations*; ax.v, axial vertebra; ca.v, caudal vertebra, ce.v, cervical vertebra; f, frontal; lac, lacrimal; n, nasal; p, parietal; pal, palatine; pof, postfrontal; prf, prefrontal; pt, pterygoid; scl, scleral plates; st, supratemporal; v, vomer. Scale bar represents 1cm.

2.4.1.2 Premaxilla

Both premaxillae are present in OMNH 74606. The premaxilla comprises a ventral subnarial ramus that bears a palatal flange medially, and a maxillary process posteriorly. Only the anteroventral portion of the base of the dorsal ramus is preserved in both the left and the right premaxilla. Nevertheless, aspects of its morphology can be reconstructed from a facet on the anterolateral process of the left nasal and from a preserved posterior section of the dorsal ramus of the right premaxilla, which remains articulated with part of the nasal (Fig.1D). Both premaxillae have five alveoli, with one tooth missing from the right premaxilla (Fig.4B). All premaxillary teeth are conical with pointed apices, and lack carinae. They are both isodont and homodont but are smaller than the maxillary teeth. The teeth are set in shallow sockets, the labial wall is slightly pronounced, and the lingual wall is absent.

The dorsal surface of the subnarial ramus, which forms the ventral floor of the external naris, grades smoothly into its mildly convex lateral surface (Fig.4A). This

is different from other early diapsids such as *Petrolacosaurus* (pers. obs. KUVP 9952) and *Araeoscelis* (pers. obs. MCZ 4380), or indeed most Palaeozoic amniotes (Reisz and Berman 2001) in which there is an angular contact between the lateral and dorsal surfaces of the subnarial ramus. Instead, the condition in *Orovenator* is similar to the rounded subnarial bar seen in some early synapsids such as the varanopids *Archaeovenator* (Reisz and Dilkes 2003) and *Mesenosaurus* (Reisz and Berman 2001). Posteriorly, the subnarial ramus narrows dorsoventrally to form a shelf that underlies the premaxillary process of the maxilla.

The maxillary process of the premaxilla comprises 48% of the total length of the premaxilla (Fig.4A). It is mediolaterally narrow and sheet-like. Its lateral surface is overlapped by the maxilla and thus obscured in lateral view. The medial surface of the maxillary process forms the anterolateral margin of the internal naris. The process extends posteriorly from the subnarial ramus of the premaxilla and tapers to a point. The process articulates with a facet on the medial surface of the alveolar shelf of the maxilla (Fig.5).

The alveolar surface of the premaxilla is approximately horizontal, sloping gently anteroventrally. The anterior surface of the truncated base of the dorsal ramus extends anterodorsally from the alveolar surface at an angle of approximately 35° from the perpendicular (Fig.3A). This forms a moderately procumbent snout ('rostral process' sensu Reisz *et al.* 2009). The 'rostral process' is absent in other early diapsids, in which the base of the anterior symphysial margin is vertical, not inclined anterodorsally (*Petrolacosaurus*, Reisz 1981; and *Araeoscelis*, Reisz *et al.* 1984). It may therefore be autapomorphic for *Orovenator* amongst early diapsids. This feature is also present in caseasaurian synapsids (*Eothyris* and *Oedaleops*, Reisz *et al.* 2009; *Ennatosaurus*, Maddin *et al.* 2008; *Euromycter*, Sigogneau-Russell and Russell 1974; Reisz *et al.* 2011b) and the diadectomorph *Limnoscelis* (Romer 1946). Maddin *et al.* (2008) considered that *Limnoscelis* and caseasaurians acquired this morphology independently, and its presence in *Orovenator* may indicate a third independent acquisition of this character state among early amniotes.

Two large foramina are located on the anterior surface of the dorsal process, and two smaller foramina are located lateral to these. The lateral surface of the premaxilla is otherwise smooth, with no sculpturing evident, unlike in *Petrolacosaurus* (Reisz 1981). The medial surface of the premaxilla bears a flat symphyseal surface for the opposing premaxilla. This surface extends posteriorly to the level of the 3rd premaxillary alveolus.

The palatal flange extends posteromedially from the medial surface of the premax-

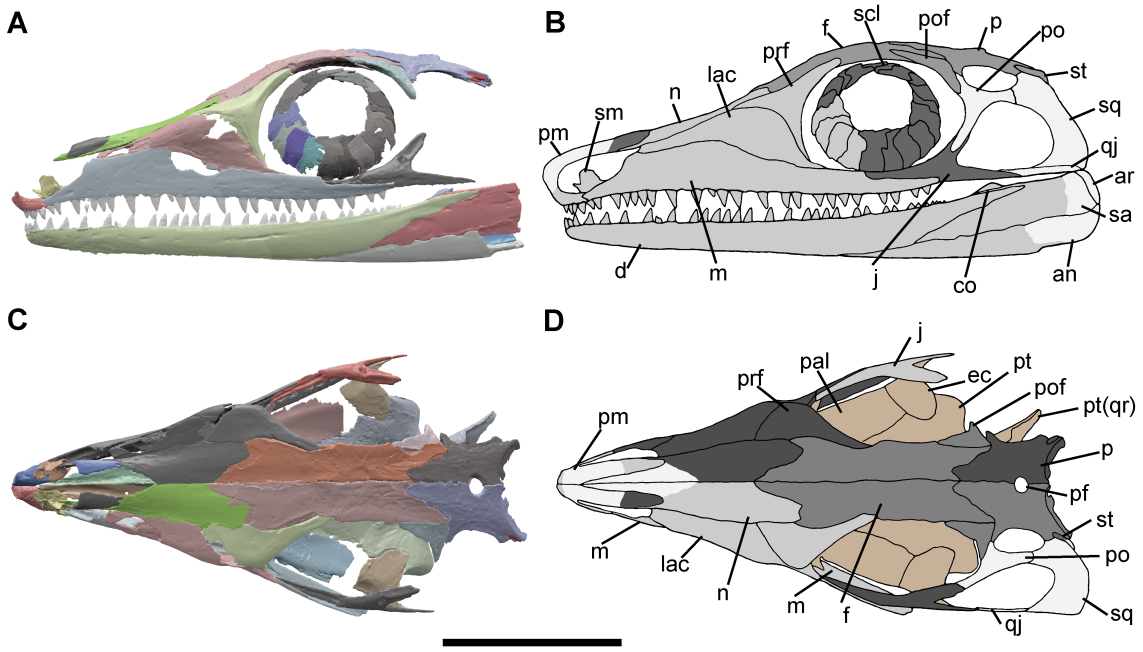


Figure 3: *Orovenator mayorum*, composite reconstruction of the skull. A, left lateral view, with mirrored or duplicated elements in dark grey; B, interpretive drawing of A, with hypothetical morphology of missing elements (white), elements from OMNH 74606 (light grey), elements from OMNH 74607 (medium grey), mirrored or duplicated elements (dark grey); C, dorsal view, with mirrored or duplicated elements in dark grey; D, interpretive drawing of B, with hypothetical morphology of missing elements (white), elements from OMNH 74606 (light grey), elements from OMNH 74607 (medium grey), mirrored or duplicated elements (dark grey), palatal elements from OMNH 74606 (beige). *Abbreviations*; an, angular; ar, articular; co, coronoid; d, dentary; ec, ectopterygoid; f, frontal; j, jugal; lac, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; pt(qr), quadrate ramus of pterygoid; qj, quadratojugal; sa, surangular; scl, scleral plates; sm, septomaxilla; sq, squamosal; st, supratemporal. Scale bar represents 1cm.

illa. The paired palatal flanges of the left and right premaxillae are recessed posteromedially such that they jointly form a midline notch that accommodates the anteromedial process of the vomer (Fig.4B). The palatal flange continues posteriorly into a short, tapering spur of bone, the vomerine process, which inserts into a notch between the anteromedial and anterolateral processes of the vomer (Fig.4C).

The dorsal rami of both premaxillae are not preserved. Nevertheless, the position of the premaxillary contact with the nasal is indicated by a facet on the anterolateral process of nasal, and from the preserved posterior section of the dorsal ramus of the right premaxilla that remains in articulation with a fragment of the right nasal. The left nasal is incomplete anteromedially but preserves a slender anterolateral process. This process has a slightly recessed lateral margin and bears a deep, anteroposteriorly elongate, groove-like facet with a prominent medial wall, which articulated with the

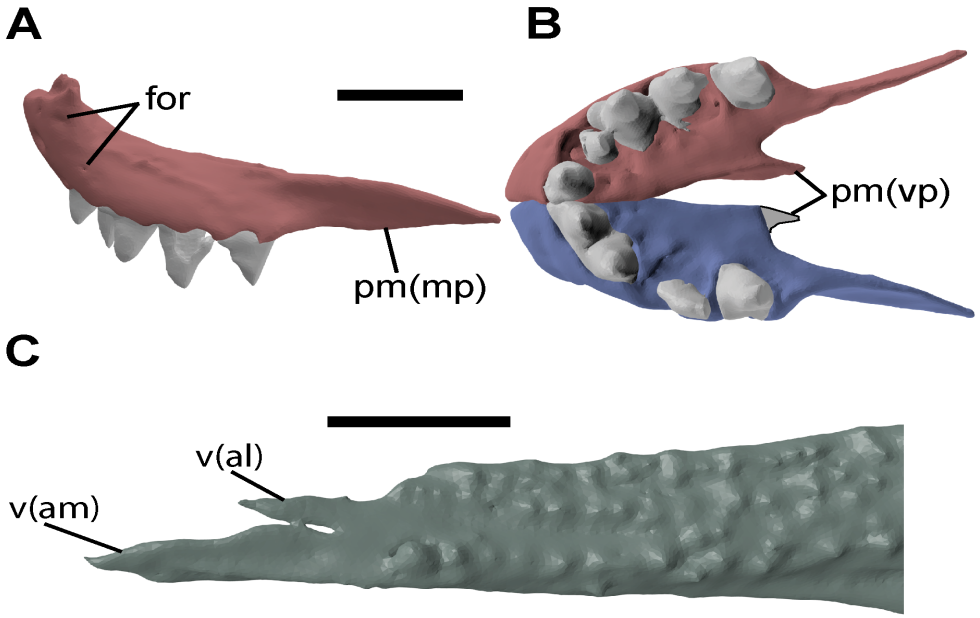


Figure 4: *Orovenator mayorum* (OMNH 74606), premaxillae and left vomer. A, left premaxilla oblique lateral view; B, reconstruction of articulated premaxillae in ventral view, with addition of right vomerine process; C, left vomer, anterior region in ventral view. *Abbreviations*; pm(mp), maxillary process of premaxilla; pm(vp), vomerine process of premaxilla; v(am), anteromedial process of vomer; v(al), anterolateral process of vomer. Scale bars represent 1mm.

ventral surface of the dorsal ramus of the premaxilla (Fig.3A).

Although the right side of the skull roof is less well preserved than the left, a fragmentary piece of bone is preserved that I identify as the posterior portion of the dorsal ramus of the right premaxilla (Fig.1D). This remains in contact with the right nasal, level with the posterior margin of the external naris. My μCT data indicate that this fragment is separated from the anterior portion of the nasal by a well-defined suture. Several vascular foramina perforate the posterior part of the dorsal ramus. Similar foramina can also be found at the base of the dorsal ramus (anteroventrally). In contrast, foramina are absent from the nasal fragment. The dorsal ramus of the premaxilla therefore extends far posteriorly in *Orovenator*, forming much of the medial margin of the external naris (Fig.3B,D), contrary to the anteroposteriorly short dorsal rami figured in Reisz *et al.* (2011a). In other early diapsids, such as *Petrolacosaurus* (Reisz 1981), this process was restricted to the anterodorsal margin of the external naris. It is likely that anteriorly the rami were in contact anteromedially, separated posteriorly by medial processes of the nasals. The external naris of *Orovenator* was therefore anteroposteriorly elongate, as noted by Reisz *et al.* (2011a).

2.4.1.3 Maxilla

The maxilla is the longest bone in the snout, and is best represented by the left maxilla of OMNH 74606 (Fig.1B). The subnarial ramus of the right maxilla is damaged: the posteriormost portion and much of the dorsal process are missing. The left maxilla is missing only a small, posterior section of the dorsal process. The subnarial process tapers anteriorly to its contact with the premaxilla, where its dorsal surface forms the posteroventral margin of the external naris. The dorsal process is an anteroposteriorly elongate, mediolaterally thin sheet of bone with a dorsal margin that increases posteriorly in dorsoventral height from the posterior border of the external naris. It reaches its maximum height level with the 13th alveolus, after which it reduces in height posteriorly before merging with the suborbital ramus level with the 20th alveolus. The suborbital ramus is long, 37% of the total length of the maxilla, and terminates anterior to the posterior orbital margin (Fig.3A). The dorsal process of the maxilla is subvertical for most of its length, but its anterior portion curves dorsomedially adjacent to the external naris. The dorsal process of the maxilla overlies the lateral surface of the lacrimal along its entire length (Fig.3A) but does not contact the nasal due to the anterior extension of the lacrimal contributing to the posterior margin of the external naris. The left maxilla shows a complete count of 30 alveoli, compared to only 25 preserved in the right maxilla.

The alveolar surface of the maxilla is sinuous, with an anterior portion that arches dorsally, and so appears mildly concave in lateral view, and a posterior portion that is bowed ventrally, and so appears mildly convex in lateral view. The lateral surface of the maxilla is smooth, but bears at least 23 small nutrient foramina, with one row of supralabial foramina, and others distributed on the surface of the dorsal process. A single, conspicuously large anterior maxillary foramen is positioned dorsal to the 3rd maxillary alveolus, from which a shallow groove extends anteriorly (Fig.3A). All foramina probably provide cutaneous egress for the maxillary branch of the trigeminal nerve (cranial nerve V) and accompanying blood vessels. Many amniotes possess a group of similar-sized supralabial foramina on the lateral surface of the maxilla (Laurin and Reisz 1995; Benoit *et al.* 2018). An anterior maxillary foramen noticeably larger than the other foramina, and often associated with an anteriorly orientated groove as seen in *Orovenator*, can be seen in many sauropsids. For example, the archosauromorphs *Prolacerta*, *Protorosuchus*, *Proterosuchus* and rhynchosaurs (e.g. *Mesosuchus*) (Modesto and Sues 2004) and the late Permian captorhinid *Saurorictus*, although absent in all earlier captorhinids (Modesto and Smith 2001). It is also present in most parareptiles (MacDougall *et al.* 2016). Despite its broad distribution amongst sauropsids it is ab-

sent in some diapsids including *Petrolacosaurus*, *Lanthanolania* and *Youngina* (Reisz 1981; Modesto and Reisz 2002; BP/1/70 pers. obs.). An enlarged anterior maxillary foramen is absent in those early synapsids in which the anterolateral surface of the maxilla is preserved (e.g. sphenacodontians, Spielmann *et al.* 2010; ophiacodontids, Berman *et al.* 1995; and edaphosaurids, Modesto 1995) with the exception of the caseasaur *Oromycter* (Reisz 2005). However, it is present in the varanopids *Archaeovenator* (Reisz and Dilkes 2003) and *Heleosaurus* (Botha-Brink and Modesto 2009).

The suborbital ramus of the maxilla is dorsoventrally high anteriorly and tapers posteriorly, contributing partly to the anteroventral margin of the orbit when seen in lateral view (Fig.3A). Posteriorly, the suborbital ramus narrows abruptly in a step-like fashion at the level of the 25th alveolus, exposing the lateral surface of the jugal (Fig.1B). From here it continues to taper posteriorly, terminating anterior to the posterior margin of the orbit. The posterior suborbital ramus of the maxilla is dorsolaterally inclined 12° from the vertical, slightly overhanging the lateral alveolar margin, in a somewhat similar fashion to that described in *Archaeovenator* (Reisz and Dilkes 2003).

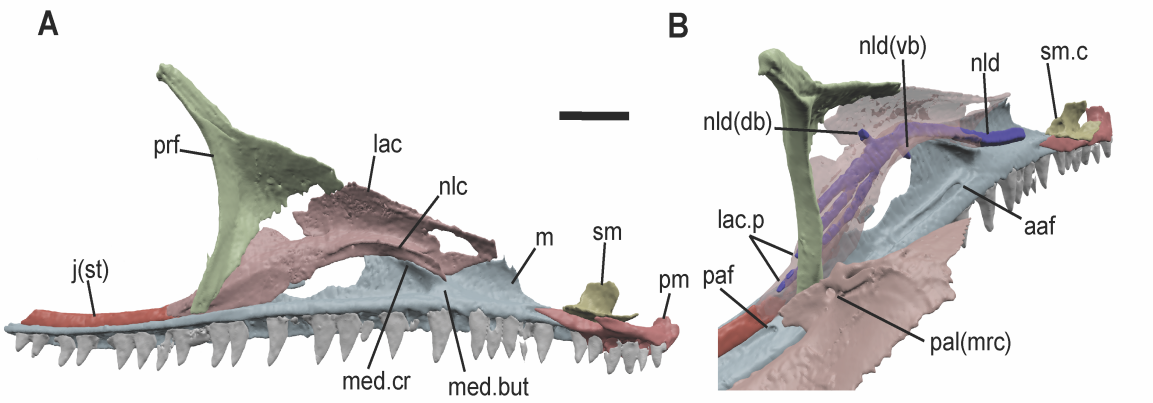


Figure 5: *Orovenator mayorum* (OMNH 74606), left preorbital region, with all elements in situ except for premaxilla and septomaxilla (reconstructed). A, medial view; B, oblique medial view, with partially transparent lacrimal. *Abbreviations*; aaf, anterior alveolar foramen; j.st, subtemporal process of jugal; lac, lacrimal; lac.p, lacrimal puncti; m, maxilla; med.but, medial buttress; med.cr, medial crest; nlc, nasolacrimal canal; nld, nasolacrimal duct; nld(db), dorsal branch of nasolacrimal duct; nld(vb), ventral branch of nasolacrimal duct; paf, posterior alveolar foramen; pal(mrc), maxillary ramus canal of palatine; pm, premaxilla; prf, prefrontal; sm, septomaxilla; sm.c, septomaxillary canal. Scale bar represents 2mm.

A transversely broad, anteroposteriorly oriented alveolar shelf projects from the medial surface of the maxilla ventrally. This shelf gradually thickens dorsoventrally from the 30th and posteriormost alveolus to a point level with the 9th alveolus. Here, the alveolar shelf produces a robust 'supracanine' buttress, which is subtriangular in

medial view (Fig.5). A mediolaterally broad crest of bone extends posterodorsally from the apex of this buttress. This crest terminates close to the dorsal margin of the maxilla. The dorsal surface of the crest provides a broad articular surface for an elliptical ventral facet on the ventromedial ridge of the lacrimal. A deep posterior cavity is formed by the 'supracanine' buttress and crest, and enclosed ventrally by the alveolar shelf. *Orovenator* does not possess a caniniform tooth or region. The maxilla is preserved only in the juvenile specimen (OMNH 74606), and caniniforms can only be assumed to be absent at older ontogenetic stages. Nevertheless, some juvenile specimens of Permian amniotes are known to exhibit distinct caniniform teeth (e.g. *Heleosaurus*, Botha-Brink and Modesto 2009). Therefore, the buttress and crest in *Orovenator* probably represents a different function (if any) than in various other taxa, in which it encloses the enlarged root of the caniniform teeth.

The medial 'supracanine' buttress and crest in *Orovenator* is an early example of this morphology in amniotes. It is absent in many early sauropsids, including captorhinids (e.g. *Euconcordia*, Müller and Reisz 2005b; and *Captorhinus laticeps*, Heaton 1979), the early parareptiles *Colobomycter vaughni* and *Delorhynchus* (Reisz *et al.* 2014; MacDougall *et al.* 2016) and the early diapsid *Petrolacosaurus* (Reisz 1981). Nevertheless, medial maxillary buttresses are present in some later diapsids. These include the *carina maxillaris* of lacertoid squamates (Augé and Smith 2009; Čerňanský and Augé 2013) and some early lepidosauromorphs, although they are less prominent (e.g. *Marmoretta*, Evans 1991; and *Diphydontosaurus*, Whiteside 1986). The morphology of the 'supracanine' buttress and crest in *Orovenator* is remarkably similar to that of non-archosauriform archosauromorph *Prolacerta* in which the buttress and crest are described as an 'internal thickening behind the nasal capsule' (Gow 1975, pp. 100/101 BP/1/2671) (Fig.18B).

The dorsoventral height of the alveolar shelf of *Orovenator* gently narrows anterior to the 'supracanine' buttress, and forms the medial premaxillary facet and premaxillary process anterior to the 5th maxillary alveolus. A shallow facet for the septomaxilla is present on the dorsal surface of the anteriormost region of the alveolar shelf.

The alveolar shelf bears two large openings for the alveolar canal, which are best seen in dorsomedial view (Fig.5B). The posterior opening lies dorsal to the 22nd alveolus, immediately posterior to the position of the maxilla/palatine suture. The anterior and somewhat larger opening lies dorsal to the 10th alveolus. A sulcus extends posteriorly from the anterior opening, terminating immediately anterior to the maxilla/palatine suture. The anterior maxillary artery and alveolar nerve were therefore not canalized entirely along the length of the maxilla. The connecting ramus of the

palatine is perforated, however, permitting the progress of the artery and nerve to the sulcus of the anterior alveolar canal. The facet for the palatine is not recessed but is a smooth area of the alveolar shelf between the posterior opening of the alveolar canal and the entrance to the sulcus of the anterior opening. A small foramen on the dorsomedial margin of the palatine facet receives a branch of the alveolar nerve/blood vessel, which exits the lateral surface of the palatine ramus. There is a shallow recess on the lateral margin of the posterior alveolar shelf, which receives the suborbital process of the jugal.

The maxillary tooth row occupies a shallow groove on the ventral surface of the alveolar shelf. Of the 30 alveoli that are present in the left maxilla, 22 contain partly or fully developed teeth. The scan reveals the apices of replacement teeth erupting from the labial surface of several alveoli. Dental implantation is broadly 'subthecodont' (*sensu* Fraser and Shelton 1988) with thin interdental plates. The labial wall of the alveolar row is slightly taller that the lingual wall, which is comprised of low, triangular paradental plates. Small ventral apices demarking the limit of each tooth position can be seen along the labial surface in lateral view. The dentition is homodont. The anterior six maxillary teeth are slightly larger that the premaxillary teeth and the 7th to 14th maxillary teeth are the largest of the marginal dentition. Thereafter the teeth reduce in size with the two posteriormost teeth slightly smaller than those of the premaxilla. All maxillary teeth are sharply pointed, conical and slightly recurved with no carinae.

2.4.1.4 Septomaxilla

Both septomaxillae of OMNH 74606 are preserved disarticulated within the narial cavity and are visible in lateral view through the left external naris (Fig.1A,B). As preserved, the right septomaxilla is anterior to the left and its medial surface is visible externally. The left septomaxilla has been displaced so its ventral surface is exposed. The septomaxilla is preserved in many early sauropsids and synapsids (e.g. the captorhinid *Euconcordia*, Müller and Reisz 2005b; Reisz *et al.* 2016; the synapsid *Archaeovenator*, Reisz and Dilkes 2003; the diapsids *Petrolacosaurus*, Reisz 1981; and *Prolacerta*, Camp 1945; and the parareptile *Delorhynchus*, Reisz *et al.* 2014). However, because the septomaxilla is typically embedded in matrix within the narial cavity, 3D information is only available for a few taxa such as *Dimetrodon limbatus* (Romer and Price 1940) and the parareptile *Milleretta* (Gow 1972).

The septomaxilla of *Orovenator* is a complex bone. A sheet-like ventral plate

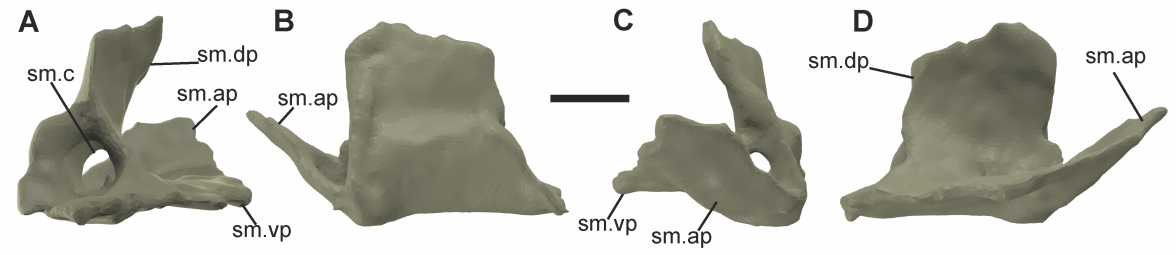


Figure 6: *Orovenator mayorum* (OMNH 74606), left septomaxilla. A, posterior view; B, lateral view; C, anterior view; D, medial view. *Abbreviations*; sm.ap, anterior process of septomaxilla, sm.c, septomaxillary canal; sm.dp, dorsal process of septomaxilla, sm.vp, ventral plate of septomaxilla. Scale bar represents 0.5 mm.

extends medially as an anteroposteriorly broad medial shelf (Fig.6A). The anterior portion of the ventral plate is inflected anterodorsally to form a sub-triangular anterior process (Fig.6B). This process extends at an angle of 45° from the ventral plate, originating at the ventral margin of the anterior opening of the septomaxillary canal and probably resting on the premaxilla ventrally. An anteroposteriorly-oriented septomaxillary canal is enclosed ventrally by the ventral plate and laterally and medially by laminae that met at the apex of the canal. From this apex a mediolaterally thin, sub-rectangular dorsal process inclines dorsomedially (Fig.6C).

The ventrolateral ridge of the septomaxilla articulates into a shallow recess on the dorsal surface of the anteriormost region of the alveolar shelf of the maxilla. The septomaxilla is therefore positioned centrally in the narial cavity (Fig.3A). The sheet-like dorsal process extends dorsomedially from the apex of the septomaxillary canal and terminates close to the dorsal margin of the external nares, virtually subdividing the narial opening into anterior and posterior orifices. This is somewhat similar to the position of the septomaxilla as described in the varanopid *Archaeovenator* (Reisz and Dilkes 2003). The ventral plate partially floors the narial chamber and encloses the anterodorsal surface of the vomer. The medial margin of the ventral plate probably extended to meet its partner at the midline of the snout.

Conflicting accounts exist of the morphology of the septomaxilla among early reptiles. The septomaxilla of *Captorhinus laticeps* (as *Eocaptorhinus laticeps*) is described as a 'thin, rectangular sheet of bone that has been curved around a basic conical form' (Heaton 1979, p. 23, fig.14). This funnel-like element had a lateral opening in the form of a C-shaped lamina visible within the narial cavity and a smaller medial opening lying adjacent to the anterior vomer. Heaton further suggested that the septomaxillae of other early sauropsids were similar to this morphology where preserved. Indeed, *Captorhinus*, along with *Paleothyris*, *Petrolacosaurus* and *Youngina*, is scored as possessing a septomaxilla shaped as a curled sheet in the character-taxon matrix of Reisz

et al. (2010). This view was questioned by Modesto *et al.* (2007), who described the septomaxilla in the early Permian captorhinid *Labidosaurus* as 'an irregular convoluted bone', with a ventral lamina, a peaked medial process and dorsal process (Modesto *et al.* 2007, p. 239).

The main features of the septomaxilla in *Orovenator* are present in several taxa where the septomaxilla has been adequately described. A ventral or horizontal plate is found in *Dimetrodon limbatus* (Romer and Price 1940), in the captorhinid *Labidosaurus* (Modesto *et al.* 2007) and in extant amphisbaenians and uropeltid snakes (Maisano *et al.* 2006; Olori and Bell 2012). The dorsal process, slightly medially inclined in *Orovenator* and *D.limbatus*, is also present in the Permian parareptiles *Colobomycter pholeter* (MacDougall *et al.* 2017a) and *Milleretta rubidgei* (Gow 1972), in the varanopid *Varanops* where it is exposed facially (Campione and Reisz 2010), the ophiacodontid *Varanosaurus* (Berman *et al.* 1995), and *Labidosaurus* (Modesto *et al.* 2007). In some extant squamates, the dorsal process curves dorsomedially to form the roof of a vaulted chamber that accommodates the vomeronasal organ (e.g. amphisbaenians, Maisano *et al.* 2006; gekkotans, Rieppel *et al.* 2008; and anilioid snakes, Rieppel 2007).

The phylogenetically broad distribution of similar features of the septomaxilla is consistent with a shared function that may be plesiomorphic for amniotes. Watson (1914) and Hillenius (2000) suggested that the septomaxillary canal of early synapsids housed the anterior progression of the nasolacrimal duct towards the vomeronasal organ (VNO), a paired chemosensory organ located in the anterior of the snout in some extant tetrapods (Bertmar 1981). In extant squamates, the VNO is enclosed by the vomer ventrally and the septomaxilla dorsally (Rieppel *et al.* 2008) and is connected to the vomeronasal duct either directly, as in snakes, or indirectly, as in most other squamates, via an opening at the anterior end of the choanal groove (Hillenius and Rehorek 2005). *Orovenator* provides the earliest known example of a three-dimensionally preserved septomaxilla in diapsids, which together with the well-developed nasolacrimal duct of the lacrimal (Fig.5B), suggests a similar function to that proposed for early synapsids (Hillenius 2000).

2.4.1.5 Lacrimal

The left lacrimal of OMNH 74606 is almost complete, lacking only a section of the anterodorsal lamina and a posterodorsal portion that contacted the prefrontal. Only fragments of the right lacrimal are preserved. The posterodorsal portion of the lacrimal, including the prefrontal contact, is best preserved in the right lacrimal of OMNH

74607. The lacrimal is comprised of a posteriorly-located ventral process that overlaps the anterolateral surface of the prefrontal and forms the anteroventral margin of the orbit ventrally, and a dorsally located anterior process that overlaps the dorsolateral margin of the nasal and attenuates anteriorly to form the posterodorsal margin of the external naris (Fig.3). The dorsal and dorsolateral surfaces are thin bone, and the sinuous ventral surface is thickened medially to accommodate the nasolacrimal canal and the epithelial tube housed within it, the nasolacrimal duct (*sensu* Witmer 1997). The contact between the lacrimal and the external naris is transversely narrow. It forms the posterior margin of a distinctive posterodorsal extension of the external naris, enclosed dorsally by the nasal and ventrally by the maxilla. A prominent posterodorsal extension is considered to be a synapomorphy of varanopids (Reisz and Dilkes 2003; Reisz *et al.* 2010).

The lacrimal has an anterodorsal surface that meets the lateral surface at a right angle, forming a rounded antorbital ridge (Reisz *et al.* 2011a). This ridge extends anteriorly along the dorsolateral surface of the snout from the prefrontal posteriorly to the posterodorsal extension of the external naris. This morphology of the lacrimal is unique amongst early amniotes and is probably autapomorphic in *Orovenator*.

The dorsal surface of the lacrimal slopes anteroventrally towards the tip of the snout where it bears a transversely narrow anterior process that makes a small contribution to the posterodorsal margin of the external naris, preventing contact between the maxilla and the nasal. The sinuous ventral margin of the lacrimal is overlapped by the maxilla along most of its anteroposterior length. Posteroventrally it contacts the anteromedial surface of the suborbital process of the jugal.

The ventral process of the lacrimal bears a posteriorly-directed orbital shelf, which extends from the mid-point of its contact with the prefrontal to the posteroventral tip of the lacrimal. This shelf contributes to the anteroventral margin of the orbit. In OMNH 74607, a deep conjunctival groove can be seen on the surface of this shelf. The ventral process of the prefrontal over-lies the orbital shelf of the lacrimal medially (Fig.5). The lacrimal/prefrontal contact extends anteromedially along the dorsal surface of the skull up to the lateral margin of the nasal. In this region the lacrimal attains its greatest mediolateral width, and overlaps a lateral shelf on the dorsal surfaces of both the prefrontal and the nasal (Fig.3C).

An anteroposteriorly elongate lacrimal that contributes to the orbit and bears a long anterior process that contacts the external naris is primitively present in amniotes (deBraga and Rieppel 1997). This morphology is retained in most early sauropsids, as seen in all non-diapsid eureptiles, including captorhinids (Fox and Bowman 1966; Car-

roll 1969; Heaton 1979) and in many early synapsids (Romer and Price 1940; Langston and Reisz 1981; Reisz and Dilkes 2003; Spindler *et al.* 2018). The lacrimal of araeoscelidian diapsids makes an extensive contact with the external naris, and this is facilitated by the presence of a dorsoventrally low maxilla (Reisz 1981; Reisz *et al.* 1984). *Orovenator* exhibits an intermediate condition, in which the presence of a dorsal process of the maxilla constricts the lacrimal contact with the external naris. In later Permian neodiapsids (*Lanthanolania*, Modesto and Reisz 2002; and *Acerosodontosaurus*, Bickelmann *et al.* 2009) and some varanopids (*Mesenosaurus*, Reisz and Berman 2001; and *Mycterosaurus*, Berman and Reisz 1982) a tall dorsal process of the maxilla excludes the lacrimal from the external naris altogether.

The thickened ventromedial surface of the lacrimal bears a prominent ridge anteriorly (Fig.5A). The ventral surface of this ridge is transversely concave (arcuate), and anterolaterally bears an elliptical facet that contacts and is supported ventrally by the medial crest of the maxilla. The ridge forms the ventral wall of the nasolacrimal canal. The pathway of the nasolacrimal canal can be traced posteriorly to three openings on the orbital shelf of the lacrimal. Two larger lacrimal puncti open into the conjunctival groove and a third smaller foramen into a medial groove close to the posterior tip of the lacrimal. The canaliculi leading from the three orbital openings conjoin anteriorly. Two more canaliculi branch off the main canal, one opens dorsally, another pierces the ventral wall of the canal (Fig.5B).

Foramina entering the posterior surface of the lacrimal from the orbital margin have been documented in several other early eureptiles. Two such foramina are reported in the basal captorhinid *Euconcordia* (Müller and Reisz 2005b), the early Permian captorhinid *Reiszorhinus* (Sumida *et al.* 2010) and in the archosauromorph *Prolacerta* (Gow 1975). Three foramina have been described in *Petrolacosaurus* and *Captorhinus laticeps* (Heaton 1979; Reisz 1981) both with two large puncti within the conjunctival groove and a third medial to them, a configuration very similar to that of *Orovenator*. The pathways of the internal canals are unknown in most of these taxa. However, the nasolacrimal canal of *Captorhinus laticeps* has been described with two canaliculi forming a single lacrimal canal, joined at their junction by a third canaliculus identified as housing the anterior orbital artery (Heaton 1979).

A deep cavity occupies the medial surface of the snout, bounded by the ventral surface of the nasolacrimal canal dorsally, the 'supracanine' buttress of the maxilla anteriorly, the alveolar shelf of the maxilla ventrally and the thin dorsal process of the maxilla laterally. This depression, and the elements that enclose it, is strikingly similar to the morphology of the medial surface of the snout in *Prolacerta*, which

lacks an antorbital fenestra (Gow 1975). The antorbital fenestra is a synapomorphy shared by crown-group archosaurs and by some members of their stem-lineage (Witmer 1997). The implications of this particular morphology are explored further below (see Discussion).

2.4.1.6 Prefrontal

The prefrontal in *Orovenator* is a triradiate element with an extensive and mildly concave dorsal surface. It provides the anterior and anterodorsal margin of the orbit. Both prefrontals are partially preserved in OMNH 74607. The most complete example is the left prefrontal of OMNH 74606, which is largely in articulation with the surrounding elements. The prefrontals are identical in both specimens, apart from several conspicuous foramina on the dorsal surface of the mature individual, OMNH 74607 (Fig.7A).

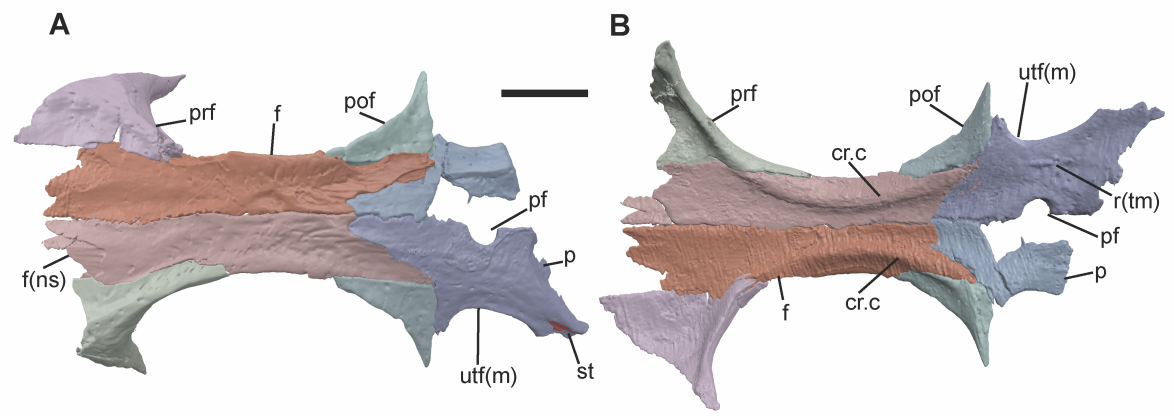


Figure 7: *Orovenator mayorum* (OMNH 74607), reconstruction of skull roof. A, dorsal view; B, ventral view. *Abbreviations*; f, frontal; f(ns), cr.c, crista cranii; narial shelf of frontal; p, parietal; pf, pineal foramen; pof, postfrontal; prf, prefrontal; r(tm), ridge for taenia marginalis; st, supratemporal, utf(m), medial margin of upper temporal fenestra. Scale bar represents 5mm.

The dorsal surface of the prefrontal is a thin sheet of bone with a triangular outline. It meets the ventral process at approximately 90° forming a distinct contrast between the dorsal and lateral surfaces of the antorbital region, which is continued anteriorly by the lacrimal (Fig.7A). The anterolateral margin bears a broad shelf-like recess that receives the lacrimal. Medially, the prefrontal overlies a similar recess on the nasal. The dorsal exposure of the prefrontal and the right-angled union with the lateral process is absent in other early diapsids (e.g. *Petrolacosaurus*; Reisz 1981 and pers. obs. KUVP 9952 and *Youngina*; pers. obs. BP/1/2871) but is present in the varanopids *Mesenosaurus* (Reisz and Berman 2001) and *Elliotsmithia* (Reisz *et al.*1998).

The posterior process of the prefrontal is a thick, posteriorly-tapering ramus of bone, which forms the anterodorsal margin of the orbit. The medial surface of this ramus is almost entirely occupied by a deep facet for the frontal. In ventral view the posterior process conjoins with the *crista crani* of the frontal, which transitions ventrally into the concave orbital rim of the prefrontal. This is best observed in OMNH 74607 (Fig.7B).

The ventral process of the prefrontal forms the anterior margin of the orbit. Much of the ventrally-tapering ramus is obscured in lateral view by the lacrimal and the suborbital process of the maxilla. Ventrally, the descending ramus remains in close contact with the medial surface of the orbital shelf of the lacrimal and extends ventrally to make a broad contact with the maxillary ramus of the palatine (Fig.5B). A small foramen pierces the medial surface of the ventral tip of the prefrontal, which coincides with a foramen on the lateral surface of the maxillary ramus of the palatine. This would have carried blood vessels from the maxillary artery as is passed through the maxillary ramus of the palatine.

The posteromedially directed orbital rim serves as an attachment for the orbitonasal membrane, separating the orbital and nasal capsules. Laterally, this rim extends to form the anteromedial wall of the orbit. This is best seen in medial view, where it joins with the dorsal and lateral regions in a deep concavity (Fig.7B). This concavity corresponds with the maximum transverse width of the antorbital region and may have housed the laterally expanded flanges of the olfactory lobe.

2.4.1.7 Nasal

Only the partial left nasal of OMNH 74606 is preserved. It is an elongate, dorsoventrally thin sheet of bone posteriorly, and becomes curved anteriorly such that the dorsal surface is mildly convex posterior to the external naris. The anteromedial process, which would have contacted the dorsal process of the premaxilla medially, is not preserved. Given the morphology of the premaxillae it is likely that the nasals had a long anteromedial process, which separated the dorsal processes of the premaxillae and terminated far anteriorly, close to the tip of the snout. The median contact surface for the right nasal cannot be distinguished. The nasal is almost entirely exposed on the dorsal surface of the snout, with a limited lateral exposure of the anterior region.

The dorsoventrally narrow supranarial process of the nasal is elongate, comprising some 25% of the lateral length of the bone, reflecting to some degree the anteroposteriorly long external naris. This is unusual in early diapsids where the contribution

of the nasal to the external naris is small compared to its anteroposterior length (e.g. *Youngina* and *Prolacerta*, Gow 1975; and *Lanthanolania*, Modesto and Reisz 2002). An elongate supranarial process of the nasal is associated with an anteroposteriorly elongate external naris in varanopids (Reisz and Dilkes 2003). In *Orovenator* the process is mediolaterally thin and would have underlain the lateral margin of the dorsal process of the premaxilla.

A narrow shelf of bone extends from the lateral surface of the nasal for the lacrimal (anteriorly) and the prefrontal (posteriorly). The posteriormost region of the lateral surface of the nasal bears a slot recess that forms a tongue and groove contact with the prefrontal. Posteriorly the nasal overlaps a broad V-shaped shelf between the anterolateral and anteromedial processes of the frontal (Fig.7A). The suture between the paired nasals and frontals is W-shaped, with a broad posterolateral extension of the nasal. The posteromedial region of the dorsal surface of the nasal is slightly depressed such that it lies below the level of the posterolateral region, and would have been overlain by the anteromedial process of the frontal.

2.4.2 Skull roof and orbital region

The skull roof of *Orovenator*, as in many early diapsids, is mildly convex, sloping gently posteroventrally in the postorbital region, and sloping more steeply anteroventrally, anterior to the orbit (Fig.3A). The postorbital region is anteroposteriorly short along the midline, and the parietals are deeply excavated posterodorsally. The large sub-circular pineal foramen is positioned on the midline within the posterior half of the parietals. The upper temporal fenestra, as indicated by the lateral excavation of the parietal, was probably the smaller of the two temporal openings. Because the postorbital, quadratojugal and squamosal are not preserved, it is not possible to confirm the completion of the ventral bar or the size and shape of the lower opening. Nevertheless, given the length of the dorsal and posterior processes of the jugal and the articular facets of the postfrontal and parietals for the postorbital, it is likely to have had at least twice the total area of the upper temporal fenestra. The orbits are large, subcircular and contain several articulated scleral ossicles. In the larger individual, OMNH 75607, the frontals, parietals, prefrontals and postfrontals bear a number of foramina, many of which are associated with small grooves in the bone surface.

2.4.2.1 Frontal

The frontals are anteroposteriorly long, paired elements of the skull roof. Only the anterior parts of the frontals of OMNH 74606 are preserved. The paired frontals of *Orovenator* are best represented in OMNH 74607, where both elements are almost complete (Fig.2). The frontals are relatively slender and elongate bones, as noted by Reisz *et al.* (2011a). They contact the nasals anteriorly and prefrontals anterolaterally, extending into the antorbital region of the snout. Posteriorly they contact the parietals and posterolaterally the postorbitals. The frontals make anteroposteriorly broad contributions to the dorsal margins of the orbits. They are slightly concave along the orbital margin and do not possess a lateral lappet. The interorbital width of the frontals is narrow, being approximately 35% of their total median length. The maximum transverse width, approximately 44% of the median length, is level with the anterior margin of the orbit. Medially the paired frontals are sutured by a scarf joint, with the right frontal providing the dorsal overlap. The ventral surface of the frontal has a prominent *crista crani* extending along the dorsal margin of the orbit (Fig.7B). The suture with the prefrontal consists of a tongue and groove anteriorly, and a dorsoventrally deep, rugose articular surface posteriorly, which fits into a wedge-shaped facet on the medial surface of the anterior process of the prefrontal.

An anteromedial process and a smaller anterolateral process extend from the anterior region of the frontal (Fig.7A). A thin sheet of bone extends from the ventral surface of the frontal between these two processes and is overlain by the posterolateral process of the nasal. The anteriormost region of the anteromedial process of the frontal overlies a shallow depression on the posteromedial surface of the nasal. Consequently, contact between the frontal and nasal is distinctive: the nasal overlies the frontal laterally, and the frontal overlies the nasal medially. The prominent posterolateral process of the frontal extends at an acute angle to make contact with the entire dorsal margin of the postfrontal, thus excluding the parietal from contact with the dorsal margin of the postfrontal. A deep facet in the posterolateral margin of the frontal accommodates the postfrontal.

In the smaller individual, OMNH 74606, the dorsal surface of the frontal is relatively smooth, with only a few foramina evident. In the larger individual, OMNH 74607, the dorsal surface of the frontal exhibits several foramina (Fig.7A). The absence of these from the smaller individual suggests that development of foramina and shallow grooves on the dermal bones occurred during ontogeny. Foramina occupy the anterodorsal surface of the frontal and continue to the supraorbital area. Some of these foramina are associated with small anteriorly or laterally directed grooves. The grooves associated

with the posterior foramina are more pronounced, such that a series of conspicuous posteriorly directed furrow-like grooves striate the posterodorsal surface of the frontal of OMNH 74607.

2.4.2.2 Parietal

The paired parietals make up the posterior skull roof. Only the left parietal of OMNH 74607 is completely preserved, together with a fragment of the right parietal.

They have a prominent anteromedial process that contacts the frontals, a concave posterolateral margin to accommodate the upper temporal fenestra, and a posterolateral process that contributes to a deeply embayed occipital margin. The dorsal surface of the parietal slopes posteroventrally and follows the curvature of the frontal.

The anteroposteriorly elongate anteromedial process of the parietal incises deeply into the frontal, extending into the supraorbital region and tapering anteriorly, as in the later diapsids *Youngina* and *Prolacerta* (pers. obs. BP/1/3859 and BP/1/4504) and varanopids (Reisz and Berman 2001). There is a small recess between the anterior tips of the paired anteromedial processes of the parietals into which fits a short posteromedial process of the frontals (Fig.7A). Contact of the parietal with the postfrontal is limited to a weakly convex surface on the posterodorsal margin of the postfrontal. A deep notch separates the suture ventrally to accommodate the dorsal process of the postorbital.

The lateral surface of the parietal is embayed by the upper temporal fenestra posteriorly. This rim lacks the ventrolateral flange present in later diapsids such as *Prolacerta* (pers. obs. BP/ 1/3575), *Claudiosaurus* (Carroll 1981) and *Pamelina* (Evans 2009). The embayment of the lateral surface of the parietal is deeper than that of *Petrolacosaurus*, as noted by Reisz *et al.* (2011a), and the upper temporal fenestra is visible in dorsal view. The posterolateral process extends posteriorly beyond the posterior margin of the upper temporal fenestra. Laterally this process bears a deep groove to receive the mediolaterally thin supratemporal and the dorsal ramus of the squamosal (Fig.7A).

A large, subcircular pineal foramen is present on the median suture of the parietals. Its anterior margin is almost level with that of the upper temporal fenestra, as in *Petrolacosaurus* (Reisz 1981). However, the pineal foramen is situated entirely in the posterior half of the parietal midline, unlike *Petrolacosaurus* where the pineal foramen is positioned at the midpoint of the parietals (Fig.7). A shallow raised platform of bone surrounds the pineal foramen. It is irregular in shape and extends from a transversely narrow region at the posterior medial margin of the parietal to an extensive region

lateral and anterolateral to the foramen.

The position of the pineal foramen varies amongst early amniotes and is phylogenetically informative (Reisz and Dilkes 2003; Reisz *et al.* 2010; Ezcurra *et al.* 2014). In all early synapsids the pineal foramen is located posteriorly, with the exception of caseasaurs in which the foramen is anteriorly positioned. Indeed, a posteriorly located pineal foramen has been proposed as a synapomorphy of 'eupelycosauria' (i.e. all early synapsids except caseasaurs and including varanopids; deBraga and Rieppel 1997). This condition, which can also be found in *Orovenator*, is otherwise rare in eureptiles, with only *Paleothyris* (pers. obs. MCZ 3483) and *Youngina* (pers. obs. BP/1/ 3859) showing a similar morphology.

There is a deep bilateral embayment on the posterior margin of the parietals. A small, posteriorly-directed spur extends from the posterior end of the parietal median suture, in the centre of this embayment. This may represent a nuchal crest. A thin lamina of bone extends posteroventrally from the embayed posterior margin of the parietal, identified as an occipital flange (Reisz *et al.* 2011a) (Fig.8A). The surface of the flange is relatively smooth, with a transverse sulcus ventral to the posterior rim of the parietal, which probably accommodated the dorsal margin of the postparietal and tabular, neither of which is preserved. The flange extends posteroventrally at an angle of approximately 45° from the posterior rim of the parietal, suggesting that the occipital region may have sloped strongly posteroventrally.

Several small foramina are present on the dorsal surface of the parietal, medial to the margin of the upper temporal fenestra. On the ventral surface, a small anteroposteriorly-orientated ridge lies between the pineal foramen and the medial margin of the upper temporal fenestra (Fig.7B). This corresponds to a similar ridge found in *Petrolacosaurus*, identified by Reisz (1981) as the point of attachment of the cartilaginous *taenia marginalis*, a dorsal extension of the chondrocranium, connecting the otic capsule with the braincase (Romer 1956).

The scan of *Orovenator* allows, for the first time, a direct comparison between the left parietal of OMNH 74607 and a right parietal (YPM 4926) described as a diapsid from the fissure-fill limestone of Fort Sill, western Oklahoma (Carroll 1968). Whilst the general morphology is strikingly similar there are significant differences (Fig.8). The pineal foramen in YPM 4926 is much larger and ovoid in shape. The embayment for the upper temporal fenestra is more extensive medially and differs from OMNH 74607 in its anterior curvature. Although only observed in the photograph provided in Carroll (1969 fig.1, the surface appears quite smooth and lacks the raised platform of *Orovenator*. The posterolateral process of YPM 4926 is significantly narrower and

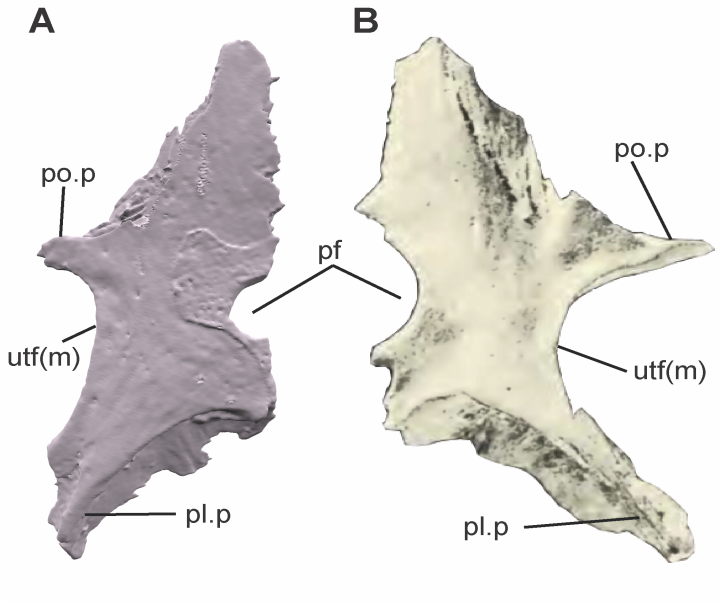


Figure 8: Comparison of diapsid-like parietals. A, left parietal of OMNH 74607; B, right parietal (YPM 4926). *Abbreviations*: pf, pineal foramen; pl.p, posterolateral process; po.p, postorbital process; utf(m), medial margin of upper temporal fenestra. Image of YPM 4926 from Carroll (1968)

more laterally orientated than OMNH 74607. I therefore agree with Reisz *et al.* (2011a) that YPM 4926 is not attributable to *Orovenator mayorum* and represents a different diapsid taxon.

2.4.2.3 Postfrontal

Both postfrontals are complete and preserved in articulation with the frontal and parietal in OMNH 75607 (Fig.2). The postfrontal is a small triangular bone that forms the posterodorsal corner of the orbital margin, contacting the frontal dorsally, the parietal posterodorsally and the postorbital posteroventrally. The anterodorsal process is slightly longer than the ventral process, which it meets posteromedially at an angle of approximately 90°. The dorsolateral surface of the postfrontal bears more than a dozen foramina of various sizes distributed principally along its medial and posterior margins.

The medial articular surface of the postfrontal for the frontal is broad and rugose. It bears a narrow, anteroposteriorly-orientated ridge that fits into a deep recess on the posterolateral surface of the frontal. A small shelf of bone extends posteriorly from the ventral surface of the posterodorsal corner of the postfrontal and is overlain by the parietal. This is unlike the situation in *Petrolacosaurus*, in which a shelf on the parietal underlies the postfrontal (Reisz 1981). The postfrontal of *Orovenator* is prevented from contributing to the upper temporal fenestra by contact between the

parietal and the postorbital, the dorsal ramus of which is accommodated by a deep notch formed between the ventrolateral processes of the postfrontal and parietal.

The exclusion of the postfrontal from the upper temporal fenestra by contact of the parietal and postorbital is plesiomorphic in diapsids. This morphology was present in the earliest diapsids *Petrolacosaurus* (Reisz 1981) and *Araeoscelis* (Vaughn 1955), and in later neodiapsids (e.g. *Lanthanolania* and *Youngina*; Reisz *et al.* 2000; Modesto and Reisz 2002). The plesiomorphic condition also appears in early archosauromorphs such as *Prolacerta* (Modesto and Sues 2004), *Macrocnemus* (pers. obs. C 111 (MCSNM)) and *Tanystropheus* (Nosotti 2007). In early non-diapsid amniotes (early synapsids, captorhinids and parareptiles) the parietal/postorbital contact is almost universal. Exceptionally, such contact is prevented by the postfrontal and supratemporal in the parareptile *Acleistorhinus* (deBraga and Reisz 1996).

The derived condition, where the postfrontal prevents contact between the parietal and postorbital, is first observed in *Acerosodontosaurus* and *Hovasaurus* (Currie 1980, 1981). Although Bickelmann *et al.* (2009) queried this interpretation in *Acerosodontosaurus* due to the poor preservation of the skull roof. It is present convergently in early lepidosauromorphs (Evans 1991; Evans and Borsuk-Białynicka 2009) and extant lepidosaurs (Evans 2008).

2.4.2.4 Supratemporal

The anterior portion of the left supratemporal is preserved in situ in OMNH 74607, within a groove on the lateral surface of the posterolateral process of the parietal (Fig.2D). It is a mediolaterally thin, anteroposteriorly-elongate bone, which probably extended to the tip of the posterolateral process of the parietal, with a slight posteromedial curve. It is excluded from any participation in the upper temporal fenestra by the squamosal and parietal. A thin lamina of bone extends from the ventral margin of the supratemporal. Anteriorly this lamina fits into a small facet on the parietal, and posteriorly it would have been overlain by the squamosal.

2.4.2.5 Jugal

The right jugal of OMNH 74606 is almost completely preserved, with only the anterior region and dorsolateral surface of the suborbital process missing (Fig.1D). A deep subcircular cavity of uncertain origin is located on the lateral surface of the dorsal process near its origin ventrally (Fig.3A). Only the suborbital process of the left jugal of OMNH 74606 is preserved, in articulation with the maxilla and lacrimal. This

element provides valuable data on the nature of the anterior contact and overall length of the jugal, which is absent on the right side.

The jugal is a distinctly triradiate bone. The suborbital process is anteroposteriorly elongate and extends to the level of the anterior orbit margin. The posterior process attenuates posteriorly to a fine point and is orientated slightly posteromedially. This process provides the anteroventral bar to the lower temporal fenestra (in taxa with 'diapsid' or 'synapsid' skulls). The dorsal process of the jugal is anteroposteriorly broad at its origin in central region of the jugal. It is orientated posterodorsally and somewhat medially, tapering to a point along its length. The suborbital and dorsal processes jointly form the posteroventral margin of the orbit.

The suborbital process of the jugal is mediolaterally thin and blade-like, tapering slightly towards the anterior tip to terminate in a smoothly round point. The ventral surface of the posterior half of the process fits into a shallow recess on the posterior part of the maxilla. Only the posterior half of the suborbital process is visible in lateral view. The anterior half contacts the medial surface of the maxilla. The posterior process of the lacrimal overlies the anterior region of the jugal medially, such that it is enclosed between the maxilla and the lacrimal (Fig.5).

The posterior or subtemporal process of the jugal is a slender, tapering component that terminates in a fine point. There is no evidence of a facet for contact with the quadratojugal on the lateral or medial surface of the posterior process, which is smooth and featureless. Nevertheless, in the absence of the preservation of the quadratojugal, the completion or non-completion of the ventral bar of the lower temporal fenestra cannot be unequivocally determined. The dorsal process of the jugal is triangular in cross-section, with a mediolaterally broad orbital rim and a blade-like posterior margin. The lateral surface bears a shallow depression that probably received the ventral process of the postorbital.

2.4.2.6 Scleral ossicles

An articulated series of seven partially or completely preserved scleral ossicles, and two further disarticulated ossicles, lie within the orbit of OMNH 74606 (Fig.1B). The more complete examples are thin irregular rectangular sheets of bone, approximately twice as long radially as wide circumferentially. Exteriorly the surface is convex along its long axis (i.e. radially). The lateral surface does not taper towards the aperture, unlike in ichthyosaurs (McGowan and Motani 2003), and inter-ossicular contact is entirely limited to unidirectional overlapping sutures rather than irregular overlapping or abutting sutures, particularly towards the aperture where the contact is most extensive. Both

internal and external surfaces are smooth. Each ossicle overlaps its neighbour in a clockwise direction.

Although many groups of vertebrates possess scleral cartilage, fewer possess both the scleral cartilage and ossicles that form the sclerotic ring. The sclerotic ring is common in teleost fish, and several groups of extant sauropsids: testudines, birds and most squamates except snakes (Atkins and Franz-Odendaal 2016). In extinct taxa, scleral ossicles were present in seymouriamorphs (Klembara 1997), early synapsids, therapsids and basal cynodonts (Angielczyk and Schmitz 2014), some captorhinids and many archosaurs, including dinosaurs (Romer 1956). Preserved examples amongst early fossil diapsids are quite rare. They are present in *Petrolacosaurus* (Reisz 1981) and some archosauromorphs (e.g. *Prolacerta*, Camp 1945; and *Tanystropheus*, Nosotti 2007).

Orovenator is estimated to have possessed 19 scleral plates, based on a virtual reconstruction of the orbit and sclerotic ring in the present study (see Appendix 3, Fig.1). This is a relatively high number of plates compared to estimates from other diapsids: 14 plates are reported in *Prolacerta* (Romer 1956), 12 in the Triassic marine reptile *Askeptosaurus* (Müller 2005) and 12 in the archosauromorph *Euparkeria* (Sookias and Butler 2013). However, the reduction in the number of scleral plates may be a derived feature of later diapsids, since up to 20 plates are reported in late Carboniferous tetrapod *Gephyrostegus bohemicus* (Klembara *et al.* 2014), up to 19 in the early Permian synapsid *Sphenacodon ferox* (Spielmann *et al.* 2010) and as many as 40 in the seymouriamorph *Discosauriscus* (Klembara 1997).

2.4.3 Palate, palatoquadrate and braincase

All elements of the palate are present in OMNH 74606, permitting an accurate reconstruction (Fig.9). The choanae are extremely elongate, incising deeply into the anterior surface of the palatines. Although the medial surface of the left pterygoid is missing, the pterygoids probably contacted each other on the midline for approximately half the length of the palatal ramus, limiting the anterior extent of the interpterygoid vacuity. All elements of the palate bear teeth, including the ectopterygoids and the cultriform process of the parabasisphenoid. The suborbital fenestrae are very narrow mediolaterally, more so anteriorly where the lateral margin of the palatine closely approaches the maxilla. The presence of a suborbital opening has been proposed as an autapomorphy of sauropsids (deBraga and Rieppel 1997). It is generally present as a small foramen in captorhinids (Romer 1956; Heaton 1979) and is enlarged to a fenestra in diapsids

(Laurin and Reisz 1995). It is absent in synapsids (Romer and Price 1940). In early diapsids such as *Petrolacosaurus* (Reisz 1981) and *Youngina* (Carroll 1981) the suborbital fenestra is anteroposteriorly long and moderately broad. Therefore, the narrow suborbital fenestra in *Orovenator* is somewhat anomalous for early diapsids.

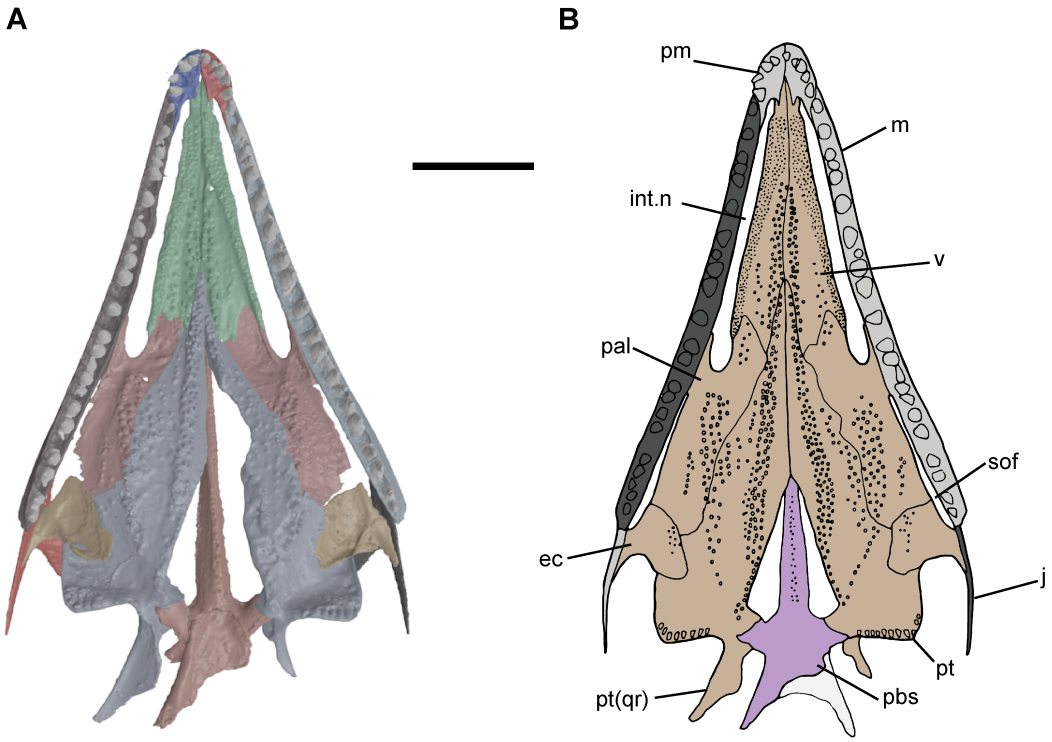


Figure 9: *Orovenator mayorum* OMNH 74606, reconstruction of palate. A, ventral view. B, interpretive drawing of A, highlighting hypothetical morphology of missing elements (white), palatal elements (beige), basicranial elements (mauve), mirrored elements (dark grey)and dermal elements (light grey). *Abbreviations*: ec, ectopterygoid; int.n, internal naris (choana); j, jugal; m, maxilla; pal, palatine; pbs, parabasisphenoid; pm, premaxilla; pt, pterygoid; pt(qr), quadrate ramus of the pterygoid; sof, suborbital fenestra; v, vomer. Scale bar represents 5 mm.

2.4.3.1 Vomer

The paired vomers are unfused anterior elements of the palate that contact the premaxillae anteriorly, the palatines posteriorly, and the pterygoids posteromedially. Both vomers are preserved in OMNH 74606. In ventral view the vomers are anteroposteriorly elongate triangular bones. They bear two distinct longitudinal series of denticles: a medial series of larger denticles and a lateral array of smaller denticles. The vomers form the medial margins of the choanae and are joined along the midline of the palate for three-quarters of their length. A narrow shelf extends medially from the right vomer and overlies the dorsal surface of the left vomer.

Anteriorly, the vomer contacts the premaxilla in an asymmetrically bifurcated suture consisting of a small anterolateral process and a larger anteromedial process which joins its partner on the midline (Fig.4C). The vomerine process of the premaxilla fits into the notch between these anterior processes of the vomer. The lateral surface of the vomer forms the medial margin of the choana along its entire length. Posteriorly it is overlain by the palatine dorsally, forming a V-shaped suture. The tapering anterior palatal process of the pterygoid contacts the posteromedial margin of the vomer.

Two irregular rows of large denticles extend anteriorly from the contact with the pterygoid along the medial region of the ventral surface the vomer. An array of smaller denticles situated on a low ridge extends from the lateral contact with the palatine and converges anteriorly with the larger denticles. A longitudinal median ridge extends along the anterodorsal surface of the vomers, similar to that of *Petrolacosaurus* (Reisz 1981), where it probably supported the cartilage of the inter-nasal septum. A low dorsal ridge is also present laterally, resulting in a U-shaped cavity on the anterodorsal surface of the vomer.

2.4.3.2 Palatine

The palatines are paired, lateral bones, both of which are preserved in OMNH 74606. Each contacts the vomer anteriorly, the pterygoid medially and the ectopterygoid posteriorly. The palatine is a dorsoventrally thin, sheet-like bone that is trapezoidal in ventral view, with a lateral maxillary ramus that anchors the palate to the alveolar shelf of the maxilla (Figs 5B, 9). The palatine is deeply incised by the choana anterolaterally such that the posterior region of the choana is enclosed between the palatine medially and laterally. A narrow field of large denticles extends anterolaterally from the posterior border with the pterygoid to the maxillary ramus. Several denticles are also present on the anteromedial region of the ventral surface of the palatine, which continue onto the posterior region of the vomer.

The anterior portion of the palatine is a triangular sheet of bone that tapers anteriorly. It overlaps the dorsal surface of the vomer. The lateral margin of the anterior portion of the palatine bears a ventral ridge posteriorly where it meets the maxillary ramus. The palatine is inflected to slope posteroventrally posterior to the choana. The medial margin of the palatine contacts the pterygoid along its entire length. The posterior region of both palatines is missing, but the contact with the ectopterygoid can be inferred from the anterior extension of the medial margin of the suborbital fenestra, which in *Orovenator* is anteroposteriorly long and mediolaterally very narrow. The suborbital fenestra is enclosed by the alveolar shelf of the maxilla laterally and by the

palatine and the ectopterygoid medially.

The maxillary ramus of the palatine is connected to the main body of the palatine by a robust, dorsally thickened flange of bone. Anteroposteriorly it is rather elongate, being approximately one-third the estimated length of the palatine, as in *Petrolacosaurus* (Reisz 1981). The lateral surface of the ramus is deeply concave and consists of two elements: a vertically orientated ventral process that contacts the medial surface of the alveolar shelf of the maxilla and a shorter but transversely broader, horizontally orientated dorsal process which overlies the dorsal surface of the alveolar shelf.

A canal, which opens via a foramen on the posterior surface of the maxillary ramus, accommodates the anterior progress of the maxillary artery and nerve (Fig.5B). It is evident from the position of the infraorbital foramen on the maxilla that the infraorbital artery and nerve, a subsidiary of the maxillary artery and nerve, enters the infraorbital foramen immediately posterior to the suture with the maxillary ramus of the palatine. Within the maxillary ramus the canal divides into two branches, one exits the ramus anteriorly and houses the main maxillary artery and nerve, which extends along a sulcus in the alveolar shelf before entering the anterior opening of the alveolar canal. The other branch is directed dorsally where it divides again into two dorsomedially orientated branches emerging as grooves on the dorsal surface of the robust flange joining the maxillary ramus to the main body of the palatine (Fig.5B). They extend across the posterodorsal surface of the anterior portion of the palatine, where they probably meet the palatine artery and nerve medially, similar to the anterior passage of these arteries and nerves in *Gephyrosaurus* (Evans 1980). The posterior dorsomedial branch has a ventral extension, which opens onto the lateral surface of the ramus adjacent to a foramen on the alveolar shelf that is overlain by the maxillary ramus. Several anastomosing capillaries are associated with the main canal.

2.4.3.3 Ectopterygoid

The ectopterygoid is an auriform posterolateral element of the palate. Both ectopterygoids are preserved in OMNH 74606. It consists of a dorsoventrally thin sheet of bone that overlies the medial part of the transverse flange of the pterygoid dorsally, contacts the posterior margin of the palatine and bears a flange on the posterolateral surface, which expands in to an anteroposteriorly elongate but dorsoventrally narrow jugal ramus. Anterolaterally the ectopterygoid forms the posteromedial and posterior margin of the suborbital fenestra.

The posterior surface of the ectopterygoid forms the anterior boundary of the sub-

temporal fenestra and bears an arcuate ventral ridge that grades into the lateral rim of the transverse flange of the pterygoid. The ventral surface of the ectopterygoid bears several small denticles, some of which continue as a cluster on to the surface of the pterygoid. The lateral margin of the jugal ramus, which contacts the medial surface of the jugal, is smooth and featureless. The nature of the suture with the palatine cannot be determined. Anterolaterally, a shallow emargination of the lateral margin encloses the posterior region of the suborbital fenestra.

2.4.3.4 Pterygoid

The pterygoids are the largest of the palatal elements and the longest bones in the cranium. Both pterygoids are present in OMNH 74606, with the right pterygoid the better preserved of the two, missing only the posterior portion of the quadrate ramus. They contact all other bones of the palate, as well as the basicranium and the quadrate. The pterygoids therefore play a key role in the structural integrity of the skull.

The pterygoid of *Orovenator* has an anteroposteriorly elongate palatal ramus, which tapers mediolaterally from the basal articulation to its anterior end, which contacts the medial surface of the vomer (Fig.9). It slopes posteroventrally as is observed in the palatine. The palatal ramus of the pterygoid bears two distinctive fields of denticles on its ventral surface. The first series occupy a ventrally raised ridge, which extends from the basal articulation along the ventromedial surface of the ramus, tapering to a point anteriorly, before continuing onto the ventromedial surface of the vomer. The denticles are tightly but irregularly spaced and are confined to the ridge. A dorsally inclined lamina extends from the denticle bearing ventromedial surface of the palatal ramus, where it probably met its partner medially. The second series of denticles are less densely clustered and extend anterolaterally from the basal articulation to the pterygoid contact with the palatine, continuing onto the ventral surface of the palatine.

The transverse flange is rectangular in outline, as in *Lanthanolania* (Modesto and Reisz 2002) and is posteroventrally orientated more steeply than the palatal ramus by an additional angle of 32°. The lateral and posterior margins of the transverse flange form an angle of approximately 85° in ventral view, and the process is orientated slightly posterolaterally, as in *Youngina* and *Prolacerta* (Gow 1975; Carroll 1981; Modesto and Sues 2004), but unlike in *Petrolacosaurus* and *Araeoscelis*, in which the transverse process extends anterolaterally (Vaughn 1955; Reisz 1981). Six large denticles, the largest of the palate, are attached to the rim of the posteroventral margin of the process, and three more extend anteriorly from the posterolateral corner. The anterior buttress of the basal articulation projects medially from the median junction of the palatal

ramus and the quadrate ramus of the pterygoid, and is formed solely by the pterygoid. It is an anteroposteriorly thin sheet of bone, which slopes slightly anterodorsally. The recess of the basal articulation is directed posteromedially and slightly dorsally. Lateral to the basal articulation the dorsal surface of the pterygoid slopes ventrally to form a narrow neck of bone that joins the quadrate ramus to the transverse flange. This surface bears a shallow longitudinal depression, which accommodates the base of the epipterygoid.

The quadrate ramus of the pterygoid extends posterolaterally from the basal articulation and is somewhat dorsally inclined. It is composed of a mediolaterally thin, vertical sheet of bone with a thickened ventral rim, the dorsal flange (Fig.10). A dorsoventrally thin arcuate flange is also present and extends medially from the ventral rim of the dorsal flange at an angle of approximately 90° (Fig.10B). Although missing its posterior region, the arcuate flange is mediolaterally broad, and the ventral surface is mildly concave. This is unlike the quadrate ramus in *Captorhinus laticeps*, where a tympanic membrane sheathed the concave medial surface of the dorsal process of the quadrate ramus (Heaton 1979). A ventral arcuate flange of the quadrate ramus appears to be plesiomorphic for amniotes, and is seen in basal captorhinids, early diapsids and early synapsids (Romer and Price 1940; Vaughn 1955; Müller and Reisz 2005b).

A mediolaterally thin, vertical septum of bone connects the dorsal flange to the arcuate flange of the anterior quadrate ramus, creating a deep posteriorly facing cavity. The smooth medial surface of this septum provides the posterior buttress for the basipterygoid process (Fig.10B). Posteriorly, the lateral surface of the dorsal flange probably contacted the medial surface of the pterygoid wing of the quadrate, but the nature of the suture cannot be determined.

2.4.3.5 Epipterygoid

Both epipterygoids are preserved in OMNH 74606. The right epipterygoid is the more complete of the two. The epipterygoid consists of a triangular base, with a convex ventral margin in lateral view. The ventral surface is anteroposteriorly long, and tapers mediolaterally towards its posterior end. Anteriorly, a small lenticular facet extends anterodorsally from the ventral surface. A mediolaterally-compressed columella projects dorsally from the apex of the triangular base.

The ventral surface of the epipterygoid is rugose. Prior to disarticulation, it was attached, probably via a connective tissue, to a shallow depression on the dorsal surface

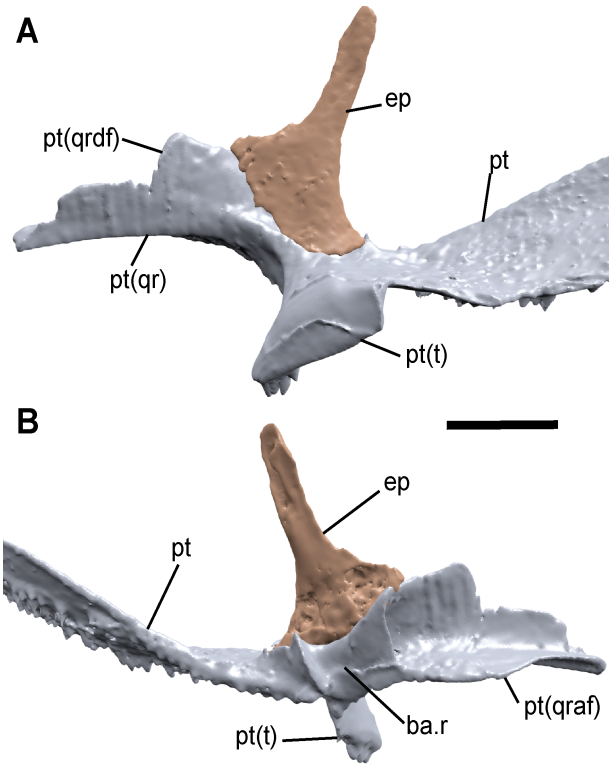


Figure 10: *Orovenator mayorum* OMNH 74606, reconstruction of articulation of right pterygoid and epipterygoid in: A, lateral; B, medial view. *Abbreviations*: ba.r, recess for basal articulation; ep, epipterygoid; pt, pterygoid; pt(qr), quadrate ramus of pterygoid; pt(qraf), arcuate flange of quadrate ramus of pterygoid; pt(qtdf), dorsal flange of quadrate ramus of pterygoid; pt(t), transverse process of pterygoid. Scale bar represents 2 mm.

of the quadrate ramus of the pterygoid, dorsolateral to the basal articulation (Fig.10A). Contrary to Reisz *et al.* (2011a) the anteroventral lenticular facet does not contribute to the basal articulation, but instead contacts a small ridge of bone that extends anterolaterally from the anterior buttress of the basal articulation. The lateral and medial surfaces of the dorsal columella are smooth, the anterior margin almost straight and the posterior margin is mildly concave. The columella of the right epipterygoid is missing the dorsal tip, but it is likely that it continued to curve posteriorly, as in *C. laticeps* (Heaton 1979), terminating in a cartilaginous extension that contacted the ventral surface of the parietal.

The shape and position of the epipterygoid of *Orovenator* is similar to that of *Youngina* as figured in lateral view by Gow (1975, p. 94, fig. E). Gow suggested that the morphology of the epipterygoid in *Youngina* might be similar to that of the late Permian parareptile *Milleretta*, in which a small anterior process of the base 'roofs' the basal articulation, rather than participates in the recess for the basipterygoid (Gow 1972, p. 236). In *Prolacerta*, the epipterygoid overlies the basal articulation in a manner

somewhat similar to *Milleretta* (Gow 1975). The base of the epipterygoid of *Orovenator* has a smooth, mildly convex lateral surface. The medial surface, which lies dorsolateral to the basal articulation, consists of unfinished bone in both epipterygoids (Fig.10B). OMNH 74606 is an immature individual and, therefore, since other elements of the palatoquadrate of this specimen are finished in cartilage (cf. quadrate), it is possible that a cartilaginous extension to the medial surface of the base of the epipterygoid capped or participated in the basal articulation.

An anteromedial exposure of the base of the epipterygoid contributes partly or wholly to the basal articulation in captorhinids (*Captorhinus aguti*; Fox and Bowman 1966 and C. *laticeps*; Heaton 1979) and early diapsids (*Petrolacosaurus*; Reisz 1981). This has also been reported in the varanopid *Varanops* (Campione and Reisz 2010). Laurin (1991) notes the epipterygoid of the varanopid *Apsisaurus* probably did not participate in the basal articulation, an interpretation disputed by other authors (Campione and Reisz 2010). In early lepidosauromorphs such as *Diphydontosaurus*, *Gephyrosaurus* and *Marmoretta* (Evans 1980, 1991; Whiteside 1986) the epipterygoid does not participate in the basal articulation.

2.4.3.6 Quadrate

Only the right quadrate of OMNH 74606 is preserved (Fig.11). It is a relatively short element, which is slightly wider anteroposteriorly than tall dorsoventrally. The condylar region is damaged or unfinished with much of the articular surface missing. A quadrate shaft extends posterodorsally from the condylar region. An anteroposteriorly broad and transversely narrow lamina or pterygoid wing extends anteromedially from the posterior shaft and condylar region. This lamina has a convex anterodorsal margin of unfinished bone, which slopes anteroventrally from the dorsal margin of the posterior shaft.

The posterior surface of the shaft is quite straight, with no evidence of the anterior curvature that is common to early members of the diapsid crown-group, Sauria (e.g. *Prolacerta*, Gow 1975; *Pamelina*, Evans 2009; and *Paliguana*, pers. obs. AM3585). A prominent shelf of bone extends from the medial surface of this shaft, transitioning ventrally into the medial condyle (Fig.11B). Reisz *et al.* (2011a) suggested that this received the distal region of the paroccipital process. However, it may alternatively have supported a cartilaginous extension of the columella of the stapes, which contacted a shallow recess in the medial surface of the quadrate shaft, similar to the structure found in *Captorhinus aguti* and *Araeoscelis* (Vaughn 1955; Fox and Bowman 1966).

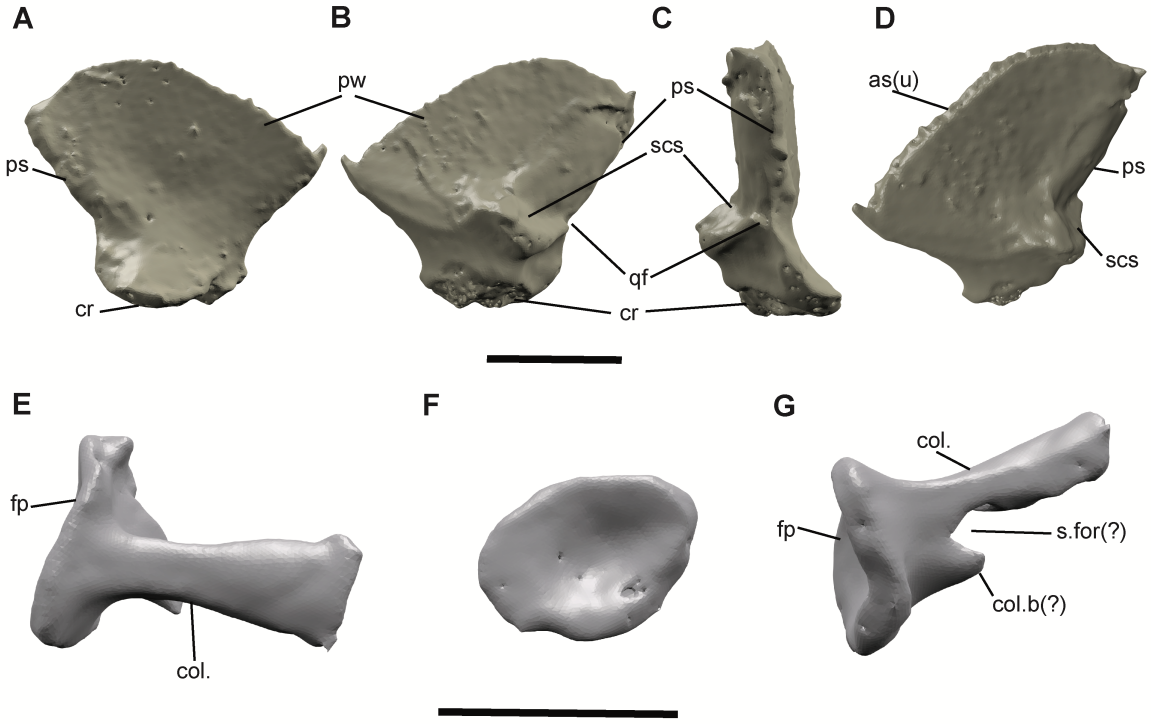


Figure 11: *Orovenator mayorum* OMNH 74606, A-D, right quadrate in: A, lateral; B, medial; C, posterior; D, anteromedial view. E-G, stapes: E, posterior view; F, footplate of stapes in proximal view; E, stapes in ventral view. *Abbreviations*: as(u), anterior surface (unfinished); col., columella; col.b(?), possible base of bridge of stapedial foramen; cr, condylar region; fp, footplate; ps, posterior shaft; pw, pterygoid wing; qf, quadrate foramen; scs, shelf for columella of stapes; s.for(?), possible stapedial foramen. Scale bars represent 2 mm.

A small notch, the quadrate foramen, is present in the posterolateral surface of the quadrate shaft, immediately lateral to this shelf (Fig.11B, C).

Orovenator has a single pterygoid wing extending anteromedially from the quadrate shaft, as in *Petrolacosaurus* and early synapsids (Romer and Price 1940; Reisz 1981). There is no lateral tympanic crest, unlike in *Prolacerta* (Modesto and Sues 2004), or anterolateral conch, as in early lepidosauromorphs (*Pamelina*, Evans 2009; and *Sophineta*, Evans and Borsuk-Białynicka 2009). The lateral surface of the pterygoid wing is relatively smooth (Fig.11A). The medial surface is slightly rugose. However, it does not bear the prominent scarring seen in some captorhinids, in which the medial surface of the pterygoid wing contacts the lateral surface of the quadrate ramus of the pterygoid (Fox and Bowman 1966; Heaton 1979). The transversely narrow, anteroventrally curving anterodorsal surface of the lamina consists of a deeply concave groove of unfinished bone (Fig.11D). It is likely that a cartilaginous anterior extension of this surface provided the main region of contact with the pterygoid, and may, given the

immature nature of OMNH 74606, have been in the process of ossification.

2.4.3.7 Parabasisphenoid

The ventral plate of the braincase (the basisphenoid) and the dermal bone that sheaths it ventrally (the parasphenoid) are difficult to delimit in *Orovenator*, and are here described as a single compound element: the parabasisphenoid (Fig.12). This bone is composed of four principal structures, the elongate and narrow cultriform process anteriorly; the dorsal surface, which bears the pituitary fossa and clinoid processes; the anterolaterally directed basipterygoid processes; and the ventral surface enclosed laterally by the *cristae ventrolaterales*. OMNH 74606 preserves all of these structures, lacking only the posterior part of the ventral surface of the parabasisphenoid.

The cultriform process is formed of two anteroposteriorly elongate lateral laminae that meet ventrally to produce a deep V-shaped trough (Fig.12). It extends anteriorly from the anterior margin of the pituitary fossa to the level of the choanae, attenuating gradually to a fine point. It bisects the interpterygoid vacuity but does not contact the medial margin of the pterygoids. The cultriform process does not extend anteriorly beyond the anterior tip of the pterygoids, unlike in *Araeoscelis* (Vaughn 1955).

The ventral surface of the cultriform process bears approximately 24 small denticles posteriorly. Reisz *et al.* (2011a), using a scanning electron microscope, also noted the bases of small denticles on the ventral surface of the parabasisphenoid and the *cristae ventrolaterales*. The presence of teeth on the parabasisphenoid is primitive for amniotes, and this trait is lost in early archosaurs, rhynchosaurs and lepidosaurs (Evans 1986). Its distribution amongst early amniotes, however, is not uniform. In captorhinids, a dentate parasphenoid is known in *Euconcordia* and *Captorhinus aguti* (Fox and Bowman 1966; Müller and Reisz 2005b) but is absent in *Captorhinus laticeps*, *Romeria* and *Protocaptorhinus* (Heaton 1979). In diapsids, denticles on the cultriform process are reported in *Petrolacosaurus* and *Lanthanolania* (Reisz 1981; Modesto and Reisz 2002) but absent in *Araeoscelis* and *Youngina* (Vaughn 1955; Gow 1975). In synapsids, both caseasaurs and varanopids have a dentate parasphenoid (Reisz and Berman 2001; Maddin *et al.* 2008; Spindler *et al.* 2018) although even within these groups the character state remains variable, as in the varanopid *Archaeovenator* where the parasphenoid is edentulous (Reisz and Dilkes 2003). Dentition is entirely absent in ophiacodontids, edaphosaurids and sphenacodontids where the parabasisphenoid is preserved (Benson 2012). The nyctiphruretid parareptile *Abyssomedon* has a few small denticles on the parasphenoid, whereas in its sister taxon *Nyctiphruretus* the cultriform parasphenoid is edentulous (MacDougall and Reisz 2014).

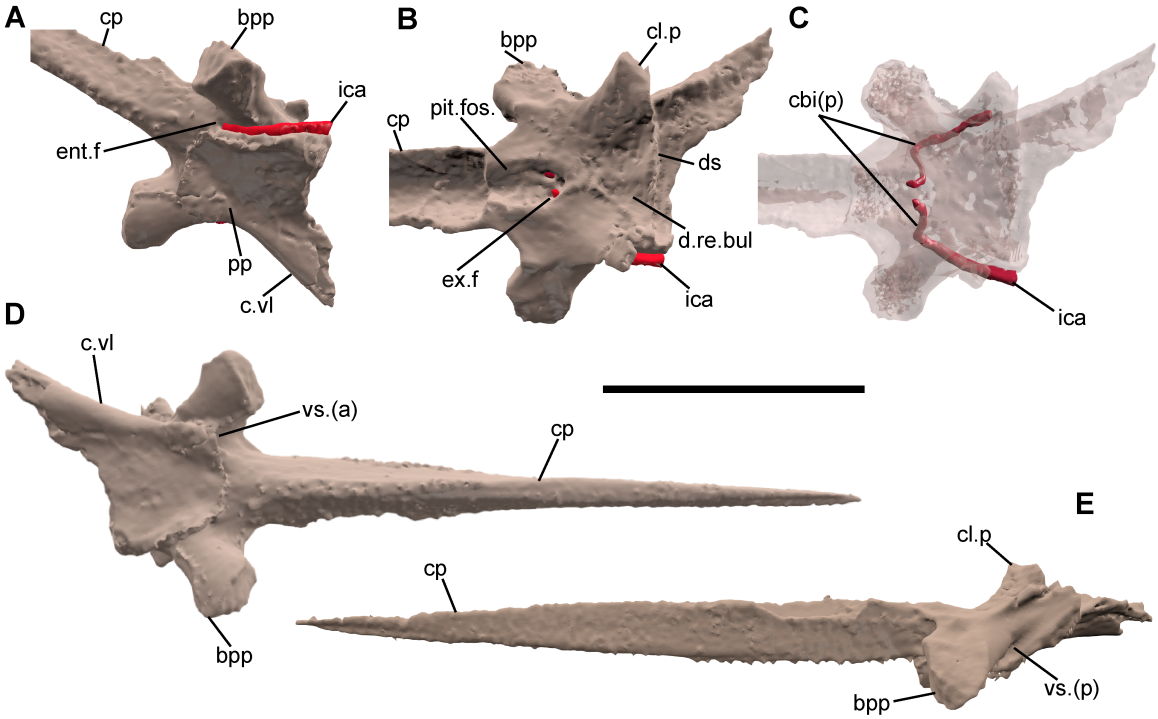


Figure 12: *Orovenator mayorum* OMNH 74606, parabasisphenoid, with pathway of internal carotid and cerebral arteries. A, ventrolateral view; B, dorsal view; C, dorsal view with partial transparency of parabasisphenoid; D, ventral view with cultriform process; E, left lateral view with cultriform process. *Abbreviations*: bpp, basipterygoid process; cbi(p), pathway of cerebral branch of internal carotid artery through parabasisphenoid; cl.p, clinoid process; cp, cultriform process; c.vl, crista ventrolaterales; d.re.bul, depression for retractor bulbi muscle; ds, dorsum sellae; ent.f, entry foramen for cerebral branch of internal carotid artery; ex.f, exit foramen for cerebral branch of internal carotid artery; ica, internal carotid artery; pit.fos, pituitary fossa; pp, parasphenoidal plate; vs.(a), anterior egress of vidian sulcus; vs.(p), posterior vidian sulcus. Scale bar represents 5 mm.

The dorsal surface of the parabasisphenoid anterior to the *dorsum sellae* is roughly pentagonal in dorsal view, with a short rostral process that narrows anteriorly from the level of the basipterygoid processes (Fig.12B). The rostral process has a flat anterior surface that marks an abrupt anatomical transition to the dorsally hollow cultriform process. It therefore lacks the anterior projections of the *cristae trabeculares*. These are paired, small, anteriorly tapering pedicels of bone on the anterolateral surface of the rostral process of the parabasisphenoid that bear facets for the *trabeculae cranii*, and are present in *Petrolacosaurus* (Reisz 1981), *Gephyrosaurus*, *Youngina* and extant squamates (Evans 1980, 1987, 2008). Trabecular facets on the rostral process are also absent in early archosauromorphs, such as *Prolacerta* and *Tanystropheus*, and early archosaurs, in which the raised dorsolateral borders of the cultriform process may represent a composite ossification of the trabeculae (Evans 1986). However, the *cristae trabeculares* are posterior extensions of the cartilaginous *trabeculae cranii* (Evans 2008)

and it is also possible that they were incompletely unossified in OMNH 74606 due to its juvenile status.

A deep ovoid pit is present on the midline of the dorsal surface of the rostral process, opening anteriorly into the cultriform recess through a V-shaped notch (Fig.12B). This is the pituitary fossa, which contained the pituitary gland. A shallower, transversely broad depression for the retractor bulbi muscles is located just posterior to the pituitary fossa. The *dorsum sellae*, an anteriorly sloping transverse sheet of bone, rises from the posterior margin of the retractor depression, supported laterally by the clinoid processes. The left clinoid process is missing its dorsal tip and some of the *dorsum sellae* attached to it is incomplete. Nevertheless, it is clear from what remains that the *dorsum sellae* was rather low. The dorsoventrally low *dorsum sellae* of the parasphenoid suggests that the proötic contributed substantially to the *dorsum sellae*, a feature usually associated with early synapsids rather than sauropsids (Romer and Price 1940). The dorsal articular surface of the clinoid process would have supported both the proötic and a cartilaginous dorsal bar, the *pila antotica* (Romer 1956).

The basipterygoid processes are robust, finger-like projections that emerge anteroventrolaterally from the parabasisphenoid, between the bases of the clinoid processes posteriorly and the rostral process anteriorly. They are somewhat ventrally orientated (Fig.12E). Distally each process bears two facets, a semicircular anterior facet that contacts the similarly shaped posterior surface of the anterior buttress on the basal articulation, and a dorsal facet that abuts the septum of bone bridging the anterior dorsal and arcuate flanges of the quadrate ramus of the pterygoid. The resulting contact would have been quite rigid and permitted little flexibility between the palate and the braincase. Posteriorly and ventrally the basipterygoid process consists of a robust shaft of smooth bone, with minimal constriction at the point of connection with the main body of the parabasisphenoid.

The ventral surface of the parabasisphenoid is smooth and concave, confined laterally by the *crista ventrolateralis*, a thickened, ventrally rounded ridge of bone that extends posterolaterally from the ventral surface of the basipterygoid process (Fig.12D). Much of the shelf of bone connecting the cristae posterior to the *dorsum sellae* is missing in OMNH 74606.

The vidian sulcus can be seen on both lateral surfaces of the parabasisphenoid. It begins as a shallow groove, becoming progressively deeper, that extends along the lateral surface of the parabasisphenoid anteroventrally from the base of the clinoid process. It passes below the basipterygoid process, where it forms a deep groove between the ventrolaterally projecting ridge of the parasphenoidal plate and the ventral

surface of the basipterygoid process. The vidian sulcus traces the route of the palatine branch of the facial nerve and the internal carotid artery (Romer 1956). A large foramen opens along the sulcus ventral to the anteroventral surface of the basipterygoid process (Fig.12A) At this point the internal carotid artery divides into the palatine artery, which continues anterodorsally along the surface of the parabasisphenoid, and the cerebral carotid, which enters the foramen (Rieppel 1993). The cerebral artery extends dorsolaterally through the body of the parabasisphenoid to open on to the dorsal surface via paired foramina at the posterior base of the pituitary fossa (Fig.12B, C). Between the cerebral carotid foramina, a third foramen opens into the pituitary fossa. The canal leading from this foramen ends abruptly a short way into the body of the parabasisphenoid.

In OMNH 74606 the course of the left sulcus can be clearly traced along the lateral surface of the parabasisphenoid. The right sulcus, however, enters an enclosed canal ventral to the basipterygoid process before entering the foramen, which is also located within the canal. It is probable that the thin septum of bone enclosing the canal was not preserved on the left sulcus, and that in life a short vidian canal was present on both sides of the parabasisphenoid, ventral to the basipterygoid processes. The septum of bone enclosing the canal derives from the ventrolateral ridge of the parasphenoid plate. The vidian canal is formed by the fusion of the lateral margin of the parasphenoid with the overlying lateral margin of the basisphenoid during development (Evans 1980). Complete closure of the vidian canal is a squamate synapomorphy (Rieppel 1993), although it is present in some parareptiles (Gow 1972; Spencer 2000). Closure of the vidian canal remains incomplete in early eureptiles (e.g. *Captorhinus laticeps*, Heaton 1979; and the diapsids *Prolacerta* and *Sphenodon*, Evans 1986). In early synapsids the grooves for the internal carotid arteries extend anteriorly along a narrow area of the ventral surface of the parasphenoid between, or just posterior to, the basipterygoid processes, where they enter foramina situated on the ventral surface of the parasphenoid. These foramina can clearly be seen in ventral view (Fig.21A-D). The vidian canal is absent (Romer and Price 1940). This may differ, however, in some varanopids, in which the course of the internal carotid artery is similar to that of *Orovenator* (see Discussion).

2.4.3.8 Stapes

The footplate and part of the columella of the stapes are preserved in OMNH 74606, in close proximity to the right quadrate. The footplate is broadly ovoid in shape with a deeply concave articular surface (Fig.11F). The rim of the footplate is thickened, apart

from what is probably the ventral region where a groove accommodates the passage of the stapedial artery. The base of the columella is damaged. There is a short pedicel of bone projecting distally from the footplate (Fig.11G), originally interpreted as the dorsal process (Reisz *et al.* 2011a). However, this may be the base of the bridge of bone forming the stapedial foramen with the columella. The presence or absence of a dorsal process, which is present in captorhinids (Fox and Bowman 1966; Heaton 1979), synapsids (Romer and Price 1940) and early diapsids (Vaughn 1955; Reisz 1981), cannot be clearly determined due to the damage to the base of the columella.

2.4.4 Mandible

The lower jaw of *Orovenator* is a slender element, with a tooth row that terminates near the level of the posterior margin of the orbit (Fig.3A, B). The dentary is the longest bone in the mandible and covers most of its lateral surface. The posterior region of the mandible, including the adductor fossa, is relatively low and elongate, and the increase in dorsoventral height from the posterior tooth row to the posterior surangular is moderate, enhancing the somewhat gracile impression of the mandible. There are two inframeckelian fossae on the medial surface. The ventral margin, in lateral view, is rather straight, and there is a slight posteromedial inflection of the surangular.

2.4.4.1 Dentary

Both dentaries are preserved in OMNH 74606. The right has an eroded anterior tip and is missing the posterodorsal process. The left dentary is complete.

The dentary is a dorsoventrally narrow and elongate bone, covering a substantial area of the lateral surface of the mandible (Fig.13A). It bears 42 alveoli on its dorsal surface. A tapering posterodorsal process terminates posteriorly level with and ventral to the inferred midpoint of the postorbital region of the skull; it bears an extensive edentulous region. More than 12 conspicuous foramina line the anterior half of the lateral surface, some associated with deep posteriorly directed grooves. An elongate groove, present on the lateral surface of both dentaries, extends posteriorly from a large foramen ventral to the 24th alveolus (Fig.13A). The dentary provides the lateral and dorsal wall to the Meckelian canal.

The anteroposterior length of the dentary accentuates its slender lateral profile, with the ratio of length to maximum dorsoventral depth approximately 12:1. Extensive su-

tural surfaces on the angular and surangular support the dentary medially. Anteriorly the dentary gradually tapers dorsoventrally from the 31st alveolus, ending in a narrow, smoothly rounded symphyseal tip. Posteriorly, the dentary tapers in dorsoventral height sharply from the 31st alveolus, forming the posterodorsal process, which terminates in a point ventral to the mid-temporal region. The ventral margin of the posterodorsal process contacts the angular anteriorly and the surangular posteriorly. Most of the edentulous region of the posterodorsal process lies within a posteriorly tapering recess on the dorsolateral surface of the surangular, where a transversely narrow ridge of the surangular separates the dentary from the coronoid dorsally. The ventromedial surface of the dentary overlies a narrow, anteriorly tapering lateral flange on the splenial, and excludes the splenial from the lateral surface of the mandible.

A broad alveolar shelf extends medially from the dorsal surface of the dentary to support the marginal dentition. It has a high lateral lamina and a low medial ridge, which extends ventrally to form the dorsomedial wall of the Meckelian canal. The symphyseal surface is a small, semi-lunate area, which lies anterior to the anteroventral extension of the splenial. Posterior to the mandibular symphysis, the dentary is exposed dorsomedially to the level of the 9th alveolus (Fig.13B). Posteriorly the medial surface of the dentary contacts an anterodorsal process of the prearticular. A narrow spur of the alveolar shelf separates the coronoid from the anterior tip of the prearticular (Fig.13B).

There are spaces for 42 teeth in the left dentary of OMNH 74606, 30 of which are occupied by small homodont teeth, similar to the marginal dentition of the maxilla. The two anterior teeth are slightly smaller than the subsequent teeth, which remain roughly isodont until the 26th tooth position, where the teeth gradually reduce in size, with the ultimate alveolus bearing the smallest tooth of the entire marginal dentition. The labial wall of the dentary is considerably taller than the lingual wall, which is reduced to a low ridge formed by thin paradental plates. The implantation remains basically 'subthecodont', although the alveoli are shallower than those of the maxilla, and the interdental plates are less prominent. The high marginal tooth count in the dentary is the highest known for a Palaeozoic neodiapsid (Reisz *et al.* 2011a).

2.4.4.2 Angular

In OMNH 74606 the right angular is missing the medial and posterior regions. The left angular is essentially complete. The angular is an anteriorly tapering sheet of bone, exposed posterolaterally on the mandible, where it provides the ventral half of

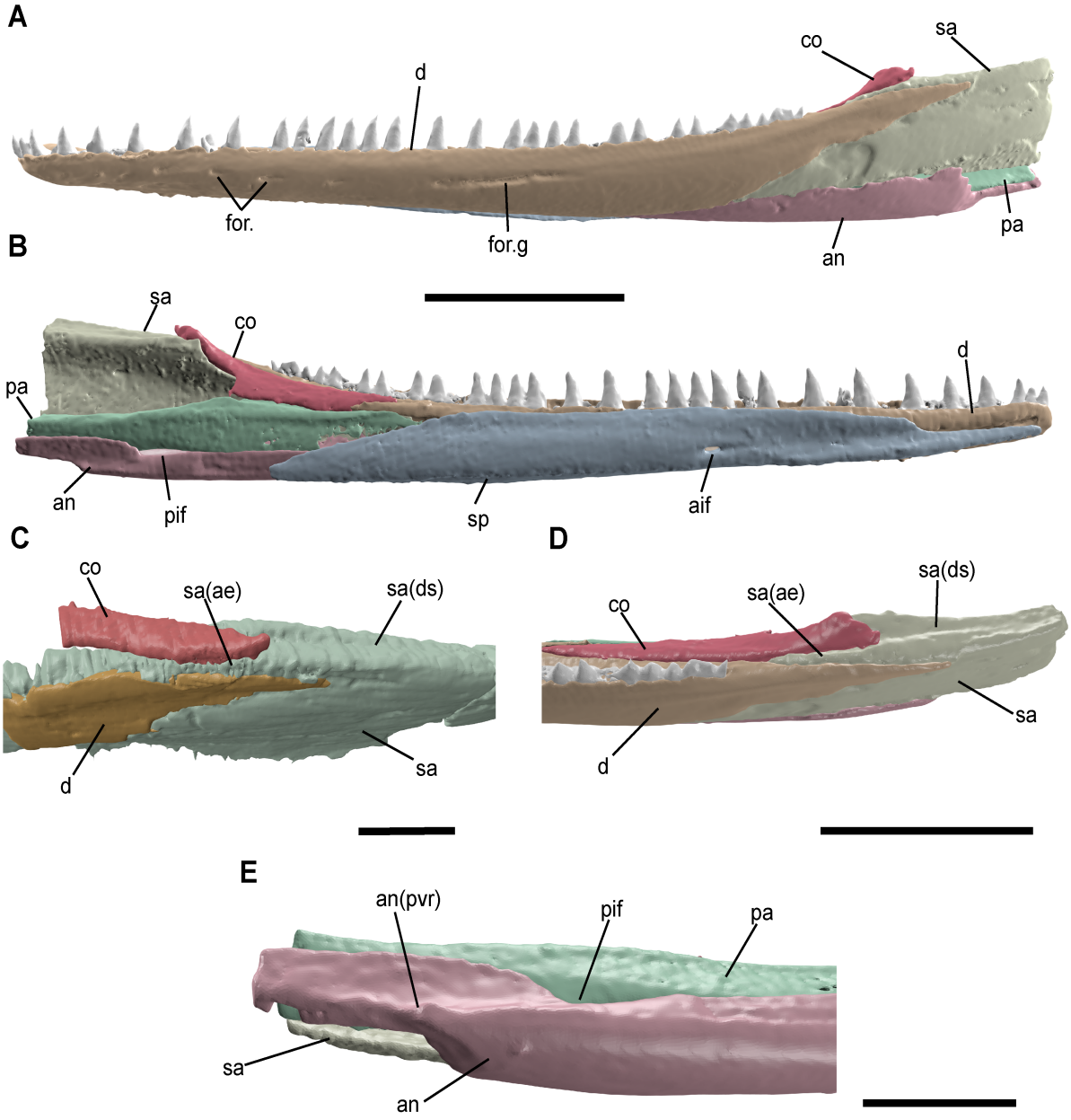


Figure 13: Mandibles of *Orovenator mayorum* and *Mycterosaurus longiceps*. A-B, OMNH 74606, reconstruction of left mandible in: A, lateral; B, medial view. C, *Mycterosaurus longiceps*, FMNH UC 692 holotype, posterior right mandible in dorsolateral view (image reversed). D-E, OMNH 74606, reconstruction of posterior left mandible in: D, dorsolateral; E, ventral view. *Abbreviations*: aif, anterior inframeckelian foramen; an, angular; an(pvr), posteroventral ridge of angular; co, coronoid; d, dentary; for, foramina; for.g, foramen and groove; pa, prearticular; pif, posterior inframeckelian foramen; sa, surangular; sa(ae), anterodorsal extension of surangular; sa(ds), dorsomedial shelf of surangular; sp, splenial. Scale bars represent 5 mm, except for E which represents 2 mm.

the surface, and posteromedially where only a narrow region is exposed ventral to the prearticular.

Anterolaterally the angular has an elongate, anteriorly attenuating, articular surface that underlies the dentary. The exposed posterolateral surface overlies a narrow shelf on the ventral surface of the surangular and provides the thin ventral ridge of the mandible for the posterior third of its length. Medially the dorsoventrally narrow exposed surface has a shallow excavation along its dorsal margin, which forms the ventral rim of the posterior inframeckelian foramen (*foramen intermandibularis caudalis* of Reisz *et al.* 2011a) (Fig.13B). Anteromedially, a narrow sheet of bone provides sutural contact for the posterior splenial.

Posteromedially it overlies the posteromedial margin of the prearticular and forms a narrow ridge of bone ventrally. Since the articular is missing from both mandibles, it is not possible to determine whether the angular contacted the articular ventrally. The narrow ridge of bone that overlies the prearticular is similar to that seen in *Archaeovenator* but is absent in later varanopids (Reisz and Berman 2001; Reisz and Dilkes 2003). The angular also bears a ventral keel in the early diapsid *Petrolacosaurus* (Reisz 1981).

2.4.4.3 Surangular

Both suranigulars are preserved in OMNH 74606, with the posterior region and articular facet present only on the right surangular. The surangular forms the dorsal region of the posterolateral surface of the mandible and the lateral wall of the adductor fossa. It is a sheet-like bone ventrally, but thickens dorsally to form a distinctive anterodorsal ridge and a transverse expansion forming a broad medial platform, the dorsomedial shelf (Fig.13D). It contacts the articular along its posterior margin.

The surangular attenuates anteriorly between its dorsal and ventral articulation with the dentary and angular respectively (Fig.13A). The articular surface for the dentary extends posteriorly to form a tapering recess on the dorsolateral surface of the surangular. The narrow anterodorsal extension of the surangular provides the dorsal margin to this recess, and substantially separates the posterior dentary from the coronoid (Fig.13D). The dorsomedial shelf is mediolaterally broad and bears a deep central anterior groove, which accommodates the posterodorsal process of the coronoid, and thus the low coronoid eminence (Fig.14B). Posterior to the coronoid, a much shallower groove continues along the dorsal surface of the shelf. The purpose is uncertain, but it may have provided a sulcus for blood vessels or nerves. The dorsomedial shelf overhangs the lateral wall of the adductor fossa (Fig.13B).

Posteriorly the surangular curves medially from the point where the dentary terminates. A flange of thin, vertically orientated bone extends medially from the pos-

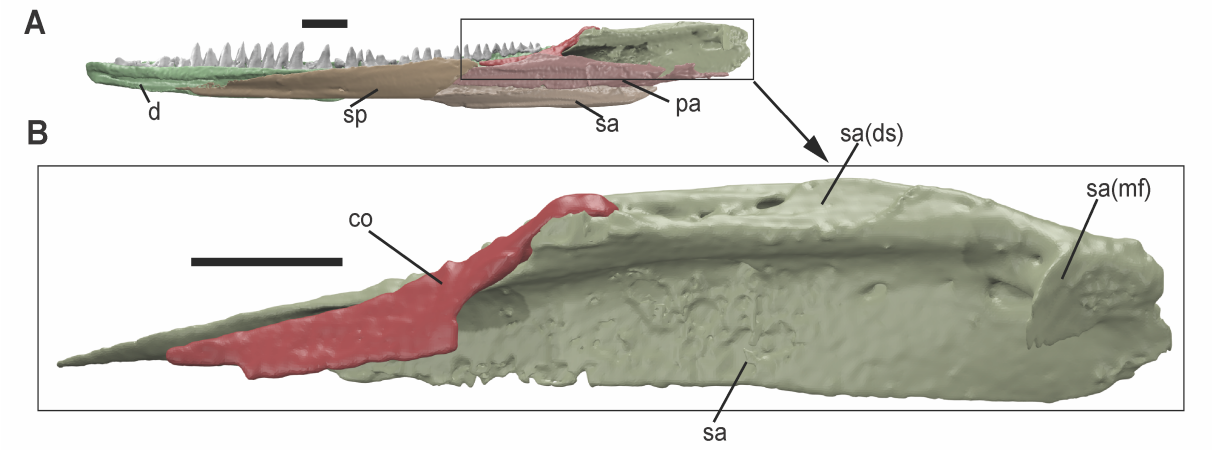


Figure 14: *Orovenator mayorum* OMNH 74606, right mandible. A, right mandible in medial view. B, right surangular and coronoid in medial view (area indicated on A). *Abbreviations*: an, angular; co, coronoid; d, dentary; pa, prearticular; sa, surangular; sa(ds), dorsal shelf of surangular; sa(mf), medial flange of surangular; sp, splenial. Scale bars represent 2 mm.

terodorsal region of the surangular (Fig.14B). Both the anterior and posterior surfaces of this flange form are smoothly concave. The posterior margin of the surangular is rugose and probably contacted the articular.

2.4.4.4 Splenial

Both splenials are present in OMNH 74606; only the left splenial is complete. Most of the anteromedial surface of the mandible, and therefore the medial wall of the Meckelian canal, is formed by the splenial. There is a small foramen, the anterior inframeckelian foramen (*foramen intermandibularis oralis*) close to the ventral margin, level with the 18th alveolus (Fig.13B). A similar foramen can be seen on the medial surface of the splenial assigned to a mycterosaurine varanopid (gen. et sp. indet.) from the Capitanian, middle Permian, of South Africa, and in an undescribed mycterosaurine from the lower Permian of Richards Spur, Oklahoma (Modesto *et al.* 2011). It is absent, however, in the varanopids *Aerosaurus* (Langston and Reisz 1981), *Varanops* (Campione and Reisz 2010) and *Varanodon* (Modesto *et al.* 2011) and indeed in all other 'pelycosaur'-grade synapsids current known (Modesto *et al.* 2011). Posteriorly, the splenial overlies the prearticular and the angular.

The splenial is a long dorsoventrally thin bone that tapers anteriorly from the 14th alveolus to a narrow ventromedial process that provides a medial wall to the anterior Meckelian canal (Fig 13B). This process terminates ventral to the 2nd alveolus, and therefore does not participate in the symphyseal joint. Dorsally, the splenial contacts the medial surface of the alveolar shelf at the 14th alveolus and continues

posteriorly until it meets the anterior process of the prearticular, from which point it tapers posteroventrally. It does not contact the anterolateral surface of the coronoid.

A dorsoventrally thin lateral process of the splenial extends posteriorly from a point level with the 8th dentary alveolus. This is overlain by the ventromedial surface of the dentary and is therefore not visible in lateral view. A narrow keel joining the medial and lateral processes of the splenial provides the floor to the Meckelian canal. The splenial tapers posteroventrally, where it overlies the prearticular and the angular. *Orovenator* does not possess a posterior splenial, a bone present in seymouriamorphs (Klembara 1997; Klembara and Ruta 2005) but not reported in any amniotes, with the exception of *Petrolacosaurus* (Reisz 1981).

2.4.4.5 Prearticular.

Both prearticulars are well preserved in OMNH 74606. The prearticular is the central element in the posteromedial surface of the mandible, forming the medial wall of the adductor fossa and providing ventral support for the coronoid (Fig.13B). It a dorsoventrally narrow bone, attenuating anteriorly. There is a thickened dorsal margin along much of its length. Posteriorly a distinct ventromedial surface is overlain by the posteromedial exposure of the angular.

The anterior portion of the prearticular is a very finely tapering thin sheet of bone that is overlain by the splenial. A thickened dorsal rim develops medial to and in contact with the narrow spur of alveolar shelf of the dentary that borders the anterior coronoid. The dorsal rim thickens posteriorly and contacts the medial margin of the coronoid posterior to the spur of the alveolar shelf. An elongate triangular lamina extends dorsomedially from the dorsal rim of the prearticular, which, along with a similar lamina on the dentary, provides support for the coronoid ventrally.

Immediately posterior to the dorsomedial lamina, the dorsal rim rises gradually to form a low eminence. The posteroventral margin of the coronoid contacts the apex of this eminence, and together they form the anterior margin of the adductor fossa. Posteriorly from this point the dorsal rim of the prearticular provides the dorsomedial margin of the adductor fossa. The posterior region of the prearticular is strongly inclined dorsoventrally, where it overlies the posteromedial flange of the angular. Anterior to this the ventral surface of the prearticular is free and forms the dorsal margin of posterior inframeckelian foramen (Fig.13B). Because the articular is not preserved, the nature of the prearticular-articular contact cannot be determined.

2.4.4.6 Coronoid

Both coronoids are preserved in OMNH 74606. The left coronoid, and its contact with the surrounding bones, is particularly well represented. The single coronoid is a mediolaterally thin bone with an anteriorly tapering anterior process and a thickened rim along its dorsal margin that develops into a posterodorsal process (Fig.14B). Almost all of the exposure is medial, apart from the low coronoid eminence of the posterodorsal process, which is visible in lateral view. Both coronoids are edentulous.

The anterior process of the coronoid has an elongate blade-like appearance, tapering anteriorly to a point. The lateral surface of the blade overlies two thin laminae of bone; anteriorly a shelf of bone recessed into a medial extension of the alveolar shelf of the dentary and posteriorly a flange projecting from the dorsal rim of the prearticular. The anterior process contacts the dentary along its dorsal margin and the prearticular along its ventral margin apart from the anteriormost region, which is bordered ventrally by a small spur of bone from the dentary. This prevents contact between the coronoid and the splenial (Fig.13B).

The thickened posterodorsal process extends from the dorsal rim of the coronoid. It bears a broad ventral facet that fits into a deep groove in the dorsomedial shelf of the surangular. A concavity on the posterior margin of the bone marks the anteromedial rim of the adductor fossa.

2.4.5 Postcranial skeleton

Four vertebrae are partially preserved in OMNH 74607 (Fig.2B, D); three have been identified as cervicals, including the axis, and the fourth as a caudal (Reisz *et al.* 2011a). They represent the only postcranial bones known for *Orovenator*. The axis and the third cervical are in semi-articulation. The left pedicel of the neural arch, which is exposed to the surface of the specimen, has been completely eroded in all three cervicals.

2.4.5.1 Cervical vertebrae

All centra are amphicoelous and notochordal. They are sharply keeled and deeply excavated ventrolaterally, such that in anterior or posterior view the notochordal canal is considerably offset towards the dorsal rim of the centrum (Fig.15A). They are relatively short anteroposteriorly, and tall in relation to their length (ratio approximately

0.60) (Fig.15B). The zygopophyses extend slightly lateral to the centrum, and the zygopophyseal facet is inclined at an angle of approximately 27°. The pedicels of the neural arch are mediolaterally narrow and firmly sutured to the centrum. The neural arch is broad and tall (Fig.15A, B).

The axis is the anterior of the two semi-articulated vertebrae, and is identified by the anteroposteriorly elongate neural spine in relation to the subsequent or third cervical vertebra (Reisz *et al.* 2011a). The anterior and dorsal region of the neural spine is missing. The posteroventral margin of the neural spine bears a notch leading to a small foramen. The neural spine of the third cervical is missing the dorsal and posterior region. The only evidence of a transverse process is on the disarticulated cervical, which is possibly the fourth cervical, where a slightly raised hourglass-shaped facet lies ventral to the prezygopophysis. There is no evidence of an accessory articulating process on the anterior or posterior margins of the neural spines (Fig.15D).

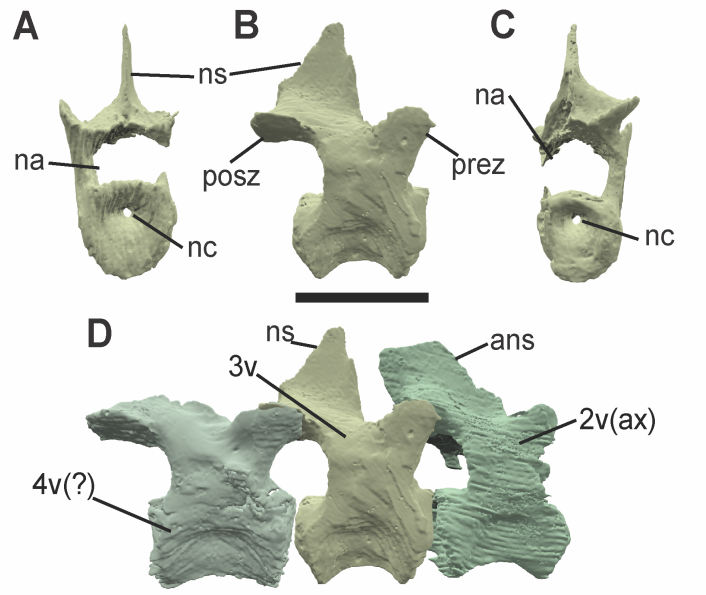


Figure 15: *Orovenator mayorum* OMNH 75607, cervical vertebrae. A-C, first post-axial vertebra (third cervical) in: A, anterior; B, right lateral;C, posterior view. D, reconstruction of cervical vertebrae (2?4) in articulation, including possible fourth cervical (anterior to right). *Abbreviations*: ans, axial neural spine; na, neural arch; nc, notochordal canal; ns, neural spine; posz, postzygopophysis; prez, prezygopophysis; 2v(ax), second cervical (axial) vertebra; 3v, third cervical vertebra; 4v(?), possible fourth cervical vertebra. Scale bar represents 5 mm.

The cervical vertebrae of *Orovenator* differ from those of earlier diapsids, particularly in the length of the centra (Vaughn 1955; Reisz 1981; Reisz *et al.* 1984). There is, however, some similarity in shape of the third cervical with cervical vertebra of *Acerosodontosaurus* (Currie 1980). The dorsoventrally low neural spine and tall neural arch of the axis in *Orovenator* differs from ophiacodontid synapsids where the neural

spine is tall and the neural arch somewhat narrow and short (Sumida 1989). A 'massive' neural arch is present in the varanopid *Archaeovenator* (Reisz and Dilkes 2003); a low axial neural spine is present in *Ascendonanus* and other small varanopids (Spindler *et al.* 2018).

Caudal vertebra. A small caudal vertebra is poorly preserved, particularly the lateral wall of the centrum, which has completely eroded ventral to the neurocentral suture. The neural spine is reduced to a posterodorsally inclined nub of bone, with an anterior margin that slopes steeply anteroventral to a deep V-shaped recess between the prominent prezygopophyses. Reisz *et al.* (2011a) considered that this element was ontogenetically separate from the cervicals and was therefore probably not associated with the other material in OMNH 74607.

2.5 Discussion

2.5.1 Palaeobiology and palaeoecology

2.5.1.1 Diel activity in *Orovenator*

The preservation of articulated scleral ossicles in the left orbit of *Orovenator*, a rare occurrence in early amniote fossils, allows a virtual reconstruction of the orbit and scleral ring (see Appendix 3). Measurements of the orbit and scleral ring can be used as palaeoecological indicators of patterns of diel activity using a derivative of generalised discriminant analysis modified for phylogenetic bias (Motani and Schmitz 2011; Schmitz and Motani 2011a). There has been some debate on the efficacy of this method in extinct taxa (Hall *et al.* 2011; Schmitz and Motani 2011b). Nevertheless, phylogenetically flexible discriminant analysis (PFDA) has also been used to investigate diel patterns in non-mammalian synapsids (Angielczyk and Schmitz 2014).

I added the measurements of *Orovenator* to the dataset of Angielczyk and Schmitz (2014), inserting *Orovenator* into their time calibrated phylogeny as a sister taxon to the 'pelycosaur'-grade synapsids (*Aerosaurus*, *Heleosaurus*, *Dimetrodon* and *Sphenacodon*), thus reflecting the synapsid/sauropsid relationship, with a terminal branch length equal to that of *Aerosaurus*, from the Abo/Cutler Formation of New Mexico (= Wolfcampian) (Langston and Reisz 1981). The PFDA of a sample of 164 extant terrestrial diapsids provides a discriminant function that can be used to infer patterns of diel activity in extinct specimens as being photopic (diurnal; prior probability = 58.6%), scotopic (nocturnal; 27.1%) or mesopic (cathemeral; 14.3%). This analysis, conducted by Ang-

ielczyk and Schmitz (2014), has an estimated phylogenetic signal parameter (Pagel's lambda) of 0.08, indicating that the relationship is essentially free from phylogenetic signal. My data for *Orovenator* is principally based on elements from a juvenile individual some 67% the size of the adult specimen, and the effects of ontogenetic status on inferences from this type of analysis have not been fully explored. Nevertheless, Angielczyk and Schmitz (2014) found the results of the two best-preserved specimens of the therapsid *Cyonosaurus* were consistently congruent despite one of them being the smallest specimen in the dataset (46% of maximum size). Furthermore, 21 of the 33 specimens included in the original study were 50% of the maximum size or larger, so my findings should be comparable to those of the original work (Angielczyk and Schmitz 2014).

The results show a 98.61% posterior probability of a scotopic ocular function in *Orovenator*, which I interpret as a strong indication of nocturnality (see Appendix 3). This represents the earliest example of nocturnality in diapsid evolution. Inferences of nocturnality in extinct amniotes were initially proposed as a predominantly mammaliaform trait that evolved in conjunction with homeothermy in Mesozoic mammals (Crompton *et al.* 1978). Studies have since suggested that a nocturnal lifestyle may have been prevalent in middle Permian parareptiles with impedance-matching hearing (Müller and Tsuji 2007) and in Mesozoic archosaurs (Schmitz and Motani 2011a), as well as early synapsids (Angielczyk and Schmitz 2014). Although the current data on diel activity in early amniotes is insufficient to imply whether nocturnality evolved independently or was homologous in the synapsid and sauropsid lineages, my findings do indicate that amniotes occupied a range of diel activity patterns quite early in their history.

2.5.1.2 Burrowing behaviour in *Orovenator*

In both general morphology and internal structure, *Orovenator* possesses a suite of features consistent with use of the snout in burrowing behaviour, which are absent in other Permian diapsids (Vaughn 1955; Gow 1975; Reisz 1981; Modesto and Reisz 2002; Bickelmann *et al.* 2009). Although the large orbits and external nares of *Orovenator* do not suggest a fully fossorial or subterranean lifestyle, a rostral process and a broad, anteriorly tapering dorsal surface of a wedge-shaped snout (Fig.16) are traits associated with burrowing in extant squamates (Wake 1993). Further, *Orovenator* possesses several features that imply mechanical reinforcement of the snout and may be associated with burrowing. The extent to which the skull is strengthened by complex articulations, and thus able to withstand greater stress, can infer a propensity towards

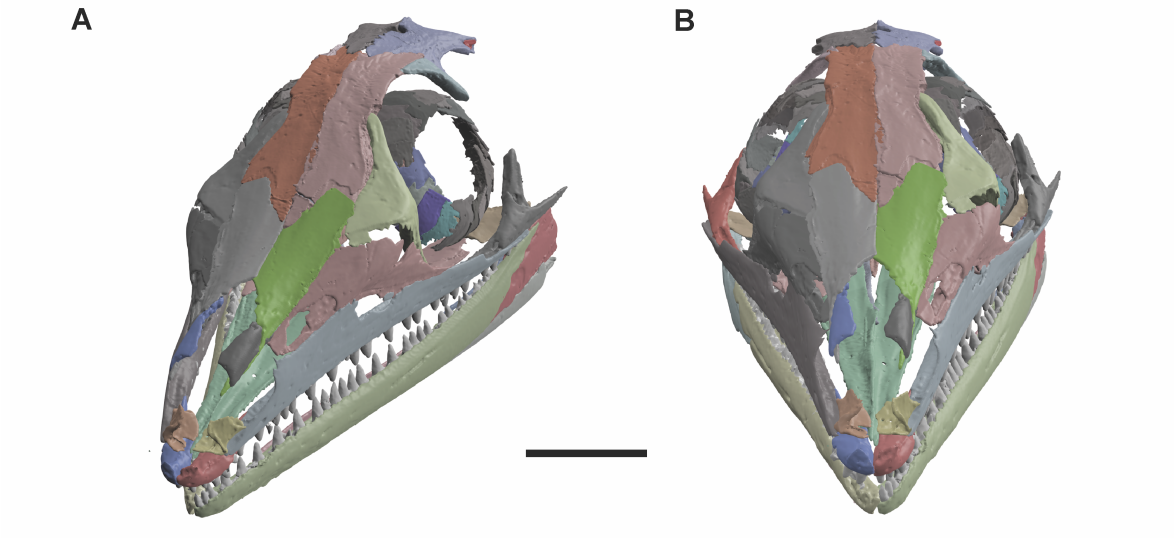


Figure 16: Composite reconstruction of the skull of *Orovenator mayorum*, with mirrored or duplicated elements in grey. A, left oblique dorsolateral view. B, anterodorsal view. Scale bar represents 5 mm.

fossoriality (Roscito and Rodrigues 2010). Such features are present in *Orovenator*, notably: (1) the anteroposteriorly long maxillary and dorsal processes of the premaxillae, and dorsoventrally thick maxillary plate, all of which serve to strengthen the anterior snout; (2) the interlocking fronto-nasal suture that braces the posterior part of the snout against lateral torsion; (3) the mutually supporting arrangement of the anterior circumorbital elements and the palate; (4) the medial buttress and crest of the maxilla which provides a firm platform for the ventromedial ridge of the lacrimal. Some other early amniotes also possess a medial buttress on the maxilla, such as ophiacodontids and sphenacodontians (Romer and Price 1940; Berman *et al.* 1995). However, in these taxa it is associated with the caniniform dentition ('supracanine' buttress), suggesting it functioned as resistance to bite forces. This is not the case in *Orovenator*, which lacked caniniform teeth and possessed a shelf on the posterodorsal crest of the medial alveolar buttress that supported the ventromedial surface of the lacrimal, thus reinforcing the snout against vertical stress.

The similarity of the skull shape of *Orovenator* with the sandfish skink (*Scincus scincus*), an extremely efficient burrower, is particularly striking (Fig.17), and a rostral process is a common feature of burrowing amphisbaenians and snakes (e.g. the North American worm lizard *Rhineura floridana* and the Mexican burrowing snake *Loxocemus bicolor*). A rostral process is also present in all caseasaurian synapsids (Romer and Price 1940). The morphology of the terminal phalanges in caseasaurs has led some authors to suggest a functional correlate with the rostral process, implying a digging behaviour in some caseid taxa (Olson 1968; Maddin and Reisz 2007). A recent study on

the long bone scaling of caseids suggests that allometric changes in forelimb morphology, even in smaller taxa, may support this hypothesis (Romano 2017). A moderate rostral process has also been suggested in the varanopids *Varanops* and *Aerosaurus* (Brinkman and Eberth 1983, though subsequently disputed by Reisz 1986).

The origin of burrowing in terrestrial vertebrates is at best obscure. Burrowing activity, particularly amongst faunivorous tetrapods, could have been used incidentally to explore the substrate for food. Exploitation of subsurface prey may have led to selection for adaptations that strengthened the structural integrity of the snout and improved prey capture (Wake 1993). Direct evidence of burrowing is rare in early Permian (Cisuralian) terrestrial vertebrates. The skull morphology of recumbirostran microsaurs from the Artinskian of Oklahoma and Texas is strongly suggestive of a burrowing lifestyle (Anderson *et al.* 2009; Maddin *et al.* 2011), an observation supported by burrows containing the putative recumbirostran *Brachydectes newberryi* (Pardo and Anderson 2016). Otherwise, there are several examples of burrowing associated with therapsids from the middle to late Permian (Guadalupian/Lopingian), such as helical burrows containing specimens of *Diictodon* (Smith 1987), fossorial adaptations in cistecephalid dicynodonts (Nasterlack *et al.* 2012), cynodont burrows from the Permo-Triassic boundary of South Africa (Damiani *et al.* 2003) and *Lystrosaurus* burrows from the Early Triassic Karoo Basin (Botha-Brink 2017). Sauropsid examples include an aggregation of five immature diapsid skeletons, referred to *Youngina*, in a possible underground burrow from the upper Permian of South Africa (Smith and Evans 1996) and potential facultative fossoriality in the stem-turtle *Eunotosaurus* (Lyson *et al.* 2016).

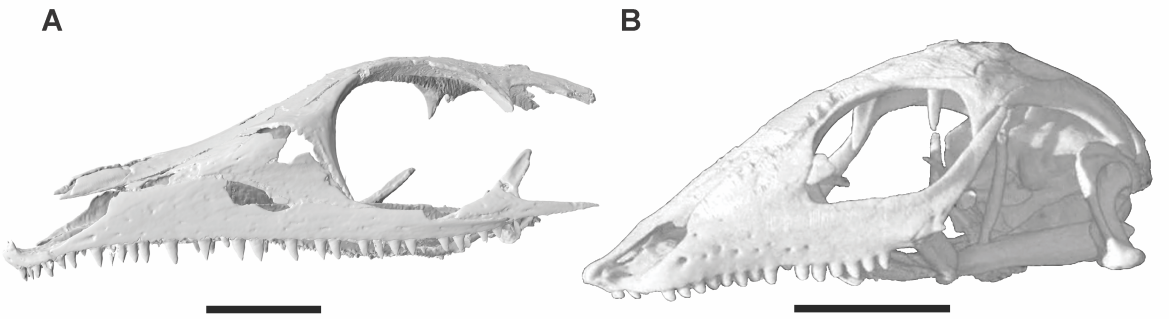


Figure 17: Crania in anterolateral view. A, composite reconstruction of *Orovenator mayorum*. B, North African sandfish (*Scincus scincus*). Scale bars represent 5 mm. CT reconstruction of *Scincus scincus* courtesy of Digital Morphology (http://digimorph.org/).

2.5.1.3 Paranasal air sinus and the origins of antorbital fenestration

The contact of the lacrimal and maxilla in *Orovenator* forms a cavity on the medial surface of the snout, bounded posteriorly and dorsally by the ventromedial ridge of the nasolacrimal canal, and anteriorly by the 'supracanine' buttress and crest of the maxilla (Fig.5). This is topologically similar to the antorbital cavity of extant archosaurs (i.e. birds and crocodilians), which takes the form of an internal space, rostral to the orbit, external to the nasal capsule, and bounded dorsally by the nasolacrimal canal (Witmer 1995). Based on its associations in extant archosaurs, the antorbital cavity has been proposed as an osteological correlate of an epithelial paranasal air sinus among crown-group archosaurs (Witmer 1995, 1997). Furthermore, a similar morphology is present in the early Triassic stem-group archosaur *Prolacerta*, which possesses a 'supracanine' buttress and crest on the medial surface of the maxilla (Gow 1975). The morphology seen in *Prolacerta* is highly similar to that of *Orovenator* (Fig.18A, B). One key difference between these taxa and the structures seen in birds/dinosaurs and most stem-group crocodylians, is the absence of an antorbital fenestra that opens from the internal antorbital cavity laterally to external space (the antorbital fenestra is secondarily closed in the crown-group of crocodylians and in some extinct groups). Witmer (1997) suggested that the origin of paranasal pneumaticity (indicated by the internal cavity) preceded the origin of crown-group Archosauria, and this is supported by the morphology of the medial surface of the snout in *Prolacerta* (Fig.18B). Witmer (1995, 1997) further hypothesised that the antorbital fenestra of early archosaurs derived from a fontanelle that failed to close during development in bones lateral to the pre-existing paranasal sinus.

The morphology of the snout in *Orovenator* is therefore consistent with the presence of paranasal pneumaticity. This is further supported in *Orovenator* by the presence of a small canaliculus that connects the nasolacrimal canal with the antorbital cavity (Fig.5B), somewhat similar to that found in birds and theropod dinosaurs (Witmer and Ridgely 2008). In contrast, this morphology is absent in the late Permian neodiapsid *Acerosodontosaurus* (Currie 1980). Furthermore, the antorbital cavity is absent in extant lepidosaurs (Witmer 1997) and fossil lepidosauromorphs (e.g. *Marmoretta*, *Gephyrosaurus*, *Sophineta*), in which a shallow depression in the medial surface of the maxilla is associated with the nasal gland cavity (Evans 1980, 1991; Evans and Borsuk-Białynicka 2009), a feature homologous with the archosaurian nasal gland rather the paranasal air sinus (Witmer 1997). In addition, the lacrimal does not extend anterodorsal to the nasal gland cavity in these taxa, as it does in the antorbital cavity in *Orovenator*. Consequently, the hypothesis of the antorbital cavity in *Orovenator* as a

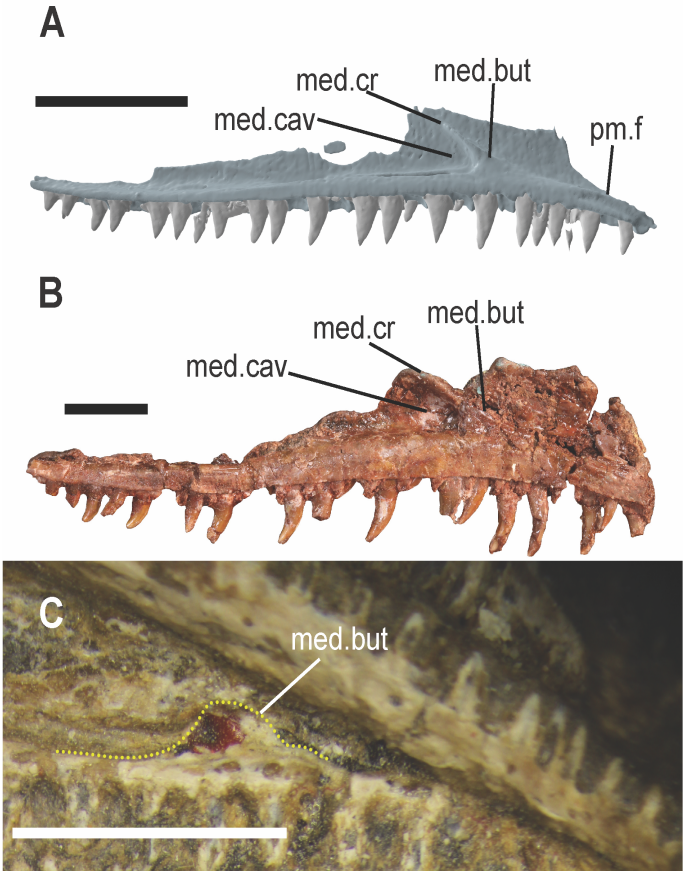


Figure 18: Maxillae in medial view. A, OMNH 74606. B, *Prolacerta broomi* (BP/I/2675). C, *Archaeovenator hamiltonensis* (KUVP 12483) (image reversed). *Abbreviations*: med.cav, medial cavity of maxilla; med.cr, medial crest; med.but, medial buttress; pm.f, facet for maxillary process of premaxilla. Scale bars represent 5 mm.

homologue of the paranasal sinus of archosaurs requires the secondary loss of this feature in lepidosaurs. The osteological evidence present in *Orovenator*, however, remains sufficiently compelling to expand this area of research in future studies.

Similarities between Orovenator and varanopids

Morphological similarities between diapsids and varanopids have long been noted, and have been the basis of protracted taxonomic and phylogenetic rearrangements (Reisz 1981; Reisz *et al.* 2010). Despite these similarities, varanopids have been assigned to Synapsida, the total-group of mammals, due to the presence of a single, lateral temporal opening (the synapsid condition). This contrasts with the presence of two temporal openings in early diapsids: the upper temporal fenestra and lower

Table 2.1: Taxa originally or secondarily assigned to Diapsida and later revised to Varanopidae

Taxon	Original description	Assignment	Revision to Varanopidae
Apsisaurus witteri	Laurin (1991)	Diapsid	Reisz et al. (2010)
Mesenosaurus romeri	Efremov (1940)	Synapsid	Reisz and Berman (2001)
	Ivakhnenko and Kurzanov (1979)	Diapsid (archosaur)	
Heleosaurus scholtzi	Broom (1907)	Diapsid	Reisz and Modesto (2007)
	Carroll (1976)	Diapsid	
	Benton (1985)	Diapsid	
Archaeovenator hamiltonensis	Reisz (1989)	Diapsids	Reisz and Dilkes (2003)

temporal fenestra or arch (the diapsid or euryapsid conditions).

The first varanopid to be described, *Varanops brevirostris*, was assigned to the Ophiacodontidae (Poliosauridae Williston, 1911). Romer and Price later erected the family 'Varanopsidae' as 'primitive sphenacodonts, retaining many ophiacodont features' (Romer and Price 1940, p. 268). Four of the fifteen genera currently recognised as varanopids were originally or secondarily described as diapsids (see Table 2.1). Furthermore, early diapsids have also been misidentified as synapsids; *Petrolacosaurus* was initially referred to the Synapsida by several authors (Lane 1945; Romer 1956; Stovall *et al.* 1966) before being comprehensively reassessed as a diapsid (Reisz 1977), and the early diapsid *Lanthanolania* was originally catalogued as a referred specimen of the varanopid *Mesenosaurus* (Modesto and Reisz 2002). One of the difficulties faced by researchers of early amniotes is that cranial characters used to distinguish between the two clades, such as the absence of the upper temporal opening and suborbital fenestra, are often not preserved or are obscured. In the case of *Apsisaurus* and *Heleosaurus*, the presence of tubercles on the lateral surface of the jugal has been a significant factor in their reassessment as varanopids rather than diapsids (Reisz and Modesto 2007; Reisz *et al.* 2010), although circumorbital ornamentation is absent in the basal varanopid *Ascendonanus nestleri* (Spindler *et al.* 2018). Altogether, it is clear that the hypothesised highly distinct phylogenetic positions of varanopids (as synapsids) and early diapsids (as sauropsids) are supported by only a small number of character states.

In contrast, numerous similarities shared by early diapsids and varanopids have already been noted, including a triradiate jugal with a dorsoventrally thin subtemporal process, a sigmoidal femur, osteoderms and serrations on the mesial edges of marginal teeth (Reisz and Modesto 2007; Reisz *et al.* 2010). In non-varanodotine varanopids, similarities also include slender limbs, relatively small body size and recurved conical teeth, as in the basal varanopids *Archaeovenator* and *Ascendonanus* (Reisz and Dilkes 2003; Spindler *et al.* 2018). Within the current paradigm (Reisz and Modesto 2007; Reisz *et al.* 2010), these similarities are interpreted as the result of convergent evolution. However, they have also been used to support alternative hypotheses of early

amniote phylogeny. Reig (1967) noted a series of features shared by varanopids and 'proterosuchians' (early Triassic stem-group archosaurs) and suggested that archosaurs evolved from varanopids in the late Permian. He subsequently listed 13 cranial and 16 postcranial similarities (Reig 1970), which Romer (1971) dismissed essentially as being plesiomorphies. Only the putative antorbital fenestra reported in the varanopid *Varanodon* (Olson 1965) appeared to support any derived affinity of varanopids with proterosuchians. This feature, however, was later interpreted as post-mortem damage to a region of thin antorbital lamina (Langston and Reisz 1981).

In my re-examination of *Orovenator*, I have identified 16 additional similarities that varanopids share with *Orovenator* and other sauropsids. This additional evidence for a clade comprising varanopids plus *Orovenator* prompted an assessment of the support for this clade, and its affinities with either synapsids or diapsids. Moreover, since this hypothesis is incongruent with the current paradigm of early amniote phylogeny, I discuss each relevant character state below. These similarities may be summarised as follows: (1) potential synapomorphies of varanopids that are also present in *Orovenator*: the rounded sub-narial shelf of the premaxilla, the posterodorsal extension of the external naris, the extensive dorsal exposure of the prefrontal with a sharp angle between the dorsal and lateral surfaces, the ventral process of the prefrontal that contacts the palatine, the prominent dorsomedial shelf of the surangular, the narrow anterodorsal extension of the surangular, the asymmetric bifurcation of the anterior vomers; (2) similarities shared by *Orovenator* and the early varanopid *Archaeovenator*: the medial 'supracanine buttress' of maxilla and absence of caniniform dentition, the dorsolateral inclination of the suborbital ramus of the maxilla, the posteroventral ridge of the angular, absence of contact between the coronoid and splenial; (3) potential synapomorphies of sauropsids that are present in varanopids: the posterolateral process of the frontal and the anteromedian process of the parietal, teeth on the cultriform process of the parasphenoid, the adductor crest and fourth trochanter of the femur absent; (4) potential synapomorphies of synapsids that are absent in most sauropsids and in varanopids: a distinct lateral lappet of the frontal (as also found in lanthanosuchoid parareptiles), the pathway of the cerebral carotid artery on the ventral surface of the parabasisphenoid and absence of the vidian sulcus.

2.5.2 Potential synapomorphies of varanopids that are also present in *Orovenator*

The character states described in this section support the inclusion of *Orovenator* in a clade with varanopids. As such, their distributions are incongruent with the presence of a diapsid or euryapsid pattern of temporal fenestration in *Orovenator*. This contrasts with the presence of a single lateral temporal fenestra in varanopids (the synapsid condition).

Rounded sub-narial shelf of the premaxilla. A broadly rounded transition between the dorsal surface of the body of the premaxilla, which forms the sub-narial shelf, and the lateral surface of the premaxilla ventral to it is a proposed unique synapomorphy of varanopids in respect to synapsids (Reisz and Dilkes 2003; Maddin *et al.* 2006) and other Palaeozoic amniotes (Reisz and Berman 2001). It differs from the situation in other taxa, in which this transition is marked by a sharp, well-defined margin. Both premaxillae in *Orovenator* exhibit the rounded morphology shared with varanopids (Fig.4A).

Posterodorsal extension of the external naris. In *Orovenator* the posterodorsal corner of the external naris is extended posteriorly, and is 'pinched' between the maxilla ventrally and the nasal dorsally (Fig.3A, B). The dorsoventrally narrow anterior process of the lacrimal forms the posterior margin of this extended region of the external naris. A similar posterodorsal expansion of the external naris between the maxilla and the nasal is present in most basal and mycterosaurine varanopids where observable, with the exception of *Ascendonanus*, which possessed a small naris with no posterodorsal extension (Spindler *et al.* 2018). This feature is also absent in other synapsids (Botha-Brink and Modesto 2009; Reisz *et al.* 2010) and early amniotes, including diapsids (Clark and Carroll 1973; Carroll 1981; Reisz 1981). In varanodontine varanopids the posterodorsal expansion is greatly enlarged (Maddin *et al.* 2006). Other than in varanopids and *Orovenator*, this morphology may also be present in weigeltisaurids, in which the posterodorsal expansion was scored as present in the taxon/character matrix of Reisz *et al.* (2010), although specimens of this group were not examined during the present study.

Extensive dorsal exposure of the prefrontal, with a sharp angle between the dorsal and lateral surfaces. The mediolaterally broad subtriangular dorsal exposure of the prefrontal in *Orovenator* forms a right angle with the lateral surface of the snout (Fig.3A,

C). This abrupt transition is also seen in the varanopids *Mesenosaurus* and *Elliotsmithia* (Reisz *et al.* 1998; Reisz and Berman 2001), and in specimens of *Varanodon* (FMNH UR 986) and *Varanops* (MCZ 1926), in which the mediolateral width of the skull roof across the prefrontals is twice the interorbital width in dorsal view. In synapsids this feature is also present in the ophiacodontids such as *Varanosaurus* (Berman *et al.* 1995). This differs from the condition in other synapsids (e.g. *Dimetrodon*, Romer and Price 1940; *Edaphosaurus*, Modesto 1995), in basal eureptiles such as *Paleothyris*, *Euconcordia* and *Romeria texana* (Carroll 1969; Müller and Reisz 2005b; pers. obs. MCZ 1480) and in the diapsid *Youngina* (pers. obs. BP/1/2871), in which the transition from the dorsal to lateral surface is gradual, and the mediolateral width of the skull roof across the prefrontals is less than twice the interorbital width.

Ventral process of the prefrontal contacts the palatine. A broad contact between the prefrontal and the maxillary ramus of the palatine is present in the varanopids *Elliotsmithia* (Modesto *et al.* 2001) and *Mesenosaurus* (Reisz and Berman 2001). A μCT scan of *Mycterosaurus* (FMNH UC 692), conducted for the present study, also shows evidence of this contact, confirming the scoring of this state in the analysis of Reisz *et al.* (1998, character 7). This contact is absent in early synapsids in which the medial surface of the antorbital region is known (e.g. *Dimetrodon* and *Ophiacodon*, Romer and Price 1940; *Haptodus*, Laurin 1993; *Ennatosaurus*, Maddin *et al.* 2008) except in *Edaphosaurus* (Modesto 1995). In *Orovenator* the prefrontal also bears a robust ventral process that lies across the medial surface of the lacrimal and makes a broad contact with the palatine (Fig.5B). *Orovenator* is the only Permian diapsid known to possess this morphology. Otherwise a broad prefrontal-palatine contact is considered to be an independently acquired synapomorphy of parareptiles, lepidosauromorphs and rhynchosaurs (deBraga and Rieppel 1997). It is also present in stem and extant turtles (Gaffney 1979).

Prominent dorsomedial shelf of the surangular. A broad dorsomedial shelf of the surangular overlies the adductor fossa dorsally, and provides a platform for the posterodorsal process of the coronoid in *Orovenator* (Fig.14). This is also present in the varanopids *Apsisaurus* (Reisz *et al.* 2010), *Mycterosaurus* (μCT scan of FMNH UC 692, Fig.13B), *Varanops* (Campione and Reisz 2010), *Varanodon* (Reisz *et al.* 2010) and *Aerosaurus* (Campione and Reisz 2010). In *Archaeovenator* there is a dorsomedial thickening of the posterior region of the surangular of the right mandible, which is exposed in medial view in the holotype (pers. obs. KUVP 12483). The same mor-

phology is seen in *Mesenosaurus* (Reisz and Berman 2001). This shelf is absent in all non-varanopid synapsids in which the dorsomedial margin of the mandible is known (e.g. *Dimetrodon* and *Ophiacodon*, Romer and Price 1940; *Varanosaurus*, Berman *et al.* 1995; *Edaphosaurus*, Modesto 1995; *Ennatosaurus*, Maddin *et al.* 2008; *Eothyris*, Reisz *et al.* 2009; and *Haptodus*, Laurin 1993). A prominent dorsomedial shelf of the surangular is also present in the parareptile *Belebey*, in which the shelf overhangs the adductor fossa (Reisz *et al.* 2007). In other early sauropsids this feature is less pronounced than in *Orovenator*, forming a thickened dorsomedial ridge of the surangular (e.g. *Acerosodontosaurus*, Currie 1980; *Petrolacosaurus*, Reisz 1981; and *Delorhynchus*, Reisz *et al.* 2014). However, it is absent in most early sauropsids in which this region can be examined (e.g. *Araeoscelis*, pers. obs. MCZ 4380; *Prolacerta*, Modesto and Sues 2004; *Captorhinus laticeps*, Heaton 1979; and *Labidosaurus*, Modesto *et al.* 2007).

Narrow anterodorsal extension of the surangular. In *Orovenator* the posterodorsal part of the dentary lies in a shallow recess on the lateral surface of the surangular. A transversely narrow and dorsoventrally thin process of the surangular extends dorsal to the dentary, substantially separating the posterior region of the dentary from the coronoid (Fig.13D) (Reisz *et al.* 2011a, Fig.3). Varanopids also exhibit this morphology where the relevant region can be examined (*Mesenosaurus*, Reisz and Berman 2001; *Apsisaurus*, pers. obs. MCZ 1474; *Mycterosaurus*, μCT scan of FMNH UC 692, Fig.13C; and *Aerosaurus*, Langston and Reisz 1981). A similar morphology can also be seen in the ophiacodontids *Ophiacodon* (Romer and Price 1940) and *Varanosaurus* (Berman *et al.* 1995), the parareptile *Delorhynchus* (Reisz *et al.* 2014), the captorhinids *Captorhinus laticeps* and *Reiszorhinus* (Sumida *et al.* 2010) and proterosuchid archosauriforms (Welman 1998; Ezcurra and Butler 2015). However, in these taxa the anterodorsal extension is dorsoventrally deeper than that of *Orovenator* and the varanopids noted above. Furthermore, the anterodorsal extension of the surangular is entirely absent in other synapsids (e.g. *Ennatosaurus*, Maddin *et al.* 2008; *Edaphosaurus*, Modesto 1995; and *Dimetrodon*, Romer and Price 1940) and in other sauropsids: the basal eureptiles *Paleothyris* (Carroll 1969) and *Protorothyris* (Clark and Carroll 1973), araeoscelidian diapsids (Vaughn 1955; Reisz 1981), in the neodiapsids *Lanthanolania* (Modesto and Reisz 2002), *Claudiosaurus* (Carroll 1981) and *Youngina* (Reisz *et al.* 2000), and in *Prolacerta* (Modesto and Sues 2004).

Asymmetrical bifurcation of the anterior vomers. In *Orovenator* the vomerine process of the premaxilla is incised deeply into the anterior surface of the vomer, which is bi-

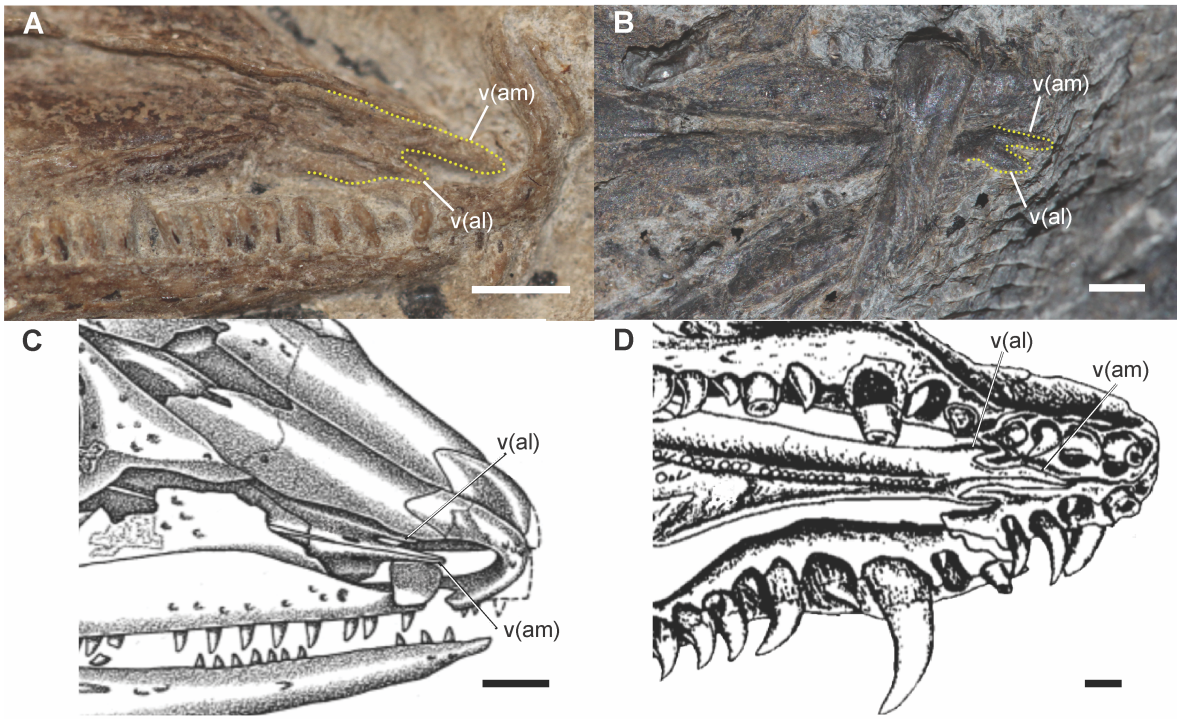


Figure 19: Asymmetric processes of anterior vomers. A, *Petrolacosaurus kansensis* (KUVP 8351). B, *Paleothyris acadiana* (MCZ 3481). C, *Archaeovenator hamiltonensis* (from Reisz and Dilkes 2003). D, *Mesenosaurus romeri* (from Reisz and Berman 2001) (image reversed). *Abbreviations*: v(al), anterolateral process of vomer; v(am), anteromedial process of vomer. Scale bars represent 2 mm.

furcated anteriorly into a short lateral process and an elongate medial process (Fig.4C). This morphology can also be found in *Paleothyris* (pers. obs. MCZ 3481; Reisz 1981), *Petrolacosaurus* (pers. obs. KUVP 8351) and in the varanopids *Mesenosaurus* (Reisz and Berman 2001) and *Archaeovenator* (Reisz and Dilkes 2003) (Fig.19). The anterior region of the vomer is insufficiently exposed or not preserved in other varanopids. A notch on the anterior surface of the vomer where it articulates with the vomerine process of the premaxilla is also present in the diadectomorph *Limnoscelis* (Berman *et al.* 2010), in the synapsids *Dimetrodon milleri* (Brink and Reisz 2012) and *Edaphosaurus boanerges* (Modesto 1995), and the parareptile *Colobomycter pholeter* (MacDougall *et al.* 2017a). However, the notch is shallow in all these taxa, and the lateral and medial processes that form the notch are short. The notch is altogether absent in more derived diapsids, such as *Prolacerta* (Gow 1975), captorhinids (*Captorhinus laticeps*, Heaton 1979; *C. aguti*; Fox and Bowman 1966; and *Labidosaurus*, Modesto *et al.* 2007) and early sphenodontians (*Clevosaurus*, Fraser 1988; and *Gephyrosaurus*, Evans 1980). A bifid anterior vomer is present in the archosauriform *Proterosuchus fergusi*, although the notch is U-shaped and the lateral and medial processes are of equal length (Ezcurra and Butler 2015).

2.5.3 Similarities of *Orovenator* and the early varanopid *Archaeovenator*

Orovenator shares several cranial similarities with *Archaeovenator* that are not present in more derived varanopids or other sauropsids. As such, they may support a sister taxon relationship of *Orovenator* with *Archaeovenator* or be primitive morphologies for a clade of *Orovenator* and Varanopidae.

Presence of a medial 'supracanine buttress' of maxilla combined with the absence of caniniform teeth. *Orovenator* possesses a thickened dorsal eminence of the alveolar shelf that extends dorsally into a triangular, tapering buttress at the level of the 9th alveolus (Fig.5A, B). *Archaeovenator* also possesses a similar buttress (Reisz and Dilkes 2003, Fig.2b) (pers. obs. KUVP 12483, right maxilla; Fig.18C), which appears to taper dorsally. This morphology is also present in ophiacodontids (Romer and Price 1940; Reisz 1972; Brinkman and Eberth 1986) and sphenacodontians (Romer and Price 1940; Reisz *et al.* 1992), and is termed a 'supracanine' buttress because members of both these groups possess caniniform teeth ventral to the maxillary buttress. Unlike in ophiacodontids and sphenacodontians, caniniform teeth are absent in both *Orovenator* and *Archaeovenator* (Reisz and Dilkes 2003). The buttress is absent in *Aerosaurus* (Langston and Reisz 1981) and its presence or absence cannot be determined in other varanopids.

Dorsolateral inclination of the suborbital portion of the maxilla. The lateral surface of the suborbital portion of the maxilla is dorsolaterally inclined by approximately 12° in *Orovenator*, such that it overhangs the alveolar margin (Fig.3A; Appendix 3, Fig.1). This also occurs in *Archaeovenator* (Reisz and Dilkes 2003), but is not found, to my knowledge, in any other early synapsid or sauropsid.

Posteroventral ridge of the angular. The posteroventral region of the angular in *Orovenator* forms a narrow ridge of bone that overlies the prearticular. Anterior to this, the ventral surface of the angular is smoothly rounded (Fig.13E). The ventral surface of the angular in *Archaeovenator* also bears a ridge posteriorly (Reisz and Dilkes 2003). In *Ascendonanus* the ventral ridge extends along the entire mandibular ramus (Spindler *et al.* 2018). This ridge is absent in derived varanopids such as

Mesenosaurus (Reisz and Berman 2001), in which the ventral margin of the angular is rounded. Amongst synapsids the ventral margin of the angular bears a thin keel in caseasaurs (e.g. *Ennatosaurus* and *Cotylorhynchus*; Maddin *et al.* 2008). In ophiacodontids, edaphosaurs and basal sphenacodontians (e.g. *Haptodus*) the posteroventral margin of the angular is expanded ventrally and transversely compressed forming a deep keel (Brinkman and Eberth 1983; Benson 2012). In derived sphenacodontians this keel is expanded ventrally to form a sheet-like lamina (Reisz 1986), a precursor of the reflected lamina of therapsids. In early eureptiles there is no posteroventral keel of the angular, which appears to be smoothly rounded in *Paleothyris*, *Protorothyris* and *Protocaptorhinus* (pers. obs. MCZ 3483, MCZ 1532 and MCZ 1478). Amongst diapsids, the angular bears a deep posteroventral keel in *Petrolacosaurus* (Reisz 1981) but is rounded in the neodiapsid *Youngina* (pers. obs. BP/1/2871).

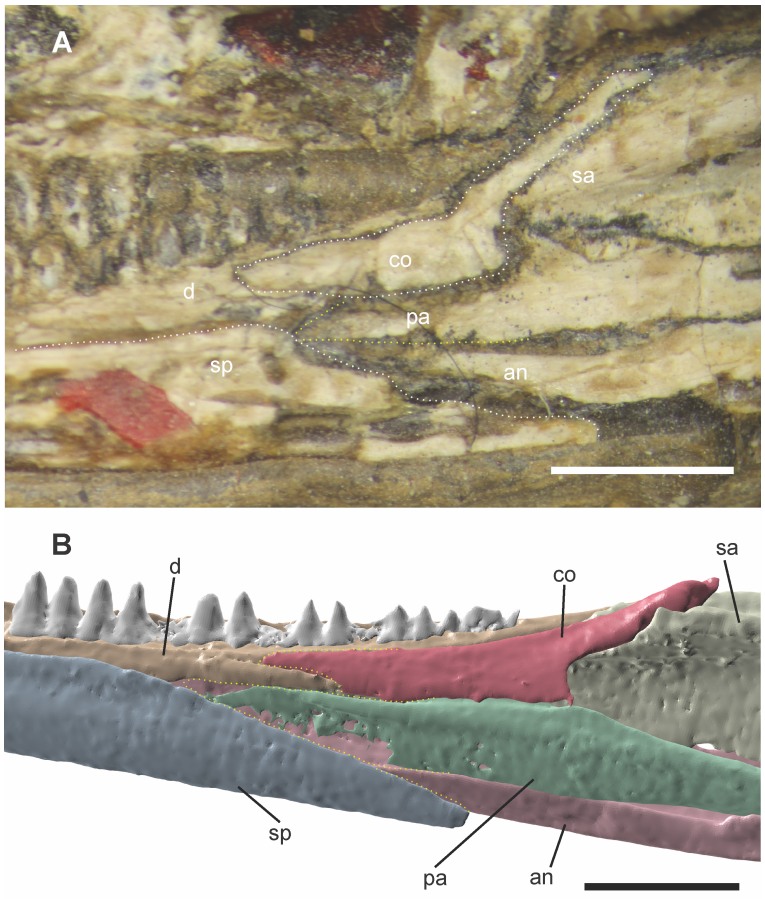


Figure 20: Coronoids in medial view. A, *Archaeovenator hamiltonensis* (KUVP 12483) right mandible. B, OMNH 74606 reconstruction of left mandible (image reversed). *Abbreviations*: an, angular; co, coronoid; d, dentary; pa, prearticular; sa, surangular; sp, splenial. Scale bars represent 2 mm.

Absence of contact between the coronoid and splenial. The morphology of the single

coronoid in *Orovenator* is similar to that found in captorhinids, basal diapsids and the posterior coronoid in early synapsids (Romer and Price 1940; Heaton 1979; Reisz 1981). In captorhinids, diapsids and archosauromorphs the splenial makes contact with the coronoid (e.g. *Captorhinus laticeps*, Heaton 1979; *Labidosaurus*, Modesto *et al.* 2007; *Petrolacosaurus*, Reisz 1981; and *Prolacerta*, Gow 1975). In contrast, the coronoid in *Orovenator* is prevented from contacting the splenial by a thin extension of the dentary (Fig.20B). This is almost identical to the condition found in *Archaeovenator*, in which the dentary also prevents contact between the coronoid and splenial (Reisz and Dilkes 2003; KUVP 12483, Fig.20A). In more derived varanopids, such as *Mesenosaurus*, the splenial contacts the anterior region of the (single) coronoid (Reisz and Berman 2001).

2.5.4 Potential synapomorphies of sauropsids that are present in varanopids and absent in other synapsids

In this section, I examine character traits found in sauropsids as a whole or in clades within the Sauropsida (e.g. diapsids) that are also present in varanopids, but absent in other early synapsid groups. These observations potentially support the existence of a clade inclusive of varanopids and diapsids.

Posterolateral process of the frontal and anterior median process of the parietal. In *Orovenator* and other early diapsids (e.g. *Araeoscelis*, Vaughn 1955; *Youngina*, pers. obs. BP/1/3859; and *Prolacerta*, pers. obs. BP/1/5375) an elongate posterolateral process of the frontal extends along the medial margin of the postfrontal at an acute angle (Fig.7A). This morphology of the frontal creates a deep V-shaped embayment in the posterior margin of the paired frontals. An anterior median process of the parietal occupies this embayment, incising into the supraorbital region of the skull roof. The posterolateral process of the frontal and the anteromedial process of the parietal were viewed as individual synapomorphies of varanopids by Reisz and Berman (2001). Here, I consider these features to be correlated, and note that both are present in *Orovenator* and varanopids (e.g. *Archaeovenator*; Reisz and Dilkes 2003; *Heleosaurus*, Botha-Brink and Modesto 2009; *Elliotsmithia*, Reisz *et al.* 1998; *Mycterosaurus*, Berman and Reisz 1982; *Mesenosaurus*, Reisz and Berman 2001; and *Varanodon*, pers. obs. FMNH UR 986). In non-varanopid synapsids, this morphology is either absent (e.g. *Dimetrodon limbatus*, Romer and Price 1940; *Ennatosaurus*, Maddin *et al.* 2008; *Sphenacodon ferox*, Spielmann *et al.* 2010) or much reduced, with the posterolateral process of the

frontal being relatively shorter and not covering the entire medial margin of the postfrontal (e.g. *Haptodus*, Laurin 1993; *Varanosaurus*, Berman *et al.* 1995; *Edaphosaurus*, Modesto 1995). It is also absent in stem amniotes (e.g. *Limnoscelis*, Berman *et al.* 2010; *Seymouria*, Laurin 1996; and *Tseajaia*, Moss 1972), in captorhinids (Fox and Bowman 1966; Heaton 1979; Müller and Reisz 2005b; Modesto *et al.* 2007; Sumida *et al.* 2010), parareptiles (*Macroleter poezicus*; Tsuji 2006) and basal eureptiles (Carroll 1964, 1969; Clark and Carroll 1973).

Teeth on the cultriform process of the parasphenoid. The presence of cultriform teeth is a derived and widespread (but variable) condition in early sauropsids. Cultriform teeth are present in *Orovenator* and other eureptiles (e.g. *Paleothyris*, Carroll 1969; *Petrolacosaurus*, Reisz 1981; *Lanthanolania*, Modesto and Reisz 2002; and *Captorhinus aguti*, Fox and Bowman 1966) but absent in *Youngina* (Gardner *et al.* 2010) and *Captorhinus laticeps* (Heaton 1979). In parareptiles they are present in *Acleistorhinus* (deBraga and Reisz 1996) and *Milleretta* (Gow 1972) but absent in *Belebey* (Reisz *et al.* 2007). Teeth on the ventral surface of the cultriform process of the parasphenoid are also present in varanopids (Langston and Reisz 1981; Berman and Reisz 1982; Reisz and Berman 2001; Reisz and Modesto 2007; Spindler *et al.* 2018). They are absent in stem-group amniotes (e.g. *Limnoscelis paludis*, Fracasso 1987; Berman *et al.* 2010; *Tseajaia* campi, Moss 1972; and *Seymouria sanjuanensis*, Klembara *et al.* 2005). They are also absent in most early synapsids (e.g. ophiacodontids, Berman *et al.* 1995; sphenacodontians, Romer and Price 1940; Laurin 1993; and edaphosaurids, Modesto 1995) except for caseasaurs (Maddin *et al.* 2008).

Adductor crest and fourth trochanter of the femur absent. In many early amniotes a prominent ridge of bone extends diagonally along the ventral surface of the femur from the internal trochanter proximally to the popliteal area of the posterior condyle distally. This ridge, the adductor crest, is interrupted approximately midshaft by the fourth trochanter when present. The fourth trochanter and adductor crest are absent in most varanopids in which the ventral surface of the femur is known (e.g. *Archaeovenator*, Reisz and Dilkes 2003; *Apsisaurus*, Laurin 1991; *Mycterosaurus*, Berman and Reisz 1982; and *Heleosaurus*, Botha-Brink and Modesto 2009). In *Varanops*, uniquely amongst varanopids, there is a moderately developed fourth trochanter (Campione and Reisz 2010). Both features are also absent in araeoscelidian diapsids (*Petrolacosaurus*, Reisz 1981; and *Araeoscelis*, Vaughn 1955), 'younginiforms' (Laurin and Reisz 1995), the archosauromorphs *Prolacerta* (Gow 1975) and *Proterosuchus* (Ezcurra *et al.* 2013),

and early sphenodontids (e.g. *Clevosaurus*; Fraser 1988). The fourth trochanter and adductor crest are present in caseasaurs, ophiacodontids and edaphosaurids (Romer and Price 1940; Reisz 1986). In sphenacodontians, these features are relatively weaker but still present, for example in *Haptodus* (Laurin 1993) or as a rugose line with a fourth trochanter in *Dimetrodon* (Reisz 1986). Both traits are also known in captorhinids (*Captorhinus aguti*; Fox and Bowman 1966) and procolophonid parareptiles (*Procolophon*; deBraga 2003). The presence of the adductor crest and fourth trochanter may be plesiomorphic for amniotes since they are present in the Permian stem-group amniotes *Limnoscelis* (Romer 1946) and *Seymouria* (White 1939).

2.5.5 Potential synapomorphies of synapsids that are absent in most sauropsids and varanopids

Lateral lappet of the frontal absent. A distinct lateral lappet of the frontal contributing to the orbital margin absent in varanopids (Langston and Reisz 1981; Reisz *et al.* 1998; Reisz and Dilkes 2003) although a small lateral lappet has been noted in *Ascendonanus* (Spindler *et al.* 2018). It is also absent in *Orovenator* and early diapsids, such as *Petrolacosaurus* (Reisz 1981), *Acerosodontosaurus* (Bickelmann *et al.* 2009) and *Lanthanolania* (Modesto and Reisz 2002). The absence of this feature is considered to be the primitive state for amniotes (deBraga and Rieppel 1997) as noted in early eureptiles (*Hylonomus lyelli*, Carroll 1964; *Paleothyris*, Carroll 1969; *Captorhinus laticeps*, Heaton 1979; and *Romeria*, Clark and Carroll 1973). In synapsids, the contribution of the frontal to the orbital margin is formed by a distinct lateral lappet (e.g. *Euromycter rutena*, Sigogneau-Russell and Russell 1974; *Ophiacodon uniformis* and *Dimetrodon limbatus*, Romer and Price 1940; *Haptodus garnettensis*, Laurin 1993; *Ianthasaurus hardestiorum*, Modesto and Reisz 1990; and *Edaphosaurus boanerges*, Modesto 1995). It is also present in lanthanosuchoid parareptiles, such as *Colobomycter pholeter* (MacDougall *et al.* 2017a) and *Delorhynchus* (Reisz *et al.* 2014). It is therefore an autapomorphy of Lanthanosuchoidea that was independently acquired in Synapsida (deBraga and Rieppel 1997).

Pathway of the cerebral carotid artery in the parabasisphenoid. The cerebral branch of the internal carotid artery (CBCA) extends through the basisphenoid from a position ventral to the basicranium into the endocranial cavity. However, its course thorough the basicranium varies among early amniotes. In particular, the condition in varanopids,

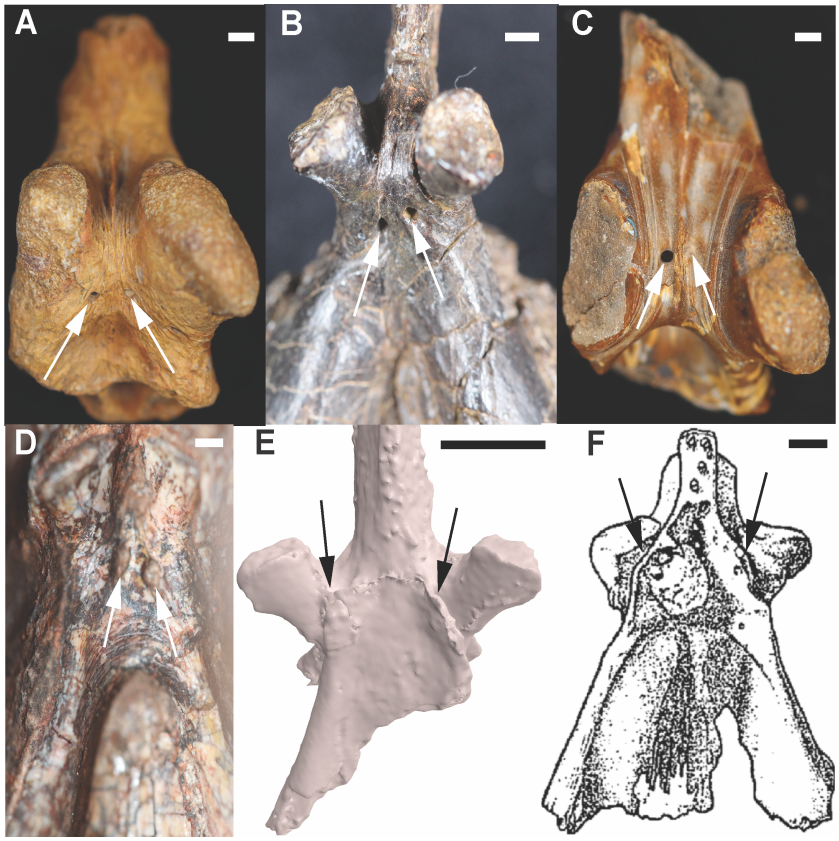


Figure 21: Parabasisphenoids in ventral view. A, *Ophiacodon retroversus* (MCZ 5792). B, *Edaphosaurus boanerges* (MCZ 1762). C, *Ophiacodon retroversus* (MCZ 4820). D, *Secodontosaurus obtusidens* (MCZ 2028). E, *Orovenator mayorum* (OMNH 74606). F, '*Basicranodon fortsillensis*' (= *Mycterosaurus longiceps*) from Vaughn (1958) (image courtesy of Washington Academy of Sciences). Arrows indicate position of entry foramina for cerebral branch of internal carotid arteries. Scale bars represent 2 mm.

stem-group amniotes, and sauropsids differs from that in synapsids. In synapsids (e.g. sphenacodontians, ophiacodontids and edaphosaurids) the point of entry of the CBCA into the endocranial cavity is located on the ventral surface of the parasphenoid medial to the basipterygoid processes, and is clearly visible in ventral view (Brinkman and Eberth 1983; Müller *et al.* 2011; Brink and Reisz 2012) (Fig.21A-D). The internal carotid artery extends along grooves on the ventral surface of the parasphenoid rather than a deep trough on ventral surface of the basipterygoid process (Romer and Price 1940).

In contrast, the varanopid *Mycterosaurus* (= '*Basicranodon*'; Reisz *et al.* 1997) possesses a pathway of the CBCA very similar to that of *Orovenator* (Fig.21E, F), with the entry point via a foramen in a deep trough or vidian sulcus formed by the lateral ridge of the parasphenoidal plate and the ventral surface the basipterygoid process, effectively obscuring the foramen in ventral view (Vaughn 1958). In the varanopid

Aerosaurus, it has been suggested that the entry point for the CBCA is situated on the lateral surface of the basisphenoid, posterior to the clinoid process, rather than via the vidian sulcus ventral to the basipterygoid process (Langston and Reisz 1981). A similar condition is only otherwise seen in taxa with vidian canals where the division of the carotid artery into the cerebral and palatine branches occurs internally (e.g. in parareptiles, squamates, crown-group turtles and birds) rather than externally as in early synapsids, early turtles and eureptiles (Müller *et al.* 2011). The pathway of the CBCA is located in a vidian sulcus ventral to the basipterygoid process in all early eureptiles in which the parabasisphenoid is preserved, for example *Prolacerta* (Evans 1986), *Youngina* (Evans 1987; Gardner *et al.* 2010), *Captorhinus laticeps* (Heaton 1979), *Gephyrosaurus* (Evans 1980), Sphenodon and basal lepidosaurs (Evans 2008). It is similarly located in the stem amniotes *Chroniosuchus* and *Seymouria baylorensis* (White 1939; Shishkin 1968) suggesting that this feature may be plesiomorphic for amniotes.

2.6 Phylogenetic analysis

Orovenator has so far been regarded as a diapsid, because of its diapsid-like temporal fenestration (Reisz *et al.* 2011a). Reisz *et al.* (2011a) therefore investigated the phylogenetic position of *Orovenator* within the framework of early diapsid evolution, using 29 neodiapsid and diapsid taxa with four out-groups. This analysis recovered *Orovenator* as the most basal member of Neodiapsida (Fig.22A). However, our new data and comparisons (discussed above) include many more observations of similarity between *Orovenator* and varanopids, which have classically been regarded as synapsids (Romer and Price 1940; Reisz 1986; Reisz and Laurin 2004; Benson 2012; Reisz and Fröbisch 2014). I therefore elected to test whether the relationship between *Orovenator* and varanopids might differ from the current consensus.

For this purpose I scored *Orovenator* into the character-taxon matrix of Reisz *et al.* (2010) designed to differentiate between diapsids and varanopids, and previously used to reassess the phylogenetic position of *Apsisaurus witteri* (Fig.22B). One change was made to the matrix: the score of character 60 (number of coronoids) was changed from two (state 0) to one (state 1) for *Mesenosaurus*, based on the absence of an anterior coronoid (Reisz and Berman 2001). This change made no difference to the tree topology prior to the inclusion of *Orovenator*. All ordered (additive) characters were analysed as such, following Reisz *et al.* (2010). The scores for *Orovenator* are

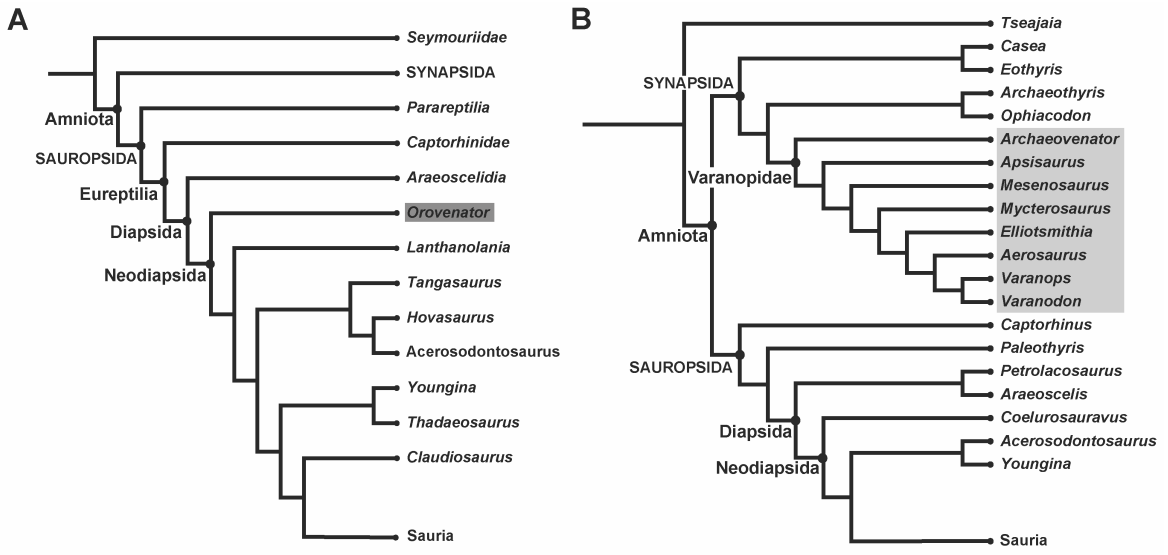


Figure 22: Phylogenetic analyses of the character-taxon matrices of: A, Reisz *et al.* (2011a); B, Reisz *et al.*(2010). Taxa recovered as Sauria in both datasets have been condensed to a single operational taxonomic unit.

provided in Appendix 3. The matrix was run in TNT v.1.5 (Goloboff *et al.* 2008) using New Technology search with drift, tree fusing, parsimony ratchet and sectorial search. The initial search level was set at 60 and additional sequence replicates at 500. Minimum length search was 30. Zero length branches are collapsed as default in TNT v.1.5. All resultant trees were subjected to final TBR branch swapping (bbreak=tbr). This analysis resulted in three MPTs with tree length of 386 (Fig.23).

The inclusion of *Orovenator* into the matrix of Reisz *et al.* (2010) results in a fundamental change to tree topology. Varanopids were previously found as synapsids but are now instead recovered within the diapsid clade as a monophyletic group, with *Orovenator* as the most basal member. This group is placed crownward of araeoscelidian diapsids and is the sister group of all remaining neodiapsids. Bremer support, however, is poor with only one additional step required to collapse all major nodes (i.e. Synapsida, Sauropsida and Diapsida). Furthermore, only one additional step is required to recover varanopids as synapsids to the exclusion of *Orovenator*. Nevertheless, this result occurs in spite of the fact that only 5 of the 16 similarities or synapomorphies between *Orovenator*/sauropsids and *Archaeovenator*/varanopids documented above are included in the character list used in this analysis. Therefore, this phylogenetic hypothesis test is conservative; the finding of an early diapsid clade comprising *Orovenator* plus varanopids occurs in the absence of the addition of extra characters that are consistent with that hypothesis. To test hypotheses of the phylogenetic position of varanopids further requires a broad-based approach to early amniote

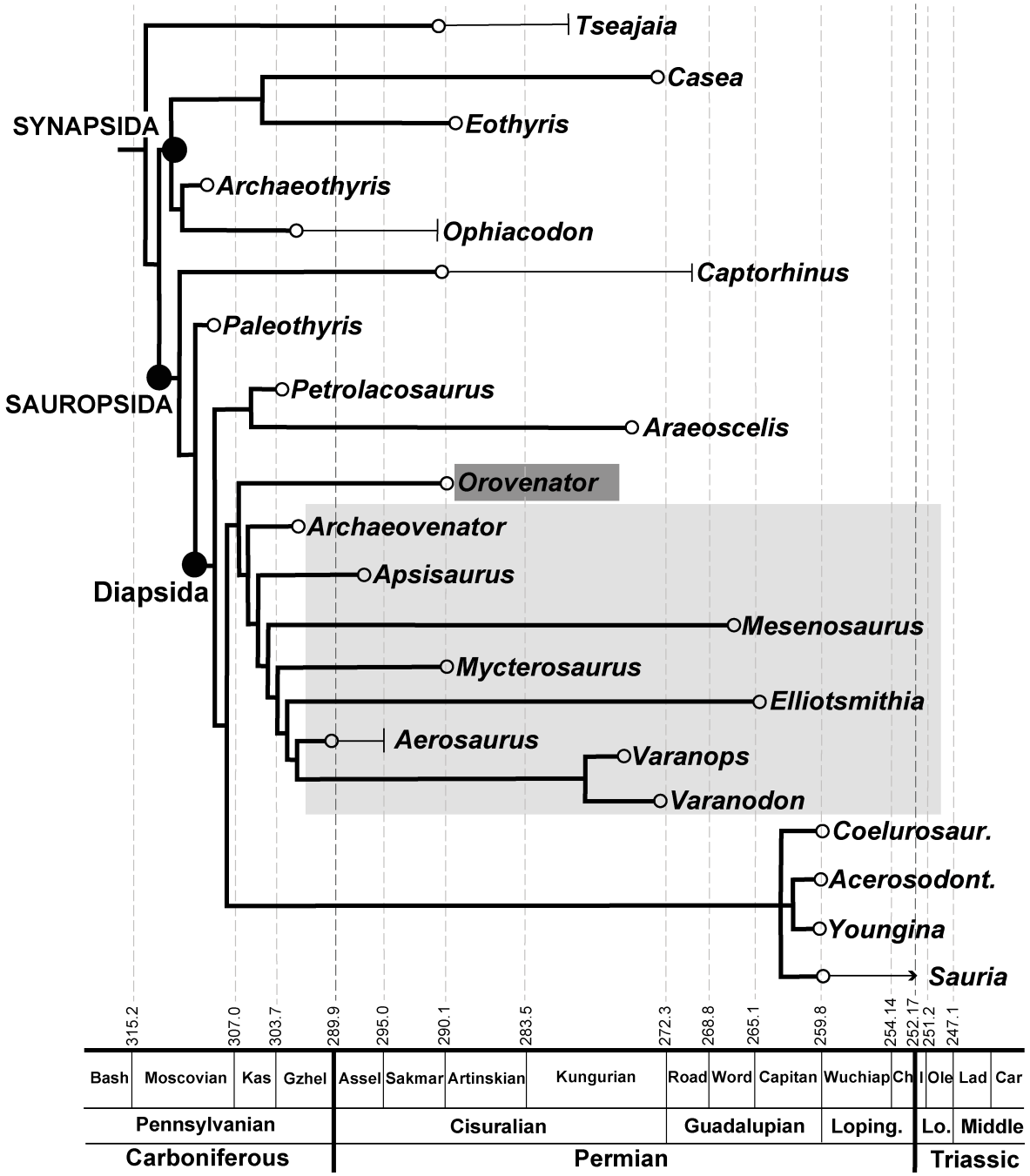


Figure 23: Time calibrated strict consensus of the three most-parsimonious trees recovered from the dataset of Reisz *et al.*(2010) after the inclusion of *Orovenator mayorum* into the character-taxon matrix. White circles denote first appearance datum, lines ending with vertical bars denote range. Taxa recovered as Sauria in have been condensed to a single operational taxonomic unit. *Abbreviations*: Coelurosaur., *Coelurosauravus*; Acerosodont., *Acerosodontosaurus*.

phylogeny, incorporating a comprehensive character-taxon matrix that may be applied across all established groups of early amniotes. This task is the subject of the research conducted and described in chapter 4.

Nevertheless, these results imply that, contrary to the current paradigm, varanopids may represent a monophyletic clade of early non-araeoscelidian diapsids that diverged from its sister group, the neodiapsids, during or prior to the late Carboniferous (late Pennsylvanian). The scarcity of diapsids during the early Permian (Reisz *et al.* 2011a) is to some extent rectified by this hypothesis, in which varanopids represent a previously-unrecognised clade of early Permian diapsids. However, it also extends the ghost lineage for neodiapsids from the late Carboniferous to the appearance of *Lanthanolania* in the late middle Permian (Modesto and Reisz 2002). This hypothesis, if correct, makes several characters that were highly congruent with previous phylogenetic hypotheses (in which varanopids are synapsids) incongruent. These are discussed below.

2.6.1 Character states that are incongruent with the hypothesis that varanopids are sauropsids

Varanopids possess only a single, lateral temporal fenestra as seen in synapsids. In contrast, *Orovenator* and all diapsids possess upper and lower temporal openings; although in some taxa the lower temporal bar is not completed, meaning that the lower temporal fenestra takes the form of an arch or emargination. Indeed, the condition of the lower temporal opening is not known in *Orovenator*, despite the elongate subtemporal process of the jugal (see Description above). If the topology recovered by my analysis is correct, then diapsid or euryapsid temporal fenestration was primitively present in the clade comprising *Orovenator* + varanopids, as indicated by the anatomy of *Orovenator*. However, the upper temporal fenestra was subsequently lost in this group, as it is absent in varanopids where the posterior process of the postorbital has closed with the lateral margin of the parietal, resulting in a dorsoventral enlargement of the lower temporal fenestra.

Hypotheses of early amniote phylogeny have placed substantial emphasis on temporal fenestration (Gauthier *et al.* 1988; Laurin and Reisz 1995; deBraga and Rieppel 1997) despite the recognition of widespread plasticity of temporal fenestrae in early amniotes (Frazzetta 1968; Müller 2003).Many examples of homoplasy have been reported relating to the loss or acquisition of temporal fenestration, suggesting a high degree of plasticity even amongst closely related taxa, with multiple independent modifications of temporal fenestration amongst parareptiles (Pineiro *et al.* 2012; MacDougall and Reisz 2014) or the opportunistic development of lower temporal fenestration in the

early synapsid *Ophiacodon* (Romer and Price 1940; Frazzetta 1968). There is also good evidence for local-scale homoplasy in temporal fenestration amongst diapsids. For example, the araeoscelidian diapsid *Petrolacosaurus* has a lower temporal fenestra with a complete ventral bar (the diapsid condition), whereas its sister taxon *Araeoscelis* lacks a lower temporal opening entirely (Vaughn 1955; Reisz *et al.* 1984). Furthermore, the euryapsid condition is widespread among late Permian neodiapsids (*Claudiosaurus*, Carroll 1981; and *Acerosodontosaurus*, Bickelmann *et al.* 2009), archosauromorphs (*Prolacerta*, Modesto and Sues 2004; and *Tanystropheus*, Nosotti 2007) and sauropterygians (Rieppel 1993), and is present in all extant squamates (Evans 2008). It has even been proposed that turtles are modified diapsids, which implies the secondary closure of the upper and lower temporal fenestrae and the emargination of the posterior and ventral temporal region (Rieppel 1993; Bever *et al.* 2015). Recent work on the patterns of ontogenetic change in the temporal region of early amniotes may provide some clues on the mechanisms of closure of fenestrae (Haridy *et al.* 2016). However, it is evident that temporal fenestration can be readily lost or gained within closely-related groups of early amniotes.

In addition to temporal fenestration, there are other morphologies that would appear to contradict the grouping of varanopids within Diapsida. However, when the presence or absence of such morphologies is reviewed for each taxon, I find that their occurrence in varanopids is variable. For example, *Orovenator* possesses a single coronoid in the mandible, a widely recognised synapomorphy of Sauropsida (deBraga and Rieppel 1997). The presence of multiple coronoids is plesiomorphic for amniotes (Moss 1972; Laurin 1996; Berman *et al.* 2010), and early synapsids possess two coronoids (anterior and posterior coronoids; Romer and Price 1940; Romer 1956). This condition has also been stated to be present in varanopids (Reisz 1986). However, although varanopids such as *Mesenosaurus*, *Mycterosaurus*, *Varanodon* and *Varanops* have been scored as possessing two coronoids in some phylogenetic studies (e.g. Reisz *et al.* 2010), I am aware of only one specimen of *Varanops* (TMM 43628-1; Campione and Reisz 2010) in which evidence of an anterior coronoid has been unequivocally documented. Moreover, the anterior coronoid is absent in *Mesenosaurus* (Reisz and Berman 2001), and it also appears to be absent in the right mandible of *Archaeovenator* (pers. obs. KUVP 12483; Reisz and Dilkes 2003). There is no evidence of an anterior coronoid in the mandible assigned to a mycterosaurine varanopid from the middle Permian of South Africa (Modesto *et al.* 2011). In *Aerosaurus*, the coronoid is not preserved, but a groove on the anteromedial surface of the dentary is interpreted as accommodating the anterior coronoid (Langston and Reisz 1981). A 'probable' anterior coronoid

was identified in *Heleosaurus* (Reisz and Modesto 2007, p. 736), although this is not conclusive. In consequence, the number of coronoids cannot be determined in many varanopids and seems to be variable. The variable nature of the coronoid count in amniotes is further exemplified in the early diapsid *Araeoscelis*, which possesses an anterior and a posterior coronoid (Vaughn 1955).

The suborbital fenestra in the suborbital region of the palate between the maxilla, palatine, pterygoid and ectopterygoid is a synapomorphy of sauropsids (deBraga and Rieppel 1997). In captorhinids and parareptiles it is present as a small gap or foramen (e.g. *Captorhinus laticeps*, Heaton 1979; and *Belebey* vegrandis, Reisz *et al.* 2007). In diapsids it commonly takes the form of an anteroposteriorly elongate and transversely broad fenestra, as seen in the earliest members of the clade (e.g. araeoscelidian diapsids; Vaughn 1955; Reisz 1981) and more derived taxa (e.g. *Prolacerta*, Gow 1975; *Youngina*, Carroll 1981; and *Gephyrosaurus*, Evans 1980). *Orovenator* possesses a slender, transversely narrow, slot-like suborbital fenestra that is particularly narrow anteriorly where the lateral margin of the palatine is dorsoventrally thin and almost contacts the maxilla (Fig.9).

The absence of a suborbital fenestra is probably primitive for amniotes since it is also absent in basal eureptiles (e.g.*Paleothyris*, Carroll 1969; *Protorothyris* and *Romeria*, Clark and Carroll 1973). All 'pelycosaur'-grade synapsids also lack the suborbital fenestra (deBraga and Rieppel 1997). In fact, many of them possess a dorsoventrally deep, firmly sutured contact between the maxilla and the palate. Although varanopids have been scored as lacking a subtemporal fenestra in phylogenetic analyses (Reisz *et al.* 2010), in fact this region is damaged or otherwise unobservable in most taxa. In *Mesenosaurus* the anterior process of the ectopterygoid contacts the jugal laterally and the palatine medially, thus effectively eliminating the possibility of a suborbital opening in the palate (Reisz and Berman 2001). In *Elliotsmithia*, only a small region of the medial margin of the right palatine is exposed (Reisz *et al.* 1998). This is mildly concave, and the nature of its contact with the maxilla cannot be ascertained. In *Heleosaurus*, the right palatine was considered too wide posteriorly to accommodate a suborbital fenestra (Reisz and Modesto 2007), although this is almost identical to the right palatine of *Orovenator*. The suborbital region of the palate is not observable in *Mycterosaurus*, *Pyozia*, *Apsisaurus*, *Ascendonanus*, *Aerosaurus*, *Varanodon*, *Watongia* and *Varanops*.

In summary, I find that the character states that are incongruent with the hypothesis of varanopids as sauropsids are either highly homoplastic amongst early amniotes (temporal fenestration), variably present or absent amongst varanopids (single or mul-

tiple coronoids) or cannot be unequivocally scored in most varanopid taxa (the absence of a suborbital fenestra).

2.7 Conclusions

I have reviewed the anatomy of the oldest non-araeoscelidian diapsid, *Orovenator mayorum*, using high resolution μCT scanning and reconstruction. I find at least 16 similarities, many of which were previously unrecognised, between *Orovenator*/sauropsids and varanopids, which are typically considered to be synapsids. I therefore propose a hypothesis that *Orovenator* forms a clade with varanopids, raising questions about whether this clade belongs to Synapsida or Sauropsida. The further evidence presented in my study supports a relationship between sauropsids and varanopids that is incongruent with the current paradigm of early amniote phylogeny. However, my findings clearly emphasise the need for further scrutiny of the base of the amniote tree, including more comprehensive character and taxon sampling across the diversity of early amniotes. I also concur with early studies that highlight the highly homoplastic nature of temporal fenestration amongst early amniotes. Finally, the present study illustrates the potential advantages in reassessing early amniote taxa using μCT scanning. Many of the earliest fossil amniotes are small-bodied taxa, for which only external cranial anatomy has been visible until now. My work on *Orovenator* demonstrates that high resolution μCT scanning can provide new insights on the comparative anatomy of the earliest amniotes. I expect that this may stimulate further debate on the systematics of amniote evolution.

Chapter 3

A Reassessment of the Characterisation of Temporal Fenestration in Early Amniotes

3.1 Temporal fenestration in a systematic framework

Almost all living amniotes (mammals, birds and reptiles; other than turtles) possess either one or two openings in the temporal (postorbital) region of the skull (Romer 1956, Moore 1981, Rieppel 1993). Primitively, these openings were entirely enclosed by dermatocranial bone, forming fenestrae, as can be seen in extant reptiles such as crocodylians (Fig.1A) and *Sphenodon* (Tuatara). Some groups have extensively modified this morphology, for example by expansion of the fenestra onto the neurocranium, and by lateral flexure of the ventral bar (zygomatic arch) in mammals (e.g. meerkat, Fig.1B). The opening may also be only partially enclosed, forming an emargination of the temporal region (e.g. iguana, Fig.1C). Birds (e.g. chicken *Gallus gallus domesticus*, Fig.1D) have highly modified openings, which often merge with the orbit. Indeed, although they lack temporal fenestrae in the formal sense, the skulls of many turtles are also emarginated externally, resulting in a functional analogue to the fenestrae of other amniotes (Frazetta 1968).

The origins and adaptive importance of temporal openings in amniotes have long been a topic of discussion among palaeontologists. Stresses resulting from muscular action (e.g. during jaw closing) are distributed unevenly in the skull, and temporal openings may have originated due to bone reduction in areas of low stress (Gregory and

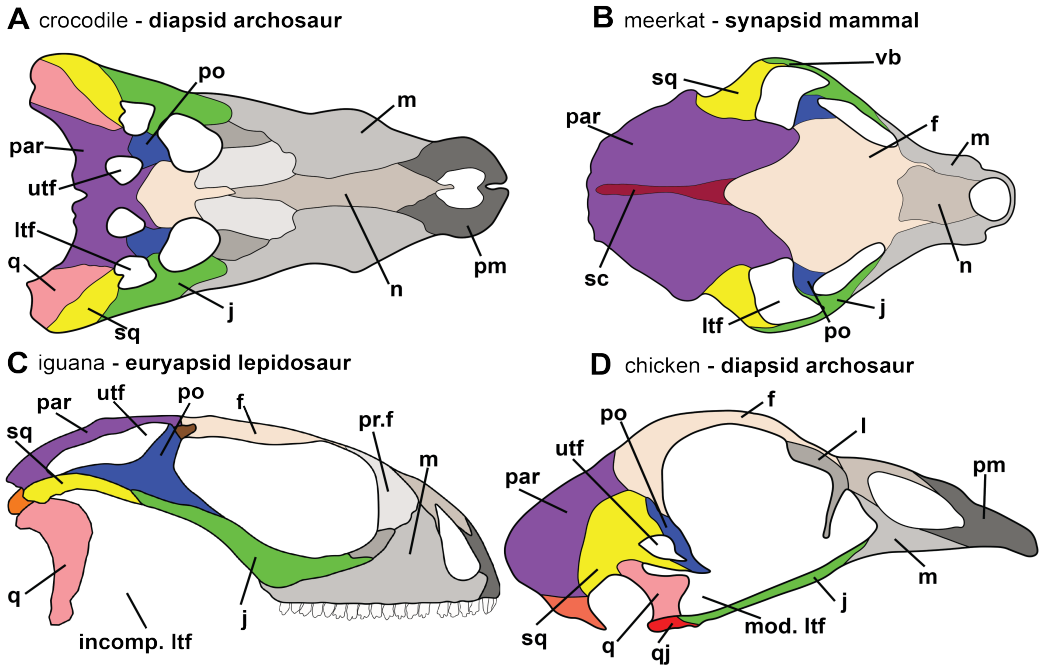


Figure 1: Diagrams of extant amniote skull types (not to scale). A, dorsal view of a crocodile (*Crocodylus moreletii*) - diapsid; B, dorsal view of a meerkat (*Suricata suricatta*) - synapsid; C, lateral view of an iguana (*Dipsosaurus dorsalis*) - euryapsid; D, lateral view of a chicken (*Gallus gallus domesticus*) - diapsid. *Abbreviations*: f, frontal; incomp.ltf, incomplete lower temporal fenestra; j, jugal; l, lacrimal; ltf, lower temporal fenestra; m, maxilla; mod. ltf, modified lower temporal fenestra; n, nasal; par, parietal; po, postorbital; pr.f, prefrontal; q, quadrate; qj, quadratojugal; sc, sagittal crest; sq, squamosal; utf, upper temporal fenestra; vb, ventral bar. All images after data from Digital Morphology (http://digimorph.org/).

Adams 1915, Case 1924). Fenestrae occur on the junctions of multiple bones, rather than within individual bones, and it is therefore likely that they resulted from separation, rather than perforation, of bones (Williston 1907). Frazetta (1968) endorsed this view, noting that the initial stages of temporal fenestration probably resulted from reduced stress at triple-junctions among temporal bones. He also suggested that, once they had originated, temporal fenestrae were retained due to other adaptive advantages: due to their convexity, the rims of fenestrae provide a more secure attachment for the adductor muscles than the concave internal surfaces of unfenestrated bones. This allows stronger jaw adductor muscles. Tarsitano *et al.* (2001) noted that in extant vertebrates the low angle attachment provided by the fenestral rim is crucial to the mineralization of the tendons during development. Mineralized tendons and a greater area of low angle attachment allow for expansion of the jaw adductor muscles, resulting in a stronger and more versatile bite force. The pattern and constituent bones of temporal fenestrae are therefore closely associated with the distribution of temporal and mandibular musculature. This results in a complex and variable morphology

with great potential to provide phylogenetically-informative characters. To make use of this potential, it is important to establish an effective method for characterising the morphology of temporal fenestration in phylogenetic character-taxon matrices.

Patterns of temporal fenestration vary considerably in all living and extinct amniotes, and have been a mainstay of taxonomic classification for over a century. Osborn (1903) consolidated earlier concepts on the division of 'reptiles' (= most early amniotes, plus crown-group reptiles) by introducing two subclasses, Synapsida and Diapsida, based principally on the presence of one (lower) fenestra in synapsids, and two (lower and upper) fenestrae in diapsids. Synapsida is the total-group mammals, and the sister taxon to Sauropsida (total group-reptiles). Diapsida is the only extant group within Sauropsida, and includes all modern birds and reptiles, although many of these have either secondarily lost their temporal openings (e.g. turtles, Bever *et al.* 2015) or modified them (e.g. squamates, Fig.1C; Evans 2008). Nevertheless, in many diapsids, and in all synapsids, the fenestrae are formed by a dorsal arch or arcade (apsis = latin 'vault' or 'arch') and a ventral bar of dermatocranial bones, completely enclosing a temporal opening (Fig.2A and 2B).

Temporal fenestration arose very early in amniote evolution. Synapsids with a single temporal fenestra are present in some of the earliest fossil assemblages that contain amniotes (e.g. *Echinerpeton intermedium* and *Archaeothyris florensis*, Middle Pennsylvanian, Florence, Nova Scotia) (Reisz 1972). These fossil occurrences, and the occurrence of the oldest fossil sauropsid (*Hylonomus lyelli*, Lower Pennsylvanian, Joggins, Nova Scotia) (Carroll 1964) are important calibration points for molecular clock studies (Müller and Reisz 2005, Benton *et al.* 2015), providing an estimated time of origin of the amniotes crown-group (synapsid/sauropsid split) of around 332.9 - 318 Ma. The oldest fenestrated sauropsids are the araeoscelidian diapsids *Petrolacosaurus* (Reisz 1981) and *Spinoequalis* (deBraga and Reisz 1995), both from the late Pennsylvanian of Kansas, USA.

3.1.1 Temporal fenestration in early amniotes

In addition to the synapsid and diapsid conditions of temporal fenestration, other morphologies of the postorbital region are found in early amniotes. The absence of fenestration or emargination, the anapsid condition, is plesiomorphic in tetrapods. Temporal fenestration is absent in stem-group amniotes, including diadectomorphs (e.g. *Tseajaia campi* and *Limnoscelis paludis*), seymouriamorphs (Moss 1972, Laurin 1996, Berman *et al.* 2010) and anthracosaurs (Clack 2012). It is also absent in some early crown-group amniotes: captorhinids, e.g. *Captorhinus laticeps* (Fig.2E) and 'protorothyridids', e.g.

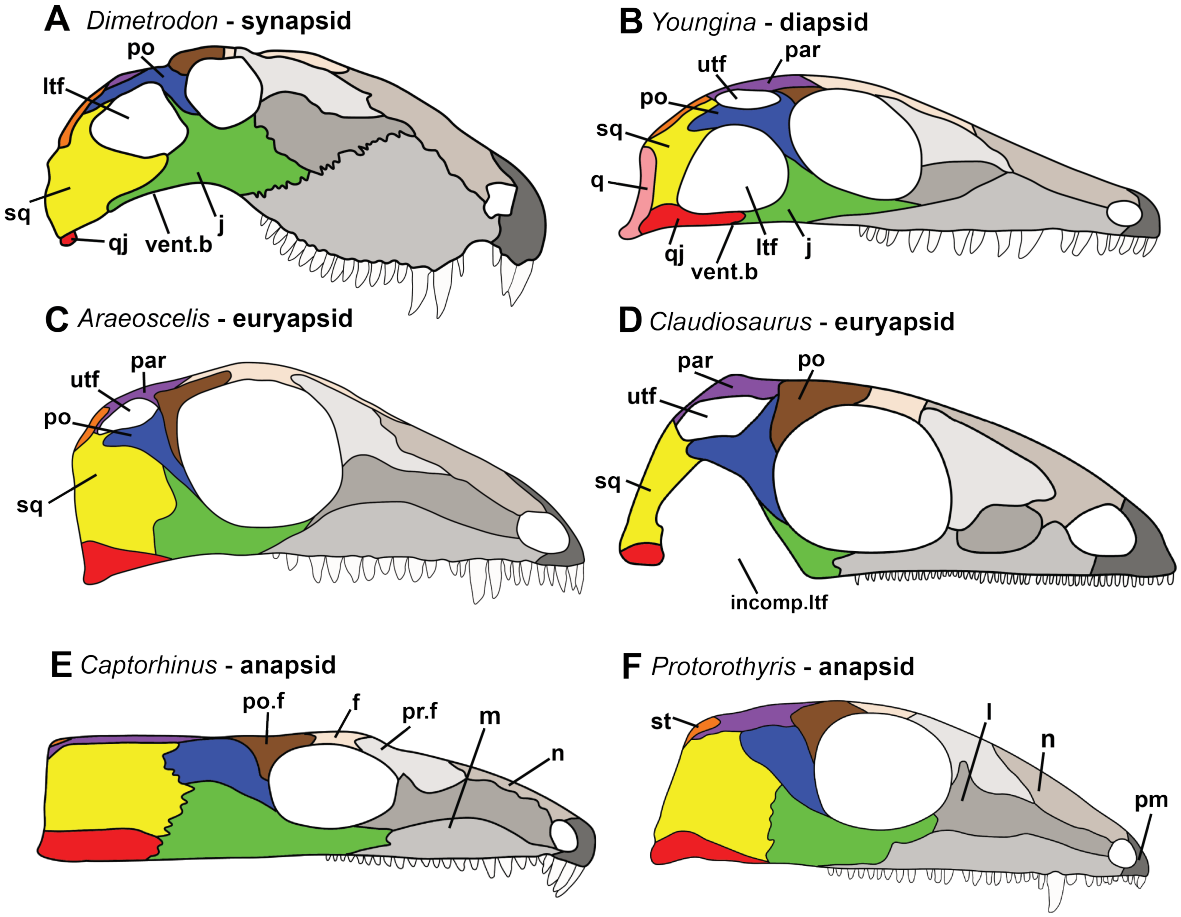


Figure 2: Diagrams of early amniote skull types in lateral view (not to scale). A, *Dimetrodon limbatus*, - synapsid (after Romer and Price 1940); B, *Youngina capensis*, - diapsid (after Carroll 1981); C, *Araeoscelis casei* - euryapsid (after Reisz *et al.* 1984); D, *Claudiosaurus germaini* - euryapsid (after Carroll 1981); E, *Captorhinus laticeps* - anapsid (after Heaton 1979); F, *Protorothyris archeri* - anapsid (after Clark and Carroll 1973). *Abbreviations*: f, frontal; incomp.ltf, incomplete lower temporal fenestra; j, jugal; l, lacrimal; ltf, lower temporal fenestra; m, maxilla; n, nasal; par, parietal; po, postorbital; po.f, postfrontal; pr.f, prefrontal; q, quadrate; qj, quadratojugal; sq, squamosal; utf, upper temporal fenestra; vent.b, ventral bar

Protorothyris archeri (Fig.2F). All of these are generally hypothesised to be members of the reptile stem-lineage (i.e. early diverging sauropsids) indicating that temporal fenestration most likely evolved independently in synapsids and diapsids (Romer and Price 1940).

Parareptiles, a diverse group of early reptiles, which, when first raised by Olson (1947), included procolophonids, pareiasaurs and turtles, have generally been characterised as possessing the anapsid condition (Olson 1947), and this view persisted in the taxonomic nomenclature of later studies (Modesto 1999, Reisz and Scott 2002). However, more recent work has provided ample evidence of widespread temporal fenestration in parareptiles, raising the possibility that this feature may be a synapomorphy

of the group, which also exhibits a high degree of homoplasy in the presence and morphology of temporal fenestrae (Cisneros *et al.* 2004, Tsuji 2006, 2010, MacDougall and Reisz 2014).

Some early reptiles possess a single upper temporal fenestra and lack an enclosed lower temporal fenestra. This is the euryapsid condition and variations of this are found in most marine reptiles (Sauropterygia and Ichthyopterygia, Rieppel 1993) and in the early Permian diapsid *Araeoscelis* (Fig.2C), prompting the hypothesis that euryapsid fenestration is a modification of the diapsid condition (Reisz *et al.* 1984, deBraga and Rieppel 1997). Many late Permian diapsids (e.g. *Lanthanolania ivakhnenkoi*, Modesto and Reisz 2002 and *Claudiosaurus germaini*, Carroll 1981), possess a version of the euryapsid condition, consisting of an enclosed upper temporal fenestra and a lower temporal arch (emargination), which most likely represents a lower temporal fenestra with an incomplete ventral bar (Fig.2D).

The euryapsid condition is also primitive for lepidosauromorphs (e.g. *Marmoretta oxoniensis*, Evans 1991; *Megachirella wachtleri*, Renesto and Bernardi 2014) and rhynchocephalians (e.g. *Gephyrosaurus bridensis*, Evans and Jones 2010), and is present in all extant squamates. It is also likely primitive for archosauromorphs as it is present in early-diverging members of their stem-lineage (e.g. *Tanystropheus longobardicus*, Nosotti 2007; *Prolacerta broomi*, Modesto and Sues 2004 and *Mesosuchus browni*, Dilkes 1998). It is likely therefore that a euryapsid condition was present in the most recent common ancestor of Sauria, the diapsid crown-group (Evans and Jones 2010). The fully diapsid condition of extant archosaurs (e.g. crocodiles, Fig.1A) and *Sphenodon* (the only extant rhynchocephalian) is therefore likely secondary, and resulted from the attainment of a complete ventral bar in the crown-ward members of these groups (e.g. *Euparkeria capensis*, Ewer 1965 and *Sphenodon punctatus*, Evans 2008). There are also at least two phylogenetically-independent origins of the ventral bar in extinct borioteiiod squamates from the late Cretaceous, (e.g. *Tianyusaurus zhengi*, Lü *et al.* 2008 and *Polyglyphanodon sternbergi*, Simões *et al.* 2016), and at least one in rhynchocephalians (*Sphenodon* has a complete lower temporal bar).

3.1.2 Coding for variation in temporal fenestration

The importance of temporal fenestration in taxonomy was further entrenched in comparative biology with the introduction of phylogenetic systematics (Henning 1950) and the increasingly popular application of cladistic analysis to palaeontological research. The earliest cladistic studies of early amniotes (Gaffney 1980, Reisz 1986, Gardiner 1982, Heaton and Reisz 1986) and later computer-assisted analyses (Gauthier *et al.*

1988a and 1988b, Laurin and Reisz 1997, deBraga and Rieppel 1997) used characters that code for the presence or absence of a lower temporal fenestra and the presence or absence of an upper temporal fenestra, and this practice has continued to the present day (Spindler *et al.* 2018, MacDougall *et al.* 2018). This method of coding, referred to here as the 'dual opening method' directly follows the diagnostic principle established by Osborn (1903), and would be justified if upper and lower fenestrae were uniquely recognisable in all taxa based on detailed observations of similarity, implying a potential for homology (Patterson 1988, de Pinna 1991). However, this is not the case, in fact the morphology of temporal openings is surprisingly variable among early amniotes. Within Synapsida, for example, there are four different configurations of bones forming the lower temporal fenestra (Figs.6, 7, 8B, 9A). In parareptiles there are three different configurations of the lower temporal fenestra (Figs.7C, 9, 11) and two different types of ventral emargination (Figs.12A, 14).

Some studies have suggested that the use of the dual opening method of coding for broad-based analyses of early amniote taxa is problematic, and that instead, the basis for coding should focus on the relationships of the bones forming the opening rather than the fenestra itself (deBraga an Rieppel 1997, MacDougall and Reisz 2014). However, this recommendation has not been followed by recent phylogenetic studies (Bever *et al.* 2015; Brocklehurst *et al.* 2016; Spindler *et al.* 2018), although some studies have used a combined approach that makes use of the dual opening method, augmented by coding for the contribution of various bones to the margins of temporal fenestrae (MacDougall *et al.* 2018).

In this chapter, I will illustrate how patterns of temporal fenestration among early amniotes are more variable than is implicit in the dual opening method, and how the atypical patterns of fenestration seen in several species of both synapsids and sauropsids introduces ambiguities to the identification of 'upper' and 'lower' temporal fenestrae. These make the dual opening method difficult to apply, in part because characters describing the presence or absence of a 'lower' temporal fenestra fail the test of conjunction (of de Pinna 1991; see below). Indeed, there are several species for which it is not possible to score the presence or absence of these fenestrae without some prior hypothesis of tree topology. This introduces circularity to phylogenetic hypothesis tests that only make use of the dual opening method in characterising temporal fenestrae.

Another drawback of the dual opening method of character construction is that it fails to capture several of the detailed points of anatomical similarities among patterns of temporal fenestration for various sets of species. As with other observations

of similarity, these provide information that can be used to test hypotheses of interrelationships amongst early amniotes, and should therefore be coded as characters in phylogenetic datasets.

3.1.3 Difficulties characterising temporal fenestration

In early synapsids a single lower temporal fenestra is considered to be universally present. There is, however, significant variation in the combinations of the bones forming this fenestra. This is exemplified in the configurations of temporal fenestrae in the early synapsids *Edaphosaurus boanerges* and *Secodontosaurus obtusidens* (Fig.3). In these taxa the ventral bar of the fenestra is formed by the jugal and squamosal, as is typical of the lower temporal fenestra of many early synapsids. However, the dorsal arcade is formed by the parietal, postorbital and squamosal, a combination that is otherwise only present in the upper temporal fenestrae of diapsid (including euryapsid) reptiles. These observations mean that the identity of the temporal fenestra of *E. boanerges* and *S. obtusidens* is ambiguous in the absence of any prior hypothesis of phylogenetic relationships. Indeed, the presence of a ventral emargination of the lower temporal bar in both species suggests that the fenestra above it could, with some justification, be described as an upper temporal fenestra. Therefore, coding for the presence of a 'lower' temporal opening in these taxa involves some degree of *a priori* assumption based on tree topology, rather than an observation of similarity (primary homology sensu de Pinna 1991) to be tested by congruence in phylogenetic analysis.

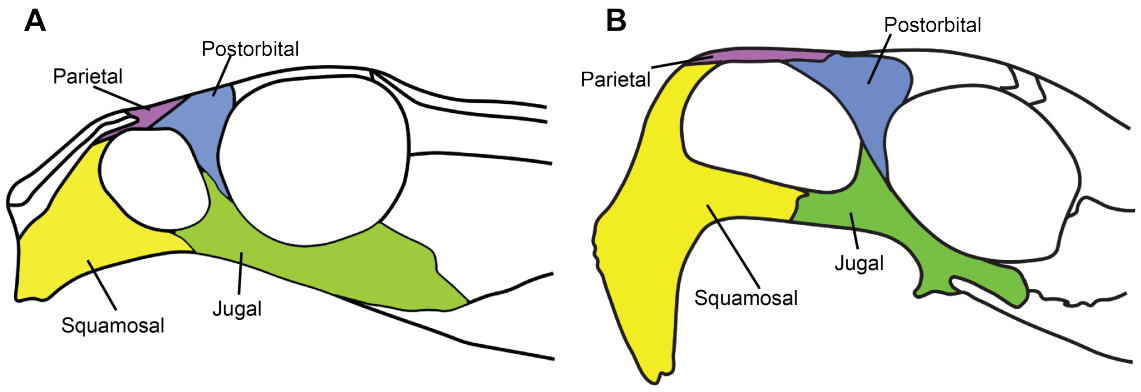


Figure 3: Diagrams of right temporal region in early synapsids. A, *Secodontosaurus obtusidens* (after Reisz *et al.* 1992); B, *Edaphosaurus boanerges* (after Modesto 1995)

The ophiacodontids *Ophiacodon retroversus* and *Varanosaurus acutirostris* present another example of these ambiguities. Both taxa possess a small additional opening posteroventral to a larger, lateral fenestra. In *O. retroversus* this small opening is

situated between the jugal, squamosal and quadratojugal (Romer and Price 1940), and between the jugal and squamosal in *V. acutirostris* (Fig.4). Although it has been assumed that the larger opening represents the 'lower' temporal fenestra seen in other synapsids, this identification is ambiguous. On one hand, the bones that contribute to the 'lower' temporal fenestra in the varanodontine *Varanodon agilis* (a presumed synapsid), and some other taxa ('Type IV' below; Fig.9A) are the same as those that form the additional opening in ophiacodontids (the quadratojugal is only marginally excluded from the rim of the fenestra in *V. acutirostris*, see Fig.4). However, on the other hand, the larger fenestra of both *O. retroversus* and *V. acutirostris* is enclosed by the postorbital, squamosal and jugal (Fig.4), which constitute the 'lower' temporal fenestrae of many other synapsids, e.g. *Dimetrodon* (Fig.2A). Therefore, in respect to the dual opening method of coding, *O. retroversus* has two 'lower' temporal fenestrae. This represents a failure of the test of conjunction (de Pinna 1991). If two structures, in this case 'lower' temporal fenestrae, are present in the same organism they must either be states of separate, independent characters or represent an error in the assessment of morphological similarity (primary homology) on which the character is based (de Pinna 1991).

Romer and Price (1940) in their review of 'pelycosaur'-grade synapsids noted of the secondary temporal opening in *O. retroversus*, "It would seem that we have here an illustration of the way in which the lateral temporal opening of a diapsid may have originated, although the ophiacodonts are not, of course, in any way related to these forms" (Romer and Price 1940 p.229). Ultimately, few would question this assertion. However, in the post-cladistic age, the interpretation of interrelatedness should be tested for congruence in a phylogenetic framework, based on morphologically consistent observations of similarity.

Difficulties of identifying fenestrae without prior knowledge of the topology are compounded by ontogenetic and individual variation. Within-species variation in some Permian amniotes illustrates the plasticity of post-orbital bones during ontogeny. For example, the closure of the fenestra between the jugal, squamosal and postorbital in adult specimens of *Milleretta rubidgei* (Gow 1972) and the closure of the upper temporal fenestra by expansion of the supratemporal in adult specimens of *Eunotosaurus africanus* (Bever *et al.* 2015). Of particular note is the ontogenetic series of temporal morphology proposed in the lanthanosuchoid parareptile *Delorhynchus cifellii* (Haridy *et al.* 2016). Juvenile specimens of this taxon possess a large 'lower' temporal fenestra (Fig.5A), whereas adult specimens have a posterior ramus of the jugal that extends towards the squamosal, almost dividing the fenestra into two smaller openings (Fig.5B).

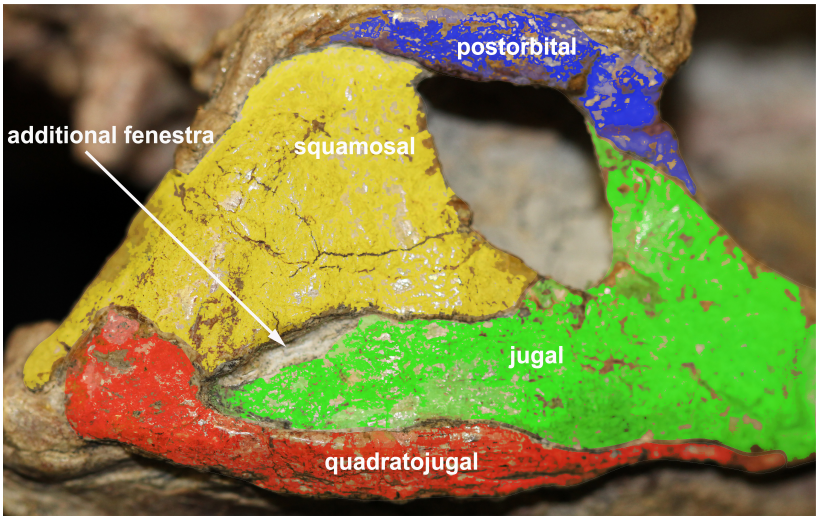


Figure 4: Right postorbital region of *Varanosaurus acutirostris* (FMNH PR 1670) showing additional fenestration.

Reisz *et al.* (2014) noted that contact of the jugal with the squamosal to form a complete bar was in fact probable in the adult specimen. This would result in two 'lower' temporal openings, both formed by bones that configure the 'lower' temporal opening in other taxa (e.g. type 1 and type 4 fenestration, see below). It is also important to note that variation occurs within individual taxa, for example the additional fenestration in *Ophiacodon retroversus* is present on only one side of the skull in several individuals (Romer and Price 1940; and also see Frazetta 1986). Therefore, we observe variation in temporal fenestration patterns at local phylogenetic scales as well as within and between higher taxonomic groups.

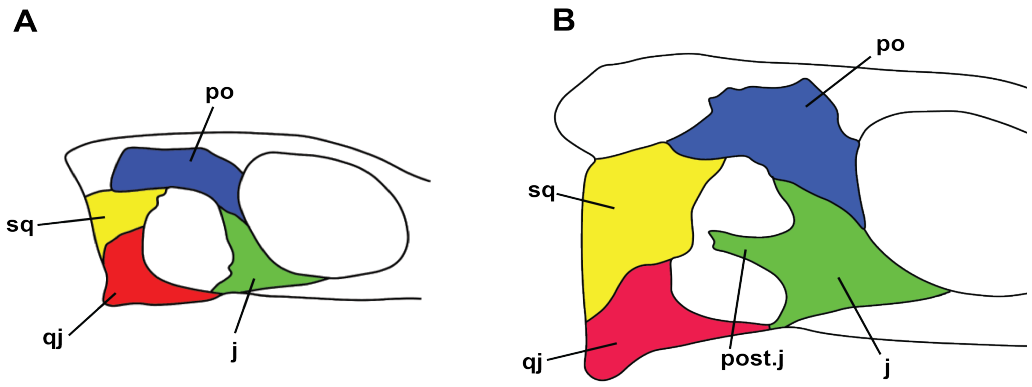


Figure 5: Diagram of right temporal region in the parareptile *Delorhynchus cifellii* (after Haridy *et al.* 2016).A, juvenile specimen: B, adult specimen . *Abbreviations*: j, jugal, po, postorbital, post.j, posterior process of the jugal; qj,quadratojugal; sq, squamosal

3.2 Patterns of temporal fenestration

Here I examine and contrast the patterns of the constituent bones forming the margins of the temporal fenestrae of all major clades of early amniotes, and note that there are nine patterns that define all fenestration or emargination of the postorbital region in early amniotes (Figs.6-14). Types 1-6 describe completely enclosed fenestrae, and incomplete fenestrae and ventral emargination are considered under types 7-9. It is not possible to adequately represent these nine patterns using characters that describe only the presence or absence of an upper temporal fenestra, and the presence or absence of a lower temporal fenestra. In Section 3, I illustrate the optimisation of the patterns of temporal fenestration in early amniotes, and in Section 4, I propose a different set of characters that aims to represent the observed variation in this morphology.

3.2.1 Type 1: postorbital, jugal, squamosal

This configuration of marginal elements is found in those taxa that have typically been considered to be 'pelycosaur'-grade (i.e. non-therapsid) synapsids (types 2, 3 and 4 below are also found some pelycosaurs). Type 1 is present in most sphenacodontians, some edaphosaurids, mycterosaurines, eothyridids, and ophiacodontids. In *Varanosaurus acutirostris* an additional, ventrally located opening is found between the squamosal and jugal (Berman *et al.* 1995) (Fig.2B), and a similar opening between the squamosal, jugal and quadratojugal is present in *Ophiacodon* (Romer and Price 1940). These are discussed in greater detail below under 'type 4'.

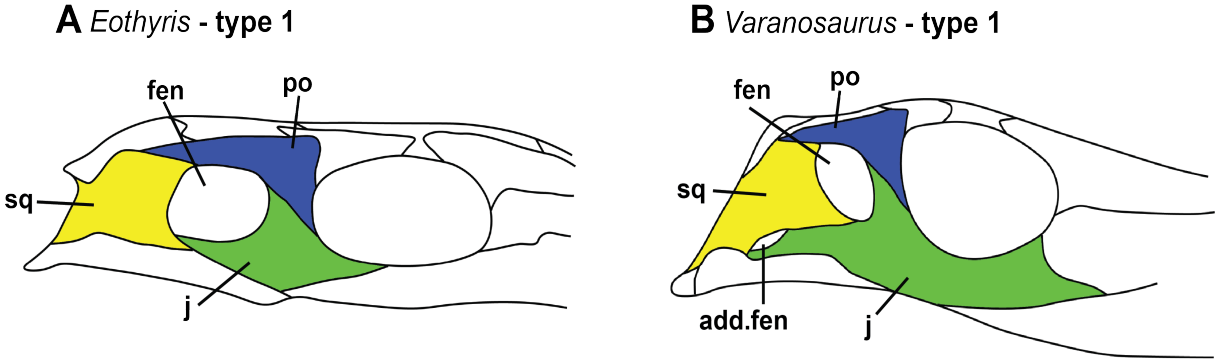


Figure 6: Diagrams of right temporal region in early amniotes with type 1 temporal fenestration. A, The eothyridid *Eothyris parkeyi* (after Reisz *et al.* 2009); B, The ophiacodontid *Varanosaurus acutirostris* (after Berman *et al.* 1995). *Abbreviations*: add.fen, additional fenestra; fen, fenestra, j, jugal; po, postorbital, sq, squamosal

Distribution: eothyridids (Fig.6A), ophiacodontids e.g. *Varanosaurus* (Fig.6B) and *Ophiacodon*, sphenacodontians (e.g. *Dimetrodon*, Fig.2A and *Haptodus*), myc-

terosaurines (e.g. *Mycterosaurus*, *Ascendonanus*, *Heleosaurus*, *Mesenosaurus*, *Elliotsmithia*) and the edaphosaurid *Ianthasaurus*.

3.2.2 Type 2: postorbital, jugal, squamosal, quadratojugal

In many early amniotes the quadratojugal participates in temporal fenestration by forming the ventral bar together with the jugal. This configuration differs from type 1 (above) by inclusion of the quadratojugal in the posteroventral margin of the fenestra. Type 2 fenestrae are present in both single opening or 'synapsid' skull types (e.g. caseids, Maddin *et al.* 2008; the varanodontine *Aerosaurus wellesi*, Langston and Reisz 1981), and parareptiles (MacDougall *et al.* 2017), and double opening or 'diapsid' skull types, e.g. the lower fenestra of *Petrolacosaurus* (Reisz 1981) and *Youngina* (Gow 1975).

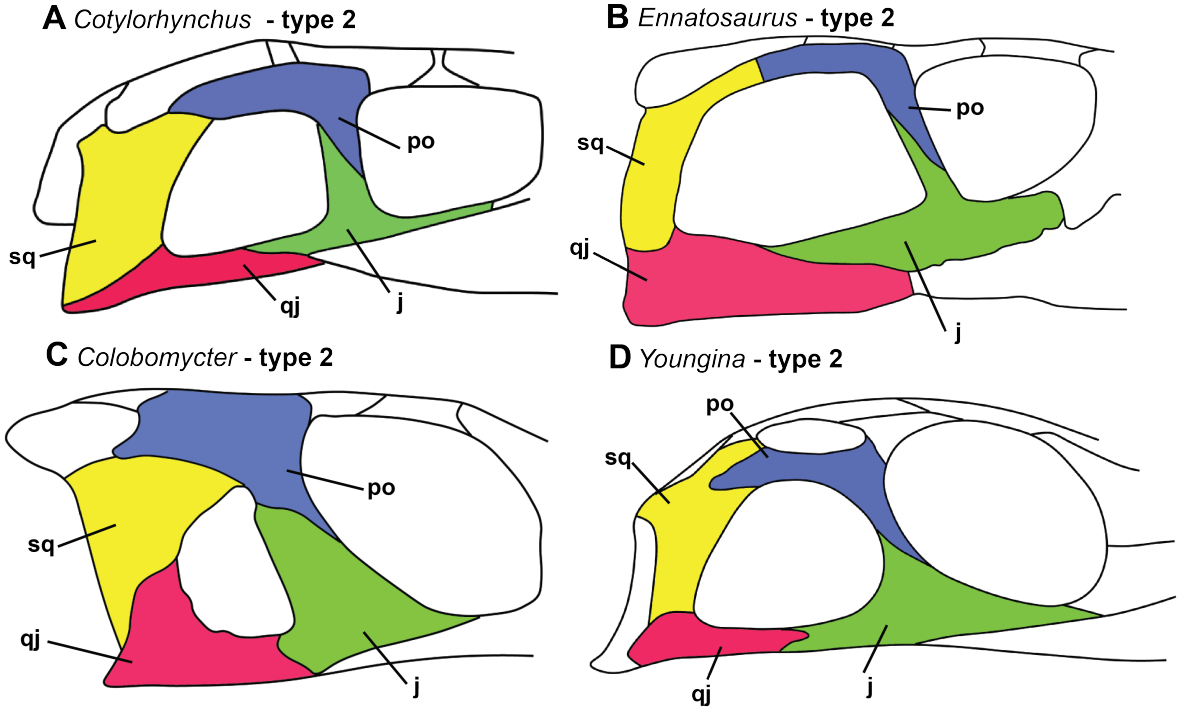


Figure 7: Diagrams of right temporal region in early amniotes with type 2 fenestration. A, the caseid *Cotylorhynchus romeri* (after Sues and Reisz 1998); B, the caseid *Ennatosaurus tecton* (after Maddin *et al.* 2008); C, the parareptile *Colobomycter pholeter* (after MacDougall *et al.* 2017); D, the diapsid *Youngina capensis* (after Carroll 1981. *Abbreviations*: j, jugal; po, postorbital, qj, quadratojugal; sq, squamosal

Distribution: caseids, e.g. *Cotylorhynchus* (Fig.7A), *Ennatosaurus* (Fig.7B), and *Eocasea*, the varanodontine *Aerosaurus*, parareptiles, e.g. *Colobomycter* (Fig.7C), *Australothyris* (Modesto *et al.* 2009) and *Millerosaurus* (Gow 1972), diapsids e.g. *Youngina* (Fig.7D) and *Petrolacosaurus* (Reisz 1981).

3.2.3 Type 3: postorbital, jugal, squamosal, parietal

Type 3 fenestration differs from type 1 fenestration by the participation of the parietal in the upper margin of the opening. The participation of the parietal in temporal fenestration is generally considered to be diagnostic of the upper fenestra in diapsid reptiles (see type 5, below). However, it is also present in some early synapsids. For example, in the sphenacodontid *Secodontosaurus obtusidens*, the postorbital and squamosal make contact on the ventral surface of the parietal, such contact is medial to the lateral edge of the parietal, which consequently contributes to the dorsal margin of the temporal fenestra (Reisz *et al.* 1992). In the edaphosaurid *Edaphosaurus boanerges*, the postorbital and squamosal do not make contact, and a concave lateral edge of the parietal forms the dorsal margin of the fenestra (Modesto 1995). In both taxa the ventral bar of the temporal fenestra is formed by the squamosal and jugal.

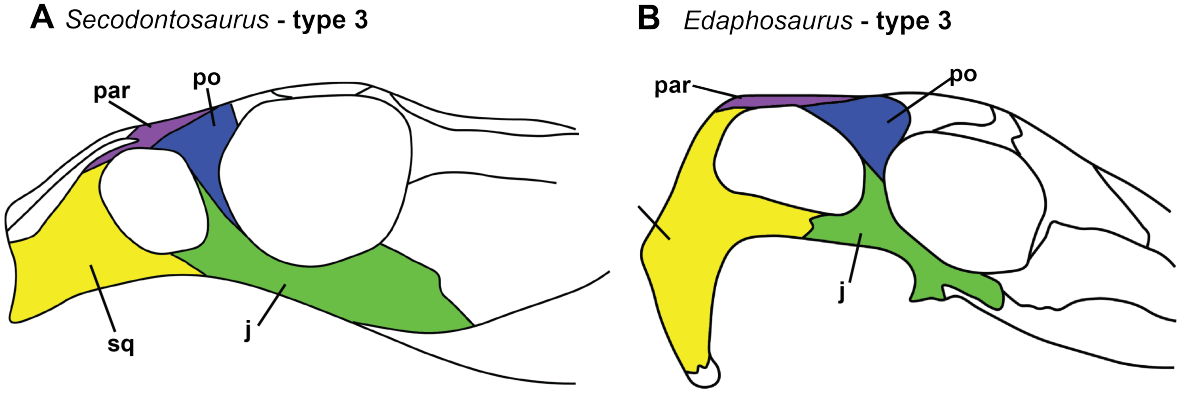


Figure 8: Diagrams of right temporal region in early synapsids with type 3 fenestration. A, *Secodontosaurus obtusidens* (after Reisz *et al.* 1992); B, *Edaphosaurus boanerges* (after Modesto 1995). *Abbreviations*: j, jugal, par, parietal; po, postorbital,; sq, squamosal

Distribution: limited to *Secodontosaurus* (Fig.8A), and *Edaphosaurus* (Fig.8B) only.

3.2.4 Type 4: jugal, squamosal, quadratojugal

This configuration differs from type 2 above in the exclusion of the postorbital from temporal fenestration. It is present in varanodontines, e.g. *Varanodon agilis* and parareptiles, e.g. *Acleistorhinus pteroticus*. In some ophiacodontids, an additional fenestra is present that conforms to type 4 fenestration. The fenestra is formed by the jugal and squamosal in the case of *Varanosaurus acutirostris* (Fig.3), and by the jugal, squamosal and quadratojugal in *Ophiacodon retroversus* (Romer and Price 1940).

Distribution: varanodontines e.g. *Varanodon agilis* (Fig.9A), *Varanops brevirostris*

(Campione and Reisz 2010), parareptiles, e.g. *Acleistorhinus pteroticus* (Fig.9B), *Macroleter poezicus* (Fig.9C), *Belebey vegrandis* (Fig.9D), *Eudibamus cursoris* (Berman *et al.* 2000) and ophiacodontids, e.g. *Ophiacodon retroversus*, *Varanosaurus acutirostris* (Fig.5B).

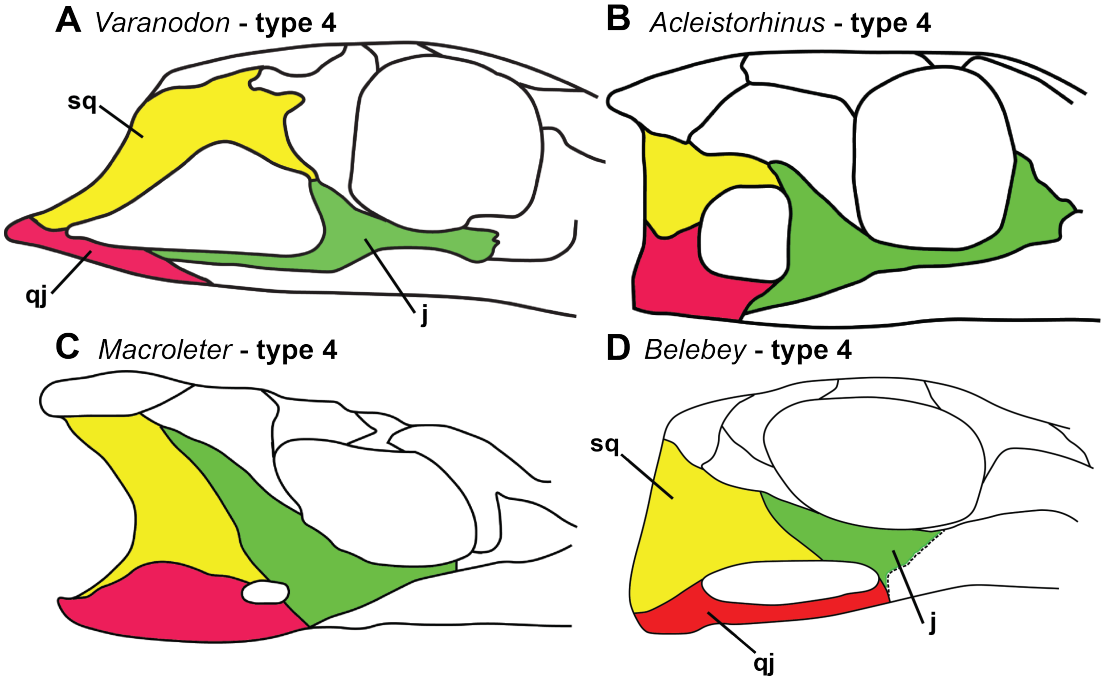


Figure 9: Diagrams of right temporal region in early amniotes with type 4 fenestration. A, the synapsid *Varanodon agilis* (after Olson 1965); B, the parareptile *Acleistorhinus pteroticus* (after deBraga and Reisz 1996); C, the parareptile *Macroleter poezicus* (after Tsuji 2006); D, the parareptile *Belebey vegrandis* (after Reisz *et al.* 2007). *Abbreviations*: j, jugal; po, postorbital; sq, squamosal

3.2.5 Type 5: postorbital, squamosal, parietal, (postfrontal)

This pattern typically constitutes the upper temporal fenestra in diapsid reptiles. It appears to be shared by all Permian diapsids other than *Hovasaurus boulei* in which the postfrontal enters the margin of the fenestra (Currie 1981). The inclusion of the postfrontal in the upper temporal fenestra was also convergently acquired in early lepidosauromorphs *Marmoretta* and *Sophineta cracoviensis* (Evans 1991, Evans and Borsuk-Białynicka 2009)(Fig.10C) and the stem-group turtle *Pappochelys* (Schoch and Sues 2015) (Fig.10D).

Distribution: diapsids, e.g. *Petrolacosaurus*, *Araeoscelis* (Fig.10A), *Youngina*, *Prolacerta* (Fig.10B) and *Proterosuchus*, early lepidosauromorphs and stem-group turtles.

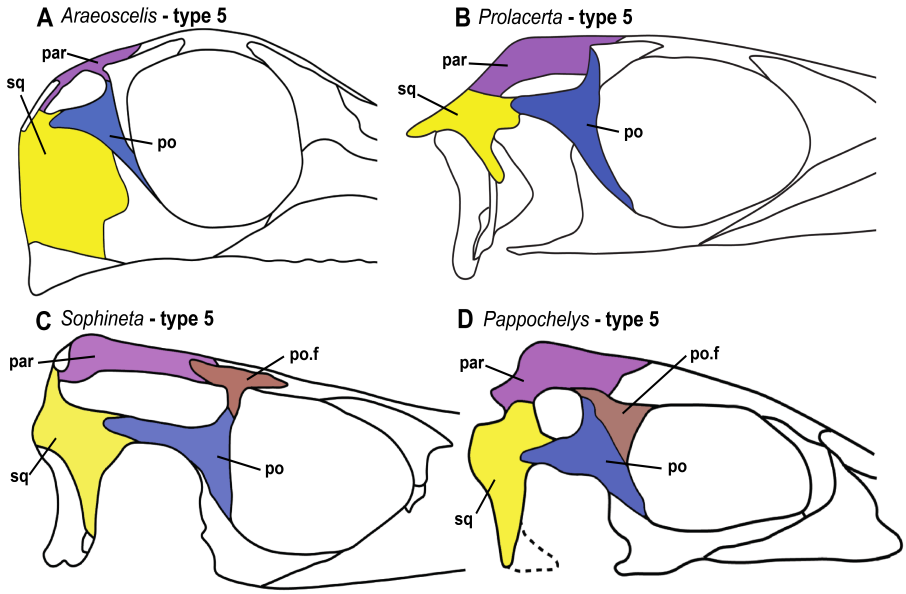


Figure 10: Diagrams of right temporal region in early amniotes with type 5 fenestration. A, the euryapsid *Araeoscelis* casei (modified from Reisz *et al.* 1984); B, the diapsid *Prolacerta broomi* (modified from Gow 1975); C, the diapsid *Sophineta cracoviensis* (after Evans and Borsuk-Białynicka 2009); D, the stem-turtle *Pappochelys rosinae* (after Schoch and Sues 2015). *Abbreviations*: par, parietal; po, postorbital; po.f, postfrontal; sq, squamosal

3.2.6 Type 6: postorbital, jugal, squamosal, supratemporal

The inclusion of the supratemporal in temporal fenestration is rare among amniotes. It is excluded from the upper temporal fenestra in *Araeoscelis* only by a thin posterolateral projection of the parietal (Fig.10A) (Reisz *et al.* 1984), and may participate marginally in the upper temporal fenestra in *Petrolacosaurus kansensis* (Reisz 1981). In the owenettid parareptile *Candelaria barbouri*, the supratemporal provides the posterodorsal margin of the temporal opening (Fig.11).

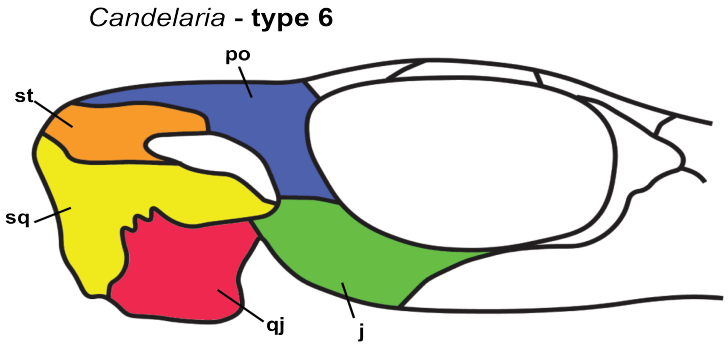


Figure 11: Diagram of right temporal region in *Candelaria barbouri* with type 6 fenestration (after Cisneros *et al.* 2004). *Abbreviations*: j, jugal; po, postorbital; qj, quadratojugal; sq, squamosal; st, supratemporal

3.2.7 Incomplete openings - patterns of emargination of the postorbital region

In many early amniotes, the elements that constitute a temporal opening do not fully enclose a fenestra, and the ventral bar is wholly or partially absent. In some taxa, e.g. the early-diverging archosauromorphs *Prolacerta broomi* (Fig.10B) and *Mesosuchus browni* (Dilkes 1997), the ventral bar, in this case a posterior process of the jugal, only marginally fails to make contact with the squamosal or quadratojugal, and the opening is considered only partially complete. In other taxa, the ventral bar is entirely absent or greatly reduced, e.g. *Claudiosaurus germaini* (Fig.2D). In sphenacodontids, edaphosaurids and some parareptiles the jugal contacts the squamosal or quadratojugal, but the ventral margin of the postorbital region is also emarginated. In *Edaphosaurus* and *Dimetrodon* (Fig.13A and 13B) and *Procolophon* (Fig.14B) this emargination is due to a concavity in the ventral margin of the jugal or squamosal. In *Candelaria*, *Owenetta* and *Nyctiphruretus*, the quadratojugal only contacts the posterodorsal margin of the jugal, forming a dorsoventrally tall but narrow emargination (Figs. 11, 14A and 14C). In all cases, the free margins of the bones forming the emarginations provide similar structures for muscle attachment and tendon development as fully enclosed fenestrae (e.g. Frazetta 1968). Emarginations have generally been assumed to have different types of evolutionary origin. For example, it is routinely assumed that the lower temporal emargination of diapsids possessing the 'euryapsid' skull morphology results from the loss of parts of the lower temporal bar in an ancestor possessing the diapsid condition (Müller 2003), but it has never been suggested that the lower temporal arch seen in some synapsids (e.g. sphenacodontids, *Edaphosaurus*) resulted from the ventral opening of a fenestra. However, it is not possible to test hypotheses of the evolutionary origins of these structures in the absence of some prior knowledge of the phylogenetic topology.

The bones that constitute the free margins of the ventral emargination in early amniotes can be categorised as follows:

Type 7: jugal, postorbital, quadratojugal and squamosal. Distribution: *Microleter* (Fig.12A) (parareptile), *Pappochelys* (Fig.12B) and *Eunotosaurus* (Fig.12C) (stem group turtles), *Sophineta* (Fig.12D) and *Paliguana* (lepidosauromorphs), *Claudiosaurus* (Fig.1D)(diapsid).

Type 8: jugal and squamosal. Distribution: *Edaphosaurus* (Fig.13A) *Dimetrodon* (fig.13B), *Secodontosaurus*, *Haptodus* (synapsids)

Type 9: jugal and quadratojugal. Distribution: *Owenetta* (Fig.14A), *Procolophon* (Fig.14B), *Candelaria* (Fig.11), *Nyctiphruretus* (Fig.14C) (parareptiles)

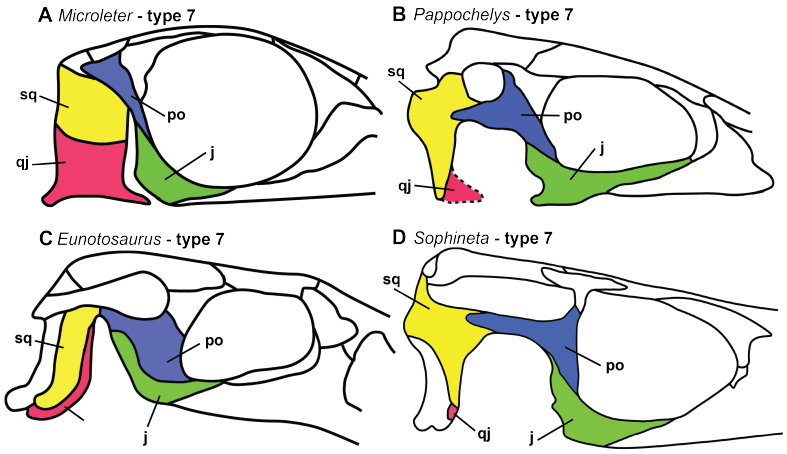


Figure 12: Diagrams of right temporal region in early amniotes with type 7 fenestration. A, the parareptile *Microleter mckinzieorum* (after Tsuji *et al.* 2010); B, the stem-turtle *Pappochelys rosinae* (after Schoch and Sues 2015); C, the stem-turtle *Eunotosaurus africanus* (after Bever *et al.* 2015); D, the lepidosauromorph diapsid *Sophineta cracoviensis* (after Evans and Borsuk-Białynicka 2009). *Abbreviations*: j, jugal; po, postorbital; qj, quadratojugal; sq, squamosal.

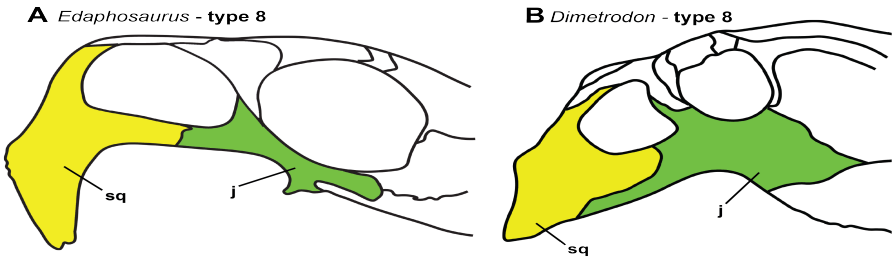


Figure 13: Diagrams of right temporal region in early synapsids with type 8 fenestration. A, *Edaphosaurus boanerges* (after Modesto 1995); B, *Dimetrodon grandis* (after Brink and Reisz 2014). *Abbreviations*: j, jugal; sq, squamosal.

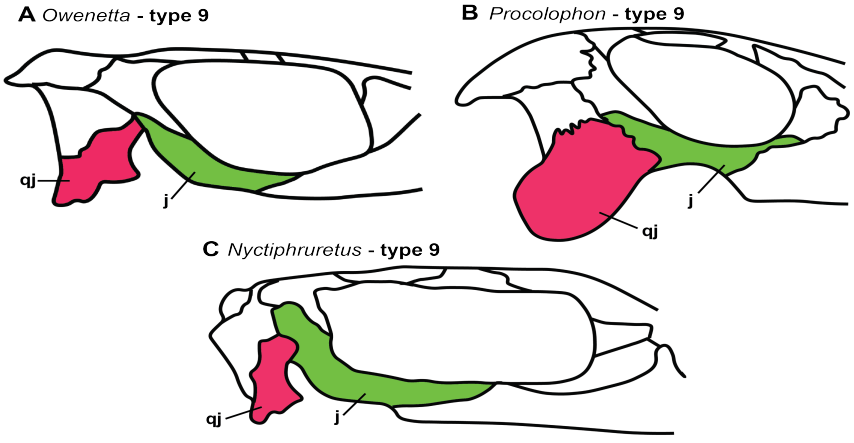


Figure 14: Diagrams of right temporal region in parareptiles with type 9 fenestration. A, *Owenetta kitchingorum* (after Reisz and Scott 2002); B, *Procolophon trigoniceps* (after Carroll and Lindsey 1985); C, *Nyctiphruretus acudens* (after Saila 2010). *Abbreviations*: j, jugal; qj, quadratojugal

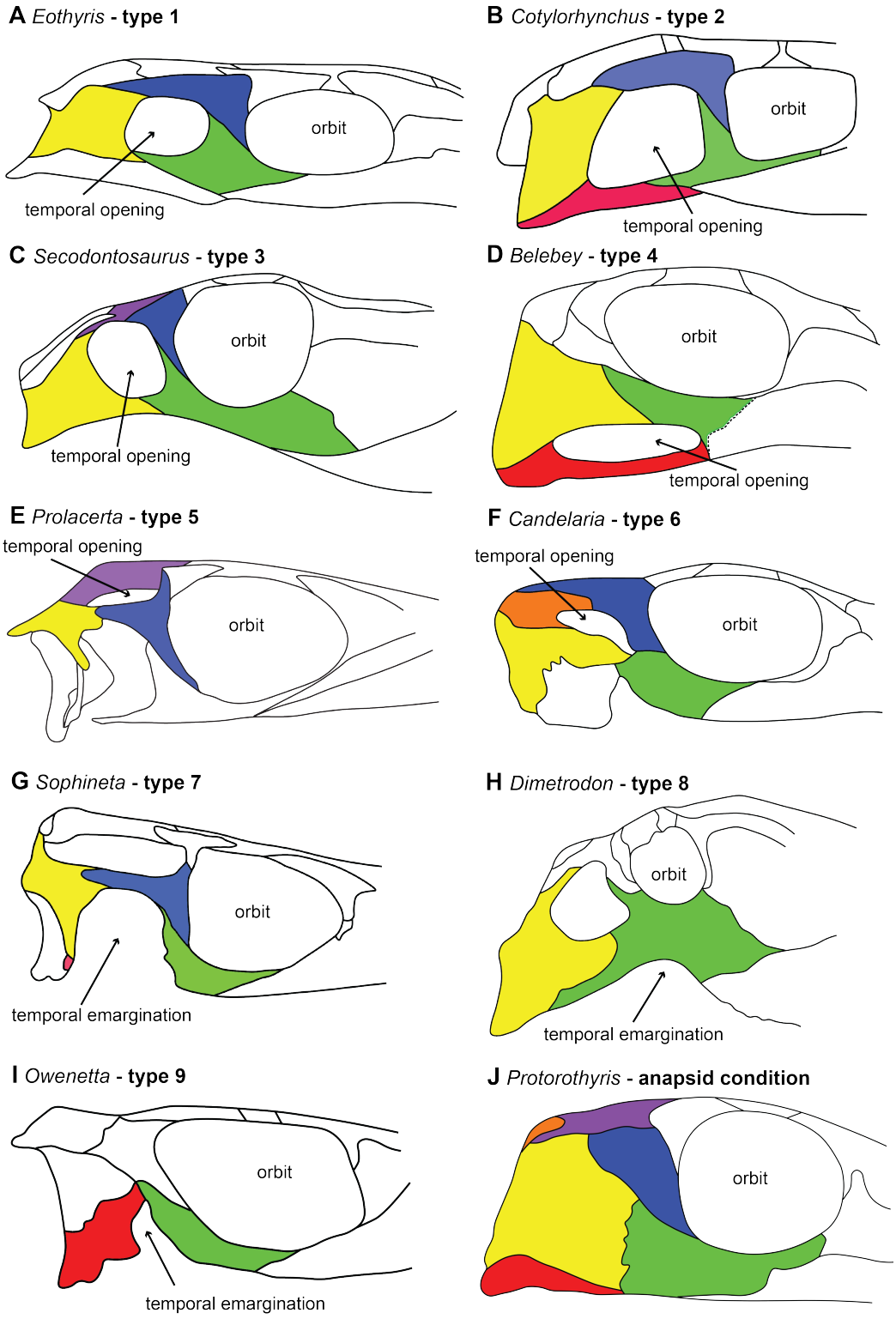


Figure 15: Summary of types of temporal fenestration in early amniotes. A, *Eothyris parkeyi* (after Reisz *et al.* 2009); B, *Cotylorhynchus romeri* (after Sues and Reisz 1998); C, *Secodontosaurus obtusidens* (after Reisz *et al.* 1992); D, *Belebey vegrandis* (after Reisz *et al.* 2007); E, *Prolacerta broomi* (modified from Gow 1975); F, *Candelaria barbouri* (after Cisneros *et al.* 2004); G, *Sophineta cracoviensis* (after Evans and Borsuk-Białynicka 2009); H, *Dimetrodon grandis* (after Brink and Reisz 2014); I, *Owenetta kitchingorum* (after Reisz and Scott 2002); J, the anapsid condition for comparison in *Protorothyris archeri* (after Clark and Carroll 1973). Key: green=jugal; blue=postorbital; mauve=parietal; red=quadratojugal; yellow=squamosal; orange=supratemporal

3.3 Optimisation of observed temporal patterns

From the observations of temporal fenestration noted above (summarised in Fig.15), it is evident that the morphology of temporal fenestrae is highly variable among early amniotes. This variation is not reflected in the hypothesised distribution of the presence of the lower and upper temporal fenestrae according to the dual opening method, as optimised on a traditional phylogeny of early amniotes (Fig.16).

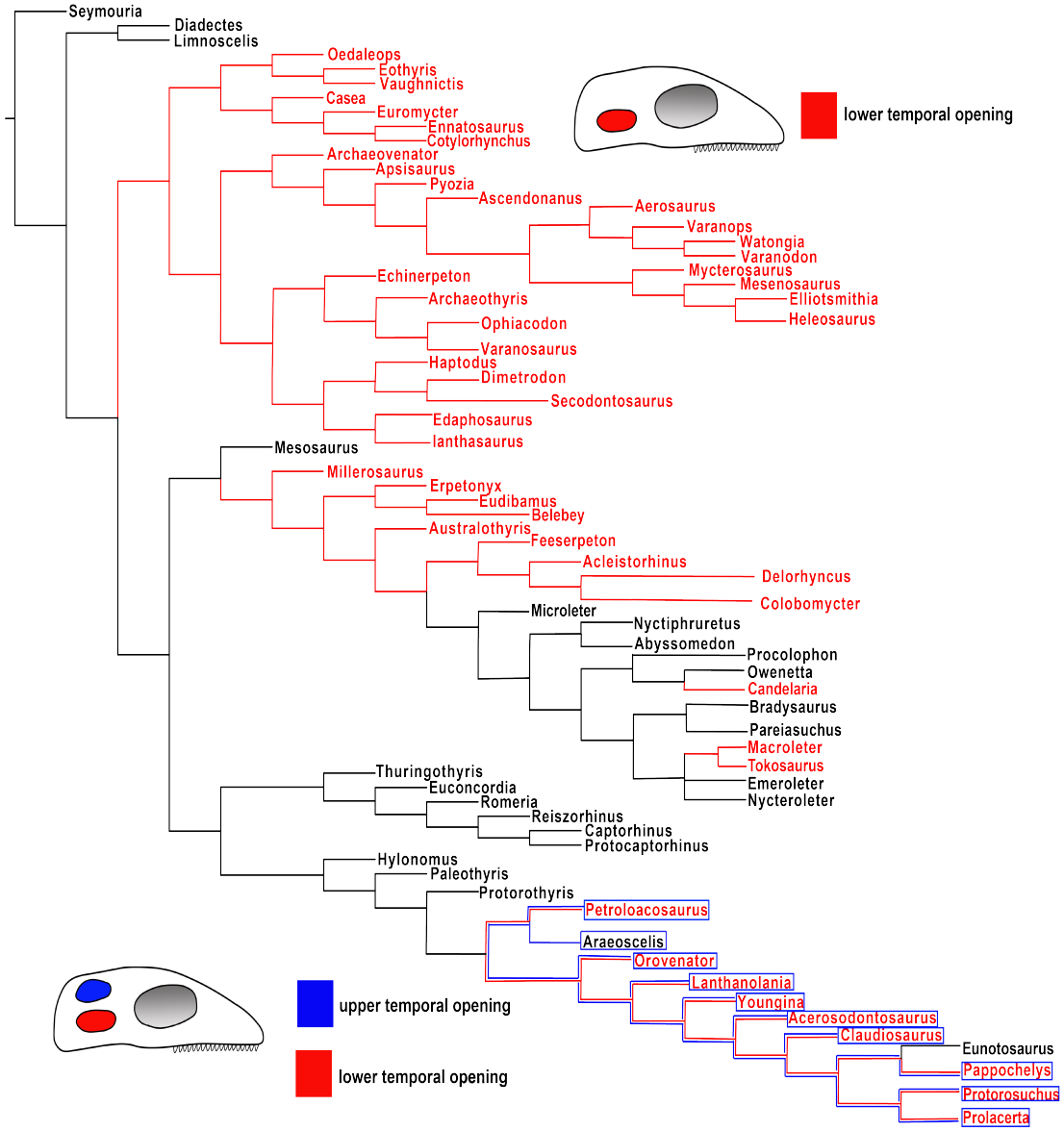


Figure 16: Non-time calibrated tree depicting a traditional phylogeny of early amniotes with the optimisation for the presence of a lower (in red) and upper (in blue) temporal fenestra. Topology is based on various phylogenetic analyses (e.g. parareptiles - MacDougall *et al.* 2017, synapsids - Brocklehurst *et al.* 2016, eureptiles - Müller and Reisz 2006, Reisz *et al.* 2011). The position of stem turtles (*Eunotosaurus*, *Pappochelys*) is based on Schoch and Sues 2015 (maximum parsimony tree), and Bever *et al.* 2015

The dual opening method distinguishes between fenestrated and non-fenestrated groups only. It fails to recognise variation within and between fenestrated groups, resulting in a broad hypothesis of convergent acquisition of a lower temporal fenestra in synapsids, diapsids and parareptiles. The upper temporal fenestra optimises as a unique synapomorphy of diapsids. A traditional tree topology also suggests at least five independent origins of temporal fenestration among early amniotes: one in synapsids, one in diapsids, and three in parareptiles, based on the hypothesis that the common ancestor of all crown amniotes lacked temporal fenestration.

When the observed types summarised in section 2 are optimised on the traditional phylogeny, however, a more complex pattern emerges (Fig.17). Although homoplasy is still evident, for example type 2 is present in at least some members of all three fenestrated groups, a number of potential homologies are also revealed. Derived varanodontines possess type 4 fenestration, which appears independently in several groups of parareptiles. Type 1 fenestration is present in many synapsids, but is absent in *Secodontosaurus*, *Edaphosaurus*, caseids and varanodontines. A type 2 pattern is found in parareptiles, with the loss of the postorbital from the fenestra (type 4) in bolosaurids and *Acleistorhinus*. Type 5 fenestration, which typifies the upper temporal fenestra, remains a diapsid synapomorphy. Type 7 signifies the euryapsid nature of derived diapsids and early saurians, type 8 is found only in sphenacodontians and edaphosaurs and type 9 unique to nyctiphruretids and procolophonoid parareptiles.

3.4 Establishing similarity using free margins and points of contact of temporal bones

Based on these observations, it is evident that the presence or absence of a temporal opening is universally indicated by the presence of free margins of a specific bone (i.e. an edge of bone that is enclosed within the skull, but nevertheless is not in contact with any other bone). For example, a free margin on the lateral surface of the parietal is always associated with a fenestra, as is a free margin at any point on the posterior surface of the jugal. In addition to this, differences in the contact between specific regions of certain bones can be used to represent differences in both the positions and relative sizes of bone in the skull. These differences define both the general skull morphology (whether fenestrae are present or absent) and pattern of temporal fenestration. For example, contact between the squamosal with the posterodorsal or posteroventral margin of the jugal, or indeed the absence of such contact, can distinguish between three different fenestral patterns (types 1 and 3, types 2 and 6 and type 4).

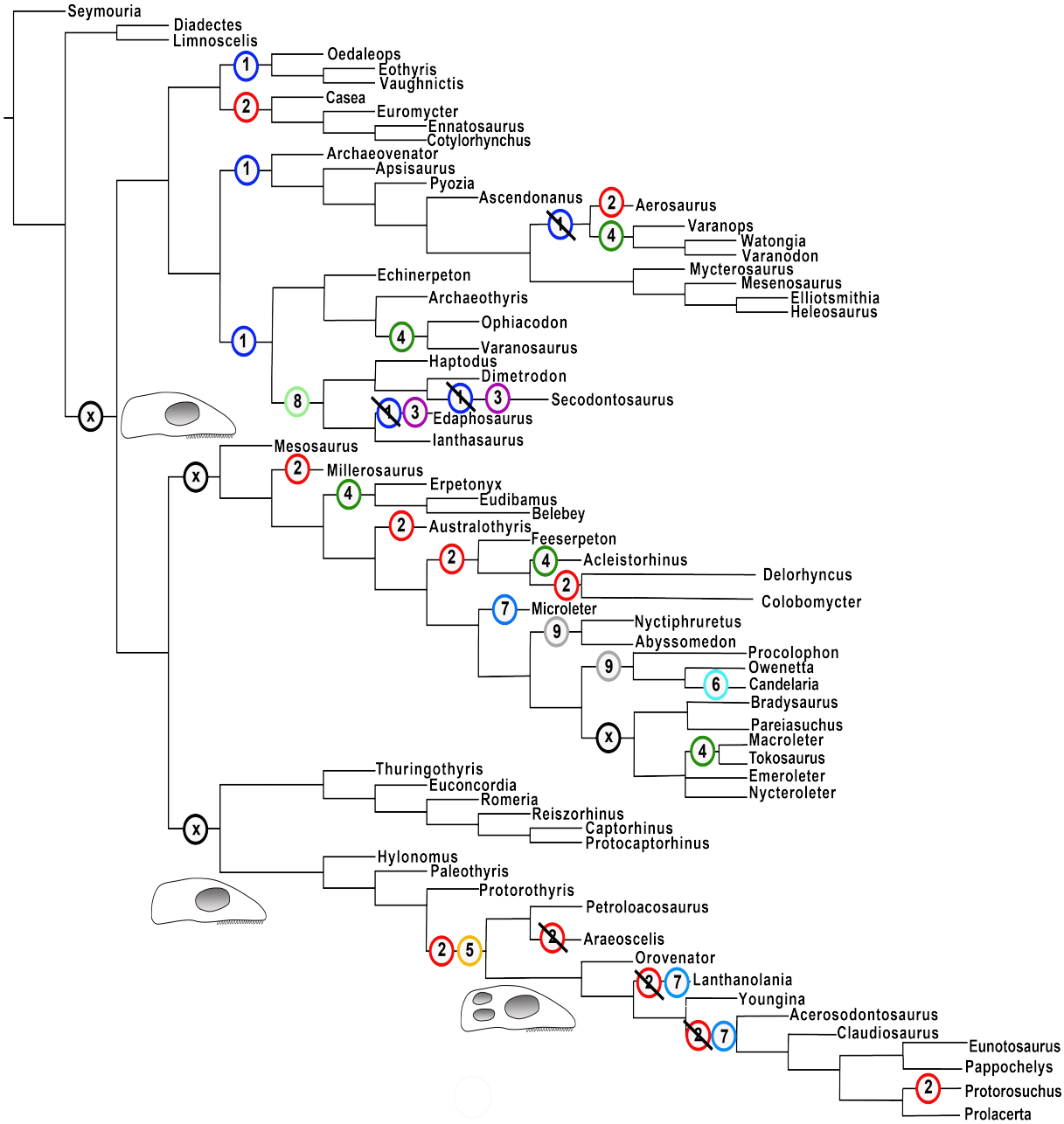


Figure 17: Non-time calibrated tree depicting a traditional phylogeny of early amniotes with the optimisation of patterns of temporal fenestration as detailed in Section 2. Topology is derived as detailed in Fig.16. Coloured circles with numerals refer to types described in Section 2; coloured circles with a diagonal black line denotes loss of fenestration type; black circles with crosses denotes absence of temporal fenestration ('anapsid' condition)

Importantly, fenestrae can appear at or disappear from the contacts among bones during evolutionary history, and the nature and positions of contacts between bones can also change during evolutionary history and ontogeny, both in the presence and absence of fenestration (i.e. changes to cranial sutural morphology do not cease once fenestrae

appear). I therefore propose separate sets of characters that embody similarities in the presence or absence of free margins (=fenestrae/emarginations) on specific bones, and in the presence or absence of contacts between particular parts of specific bones. Together, these characters summarise the observed types of fenestration, and express them as binary characters.

I summarise below seven new characters, which are designed to replace the dual opening method of coding. Each character is then optimised on a non-time calibrated traditional tree topology of early amniotes.

1. Jugal, free posterior margin: absent (0); present (1)
2. Jugal, free concave ventral margin: absent (0); present (1); inapplicable, free ventral margin absent (-)
3. Quadratojugal, contact with posteroventral margin of jugal: present (0); absent (1)
4. Quadratojugal, contact with posterodorsal margin of jugal: absent (0); present (1)
5. Squamosal, contacts posterodorsal margin of jugal: absent (0); present (1)
6. Squamosal, contacts posteroventral margin of jugal: absent (0); present (1)
7. Parietal, free lateral margin: absent (0); present (1)

Character 1: Jugal, free posterior margin: absent (0); present (1) (Fig.18)

A free margin at any point on the posterior surface of the jugal will define the presence of a 'lower' fenestra. However, unlike the traditional scoring for the presence or absence of a 'lower' temporal fenestra, state 1 of this character describes not only those taxa with a fully enclosed 'lower' temporal fenestra (i.e. those possessing a complete ventral bar: types 1-4), but also those with type 7 and type 9 ventral emargination (excluding *Procolophon*, in which the posterior margin of the jugal contacts the quadratojugal along its entire length). Consequently this character recognises the presence (i.e. synapsid, diapsid or euryapsid condition) or absence (anapsid condition) of a fenestra or emargination in the lower temporal region.

Character 2: Jugal, free ventral margin of jugal is concave: absent (0); present (1); inapplicable, ventral margin of jugal is not free, but is covered by other bones (-)(Fig.19)

Character state (1) describes the concavity on the ventral margin of the jugal that contributes to a distinct ventral emargination of the postorbital region in sphenacodontids (e.g. *Secodontosaurus* MCZ 1124, Reisz *et al.* 1992; *Dimetrodon*, Romer and Price 1940; *Sphenacodon*, Spielmann *et al.* 2010), and *Edaphosaurus* (Modesto 1995 fig.2/fig.6) and the parareptile *Procolophon* (Fig.13B)(Carroll and Lindsay 1985).

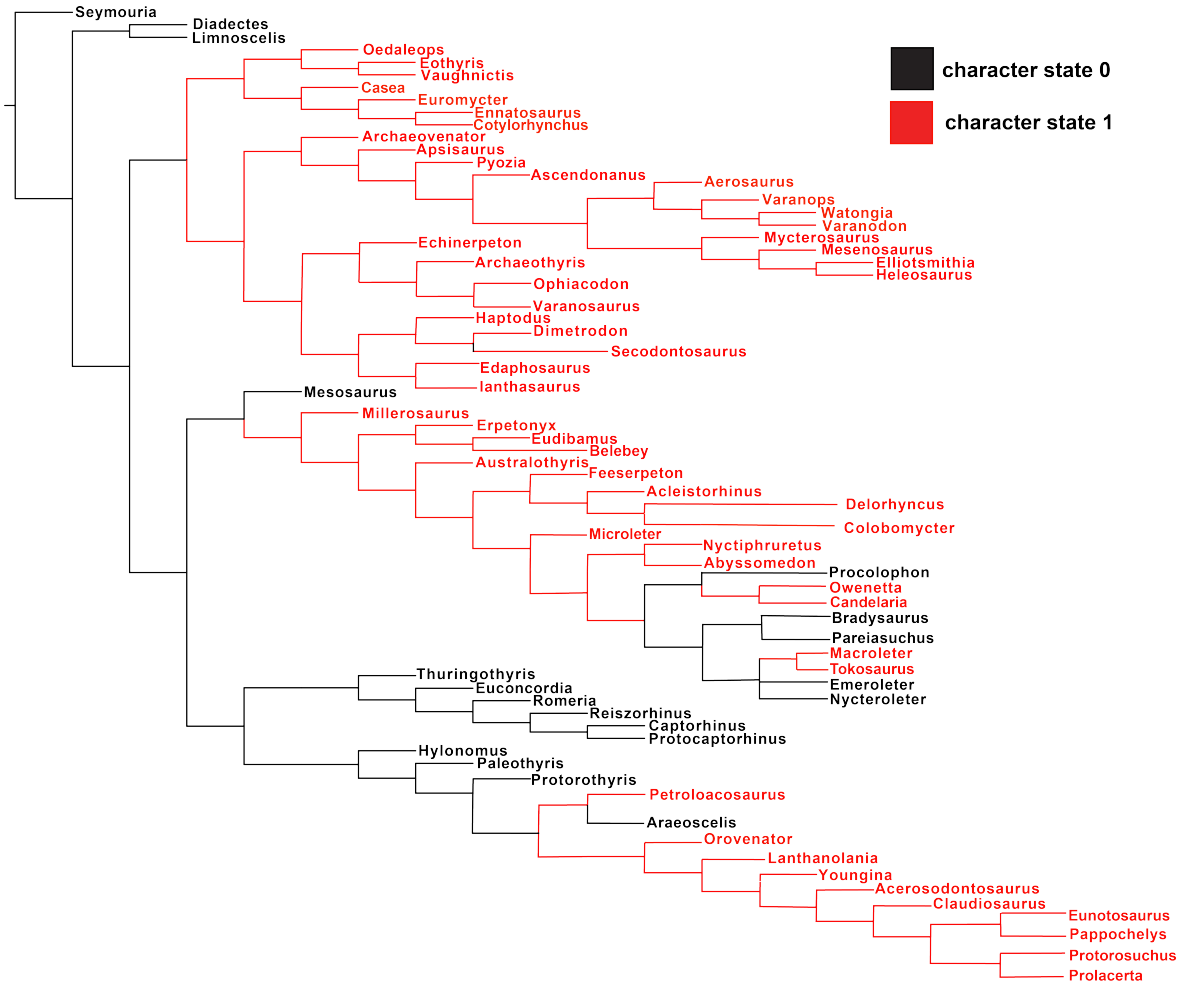


Figure 18: Optimisation of character 1, free posterior margin of jugal, on non-time calibrated traditional phylogeny of early amniotes. Topology is derived as detailed in Fig.15. Key: black = taxa coding for state 0, red = taxa coding for state 1

Character 3: Quadratojugal, contact with posteroventral margin of jugal: present (0); absent (1)(Fig.20)

The anteroventral process of the quadratojugal, when present, contacts the posteroventral margin of the jugal. This occurs in both fenestrated and unfenestrated taxa. When a fenestra is present, dorsal to the jugal, this contact forms a ventral bar that encloses the ventral margin of the fenestra. This contact is absent in all taxa that possess an emargination of the ventral surface of the temporal region (most neodiapsids and several parareptiles), with the exception of *Procolophon*, in which the quadratojugal contacts the jugal along the entire posterior margin. It is also absent in

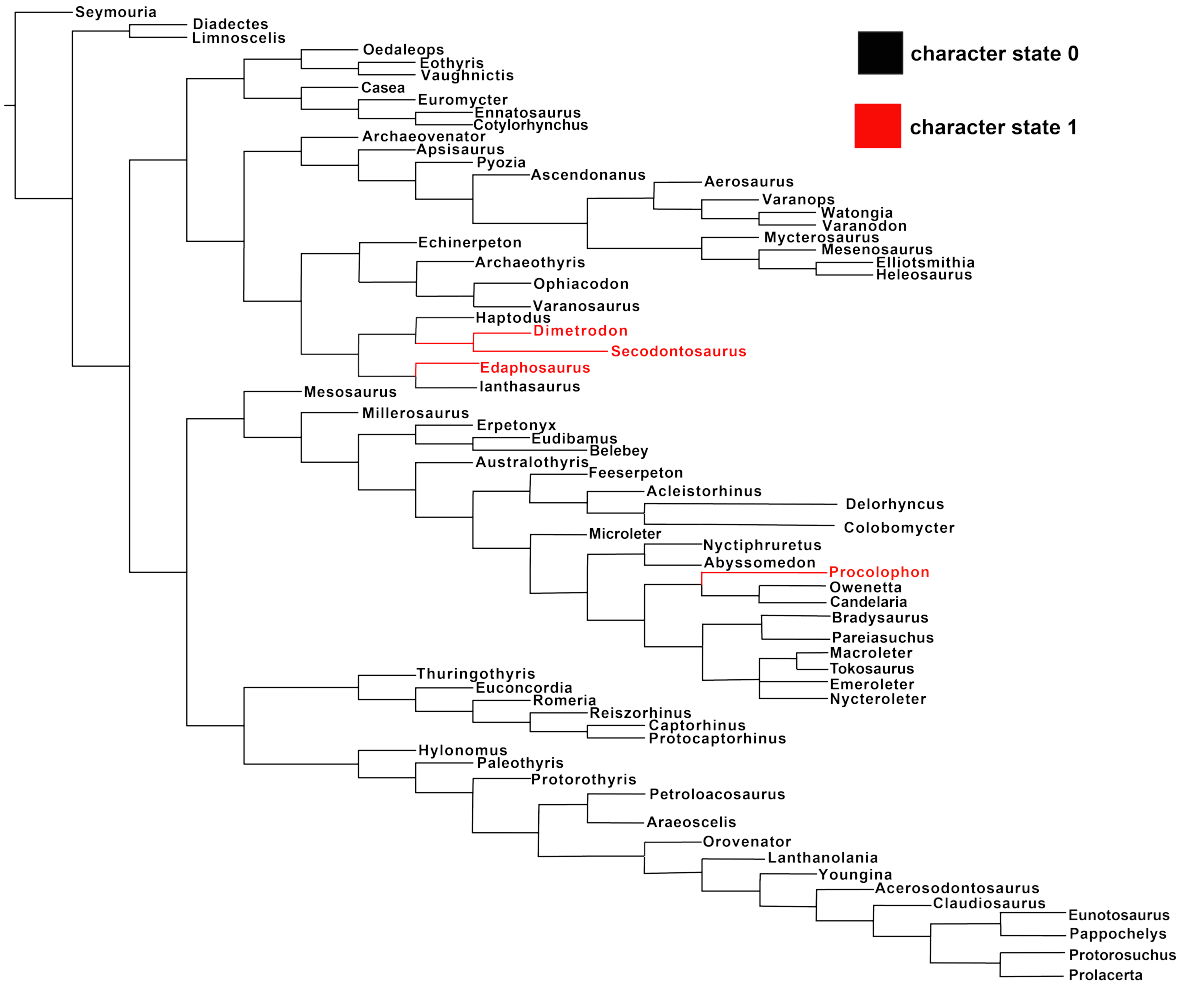


Figure 19: Optimisation of character 2, free concave margin on ventral surface of jugal, on non-time calibrated traditional phylogeny of early amniotes. Topology is derived as detailed in Fig.16. Key: black = taxa coding for state 0, red = taxa coding for state 1

edaphosaurids and sphenacodontians, which have a reduced quadratojugal, and some of which have a ventrally-concave lower temporal bar that therefore has the appearance of an emargination.

Character 4: Quadratojugal, contact with posterodorsal margin of jugal: absent (0); present (1)(Fig.21)

Contact between the jugal and quadratojugal is widespread among early amniotes. The location(s) of this contact, however, varies among taxa. A contact of the quadratojugal with the posteroventral margin of the jugal is present in many taxa (state 0 in character 3 above e.g. *Captorhinus laticeps*, Fig.2E; *Protorothyris archeri*, Fig.2F; *Procolophon*, Fig.14B and all taxa with types 1,2 and 4 fenestration). The contact of the quadratojugal with the jugal is restricted to the dorsal process of the jugal (state 1) in the present character (e.g. nyctiphruretids and owenettids, Figs.11, 14A, and

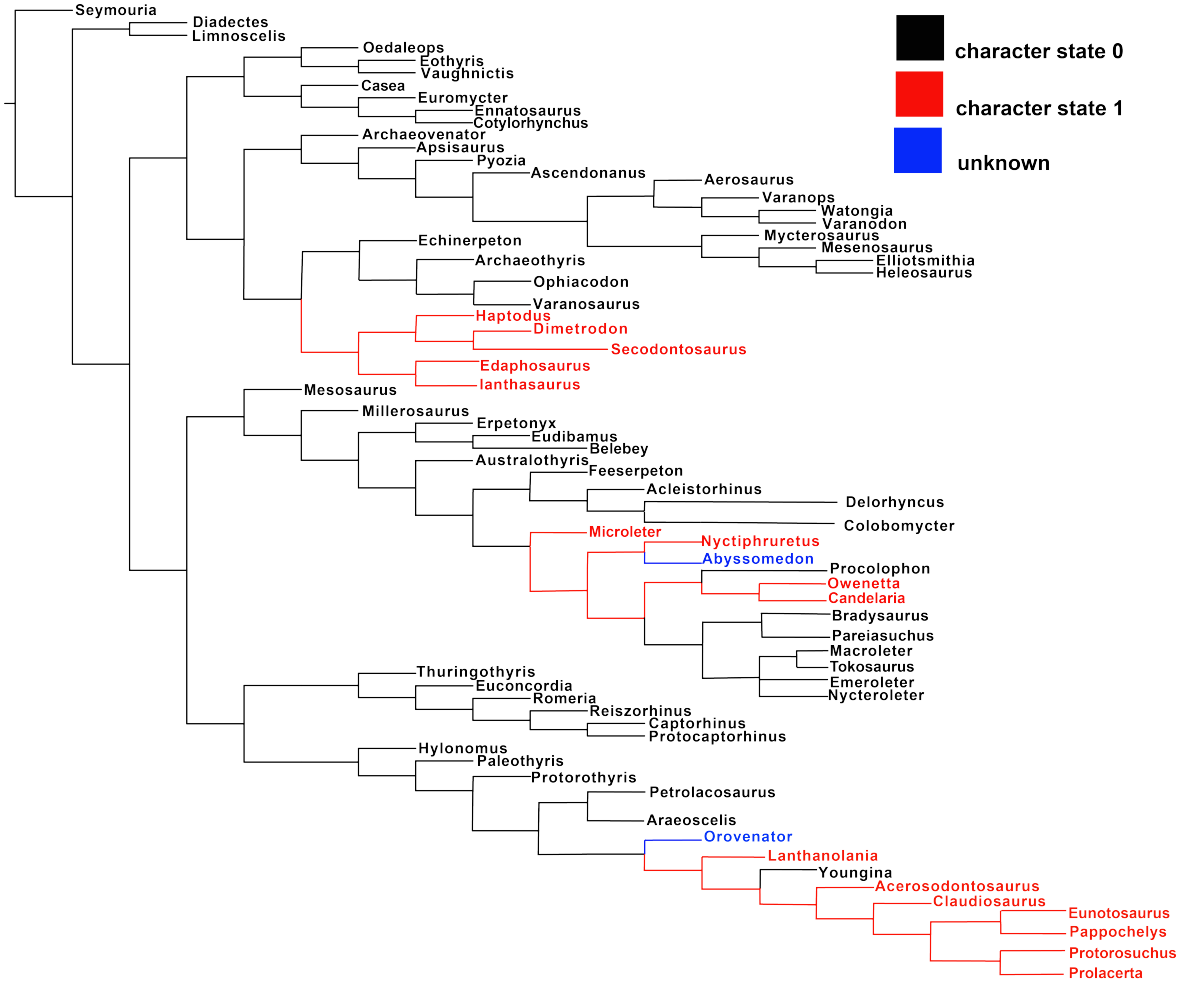


Figure 20: Optimisation of character 3, contact between the quadratojugal and the posteroventral margin of the jugal, on a non-time calibrated traditional phylogeny of early amniotes. Topology is derived as detailed in Fig.16. Key: black = taxa coding for state 0, red = taxa coding for state 1, blue = unknown

14C). These contacts are logically independent of each other, and indeed they co-occur in *Procolophon*, and so are coded as states of separate characters.

Character 5: Squamosal, contacts posterodorsal margin of jugal: absent (0); present (1)(Fig.22)

The distribution of the squamosal contact with the posterodorsal margin of the jugal is somewhat similar to that of the absence of contribution of the postorbital to the lower temporal fenestra (e.g. MacDougall *et al.* 2018 c.44). The scores of the present character however are not dependent upon the presence of a temporal opening, but rely only on the specified contact between the two bones. Consequently, many taxa that lack temporal fenestration are scored possessing state 1 of the present character (presence of the contact; Figs 2E, 2F) along with taxa that possess type 4 fenestration (e.g.

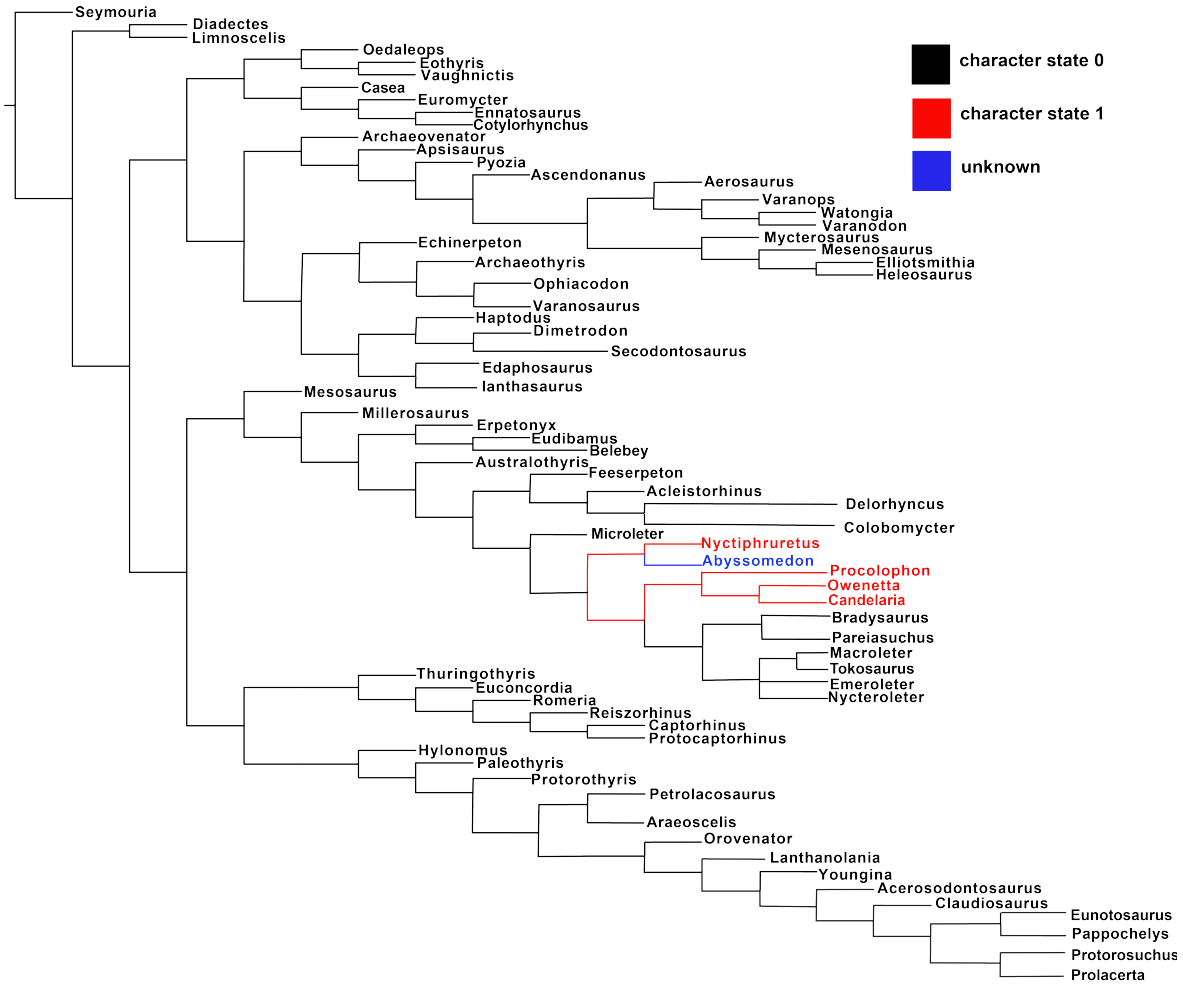


Figure 21: Optimisation of character 4, contact between the quadratojugal and the posterodorsal margin of the jugal, on a non-time calibrated traditional phylogeny of early amniotes. Topology is derived as detailed in Fig.16. Key: black = taxa coding for state 0, red = taxa coding for state 1, blue = unknown

varanodontines, bolosaurids and *Acleistorhinus*; Fig.9). The contact is also present in several parareptile groups, including procolophonoids, nyctiphruretids, pareiasaurs and nycteroleterids (Fig.14). It is absent in ophiacodontids, despite their additional type 4 fenestration, because the squamosal contacts the jugal posteroventrally (Fig.4). It is also absent in all caseasaurs, mycterosaurines, edaphosaurids, sphenacodontians, diapsids (with the exception of *Araeoscelis*) and some parareptiles.

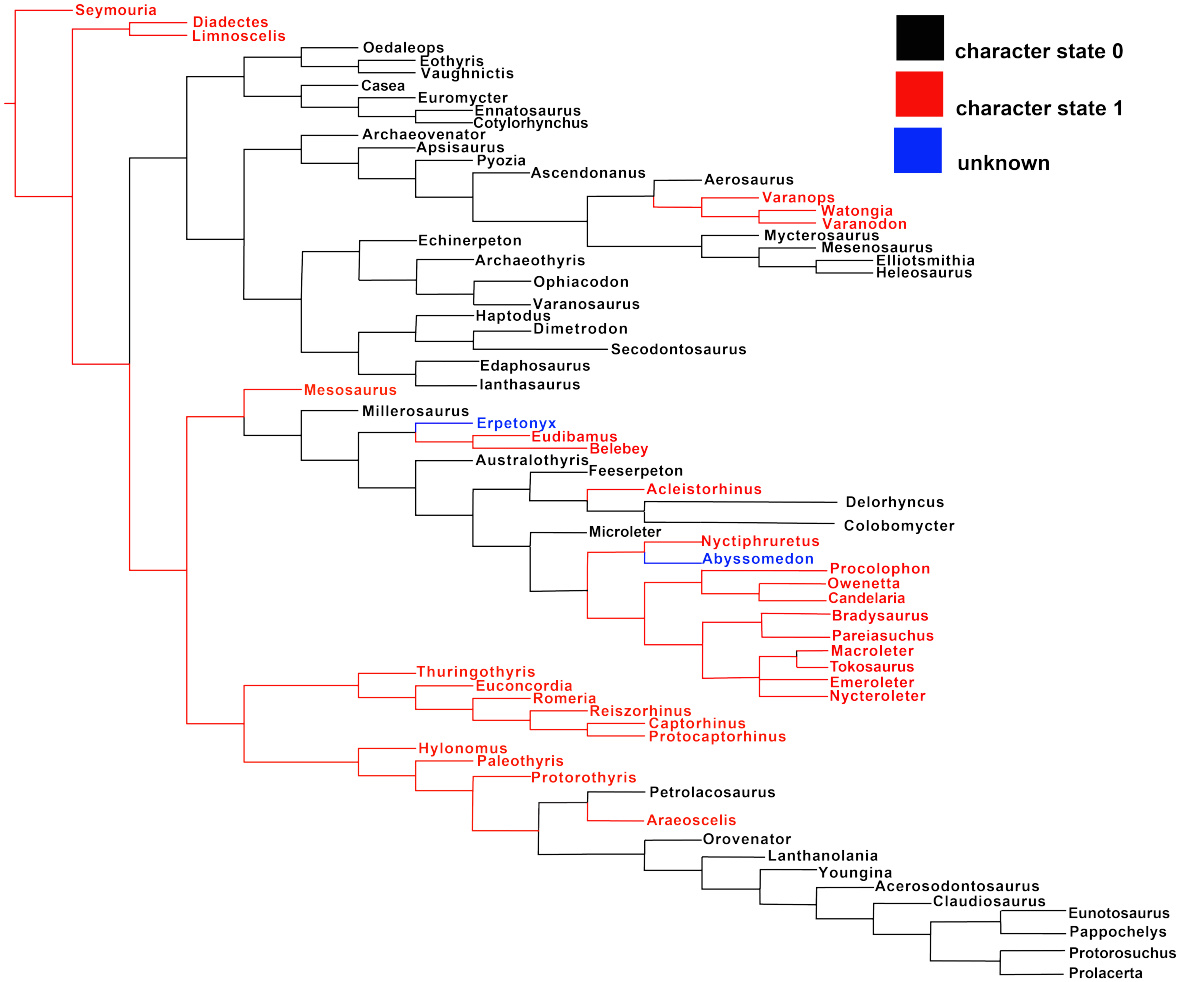


Figure 22: Optimisation of character 5, contact between squamosal and posterodorsal margin of the jugal, on a non-time calibrated traditional phylogeny of early amniotes. Topology is derived as detailed in Fig.16. Key: black = taxa coding for state 0, red = taxa coding for state 1, blue = unknown

Character 6: Squamosal, contacts posteroventral margin of jugal: absent (0); present (1)(Fig.23)

This character defines a point of contact between two bones that describes the morphology of the temporal fenestra in many traditionally synapsid taxa with type 1 and 3 fenestration (e.g. eothyridids, ophiacodontids, mycterosaurines, sphenacodontians and edaphosaurids).

It is also present in taxa that lack any temporal fenestrae, although in some taxa the posteroventral margin of the jugal is excluded from the squamosal by a broad dorsoventral contact with the anterior margin of the quadratojugal (e.g. *Captorhinus laticeps*; Fig.1E). This contact is also absent in caseids, varanodontines, diapsids (although it is present in *Araeoscelis*) and all parareptiles except bolosaurids and *Mesosaurus*.

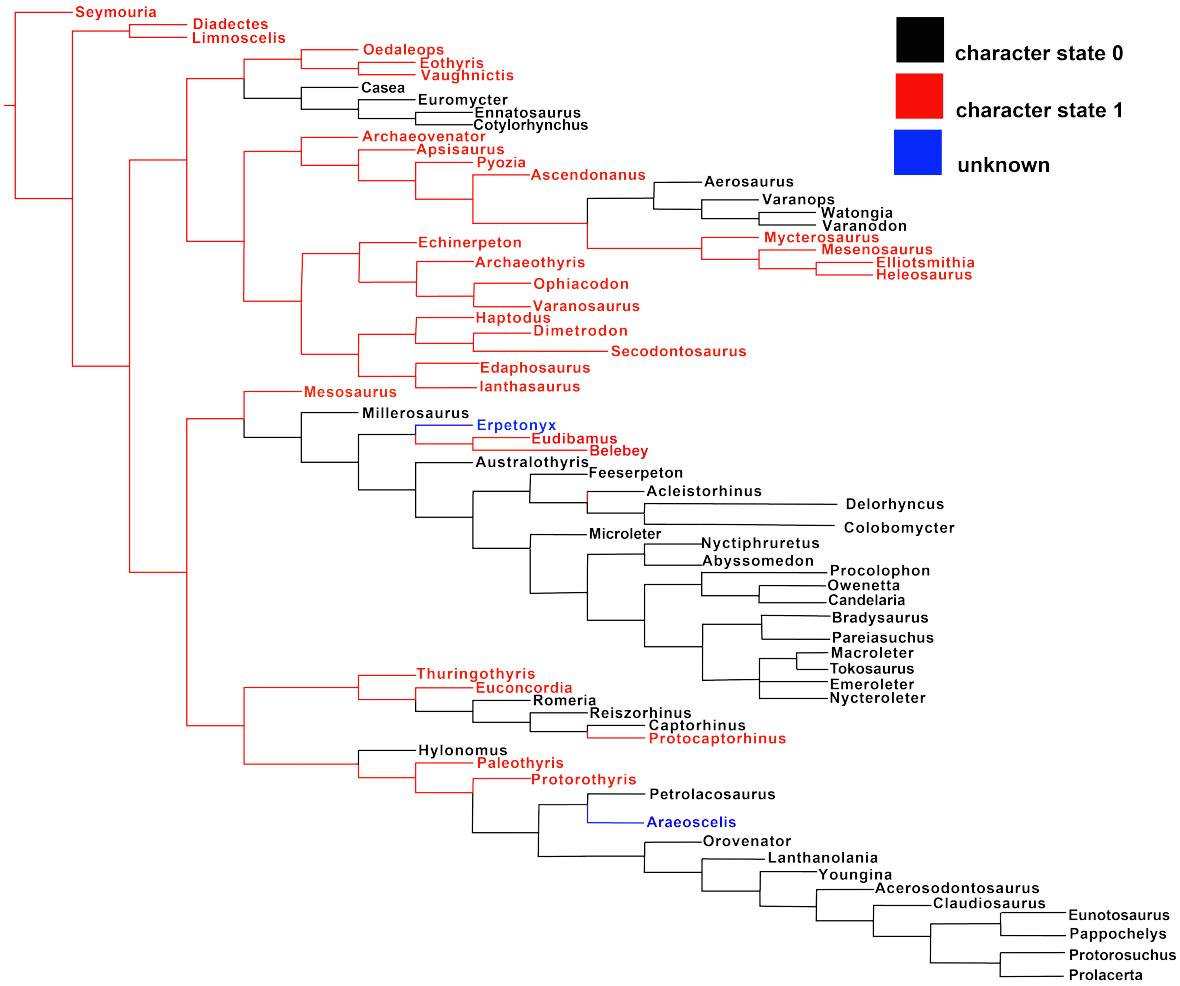


Figure 23: Optimisation of character 6, contact between squamosal and posteroventral margin of the jugal, on a non-time calibrated traditional phylogeny of early amniotes. Topology is derived as detailed in Fig.16. Key: black = taxa coding for state 0, red = taxa coding for state 1, blue = unknown.

Character 7: Parietal, free lateral margin: absent (0); present (1)(Fig.24)

A free lateral margin of the parietal (state 1) consistently defines the upper temporal fenestra in all diapsids (type 5 fenestration), and is also present in *Secodontosaurus* and *Edaphosaurus* (type 3 fenestration).

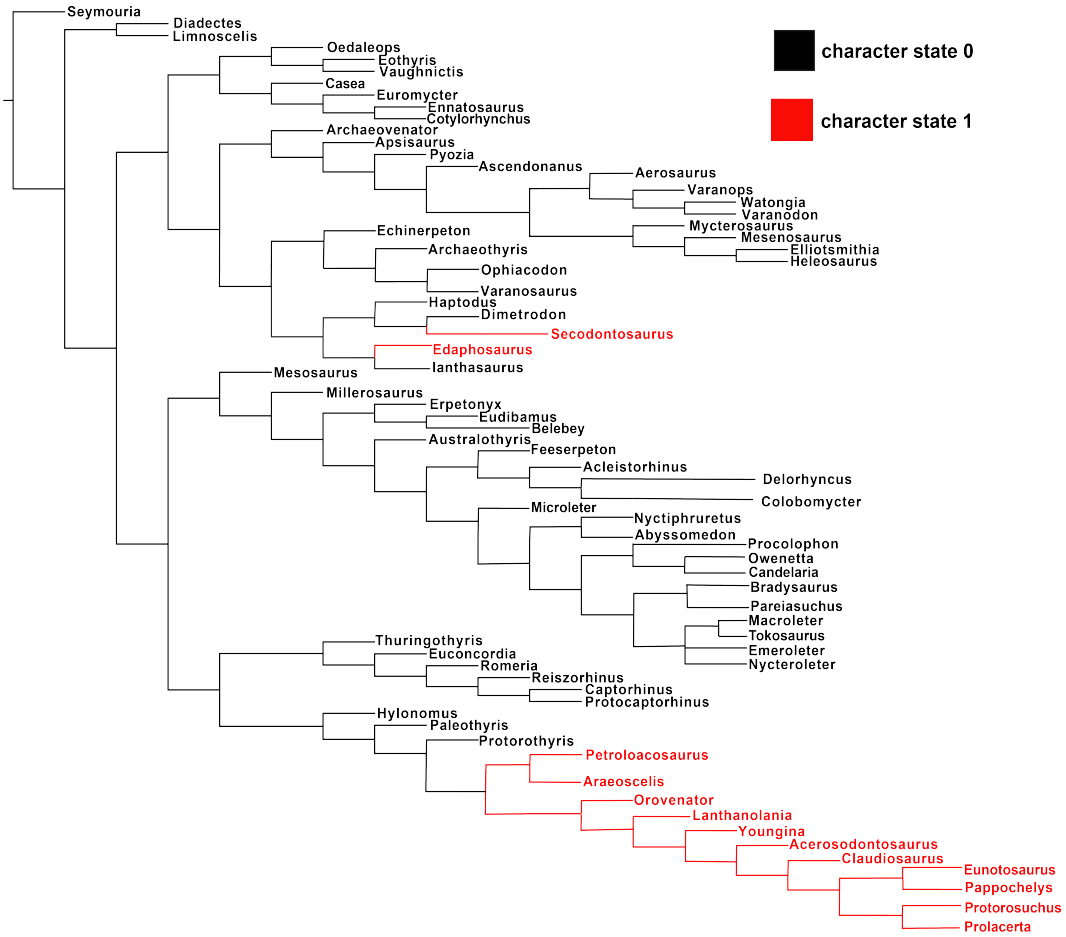


Figure 24: Optimisation of character 7, free lateral margin of parietal, on non-time calibrated traditional phylogeny of early amniotes. Topology is derived as detailed in Fig.16. Key: black = taxa coding for state 0; red = taxa coding for state 1

In summary, observations on the composite elements of temporal fenestrae and emarginations provide conjectures of homology that are otherwise absent when coding is limited to the presence or absence of the upper and lower fenestrae. In particular, characters that focus on the free margins of the parietal and jugal, and the points of contact between the jugal, squamosal and quadratojugal support relationships both within clades, e.g. caseids (character 6), bolosaurids (characters 5 and 6), varanodontines (characters 5 and 6), non-lanthanosuchoid ankyramorphs (character 5), nyctiphruretids + owenettids (characters 3 and 4), sphenacodontids + edaphosaurids (characters 2 and 3), and between clades, e.g. diapsids (character 7) and synapsids (character 6). In addition, any observations of potential homology derived from the

dual opening method of are retained in characters 1 and 7.

The new scheme for coding characters related to temporal fenestration is not free of probable homoplasy. For example, the free lateral margin of the parietal is present in *Secodontosaurus* and *Edaphosaurus* as well as in neodiapsids (character 5). Nevertheless, characterisation of temporal openings derived from the constituent elements provides an effective alternative to the traditional approach to coding in early amniotes.

3.5 Synthesising new characters for temporal fenestration into existing datasets

In practise, character lists are constructed to fit the purpose of the phylogenetic exercise, i.e. the taxonomic focus of the study, and the relevance of characters may therefore vary. In past phylogenetic analyses, particularly those concerned with parareptile phylogeny, researchers have recognised that the morphology of temporal fenestration is complex, and cannot be adequately represented by characters that only describe the presence or absence of fenestrae (MacDougall and Reisz 2014). Characters describing the contribution of the quadratojugal and postorbital to the lower temporal fenestra, for example, were introduced by deBraga and Reisz (1996 c.16 and c.20), and have since been widely used in parareptile character lists, together with the traditional dual opening characters (e.g. Tsuji 2012, MacDougall *et al.* 2018).

The series of seven characters outlined above are designed to replace the two characters traditionally used in the dual opening method, and are applicable to most datasets on early amniotes. Care should be taken, however, to avoid redundancy with other characters when incorporating the new series into existing datasets. For example, character 6 of the new series is similar in respect to scoring as the contribution of the quadratojugal to the lower temporal fenestra (e.g. Laurin and Reisz 1995 c.16). This is because contact between the squamosal and the posteroventral margin of the jugal often excludes the quadratojugal from the 'lower' temporal fenestra. However, the new character additionally recognises the morphology of bolosaurids, in which the contact of the squamosal and jugal is maintained dorsal to the fenestra, whilst the quadratojugal provides the ventral margin (Fig.9). Furthermore, the new character can be scored for 'anapsid' taxa, which would usually score as 'inapplicable' for the contribution of the quadratojugal to the fenestra.

Character lists focusing on synapsids and parareptiles often include a character describing the participation of the postorbital to the lower temporal fenestra (deBraga and Reisz 1996 c.20). Benson (2012) omitted this character, but instead included a

character describing the contact of the squamosal with the postorbital process of the jugal in varanodontines, which excludes the postorbital from the temporal fenestra (i.e. equivalent to deBraga and Reisz 1996 c.20). The coding of Benson (2012), with some modification, is included in the new series as character 5.

3.6 Testing the hypothesis using parsimony

In chapter 4, I present the results of a new and comprehensive phylogenetic analysis of early amniotes, for which a novel character-taxon matrix has been created to reflect the broad range of amniotes used as operational taxonomic units (also see Appendices 1 and 2). The new series of seven characters as defined above has been incorporated into this dataset as characters 72, 73, 81, 82, 84, 85 and 90. The traditional characters coding for the presence or absence of upper and lower temporal fenestrae have been omitted, together with characters 16 and 20 of deBraga and Reisz (1996), which, as noted in section 3.5, are partially or wholly redundant with those of the new series. The analysis was performed using the new technology driven search in TNT (Goloboff *et al.* 2008) (see chapter 4 for further details). The inclusion of the new series of characters into the character-taxon matrix of this analysis results in 16 most parsimonious trees (MPT's). A strict consensus of the 16 MPT's produces a tree topology with a high degree of within and between clade resolution, particularly among the monophyletic group comprised of neodiapsids, parareptiles and varanopids (Fig.25A). Early synapsids, with the exception of varanopids, remain a monophyletic group.

This character-taxon matrix was then revised, omitting the seven new characters detailed above, but including the two binary characters usually used to describe the presence/absence of the lower and upper temporal fenestrae, plus characters 16 and 20 of deBraga and Reisz (1996) describing the contribution of the postorbital and quadratojugal to the lower temporal fenestra. The tree topology resulting from the revised dataset is based on a strict consensus of 140 MPT's and reflects a broad polytomy between and within the three groups of neodiapsids, parareptiles and varanopids (Fig.25B). The results also show a polytomy between sauropsids, caseasaurs and the remaining group of early synapsids. This implies that the new series of characters on temporal fenestration recognise morphological disparity and similarity within and between groups. This is particularly relevant to in-group resolution in parareptiles and varanopids, and neodiapsids.

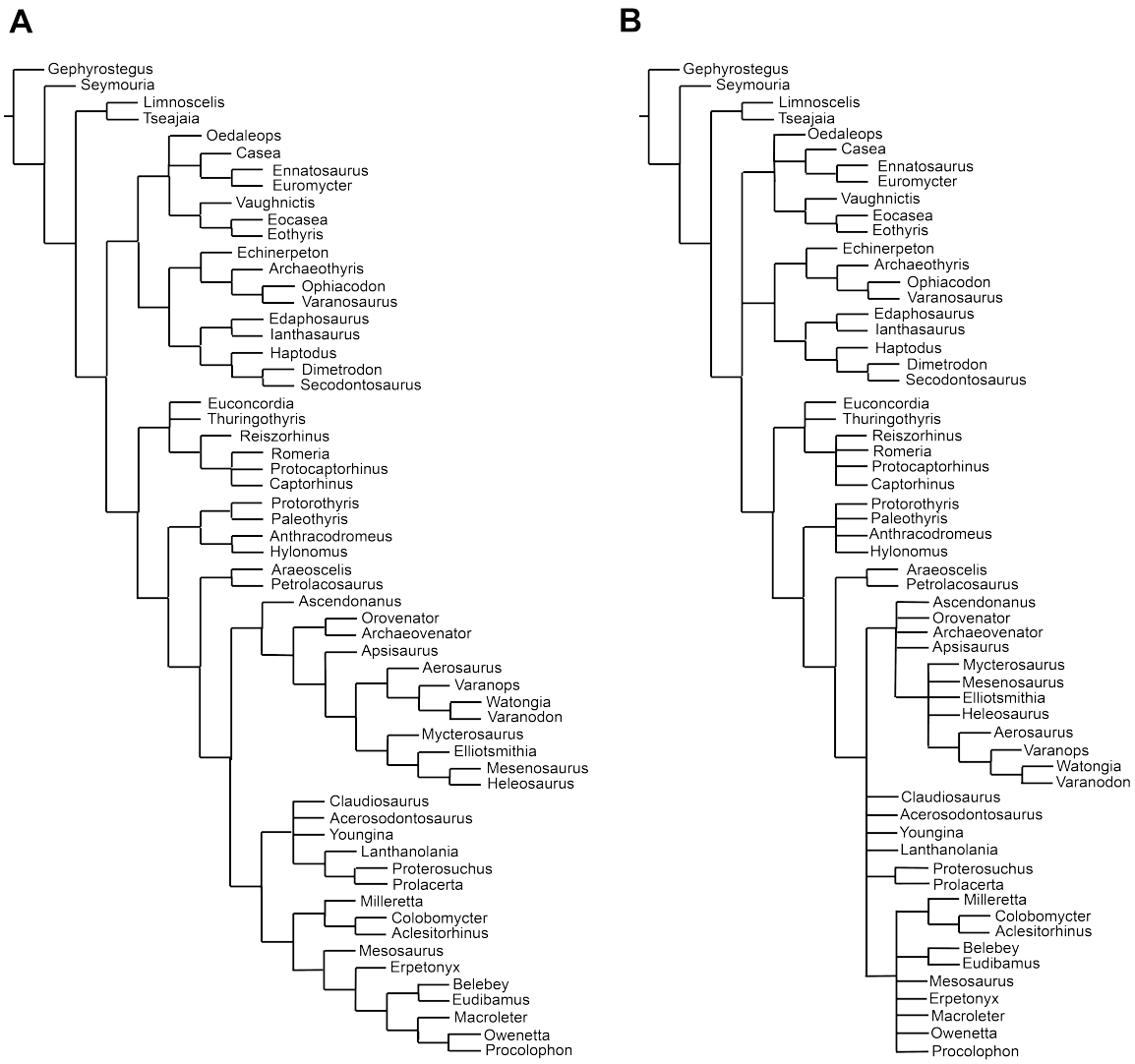


Figure 25: A, strict consensus tree incorporating the new series of seven characters detailed in section 3.4; B, strict consensus tree substituting two characters for the presence/absence of the upper and lower temporal fenestrae plus two characters for the participation of the postorbital and quadratojugal in the lower temporal fenestra for the seven new series characters.

3.7 Conclusions

The problems of coding for temporal fenestration across early amniote taxa has been recognised for over two decades, and the focus on the constituent bones forming the margins of fenestrae has been suggested as an alternative approach (deBraga and Rieppel 1997). However, despite continued concerns raised by more recent studies (MacDougall and Reisz 2014, MacDougall *et al.* 2018), little has been attempted by way of a systematic analysis of fenestral patterns or in proposing alternative methods. In this chapter I have shown that the variation in the patterns of temporal fenestration in early amniotes can be defined and condensed into a series of seven binary characters

that provide consistent observations of primary homology. When placed in a phylogenetic framework of a large and broad-based amniote dataset, the inclusion of these new characters results in a highly resolved topology. Recovery of a more highly-resolved tree does not necessarily indicate that a particular method or dataset is better than others. Nevertheless, it is consistent with the hypothesis that detailed observations of temporal fenestra morphology can play a role in resolving the phylogeny of early amniotes. Although care should be taken to ensure that the redundancy and non-independence is avoided in existing datasets, the implementation of the new series of characters addresses, for the first time, concerns on the effectiveness of character coding for temporal fenestration in a global phylogenetic analysis of early amniotes.

Chapter 4

A New Phylogeny of Early Amniotes

4.1 Introduction

The colonisation of the land by vertebrates was initially confined to semiaquatic environments. Early tetrapods, in common with most extant lissamphibians, probably relied on cutaneous gas exchange, particularly for expelling CO_2, and were therefore dependent on wet conditions to balance water loss (Janis and Keller 2001). The ability to survive and reproduce outside these environments required a series of novel physiological and anatomical changes (Martin and Nagy 1997). The evolution of the amniotic egg, regarded by Romer (1967:1634) as"the most marvellous 'invention' in vertebrate history" was certainly a factor in the radiation of early amniotes, allowing reproduction away from water (Sander 2012). However, changes in the mode of respiration, in locomotion and feeding mechanisms in stem- and crown-amniotes were likely to have been equally important and also underwent substantial transformation (Sumida 1997, Janis and Keller 2001).

Molecular and total evidence analyses suggests that stem-amniotes first appeared in the late Devonian/early Carboniferous, with estimated divergence times for the amphibian/amniote split ranging from 367.5 million years ago (Ma) (95% HDP 354.9-380.6 Ma) based on total evidence Bayesian analysis (Pyron 2011) to a mean of 370 Ma, based on Bayesian posterior distribution of nuclear-encoded proteins (Blair and Hedges 2005). The earliest crown-group amniote fossil, the small lizard-like *Hylonomus lyelli*, was discovered in fossilised lycopod stumps from the coal measures of Joggins, Nova Scotia (latest Bashkirian 319 - 318 Ma) (Carroll 1964, Benton *et al.* 2015,). *Hylonomus* provides evidence that deep divergences of the amniote crown-group had

occurred by this time, since morphological phylogenetic studies have found *Hylonomus* to be the earliest known stem reptile (Müller and Reisz 2006).

Initial hypotheses on the interrelationships of early amniotes were established according to distinctive characteristic of the skull: the presence/absence and number of temporal fenestrae (see chapter 3 for more detailed discussion), and this systematic approach has undergone remarkably little change since the work of Osborn and others in the early 1900's (Osborn 1903, Williston 1917). This view was formalised by substantive studies on early synapsids (Romer and Price 1940) and reptiles (Romer 1956). Later comparative and phylogenetic studies (Carroll 1969, Carroll and Baird 1972, Clark and Carroll 1973, Reisz 1980,1986, Brinkman and Eberth 1982, Benton 1985) firmly established the principle relationships in the dichotomy of early amniotes: synapsids, the total-group mammals (caseasaurs, varanopids, ophiacodontids, edaphosaurids and sphenacodontians) and sauropsids, the total-group reptiles (captorhinids, romeriids - later referred to 'protorothyridids' - araeoscelidians and 'eosuchians', a 'waste-basket' taxon to which most non-archosauromorph diapsids were referred).

Despite the apparent consensus on key relationships among early amniotes, some uncertainty remained in respect to the position of turtles. Turtle origins became the focus of rigorous debate, producing a number of morphological studies on early amniote phylogeny (Gauthier *et al.* 1988a and 1988b, Lee 1997, Laurin and Reisz 1995, deBraga and Rieppel 1997, Rieppel and Reisz 1999), as well as early molecular phylogenies (Zardoya and Meyer 1998).

This episode of phylogenetic research resulted in the emergence of a broad consensus on many more detailed aspects of early amniote, and particularly reptilian, interrelationships including the current paradigm of a basal reptile dichotomy between Parareptilia and Eureptilia (Laurin and Reisz 1995). Parareptilia Olson, 1947 currently includes Mesosauridae, Millerettidae, Lanthanosuchoidea, Bolosauridae, Procolophonoidea, Pareaisauria and Nycteroleteridae (Tsuji and Müller 2009, Tsuji *et al.* 2012) and Eureptilia Olson, 1947 currently includes Captorhinidae, the paraphyletic grade 'protorothyridids' and Diapsida (Müller and Reisz 2006). The question of the origin of turtles is now partly resolved, with molecular studies finding turtles as the extant sister group of archosaurs (Chiari *et al.* 2012, Field *et al.* 2014), whereas morphological studies, which include fossils, find them as a sister taxon to lepidosaurs (Bever *et al.* 2015 - parsimony analysis), or within Diapsida, but outside crown-group diapsids (Bever *et al.* 2015 - Bayesian analysis, Schoch and Sues 2017). This issue aside, a basic phylogeny of early amniotes has become widely accepted (Fig.1).

Over the past 15 years, since the height of the debate on turtle relationships, system-

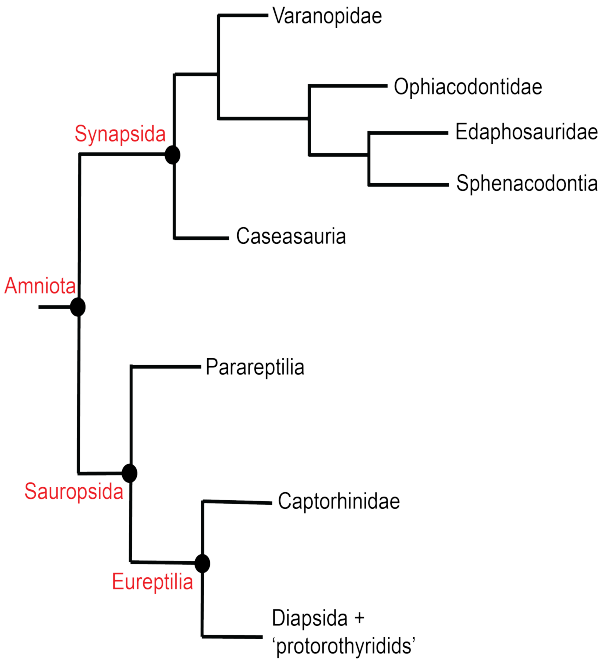


Figure 1: General consensus of higher taxonomic relationships among early amniotes

atic studies of early amniotes have tended to focus on the relationships of taxa within established clades (e.g. Synapsida, Benson 2012, Reisz and Fröbisch 2014, Brocklehurst *et al.* 2016; Varanopidae, Maddin *et al.* 2006, Spindler *et al.* 2018; Caseasauria, Reisz *et al.* 2009, Romano and Nicosia 2015; Diapsida, Müller 2004, Bickelmann *et al.* 2009; Eureptilia, Müller and Reisz 2006, Captorhinidae, Sumida *et al.* 2010, Reisz *et al.* 2015, Modesto *et al.* 2018 and Parareptilia, Tsuji *et al.* 2012, Modesto *et al.* 2015, MacDougall *et al.* 2016). In almost all cases, the inclusion of terminal units outside the group of interest has been limited to a few individual taxa or otherwise a single terminal unit of a higher-level taxonomic group (see Table 4.1). The direction of research, therefore, has been primarily concerned with resolving within-group relationships rather than exploring broader systematic issues. To this extent, relationships among higher clades of early amniotes have generally been assumed, and not tested. Nevertheless, some recent work on the interrelationships of the early Permian reptile *Mesosaurus* has galvanised interest in early amniote systematics, resulting in a more comprehensive approach to taxon inclusion in phylogenetic analyses (Piñeiro and Laurin 2017, MacDougall *et al.* 2018).

Another recent development in the study of early amniotes has been a marked increase in the application of high-resolution X-ray micro-computed tomographic techniques (μCT) to fossils specimens. This has enabled detailed examination of the anatomy of fossils, which were previously impossible due to the constraints of non-

Table 4.1: Selection of early amniote phylogenetic analyses from 2003 to date, showing the number of terminal units of the main focus group (focus N) compared to those outside the main focus group (other N). Abbreviations: stem= stem-amniotes, cap= captorhinids, proto= 'protorotyhridids', diap= diapsids, para= parareptiles, synap= synapsids, rept= reptile or eureptiles as a single terminal unit, dash=inapplicable

Author(s)	year	focus	focus N	other N	stem	cap	proto	diap	para	synap	rept
Reisz and Dilkes	2003	synapsids	12	1	0	-	-	-	-	-	1
Müller	2004	diapsids	29	4	1	1	0	-	1	1	-
Maddin *et al.*	2006	synapsids	14	1	0	-	-	-	-	-	1
Müller & Reisz	2006	eureptiles	19	6	2	-	-	-	3	1	-
Tsuji	2006	parareptiles	14	2	0	1	0	0	-	1	-
Müller *et al.*	2006	captorhinids	10	5	0	-	2	1	1	1	-
Reisz *et al.*	2009	synapsids	11	2	1	-	-	-	1	-	1
Bickelmann *et al.*	2009	diapsids	34	4	1	1	0	-	1	1	-
Sumida *et al.*	2010	captorhinids	11	1	0	-	1	0	0	0	-
Reisz *et al.*	2011	diapsids	30	4	1	1	0	-	1	1	-
Benson	2012	synapsids	44	4	2	1	0	1	0	-	-
Tsuji *et al.*	2012	parareptiles	22	7	3	1	1	2	-	1	-
Ezcurra *et al.*	2014	diapsids	25	15	1	1	1	-	0	12	-
Romano & Nicosia	2015	synapsids	22	2	1	1	0	0	0	-	-
Reisz *et al.*	2015	captorhinids	20	1	0	-	1	0	0	0	-
Modesto *et al.*	2015	parareptiles	28	9	2	2	0	3	-	2	-
Brocklehurst *et al.*	2016	synapsids	51	4	2	1	0	1	0	-	-
MacDougall *et al.*	2016	parareptiles	28	4	2	-	-	-	-	1	1
Splindler *et al.*	2018	synapsids	38	8	2	1	2	0	3	-	-
Modesto *et al.*	2018	captorhinids	21	1	0	-	1	0	0	0	-

destructive preparation and size limitation. This method has greatly augmented our understanding of early amniotes systematics, often revealing new aspects of anatomy, supporting new or modified phylogenetic hypotheses (e.g. Bever *et al.* 2015, Simões *et al.* 2018). In chapter 2, I described the results of μCT data on the early Permian neodiapsid *Orovenator mayorum* (Reisz *et al.* 2011a) and presented the hypothesis that this taxon formed a clade with varanopids, a group of early amniotes typically considered as synapsids (Reisz and Fröbisch 2014, Brocklehurst *et al.* 2016, Spindler *et al.* 2018). The phylogenetic analysis supporting this hypothesis was performed using a previously published dataset (see below) that was conservative in the respect that it included the previously proposed synapsid-like traits of varanopids, but did not include the newly-observed traits shared between varanopids and diapsids. A more robust test of the hypothesis requires the construction of a broad-based character-taxon matrix for early amniotes.

The aim of this chapter is to present the results of this endeavour, which is, to my knowledge, one of the largest and most comprehensive phylogenetic analyses of early amniotes to date. The results confirm my initial hypothesis that varanopids and *Orovenator mayorum* form a monophyletic group within Sauropsida, challeng-

ing the traditional view of varanopids as 'pelycosaur'-grade early synapsids, which was established over 75 years ago by Romer and Price (1940), and reaffirmed in numerous subsequent studies (e.g. Olson 1965, Reisz 1980, Langston and Reisz 1981, Berman and Reisz 1982, Reisz 1986, Reisz and Dilkes 2003, Maddin *et al.* 2006, Campione and Reisz 2010, Benson 2012, Spindler *et al.* 2018). My results also support a sister group relationship between neodiapsids and parareptiles, with Captorhinidae positioned stemward to this group within the total-group reptiles (Sauropsida). This conflicts with the conventional hypothesis of captorhinids as the sister taxon to diapsids within Eureptilia, first proposed by Laurin and Reisz (1995). My results have implications for hypotheses concerning the transition between 'pelycosaur'-grade synapsids of the early Permian and therapsid-grade synapsids of the middle Permian, and on patterns of evolution of temporal fenestration in early amniotes. I also find an unexpected degree of uncertainty over the affinities of caseasaurs as synapsids, stem-amniotes or stem-reptiles.

4.2 Methods

The compilation of an inclusive taxon list, encompassing a broad range of early amniotes, was central to the current analysis. My objective was not to resolve the in-group relationships of early amniote subclades, but to resolve the relationships among higher taxonomic groups. Therefore, my taxon sample was focused on the basal chronologically early members of each clade (see Table 4.3). In total, 60 taxa were selected, including 4 species of stem-group amniotes (*Gephyrostegus*, *Seymouria*, and the diadectomorphs *Tseajaia* and *Limnoscelis*) and 56 species that have previously been considered as crown-group amniotes. Most operational taxonomic units (OTUs) were selected at species level, with eight taxa considered at the generic level to improve scoring completeness (*Seymouria*, *Ophiacodon*, *Dimetrodon*, *Aerosaurus*, *Araeoscelis*, *Proterosuchus*, *Captorhinus* and *Romeria*). All OTUs are Carboniferous or Permian in age, with the exception of those representing archosauromorphs and procolophonoids, both from the earliest Triassic. All OTUs were scored for 286 discrete characters, and all characters are parsimony informative, although limited non-parsimony informative scoring has been retained in some multistate characters for information purposes.

My character list was assembled by undertaking a comprehensive review of key phylogenetic studies on stem-amniotes (e.g. Klembara *et al.* 2014), early amniotes (e.g. Benton 1985, Gauthier *et al.* 1988a, Laurin and Reisz 1995, deBraga and Rieppel 1997), early synapsids (e.g. Brinkman and Eberth 1982, Reisz 1986, Reisz *et al.* 1992,

Modesto 1995, Reisz and Dilkes 2003, Fröbisch *et al.* 2011, Benson 2012), parareptiles (e.g. deBraga and Reisz 1996, Reisz *et al.* 2007, MacDougall and Reisz 2017, Schoch and Sues 2018), diapsids (e.g. Carroll and Currie 1991, Müller 2004, Müller and Reisz 2006, Ezcurra 2016) and captorhinids (e.g. Heaton and Reisz 1986, Dodick and Modesto 1995, Modesto *et al.* 2007, Modesto *et al.* 2018). The characters were compiled in to a single database from which 286 characters were selected, with the omission of similar or redundant characters, or those that were parsimony uninformative.

There are 19 new characters (see Table 4.2); seven (72,73,81,82,84,85,90) represent a novel series of characters describing temporal fenestration (see chapter 3), together with six new characters of the mandible (159,169,170,175,189,190), three of the palate (128,129,133) and one each for the maxilla (39), prefrontal (60) and manus (258). There are 55 multistate characters, all of which are unordered. Equal weighting was applied across all characters. A full character list with annotations on their use in previous analyses, optimisation and, where appropriate, explanatory comments are provided in Appendix 1, and a character-taxon matrix is detailed in Appendix 2.

Phylogenetic analysis was performed using both maximum parsimony and Bayesian inference. Both methods were used in order to present a fully comprehensive series of results, particularly in light of recent conflicting opinions on the comparative performance of both methods for discrete morphological datasets (Wright and Hillis 2014, Puttick *et al.* 2017, Sansom *et al.* 2018, O'Reilly *et al.* 2018).

Furthermore, the estimation of branch lengths derived from Bayesian analysis using a fossilised birth-death (FBD) model (see below) can offer insights into macroevolutionary patterns and the timing of major evolutionary divergence. The topologies I recovered using both maximum parsimony analysis and Bayesian inference are fundamentally similar in respect to higher taxonomic levels, although several differences are evident, and these are discussed below.

Table 4.2: List of 19 new characters included in character/taxon matrix. Refer to Appendix 1 for discussion on each character

character number	character description
39	Maxilla, lateral surface, orientation of suborbital ramus only:vertical, with no lateral overhang of tooth row (0); dorsolaterally inclined, overhangs tooth row (1)
60	Prefrontal, sharp angle between the dorsal and lateral surface:absent (0), present (1)
72	Jugal, free posterior margin:absent (0); present (1)
73	Jugal, free concave ventral margin:absent (0); present (1)
81	Quadratojugal, contact with posteroventral margin of jugal:present (0); absent (1)
82	Quadratojugal, contact with posterodorsal margin of jugal:absent (0); present (1)
84	Squamosal, contacts posterodorsal margin of jugal:absent (0); present (1)
85	Squamosal, contacts posteroventral margin of jugal:absent (0); present (1)
90	Parietal, free lateral margin:absent (0); present (1)
128	Vomer, asymmetric bifurcated anterior processes: present, vomer terminates anteriorly in short lateral and elongate medial projections (0); absent (1)
129	Vomer, medial contact with pterygoid:absent (0); present (1); inapplicable pterygoid does not contact the vomer (-)
133	Palatine, incision of anterior surface to accommodate internal naris (choana): shallow to moderate anterior incision (0); deep anterior incision (1); palatine is not incised (2)
159	Mandible, anterodorsal curvature of anterior mandible in lateral view: absent, alveolar margin of anterior mandible approximately horizontal (0); present, dorsal margin of anterior mandible shows distinct concavity (1)
169	Mandible, contribution of the splenial or post-splenial to the posterior inframeckelian foramen:absent (0); present (1); inapplicable, foramen is absent (-)
170	Mandible, contribution of the prearticular to the posterior inframeckelian foramen:absent (0); present (1); inapplicable, foramen is absent (-)
175	Dentary, region posterior to tooth row:contacts the angular ventrally (0); does not contact the angular ventrally (1); inapplicable, dentary does not extend posterior to tooth row (-)
189	Surangular, anterodorsal process preventing posterior contact of dentary and coronoid:absent (0); present (1)
190	Surangular, morphology of anterodorsal process, if present:narrow splint-like process (0); dorsoventrally broad posteriorly, tapering anteriorly (1), inapplicable, anterodorsalprocess absent (-)
258	Manus, ungual (terminal) phalanges, shape:hoof-like or bluntly spade-shaped distally with no ventral curvature (0); taper distally to a point, and curve ventrally (1)

Table 4.3: Taxon list for terminal units used in this analysis, with principle reference sources(s) and accession numbers of examined specimens. Missing data expressed as a percentage of the 286 characters used in this analysis for cranial and postcranial characters and all characters combined.

Taxon	Primary references and specimens examined	missing data total	missing data cranial	missing data postcranial
Gephyrostegus bohemicus	Brough, Brough and White 1967, Carroll 1970, Godfrey and Reisz 1991, Klembara et al. 2014 White 1939, Laurin 1996	46%	32%	74%
Seymouria spp	Berman et al. 2000, Klembara et al. 2005 MCZ 1098, MCZ 1643, MCZ 1083 FMNH UC 666, FNHN C.145	19%	19%	19%
Tseajaia campi	Moss 1972	20%	20%	19%
Limnoscelis plaudis	Romer 1946, Fracasso 1987, Berman et al. 2010 FMNH UC 676	17%	18%	16%
Oedaleops campi	Langston 1965, Reisz et al. 2009	35%	53%	64%
Eothyris parkeyi	Reisz et al. 2009, Sumida et al.2014 MCZ 1161	52%	28%	100%
Vaughnictis smithae	Brocklehurst et al.2016 MCZ 2985	73%	65%	88%
Eocasea martini	Reisz and Fröbisch 2014	73%	79%	60%
Euromycter rutena	Sigogneau-Russell and Russell 1974	41%	25%	72%
Casea broilii	Williston 1913, Romer and Price 1940, Olson 1968, LeBlanc and Reisz 2014 FMNH UC 656, FMNH UR 1011, FMNH UR 2512, FMNH UC 657	19%	23%	9%
Ennatosaurus tecton	Olson 1968, Maddin et al. 2008	30%	20%	49%
Echinerpeton intermedium	Reisz 1972 MCZ 4090,4091, 4092,4093,4094	82%	87%	72%
Archaeothyris florensis	Reisz 1972,1975 MCZ 4079, 4085,4089	65%	68%	60%
Varanosaurus acutirostris	Berman et al. 1995, Sumida 1990 FMNH PR 1670, FMNH UC 34	25%	12%	51%
Ophiacodon spp	Romer and Price 1940 MCZ 1203, 1206, 1350, 1366, 1435, 1486, 1971, 2934,4820, 4827, 4829, 4854, 4895 ,4938, 5051, 5719, 5792, 5933, 5934, 5963, 6845, 7452	8%	11%	1%

Table 4.3: Taxon list for terminal units used in this analysis, with principle reference sources(s) and accession numbers of examined specimens. Missing data expressed as a percentage of the 286 characters used in this analysis for cranial and postcranial characters and all characters combined.

Taxon	Primary references and specimens examined	missing data total	missing data cranial	missing data postcranial
Haptodus garnettensis	Currie 1977, Laurin 1993 ROM 29872, 30099, 43601, 43602, 43603, 43604, 43605, 43606, 43607, 43608	16%	15%	18%
Secodontosaurus obtusidens	Reisz et al. 1991, 1992, Fröbisch et al. 2010, MCZ 1124, 2028, 3427, 3628, 5203, 5064, 5355, 8677, 7013, 7080	25%	12%	52%
Dimetrodon spp	Romer and Price 1940 MCZ 1114, 1365, 4443, 4982, 6148, 7074	8%	10%	5%
Ianthasaurus hardestiorum	Reisz and Berman 1986, Modesto and Reisz 1990, Mazierski and Reisz 2010 ROM 29941, 37751, 59933	57%	51%	67%
Edaphosaurus boanerges	Modesto 1995 MCZ1531, 1680, 1762, 3417, 3420, 3421, 4309, 4315, 4316	13%	13%	15%
Archaeovenator hamiltonensis	Reisz and Dilkes 2003 KUVP 12483	27%	23%	36%
Ascendonanus nestleri	Spindler et al. 2018	48%	48%	49%
Aerosaurus spp	Langston and Reisz 1981, Pelletier 2014	27%	31%	20%
Apsisaurus witteri	Laurin 1991, Reisz et al.2010 MCZ 1474	71%	76%	62%
Heleosaurus scholtzi	Carroll 1995, Reisz and Modesto 2007, Botha-Brink and Modesto 2007,2009	37%	32%	46%
Mesenosaurus romeri	Reisz and Berman 2001	29%	12%	62%
Mycterosaurus longiceps	Vaughn 1958, Berman and Reisz 1982 FMNH UC 692, FMNH UC169	40%	32%	55%
Elliotsmithia longiceps	Dilkes and Reisz 1996, Resiz et al. 1998, Modesto et al. 2001	69%	55%	97%
Varanops brevirostris	Maddin et al. 2006, Campione and Reisz 2010 FMNH UC 644, FMNH UR 2423, MCZ 1928, FMNH P 12841, FMNH UC 677	15%	17%	11%
Varanodon agilis	Olson 1965 FMNH 986	45%	42%	53%
Watongia meieri	Reisz and Laurin 2004	85%	95%	64%

Table 4.3: Taxon list for terminal units used in this analysis, with principle reference sources(s) and accession numbers of examined specimens. Missing data expressed as a percentage of the 286 characters used in this analysis for cranial and postcranial characters and all characters combined.

Taxon	Primary references and specimens examined	missing data total	missing data cranial	missing data postcranial
Hylonomus lyelli	Carroll 1964, Meyer and Anderson 2013 NHMUK R 4168	46%	43%	51%
Anthracodromeus longipes	Carroll and Baird 1972	70%	78%	54%
Paleothyris acadiana	Carroll 1969 MCZ 3481, 3482, 3483, 3485, 3486, 3487, 3489, 3490	19%	21%	15%
Protorothyris archeri	Clark and Carroll 1973 MCZ 1532, 2148	35%	22%	60%
Petrolacosaurus kansensis	Reisz 1981 KUVP 1424, 8351, 9951, 9952, 9957, 9958, 33603	9%	11%	4%
Araeoscelis spp	Williston 1913, Vaughn 1955, Reisz et al.1984 MCZ 4380, 8828	16%	19%	12%
Orovenator mayorum	Reisz et al. 2011, Ford and Benson 2018 OMNH 74606, 74607	49%	26%	96%
Youngina capensis	Gow 1975, Currie 1980, Carroll 1981 BP/1/70, 2614, 2871,3859,	20%	22%	17%
Acerosodontosaurus piveteaui	Currie 1980, Bickelmann et al.2009 MNHN 1908-32-57	66%	72%	56%
Lanthanolania ivakhnenkoi	Modesto and Reisz 2002	79%	68%	100%
Claudiosaurus germaini	Carroll 1981 MNHN 1978-6-1, MNHN 1978-6-2	26%	28%	22%
Prolacerta broomi	Gow 1975, Modesto and Sues 2004 BP/1/471, 2675, 4504, 5375, 5066, 588,	15%	14%	17%
Proterosuchus spp	Wellman 1998, Ezcurra et al. 2013,2015, Ezcurra 2016	29%	25%	38%
Thuringothyris malendorffae	Müller et al. 2006	41%	38%	48%
Captorhinus spp	Fox and Bowman 1966, Heaton 1979, Heaton and Reisz 1980, Modesto 1998, Holmes 2003 FMNH UC 242, 687, 701, FMNH PR 912, 913, MCZ 1746, OMNH 15003, 15101, 52331, 56819	9%	11%	4%
Protocaptorhinus pricei	Clark and Carroll 1973 MCZ 1160, 1478	51%	36%	81%

Table 4.3: Taxon list for terminal units used in this analysis, with principle reference sources(s) and accession numbers of examined specimens. Missing data expressed as a percentage of the 286 characters used in this analysis for cranial and postcranial characters and all characters combined.

Taxon	Primary references and specimens examined	missing data total	missing data cranial	missing data postcranial
Romeria spp	Clark and Carroll 1973 MCZ 1480, 1963,	51%	28%	98%
Euconcordia cunninghami	Müller and Reisz 2005, Reisz et al. 2016	56%	34%	100%
Reiszorhinus olsoni	Sumida et al.2010 FMNH UC 183	57%	35%	100%
Eudibamus cursoris	Berman et al. 2000	71%	73%	66%
Mesosaurus tenuidens	Modesto 2006, 2010, Piñiero et al. 2012, 2016	20%	23%	14%
Erpetonyx arsenaultorum	Modesto et al.2015 ROM 55402	69%	75%	58%
Belebey vegrandis	Reisz et al. 2007	46%	21%	96%
Macroleter poezicus	Tsuji 2006	44%	23%	86%
Milleretta rubidgei	Watson 1957, Gow 1972 BP/1/720, 3818, 3822	33%	21%	57%
Acleistorhinus pteroticus	Daly 1969, deBraga and Reisz 1996 FMNH UR 1038	52%	28%	100%
Colobomycter pholeter	Vaughn 1958b, Laurin and Reisz 1989, Modesto 1999b, MacDougall et al. 2016, 2017	50%	25%	100%
Procolophon trigoniceps	FMNH UR 272, BMRP 2008.3.1, 2008.3.3, 2008.3.10, Carroll and Lindsey 1985, deBraga 2003, Cisneros 2008 BP/1/962, 5927	20%	19%	22%
Owenetta kitchingorum	Reisz and Scott 2002 BP/1/ 4195	30%	16%	59%

4.2.1 Maximum parsimony

The underlying premise of parsimony analysis is to find the tree topology that minimises the amount of implied evolutionary change (i.e. the tree topology that implies the smallest number of character state changes that best explains the data; Felsenstein 1982, 1985). There are two stages required to achieve this outcome, (i) calculate the number of characters changes (or steps) required for any given tree, and (ii) search all possible tree combinations that produce the minimum number of steps (Swofford and Sullivan 2009). Although point (i) is effectively resolved with minimal computational requirement using Fitch (1970) or Sankoff (1985) algorithms, there are difficulties in achieving point (ii) due to the sheer number of tree combinations generated by even a small number of taxa. The 60 OTUs in this analysis would produce an astronomically high number of possible trees, making an exhaustive search computationally unfeasible; for example only 15 OTUs can be arranged in 8 x 10^{12} different topologies. Consequently, exhaustive search methods are only practical for small datasets of less than 10 taxa. The branch-and-bound method (Hendy and Penny 1982) provides a partial solution to an exhaustive search by arresting the path of search if it cannot lead to an optimal tree, and is suitable for up to 25 OTUs (Swofford and Sullivan 2009). Larger datasets, however, require heuristic (i.e. non-exhaustive) search criteria based on algorithms that consider trees sequentially or use branch-swapping methods, such as tree bisection and reconnection (TBR). Parsimony is an older method of phylogenetic analysis, with few recent developments compared to Bayesian inference, but nevertheless remains an important and practical tool in systematics (Swofford and Sullivan 2009). Parsimony analysis is implemented in several different software packages, including TNT, which uses a number of algorithms including tree fusing (for sub-tree exchanges), tree-drifting (cyclic perturbation and search) and sectorial searches that are appropriate for rapid analysis of large datasets (Goloboff *et al.* 2008), although non-exhaustive algorithms give no guarantee of recovering the optimal tree.

The maximum parsimony analysis was performed in TNT v.1.5-beta (Goloboff *et al.* 2008), using the new technology driven search with sectorial, drift and tree fusing algorithms, set at an initial level of 100, with 1000 random additional sequences and the minimum tree length searched for 100 times. *Gephyrostegus bohemicus* was set as the out-group. No constraints were applied to the original analysis. The resulting 16 most parsimonious trees (MPTs) of 1380 steps were then subjected to an additional round of tree bisection reconnection (TBR) branch swapping, with no additional trees recovered. Decay indices (Bremer support) also were calculated in TNT v.1.5-beta.

Bootstrap analysis (100 replicates, full heuristic search) was performed using PAUP*v.

4.0a for Macintosh (Swofford 2003). Since the setting in TNT in respect to character optimisation is restricted to unambiguous synapomorphies (i.e. where ACCTRAN and DELTRAN agree), the parsimony analysis was also performed in PAUP*v.4.0a, using a heuristic search and TBR, with 1000 random additional replicates, resulting in 16 MPTs of 1380 steps. The ACCTRAN/DELTRAN optimisations of character states were subsequently produced, which are detailed in Appendix 1. The retention index (RI), consistency index (CI) and rescaled consistency index (RCI) were also calculated in PAUP* v4.0a. The tree topology, tree length and number of MPTs recovered in PAUP*v.4.0a were identical to those recovered in TNT v.1.5-beta. The nexus file for the character-taxon matrix is provided in Appendix 4.

4.2.1.1 Constrained topologies and Templeton tests

A series of additional parsimony analyses were run, which included topological constraints, to compare tree lengths of alternative phylogenetic hypotheses. Pairwise Templeton tests were used to statistically compare the topologically-constrained analyses to the most parsimonious trees. The Templeton test is a non-parametric statistical test (Wilcoxon signed-rank test) adapted to phylogenetic data (Templeton 1983). It uses a critical threshold applied to the P-value (P=probability) to accept or reject the null hypothesis that both topologies are statistically equivalent explanations of the data. The rejection of the null hypothesis (with a critical one-tailed p-value below 0.05) implies that the most parsimonious tree topology is a (statistically) significantly better explanation of the data than the constrained tree topology. Templeton tests for a one-tailed P-value were performed in PAUP* v.4.0a for Macintosh (Swofford 2003).

The alternative phylogenetic hypotheses tested by this method were (i) all varanopids, including *Orovenator*, are positioned within a monophyletic Synapsida (i.e. to the group containing caseasaurs + ophiacodontids + edaphosaurids + sphenacodontians), (ii) captorhinids are recovered as the sister taxon to 'protorothyridids' + diapsids within a monophyletic Eureptilia and (iii) caseasaurs form a monophyletic group of stem-amniotes or stem-sauropsids.

4.2.2 Bayesian inference

Statistical methods are often used to infer the probability of an outcome for a given set of known data. As these data become more clearly defined or more numerous, so the probability of the outcome becomes relatively greater. This is an example of forward probability, a system of logic in everyday use. If, on the other hand, the outcome,

rather than the data, is known, what can it tell us about the data? This is a problem of inverse probability, a mathematical solution to which was first proposed by Thomas Bayes (c.1720-1761). Bayes realised that a solution was only possible if prior conditions in respect to the data were known. For example, the prior conditions of throwing a six on a dice roll are uniform, i.e. the outcome has the same probability for each roll. Conversely, variable priors may favour some outcomes over others, by implying differential probability. Either way, the prior, or prior probability distribution, is key to the problem of inverse probability. Bayes used this concept to formulate a theorem, which infers the probability of the data (called the posterior probability distribution) based on the prior conditions. Bayes' theorem means we can derive the posterior distribution as:

$$f(A|X) = \frac{f(A)f(X|A)}{f(X)}$$

Where $f(A|X)$ is the probability of the model parameters A given that data X are true, or the posterior probability function.
Where$f(X|A)$ is the probability of the data X given the model parameters A are true, or the likelihood function
Where $f(A)$ is probability of model parameters A independent of all other information, or the prior probability distribution
Where $f(X)$ is the probability of the data X independent of all other information, or the normalising constant
The likelihood function/the normalising content, $\frac{f(X|A)}{f(X)}$ gives the likelihood ratio.
So the theorem can also be expressed as: the posterior probability is equal to the prior probability times the likelihood ratio. Therefore, Bayesian inference is a probabilistic model that involves the computation of a series of likelihoods based on the prior knowledge of an event.

4.2.2.1 Bayesian inference and phylogenetic analysis

Bayesian inference can be used in phylogenetic analysis, since the data for each OTU, whether molecular or morphological, can be analysed in conjunction with a series of priors which can inform a posterior probability distribution. In the context of a phylogenetic analysis, the posterior distribution means the probabilities of all possible phylogenies (tree topologies, including their branch lengths; note that this differs from parsimony analysis, which infers only the tree topology). This presents the same computational problem as discussed above for maximum parsimony, i.e. the large number

of trees produced by even relatively small datasets. Therefore, the posterior probability distribution is estimated using a sampling method called Markov chain Monte Carlo sampling (MCMC) coupled with a search algorithm (Metropolis-Hastings method), which helps the Markov sampling chains converge towards the maxima of the posterior probability distribution (Ronquist *et al.* 2009). This process involves the Markov chain sampling each topology in the 'landscape' of posterior distribution in a stepwise manner, starting at an arbitrary point on a random tree 'island' in the 'landscape' (point A). A small random move (to point B) on the 'island' is either accepted or rejected according to the ratio of posterior probability between the points A and B. In this way, each Markov chain (there are usually two running simultaneously) explores the 'landscape' of posterior distribution by moving in small increments on or between 'islands' (Ronquist *et al.* 2009).

A problem inherent to this method is that Markov chains can become trapped on suboptimal maxima, and unable to continue exploring the posterior distribution (Ronquist *et al.* 2009). The Metropolis-Hastings algorithm attempts to rectify this by adding additional 'heated' chains in each run. These chains move across the 'landscape' with greater freedom by raising the posterior probability to a power smaller than 1, effectively flattening the 'landscape' of the posterior distribution (Ronquist *et al.* 2009). At regular periods the 'heated' chains offer a positional swap with a random chain in the run. If the 'cold' chain is one of the random choices, it can swap with the 'heated' chain, and continue to explore the 'landscape'. When both the 'cold' chains from the two runs converge on the target distribution, the runs may have reached 'stationarity', producing a good sample of the posterior probability distribution (Ronquist *et al.* 2009).

Using Bayesian inference as an alternative phylogenetic method for morphological datasets was first proposed for extant taxa by Lewis (2001), and later for combined (i.e. molecular and morphological) datasets by Nylander *et al.* (2004). One of the first studies to apply Bayesian inference to a fossil-only dataset of early amniotes recovered a similar tree topology to that of their maximum parsimony analysis (Müller and Reisz 2006). This study used a Markov (Mk) model for their Bayesian analysis (where k = the number of states observed), corrected for acquisition bias (Lewis 2001). Morphological datasets are biased in that they generally include only or predominantly those characters whose character states vary among the sampled taxa in a parsimony-informative way. The acquisition bias correction addresses this problem, by assuming that only variable characters, rather than all characters, are included in the dataset, and this avoids overestimation of evolutionary rates of character state transi-

tions (Lewis 2001). This modification is usually referred to as the Mkv model (where v = variable). The model incorporates the Jukes-Cantor 69 basic substitution model, a time-homogenous time-continuous stationary Markov model in which the probability of transitions between all character states for each character is equal at all points on phylogenetic branch lengths (Lewis 2001, Strimmer and von Haeseler 2009). The Mkv model has been used in several recent fossil-only datasets of early amniotes in non-time calibrated analyses, i.e. where the nodes are based on the number of changes on each of the branch lengths (Tsuji *et al.* 2012, Sobral *et al.* 2015, Bever *et al.* 2015, Modesto *et al.* 2015, Brocklehurst *et al.* 2016).

4.2.2.2 Non-time calibrated Bayesian analysis

In the Mkv model, branch length is a function of the number of changes per character for each branch, and is therefore a structural rather than incidental parameter (Lewis 2001). Branch lengths, however, are not directly proportional to the number of changes per character per branch, since the model includes the occurrence of unobserved state changes, and longer branches may have proportionately fewer character state transitions than shorter ones. Although branch lengths can be implied in parsimony analysis by mapping the changes to character states on the MPTs, Mkv uses branch lengths to calculate the likelihood values that ultimately determine the posterior distribution (Lewis 2001).

The most widely-used historical implementation of this method involves using fossils as constraints for minimum or maximum ages of internal nodes, or node dating (Arcila *et al.* 2014). More recently, fossils have been used as terminal taxa, in conjunction with extant taxa, incorporating absolute age data from the fossil record with customised tree priors and a substitution model, referred to as total evidence or tip dating (Pyron 2011, Ronquist *et al.* 2012, O'Reilly *et al.* 2015). Since the Mkv model can be used as the substitution model in clock methods, I clarify this distinction herein by reference to the non-time calibrated model as Mkv (no ages).

I performed a Bayesian analysis using the Mkv (no ages) model with the new dataset of 286 discreet morphological characters and 60 OTUs. The 'standard' datatype was used for morphological data, and the coding was set at 'variable', i.e. only variable characters being sampled (see above), with rates set to a gamma distribution (alpha=1). Gamma distribution modifies the Mkv substitution model to allow variation in the rates of evolution among characters (Yang 1993). The alpha parameter determines one aspect of the shape of the gamma distribution. *Gephyrostegus* and *Seymouria* were constrained as the out-group taxa. The Mkv (no ages) analysis was performed with 2

runs of 4 chains each (one 'cold', three 'heated'), with temperature set at 0.10. The analysis was run for 50 million generations, sampling every 500th generation, with a burn-in of the first 2,500 sampled trees (25%). The effective sample size (ESS) for the two parameters (Tree Length and shape of gamma distribution) were in excess of 60,000, and the average potential scale reduction factor (PSRF) was < 1.001. The script for this analysis is provided in Appendix 4.

4.2.2.3 Time-calibrated Bayesian analysis

Estimations of the absolute timing of clade divergence in phylogenetic analysis are of great interest to both palaeontologists and neontologists, since they provide key data on the tempo and mode of macroevolutionary processes (dos Reis *et al.* 2012, 2016, Pennell and Harmon 2013). Initial hypotheses on the molecular clock method were proposed over 50 years ago, based on differences in amino acid sequences in mammals correlating with estimated fossil divergence times (Zuckerkandl and Pauling 1962, 1965, Dickerson 1971). Initially, an almost constant rate of evolutionary change ('strict' clock) was assumed, which was later shown to contradict the stochastic rate indicated by the fossil record, although it can apply to closely related species or population data (dos Reis *et al.* 2016).

4.2.2.4 Node dating model

The application of Bayesian statistical methods to phylogenetic analysis led to the development of a 'relaxed' clock model for molecular data, which allowed for variation in the evolutionary rate (Thorne *et al.* 1998, Kishino *et al.* 2001). This model used priors on evolutionary rates, incorporating a birth-death process and fossil age calibration data (Yang and Rannala 2006). Often referred to as node dating, this method requires data from the fossil record to calibrate node age (usually the earliest clade age) and then calculates a prior calibration density beyond the estimated node age, which is used as the prior probability distribution of the node age (Gavryushinka *et al.* 2017). There are several areas where problems can occur with this process:
(i) The methods used to calculate the node age prior distribution may be based on arbitrary criteria. The standard approach is to apply a simple probability distribution (e g. uniform, gamma or exponential), which is rarely informed by biological processes or by the fossil record (Heath *et al.* 2014). The posterior distribution of node age is particularly sensitive to the prior calibration density, regardless of the amount of data, and ad hoc estimates can result in precise but inaccurate posterior divergence dates (dos Reis *et al.* 2016).

(ii) Uncertainties in the taxonomic affinities of fossils and the absolute dating of nodes can lead to inaccurate calibration densities (Ronquist *et al.* 2012, Bromham 2018). This occurs because the affinities of fossil species used to calibrate node age are assigned *a priori*, and not tested during the analysis itself.
(iii) Tree priors, calibration density and phylogeny dating are sequential processes. This implies an independence that can lead to statistical error. There is no efficient method to specify tree priors jointly with calibration distributions, leading to a degree of incoherence in posterior divergence ages (Heath *et al.* 2014, Gavryushinka *et al.* 2017).

4.2.2.5 Total evidence dating model

Total evidence dating, or tip dating, provides the basis for a unified probabilistic model, encompassing fossil age, molecular and morphological data in a single analysis, using all the data simultaneously rather than sequentially (Pyron 2011, Ronquist *et al.* 2012). This model uses absolute dates of individual fossil and extant OTUs as strict priors for the ages of terminals in the phylogeny, thus avoiding the use of calibration densities for node ages and their inherent problems (described above). A relaxed clock model is applied to the molecular data and a tree prior distribution with a substitution model for the morphological data, which is required for both fossil and extant OTUs. This method can also be applied to fossil-only datasets, using the relaxed clock model. However, whilst tip dating does provide a number of advantages over node dating, its early uses were made in conjunction with simple tree priors for the distribution of speciation events over time (e.g. Yule model and birth-death process), none of which model the fossilisation and sampling processes or allow for direct ancestors in the sample (Zhang *et al.* 2015, Gavryushinka *et al.* 2017).

4.2.2.6 Fossilised birth-death (FBD) model

The standard birth-death process assumes that speciation and extinction rates are constant over time, and that no fossils are sampled (Yang and Rannala 1998). Stadler (2010) extended this process to account for sampled fossil lineages, called the fossilised birth-death process (FBD). The FBD process has therefore become central to the application of tip dating methods, by introducing a tree prior specifically designed for divergence time dating of both fossil data and molecular sequences (Heath *et al.* 2014). Heath *et al.* (2014) applied this process (now referred to as the FBD model) where fossils were identified with specific clades *a priori* and fossil branch lengths were only informed by the prior rather than the character data (Zhang *et al.* 2015). The

FBD model can also be used for morphological datasets in the absence of extant tips (i.e. fossil-only), and the relaxed Mkv model can be applied so that the phylogenetic positions of fossils and their branch lengths in units of time can be used as part of the analysis, and therefore inform divergence times. The prior to this model included four parameters that are the only quantities that require prior assumptions:
(i) A constant speciation rate (λ)
(ii) A constant extinction rate (μ)
(iii) A fossil recovery rate (ψ) that follows a Poisson distribution for the probability of fossil production for a given lineage.
(iv) The proportion of sampled extant OTUs to all extant members of the group (ρ)

As for all tip dating methods, the potentially arbitrary nature of choosing and parameterising calibration densities for multiple nodes is eliminated since posterior distribution of nodes ages is controlled entirely by the priors (Heath *et al.* 2014). Extensions to the FBD model have since been introduced, including allowing λ, μ and ψ to change through time (Gavryushinka *et al.* 2014), and modelling the diversified sampling of extant tips, instead of a complete or strictly random sampling of fossil and extant OTUs (Zhang *et al.* 2015).

The FBD process is a unified model, with a non-sequential approach to tree and dating priors, incorporating a fossil sampling process and allowing for the possibility of sampled direct ancestors (Gavryushinka *et al.* 2017). It is therefore an appropriate probabilistic method for exploring fossil phylogenies. Several recent studies have used the FBD model: Puttick *et al.* (2016) for comparing node dates with molecular data in placental mammals, Wright (2017) for a fossil-only dataset of Paleozoic crinoids, Simões *et al.* (2018) for Lepidosauria; Varela *et al.* (2018) for sloths.

A second Bayesian phylogenetic analysis on the new amniote dataset was performed using MrBayes v3.2.6 (Ronquist *et al.* 2012), with the FBD prior, using a relaxed clock model (rates=gamma, coding=variable, clockvarpr=igr). The ages of all OTUs were specified using a uniform distribution between the minimum and maximum stratigraphic boundaries according to published data, unless more specific age data was available (see Appendix 5 for details). Options specifying proportional sampling of extant taxa (sampleprob) were omitted since the analysis is limited to fossil data. The setting for the tree age prior, the age of the most recent common ancestor of the tree, was set to offsetexponential (x,y), where x is the oldest fossil in the taxon list (*Hylonomus lyelli* 318.1 Ma), and y the mean density of the cumulative density function between the oldest taxon and earliest putative date of the appearance of a common tree ancestor (in this case the earliest Carboniferous, 358.9 Ma). Two runs, each consisting

of 4 chains at a temperature of 0.09, were performed for 50 million generations, and sampled every 500th generation, with a burn-in of the first 2,500 sampled trees (25%). The ESS was greater than 200 for all tested parameters and an average PSRF was < 1.001 on all parameters. The script for this analysis is provided in Appendix 4.

4.3 Results

4.3.1 Maximum parsimony

The phylogenetic analysis of 60 taxa and 286 characters resulted in 16 MPT's, with a length of 1380 (RI=0.5733, CI=0.2553 rescaled CI=0.1463). A strict consensus of the 16 MPT's (Fig.2) shows two substantive differences in topology when compared to the traditional phylogeny of early amniotes (Fig.1). In particular (i) Parareptilia are recovered as a sister taxon to neodiapsids (Clade D), and Captorhinidae form a monophyletic group at the base of Sauropsida, (ii) Varanopidae form a monophyletic group with *Orovenator mayorum*, within the total group reptiles (Sauropsida). Each of these new hypotheses is considered under 'Discussion' below.

Synapsida are recovered in the traditional position as a monophyletic sister group to Sauropsida at the base of the crown-group amniotes. Caseasaurs are the early diverging synapsid group, in accordance with previous studies (Reisz and Fröbisch 2014, Brocklehurst *et al.* 2016, Spindler *et al.* 2018). There is, however, some uncertainty in the resolution of the group, with *Oedaleops* forming a polytomy with eothyridids and caseids. Brocklehurst *et al.* (2016) recovered *Oedaleops* as the most basal eothyridid, and noted eothyridids in general were poorly supported (relative fit difference=20).

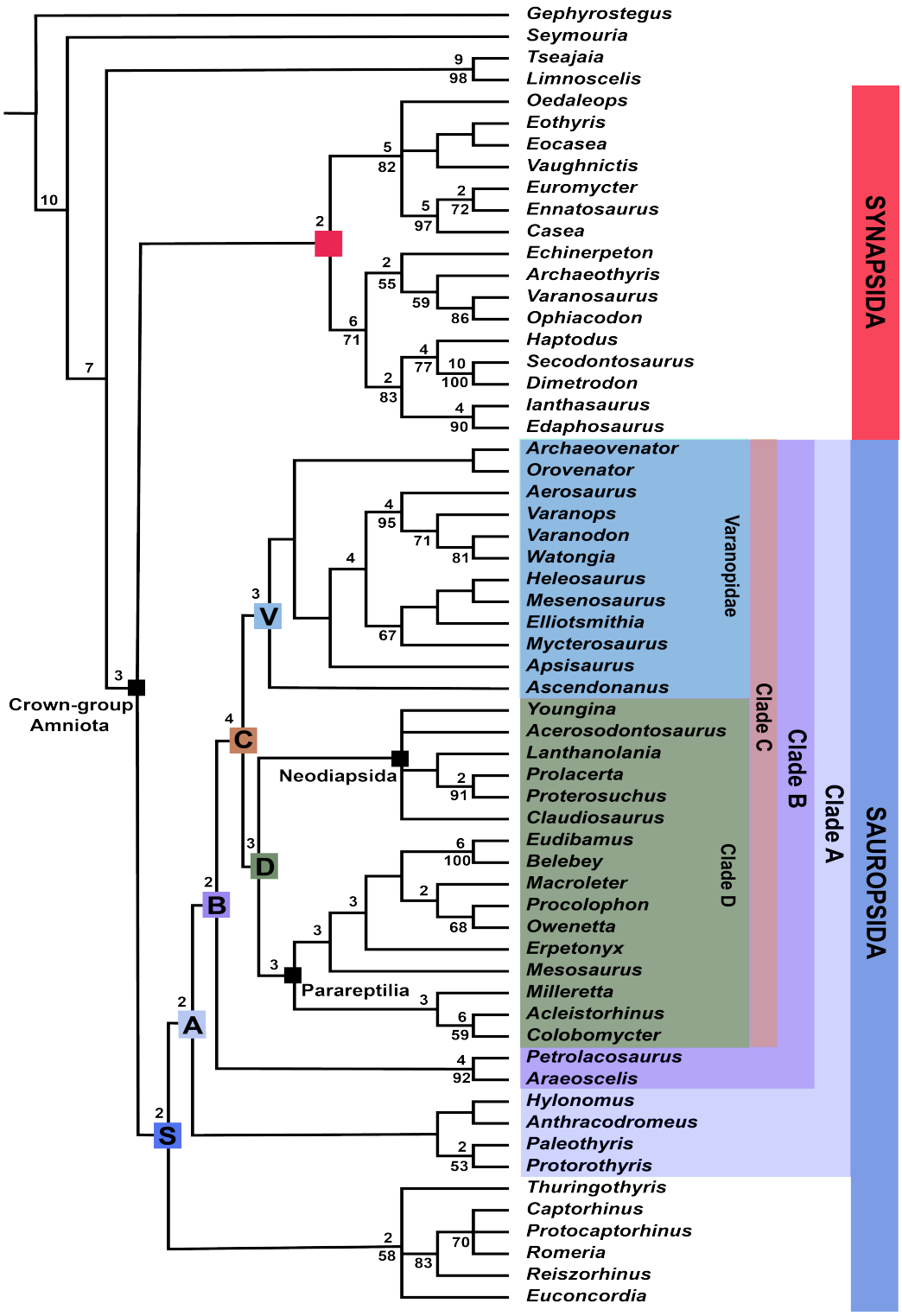


Figure 2: Strict consensus of 16 MPT's recovered in the maximum parsimony analysis. Figures above the nodes are Bremer support indices; figures below the node are bootstrap support indices. Bremer support below 2 or bootstrap below 50 is omitted

The position of *Eocasea* within eothyridids is unexpected, since this taxon has been considered by previous studies as the most basal caseid (Reisz and Fröbisch 2014, Brocklehurst *et al.* 2016). All other caseids form a monophyletic group with strong bootstrap and Bremer support. Bootstrap support is also strong for the monophyly of Caseasauria. However, I find support levels for caseasaurs within a monophyletic Synapsida are poor (bootstrap below 50, Bremer=2). All remaining synapsids (ophiacodontids + edaphosaurids + sphenacodontians) form a well-supported group, with all taxa occupying traditional positions within it.

Thuringothyris and *Euconcordia* are recovered in a polytomy with other (monophyletic) captorhinids. This is consistent with previous studies, which consider these taxa to be the most basal members of the clade (Müller and Reisz 2006, Sumida *et al.* 2010, Reisz *et al.* 2011, Modesto *et al.* 2018). Support levels for the monophyly of the group are low. All taxa traditionally described as 'protorothyridids' are recovered as a monophyletic sister group to Clade B. Many analyses of early reptiles include only one 'protorothyridid' (e.g. Laurin and Reisz 1995, deBraga and Rieppel 1997) so cannot provide information on the monophyly of the group. Müller and Reisz (2006) was the first study to investigate the interrelationships of 'protorothyridids' with their close relatives captorhinids and araeoscelidians. This study found them to be a paraphyletic group stemward to the earliest diapsids. The 'protorothyridid' clade recovered in my parsimony analysis, however, is poorly supported (bootstrap support below 50, Bremer support below 2). The close relationship between basal captorhinids and 'protorothyridids' often results in some 'protorothyridids' being recovered as captorhinids (Müller and Reisz 2006, MacDougall *et al.* 2018). In common with all previous studies, araeoscelidian diapsids are recovered as a monophyletic group, and sister to Clade C.

In respect to the internal grouping of varanopids, I find *Ascendonanus* the sister taxon of all other varanopids, in concurrence with Spindler *et al.* (2018). *Orovenator* is the sister taxon to *Archaeovenator* in an early branching sub-group. *Mycterosaurus* is recovered as the basal member of the mycterosaurines (contra Spindler *et al.* 2018), supporting the traditional subdivision of varanodontines and mycterosaurines.

Milleretta and lanthanosuchoids form a monophyletic sister group to all other parareptiles, which consists of *Mesosaurus* and *Erpetonyx* basal to a traditional array of bolosaurids, nycteroleterids and procolophonoids. Apart from the unexpected recovery of a monophyletic *Milleretta* + lanthanosuchoids, the positions of all other parareptiles are along traditional lines (MacDougall *et al.* 2018). The position of *Mesosaurus* in this and the Bayesian analyses shall be expanded in 'Discussion' below. Support levels for many groups are low (bootstrap below 50) to moderate (Bremer=3),

with only derived bolosaurids finding strong support (Fig. 2). Low support indices are common in analyses of early amniotes, particularly at nodes that designate more inclusive clades (e.g. Benson 2012, Ezcurra *et al.* 2014, Modesto *et al.* 2015, Brocklehurst *et al.* 2016, Laurin and Piñeiro 2017, Spindler *et al.* 2018).

4.3.2 Bayesian inference with Mkv (no ages) model

4.3.2.1 Mkv (no ages) with all posterior probabilities

I have opted to use the maximum clade credibility (MCC) tree to summarise the results of the Bayesian inference analysis. The MCC is the single tree in the posterior sample with the maximum sum of the posterior clade probabilities across all its constituent bifurcations (Heled and Bouckarert 2013). The posterior probability represents the confidence estimate of the evolutionary relationships reflected in the tree topology based on the data, the prior distribution of the model parameters, and the substitution model (Yang and Rannala 2005, Vandamme 2009).

The MCC tree resulting from the Mkv (no ages) analysis closely resembles the topology of the parsimony analysis (Fig. 3). The principle differences when compared to traditional phylogenies (i.e. varanopids within Sauropsida and parareptiles as a sister taxon to diapsids) are maintained within Clades A-D.

Within-group topologies are largely consistent with current convention, (i) caseasaurs are resolved into two traditional sub-clade: eothyridids and caseids, although *Eocasea* is recovered as an eothyridid as in the parsimony analysis, (ii) only the derived position of *Romeria* differs from the traditional resolution of captorhinids, (iii) the position and interrelationships of 'protorothyridids' and araeoscelidians are in accord with traditional views (e.g. Müller and Reisz 2006), with 'protorothyridids' forming a paraphyletic group, (iv) *Mesosaurus* is recovered within Parareptilia as the most basal taxon, and *Erpetonyx* as a basal bolosaurid.

The resolution of varanopids in respect to the recovery of the derived sub-groups of mycterosaurines and varanodontines is unusual. Mycterosaurines form a paraphyletic grade with respect to varanodontines, which retain a more derived position. This topology is inconsistent with the younger stratigraphic ranges of many mycterosaurines. *Ascendonanus* is recovered in a more derived position, with the group comprised of *Orovenator* + *Archaeovenator* + *Apsisaurus* now the basal-most varanopids.

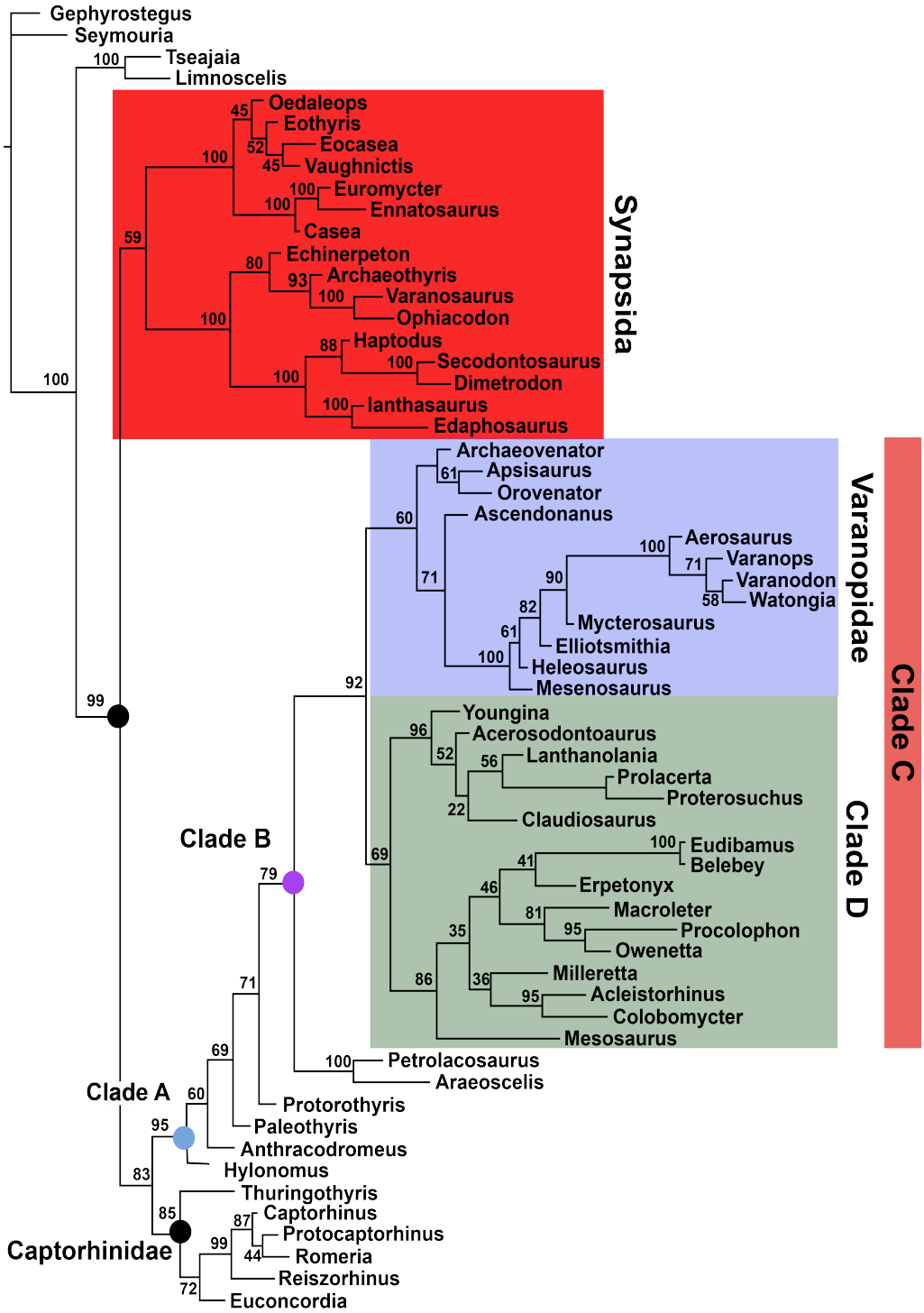


Figure 3: Maximum clade credibility tree recovered from Bayesian analysis using the Mkv (no ages) model. Figures adjacent to nodes are the posterior probability value of the node

Posterior probability values supporting the main clades are good (i.e. Sauropsida=0.83, Captorhinidae= 0.85, Clade A=0.95, Clade B=0.79, Clade C=0.92). The posterior probability for the node supporting synapsid monophyly is low (=0.59), although support for a monophyletic Caseasauria is high (=1), as is that for all other synapsids (=1).

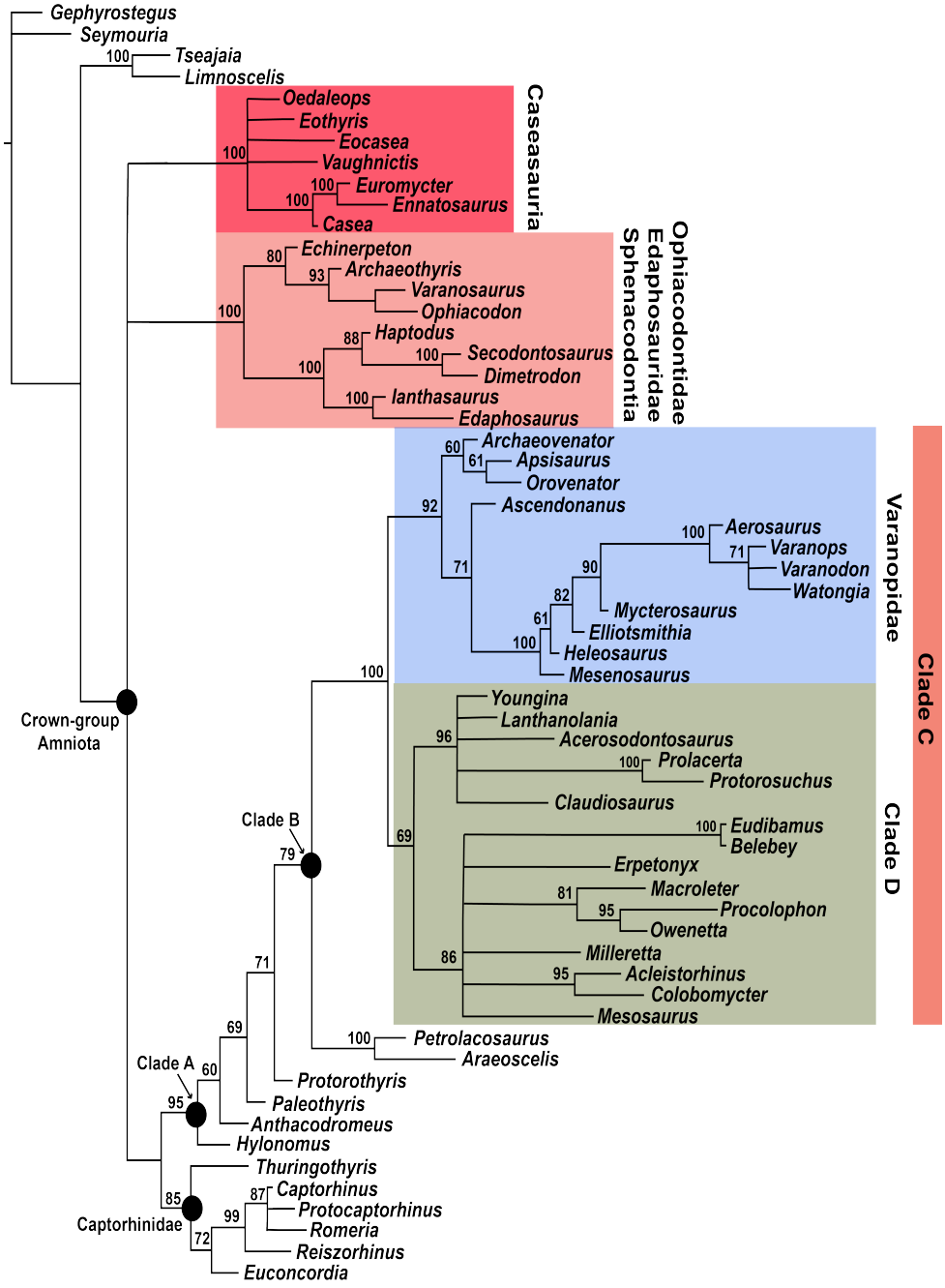


Figure 4: Maximum clade credibility tree recovered from Bayesian analysis using the Mkv (no ages) model only, with all nodes with a posterior probability < 60 have been collapsed

4.3.2.2 Mkv (no ages) with posterior probabilities ≥0.60

Since several nodes in the MCC tree reflect poor support, I also show the MCC tree where nodes are collapsed unless supported by a posterior probability ≥0.60 (Fig. 4). Although there is relative little change to the topology, with Clades A-D maintained, some within-group resolution is lost, i.e. neodiapsids and parareptiles. The monophyly of Synapsida is lost, with caseasaurs + all other synapsids + sauropsids forming a polytomy at the base of crown-group amniotes.

4.3.3 Bayesian inference with FBD model

4.3.3.1 FBD model with all posterior probabilities

The results of the Bayesian inference analysis with the FBD model (using the FBD process as the tree prior, strict age prior assigned to all dated tips and the relaxed clock model with the JC69 substitution model) are shown using the MCC tree (Fig. 5). The tree topology is very similar to that recovered by maximum parsimony analysis, with Clades A (all sauropsids excluding captorhinids), C (varanopids + neodiapsids + parareptiles) and D (neodiapsids + parareptiles) maintained and with synapsids as a monophyletic sister group to sauropsids. Araeoscelidians form a monophyletic group with *Paleothyris* and *Protorothyris*, although this is very poorly supported (see below).

The principle differences between the results of the FBD model and maximum parsimony analyses are the within-group positions of individual taxa. Caseasaurs are a sister taxon to all other early synapsids, as in the parsimony topology, although *Eocasea* and *Vaughnictis* are recovered as successively basal to both eothyridids and caseids. The phylogeny of captorhinids is in close agreement with earlier studies (Müller and Reisz 2005, Müller *et al.* 2006, Sumida *et al.* 2010). *Hylonomus* is recovered as the basal-most member of Clade A. The monophyly of *Paleothyris* + *Protorothyris* + araeoscelidians is inconsistent with both the MP results and the conventional view of araeoscelidians as basal diapsids. *Mesosaurus* and *Erpetonyx* form a group basal to all other members in a monophyletic Parareptilia. In Varanopidae, the position of *Apsisaurus*, which is now included in a group with *Orovenator* and *Archaeovenator*, is the only change from the parsimony result.

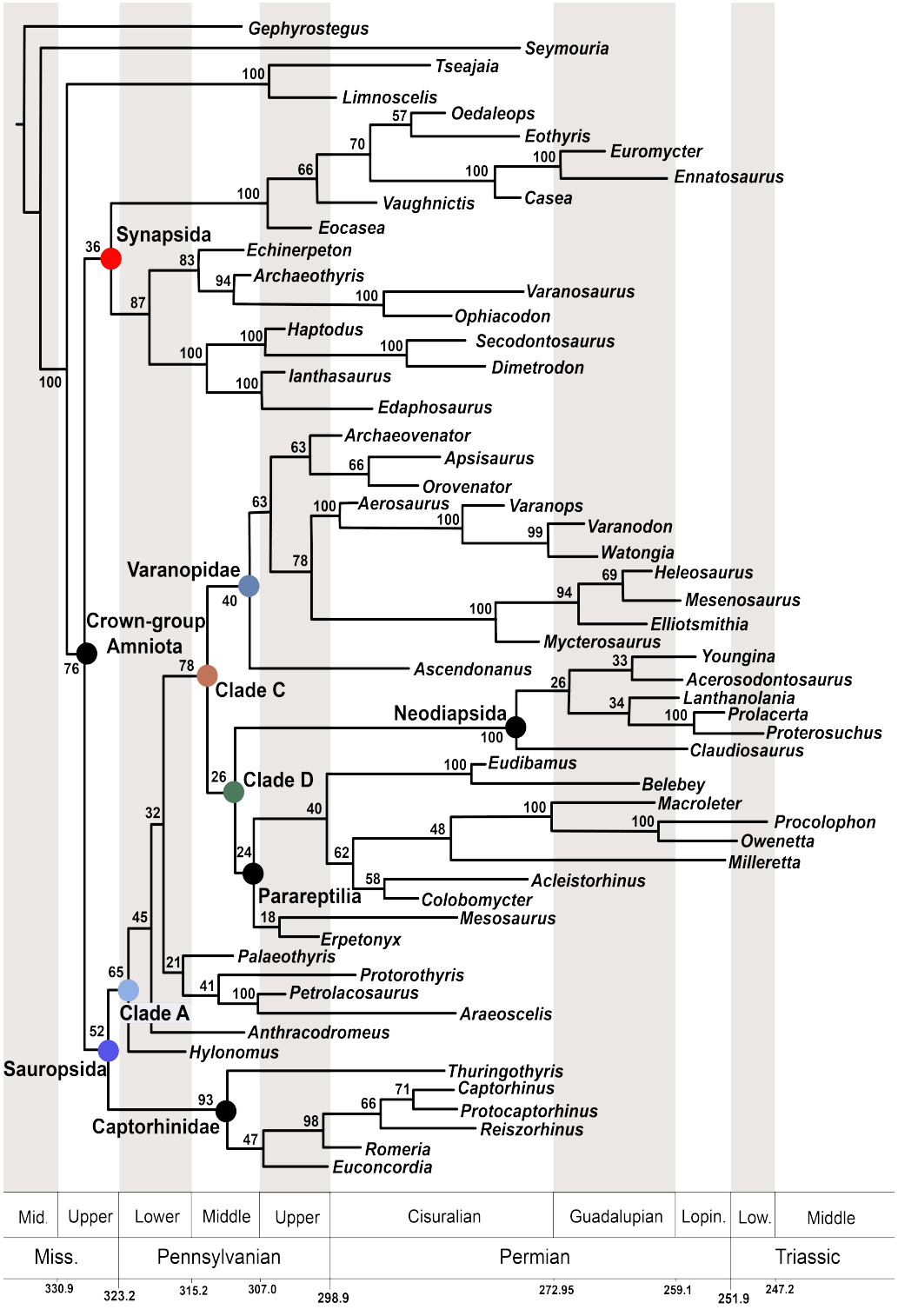


Figure 5: Maximum clade credibility tree recovered from Bayesian analysis with FDB model. Figures adjacent to nodes are posterior probability values. Abbreviations: Lopin. =Lopingian, Low. =Lower, Mid..=Middle, Miss.=Mississippian

Some of the key nodes in the maximum clade credibility tree have low posterior probabilities (Fig. 5), and the distribution of posterior probabilities is essentially consistent with that of support indices derived from the maximum parsimony analysis. The inclusion of *Ascendonanus* within Varanopidae has poor support (= 0.40), as do nodes at the base of parareptiles. In contrast, there is good support (= 0.90 to 1) for several monophyletic groups, i.e. ophiacodontids + edaphosaurids + sphenacodontians, varanodontines, mycterosaurines, neodiapsids, captorhinids, bolosaurids (excluding *Erpetonyx*), procolophonoids and caseasaurs. Support for the crown-group Amniota is only moderate (=0.76).

4.3.3.2 FBD model with posterior probabilities ≥0.60

As with the Mkv (no ages) model discussed above, I show the MCC tree where nodes are collapsed unless supported by a posterior probability ≥0.60 (Fig. 6).

Varanopidae, Neodiapsida and Parareptilia form a polytomy, with *Ascendonanus* and several subclades that were otherwise found within Parareptilia participating in the base of this polytomy. Caseasaurs, other synapsids, captorhinids and Clade A form a polytomy at the base of crown-group amniotes. Of the more inclusive groups, only Clade A (all sauropsids excluding captorhinids) and Clade C (varanopids + neodiapsids + parareptiles) are maintained.

4.3.4 Clade divergence and ghost lineages

Bayesian inference with tip dating provides estimates of the absolute branch length, and therefore node dates, throughout the tree (Fig. 7). Each node is associated with a Highest Posterior Density interval (HPD). This gives the shortest possible period of fixed probability (i.e. 95%) for the absolute date of the node of interest.

The results suggest the basal divergence of crown amniotes (mammal/bird split) occurred between 337-322 Ma (Middle Mississippian to Lower Pennsylvanian, median age 328.47 Ma). This is consistent with results from molecular clock analyses of deuterostomes, which gives a mean divergence time for mammals and birds of 326 Ma, with a 95% HPD between 354 -311 Ma (Blair and Hedges 2005). Currently, the oldest bird-lineage fossil, *Hylonomus lyelli*, has an estimated age of 319-318 Ma (Benton *et al.* 2015), and the earliest undisputed mammal line fossil, *Archaeothyris florensis* (Reisz 1972) from Florence, Nova Scotia, is from the Westphalian D, approximately 315.2 -307 Ma (= Moscovian). This would give an estimated ghost lineage for crown-group amniotes of 10 million years.

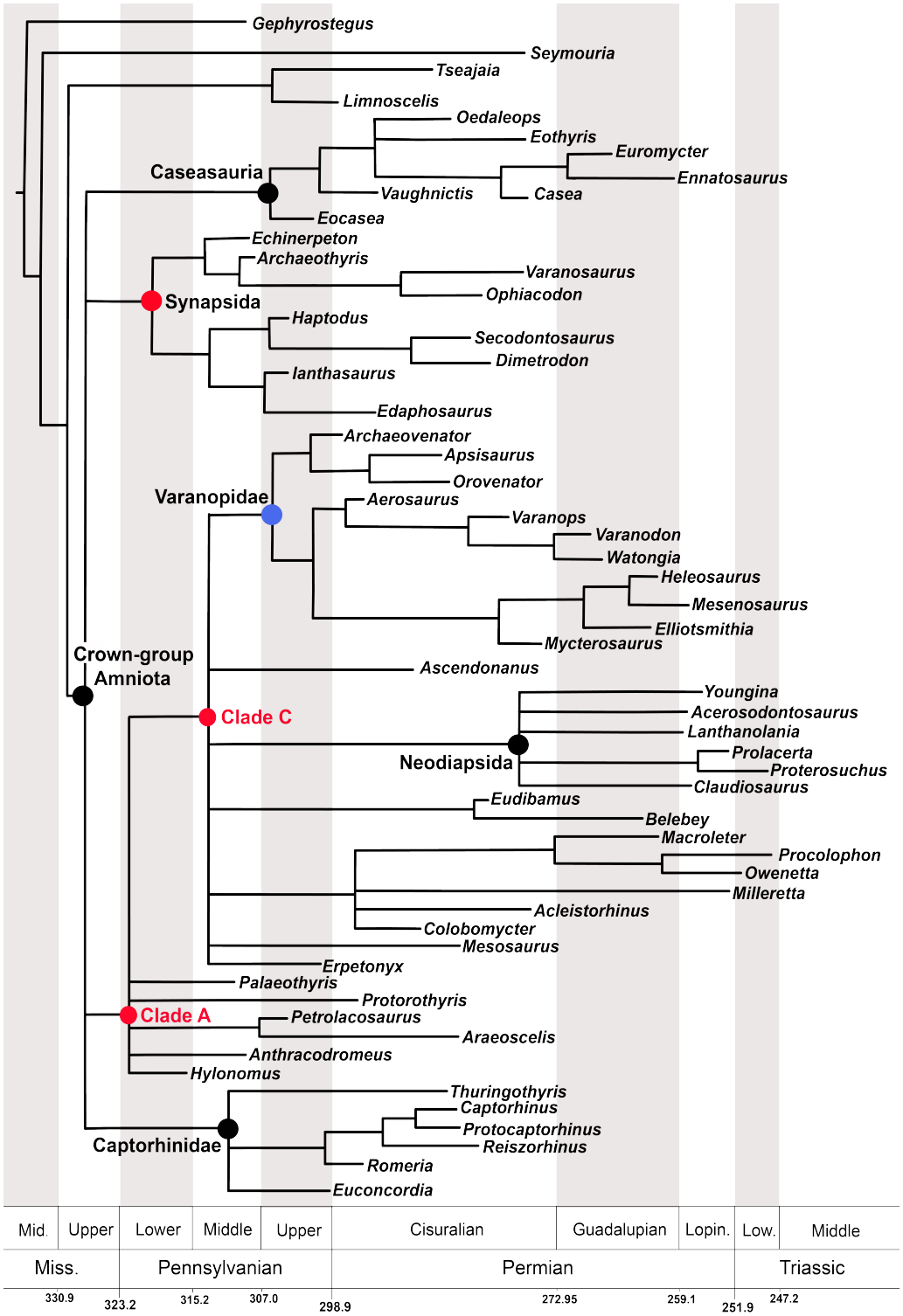


Figure 6: Maximum clade credibility tree recovered from Bayesian analysis with FBD model, nodes are collapsed unless supported by a posterior probability ≥60. Abbreviations as in Fig.5

The median divergence time of captorhinids from all other sauropsids is estimated at 325.72 Ma, suggesting the basal split in early sauropsids took place within 3 million years after the divergence of crown amniotes, implying a ghost-lineage of over 20 million years from the oldest known captorhinid (*Euconcordia*, Müller and Reisz 2006, Reisz *et al.* 2016).

The oldest parareptile currently known is the bolosaurid *Erpetonyx* from the latest Pennsylvanian (Gzhelian 303.7-298.9) of Prince Edward Island, Canada (Modesto *et al.* 2015). As noted above, the divergence age estimated by the FBD model analysis for the captorhinid/'protorothyridid' split is 325.72 Ma. In the traditional hypothesis of early sauropsid phylogeny, this would require a ghost lineage for parareptiles of approx. 22 million years., i.e. earlier than the captorhinid/'protorothyridid' divergence. Based on my new hypothesis the estimated median divergence of neodiapsids and parareptiles is 310.93 Ma, reducing the parareptilian ghost lineage to approximately 7 million years.

4.3.5 Examining the novel groupings and Templeton tests

The maximum parsimony and Bayesian inference analyses of my new early amniote dataset have resulted in a series of fundamentally similar tree topologies that recover novel groupings. These groupings differ substantially from the traditional view of early amniote phylogeny in several respects. Below I discuss the character evidence for these new groups and compare them to character evidence from previous hypotheses. I also perform a series of constraint analyses and Templeton tests on the statistical significance of the differences in tree length between the optimal trees (which recover the new groupings) and sub-optimal trees constrained to reflect the previous hypotheses supporting the traditional tree topology (Fig. 1). Additionally, in respect to the weak support found in all analyses of a monophyletic Synapsida, I also apply constraint analyses and Templeton tests to the position of caseasaurs.

4.3.5.1 Varanopidae as stem-group reptiles

Varanopids are a group of faunivorous predators, ranging in size from small (e.g. estimated 0.4 m total length for *Ascendonanus*, Spindler *et al.* 2018) to large body sizes (e.g. estimated 2 m total length for *Watongia*, Laurin and Reisz 2004), and whose fossil records extends from the late Carboniferous (Reisz and Dilkes 2003) to the late middle Permian (Botha-Brink and Modesto 2009; also see stratigraphic data and range charts in Day *et al.* 2015), an unusually long stratigraphic range among monophyletic groups of Palaeozoic amniotes (Dilkes and Reisz 1996).

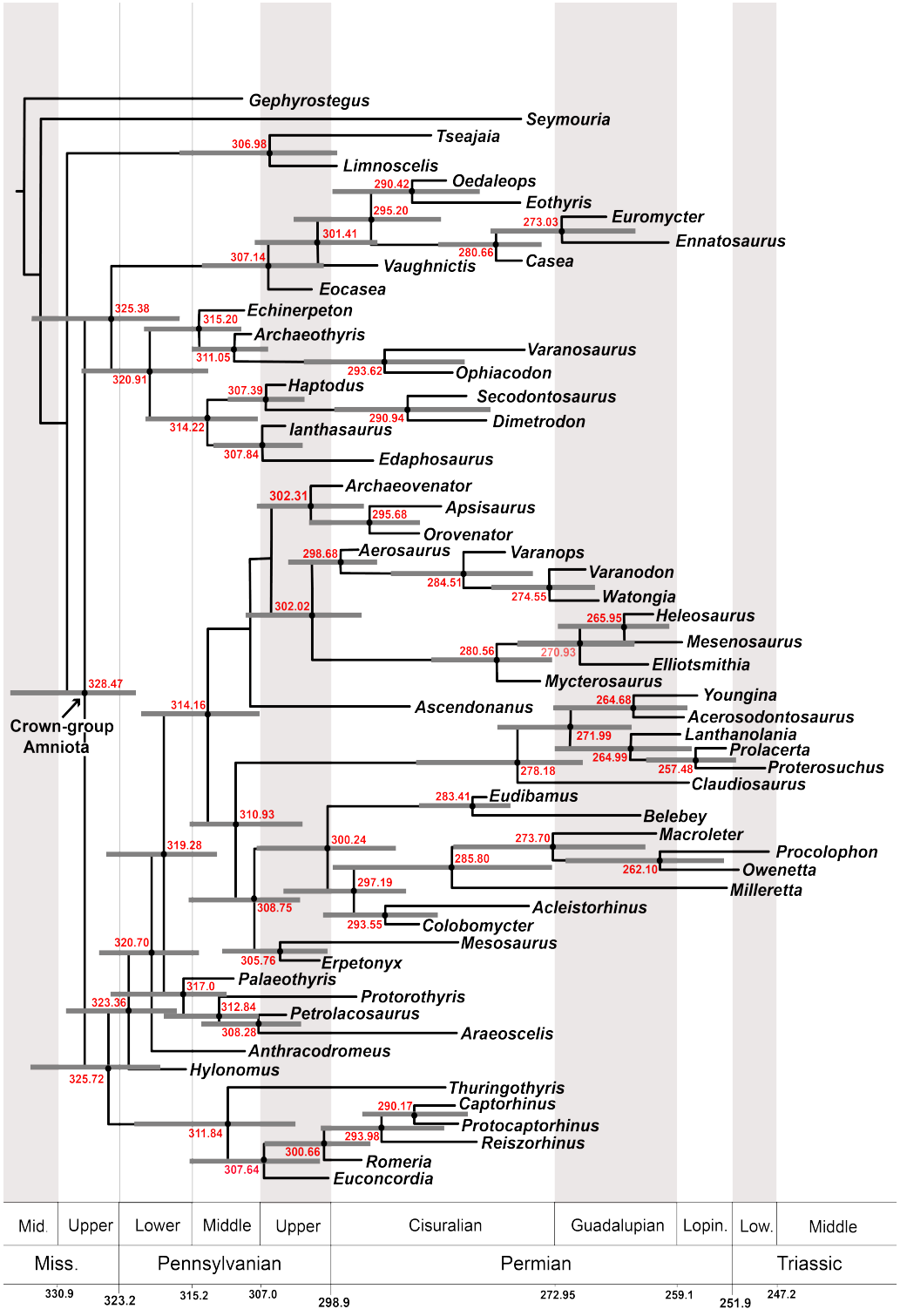


Figure 7: Maximum credibility clade tree recovered from Bayesian analysis with FDB model. Grey horizontal bars represent 95% HPD interval of node age. Red figures represent median node ages. Abbreviations as in Fig. 5

First recognised as the family 'Varanopsidae' by Romer and Price (1940), the position of varanopids as early synapsids has never been questioned, although several species have been reassigned to Varanopidae from reptilian clades, and the similarities between varanopids and early diapsids have been frequently discussed (Reisz and Berman 2001, Reisz and Modesto 2007, Reisz *et al.* 2010; Ford and Benson 2018).

Studies on the interrelationships within Varanopidae have resolved three subdivisions: (i) the paraphyletic basal members of the group (e.g. *Archaeovenator*, *Ascendonanus*, *Apsisaurus* and *Pyozia*); (ii) the monophyletic sub-family Mycterosaurinae (Reisz and Berman 2001) including *Mycterosaurus* (North America), *Mesenosaurus* (Russia), *Elliotsmithia* and *Heleosaurus* (South Africa); (iii) the monophyletic sub-family Varanodontinae (Reisz and Berman 2001), comprising the North American taxa *Aerosaurus*, *Varanodon*, *Varanops*, *Watongia* and the European taxon *Tambacarnifex*. Recently, Spindler *et al.* (2018) presented a phylogenetic analysis focused on varanopids and recovered *Mycterosaurus* as more closely related to varanodontines.

The possibility that varanopids are non-synapsid amniotes has rarely been tested. Even in generalised amniote phylogenies (e.g. Laurin and Reisz 1995, deBraga and Rieppel 1997, Rieppel and Reisz 1999, Hill 2005, Laurin and Piñeiro 2017) synapsids have been included as a single taxonomic unit or varanopids have been omitted from analysis. Two recent studies have included varanopid genera along with a wide range of other amniotes. Reisz *et al.* (2010) analysed a matrix of 14 eureptiles, seven varanopids, and four other synapsids using 113 characters to examine the affinities of *Apsisaurus witteri*, which was consequently recovered as a varanopid. This analysis recovered a monophyletic Varanopidae within Synapsida, supported by 15 unambiguous synapomorphies, which are discussed in detail below. MacDougall *et al.* (2018) included two varanopids in a dataset of seven other synapsids, eight eureptiles and 28 parareptiles with 178 characters. This main focus of this study was the phylogenetic position of *Mesosaurus* among early amniotes, but a noteworthy aspect of the result was the recovery of both varanopids (*Mycterosaurus* and *Archaeovenator*) outside the main body of synapsid taxa, in a polytomy with sauropsids.

In chapter 2, I presented a phylogenetic analysis of *Orovenator* based on the dataset of Reisz *et al.* (2010) and scored *Orovenator* based on the re-examination of this taxon using high resolution μCT data. This was a preliminary analysis, with several novel anatomical observations missing from the character list, pending a more broad based analysis of early amniotes, including *Orovenator*. The current analysis meets this criterion, and provides support for the hypothesis, originally posited in chapter 2, that varanopids, including *Orovenator*, are a group of early reptiles closely related

to diapsids. This hypothesis clearly has implication for our current understanding of synapsid evolution during the Permian, and in particular the 'pelycosaur'/therapsid transition. This shall be considered in the discussion of the present chapter.

To fully evaluate the morphological evidence supporting the new hypothesis of varanopid phylogeny, I examine below the synapomorphies that have been highlighted in previous analyses supporting the inclusion of varanopids within Synapsida, and varanopids as a monophyletic group within Synapsida. I also list the synapomorphies supporting varanopids as members of the hierarchical clades within Sauropsida, resulting from the analysis of my new dataset. For each synapomorphy in sections 1 and 2, I have provided data on the previous study for which the character number is given (prefixed with 'c.') and the corresponding character number in the present study is also provided (prefixed with 'ch.'). In sections 3-7, the character number in the present study is given, followed by the optimisation at the node. These sections are presented under the following sub-headings:

1. Similarities of synapsids shared by varanopids (from previous studies)
2. Synapomorphies of varanopids (from Reisz *et al.* 2010)
3. Synapomorphies of sauropsids (from this study)
4. Synapomorphies of Clade A (from this study)
5. Synapomorphies of Clade B (from this study)
6. Synapomorphies of Clade C (from this study)
7. Synapomorphies of varanopids + *Orovenator* (from this study)

1. **Similarities of synapsids shared by varanopids** (from previous studies).

a) Lateral lappet of frontal present: deBraga and Rieppel (1997 c.24). This character state has a broad distribution amongst early synapsids, including eothyridids, but excluding *Ennatosaurus* and *Varanosaurus*. It is absent in varanopids, diapsids and parareptiles, apart from lanthanosuchoids, *Claudiosaurus* and *Romeria*. In stem-amniotes, the frontal does not contribute to the orbital margin. Like deBraga and Rieppel suggested, this is a synapsid synapomorphy, and this is also the case according to my optimisation (Appendix 1), but it is absent in all varanopids and therefore doesn't provide evidence for synapsid affinities of Varanopidae (ch.62).

b) Elongation of posterior process of postorbital, contacts supratemporal: deBraga and Rieppel (1997 c.32). A long posterior process of the postorbital that contacts the supratemporal is found in all caseasaurs, and in varanopids where the postorbital is known, apart from *Mesenosaurus*. It is also present in *Acleistorhinus*, *Macroleter* and procolophonoids, although absent in other sauropsids and synapsids (e.g. *Varanosaurus*, *Haptodus*, *Edaphosaurus* and *Secodontosaurus*), apart from *Dimetrodon* and

Ophiacodon. It therefore provides support for a caseasaur/varanopid relationship, and potentially for varanopids as synapsids. See Appendix 1 for further details. (ch.66/67).

c) Angle of occiput at least 45° from vertical: deBraga and Rieppel (1997 c.58) (synapsid synapomorphy). The anterodorsal inclination of the occipital margin in varanopids varies from strongly inclined in varanodontines (i.e. $> 60°$), to subvertical in *Archaeovenator* and *Mycterosaurus*. *Ascendonanus*, *Elliotsmithia*, *Mesenosaurus* and *Heleosaurus* share an inclination of the occiput of between 10 and 55°, and this range of inclination is also present in caseasaurs and ophiacodontids. In sphenacodontians and edaphosaurids the occipital margin is subvertical. All sauropsids have subvertical occiputs, except the 'protorothyridid' *Paleothyris* and the archosauromorph *Proterosuchus*. This character state is therefore somewhat ambiguous among synapsids (ch.152).

d) Small posttemporal fenestra: deBraga and Rieppel (1997 c.59) proposed that a small posttemporal fenestra was present in all synapsids. The size of the posttemporal fenestra is dependent upon a number of morphologies of the occipital area, i.e. tabular, squamosal, opisthotic and supraoccipital, which are the subject of several independent characters in the present study. In sauropsids, the morphology of the tabular (or its absence as in most captorhinids, derived neodiapsids and some parareptiles) determines the size of the posttemporal fenestra, which is large when compared to synapsids and most varanopids. In the basal varanopid *Archaeovenator*, the tabular is a small bone, although the size of the posttemporal fenestra cannot be determined. The posttemporal fenestra in varanopids where the occiput is known is small. See Appendix 1 characters 87, 99, 101 and 110.

e) Suborbital fenestra absent: deBraga and Rieppel (1997 c.74). In synapsids and 'protorothyridids' the suborbital fenestra is absent. In varanopids, apart for *Mesenosaurus*, the palate is either not observable or its morphology is uncertain. Refer to chapter 2 - character states that are incongruent with the hypothesis that varanopids are sauropsids - for detailed comments on this character state (ch.147).

f) Keeled ventral edge of angular: deBraga and Rieppel (1997 c.90). A weakly keeled posteroventral border of the angular is plesiomorphic for amniotes, and can be found in stem-amniotes, caseasaurs, some captorhinids, parareptiles, araeoscelidians, and basal varanopids, including *Orovenator*. In mycterosaurines, varanodontines and neodiapsids the angular is rounded posteroventrally. Only more derived synapsids possess an angular with a sheet-like keel (ophiacodontids, edaphosaurids and *Haptodus*) or a reflected lamina (sphenacodontids). This does not provide evidence for synapsid affinities of Varanopidae, since a keeled ventral edge of the angular is a plesiomor-

phic feature of basal varanopids and its absence is derived for mycterosaurines and varanodontines (ch. 183).

g) Maxilla is separated from the quadratojugal: Laurin and Reisz (1995 c.22). Contact between the maxilla and quadratojugal is a derived state in amniotes. Among synapsids it is only present in caseasaurs. It is also present in several derived parareptiles, varanodontines and some mycterosaurines (*Mycterosaurus* and *Elliotsmithia*) but absent in others (*Mesenosaurus* and *Heleosaurus*). It is absent in all basal varanopids, including *Orovenator*, and all diapsids, captorhinids, some parareptiles and 'protorothyridids'. The presence of this character state is therefore independently acquired in caseasaurs, derived varanopids and some parareptiles, and is not supportive of the synapsid affinities of Varanopidae (ch.74/75).

h) Caniniform maxillary teeth: Laurin and Reisz (1995 c.25). The presence of caniniform teeth is plesiomorphic for amniotes, and can be found in eothyridids, all synapsids (with the exception of *Edaphosaurus*), all captorhinids (with the exception of *Thuringothyris*), araeoscelidians, mycterosaurines and varanodontines. The absence of caniniform teeth (the derived condition) is present in the basal varanopids *Archaeovenator* and *Orovenator*, all neodiapsids and basal parareptiles. I find that the derived condition is a synapomorphy of parareptiles + neodiapsids (Clade D in the present study), and does not, therefore, support the synapsid affinities of Varanopidae (ch.30).

i) Lower temporal fenestra: Laurin and Reisz (1995 c.30). The 'lower' temporal fenestra is present in all synapsids, diapsids (with the exception of *Araeoscelis*) and many parareptiles. Its presence is therefore a derived feature of both synapsids and Clade B of the present study. The presence of an 'upper' temporal fenestra is unique to *Orovenator* and diapsids. However, temporal fenestrae are clearly highly homoplastic among early amniotes, and I have proposed an alternative method of characterisation in chapter 3 of this thesis. See chapter 2 - character states that are incongruent with the hypothesis that varanopids are sauropsids - for further discussion. (ch.72/81/82).

j) Paroccipital process contacts tabular: Laurin and Reisz (1995 c.57). The paroccipital process of the opisthotic contacts the tabular in stem-amniotes (e.g. *Seymouria* and *Limnoscelis*), and in all synapsids and varanopids where the occipital region is adequately known. This feature is also present in the araeoscelians diapsid *Araeoscelis*. It is absent in the neodiapsids *Youngina* and *Prolacerta*, and the parareptile *Acleistorhinus*. Its presence is therefore plesiomorphic for amniotes and its absence (the derived condition) is found only in Clade D of the present study. It does not, therefore, provide evidence of synapsid affinities of Varanopidae. Instead it suggests affinities between parareptiles and neodiapsids, although since it cannot be confidently scored in many

amniotes this character may be ambiguous (ch.110).

k) Narrow neural arches on trunk: Laurin and Reisz (1995 c.86). Swollen neural arches are present in stem-amniotes, captorhinids and parareptiles, apart from *Milleretta* and *Erpetonyx*. Most synapsids, 'protorothyridids', neodiapsids and basal varanopids have narrow neural arches. Some taxa, i.e. sphenacodontians, *Ianthasaurus*, araeoscelidians, archosauromorphs and *Erpetonyx* have narrow neural arches with excavations on the lateral surface. Therefore the presence of narrow neural arches could be either a synapomorphy of varanopids with Synapsida or within Sauropsida, as in my optimisation (Appendix 1) (ch. 216).

l) Two coronoids on each ramus of mandible: Reisz (1986, p.7). Two coronoids on the mandibular ramus is plesiomorphic for amniotes, and is found in the diadectomorphs *Limnoscelis* and *Tseajaia*, and in all synapsids. Two coronoids are also present in *Hylonomus*, *Araeoscelis* and *Varanops*, the only varanopid where both coronoids have been identified. A single coronoid (the derived condition) is present in sauropsids, including the varanopids *Archaeovenator*, *Orovenator* and *Mesenosaurus*. Consequently the derived condition supports the sauropsid affinities of Varanopidae, rather than synapsid affinities, with the independent acquisition of two coronoids in *Varanops*. See Appendix 1 for further discussion, and chapter 2 - character states that are incongruent with the hypothesis that varanopids are sauropsids (ch.181).

m) Tabular is a large element of occiput: Reisz (1986, p.7). Synapsids are often considered as possessing large tabulars. This is true of eothyridids and ophiacodontids (very broad tabulars), edaphosaurids and sphenacodontians (deep and broad 'L' shaped tabulars). Basal varanopids, such as *Archaeovenator* and *Ascendonanus* have quite small, narrow tabulars. They remain narrow in other varanopids, but are elongate dorsoventrally. Tabulars in sauropsids, where present, are small, narrow bones, except in *Araeoscelis* and bolosaurids where, like derived varanopids, they are dorsoventrally elongate. Consequently, I consider this character to be a poor observation of primary homology, since it does not account for the wide variation in tabular morphology (ch.99).

n) Height of skull exceeds width of snout: Reisz (1986 table 3b). All varanopids, with the exclusion of *Orovenator*, and all synapsids, with the exception of caseasaurs, have a narrow and tall snout, where the nasal has a largely vertical contribution. This character does support the synapsid affinities of Varanopidae (ch.2).

o) Frontal forms at least one third of dorsal orbital margin: Reisz (1986 table 3b). Most caseasaurs and captorhinids have a narrow contribution of the frontal to the dorsal orbital margin. The derived state, where the frontal makes up at least one third of the

dorsal orbital margin, is present in all remaining synapsids and sauropsids, including varanopids, with the exception of *Ascendonanus* and some parareptiles. This character is therefore ambiguous because it is consistent with both synapsid and sauropsids affinities of Varanopidae (ch.61).

p) Supratemporal fits in groove formed by parietal and squamosal: Reisz (1986 table 3b). A broad supratemporal is plesiomorphic for early amniotes, being present in all out-group stem-amniotes and all caseasaurs. All other synapsids, and sauropsids have narrow supratemporals, with the exception of *Archaeovenator* and Parareptiles that have independently acquired broad supratemporals. This character is therefore ambiguous in respect to the varanopid affinities (ch.95).

q) Pineal foramen posterior to midpoint of parietal: Reisz 1986 (table 3b). All synapsids, except caseasaurs, and all varanopids, including *Orovenator*, have a posteriorly positioned pineal foramen. This is also the condition also found convergently in *Youngina* and some parareptiles. This character does support synapsid affinities of Varanopidae, inclusive of *Orovenator*; see section 7(b) below (ch.92).

2. **Synapomorphies of varanopids** (from Reisz *et al.* 2010)

a) Premaxilla narial shelf rounded, transitions smoothly ventrally: Reisz *et al.* (2010 c.11). This condition is present in *Archaeovenator*, *Mycterosaurus*, *Mesenosaurus*, *Aerosaurus*, *Pyozia*, and *Orovenator*. It is absent in *Varanops*, and is unknown in *Heleosaurus*, *Varanodon* and *Ascendonanus*. It is therefore a synapomorphy of Varanopidae, including *Orovenator*, as defined in this study. It is convergently present in *Varanosaurus* (ch.19).

b) Posterodorsal expansion of external naris: Reisz *et al.* (2010 c.21). The posterodorsal extension of the naris is present in all varanopids, including *Orovenator*, where the morphology is known, apart from *Aerosaurus*. It is a unique synapomorphy of Varanopidae, as defined in this study (ch. 44/45).

c) Lacrimal does not reach external naris: Reisz *et al.* (2010 c.24). The participation of the lacrimal either in the margin of the external naris or in direct contact with the septomaxilla, is the plesiomorphic condition in early amniotes, being present in stem-amniotes, all synapsids with the exception of sphenacodontids, captorhinids, 'protorothyridids' and araeoscelidians. It is also present in basal and varanodontine varanopids, including *Orovenator*, and basal parareptiles. The derived condition is independently acquired in mycterosaurines, neodiapsids, derived parareptiles and sphenacodontids (ch. 49/50).

d) Parietal extension over interorbital region more than marginal: Reisz *et al.* (2010 c.28). The interorbital extension of the anterior process of the parietal is redundant

with the character coding for the posterolateral process of the frontal (ch. 64 of the present study). This character is therefore omitted. Refer to section 5(a) below for comments on the character coding for the posterolateral process of the frontal.

e) Squamosal occipital shelf narrow: Reisz *et al.* (2010 c.38). The occipital margin of the squamosal is narrow in all varanopids, and all diapsids and parareptiles. This is the derived condition in early amniotes, and is therefore a synapomorphy of Clade B as recovered in the present study; see section 5(b) below (ch. 87).

f) Ventral temporal bar narrow, > 20% of skull height: Reisz *et al.* (2010 c.41). The ventral temporal bar is narrow in varanopids and neodiapsids and most parareptiles where temporal fenestration is present. It is therefore a synapomorphy of Clade C as recovered in the present study, which is also convergently present in edaphosaurids and *Haptodus* (ch.71).

g) Anterior extent of quadratojugal and anterior process of ventral part of squamosal: Reisz *et al.* (2010 c.46). Characters 81 and 85 in my character list (Appendix 1) are concerned with the contact between the anterior processes of the squamosal and quadratojugal with the posteroventral margin of the jugal. They preclude the inclusion of this character as non-independent, and this character is therefore omitted.

h) Wing-like basipterygoid process: Reisz *et al.* (2010 c.51). All varanopids, excluding *Orovenator*, possess a laterally directed basipterygoid process, which is also present convergently in in caseasaurs, *Prolacerta* and *Mesosaurus*. Sphenacodontians, edaphosaurs and sauropsids have anterolaterally directed process. Ophiacodontids have a posteroventrally directed basipterygoid process. This character is therefore a shared feature of varanopids and caseasaurs (ch.117).

i) Tabular, narrow and slender, no ventral expansion: Reisz *et al.* (2010 c.54). Refer to 1(m) above (ch.99).

j) Hindlimb almost as long or longer than trunk: Reisz *et al.* (2010 c.101). Uniquely among traditional synapsids, varanopids possess hind limbs at least 90% as long as the trunk. This feature is also present in diapsids and the exceptionally long limbed parareptile *Eudibamus*. It is absent in the basal varanopid *Ascendonanus*, and this may be a related to the possible arboreal habitat of this taxon. This character is a synapomorphy of Clade C in the present study, with secondary loss in some parareptiles (ch.267).

k) Tuberous ornamentation on prefrontal and/or jugal: Reisz *et al.* (2010 c.34). This is a unique synapomorphy among derived varanopids, with the exception of *Varanodon*. It is absent in the basal varanopids *Archaeovenator*, *Orovenator* and *Ascendonanus* (ch.79).

l) Cervical central longer than dorsal centra: Reisz *et al.* (2010 c.69). In varanodontines the cervical centra are longer than the dorsal centra. This is an unusual condition among early amniotes, otherwise only convergently present in araeoscelidian diapsids, archosauromorphs and *Secodontosaurus* (ch.199).

m) Ventral surface of cervical centra strongly keeled: Reisz *et al.* (2010 c.70). Keeled cervical central are plesiomorphic for amniotes, and present in stem-amniotes, captorhinids, 'protorothyridids', diapsids, ophiacodontids and varanopids, including *Orovenator*. Sphenacodontids have sheet-like keels. Only caseasaur have a rounded ventral margin on the cervical central (ch.200).

n) Cervical neural arches shallowly excavated: Reisz *et al.* (2010 c.71) Mycterosaurine and varanodontine varanopids both possess excavated neural arches, convergently present in araeoscelids, *Dimetrodon* and *Proterosuchus*. Excavations are absent in basal varanopids (i.e. *Archaeovenator*, *Orovenator* and *Apsisaurus*)(ch.201).

3. **Synapomorphies of sauropsids** (from this study)

a) Tabular morphology short and narrow (ch.99 0 → 1). The tabular is short and narrow (state 1) in most sauropsids, including the basal varanopids *Archaeovenator* and *Ascendonanus*. The tabular is narrow but dorsoventrally elongate in derived varanopids, bolosaurids and *Araeoscelis* (state 2). It is broad (state 0) in Eothyris and ophiacodontids and large and 'L' shaped in edaphosaurids and sphenacodontids. Also refer to 1(m) above.

b) Single coronoid present in mandible (ch.181 1 → 2). All synapsids have two coronoids in the mandibular ramus, which is also convergently present in some sauropsids, (e.g. *Araeoscelis*, *Hylonomus*and *Varanodon*). All other sauropsids, including the basal varanopids *Archaeovenator* and *Mycterosaurus*, have a single coronoid in the mandible.

c) Coronoid teeth absent (ch.182 0 → 1). Teeth on the coronoid (or posterior coronoid in those taxa with multiple coronoids) is the plesiomorphic condition in early amniotes. Coronoid teeth are present in stem-amniotes, caseasaurs, *Edaphosaurus* and *Haptodus*, and convergently in the earliest sauropsid *Hylonomus*. The derived condition is present in all sauropsids, including all varanopids. Ophiacodontids and sphenacodontids also possess the derived condition.

d) Tarsus, one centrali present (ch.283 0 → 1). *Ophiacodon*, *Edaphosaurus* and *Dimetrodon* all possess two centrali in the tarsus. More than one pedal centrali may have been plesiomorphic for amniotes, since the stem-amniote *Seymouria* possesses three pedal centrali. There are two centrali in the pes of *Diadectes*, although one, the proximal centrali, is firmly sutured to the tibiale and intermedium in a proto-astragalus. Sauropsids possess a single centrale in the tarsus, as does the basal vara-

nopid *Archaeovenator*. The tarsus is unknown in other varanopids.

4. **Synapomorphies of Clade A** (from this study)

I find Captorhinidae as the most basal group within Sauropsida, and the more inclusive sauropsid clade of 'protorothyridids' + diapsids + parareptiles + varanopids is therefore designated Clade A (Fig. 2). This is contrary to many previous studies that recovered a monophyletic Eureptilia comprising captorhinids + 'protorothyridids' + diapsids. The synapomorphies supporting the traditional definition of Eureptilia are considered in the section 'Parareptiles as the sister taxon to neodiapsids' later in this chapter.

a) Lacrimal, suture with jugal small in lateral view (ch.54 $1 \rightarrow 0$). Diadectomorphs, captorhinids and all synapsids, with the exceptions of *Euromycter* and *Oedaleops* possess a broad suture of the jugal and lacrimal in lateral view. In the varanopids *Aerosaurus*, *Varanops* and *Varanodon*, and all members of Clade A where the lacrimal contacts the jugal in lateral view, the suture is less than 50% of the height of the suborbital bar. Bolosaurids are an exception to this. In other varanopids, i.e. *Archaeovenator*, *Orovenator* and *Mesenosaurus*, the lacrimal contacts the jugal medial to the suborbital process of the maxilla, and is not visible in lateral view.

b) Mandible long and dorsoventrally slender, height less than 0.18 of total length (ch.158 $0 \rightarrow 2$). The mandible is long and dorsoventrally slender in all members of Clade A, including all varanopids, with the exception of *Araeoscelis* and most parareptiles. This condition is convergently present in ophiacodontids and *Secodontosaurus*. However, most other synapsids, captorhinids and stem-amniotes have mandibles of intermediate height/length ratio (0.20-0.26), with some OTUs (*Ennatosaurus*, *Euromycter*, *Edaphosaurus* and *Procolophon*) possessing robust mandibles (ratio > 0.30) adapted for high-fibre herbivory.

c) Humerus, ratio of width of distal head to length less than 0.40 (ch.242 $0 \rightarrow 1$). The distal head of the humerus is narrow compared to humeral length (state 1) in basal varanopids and mycterosaurines, i.e. *Ascendonanus*, *Apsisaurus* and *Heleosaurus*. This condition is also found in 'protorothyridids', most diapsids and the basal parareptile *Mesosaurus*. Exceptions to this in Clade A are all varanodontines, most parareptiles and the some diapsids, i.e. *Hovasaurus* and *Thadeosaurus*, where the ratio is > 0.40 (state 0). All stem-amniotes, synapsids and captorhinids also have width to distal head ratio > 0.40 (state 0), which is therefore probably plesiomorphic for amniotes.

d) Transverse width across carpus less than length of 4th metacarpal (ch.253 $0 \rightarrow 1$). *Ascendonanus* and *Heleosaurus* have a narrow carpus and long metacarpals (state 1), in common with 'protorothyridids', araeoscelidian diapsids and some neodiapsids. The

condition is reversed in varanodontines and parareptiles (state 0). In all stem-amniotes, captorhinids and synapsids the transverse width of the carpus is greater than the 4th metacarpal (state 0).

e) Femur, long and slender, length more than 3 times distal width (ch.270 0 → 1). In all members of clade A, including the varanopids *Ascendonanus*, *Archaeovenator*, *Apsisaurus*, *Mycterosaurus*, *Mesenosaurus* and *Heleosaurus*, but with the exception of varanodontines, the length of the femur is greater then 3 times the distal width (state 1). This condition is convergently present in *Secodontosaurus*, but otherwise absent in all stem-amniotes, captorhinids and synapsids (state 0).

f) 4th trochanter of the femur absent (ch. 271 0 → 1). The 4th trochanter is absent (state 1) in all members of Clade A, with the exception of *Varanops*. It is present (state 0) in stem-amniotes, synapsids and *Captorhinus* (see Appendix 1 for further details).

g) Transverse width across tarsus less than length of 4th metatarsal (ch.277 0 → 1). In 'protorothyridids', diapsids and the basal varanopids *Archaeovenator* and *Ascendonanus* the width across the tarsus is narrow, less than the proximodistal length of the 4th metatarsal (state 1). All stem-amniotes, synapsids and captorhinids have a broad tarsus relative to the 4th metatarsal (state 0), which is convergently present in varanodontines and parareptiles.

5. **Synapomorphies of Clade B** (from this study)

My analyses have recovered tree topologies (Figs. 2, 3) that includes parareptiles and varanopids in a monophyletic group with diapsids (including araeoscelidians). The node-based definition of Diapsida (i.e. the most recent common ancestor of Araeoscelidia, *Claudiosaurus*, Younginiformes, and Sauria and all their descendants, deBraga and Rieppel 1997) is therefore invalid for this group. For ease of reference, therefore, this group is designated Clade B.

a) Posterolateral process of frontal long and narrow (ch.64 0 → 2). The posterolateral process of the frontal substantially or fully separates the parietal from the postfrontal (state 2) in all diapsids (except *Petrolacosaurus*), varanopids, basal parareptiles and procolophonoids. The same condition is convergently present in ophiacodontids. In all other taxa, the posterolateral process forms a right-angle to the parasagittal plane (state 0 in caseids, sphenacodontids, captorhinids, 'protorothyridids' and *Belebey*) or only partially separates the postfrontal from the parietal forming an obtuse angle (state 1 in eothyridids, edaphosaurids, *Haptodus*, *Petrolacosaurus* and some parareptiles)

b) Occipital flange of squamosal is absent or narrow (ch.87 0 → 1). In varanopids and all other members of Clade B, with the exception of some parareptiles, the occipital flange of the squamosal is narrow or absent. See Appendix 1 for further details and

section 2(b) above.

c) Sub-rectangular outline of dorsal neural spines in lateral view (ch.209 0 →1). Araeoscelidians, neodiapsids and varanopids all possess sub-rectangular dorsal neural spines. This condition is shared convergently by most synapsids, with the exception of edaphosaurids and some sphenacodontids, where the neural spines are particularly elongate. This synapomorphy is therefore ambiguous to Clade B and Synapsida. Captorhinids and 'protorothyridids' share subtriangular outlines of the dorsal neural spines.

d) Supinator process on humerus transversely narrow and almost confluent with the humeral shaft (ch.246 0 → 1). In almost all members of Clade B, where the morphology of the supinator process of the humerus is known, the process is narrow and almost confluent with the shaft, e.g. the varanopids *Apsisaurus* and *Heleosaurus*. In stem-amniotes, synapsids and *Paleothyris* the process is broad and extends laterally or anterolaterally (state 0). This condition is convergently present in varanodontines.

6. **Synapomorphies of Clade C** (from this study)

Varanopids, neodiapsids and parareptiles are recovered in a monophyletic group that is designated Clade C (Figs.2, 3, 5).

a) Ventral temporal bar height narrow (ch.71 0 → 1). The temporal (zygomatic) bar of the lower temporal fenestra is less than 20% of the height of the postorbital skull region (state 1) in all members of Clade C that possess the opening, with the exception of *Milleretta*. This is convergently present in edaphosaurids and *Haptodus*. In all other synapsids and *Petrolacosaurus*, the temporal bar is dorsoventrally taller, occupying more than 20% of the skull height.

b) Absence of teeth on the ectopterygoid (ch.145 0 → 1). The ectopterygoid is edentulous (state 1) in *Archaeovenator*, *Apsisaurus*, *Mesenosaurus* and all other members of Clade C, where the morphology is known, with the exception of *Orovenator*. Teeth are also absent convergently in some synapsids (*Varanosaurus*, *Haptodus* and *Secodontosaurus*). *Ennatosaurus*, *Edaphosaurus* and *Dimetrodon* all possess teeth on the ectopterygoid, and they are convergently present in 'protorothyridids' and araeoscelidians. The ecopterygoid is absent in *Mesosaurus* and captorhinids, with the possible except of *Euconcordia*.

c) Retroarticular process on the mandible (ch.163 0 →1). All varanopids, diapsids and parareptiles possess a retroarticular process, with the exception of *Claudiosaurus* and derived bolosaurids. A retroarticular process is convergently present in edaphosaurids and sphenacodontians and derived captorhinids. It is absent in diadectomorphs, caseasaurs, ophiacodontids, basal captorhinids, 'protorothyridids' and araeoscelidians.

d) Trunk ribs single headed (holocephalous) (ch.218 0 → 1). Holocephalous ribs are present in the trunk of all diapsids and most parareptiles. In varanopids they are present in basal taxa, i.e. *Ascendonanus* and *Archaeovenator*, and Mycterosaurines, but double-headed in *Apsisaurus* and varanodontines. *Ascendonanus*, *Archaeovenator* and all mycterosaurines have holocephalous trunk ribs. Synapsids, captorhinids, 'protorothyridids' and araeoscelidians also have double-headed ribs in the trunk region.

e) Supraglenoid foramen is absent (ch.232 0 →1). The Supraglenoid foramen is absent in all members of Clade C, with the exception of *Aerosaurus*. It is also convergently absent in caseasaurs. *Varanodon* may be polymorphic for this character. See Appendix 1 for further details.

f) Capitellum and trochlea of humerus poorly developed (ch.239 0 → 1). The capitellum and the trochlea are well developed (state 0) in stem-amniotes, synapsids, derived captorhinids (e.g. *Captorhinus*) and 'protorothyridids'. The varanopids *Aerosaurus* and *Varanops* have a very inconspicuous capitellum and trochlea (state 1), a feature that is shared with most members of Clade C and convergently in basal captorhinids (e.g. *Thuringothyris*). In Archosauromorphs and *Mesosaurus* the capitellum and trochlea are indistinct from the distal surface of the humerus.

g) Entepicondyle of the humerus reduced or confluent with the ectepicondyle (ch.244 0 → 1). The varanopids *Ascendonanus*, *Apsisaurus* and *Heleosaurus*, the diapsids *Youngina* and *Prolacerta*, and the basal parareptile *Mesosaurus* have much reduced entepicondyles (state 1). Stem-amniotes, synapsids, captorhinids, 'protorothyridids' and araeoscelidians have entepicondyles that make up around half the distal width of the humerus (state 0), which is convergently present in varanodontines, *Claudiosaurus* and *Acerosodontosaurus*. *Ophiacodon* and *Procolophon* have broad entepicondyles, which make up at least two thirds of the distal humerus.

h) Olecranon process of the ulna is absent or very low (ch. 250 2 → 0). The olecranon process is low or absent in *Ascendonanus*, *Apsisaurus*, *Watongia*, *Varanodon* and *Heleosaurus* and most other members of Clade C, with the exception of *Aerosaurus*, *Varanops*, *Mesenosaurus* and some derived parareptiles. It is moderate to well developed in stem-amniotes, synapsids, captorhinids, 'protorothyridids' and araeoscelidians.

7. **Synapomorphies of varanopids + *Orovenator*** (from this study)

a) Lacrimal contribution to orbital margin in lateral view less than 5% (ch.51 0 → 1). In *Orovenator*, other basal varanopids and mycterosaurines the ventral process of the prefrontal restricts the orbital exposure of the lacrimal (state 1). This condition is convergently present in some diapsids and parareptiles. In stem-amniotes, synapsids, captorhinids, 'protorothyridids' and araeoscelidians, and convergently in varanodon-

tines, the lacrimal contribution to the orbital margin is greater than 7% (state 0).

b) Pineal foramen located on the posterior portion of the parietal (ch.92 state change 1 → 2). In all varanopids (including *Orovenator*) the pineal foramen is posteriorly positioned on the midline of the parietal. This condition is also present in ophiacodontids, edaphosaurids and sphenacodontians, some parareptiles, *Paleothyris* and *Youngina*. This character supports the synapsid affinities Varanopidae; see section 1(r) above.

c) Palatine deeply incised anteriorly (ch.133 0 → 1). The anterior margin of the palatine in *Orovenator*, *Archaeovenator*, *Mesenosaurus* and *Heleosaurus* is deeply embayed by the internal naris (state 1). This is also present convergently in *Proterosuchus* and some stem-amniotes. In all other OTUs the emargination very shallow or moderate.

d) Dorsomedial shelf on surangular (ch.187 0 → 1). *Orovenator* and other varanopids, with the exception of *Archaeovenator* and *Mesenosaurus*, possess a medial expansion of the dorsal surface of the surangular. It is convergently present in *Acerosodontosaurus*. It is absent in all other OTUs.

e) Narrow anterodorsal process of surangular present (ch.189/190 0 → 1). All varanopids, where this portion of the mandible is exposed, possess a narrow anterodorsal process of the surangular that separates the posterodorsal margin of the dentary from the coronoid.

4.3.5.2 Testing the varanopid/reptile hypothesis

When I constrained individual varanopid OTUs to be members of Synapsida (see 'Methods' above), constrained topologies for six of the 12 varanopids produced a monophyletic Synapsida, including all varanopids, in all or some of the resulting MPTs. Varanopids formed a polytomy at the base of the group in all cases. The remaining varanopid taxa, when constrained individually within Synapsida, did not produce any trees in which all varanopids were recovered within a monophyletic Synapsida. Differences in tree length and their statistical significance for the six varanopids that produced a monophyletic Synapsida including all varanopids are summarised in Table 4.4.

Table 4.4: Constrained varanopid topology resulting in a monophyletic Synapsida, where add. steps= number of steps in addition to the optimal MPT's, N= the number of positive or negative differences in steps for the pairwise comparison of each character, P-value= probability value of test, Null Hypothesis= the hypothesis that there is no statistical difference in the topologies of both datasets.

taxon	Tree Length	add. steps	MPT's	min P-value	N	max P-value	N
Mycterosaurus	1411	31	12	0.0011	72	0.0024	79
Varanodon	1411	31	60	0.0001	64	0.0032	72
Aerosaurus	1404	24	16	0.0011	59	0.0099	73
Mesenosaurus	1412	32	8	0.0001	67	0.0002	75
Varanops	1409	29	10	0.0001	67	0.0003	74
Heleosaurus	1414	34	164	0.0001	68	0.0002	74

All tree lengths exceed the tree length of the MPTs by between 24 and 34 additional steps. The results strongly support the rejection of the Null Hypothesis in all cases (P$<$ 0.01=highly significant), and the alternative hypothesis that varanopids form a monophyletic group within Synapsida can be rejected as being a statistically equivalent explanation of the data. Analysis of my new dataset of early amniotes using maximum parsimony and Bayesian inference confirms the observations presented in chapter 2, and supports the hypothesis that *Orovenator mayorum* + Varanopidae form a monophyletic group. This group, for which I maintain the existing nomenclature Varanopidae, is recovered within Sauropsida (total-group reptiles), and is the sister taxon of the group comprised of neodiapsids and parareptiles. The position of parareptiles is the second of the non-traditional outcomes of this analysis, and requires further examination, which I detail below.

4.3.5.3 Parareptiles as the sister taxon to neodiapsids

Parareptilia was first erected as a sub-class of reptiles by Olson (1947), and included stem-amniotes (diadectomorphs and seymouriamorphs), procolophonids and pareiasaurs (including turtles). Later work on amniote phylogeny excluded stem-amniotes from this group, and revised the definition of parareptiles as a monophyletic sister group of all other reptiles (Eureptilia), either including (Reisz and Laurin 1995, Lee 1997) or excluding (deBraga and Rieppel 1997, Rieppel and Reisz 1999) turtles. The basal dichotomy of the total-group reptiles (Sauropsida) into eureptiles (diapsids and captorhinids) and parareptiles has therefore been a convention since a revised definition of both groups was first proposed by Laurin and Reisz (1995), and reaffirmed by various studies since (Reisz *et al.* 2007, Tsuji *et al.* 2012, MacDougall and Reisz 2014, Reisz *et al.* 2014, Modesto *et al.* 2015, MacDougall *et al.* 2016, MacDougall *et al.* 2018).

The results of my analysis challenge this view by recovering parareptiles as a sister taxon to neodiapsids (Fig. 2). In agreement, however, with many previous studies, I find parareptiles to be a monophyletic group, which includes the early Permian amniote *Mesosaurus*. The position of this taxon has been the subject of recent debate, and I shall discuss this result in detail below. In order to explore the validity of the hypothesis of a parareptile + neodiapsid group, I list below the previously established synapomorphies that support the sister relationship of captorhinids + diapsids + 'protorothyridids' within Eureptilia, to the exclusion of parareptiles, together with their source, comments and the corresponding characters in my analysis as detailed in Appendix 1. I subsequently list the synapomorphies supporting Clade D, i.e. parareptiles + neodiapsids (Fig.2), resulting from the analysis of my new dataset.

1. **Synapomorphies of Eureptilia** (from previous studies)

a) Postorbital/supratemporal contact absent: Laurin and Rieppel (1995), deBraga and Reisz (1997), Müller and Reisz (2006), Laurin and Piñeiro (2017). The contact of the postorbital and supratemporal is considered a synapomorphy of synapsids (deBraga and Reisz 1997). It is present in all caseasaurs, but varies within other synapsids, i.e. it is absent in *Varanosaurus*, edaphosaurids, *Haptodus* and *Secodontosaurus*. It is absent in all captorhinids, 'protorothyridids', araeoscelidians and neodiapsids and is therefore supportive of a traditional eureptile clade. It is also absent, however, in the basal parareptiles *Mesosaurus* and *Milleretta*, although present in more derived parareptiles. The absence of contact between the postorbital and supratemporal could also be considered, therefore, as a sauropsid synapomorphy, reversed in derived parareptiles and several varanopids. See Appendix 1 for further details (ch.66/67).

b) Squamosal contribution to posttemporal fenestra present: Laurin and Reisz (1995), deBraga and Rieppel (1997), Müller and Reisz (2006), Laurin and Piñeiro (2017). In captorhinids and 'protorothyridids' the occipital exposure of the squamosal is mediolaterally wide, and when the tabular is absent (as in captorhinids) the squamosal contributes broadly to the posttemporal fenestra. This may be supportive of eureptiles, although this condition is ambiguous in araeoscelidians and neodiapsids. See Appendix 1 for further comments (ch.89)

c) Supratemporal small: Laurin and Reisz (1995), deBraga and Rieppel (1997), Müller and Reisz (2006), Laurin and Piñeiro (2017). The supratemporal is reduced in captorhinids, 'protorothyridids' and diapsids. The same condition is found in most synapsids and varanopids. Only stem-amniotes, caseasaurs and parareptiles have distinctively broad supratemporals, and broad supratemporal is probably a plesiomorphic for amniotes, with a reversal in parareptiles. Alternatively, this character suggests a

more basal position for parareptiles within Sauropsida, and it supportive of a traditional Eureptilia (ch.95).

d) Posterolateral corner of skull formed mostly by supratemporal: Laurin and Reisz (1995), Müller and Reisz (2006), Laurin and Piñeiro (2017). The size of the supratemporal will determine the nature of the posterolateral corner of the skull roof (see above). This character is therefore redundant with the supratemporal size (refer c.47 and c.48 in Müller and Reisz 2006, where these scores are identical). This character is therefore omitted. As noted above (1c) a broad supratemporal is supportive of a eureptile clade excluding parareptiles.

e) Nasal shorter than frontal: Müller and Reisz (2006). The nasal is distinctly shorter than the frontal in captorhinids, 'protorothyridids' and araeoscelidian diapsids, and this character can be considered a synapomorphy of eureptiles. It is also present in most parareptiles, basal varanopids (*Orovenator* and *Archaeovenator*) and *Claudiosaurus*, and could also be considered a synapomorphy of sauropsids, reversed in derived varanopids, *Youngina* and *Belebey* (where the nasal and frontal are for equal length) and in *Mesosaurus* and archosauromorphs (nasal longer than frontal) (ch.47).

f) Arcuate flange of pterygoid absent: Laurin and Reisz (1995), Laurin and Piñeiro (2017). An arcuate flange on the quadrate ramus of the pterygoid is absent in derived captorhinids, but present in the basal captorhinid *Euconcordia*. It is absent in 'protorothyridids' where known. The absence of the pterygoid flange is ambiguous in araeoscelidians (present in *Araeoscelis* and absent in *Petrolacosaurus*. It is present in many other diapsids (e.g. *Araeoscelis*, *Youngina*, *Lanthanolania* and *Prolacerta*), all varanopids (excluding *Mesenosaurus*) and all parareptiles. The presence, rather than absence, of an arcuate flange on the quadrate ramus of the pterygoid is there supportive of the affinities of varanopids + neodiapsids + parareptiles, i.e. Clade C (ch.140).

g) Bilaterally embayed posterior skull margin: Müller and Reisz (2006). This is present in basal captorhinids (*Euconcordia*, *Thuringothyris* and *Romeria*), most 'protorothyridids' and araeoscelidians. A bilateral embayment of the posterior skull margin is also found in all varanopids. This may indeed be plesiomorphic for amniotes since it is present in caseasaurs and ophiacodontids, although absent in edaphosaurids and sphenacodontians, where there is a single embayment. Neodiapsids and many parareptiles also possess a single median embayment. Consequently, this is more likely to be a synapomorphy that supports the affinities of neodiapsids and parareptiles (see below) (ch.5).

h) Narrow iliac blade: Müller and Reisz (2006). A narrow tapering iliac blade, extending beyond the posterior edge of the iliac body is present in all sauropsids as

defined in the present study (i.e. including varanopids), with the exception of *Milleretta* and *Procolophon* (ch.264).

i) Strong ventrolateral constriction of dorsal centra: Müller and Reisz (2006). Among captorhinids, only *Thuringothyris* has ventrolaterally constricted dorsal centra, which is absent in more derived captorhinids. It is present in 'protorothyridids' and araeoscelidians, and as such could be considered a synapomorphy of Eureptilia. However, it may be plesiomorphic for sauropsids, since a ventral keel on the dorsal centra is present in varanopids, but absent, where known, in neodiapsids and basal parareptiles, where the ventral surface of the centra are rounded (ch. 207).

j) Anterior process of quadrate less than 55% of the length of the distance between the quadrate condyle and the transverse process of the pterygoid: Laurin and Reisz (1995), deBraga and Rieppel (1997), Laurin and Piñeiro (2017). The pterygoid flange (anterior process) of the quadrate in combination with the length of the quadrate ramus of the pterygoid is not sufficiently well known in most sauropsid OTUs in the present study to accurately determine the state of this character. This character is therefore omitted.

k) Caniniform maxillary tooth present Laurin and Reisz (1995). Caniniform teeth are present in all captorhinids (except *Thuringothyris*), and this is probably plesiomorphic for amniotes since they are also present in all 'protorothyridids', araeoscelidians and synapsids (except caseids). Their absence is a synapomorphy of neodiapsids and basal parareptiles, Clade D (see below) (ch.30).

l) Paroccipital process ends freely: Laurin and Reisz (1995). The paroccipital process ends freely in captorhinids and 'protorothyridids'. The condition in diapsids and parareptiles is ambiguous; the process ends freely in *Petrolacosaurus*, *Claudiosaurus*, *Milleretta*, *Mesosaurus* and *Belebey*, but contacts the skull laterally in other diapsids and parareptiles (ch.109).

m) Interpterygoid vacuity long: Laurin and Reisz (1995). The interpterygoid vacuity is long, i.e. it reaches beyond posterior margin of palatine, in all sauropsids with the exception of *Thuringothyris* and some parareptiles, and may be plesiomorphic for amniotes. It is short in synapsids, with the exception of Casea broilii. This character state could therefore equally be considered as a eureptile synapomorphy or a synapomorphy of sauropsids (ch.143).

n) Two coracoid ossifications: deBraga and Rieppel (1997). Captorhinids have two ossifications of the coracoid. This may be plesiomorphic for amniotes since this condition is present in araeoscelidians and all synapsids where known. Basal parareptiles, e.g. *Mesosaurus* and *Milleretta*, and neodiapsids have one coracoid ossification

(ch.236).

2. **Synapomorphies of Clade D - parareptiles and neodiapsids** (from this study)

Many of the synapomorphies detailed in section 1 above are plesiomorphic for early amniotes or sauropsids, and the derived state can often be considered a synapomorphy of Clade D, some of which are included in the following section of eight unambiguous synapomorphies derived from the present study that support the monophyletic group neodiapsids + parareptiles, which is designated as Clade D (Fig.2).

a) Posterior margin of skull with a single medial embayment (ch.5 2 → 1). The posterior margin of the skull in most sauropsids is bilaterally embayed. In neodiapsids and many parareptiles, including *Mesosaurus* and *Milleretta*, the margin has a single embayment. This is reversed in bolosaurids and procolophonoids.

b) Absence of caniniform teeth (ch.30 1 → 0). The presence of caniniform teeth is plesiomorphic for most early amniotes. They are absent in neodiapsids and parareptiles (apart from *Colobomycter* and *Macroleter*, although absent in other nycteroleterids).

c) Lacrimal duct opens on lateral surface of lacrimal, near posterior edge (ch.52 0 → 1). In many early amniotes the lacrimal duct opens on the orbital rim of the lacrimal. In neodiapsids and some parareptiles, i.e. *Mesosaurus*, *Belebey* and *Acleistorhinus*, the opening is on the lateral surface of the lacrimal. The lateral opening is also present in several varanopids.

d) Paroccipital process does not contact tabular (ch.110 0 → 1). In stem- and early crown-amniotes, where the paroccipital process contacts the skull laterally, contact is made with the tabular. In *Youngina*, *Prolacerta* and *Acleistorhinus* contact is with the parietal and supratemporal. This character may be ambiguous, however, since the morphology of the occipital region is unknown in most diapsids and parareptiles.

e) First sacral rib subequal to or only slightly larger than second sacral rib (ch.221 0 → 1). In neodiapsids and parareptiles, with the exception of *Eudibamus*, both sacral ribs are of similar size. This is convergently found in caseids, edaphosaurids and sphenacodontids. In *Araeoscelis* and most varanopids, apart from *Archaeovenator*, the first sacral is distinctively larger than the second.

f) Notch on margin of scapula/coracoid contact (ch.235 0 → 1). The anterior margin of the scapulocoracoid in *Mesosaurus*, *Youngina* and *Prolacerta* is notched at the junction of the scapula and coracoid. This is absent in other sauropsids, apart from varanodontines. It is convergently present in *Ophiacodon* and *Haptodus*.

g) Single ossification of the coracoid (ch.236 1 → 0). Neodiapsids and basal parareptiles, i.e. *Mesosaurus* and *Milleretta*, have single ossification of the coracoid. Procolophonoids have two ossifications, as do all other amniotes where the morphology

Table 4.5: Constrained captorhinid topology, where additional steps= number of steps in addition to the optimal MPT's, N= the number of positive or negative differences in steps for the pairwise comparison of each character, min P-value= minimum probability value of constrained MPT's, max P-value= minimum probability value of constrained MPT's

Taxon	Tree Length	add. steps	MPT's	min P-value	N	max P-value	N
Thuringothyris	1401	21	6	0.0323	91	0.0385	96
Captorhinus	1417	37	12	0.0007	105	0.0008	106
Protocaptorhinus	1413	33	14	0.0017	103	0.0024	105
Romeria	1411	31	14	0.0044	102	0.0059	106
Euconcordia	1401	21	39	0.0333	79	0.0509	104
Reiszorhinus	1408	28	56	0.0042	91	0.0114	101

can be distinguished. A single ossification of the coracoid is present in stem-amniotes, so the condition in neodiapsids and the basal parareptiles may represent a reversal.

h) Distal articular condyles of the femur extend to same level (ch.268 0 → 1). The subequal distal extension of the anterior and posterior condyles of the femur is present in neodiapsids and the basal parareptiles *Mesosaurus* and *Milleretta*, although absent in *Erpetonyx*. It is also absent in other early amniotes, with the exception of eothyridids and *Apsisaurus*.

4.3.5.4 Testing the parareptile/neodiapsid hypothesis

The position of parareptiles in the present analysis was also examined using a series of constraint analyses and Templeton tests, according to the methods detailed above. A constraint was applied individually to each captorhinid to form a monophyletic group with diapsids and 'protorothyridids', with all other taxa allowed to move freely. This protocol resulted in a broad polytomy when applied to each captorhinid. However, when parareptiles were simultaneously constrained to a separate monophyletic group, the effect of this constraint, in most cases, was to position all captorhinids within the traditional Eureptilia. The captorhinid taxon selected for constraint, however, was positioned as a single terminal unit more closely related to 'protorothyridids' and diapsids than other captorhinids. The results are summarised in Table 4.5.

One important observation that results from this series of constraints is that for several taxa (*Thuringothyris*, *Captorhinus*, *Protocaptorhinus* and *Romeria*) the strict consensus of the constrained MPTs produced a traditional sauropsid grouping (parareptiles + Eureptilia) and recovered Varanopidae (varanopids + *Orovenator*) within Synapsida, essentially the conventional view of early amniote phylogeny (see Fig. 1). This topology is also found in several MPTs in *Euconcordia* and *Reiszorhinus*.

Nevertheless, between 21 and 37 additional steps are required for each of the con-

strained runs, and the Templeton test results on these trees allow a statistically significant rejection of the null hypothesis that captorhinids form a monophyletic group with 'protorothyridids' and diapsids. However, in seven of the 39 MPTs resulting from the constraint analysis of *Euconcordia*, the test results for the P-value are marginally higher than the critical threshold of P=0.05, even though there are 21 additional steps required in each case.

These results are intriguing, not because of the marginal P-value value in respect to the critical threshold in some MPTs of a single captorhinid, but the implication that the position of both varanopids and parareptiles in a crownward clade with neodiapsids (Fig. 2, Clade C) may be interdependent, since when one group (parareptiles) is removed from the clade by constraint, the other (varanopids) is more parsimoniously recovered within Synapsida, if captorhinids are constrained within a traditional Eureptilia. To test this concept further, an analysis of the optimal dataset was made, first excluding all parareptiles and then all varanopids. The results do not support an interdependent position in the tree for these groups. If all parareptiles are excluded, varanopids are still recovered in a monophyletic group with neodiapsids; if all varanopids are excluded, parareptiles are still recovered in a monophyletic group with diapsids

4.3.5.5 Testing the monophyly of synapsids

It is worth noting that the results of both the parsimony and Bayesian analyses detailed above show particularly poor support for the clade that unites caseasaurs with other synapsids. A monophyletic Synapsida is supported by a posterior probability of < 60 in both the Mkv (no ages) and FBD model (Figs. 3 and 6). In the parsimony analysis, the node supporting synapsid monophyly collapses in one step under Bremer support indices and has bootstrap support below 50 (Fig. 2). Although both parsimony and Bayesian analysis recovers a topology with a monophyletic synapsid clade, this appears to be a particularly weak hypothesis.

To further test this hypothesis, I applied two hierarchical constraints to all caseasaurs, (i) to test the position of caseasaurs as a monophyletic clade of stem-amniotes, (ii) to test the position of caseasaurs as a monophyletic clade of stem-sauropsids. The results are shown in Table 4.6.

Each of the 6 MPT's of the stem-amniotes hypothesis was subjected to Templeton tests as described above. For the stem-sauropsid hypothesis, 6 trees were chosen at random from the 633 MPT's for Templeton test analysis. Both sets of results the P-values are well above the critical threshold of P=0.05. With only two addition steps

Table 4.6: Constrained caseasaur topology, where additional steps= number of steps in addition to the optimal MPT's, N= the number of positive or negative differences in steps for the pairwise comparison of each character, min P-value= minimum probability value of constrained MPT's, max P-value= minimum probability value of constrained MPT's

Hypothysis	Tree Length	add. Steps	MPT's	min. P-value	N	max P-Value	N2
Caseasaurs form a monophyletic group of stem-amniotes	1382	2	6	0.7819	46	0.8011	51
Caseasaurs form a monophyletic group of stem-sauropsids	1382	2	633	0.6698	22	0.7928	54

required, I am unable to reject the Null Hypothesis. There is no statistical significance, therefore, in the optimal and sub-optimal trees showing either: (i) a monophyletic clade of caseasaurs + other synapsids or (ii) caseasaurs as stem-amniotes/stem-sauropsids.

4.4 Discussion

Phylogenetic analysis of my new character-taxon matrix, using both maximum parsimony and Bayesian inference, suggests a new hypothesis of interrelationships of early amniotes that challenges the current paradigm in two main areas:

(i) Varanopidae (including *Orovenator*) are recovered as a monophyletic group within Sauropsida, and this may have implications for the timing of the transition from 'pelycosaur'-grade to therapsid-grade synapsids.

(ii) Parareptiles are recovered as a sister taxon to neodiapsids, with captorhinids as an early branching basal member of Sauropsida.

My results also support a basal position within Parareptilia for *Mesosaurus*, and suggest a more parsimonious explanation of the evolution of temporal fenestration in early amniotes than previous topologies. Each of these hypotheses is discussed in detail below.

4.4.1 The 'pelycosaur'/therapsid transition

The decline and extinction of many 'pelycosaur'-grade synapsids towards the close of the early Permian (Cisuralian) and their replacement in global faunas by therapsids from the early middle Permian (Guadalupian), has been recognised as an important transition in vertebrate evolution for many decades (Olson 1962, Benton 2015, Brocklehurst *et al.* 2013, 2017). Kemp (1982) argued the faunal change was an example of 'incumbent replacement' of 'pelycosaur'-grade synapsids by therapsids, and proposed a broad hypothesis to account for the transition (Kemp 2005, 2006). Major groups that have been consistently assigned to Synapsida (Caseasauria, Varanopidae, Ophia-

codontidae, Edaphosauridae and Sphenacodontia) make their first appearances late in the Carboniferous (Reisz 1972, Currie 1977, Reisz and Berman 1986, Reisz and Dilkes 2003, Reisz and Fröbisch 2014). Most of these persist to late in the Cisuralian but are absent from early Middle Permian deposits. Varanopids, on the other hand, are present in the fossil record from the late Carboniferous until the end of the Guadalupian (late Capitanian; late middle Permian) (Day *et al.* 2015). Unlike varanopids, caseids make their last appearance relatively early in the middle Permian. The youngest caseid, *Ennatosaurus tecton*, from the Mezen River assemblage of Russia, was thought to be early Tatarian (Capitanian) in age (Maddin *et al.* 2008), although the latest upper boundary for the Mezen assemblage is now considered to be equivalent to the early Wordian (Golubev and Bulanov 2018).

The survival of sphenacodontids into the earliest middle Permian (Roadian) is uncertain. Synapsid material from the San Angelo Formation of Texas, originally described as therapsid (Olson 1962), has since been assigned to Sphenacodontidae indet. (Kammerer 2011). Caseids are also present in the San Angelo Formation, and the contemporaneous Chickasha Formation of Oklahoma (Lucas 2006). However, the age of the San Angelo Formation is disputed, with some studies proposing a Kungurian age (late early Permian) (Lucas 2006) and others that the San Angelo Formation and Chickasha Formation of Texas, is Roadian in age (Reisz and Laurin 2001, Lozovsky 2003, Benton 2012). Lucas (2004, 2006) considered the San Angelo and Chickasha formations as Leonardian (Kungurian) in age, based on intercalated marine strata with Leonardian fusulinids, and an overlying strata of Leonardian ammonoids. He proposed a global stratigraphic gap, consisting of the greater part of the 4 million year duration of the Roadian, between these formations and the middle Permian tetrapod-bearing assemblage of Russia and South Africa. Reisz and Laurin (2001, 2002) argued that the formations were contemporaneous Roadian age beds, and shared similar fauna, including caseids, varanopids, and the nycteroleterid parareptile *Macroleter*. If correct, then the San Angelo formation sphenacodontid material is Roadian (early middle Permian). Putting this debate to one side, it is clear that even if sphenacodontids did occur in the Roadian, that they did not persist for long into the middle Permian. Furthermore, unlike caseids, varanopids and *Macroleter*, sphenacodontids are not currently known from the indisputably middle Permian faunas of Russia or South Africa (Ivakhnenko 2005, Brocklehurst *et al.* 2013, 2017, Day *et al.* 2018).

Kemp (2006) proposed that a gradual rise in global temperatures and increasing seasonal aridity during the early to middle Permian could explain the turnover between 'pelycosaur'-grade synapsids and therapsid-grade synapsids. The occurrence of these

climate changes has been inferred based on geochemical proxies and palaeobotanical data from South Africa, North America and Europe (Scheffler *et al.* 2006, DiMichele *et al.* 2006, Schneider *et al.* 2006, Tabor and Poulsen 2008). In Kemp's (2006) hypothesis, 'pelycosaur'-grade synapsids, with low activity levels and ectothermic temperature physiology, were confined to wet and humid equatorial environments. Therapsid character evolution, stimulated by high atmospheric oxygen levels, resulted in higher levels of metabolic activity and homeostatic regulation, expanding their habitat into seasonally arid biomes.

Varanopids have long been problematic to this theory, since the clade survived at least to the end of the Guadalupian (middle Permian) in both South Africa (*Heleosaurus*, *Elliotsmithia*; approx. 260 Ma; latest *Tapinocephalus* Assemblage Zone, Day *et al.* 2015) and Russia (*Mesenosaurus*; late Kazanian/early Tatarian; Capitanian; Reisz and Berman 2001), where they occur alongside abundant therapsids (Kemp 2006, Day *et al.* 2015, 2018). One fragmentary specimen assigned to Mycterosaurinae has also been found in the slightly younger *Pristerognathus* Assemblage Zone of South Africa (Modesto *et al.* 2011). Therefore, if varanopids are 'pelycosaur'-grade synapsids, the duration of co-occurrence between 'pelycosaur'-grade synapsids and therapsid-grade synapsids spanned the entire middle Permian (Guadalupian), an interval of approximately 13 million years, and varanopids (and so perhaps other non-therapsid synapsids) shared the hypothesised environmental tolerances of therapsids.

However, my new hypothesis suggests that varanopids were reptiles, not synapsids. This has two main implications. First, it reduces the maximum time of co-occurrence between 'pelycosaur'-grade synapsids and therapsid-grade synapsids to include only the span of the Guadalupian occurrences of caseids (Maddin *et al.* 2008, Brocklehurst *et al.* 2017, Romano *et al.* 2017, although see below uncertainties about the affinities of caseasaurs) and possible sphenacodontids (discussed above), a shorter duration that extends to the early Roadian. Secondly, it provides an explanation of why varanopids (and other sauropsids) may not have shared the narrow environmental tolerances of pelycosaur-grade synapsids that were hypothesised by Kemp (2006). Consistent with this possibility, varanopid fossils have been found in a variety of horizons including dry up-land environments (e.g. *Orovenator* and *Mycterosaurus*; MacDougall *et al.* 2017), and forests (*Ascendonanus*; Spindler *et al.* 2018) and do not appear to have been limited to tropical, wet environments, as posited for other 'pelycosaur'-grade synapsids (Kemp 2006). Varanopids were therefore already adapted for a changing climate and increasingly seasonal environments, such as the semi-arid alluvial plains of the Abrahamskraal Formation of South Africa (*Elliotsmithia* and *Heleosaurus*; Smith *et*

al. 1993). As early reptiles, varanopids are no longer an exception to the 'pelycosaur'/ therapsid transition, and they survive into the latest middle Permian as contemporaries of more closely related taxa (i.e. parareptiles and diapsids).

4.4.2 Are caseasaurs synapsids?

Based on my phylogenetic hypothesis, only caseids, among synapsids, extended their range beyond the early Permian with certainty: *Ennatosaurus*, the youngest caseid occurs in the Mezen assemblage (Wordian) of Russia. Derived caseids were specialised herbivores (Olson 1968, Angielczyk and Kammerer 2018), coexisting with small herbivorous therapsids, for example, in the Mezen assemblage (Kemp 2006). The eventual disappearance of caseids has been linked to the emergence of pareiasaurian parareptiles rather than therapsid herbivores, since both share a similar body-plan and dental morphology and were therefore more plausible as competitors (Maddin *et al.* 2008). My Templeton tests are unable to reject possible alternative phylogenetic positions of caseasaurs as either stem-amniotes or stem-sauropsids, (see above). These alternatives are therefore statistically equally well supported by the data as the most parsimonious hypothesis that caseasaurs belong within a monophyletic Synapsida. I also find very low posterior probabilities for a monophyletic Synapsida, inclusive of caseasaurs, in both the Mkv (no ages) and FBD model Bayesian analyses, the caseasaurs and all other synapsids form a polytomy when posterior probabilities below 60 are collapsed (Figs. 4 and 6).

In respect to the 'pelycosaur'/therapsid replacement hypothesis, this implies a possible scenario where all 'pelycosaur'-grade synapsids were extinct by the latest Cisuralian, and the transition to the therapsid dominated faunas of the middle and late Permian were the result of a complete and relatively rapid demise of the three remaining early synapsid clades of ophiacodontids, edaphosaurids and sphenacodontians (also see Brocklehurst *et al.* 2017).

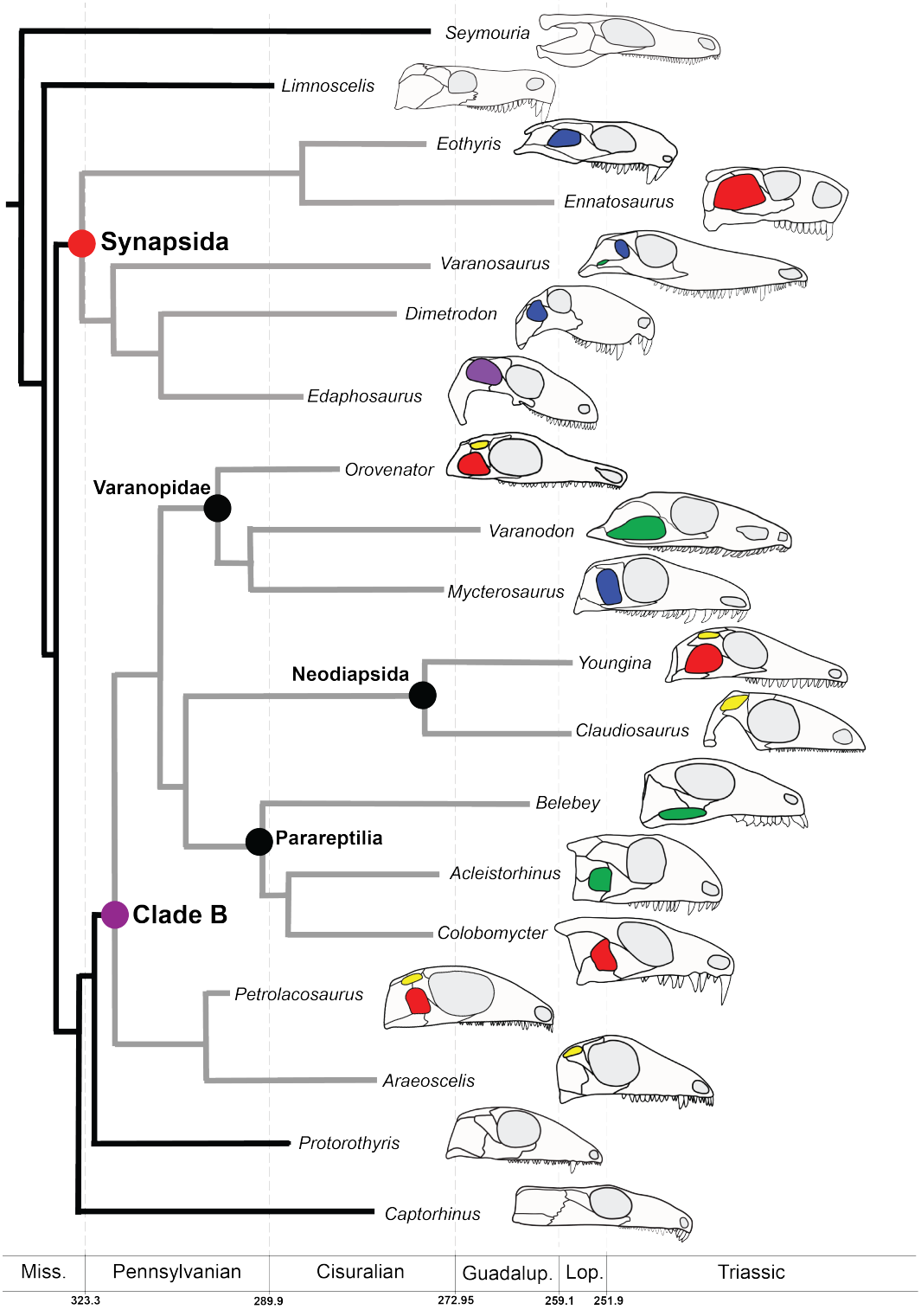


Figure 8: Simplified phylogeny based on this study indicating the origins of temporal fenestration in early amniotes. Black lines indicate lineages where fenestration is absent, grey lines indicate where fenestration is present. Key to fenestration types: Blue = type 1, red = type 2, mauve = type 3, green = type 4, yellow = type 5 (see chapter 3 for details of fenestration types). Abbreviations: Miss.= Mississippian, Guadalup.= Guadalupian, Lop.= Lopingian. Skulls are not drawn to scale.

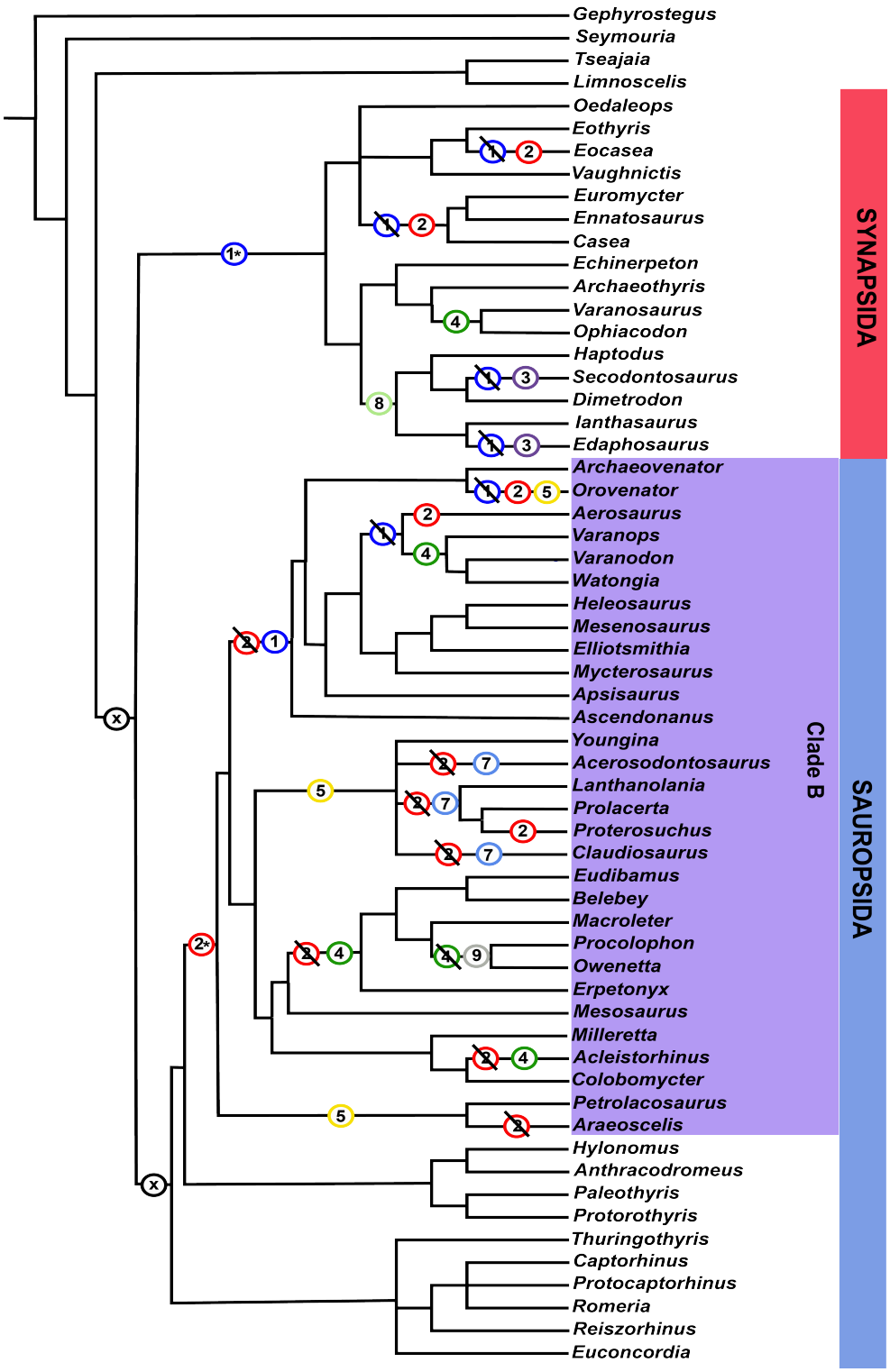


Figure 9: Phylogeny based on maximum parsimony from this study, optimised for the types of fenestration patterns detailed in chapter 3. Key to fenestration types: Blue = type 1, red = type 2, mauve = type 3, green = type 4, yellow = type 5, light blue = type 7, light green = type 8, grey = type 9. Black circles with x denotes fenestration absent. Figures with asterisk indicate putative ancestral condition of clade

4.4.3 Temporal fenestration

Based on the traditional phylogenetic hypothesis (Fig.1), three major clades of early amniotes possess independently acquired fenestrae; synapsids, diapsid and parareptiles. When the presence of temporal fenestration is optimised based on the new phylogenetic hypothesis, the acquisition of temporal fenestration is implied only in two major clades; Synapsida and the sauropsid Clade B that includes varanopids, diapsids and parareptiles (Figs. 8, 9).

This poses intriguing questions in respect to the condition of *Mesosaurus*, recovered in this study as a basal parareptile. If, as posited by some studies (Modesto 2006, MacDougall *et al.* 2018) temporal fenestrae are absent in *Mesosaurus*, this can only be due to a secondary loss. Alternatively, the presence of temporal fenestrae in *Mesosaurus*, as argued by other studies (Piñeiro *et al.* 2012, Laurin and Piñeiro 2017), may be plesiomorphic for the group, rather than synapomorphic as implied by others (Cisneros *et al.* 2004).

4.4.4 Position of *Mesosaurus*

The maximum parsimony and both Bayesian analyses recover *Mesosaurus* as a parareptile. The results of the Mkv (no ages) analysis recover a broadly unresolved, but monophyletic, Parareptilia, which includes *Mesosaurus*. In the FBD model analysis, *Mesosaurus* is the sister taxon to all other parareptiles, a position also recovered in several previous studies (Modesto 2006, Reisz *et al.* 2007, Tsuji *et al.* 2010, Modesto *et al.* 2012, Tsuji *et al.* 2012, MacDougall and Reisz 2012, 2014, MacDougall *et al.* 2016). Some analyses have proposed alternative phylogenetic positions for *Mesosaurus*. Laurin and Reisz (1995) found *Mesosaurus* to be a sister taxon of all other sauropsids, and Hill (2005) as the sister taxon to all other amniotes. Recently, Laurin and Piñeiro (2017) reassessed the position of *Mesosaurus*, based on the dataset of Laurin and Reisz (1995), reaffirming the hypothesis of a sister taxon relationship to all other sauropsids. This study scored *Mesosaurus* as possessing temporal fenestration, based on observations from previous work (Piñeiro *et al.* 2012), contrary to the view of Modesto (2006), who considered that temporal fenestration was absent in *Mesosaurus*. MacDougall *et al.* (2018), although scoring this taxon as lacking temporal fenestration, attempted to resolve the issue by removing all characters concerned with temporal fenestration from their dataset, and comparing the results to an analysis including fenestration characters. Both tree topologies recovered *Mesosaurus* in the same position, as sister taxon to all other parareptiles, and this result was repeated for an analysis where *Mesosaurus*

was scored as polymorphic for temporal fenestration (MacDougall *et al.* 2018).

In my scorings for this study I have followed the view of Modesto (2006), that *Mesosaurus* lacks temporal fenestration. However, I conducted an additional parsimony analysis to compare alterative phylogenetic hypotheses for *Mesosaurus* using TNT v.1.5beta. All characters concerned with the temporal region and fenestration were reviewed, and scored in accordance with the morphology described by Piñeiro *et al.* (2012) and Laurin and Piñeiro (2017) (my characters 71, 72, 77, 78, 79 and 84). Analysis of this modified dataset resulted in 16 MPTs, with a tree length of 1379 steps (1 step shorter than the original analysis). The strict consensus tree recovered a topology identical in all respects to the original analysis. Therefore, the position of *Mesosaurus* recovered in my analysis is not predicated by the presence or absence of temporal fenestration. However, based on the parareptile/neodiapsid sister relationship, the presence of temporal fenestration in *Mesosaurus* would be a more parsimonious explanation of the results.

4.4.5 Turtles as diapsids

The diapsid affinity of turtles (Testudinata), as the extant sister taxon of Archosauria, is now widely accepted based on molecular phylogenetic studies (Chiari *et al.* 2012, Crawford *et al.* 2012, Field *et al.* 2014). However, the morphological evidence and fossil record continues to suggest to some researchers that a parareptilian origin is still open to debate (e.g. Lyson *et al.* 2013, Laurin and Piñeiro 2017). *Eunotosaurus africanus* from the middle Permian of South Africa has been variously described as a chelonian (Romer 1956), a 'captorhinomorph' (Cox 1969, Keyser and Gow 1981) and more recently as a parareptile (Gow and de Klerk 1997, Rubidge *et al.* 1999). Several recent papers have provided evidence consistent with the hypothesis that *Eunotosaurus* is a stem-group turtle, and also that it shares features with younger stem-group turtles like *Odontochelys* and *Pappochelys* (Lee 2013, Bever *et al.* 2015, Schoch and Sues 2015). However, the hypothesis that *Eunotosaurus* is a stem-group turtle does not clarify the position of turtles within Amniota, with questions over the possible systematic bias of the molecular data, and the highly apomorphic morphology of the turtle bauplan (Joyce 2015). Nevertheless, detailed μCT analysis of the skull of *Eunotosaurus* has revealed the presence of an upper temporal fenestra in juvenile specimens, suggesting that the fenestra closed during ontogeny due to the expansion of the dermal roof elements (Bever *et al.* 2015). Based on this evidence, Bever *et al.* (2015) reassessed the affinities of *Eunotosaurus* and recovered it as a diapsid rather than a parareptile. This would appear to give some degree of morphological support to the hypothesis of

diapsid affinities for turtles, although neither hypothesis, i.e. as a stem-group diapsid or a parareptile, is consistent with the molecular analysis of a sister taxon relationship with archosaurs.

My phylogenetic results also shed some light on the possible causes of some of these historical uncertainties. Both the parsimony and Bayesian analyses of my dataset suggest a sister relationship between diapsids and parareptiles, and this is supported by statistical hypothesis tests (Table 4.4). This indicates that parareptiles and neodiapsids shared a common ancestor that probably possessed temporal fenestration. In addition, the divergence age between these clades may be 10 million years younger than the traditional parareptile/eureptile divergence implies (see 'clade divergence and ghost lineages' above). The presence of parareptile-like and diapsid-like traits in combination among some fossil taxa, such as *Mesosaurus* and *Eunotosaurus*, is consistent with the hypothesis of a close relationship between Parareptilia and Diapsida (as also suggested by Laurin and Piñeiro 2017).

4.5 Conclusions

The purpose of the phylogenetic analyses in this chapter was to provide a vigorous and detailed review of early amniote interrelationships using a broad-based dataset of early amniotes. The specific goal, as outlined in chapter 2, was to test the hypothesis that varanopids formed a monophyletic clade with the early Permian amniote *Orovenator mayorum*. The results fully support my initial hypothesis and, moreover, confirm the position of varanopids within Sauropsida.

The results of my phylogenetic analyses also have implications for several other questions in early amniote evolution, including:

-the period of co-occurrence of a 'pelycosaur' to a therapsid global fauna is significantly reduced, implying a short macroevolutionary transition across the Cisuralian/ Guadalupian boundary.

-The recovery of a parareptile/neodiapsid sister group is a relatively novel finding, recently posited by Laurin and Piñeiro (2017), with implications for our current understanding the affinities of *Eunotosaurus* and the phylogeny of stem-turtles.

Chapter 5

Conclusions and future research directions

In this thesis, I have provided a brief overview on the history of research into early amniote systematics and discussed some of the macroevolutionary transitions that led to the emergence of amniotes in the Lower Pennsylvanian of the Carboniferous. I have also discussed the relationships of early amniotes with other Carboniferous and Permian tetrapods. In this chapter, I summarise the results of my research, and discuss possible directions of future research.

5.1 Summary of conclusions

In chapter 2, I described the anatomy of the early neodiapsid *Orovenator mayorum* (Reisz *et al.* 2011) using 3-D digital visualisation from μCT scans. Both specimens of *Orovenator mayorum* are small, some three or four centimetres in length. The exceptional preservation of these specimens from the Dolese quarry, Richards Spur, Oklahoma, is typical of the material from the fissure fills in the Ordovician limestone (MacDougall *et al.* 2017, Reisz pers. comm.). This made them particularly well suited to μCT scanning. The μCT data allowed me to examine cranial elements in very high resolution. I was able to use this data to redescribe the cranial morphology of *Orovenator* in some detail. It also allowed me to reconstruct the palate, noting the transversely narrow suborbital fenestra, the bifurcated anterior vomers, and the autapomorphic medial buttressing of the maxilla by the lacrimal. The complete left septomaxilla is one of the best examples of this element in early amniotes. Together with the tracing of the pathways of the lacrimal canal, this data will prove useful to researchers in the evolution of the vomeronasal organ in vertebrates.

I have also presented hypotheses in the palaeoecology of *Orovenator*, based on a reconstruction of the orbit and the anatomy of the snout, suggesting that *Orovenator* may have been a nocturnal predator, exploring the substrate for invertebrates. I discussed the 16 similarities that *Orovenator* shares with varanopids, as well as the potential synapomorphies that are present in both varanopids and sauropsid taxa other than *Orovenator*. A phylogenetic analysis of the interrelationships of *Orovenator* with both varanopids and sauropsids was performed, using the existing dataset of Reisz *et al.* (2010). I concluded from this analysis that *Orovenator* forms a clade with varanopids, and I proposed that this clade is positioned within Sauropsida.

In my concluding comments to chapter 2, I expressed some concern over the emphasis placed on temporal fenestration and its characterisation in the systematic studies of early amniotes that had prevailed since Osborn (1903). As Romer (1956:467) noted of Osborn's classification "use of the temporal arches was to lead to fruitful results but, as may be seen in retrospect, was (and is) fraught with danger", adding "fenestrae might arise independently and vary greatly, in parallel fashion".

My work on chapter 3 began as a series of notes to improve my understanding of the anatomy of temporal fenestrae across a wide range of early amniotes. I realised that the bones that formed the fenestrae were highly variable, not just between major groups, but within them. Based on the contributing elements, there are four difference types of 'lower' temporal fenestrae in the traditional groups that comprise 'pelycosaur'-grade synapsids, and three in parareptiles, not including various forms of emargination in both groups. In chapter 3, I presented a systematic review of temporal fenestration in early amniotes, highlighting a number of conceptual problems in the traditional coding. I devised a series of characters that use the points of contact of temporal bones and the free margins defined by the openings as the main criteria of primary homology.

The resulting series of seven characters were incorporated in to my new early amniote character-taxon matrix, which is discussed in detail in chapter 4. I then substituted these seven characters with the traditional presence/absence characters, including characters for the contribution of the postorbital and quadratojugal to the lower temporal fenestra, and performed a parsimony analysis on both datasets. The tree topology of the revised dataset was poorly resolved when compared to the topology of the dataset including the seven new fenestration characters. I concluded that detailed observation and characterisation of temporal fenestrae plays an important role in resolving phylogenies of early amniotes, and that future phylogenetic studies on early amniotes should consider replacing the traditional method of presence/absence coding with the new characters proposed in chapter 3.

In my final research chapter, I presented the results of a new character-taxon matrix of 286 characters, including 19 new characters, and 60 taxa. Each character was chosen after a thorough review of phylogenetic research across a range of stem-group and crown-group amniotes from 1982 to the present date. The operational taxonomic units were selected to ensure that basal members of each clade were represented. For the phylogenetic analyses I used both parsimony and probabilistic Bayesian methods. One of the aims of this study was to test the hypothesis posited in chapter 2, that *Orovenator* formed a clade with varanopids within Sauropsida. My results confirm this initial hypothesis. Some unexpected results of my analysis were also recovered. I found parareptiles to be the sister taxon of neodiapsids, with captorhinids as the early diverging sauropsid clade, and the sister taxa of the crownward group comprised of 'protorothyridids' + diapsids + parareptiles + varanopids.

The main implications of my new topology are two-fold, (i) the co-occurrence of the 'pelycosaur'-grade synapsids and therapsids in the middle Permian is significantly reduced with the removal of varanopids from Synapsida and (ii) the origins of temporal fenestration are more parsimoniously explained with parareptiles as a sister taxon to neodiapsids. In addition, I recover *Mesosaurus* as a basal parareptile rather than a basal sauropsid, regardless of the scoring for temporal fenestration.

5.2 Direction of future research

5.2.1 Microsaurs and early amniotes

μCT data of a partial growth series of nine skulls of the lysorophian lepospondyl *Brachydectes newberryi* from the early Permian of Nebraska and Kansas revealed remarkable detail of the neurocranial anatomy (Pardo and Anderson 2015). Pardo and Anderson noted a number of derived characters in the neurocranium and suspensorium of *Brachydectes* that are shared by early amniotes, although no phylogenetic analysis was attempted for this study. In a later study of the aïstopod lepospondyls *Lethiscus stocki* and *Coloraderpeton*, also using μCT data, a phylogenetic analysis was conducted, including *Brachydectes* (Pardo *et al.* 2017). The results of this analysis recovered aïstopods as basal tetrapods, and lysorophian and recumbirostran microsaurs as crown-group amniotes (see chapter 1, Fig.4).

Included in this study was the basal captorhinid *Opisthodontosaurus carrolli*, a taxon named by Reisz *et al.* (2015) after new skull and post-cranial material showed that similar dentigerous jaw elements had been mistakenly assigned to the recumbiros-

tran lepospondyl *Euryodus primus*. In this study Reisz and colleagues noted that the mistaken identity of the original material indicted a 'dramatic level of convergence' between microsaurs and captorhinids (Reisz *et al.* 2015:1). In the analysis of Pardo *et al.* (2017) only one other captorhinid was included (*Captorhinus laticeps*) and only one diapsid (*Petrolacosaurus*). *Opisthodontosaurus* was recovered as the taxon most closely related to *Captorhinus laticeps* (see chapter 1, Fig. 4).

I suggest that a more robust test of this intriguing hypothesis would be to include microsaurs into my new dataset, along with an expanded out-group of non-recumbirostran lepospondyls, anthracosaurs and temnospondyls. This would require an augmented character list to incorporate anamniote traits. In a traditional amniote phylogeny, parareptiles are the sister taxon to Eureptiles, which include captorhinids. Since parareptiles are excluded from the Pardo *et al.* (2017) analysis, the position of recumbirostran microsaurs within Amniota must be considered uncertain. It may be that microsaurs, should they prove to be early amniotes, are more closely related to diapsids than parareptiles. This would indeed be the case if microsaurs are the sister taxon to the traditional definition of eureptiles. However, in my new phylogeny, microsaurs may represent an early diverging, basal sauropsid group, closer to the basal amniote dichotomy with synapsids.

5.2.2 *Eunotosaurus* and stem-group turtles

The position of *Eunotosaurus africanus* has been briefly discussed in chapter 4. I believe it would be an interesting project to include *Eunotosaurus*, together with several stem-group turtles (e.g. *Pappochelys*, *Proganochelys* and *Odontochelys*) into an augmented dataset together with a revised character list. It would be desirable, I believe, to include a number of more derived archosauromorphs, and some basal lepidosauromorphs.

In tandem with this, I would like to examine in more detail the cranial and neurocranial anatomy of South African taxa, which may be closely related to *Eunotosaurus*. I have recently been working in collaboration with colleagues at the Evolutionary Studies Institute, University of Witwatersrand, Johannesburg. We have been able to arrange for several skulls of key South African taxa to be scanned at the European Synchrotron Radiation Facility in Grenoble. This will enable a very high resolution study of these specimens, with exceptional fossil/matrix contrast. The taxa include the procolophonids *Procolophon* and *Owenetta*, the diapsids *Youngina* and *Prolacerta*, and, I think crucially, a number of millerettid skulls and the only known specimen of the putative basal lepidosauromorph *Paliguana*.

There have been no extensive studies on the skull of millerettids since Watson (1957) and Gow (1972), yet this taxon is rather enigmatic, often recovered as a sister taxon to *Eunotosaurus* (MacDougall and Reisz 2012, MacDougall *et al.* 2017), or as a sister taxon to procolophonoids (Laurin and Pinero 2017), or as the basal most parareptile after *Mesosaurus* (Modesto *et al.* 2009, MacDougall *et al.* 2018). In my analysis it is recovered as a sister taxon to lanthanosuchoids (parsimony and Mkv model) or to procolophonoids (FBD model).

Very little is known of the skull of *Paliguana*. In 2016, the skull was μCT scanned at the ESI, and I completed the segmentation work. The results allowed some clearer understanding of the structure of the temporal region, but the contrast with the matrix was generally poor. The preliminary results of the synchrotron scan are very encouraging, however, and I am hopeful that this will provide valuable new information on the anatomy of this key fossil. I believe that this potential project, together with my new dataset on early amniotes augmented with *Eunotosaurus* and stem-group turtles, will provide interesting results.

In my thesis, I have argued that applying μCT analysis to new and previously examined fossil specimens can reveal new data, allowing us to improve and augment phylogenetic matrices. This is an increasingly popular approach, partly due to the widespread availability of imaging resources. I believe that, prompted by advances in X-Ray tomography and new models of probabilistic methods, systematic palaeontology is entering a new phase. The paradigms of established relationships are being challenged, and regardless of whether or not new hypotheses achieve consensus, they have a galvanising effect on phylogenetic studies. We are still unravelling the complexities of tetrapod phylogeny during the Carboniferous and early Permian. It is an exciting time to be involved in this fascinating area of research.

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Appendix 1 - Character List

The character list used in the phylogenetic analysis has been compiled from a number of sources that reflect the broad scope of the terminal taxa. I list below each character with notes on its derivation and optimisation, together with any comments on the interpretative issues that have some bearing on the past or current scoring. The institutional abbreviation and accession number indicate all specimens personally examined by the author. Characters relating to the present study are prefixed 'ch'; characters relating to referenced studies are prefixed 'c'.

Cranial characters

1. Skull, antorbital-postorbital length ratio: antorbital part of skull (anterior margin of orbit to anteriormost extremity of skull) equal to or longer than the postorbital part (posterior margin of orbit to posteriormost extremity of skull) (0); postorbital part longer than antorbital part (1)

Modified from Rieppel (1994 c.9), Laurin and Reisz (1995 c.32), Modesto (1995 c.17), deBraga and Rieppel (1997 c.19), Müller (2004 c.8), Reisz *et al.* (2010 c.6), Benson (2012 c.2), Modesto *et al.* (2015 c.47).

State 1 is present in caseasaurs (Maddin *et al.* 2008) and some captorhinids (e.g. *Protocaptorhinus pricei*, MCZ 1478, Clack and Carroll 1973 and *Romeria texana*, MCZ 1480, Clark and Carroll 1973). Due to the increased length resulting from the strong anterodorsal inclination of the posterior margin of the skull in *Varanodon*, this taxon is scored as (1), in accordance with Reisz *et al.* 2010.

Unambiguous: *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), Caseasauria (0→1). DELTRAN: *Varanodon agilis* (0→1). ACCTRAN: *Varanodon* + *Watongia* (0→1).

2. Skull, shape of antorbital region: mediolaterally broad, nasal largely dorsal element (0); mediolaterally narrow and dorsoventrally tall, nasal has nearly vertical contribution to snout (1)

From Modesto (1994 c.9), Reisz (1998 c.12), Reisz and Dilkes (2003 c.12), Maddin *et al.* (2006 c.43), Reisz *et al.* (2010 c.5), Benson (2012 c.3), Spindler *et al.* (2018 c.4).

State (1) is considered as a synapomorphy of 'eupelycosaur'-grade synapsids, i.e. non-therapsid synapsids excluding caseasaurs (Reisz 1986, Kemp 2005, Brocklehurst *et al.* 2016).

Unambiguous: Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1). DELTRAN: *Archaeovenator hamiltonensis* (0→1), Mycterosaurinae + Varanodontinae (0→1). ACCTRAN: *Varanodon* + *Watongia* (0→1), *Orovenator mayorum* (1→0).

3. Skull, extensive dermal sculpturing of skull roof: present (0), absent or weakly developed (1)

Modified from Laurin and Reisz (1995 c.38), Reisz *et al.* (2007 c.38), Maddin *et al.* (2008 c.48), Reisz *et al.* (2009 c.1), Benson 2012 (c.11), Tsuji *et al.* (2102 c.38), MacDougall and Reisz (2014 c.54).

This character describes the widely distributed pattern of pits, grooves and ridges found on the skull roof. A binary version of this character was adopted by MacDougall and Reisz 2014 (c.54), establishing the presence/absence of dermal sculpturing, with a new character to describe the nature of the sculpturing (MacDougall and Reisz 2014 c.55), and modified versions of these characters are included in the present study (the present character and ch.4 below). This character should not be confused with the presence or absence of circumorbital ornamentation in the form of tuberous ridges (ch.65 and ch.79 below).

Unambiguous: *Hylonomus lyelli* (0→1),*Macroleter poezicus* (1→0), *Milleretta* + *Colobomycter* + *Acleistrohinus* (1→0), Diadectomorpha (0→1),*Ophiacodon* spp (0→1), *Vaughnictis smithae* (0→1). DELTRAN: *Araeoscelis* spp (0→1), *Edaphosaurus boanerges* (0→1), clade C (0→1), Sphenacodontidae (0→1), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: *Haptodus garnettensis* (1→0), clade

B (0→1),Sphenacodontia + Edaphosauridae (0→1), *Petrolacosaurus kansensis* (1→0), *Thuringothyris mahlendorffae* (0→1).

4. Skull, dermal sculpturing, if present: composed of ridges and pits arranged in a honeycomb pattern (0); an irregular distribution of rounded pits (1); anastomosing narrow grooves and low ridges (2); deep pits with prominently raised knobs (3); inapplicable, sculpturing absent or weakly developed (-)

Modified from Laurin and Reisz (1995 c.38), Dodick and Modesto (1995 c.25), MacDougall and Reisz (2014 c.55), Reisz and Fröbisch (2014 c.48).

Unambiguous: *Ennatosaurus tecton* (1→2), *Gephyrostegus bohemicus* (0→3), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→2), *Colobomycter* + *Acleistrohinus* (3→1), *Paleothyris acadiana* (0→2), *Reiszorhinus olsoni* (0→2). DELTRAN: Parareptilia (0→3), Caseasauria (0→1), *Petrolacosaurus kansensis* (0→2). ACCTRAN: clade C (2→3), clade B (0→2), Synapsida (0→1).

5. Skull, posterior margin in dorsal view: roughly straight (0); with a single, median embayment (1); embayed bilaterally (2)

Modesto (1999 c.125), Tsuji (2006 c.41), Modesto *et al.* (2015 c.58).

Unambiguous: *Hylonomus lyelli* (2→0), clade D (2→1), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (2→1), Amniota (0→2),Sphenacodontia + Edaphosauridae (2→1), *Romeria* spp (1→2). DELTRAN: Diadectomorpha (0→1), *Eudibamus* + *Belebey* (1→0), Procolophonoidea (1→0). ACCTRAN:*Macroleter poezicus* (0→1), Diadectomorpha + Amniota (0→1), Bolosauridae + Procolphonoidea + *Macroleter* (1→0).

6. Teeth, distal recurvature of marginal teeth: present (0); absent (1)

Modified from Reisz *et al.* (1998 c.1), Maddin *et al.* (2008 c.67), Benson (2012 c.41), Reisz and Fröbisch (2014 c.67), Spindler *et al.* (2018 c.99).

In the present study, recurvature of marginal teeth is defined as the apex of the tooth being situated

distal to the distal margin of the crown base. When character state (0) is present the distal margin appears concave in lateral view. Character state (1) is scored in taxa possessing marginal teeth that that have a dorsoventrally straight distal margin in lateral view, even when a dorsoventrally convex mesial margin is present. A slight distal recurvature of the marginal dentition (state 0) is present in diadectomorphs (e.g. *Tseajaia*, Moss 1972 on dentary teeth only; *Limnoscelis*, Berman *et al.* 2010), *Seymouria* and *Gephyrostegus* (Klembara *et al.* 2005, 2014). Recurvature of marginal teeth (state 0) is also present in many early amniotes groups, including ophiacodontids, sphenacodontians, mycterosaurines, varanodontines, diapsids and some parareptiles.

Unambiguous: *Claudiosaurus germaini* (0→1), *Colobomycter pholeter* (0→1), *Mesosaurus tenuidens* (0→1), Amniota (0→1), *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (1→0), Sphenacodontia (1→0), *Eudibamus* + *Belebey* (0→1), *Procolophon trigoniceps* (0→1), *Reiszorhinus olsoni* (1→0), *Vaughnictis smithae* (1→0). DELTRAN: clade C (1→0), *Petrolacosaurus kansensis* (1→0). ACCTRAN: *Araeoscelis* spp (0→1), clade B (1→0).

7. Teeth, distal recurvature of marginal teeth, if present: slight to moderate (0); strong (1); inapplicable, distal recurvature absent (-)

Modified from Reisz *et al.* (1998 c.1), Maddin *et al.* (2008 c.67), Ezcurra *et al.* (2014 c.2), Benson (2012 c.41), Spindler *et al.* (2018 c.100).

Strong recurvature of the margin dentition (state 1) is present in mycterosaurines, varanodontines and archosauromorphs. In all other taxa scored as state (0) in ch.6 above, the recurvature is slight to moderate (state 0)

Unambiguous: Mycterosaurinae + Varanodontinae (0→1), Archosauromorpha (0→1).

8. Teeth, marginal dentition, cutting edges (carinae) on the mesial and distal surfaces: absent or only present distally (0); present (1)

From Reisz *et al.* (1992 c.58), Laurin (1993 c.64), Berman *et al.* (1995 c.66), Modesto (1995 c.2), Maddin *et al.* (2006 c.3); Mazierski and Reisz (2010 c.2), Fröbisch *et al.* (2011 c.50).

Unambiguous: *Colobomycter pholeter* (0→1), *Euconcordia cunninghami* (0→1), *Limnoscelis plaudis* (0→1),*Macroleter poezicus* (0→1), Mycterosaurinae + Varanodontinae (0→1). DELTRAN: Sphenacodontidae (0→1), Edaphosauridae (0→1), Archosauromorpha (0→1). ACCTRAN: *Haptodus garnettensis* (1→0),Sphenacodontia + Edaphosauridae (0→1), *Lanthanolania* + Archosauromorpha (0→1).

9. Teeth, serrations on crown of marginal teeth: absent (0); present (1)

Modified from Gauthier *et al.* (1988 c.108), Modesto *et al.* (2001 c.32), Reisz and Dilkes (2003 c.32), Campione and Reisz (2010 c.3), Ezcurra (2014 c.3).

Character state 1 is present in *Dimetrodon* (Romer and Price 1940), *Edaphosaurus* (Modesto 1995), *Mesenosaurus*, Reisz and Berman 2001) and *Proterosuchus* (Ezcurra *et al.* 2013). Serrations are present in the ophiacodontid *Archaeothyris*, although they are found only on the lingual surface of the anterior maxillary teeth (Reisz 1972).

Unambiguous: *Archaothyris florensis* (0→1), *Dimetrodon* spp (0→1), *Proterosuchus* spp (0→1). DELTRAN: *Edaphosaurus boanerges* (0→1), *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (0→1). ACCTRAN: Edaphosauridae (0→1), Mycterosaurinae (0→1).

10. Teeth, lateral compression of marginal dentition: only apicially or nowhere (0); over two-thirds of tooth (1)

Modified from Reisz (1998 c.1), Reisz and Dilkes (2003 c.1), Reisz *et al.* (2010 c.4), Benson (2012 c.40), Ezcurra (2014 c.4).

Extensive labiolingual compression of the marginal dentition is present in derived mycterosaurines and in archosauromorphs. It is also present in the captorhinid *Reiszorhinus* (Sumida *et al.* 2010) and the sphenacodontid *Dimetrodon* (Romer and Price 1940).

Unambiguous: *Dimetrodon* spp (0→1), Mycterosaurinae + Varanodontinae (0→1), *Reiszorhinus olsoni* (0→1). DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

11. Teeth, multiple apical cusps on marginal dentition: absent (0); present (1)

Modified from Maddin *et al.* (2008 c70), Reisz *et al.* (2009 c.21), Benson (2012 c.44), Reisz and Fröbisch (2014 c.70).

Previous studies presented this character as a multistate count of apical cusps. In the present study this approach is parsimony uninformative, since the condition of multiple cusps is present only in caseids (e.g. *Casea*, *Euromycter* and *Ennatosaurus*, Maddin *et al.* 2008).

Unambiguous: Caseidae (0→1).

12. Premaxilla, number of teeth: five or more (0); four or fewer (1)

Carroll and Currie (1991 c.27), Berman *et al.* (1995 c.70), Modesto *et al.* (2001 c.2), Reisz and Dilkes (2003 c.41) Reisz *et al.* (2010 c.8), Benson (2012 c.17), Ezcurra (2014 c.8), Spindler *et al.* (2018 c.17).

Unambiguous: *Aerosaurus* spp (0→1), *Dimetrodon* spp (0→1), *Mycterosaurus longiceps* (0→1), *Milleretta* + *Colobomycter* + *Acleistrohinus* (0→1), Diadectomorpha (0→1), Caseasauria (0→1), *Eudibamus* + *Belebey* (0→1), *Procolophon trigoniceps* (0→1), *Youngina capensis* (0→1). DELTRAN: *Archaeovenator hamiltonensis* (0→1), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: *Archaeovenator hamiltonensis* (0→1), *Thuringothyris mahlendorffae* (0→1).

13. Premaxilla, orientation of ascending (supranarial) process: subvertical at base, then slopes posterodorsally (0); slopes anterodorsally, overhanging tooth row ('rostral process' present) (1); slopes posterodorsally at an angle $< 75°$(2)

Modified from Brinkman and Eberth (1983 c.5), Reisz (1986 table 3a), Reisz and Dilkes (2003 c.51), Maddin *et al.* (2006 c.6), Maddin *et al.* (2008 c.1), Benson (2012 c.14), Spindler *et al.* (2018 c.16).

In previous studies character state (1) has been has been scored as present in caseasaurs and the diadectomorph *Limnoscelis* (Maddin 2008, Benson 2012, Spindler *et al.* 2018). Spindler *et al.* (2018) also scored this state for *Tseajaia*, although I consider this to be ambiguous given the compression of the snout and the displacement of the anterior premaxillary tooth (Moss 1972). A rostral process of the

premaxilla (state 1) has been acquired independently in *Orovenator* and *Procolophon* (Cisneros 2008, Ford and Benson 2018). Langston and Reisz (1981) argued that a slight anterior slope (equivalent to a 'rostral process' in other taxa) of the premaxilla in *Aerosaurus wellesi* was due to post-mortem distortion. Brinkman and Eberth (1983) disagreed with this view, suggesting this feature was present in both *Aerosaurus* and *Varanops*. Later studies have been consistent in scoring the rostral process as absent in one or both these taxa (Reisz and Dilkes 2003, Maddin *et al.* 2008, Benson 2012, Spindler *et al.* 2018). Close examination of *Varanops* during the present study (MCZ 1961) confirms that a slight anterodorsal inclination of the premaxilla is present. I also concur with Brinkman and Eberth (1983) in that there is no clear evidence for distortion of the premaxilla in *Aerosaurus*. Consequently both taxa are scored as (1) in the present study. An acute posterodorsal slope of premaxilla, state (2), is an autapomorphy of derived ophiacodontids (e.g. *Varanosaurus*, FMNH PR 1670, Berman *et al.* 1995 and *Ophiacodon*, MCZ 1366).

Unambiguous: Caseasauria (0→1), *Orovenator mayorum* (0→1), *Procolophon trigoniceps* (0→1). DELTRAN: *Aerosaurus* spp (0→1), *Limnoscelis plaudis* (0→1), *Varanosaurus* + *Ophiacodon* (0→2), *Varanops brevirostris* (0→1). ACCTRAN: Diadectomorpha (0→1), Ophiacodontidae (0→2), *Varanodon* + *Watongia* (1→0), Varanodontinae (0→1).

14. Premaxilla, subnarial process excludes maxilla from margin of external naris or septomaxilla: absent (0); present (1)

Modified from Reisz *et al.* (2009 c.19), Benson (2012 c.16).

In the current taxon list *Tseajaia*, eothyridids, archosauromorphs and *Procolophon* possess a posterodorsal spur of the subnarial process of the premaxilla, which prevents the maxilla from contacting the septomaxilla or participating in the external naris (state 1). This morphology is absent in all other taxa where known (state 0).

Unambiguous: Eothyrididae (0→1), Archosauromorpha (0→1), *Procolophon trigoniceps* (0→1), *Tseajaia campi* (0→1).

15. Premaxilla, posterior surface of subnarial process, if present: contacts the lacrimal only (0); contacts the nasal (1); inapplicable, subnarial process does not exclude maxilla

from external naris or septomaxilla (-)

Modified from Gauthier *et al.* (1988 c.2), Berman *et al.* (1995 c.11), Modesto *et al.* (2001 c.3), Müller 2004 c.2), Reisz *et al.* (2009 c. 19), Reisz *et al.* (2010 c.12), Spindler *et al.* (2018 c.15).

In eothyridids and the diadectomorph *Tseajaia* a posterodorsal spur of the subnarial process of the premaxilla contacts the lacrimal only posterior to the external naris (state 0)(MCZ 1161, Reisz *et al.* 2009, Moss 1972). In archosauromorphs the posterodorsal spur of the subnarial process of the premaxilla contacts the nasal (state 1)(e.g. *Prolacerta*, Modesto and Sues 2004; *Proterosuchus*, Ezcurra and Butler 2015). A similar process is also present in *Procolophon* (Carroll and Lindsey 1985).

DELTRAN: clade D (0→1). ACCTRAN: Sauropsida (0→1).

16. Premaxilla, supranarial (dorsal) process, extending posteriorly level with or beyond the posterior margin of the external naris: absent (0), present (1)

Modified from Reisz (1992 c.5), Laurin (1993 c.2), Fröbisch *et al.* (2011 c.1).

An anteroposteriorly long dorsal process of the premaxilla is present in ophiacodontids (Berman *et al.* 1995, Romer and Price 1940), *Mesenosaurus* (Reisz and Berman 2001), *Araeoscelis*, *Orovenator* and early diapsids (Carroll 1981, Reisz *et al.* 1984, Ford and Benson 2018).

Unambiguous: *Araeoscelis* spp (0→1), *Mesenosaurus romeri* (0→1), *Orovenator mayorum* (0→1), *Proterosuchus* spp (0→1). DELTRAN: *Claudiosaurus germaini* (0→1), *Varanosaurus* + *Ophiacodon* (0→1). ACCTRAN: Ophiacodontidae (0→1).

17. Premaxilla, supranarial (dorsal) process, suture with naris: single pronged or transversely flat (0); two-pronged (alary process present) (1)

Modesto *et al.* (2007 c.2), Modesto *et al.* (2014 c.2).

State 1 has been considered to be a synapomorphy of basal and derived captorhinids (Müller and Reisz 2005, Modesto *et al.* 2007). This state is also independently present in *Varanosaurus* (Berman

et al. 1995).

Unambiguous: Captorhinidae except *Thuringothyris* (0→1). DELTRAN: *Varanosaurus acutirostris* (0→1). ACCTRAN: *Varanosaurus acutirostris* (0→1).

18. Premaxilla, anteroventral slope of alveolar margin: absent (0); slight, less than 15°from horizontal (1); moderate, 15-45°from horizontal (1); strong, > 45°from horizontal (2)

Modified from Carroll and Currie (1991 c.16), Reisz (1992 c.3), Berman *et al.* (1995 c.3), Dodick and Modesto (1995 c.1), Dilkes (1998 c.6), Reisz *et al.* (2010 c.10), Fröbisch *et al.* (2011 c.96), Ezcurra *et al.* (2014 c.10), Benson (2012 c.13).

State (1) of this character is present in some caseasaurs (e.g. *Eothyris*, MCZ 1161, Reisz *et al.* 2009 and *Euromycter*, Reisz *et al.* 2010 Appendix S1 c.10) and diadectomorphs (Romer 1946, Moss 1972), as well as *Orovenator* and some parareptiles (e.g. *Acleistorhinus*, deBraga and Reisz 1996, Ford and Benson 2018). Derived captorhinids possess a more pronounced inclination, with up to 45°in *Labidosaurus* (Modesto *et al.* 2007). The extreme state of anteroventral inclination (state 2) is present only in *Proterosuchus* in the context of the present study, and as such is phylogenetically uninformative, but is included for information only.

Unambiguous: *Euromycter rutena* (0→1), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→2), Diadectomorpha (0→1), Sphenacodontia (0→1), *Orovenator mayorum* (0→1), *Proterosuchus* spp (0→3). DELTRAN: *Acleistorhinus pteroticus* (0→1), *Eothyris parkeyi* (0→1), *Milleretta rubidgei* (0→1), *Prolacerta broomi* (0→1). ACCTRAN: *Colobomycter pholeter* (1→0), *Milleretta* + *Colobomycter* + *Acleistrohinus* (0→1), Eothyrididae (0→1), *Lanthanolania* + Archosauromorpha (0→1).

19. Premaxilla, narial shelf: more or less sharp edge between lateral (= sculptured, if sculpture is present) surface of skull and ventral wall of naris (0); rounded ventral narial shelf that transitions smoothly into ventral edge of skull (1); inapplicable, premaxilla does not participate in narial shelf (-)

Modified from Reisz *et al.* (1998 c.2), Reisz and Dilkes (2003 c.2), Anderson and Reisz (2004 c.2),

Reisz and Laurin (2004 c.2), Reisz *et al.* (2009 c.5), Maddin *et al.* (2006 c.7), Campione and Reisz (2010 c.7), Ezcurra *et al.* (2014 c.11), Benson (2012 c.15), Spindler *et al.* (2018 c.14).

Character state 1 has been considered by previous studies as a synapomorphy of all 'varanopids' (i.e. basal and derived mycterosaurines plus varanodontines, Reisz *et al.* 1998, Reisz and Berman 2001, Reisz and Dilkes 2003, Anderson and Reisz 2004), and is also present in *Orovenator* (Ford and Benson 2018). However, Benson (2012) noted that a rounded narial shelf was present in the ophiacodontid *Varanosaurus*, and absent in the mycterosaurine *Heleosaurus* and in the varanodontines *Varanops* and *Varanodon*. Having examined the varanodontine specimens for the present study, I conclude that state (1) is indeed absent in *Varanops* (MCZ 1926), but that the condition in *Varanodon* is uncertain. I further consider the condition in *Heleosaurus* to be unknown, in accordance with the scoring of Botha-Brink and Modesto (2009).

ELTRAN: Varanopidae except *Ascendonanus* (0→1), *Varanops brevirostris* (1→0), *Varanosaurus acutirostris* (0→1). ACCTRAN: *Varanops* + *Varanodon* + *Watongia* (1→0), Varanopidae (0→1), *Varanosaurus acutirostris* (0→1).

20. Premaxilla, tooth size compared to marginal maxillary teeth: small or subequal to (non-caniniform) maxillary teeth (0); premaxillary teeth larger (1)

Modified from Gauthier *et al.* (1988 c.114), Reisz *et al.* (1992 c.60), Laurin (1993 c.6), (Modesto 1994 c.2), Modesto *et al.* (2007 c.34), Reisz *et al.* (2011 c.36), Benson (2012 c.18).

Diadectomorphs (Moss 1972, Berman *et al.* 2010), eothyridids (Reisz *et al.* 2009) and captorhinids (Modesto *et al.* 2007, Fox and Bowman 1966) all possess premaxillary teeth that are substantially larger than the non-caniniform maxillary teeth. This state is also shared by sphenacodontians (Romer and Price 1940, Reisz *et al.* 1992; including many therapsids), ophiacodontids (Berman *et al.* 1995, Romer and Price 1940), *Hylonomus* (Carroll 1969), *Petrolacosaurus* (Reisz 1981) and *Colobomycter* (MacDougall *et al.* 2017).

Unambiguous: *Colobomycter pholeter* (0→1), *Ennatosaurus tecton* (0→1), Captorhinidae except *Thuringothyris* (0→1). DELTRAN: *Hylonomus lyelli* (0→1), Diadectomorpha (0→1), Eothyrididae (0→1), *Varanosaurus* + *Ophiacodon* (0→1), Sphenacodontia (0→1), *Petrolacosaurus kansensis* (0→1). ACCTRAN:

Anthracodromeus + *Hylonomus* (0→1), Sauropsida (1→0), Diadectomorpha + Amniota (0→1), Caseidae (1→0), Edaphosauridae (1→0), *Petrolacosaurus kansensis* (0→1).

21. Premaxilla, tooth size: isodont (0); anterior teeth larger than posterior teeth (1)

Modified from Laurin (1993 c.67), Fröbisch *et al.* (2011 c.53).

Variation in the size of premaxillary teeth might be considered as non-independent from the preceding character. However, several taxa possess the derived state of ch.20 above, but nevertheless have an isodont array of premaxillary dentition (e.g. *Tseajaia*, Moss 1972 and *Euconcordia*, Müller and Reisz 2005), whereas others possess large anterior premaxillary teeth that are subequal to the non-caniniforms (e.g. varanodontines, FMNH UC 986, Campione and Reisz 2010; *Protorothyris*, Clark and Carroll 1973 and *Macroleter*, Tsuji *et al.* 2006). Therefore, ch.20 and ch.21 vary independently of each other and are both included in the analysis.

Unambiguous: *Colobomycter pholeter* (0→1), *Ennatosaurus tecton* (0→1),*Macroleter poezicus* (0→1), Varanodontinae (0→1), *Protorothyris archeri* (0→1). DELTRAN: *Limnoscelis plaudis* (0→1), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), Eothyrididae (0→1), *Varanosaurus* + *Ophiacodon* (0→1), Sphenacodontia (0→1), *Petrolacosaurus kansensis* (0→1), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: *Euconcordia cunninghami* (1→0), clade A (1→0), Diadectomorpha + Amniota (0→1), Caseidae (1→0), Edaphosauridae (1→0), *Petrolacosaurus kansensis* (0→1), *Tseajaia campi* (1→0).

22. Septomaxilla, morphology in lateral view: a thin superficial bone that forms the ventral margin of the external naris (0); a rectangular sheet of bone shaped as a conical funnel (1); an anteroposteriorly broad sheet of bone, which lies medial to the superficial surface of the circumnarial bones, and fully or partially partitions the external naris (2); a pillar of bone, partitioning the naris or forming the posterior margin of the external naris, with superficial exposure (3)

Modified from Modesto (1994 c.8), Reisz and Dilkes (2003 c.42), Maddin *et al.* (2006 c.8), Reisz *et al.* (2009 c.10/11), Reisz *et al.* (2010 c.18/19), Benson (2012 c.19).

Character states for the septomaxillae used in early studies focused almost exclusively in the absence or presence of a superficial contact with the circumnarial elements (Gauthier *et al.* 1988 c.3, Reisz 1992 c.6, Laurin 1993 c.4, deBraga and Rieppel 1997 c.5, Berman *et al.* 1995 c.7). This distinction is maintained here (state 3), and is present in sphenacodontians (Romer and Price 1940, Laurin 1993), edaphosaurs (Modesto 1995), varanodontines (Campione and Reisz 2010) and *Procolophon* (Carroll and Lindsey 1985). The 'conical funnel' morphology (state 1) is a synapomorphy of the captorhinids included in the present taxon list, where this element is preserved (Fox and Bowman 1966, *Captorhinus aguti* OMNH 15101, *Protocaptorhinus pricei* MCZ 1478, *Romeria primus* MCZ 1963, Sumida *et al.* 2010). In *Limnoscelis* (Berman *et al.* 2010), caseids (Olson 1968, Sigogneau-Russell and Russell 1974), *Archaeovenator* (Reisz and Dilkes 2003), *Orovenator* (Reisz *et al.* 2011), *Araeoscelis* (MCZ 4380), archosauromorphs (Modesto and Sues 2004, Ezcurra and Butler 2015) and most parareptiles (MacDougall *et al.* 2017, Daly 1969), there is no superficial exposure of the septomaxilla, which forms a sheet-like element within the naris (state 2). *Seymouria* and the basal parareptile *Mesosaurus* possess a dorsoventrally narrow septomaxilla that is situated on the ventral surface of the external naris (state 0).

Unambiguous: Diadectomorpha + Amniota (0→2), Ophiacodontidae + Sphenacodontia + Edaphosauridae (2→3). DELTRAN: *Mesosaurus tenuidens* (2→0), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (2→1), *Procolophon trigoniceps* (2→3), *Varanops brevirostris* (2→3). ACCTRAN: Captorhinidae (2→1), Mycterosaurinae + Varanodontinae + *Apsisaurus* (2→3), Bolosauridae + Procolphonoidea + *Macroleter* (0→3), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (2→0).

23. Maxilla, preorbital ascending process: convex dorsal margin that does not divide lacrimal (0); divides lacrimal in lateral view (1)

Modified from Reisz (1992 c.29), Berman *et al.* (1995 c.34), Reisz *et al.* (1998 c.5), Maddin *et al.* (2006 c.9), Benson (2012 c.25).

This character describes the acumate dorsal process of the maxilla that overlaps the surface of the lacrimal, dividing it into a pre- and post-maxillary dorsal process regions. This is present in *Varanodon* and *Varanops* (FMNH UC 986, MCZ 1926), and independently in the parareptiles *Colobomycter pholeter* (MacDougall *et al.* 2017) and *Delorhynchus* (Reisz *et al.* 2014).

Unambiguous: *Colobomycter pholeter* (0→1), *Varanops* + *Varanodon* + *Watongia* (0→1).

24. Maxilla, preorbital ascending process, maximum dorsoventral height in respect to the height of the maxilla at the anterior orbital margin: less than 1.5 times the height (0); between 1.5 and twice the height (1); greater than twice the height (2)

Modified from Laurin (1993 c.29), Berman *et al.* (1995 c.34), Reisz and Dilkes (2003 c.5), Benson (2012 c.25), Spindler *et al.* (2018 c.21).

The dorsoventral extension of the preorbital ascending process of the maxilla is a distinctive morphology of many early amniotes. Previous studies only describe this quantitatively, as either 'tall' or 'short', or described the position of the apex of the process relative to the external naris e.g. Laurin and Reisz (1995 c.19), Reisz *et al.* (2007 c.19). The lowest ratio, state (0), describes the process found in diadectomorphs, caseasaurs, 'protorothyridids', araeoscelidians and most captorhinids. This distribution suggests that state (0) represents the plesiomorphic condition. Derived ophiacodontids, sphenacodontids, varanodontines, some mycterosaurines and diapsids possess the highest ratio state (2).

Unambiguous: *Claudiosaurus germaini* (2→1),*Macroleter poezicus* (0→1), Sphenacodontidae (1→2), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), Neodiapsida (0→2),*Ophiacodon* spp (1→2), *Owenetta kitchingorum* (0→2), *Protocaptorhinus pricei* (0→1), *Seymouria* spp (0→1). DELTRAN: *Mesosaurus tenuidens* (0→1), *Varanops* + *Varanodon* + *Watongia* (1→2), Mycterosaurinae (1→2), Varanopidae (0→1), *Colobomycter* + *Acleistrohinus* (0→1). ACCTRAN: *Aerosaurus* spp (2→1), *Milleretta rubidgei* (1→0), clade C (0→1), Mycterosaurinae + Varanodontinae + *Apsisaurus* (1→2), Bolosauridae + Procolphonoidea + *Macroleter* (1→0).

25. Maxilla, position of apex of preorbital ascending process: process absent or very low (0); tallest point located centrally (1); tallest point located anteriorly, immediately posterior to the external naris (2).

From Laurin and Reisz (1995 c.19), Reisz *et al.* (2007 c.19), Maddin *et al.* (2008 c.9).

Unambiguous: *Claudiosaurus germaini* (1→2), Amniota (0→1), *Euromycter* + *Ennatosaurus* (1→2), *Prolacerta broomi* (1→2), *Seymouria* spp (0→2). DELTRAN: *Acleistorhinus pteroticus* (1→2),*Macroleter poezicus* (1→2), *Owenetta kitchingorum* (1→2). ACCTRAN: *Acleistorhinus pteroticus* (1→2), *Macroleter* + Procolophonoidea (1→2), *Procolophon trigoniceps* (2→1).

26. Maxilla, contact with prefrontal: absent, separated by the anterior extension of the lacrimal (0); present, lacrimal is reduced anteriorly allowing contact (1)

Modified from Gauthier *et al.* (1988 c.27), Laurin (1993, c.27), Reisz *et al.* (1998 c.6), Maddin *et al.* (2006 c.10), Reisz *et al.* (2009 c.24), Fröbisch *et al.* (2011 c.10), Benson (2012 c.53), Spindler *et al.* (2018 c.20).

Character state 1 is present in mycterosaurines, some diapsids and lanthanosuchoid parareptiles. Spindler *et al.* (2018) noted that in their analysis this character is redundant with the character defining the contribution of the lacrimal to the external nares (ch. 49 present study). However, in sphenacodontids (Romer and Price 1940, Reisz *et al.* 1992), diapsids (Carroll 1981, Modesto and Reisz 2003), archosauromorphs (Modesto and Sues 2004, Ezcurra and Butler 2015) and some parareptiles (Tsuji 2006, Carroll and Lindsey 1985) the lacrimal prevents contact between the maxilla and the prefrontal (state 0) and does not contribute to the external naris or the septomaxilla. Consequently both characters are maintained here.

Unambiguous: Mycterosaurinae (0→1), *Colobomycter* + *Acleistrohinus* (0→1), *Youngina capensis* (0→1). DELTRAN: *Acerosodontosaurus piveteaui* (0→1). ACCTRAN: *Acerosodontosaurus piveteaui* (0→1).

27. Maxilla, parallel row of lateral (supralabial) maxillary foramina: absent (0); present (1)

Modified from Laurin and Reisz (1995 c.20 state 2).

Many early amniotes have a distinctive row of supralabial foramina (state 1) located ventrally on the lateral surface of the maxilla (e.g. varanodontines and mycterosaurines, Reisz and Dilkes 2003, Anderson and Reisz 2004, Langston and Reisz 1981, Campione and Reisz 2010; *Orovenator*, Reisz *et*

al. 2011; *Petrolacosaurus*, Reisz 1981; *Lanthanolania*, Modesto and Reisz 2003; *Macroleter poezicus*, Tsuji 2006 and archosauromorphs, Modesto and Sues 2004). The caseid *Ennatosaurus* also has a row of large maxillary foramina extending dorsally along the lateral surface of the maxilla (Maddin *et al.* 2008), with a similar arrangement ventrally on the lateral surface in *Euromycter* (Sigogneau-Russell and Russell 1974). Ophiacodontids, sphenacodontians and edaphosaurids do not possess a distinctive row of maxillary foramina.

Unambiguous:*Macroleter poezicus* (0→1), *Euromycter* + *Ennatosaurus* (0→1), *Lanthanolania* + Archosauromorpha (0→1). DELTRAN: Varanopidae except *Ascendonanus* (0→1), *Petrolacosaurus kansensis* (0→1). ACCTRAN: Varanopidae (0→1), *Petrolacosaurus kansensis* (0→1).

28. Maxilla, anterior lateral (supralabial) maxillary foramen: equal in size to other maxillary foramina, if present (0); much larger than other foramina or a single large foramen (1); inapplicable, maxillary foramina absent (-)

Modified from Laurin and Reisz (1995 c.20), Dilkes (1998 c.17), Modesto and Sues (2004 c.17), Tsuji (2006 c.21), Maddin *et al.* (2008 c.3), Benson (2012 c.24), Modesto *et al.* (2015 c.30).

The anterior-most maxillary foramen is distinctly larger than the other maxillary foramina in some taxa, and gives rise to an anteriorly directed groove. This condition is found in *Orovenator* (Ford and Benson 2018), some mycterosaurines (Reisz and Dilkes 2003, Botha-Brink and Modesto 2009) and archosauromorphs (Modesto and Sues 2004). In parareptiles, a row of supralabial foramina is often absent, with the exception of *Macroleter poezicus* in the current taxon list. Instead a single large foramen is present, which is a synapomorphy of parareptiles (Tsuji 2006).

Unambiguous: *Heleosaurus scholtzi* (0→1). DELTRAN: Parareptilia (0→1), *Archaeovenator* + *Orovenator* (0→1), Archosauromorpha (0→1). ACCTRAN: *Lanthanolania ivakhnenko* (1→0), clade C (0→1), Mycterosaurinae + Varanodontinae + *Apsisaurus* (1→0).

29. Maxilla, tooth number (count): 10 or fewer (0); 13-27 (1); 28-34 (2); 35 or more (3)

Modified from Carroll and Currie (1991 c.29), Laurin (1993 c.73), Berman *et al.* (1995 c.65), Reisz *et al.* (1998 c.28), Maddin *et al.* (2006 c.2), Maddin *et al.* (2008 c.64), Reisz *et al.* (2009 c.20), Benson

(2012 c.29), Spindler *et al.* (2018 c.27).

Many studies omit characters defining the total maxillary tooth count (Gauthier *et al.* 1988, Reisz 1992, Laurin and Reisz 1995, Modesto 1995, deBraga and Reisz 1996, Fröbisch *et al.* 2011 - post-caniniform teeth only). Analysis of the tooth count in the current taxon list exhibits clustering from which I derive the defined states. Several groups (e.g. derived mycterosaurines, varanodontines, captorhinids, most parareptiles and caseasaurs) are scored as state (1). The out-group taxon, *Gephyrostegus*, possessed at least 35 maxillary teeth (Klembara *et al.* 2014), which is also the condition in derived ophiacodontids, *Ianthasaurus hardestiorum*, some 'protorothyridids' and some diapsids. Basal mycterosaurines (e.g. *Archaeovenator* and *Pyozia*), *Orovenator* and *Youngina* are scored as state (2). The reduction of maxillary teeth to 10 or less is shared by derived herbivores (e.g. *Ennatosaurus*, Maddin *et al.* 2008; *Procolophon*, Cisneros 2008 and *Belebey*, Reisz *et al.* 2007).

Unambiguous: *Ennatosaurus tecton* (1→0), *Gephyrostegus bohemicus* (1→3), Protorothyrididae (1→3), *Varanosaurus* + *Ophiacodon* (1→3), *Archaeovenator* + *Orovenator* (1→2), *Procolophon trigoniceps* (1→0), *Protorothyris archeri* (3→2), *Youngina capensis* (1→2). DELTRAN: *Archaothyris florensis* (1→2), *Belebey vegrandis* (1→0), *Ianthasaurus hardestiorum* (1→3), *Petrolacosaurus kansensis* (1→3). ACCTRAN: *Ianthasaurus hardestiorum* (1→3), *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (1→2), *Eudibamus* + *Belebey* (1→0), *Petrolacosaurus kansensis* (1→3).

30. Maxilla, 'caniniform' teeth: absent (0); present (1)

Dodick and Modesto (1995 c.35), Laurin and Reisz (1995 c.24/25), Modesto (1994 c.4), Dilkes (1998 c.56), Reisz and Dilkes (2003 c.39), Maddin *et al.* (2006 c.4), Maddin *et al.* (2008 c.69), Benson (2012 c34), Spindler *et al.* (2018 c.30).

For clarity, I define caniniform teeth as anterior maxillary teeth distinctively larger than all other maxillary teeth. They are found in many early amniotes and their close relatives. Where more than two caniniform teeth are present I define this as a caniniform region. Caniniform maxillary teeth, as a region or as one or two teeth, are present in *Seymouria* (Berman *et al.* 2000) and diadectomorphs (Moss 1972, Berman *et al.* 2010), eothyridids (Reisz *et al.* 2009), ophiacodontids and sphenacodontians (Romer and Price 1940), captorhinids (Sumida *et al.* 2010), varanodontines, (Maddin *et al.* 2006), derived mycterosaurines (Berman and Reisz 1982), 'protorothyridids' (Carroll 1969), araeoscelidian

diapsids (Reisz 1981) and some parareptiles (e.g. *Macroleter poezicus*, Tsuji 2006). Caniniforms are absent in neodiapsids (Gow 1975, Modesto and Sues 2004), some parareptiles (Modesto *et al.* 2015), basal mycterosaurines (e.g. *Archaeovenator*, Reisz and Dilkes 2003) and derived herbivores (parallel adaptation in caseids and edaphosaurs as suggested by Reisz 1980).

Unambiguous: *Colobomycter pholeter* (0→1), *Edaphosaurus boanerges* (1→0), clade D (1→0), *Seymouria* + Diadectomorpha + Amniota (0→1), Caseidae (1→0), *Archaeovenator* + *Orovenator* (1→0). DELTRAN:*Macroleter poezicus* (0→1), *Owenetta kitchingorum* (0→1), *Thuringothyris mahlendorffae* (1→0). ACCTRAN: *Macroleter* + Procolophonoidea (0→1), *Procolophon trigoniceps* (1→0), *Thuringothyris mahlendorffae* (1→0).

31. Maxilla, 'caniniform' teeth number (count): more than two caniniform teeth present (caniniform region) (0); one or two caniniform teeth present (1); inapplicable, caniniform teeth absent (-)

Modified from Modesto (1994 c.3), Benson (2012 c.34) , Spindler *et al.* (2018 c.32).

Unambiguous: *Aerosaurus* spp (1→0), *Euconcordia cunninghami* (1→0), *Limnoscelis plaudis* (1→0), *Mycterosaurus longiceps* (1→0),*Ophiacodon* spp (1→0). DELTRAN: *Macroleter* + Procolophonoidea (1→0). ACCTRAN: *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (1→0).

32. Maxilla, 'caniniform' teeth, size: slightly larger than the adjacent maxillary teeth (0); at least 1.5 times as large as adjacent maxillary teeth (1); inapplicable, caniniform teeth absent (-)

Modified from Reisz *et al.* (1992 c.59), Reisz *et al.* (2009 c.17), Benson (2012 c.34), Spindler *et al.* (2018 c.31).

Unambiguous: Araeoscelidia (0→1), *Protorothyris* + *Paleothyris* (0→1), *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), Synapsida (0→1),*Ophiacodon* spp (1→0), *Tseajaia campi* (0→1). DELTRAN: *Colobomycter pholeter* (0→1). ACCTRAN: *Milleretta* + *Colobomycter* + *Acleistrohinus* (0→1).

33. Maxilla, secondary 'caniniform' region: absent (0); present (1); inapplicable, canini-

form teeth absent (-)

Maddin *et al.* (2008 c.66), Reisz *et al.* (2009 c.18), Benson (2012 c.39), Spindler *et al.* (2018 c.33).

The eothyridids *Eothyris* and *Oedaleops* possess a secondary series of 'caniniform' teeth posterior to the two large caniniforms (Langston 1965, Reisz *et al.* 2009).

DELTRAN: Eothyrididae (0→1). ACCTRAN: Caseasauria (0→1).

34. Maxilla, number of pre-caniniform maxillary teeth: five or less (0); six or more (1); inapplicable, 'caniniform' teeth absent (-)

Modified from Reisz *et al.* (1992 c.62), Laurin (1993 c.71), Berman *et al.* (1995 c.69), Maddin *et al.* (2008 c.65), Reisz *et al.* (2009, c.16), Fröbisch *et al.* (2011 c.57), Benson (2012 c.32), Spindler *et al.* (2018 c.29).

Unambiguous: *Protorothyris* + *Paleothyris* (0→1), *Varanosaurus* + *Ophiacodon* (0→1), *Varanops* + *Varanodon* + *Watongia* (0→1). DELTRAN: *Haptodus garnettensis* (0→1), *Petrolacosaurus kansensis* (0→1), *Secodontosaurus obtusidens* (0→1). ACCTRAN: *Dimetrodon* spp (1→0),Sphenacodontia + Edaphosauridae (0→1), *Petrolacosaurus kansensis* (0→1).

35. Maxilla, lateral 'supracanine' buttress: absent or slight swelling (0), distinct lateral swelling or dorsally oriented ridge on the maxilla, dorsal to the caniniform dentition (1)

Reisz *et al.* (1998 c.10), Reisz and Dilkes (2003 c.10), Maddin *et al.* (2006 c.11), Reisz *et al.* (2009 c.13), Benson (2010 c.36), Brocklehurst *et al.* (2016 c.25), Spindler *et al.* (2018 c.24).

Several early amniotes possess a lateral extension of the maxilla immediately dorsal to the 'caniniform' dentition. This is often present as a swelling on the lateral surface of the maxilla (e.g. *Eothyris*, Reisz *et al.* 2009; *Varanosaurus*, Berman *et al.* 1995 and *Dimetrodon* milleri, MCZ 1365), or forms a dorsoventral ridge that overlies the lacrimal (e.g. *Varanops* and *Varanodon*, Campione and Reisz 2010, FMNH UC 986). In the mycterosaurines *Heleosaurus* (Botha-Brink and Modesto 2009) and *Mesenosaurus* (Reisz and Berman 2001) only a slight lateral swelling of the maxilla is present, which

is not sufficiently well developed to be considered as state (1), in accordance with Spindler *et al.* (2018). Langston and Reisz (1981) noted a 'suggestion of a lateral ridge' in *Aerosaurus wellesi*, somewhat similar to that of *Varanops* and *Varanodon*, which I also consider as insufficient evidence to score as the derived state, in agreement with the coding of Benson (2012) and Spindler *et al.* (2018).

Unambiguous: *Dimetrodon* spp (0→1), *Varanops* + *Varanodon* + *Watongia* (0→1). DELTRAN: *Eothyris parkeyi* (0→1), *Varanosaurus acutirostris* (0→1). ACCTRAN: *Eothyris* + *Eocasea* + *Vaughnictis* (0→1), *Varanosaurus acutirostris* (0→1).

36. Maxilla, 'supracanine' buttress on medial surface: absent, alveolar shelf has uniform or gradually tapering dorsoventral height (0); present, subtriangular dorsal thickening of anterior alveolar shelf (1)

Modified from Reisz *et al.* (1992 c.27), Laurin (1993 c.28/70), Berman *et al.* (1995 c.33), Fröbisch *et al.* (2011 c.21/56), Benson (2012 c.37), Spindler *et al.* (2018 c.25).

In some early amniotes, where 'caniniform' teeth are present, a thickening and dorsal expansion of the alveolar ridge onto the medial surface of the maxillary lamina is also present, which contains the roots of the larger teeth (Reisz 1986). Although, this medial buttress is absent in the caseasaur *Oedaleops*, which possesses large 'caniniform' teeth (Langston 1965). Conversely, in *Archaeovenator*, *Orovenator* and *Prolacerta*, where 'caniniform' teeth are absent, a medial buttress of the maxilla is present (KUVP 12483, Modesto and Sues 2004, Ford and Benson 2018).

Unambiguous: *Archaeovenator* + *Orovenator* (0→1). DELTRAN: Ophiacodontidae (0→1), Sphenacodontia (0→1), *Prolacerta broomi* (0→1). ACCTRAN: Edaphosauridae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), Neodiapsida (0→1).

37. Maxilla, morphology of dorsal portion of 'supracanine' buttress: anteroposteriorly broad region of thickened bone (0); narrow, strut-like ascending process extends posterodorsally from supracanine buttress (1); inapplicable, supracanine buttress absent (-)

Modified from Reisz *et al.* (1992 c.27), Laurin (1993 c.28), Fröbisch *et al.* (2011 c.21), Benson (2012 c.38).

A narrow, posterodorsal extension of the 'supracanine' buttress (state 1) is present in derived ophiacodontids (Romer and Price 1940, Berman *et al.* 1995), in *Orovenator* (Ford and Benson 2018) and in *Prolacerta* (Gow 1975).

Unambiguous: *Varanosaurus* + *Ophiacodon* (0→1). DELTRAN: clade C (0→1). ACCTRAN: Sauropsida (0→1).

38. Maxilla, lateral surface, orientation of dorsal lamina: vertical or slopes weakly dorsomedially (0); slopes dorsolaterally, overhanging tooth row (1)

Modified from Maddin *et al.* (2008 c.2), Reisz *et al.* (2009 c.14), Benson (2012 c.21), Romano *et al.* (2015 c.324), Brocklehurst *et al.* (2016 c.21), Spindler *et al.* (2018 c.26).

The derived state (state 1) of this character is present in caseasaurs (Reisz *et al.* 2009, Maddin *et al.* 2008). Most of the previous studies using this character have also scored for state (1) in diadectomorphs, with only Reisz *et al.* (2009) scoring for state (0) in this clade. I have not been able to examine any specimens that support presence of either state in diadectomorphs. Neither do I find any confirmation of this feature in the available literature. Consequently I score *Tseajaia* and *Limnoscelis* as unknown. Several studies (Benson 2012, Romano *et al.* 2015, Brocklehurst *et al.* 2016, Spindler *et al.* 2018) scored *Captorhinus* as possessing state (1). Recent phylogenetic studies concerned with the interrelationships of captorhinids omit this character altogether (e.g. Modesto *et al.* 2018, Reisz *et al.* 2015, Modesto *et al.* 2014, Modesto *et al.* 2007, Sumida *et al.* 2010, Müller and Reisz 2005). Heaton (1979) noted that the lateral surface of the maxilla is vertical in both *Captorhinus laticeps* and C. *aguti*. Personal examination of several specimens (C. *aguti* FMNH UC 242, MCZ 1768, OMNH 56819; C. *laticeps* FMNH UC 701, OMNH 15101) and other literature sources (Fox and Bowman 1966, Modesto 1998) do not support the presence of state (1) in *Captorhinus*. Likewise, specimens of *Protocaptorhinus pricei* (MCZ 1478), *Romeria primus* (MCZ 1963) and *Romeria texana* (MCZ 1480) show no evidence of a dorsolaterally orientated maxillary lamina. However the holotype specimen of *Reiszorhinus* olsoni (FMNH UC 183) does possess a distinctive dorsolateral inclination of the maxilla, and is scored as state (1) herein.

Unambiguous: Caseasauria (0→1), *Reiszorhinus olsoni* (0→1).

39. Maxilla, lateral surface, orientation of suborbital ramus only: vertical, with no lateral overhang of tooth row (0); dorsolaterally inclined, overhangs tooth row (1)

NEW

Both *Archaeovenator* and *Orovenator* share a feature of the suborbital ramus of the maxilla where a distinct dorsolateral inclination causes the dorsal edge of the maxilla to overhang the marginal tooth row (Reisz and Dilkes 2003, Ford and Benson 2018).

Unambiguous: *Archaeovenator* + *Orovenator* (0→1).

40. Maxilla, shape: relatively straight or mildly convex (0); posterior end flexed laterally resulting in concave outline seen in dorsal/ventral view (1)

Modified from Dodick and Modesto (1995 c.2), Müller *et al.* (2006 c.2), Modesto *et al.* (2007 c.3), Modesto *et al.* (2018 c.4).

The lateral flexure of the maxilla is a synapomorphy of derived captorhinids (Müller *et al.* 2006, Modesto *et al.* 2018), which is also present in diadectomorphs (Heaton and Reisz 1986, Berman *et al.* 2010). A similar condition is found independently in the early synapsid *Edaphosaurus* (Modesto 1995) and the parareptile *Procolophon* (Carroll and Lindsey 1985) suggesting that this feature may be a parallel adaptation for derived herbivory.

Unambiguous: *Edaphosaurus boanerges* (0→1), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), Diadectomorpha (0→1), *Procolophon trigoniceps* (0→1).

41. Maxilla, posterior extension: maxilla terminates posteriorly at the level of or posterior to the posterior orbital rim (0); anterior to the posterior orbital rim (1)

Modified from Modesto (1994 c.7), deBraga and Rieppel (1997 c.14), Müller (2004 c.127), Ezcurra *et al.* (2014 c.122).

Unambiguous: *Protorothyris* + *Paleothyris* (1→0), *Protocaptorhinus pricei* (1→0), *Seymouria* + Diadectomorpha + Amniota (0→1), *Heleosaurus* + *Mesenosaurus* (0→1), Mycterosaurinae + Varanodontinae (1→0), *Colobomycter* + *Acleistorhinus* (1→0). DELTRAN: *Lanthanolania ivakhnenko* (1→0), *Eothyris* + *Eocasea* + *Vaughnictis* (1→0), Caseidae (1→0), *Proterosuchus* spp (1→0), *Thuringothyris mahlendorffae* (1→0). ACCTRAN: Caseasauria (1→0), *Lanthanolania* + Archosauromorpha (1→0), *Oedaleops campi* (0→1), *Prolacerta broomi* (0→1), *Thuringothyris mahlendorffae* (1→0).

42. Maxilla, posterior extent of dentition if posterior extension level with or posterior to posterior orbital rim: anterior to the posterior orbital rim exclusively (0); terminates ventral to the posterior orbital rim (1); continues posterior to the posterior orbital rim (2) inapplicable, maxilla terminates anterior to the posterior orbital rim (-)

Modified from Rieppel (1999 c.57), Müller (2004 c.118), Maddin *et al.* (2008 c.11), Reisz *et al.* (2009 c.15), Benson (2012 c.30), Reisz and Fröbisch (2014 c.11), Spindler *et al.* (2018 c.28).

The posterior extent of the maxilla (ch.41) and the posterior extent of the maxillary tooth row are partially independent characters that provide separate and phylogenetically informative data. The maxilla extends posterior to the posterior orbital rim in varanodontines, *Mycterosaurus* (Berman and Reisz 1982) and *Elliotsmithia* (Reisz *et al.* 1998). In previous studies (Maddin *et al.* 2008, Reisz and Fröbisch 2014, Benson 2012, Spindler *et al.* 2018) *Mycterosaurus* is scored as possessing a tooth row that extends beyond the posterior orbital rim. However, a microCT scan of the holotype of this taxon (FMNH UC 692, Berman and Reisz 1982) has revealed the tooth row terminates anterior to the posterior orbital rim, a condition shared with *Elliotsmithia*. Consequently, in the present study the tooth row is scored as extending posterior to the posterior orbital rim in varanodontines (state 2), and as terminating anteriorly in *Mycterosaurus* and *Elliotsmithia* (state 0).

Unambiguous: *Gephyrostegus bohemicus* (1→2), Varanodontinae (0→2), *Romeria* spp (1→0). DELTRAN: *Acleistorhinus pteroticus* (0→1), clade C (1→0), *Proterosuchus* spp (0→1), *Protorothyris archeri* (1→0). ACCTRAN: *Acleistorhinus pteroticus* (0→1), clade A (1→0), Archosauromorpha (0→1), *Paleothyris acadiana* (0→1).

43. Maxilla, ventral surface in lateral view: straight or weakly convex (0); pronounced convexity (1)

Modified from Gauthier *et al.* (1988 c.30), Reisz *et al.* (1992 c.25), Berman *et al.* (1995 c.31), Reisz and Dilkes (2003 c.52), Maddin *et al.* (2008 c.12), Benson (2012 c.27 with state (2) omitted as uninformative).

In the current taxon list, state (1) is present in diadectomorphs, derived ophiacodontids and sphenacodontians. Benson (2012) included a third state to account for the 'pre-canine' step in *Dimetrodon* and more derived sphenacodontids/therapsids. This state is omitted here as parsimony uninformative (the step is only present in *Dimetrodon* among the taxa in the analysis). The mild convexity in the anterior part of the ventral margin of the maxilla in *Ennatosaurus* is scored as state (0) herein contra Maddin *et al.* 2008.

Unambiguous: Diadectomorpha (0→1), *Varanosaurus* + *Ophiacodon* (0→1), Sphenacodontia (0→1).

44. External naris, posterodorsal expansion: absent (0); present (1)

Modified from Reisz and Dilkes (2003 c.43), Maddin *et al.* (2006 c.42), Reisz *et al.* (2009 c.9), Reisz *et al.* (2010 c.21), Benson (2012 c.4 in part), Spindler *et al.* (2018 c.5).

Reisz and Dilkes (2003 c.43) introduced a multistate character describing the presence, absence, size and composition of the narial posterodorsal expansion in mycterosaurines and varanodontines. I instead score a pair of hierarchically related characters (the present character and ch.45 below) in which the presence/absence and composition are coded as binary characters. The posterodorsal expansion of the naris is present in mycterosaurines and varanodontines (Reisz and Dilkes 2003, Reisz *et al.* 2010, Campione and Reisz 2010), with the exception of *Aerosaurus* (Langston and Reisz 1981). It is also present in *Orovenator* (Ford and Benson 2018).

Unambiguous: *Aerosaurus* spp (1→0). DELTRAN: Varanopidae except *Ascendonanus* (0→1). ACCTRAN: Varanopidae (0→1).

45. External naris, morphology of posterodorsal expansion if present: pinched between nasal and maxilla (0); greatly enlarged, between nasal and lacrimal (1); inapplicable, posterodorsal expansion absent (-)

Modified from Reisz and Dilkes (2003 c.43), Maddin *et al.* (2006 c.42), Reisz *et al.* (2009 c.9), Reisz *et al.* (2010 c.21), Benson (2012 c.4 in part), Spindler *et al.* (2018 c.5).

In *Orovenator* and some mycterosaurines the posterodorsal expansion of the naris is narrow, and is pinched between the nasal and the maxilla (state 0) (Berman and Reisz 1982, Reisz and Dilkes 2003, Ford and Benson 2018) In *Archaeovenator* and varanodontines the posterodorsal expansion is significantly larger, with the lacrimal forming the ventral margin (state 1) (Reisz and Dilkes 2003, Maddin *et al.* 2006).

DELTRAN: *Archaeovenator hamiltonensis* (0→1), *Varanops* + *Varanodon* + *Watongia* (0→1). ACCTRAN: *Archaeovenator hamiltonensis* (0→1), Varanodontinae (0→1).

46. External naris, position: marginal (minimal distance between nares ≥0.35 snout width at same level) (0); close to midline (1)

Laurin (1991 F.2), deBraga and Rieppel (1991 c.6/7), Dilkes (1998 c.11), Reisz *et al.* (2010 c.20).

Laurin (1991) included state (1) of this character as a synapomorphy of Archosauromorpha. I score it also as being present in the late Permian neo-diapsid *Claudiosaurus*. Reisz *et al.* (2010) scored the derived state present in *Varanodon*, but examination of FMNH UR 986 leads us to score this taxon as state (0) herein.

DELTRAN: *Claudiosaurus germaini* (0→1), Archosauromorpha (0→1). ACCTRAN: Neodiapsida (0→1), *Youngina capensis* (1→0).

47. Nasal, length: distinctly shorter than the frontal (0); approximately equal to the frontal (1); longer than frontal (2)

Modified from Gauthier (1988 c.4), Reisz *et al.* (1992 c.7), Laurin (1993 c.5), Berman *et al.* (1995, c8/9), Reisz and Dilkes (2003 c.50), Müller (2004 c.4), Reisz *et al.* (2009 c.7), Maddin *et al.* (2006 c.14) Fröbisch *et al.* (2011 c.4), Benson (2012 c.47), Spindler *et al.* (2018 c.35).

Unambiguous: *Mesosaurus tenuidens* (0→2), Sphenacodontidae (0→2). DELTRAN: *Belebey vegrandis* (0→1), *Casea broilii* (0→1), *Euromycter rutena* (0→1), Diadectomorpha (0→1), *Varanosaurus* + *Ophiacodon* (0→2), Mycterosaurinae + Varanodontinae (0→1), Archosauromorpha (0→2), *Seymouria* spp (0→1), *Youngina capensis* (0→1). ACCTRAN: *Ennatosaurus tecton* (1→0), Amniota (1→0), *Seymouria* + Diadectomorpha + Amniota (0→1), Caseidae (0→1), Ophiacodontidae (0→2), Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→1), *Lanthanolania* + Archosauromorpha (1→2),*Eudibamus* + *Belebey* (0→1).

48. Nasal, external narial shelf: absent (0); present as a lateral fossa (1)

Modified from Reisz 1986 (table 3a), Laurin and Reisz (1995 c.1), Reisz and Dilkes (1998 c.49), Maddin *et al.* (2006 c.13), Reisz *et al.* (2007 c.1), Reisz *et al.* (2009 c.6), Benson (2012 c.48), MacDougall and Reisz (2014 c.1), Modesto *et al.* (2015 c.1), Spindler *et al.* (2018 c.36).

State (1) of this character has long been recognised as being present in all caseasaurs (Olson 1968, Reisz 1986, Reisz *et al.* 2009). Laurin and Reisz (1995) considered the lateral narial fossa as an independently derived autapomorphy of Procolphonidae. More recent studies have recognised the wider distribution of this feature amongst ankyramorph parareptiles (Modesto *et al.* 2015).

Unambiguous: *Colobomycter pholeter* (0→1), Caseasauria (0→1), *Procolophon trigoniceps* (0→1).

49. Lacrimal, length: participates in margin of external naris or contacts the posterior margin of the septomaxilla (0); does not reach external naris or septomaxilla (1)

Modified from Gauthier *et al.* 1988 (c.33), Laurin (1991 B.2), Reisz *et al.* (1992 c.30), Berman *et al.* (1995 c.35), Rieppel (1999 c.9), Müller (2004 c.6), Reisz *et al.* (2010 c.24), Benson (2012 c.22).

This character was modified to include the septomaxilla to account for those taxa where the septomaxilla forms the posterior margin of the naris. The position of the septomaxilla in this respect is considered elsewhere (ch.22 above). State (1) of the present character is found in mycterosaurines (Botha-Brink and Modesto 2009, Reisz and Berman 2001), diapsids (Gow 1975, Bickelmann *et al.* 2009, Modesto and Sues 2004), ankyramorph parareptiles (Tsuji 2006, deBraga and Reisz 1996, Carroll and Lindsey 1985) and derived sphenacodontids (Romer and Price 1940).

Unambiguous: Sphenacodontidae (0→1), Mycterosaurinae (0→1), Neodiapsida (0→1), *Macroleter* + Procolophonoidea (0→1), *Colobomycter* + *Acleistorhinus* (0→1).

50. Lacrimal, contribution to margin of external naris: broad (0); narrow (1); inapplicable, contact absent (-)

Modified from Berman *et al.* (1995 c.36), Benson (2012 c.49).

nambiguous: *Orovenator mayorum* (0→1). DELTRAN: *Haptodus garnettensis* (0→1), *Varanosaurus acutirostris* (0→1). ACCTRAN: Sphenacodontia (0→1), *Varanosaurus acutirostris* (0→1).

51. Lacrimal, contribution to orbit margin as seen in lateral view: large, greater than 7% of the orbital circumference (0); small less than 5% of the orbital circumference or absent, restricted by a prominent ventral process of the prefrontal (1)

Modified from Laurin (1993 c.32), Müller (2004 c.181), Maddin *et al.* (2006 c.16), Reisz *et al.* (2009 c.26), Fröbisch *et al.* (2011 c.25), Benson (2012 c.51).

The lack of quantitative criteria has led to inconsistencies among previous studies in scoring this character (e.g. Benson 2012 and Fröbisch *et al.* 2011 disagree in respect to *Secodontosaurus*, with Benson scoring as narrow, and Fröbisch *et al.* as large). In *Dimetrodon limbatus* (Romer and Price 1940 plate 6) the contribution of the lacrimal to the orbital circumference is between 7 and 8% (state 0), and both the anterodorsal extension of the jugal and the ventral process of the prefrontal restrict the contribution of the lacrimal. In *Archaeovenator* the lacrimal is 'virtually excluded' from the orbital margin (state 1)(Reisz and Dilkes 2003:671). In *Mesenosaurus* and *Mycterosaurus* the lacrimal is equally restricted from the orbital margin (Berman and Reisz 1982, Reisz and Berman 2001). In *Orovenator* lacrimal contribution is less than 4% (state 1)(OMNH 74606). In all the cases that share state (1) the ventral process of the prefrontal is the principle restricting element to the orbital contribution of the lacrimal. A similar morphology is seen in *Prolacerta* (Gow 1975), *Proterosuchus* (Ezcurra and Butler 2015), *Mesosaurus* (Piñeiro *et al.* 2012) and *Macroleter* (Tsuji 2006). The condition present in *Dimetrodon* is more similar to other early synapsids (state 0), where the contribution of the lacrimal is relatively greater than the foregoing examples. In the present study the scoring for state (1) of this

character is applicable only to mycterosaurines, derived diapsids and some parareptiles.

Unambiguous: *Colobomycter pholeter* (0→1),*Macroleter poezicus* (0→1), *Mesosaurus tenuidens* (0→1), Varanodontinae (1→0), Varanopidae (0→1), Archosauromorpha (0→1). DELTRAN: *Claudiosaurus germaini* (0→1).

52. Lacrimal, duct: opens on posterior (orbital rim) surface of lacrimal (0); opens laterally near posterior edge of lacrimal (1); opens laterally on concave surface of lacrimal (2)

From Reisz *et al.* (1998 c.19), Maddin *et al.* (2006 c.15), Reisz *et al.* (2009 c.25), Campione and Reisz (2010 c.15), Reisz *et al.* (2010 c.25), Benson (2012 c.52), Spindler *et al.* (2018 c.34).

The position of the anterior opening(s) of the lacrimal duct is primitively found on the posterior surface (orbital rim) of the lacrimal (state 0). In mycterosaurines, *Acerosodontosaurus*, *Prolacerta* and some parareptiles the opening is located instead on the posterolateral surface of the lacrimal, and so can be seen lateral view. Reisz *et al.* (1998) considered that the condition in varanodontines (*Aerosaurus* + *Varanops* + *Varanodon*), with an opening more anteriorly placed within the concavity on the surface of the lacrimal, was sufficiently different to warrant a third state (state 2). This scoring was followed in all subsequent studies until Spindler *et al.* (2018), where the presence of state (2) in any varanodontine was questioned. Campione and Reisz (2010) noted the exit of the lacrimal duct was via the infraorbital foramen located on the orbital rim of *Varanops*, yet maintained the scoring of this taxon as state (2) in the same study (Campione and Reisz 2010 c.15). Based on the examination of the holotype and two referred specimens of *Varanops* (FMNH UC 644, MCZ 1926, FMNH UR 2423) I concur with Campione and Reisz in the location of the exit foramen for the lacrimal duct being on the orbital rim (state 0) in *Varanops*, and score this taxon accordingly herein.

Unambiguous: *Colobomycter pholeter* (1→0), clade D (0→1). DELTRAN: *Aerosaurus* spp (0→2), Mycterosaurinae (0→1), Procolophonoidea (1→0), *Varanodon agilis* (0→2). ACCTRAN: Varanodontinae (1→2), Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→1), *Macroleter* + Procolophonoidea (1→0), *Varanops brevirostris* (2→0).

53. Lacrimal, contact with jugal in lateral view: present (0); absent and maxilla partic-

ipates in orbital margin (1)

Modified from Reisz 1986 (table 3a), Benson (2012 c.72).

In most of the taxa considered in the present study, including varanodontines (e.g. *Aerosaurus*, Langston and Reisz 1981, *Varanops*, FMNH UR 2423 and *Varanodon*, FMNH UR 986), the lacrimal contacts the anterior process of the jugal either anteroventral or ventral to the orbit (state 0). This contact excludes the maxilla from participating in the rim of the orbit. In contrast to this, in the eothyridids *Eothyris* and *Vaughnictis* the short anterior process of the jugal does not meet the lacrimal and the maxilla contributes substantially to the ventral margin of the orbit (state 1)(MCZ 1161, Reisz *et al.* 2009 and MCZ 2985, Brocklehurst *et al.* 2016). In *Orovenator* (Reisz *et al.* 2011) and *Mesenosaurus* (Reisz and Berman 2001) the jugal and lacrimal also do not meet in lateral view (state 1). Instead contact between these two elements is medial to the maxillary orbital margin in these taxa (Reisz and Berman 2001, Ford and Benson 2018). In *Archaeovenator*, contact between the jugal and lacrimal is likely (Reisz and Dilkes 2003), but this would probably have also been medial to the maxillary orbital margin given the dorsoventrally high 'up-step' in the anterior suborbital ramus of the maxilla, morphology very similar to that of *Orovenator*. *Archaeovenator* is accordingly scored as state (1) herein. In *Mycterosaurus*, jugal/lacrimal contact is uncertain since the lacrimal is poorly preserved (Berman and Reisz 1982), as is the case in other mycterosaurines (e.g. *Elliotsmithia*, Reisz *et al.* 1998 and *Heleosaurus*, Botha-Brink and Modesto 2009).

Unambiguous: *Claudiosaurus germaini* (0→1), *Milleretta rubidgei* (0→1), *Eothyris* + *Eocasea* + *Vaughnictis* (0→1). DELTRAN: *Mesenosaurus romeri* (0→1), *Archaeovenator* + *Orovenator* (0→1). ACCTRAN: Varanodontinae (1→0), Varanopidae except *Ascendonanus* (0→1).

54. Lacrimal, suture with jugal in lateral view: small, less than 50% of the minimum dorsoventral height of the suborbital bar (0); well developed, greater than 50% of the minimum dorsoventral height of the suborbital bar (1); inapplicable, lateral contact absent (-)

Modified from Dodick and Modesto (1995 c.4), Modesto *et al.* (2007 c.5), Sumida *et al.* (2010 c.7), Modesto *et al.* (2018 c.13).

Unambiguous: clade A (1→0), *Seymouria* spp (1→0). DELTRAN: *Belebey vegrandis* (0→1), *Euromycter rutena* (1→0), *Oedaleops campi* (1→0). ACCTRAN: *Ennatosaurus tecton* (0→1), Caseasauria (1→0), *Eudibamus* + *Belebey* (0→1).

55. Prefrontal, contact with postfrontal: contact of prefrontal and postfrontal excludes the frontal from the dorsal margin of the orbit (0); prefrontal and postfrontal separated by the frontal along the dorsal margin of the orbit (1)

Modified from Laurin and Reisz (1995 c.2), deBraga and Rieppel (1997 c.22), Rieppel *et al.* (1999 c.10), Müller (2004 c.7), Tsuji (2006 c.2), MacDougall and Reisz (2014 c.3), Modesto *et al.* (2015 c.3).

Character state (0) is present only in diadectomorphs, *Seymouria* and *Gephyrostegus* in the current taxon list. *Eothyris* has a very narrow lappet, less than 1mm in width, separating the pre- and postfrontals (Reisz *et al.* 2009, MCZ 1161).

Unambiguous: Amniota (0→1).

56. Prefrontal, palatal contact: absent (0); present (1)

Modified from Wu and Chatterjee (1993 c.10), Laurin and Reisz (1995 c.6), Reisz *et al.* (1998 c.7), Reisz *et al.* (2007 c.6), MacDougall and Reisz (2014 c.11), Modesto *et al.* (2015 c.11).

State (1) of this character is present in most parareptiles (Laurin and Reisz 1995), mycterosaurines (Berman and Reisz 1982, Reisz and Berman 2001), *Orovenator* (Ford and Benson 2018) and *Edaphosaurus* (Modesto 1995) in the current taxon list. State (1) has also been considered as present in captorhinids in some studies (e.g. Laurin and Reisz 1995, Modesto 2015). However, Heaton (1979 fig.9) noted that the sutural scar on the medial surface of the lacrimal for the prefrontal is dorsal to the sutural contact with the palatine in *Captorhinus laticeps*. It is also interesting to note that phylogenetic datasets focusing in captorhinids do not include this character (e.g. Modesto *et al.* 2018, Sumida *et al.* 2010, Dodick and Modesto 1995).Consequently captorhinids are scored as (0) herein.

Unambiguous: *Edaphosaurus boanerges* (0→1), *Seymouria* spp (0→1). DELTRAN: *Milleretta* + *Colobomycter* + *Acleistorhinus* (0→1), Mycterosaurinae (0→1), Bolosauridae + *Macroleter* + Pro-

colophonoidea (0→1), *Orovenator mayorum* (0→1). ACCTRAN: *Mesosaurus tenuidens* (1→0), clade C (0→1), Varanodontinae (1→0), Neodiapsida (1→0).

57. Prefrontal, width of palatal contact: narrow, forming less that one third of the transverse distance between the orbits (0); wide, forming at least one half of the distance (1); inapplicable, palatal contact absent (-)

Modified from Laurin and Reisz (1997 c.7), deBraga and Rieppel (1997 c.20), Müller (2004 c.130), Modesto *et al.* (2015 c.12/13).

This character differentiates between the prefrontal/palatal contact in parareptiles, which takes the form of a mediolaterally wide flange (state 1) and the more transversely narrow morphology in all other taxa (state 0).

DELTRAN: Parareptilia (0→1). ACCTRAN: clade D (0→1).

58. Prefrontal, suture with nasal: parasagittal, at least in its caudal third (0); anterolateral (1)

Modified from Laurin (1991 E.1), Reisz *et al.* (2010 c.33), Ezcurra *et al.* (2014 c.32), Pritchard *et al.* (2015 c.9), Pinheiro *et al.* (2016 c.38).

An anterolaterally orientated suture of the nasal and prefrontal was considered as a synapomorphy of the Sauria by Laurin (1991). However, Ezcurra *et al.* (2014) observed that it was also present in non-saurian diapsids (*Youngina* BP/1/3859). It is also present in *Lanthanolania* (Modesto and Reisz 2003) and *Claudiosaurus* (Carroll 1981).

Unambiguous: *Lanthanolania* + Archosauromorpha (0→1).

59. Prefrontal, lateral surface: approximately flat or convex (0); concave, forming antorbital recess (prefrontal pocket) (1)

Reisz *et al.* (1992 c.9), Berman *et al.* (1995 c.12), Laurin (1993 c.11), Fröbisch *et al.* (2011 c.10),

Benson (2012 c.54), Spindler *et al.* (2018 c.38).

Unambiguous: *Proterosuchus* spp (0→1). DELTRAN: *Varanosaurus* + *Ophiacodon* (0→1), Sphenacodontia (0→1). ACCTRAN: Edaphosauridae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1).

60. Prefrontal, sharp angle between the dorsal and lateral surface: absent (0), present (1)

NEW

In ophiacodontids (*Varanosaurus* FMNH PR 1670, *Ophiacodon uniformis* MCZ 5934), mycterosaurines and varanodontines (Reisz and Dilkes 2003, Berman and Reisz 2001, *Mycterosaurus* FMNH UC 692, Reisz *et al.* 1998) the dorsal and lateral surfaces of the prefrontal meet at an angle of around 90 degrees, rather than transitioning gradually. This morphology is also present in *Orovenator* (Ford and Benson 2018).

DELTRAN: *Varanosaurus* + *Ophiacodon* (0→1), Varanopidae except *Ascendonanus* (0→1). ACCTRAN: Ophiacodontidae (0→1), Varanopidae (0→1).

61. Frontal, contribution to orbital margin: narrow (0); broad, >1/4 of maximum orbital length (1); inapplicable, frontal does not contribute to orbital margin (-)

Modified from Reisz *et al.* (1992 c.11), Reisz *et al.* (1998 c.13), Reisz and Dilkes (2003 c.13), Maddin *et al.* 2006 c.18, Reisz *et al.* 2009 c.19, Reisz *et al.* (2010 c.26), Benson (2012 c.60), Spindler *et al.* (2018 c.40).

This character deals with the anteroposterior length of the frontal contribution to the orbital margin rather than the morphology of the frontal, i.e. if the orbital exposure is provided by a distinct lateral lappet of the frontal (see ch.62 below). A narrow frontal exposure is plesiomorphic for amniotes (caseasaurs and captorhinids). Parareptiles, notably *Mesosaurus* (Piñeiro *et al.* 2012) and some ankyramorphs (Tsuji 2006, *Acleistorhinus* FMNH UR 1038, Carroll and Lindsey 1985), are also scored for state (0), probably representing a reversal.

Unambiguous: *Ascendonanus nestleri* (1→0), *Ennatosaurus tecton* (0→1), *Mesosaurus tenuidens* (1→0),

clade A (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Macroleter* + Procolophonoidea (1→0), *Acleistorhinus pteroticus* (1→0).

62. Frontal, contribution to orbital margin formed by lateral lappet: absent (0); present (1); inapplicable, frontal does not contribute to orbital margin (-)

Modified from Gauthier *et al.* (1988 c.8), Brinkman and Eberth (1983 c.10), deBraga and Reisz (1996 c.7), Tsuji (2006 c.3), MacDougall and Reisz (2014 c.5), Modesto *et al.* (2015 c.5), Spindler *et al.* (2018 c.41).

Brinkman and Eberth (1983) described the distinct lateral lappet of the frontal that contributes to the orbital margin in basal synapsids as being greater in mediolateral width than the posterior region of the frontal. Reisz (1986) recognised a lateral expansion of the frontal contributing to the orbital margin in early synapsids. Benson (2012) omitted this character, concluding that the lappet formed a continuum in early synapsids, making scoring problematic. Indeed, for some datasets the presence of a lateral expansion of the frontal and the presence of a frontal contribution to the orbital rim are synonymous (e.g. Modesto 1995 c.9). In the current taxon list, however, this character forms a clear morphological dichotomy and provides salient phylogenetic data. Herein these two morphologies are considered as independent characters in accordance with more recent studies (Modesto *et al.* 2015 c.5, Spindler *et al.* 2018 c.41). State (1), the presence of a lateral lappet, has a broad distribution amongst early synapsids (Reisz 1986), although I concur with Brinkman and Eberth (1983) that it is absence in mycterosaurines and varanodontines. A large frontal lappet is considered an autapomorphy of lanthanosuchoid parareptiles (deBraga and Reisz 1996) (e.g. *Acleistorhinus* and *Colobomycter* in the current taxon list). The lappet is absent in 'protorothyridids', diapsids (with exception of *Claudiosaurus*), captorhinids (with exception of *Romeria texana*) and most parareptiles.

Unambiguous: *Claudiosaurus germaini* (0→1), *Ennatosaurus tecton* (1→0), Synapsida (0→1), *Colobomycter* + *Acleistorhinus* (0→1), *Romeria* spp (0→1), *Varanosaurus acutirostris* (1→0).

63. Frontal, anteroposterior length at the midline: less than 1.5 times parietal length (0); equal to or greater than 1.5 times parietal length (1); greater than 2.5 times parietal length (2)

Modified from Sidor and Hopson (1998 c.47), Dilkes (1998 c.19), Maddin *et al.* (2008 c.25), Benson

(2012 c.56).

The frontal is short anteroposteriorly relative to the parietal (state 0) in caseasaurs (Langston 1965, Reisz *et al.* 2009, *Casea broilii* FMNH UC 656, Maddin *et al.* 2008), captorhinids (*Captorhinus laticeps* FMNH UC 701, OMNH 15101, *Protocaptorhinus pricei* MCZ 1160, *Romeria primus* MCZ 1963,Reisz *et al.* 2016) and some parareptiles (Tsuji 2006, MacDougall *et al.* 2017, *Acleistorhinus pteroticus* FMNH UR 1038). Diapsids, mycterosaurines, varanodontines and ophiacodontids are scored for state (1). Only sphenacodontids (Romer and Price 1940, Reisz *et al.* 1992) and the archosauromorph *Proterosuchus* (Ezcurra and Butler 2015) possess the greatly enlarged frontals relative to the parietals (state 2) in the current taxon list.

Unambiguous: *Edaphosaurus boanerges* (1→0), Captorhinidae (1→0), Caseasauria (1→0), Sphenacodontidae (1→2), *Colobomycter* + *Acleistorhinus* (1→0), *Owenetta kitchingorum* (0→1), *Proterosuchus* spp (1→2), *Reiszorhinus olsoni* (0→1), *Seymouria* spp (1→0). DELTRAN: *Hylonomus lyelli* (1→0), Bolosauridae + *Macroleter* + Procolophonoidea (1→0). ACCTRAN: *Anthracodromeus* + *Hylonomus* (1→0), Bolosauridae + Procolphonoidea + *Macroleter* (1→0).

64. Frontal, posterolateral process: absent, frontoparietal suture forming right angle to parasagittal plane (0); short, only partially separating parietal from dorsolateral margin of postfrontal or forming obtuse posterolateral angle to parasagittal plane (1); long, narrow, frontoparietal suture forming acute posterolateral angle with parasagittal plane, substantially or fully separating parietal from dorsomedial margin of postfrontal (2)

Modified from Reisz *et al.* (1998 c.4), Rieppel *et al.* (1999 c.15), Reisz and Dilkes (2003 c.4), Müller (2004 c.10) Maddin *et al.* (2006 c.17), Reisz *et al.* (2009 c.28), Reisz *et al.* (2010 c.27), Benson (2012 c.61), Spindler *et al.* (2018 c.39).

The character state 0 is found in *Seymouria* and *Gephyrostegus* (Klembara *et al.* 2005, 2014), captorhinids (*Protocaptorhinus pricei* MCZ 1478, Reisz *et al.* 2016) and 'protorothyridids' (Carroll 1964, 1969) and as a secondary reversal in sphenacodontids (Romer and Price 1940, Reisz *et al.* 1992). An elongate posterolateral process of the frontal (state 2) is present in ophiacodontids, mycterosaurines, varanodontines, diapsids and some parareptiles. Most other taxa herein share state (1), including diadectomorphs (Moss 1972, Berman *et al.* 2010) and eothyridids (Langston 1965, Reisz *et al.* 2009,

Brocklehurst *et al.* 2016).

Unambiguous:*Macroleter poezicus* (2→1), clade B (0→2), *Colobomycter* + *Acleistorhinus* (2→1). DELTRAN: *Belebey vegrandis* (2→0), *Haptodus garnettensis* (0→1), Diadectomorpha (0→1), Eothyrididae (0→1), *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (0→2), Edaphosauridae (0→1), *Petrolacosaurus kansensis* (2→1), *Protorothyris archeri* (0→1). ACCTRAN: Sauropsida (1→0), Diadectomorpha + Amniota (0→1), Caseidae (1→0), Ophiacodontidae (1→2), Sphenacodontidae (1→0), *Eudibamus* + *Belebey* (2→0), *Petrolacosaurus kansensis* (2→1), *Protorothyris archeri* (0→12).

65. Postorbital, lateral tuberosity at orbital margin: absent (0); present (1)

Modified from Reisz *et al.* (1998 c.14), Reisz and Dilkes (2003 c.37), Maddin *et al.* (2006 c.23), Reisz *et al.* (2009 c.33), Reisz *et al.* (2010 c.44), Benson (2012 c.67), Spindler *et al.* (2018 c.47).

Character state 1, describing the presence of a freely exposed lateral boss on the prefrontal is present in most derived mycterosaurines and varanodontines (Botha-Brink and Modesto 2009, microCT data *Mycterosaurus longiceps* FMNH UC 692, Reisz and Laurin 2004) with the exception of basal mycterosaurines (Reisz *et al.* 2011, Spindler *et al.* 2018) and *Varanops* (Campione and Reisz 2010). It is also present in the parareptile *Macroleter poezicus* (Tsuji 2006). The raised area of bone on the postorbital of some sphenacodontians is scored as state (0) herein, following the comments of Spindler *et al.* (2018 c.47), who interpreted the raised ridge forming the orbital rim on the postorbital as a lateral extension supporting the postfrontal, and creating a vertical trough in the postorbital, rather than a freely exposed boss.

Unambiguous:*Macroleter poezicus* (0→1). DELTRAN: *Varanodon* + *Watongia* (0→1), Mycterosaurinae (0→1). ACCTRAN: Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→1), *Varanops brevirostris* (1→0).

66. Postorbital, posterior process, contact with supratemporal: present (0); absent (1)

Modified form Reisz *et al.* (1992 c.20), Laurin (1993 c.25), Laurin and Reisz (1995 c.12), Berman *et al.* (1995 c.26), deBraga and Rieppel (1997 c.30), Maddin *et al.* (2008 c.27), Fröbisch *et al.* (2011 c.19), Benson (2012 c.66), Modesto *et al.* (2015 c.22), Spindler *et al.* (2018 c.49).

Contact between the postorbital and supratemporal is absent (state 0) in *Seymouria*, *Gephyrostegus* and *Tseajaia* (Laurin 1996, Evans 1980, Moss 1972), although it is present (state 1) in *Limnoscelis* (Romer 1946, Berman *et al.* 2010). All diapsids and captorhinids in the current taxon list possess state (0), together with basal parareptiles. State (1) is found in all caseasaurs (e.g. *Eothyris* MCZ 1161, *Casea* FMNH UC 656), but varies within other groups. It is present in *Ophiacodon* (Romer and Price 1940), but absent in *Varanosaurus* (FMNH PR 1670), where a narrow process of the parietal separates the two bones. It is present in *Dimetrodon* and *Sphenacodon*, but absent in *Secodontosaurus* (Reisz *et al.* 1992). It is present in *Archaeovenator* (Reisz and Dilkes 2003) but absent in *Mesenosaurus* (Reisz and Berman 2001).

Unambiguous: *Dimetrodon* spp (0→1), *Limnoscelis plaudis* (0→1), *Mesenosaurus romeri* (1→0), Caseasauria (0→1), Varanopidae except *Ascendonanus* (0→1),*Ophiacodon* spp (0→1). DELTRAN: *Acleistorhinus pteroticus* (0→1), *Macroleter* + Procolophonoidea (0→1). ACCTRAN: Bolosauridae + Procolphonoidea + *Macroleter* (0→1), *Colobomycter* + *Acleistorhinus* (0→1).

67. Postorbital, anteroposterior length of posterior process: short (0); long, extending more than half of temporal length (1)

Modified from Laurin (1993 c.25), Berman (1995 c.25), Reisz *et al.* (1998 c.23), Maddin *et al.* (2006 c.21), Maddin *et al.* (2008 c.15), Reisz *et al.* (2009 c.31), Benson (2012 c.68), Spindler *et al.* (2018 c.45)

This character is considered independent to ch.66 above, since other factors can determine contact with the supratemporal e.g. *Mesenosaurus*, where the contact is absent but the posterior process is long (Reisz and Berman 2001), whereas in varanodontines the posterior process is short but still makes contact with the supratemporal (Campione and Reisz 2010).

Unambiguous: *Dimetrodon* spp (0→1), *Limnoscelis plaudis* (0→1), *Mesosaurus tenuidens* (1→0), Procolophonoidea (1→0), *Prolacerta broomi* (1→0). DELTRAN: *Araeoscelis* spp (0→1), clade C (0→1), Caseasauria (0→1), *Varanosaurus* + *Ophiacodon* (0→1), *Varanops* + *Varanodon* + *Watongia* (1→0). ACCTRAN: clade B (0→1),Sphenacodontia + Edaphosauridae (1→0), Synapsida (0→1), Varanodontinae (1→0), *Petrolacosaurus kansensis* (1→0).

68. Postorbital, posterior process, transverse (dorsoventral) width: broad, at least 25% of dorsoventral height of temporal region (0); narrow, no more than 20% of dorsoventral height of temporal region (1)

Modified from Reisz *et al.* (1992 c.22), Laurin (1993 c.15), Berman (1995 c.26), Maddin *et al.* (2008 c.28), Fröbisch *et al.* (2011 c.13), Benson (2012 c.69), Spindler *et al.* (2018 c.46).

This character has been modified from that used in previous studies by quantifying the relative transverse width of the posterior process in relation to the height of the temporal region at the same level. This is a similar approach to that taken with the dorsoventral height of the ventral temporal (zygomatic) bar in ch.71 below.

Unambiguous: *Milleretta rubidgei* (0→1), *Eothyris* + *Eocasea* (1→0), *Heleosaurus* + *Mesenosaurus* (1→0). DELTRAN: Araeoscelidia (0→1), Synapsida (0→1), Varanopidae except *Ascendonanus* (0→1), Neodiapsida (0→1), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: *Ascendonanus nestleri* (1→0), Parareptilia (1→0), Protorothyrididae (1→0), Captorhinidae except *Thuringothyris* (1→0), Amniota (0→1).

69. Postorbital, dorsal and lateral surfaces: form smooth curve (or dorsal surface absent, postorbital not participating in skull roof) (0); sharply divided (meeting at edge) (1)

Modified from Reisz *et al.* (1998 c.25), Reisz and Dilkes (2003 c.25), Maddin *et al.* (2006 c.22), Reisz *et al.* (2009 c.32), Reisz *et al.* (2010 c.43), Campione and Reisz (2010 c.22)

Recent studies have rejected a modified version of this character due to uncertainty of the distinction between states (Benson 2012 c.X1, Spindler *et al.* 2018). This character describes the same morphology for the postorbital as ch.60 above does for the prefrontal, and is coded as present in some mycterosaurines (Reisz and Berman 2001, Berman and Reisz 1982). Maddin *et al.* (2008:173) note that a 'well-defined right angle' between the skull table and temporal surface of the postorbital is present in derived caseasaurs such as *Ennatosaurus* and *Cotylorhynchus*.

Unambiguous: *Ennatosaurus tecton* (0→1), Mycterosaurinae (0→1).

70. Postorbital, contact with parietal: absent (0); present (1)

Modified from Dilkes (1998 c.22), Müller (2004 c.89).

The postorbital contacts the parietal in all terminal taxa in the present study with some exceptions. In *Seymouria* and *Gephyrostegus* the intertemporal bone prevents contact with the parietal (Klembara *et al.* 2005, 2014). A broad contact between the postfrontal and supratemporal in the parareptile *Acleistorhinus* prevents contact of the postorbital and parietal (deBraga and Reisz 1996). In archosauriforms, represented by *Proterosuchus* in the present study, postfrontal/supratemporal contact also excludes the postorbital from contact with the parietal (Ezcurra and Butler 2015).

Unambiguous: Diadectomorpha + Amniota (0→1), *Owenetta kitchingorum* (1→0), *Proterosuchus* spp (1→0). DELTRAN: *Acleistorhinus pteroticus* (1→0). ACCTRAN: *Acleistorhinus pteroticus* (1→0).

71. Temporal (=Postorbital) region, height of ventral temporal (zygomatic) bar (complete or partially complete): tall, occupying more than 20% of skull height (0); narrow, occupying less than 20% of postorbital skull height (1) inapplicable, ventral temporal bar absent (-)

Modified from Laurin (1991 B.4), Dilkes (1998 c.32), Reisz and Dilkes (2003 c.18), Müller (2004 91), Reisz *et al.* (2010 c.41), Ezcurra *et al.* (2014 c.40)

All diapsids, mycterosaurines, varanodontines and parareptiles, with the exception of *Petrolacosaurus* (Reisz 1981, Reisz *et al.* 2010 c.41), share state (1), describing a narrow ventral temporal bar. The ventral temporal bar of *Haptodus* (Laurin 1993) and edaphosaurids (Modesto 1995, Modesto and Reisz 1990) are also scored as narrow. Caseasaurs, ophiacodontids and sphenacodontids possess tall ventral bars (state 0).

Unambiguous: *Milleretta rubidgei* (1→0), clade C (0→1). DELTRAN: *Haptodus garnettensis* (0→1), Edaphosauridae (0→1). ACCTRAN: Sphenacodontidae (1→0),Sphenacodontia + Edaphosauridae (0→1).

72. Jugal, free posterior margin: absent (0); present (1)

NEW

This character is the first of seven new characters coded to describe temporal fenestrae and emarginations. See Chapter 3 for detailed discussion on this character and others relating to temporal openings. A free surface at any point on the posterior margin of the jugal (state 1) indicates the presence of a lateral temporal fenestration or emargination.

Unambiguous: *Mesosaurus tenuidens* (1→0), Synapsida (0→1), *Procolophon trigoniceps* (1→0). DELTRAN: clade C (0→1), *Petrolacosaurus kansensis* (0→1). ACCTRAN: *Araeoscelis* spp (1→0), clade B (0→1).

73. Jugal, free concave ventral margin: absent (0); present (1)

NEW

This character is the second of seven new characters coded to describe temporal fenestrae and emarginations. See Chapter 3 for detailed discussion on this character and others relating to temporal openings. Character state (1) describes the concavity on the ventral margin of the jugal that contributes to a distinct ventral emargination of the postorbital region in sphenacodontids (e.g. *Secodontosaurus* MCZ 1124, Reisz *et al.* 1992; *Dimetrodon*, Romer and Price 1940; *Sphenacodon*, Spielmann *et al.* 2010), *Edaphosaurus* (Modesto 1995 fig.2/fig.6) and the parareptile *Procolophon* (Carroll and Lindsay 1985).

Unambiguous: *Edaphosaurus boanerges* (0→1), Sphenacodontidae (0→1), *Procolophon trigoniceps* (0→1).

74. Jugal, contribution to ventral margin of the skull: present (0); absent (1)

Modified from, Reisz *et al.* (1992 c.31), Berman (1995 c.37), Maddin *et al.* (2008 c.13), Benson (2012 c.71 in part).

The jugal is excluded from the ventral margin of the skull (state 1) in caseasaurs, *Mycterosaurus*,

Elliotsmithia, varanodontines and some parareptiles. This exclusion of the jugal from the ventral margin is achieved in all cases by the contact of the maxilla with the quadratojugal. However, the nature of this contact derives from two distinct morphologies (Langston and Reisz 1981, Reisz 1986), which differ between and within these groups, and forms the basis of the subsequent character (ch.75).

Unambiguous: Caseasauria (0→1), *Heleosaurus* + *Mesenosaurus* (1→0), Mycterosaurinae + Varanodontinae (0→1), *Colobomycter* + *Acleistorhinus* (0→1). DELTRAN: *Belebey vegrandis* (0→1),*Macroleter poezicus* (0→1). ACCTRAN: Procolophonoidea (1→0), Bolosauridae + Procolphonoidea + *Macroleter* (0→1).

75. Jugal, if contribution to ventral margin of skull is absent: jugal excluded from ventral margin by maxilla-quadratojugal contact achieved by a long posterior extension of the maxilla (0); maxilla-quadratojugal contact achieved by long anterior extension of the quadratojugal (1); inapplicable, jugal contributes to ventral margin of skull (-)

Modified from Brinkman and Eberth (1983 c.2), Modesto (1994 c.6), Laurin and Reisz (1995 c.22), Tsuji (2006 c.22), Reisz *et al.* (2009 c.46), Reisz *et al.* (2010 c.46 in part), Benson (2012 c.71 in part), Modesto *et al.* (2015 c.31), Spindler *et al.* (2018 c.62).

A long posterior extension of the maxilla is present in *Vaughnictis* (Brocklehurst *et al.* 2016), varanodontines (Campione and Reisz 2010), *Mycterosaurus* (Berman and Reisz 1982) and *Acleistorhinus* (deBraga and Reisz 1986). In *Elliotsmithia* (Modesto *et al.* 2001), all other caseasaurs apart from *Vaughnictis* and parareptiles the quadratojugal possesses an extended anterior process, which meets the maxilla closer to the orbital margin.

Unambiguous: *Vaughnictis smithae* (1→0). DELTRAN: *Acleistorhinus pteroticus* (1→0), *Mycterosaurus longiceps* (1→0), Varanodontinae (1→0). ACCTRAN: *Acleistorhinus pteroticus* (1→0), *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (0→1), Varanopidae (1→0).

76. Jugal, suborbital ramus: does not extend to anterior orbital rim (0); extends at least to level of anterior orbital rim (1)

From Laurin and Reisz (1995 c.11), Tsuji (2006 c.12), Tsuji *et al.* (2012 c.12), MacDougall and Reisz

(2014 c.18), Modesto *et al.* (2015 c.18), Modesto *et al.* (2018 c.20).

This character has typically been used in parareptile phylogenies, where state (1) is present in *Macroleter*, pareiasaurs and procolophonoids (Modesto *et al.* 2015). Modesto *et al.* (2015) also score araeoscelidians and diapsids as possessing state (1). However, the ramus does not extend to the anterior orbital rim in *Petrolacosaurus* (Reisz 1981, KUVP 9952), *Youngina* (BP/1/2871, FMNH UC 1528) and *Acerosodontosaurus* (Bickelmann *et al.* 2009). In derived ophiacodontids, sphenacodontians and some captorhinids the ramus extends beyond the anterior orbital rim (state 1). Among stem-amniotes, a short ramus is present in *Tseajaia* and *Gephyrostegus* (state 0) and the ramus length is polymorphic among species of *Seymouria* e.g. *S. baylorensis* shows state (0) (Laurin 1996), and *S. sanjuanensis* shows state (1) (Klembara *et al.* 2005). Spindler *et al.* (2018) rejects the concept of describing the anterior extent of the suborbital ramus by its relative position to the orbit as interdependent with proportional constraints, opting instead for the presence or absence of contact with the lacrimal (Spindler *et al.* 2018 online resource 3 c.44). However, I find that the scores of this character are independent of the scores of characters concerned with the lacrimal/jugal contact and extent of the suture (ch.53 and ch.54 above), and therefore I use all of these characters in the study.

Unambiguous: *Limnoscelis plaudis* (0→1), *Protocaptorhinus* pricei (1→0), Captorhinidae (0→1), *Proterosuchus* spp (0→1). DELTRAN:*Macroleter poezicus* (0→1), *Mesosaurus tenuidens* (0→1), *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (0→1), Sphenacodontia (0→1), *Procolophon trigoniceps* (0→1). ACCTRAN: Edaphosauridae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Eudibamus* + *Belebey* (1→0), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1), *Owenetta kitchingorum* (1→0).

77. Jugal, anteroposterior thickness of dorsal ramus (forming postorbital bar): broad, temporal fenestra only weakly emarginates the jugal (0); narrow, (1); inapplicable, temporal fenestration absent or jugal lacks dorsal ramus (-)

From Benson (2012 c.73) modified from Maddin *et al.* (2008 c.20), Reisz and Fröbisch (2014 c.73).

State (0) of this character is present in most basal caseasaurs (Reisz *et al.* 2009, Brocklehurst *et al.* 2016, Reisz and Fröbisch 2014) and those parareptiles in which temporal fenestration is present (Tsuji 2006, MacDougall *et al.* 2017, deBraga and Reisz 1996)

Unambiguous: Parareptilia (1→0). DELTRAN: *Casea broilii* (1→0), *Euromycter rutena* (1→0), *Eothyris* + *Eocasea* + *Vaughnictis* (1→0). ACCTRAN: *Ennatosaurus tecton* (0→1), Caseasauria (1→0), *Oedaleops campi* (0→1).

78. Jugal, posterior ramus length: short, extending to, or less than, temporal midlength (0); long, extending to the posterior end of temporal fenestra (or past temporal midlength in taxa that lack a temporal fenestra) (1); inapplicable, jugal lacks posterior process (-)

Modified from Gauthier *et al.* (1988 c.34), deBraga and Rieppel (1997 c.33), Rieppel (1999 c.24), Müller (2004 c.16), Reisz *et al.* (2009 c.49), Benson (2012 c.75).

Unambiguous: *Dimetrodon* spp (0→1), *Eothyris parkeyi* (0→1), Diadectomorpha (0→1), Mycterosaurinae (0→1), *Oedaleops campi* (0→1), *Proterosuchus* spp (0→1), *Reiszorhinus olsoni* (0→1), *Romeria* spp (0→1). DELTRAN: *Varanosaurus* + *Ophiacodon* (0→1). ACCTRAN: Ophiacodontidae (0→1).

79. Jugal, tuberous ornamentation on lateral surface: absent (0); present (1)

Modified from Reisz *et al.* 1998 c.14, Reisz and Dilkes 2003 c.17, Maddin *et al.* 2006 c.44, Reisz *et al.* 2010 c.34, Benson (2012 c.12).

Distinctive ornamentation in the form of a series of dorsoventral serrations on the ventral margin of the suborbital ramus of the jugal is present in *Aerosaurus* (Langston and Reisz 1981). A similar pattern on the ventral margin of the jugal is present in *Varanops*, although it is absent in *Varanodon* (Campione and Reisz 2010, FMNH UR 986). *Heleosaurus*, *Elliotsmithia* and *Mesenosaurus* also possess tubercular ornamentation on the lateral surface of the jugal (Reisz and Modesto 2007, Reisz *et al.* 1998, Reisz and Berman 2001), and a small irregular raised ridge is present on the orbital margin of the left jugal in *Mycterosaurus*, based on microCT data of the holotype FMNH UC 692). Reisz *et al.* (2010) noted a small tubercle on the left jugal in *Apsisaurus*, although this appears to be absent from the right jugal (MCZ 1474). Circumorbital ornamentation is absent in the basal mycterosaurines *Archaeovenator* and *Ascendonanus* (Reisz and Dilkes 2003, Spindler *et al.* 2018).

Unambiguous: Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→1). DELTRAN: *Varanodon agilis* (1→0). ACCTRAN: *Varanodon* + *Watongia* (1→0).

80. Jugal, ventral contact with squamosal perforated by small elongate fenestra: absent (0); present, upper margin enclosed by anteroventral extension of the squamosal (1); inapplicable jugal does not contact squamosal ventrally (-)

From Benson (2012 c.76), modified from Berman *et al.* (1995 c.17)

A small 'half moon' shaped fenestra has been observed in some specimens of *Ophiacodon retroversus* at the junction of the squamosal, jugal and quadratojugal, which appears to be polymorphic for this genus (Romer and Price 1940). A similar condition is present in the only specimen of *Varanosaurus* where the temporal region is preserved (Berman *et al.* 1995, FMNH PR 1670).

Unambiguous: *Varanosaurus* + *Ophiacodon* (0→1).

81. Quadratojugal, contact with posteroventral margin of jugal: present (0); absent (1)

NEW

This character is the third of seven new characters coded to describe temporal fenestrae and emarginations. See Chapter 3 for detailed discussion on this character and others relating to temporal openings. The quadratojugal is in contact with the posteroventral margin of the jugal (state 0) in most taxa included in the present study, and this state is universally associated with the presence of an anteroventral process of the quadratojugal. Contact between the quadratojugal and posteroventral margin of jugal is absent (state 1) in all taxa included herein that possess an emargination or concavity of the ventral surface of the temporal region (e.g. sphenacodontians, edaphosaurids, some neo-diapsids and owenettids), with the exception of *Procolophon*, in which the quadratojugal contacts the jugal along the entire posterior margin and is scored as state (0). This character replaces a character used in recent studies describing the presence, absence or size limitation of the anterior process of the quadratojugal (e.g. Benson 2012 c.77, Pritchard *et al.* 2015 c.39, Spindler *et al.* 2018 c.60).

Unambiguous:Sphenacodontia + Edaphosauridae (0→1), *Owenetta kitchingorum* (0→1). DELTRAN:

Lanthanolania + Archosauromorpha (0→1). ACCTRAN: Neodiapsida (0→1), *Youngina capensis* (1→0).

82. Quadratojugal, contact with posterodorsal margin of jugal: absent (0); present (1)

NEW

This character is the fourth of seven new characters coded to describe temporal fenestrae and emarginations. See Chapter 3 for detailed discussion on this character and others relating to temporal openings. Contact between the quadratojugal and the posterodorsal margin of the jugal is present (state 1) in procolophonoids (e.g. *Procolophon*, *Owenetta* and *Candelaria*), and absent (state 0) in all other taxa.

Unambiguous: Procolophonoidea (0→1).

83. Quadratojugal, shape of anterior margin of anteroventral process: square-tipped (0); acuminate (tapering to a point) (1); inapplicable, anteroventral process absent (-)

From Dodick and Modesto 1995 c.10, Müller and Reisz (2005 c.10), Müller *et al.* (2006 c.10), Müller and Reisz (2006 c.10), Modesto *et al.* (2007 c.12), Modesto *et al.* (2018 c.23).

The anterior tip of the quadratojugal in the out-group taxon *Gephyrostegus* meets the jugal in a dorsoventrally straight suture (Klembara *et al.* 2014). The same condition is found in basal 'protorothyridids' e.g. *Hylonomus* (Carroll 1964 - based on the morphology of jugal and squamosal) and *Cephalerpeton* (Carroll and Baird 1972), and some captorhinids e.g. *Romeria primus* (Clark and Carroll 1973) and *Captorhinus aguti* (Fox and Bowman 1966). *Ennatosaurus* (Maddin *et al.* 2008) and *Milleretta rubidgei* (Gow 1972) also share state (0).

Unambiguous: *Ennatosaurus tecton* (1→0), *Hylonomus lyelli* (1→0), *Milleretta rubidgei* (1→0), *Seymouria* + Diadectomorpha + Amniota (0→1). DELTRAN: *Captorhinus* spp (1→0), *Romeria* spp (1→0). ACCTRAN: *Captorhinus* + *Protocaptorhinus* + *Romeria* (1→0), *Protocaptorhinus pricei* (0→1).

84. Squamosal, contacts posterodorsal margin of jugal: absent (0); present (1)

NEW

This character is the fifth of seven new characters coded to describe temporal fenestrae and emarginations. See Chapter 3 for detailed discussion on this character and others relating to temporal openings. State (1) is present in all taxa that do not possess a lateral temporal opening, the anapsid condition (e.g. diadectomorphs, *Seymouria*, *Gephyrostegus*, 'Protorothyridids', *Araeoscelis*, captorhinids and *Mesosaurus*), and in some that do, such as derived varanodontines (e.g. *Varanops*, *Varanodon*) and parareptiles (e.g. bolosaurids, *Acleistorhinus* and *Colobomycter*)

Unambiguous: Synapsida (1→0), *Varanops* + *Varanodon* + *Watongia* (0→1), Procolophonoidea (1→0), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1). DELTRAN: *Acleistorhinus pteroticus* (0→1), clade C (1→0), *Petrolacosaurus kansensis* (1→0). ACCTRAN: *Acleistorhinus pteroticus* (0→1), *Araeoscelis* spp (0→1), clade B (1→0).

85. Squamosal, contacts posteroventral margin of jugal: absent (0); present (1)

NEW

This character is the sixth of seven new characters coded to describe temporal fenestrae and emarginations. See Chapter 3 for detailed discussion on this character and others relating to temporal openings. State (1) is present in eothyridids, ophiacodontids, sphenacodontians, edaphosaurids, mycterosaurines and bolosaurid parareptiles. It is also present in some anapsid taxa where the anterior region of the quadratojugal tapers to a point contact with the jugal, permitting the squamosal to contact the posteroventral margin of the jugal (e.g. *Paleothyris*, *Protorothyris*) and in *Araeoscelis*. In all taxa scoring as state (1) the quadratojugal does not participate in the lateral temporal fenestration (if present). Therefore, this character replaces a character used in several studies to describe the contribution of the quadratojugal to the lateral temporal fenestra (e.g. Tsuji 2006 c.32, Benson 2012 c.77/78 in part, MacDougall and Reisz 2014 c.46, Modesto *et al.* 2015 c.46, Spindler *et al.* 2018 c.61).

Unambiguous: *Araeoscelis* spp (0→1), *Protorothyris* + *Paleothyris* (0→1), Varanodontinae (1→0), Varanopidae (0→1), *Protocaptorhinus pricei* (0→1). DELTRAN: *Mesosaurus tenuidens* (0→1), Eothyrididae (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Eudibamus* + *Bele-*

bey (0→1). ACCTRAN: Caseidae (1→0), Synapsida (0→1), *Macroleter* + Procolophonoidea (1→0), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1).

86. Squamosal, anteroposterior breadth of post-fenestral portion on lateral surface of skull: narrow (0); broad, just over half the breadth of the temporal region, restricting the posterior extent of the temporal fenestra (1); inapplicable, temporal fenestra absent (-)

From Benson (2012 c.79), modified in Spindler *et al.* (2018 c.55).

Ophiacodontids possess an anteroposteriorly broad region of the squamosal posterior to the temporal fenestra (state 1) (Romer and Price 1940, Berman *et al.* 1995, Modesto and Reisz 1990). State (1) is also present in the eothyridid *Vaughnictis* (Brocklehurst *et al.* 2016), and some parareptiles (e.g. *Macroleter poezicus*, Tsuji 2006 and *Belebey*, Reisz *et al.* 2007).

Unambiguous: *Vaughnictis smithae* (0→1). DELTRAN: *Milleretta rubidgei* (0→1), *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (0→1), Bolosauridae + *Macroleter* + Procolophonoidea (0→1). ACCTRAN: Parareptilia (0→1), Ophiacodontidae (0→1), *Colobomycter* + *Acleistorhinus* (1→0).

87. Squamosal, occipital shelf (flange): mediolaterally broad, contributes to occipital surface of skull, obscuring much of the posterior margin of the quadrate (0); absent or mediolaterally very narrow, posterior margin of quadrate exposed in occipital view (1)

Modified from Laurin (1991 D.2, E.4), Berman *et al.* (1995 c.48), Laurin and Reisz (1995 c.27), deBraga and Rieppel (1997 c.37), Reisz *et al.* (1998 c.15), Reisz and Dilkes (2003 c.33), Müller (2004 c.132), Maddin *et al.* (2006 c.35), Reisz *et al.* (2009 c.39), Reisz *et al.* (2010 c.38), Benson (2012 c.80), Spindler *et al.* (2018 c.59).

Many early amniotes have a mediolaterally broad occipital flange of the squamosal e.g. captorhinids (Heaton 1979 fig.1, Sumida *et al.* 2010 fig.3), 'protorothyridids' (Clark and Carroll 1973 fig.2), caseasaurs (Reisz *et al.* 2009 fig.4, Maddin *et al.* 2008 fig.1) and early synapsids (Berman *et al.* 1995 fig.9, Romer and Price 1940 plate 14, Modesto *et al.* 1995 fig.1). In mycterosaurines (Reisz and Berman 2001 fig.4, Berman and Reisz 1982 fig.5), varanodontines (FMNH UR 986), diapsids (Vaughn

1955 fig.4, Modesto and Sues 2004 fig.5) and some parareptiles (deBraga and Reisz 1996 fig.1, Modesto 2006 fig.2) the flange is narrower or is absent altogether.

88. Squamosal, posterodorsal process: absent (0); present (1)

Modesto *et al.* (2001 c.33), Maddin *et al.* (2006 c.27), Reisz *et al.* (2009 c.40), Botha-Brink and Modesto (2009 c.27), Reisz *et al.* (2010 c.36), Benson (2012 c.81), Spindler *et al.* (2018 c.56).

Modesto *et al.* (2001) observed that a small spur of bone extending posteriorly from the posterodorsal corner of the squamosal in *Elliotsmithia* was also present in *Mesenosaurus* (state 1). Subsequently, the same morphology has been observed in *Heleosaurus* (Botha-Brink and Modesto 2009) and Spindler *et al.* (2018) noted a posterodorsal process in the *Ascendonanus* (Spindler *et al.* 2018 fig.25). Several studies have also scored the derived state for caseasaurs (Maddin *et al.* 2006, Reisz *et al.* 2009, Spindler *et al.* 2018). I have not been able to determine the presence or absence of this feature in *Eothyris* (MCZ 1161) where the posterodorsal margin of the squamosal is obscured by the supratemporal, and I score this taxon as (?) herein. In *Oedaleops* there is a slight concavity in the posteroventral margin of the squamosal (Langston 1965 fig.1A), which does not represent the derived morphology of this character. A posterodorsal process of the squamosal is clearly present in the archosauromorphs *Prolacerta* (Modesto and Sues 2004) and *Proterosuchus* (Ezcurra and Butler 2015).

Unambiguous: *Ascendonanus nestleri* (0→1). DELTRAN: *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (0→1), Archosauromorpha (0→1). ACCTRAN: Mycterosaurinae (0→1).

89. Squamosal, contribution to the posttemporal fenestra: absent (0); present (1)

Laurin and Reisz (1995 c.26), deBraga and Rieppel (1997 c.36), Müller and Reisz (2006 c.49), Tsuji (2006 c.26), Tsuji *et al.* (2012 c.25), Laurin and Piñeiro (2017 c.25).

This participation of the occipital flange of the squamosal in margin of the posttemporal fenestra is considered by several studies to be a synapomorphy of Eureptilia (Laurin and Reisz 1995, deBraga and Rieppel 1997, Laurin and Piñeiro 2017). The mediolaterally broad occipital exposure of the squamosal in captorhinids and 'protorothyridids' (Fox and Bowman 1966, Carroll 1969, Clark and Carroll 1973, Müller *et al.* 2006) and in *Petrolacosaurus* (Reisz 1981), coupled with the absence of a tabular (in the

case of most captorhinids) or an anteroposteriorly short tabular (in *Petrolacosaurus*), does allow an extensive exposure of the squamosal to the posttemporal fenestra (state 1). However, this is not the case in all early diapsids, such as *Araeoscelis*, where the tabular is elongate (Vaughn 1955), or in *Prolacerta*, where the occipital exposure of the squamosal in limited (Gow 1975, Modesto and Sue 2004). State (1) is also present, however, in some parareptiles (e.g. *Mesosaurus*, Modesto 2006; bolosaurids and *Acleistorhinus*, scoring of Tsuji 2006 c.26). In derived ophiacodontids, the squamosal forms the lateral margin of the posttemporal fenestra (state 1)(e.g. *Ophiacodon* uniformis, Romer and Price 1940 pl.4, and *Varanosaurus*, Berman *et al.* 1995).

Unambiguous: *Araeoscelis* spp (1→0), *Milleretta rubidgei* (1→0), Sauropsida (0→1), *Macroleter* + Procolophonoidea (1→0). DELTRAN: *Varanosaurus* + *Ophiacodon* (0→1), Mycterosaurinae + Varanodontinae (1→0), *Prolacerta broomi* (1→0). ACCTRAN: Ophiacodontidae (0→1), Varanopidae (1→0), *Lanthanolania* + Archosauromorpha (1→0).

90. Parietal, free lateral margin: absent (0); present (1)

NEW

This character is one of a suite of new characters coded to describe temporal fenestrae and emarginations. See Chapter 3 for detailed discussion on this character and others relating to temporal openings. State (1) is present in all diapsids, in which it describes the morphology of the dorsal arcade of the upper temporal fenestra. It is also present in the early synapsids *Secodontosaurus* (Reisz *et al.* 1992) and *Edaphosaurus* (Modesto 1995).

Unambiguous: *Edaphosaurus boanerges* (0→1), Araeoscelidia (0→1), Neodiapsida (0→1), *Orovenator mayorum* (0→1). DELTRAN: *Secodontosaurus obtusidens* (0→1). ACCTRAN: *Secodontosaurus obtusidens* (0→1).

91. Parietal, anteroposterior diameter of pineal foramen: small, less than 25% of mid-parietal length (0); large, more than 25% of mid-parietal length (1); absent (2)

Modified from Gauthier *et al.* (1988 c.17), Reisz *et al.* (1992 c.17), Berman *et al.* (1995 c.22), Müller (2004 c.12), Reisz *et al.* (2009 c.84), Reisz *et al.* (2010 c.31), Benson (2012 c.35), Spindler *et al.* (2018

c.52).

A proportionally large pineal foramen is present in all caseasaurs (Olson 1968, Reisz *et al.* 2009) and ophiacodontids (Romer and Price 1940, FMNH PR 1670, MCZ 4070), some mycterosaurines (Reisz and Berman 2001, Berman and Reisz), *Aerosaurus* (Langston and Reisz 1981) and *Secodontosaurus* (MCZ 1124).

Unambiguous: *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1), *Tseajaia campi* (0→1). DELTRAN: *Aerosaurus* spp (0→1), *Claudiosaurus germaini* (0→1), Caseasauria (0→1), *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (0→1), Mycterosaurinae (0→1), *Secodontosaurus obtusidens* (0→1). ACCTRAN:Sphenacodontia + Edaphosauridae (1→0), Synapsida (0→1), *Varanops* + *Varanodon* + *Watongia* (1→0), Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→1), *Secodontosaurus obtusidens* (0→1).

92. Parietal, pineal foramen location: anteriorly on parietal midline suture, such that the anterior rim of the foramen lies within the anterior third of the midline suture (0); midlength on parietal midline suture, such that the anterior and posterior rims of the foramen both lie within the middle third of the midline suture (1); posteriorly on parietal midline suture, such that the posterior rim of the foramen lies within the posterior third of the midline suture (2)

Modified from Reisz (1986 table 3.b), Laurin (1993 c.20), Modesto (1994 c.13), Laurin and Reisz (1995 c.3), deBraga and Rieppel (1997 c.47), Reisz *et al.* (1998 c.17), Rieppel (1999 c.18), Müller (2004 c.12), Maddin *et al.* (2006 c.20), Maddin *et al.* (2008 c.26), Reisz *et al.* (2009 c.35), Fröbisch *et al.* (2011 c.17), Benson (2012 c.85), Schoch and Sues (2015 c.49), Pritchard *et al.* (2015 c.23), Modesto *et al.* (018 c.28), Spindler *et al.* (2018 c.51).

This character has been used in various forms from the earliest cladistic analyses of 'pelycosaur'-grade synapsids, (e.g. Reisz 1986 table 3b) to the most recent analyses of captorhinids and synapsids (e.g. Modesto *et al.* 2018 c.28 and Spindler *et al.* 2018 c.51). Here, the definitions of the character states are clarified based on the position of the rim of the foramen in respect to the midline suture. I agree with the conclusion of Reisz (1986) that a posteriorly located foramen (state 2) is a synapomorphy of ophiacodontids, sphenacodontians, edaphosaurids, mycterosaurines and varanodontines. State (2) is

also shared with *Paleothyris* (MCZ 3483), *Orovenator* (Reisz *et al.* 2011), *Youngina* (BP/1/, 3895) and some parareptiles (*Macroleter poezicus*, Tsuji 2006, *Belebey*, Reisz *et al.* 2007). Captorhinids are united by an anteriorly placed foramen, as are caseids. Eothyridids share a centrally placed foramen as noted by Langston (1965).

Unambiguous: *Milleretta rubidgei* (1→2), Captorhinidae (1→0), *Seymouria* + Diadectomorpha + Amniota (0→1), Caseidae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (1→2), Varanopidae (1→2), Procolophonoidea (2→0), *Paleothyris acadiana* (1→2), *Tseajaia campi* (1→2), *Youngina capensis* (1→2). DELTRAN: *Anthracodromeus longipes* (1→0), Bolosauridae + *Macroleter* + Procolophonoidea (1→2). ACCTRAN: *Anthracodromeus* + *Hylonomus* (1→0), Bolosauridae + Procolphonoidea + *Macroleter* (1→2).

93. Parietal, dorsoventrally narrow flange extending ventrally from the lateral margin of the parietal (ventrolateral flange): absent (0); present (1); inapplicable, lateral margin of parietal is not free (-)

From Laurin (1991 D.1), deBraga and Reisz (1995 c.6), deBraga and Rieppel (1997c.48), Müller (2004 c.157), Reisz *et al.* (2010 c.29).

This character can only be scored for taxa where the parietal possesses a free lateral margin (ch.90 state1) i.e. diapsids, and the early synapsids *Edaphosaurus* and *Secodontosaurus*. Character state (1) is a synapomorphy of derived neodiapsids (Laurin 1991).

DELTRAN: Neodiapsida (0→1). ACCTRAN: clade D (0→1).

94. Supratemporal: present (0); absent (1)

From Laurin and Reisz (1995 c.18), Müller (2004: 21), Reisz *et al.* (2007 c.18), Benson (2012 c.88 state 3), Modesto *et al.* (2015 c.26).

In the current taxon list, the supratemporal is absent in the bolosaurid parareptiles *Belebey* and *Eudibamus* (Reisz *et al.* 2007). It is present in all other taxa.

Unambiguous: *Eudibamus* + *Belebey* (0→1).

95. Supratemporal, size: broad element of skull table, mediolateral width is greater than 30% of width of posterior skull table from lateral margin of supratemporal to midline (0); slender, in parietal or parietal/squamosal trough, mediolateral width approximately 15% (1); inapplicable, supratemporal absent (-)

Modified from Reisz *et al.* (1998 c.22), Reisz and Dilkes (2003: 22), Maddin *et al.* 2006 c.28), Maddin *et al.* (2008 c.28), Reisz *et al.* (2009 c.37), Reisz *et al.* (2010 c.52) Benson (2012 c.88 in part), Modesto *et al.* (2018 c.31), Spindler *et al.* (2018 c.53).

Gephyrostegus (Klembara *et al.* 2014), *Seymouria* (Klembara *et al.* 2005) and diadectomorphs (Moss 1972, Berman *et al.* 2010) all possess a broad supratemporal (state 0) that occupies the posterolateral corner of the skull roof, with a minimum width of 30% of the posterior skull table from the lateral margin of the supratemporal to the midline. This condition is also present in caseasaurs such as *Eothyris*, *Oedaleops* and *Vaughnictis* and caseids (Reisz *et al.* 2009, Langston 1965, MCZ 2985, FMNH UC 656) and in parareptiles (deBraga and Reisz 1996, Reisz and Scott 2002, MacDougall *et al.* 2017). Maddin *et al.* (2008 c.28) and Reisz *et al.* (2009 c.37) added a third state to that of Maddin *et al.* (2006) to describe the posteroventral extent of the supratemporal in certain caseids (e.g. *Euromycter*, *Ennatosaurus*, *Cotylorhynchus* and *Angelosaurus* (Maddin *et al.* 2008). In the present study, the increased posteroventral extent of the supratemporal of these taxa is described in the next character (ch.96). The supratemporal of captorhinids is a slender element (Fox and Bowman 1966, *Reiszorhinus* FMNH UC 183, *Romeria texana* MCZ 1480) and is scored as state (1), as are all diapsids (e.g. *Petrolacosaurus* Reisz 1981, *Youngina* Gow 1975 and *Prolacerta* Modesto and Sues 2004), ophiacodontids (e.g. *Varanosaurus* Berman *et al.* 1995), sphenacodontians (e.g. *Secodontosaurus* Reisz *et al.* 1992), edaphosaurids (e.g. *Edaphosaurus* Modesto 1995), varanodontines (e.g. *Aerosaurus* Langston and Reisz 1981) and mycterosaurines (e.g. *Mesenosaurus* Reisz and Berman 2001), with the exception of *Archaeovenator* (Reisz and Dilkes 2003). This character scores identically to a character describing the morphology of the posterolateral corner of skull (i.e. formed by parietal and small supratemporal or by supratemporal only) used in several analyses (e.g. Laurin and Reisz,1995 c.26; Müller and Reisz, 2006 c.49; Laurin and Piñeiro, 2017 c.25) but is omitted from the current character list.

Unambiguous: Parareptilia (1→0). DELTRAN: *Archaeovenator hamiltonensis* (1→0), Sauropsida (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1). ACCTRAN: *Archaeovenator*

hamiltonensis (1→0), Amniota (0→1), Caseasauria (1→0).

96. Supratemporal, posteroventral extent: approximately equal to or less than that of the tabular (0); greatly exceeds that of the tabular (1)

Modified from Maddin *et al.* (2009 c.28 state 2), Reisz *et al.* (2009 c.37 state 0)

Reisz and Fröbisch (2014) noted that in all synapsids, with the exception of caseids, the posteroventral extent of the supratemporal matches that of the tabular. In caseids (Reisz *et al.* 2009, Reisz and Fröbisch 2014) and in basal parareptiles (Modesto 2006, Reisz and Fröbisch 2014, Gow 1972) the posteroventral extension of the supratemporal significantly exceeds that of the tabular.

DELTRAN: *Eocasea martini* (0→1), *Milleretta rubidgei* (0→1), Caseidae (0→1), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1). ACCTRAN: *Eothyris parkeyi* (1→0), Parareptilia (0→1), Caseasauria (0→1), *Colobomycter* + *Acleistorhinus* (1→0).

97. Intertemporal: present (0), absent (1)

From Laurin and Reisz (1995 c.14), deBraga and Rieppel (1997 c.54), Klembara *et al.* (2014 c.23).

The intertemporal bone is present only in *Gephyrostegus* and *Seymouria* in the current taxon list (Klembara *et al.* 2005, 2014)

nambiguous: Diadectomorpha + Amniota (0→1).

98. Tabular: present (0); absent (1)

From Laurin (1991 E.3), deBraga and Reisz (1996 c.15), deBraga and Rieppel (1997 c.55), Jalil (1997 c.2), Reisz and Dilkes (2003 c.46), Müller (2004 c.15), Reisz *et al.* (2010 c.53), Sumida *et al.* (2010 c.22), Benson (2012 c.86 state 3), Modesto *et al.* (2015 c.24), Pritchard *et al.* (2015 c.37).

The tabular is present in most of the taxa included in the present study. It is absent in captorhinids (Müller and Reisz 2005), *Claudiosaurus* (Carroll 1981), archosauromorphs (e.g. *Prolacerta* Gow 1975 and *Proterosuchus* Ezcurra 2016) and the parareptiles *Colobomycter pholeter* (MacDougall *et al.*

2017), *Macroleter poezicus* (Tsuji 2006), *Owenetta* (Reisz and Scott 2002) and *Procolophon* (Carroll and Lindsey 1985).

Unambiguous: *Colobomycter pholeter* (0→1), Captorhinidae except *Thuringothyris* (0→1), *Macroleter* + Procolophonoidea (0→1). DELTRAN: *Claudiosaurus germaini* (0→1), Archosauromorpha (0→1). ACCTRAN: Neodiapsida (0→1), *Youngina capensis* (1→0).

99. Tabular, morphology: broad sub-rectangular sheet located dorsal to the fenestra (0); small and wedge-shaped, located dorsal to the post-temporal fenestra (1); long and narrow, displaced laterally, located dorsolateral to post-temporal fenestra (2); large L-shaped bone enclosing post-temporal fenestra dorsally and laterally (3); inapplicable tabular absent (-)

Modified from deBraga and Rieppel (1997 c.55), Sidor and Hopson (1998 c.54), Reisz and Dilkes (2003 c46), Maddin *et al.* (2006 c.29), Reisz *et al.* (2009 c.51), Berman *et al.* (1995 c.55), Benson (2012 c.86), Schoch and Sues (2015 c.55), Spindler *et al.* (2018 c.64/c.65).

The morphology of the tabular varies considerably among the terminal taxa of the present study, and presents challenges in describing character states that reflect potential homologies. In previous studies the descriptive emphasis has been focused on (i) the degree or absence of ventral expansion (deBraga and Rieppel 1997, Schoch and Sues 2015), (ii) mediolateral expansion (Reisz and Dilkes 2003, Maddin *et al.* 2006, Reisz *et al.* 2009, Spindler *et al.* 2018), (iii) description of the ventral expansion in respect to the post-temporal fenestra (Sidor and Hopson 1998, Berman *et al.* 1995). In all of these examples the character is binary. Benson (2018) introduced a multistate character that encapsulates these morphological aspects, including the absence of the tabular (state 3). Herein I present a modified version of Benson (2012 c.86), with absence/presence removed to form a separate binary character (ch.98 above) and include a new state (state 1) that describes the tabular morphology in 'protorothyridids', *Petrolacosaurus*, *Youngina*, some parareptiles and basal mycterosaurines.

Unambiguous: *Araeoscelis* spp (1→2), Sauropsida (0→1),Sphenacodontia + Edaphosauridae (0→3), *Tseajaia campi* (0→2). DELTRAN: *Belebey vegrandis* (1→2), *Ennatosaurus tecton* (0→1), *Erpetonyx arsenaultorum* (1→2), Mycterosaurinae + Varanodontinae (1→2). ACCTRAN: Caseidae (0→1), Mycterosaurinae + Varanodontinae + *Apsisaurus* (1→2), *Macroleter* + Procolophonoidea (2→1), Bolosauri-

dae + Procolphonoidea + *Macroleter* (1→2).

100. Tabular, posteromedial process that contacts the dorsolateral corner of the supraoccipital: absent (0); present (1); inapplicable, tabular absent (-)

Modified from Benson (2012 c.87).

In *Heleosaurus* (Botha-Brink and Modesto 2009) and *Mesenosaurus* (Reisz and Berman 2001) a posteromedial semi-cylindrical hook-like process contacts the supraoccipital to provide the ventral margin of a small, dorsally positioned post-temporal fenestra.

DELTRAN: *Heleosaurus* + *Mesenosaurus* (0→1). ACCTRAN: Mycterosaurinae (0→1).

101. Supraoccipital, lateral expansion providing dorsal margin of post temporal fenestra: absent (0); present (1)

Modified from Brinkman and Eberth (1983 c.15), Heaton and Reisz (1986 C), Laurin (1993 c.43), Benson (2012 c.92).

The presence of a lateral process of the supraoccipital (state 1) is variable among early synapsids, and absent in other early amniotes. In sphenacodontians the presence of state (1) is well documented (Romer and Price 1940, Brinkman and Eberth 1983, Reisz 1986), and with the elongate ventrolateral extension of the paroccipital process, this gives the supraoccipital/paroccipital plate a butterfly-like outline shape when seen in posterior view (Romer and Price 1940 plate 14). The lateral process of the supraoccipital forms the dorsal margin of the small post-temporal fenestra in these taxa. A similar morphology is present in *Edaphosaurus* (Modesto 1995). In varanodontines the presence of the lateral process (State 1) is quite distinct and forms the dorsal margin of the post-temporal fenestra (e.g. *Varanodon* FMNH UR 986, *Aerosaurus* Langston and Reisz 1981, *Varanops* Campione and Reisz 2010), although the paroccipital process is more dorsally orientated. In mycterosaurines, however, the lateral process is much reduced or absent (Reisz *et al.* 1998, Reisz and Berman 2001,). The lateral process is absent in *Ophiacodon*, *Eothyris* and *Casea* (Heaton and Reisz 1986), although Benson (2012) coded eothyridids as possessing the derived state. In *Eothyris* the supraoccipital forms the medial border of the post-temporal fenestra, and there is little evidence of a lateral extension,

with the tabular providing the dorsal margin to the post-temporal fenestra (Reisz *et al.* 2009, MCZ 1161). Consequently, *Eothyris* is scored for state (0) herein, and *Oedaleops* as (?).

Unambiguous:Sphenacodontia + Edaphosauridae (0→1), Varanodontinae (0→1).

102. Postparietals: present (0); absent (1)

From Benton (1985 L.1), Carroll and Currie (1991 c.7b), Laurin and Reisz (1995 c.4), (deBraga and Rieppel 1997 c.52).

The loss of the postparietals was considered a synapomorphy of derived archosaurs by Benton (1985), and of 'testudinomorpha' (i.e. procolophonoids + testudines) by Laurin and Reisz (1995). In the current taxon list, postparietals are absent (state 1) in *Claudiosaurus* (Carroll 1981), *Prolacerta* (Modesto and Sues 2004) and *Procolophon* (Carroll and Lindsey 1985). *Proterosuchus* scores as state (0) (Ezcurra and Butler 2015).

Unambiguous: *Procolophon trigoniceps* (0→1), *Prolacerta broomi* (0→1). DELTRAN: *Claudiosaurus germaini* (0→1).

103. Postparietals: unfused/paired (0); fused to form a midline element (1); inapplicable, postparietals absent (-)

Modified from Reisz *et al.* (1992 c.24), Laurin and Reisz (1995 c.4), Berman *et al.* (1995 c.30), deBraga and Rieppel (1997 c.52), Maddin *et al.* (2008 c.43), Benson (2012 c.91), Spindler *et al.* (2018 c.67).

Laurin and Reisz (1995) noted that the postparietals in all early amniotes, where present (i.e. ch.102 state (0) above), were paired elements. However, the postparietals are fused to form a single element (state 1) in several taxa (e.g. *Oedaleops*, Reisz *et al.* 2009; *Euromycter*, Sigogneau-Russell and Russell 1974 fig.6; *Archaeothyris*, Reisz 1972; *Ophiacodon* and *Dimetrodon*, Romer and Price 1940 plates 3 and 10; *Secodontosaurus*, Reisz *et al.* 1992; *Proterosuchus*, Ezcurra 2016 and *Acleistorhinus*, deBraga and Reisz 1996, FMNH UR 1038). *Mycterosaurus* had been scored as lacking fusion between the postparietals by many studies. Spindler *et al.* (2018) recently differed from these, instead scoring

the presence of fusion. Examination of the holotype FMNH UC 692 does appear to show a suture between the paired postparietals. However, Berman and Reisz (1982) attributed this feature in *Mycterosaurus* to a break along the midline due to crushing, and note its absence in a referred specimen. Consequently, *Mycterosaurus* is scored as possessing state (1) herein.

Unambiguous: *Ennatosaurus tecton* (1→0). DELTRAN: *Acleistorhinus pteroticus* (0→1), *Limnoscelis plaudis* (0→1), *Mycterosaurus longiceps* (0→1), *Eothyris* + *Eocasea* (1→0), Synapsida (0→1), *Proterosuchus* spp (0→1), *Varanops brevirostris* (0→1), *Varanosaurus acutirostris* (1→0). ACCTRAN: *Acleistorhinus pteroticus*u (0→1), Sauropsida (1→0), Diadectomorpha + Amniota (0→1), *Eothyris* + *Eocasea* + *Vaughnictis* (1→0), *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (1→0), Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→1), *Lanthanolania* + Archosauromorpha (0→1), *Varanosaurus acutirostris* (1→0).

104. Postparietals, incised by a median ascending process of the supraoccipital: absent, postparietals in contact along median height (0); present, postparietals separated from the midline ventrally by the supraoccipital (1); inapplicable, postparietals absent (-)

Modified from Dodick and Modesto (1995 c.14), Müller *et al.* (2006 c.14), Sumida *et al.* (2010 c.17), Modesto *et al.* (2018 c.33).

State (1) has been found as a synapomorphy of captorhinids (Heaton 1979, Modesto *et al.* 1998, Modesto *et al.* 2018), and is also scored as present in all captorhinids herein. It is also present in *Youngina* (Reisz *et al.* 2000).

Unambiguous: Captorhinidae (0→1), *Reiszorhinus olsoni* (1→0), *Youngina capensis* (0→1).

105. Postparietals, size, transverse width of paired or single medial element: equal to or greater than the transverse width of one parietal at its widest point (0); less than the transverse width of one parietal (1); inapplicable, postparietals absent (-)

Modified from Laurin and Reisz (1995 c.4), MacDougall and Reisz (2014 c.9), Modesto *et al.* (2015 c.9).

The postparietals are transversely narrow in most derived parareptiles (Modesto *et al.* 2015), and independently in *Tseajaia* (Moss 1972) and *Eocasea* (Reisz and Fröbisch 2014).

Unambiguous: *Colobomycter pholeter* (0→1), *Eocasea martini* (0→1), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1), *Tseajaia campi* (0→1).

106. Postparietals, contribution to margin of post-temporal fenestra: absent (0); present (1); inapplicable, postparietals absent (-)

From Maddin *et al.* (2008 c.14).

The postparietals contribute to the dorsal margin of the post-temporal fenestra in the caseids *Euromycter* and *Ennatosaurus* (Maddin *et al.* 2008 c.14), and independently in *Procolophon* (Carroll and Lindsey 1985).

Unambiguous: *Euromycter* + *Ennatosaurus* (0→1), *Procolophon trigoniceps* (0→1).

107. Opisthotic, paroccipital process, posterior extension: not visible in lateral view (0); visible in lateral view (1)

Modified from Benson (2012 c.96 in part), modified from Berman *et al.* (1995 c.54), deBraga and Reisz (1996 c.44), Maddin *et al.* (2006 c.33), Maddin *et al.* (2008 c.39), Reisz *et al.* (2009 c.53), Modesto *et al.* (2015 c.91).

Maddin *et al.* (2008) noted that the paroccipital process in caseasaurs projects posterior to the squamosal and is visible in lateral view (state 1), suggesting this feature was autapomorphic for caseasaurs. This feature can also be found in *Seymouria* (Laurin 1996), *Edaphosaurus* (Modesto *et al.* 1995) and the parareptiles *Acleistorhinus* and *Procolophon* (FMNH UR 1038, Carroll and Lindsay 1985).

Unambiguous: Caseasauria (0→1), *Owenetta kitchingorum* (0→1), *Seymouria* spp (0→1). DELTRAN: *Acleistorhinus pteroticus* (0→1), *Edaphosaurus boanerges* (0→1). ACCTRAN: *Milleretta* + *Colobomycter* + *Acleistorhinus* (0→1), Edaphosauridae (0→1).

108. Opisthotic, morphology and orientation of paroccipital process: robust and rod-like, extends laterally or ventrolaterally (0); slender and rod-like, extends posteroventrolaterally (1); dorsoventrally broad sheet with short lateral extension (2); dorsoventrally broad sheet, extends laterally or dorsolaterally (3)

Modified from Benson (2012 c.97), modified from Reisz (1986 table 3.E), Gauthier *et al.* 1988 c.77/78/79), Laurin (1993 c.48/49), Laurin and Reisz (1995 c.56), Reisz *et al.* (1992 c.46/47/48), Laurin (1993 c.48/49/50), Berman *et al.* (1995 c.56), Reisz *et al.* (1998 c.26), Sidor and Hopson (1998 c.65), Fröbisch *et al.* (2011 c.35/36/37), Modesto *et al.* (2015 c.90).

Benson (2012) added state (3) to describe the condition in caseids, where the paroccipital process forms a broad rectangular sheet (Maddin *et al.* 2008). This score can also be applied to *Eothyris* (MCZ 1161). In sphenacodontids (e.g. *Dimetrodon*, Romer and Price 1940 plate 8, and *Secodontosaurus*, Reisz *et al.* 1992) and in *Edaphosaurus* (Modesto 1995) the paroccipital process is slender distally and rod-like, extending ventrolaterally and somewhat posteriorly. In ophiacodontids (e.g. *Ophiacodon* Romer and Price 1940 plate 4 and *Varanosaurus* Berman *et al.* 1995) the process is dorsoventrally broad with a short lateral extension (Reisz 1986).

Unambiguous: *Araeoscelis* spp (0→2), Caseasauria (0→3). DELTRAN: *Anthracodromeus longipes* (0→2), *Edaphosaurus boanerges* (0→1), *Varanosaurus* + *Ophiacodon* (0→2), Sphenacodontidae (0→1). ACCTRAN: *Haptodus garnettensis* (1→0), Protorothyrididae (0→2), Ophiacodontidae (1→2), Synapsida (0→1).

109. Opisthotic, paroccipital process attachment: contacts skull laterally (0); ends freely (1)

Modified from Laurin (1991 A.4/E.6 with polarity reversal), Laurin and Reisz (1995 c.57 in part), Reisz and Dilkes (2003 c.26) Reisz *et al.* (2010 c.58), Modesto *et al.* (2015 c.92), Spindler *et al.* (2018 c.83 in part).

An osseous contact of the opisthotic with the dermatocranium is present in *Seymouria* (Laurin 1996) and *Limnoscelis* (Romer 1946, Berman *et al.* 2010), and this condition is considered plesiomorphic

for the current taxon list. The derived condition, where the paroccipital process ends freely, is seen in *Varanosaurus* (Berman *et al.* 1995), *Ennatosaurus* (Maddin *et al.* 2008), some captorhinids (Heaton 1979), 'protorothyridids' (Carroll 1969, Clark and Carroll 1973), *Petrolacosaurus* (Reisz 1981) and basal parareptiles (Modesto *et al.* 2015).

Unambiguous: *Araeoscelis* spp (1→0), *Ennatosaurus tecton* (0→1), Sauropsida (0→1), *Macroleter* + Procolophonoidea (1→0), *Tseajaia campi* (0→1). DELTRAN: *Acleistorhinus pteroticus* (1→0), Varanodontinae (1→0), *Varanosaurus acutirostris* (0→1). ACCTRAN: Varanopidae (1→0), *Colobomycter* + *Acleistorhinus* (1→0), *Varanosaurus acutirostris* (0→1).

110. Opisthotic, if paroccipital process contacts skull laterally contact is made with tabular: present (0); absent (1); inapplicable, process ends freely or tabular is absent (-)

Modified from Laurin and Reisz (1995 c.57 in part), Reisz *et al.* (1998 c.26), Maddin *et al.* (2006 c.33), Campione and Reisz (2010 c.33), Spindler *et al.* (2018 c.83).

Contact between the paroccipital process of the opisthotic and the tabular is present in *Limnoscelis* (Romer 1946, Fracasso 1987, Berman *et al.* 2010) and *Seymouria* (Laurin 1996), and some caseasaurs (e.g. *Eothyris* MCZ1161, *Casea* Olson 1968), sphenacodontids (Romer and Price 1940, Reisz *et al.* 1992) and *Edaphosaurus* (Modesto 1995). Previous studies agree that the paroccipital process contacts the tabular in varanodontines (Reisz *et al.* 1998, Maddin *et al.* 2006, Campione and Reisz 2010, Spindler *et al.* 2018), but disagree on *Mesenosaurus*, with only Spindler *et al.* (2018) scoring as present. I concur that contact between the tabular and paroccipital process was probably present in *Varanops* and *Varanodon* (FMNH UR 986, FMNH UC 644), but find no evidence for its presence in mycterosaurines, which I score as (?) until further data is available.

Unambiguous: clade D (0→1).

111. Prootic, lateral surface: continuous and slightly convex, lacking crista prootica (0); crista prootica present (1)

From Jalil (1997 c.69), Dilkes (1998 c.47), Ezcurra *et al.* (2014 c.153), Pritchard *et al.* (2015 c.73).

The crista prootica is a prominent ridge of bone that extends anteroposteriorly along the lateral surface of the prootic in archosaurs and derived lepidosaurs (Evans 1986), often extending ventrolaterally to overhang the foramina for the facial nerves (Rieppel and Zaher 2000). It is absent in *Youngina* (Evans 1987), but present in *Prolacerta* and *Proterosuchus* (Evans 1986, Ezcurra *et al.* 2014).

DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).//

112. Prootic, anterior inferior process: absent (0); present (1)

From Dilkes (1998 c.48), Ezcurra *et al.* (2014 c.154), Pritchard *et al.* (2015 c.74).

The anterior inferior process of the prootic articulates with the clinoid process of the parabasisphenoid and supports the pila antotica. It is present in *Prolacerta* and *Proterosuchus* (Evans 1986, Ezcurra *et al.* 2014). Evans (1987) noted its absence in *Youngina*, although this was subsequently reported as being present based on microCT analysis (Gardner *et al.* 2010).

LTRAN: *Lanthanolania* + Archosauromorpha (0→1). ACCTRAN: clade D (0→1).

113. Exoccipital, lateral wing: tall and narrow (0); broad, extending ventral to paroccipital process (1)

From Laurin and Reisz (1995 c64), Tsuji (2006 c.74), Reisz *et al.* (2009 c.52), Benson (2012 c.95), Modesto *et al.* (2015 c.102), Spindler *et al.* (2018 c.84).

In some early amniotes the ventral region of the exoccipital extends laterally to form a flange of bone that extends ventral to or contacts the ventral process of the opisthotic. This condition (state 1) is present in caseasaurs (Reisz *et al.* 2009, Olson 1968), some 'protorothyridids' (Carroll 1969), *Youngina* (Evans 1987), *Prolacerta* (Evans 1986) and *Macroleter* (the 'lateral flange' of Modesto *et al.* 2015).

Unambiguous: *Archaeothyris florensis* (0→1),*Macroleter poezicus* (0→1), *Protorothyris* + *Paleothyris* (0→1), Caseasauria (0→1), *Lanthanolania* + Archosauromorpha (0→1).

114.Exoccipitals enclose the complete ventral margin of the foramen magnum: absent, margin provided by the basioccipital (0) present (1)

Modified from deBraga and Rieppel (1997 c.62 with polarity reversal), Nesbitt (2011 c.115), Schoch and Sues (2015 c.52), Pritchard *et al.* (2015 c.61).

In diadectomorphs (Romer 1946, Moss 1973), caseasaurs (Olson 1968, Reisz *et al.* 2009), sphenacodontians (Romer and Price 1940, Laurin 1993), *Edaphosaurus* (Modesto 1995), *Mesenosaurus* (Reisz and Berman 2001), *Aerosaurus* (Langston and Reisz 1981), 'protorothyridids' and captorhinids (Clark and Carroll 1973), diapsids (Reisz 1981, Evans 1986) and some parareptiles (e.g. *Milleretta* Gow 1972, *Acleistorhinus* deBraga and Reisz 1996) the basioccipital contributes to the ventral margin to the foramen magnum (state 0). In the current taxon list, the contact of the exocciptals ventral to the foramen magnum, excluding the basioccipital from this margin (state 1), is present in derived ophiacodontids (Romer and Price 1940, Berman *et al.* 1995,), *Varanops* (Campione and Reisz 2010) and some parareptiles (e.g. *Macroleter*, Tsuji 2006; *Belebey*, Reisz *et al.* 2007).

Unambiguous: *Procolophon trigoniceps* (1→0). DELTRAN: *Varanosaurus* + *Ophiacodon* (0→1), Bolosauridae + *Macroleter* + Procolophonoidea (0→1), *Varanops brevirostris* (0→1). ACCTRAN: Ophiacodontidae (0→1), *Varanops* + *Varanodon* + *Watongia* (0→1), Bolosauridae + Procolphonoidea + *Macroleter* (0→1).

115. Basioccipital, occipital condyle orientation: posteriorly directed (0); posteroventrally directed (1)

From Maddin *et al.* (2008 c.42), Benson (2012 c.98).

A posteroventrally directed occipital condyle (state 1) is present only in caseids (Maddin *et al.* 2008, Olson 1968) and *Edaphosaurus* (MCZ 4309) in the current taxon list. This may be associated with convergent adaptation to herbivory.

Unambiguous: Caseidae (0→1). DELTRAN: *Edaphosaurus boanerges* (0→1). ACCTRAN: Edaphosauridae (0→1).

116. Basal articulation, position: approximately level with posterior rim of the transverse flange of pterygoid (0); anterior to rim of the transverse flange (1); posterior to

the rim transverse flange (2)

Modified from Reisz *et al.* (1992 c.42), Berman *et al.* (1995 c.50), Sidor and Hopson (1998 c.73), Maddin *et al.* (2008 c.34), Fröbisch *et al.* (2011 c.104), Benson (2012 c.101).

Most early amniotes have a basal articulation of the pterygoid that is level with the posterior rim of the transverse flange (state 0). Caseids (*Casea broilii* FMNH UR 1011, Maddin *et al.* 2008) are autapomorphic for the basal articulation being situated anterior to the rim (state 1). A posteriorly located basal articulation (state 2) is present in diadectomorphs (Moss 1972, Berman *et al.* 2010), sphenacodontians (Romer and Price 1940, Reisz *et al.* 1992, *Haptodus garnettensis* ROM 43606), captorhinids (C. *laticeps* OMNH 15101, R. *texana* MCZ 1480) and ankyramorph parareptiles (MacDougall *et al.* 2017, Tsuji 2006, Cisneros 2008).

Unambiguous: Parareptilia (0→2), Diadectomorpha (0→2), Caseidae (0→1), Sphenacodontia (0→2). DELTRAN: *Belebey vegrandis* (2→0), *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→2). ACCTRAN: *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→2), *Eudibamus* + *Belebey* (2→0).

117. Basal articulation, orientation of basipterygoid process: anteroventrolaterally directed (0); laterally directed (1); distinctly ventrally or posteroventrally directed (2)

Modified from Brinkman and Eberth (1983 c.3), Reisz *et al.* (1992 c43), Berman *et al.* (1995 c.51), Dilkes (1998 c.43), Reisz and Dilkes (2003 c.20), Müller (2004 c.96), Maddin *et al.* (2006 c.39), Benson (2012 c.102), Pritchard *et al.* (2015 c.70), Spindler *et al.* (2018 c.74/75)

Characters concerning the basipterygoid processes of the parabasisphenoid have tended to focus on two aspects of its morphology, (i) the orientation of the process and (ii) the direction of the articulating facets. The paroccipital process is directed anteroventrolaterally (state 0) in most terminal taxa herein. Caseasaurs (*Eothyris* MCZ 1161, *Casea broilii* FMNH UR 1011), mycterosaurines (*Archaeovenator* KUVP 12483, Vaughn 1958, Reisz and Berman 2001, Spindler *et al.* 2018), varanodontines (Langston and Reisz 1981) and *Prolacerta* (BP/1/5066) share the condition of a laterally directed process (state 1). Derived ophiacodontids (*Ophiacodon retroversus* MCZ 4820, *Varanosaurus* FMNH PR 1670) have a strongly ventrally or posteroventrally directed basipterygoid process (state 2).

Unambiguous: *Mesosaurus tenuidens* (0→1), Caseasauria (0→1), Varanopidae (0→1), *Orovenator mayorum* (1→0). DELTRAN: *Varanosaurus* + *Ophiacodon* (0→2), *Prolacerta broomi* (0→1). ACCTRAN: Ophiacodontidae (0→2), Archosauromorpha (0→1).

118. Parabasisphenoid, dentition posterior to level of transverse flange: absent (0); present (1)

Modified from Laurin and Reisz (1995 c.53), Reisz and Dilkes (2003 c.45), Reisz *et al.* (2009 c.54), Reisz *et al.* (2010 c.50), Benson (2012 c.109 state 1).

Teeth are absent from the ventral surface of the parasphenoidal plate posterior to the transverse flange of the pterygoid (state 0) in *Gephyrostegus* (Klembara *et al.* 2014), *Seymouria* (White 1939, Laurin 1996) and diadectomorphs (Moss 1972, Berman *et al.* 2010) and most early amniotes. Teeth are present (state 1) in most mycterosaurines and varanodontines, although they are absent in *Archaeovenator* (Reisz and Dilkes 2003, Spindler *et al.* 2018). They are also present in 'protorothyridids' (Carroll 1964,1969), *Orovenator* (Reisz *et al.* 2011), *Petrolacosaurus* (Reisz 1981), the basal captorhinid *Euconcordia* (Müller and Reisz 2005) and some parareptiles (MacDougall *et al.* 2017, deBraga and Reisz 1996, Gow 1972).

Unambiguous: *Euconcordia cunninghami* (0→1), *Milleretta* + *Colobomycter* + *Acleistorhinus* (0→1). DELTRAN: *Archaeovenator hamiltonensis* (1→0), *Euromycter rutena* (0→1), *Hylonomus lyelli* (0→1), Varanopidae (0→1), *Petrolacosaurus kansensis* (0→1). ACCTRAN: *Araeoscelis* spp (1→0), *Archaeovenator hamiltonensis* (1→0), clade D (1→0), clade A (0→1), *Euromycter* + *Ennatosaurus* (0→1).

119. Parabasisphenoid, dentition on ventral surface of cultriform process: absent (0); present (1)

Modified from Laurin and Reisz (1995 c.53), Maddin *et al.* (2008 c.30), Reisz and Fröbisch (2014 c.30).

The presence of teeth on the ventral surface of the cultriform process (state 1) is a derived condition in early amniotes and follows a similar distribution pattern for the preceding character (ch. 118), except for its additional presence in caseasaurs (Maddin *et al.* 2008, Brocklehurst *et al.* 2016), *Lanthanolania*

(Modesto and Reisz 2002) and *Captorhinus aguti* (Fox and Bowman 1966).

Unambiguous: *Milleretta* + *Colobomycter* + *Acleistorhinus* (0→1). DELTRAN: *Lanthanolania ivakhnenko* (0→1), Protorothyrididae (0→1), Captorhinidae except *Thuringothyris* (0→1), Caseasauria (0→1), Varanopidae except *Ascendonanus* (0→1), *Petrolacosaurus kansensis* (0→1). ACCTRAN: *Araeoscelis* spp (1→0), *Lanthanolania ivakhnenko* (0→1), clade D (1→0), Amniota (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (1→0), *Thuringothyris mahlendorffae* (1→0).

120. Parabasisphenoid, entry foramen for the internal carotid arteries: on the ventral surface of the parabasisphenoid, medial to the basipterygoid process (0); within the lateral wall of braincase, dorsal to the basipterygoid process (1) within ventral surface of the parabasisphenoid.

Modified from Gower and Sennikov (1996 c.1), Dilkes (1998 c.45), Nesbitt (2011 c.95), Pritchard *et al.* (2015 c.67), Ezcurra (2016 c.240)

The position of the entry foramina for the internal carotid artery has long been used as a character in phylogenetic studies of archosaurs (Parrish 1993 c.7, Gower and Sennikov 1996 c.1), and also varies among early amniotes. State (1) describes the presence of entry foramina on the lateral surface of the parabasisphenoid, anterior to the suture with the prootic and dorsal to the basipterygoid process. This condition is present in some parareptiles, e.g. *Procolophon* (Carroll and Lindsey 1985) and *Milleretta* (Gow 1972) as well as in squamates, crown-group turtles and birds (Müller *et al.* 2011). State (0), describing entry foramina located on the ventral surface of the parabasisphenoid, is present in most early amniotes (Brinkman and Eberth 1983, Müller *et al.* 2011, Ford and Benson 2018). Langston and Reisz (1981) suggested that the position of the entry foramen in the varanodontine *Aerosaurus* is located on the lateral surface of the parabasisphenoid, but I consider this interpretation uncertain since (i) a foramen is also observed at the base of the basipterygoid process in this taxon, in a position similar to that of *Mycterosaurus* (Vaughn 1958, Reisz *et al.* 1997) and *Orovenator* (Ford and Benson 2018), (ii) the pathway of the internal carotid suggested by Langston and Reisz is associated with the division of this artery into the cerebral and palatal branches taking place within the bone of the basisphenoid, a condition only found in parareptiles, squamates, crown-group turtles and birds (Müller *et al.* 2011), (iii) in *Aerosaurus*, the pathway of the cerebral branch of the internal carotid to the exit foramina, located in the pituitary fossa on the dorsal surface of the basisphenoid, remains

hypothetical. I have therefore scored *Aerosaurus* as (?) herein.

DELTRAN: *Milleretta rubidgei* (0→1), *Procolophon trigoniceps* (0→1). ACCTRAN: Parareptilia (0→1), *Eudibamus* + *Belebey* (1→0).

121. Parabasisphenoid, lateral parasphenoidal crests: present as prominent lateral extensions framing the ventromedial floor of the vidian sulcus, and obscuring the entry foramen of the internal carotid artery from ventral view (0); absent, such that there is no ventral floor to the passage of the internal carotid artery, and the entry foramina of the internal carotid are visible in ventral view (1); inapplicable, entry foramen is located on the lateral surface of the parabasisphenoid (-)

Modified from Pritchard *et al.* (2015 c.66), Ezcurra (2016 c.246).

In *Seymouria* (Shishkin 1968 fig.5), *Casea broilii* (Brinkman and Eberth 1983, FMNH UR 1011), some captorhinids (Fox and Bowman 1966, Müller and Reisz 2005), diapsids (Evans 1986, 1987, Ford and Benson 2018), varanodontines (cf. *Varanops*, Maddin *et al.* 2006) and *Mycterosaurus* (Vaughn 1958, Reisz *et al.* 1997) a lateral expansion of the parasphenoidal plate provides a floor for the passageway (vidian sulcus) of the internal carotid artery, all but enclosing the entry foramen between the basipterygoid process and the parasphenoidal crest (state 0). In sphenacodontians, ophiacodontids and *Edaphosaurus*, the entry foramina for the cerebral branch of the internal carotid artery is located on the ventral surface of parabasisphenoid close to the median line, between the basipterygoid processes (Brinkman and Eberth 1983 fig.7). A similar condition can be seen in the parareptile *Belebey* (Reisz *et al.* 2007 fig.8).

Unambiguous: Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1). DELTRAN: *Belebey vegrandis* (0→1). ACCTRAN: Parareptilia (0→1).

122. Parabasisphenoid, body shape: transversely broad, width greater than length from basipterygoid processes to posterior end (0); transversely narrow, length greater than width (1)

Modified from Reisz *et al.* (1992 c.44), Laurin (1993 c.41), Berman *et al.* (1995 c.52), Maddin *et al.*

(2008 c.31), Benson (2012 c.104).

The body of the parabasisphenoid posterior to the basipterygoid processes is long and narrow (state 1) in *Ophiacodon* and sphenacodontids (Romer and Price 1940, *Secodontosaurus* MCZ 2028). In other terminal taxa, the parabasisphenoid becomes mediolaterally broader posteriorly.

Unambiguous: Sphenacodontidae (0→1),*Ophiacodon* spp (0→1).

123. Parabasisphenoid, outline of lateral margin, anterior 'shoulder' level with the basal articulation in ventral view: absent (0); present (1)

From Maddin *et al.* (2006 c.36) , Campione and Reisz (2010 c.36), Benson (2012 c.105) Spindler *et al.* (2018 c.78).

This character describes the abrupt lateral expansion of the transverse width of the anterior region of the parabasisphenoid instead of a gradual increase in transverse width. State (1) is only seen in *Mesenosaurus* (Reisz and Berman 2001) and *Aerosaurus* (Langston and Reisz 1981). The scoring of the derived state for *Pyozia*, *Heleosaurus* and *Mycterosaurus* (Spindler *et al.* 2018) is rejected herein, since the parabasisphenoid is either too poorly preserved to be scored (e.g. *Pyozia*, Anderson and Reisz 2004) or the anterior 'shoulder' is absent (e.g. *Heleosaurus*, Reisz and Modesto 2007 fig.3 and *Mycterosaurus*, Vaughn 1958 fig.1).

Unambiguous: *Aerosaurus* spp (0→1), *Mesenosaurus romeri* (0→1).

124. Parabasisphenoid, ventral plate, medial excavation: depression or concavity between the *cristae ventrolaterales* (0); deep median recess present (1); absent, ventral surface flat (2)

Modified from Benson (2012 c.106) modified from Laurin (1993 c.41), Laurin and Reisz (1995 c.50), Berman (1995 c.52), Maddin *et al.* (2006 c.37), Tsuji (2006 c.60), Nesbitt (2011 c.100), MacDougall and Reisz (2014 c.81/82), Modesto *et al.* (2015 c.82/83), Modesto *et al.* (2018 c.47)

The region medial to the *cristae ventrolaterales* of the parabasisphenoid has a moderate concavity

(state 0), possibly for the insertion of cervical musculature, in diadectomorphs (Moss 1972, Fracasso 1987), *Seymouria* (White 1939) and many early amniotes. A much deeper median recess (state 1) is present in ophiacodontids (Berman *et al.* 1995) and sphenacodontians (Reisz *et al.* 1992). In archosauromorphs the surface is relatively flat (state 2) (Nesbitt 2011), although Modesto and Sues (2004:344) note a 'deep parabolic depression' in *Prolacerta* (BP/1/5006), which I score as [1,2] for uncertainty.

Unambiguous: *Milleretta rubidgei* (0→2), *Procolophon trigoniceps* (0→2). DELTRAN: *Varanosaurus* + *Ophiacodon* (0→1), Sphenacodontia (0→1), Archosauromorpha (0→2). ACCTRAN: Edaphosauridae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Lanthanolania* + Archosauromorpha (0→2).

125. Parabasisphenoid, ventral plate, median longitudinal septum or ridge: absent (0); present (1)

From Benson (2012 c.108), Spindler *et al.* (2018 c.79)

A raised ridge is present on the midline of the ventral surface of the parabasisphenoid (state 1) in diadectomorphs (Moss 1972, Berman *et al.* fig.10a), mycterosaurines (Vaughn 1958, Anderson and Reisz 2004 fig.1), *Varanosaurus* (FMNH PR 1670) and *Mesosaurus* (Modesto 2006), dividing the concavity between the *cristae ventrolaterales* into paired fossae. Modesto (2006) noted that the median ridge was absent in most Palaeozoic amniotes, but present in the holotype of *Paleothyris acadiana* based on illustrations in Carroll (1996 fig.1). However, close examination of this specimen (MCZ 3481) shows the medial ridge to be absent in this taxon.

Unambiguous: *Mesosaurus tenuidens* (0→1), Diadectomorpha (0→1), Mycterosaurinae (0→1), *Varanosaurus acutirostris* (0→1.

126. Vomer, teeth or shagreen: present (0); absent (1)

From Gauthier *et al.* (1988 c.120), Reisz *et al.* (1992 c.64), Laurin (1993 c.77), Berman *et al.* (1995 c.71), Sidor and Hopson (1998 c.40), Fröbisch *et al.* (2011 c.61), Benson (2012 c.112), Modesto *et al.* (2018 c.37)

Most early amniotes share state (0), the presence of teeth or shagreen of denticles on the vomer. However, they are independently absent in some groups, including sphenacodontids (Romer and Price 1940, Fröbisch *et al.* 2011 c.61), captorhinids (Fox and Bowman 1966, Heaton 1979, Modesto *et al.* 2018) and bolosaurian parareptiles (Berman *et al.* 2000, Reisz *et al.* 2007). Vomerine teeth are also absent in *Limnoscelis* (Romer 1946, Berman *et al.* 2010).

Unambiguous: *Limnoscelis plaudis* (0→1), Sphenacodontidae (0→1), *Eudibamus* + *Belebey* (0→1). DELTRAN: *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: *Euconcordia cunninghami* (1→0), Captorhinidae (0→1).

127. Vomer, fangs: present (0); absent (1)

From Klembara *et al.* (2014 c.68)

In the current taxon list only *Gephyrostegus* and *Seymouria* (Klembara *et al.* 2005, 2014) possess vomerine fangs. This is also a feature of temnospondyl anamniotes (Laurin and Reisz 1997).

Unambiguous: Diadectomorpha + Amniota (0→1).

128. Vomer, asymmetric bifurcated anterior processes: present, vomer terminates anteriorly in short lateral and elongate medial projections (0); absent (1)

NEW

Some early amniotes possess a distinctive bifurcation of the anterior tip of the vomer, separated by the vomerine process of the premaxilla, with a short lateral process and long medial process that meets its partner at the midline of the palate. This feature is present in mycterosaurines (e.g. *Archaeovenator*, Reisz and Dilkes 2003 and *Mesenosaurus*, Reisz and Berman 2001), the 'protorothyridid' *Paleothyris* (MCZ 3481, Carroll 1969 fig.1b), araeoscelidians (e.g. *Petrolacosaurus*, KUVP 8351, Reisz 1981), *Orovenator* (Ford and Benson 2018) and the basal parareptile *Erpetonyx* (ROM 55402, Modesto *et al.* 2015 fig.2a). In most early synapsids in which this region can be observed, the premaxillae meets the vomers with medially directed processes (e.g. *Ennatosaurus* and *Dimetrodon limbatus*; Olson

1968 fig.3b, Romer and Price plate 13), laterally directed processes forming the anterior margin to the internal nares (e.g. *Varanosaurus*; Berman *et al.* 1995), or in a short butt joint (e.g. *Secodontosaurus*; Reisz *et al.* 1992). The presence of this character state may be plesiomorphic, however, as *Limnoscelis* possesses a bifurcated anterior tip of the vomer, which is slightly differentiated in length (Berman *et al.* 2010).

Unambiguous: *Erpetonyx arsenaultorum* (1→0). DELTRAN: *Limnoscelis plaudis* (1→0), Varanopidae except *Ascendonanus* (1→0), *Paleothyris acadiana* (1→0), *Petrolacosaurus kansensis* (1→0). ACCTRAN: clade D (0→1), clade A (1→0), Diadectomorpha (1→0), *Protorothyris archeri* (0→1).

129. Vomer, medial contact with pterygoid: absent (0); present (1); inapplicable pterygoid does not contact the vomer (-)

NEW

An incision of the pterygoid between the posteromedial margins of the vomers is absent in several early amniotes (state 0), and the vomers remain in contact at the midline throughout their anteroposterior length (e.g. *Tseajaia*, Moss 1972; *Gephyrostegus*, Carroll 1970; *Casea*, FMNH UR 1011; *Edaphosaurus*, Modesto 1995; *Haptodus*, Laurin 1993 and *Ophiacodon*, Romer and Price 1940). An extensive incision (state 1) is present in mycterosaurines (Reisz and Dilkes 2003, Reisz and Berman 2001), *Orovenator*, (Ford and Benson 2018), 'protorothyridids' (Clark and Carroll 1973), captorhinids (Fox and Bowman 1966), *Petrolacosaurus* (Reisz 1981), diapsids (Gow 1975) and most parareptiles (Tsuji 2006, MacDougall *et al.* 2017). A smaller medial incision is found in *Dimetrodon* (Romer and Price 1940), which is scored herein as state (1). In the parareptile *Belebey* there is small fenestra preventing contact between the pterygoid and the vomer, which possibly functioned as a secondary palate (Reisz *et al.* 2007), and is therefore scored as state (0).

DELTRAN: *Belebey vegrandis* (1→0), *Dimetrodon* spp (0→1), *Limnoscelis plaudis* (0→1), Sauropsida (0→1), *Seymouria* spp (0→1). ACCTRAN: *Seymouria* + Diadectomorpha + Amniota (0→1), Sphenacodontidae (0→1), Synapsida (1→0), *Eudibamus* + *Belebey* (1→0), *Tseajaia campi* (1→0).

130. Vomer, if medial contact with pterygoid is present it is: extensive (≥50% median border of vomer) (0); short (≥33% median border of vomer) (1); inapplicable, medial

contact absent (-)

From Modesto *et al.* (2007 c.19), Sumida *et al.* (2010 c.26), Modesto *et al.* (2014 c.38), Modesto *et al.* (2018 c.38)

This character distinguishes between basal (with extensive medial contact) and derived (short medial contact) captorhinids in the above referenced studies. Extensive medial contact is also present in *Pyozia* (Anderson and Reisz 2004), *Seymouria* (Klembara *et al.* 2005), *Protorothyris* (Clark and Carroll 1973) and *Romeria texana* (MCZ 1480).

Unambiguous: Diadectomorpha + Amniota (0→1). DELTRAN: *Protorothyris archeri* (1→0), *Romeria* spp (1→0). ACCTRAN: Protorothyrididae (1→0), *Protocaptorhinus* pricei (1→0, *Romeria* (1→0).

131. Palatine, teeth or shagreen: present (0); absent (1)

From Gauthier *et al.* (1988 c.121), Laurin (1993 c.78), Dilkes (1998 c.67), Sidor and Hopson (1998 c. 36), Müller (2004 c.99), Benson (2012 c.114), Spindler *et al.* (2018 c.68), Modesto *et al.* (2018 c.39)

Palatine dentition is present in *Seymouria* and *Gephyrostegus* (Klembara *et al.* 2005, 2014), and also in most early amniotes. Klembara and Ruta (2005) scored palatine dentition as absent in *Limnoscelis*. However, Berman *et al.* (2010) noted a narrow field of small denticles on the palatine, and this taxon has been scored accordingly as state (0). Palatine teeth are absent in *Tseajaia* (Moss 1972), derived ophiacodontids (Romer and Price 1940, Berman *et al.* 1995) and in bolosaurian parareptiles (Berman *et al.* 2000, Reisz *et al.* 2007).

Unambiguous: *Eudibamus* + *Belebey* (0→1), *Tseajaia campi* (0→1). DELTRAN: *Varanosaurus* + *Ophiacodon* (0→1). ACCTRAN: Ophiacodontidae (0→1).

132. Palatine, fangs: present (0), absent (1)

From Klembara *et al.* (2014 c.62)

Unambiguous: Diadectomorpha + Amniota (0→1).

133. Palatine, incision of anterior surface to accommodate internal naris (choana): shallow to moderate anterior incision (0); deep anterior incision (1); palatine is not incised (2)

NEW

In mycterosaurines (e.g. *Archaeovenator*, Reisz and Dilkes 2003; *Heleosaurus*, Reisz and Modesto 2007; *Mesenosaurus*, Reisz and Berman 2001), *Orovenator* (Ford and Benson 2018) and *Proterosuchus* (Wellman 1998) the anterior surface of the palatine is deeply incised, and forms the posterolateral and posteromedial margin of the internal naris. The incision of the palatine by the external naris is absent in most early synapsids (e.g. *Dimetrodon limbatus*, *Ophiacodon uniformis*, Reisz 1986; *Haptodus*, Laurin 1993; *Casea*, FMNH UR 1011, Olson 1968) and *Edaphosaurus* (Modesto 1995). It is also absent in captorhinids (Fox and Bowman 1966, *Romeria texana* MCZ 1480) and the parareptile *Belebey* (Reisz *et al.* 2007). In the current taxon list, all 'protorothyridids', most diapsids and parareptiles possess a moderate or shallow incision to the anterior palatine.

Unambiguous: Synapsida (0→2), *Proterosuchus* spp (0→1), *Seymouria* spp (0→1), *Tseajaia campi* (0→1). DELTRAN: *Belebey vegrandis* (0→2), *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→2), Varanopidae except *Ascendonanus* (0→1). ACCTRAN: *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→2), Varanopidae (0→1), *Eudibamus* + *Belebey* (0→2).

134. Pterygoid, transverse flange: large, approaches cheek, a noticeable lateral projection (0); small, does not approach cheek (1)

From Modesto *et al.* (2015 c.68), modified from Lee (1997 c.19), Tsuji (2006 c.50), Tsuji *et al.* (2012 c.47), MacDougall and Reisz (2014 c.68)

State (1) of this character describes a synapomorphy of bolosaurian parareptiles *Eudibamus* and *Belebey*. All other terminal taxa, where the pterygoid can be observed, as scored as state (0) including stem-group amniotes (e.g. *Gephyrostegus*, *Seymouria*, *Tseajaia* and *Limnoscelis*), where the transverse flange is also present.

Unambiguous: *Eudibamus* + *Belebey* (0→1).

135. Pterygoid, teeth on transverse flange: present (0); absent (1)

From Gauthier *et al.* (1988 c.123), Laurin and Reisz (1995 c.46), deBraga and Rieppel (1997 c.78), Reisz *et al.* (2007 c.46), Modesto *et al.* (2015 c.70), Laurin and Piñeiro (2017 c.46)

The presence of teeth on the transverse flange is a symplesiomorphy that is present in almost all early amniotes. Exceptionally, bolosaurian and procolophonoid parareptiles lack any dentition on the transverse process of the pterygoid (Reisz *et al.* 2007, Berman *et al.* 2000, Carroll and Lindsey 1985, Modesto *et al.* 2015 - although in this study there is an error in the caption of fig.2 in respect to the unambiguous synapomorphies of Bolosauria, since character 70, state 1 = 'absent' rather than 'present')

Unambiguous:*Macroleter poezicus* (1→0), Bolosauridae + Procolphonoidea + *Macroleter* (0→1).

136. Pterygoid, arrangement of teeth on transverse flange: a field or shagreen of teeth covering the ventral surface of the flange (0); additional teeth anterior to a single row of large teeth on ventral rim of flange (1); single row of large teeth on ventral rim of flange (2); inapplicable, teeth absent from transverse flange (-)

Modified from Laurin (1991 E.5), Reisz *et al.* (1998 c.30), Reisz and Dilkes (2003 c.30), Müller (2004 c.163), Maddin *et al.* (2006 c.35), Reisz *et al.* (2009 c.56), Reisz *et al.* (2010: 49), Benson (2012 c.123), Pritchard *et al.* (2015 c.51), Spindler *et al.* (2018 c.69), Modesto *et al.* (2018 c.42)

State (0) describes a field of teeth covering most of the ventral surface of the transverse process, and is present in *Gephyrostegus*, *Seymouria* and *Tseajaia*, captorhinids (e.g. C. *laticeps*, OMNH 15101) and *Euconcordia* (Reisz *et al.* 2016), the basal 'protorothyridid' *Hylonomus* (Carroll 1964), some caseasaurs (e.g. *Casea*, FMNH UC 1011, Olson 1968; *Vaughnictis*, Brocklehurst *et al.* 2016) and edaphosaurids (e.g. *Ianthasaurus*, ROM 59933; *Edaphosaurus*, Modesto 1995), in which it may represent a secondary reacquisition. A single row of teeth is found in ophiacodontids (e.g. *Ophiacodon*, Romer and Price 1940; *Varanosaurus*, Berman *et al.* 1995)), sphenacodontids (e.g. *Dimetrodon*, Romer and Price 1940; *Secodontosaurus*, Reisz *et al.* 1992), varanodontines (e.g. *Aerosaurus*, Langston and Reisz 1981), several mycterosaurines (e.g. *Ascendonanus*, Spindler *et al.* 2018; *Elliotsmithia*, Reisz

et al. 1998), diapsids (e.g. *Youngina*, Gow 1975; *Prolacerta*, Modesto and Sues 2004) and the parareptile *Macroleter* (Tsuji 2006).

Unambiguous: *Apsisaurus witteri* (2→1), *Ennatosaurus tecton* (0→1), *Haptodus garnettensis* (0→1), *Limnoscelis plaudis* (0→1), *Mesenosaurus romeri* (2→1), *Mycterosaurus longiceps* (2→1), *Milleretta* + *Colobomycter* + *Acleistorhinus* (0→1), *Orovenator mayorum* (2→1), *Protorothyris archeri* (0→2), *Varanops brevirostris* (2→1). DELTRAN: *Eothyris parkeyi* (0→1),*Macroleter poezicus* (0→2), Araeoscelidia (0→1), *Varanosaurus* + *Ophiacodon* (0→2), Sphenacodontidae (0→2), Varanopidae (0→2), *Lanthanolania* + Archosauromorpha (0→2), *Paleothyris acadiana* (0→1). ACCTRAN: *Mesosaurus tenuidens* (2→0), clade C (1→2), *Anthracodromeus* + *Hylonomus* (1→0), clade A (0→1), *Eothyris* + *Eocasea* (0→1), Edaphosauridae (2→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→2).

137. Pterygoid, orientation of the transverse flange: directed predominately laterally or posterolaterally (0); directed anterolaterally (1); directed anteriorly (2)

Modified from Laurin and Reisz (1995 c.45), deBraga and Rieppel (1997 c.77), Müller (2004 c.140), Maddin *et al.* (2008 c.37), Benson (2012 c.118), Modesto *et al.* (2015 c.69), Pritchard *et al.* (2015 c.53)

Most terminal taxa possess state (0), a laterally or posterolaterally directed pterygoid flange. Caseids (FMNH UC 1011, Maddin *et al.* 2008), araeoscelidians (Reisz 1981, Vaughn 1955), *Mesenosaurus* (Reisz and Berman 2001), procolophonids (e.g. *Owenetta*, Reisz and Scott 2002) and *Claudiosaurus* (Carroll 1981) are the only taxa herein coded as state (1). The unusual transverse process of the pterygoid found in bolosaurids, where the transverse process remains in the same plane as the palatal process of the pterygoid, unlike all other early amniotes where the transverse process has a ventral inclination, is scored as state (2) in *Belebey* and *Eudibamus* (Reisz *et al.* 2007, Modesto *et al.* 2017).

Unambiguous: *Mesenosaurus romeri* (0→1), Araeoscelidia (0→1), Caseidae (0→1), *Eudibamus* + *Belebey* (0→2), Procolophonoidea (0→1). DELTRAN: *Claudiosaurus germaini* (0→1).

138. Pterygoid, anterior extent of palatal process: terminates anteriorly level with or posterior to the anterior margin of the palatine (0); extends anterior to the palatine (1)

Modified and polarity reversed from Laurin and Reisz (1995 c.44), deBraga and Rieppel (1997 c.76),

Müller (2004 c.139), Ezcurra *et al.* (2014 c.140), Laurin and Piñeiro (2017 c.44)

State (0) is present in *Gephyrostegus* (Klembara *et al.* 2014), *Tseajaia* (Moss 1972), most synapsids and all parareptile terminal taxa herein in which the anterior portion of the palate can be observed. State (1) is found in *Seymouria* (Klembara *et al.* 2005), *Limnoscelis* (Berman *et al.* 2010), *Protorothyris* (MCZ 1532), diapsids (Reisz 1981, Gow 1975), *Orovenator* (Ford and Benson 2018), *Archaeovenator* (KUVP 12483, Reisz and Dilkes 2003) and captorhinids (Reisz *et al.* 2016, Heaton 1979).

Unambiguous: Parareptilia (1→0). DELTRAN: *Limnoscelis plaudis* (0→1), *Mesenosaurus romeri* (1→0), Sauropsida (0→1), *Seymouria* spp (0→1). ACCTRAN: *Seymouria* + Diadectomorpha + Amniota (0→1), Synapsida (1→0), Mycterosaurinae + Varanodontinae + *Apsisaurus* (1→0), *Tseajaia campi* (1→0)

139. Pterygoids, median contact between each other: median contact present only anteriorly (0); median contact extensive, pterygoids meet medially along > 50% of their anteroposterior length (1); no median contact between the pterygoids (2)

Modified from Dilkes (1998 c.126), Ezcurra *et al.* (2014 c.137), Pritchard *et al.* (2015 c.52)

The paired palatal flanges of the pterygoids make contact on the midline (states 0 or 1) in all terminal taxa with the exception of early archosauromorphs (state 2) (Modesto and Sues 2004, Ezcurra and Butler 2015). The median contact of the pterygoids is extensive (state 0) in ophiacodontids (Berman *et al.* 1995, Romer and Price 1940), sphenacodontians (Reisz 1986, Reisz *et al.* 1992, Laurin 1993), mycterosaurines (Anderson and Reisz 2004, Reisz and Berman 2001), *Orovenator* (Ford and Benson 2018), and some parareptiles (Reisz *et al.* 2007, Tsuji 2006).

Unambiguous: *Ennatosaurus tecton* (0→1), Procolophonoidea (1→0), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1). DELTRAN: *Varanosaurus* + *Ophiacodon* (0→1), Sphenacodontia (0→1), Varanopidae except *Ascendonanus* (0→1), Archosauromorpha (0→2). ACCTRAN: Edaphosauridae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), Varanopidae (0→1), *Lanthanolania* + Archosauromorpha (0→2).

140. Pterygoid, quadrate ramus, medial shelf ('posteromedian flange'; 'tympanic flange';'arcuate

flange'): absent (0); present (1)

Modified from Benson (2012 c.120) modified from Brinkman and Eberth (1983 c.14); Reisz (1986 table 3d), Reisz *et al.* (1992 c.37), Laurin (1993 c.40), Berman *et al.* (1995 c.46), Fröbisch *et al.* (2011 c.102), MacDougall and Reisz (2014 c.65), Modesto *et al.* (2015 c.65)

A medial transverse shelf extends from the ventral edge of the quadrate ramus (state 1) in all diapsid terminal taxa herein, with the exception of *Petrolacosaurus*, where the ventral edge forms a thickened ridge only (Reisz 1981).Is it present in parareptiles where the quadrate ramus of the pterygoid can be observed. In *Archaeovenator* the medial shelf of the right quadrate ramus is present, exposed adjacent to the *crista ventrolaterales* of the parabasisphenoid in KUVP 12483. State (1) is also present in *Varanops* (Romer and Price 1940), *Apsisaurus* (Laurin 1991), and *Aerosaurus* (Langston and Reisz 1981). The medial shelf is also present in caseasaurs and *Ophiacodon* (*Eothyris* MCZ 1161, Brinkman and Ebert 1983). The shelf is probably absent (state 0) in *Mesenosaurus*, where the thickened ventral edge of the vertical lamina is smoothly rounded (Reisz and Berman 2001). The quadrate ramus has a rounded ventral edge, with no trace of a medial shelf (state 0) in sphenacodontids and *Edaphosaurus* (Brinkman and Ebert 1983). This shelf is also absent in *Varanosaurus* (FMNH PR 1670), in the protorothyridids *Paleothyris* and *Protorothyris*. It is absent in captorhinids, except *Euconcordia* (Müller and Reisz 2005).

Unambiguous:*Ophiacodon* spp (0→1). DELTRAN: *Araeoscelis* spp (0→1), *Euconcordia cunninghami* (0→1), *Limnoscelis plaudis* (0→1), *Mesenosaurus romeri* (1→0), clade C (0→1), Caseasauria (0→1). ACCTRAN: Protorothyrididae (1→0), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (1→0), Diadectomorpha + Amniota (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (1→0), Mycterosaurinae (1→0), *Petrolacosaurus kansensis* (1→0).

141. Pterygoid, teeth on the quadrate flange: absent (0); present (1)

From MacDougall *et al.* (2018 c.72)

In *Gephyrostegus* (Klembara *et al.* 2014) and some parareptiles (e.g. *Mesosaurus*, *Colobomycter pholeter*, *Feeserpeton* and *Delorhynchus*, MacDougall *et al.* 2018 c.72) teeth extend posteromedially from the transverse flange of the pterygoid on to the anteroventral surface of the quadrate ramus of the

pterygoid (state 1). This feature is absent in all other taxa included in this study (state 0).

Unambiguous: *Colobomycter pholeter* (0→1), *Gephyrostegus bohemicus* (0→1), *Mesosaurus tenuidens* (0→1).

142. Pterygoid, ascending dorsal lamina of the anterior (palatal) ramus: absent or low (0); tall (1)

From Reisz *et al.* (1992 c.36), Berman *et al.* (1995 c.45), Fröbisch *et al.* (2011 c.101), Benson (2012 c.116), Spindler *et al.* (2018 c.71)

State (1) of this character is present in sphenacodontians (Romer and Price 1940, *Haptodus* ROM 34602), edaphosaurids (*Ianthasaurus* ROM 59933, Modesto 1995) and *Ophiacodon* (Romer and Price 1940).

Unambiguous: Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1).

143. Pterygoid, anterior extent of interpterygoid vacuity: reaches beyond posterior margin of palatine (0); reaches level of palatine or less (1)

Modified from Laurin and Reisz (1995 c.39), Reisz *et al.* (2007 c.127), MacDougall and Reisz (2014 c.61), Modesto *et al.* (2015 c.61)

An anteroposteriorly short interpterygoid vacuity is present in ophiacodontids, sphenacodontians, edaphosaurids and the caseid *Ennatosaurus* (Maddin *et al.* 2008, Olson 1968). It is also found in some parareptiles (Tsuji 2006, Reisz *et al.* 2007, MacDougall *et al.* 2017).

Unambiguous: *Colobomycter pholeter* (0→1). DELTRAN: *Belebey vegrandis* (0→1), *Ennatosaurus tecton* (0→1),*Macroleter poezicus* (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: *Casea broilii* (1→0), Synapsida (0→1), Procolophonoidea (1→0), Bolosauridae + Procolphonoidea + *Macroleter* (0→1), *Thuringothyris mahlendorffae* (0→1).

144. Ectopterygoid: present (0); absent (1)

From Gauthier *et al.* (1988 c.55), Carroll and Currie (1991 c.33b), Laurin and Reisz (1995 c.47), Dodick and Modesto (1995 c.17), deBraga and Rieppel (1997 c.81 in part), Müller (2004 c.34), Sumida *et al.* (2010 c.24), Modesto *et al.* (2015 c.77), Modesto *et al.* (2018 c.40 in part)

The absence of the ectopterygoid (state 1) is synapomorphy of derived captorhinids, in which it is replaced with a medial 'alary' process of the jugal (Lauren and Reisz 1995, Heaton 1979, Reisz *et al.* 2016). The ectopterygoid is also absent in *Mesosaurus* (Modesto 2006).

Unambiguous: *Mesosaurus tenuidens* (0→1). DELTRAN: *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1). ACCTRAN: Captorhinidae except *Thuringothyris* (0→1).

145. Ectopterygoid, dentition: present (0); absent (1); inapplicable, ectopterygoid absent (-)

From Gauthier *et al.* (1988 c.122), Laurin and Reisz (1995 c.48), Berman *et al.* (1995 c.72), deBraga and Rieppel (1997 c.81 in part), Reisz *et al.* (2007 c.48), Benson (2012 c.124), Klembara *et al.* (2014 c.67/68), Modesto *et al.* (2015 c.76)

Teeth are present on the ventral surface of the ectopterygoid in *Gephyrostegus* and *Seymouria* (Klembara *et al.* 2014, 2005), *Protorothyris* (MCZ 1532), araeoscelidians diapsids (e.g. *Petrolacosaurus*, Reisz 1981; *Araeoscelis*, Vaughn 1955) and *Orovenator* (Ford and Benson 2018). They are also present in several derived early synapsids (e.g. *Dimetrodon*, Romer and Price 1940; *Edaphosaurus*, Modesto 1995) and the caseid *Ennatosaurus* (Olson 1968, although not confirmed by Maddin *et al.* 2008).

Unambiguous: clade C (0→1), Diadectomorpha (0→1), *Orovenator mayorum* (1→0). DELTRAN: *Haptodus garnettensis* (0→1), *Secodontosaurus obtusidens* (0→1), *Varanosaurus acutirostris* (0→1). ACCTRAN: *Dimetrodon* spp (1→0), Edaphosauridae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1).

146. Ectopterygoid, contact restricted to maxilla: present (0); absent, ectopterygoid contacts the jugal (1); inapplicable, ectopterygoid absent (-)

From Dilkes (1998 c.40), Müller (2004 c.94), Ezcurra *et al.* (2014 c.144), Ezcurra (2016 c.142)

This character has been used principally to describe the lateral sutural contact of the ectopterygoid in archosauromorphs, in which contact with the maxilla (state 0) has been considered to be the derived state (Dilkes 1998). Nevertheless, contact with the maxilla (state 0) is also present in stem-group amniotes such as *Tseajaia*, *Limnoscelis* and *Gephyrostegus* (Moss 1972, Berman *et al.* 2010, Klembara *et al.* 2014) and early synapsids (e.g. *Dimetrodon* and *Ophiacodon*, Romer and Price 1940; *Secodontosaurus*, Reisz *et al.* 1992, and *Varanosaurus*, Berman *et al.* 1995). In mycterosaurines the lateral margin of the ectopterygoid is rarely exposed. It appears to contact the maxilla in *Mesenosaurus* (Reisz and Berman 2001), but in *Archaeovenator* (KUVP 12483) the right ectopterygoid, which is preserved in articulation with the surrounding elements of the palate and the maxilla, is located posterior to the posterior extremity of the maxilla, and therefore was probably limited to lateral contact with the jugal (state 1), as in *Orovenator* (Ford and Benson 2018). Contact is also restricted to the jugal in *Ennatosaurus* (Maddin *et al.* 2008), *Edaphosaurus* (Modesto 1995) and in *Petrolacosaurus* and other early diapsids (Reisz 1981, Carroll 1981, Gow 1975). State (1) is present in *Macroleter* (Tsuji 2006), but absent in other parareptiles.

Unambiguous:*Macroleter poezicus* (0→1). DELTRAN: *Edaphosaurus boanerges* (0→1), *Ennatosaurus tecton* (0→1), *Archaeovenator* + *Orovenator* (0→1), Neodiapsida (0→1), *Petrolacosaurus kansensis* (0→1), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: *Araeoscelis* spp (1→0), Parareptilia (1→0), Amniota (0→1), Edaphosauridae (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (1→0), Mycterosaurinae + Varanodontinae + *Apsisaurus* (1→0).

147. Suborbital opening: absent (0); present (1)

From Laurin (1991 A.3), Carroll and Currie (1991 c.3), Laurin and Reisz (1995 c.49 in part), Rieppel (1999 c.43), Müller (2004 c.32), Reisz *et al.* (2010 c.48), Klembara *et al.* (2014 c.83), Modesto *et al.* (2015 c.79)

The presence of a suborbital fenestra has long been considered a synapomorphy of Diapsida (Benton 1985, Carroll and Currie 1991). Captorhinids and parareptiles possess a small foramen close to, or forming part of, the junction of the palatine, pterygoid and ectopterygoid, and the presence of an opening of any size in this area has been suggested as a synapomorphy of Reptilia (=Sauropsida)

(Laurin and Reisz 1995), although the opening is absent in 'protorothyridids' (e.g. *Protorothyris*, Clark and Carroll 1973). *Seymouria sanjuanensis* possesses an elongate fenestra between the palatine, ecopterygoid and maxilla (Klembara *et al.* 2005), which is absent in *S. baylorensis* (Laurin 1996, White 1939) and other stem-group amniotes such as diadectomorphs (Moss 1972, Berman *et al.* 2010) and *Gephyrostegus* (Klembara *et al.* 2014). This current character describes the presence or absence of a suborbital opening, regardless of size, athe following character (ch.148) describes the morphology of this opening.

Unambiguous: *Mesosaurus tenuidens* (1→0), *Orovenator mayorum* (0→1), *Seymouria* spp (0→1). DELTRAN: clade D (0→1), Araeoscelidia (0→1), Captorhinidae except *Thuringothyris*(0→1). ACCTRAN: Protorothyrididae (1→0), Sauropsida (0→1), Varanopidae (1→0).

148. Suborbital opening, morphology if present: present as anteroposteriorly elongate fenestra (0); present as small foramen (1); inapplicable, opening absent (-)

Modified from Laurin and Reisz (1995 c.49 in part), Tsuji (2006 c.57), Reisz *et al.* (2007 c.49)

Unambiguous: Parareptilia (0→1). DELTRAN: Captorhinidae except *Thuringothyris* (0→1). ACCTRAN: Captorhinidae (0→1).

149. Quadrate, jaw articulation position (anteroposterior aspect): approximately level with occiput (0); posterior to occiput (1); anterior to occiput (2)

Modified from Laurin (1993 c.46), Laurin and Reisz (1995 c.36), Tsuji (2006 c.37), Maddin *et al.* (2008 c.46), Fröbisch *et al.* (2011 c.34), Benson (2012 c.10)

The jaw articulation is located anterior to the position of the occiput (state 2) in ankyramorph parareptiles (Tsuji 2006, deBraga and Reisz 1996, Carroll and Lindsey 1985) and the caseid *Ennatosaurus* (Maddin *et al.* 2008). This contrasts with the condition in most other early amniotes, in which the jaw articulation and occiput are approximately level with each other (state 0). In varanodontines (Langston and Reisz 1981) and ophiacodontids (Romer and Price 1940, FMNH PR 1670), *Proterosuchus* (Ezcurra 2016) and *Mesosaurus* (MacDougall *et al.* 2018 c.52) the jaw articulation is posterior to the occiput (state 1).

Unambiguous: *Ennatosaurus tecton* (0→2), *Mesosaurus tenuidens* (0→1), *Proterosuchus* spp (0→1), *Tseajaia campi* (0→1). DELTRAN: *Milleretta* + *Colobomycter* + *Acleistorhinus* (0→2), *Varanosaurus* + *Ophiacodon* (0→1), *Varanops* + *Varanodon* + *Watongia* (0→1), *Macroleter* + Procolophonoidea (0→2). ACCTRAN: Parareptilia (0→2), Ophiacodontidae (0→1), Varanodontinae (0→1), *Eudibamus* + *Belebey* (2→0).

150. Quadrate, jaw articulation position (dorsoventral aspect): at level of alveolar margin of maxillary tooth row (0); quadrate projects far ventral to level of alveolar margin of maxillary tooth row (1)

Modified from Laurin (1993 c. 54), Modesto (1995 c.15), Mazierski and Reisz (2010 c.16), Fröbisch *et al.* (2011 c.40, c.122), Benson (2012 c.125).

In sphenacodontians, with the exception of *Secodontosaurus* (MCZ 1124, Reisz *et al.* 1992), edaphosaurids, *Araeoscelis* (Reisz *et al.* 1984) and *Procolophon* (Carroll and Lindsay 1985) the point of articulation between the quadrate condyle and the mandible is ventral (state 1) to the lowest point of the alveolar margin of the maxillary tooth row.

Unambiguous: *Araeoscelis* spp (0→1),Sphenacodontia + Edaphosauridae (0→1), *Procolophon trigoniceps* (0→1). DELTRAN: *Secodontosaurus obtusidens* (1→0). ACCTRAN: *Secodontosaurus obtusidens* (1→0).

151. Quadrate, condyles: distinct, separate (0); confluent, forming a saddle-shaped articular facet (1)

Modified from Laurin and Reisz (1995 c.65), Modesto (1995 c.14), Mazierski and Reisz (2010 c.15), Benson (2012 c.89), Modesto *et al.* (2015 c.51)

Modesto (1995) described the derived condition (state 1) as 'yoke-shaped' in posterior view rather than anteroposteriorly elongate rounded ridges. Both *Edaphosaurus* (Modesto 1995) and *Ianthasaurus* (Mazierski and Reisz 2010) are scored as possessing state (1), which is also present in some parareptiles (Modesto *et al.* 2015).

Unambiguous: *Erpetonyx arsenaultorum* (0→1), Edaphosauridae (0→1), *Procolophon trigoniceps* (0→1). DELTRAN: *Acleistorhinus pteroticus* (0→1). ACCTRAN: *Colobomycter* + *Acleistorhinus* (0→1).

152. Quadrate, slope of occipital margin: approximately vertical (0); inclined anterodorsally by 10-55 degrees (1); strongly inclined anterodorsally by >60 degrees (2); inclined posterodorsally (3)

Modified from Modesto (1994 c.20), Reisz *et al.* (1998 c.27), Sidor and Hopson (1998 c.42), Maddin *et al.* (2006 c.34, 2008 c.41), Reisz *et al.* (2009 c.50), Campione and Reisz (2010 c.34), Reisz *et al.* (2010 c.56), Benson (2012 c.90), Spindler *et al.* (2018 c.12)

In the current taxon list, the occipital margin is vertical (state 0) in most early amniotes, including sphenacodontians (Romer and Price 1940, Reisz *et al.* 1992, Laurin 1993), edaphosaurids (Modesto *et al.* 1995) most 'protorothyridids' (Carroll 1964, 1969), diapsids (Reisz 1981, Reisz *et al.* 1984), with the exception of *Proterosuchus* (e.g. *P. fergusi* Ezcurra *et al.* 2015), and many parareptiles (Gow 1972, deBraga and Reisz 1996). The occipital margin is also vertical in *Archaeovenator* (Reisz and Dilkes 2003 fig.3, Reisz *et al.* 2009 c.50) and *Mycterosaurus* (Berman and Reisz 1982), although anterodorsally inclined (state 1) in other mycterosaurines (e.g. *Elliotsmithia*, Modesto *et al.* 2001; *Ascendonanus*, Spindler *et al.* 2018), and strongly inclined (state 2) in varanodontines (e.g. *Varanodon*, FMNH UR 986; *Varanops*, MCZ 1926). The parareptiles *Owenetta* (Reisz and Scott 2002), *Procolophon* (Carroll and Lindsey 1985) and *Colobomycter* (MacDougall *et al.* 2017) have slightly posterodorsally inclined occipital margins (state 3).

Unambiguous: *Ascendonanus nestleri* (0→1), *Colobomycter pholeter* (0→3), *Limnoscelis plaudis* (1→0), Sauropsida (1→0),Sphenacodontia + Edaphosauridae (1→0), Varanodontinae (0→2), *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (0→1), *Paleothyris acadiana* (0→1), *Proterosuchus* spp (0→1). DELTRAN: Procolophonoidea (0→3). ACCTRAN: *Macroleter* + Procolophonoidea (0→3).

153. Quadrate, shape: straight posteriorly (0); shallowly emarginated (1)

From Laurin (1991 E.7), deBraga and Rieppel (1997 c.38), Rieppel (1999 c.37), Müller (2004 c.26), Reisz *et al.* (2010 c.55), Pritchard *et al.* (2015 c.41), Ezcurra (2016 c.176)

In archosauromorphs a shallow emargination of the posterior margin of the quadrate probably provides attachment for the tympanum (Modesto and Sues 2004, Ezcurra and Butler 2015).

DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

154.Temporal 'otic' notch: absent (0), present (1)

Modified from Müller and Tsuji (2007 c. 134), MacDougall and Reisz (2014 c.59), Modesto *et al.* (2015 c.59)

The emargination of the posterior margin of the temporal region of the skull (state 1) is present in the stem-group amniote *Seymouria* (e.g. *Seymouria sanjuanensis* Klembara *et al.* 2005; *S. baylorensis*, Laurin 1996), and derived parareptiles such as procolophonoids (e.g. *Procolophon*, Carroll and Lindsey 1985; *Owenetta*, Reisz and Scott 2002) and nycteroleterids (*Macroleter poezicus* and *Baskyroleter mesenis*, Müller and Tsuji 2007). The emargination is formed principally by a concavity in the posterior margin of the squamosal and a posterior extension of the supratemporal. In parareptiles, the emargination of the posterior margin of the temporal region has been linked to the possession of impedance-matching hearing (Müller and Tsuji 2007).

Unambiguous: *Macroleter* + Procolophonoidea (0→1), *Seymouria* spp (0→1).

155. Stapes, stapedial foramen: present (0); absent (1)

From Laurin (1991 E.9), Laurin and Reisz (1995 c.66), Reisz *et al.* (2010 c.66), Pritchard *et al.* (2015 c.77), Ezcurra (2016 c.297)

A perforating foramen close to the footplate of the stapes is present in most terminal taxa. The loss of the stapedial foramen has been considered a synapomorphy of archosauromorphs (Ezcurra 2016). However, Olson (1968) notes it is absent in *Casea broilii*.

DELTRAN: Caseidae (0→1), Archosauromorpha (0→1). ACCTRAN: Caseasauria (0→1), *Lanthanolania* + Archosauromorpha (0→1).

156. Stapes, dorsal process: present as a clearly defined process (0); absent or greatly reduced (1)

Modified from Reisz *et al.* (1992 c.31 state 3)

In several early synapsids (e.g. *Dimetrodon* and *Ophiacodon*, Romer and Price 1940, Reisz 1986; *Edaphosaurus*, Brinkman and Eberth 1983; *Mycterosaurus*, Berman and Reisz 1982), 'protorothyridids' (e.g. *Hylonomus*, Carroll 1964; *Paleothyris*, Carroll 1969), araeoscelidians (e.g. *Petrolacosaurus*, Reisz 1981; *Araeoscelis*, Vaughn 1955) and captorhinids (e.g. *Captorhinus aguti*, Fox and Bowman 1966) a distinct dorsal process is present on the stapes (state 0). This is absent (state 1) in *Orovenator* (Ford and Benson 2018), *Youngina* (Gardner *et al.* 2010), and in parareptiles in which the stapes is known (e.g. *Macroleter*, Müller and Tsuji 2007; *Procolophon*, Carroll and Lindsay 1985). In the mycterosaurine *Mesenosaurus*, the stapes is slender and rod-like, and the dorsal process is rudimentary (state 1) (Reisz and Berman 2001).

Unambiguous: *Mesosaurus tenuidens* (1→0), *Seymouria* spp (0→1). DELTRAN: *Mesenosaurus romeri* (0→1), clade D (0→1), *Orovenator mayorum* (0→1). ACCTRAN: clade C (0→1), *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (0→1), Mycterosaurinae + Varanodontinae + *Apsisaurus* (1→0).

157. Stapes, dorsal process, articulation with the paroccipital process of the opisthotic: absent (0); present (1); inapplicable, dorsal process is absent or greatly reduced (-)

From Brinkman and Eberth (1983 c.6), Gauthier *et al.* (1988 c.69), Reisz *et al.* (1992 c.39).

Reisz (1986) described the presence of a dorsal process of the stapes that contacts the paroccipital process of the opisthotic as a synapomorphy shared by ophiacodontids, sphenacodontians and edaphosaurids. However, in *Varanosaurus* the dorsal process contacts the tabular rather than the paroccipital process (state 0) (Berman *et al.* 1995). The dorsal process of the stapes articulates with the conjoined margin of the prootic and opisthotic in *Araeoscelis* (Vaughn 1955) and is scored as (0) herein. There is a small depression on the ventral margin of the opisthotic in *Euconcordia* that may have received the dorsal process of the stapes (Müller and Reisz 2005), which I score as state (1).

Unambiguous: *Euconcordia cunninghami* (0→1). DELTRAN:Sphenacodontia + Edaphosauridae (0→1),*Ophiacodon*

spp (0→1). ACCTRAN: Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Varanosaurus acutirostris* (1→0).

158. Mandible, proportions (not including laminar portion of the angular): intermediate proportions, dorsoventral height 0.20-0.26 of total length (0); short and robust, dorsoventral height >0.30 of total length (1); very long and dorsoventrally slender, maximum height <0.18 of total length (2)

From Benson (2012 c.126) modified from Modesto (1995 c.20), Mazierski and Reisz (2010 c. 22), Sidor (2003 c.3), Spindler *et al.* (2018 c.85)

Short, robust mandibles (state 1) are present in terminal taxa with adaptations for advanced herbivory (e.g. *Ennatosaurus*, Maddin *et al.* 2008; *Edaphosaurus*, Modesto 1995; *Procolophon*, Carroll and Lindsey 1985). Most captorhinids, sphenacodontians, with the exception of *Secodontosaurus*, and parareptiles are scored as possessing state (0). State (2) is present in ophiacodontids, mycterosaurines, varanodontines, 'protorothyridids', diapsids and the parareptiles *Mesosaurus* (Modesto 2006) and *Owenetta* (Reisz and Scott 2002).

Unambiguous: *Araeoscelis* spp (2→0), *Edaphosaurus boanerges* (0→1), *Milleretta* + *Colobomycter* + *Acleistorhinus* (2→0), clade A (0→2), *Euromycter* + *Ennatosaurus* (0→1), Ophiacodontidae (0→2), *Procolophon trigoniceps* (2→1). DELTRAN: *Belebey vegrandis* (2→0), *Secodontosaurus obtusidens* (0→2). ACCTRAN: *Eudibamus* + *Belebey* (2→0), *Secodontosaurus obtusidens* (0→2).

159. Mandible, anterodorsal curvature of anterior mandible in lateral view: absent, alveolar margin of anterior mandible approximately horizontal (0); present, dorsal margin of anterior mandible shows distinct concavity (1)

NEW

In *Gephyrostegus* (Klembara *et al.* 2014), *Seymouria* (Laurin 1996) and basal 'protorothyridids' (e.g. *Hylonomus lyelli*, NHM R 4168, Carroll 1964) the anterior region of the mandible curves dorsally. This character is independent of the convexity of the ventral margin of the maxilla (ch.43), although also present in ophiacodontids and sphenacodontids.

Unambiguous: Diadectomorpha + Amniota (1→0), Ophiacodontidae (0→1), Sphenacodontidae (0→1), *Proterosuchus* spp (0→1). DELTRAN: *Hylonomus lyelli* (0→1). ACCTRAN: *Anthracodromeus* + *Hylonomus* (0→1).

160. Mandible, position of coronoid eminence: posteriorly, within posterior 1/3 of total length (0); anteriorly, approximately 2/5 of total length from posterior end (1)

From Benson (2012 c.129), Maddin *et al.* (2008 c.59)

The coronoid eminence is located further anteriorly on the mandible in caseasaurs, captorhinids, *Edaphosaurus* (Maddin *et al.* 2008) and procolophonoids (e.g. *Procolophon*, Carroll and Lindsey 1985). This character is independent of the scores for the proportions of the mandible (ch.158).
Unambiguous: *Edaphosaurus boanerges* (0→1), Caseasauria (0→1). DELTRAN: *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), Procolophonoidea (0→1). ACCTRAN: Captorhinidae (0→1), *Macroleter* + Procolophonoidea (0→1).

161. Mandible, shape of coronoid eminence: slightly convex or low (0); strongly convex (1); subhorizontal/flat (2); dorsoventrally tall (3)

Benson (2012 c.130) modified from Reisz *et al.* (1992 c.51), Laurin (1993 c.53), Berman *et al.* (1995 c.61), Sidor (2003 c.12), Fröbisch *et al.* (2011 c.39), Spindler *et al.* (2018 c.89)

Most terminal taxa have a low coronoid eminence, which is little more than a slight to moderate convexity along the dorsal margin of the mandible, posterior to the tooth row (state 0). In *Varanops* (Campione and Reisz 2010) and *Varanodon* (FMNH PR 1670) the coronoid region of the mandible is flat (state 2). Sphenacodontians and edaphosaurs have a strongly convex coronoid eminence (state 1). *Procolophon* (Carroll and Lindsay 1985), *Owenetta* (Reisz and Scott 2002) and some bolosaurid parareptiles (e.g. *Belebey*, Reisz *et al.* 2007; *Eudibamus*, Berman *et al.* 2000) possess a coronoid eminence that is noticeably tall (state 3)

Unambiguous: Diadectomorpha + Amniota (1→0),Sphenacodontia + Edaphosauridae (0→1), Bolosauridae + *Macroleter* + Procolophonoidea (0→3). DELTRAN: *Varanops* + *Varanodon* + *Watongia* (0→2).

ACCTRAN: Varanodontinae (0→2).

162. Mandible, contribution of dentary to coronoid eminence: absent (0); present (1); inapplicable, coronoid eminence absent (-)

Modified from Laurin and Reisz (1995 c.79), deBraga and Rieppel (1997 c.83), Tsuji *et al.* (2012 c.87), Modesto *et al.* (2015 c.120), Schoch and Sues (2015 c.83), Ezcurra (2016 c.261)

Character state (1) is present in sphenacodontians (e.g. *Dimetrodon*, Romer and Price 1940; *Secodontosaurus*, Reisz *et al.* 1992), some parareptiles (e.g. *Belebey*, Reisz *et al.* 2006; *Milleretta*, Gow 1972) and the diapsid *Araeoscelis* (Reisz *et al.* 1984).

Unambiguous: *Araeoscelis* spp (0→1), Sphenacodontia (0→1). DELTRAN: *Milleretta rubidgei* (0→1), *Eudibamus* + *Belebey* (0→1). ACCTRAN: Parareptilia (0→1), *Macroleter* + Procolophonoidea (1→0).

163. Mandible, retroarticular process: absent (0); present (1)

From Carroll and Currie (1991 c.44), Laurin (1991 B.6), Laurin (1993 c.61 in part), Berman *et al.* (1995 c.64 in part), deBraga and Rieppel (1997 c.92), Dilkes (1998 c.74 in part), Rieppel (1999 c.48), Müller (2004 c.35), Maddin *et al.* (2006 c.41), Tsuji (2006 c.85 in part), Benson (2012 c.132), Modesto *et al.* (2015 c.115), Pritchard *et al.* (2015 c.86), Spindler *et al.* (2018 c.98)

The retroarticular process of the mandible is absent in diadectomorphs (Moss 1972, Berman *et al.* 2010), caseasaurs (Reisz *et al.* 2009, Reisz and Fröbisch 2014), most 'protorothyridids' (Carroll 1969, Clark and Carroll 1973), araeoscelidians (Reisz 1981, Vaughn 1955), basal bolosaurid parareptiles (Reisz *et al.* 2007) and basal captorhinids (Müller and Reisz 2005, Sumida *et al.* 2010). The absence of a clearly defined retroarticular process in ophiacodontids has been noted in previous studies (e.g. Reisz *et al.* 1992; Reisz and Dilkes 2003). The retroarticular process is present (state 1) in some stem-amniotes (e.g. *Seymouria*, Laurin 1996)), sphenacodontians (e.g. *Dimetrodon*, Romer and Price 1940; *Haptodus*, Laurin 1993), *Edaphosaurus* (Modesto 1995) neodiapsids (e.g. *Acerosodontosaurus*, Bickelmann *et al.* 2009; *Prolacerta*, Modesto and Sues 2004), some captorhinids (e.g. *Captorhinus*, Heaton 1979) and most parareptiles (e.g. *Mesosaurus*, Modesto 2006; *Macroleter*, Tsuji 2006; *Acleistorhinus*, deBraga and Reisz 1996; *Procolophon*, Carroll and Lindsay 1985). The presence of a small

retroarticular process has been questioned in basal mycterosaurines (Reisz *et al.* 2010, Benson 2012). However, a small process is present in *Archaeovenator* (KUVP 12483, Reisz and Dilkes 2003) and *Ascendonanus* (Spindler *et al.* 2018). Indeed, the process is present but poorly developed in all mycterosaurines (Reisz and Berman 2001, Botha-Brink and Modesto 2009) and varanodontines (Langston and Reisz 1981, FMNH UR 986).

Unambiguous: *Claudiosaurus germaini* (1→0), clade C (0→1),Sphenacodontia + Edaphosauridae (0→1), *Eudibamus* + *Belebey* (1→0), *Seymouria* spp (0→1). DELTRAN: *Captorhinus* spp (0→1), *Protocaptorhinus pricei* (0→1). ACCTRAN: *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), *Romeria* spp (1→0).

164. Mandible, retroarticular process if present, size: small (0); large (1); inapplicable, process is absent (-)

Modified from Laurin (1991 E.10), Laurin (1993 c.61 in part,) Laurin and Reisz (1995 c.76), Dilkes (1998 c.74 in part), Tsuji (2006 c.85 in part), Reisz *et al.* (2010 c.63), Modesto *et al.* (2015 c.116)

The retroarticular process is large in sphenacodontids (Romer and Price fig.16, Reisz *et al.* 1992), archosauromorphs (Gow 1975, Ezcurra and Butler 2005), and some basal parareptiles and procolophonoids (Modesto 2006, Modesto *et al.* 2015, Reisz and Scott 2002).

Unambiguous:*Macroleter poezicus* (1→0), Sphenacodontidae (0→1), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1). DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

165. Mandible, retroarticular process, composition: composite, formed by articular, angular and surangular (0); formed only by articular (1); inapplicable process is absent (-)

Modified from Laurin (1991 J.5), Laurin and Reisz (1995 c.77), Berman *et al.* (1995 c.64 in part), Dilkes (1998 c.74 in part), Tsuji (2006 c.86), Maddin *et al.* (2006 c.41 in part), Reisz *et al.* (2010 c.64), Benson (2012 c.133 in part), Modesto *et al.* (2015 c.117), Pritchard *et al.* (2015 c.87)

Unambiguous: *Milleretta* + *Colobomycter* + *Acleistorhinus* (0→1), Sphenacodontidae (0→1).

166. Mandible, retroarticular process, orientation: posteriorly directed (0); upturned posterodorsally (1); curves posteroventrally (2) inapplicable process is absent (-)

Modified from Reisz (1986 table 3e), Gauthier *et al.* (1988 c.105), Dilkes (1998 c.75), Müller (2004 c.101), Benson (2012 c.133 in part)

A downturned retroarticular process (state 2) is present in sphenacodontians (*Dimetrodon*, *Secodontosaurus*, Reisz *et al.* 1992 and *Haptodus*, ROM 92872). It is upturned (state 1) in varanodontines (e.g. *Varanodon*, Olson 1965 fig. A, FMNH UC 986) and some neodiapsids (e.g. *Prolacerta*, Gow 1975 fig.20; *Proterosuchus* Ezcurra and Butler 2015 fig. 6J). All other terminal taxa, in which the morphology can be observed, possess a posteriorly directed process (state 0).

Unambiguous: Sphenacodontia (0→2), *Varanops* + *Varanodon* + *Watongia* (0→1), Neodiapsida (0→1).

167. Mandible, lateral mandibular fenestra between dentary and angular: absent (0); present (1)

From Gauthier *et al.* (1988 c.87), Reisz *et al.* (1992 c.49), Berman *et al.* (1995 c.57), Dilkes (1998 c.76), Sidor (2003 c. 64), Nesbitt (2011 c.138), Benson (2012 c.137), Pritchard *et al.* (2015 c.84), Ezcurra (2016 c.261)

A lateral (or external) mandibular fenestra is present on the mandible in archosauriforms (Nesbitt 2011), represented herein only by *Proterosuchus*, and in ophiacodontids (Reisz 1972, Berman *et al.* 1995, MCZ1366).

Unambiguous: *Proterosuchus* spp (0→1). DELTRAN: *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (0→1). ACCTRAN: Ophiacodontidae (0→1).

168. Mandible, posterior inframeckelian foramen (*foramen intermandibularis caudalis*): present (0); absent (1)

Modified from Laurin and Reisz (1995 c.69), Tsuji (2006 c.78), Reisz *et al.* (2007 c69), Tsuji *et al.*

(2012 c.77), MacDougall and Reisz (2014 c.106), Modesto *et al.* (2015 c.106)

The posterior inframeckelian foramen is located on the medial surface of the mandible, ventral to the posterior or single coronoid, in many early amniotes (Romer 1956). It is absent in sphenacodontians (Romer and Price 1940, Reisz *et al.* 1992, *Haptodus* ROM 43602), *Araeoscelis* (Vaughn 1955) and *Mesosaurus* (Modesto 2006).

Unambiguous: *Mesosaurus tenuidens* (0→1), Sphenacodontia (0→1). DELTRAN: *Araeoscelis* spp (0→1). ACCTRAN: Araeoscelidia (0→1).

169. Mandible, contribution of the splenial or post-splenial to the posterior inframeckelian foramen: absent (0); present (1); inapplicable, foramen is absent (-)

NEW

Character state (1) is found in stem-amniotes, most parareptiles (e.g. *Colobomycter*, MacDougall *et al.* 2017; *Procolophon*, Carroll and Lindsay 1985; *Macroleter*, Tsuji 2006), captorhinids (e.g. *Captorhinus*, Fox and Bowman 1966; *Reiszorhinus*, Sumida *et al.* 2010 fig. 2B), *Protorothyris* (Clark and Carroll 1973) and *Edaphosaurus* (Modesto 1995).

DELTRAN: *Belebey vegrandis* (1→0), *Claudiosaurus germaini* (1→0), Caseidae (1→0), *Varanosaurus* + *Ophiacodon* (1→0), Varanopidae except *Ascendonanus* (1→0). ACCTRAN: Parareptilia (0→1), clade B (1→0),Sphenacodontia + Edaphosauridae (0→1), Synapsida (1→0), *Eudibamus* + *Belebey* (1→0).

170. Mandible, contribution of the prearticular to the posterior inframeckelian foramen: absent (0); present (1); inapplicable, foramen is absent (-)

NEW

The prearticular contributes to the posterior inframeckelian foramen (state 1) in stem-amniotes, neodiapsids (e.g. *Orovenator*, Ford and Benson 2018; *Claudiosaurus*, Carroll 1981), caseids (e.g. *Ennatosaurus*, Maddin *et al.* 2008), ophiacodontids (Romer and Price 1940), *Edaphosaurus* (Modesto

1995), mycterosaurines (e.g. *Archaeovenator*, Dilkes and Reisz 2003), varanodontines (e.g. *Aerosaurus*, Langston and Reisz 1981; *Varanops*, Campione and Reisz 2010) and some parareptiles (e.g. *Belebey*, Reisz *et al.* 2007; *Colobomycter*, MacDougall *et al.* 2017; *Procolophon*, Carroll and Lindsay 1985

Unambiguous: *Milleretta rubidgei* (1→0). DELTRAN:*Macroleter poezicus* (1→0), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (1→0), *Owenetta kitchingorum* (1→0), *Protorothyris archeri* (1→0). ACCTRAN: clade B (0→1), Sauropsida (1→0), *Macroleter* + Procolophonoidea (1→0), *Procolophon trigoniceps* (0→1).

171. Mandible, posterior inframeckelian foramen (foramen intermandibularis caudalis), size: large, greater than 25% of jaw length (0); small, less than 16% of jaw length (1); inapplicable, foramen is absent. (-)

Modified from Maddin *et al.* (2008 c.60), Benson (2012 c.128), Spindler *et al.* (2018 c.88)

Unambiguous: Diadectomorpha (1→0), *Owenetta kitchingorum* (1→0), *Reiszorhinus olsoni* (1→0). DELTRAN: *Colobomycter pholeter* (1→0). ACCTRAN: *Colobomycter* + *Acleistorhinus* (1→0).

172. Mandible, symphysis: dorsoventrally low, mandible tapers anteriorly (0); dorsoventrally thick, symphysis almost as deep as mandible at midlength of the tooth row (1)

From Maddin *et al.* (2008 c.53), Reisz *et al.* (2009 c.57), Fröbisch *et al.* (2011 c.120), Benson (2012 c.127), Spindler *et al.* (2018 c.87)

Unambiguous: *Limnoscelis plaudis* (0→1), Caseidae (0→1),Sphenacodontia + Edaphosauridae (0→1), *Reiszorhinus olsoni* (0→1), *Seymouria* spp (0→1). DELTRAN: *Belebey vegrandis* (0→1), *Secodontosaurus obtusidens* (1→0). ACCTRAN: *Eudibamus* + *Belebey* (0→1), *Secodontosaurus obtusidens* (1→0).

173. Dentary, size: comprises equal to or greater than 70% of the anteroposterior length of the mandible (0); equal to or less than 65% (1)

From Modesto (1995 c.21), Mazierski and Reisz (2010 c.23), Benson (2012 c.134)

All caseids (e.g. *Ennatosaurus*, Maddin *et al.* 2008; *Euromycter*, Sigogneau-Russell and Russell 1974), some captorhinids (e.g. *Captorhinus laticeps*, OMNH 15101), *Edaphosaurus* (MCZ 4309, Modesto 1995 fig.17B), *Procolophon* (Carroll and Lindsay 1985), *Owenetta* (Reisz and Scott 2002) and the diadectomorph *Tseajaia* (Moss 1972) have short dentaries relative to the length of the mandible (state 1). Character state (1) can also be found in taxa with long and slender mandibles e.g. archosauromorphs.

Unambiguous: *Edaphosaurus boanerges* (0→1), *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), Caseidae (0→1), *Tseajaia campi* (0→1). DELTRAN: Archosauromorpha (0→1), Procolophonoidea (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1), *Macroleter* + Procolophonoidea (0→1).

174. Dentary, orientation of anteriormost marginal tooth: mainly vertically (0); leans anteriorly (1); leans strongly anteriorly, greater than 45 degrees from perpendicular of the alveolar margin (2)

Modified from Dodick and Modesto (1995 c.39), Müller and Reisz (2006 c.39), Sumida *et al.* (2010 c.48), Modesto *et al.* (2018 c.57)

This character has principally been used in studies concerned with the interrelationships of captorhinids. Character state (1) is present in *Captorhinus*, *Romeria* and *Reiszorhinus*. I also find that the orientation of the anteriormost marginal tooth of the dentary varies within other groups of early amniotes. Reisz (1981) noted a slight anterior inclination of the first three teeth on the dentary of *Petrolacosaurus*. A similar condition can be seen in *Araeoscelis* (MCZ 4380), *Orovenator* (Ford and Benson fig.13A) and in the anteriormost dentary tooth in *Archaeovenator* (KUVP 12483), *Elliotsmithia* (Modesto *et al.* 2001 fig.1), *Secodontosaurus* (MCZ 1124, Reisz *et al.* 1992), *Haptodus* (Laurin 1993 fig.1) and in edaphosaurids (e.g. *Edaphosaurus*, MCZ 4309; *Ianthasaurus*, Mazierski and Reisz 2010 fig.2B)). Amongst parareptiles it is present in *Colobomycter pholeter* (BMRP 2008.3.1, MacDougall *et al.* 2017) and *Belebey* (Reisz *et al.* 2007). *Mesosaurus*, with the distinctively strong anterior inclination of the first dentary tooth (Modesto 2006) is the only terminal taxon coded for state (2) herein. Although parsimony uninformative, character state (2) is included here for future reference.

Unambiguous: *Dimetrodon* spp (1→0), *Elliotsmithia longiceps* (0→1), *Mesosaurus tenuidens* (0→2), Araeoscelidia (0→1), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), *Archaeovenator* + *Orovenator* (0→1). DELTRAN: *Belebey vegrandis* (0→1), *Colobomycter pholeter* (0→1), *Echinerpeton intermedium* (0→1),Sphenacodontia + Edaphosauridae (0→1). ACCTRAN: *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Eudibamus* + *Belebey* (0→1), *Colobomycter* + *Acleistorhinus* (0→1).

175. Dentary, region posterior to tooth row: contacts the angular ventrally (0); does not contact the angular ventrally (1); inapplicable, dentary does not extend posterior to tooth row (-)

NEW

State (1) of this character describes a condition in which the dentary tapers posterior to the marginal dentition, and contact with the angular ventrally is prevented by the surangular. In several of the taxa possessing state (1) (e.g. *Orovenator*, Ford and Benson 2018 fig.13A; *Archaeovenator*, Reisz and Dilkes 2003 fig. 2B; *Mesenosaurus*, Reisz and Berman 2001 fig.6B and *Mycterosaurus*, FMNH UC 692) this region is anteroposteriorly long. In others, such as *Limnoscelis* (Berman *et al.* fig.3B), *Gephyrostegus* (Klembara *et al.* 2014 fig.7B) and *Mesosaurus* (Piñeiro *et al.* 2012) the posterior region is anteroposteriorly short. In all other terminal taxa, where this area is exposed, contact between the dentary and angular is present to varying degrees.

Unambiguous: *Gephyrostegus bohemicus* (0→1), *Mesosaurus tenuidens* (0→1). DELTRAN: *Limnoscelis plaudis* (0→1), *Archaeovenator* + *Orovenator* (0→1), Mycterosaurinae (0→1). ACCTRAN: Diadectomorpha (0→1), Varanodontinae (1→0), Varanopidae (0→1).

176. Splenial, contribution to mandibular symphysis: present, symphysis formed from dentary and splenial (0); absent, symphysis formed solely by dentary (1)

Form Berman *et al.* (1995 c.58), Sidor (2003 c.25), Maddin *et al.* (2008 c.59), Fröbisch *et al.* (2011, c 121), Benson (2012 c.138), Spindler *et al.* (2018 c.92)

The splenial participates in the mandibular symphysis in *Seymouria* (Klembara *et al.* 2005) and

diadectomorphs (e.g. *Limnoscelis*, Berman *et al.* 2010). This state (0) is probably plesiomorphic for amniotes, and is present in caseids (e.g. *Euromycter*, Sigogneau-Russell and Russell 1974; *Ennatosaurus*, Maddin *et al.* 2008), captorhinids (e.g. *Thuringothyris*, Müller *et al.* 2006; *Reiszorhinus*, Sumida *et al.* 2010; *Captorhinus*, Heaton 1979), *Edaphosaurus* (Modesto 1995) and sphenacodontians (other than *Secodontosaurus*, Reisz *et al.* 1992). The symphysis is formed by the dentary only in ophiacodontids, mycterosaurines, varanodontines, 'protorothyridids', diapsids and parareptiles, with the exception of *Mesosaurus*.

Unambiguous: *Euconcordia cunninghami* (0→1), *Mesosaurus tenuidens* (1→0), clade A (0→1). DELTRAN: *Varanosaurus* + *Ophiacodon* (0→1), *Secodontosaurus obtusidens* (0→1). ACCTRAN: Ophiacodontidae (0→1), *Secodontosaurus obtusidens* (0→1).

177. Splenial, anterior dorsoventral height: narrow, splenial tapers anteriorly (0); deep, maintains dorsoventral height anteriorly (1)

Modified from Maddin *et al.* (2008 c.55)

In most terminal taxa the splenial narrows anteriorly as it approaches the mandibular symphysis. In *Ennatosaurus* and *Euromycter* the splenial maintains its dorsoventral height anteriorly (Maddin *et al.* 2008 c.55). A similar condition is found in *Limnoscelis* (Berman *et al.* 2010).

Unambiguous: *Euromycter* + *Ennatosaurus* (0→1). DELTRAN: *Limnoscelis plaudis* (0→1). ACCTRAN: Diadectomorpha (0→1).

178. Splenial, exposure on lateral surface of mandible: present (0); absent (1)

Modified from Berman *et al.* (1995 c.59), Modesto (1995 c.22), Sidor and Hopson (1998, c.90), Sidor (2003 c.26/28), Maddin *et al.* (2008 c.55), Mazierski and Reisz (2010 c.24), Fröbisch *et al.* (2011 c.121), Benson (2012 c.139)

Unambiguous: *Araeoscelis* spp (1→0), *Mesosaurus tenuidens* (1→0), Diadectomorpha + Amniota (0→1), *Euromycter* + *Ennatosaurus* (1→0),Sphenacodontia + Edaphosauridae (1→0).

179. Splenial, contact with posterior coronoid: absent (0); present (1)

Maddin *et al.* (2008 c.57), Benson (2012 c.140), Spindler *et al.* (2018 c.93)

In *Ophiacodon* contact between the posterior coronoid and splenial is prevented by a thin point contact between the anterior coronoid and the prearticular (Romer and Price 1940 plate 2), morphology very similar to that of *Varanops* (Campione and Reisz 2010 fig.3C, 3D). Therefore, both taxa are scored as state (0) herein. This is contrary to the approach of Spindler *et al.* (2018), where character state (1) is described as 'closely located to contacting' the posterior coronoid (Spindler *et al.* 2018 online resource 3, c.93), and allowed the score of *Ophiacodon* to match that of *Varanosaurus*, in which sutural contact between the posterior coronoid and splenial is present (state 1).

DELTRAN: *Mesenosaurus romeri* (0→1), *Milleretta rubidgei* (0→1), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), Procolophonoidea (0→1), *Petrolacosaurus kansensis* (0→1), *Prolacerta broomi* (0→1), *Secodontosaurus obtusidens* (0→1), *Varanosaurus acutirostris* (0→1). ACCTRAN: *Araeoscelis* spp (1→0), Sauropsida (0→1), Mycterosaurinae (0→1), Varanopidae (1→0), *Eudibamus* + *Belebey* (1→0), *Secodontosaurus obtusidens* (0→1), *Varanosaurus acutirostris* (0→1).//

180. Postsplenial: present (0); absent (1)

Klembara et al 2014 c.104

The postsplenial is plesiomorphically present in *Gephyrostegus* (Klembara *et al.* 2014) and *Seymouria* (Klembara *et al.* 2005). It is also present in *Petrolacosaurus* (Reisz 1981).

Unambiguous: Diadectomorpha + Amniota (0→1). DELTRAN: *Petrolacosaurus kansensis* (1→0). ACCTRAN: *Petrolacosaurus kansensis* (1→0).

181. Coronoids, number in mandible: three (0); two (1); one (2)

Modified from Gauthier *et al.* (1988 c.100), Laurin (1993 c.55), Laurin and Reisz (1995 c.74), deBraga and Rieppel (1997 c.84), Sidor and Hopson (1998 c.89), Sidor (2003 c.58), Müller and Reisz (2006 c.67), Maddin *et al.* (2008 c.61), Fröbisch *et al.* (2011 c.41), Benson (2012 c.141), Klembara *et al.* (2014 c.95), Modesto *et al.* (2015 c.113), Spindler *et al.* (2018 c.94)

This character describes one of the key diagnostic features that support the early divergence of amniotes into the synapsid total-group, in which two coronoids are present (state 1), and the reptile total-group, in which only a singe coronoid is present (state 2). The current paradigm suggests a single coronoid (state 2) is present in captorhinids, parareptiles (including mesosaurs), 'protorothyridids' and diapsids (Laurin and Reisz 1995, deBraga and Reisz 1997). I note there are exceptions to this hypothesis. Two coronoids are present in the diapsid *Araeoscelis* (Vaughn 1955). Carroll (1964) described isolated edentulous anterior coronoids in two specimens, and a rugose area on the medial surface of the dentary level with the 10th tooth position in the basal 'protorothyridid' *Hylonomus*. *Hylonomus* has nevertheless been scored as possessing a single coronoid in previous analyses (Müller and Reisz 2006 c.57), and here it is scored as state (1). The primitive condition, the presence of three coronoids, is only known in the most basal stem-group terminals *Gephyrostegus* and *Seymouria* (Klembara *et al.* 2014, Laurin 1996). Some, if not all, diadectomorphs possess just two coronoids e.g. *Limnoscelis* (Berman *et al.* 2010). Many previous analyses have scored all taxa considered to be early synapsids, including caseasaurs, sphenacodontians and edaphosaurs as possessing two coronoids (state 1), and this is supported by various descriptive studies (Sigogneau-Russell and Russell 1974, Maddin *et al.* 2008, Reisz *et al.* 1992, Currie 1977, Modesto 1995). An anterior coronoid has also been described in the varanodontine *Varanops* (Campione and Reisz 2010). However, the condition in mycterosaurines is different, some of which seem to lack the anterior coronoid and therefore possess only a single coronoid: the anterior coronoid is absent in *Archaeovenator* (Dilkes and Reisz 2003) and *Mesenosaurus* (Reisz and Berman 2001), and these taxa are scored as state (2) herein. The condition in other varanodontines and mycterosaurines cannot be determined (reviewed by Ford and Benson 2018), and they are scored as (?) in agreement with Benson (2012).

Unambiguous: *Araeoscelis* spp (2→1), Sauropsida (1→2), Diadectomorpha + Amniota (0→1). DELTRAN: *Hylonomus lyelli* (2→1), *Varanops brevirostris* (2→1). ACCTRAN: *Anthracodromeus* + *Hylonomus* (2→1), Varanodontinae (2→1).

182. Coronoid, teeth: present (0); absent (1)

From Laurin (1993 c.81), Maddin *et al.* (2008 c.62), Fröbisch *et al.* (2011 c.63), Benson (2012 c.142), Klembara *et al.* (2014 c.119/120/121), Spindler *et al.* (2018 c.95)

Amongst early amniotes coronoid teeth are present (state 0) in out-group-taxa (e.g. *Seymouria*, Laurin 1996; *Gephyrostegus*, Klembara *et al.* 2014 fig.7C), caseasaurs (Maddin *et al.* 2008, Brocklehurst *et al.* 2016), the 'protorothyridid' *Hylonomus* (Carroll 1964), the sphenacodontian *Haptodus* (ROM 43601, Laurin 1993 fig. 8D) and the edaphosaurid *Edaphosaurus* (Modesto 1995).

Unambiguous: Sauropsida (0→1), Sphenacodontidae (0→1). DELTRAN: *Hylonomus lyelli* (1→0), *Varanosaurus* + *Ophiacodon* (0→1). ACCTRAN: *Anthracodromeus* + *Hylonomus* (1→0), Ophiacodontidae (0→1).

183. Angular, cross-section shape of posteroventral border of angular: weakly developed ridge or keel (0); prominent, sheet-like keel with strongly convex posterior edge (1); reflected lamina separated from mandible by a posterior notch in lateral view (2); ridge or keel absent from ventral surface of angular (3).

Modified from Benson (2012 c.143) modified from Brinkman and Eberth (1983 c.7), Reisz *et al.* (1992 c.50), Berman *et al.* (1995 c.60/63), Sidor (2003 c.30), Reisz and Dilkes (2003 c.38), Maddin *et al.* (2006 c.40), Maddin *et al.* (2008 c.56), Reisz *et al.* (2009 c.58), Spindler *et al.* (2018 c.91)

A weakly keeled angular (state 0) is present in diadectomorphs, caseasaurs, basal mycterosaurines, araeoscelidians, parareptiles and *Orovenator*. Ophiacodontids, edaphosaurids and *Haptodus* share state (1). State (2) is restricted to sphenacodontids. The keel is absent (state 3) in derived mycterosaurines, varanodontines, diapsids and captorhinids. The definition of state (3) has been revised to describe the absence of a ridge or keel rather than the presence of an evenly rounded edge e.g. Benson (2012 c.143), since the curvature of the ventral surface of the angular can differ in those taxa where the keel is absent, as noted by Spindler *et al.* (2018 c.91).

Unambiguous: *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→3), Sphenacodontidae (1→2), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), Mycterosaurinae + Varanodontinae (0→3), *Paleothyris acadiana* (0→3), *Seymouria* spp (0→3). DELTRAN: *Lanthanolania* + Archosauromorpha (0→3). ACCTRAN: Neodiapsida (0→3).

184. Surangular, anterior extension: extends anteriorly beyond coronoid eminence (0); terminates posterior to or level with the anterior border of the coronoid eminence (1)

Modified from Laurin and Reisz (1995 c.72), deBraga and Rieppel (1997 c.86), Müller (2004 c.146), Reisz *et al.* (2007 c.72), Tsuji *et al.* (2012 c.80), Ezcurra *et al.* (2014 c.162), Ezcurra (2016 c.285)

This character has more recently been used to describe morphological similarities among ankyramorph parareptiles (Tsuji *et al.* 2012 c.80) and lepidosauromorphs (Ezcurra 2016 c.285). In the current taxon list, the anterior extension of the surangular does not extend beyond the coronoid eminence (state 1) in captorhinids (Clark and Carroll 1973, Heaton 1979), caseids (Sigogneau-Russell and Russell 1974, Maddin *et al.* 2008) ophiacodontids (Romer and Price 1940, Berman *et al.* 1995) edaphosaurids (Modesto 1995), sphenacodontids (Romer and Price 1940), *Mycterosaurus* (Berman and Reisz 1982), *Heleosaurus* (Botha-Brink and Modesto 2009), *Araeoscelis* (Reisz *et al.* 1984) and *Claudiosaurus* (Carroll 1981).

Unambiguous: *Araeoscelis* spp (0→1), *Heleosaurus scholtzi* (0→1), *Mycterosaurus longiceps* (0→1), Bolosauridae + *Macroleter* + Procolophonoidea (0→1), *Paleothyris acadiana* (0→1). DELTRAN: *Acleistorhinus pteroticus* (0→1), *Claudiosaurus germaini* (0→1), *Reiszorhinus* + *Captorhinus* + *Protocaptorhinus* + *Romeria* (0→1), Caseidae (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1). ACCTRAN: clade A (1→0), Amniota (0→1), Eothyrididae (1→0), *Colobomycter* + *Acleistorhinus* (0→1).

185. Surangular, anterior surangular foramen: absent (0); present (1)

From Modesto and Sues (2004 c.145), Ezcurra *et al.* (2014 c.164), Pritchard *et al.* (2015 c.80), Ezcurra (2016 c.288)

As noted by Modesto and Sues (2004) an anteriorly opening foramen and groove is located on the lateral surface of the surangular at the base of the coronoid eminence in *Prolacerta* and *Proterosuchus*, and is considered homologous with similar opening in archosaurs and squamates. It is absent in all other terminal taxa included in the analysis.

DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

186. Surangular, posterior surangular foramen: absent (0); present (1)

From Modesto and Sues (2004 c.146), Nesbitt (2011 c.163), Ezcurra *et al.* (2014 c.165), Pritchard *et al.* (2015 c.81), Ezcurra (2016 c.289)

This is a second opening on the surangular, located ventral to the articulating facet for the quadrate. The posterior surangular foramen is present in archosauromorphs, such as *Proterosuchus* and *Prolacerta* (Modesto and Sues 2004), nyctiphruretid parareptiles (Modesto *et al.* 2015 c.112) and *Milleretta* (Gow 1975 identified a small foramen on the posterolateral surface of the surangular in *Milleretta* as the entry point for the chorda tympani branch of cranial nerve VII).

Unambiguous: *Milleretta rubidgei* (0→1). DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

187. Surangular, medial expansion of dorsal surface: thin, sheet-like surangular, unexpanded (0); medially expanded along the dorsal margin, forming a broad dorsally facing platform (1).

From Benson (2012 c.145), Spindler *et al.* (2018 c.90)

This character was first introduced by Benson (2012) to describe the medial expansion of the dorsal surface of the surangular (state 1) as a varanodontine synapomorphy. State (1) is also present in *Apsisaurus* (MCZ 1474, Reisz *et al.* 2010), *Mycterosaurus* and *Orovenator* (Ford and Benson 2018 fig. 13C/13D, based on 'CT data). A similar condition is also found in some diapsids (e.g. *Acerosodontosaurus*, Currie 1980). Laurin and Reisz (1995) described an accessory lateral shelf on the dorsal surface of the surangular in procolophonids and testudines, and Modesto *et al.* (2015 c.112) scored this feature as being present in several ankyramorph parareptiles. Here, I treat the presence of a lateral shelf as a separate morphology, which is described in the subsequent character (ch.188).

DELTRAN: *Acerosodontosaurus piveteaui* (0→1), *Mesenosaurus romeri* (1→0), Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→1), *Orovenator mayorum* (0→1). ACCTRAN: *Archaeovenator hamiltonensis* (1→0), Parareptilia (1→0), clade C (0→1), *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (1→0).

188. Surangular, accessory lateral shelf anterior to articular region: absent (0); present (1)

From Laurin and Reisz (1995 c.73), Modesto *et al.* (2015 c.111)

Character state (1) is present in several ankyramorph parareptiles, including *Macroleter* and *Procolophon* (Modesto *et al.* 2015 c.111). In *Belebey* a ridge overhangs the mandible laterally (Reisz *et al.* 2007) which I also score as state (1).

Unambiguous: Bolosauridae + *Macroleter* + Procolophonoidea (0→1), *Owenetta kitchingorum* (1→0).

189. Surangular, anterodorsal process preventing posterior contact of dentary and coronoid: absent (0); present (1)

NEW

In *Seymouria* (Laurin 1996 fig.3E, MCZ 1083), ophiacodontids (Romer and Price 1940 plate 1, *Varanosaurus* FMNH PR 1670), mycterosaurines (Reisz and Berman 2001), varanodontines (Langston and Reisz 1981), derived captorhinids (Heaton 1979, *Reiszorhinus* FMNH UC 183) and *Orovenator* (Ford and Benson 2018) a conspicuous anterodorsal process of the surangular prevents contact between the posterior region of the dentary and the coronoid on the dorsal margin of the mandible.

Unambiguous: *Seymouria* spp (0→1). DELTRAN: *Captorhinus* spp (0→1), *Varanosaurus* + *Ophiacodon* (0→1), Varanopidae except *Ascendonanus* (0→1), *Reiszorhinus olsoni* (0→1). ACCTRAN: *Protocaptorhinus* pricei (1→0), Captorhinidae (0→1), Ophiacodontidae (0→1), Varanopidae (0→1).

190. Surangular, morphology of anterodorsal process, if present: narrow splint-like process (0); dorsoventrally broad posteriorly, tapering anteriorly (1), inapplicable, anterodorsal process absent (-)

NEW

In several terminal taxa the anterodorsal process of the surangular (state 1 ch.189), where present, is

a mediolaterally narrow splint-like process, principally exposed dorsally e.g. in mycterosaurines and varanodontines (Campione and Reisz 2010, *Mycterosaurus* FMNH UC 692) and *Orovenator* (Ford and Benson 2018 fig.13A, D). In other taxa where this morphology is present the process is broad at its base and prominent in lateral view, tapering anteriorly (e.g. *Ophiacodon*, Romer and Price 1940; *Reiszorhinus*, Sumida *et al.* 2010 and *Seymouria*, Laurin 1996).

DELTRAN: Varanopidae except *Ascendonanus* (0→1). ACCTRAN: clade A (0→1).

191. Prearticular, medial surface: nearly straight (0); twisted posteriorly (1)

From Brinkman and Eberth (1983 c.12), Reisz (1986 table 3d), Reisz *et al.* (1992 c.52), Berman *et al.* (1995 c.62), Fröbisch *et al.* (2011 c.105), Benson (2012 c.146)

A conspicuous twisting of the posterior surface of the prearticular is present in sphenacodontians and edaphosaurs (Romer and Price 1940, Brinkman and Eberth 1983, Reisz 1986).

Unambiguous:Sphenacodontia + Edaphosauridae (0→1).

Postcranial characters

192. Vertebrae, notochordal canal: present throughout ontogeny (0); absent in adults (1)

From Gauthier *et al.* (1988 c.124), Laurin (1991: F3), deBraga and Rieppel (1997 c.99), Dilkes (1998 c.83), Rieppel (1999 c.59), Müller (2004 c.40), Reisz *et al.* (2010 c.68), Ezcurra *et al.* (2014 c.67), Schoch and Sues (2015 c.99)

The notochordal canal is closed in adults of saurians and in derived therapsids (deBraga and Rieppel 1997). In the current taxon list it is scored as (1) in *Prolacerta* and *Proterosuchus*. A continuous notochordal canal appears to be present in adult individuals of all other terminal taxa in which vertebrae have been preserved, with the exception of *Milleretta* (Gow 1972).

DELTRAN: *Milleretta rubidgei* (0→1), Archosauromorpha (0→1). ACCTRAN: Parareptilia (0→1), *Lanthanolania* + Archosauromorpha (0→1).

193. Vertebrae, presacral, count: 27 or more (0); fewer than 27 (1)

From Benson (2012 c.148), Spindler *et al.* (2018 c.105) modified from Carroll and Currie (1991 c.46), deBraga and Rieppel (1997 c. 97), Klembara *et al.* (2014 c.123), Laurin and Piñeiro (2017 c. 84)

Previous studies select different numerical boundaries between the states of this character depending on their taxonomic focus. Laurin and Piñeiro (2017) and deBraga and Rieppel (1997), for example, chose 20 presacral vertebrae as the boundary for the primitive and derived states in a broad based analyses of early amniotes focusing on turtles, whereas both Benson (2012) and Spindler *et al.* (2018) used 27 presacrals for synapsid-focused studies. Klembara *et al.* (2014) employed a multistate approach (minimum 28 to more than 38) for anamniotes, and Carroll and Currie (1991) use 26 vertebrae for diapsids. Here I use the 27 presacral count of Benson (2102) and Spindler *et al.* (2018), and find that *Seymouria* (Berman *et al.* 2000), *Gephyrostegus* (Carroll 1970) and diadectomorphs (Moss 1972, Romer 1946) have fewer that 27 presacral vertebrae, a condition that also occurs in Captorhinids (e.g. *Thuringothyris* Müller *et al.* 2006 and *Captorhinus aguti*, Fox and Bowman 1966), *Petrolacosaurus* (Reisz 1981) and neodiapsids (e.g. *Youngina*, Smith and Evans 1996; *Acerosodontosaurus*, Bickelmann *et al.* 2009; *Claudiosaurus*, Carroll 1981; and *Prolacerta*, Gow 1975). Where known, all other terminal taxa share state (0), with the exception of *Casea* (Olson 1968), *Eudibamus* (Berman *et al.* 2000) and *Milleretta* (Gow 1972).

Unambiguous: *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (1→0). DELTRAN: *Araeoscelis* spp (1→0), *Eocasea martini* (1→0), *Eudibamus cursoris* (0→1), Protorothyrididae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (1→0), Varanopidae (1→0). ACCTRAN: clade D (0→1), Captorhinidae (0→1), Amniota (1→0), Caseidae (0→1), *Eudibamus* + *Belebey* (0→1), *Petrolacosaurus kansensis* (0→1).

194. Cervical vertebrae, atlantal ribs: present (0); absent (1)

From deBraga and Rieppel (1997 c.102), Schoch and Sues (2015 c.102)

The loss of an ossified atlantal rib (state 1) is an autapomorphy of derived diapsids (deBraga and Rieppel 1997), and is scored as absent (state 1) in *Claudiosaurus*, *Prolacerta* and *Proterosuchus*. How-

ever, both Currie (1980) and Bickelmann *et al.* (2009) note an articulation facet for the atlantal rib on the atlantal neural arch in *Acerosodontosaurus*.

DELTRAN: *Claudiosaurus germaini* (0→1), Archosauromorpha (0→1). ACCTRAN: *Acerosodontosaurus piveteaui* (1→0), Neodiapsida (0→1).

195. Cervical vertebrae, atlas-axis complex, atlantal and axial intercentra: contact ventrally or in very close proximity (0); widely separated by ventral extension of the atlantal centrum (1)

From Benson (2012 c.150) modified from Reisz *et al.* (1992 c.67), Laurin (1993 c.89), Berman *et al.* (1995 c.73)

In sphenacodontids, an extension of the atlantal centrum reaches the ventral surface of the column and prevents contact between the atlantal and axial intercentra (state 1)(Reisz 1986). Reisz (1980) suggested that this state might also be present in mycterosaurines and varanodontines, as noted by Benson (2012), who scored *Archaeovenator* and *Varanodon* as possessing state (1). In *Archaeovenator*, however, the wedge-shaped axial intercentrum is fused to the ventral margin of the atlantal centrum, preventing the centrum from reaching the ventral surface of the column (Reisz and Dilkes 2003). The examination of *Archaeovenator* (KUVP 12483) also indicates that the atlantal intercentrum is somewhat displaced, but would originally have made contact with the anterior margin of the fused atlantal centrum/axial intercentrum. This is similar to the configuration of these elements in *Ophiacodon* (Reisz 1986 fig. 17A) and *Varanosaurus* (Sumida 1989 fig. 26B), so I score *Archaeovenator* instead as possessing state (0). Laurin (1996) suggested that the condition in *Haptodus* might be similar to that of sphenacodontids, since the axial and atlantal intercentra do not meet ventral to the atlantal centrum (Laurin 1993 fig.14). However, the intercentra are in close proximity and the atlantal centrum lacks the flat ventral margin of more derived sphenacodontians, and is therefore scored as state (0).

Unambiguous: Sphenacodontidae (0→1). DELTRAN: *Varanodon agilis* (0→1). ACCTRAN: Varanopidae (0→1).

196. Cervical vertebrae, axial neural spine, anteroposterior length of apex: longer than or equal to the centrum (0); shorter than centrum (1); short and spine inclined an-

terodorsally (2)

From Benson (2012 c.151) modified from Gauthier *et al.* (1988 c.126), Reisz *et al.* (1992 c.68), Berman *et al.* (1995 c.74), Fröbisch *et al.* (2011 c.108) Maddin *et al.* (2008 c.80)

In most terminal taxa, including mycterosaurines (*Archaeovenator* KUVP 12483), varanodontines (Langston and Reisz 1981), ophiacodontids (Sumida 1989, Reisz 1986) and *Haptodus* (Laurin 1996) the apex of the axial neural spine is anteroposteriorly longer than the axial centrum (state 0). Sphenacodontians (Reisz 1986, Reisz *et al.* 1992) have a dorsally tapering neural spine, the apex of which is shorter anteroposteriorly than the centrum (state 1). The additional state of Benson (2018) (state 2) describes the distinctive anterodorsal inclination of the axial neural spine in caseids (Reisz and Fröbisch 2014) and edaphosaurids (Modesto and Reisz 1990). The early diapsid *Araeoscelis* (Vaughn 1955) is scored as possessing state (1) due to its unusually elongate cervical centra.

Unambiguous: *Araeoscelis* spp (0→1), Sphenacodontidae (0→1), Edaphosauridae (0→2). DELTRAN: *Eocasea martini* (0→2), *Euromycter* + *Ennatosaurus* (0→2). ACCTRAN: *Casea broilii* (2→0), Caseasauria (0→2).

197. Cervical vertebrae, axial neural spine, dorsoventral height: low, subequal to the centrum height (0); tall, approximately 1.5 times the height of the centrum (1); very tall, many times the centrum height (2)

From Benson (2012 c.152), Spindler *et al.* (2018 c. 106)

Unambiguous: *Dimetrodon* spp (1→2), Protorothyrididae (0→1), Sphenacodontia (0→1), Varanodontinae (0→1). DELTRAN: *Archaeothyris florensis* (0→1), *Ianthasaurus hardestiorum* (0→2),*Ophiacodon* spp (0→1), *Procolophon trigoniceps* (0→1). ACCTRAN: *Ianthasaurus hardestiorum* (0→2), Parareptilia (0→1), *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (0→1), *Varanosaurus acutirostris* (1→0).

198. Cervical vertebrae - ribs, slender and tapering at low angle to vertebrae: absent (0); present (1)

Modified from Dilkes (1998 c.77), Müller (2004 c.102), Nesbitt (2011 c.196), Ezcurra *et al.* (2014

c.173), Pritchard *et al.* (2015 c.104), Ezcurra (2016 c.349)

Character state (1) is present in archosauriforms (e.g. *Proterosuchus*)(Nesbitt 2011). It is also present in *Prolacerta* (Gow 1975).

DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

199. Cervical vertebrae, centra length: shorter than or subequal to the dorsal centra (0); markedly longer than dorsal centra (1)

From Spindler *et al.* (2018 c.107) modified from Laurin (1993 c.93), Fröbisch *et al.* (2011 c.70), Benson (2012 c.153) modified from Reisz *et al.* (1992 c.70), Modesto (1994 c.25, 1995 c.23), Reisz *et al.* (2010 c.69), Mazierski and Reisz (2010 c.25), Nesbitt (2011 c.181)

State (1) of this character is present in sphenacodontids, and in the varanodontines *Varanops* and *Aerosaurus greenleeorum* (Romer and Price 1940, table 3). However, there is some degree of intraspecific and sexual dimorphism in *Dimetrodon*, and in *Aerosaurus wellesi* the cervical centra are marginally shorter than the mid-dorsals, although this measurement is 'uncorrected for distortion' (Langston and Reisz 1981 table 1). I therefore score both *Dimetrodon* and *Aerosaurus* as [0,1]. There is a conspicuous elongation of the cervical centra relative to the dorsal centra (state 1) in araeoscelidian diapsids (Vaughn 1955, Reisz 1981), and the archosauromorphs *Prolacerta* and *Proterosuchus* (Nesbitt 2011).

Unambiguous: Araeoscelidia (0→1). DELTRAN: *Varanops* + *Varanodon* + *Watongia* (0→1), Archosauromorpha (0→1), *Secodontosaurus obtusidens* (0→1). ACCTRAN: Sphenacodontidae (0→1), Varanodontinae (0→1), *Lanthanolania* + Archosauromorpha (0→1).

200. Cervical vertebrae, ventral surface of cervical centra: rounded (0); bearing a low keel or ridge (1), bearing a prominent, transversely narrow, sheet-like keel (2)

Modified from Gauthier *et al.* (1988 c.139), Laurin (1991 H.2), Reisz *et al.* (1992 c.69 in part), Laurin (1993 c.92), deBraga and Rieppel (1997 c.103), Reisz *et al.* (2010 c.70), Nesbitt (2011 c.190), Benson (2012 c.154), Pritchard *et al.* (2015 c.108), Ezcurra (2016 c.327), Spindler *et al.* (2018 c.109)

State (1) of this character is present in *Procolophon* (deBraga 2003), *Haptodus* (Laurin 1993) mycterosaurines (Reisz and Dilkes 2003, Anderson and Reisz 2004, Reisz and Modesto 2007), varanodontines (Maddin *et al.* 2006, Campione and Reisz 2010), ophiacodontids (Romer and Price 1940, Sumida 1989) and captorhinids (deBraga and Rieppel 1997). It is also present in *Orovenator* (Reisz *et al.* 2011), araeoscelidians (Reisz 1981, Vaughn 1955), *Acerosodontosaurus* (Currie 1980) and basal archosauromorphs (Ezcurra *et al.* 2014 Appendix S1). In sphenacodontids, the keel is dorsoventrally deeper and sheet-like (state 2) (Reisz 1986). Caseids (Olson 1968) possess a rounded ventral surface of the cervical centra (state 0).

Unambiguous: Caseasauria (1→0), Sphenacodontidae (1→2).

201. Cervical vertebrae, neural arch excavation (lateral to the base of the neural spine): absent (0); present (1)

Modified from Reisz *et al.* (2010 c.71) modified from Reisz and Dilkes (2003 c.47), Ezcurra *et al.* (2014 c.70), Ezcurra (2016 c.337)

Shallow depressions in the dorsolateral of the cervical neural arches (state 1) are present in some mycterosaurines (e.g. *Heleosaurus* and *Mesenosaurus*, Reisz and Modesto 2007; *Mycterosaurus*, Berman and Reisz 1982) and varanodontines (e.g. *Varanops*, Maddin *et al.* 2006). State (1) is also present on the axial neural arch of *Dimetrodon milleri* (MCZ 1365), but is absent in *Secodontosaurus* (MCZ 5203). It can also be found in araeoscelidians (Reisz 1981, Vaughn 1955) and *Proterosuchus* (Ezcurra 2016).

Unambiguous: *Dimetrodon* spp (0→1), Araeoscelidia (0→1), Mycterosaurinae + Varanodontinae (0→1), *Proterosuchus* spp (0→1).

202. Cervical vertebrae, outline of neural spines in lateral view: sub-triangular (0); sub-rectangular (1)

From Reisz *et al.* (2010 c.72), Ezcurra *et al.* (2014 c.71), Ezcurra (2016 c.339)

In the current taxon list, state (0) is scored as being present in captorhinids (Heaton and Reisz 1980, *Protocaptorhinus* MCZ 1478).

DELTRAN: *Captorhinus* + *Protocaptorhinus* + *Romeria* (1→0). ACCTRAN: Captorhinidae (1→0).

203. Cervical ribs, accessory process on anterolateral surface: absent (0); present (1)

From Laurin (1991 H.4), Rieppel (1999 c.71), Müller (2004 c.48), Reisz *et al.* (2010 c.77), Ezcurra *et al.* (2014 c.76), Pritchard *et al.* (2015 c.105)

Character state (1), an anteriorly projecting acumate process on the anterolateral margin of the cervical ribs, is present in araeoscelidians (Reisz 1981) and archosauromorphs (Ezcurra 2016).

Unambiguous: Araeoscelidia (0→1). DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

204. Cervical ribs, proximal heads: some or all holocephalous (single-headed)(0); all dichocephalous (double-headed)(1)

Modified from Laurin (1991 F.4), Reisz *et al.* (2010 c.78), Müller (2004 c.104) Bickelmann *et al.* (2009 c.104), Ezcurra *et al.* (2014 c. 77)

There is some ambiguity in previous discussions of this character and of ch.218 below. In many taxa the region of articular surface of the rib is triangular in shape, and consists of thickened ridges of bone on the dorsal (the tuberculum) and ventral (the capitulum) articular surface, which correspond with the tubercular (upper: diapophysis) and capitular (lower: parapophysis) facets on the vertebra. These thickened areas are often connected by a thin, dorsoventrally oriented lamina or webbing, and together form a continuous contact with the vertebra. Romer and Price (1940:110) noted, 'this may be regarded as a holocephalous condition, but actually the rib is double-headed'. However, Moss (1972:27) notes of *Tseajaia* that the ribs are 'holocephalous, the capitulum and tuberculum being connected by a thin web of bone'. Likewise, Laurin (1993) on the axial rib of the sphenacodontian *Haptodus* noted, ' the axial rib is holocephalous because there is no notch in the web connecting the tuberculum and the capitulum' (Laurin 1993:214). In the diapsid *Acerosodontosaurus*, the distinct tubercular and

capitular regions are joined by a bridge of bone, and were also considered as holocephalous by Currie (1980). In a later study on the same specimen, the ribs were described as double-headed, although in the phylogenetic matrix of the same study they were scored as holocephalous (Bickelmann *et al.* 2009). Ezcurra *et al.* (2014) then scored *Acerosodontosaurus* as possessing dichocephalous ribs, based on the comments of Bickelmann *et al.* (2009). To clarify this issue I take the following approach to both cervical and dorsal ribs (partly based on the definition of Müller 2004 c.104): (i) Where a lamina of bone forms a continuous ridge of uninterrupted contact between the tubercular and capitular regions of the articular surface of the rib, the condition is holocephalous (contra Romer and Price 1940) (state 0). In respect to the cervical ribs, this occurs in *Gephyrostegus* (Godfrey and Reisz 2009) *Hylonomus* (Carroll 1964), *Limnoscelis* (Williston 1911, Romer 1946, Kennedy 2010), *Ianthasaurus hardestiorum* (Reisz and Berman 1986), *Haptodus* (Laurin 1993), mycterosaurines (e.g. *Archaeovenator*, Reisz and Dilkes 2003; *Heleosaurus*, Botha-Brink and Modesto 2009), *Proterosuchus* (Ezcurra 2016), *Captorhinus aguti* (Fox and Bowman 1966), *Mesosaurus* (Modesto 2010) and *Araeoscelis* (Vaughn 1955). (iii) Where the lamina of bone is proximally notched or interrupted between the tubercular and capitular regions of the articular surface of the rib or there is a clear bifurcation of the capitulum and tuberculum, the condition is dichocephalous (state 1). This condition is present in the cervical ribs of *Seymouria* (White 1939), caseids (Olson 1968) ophiacodontids (e.g. *Ophiacodon* MCZ 1366, Romer and Price 1940), *Dimetrodon* and *Edaphosaurus* (Romer and Price 1940), varanodontines (e.g. *Aerosaurus*, Langston and Reisz 1981; *Varanodon*, Olson 1965), some 'protorothyridids' (e.g. *Coelostegus*, Carroll and Baird 1972; *Paleothyris*, Carroll 1969), *Petrolacosaurus* (Reisz 1981), some captorhinids (e.g. *Thuringothyris*, Müller *et al.* 2006; *Protocaptorhinus*, Clark and Carroll 1973) and procolophonoids (e.g. *Owenetta*, Reisz and Scott 2002; *Procolophon*, deBraga 2003).

Unambiguous: *Captorhinus* spp (1→0), *Haptodus garnettensis* (1→0), *Hylonomus lyelli* (1→0). DELTRAN: *Araeoscelis* spp (1→0), *Archaeovenator hamiltonensis* (1→0), *Ianthasaurus hardestiorum* (1→0), *Mesosaurus tenuidens* (1→0), Amniota (0→1), Mycterosaurinae (1→0), *Lanthanolania* + Archosauromorpha (1→0), *Seymouria* spp (0→1). ACCTRAN: *Ianthasaurus hardestiorum* (1→0), clade B (1→0), *Seymouria* + Diadectomorpha + Amniota (0→1), Diadectomorpha (1→0), Varanodontinae (0→1), Bolosauridae + Procolphonoidea + *Macroleter* (0→1), *Petrolacosaurus kansensis* (0→1).

205. Cervicodorsal vertebrae, mammillary processes on posterior cervical and anterior dorsal neural spines: absent (0); present (1)

From Laurin (1991 H.3), Reisz *et al.* (2010 c.76), Ezcurra *et al.* (2014 c.75), Pritchard *et al.* (2015 c.125), Ezcurra (2016 c.320)

The mammillary process is a small lip of dorsolaterally directed bone that is located on the lateral surface of the neural spine close to the dorsal margin (Reisz 1981, Ezcurra 2016). It is present in several diapsid taxa (e.g. *Petrolacosaurus*, Reisz 1981; *Araeoscelis*, Vaughn 1955) and archosauromorphs (Ezcurra 2016). Modesto (2010) notes that mammillary processes are present on the cervical and dorsal vertebrae of *Mesosaurus*. However, the position of these processes, directly dorsal to the postzygopophyses, and their posterodorsal orientation, makes it unlikely that they are homologous with the processes found in diapsid taxa. Therefore, *Mesosaurus* is scored as possessing state (0) here.

Unambiguous: Araeoscelidia (0→1). DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

206. Dorsal vertebrae, anteroposterior length of centra: short, subequal to height (0); long, at least 1.5 times as long as high (1)

From Benson (2012 c.155), Ezcurra *et al.* (2014 c.176), Spindler *et al.* (2018 c.108), Ezcurra (2016 c.351, 352)

Unambiguous: *Araeoscelis* spp (0→1), *Claudiosaurus germaini* (0→1), *Haptodus garnettensis* (1→0), Captorhinidae (0→1), *Varanosaurus* + *Ophiacodon* (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Protorothyris archeri* (0→1), *Vaughnictis smithae* (0→1). DELTRAN: *Archaeovenator hamiltonensis* (0→1), *Heleosaurus scholtzi* (0→1), *Mesosaurus tenuidens* (0→1). ACCTRAN: *Archaeovenator* + *Orovenator* (0→1), *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (0→1), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1).

207. Dorsal vertebrae, ventral surface of dorsal centra: rounded (0); bearing a low ridge or keel (1); bearing a prominent, transversely narrow, sheet-like keel (2); bearing a ventrally raised platform or keel with longitudinal trough (3)

Modified from Laurin (1991 H.2), Berman *et al.* (1995 c.75), Reisz and Dilkes (2003 c.44), Maddin *et al.* (2006 c.50), Reisz *et al.* (1992 c.71), Reisz *et al.* (2009 c.62), Fröbisch *et al.* (2011 c.109), Reisz

and Dilkes (2003 c.44), Reisz *et al.* (2010 c.74) Benson (2012 c.156 state 3), Spindler *et al.* (2018 c.110)

State (3) describes the condition found in some ophiacodontids, including *Ophiacodon* (Romer and Price 1940). It is also present in *Heleosaurus* (Reisz and Modesto 2007) and *Procolophon* (deBraga 2003). State (2) is present in sphenacodontids. Most other terminal taxa herein possess a ridge or keel on the dorsal vertebrae (state 1), with the exception of caseasaurs, that possess the rounded ventral surface described by state (0).

Unambiguous: *Heleosaurus scholtzi* (1→3), clade D (1→0), Ophiacodontidae (0→1), Sphenacodontidae (0→2),*Ophiacodon* spp (1→3), *Tseajaia campi* (0→1). DELTRAN: *Ianthasaurus hardestiorum* (0→1), clade A (0→1), *Procolophon trigoniceps* (0→3), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: *Ianthasaurus hardestiorum* (0→1), Captorhinidae except *Thuringothyris* (1→0), Sauropsida (0→1), Bolosauridae + Procolphonoidea + *Macroleter* (0→3).

208. Dorsal vertebrae, transverse processes in trunk: short, projecting equal with or only slightly beyond the lateral surface of the neural arch (0); moderately long, projecting clearly beyond the lateral surface of the neural arch (1)

Modified from Laurin (1991 F.5), Reisz *et al.* (2010 c.75), Benson (2102 c.158), Ezcurra *et al.* (2014 c.74), Ezcurra (2016 c.358)

The transverse process is moderately long (state 1) in *Seymouria* (White 1939, anterior dorsals only), caseids (e.g., *Casea broilii*, FMNH UC 656; *Ennatosaurus*, Olson 1968), with the exception of *Eocasea* (Reisz and Fröbisch 2014), sphenacodontians (Romer and Price 1940), ophiacodontids (e.g. *Ophiacodon*, Romer and Price 1940 fig. 44; *Archaeothyris*, Reisz 1972 fig. 6c; *Varanosaurus*, Sumida 1989) and archosauromorphs (Ezcurra 2016).

Unambiguous: *Seymouria* spp (0→1). DELTRAN: *Anthracodromeus longipes* (0→1), *Ianthasaurus hardestiorum* (1→0), Caseidae (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), Archosauromorpha (0→1). ACCTRAN: *Ianthasaurus hardestiorum* (1→0), *Anthracodromeus* + *Hylonomus* (0→1), Eothyrididae (1→0), Synapsida (0→1), *Lanthanolania* + Archosauromorpha (0→1).

209. Dorsal vertebrae, outline of anterior and middle dorsal neural spines in lateral view:

sub-triangular (0); sub-rectangular (1); dorsal neural spines are long and thin (2)

Modified from Ezcurra *et al.* (2014 c.179)

Unambiguous: *Dimetrodon* spp (1→2), Parareptilia (1→0), clade B (0→1), Edaphosauridae (1→2), Synapsida (0→1). DELTRAN: *Anthracodromeus longipes* (0→1). ACCTRAN: *Anthracodromeus longipes* (0→1).

210. Dorsal vertebrae, posterior dorsal neural spines, orientation: approximately vertical (0); moderately anterodorsally inclined (1); strongly posterodorsally inclined (2)

Modified from Benson (2012 c.165), Spindler *et al.* (2018 c.112), Ezcurra (2016 c.362 in part)

There is a moderate anterodorsal inclination in the neural spines of *Archaeovenator* (Reisz and Dilkes 2003), *Mycterosaurus* (Berman and Reisz 1982 fig.9B) and most varanodontines (e.g. *Varanodon*, Williston 1911 plate 2). Edaphosaurids are scored as possessing state (2) (Modesto and Reisz 1990, Romer and Price 1940).

Unambiguous: Edaphosauridae (0→2). DELTRAN: Varanopidae except *Ascendonanus* (0→1). ACCTRAN: Varanopidae (0→1).

211. Dorsal vertebrae, anterodorsally inclined posterior dorsal neural spines: posteriormost one or two (0); several posterior dorsal neural spines (1); inapplicable, anterodorsally inclined dorsal neural spines are absent (-)

Modified from Benson (2012 c.165)

This character describes the variation between groups in the number of anterodorsally inclined posterior dorsal neural spines (209 state 1). Mycterosaurines are scored as state (0), and varanodontines as state (1), where the condition can be observed.

DELTRAN: *Varanops* + *Varanodon* + *Watongia* (0→1). ACCTRAN: Varanodontinae (0→1).

212. Dorsal vertebrae, neural spines, height: short, approximately 1.5 times centrum height or lower (0); intermediate, 2-3 times centrum height (1); very tall (2).

From Benson (2012 c.164) modified from Reisz *et al.* (1992 c73, 74), Laurin (1993 c.82), Berman *et al.* (1995 c.77), Modesto (1995 c.24), Reisz *et al.* (1998 c.31), Maddin *et al.* (2006 c.52), Reisz *et al.* (2009 c.61), Mazierski and Reisz (2010 c.26, 27), Fröbisch *et al.* (2011 c.64) Ezcurra *et al.* (2014 c.72), Spindler *et al.* (2018 c.111)

The tall dorsal neural spines of sphenacodontids and edaphosaurids are scored as state (2) (Romer and Price 1940). In *Haptodus* (ROM 29872), *Ophiacodon* (MCZ 1366), *Mycterosaurus* and varanodontines (FMNH UR 986, Reisz and Laurin 2004, Langston and Reisz 1981), *Procolophon* (deBraga 2003) and *Mesosaurus* (Modesto 2010) the dorsal neural spines are at least twice the height of the centrum (state 1). This differs from the condition in most other early amniotes (e.g. caseasaurs, most mycterosaurines, 'protorothyridids' and diapsids) in which the dorsal neural spines are short (state 0).

Unambiguous: *Haptodus garnettensis* (2→1),Sphenacodontia + Edaphosauridae (0→2),*Ophiacodon* spp (0→1). DELTRAN: *Mesosaurus tenuidens* (0→1), *Mycterosaurus longiceps* (0→1), Varanodontinae (0→1), *Procolophon trigoniceps* (0→1). ACCTRAN: *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (1→0), Mycterosaurinae + Varanodontinae (0→1), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1), *Owenetta kitchingorum* (1→0).

213. Dorsal vertebrae, neural spines, lateral tubercles: absent (0); present (1)

From Reisz *et al.* (1992 c.77), modified from Modesto (1994 c.29, 1995 c.26), Mazierski and Reisz (2010 c.29), Benson (2012 c.169)

State (1) is a unique synapomorphy of edaphosaurids (Reisz 1986, Reisz and Berman 1986)

Unambiguous: Edaphosauridae (0→1).

214. Dorsal vertebrae, neural spines morphology: consistent along column (0); alternating (1)

From Benson (2012 c.167)

Alternating height or morphology of the dorsal neural spine is present (state 1) in *Varanosaurus* (Sumida 1989), *Seymouria*, diadectomorphs (e.g. *Limnoscelis*, *Tseajaia*), araeoscelidians (e.g. *Petrolacosaurus* and *Araeoscelis*) and captorhinids (e.g. *Captorhinus* and *Protocaptorhinus*, Sumida 1990). Gow (1975) also notes the dorsal neural spines of the archosauromorph *Prolacerta* show a slight but distinct alternation in length (state 1).

Unambiguous: *Prolacerta broomi* (0→1), *Romeria* spp (1→0). DELTRAN: clade C (1→0), *Anthracodromeus* + *Hylonomus* (1→0), Synapsida (1→0), *Varanosaurus acutirostris* (0→1). ACCTRAN: Araeoscelidia (0→1), Captorhinidae (0→1), Amniota (1→0), *Varanosaurus acutirostris* (0→1).

215. Dorsal vertebrae, anterior centrodiapophyseal lamina: absent (0); present (1)

From Brinkman and Eberth (1983 c.17), Ezcurra *et al.* (2014 c.180), Benson (2012 c. 158 in part), Ezcurra (2016 c.315)

In the dorsal vertebrae of several terminal taxa a conspicuous lamina extends anteroventrally from the base of the transverse process to the anterodorsal corner of the centrum. This morphology is very similar to the anterior centrodiapophyseal lamina used to describe the vertebrae of basal archosauromorphs (Ezcurra 2016) and saurischian dinosaurs (Wilson 1999), and this term is adopted herein. An anterior centrodiapophyseal lamina is present in derived ophiacodontids (Brinkman and Eberth 1983, Sumida 1989, Romer and Price 1940 fig.44F), and the archosauromorphs *Prolacerta* and *Proterosuchus* (Ezcurra 2016). In *Petrolacosaurus* a thin ridge runs anteroventrally from the transverse process to the anterior centrosphene in both dorsal and cervical vertebrae (Reisz 1981). Ezcurra *et al.* (2014) scored this condition as an anterior centrodiapophyseal lamina, although later noting its absence in *Petrolacosaurus* (Ezcurra 2016 c.315: 199). Herein I score this as state (1).

Unambiguous: Ophiacodontidae (0→1). DELTRAN: Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→1), Neodiapsida (0→1), *Petrolacosaurus kansensis* (0→1). ACCTRAN: *Araeoscelis* spp (1→0), Parareptilia (1→0), clade B (0→1).

216. Dorsal vertebrae, dorsolateral surface: flat or weakly concave (0); swollen and convex (1); excavated by a depression lateral to the base of the neural spine (2)

Modified from Brinkman and Eberth (1983 c.16), Reisz *et al.* (1992 c.79), Laurin (1993 c.84), Modesto (1994 c.30, 1995 c.28), Berman *et al.* (1995 c.79), Laurin and Reisz (1995 c.86), Dilkes (1998 c.84), Reisz and Dilkes (2003 c.47), Müller (2004 c.103 in part), Maddin *et al.* (2006 c.51), Maddin *et al.* (2008 c.74), Reisz *et al.* (2009 c.60), Mazierski and Reisz (2010 c.31), Fröbisch *et al.* (2011 c.66), Benson (2012 c.163), Ezcurra *et al.* (2014 c.184), Modesto *et al.* (2015 c.127), Ezcurra (2016 c.361), Spindler *et al.* (2018 c.115)

Among out-group taxa, the dorsal neural arches are swollen (state 1) in *Seymouria* and diadectomorphs (Sumida 1990). They are flat (state 0) in most early amniotes, including caseasaurs (Sumida *et al.* 2014, Brocklehurst *et al.* 2016, Reisz and Fröbisch 2014), ophiacodontids (Romer and Price 1940), with the exception of *Varanosaurus*, basal mycterosaurines (Reisz and Dilkes 2003, Spindler *et al.* 2018), 'protorothyridids' (Carroll 1964, 1969), early neo-diapsids (Currie 1980) and *Milleretta* (Gow 1972). The neural arches are swollen and convex in *Varanosaurus* (Sumida 1990), captorhinids (Heaton and Reisz 1986, Sumida 1990) and many basal and derived parareptiles (e.g. *Mesosaurus*, Modesto 2010; bolosaurids, Berman *et al.* 2000, with the exception of *Erpetonyx*, Modesto *et al.* 2015;*Macroleter*, Tsuji 2006 and *Procolophon*oids, deBraga 2003,Reisz and Scott 2002). Lateral excavations are present in sphenacodontians (Romer and Price 1940, Currie 1977), *Ianthasaurus* (Mazierski and Reisz 2010), derived mycterosaurines (Reisz *et al.* 2010, Berman and Reisz 1982) and varanodontines (Reisz and Laurin 2004). Among diapsids, araeoscelidians, *Prolacerta* and *Proterosuchus* are also scored as state 1 (Reisz 1981, Ezcurra 2016). Modesto *et al.* (2015) noted paired excavations in the dorsolateral surface of the neural arch in in the *Erpetonyx*.

Unambiguous: *Erpetonyx arsenaultorum* (1→2), Araeoscelidia (0→2), Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→2), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1). DELTRAN: *Ianthasaurus hardestiorum* (0→2), clade A (1→0), Sphenacodontia (0→2), Synapsida (1→0), Archosauromorpha (0→2), *Varanosaurus acutirostris* (0→1). ACCTRAN: *Edaphosaurus boanerges* (2→0), Captorhinidae (0→1), Amniota (1→0),Sphenacodontia + Edaphosauridae (0→2), *Lanthanolania* + Archosauromorpha (0→2), *Varanosaurus acutirostris* (0→1).

217. Dorsal vertebrae, postzygapophyses: widely spaced (0); contact on midline (1).

From Benson (2012 c.161), Spindler *et al.* (2018 c.118)

Unambiguous: *Edaphosaurus boanerges* (0→1), Sphenacodontidae (0→1), *Varanodon* + *Watongia* (0→1),*Ophiacodon* spp (0→1). DELTRAN: *Prolacerta broomi* (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

218. Dorsal vertebrae, trunk ribs: mostly dichocephalous (double-headed)(0); mostly holocephalous (single-headed)(1)

From Laurin (1991 D.3), Dilkes (1998 c.86), Müller (2004 c.104), Reisz *et al.* (2010 c.79), Ezcurra *et al.* (2014 c.78), Spindler *et al.* (2018 c.119)

Refer to ch.204 above for a discussion on the morphology of single- and double-headed ribs. In the current taxon list a single-headed (holocephalous) rib attachment to the dorsal vertebrae (state 1) is present in diadectomorphs (Moss 1972, Romer 1946), diapsids (Currie 1980, a synapomorphy in Laurin 1991, Ezcurra 2016) and most parareptiles (Gow 1997, deBraga 2003, Modesto 2010, Modesto *et al.* 2015). The articular surfaces of the pre-sacral trunk ribs in *Heleosaurus* are triangular in outline and holocephalous (State 1) (Botha-Brink and Modesto 2009). This is similar to the condition found in *Mycterosaurus* (Berman and Reisz 1982), *Archaeovenator* (Reisz and Dilkes 2003) and *Ascendonanus* (Spindler *et al.* 2018). The dichocephalous condition (state 0) is present in *Seymouria* (White 1939), varanodontines (Pelletier 2014), *Apsisaurus* (Laurin 1991), ophiacodontids, caseids, sphenacodontians and edaphosaurids (Romer and Price 1940, Laurin 1993, Mazierski and Reisz 2010), *Araeoscelis* (Vaughn 1955), *Petrolacosaurus* (Reisz 1981), captorhinids (e.g. *Thuringothyris* Müller *et al.* 2006; *Captorhinus*, Fox and Bowman 1966) and *Owenetta* (Reisz and Scott 2002).

Unambiguous: clade C (0→1), Diadectomorpha (0→1), *Owenetta kitchingorum* (1→0). DELTRAN: *Apsisaurus witteri* (1→0), Varanodontinae (1→0). ACCTRAN: Mycterosaurinae (0→1), Mycterosaurinae + Varanodontinae + *Apsisaurus* (1→0).

219. Dorsal vertebrae, trunk ribs, curvature: curved proximally, only weakly curved distally (0); strongly arched proximally, curved throughout length enclosing expanded, 'barrel- shaped' trunk (1)

From Benson (2012 c.170) modified from Modesto (1994 c.32, 1995 c.34), Maddin *et al.* (2008 c.79), Mazierski and Reisz (2010 c.37)

Caseids and *Edaphosaurus* share the derived state, which is an adaptation for high-fibre herbivory. The trunk ribs in *Procolophon* are only gently curved (state 0)(deBraga 2003).

Unambiguous: *Edaphosaurus boanerges* (0→1), Caseidae (0→1).

220. Osteoderms: absent (0); present dorsally on trunk (1)

From Botha-Brink and Modesto (2009 c.62), Nesbitt 2011 (c.401), Ezcurra (2016 c.588), Spindler *et al.* (2018 c.1)

Osteoderms are present (state 1) in *Heleosaurus* (Reisz and Modesto 2007), *Elliotsmithia* (Reisz *et al.* 1998) and *Youngina* (Gow 1975).

Unambiguous: *Youngina capensis* (0→1). DELTRAN: *Elliotsmithia longiceps* (0→1), *Heleosaurus scholtzi* (0→1). ACCTRAN: *Mesenosaurus romeri* (1→0), Mycterosaurinae (0→1).

221. Sacral vertebrae, morphology of first sacral rib: greatly enlarged in comparison with the second sacral rib (0); subequal to or only slightly larger than the second sacral rib (1).

Modified from Berman *et al.* (1995 c.76), reversed from Maddin *et al.* (2008 c.76, 77) modified from Reisz and Dilkes (2003 c.48), Maddin *et al.* (2006 c.53), Reisz *et al.* (2009 c.63), Benson (2012 c.173), Ezcurra 2016 c.372), Spindler *et al.* (2018 c.122)

Unambiguous: clade D (0→1), *Protorothyris* + *Paleothyris* (0→1), Caseidae (0→1),Sphenacodontia + Edaphosauridae (0→1). DELTRAN: *Archaeovenator hamiltonensis* (0→1), *Eudibamus cursoris* (1→0). ACCTRAN: *Archaeovenator* + *Orovenator* (0→1), *Eudibamus* + *Belebey* (1→0).

222. Sacral vertebrae, second sacral rib: not bifurcate (0); bifurcate (1)

From Dilkes (1998 c.87), Müller (2004: 105), Nesbitt (2011 c. 203), Ezcurra *et al.* (2014 c.187), Pritchard *et al.* (2015 c.131), Ezcurra (2016 c.373)

State (1) of this character is present in a few basal archosauromorphs e.g. Mesosuchus, *Prolacerta* and *Proterosuchus* (Dilkes 1998, Nesbitt 2011). The first, rather than the second, sacral rib in *Aerosaurus* is 'Y' shaped (Langston and Reisz 1981), and is therefore scored here as state (0).

DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

223. Sacral vertebrae, count: two or fewer (0); three or greater (1)

From Reisz *et al.* (1992 c.72), Laurin (1993 c.94), Laurin and Reisz (1995 c.88), Reisz and Dilkes (2003 c.48), Maddin *et al.* (2006 c.53, 2008 c.75), Reisz *et al.* (2009 c.63), Tsuji *et al.* (2012 c. 96), Benson (2012 c.172), Modesto *et al.* (2015 c.129), Spindler *et al.* (2018 c.121).

Three or more sacral vertebrae (state 1) are present in most caseids (e.g. *Casea*, Olson 1968), most edaphosaurids (e.g. *Edaphosaurus*, Romer and Price 1940) and in sphenacodontians (Romer and Price 1940, Currie 1979). LeBlanc and Reisz (2014) posited that state (1) arose independently within each of these groups, since basal members possess only two sacral vertebrae e.g. *Eocasea* (Reisz and Fröbisch 2014), and *Ianthasaurus* (LeBlanc and Reisz 2014). Three sacral vertebrae are also present in non-lanthanosuchoid ankyramorphs and the basal bolosaurid *Erpetonyx* (Modesto *et al.* 2015), as well as the varanodontine *Aerosaurus* (Langston and Reisz 1981). There are two sacral vertebrae (state 0) in most out-group taxa (e.g. *Seymouria*, White 1939; *Limnoscelis*, Kennedy 2010; *Tseajaia*, Moss 1972). Two sacral vertebrae are present in 'protorothyridids' (e.g. *Paleothyris*, Carroll 1969), diapsids (e.g. *Petrolacosaurus*, Reisz 1981; *Youngina* and *Prolacerta*, Gow 1975), captorhinids (e.g. *Captorhinus aguti*, Fox and Bowman 1966), *Archaeovenator* (Reisz and Dilkes 2003) and other mycterosaurines, the varanodontine *Varanodon* (FMNH UR 986), ophiacodontids (Romer and Price 1940 fig.45A, Reisz 1972), and the parareptiles *Mesosaurus* (Modesto 2010) and *Milleretta* (Gow 1972).

Unambiguous: *Aerosaurus* spp (0→1). DELTRAN: *Casea broilii* (0→1), *Edaphosaurus boanerges* (0→1), *Erpetonyx arsenaultorum* (0→1), Sphenacodontia (0→1), *Macroleter* + Procolophonoidea (0→1). ACCTRAN: *Ianthasaurus hardestiorum* (1→0), Caseidae (0→1),Sphenacodontia + Edaphosauridae (0→1), *Eudibamus* + *Belebey* (1→0), Bolosauridae + Procolphonoidea + *Macroleter* (0→1).

224. Caudal vertebrae, anterior caudal neural spine height: moderately tall with height/length between >1.0 and <2.0 (0); low with height/length <1.0 (1); tall with height/length >2.0 and <3.0 (2); very tall with height/length >3.0 (3)

From Dilkes (1998 c.88), Müller (2004 c.106), Ezcurra *et al.* (2014 c.189), Ezcurra (2016 c.379)

Unambiguous: *Haptodus garnettensis* (3→1), *Limnoscelis plaudis* (0→2), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→3), *Youngina capensis* (0→1). DELTRAN: Caseasauria (0→1), *Tseajaia campi* (0→1), *Varanodon agilis* (0→2), *Varanosaurus acutirostris* (3→1). ACCTRAN: Sauropsida (1→0), Diadectomorpha + Amniota (0→1), Mycterosaurinae + Varanodontinae (0→2), *Varanosaurus acutirostris* (3→1).

225. Caudal vertebrae, chevrons, distal width of haemal spine: equivalent to proximal width (0); tapering (1); wider than proximal width (2)

From Dilkes 1998 c.91), Müller (2004 c.108), Ezcurra *et al.* (2014 c.192)

Unambiguous: Sauropsida (0→1). DELTRAN: *Archaeovenator hamiltonensis* (1→0), *Edaphosaurus boanerges* (0→1), *Lanthanolania* + Archosauromorpha (1→2). ACCTRAN: Edaphosauridae (0→1), Varanopidae (1→0), Neodiapsida (1→2).

226. Clavicle, orientation of long axis of ventromedial plate relative to shaft: highly obtuse angle (0); almost perpendicular (1)

From Benson (2012 c.188)

Unambiguous:Sphenacodontia + Edaphosauridae (0→1), *Seymouria* spp (0→1). DELTRAN: *Captorhinus* spp (0→1), Protorothyrididae (0→1), *Youngina capensis* (0→1). ACCTRAN: clade B (1→0), Sauropsida (0→1), Neodiapsida (0→1).

227. Clavicle, anteroposterior width of ventromedial plate: narrow, less than three times the width of the midpoint of the dorsal shaft (0); narrow, but with a distinct anterior

process of the ventromedial plate (1); intermediate, equal to or more than 3 times the width of the midpoint of the dorsal shaft (2), deep, at least 4 times the width of the midpoint of the dorsal shaft (3)

Modified from Benson (2012 c.187) modified from Berman *et al.* (1995 c.83), Laurin and Reisz (1995 c.96), Maddin *et al.* (2006 c.54, 2008 c.82), Reisz *et al.* (2009 c.65), Spindler *et al.* (2018 c.123)

In previous studies the description of the anteroposterior width of the ventromedial plate has been a qualitative (narrow, intermediate, deep) assessment. Here I introduce a quantitative parameter to the character based on the width of the dorsal shaft at the midpoint. In the out-group taxon *Gephyrostegus*, the ventromedial plate is narrow (state 0) (Klembara *et al.* 2014), and this is probably the plesiomorphic state for amniotes (contra Reisz 1986) as this is condition is also present in *Tseajaia* (Moss 1972), *Oedaleops* (Sumida *et al.* 2014), ophiacodontids (e.g. *Ophiacodon*, MCZ 2934), basal mycterosaurines (*Archaeovenator* KUVP 12483, Spindler *et al.* 2018) and 'protorothyridids' (Carroll 1964, Carroll and Baird 1972), with the exception of *Protorothyris* (see below). The intermediate state (2) is present in *Seymouria* (White 1939), *Petrolacosaurus* (KUVP 9958) and the varanodontines *Aerosaurus* and *Varanops* (Pelletier 2014, MCZ 1926). A deep width of the ventromedial plate (state 3) is present in sphenacodontians (e.g. *Dimetrodon* (MCZ 1365) and edaphosaurids (e.g. *Edaphosaurus*, MCZ 4316) as noted by Reisz (1986). Benson (2012) introduced a new state to account for an additional anterior process on the ventromedial plate in *Captorhinus* and *Protorothyris*. A distinctive anterior process is present in *Captorhinus aguti* (OMNH 15003) and *Limnoscelis* (Romer 1946)(state 1). However, it is absent in *Protorothyris archeri* (MCZ 1532, MCZ 2148), which is scored for the intermediate state (2) herein.

Unambiguous: *Limnoscelis plaudis* (0→1), *Mesosaurus tenuidens* (0→2), *Protorothyris archeri* (0→2), *Seymouria* spp (0→2). DELTRAN: *Aerosaurus* spp (0→2), *Captorhinus* spp (0→1), *Dimetrodon* spp (0→3), *Edaphosaurus boanerges* (0→3), *Petrolacosaurus kansensis* (0→2), *Varanops brevirostris* (0→2). ACCTRAN: *Haptodus garnettensis* (3→0), Araeoscelidia (0→2), Captorhinidae (0→1),Sphenacodontia + Edaphosauridae (0→3), *Varanodon* + *Watongia* (2→0), Varanodontinae (0→2).

228. Interclavicle, median notch on anterior margin: absent (0); present (1)

From Ezcurra *et al.* (2014 c.195) modified from Dilkes (1998 c.97), Müller 2004 c.111), Pritchard *et*

al. (2015 c.134), Ezcurra (2016 c.407)

A median notch is present in *Limnoscelis* (Williston 1911 fig.11A), *Archaeovenator* (KUVP 12483), *Paleothyris* (pers. obs. microCT data from MCZ 3481), *Petrolacosaurus* (Reisz 1981) and archosauromorphs (Ezcurra 2016).

Unambiguous: *Paleothyris acadiana* (0→1). DELTRAN: *Archaeovenator hamiltonensis* (0→1), *Limnoscelis plaudis* (0→1), Archosauromorpha (0→1), *Petrolacosaurus kansensis* (0→1). ACCTRAN: Diadectomorpha (0→1), *Archaeovenator* + *Orovenator* (0→1), *Lanthanolania* + Archosauromorpha (0→1), *Petrolacosaurus kansensis* (0→1).

229. Interclavicle, posterior stem: little change in width along entire length or attenuates posteriorly (0); expansion present (1)

Modified from (Dilkes 1998 c.98), Müller (2004 c.112), Ezcurra *et al.* (2014 c.196), Pritchard *et al.* (2015 c.144), Ezcurra (2016 c.411)

Unambiguous: Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (0→1), *Prolacerta broomi* (0→1), *Seymouria* spp (0→1), *Tseajaia campi* (0→1). DELTRAN: *Petrolacosaurus kansensis* (0→1), *Varanops brevirostris* (0→1). ACCTRAN: *Varanops* + *Varanodon* + *Watongia* (0→1), *Petrolacosaurus kansensis* (0→1).

230. Interclavicle, shape of interclavicular head in ventral view: paddle-shaped (0); diamond or spade shaped with anteroposterior length sub-equal to or greater than the transverse width (1); lateral processes or wings present, with transverse width approximately two times greater than anteroposterior length of interclavicular head (2)

Modified from (Laurin 1991 J.6), Berman *et al.* (1995 c.8), Laurin and Reisz (1995 c.92), Benson (2012 c.190), Spindler *et al.* (c.125, 126)

There is some degree of variation in the morphology of the interclavicular head among early amniotes. Herein I identify three principle morphologies associated with the current taxon list: state (1), a broad, paddle-shape with a smoothly convex lateral margin (e.g. *Seymouria*, White 1939), state

(2), anteroposterior length sub-equal to or greater than the transverse width, with no clearly defined lateral wings, and a diamond or spade-like outline (e.g. *Dimetrodon* sp. MCZ 4443; *Ophiacodon mirus*, MCZ 294; *Edaphosaurus boanerges*, MCZ 4315; *Varanops brevirostris*, MCZ 1926), state (3), distinct lateral processes, where the transverse width is around double that of the anteroposterior length (e.g. *Oedaleops*, Sumida *et al.* 2014; *Archaeovenator*, KUVP 12483; *Ascendonanus*, Spindler *et al.* 2018; *Ophiacodon uniformis*, Romer and Price 1940 fig.21; *Petrolacosaurus*, Reisz 1981; *Prolacerta* and *Proterosuchus* (Ezcurra 2016 fig.38). For those taxa possessing distinct lateral wings there is a further subdivision in the presence or absence of an anterior process. This distinction is the subject of ch. 231 below. State (1) is scored only *Seymouria*, and as such is parsimony uninformative, but is maintained for information purposes.

Unambiguous: Diadectomorpha + Amniota (0→2). DELTRAN: *Dimetrodon* spp (2→1), *Edaphosaurus boanerges* (2→1), *Varanops brevirostris* (2→1). ACCTRAN: *Haptodus garnettensis* (1→2),Sphenacodontia + Edaphosauridae (2→1), *Varanops* + *Varanodon* + *Watongia* (2→1).

231. Interclavicle, if lateral processes or wings are present, an anterior process extends between the clavicles: absent, or reduced to a small nub/mild convexity (0); present (1); inapplicable, lateral wings are absent (-)

Modified from deBraga and Reisz (1995 c.115), Rieppel (1999 c.82), Müller (2004 c.55), Reisz *et al.* (2010 c.82), Ezcurra *et al.* (2014 c.81) Spindler *et al.* (2018 c.124)

State (1) of this character describes the anterior process that partially or fully separates the medial margin of the ventral plate of the clavicles in those taxa with mediolaterally broad lateral processes (ch.230 state 2). It is present in basal mycterosaurines (e.g. *Archaeovenator*, Reisz and Dilkes 2003; *Pyozia*, Anderson and Reisz 2004 and *Ascendonanus*, Spindler *et al.* 2018 fig.18B), araeoscelidians (e.g. *Petrolacosaurus*, Reisz 1981), *Protorothyris archeri* (MCZ 1532, Clark and Carroll 1973) and some captorhinids (e.g. *Thuringothyris*, Müller *et al.* 2006). It is absent (state 0) in all ankyramorph parareptiles, in which the mediolaterally broad lateral processes form a 'T-shaped' interclavicle with the posterior stem (Modesto *et al.* 2015 c.134 state 1). State (0) is also scored for caseasaurs (e.g. *Oedaleops*, Sumida *et al.* 2014; *Euromycter*, Sigogneau-Russell and Russell 1974), the varanodontine *Aerosaurus* (Langston and Reisz 1981) and the some neodiapsids (e.g. *Youngina* and *Prolacerta*, Gow 1975 and *Proterosuchus*, Ezcurra 2016).

Unambiguous: *Captorhinus* spp (1→0), Sauropsida (0→1), *Lanthanolania* + Archosauromorpha (1→0), *Mesosaurus* + Bolosaurinae + Procolophonoidea + *Macroleter* (1→0), *Paleothyris acadiana* (1→0). DELTRAN: *Aerosaurus* spp (1→0),*Ophiacodon* spp (0→1). ACCTRAN: *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (0→1), Mycterosaurinae + Varanodontinae + *Apsisaurus* (1→0).

232. Scapula, supraglenoid foramen: present (0); absent (1)

From Laurin and Reisz (1995 c.97), Reisz *et al.* (1998 c.29), Reisz and Dilkes (2003 c.29), Reisz and Laurin (2004 c.54), Maddin *et al.* (2006 c.59, 2008 c.84), Reisz *et al.* (2010 c.87), Fröbisch *et al.* (2011 c.112), Ezcurra *et al.* (2014 c.86), Benson (2012 c.179), Modesto *et al.* (2015 c.139), Ezcurra (2016 c.393 polarity reversed), Spindler *et al.* (2018 c.128)

The supraglenoid foramen is located on the posterolateral or posterior surface of the scapula, immediately dorsal to the glenoid. The absence of the supraglenoid foramen is hypothesised to be a derived condition that evolved independently in several lineages of early amniotes (Laurin and Reisz 1995). The foramen is absent in caseasaurs (e.g. *Oedaleops*, Sumida *et al.* 2014 and *Casea*, Williston 1911), diapsids (e.g. *Youngina*, BP/1/3859; *Prolacerta*, Gow 1975 and *Proterosuchus*, Ezcurra 2016), parareptiles (e.g. *Mesosaurus*, Modesto 2010 and *Procolophon*, BP/1/692) and mycterosaurines (e.g. *Archaeovenator*, Reisz and Dilkes 2003; *Heleosaurus*, Reisz and Modesto 2007, Botha-Brink and Modesto 2009 and *Mycterosaurus*, Berman and Reisz 1982). Pelletier (2014) stated that a supraglenoid foramen is present in the basal mycterosaurine *Pyozia*. However, the foramen is 'not evident' in the fragmented scapulocoracoid (Anderson and Reisz 2004:176). Spindler *et al.* (2018) suggested that the foramen is present in *Apsisaurus*. Close examination of the scapula of this taxon has determined that the foramen is absent (MCZ 1474). The foramen-like feature appearing in the illustration of Laurin (1991 fig.7D) in fact is an irregularly shaped discolouration of the bone surface. Consequently, the condition in *Apsisaurus* is scored as (1) herein. The supraglenoid foramen has been scored as absent in the varanodontine *Watongia* (Reisz and Laurin 2004 c.54), but I have not been able to confirm this in the examination of this taxon, and here I score *Watongia* as (?). The condition in other varanodontines is also uncertain. Campione and Reisz (2010 fig.10A) noted the presence of a supraglenoid foramen in *Varanops brevirostris*, which is absent in other scapulae assigned to this taxon (MCZ 1926). I therefore score *Varanops* as [0,1] for uncertainty. The supraglenoid foramen is present (state 0) in *Aerosaurus* (Langston and Reisz 1981).

Unambiguous: clade C (0→1), Caseasauria (0→1). DELTRAN: *Aerosaurus* spp (1→0). ACCTRAN: Varanodontinae (1→0).

233. Scapula, supraglenoid foramen, location: posterior to the apex of the supraglenoid buttress (0); located on or anterior to the apex of the buttress (1); inapplicable, supraglenoid foramen absent (-)

Modified from Benson (2012 c.180) modified from Reisz *et al.* (1992 c.82), Fröbisch *et al.* (2011 c.112) Spindler *et al.* (2018 c.129)

Character state (0) is present in out-group taxa (e.g. *Seymouria*, White 1939 fig.17A; *Tseajaia*, Moss 197 fig.8A). The supraglenoid foramen is located anterior to the apex of the glenoid buttress (state 1) in sphenacodontians (Romer and Price 1940, *Dimetrodon milleri* MCZ 1365, *Haptodus garnettensis* ROM 43605), 'protorothyridids' (*Paleothyris* MCZ 3485, Carroll 1969, *Protorothyris* MCZ 2148) araeoscelidians (Reisz 1981, Vaughn 1955) and varanodontines (Langston and Reisz 1981, Campione and Reisz 2010).

Unambiguous: clade A (0→1), Sphenacodontia (0→1).

234. Scapula, anterior margin: straight or slightly concave, at least dorsally (0); convex along entire length (1)

From deBraga and Reisz (1995 c.27), Reisz *et al.* (2010 c.86), Nesbitt (2011 c.217), Ezcurra *et al.* (2014 c.85), Spindler *et al.* (2018 c.131)

State (1) of this character was introduced by deBraga and Reisz (1995) to describe the broadly convex anterior margin of the scapula in araeoscelidian diapsids (e.g. *Petrolacosaurus*, Reisz 1981 and *Araeoscelis*, Vaughn 1955). State (1) is also convergently present in the eothyridid *Oedaleops* (Sumida *et al.* 2014 fig. 2.5b) and the parareptile *Mesosaurus* (Modesto 2010).

Unambiguous: *Mesosaurus tenuidens* (0→1), Araeoscelidia (0→1). DELTRAN: *Oedaleops campi* (0→1). ACCTRAN: Eothyrididae (0→1).

235. Scapula, scapulocoracoid notch on anterior margin on scapula/coracoid contact: absent (0); present (1)

From Laurin (1993 c.100), Fröbisch *et al.* (2011 c.76), Benson (2012 c.183), Spindler *et al.* (2018 c.132)

A notch is present on the anterior margin of the scapulocoracoid (state 1) in *Youngina* (Gow 1975), *Prolacerta* (BP/1/2675) and *Mesosaurus* (Modesto 2010). As noted by Benson (2012 c.183) it is also found in varanodontines, *Ophiacodon* and *Haptodus*.

Unambiguous: *Haptodus garnettensis* (0→1), clade D (0→1), Varanodontinae (0→1), *Proterosuchus* spp (1→0). DELTRAN:*Ophiacodon* spp (0→1). ACCTRAN: Ophiacodontidae (0→1).

236. Coracoids, number: one (0); two (1)

From Gauthier *et al.* (1988 c.148), Laurin and Reisz (1995 c.95), Maddin *et al.* (2008 c.85), Benson (2012 c.184), Spindler *et al.* (2018 c.133)

The stem-group amniotes *Seymouria* and diadectomorphs have a single coracoid (state 0)(White 1939, Moss 1972, Kennedy 2010). However, most early amniotes have instead two ossifications of the coracoid (state 1)(e.g. caseasaurs, Williston 1911; sphenacodontians, Romer and Price 1940; ophiacodontids, Watson 1914; edaphosaurids, Romer and Price 1940; the varanodontine *Varanops*, Campione and Reisz 2010; the 'protorothyridid' *Cephalerpeton*, Carroll and Baird 1972; the araeoscelidian diapsids *Petrolacosaurus* and *Araeoscelis*, Reisz 1981, Vaughn 1955; the captorhinid *Captorhinus aguti*, Fox and Bowman 1966 and the procolophonid *Procolophon*, deBraga 2003). In many taxa the anterior and posterior ossifications of the coracoid fuse in mature specimens and the suture between them is lost. For example, immature specimens of *Petrolacosaurus* show post-mortem separation of the anterior and posterior coracoids (Reisz 1981), although there are no sutures separating the coracoids in adult specimens of *Petrolacosaurus*. In some 'protorothyridids' there is no trace of a suture between the two coracoid elements (e.g. *Paleothyris*, Carroll 1969 and *Protorothyris*, Clark and Carroll 1973). The condition in mycterosaurines requires further clarification. The right scapulocoracoid of *Archaeovenator* (KUVP 12483) is fully exposed on the medial surface and, despite some mediolateral compression, is undamaged. There is no visible suture between the scapula and coracoid (Reisz and Dilkes 2003),

and neither does there appear to be any suture separating the anterior and posterior coracoid, making it impossible to determine confidently how many coracoids were present. Equally, in *Mycterosaurus* there is no evidence of a suture between the coracoid elements, although a small ridge probably traces the line of the suture between the scapula and anterior region of the coracoid (Berman and Reisz 1982). Consequently I score these taxa as (?). A single coracoid is present in neodiapsids (Carroll 1981, Smith and Evans 1996) and the parareptiles *Mesosaurus* (Modesto 2010) and *Milleretta* (Gow 1972)

Unambiguous: clade D (1→0), Amniota (0→1). DELTRAN: Procolophonoidea (0→1). ACCTRAN: Bolosauridae + Procolphonoidea + *Macroleter* (0→1).

237. Coracoid, triceps process: absent or small (0); large (1)

From Laurin (1991 H.5), Reisz *et al.* (1992 c.83), Berman *et al.* (1995 c.82), Reisz *et al.* (2010 c.88), Benson (2012 c.186), Ezcurra *et al.* (2010 c.87), Fröbisch *et al.* (2011 c.113), Spindler *et al.* (2018 c.134)

Unambiguous: Araeoscelidia (0→1), Sphenacodontia (0→1), *Protorothyris archeri* (0→1).

238. Sternum: not mineralised (0); mineralised (1)

From Laurin and Reisz (1995 c.100).

A sternum composed of calcified cartilage or bone is present in *Araeoscelis* (Vaughn 1955) and *Youngina* (Smith and Evans 1996).

Unambiguous: *Araeoscelis* spp (0→1). DELTRAN: *Youngina capensis* (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

239. Humerus, capitellum (radial condyle) and trochlea (ulnar condyle): strongly developed as distinct ball-shaped and saddle-shaped structures (0); poorly developed but distinct from the ectepicondyle and entepicondyle (1); indistinct from the ectepicondyle and entepicondyle (2)

From Ezcurra *et al.* (2014 c.198), Pritchard *et al.* (2015 c.156), Ezcurra (2016 c.428)

Almost all early amniotes possess a well-developed capitellum and trochlea (state 0) (e.g. diadectomorphs, Moss 1972; *Limnoscelis*, FMNH UC 676; caseasaurs, Sumida *et al.* 2014, *Casea broilii* FMNH UC 656; ophiacodontids, *Ophiacodon* uniformis MCZ 5935; sphenacodontians, *Dimetrodon* sp. MCZ 7074; edaphosaurids, *Edaphosaurus boanerges* MCZ 3417; captorhinids, Fox and Bowman 1966; 'protorothyridids', *Hylonomus* NHM R 4168, *Paleothyris* MCZ 3485 and araeoscelidian diapsids, Reisz 1981). Character states (1) is present in varanodontines (e.g. *Aerosaurus*, Langston and Reisz 1981 fig.2; *Varanops*, MCZ 1926), diapsids (e.g. *Youngina*, BP/1/3859, Currie 1980), *Erpetonyx* (Modesto *et al.* 2015) and *Procolophon* (BP/1/962, deBraga 2003). Character state (2) is present in archosauromorphs (e.g. *Prolacerta* and *Proterosuchus*, Ezcurra 2016) and *Mesosaurus* (Modesto 2010).

Unambiguous: *Mesosaurus tenuidens* (1→2), clade C (0→1). DELTRAN: Archosauromorpha (1→2), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (1→2), *Thuringothyris mahlendorffae* (0→1).

240. Humerus, ridge connecting deltopectoral crest to head: double, paired ridge enclosing proximolateral fossa, deltopectoral crest anteroposteriorly expanded and 'tuberous' (0); single, fossa is absent (1)

From Brinkman and Eberth (1983 c.1), Reisz *et al.* (1992 c.85), Berman *et al.* (1995 c.88) Benson (2012 c.192), Spindler *et al.* (2018 c.150)

Brinkman and Eberth (1983 fig.13) noted a distinctive double ridge, enclosing a fossa, connecting the distal tip of the deltopectoral crest to the femoral head in caseids and varanodontines. The double ridge is absent (state 1) in sphenacodontians, edaphosaurids and ophiacodontids. It is also absent in araeoscelidian diapsids (e.g. *Petrolacosaurus*, Reisz 1981 and *Araeoscelis*, Vaughn 1955).

Unambiguous: Araeoscelidia (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1).

241. Humerus, diaphysis (shaft): absent, distal and proximal heads merge and lack dis-

crete shaft (0); distinct shaft present (1)

From Laurin and Reisz (1995 c.104), Reisz *et al.* (2007 c.104), Tsuji *et al.* 2012 c.111)

In the current taxon list state (0) is found only in diadectamorphs (e.g. *Tseajaia*, Moss 1972; *Limnoscelis*, FMNH UC 676) and *Seymouria* (FMNH C.145).

Unambiguous: Amniota (0→1).

242. Humerus, ratio of width of distal head to humerus length: equal to or greater than 0.40 (0); less than 0.40 (1)

Modified from Laurin (1991 D.4), Reisz *et al.* (2010 c.89), Nesbitt (2011 c.235), Ezcurra *et al.* (2014 c.88), Spindler *et al.* (2018 c.155)

State (1) describes the slender distal humerus that occurs in mycterosaurines (e.g. *Apsisaurus*, Laurin 1991; *Heleosaurus*, Botha-Brink and Modesto 2009; *Ascendonanus*, Spindler *et al.* 2018), 'protorothyridids' (e.g., *Hylonomus*, Carroll 1964; *Paleothyris*, Carroll 1969), araeoscelidians (e.g. *Petrolacosaurus*, Reisz 1981; *Araeoscelis*, Vaughn 1955) and diapsids (e.g. *Youngina*, BP/1/3859; *Claudiosaurus*, MNHN 1978-6-1 and -2). It is also found in *Mesosaurus* (Modesto 2010). The state threshold for this character was originally set at 30% of the humeral shaft e.g. Laurin (1991), Reisz *et al.* (2010), Ezcurra *et al.* (2014). Nesbitt (2011) revised the ratio measurement to the humeral length/distal width rather than the more subjective shaft length, but maintained the 30% threshold. Spindler *et al.* (2018) maintained this definition, but increased the threshold to 50%. I find that for the current taxon list a threshold of 40% defines a phylogenetically consistent morphology in some groups of early amniotes.

Ch. 242: Unambiguous: clade A (0→1), Varanodontinae (1→0). DELTRAN: *Milleretta rubidgei* (1→0), Bolosauridae + *Macroleter* + Procolophonoidea (1→0). ACCTRAN: *Mesosaurus tenuidens* (0→1), Parareptilia (1→0).

243. Humerus, entepicondylar foramen: present (0); absent (1)

From Gauthier *et al.* (1988 c.164), Laurin (1991 F.6), Laurin and Reisz (1995 c.103), Müller (2004 c.65), Reisz *et al.* (2010 c.91, Ezcurra *et al.* (2014 c.90), Pritchard *et al.* (2015 c.153), Modesto *et al.* (2015 c.146), Ezcurra (2016 c.426)

The absence of the entepicondylar foramen (state 1) is a synapomorphy of Archosauromorpha (Laurin 1991), and is scored as state (1) in *Prolacerta* (Gow 1975) and *Proterosuchus* (Ezcurra *et al.* 2013). The entepicondylar foramen is also absent in owenettid parareptiles (e.g. *Owenetta* and *Barasaurus*, Reisz and Scott 2002). Laurin and Reisz (1995) considered the derived state an autapomorphy of *Mesosaurus*, but the presence of an entepicondylar foramen in *Mesosaurus* is clearly shown in Modesto (2010 figs.3, 5, 10).

Unambiguous: *Owenetta kitchingorum* (0→1). DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

244. Humerus, entepicondyle (ulnar epicondyle), transverse width: moderate makes up just less than half of transverse width of distal expansion (0); reduced or confluent with the ectepicondyle (1); enlarged, makes up more than 2/3 of the distal transverse width (2)

Modified from Laurin (1991 F.6), Berman *et al.* (1995 c.86), Reisz *et al.* (2010 c.90), Benson (2012 c.199), Ezcurra *et al.* (2014 c.89), Ezcurra (2016 c.245)

Unambiguous: clade C (0→1), Varanodontinae (1→0). DELTRAN: *Anthracodromeus longipes* (0→1),*Ophiacodon* spp (0→2), *Procolophon trigoniceps* (1→2). ACCTRAN: *Anthracodromeus* + *Hylonomus* (0→1), *Varanosaurus* + *Ophiacodon* (0→2), Bolosauridae + Procolphonoidea + *Macroleter* (1→2).

245. Humerus, ectepicondylar (radial epicondylar) foramen: absent, ectepicondylar groove not enclosed and supinator process proximodistally short (0); present (1); long supinator process, but epicondylar foramen not enclosed (2); supinator process very low or absent (3)

Modified from Benson (2012 c.198) modified from Laurin (1993 c.103), Berman *et al.* (1995 c.87), Sidor and Hopson (1998 c.142, 143), Maddin *et al.* (2008 c.87), Fröbisch *et al.* (2011 c.79), Mac-

Dougall and Reisz (2014 c.145), Modesto *et al.* (2015 c.145)

In most early amniotes the supinator process is proximodistally short, and forms a small, unclosed groove or notch on the posterior surface of the humerus (state 0). Basal caseids possess a long supinator process, which does not fully enclose the ectepicondyle, but instead forms an elongate open groove (state 2) (Olsen 1968). The foramen is virtually absent and the supinator process is not differentiated from the ectepicondyle to any marked degree (state 3) in 'protorothyridids' (e.g. *Hylonomus*, Carroll 1964; *Protorothyris*, Clark and Carroll 1973) and captorhinids (e.g. *Protocaptorhinus*, MCZ 1473). Several terminal taxa have a fully enclosed ectepicondylar foramen (state 1)(e.g. *Edaphosaurus*, MCZ 3417; *Ascendonanus*, Spindler *et al.* 2018; *Heleosaurus*, Botha-Brink and Modesto 2009; *Araeoscelis*, Vaughn 1955; *Acerosodontosaurus*, Bickelmann *et al.* 2009 and some basal parareptiles, Modesto 2010, Modesto *et al.* 2015).

Unambiguous: *Araeoscelis* spp (0→1), *Ascendonanus nestleri* (0→1), *Edaphosaurus boanerges* (0→1), *Hylonomus lyelli* (0→3), Parareptilia (0→1), Captorhinidae (0→3), Caseidae (0→2), *Protorothyris archeri* (0→3). DELTRAN: *Acerosodontosaurus piveteaui* (0→1), *Eudibamus cursoris* (1→0), *Heleosaurus scholtzi* (0→1), *Procolophon trigoniceps* (1→0). ACCTRAN: *Acerosodontosaurus piveteaui* (0→1),*Macroleter poezicus* (0→1), *Heleosaurus* + *Mesenosaurus* + *Elliotsmithia* (0→1), Bolosauridae + *Macroleter* + Procolophonoidea (1→0).

246. Humerus, supinator process: transversely broad and extends laterally or anterolaterally (0); transversely narrow and almost confluent with humeral shaft (1); inapplicable, supinator process is low or absent (-)

Modified from Laurin and Reisz (1995 c.101), deBraga and Rieppel (1997 c.126), Reisz *et al.* (2007 c.101), Schoch and Sues (2015 c.125), Modesto *et al.* (2015 c.143), Modesto *et al.* (2018 c.72 in part)

The supinator process is parallel or confluent with the humeral shaft (state 1) in *Heleosaurus* (Botha-Brink and Modesto 2009), *Apsisaurus* (Laurin 1991), araeoscelidians (Reisz 1981, Vaughn 1955), diapsids (Gow 1975, *Claudiosaurus* MNHN 1978-6-1 and -2) and parareptiles (Modesto *et al.* 2015, Reisz *et al.* 2007).

Unambiguous: clade B (0→1), Varanodontinae (1→0).

247. Radius-humerus, length ratio: less than 0.68 (0); 0.68 to 0.82 (1); greater than 0.82 (2)

From Ezcurra *et al.* (2014 c.92) modified from Laurin (1991 A.6, H.7). Reisz *et al.* (2010 c.93), Nesbitt (2011 c.241), Ezcurra (2016 c.435), Spindler *et al.* (2018 c. 158)

Unambiguous: Araeoscelidia (0→2), *Tseajaia campi* (0→1), *Varanodon agilis* (1→0), *Varanops brevirostris* (1→2). DELTRAN: *Erpetonyx arsenaultorum* (0→1), *Heleosaurus scholtzi* (1→2), *Varanosaurus* + *Ophiacodon* (0→1), Sphenacodontia (0→1), Mycterosaurinae + Varanodontinae + *Apsisaurus* (0→1), Archosauromorpha (0→2), *Owenetta kitchingorum* (0→1), *Thuringothyris mahlendorffae* (0→2), *Youngina capensis* (0→1). ACCTRAN: Edaphosauridae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), Mycterosaurinae (1→2), Varanopidae except *Ascendonanus* (0→1), *Lanthanolania* + Archosauromorpha (1→2), *Lanthanolania* + Archosauromorpha (0→1), Bolosauridae + Procolphonoidea + *Macroleter* (0→1), *Procolophon trigoniceps* (1→0), *Thuringothyris mahlendorffae* (0→2).

248. Radius, length: shorter than ulna (0); longer than or approximately of the same length as the ulna (1)

Ezcurra *et al.* (2014 c.202) modified from Rieppel (1999 c.98), Müller (2004 c.66), Ezcurra (2016 c.436)

The proximodistal measurement of the ulna does not include the olecranon process.

Unambiguous: *Haptodus garnettensis* (1→0), clade B (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Watongia meieri* (1→0). DELTRAN: *Milleretta rubidgei* (1→0), *Procolophon trigoniceps* (1→0). ACCTRAN: *Milleretta* + *Colobomycter* + *Acleistorhinus* (1→0), Bolosauridae + *Macroleter* + Procolophonoidea (1→0).

249. Radius, shape: straight (0); distinctly sigmoidal in lateral view (1)

From Laurin (1991 I.3), Reisz *et al.* (2010 c.94), Ezcurra *et al.* (2010 c.93), Ezcurra (2016 c.437)

The radius is sigmoidal or 'twisted' in lateral view in *Youngina* (Gow 1975) and *Acerosodontosaurus* (Bickelmann *et al.* 2009).

DELTRAN: *Acerosodontosaurus piveteaui* (0→1), *Euromycter rutena* (0→1), *Youngina capensis* (0→1). ACCTRAN: *Euromycter* + *Ennatosaurus* (0→1), *Lanthanolania* + Archosauromorpha (1→0), Neodiapsida (0→1).

250. Ulna, olecranon process: absent or very low (0); prominent but lower than its transverse depth at base (1); strongly developed, being higher than its transverse depth at base (2)

Modified from Ezcurra *et al.* (2014 c.94), Laurin (1991 C.2), Laurin and Reisz (1995 c.105), deBraga and Rieppel (1997 c.130) modified from Müller (2004 c.147), Reisz *et al.* (2010 c.95), Modesto *et al.* (2015 c.148), Pritchard *et al.* (2015 c.157 in part), Ezcurra (2016 c. 430)

Unambiguous: *Haptodus garnettensis* (2→1), clade C (2→0), Amniota (1→2). DELTRAN: *Aerosaurus* spp (0→1), *Casea broilii* (2→1), *Ennatosaurus tecton* (2→1),*Macroleter poezicus* (0→1), *Mesenosaurus romeri* (0→1), *Procolophon trigoniceps* (0→1), *Thuringothyris mahlendorffae* (2→1), *Varanops brevirostris* (0→1). ACCTRAN: *Euromycter rutena* (1→2), *Heleosaurus scholtzi* (1→0), Caseidae (2→1), *Varanodon* + *Watongia* (1→0), Mycterosaurinae + Varanodontinae (0→1), Bolosauridae + *Macroleter* + Procolophonoidea (0→1), *Owenetta kitchingorum* (1→0), *Thuringothyris mahlendorffae* (2→1).

251. Carpus, width to length ratio of radiale: subequal or less than 1.0 (0); greater than 1.0 (1)

From Reisz and Laurin (2004 c.56), Maddin *et al.* (2006 c.55), Benson (2012 c.201)

DELTRAN: *Casea broilii* (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (1→0). ACCTRAN: *Euromycter* + *Ennatosaurus* (0→1), Synapsida (1→0).

252. Carpus, ulnare proximodistal proportions: longer than wide, width less than 0.7 times length (0); short, width equal to or greater than 0.7 times length (1)

From Benson (2012 c.204) modified from Bickelmann *et al.* (2009 c.188)

Unambiguous: *Erpetonyx arsenaultorum* (1→0), *Euromycter rutena* (1→0). DELTRAN: Araeoscelidia (1→0), Sphenacodontia (1→0),*Ophiacodon* spp (1→0), *Paleothyris acadiana* (1→0). ACCTRAN: clade C (0→1), clade A (1→0), Edaphosauridae (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (1→0).

253. Carpus, transverse width across carpus at widest point (excluding pisiform): subequal to or greater than 4th metacarpal (0); less than 4th metacarpal (1)

Modified from Laurin and Reisz (1995 c. 114 in part)

Heaton and Reisz (1986) noted that the presence of a broad carpus/tarsus and short metacarpals/metatarsals (state 0) is a primitive condition in amniotes, and that the maximum transverse width of the carpus/tarsus is less than the length of the longest metacarpal/metatarsal in more derived taxa (state 1). In the current taxon list, state (1) is present in mycterosaurines (e.g. *Ascendonanus*, Spindler *et al.* 2018 and *Heleosaurus*, Botha-Brink and Modesto 2009), *Paleothyris* (Heaton and Reisz 1986) and araeoscelidians (Reisz 1981, Vaughn 1955), *Youngina* (Smith and Evans 1996) and *Prolacerta* (Gow 1975).

Unambiguous: *Erpetonyx arsenaultorum* (1→0), *Euromycter rutena* (1→0). DELTRAN: Araeoscelidia (1→0), Sphenacodontia (1→0),*Ophiacodon* spp (1→0), *Paleothyris acadiana* (1→0). ACCTRAN: clade C (0→1), clade A (1→0), Edaphosauridae (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (1→0).

254. Carpus, pisiform size: subequal to or smaller than the 4th distal carpal (0); conspicuously larger than the 4th distal carpal (1)

Modified from Spindler *et al.* (2018 c.163)

Spindler *et al.* (2018 online resource 3 c.163) noted that a large pisiform is characteristic of 'pelycosaur'-grade synapsids and captorhinids, although did not suggest a comparative method for defining its size. Herein I compare the size of the pisiform to the 4th distal carpal of the manus. I find that the pisiform

is enlarged (state 1) in those early synapsids where both elements are preserved (e.g. *Ophiacodon* and *Dimetrodon*, Romer and Price 1940; *Edaphosaurus*, MCZ 4320; *Varanops*, Williston 1911 plate VIII, Olson 1965 fig.4E, *Watongia*, Reisz and Laurin 2005 fig. 5B) and in the diapsid *Claudiosaurus* (Carroll 1981 fig.19D and MNHN 1978-6-1). However, it is subequal to the 4th distal carpal (State 0) in *Casea* (Williston 1911). In *Captorhinus aguti* the pisiform is also subequal in size to the 4th distal carpal (Holmes 1977 fig. 10A and Fig. 11E).

Unambiguous: *Claudiosaurus germaini* (0→1), *Limnoscelis plaudis* (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1). DELTRAN: *Varanops* + *Varanodon* + *Watongia* (0→1). ACCTRAN: Varanopidae (0→1).

255. Metacarpus, length of McIV: less than 45% of radius length (0); greater than 45% (1)

From Spindler *et al.* (2018 c.165) modified from Maddin *et al.* (2008 c. 57), Campione and Reisz (2010 c.56), Benson (2012 c.205), Reisz and Fröbisch (2014 c.93)

The manus is proximodistally elongate compared to the zeugopodium (state 1) in several terminal taxa (e.g. varanodontines, Olson 1965, Williston 1911, Reisz and Laurin 2004; *Ascendonanus*, Spindler *et al.* 2018; *Paleothyris*, Carroll 1969; *Youngina*, Gow 1975 and *Erpetonyx*, ROM 55402).

Unambiguous: *Erpetonyx arsenaultorum* (0→1), *Youngina capensis* (0→1). DELTRAN: *Ascendonanus nestleri* (0→1), Varanodontinae (0→1), *Paleothyris acadiana* (0→1), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: Protorothyrididae (0→1), Mycterosaurinae (1→0), Varanopidae (0→1), *Thuringothyris mahlendorffae* (0→1).

256. Metacarpus, McV to McIV length ratio: greater than 0.65 (0); less than 0.65 (1)

Modified from deBraga and Rieppel (1997 c.132), Reisz and Laurin (2004 c.57), Maddin *et al.* (2006 c.56), Reisz *et al.* (2009 c.68), Benson (2012 c.207)

Unambiguous: *Watongia meieri* (1→0). DELTRAN: Varanopidae (0→1), *Petrolacosaurus kansensis* (0→1), *Thuringothyris mahlendorffae* (0→1), *Youngina capensis* (0→1). ACCTRAN: clade D (1→0),

Captorhinidae except *Thuringothyris* (1→0), Sauropsida (0→1), *Lanthanolania* + Archosauromorpha (0→1).

257. Manus, ungual (terminal) phalanges, height to width ratio: low, ratio <1.1 and blood vessel grooves may be visible on the dorsolateral surface of the phalanx (0); high, ratio >1.5, strongly recurved and blood vessel grooves are located on the lateral surface of the phalanx (1)

Modified from Maddin *et al.* (2006 c.58), Maddin *et al.* (2008 c.95), Reisz *et al.* (2009 c.69), Benson (2010 c.212)

Unambiguous: *Ascendonanus nestleri* (0→1),Sphenacodontia + Edaphosauridae (0→1). DELTRAN: *Procolophon trigoniceps* (0→1). ACCTRAN: Bolosauridae + Procolphonoidea + *Macroleter* (0→1).

258. Manus, ungual (terminal) phalanges, shape: hoof-like or bluntly spade-shaped distally with no ventral curvature (0); taper distally to a point, and curve ventrally (1)

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A keratinous claw, which sheaths the ungual (terminal) phalanx of the manus, is considered to be a feature unique to amniotes (Maddin and Reisz 2007). In all amniote taxa included in the current study where the manual unguals are known, with the exception of *Mesosaurus*, the ungual tapers to a point distally with a distinct ventral curvature (state 1). In *Mesosaurus*, the manual unguals are bluntly spade-shaped in dorsal view (state 0)(Modesto 2010). In out-group taxa such as *Seymouria* (White 1939) and diadectomorphs (e.g. *Tseajaia*, Moss 1972 and *Limnoscelis*, Kennedy 2010) the ungual phalanx is hoof-like (state 0), although a keratinous sheaf may have been present in life based on a series of pits and grooves on the distal surface of the phalanx in *Diadectes absitus* (Maddin and Reisz 2007). The stem-amniote *Gephyrostegus* is shown by Carroll (1970 fig.2) to possess small tapering manual unguals, however, postcranial remains attributed to this taxon are possibly related to other taxa (Clack 2012) and *Gephyrostegus* is scored as (?) herein.

Unambiguous: *Mesosaurus tenuidens* (1→0), Amniota (0→1).

259. Pelvic girdle, acetabulum: elongate, sub-oval and shallow (0); subcircular and deep (1)

Modified from Laurin (1991 B.7) Reisz *et al.* (2010 c.100), Benson (2012 c.214), Ezcurra *et al.* (2014 c.99), Ezcurra 2016 (c.469 in part)

Unambiguous: clade D (0→1), *Youngina capensis* (1→0).

260. Pubis, anteroposterior length relative to acetabulum:>1.5 times (0); 1.0-1.5 times (1)

From Benson (2012 c. 218), modified from Sidor and Hopson (1998 c.161), Ezcurra (2016 c.472).

In diadectomorphs (e.g. *Tseajaia*, Moss 1972 and *Limnoscelis*, Romer 1946, Kennedy 2010) the pubis is short anteroposteriorly when compared to the length of the acetabulum (state 1). This condition is also present in *Captorhinus aguti* (fox and Bowman 1966), and some diapsids (e.g. *Petrolacosaurus*, Reisz 1981 fig.18; *Youngina*, BP/1/3859; *Acerosodontosaurus*, Currie 1980 and *Prolacerta*, Gow 1975). In the basal mycterosaurine *Archaeovenator* the pubis is unusually short anteroposteriorly compared to basal synapsids (MCZ 12483, Reisz and Dilkes 2003), and is scored as state (1) herein.

Unambiguous: Diadectomorpha (0→1), Neodiapsida (0→1), *Proterosuchus* spp (1→0). DELTRAN: *Archaeovenator hamiltonensis* (0→1), *Captorhinus* spp (0→1), *Petrolacosaurus kansensis* (0→1). ACCTRAN: Captorhinidae (0→1), *Archaeovenator* + *Orovenator* (0→1), *Petrolacosaurus kansensis* (0→1).

261. Pubis, ventrolateral surface of pubic apron: flat or convex, pubes extends ventromedially (0); strongly concave, pubes extend approximately medially (1).

From Benson (2012 c.221)

In the varanodontine *Varanops*, the ventral region of the pubic apron inclined medially, forming a strongly concave region on the ventrolateral surface (MCZ 1926, Campione and Reisz 2010 fig.13). The same condition can be found in sphenacodontians (e.g. *Dimetrodon*, MCZ 1365, Romer and Price 1940 plate 28), some mycterosaurines (e.g. *Heleosaurus*, *Mycterosaurus*) and araeoscelidian diapsids

(e.g. *Petrolacosaurus*, Reisz 1981 fig.18 and *Araeoscelis*, Vaughn 1955 fig.11)

Unambiguous: *Mesenosaurus romeri* (1→0). DELTRAN: *Dimetrodon* spp (0→1), Araeoscelidia (0→1), Mycterosaurinae + Varanodontinae (0→1). ACCTRAN: clade D (1→0), clade B (0→1), Sphenacodontia (0→1).

262. Pubis, pubic tubercle anteroventral to acetabulum: absent (0); present, projects laterally (1); present, projects dorsally (2); highly striated region bounded by a longitudinal crest dorsally (3)

Modified from Benson (2012 c.219) modified from Reisz *et al.* (1992 c.90), Berman *et al.* (1995 c.91), Maddin *et al.* (2008 c.100), Spindler *et al.* (2018 c.139)

Character state (3) of Benson (2012 c.219) is omitted since the derived caseids scored for this state are not included in the current taxon list. *Edaphosaurus* is scored as state (3) herein, i.e. state (4) in Benson (2012), although this is parsimony uninformative, and is included for information purposes only.

Unambiguous: *Ascendonanus nestleri* (1→0), *Mesosaurus tenuidens* (1→0),*Ophiacodon* spp (2→0). DELTRAN: *Captorhinus* spp (1→2), *Casea broilii* (1→2), *Edaphosaurus boanerges* (1→3), *Mycterosaurus longiceps* (1→2), *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (1→2). ACCTRAN: Captorhinidae (1→2), Caseidae (1→2), Ophiacodontidae (1→2), Edaphosauridae (1→3), Mycterosaurinae (1→2).

263. Ilium, medial surface: weakly concave or flat (0); anteroventrally oriented ridge contacts pubic articulation (1)

From Benson (2012 c.215).

In *Limnoscelis*, ophiacodontids (e.g. *Varanosaurus*, MCZ 1353, Benson 2012 appendix 1 fig.A9B), *Varanops*, (Benson 2012 appendix 1 fig.A9D), *Captorhinus aguti* (Fox and Bowman fig.32), some 'protorothyridids' (e.g. *Hylonomus*, Carroll 1964 and *Paleothyris*, MCZ 3485, Carroll 1969) and *Petrolacosaurus* (Reisz 1981 fig.18) a ridge on the medial surface of the ilium extends anteroventrally to the suture with the pubic plate.

Unambiguous: Diadectomorpha + Amniota (0→1),Sphenacodontia + Edaphosauridae (1→0). DELTRAN: *Araeoscelis* spp (1→0), *Casea broilii* (1→0), clade C (1→0), *Varanops brevirostris* (0→1). ACCTRAN: clade B (1→0), Caseidae (1→0), Varanodontinae (0→1), *Petrolacosaurus kansensis* (0→1).

264. Ilium, dorsal process morphology: long, tapering posterodorsal blade, extending beyond the posterior edge of iliac body, anterodorsal blade small or absent (0); marked anterodorsal expansion present, dorsal process tall and plate-like (1); dorsal expansion directly above acetabulum, short posteriorly, not extending beyond posterior edge of iliac body (2)

Modified from Benson (2012 c.216) modified from Reisz *et al.* (1992 c.88, 89), Laurin (1993 c.107), Modesto (1994 c.34), Laurin and Reisz (1995 c.108), Berman *et al.* (1995 c.90), Maddin *et al.* (2008 c.97), Fröbisch *et al.* (2011 c.82), Modesto *et al.* (2015 c.152), Spindler *et al.* 2018 c.135)

Most terminal taxa, where the ilium is known, share state (0). Caseasaurs (Sumida *et al.* 2014, Olson 1968, FMNH UC 656), sphenacodontians (Romer and Price 1940, MCZ 1114) and edaphosaurids (Romer and Price 1940) share a posterodorsally directed plate-like ilium with an anterodorsal projection (state 1). In some parareptiles the ilium has a short, dorsally orientated process with limited posterior or anterior projection (state 2) (e.g. *Procolophon*, deBraga 2003; *Milleretta*, Gow 1972).

Unambiguous: *Procolophon trigoniceps* (0→2). DELTRAN: *Milleretta rubidgei* (0→2), Caseasauria (0→1),Sphenacodontia + Edaphosauridae (0→1). ACCTRAN: *Milleretta* + *Colobomycter* + *Acleistorhinus* (0→2), Ophiacodontidae (1→0), Synapsida (0→1).

265. Ilium, mediolateral expansion on dorsal surface: absent, ilium is plate-like with no mediolateral expansion along the dorsal surface (0); present, and forms a trough or well-defined fossa (1); present, and forms a shelf with no discernable fossa (2)

Modified from Reisz *et al.* (1992 c.87), Laurin (1993 c.106), Laurin and Reisz (1995 c.107), Berman *et al.* (1995 c.89), Maddin *et al.* (2008 c.98), Fröbisch *et al.* (2011 c.81), Benson (2012 c.217), Modesto *et al.* (2015 c.151)

Many early amniotes possessed ilia with mediolaterally thin, plate-like dorsal margins (e.g. *Seymouria*, caseasaurs, sphenacodontians, edaphosaurids, *Ascendonanus*, *Varanops*, *Mesosaurus* and several neodiapsids. State (1), in which the mediolaterally expanded dorsal surface of the ilium forms a double ridge and longitudinal fossa, is present in *Limnoscelis* (Romer 1946), ophiacodontids (Romer and Price 1940) and *Petrolacosaurus* (Reisz 1981). Other taxa possessed a flat shelf along the dorsal surface of the ilium, but with no fossa (e.g. *Tseajaia*, Moss 1972; *Aerosaurus*, Langston and Reisz 1981; *Archaeovenator*, Reisz and Dilkes 2003; *Paleothyris*, Carroll 1969, MCZ 3481, 3485; *Captorhinus aguti*, Holmes 2003 and *Araeoscelis*, Reisz 1981, Vaughn 1955). Modesto *et al.* (2015) scored for state (2) in the bolosaurid parareptile *Eudibamus*. A mediolateral expansion (state 2) is also present on the dorsal surface of the ilium in *Erpetonyx* (ROM 55402).

Unambiguous: *Limnoscelis plaudis* (0→1). DELTRAN: *Hylonomus lyelli* (2→0), *Mesosaurus tenuidens* (2→0), Sauropsida (0→2), *Varanosaurus* + *Ophiacodon* (0→1), Neodiapsida (2→0), Procolophonoidea (2→0), *Petrolacosaurus kansensis* (2→1), *Tseajaia campi* (0→2), *Varanops brevirostris* (2→0). ACCTRAN: clade D (2→0), *Anthracodromeus* + *Hylonomus* (2→0), Diadectomorpha + Amniota (0→2), Ophiacodontidae (0→1), Synapsida (2→0), *Varanops* + *Varanodon* + *Watongia* (2→0), *Macroleter* + Procolophonoidea (2→0), Bolosauridae + Procolphonoidea + *Macroleter* (0→2), *Petrolacosaurus kansensis* (2→1).

266. Ischium, shape: slender, tapering posteriorly (0); expanded posterodorsally (1)

Reisz *et al.* (1992 c.91), Fröbisch *et al.* (2011 c.116), Benson (2012 c.222)

Unambiguous:Sphenacodontia + Edaphosauridae (0→1).

267. Hindlimb-trunk, length ratio: hindlimb much shorter than trunk (0); hindlimb not less than 90% of the anteroposterior length of the trunk or longer (1)

Modified from Reisz *et al.* (2010 c.101), Ezcurra *et al.* (2014 c.100), Spindler *et al.* (2018 c.143)

For clarity, I define the trunk as that part of the torso between the fore and hindlimbs, represented by the anteroposterior length of the dorsal vertebral series. *Araeoscelis* (Vaughn 1955, MCZ 4380) and neodiapsids (e.g. *Claudiosaurus*, MNHN 1978-6-1 and *Youngina*, Smith and Evans 1996 fig.4),

some mycterosaurines (e.g. *Mycterosaurus*) and varanodontines (e.g. *Aerosaurus* and *Varanops*) possessed relatively long hindlimbs (state 1). The parareptile *Eudibamus* possessed an unusually elongate hindlimb, suggesting facultative bipedalism (Berman *et al.* 2000).

DELTRAN: *Eudibamus cursoris* (0→1), Araeoscelidia (0→1), Mycterosaurinae + Varanodontinae (0→1), Neodiapsida (0→1). ACCTRAN: *Ascendonanus nestleri* (1→0), Parareptilia (1→0), clade B (0→1), *Eudibamus* + *Belebey* (0→1).

268. Femur, distal articular surface: uneven, posterior (fibular) condyle projecting distinctly beyond the anterior (tibial) condyle (0); both condyles extend distally to approximately at same level (1)

Modified from Gauthier *et al.* (1988 c.187), Laurin (1991 B.8), Müller (2004 c.72), Reisz *et al.* (2010 c.102), Fröbisch *et al.* (2011 c.88), Benson (2012 c.232 with states (1) and (2) combined), Ezcurra *et al.* (2014 c.101), Spindler *et al.* (2018 c.169)

Eothyridids and *Eocasea* possess state (1) (Brocklehurst *et al.* 2016, Sumida *et al.* 2014), as do some diapsids (e.g. *Acerosodontosaurus*, Currie 1980; *Claudiosaurus*, MNHN 1978-6-1; *Proterosuchus*, Ezcurra 2016) and some parareptiles (e.g. *Mesosaurus*, Modesto 2010 and *Milleretta*, Gow 1972). *Prolacerta* (Ezcurra 2016) and *Erpetonyx* (ROM 55402) are scored as state (0). In sphenacodontians, edaphosaurids, ophiacodontids, mycterosaurines and varanodontines the fibular condyle extends beyond the tibial condyle (state 0), except in the varanodontine *Aerosaurus* (Laurin 1991), which is scored as state (1).

Unambiguous: *Apsisaurus witteri* (0→1), clade D (0→1), Eothyrididae (0→1), *Prolacerta broomi* (1→0). DELTRAN: *Erpetonyx arsenaultorum* (1→0), *Procolophon trigoniceps* (1→0). ACCTRAN: *Eudibamus* + *Belebey* (0→1), Bolosauridae + Procolphonoidea + *Macroleter* (1→0).

269. Femur, length to humerus ratio: greater than or equal to 1.2 (0); less than 1.2 (1)

Modified from Laurin (1991 C.3), Reisz *et al.* (2010 c.104), Nesbitt (2011 c.231), Ezcurra *et al.* (2014 c.103), Ezcurra (2016 c.489 in part), Spindler *et al.* (2018 c.145)

The femur is longer than the humerus by at least 20% in several terminal taxa; mycterosaurines (e.g. *Apsisaurus*, Laurin 1991), varanodontines (e.g. *Varanops*, MCZ 1926), diapsids (e.g. *Youngina*, Smith and Evans 1996 and *Prolacerta*, Gow 1975), and parareptiles (e.g. *Eudibamus*, Berman *et al.* 2000) and *Milleretta*, Gow 1972). In *Ophiacodon* the condition is polymorphic (Romer and Price 1940 table 5).

DELTRAN: *Apsisaurus witteri* (0→1), *Eudibamus cursoris* (0→1), *Milleretta rubidgei* (0→1), *Lanthanolania* + Archosauromorpha (0→1), *Owenetta kitchingorum* (0→1), *Thuringothyris mahlendorffae* (0→1), *Varanops brevirostris* (0→1). ACCTRAN: *Aerosaurus* spp (1→0), *Ascendonanus nestleri* (1→0), *Erpetonyx arsenaultorum* (1→0), clade C (0→1), *Procolophon trigoniceps* (1→0), *Thuringothyris mahlendorffae* (0→1).

270. Femur, proportions: short and broad, maximum length less than three times distal width (0); long and slender, maximum length more than three times distal width (1).

From Reisz *et al.* (1998 c.21) modified from Reisz *et al.* (1992 c.84), Laurin and Reisz (1995 c.113) Maddin *et al.* (2006 c.60), Reisz *et al.* (2007 c.113), Reisz *et al.* (2009 c.66), Reisz *et al.* (2010 c.103), Benson (2012 c.224), Ezcurra *et al.* (2014 c.102), Modesto *et al.* (2015 c.157), Spindler *et al.* (2018 c.167)

Character state (1), in respect to the current taxon list, is present in all mycterosaurines (e.g. *Archaeovenator*, KUVP 12483 and *Apsisaurus*, Laurin 1991), diapsids (e.g. *Petrolacosaurus*, Reisz 1981 and *Youngina*, Gow 1975), parareptiles (e.g. *Mesosaurus*, Modesto 2010 and *Erpetonyx*, ROM 55402), and the 'protorothyridid' *Paleothyris* (MCZ 3490). It is also found in sphenacodontids, (e.g. *Secodontosaurus*, MCZ 5355, 8677) and is polymorphic in *Dimetrodon* spp. (Romer and Price 1940 table 5).

Unambiguous: clade A (0→1), Varanodontinae (1→0). DELTRAN: *Secodontosaurus obtusidens* (0→1). ACCTRAN: Sphenacodontidae (0→1).

271. Femur, 4th trochanter: present as a raised ridge on the ventral surface of the femoral shaft (0); absent (1)

From Gauthier *et al.* (1988 c.193) modified from Nesbitt (2011 c.315, 316 in part), Benson (2012

c.228), Ezcurra (2016 c.504 in part).

In early amniotes the internal trochanter of the femur, a conspicuous raised ridge located on the margin of the proximal intertrochanteric fossa, extends distally as a low ridge on the ventral surface of the femur. Close to the distal margin of the intertrochanteric fossa this ridge may increase in height and form an area for the insertion of the coccygeofemoralis called the 4th trochanter (Romer 1956). This series of ridges is often referred to as the ventral ridge system of the femur, i.e. the internal and 4th trochanters (Gauthier *et al.* 1988, Benson 2012 c.228). The 4th trochanter is present (state 0) in many early amniotes, and can vary in morphology. It may form a low, angular ridge originating at the posterior margin of the intertrochanteric fossa as in *Ophiacodon* (Romer and Price 1940), or a prominent raised rugose area originating from the anterior margin of the intertrochanteric fossa as in sphenacodontians, edaphosaurids and caseasaurs (Romer and Price 1940, Laurin 1993, Sumida *et al.* 2010, Brocklehurst *et al.* 2016). A 4th trochanter is present in diadectomorphs (e.g. *Tseajaia*, Moss 1972 and *Limnoscelis*, Romer 1946) and the captorhinid *Captorhinus aguti* (Holmes 2003). In the varanodontine *Varanops*, the 4th trochanter is also present as a low but distinctive raised ridge of bone close to the distal anterior margin of the intertrochanteric fossa (MCZ 1926). In other taxa, the 4th trochanter is absent (state 1)(e.g. *Archaeovenator*, Reisz and Dilkes 2003; *Apsisaurus*, Laurin 1991; *Heleosaurus* Botha-Brink and Modesto 2009, *Mycterosaurus* Berman and Reisz 1982), *Paleothyris* (MCZ 3490), araeoscelidians (Reisz 1981, Vaughn 1955), neodiapsids (Gow 1975) and parareptiles (e.g. *Procolophon*, deBraga 2003; *Mesosaurus*, Modesto 2010, *Erpetonyx*, ROM 55402).

Unambiguous: clade A (0→1). DELTRAN: *Varanops brevirostris* (1→0). ACCTRAN: Varanodontinae (1→0).

272. Femur, distal adductor crest on ventral surface: prominent (0); low and feebly developed (1); absent or reduced to a rugosity on the surface of the bone (2).

Gauthier *et al.* 1988 c.190 Reisz *et al.* (1992 93), Laurin (1993, 116), Berman *et al.* (1995 93), Fröbisch *et al.* (2011, 91), Ezcurra (2016 c.507)

In some terminal taxa, a low ridge of bone extends distally from the 4th trochanter towards the posterior (fibular) condyle; I refer to this ridge as the distal adductor crest. In some taxa a prominent distal adductor crest extends longitudinally (e.g. *Ophiacodon*, Romer and Price 940) or diagonally

(e.g. *Edaphosaurus*, Romer and Price 1940) from the 4th trochanter to the posterior condyle (state 0)(Romer and Price 1940). In others (e.g. sphenacodontians, Romer and Price 1940, Laurin 1993), the distal adductor crest is low (state 1). The distal adductor ridge is absent or is reduced to a flat rugose line of insertion (linea aspera)(state 2) in *Archaeovenator* (Reisz and Dilkes 2003), *Apsisaurus* (Laurin 1991), *Mycterosaurus* (Berman and Reisz 1982), *Petrolacosaurus* (Reisz 1981), *Araeoscelis* (Vaughn 1955), *Prolacerta* (Gow 1975), *Proterosuchus*, Ezcurra *et al.* 2013, *Mesosaurus* (Modesto 2010) and *Milleretta* (Gow 1972) in respect to the taxa included in this study.

Unambiguous: clade B (0→2), Bolosauridae + Procolphonoidea + *Macroleter* (2→1),*Ophiacodon* spp (1→0). DELTRAN: Protorothyrididae (0→1), Ophiacodontidae (0→1), Sphenacodontia (0→1), *Procolophon trigoniceps* (1→0), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: Captorhinidae except *Thuringothyris* (1→0), Amniota (0→1), Caseasauria (1→0), Edaphosauridae (1→0), Procolophonoidea (1→0).

273. Femur, anterior condyle: dorsoventrally thick, at least 0.6 of the dorsoventral depth of the posterior condyle (0); dorsoventrally compressed, approx. 0.5 or less of the dorsoventral depth of the posterior condyle (1)

Modified from Benson (2012 c.233)

The anterior (tibial) condyle of the femur is compressed dorsoventrally relative to the dorsoventral depth of the posterior (fibular) condyle (state 1) in *Seymouria baylorensis* (FMNH UC 1313, White 1939 fig.28C), *Casea broilii* (FMNH UR 656), *Edaphosaurus boanerges* (Benson appendix S1 fig.A10D), 'protorothyridids' (e.g. *Hylonomus*, Carroll 1964 and *Paleothyris*, Carroll 1969), and *Captorhinus aguti* (Holmes 2003).

Unambiguous: Protorothyrididae (0→1), *Seymouria* spp (0→1). DELTRAN: *Captorhinus* spp (0→1), *Casea broilii* (0→1), *Edaphosaurus boanerges* (0→1). ACCTRAN: Captorhinidae except *Thuringothyris* (0→1), Caseidae (0→1), Edaphosauridae (0→1).

274. Tibia, cnemial crest: low (0); prominent and distinct (1)

From Benson (2012 c.235)

The cnemial crest is a flange of bone that extends distally from the dorsal (extensor) surface of the proximal end of the tibia for the insertion of the triceps femoris. In some taxa it forms a rounded knob of bone proximally. It is a prominent and distinctive element (state 1) in *Seymouria baylorensis* (White 1939), *Limnoscelis* (Kennedy 2010), caseasaurs (e.g. *Oedaleops* and *Vaughnictis*, Brocklehurst *et al.* 2016; *Casea broilii*, FMNH UR 656), sphenacodontids (e.g. *Dimetrodon* and *Secodontosaurus*, Romer and Price 1940), *Edaphosaurus* (Romer and Price 1940), 'protorothyridids' (e.g. *Hylonomus*, Carroll 1964 and *Paleothyris*, Carroll 1969), araeoscelidians (e.g. *Petrolacosaurus*, Reisz 1981 and *Araeoscelis*, Vaughn 1955), *Captorhinus aguti* (Holmes 2003) and *Procolophon* (deBraga 2003).

Unambiguous: clade C (1→0), *Procolophon trigoniceps* (0→1). DELTRAN: *Varanosaurus* + *Ophiacodon* (1→0). ACCTRAN: Ophiacodontidae (1→0).

275. Tibia, lower leg-foot length, ratio: articulated tibia + tibiale/astragalus longer than articulated 4th metatarsal + digit (0); shorter (1)

From Reisz *et al.* (2010 c.106) modified from deBraga and Reisz (1995 c.33, 42), Ezcurra *et al.* (2014 c.105), Spindler *et al.* (2018 c.171)

Unambiguous: Varanodontinae (1→0). DELTRAN: *Casea broilii* (0→1), *Eudibamus cursoris* (1→0), clade C (0→1), *Paleothyris acadiana* (0→1), *Prolacerta broomi* (1→0), *Varanosaurus acutirostris* (0→1). ACCTRAN: Araeoscelidia (1→0), clade A (0→1), Caseasauria (0→1), *Lanthanolania* + Archosauromorpha (1→0), Bolosauridae + *Macroleter* + Procolophonoidea (1→0), *Varanosaurus acutirostris* (0→1).

276. Tarsus, tibio-astragalar joint: flat (0); tibial ridge fits into astragalar groove (1); inapplicable, astragalus absent (-)

From Gauthier *et al.* (1988 c.195), Laurin (1991 J.9), Laurin and Reisz (1995 c.116), Reisz *et al.* (2010 c.107)

State (1) was recognised by Laurin and Reisz (1995) as a diapsid synapomorphy, and is scored for several diapsids in the present study (e.g. *Petrolacosaurus*, Reisz 1981; *Araeoscelis*, Vaughn 1955;

Youngina and *Prolacerta*, Gow 1975) with the exception of *Claudiosaurus*, in which Carroll (1982) states that the astragalus and calcaneum abut with a nearly flat surface, and this is confirmed in examining specimens MNHN 1978-6-1 and 1978-6-2.

Unambiguous: Araeoscelidia (0→1).

277. Tarsus, transverse width across tarsus at widest point: subequal to or greater than 4th metatarsal (0); less than 4th metatarsal (1)

Modified from Laurin and Reisz (1995 c.114 in part)

Refer ch.253 above for derivation of this character. State (1) is present in basal mycterosaurines and diapsids.

Unambiguous: Parareptilia (1→0), clade A (0→1). DELTRAN: Varanodontinae (1→0). ACCTRAN: Mycterosaurinae + Varanodontinae + *Apsisaurus* (1→0).

278. Tarsus, astragalus: absent (0); present (1)

From deBraga and Rieppel (1997 c.148), Benson (2012 c.236), Spindler *et al.* (2018 c.172)

The fusion of the astragalus from independent elements of the tarsus is considered a diagnostic feature of amniotes (Meyer and Anderson 2013). A discrete astragalus is absent in diadectomorphs (Moss 1972, Kennedy 2010), *Seymouria* (Berman *et al.* 2000) and *Gephyrostegus* (Rieppel 1993).

Unambiguous: Amniota (0→1).

279. Tarsus, astragalus, proximal neck region: short (0); long, equal to or > 0.4 of the proximodistal length of astragalus (1); inapplicable, astragalus absent (-)

From Reisz *et al.* (1992 c.95), Fröbisch *et al.* (2011 c.118), Benson (2012 c.238), Spindler *et al.* (2018 c.175)

An elongated proximal region of the astragalus is a derived feature in amniotes. Herein I define the neck region as state (1) if it is equal to or longer than 0.4 of the proximodistal length of the astragalus. The derived state is therefore present in sphenacodontians and edaphosaurids. Reisz and Dilkes (2003) noted that the proximal neck in *Archaeovenator* is longer than other 'varanopids', and examination of KUVP 12483 confirms this taxon should be scored as state 1. State (1) is also scored for *Paleothyris* (MCZ 3481), *Petrolacosaurus* (KUVP 1424), *Erpetonyx* (ROM 55402), *Eudibamus* (Berman *et al.* 2000) and *Procolophon* (deBraga 2003).

Unambiguous: Bolosauridae + Procolphonoidea + *Macroleter* (0→1). DELTRAN: *Archaeovenator hamiltonensis* (0→1), *Echinerpeton intermedium* (0→1),Sphenacodontia + Edaphosauridae (0→1), *Paleothyris acadiana* (0→1), *Petrolacosaurus kansensis* (0→1). ACCTRAN: *Protorothyris* + *Paleothyris* (0→1), *Archaeothyris* + *Varanosaurus* + *Ophiacodon* (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Archaeovenator* + *Orovenator* (0→1), *Petrolacosaurus kansensis* (0→1).

280. Tarsus, calcaneum (fibulare), proportions: length approximately equal to width (0); length conspicuously greater than width (1)

From Reisz *et al.* (1992 c.96), Berman *et al.* (1995 c.94), Fröbisch *et al.* (2011 c.119), Benson (2012 c.239), Spindler *et al.* (2018 c.176)

Unambiguous: *Araeoscelis* spp (1→0), *Anthracodromeus* + *Hylonomus* (1→0), Amniota (0→1),*Ophiacodon* spp (1→0). DELTRAN: *Edaphosaurus boanerges* (1→0), *Eocasea martini* (1→0), *Mesosaurus tenuidens* (1→0), Neodiapsida (1→0), *Varanops brevirostris* (1→0). ACCTRAN: clade D (1→0), Eothyrididae (1→0), Edaphosauridae (1→0), *Varanops* + *Varanodon* + *Watongia* (1→0), Bolosauridae + Procolphonoidea + *Macroleter* (0→1).

281. Tarsus, notch or trough for perforating foramen: on astragalus only (0); on the astragalus and calcaneum (1), inapplicable, perforating foramen or astragalus absent (-)

From Spindler *et al.* (2018 c.174) modified from Reisz *et al.* (2010 c.107 in part)

Unambiguous: *Ascendonanus nestleri* (1→0). DELTRAN: *Ennatosaurus tecton* (1→0), *Erpetonyx arsenaultorum* (1→0), *Hylonomus lyelli* (1→0), *Mycterosaurus longiceps* (1→0), *Thuringothyris mahlen-*

dorffae (1→0). ACCTRAN: *Anthracodromeus* + *Hylonomus* (1→0), *Euromycter* + *Ennatosaurus* (1→0), Mycterosaurinae (1→0), Bolosauridae + Procolphonoidea + *Macroleter* (1→0), *Thuringothyris mahlendorffae* (1→0).

282. Tarsus, fifth distal tarsal: present (0); absent (1)

From Laurin (1991 E.13), Laurin (1993 c.120), Laurin and Reisz (1995 c.119), Reisz *et al.* (2010 c.112), Ezcurra (2014 c.111), Modesto *et al.* (2015 c.163), Pritchard *et al.* (2015 c.195), Ezcurra (2016 c.563)

The loss of the fifth distal tarsal was considered a synapomorphy of pareiasaurs, procolophonids and testudines (Laurin and Reisz 1995). More recently deBraga (2003) noted that the 5th distal tarsal was likely present in *Procolophon*, but not preserved, and is scored as present (state 0) herein. Benson (2012) recognised that the fifth distal tarsal was also absent in therapsids, a group not represented in the present study. Ezcurra (2016) noted the absence of the fifth distal tarsal in archosauromorphs. It is scored accordingly in *Prolacerta* and *Proterosuchus*.

DELTRAN: Archosauromorpha (0→1). ACCTRAN: *Lanthanolania* + Archosauromorpha (0→1).

283. Tarsus, number of centralia: two centralia present (0); only one centrale is present (1)

Modified from deBraga and Rieppel (1997 c.158), Müller (20041 c.151), Ezcurra *et al.* (2014 c.214), Modesto *et al.* (2015 c.162)

Reisz (1986) noted the presence of two subequal pedal centralia in ophiacodontids, and two in all other 'pelycosaur' ' grade synapsids, although the medial centrale (sensu Romer and Price 1940 fig.35D) is much larger than the lateral centrale. There is some uncertainty, however, in the condition in *Casea broilii*, where some studies consider only one centrale is present (Williston 1911, Olson 1968). Reisz (1986 fig.33D) figures the lateral centrale as a small element in *Casea broilii*, although absent in the more derived caseid *Cotylorhynchus* romeri (Reisz 1986 fig.33E), in accordance with Stovall *et al.* (1966). Consequently *Casea broilii* is coded as (?) herein. The configuration of the tarsus is poorly known in most varanopids, although state (1) is applicable to *Archaeovenator* (Reisz and Dilkes 2003).

In respect to the current taxon list, only one pedal centrale (state 1) is present in 'protorothyridids' (Carroll 1964), diapsids (Reisz 1981, Carroll 1981, Gow 1975) parareptiles (Modesto *et al.* 2015 c.162) and *Captorhinus* (Holmes 2003).

Unambiguous: Sauropsida (0→1).

284. Metatarsus, ratio of lengths of metatarsals I and IV: equal or greater than 0.42 (0); less than 0.42 (1)

Modified from Ezcurra *et al.* (2014 c.216) modified from Dilkes (1998 c.123), Müller (2004 c.173), Modesto and Sues (2004 c.123)

A third state, equal to or less than 0.32, was omitted from this character, since it only applied to *Eudibamus* in the current taxon list and was therefore parsimony uninformative.

Unambiguous: *Ascendonanus nestleri* (0→1), *Seymouria* spp (0→1), *Youngina capensis* (0→1). DELTRAN: *Dimetrodon* spp (0→1), *Eudibamus cursoris* (0→1),*Ophiacodon* spp (0→1), *Thuringothyris mahlendorffae* (0→1). ACCTRAN: Ophiacodontidae (0→1), Sphenacodontidae (0→1), Bolosauridae + Procolphonoidea + *Macroleter* (0→1), *Thuringothyris mahlendorffae* (0→1).

285. Metatarsus, metapodials overlapping proximally: absent (0); present (1)

From Laurin and Reisz (1995 c.121), deBraga and Reisz (1995 c.43), Reisz *et al.* (2010 c.110), Ezcurra *et al.* (2014 c.109)

State (1) is present in *Dimetrodon*, *Ophiacodon*, varanodontines and mycterosaurines (with the exception of *Ascendonanus*, Spindler *et al.* 2018), and diapsids.

DELTRAN: *Dimetrodon* spp (0→1), *Eudibamus cursoris* (0→1), Araeoscelidia (0→1), Varanopidae except *Ascendonanus* (0→1), Neodiapsida (0→1),*Ophiacodon* spp (0→1). ACCTRAN: *Ascendonanus nestleri* (1→0), Parareptilia (1→0), clade B (0→1), Edaphosauridae (1→0), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), *Eudibamus* + *Belebey* (0→1).

286. Metatarsus, fourth metatarsal: short (0); long (at least 40% of digit IV) (1)

From Laurin (1991 F.10), Reisz *et al.* (2010 c.111), Ezcurra *et al.* (2014 c.110)

DELTRAN: *Limnoscelis plaudis* (0→1), Araeoscelidia (0→1), Ophiacodontidae + Sphenacodontia + Edaphosauridae (0→1), Varanopidae except *Ascendonanus* (0→1), Neodiapsida (0→1). ACCTRAN: *Ascendonanus nestleri* (1→0), Parareptilia (1→0), Protorothyrididae (1→0), Diadectomorpha + Amniota (0→1), Caseasauria (1→0).

Appendix 2 - Character/Taxon Matrix

Character/Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Gephyrostegus	0	0	0	3	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Seymouria	0	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0	0	0	0	0
Tseajaia	0	0	1	-	1	0	0	0	0	0	0	1	?	1	0	0	0	1	?	1
Limnoscelis	0	0	1	-	1	0	0	1	?	0	0	1	1	0	-	0	0	1	0	1
Oedaleops	1	0	0	?	2	1	-	0	0	0	0	1	1	1	0	0	0	?	?	1
Eothyris	1	0	?	?	2	1	-	0	0	0	0	1	1	1	0	0	0	1	0	1
Vaughnictis	?	0	1	-	?	0	0	0	0	0	0	1	?	?	?	?	?	?	?	1
Eocasea	?	?	0	1	2	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Euromycter	1	0	0	1	2	1	-	0	0	0	1	1	1	0	-	0	0	1	0	0
Casea	1	0	0	1	2	1	-	0	0	0	1	1	1	0	-	0	0	0	0	0
Ennatosaurus	1	0	0	2	2	1	-	0	0	0	1	1	1	0	-	0	0	0	0	1
Echinerpeton	?	?	?	?	?	1	-	?	0	0	0	?	?	?	?	?	?	?	?	?
Archaeothyris	0	?	0	?	2	0	0	?	1	0	0	?	?	0	-	?	?	?	?	?
Varanosaurus	0	1	0	2	2	0	0	0	0	0	0	0	2	0	-	1	1	0	1	1
Ophiacodon	0	1	1	-	2	0	0	0	[01]	0	0	0	2	0	-	1	0	0	0	1
Haptodus	0	1	0	2	1	0	0	0	0	0	0	0	0	0	-	0	0	1	0	1
Secodontosaurus	0	1	1	-	1	0	0	1	0	0	0	0	0	0	-	0	0	1	0	1
Dimetrodon	0	1	1	-	1	0	0	1	1	1	0	1	0	0	-	0	0	1	0	1
Ianthasaurus	0	?	?	?	1	1	-	1	?	0	0	?	?	0	-	?	?	?	?	?
Edaphosaurus	0	1	1	-	1	1	-	1	1	0	0	0	0	0	-	0	0	0	0	0
Hylonomus	0	0	1	-	0	1	-	0	0	0	0	0	0	0	-	0	0	0	0	1
Anthracodromeus	0	?	0	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paleothyris	0	0	0	2	2	1	-	0	0	0	0	0	0	0	-	0	0	0	0	0
Protorothyris	0	0	0	0	2	1	-	0	0	0	0	[01]	0	0	-	0	0	0	?	0
Petrolacosaurus	0	0	0	2	2	0	0	0	0	0	0	0	0	0	-	0	0	0	0	1
Araeoscelis	0	0	1	-	2	1	-	0	0	0	0	0	0	0	-	1	?	0	0	0
Orovenator	0	0	1	-	2	0	0	0	0	0	0	0	1	0	-	1	0	1	1	0
Archaeovenator	0	1	1	-	2	0	0	0	0	0	0	1	0	0	-	0	0	0	1	0
Ascendonanus	0	?	1	-	2	0	0	0	0	0	0	0	0	?	?	?	?	?	?	0
Aerosaurus	0	1	1	-	2	0	1	1	0	1	0	1	1	0	-	0	0	0	1	0
Apsisaurus	?	?	?	?	?	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?
Heleosaurus	0	1	1	-	2	0	1	1	?	1	0	0	0	0	-	0	0	0	?	0
Mesenosaurus	0	1	1	-	2	0	1	1	1	1	0	0	0	0	-	1	0	0	1	0
Mycterosaurus	0	1	1	-	2	0	1	1	?	1	0	1	0	0	-	?	0	0	1	0
Elliotsmithia	0	?	1	-	2	0	1	1	1	1	0	?	?	?	?	?	?	?	?	?
Varanops	0	1	1	-	?	0	1	1	0	1	0	0	1	0	-	0	0	0	0	0
Varanodon	1	1	1	-	[12]	0	1	1	0	1	0	0	0	0	-	0	?	0	?	0
Watongia	?	?	?	?	?	0	1	1	0	1	0	?	?	0	-	?	?	?	?	?
Youngina	0	0	1	-	1	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0
Acerosodont.	0	?	?	?	?	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?
Lanthanolania	0	0	?	?	?	0	0	?	?	?	0	?	?	0	-	?	?	?	?	?
Claudiosaurus	0	0	1	-	1	1	-	?	0	0	0	0	0	0	-	1	0	0	0	0
Prolacerta	0	0	1	-	1	0	1	1	0	1	0	0	0	1	1	0	0	1	0	0
Proterosuchus	0	0	1	-	1	0	1	1	1	1	0	0	0	1	1	1	0	3	0	0
Thuringothyris	0	0	1	-	2	1	-	0	0	0	0	1	0	0	-	0	0	0	0	0
Captorhinus	1	0	0	0	1	1	-	0	0	0	0	[01]	0	0	-	0	1	2	0	1
Protocaptorhinus	1	0	0	0	1	1	-	0	0	0	0	0	0	0	-	0	1	2	0	1
Romeria	1	0	0	0	2	1	-	?	0	0	0	[01]	0	0	-	0	[01]	2	0	1
Euconcordia	?	0	0	0	2	1	-	1	0	0	0	0	0	0	-	0	1	0	?	1
Reiszorhinus	0	0	0	2	1	0	0	0	?	1	0	0	0	0	-	0	1	2	0	1
Eudibamus	?	?	1	-	0	1	-	0	0	0	0	1	?	?	?	?	?	0	?	?
Mesosaurus	0	0	1	-	1	1	-	0	0	0	0	0	0	0	-	0	0	0	-	0
Erpetonyx	?	?	1	-	?	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?
Belebey	0	0	1	-	0	1	-	0	0	0	0	1	0	0	-	0	0	0	0	0
Macroleter	0	0	0	3	1	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0
Milleretta	0	0	0	3	1	0	0	0	0	?	0	1	0	0	-	?	0	1	0	0
Acleistorhinus	0	0	0	1	1	0	0	0	0	0	0	1	?	0	-	0	?	1	0	0
Colobomycter	0	0	0	1	1	1	-	1	0	0	0	1	0	0	-	0	0	0	0	1
Procolophon	0	0	1	-	0	1	-	0	0	0	0	1	1	1	1	0	0	0	0	0
Owenetta	0	0	1	-	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0

Character/Taxon	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Gephyrostegus	0	?	0	0	0	0	0	-	3	0	-	-	-	-	0	?	?	0	0	0
Seymouria	0	0	0	1	2	0	0	-	1	1	1	0	0	0	0	?	?	0	0	0
Tseajaia	0	?	0	0	0	0	0	-	1	1	1	1	0	0	0	?	?	?	0	1
Limnoscelis	1	2	0	0	0	0	0	-	1	1	0	0	0	0	0	?	?	?	0	1
Oedaleops	1	?	0	0	1	0	0	-	1	1	1	1	1	0	0	0	-	1	0	0
Eothyris	1	?	0	0	1	0	0	-	1	1	1	1	1	0	1	?	?	1	0	0
Vaughnictis	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eocasea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euromycter	0	2	0	0	2	0	1	0	1	0	-	-	-	-	0	0	-	1	0	0
Casea	0	?	0	0	1	0	0	-	1	0	-	-	-	-	0	0	-	1	0	0
Ennatosaurus	1	2	0	0	2	0	1	0	0	0	-	-	-	-	0	0	-	1	0	0
Echinerpeton	?	?	0	1	1	?	?	?	1	1	1	1	0	0	?	1	0	0	0	?
Archaeothyris	?	?	0	1	1	?	?	?	2	1	1	1	0	0	?	1	0	?	?	0
Varanosaurus	1	3	0	1	1	0	0	-	3	1	1	1	0	1	1	1	1	0	0	0
Ophiacodon	1	?	0	2	1	0	0	-	3	1	0	0	0	1	0	1	1	0	0	0
Haptodus	1	3	0	1	1	0	0	-	1	1	1	1	0	1	0	1	0	0	0	0
Secodontosaurus	1	3	0	2	1	0	0	-	1	1	1	1	0	1	0	1	0	0	0	0
Dimetrodon	1	3	0	2	1	0	0	-	1	1	1	1	0	0	1	1	0	0	0	0
Ianthasaurus	?	?	0	1	1	0	0	-	3	1	1	[01]	0	[01]	0	?	?	0	0	0
Edaphosaurus	0	3	0	1	1	0	0	-	1	0	-	-	-	-	0	0	-	0	0	1
Hylonomus	?	?	0	0	1	0	0	-	3	1	1	0	0	0	0	0	-	0	0	0
Anthracodromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
Paleothyris	0	?	0	0	1	0	0	-	3	1	1	1	0	1	0	0	-	0	0	0
Protorothyris	1	?	0	0	1	0	0	-	2	1	1	1	0	1	0	?	?	0	0	0
Petrolacosaurus	1	?	0	0	1	0	1	0	3	1	1	1	0	1	0	0	-	0	0	0
Araeoscelis	0	2	0	0	1	0	0	-	1	1	1	1	0	0	0	?	?	0	0	0
Orovenator	0	2	0	1	1	0	1	1	2	0	-	-	-	-	0	1	1	0	1	0
Archaeovenator	0	2	0	1	1	0	1	1	2	0	-	-	-	-	0	1	?	0	1	0
Ascendonanus	0	?	0	1	1	0	?	?	1	1	1	0	?	0	0	0	-	0	0	0
Aerosaurus	1	?	0	1	1	0	1	0	1	1	0	0	0	0	0	0	-	0	?	0
Apsisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Heleosaurus	0	?	0	2	1	1	1	1	1	1	1	0	0	?	0	?	-	0	0	0
Mesenosaurus	0	?	0	2	1	1	1	0	1	1	1	0	0	0	0	?	?	0	0	0
Mycterosaurus	?	?	0	2	1	1	1	?	1	1	0	0	0	0	0	0	?	0	0	0
Elliotsmithia	?	?	?	?	?	1	?	?	?	1	1	?	0	0	?	?	?	0	?	0
Varanops	1	3	1	2	1	0	1	0	1	1	1	0	0	1	1	0	-	0	0	0
Varanodon	1	?	1	2	1	0	?	?	1	1	1	0	0	1	1	?	?	0	0	0
Watongia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	0	?	0	2	1	1	0	-	2	0	-	-	-	-	-	?	?	0	0	0
Acerosodont.	?	?	0	2	1	1	?	?	3	?	?	?	?	?	?	?	?	0	0	?
Lanthanolania	?	?	0	2	1	0	1	0	?	0	-	-	-	-	0	?	?	0	0	0
Claudiosaurus	0	?	0	1	2	0	0	-	3	0	-	-	-	-	0	?	?	0	0	0
Prolacerta	0	2	0	2	2	0	1	1	1	0	-	-	-	-	0	1	1	0	0	0
Proterosuchus	0	2	0	2	1	0	1	1	[12]	0	-	-	-	-	0	?	?	0	?	0
Thuringothyris	1	?	0	0	1	0	0	-	1	0	-	-	-	-	0	?	?	0	?	0
Captorhinus	1	1	0	[01]	1	0	0	-	1	1	1	1	0	0	0	0	-	0	0	1
Protocaptorhinus	1	1	0	1	1	0	0	-	1	1	1	1	0	0	0	?	?	0	0	1
Romeria	1	1	0	0	1	0	0	-	1	1	1	1	0	0	0	?	?	0	0	1
Euconcordia	0	?	0	0	1	0	0	-	1	1	0	0	0	0	0	?	?	?	0	0
Reiszorhinus	1	1	0	0	1	0	0	-	1	1	1	0	0	0	0	?	?	1	0	1
Eudibamus	?	?	?	?	?	?	?	1	?	0	-	-	-	-	?	?	?	?	?	?
Mesosaurus	0	0	0	1	?	0	0	-	1	0	-	-	-	-	0	0	-	0	?	0
Erpetonyx	?	?	0	?	?	?	?	?	1	0	-	-	-	-	?	0	-	?	?	0
Belebey	0	?	0	0	1	0	0	1	0	0	-	-	-	-	0	?	?	0	0	0
Macroleter	1	?	0	1	2	0	1	1	1	1	0	0	0	0	0	0	-	0	0	0
Milleretta	?	2	0	0	1	0	0	1	1	0	-	-	-	-	0	?	?	0	0	0
Acleistorhinus	0	2	0	1	2	1	0	1	1	0	-	-	-	-	0	?	?	0	0	0
Colobomycter	1	2	1	1	1	1	0	1	1	1	1	1	0	0	0	0	-	0	0	0
Procolophon	0	3	0	0	1	0	0	1	0	0	-	-	-	-	0	0	-	0	0	1
Owenetta	0	?	0	2	2	0	0	1	1	1	0	0	0	0	0	?	?	0	0	0

Character/Taxon	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Gephyrostegus	0	2	0	0	-	0	0	0	0	0	0	?	0	1	0	?	?	0	0	0
Seymouria	1	-	0	0	-	0	1	0	0	0	0	?	0	0	0	1	0	0	0	0
Tseajaia	1	-	1	0	-	0	1	0	0	0	0	0	0	1	0	0	?	?	0	0
Limnoscelis	1	-	1	0	-	0	1	0	0	0	0	0	0	1	0	0	?	?	0	0
Oedaleops	1	-	0	0	-	0	0	1	0	0	0	0	0	0	1	0	-	0	0	0
Eothyris	0	1	0	0	-	0	0	1	0	0	0	0	1	-	1	0	-	0	0	0
Vaughnictis	0	1	?	?	?	?	?	?	?	?	0	?	1	-	1	?	?	?	?	0
Eocasea	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euromycter	0	1	0	0	-	0	1	1	0	0	0	0	0	0	1	?	?	0	0	0
Casea	0	1	0	0	-	0	1	1	?	0	0	0	?	-	1	?	?	0	0	0
Ennatosaurus	0	1	0	0	-	0	0	1	0	0	0	?	0	1	1	0	-	?	0	0
Echinerpeton	?	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Archaeothyris	?	?	0	?	-	0	?	0	?	?	?	?	0	1	1	?	?	?	?	?
Varanosaurus	1	-	1	0	-	0	2	0	0	1	0	?	0	1	1	0	-	0	1	1
Ophiacodon	1	-	1	0	-	0	2	0	0	0	?	0	0	1	1	0	-	0	1	1
Haptodus	1	-	1	0	-	0	0	0	0	1	0	0	0	1	1	0	-	0	1	0
Secodontosaurus	1	-	1	0	-	0	2	0	1	-	0	0	0	1	1	0	-	0	1	0
Dimetrodon	1	-	1	0	-	0	2	0	1	-	0	0	0	1	1	0	-	0	1	0
Ianthasaurus	1	-	0	0	-	0	?	0	0	0	0	0	0	1	1	0	-	0	0	?
Edaphosaurus	1	-	0	0	-	0	0	0	0	0	0	?	0	1	1	1	0	0	0	0
Hylonomus	1	-	0	0	-	0	0	0	0	0	0	0	0	0	1	?	?	0	0	0
Anthracodromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paleothyris	0	1	0	0	-	0	0	0	0	0	0	0	0	0	1	0	-	0	0	?
Protorothyris	0	0	0	0	-	0	0	0	0	0	0	0	0	0	1	?	?	?	0	0
Petrolacosaurus	1	-	0	0	-	0	0	0	0	0	0	0	0	0	1	?	?	0	0	0
Araeoscelis	1	-	0	0	-	0	0	0	0	0	0	0	0	0	1	0	-	0	0	0
Orovenator	1	-	0	1	0	0	0	0	0	1	1	0	1	-	1	1	0	0	0	1
Archaeovenator	1	-	0	1	1	0	0	0	0	0	1	0	1	-	1	?	?	0	0	1
Ascendonanus	1	-	0	?	?	0	[01]	?	0	?	1	0	0	0	1	?	?	?	0	?
Aerosaurus	0	2	0	0	-	0	?	0	0	0	0	2	0	0	1	?	?	0	0	?
Apsisaurus	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Heleosaurus	1	-	0	1	0	0	1	0	1	-	1	?	?	?	1	?	?	0	0	?
Mesenosaurus	1	-	0	1	0	0	1	0	1	-	1	1	1	-	1	1	0	0	0	1
Mycterosaurus	0	0	0	1	0	0	1	0	1	-	1	1	?	?	1	1	0	0	0	1
Elliotsmithia	0	0	?	?	?	?	?	?	?	?	1	?	?	-	1	1	0	?	0	1
Varanops	0	2	0	1	1	0	1	0	0	0	0	0	0	0	1	0	-	0	0	1
Varanodon	0	2	0	1	1	0	1	0	0	0	0	2	0	0	1	0	-	0	0	1
Watongia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	1	-	0	0	-	0	1	0	1	-	0	?	0	0	1	0	-	1	0	0
Acerosodont.	1	-	?	?	?	?	?	?	1	-	?	1	0	0	1	0	-	?	?	0
Lanthanolania	0	0	0	?	?	?	?	?	1	-	0	?	0	0	1	?	?	1	0	0
Claudiosaurus	1	-	0	0	-	1	0	0	1	-	1	?	1	-	1	?	?	0	0	0
Prolacerta	1	-	0	0	-	1	2	0	1	-	1	1	0	0	1	0	-	1	0	0
Proterosuchus	0	1	0	0	-	1	2	0	1	-	1	?	0	0	1	?	?	1	1	?
Thuringothyris	0	1	0	0	-	0	0	0	0	0	0	?	0	1	1	0	-	0	0	0
Captorhinus	1	-	0	0	-	0	0	0	0	0	0	0	0	1	1	0	-	0	0	0
Protocaptorhinus	0	1	0	0	-	0	0	0	0	0	0	?	0	1	1	?	?	0	0	0
Romeria	0	0	0	0	-	0	0	0	0	0	0	?	0	1	1	?	?	0	0	0
Euconcordia	1	-	0	0	-	0	0	0	0	0	0	0	0	1	1	0	-	0	0	0
Reiszorhinus	1	-	0	0	-	0	0	0	0	0	0	0	0	1	1	0	-	0	0	0
Eudibamus	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1	1	1	?	?	?
Mesosaurus	1	0	0	0	-	0	2	0	0	-	1	1	0	0	1	0	-	0	0	0
Erpetonyx	?	?	0	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	0
Belebey	1	-	0	0	-	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0
Macroleter	1	-	0	0	-	0	0	0	1	-	1	?	0	0	1	1	1	0	0	0
Milleretta	1	-	0	0	-	0	0	0	0	0	0	?	1	-	1	1	1	?	0	0
Acleistorhinus	0	1	0	0	-	0	0	0	1	-	0	1	0	0	1	?	?	0	0	0
Colobomycter	0	0	0	0	-	0	0	1	1	-	1	0	[01]	-	1	1	1	0	0	0
Procolophon	1	-	0	0	-	0	0	1	1	-	0	0	0	0	1	1	1	0	0	0
Owenetta	1	-	0	0	-	0	0	0	1	-	0	0	0	0	1	1	1	?	0	0

Character/Taxon	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Gephyrostegus	-	-	1	0	0	0	0	0	?	0	-	0	0	0	-	0	-	-	0	0
Seymouria	-	-	0	0	0	0	0	0	?	0	-	0	0	0	-	[02]	-	-	0	0
Tseajaia	-	-	1	1	0	0	0	0	0	1	-	0	0	0	-	0	-	1	0	0
Limnoscelis	-	-	1	1	0	1	1	0	0	1	-	0	0	0	-	1	-	1	0	0
Oedaleops	0	1	0	1	0	1	1	1	0	1	0	1	0	?	-	0	1	1	0	0
Eothyris	0	1	0	1	0	1	1	0	0	1	0	1	0	1	1	0	0	1	0	0
Vaughnictis	?	?	?	1	0	1	1	1	0	1	0	1	0	1	0	0	0	0	?	0
Eocasea	?	?	?	?	?	1	1	0	0	1	?	1	0	?	?	?	0	0	?	0
Euromycter	0	1	0	0	0	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0
Casea	0	?	0	?	0	1	?	?	0	1	0	1	0	1	1	0	0	0	0	0
Ennatosaurus	1	0	0	0	0	1	1	1	1	1	0	1	0	1	1	0	1	0	0	0
Echinerpeton	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?
Archaeothyris	1	?	1	2	0	?	?	?	?	1	0	1	0	0	-	1	?	?	0	0
Varanosaurus	1	0	1	2	0	0	1	1	0	1	0	1	0	0	-	1	1	1	0	1
Ophiacodon	1	1	1	2	0	1	1	1	0	1	0	1	0	0	-	1	1	1	0	1
Haptodus	1	1	1	1	0	0	0	1	0	1	1	1	0	0	-	1	1	0	0	0
Secodontosaurus	1	1	2	0	0	0	0	1	0	1	0	1	1	0	-	1	1	0	0	0
Dimetrodon	1	1	2	0	0	1	1	1	0	1	0	1	1	0	-	1	1	1	0	0
Ianthasaurus	1	1	1	1	0	0	0	1	?	1	1	1	0	0	-	0	1	0	0	0
Edaphosaurus	1	1	0	1	0	0	0	1	0	1	1	1	1	0	-	0	1	0	0	0
Hylonomus	1	0	0	0	0	0	0	0	0	1	-	0	0	0	-	0	-	-	0	0
Anthracodromeus	?	?	?	?	?	0	0	0	0	1	-	0	0	0	-	?	-	-	?	?
Paleothyris	1	0	1	0	0	0	0	0	0	1	-	0	0	0	-	0	-	-	0	0
Protorothyris	1	0	1	[12]	0	0	0	0	0	1	-	0	0	0	-	0	-	-	0	0
Petrolacosaurus	1	0	1	1	0	0	0	1	0	1	0	1	0	0	-	0	1	0	0	0
Araeoscelis	1	0	?	2	0	0	1	1	0	1	-	0	0	0	-	0	?	?	0	0
Orovenator	1	0	1	2	?	?	?	?	?	1	1	1	0	0	-	0	1	?	0	0
Archaeovenator	1	0	1	2	0	1	1	1	?	1	1	1	0	0	-	0	1	0	0	0
Ascendonanus	0	?	?	2	0	0	1	0	?	1	1	1	0	0	-	0	1	0	0	0
Aerosaurus	1	0	?	2	?	?	?	?	?	1	1	1	0	1	0	0	1	0	1	?
Apsisaurus	?	?	?	?	?	?	?	?	?	?	1	1	0	0	-	?	1	0	1	0
Heleosaurus	1	0	1	2	1	1	1	0	?	1	1	1	0	0	-	0	1	1	1	0
Mesenosaurus	1	0	1	2	1	0	1	0	1	1	1	1	0	0	-	0	1	1	1	0
Mycterosaurus	1	0	?	2	1	?	1	1	1	1	1	1	0	1	0	0	1	1	1	0
Elliotsmithia	1	0	?	2	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	0
Varanops	1	0	1	2	0	1	0	1	0	1	1	1	0	1	0	0	1	?	1	0
Varanodon	1	0	1	2	1	?	0	?	0	1	1	1	0	1	0	0	1	0	0	0
Watongia	?	?	?	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	1	0	1	2	0	0	1	1	0	1	1	1	0	0	-	0	1	0	0	0
Acerosodont.	1	0	?	2	?	?	1	1	?	?	1	1	0	0	-	0	1	0	?	0
Lanthanolania	1	0	?	?	0	?	?	1	0	1	-	1	0	0	-	0	1	-	0	0
Claudiosaurus	1	1	?	2	0	0	1	1	?	1	-	1	0	0	-	0	1	-	0	0
Prolacerta	1	0	1	2	0	0	0	1	0	1	1	1	0	0	-	0	1	0	0	0
Proterosuchus	1	0	2	[012]	0	0	1	1	0	0	1	1	0	0	-	1	1	1	0	0
Thuringothyris	0	0	0	0	0	0	0	1	0	1	-	0	0	0	-	1	-	0	0	0
Captorhinus	0	0	0	[01]	0	0	0	0	0	1	-	0	0	0	-	1	-	0	0	0
Protocaptorhinus	0	0	0	0	0	0	0	0	0	1	-	0	0	0	-	0	-	0	0	0
Romeria	0	1	[01]	[01]	0	0	0	0	0	1	-	0	0	0	-	0	-	1	0	0
Euconcordia	0	0	0	0	0	0	0	0	0	1	-	0	0	0	-	1	-	0	0	0
Reiszorhinus	0	0	1	0	0	0	0	0	0	1	-	0	0	0	-	1	-	1	0	0
Eudibamus	1	0	?	?	?	?	?	0	?	?	1	1	0	?	?	0	?	?	?	0
Mesosaurus	0	0	1	2	0	0	0	?	0	1	-	0	0	0	-	1	-	-	0	0
Erpetonyx	1	0	?	2	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	0
Belebey	1	0	0	0	0	?	1	0	0	1	1	1	0	1	1	0	-	0	0	0
Macroleter	0	0	0	1	1	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0
Milleretta	1	0	1	2	0	0	1	1	0	1	0	1	0	0	-	0	0	0	0	0
Acleistorhinus	0	1	0	1	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0
Colobomycter	1	1	0	1	0	?	1	0	0	1	1	1	0	1	1	0	0	0	0	0
Procolophon	0	0	0	2	0	1	0	?	0	1	-	0	1	0	-	1	-	-	0	0
Owenetta	0	0	1	2	0	1	0	0	0	0	-	1	0	0	-	0	-	-	0	0

Character/Taxon	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Gephyrostegus	0	0	0	1	0	-	?	0	?	0	0	0	-	0	0	0	0	0	0	0
Seymouria	0	0	1	1	0	-	0	0	?	0	0	[12]	-	0	0	0	0	0	0	0
Tseajaia	0	0	1	1	0	-	1	?	?	0	1	2	-	0	0	0	1	0	2	0
Limnoscelis	0	0	1	1	0	-	0	0	0	0	0	1	-	0	0	0	1	0	0	0
Oedaleops	0	0	1	0	1	0	0	0	?	0	1	1	-	0	0	?	1	0	?	?
Eothyris	0	0	1	0	1	0	0	?	0	0	1	1	-	0	0	0	1	0	0	0
Vaughnictis	0	0	1	0	1	1	?	?	?	0	1	1	-	0	0	?	1	0	?	?
Eocasea	?	?	?	?	?	?	?	?	?	0	?	?	-	0	0	1	1	0	?	?
Euromycter	0	0	1	0	0	0	0	0	0	0	1	0	-	0	0	1	1	0	?	0
Casea	0	0	?	0	0	0	0	0	?	0	1	0	-	0	0	1	1	0	?	0
Ennatosaurus	0	0	0	0	0	?	0	?	0	0	1	0	-	0	0	1	1	0	1	?
Echinerpeton	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Archaeothyris	0	0	1	0	1	1	?	0	?	0	1	2	-	0	?	?	1	?	?	?
Varanosaurus	0	0	1	0	1	1	0	0	1	0	1	2	-	0	1	0	1	0	0	0
Ophiacodon	0	0	1	0	1	1	0	0	1	0	1	2	-	0	1	0	1	0	0	0
Haptodus	1	0	-	0	1	0	0	0	0	0	0	2	-	0	1	0	1	0	?	0
Secodontosaurus	1	0	-	0	1	0	0	0	0	1	1	2	0	0	1	0	1	0	3	0
Dimetrodon	1	0	-	0	1	0	0	0	0	0	0	2	-	0	1	0	1	0	3	0
Ianthasaurus	1	0	-	0	1	0	?	0	?	0	0	2	-	0	1	?	1	0	?	0
Edaphosaurus	1	0	-	0	1	0	0	0	0	1	0	2	0	0	1	0	1	0	3	0
Hylonomus	0	0	0	1	0	-	0	?	?	0	0	?	-	?	?	?	1	0	1	?
Anthracodromeus	0	0	1	1	0	-	0	0	?	0	0	0	-	0	1	0	1	0	1	0
Paleothyris	0	0	1	1	1	-	0	0	1	0	0	2	-	0	1	?	1	0	1	0
Protorothyris	0	0	1	1	1	-	0	0	1	0	0	1	-	0	1	?	1	0	1	0
Petrolacosaurus	0	0	?	0	0	0	1	0	1	1	0	1	0	0	1	0	1	0	1	0
Araeoscelis	0	0	1	1	1	-	1	0	0	1	0	1	0	0	1	0	1	0	2	0
Orovenator	?	?	?	0	?	?	?	?	?	1	0	2	0	0	1	?	1	?	?	?
Archaeovenator	0	0	1	0	1	0	1	?	?	0	0	2	-	0	0	?	1	0	1	?
Ascendonanus	0	0	1	0	1	0	?	1	?	0	0	2	-	0	1	?	1	0	1	?
Aerosaurus	0	0	1	0	0	0	?	?	0	0	1	2	-	0	1	0	?	0	2	?
Apsisaurus	0	0	1	0	1	?	1	0	?	?	?	?	?	?	?	?	1	?	?	?
Heleosaurus	0	0	1	0	1	0	1	1	0	0	1	2	-	0	1	?	1	0	2	1
Mesenosaurus	0	0	1	0	1	0	1	1	0	0	1	2	-	0	1	?	1	0	2	1
Mycterosaurus	0	0	1	0	1	0	1	?	?	0	1	2	-	0	1	?	1	?	?	?
Elliotsmithia	0	0	1	0	1	0	1	1	0	0	1	2	-	0	1	0	1	0	2	?
Varanops	0	0	1	1	0	0	1	0	0	0	0	2	-	0	1	0	1	0	2	0
Varanodon	0	0	1	1	0	0	1	0	?	0	?	2	-	0	1	?	1	?	?	?
Watongia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	0	0	1	0	0	0	1	?	1	1	0	2	1	0	1	0	1	0	1	0
Acerosodont.	1	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	1	?	?	?
Lanthanolania	1	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?
Claudiosaurus	1	0	-	0	0	0	1	0	?	1	1	1	1	0	1	-	1	1	-	-
Prolacerta	1	0	-	0	0	0	1	1	0	1	[02]	1	1	0	1	-	1	1	-	-
Proterosuchus	[01]	0	-	0	0	0	1	1	?	1	[02]	1	1	0	1	-	1	1	-	-
Thuringothyris	0	0	1	1	?	-	0	0	1	0	0	0	-	0	1	0	1	0	1	0
Captorhinus	0	0	0	1	0	-	0	0	1	0	0	0	-	0	1	-	1	1	-	-
Protocaptorhinus	0	0	1	1	1	-	0	0	1	0	0	0	-	0	1	-	1	1	-	-
Romeria	0	0	0	1	0	-	0	0	1	0	0	0	-	0	1	-	1	1	-	-
Euconcordia	?	?	?	1	?	-	0	0	1	0	0	0	-	0	1	-	1	1	-	-
Reiszorhinus	0	0	1	1	0	-	0	0	1	0	0	0	-	0	1	-	1	1	-	-
Eudibamus	0	0	?	1	1	?	?	0	1	?	?	?	?	1	-	-	1	?	?	?
Mesosaurus	0	0	1	1	1	-	1	0	1	0	1	1	-	0	0	1	1	0	1	0
Erpetonyx	?	?	?	?	?	?	?	0	?	?	?	?	?	0	0	1	1	0	2	?
Belebey	0	0	1	1	1	1	0	0	1	0	1	2	-	1	-	-	1	0	2	0
Macroleter	0	0	1	1	0	1	?	?	0	0	1	2	-	0	0	-	1	1	1	0
Milleretta	0	0	0	0	0	1	0	0	0	0	0	2	-	0	0	1	1	0	1	0
Acleistorhinus	0	0	1	1	0	0	1	0	1	0	0	1	-	0	0	0	1	0	1	?
Colobomycter	0	0	1	0	0	0	?	0	?	0	0	1	-	0	0	-	1	1	-	-
Procolophon	0	1	1	0	0	-	0	0	0	0	1	0	-	0	0	-	1	1	-	-
Owenetta	1	1	1	0	0	-	0	0	0	0	1	0	-	0	0	-	1	1	-	-

Character/Taxon	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119
Gephyrostegus	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	0	0	0	0
Seymouria	0	0	0	0	0	?	1	0	0	0	?	?	?	?	0	0	0	0	0
Tseajaia	0	0	[01]	0	1	?	0	0	1	-	0	0	0	0	0	2	0	0	0
Limnoscelis	0	0	1	0	0	0	0	0	0	0	?	?	0	0	0	2	?	0	0
Oedaleops	?	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Eothyris	0	0	0	0	0	0	1	3	0	0	?	?	1	?	0	0	1	?	?
Vaughnictis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
Eocasea	0	0	0	0	1	0	?	?	?	?	?	?	?	?	?	0	?	?	?
Euromycter	0	0	1	0	0	1	1	3	0	0	?	?	1	0	1	1	1	1	1
Casea	?	0	1	0	0	0	1	3	0	0	?	?	1	0	1	1	1	0	1
Ennatosaurus	?	0	0	0	0	1	1	3	1	-	?	?	1	0	1	1	?	?	1
Echinerpeton	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Archaeothyris	?	0	1	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?
Varanosaurus	0	0	0	0	0	0	0	2	1	-	?	?	0	1	0	0	2	0	0
Ophiacodon	0	0	1	0	0	0	0	2	0	-	0	0	0	1	0	0	2	0	0
Haptodus	1	?	?	?	?	0	?	0	0	?	?	?	0	0	?	2	0	0	0
Secodontosaurus	1	0	1	0	0	0	0	1	0	0	?	?	0	0	0	2	?	0	0
Dimetrodon	1	0	1	0	0	0	0	1	0	0	?	?	0	0	0	2	0	0	0
Ianthasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Edaphosaurus	1	?	1	0	0	0	1	1	0	0	?	?	0	0	1	0	0	0	0
Hylonomus	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	0	0	1	1
Anthracodromeus	0	0	0	0	0	0	0	2	1	-	?	?	0	0	?	?	?	?	?
Paleothyris	0	0	0	0	0	?	?	?	1	-	?	?	1	0	0	0	0	[01]	1
Protorothyris	0	0	0	0	0	0	?	?	1	-	?	?	1	0	0	0	0	?	?
Petrolacosaurus	0	0	0	0	0	0	0	0	1	-	0	0	0	0	0	0	0	1	1
Araeoscelis	0	0	0	0	0	0	0	2	0	0	?	?	0	0	0	?	0	0	0
Orovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1
Archaeovenator	?	0	0	?	0	?	?	?	?	?	?	?	?	?	0	0	1	0	?
Ascendonanus	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	1	1	?
Aerosaurus	1	?	?	?	?	?	0	0	0	?	0	0	0	0	0	0	1	1	1
Apsisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Heleosaurus	0	0	0	0	0	?	0	0	?	?	?	?	?	?	?	0	1	1	1
Mesenosaurus	0	0	0	0	0	0	0	0	?	?	?	?	0	0	0	0	1	1	1
Mycterosaurus	0	0	1	0	0	0	0	?	?	?	?	?	0	?	?	?	1	1	1
Elliotsmithia	0	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Varanops	1	0	1	?	0	?	?	?	0	0	0	0	?	1	0	0	1	1	1
Varanodon	1	0	?	?	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?
Watongia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	0	0	0	1	0	?	0	0	0	1	0	1	1	0	0	0	[01]	0	0
Acerosodont.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lanthanolania	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1
Claudiosaurus	?	1	-	-	-	-	0	0	1	-	?	?	0	0	0	?	0	0	0
Prolacerta	0	1	-	-	-	-	0	0	0	1	1	1	1	0	0	0	1	0	0
Proterosuchus	?	0	1	0	0	?	?	?	0	?	1	1	?	0	?	?	?	0	0
Thuringothyris	0	0	0	1	0	?	?	?	1	-	?	?	0	0	?	0	0	0	0
Captorhinus	0	0	0	1	0	0	0	0	[01]	-	?	?	?	0	0	2	0	0	1
Protocaptorhinus	0	0	0	1	0	0	0	0	1	-	?	?	?	0	0	?	?	?	?
Romeria	0	0	0	1	0	0	?	?	1	-	?	?	?	0	0	2	0	0	?
Euconcordia	0	0	0	1	0	0	0	?	1	-	?	?	?	?	?	0	0	1	1
Reiszorhinus	0	0	0	0	0	0	?	?	?	-	?	?	?	?	?	?	?	?	?
Eudibamus	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	0
Mesosaurus	0	0	0	0	1	?	0	0	1	-	?	?	0	0	?	2	1	0	0
Erpetonyx	?	0	0	?	1	?	0	0	?	?	?	?	0	?	?	?	?	?	?
Belebey	?	0	0	?	1	?	0	?	1	-	?	?	0	1	?	0	0	0	0
Macroleter	0	0	[01]	0	1	?	?	?	0	-	?	?	1	1	?	2	0	0	0
Milleretta	0	0	0	0	0	?	?	0	1	-	?	?	0	0	0	?	0	1	1
Acleistorhinus	?	0	1	0	0	?	1	?	0	1	?	?	0	0	?	?	?	1	1
Colobomycter	?	0	0	0	1	?	?	?	?	-	?	?	?	?	?	2	0	1	1
Procolophon	0	1	-	-	-	1	0	0	0	-	?	?	0	0	0	2	0	?	0
Owenetta	0	0	0	0	1	0	1	0	0	-	?	?	0	1	0	2	0	0	0

Character/Taxon	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138
Gephyrostegus	?	?	0	0	?	?	0	0	?	0	-	0	0	0	0	0	0	0	0
Seymouria	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1
Tseajaia	?	?	0	0	0	1	0	1	?	0	-	1	1	1	0	0	0	0	0
Limnoscelis	?	?	0	0	0	1	1	1	0	1	1	0	1	0	0	0	1	0	1
Oedaleops	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eothyris	?	?	0	0	0	?	?	1	?	?	?	?	?	?	0	0	1	0	?
Vaughnictis	?	?	?	?	?	?	0	1	?	?	?	0	1	?	0	0	0	?	?
Eocasea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euromycter	?	0	0	0	0	0	?	?	?	?	?	0	1	?	0	0	0	1	?
Casea	0	0	0	0	?	?	0	1	?	0	-	0	1	2	0	0	0	1	0
Ennatosaurus	?	?	0	0	?	?	0	1	1	0	-	0	1	?	0	0	1	1	0
Echinerpeton	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Archaeothyris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Varanosaurus	0	1	0	0	1	1	0	1	1	?	?	1	1	2	0	0	2	0	0
Ophiacodon	0	1	1	0	1	0	?	1	1	0	-	1	1	2	0	0	2	0	?
Haptodus	0	1	0	0	1	0	0	1	1	0	-	0	1	2	0	0	1	0	0
Secodontosaurus	0	1	1	0	1	0	1	1	1	?	?	0	1	2	0	0	2	0	0
Dimetrodon	0	1	1	0	1	0	1	1	1	1	1	0	1	2	0	0	2	0	0
Ianthasaurus	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0	0	?	?
Edaphosaurus	0	1	0	0	0	0	0	1	?	0	-	0	1	2	?	0	0	?	0
Hylonomus	?	?	?	0	?	0	0	1	?	?	?	0	1	0	0	0	0	?	?
Anthracodromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paleothyris	?	?	0	0	0	0	0	1	0	?	?	0	1	0	0	0	1	0	?
Protorothyris	?	?	0	0	0	0	0	1	1	1	0	0	1	0	0	0	2	0	1
Petrolacosaurus	?	?	0	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1	1
Araeoscelis	0	0	0	0	0	0	?	1	?	?	?	?	?	?	0	0	1	1	?
Orovenator	0	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	0	1
Archaeovenator	?	?	0	0	0	0	?	1	0	1	?	0	1	1	0	0	2	0	1
Ascendonanus	?	?	?	0	?	0	0	?	?	?	?	0	1	?	0	0	2	?	?
Aerosaurus	?	?	0	1	0	0	?	?	?	?	?	?	?	?	?	0	2	?	?
Apsisaurus	?	?	0	0	?	?	?	?	?	?	?	?	?	?	0	0	1	0	?
Heleosaurus	?	?	0	0	0	1	0	1	?	?	?	0	1	1	0	0	2	0	?
Mesenosaurus	?	?	0	1	0	1	0	1	0	1	1	0	1	1	0	0	1	1	0
Mycterosaurus	0	0	0	0	0	1	0	1	?	?	?	0	1	?	0	0	1	0	?
Elliotsmithia	?	?	?	?	?	?	?	1	?	?	?	?	?	?	0	0	2	0	?
Varanops	?	0	0	0	0	0	?	1	?	?	?	?	?	?	?	0	1	?	?
Varanodon	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0	2	?	?
Watongia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	0	0	0	0	?	0	0	1	1	1	1	0	1	0	0	0	2	0	?
Acerosodont.	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
Lanthanolania	0	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
Claudiosaurus	?	?	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	1	1
Prolacerta	0	0	0	0	[12]	0	0	1	1	1	1	0	1	0	0	0	2	0	1
Proterosuchus	0	0	?	?	2	0	0	1	1	1	1	0	1	1	0	0	2	0	1
Thuringothyris	0	?	?	0	?	?	1	1	1	1	?	0	1	?	0	0	0	0	?
Captorhinus	0	0	0	0	0	0	1	1	1	1	1	0	1	2	0	0	0	0	1
Protocaptorhinus	?	?	?	?	?	?	?	1	?	?	?	?	?	?	0	0	0	0	?
Romeria	?	?	?	?	?	?	1	1	?	1	0	0	1	2	0	0	0	0	1
Euconcordia	0	0	0	0	0	0	0	1	?	?	?	0	1	0	0	0	0	0	1
Reiszorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eudibamus	?	?	?	?	0	?	1	1	?	?	?	1	1	?	1	1	-	2	?
Mesosaurus	?	?	0	0	0	1	0	1	?	1	1	0	1	0	0	0	0	0	0
Erpetonyx	?	?	?	?	0	?	?	?	0	?	?	?	?	?	0	1	?	0	?
Belebey	0	1	0	?	0	?	1	1	?	0	-	1	1	2	1	1	-	2	0
Macroleter	?	?	?	0	0	0	0	1	?	1	1	0	1	0	0	0	2	0	0
Milleretta	1	-	?	?	2	?	0	1	1	?	?	0	1	?	0	0	1	0	?
Acleistorhinus	?	?	?	?	0	0	0	1	1	1	1	0	1	0	0	0	1	0	?
Colobomycter	?	?	?	0	?	?	0	1	1	1	1	0	1	0	0	0	1	0	0
Procolophon	1	-	0	?	2	0	0	1	1	1	1	0	1	0	0	1	-	1	0
Owenetta	?	?	0	0	0	0	0	1	1	1	1	0	1	0	0	1	-	1	0

Character/Taxon	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157
Gephyrostegus	0	?	1	?	0	0	0	0	0	-	?	0	?	1	?	?	?	?	?
Seymouria	0	0	0	?	0	0	0	?	1	0	0	0	0	?	?	1	?	1	-
Tseajaia	0	?	0	?	0	0	1	0	0	-	1	0	0	1	0	0	0	0	?
Limnoscelis	?	1	0	?	0	0	1	0	0	?	0	0	0	0	0	0	?	0	?
Oedaleops	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?
Eothyris	?	1	0	?	?	?	?	?	0	-	0	0	0	1	0	0	?	?	?
Vaughnictis	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eocasea	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	?	0	?
Euromycter	0	1	0	?	?	0	?	?	0	-	0	0	0	1	0	0	1	0	0
Casea	0	1	0	?	0	?	?	?	0	-	0	0	?	1	0	0	1	0	0
Ennatosaurus	1	1	0	0	1	0	0	1	0	-	2	0	0	1	?	0	?	?	?
Echinerpeton	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Archaeothyris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?
Varanosaurus	1	0	0	?	1	0	1	0	0	-	1	0	0	1	?	0	0	0	0
Ophiacodon	1	1	0	1	1	0	?	0	0	-	1	0	0	1	0	0	0	0	1
Haptodus	1	0	0	1	1	0	1	?	0	-	0	1	0	0	0	0	0	0	1
Secodontosaurus	1	0	0	1	1	0	1	0	0	-	0	0	0	0	0	0	0	0	1
Dimetrodon	1	0	0	1	1	0	0	0	0	-	0	1	0	0	0	0	0	0	1
Ianthasaurus	?	?	0	1	?	?	?	?	?	?	?	1	1	?	0	0	?	?	?
Edaphosaurus	0	0	0	1	1	0	0	1	0	-	0	1	1	0	0	0	0	0	1
Hylonomus	?	?	0	0	?	?	?	?	?	?	0	0	?	?	?	?	0	0	?
Anthracodromeus	?	?	?	?	?	?	?	?	0	-	?	?	?	?	?	?	?	?	?
Paleothyris	0	0	0	0	0	0	?	?	0	-	0	0	?	1	0	0	0	0	?
Protorothyris	0	0	0	?	0	0	0	?	0	-	0	0	0	0	?	0	?	0	?
Petrolacosaurus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	?
Araeoscelis	0	1	0	?	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Orovenator	1	1	0	0	0	0	0	1	1	0	?	0	0	?	0	?	0	1	-
Archaeovenator	?	1	0	0	0	0	1	1	0	-	?	0	?	0	0	0	?	?	?
Ascendonanus	?	?	0	?	?	0	?	?	?	?	0	0	0	1	?	?	?	?	?
Aerosaurus	?	1	0	?	?	?	?	?	?	?	?	0	?	2	0	0	?	0	0
Apsisaurus	?	1	0	0	?	0	1	?	0	?	?	?	?	?	0	?	?	?	?
Heleosaurus	?	?	0	0	?	0	?	?	0	-	0	0	?	1	?	0	?	?	?
Mesenosaurus	1	0	0	0	0	0	1	0	0	-	0	0	0	1	0	0	0	1	-
Mycterosaurus	?	?	0	?	?	?	?	?	?	?	0	0	?	0	0	0	0	0	0
Elliotsmithia	?	?	0	?	?	0	?	?	?	?	0	0	?	1	0	0	?	?	?
Varanops	?	1	0	?	?	?	?	?	0	-	1	0	0	2	0	0	0	0	0
Varanodon	?	?	0	?	?	?	?	?	?	?	1	0	?	2	0	0	?	?	?
Watongia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	-
Acerosodont.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?
Lanthanolania	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Claudiosaurus	?	1	0	?	0	0	1	1	1	0	?	0	0	0	0	0	?	?	?
Prolacerta	2	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	-
Proterosuchus	2	?	0	0	?	0	1	1	1	0	1	0	?	1	1	0	1	1	-
Thuringothyris	0	?	0	?	1	0	?	1	?	?	0	?	?	0	?	0	0	0	0
Captorhinus	0	0	0	0	0	1	-	-	1	1	0	0	0	0	0	0	0	0	0
Protocaptorhinus	?	?	0	?	0	1	-	-	1	1	0	0	?	0	0	0	0	0	?
Romeria	0	0	0	?	0	1	-	-	1	1	0	0	?	0	?	0	0	0	0
Euconcordia	0	1	0	?	0	?	?	?	1	1	0	0	0	?	?	0	0	0	1
Reiszorhinus	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	0	?	?	?
Eudibamus	?	?	0	?	?	0	1	?	?	?	0	?	?	?	?	0	?	?	?
Mesosaurus	1	1	1	0	0	1	-	-	0	?	1	0	0	0	?	0	?	0	?
Erpetonyx	?	?	0	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?
Belebey	1	1	0	0	1	0	1	0	1	1	0	0	0	0	?	0	?	?	?
Macroleter	1	1	0	0	1	0	1	1	1	1	2	0	?	?	?	1	?	1	-
Milleretta	?	1	0	?	0	0	1	0	1	1	2	0	0	0	?	0	0	1	-
Acleistorhinus	0	1	0	?	0	0	1	?	1	1	2	0	1	0	?	0	0	?	?
Colobomycter	0	1	1	?	1	0	1	0	?	?	2	0	?	3	0	0	?	?	?
Procolophon	0	1	0	0	0	0	1	0	1	1	2	1	1	3	0	1	?	1	-
Owenetta	0	1	0	0	0	0	1	?	1	1	2	0	0	3	0	1	?	?	?

Character/Taxon	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176
Gephyrostegus	0	1	0	1	0	?	?	?	?	0	0	1	1	1	0	0	0	1	?
Seymouria	0	1	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0
Tseajaia	0	0	0	0	0	0	-	-	-	0	0	1	1	0	0	1	?	?	0
Limnoscelis	0	0	0	0	0	0	-	-	-	0	0	1	1	0	1	0	0	1	0
Oedaleops	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Eothyris	0	0	1	0	0	0	-	-	-	0	?	?	?	?	0	0	?	0	?
Vaughnictis	?	0	?	0	0	?	?	?	?	0	?	?	?	?	0	0	?	?	?
Eocasea	?	?	?	0	0	0	-	-	-	0	?	?	?	?	?	?	?	?	?
Euromycter	1	0	?	?	?	0	-	-	-	0	?	?	?	?	?	1	?	?	0
Casea	0	0	1	0	0	0	-	-	-	0	0	0	1	?	1	1	?	?	0
Ennatosaurus	1	0	1	0	0	0	-	-	-	0	0	0	1	1	1	1	0	0	0
Echinerpeton	2	1	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	?	?
Archaeothyris	2	1	?	?	?	?	?	?	?	1	?	?	?	?	0	?	0	?	?
Varanosaurus	2	1	0	0	0	0	-	-	-	1	0	0	1	1	0	0	0	0	1
Ophiacodon	2	1	0	0	0	0	-	-	-	1	0	0	1	1	0	0	0	0	1
Haptodus	0	0	0	1	1	1	0	0	2	0	1	-	-	-	1	0	1	0	0
Secodontosaurus	2	1	0	1	1	1	1	1	2	0	1	-	-	-	0	0	1	0	1
Dimetrodon	0	1	0	1	1	1	1	1	2	0	1	-	-	-	1	0	0	0	0
Ianthasaurus	0	0	0	1	?	?	?	?	?	0	?	?	?	?	1	0	1	?	0
Edaphosaurus	1	0	1	1	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0
Hylonomus	2	1	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	1
Anthracodromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paleothyris	2	0	0	0	?	0	-	-	-	0	?	?	?	?	0	0	0	0	?
Protorothyris	2	0	0	0	0	0	-	-	-	0	0	1	0	1	0	0	0	0	1
Petrolacosaurus	2	0	0	0	0	0	-	-	-	0	?	?	?	?	0	0	1	?	1
Araeoscelis	0	0	0	0	1	0	-	-	-	0	1	-	-	-	0	0	1	?	1
Orovenator	2	0	0	0	0	?	?	?	?	0	0	0	1	1	0	0	1	1	1
Archaeovenator	2	0	0	0	0	1	0	?	0	0	0	0	1	1	0	0	1	1	1
Ascendonanus	2	0	0	0	?	1	0	?	?	0	?	?	?	?	0	0	0	?	?
Aerosaurus	2	0	0	?	?	1	0	0	0	0	0	0	1	1	0	0	0	0	1
Apsisaurus	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Heleosaurus	2	0	0	0	?	1	0	0	?	0	?	?	?	?	0	0	?	?	?
Mesenosaurus	2	0	0	0	0	1	0	0	0	0	?	?	?	?	0	0	0	1	1
Mycterosaurus	2	0	0	0	0	?	?	?	?	0	?	?	?	?	?	0	?	1	?
Elliotsmithia	?	0	?	?	?	1	0	0	?	0	?	?	?	?	0	?	1	?	?
Varanops	2	0	0	2	-	1	0	0	1	0	0	0	1	1	0	0	0	?	1
Varanodon	2	0	0	2	-	1	0	0	1	0	?	?	?	?	0	?	0	?	?
Watongia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	2	0	?	?	?	?	?	?	?	0	?	?	?	?	0	0	0	?	1
Acerosodont.	?	?	?	0	0	1	0	?	1	?	?	?	?	?	?	?	?	?	?
Lanthanolania	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
Claudiosaurus	2	0	0	0	0	0	-	-	-	0	0	0	1	1	0	0	0	0	1
Prolacerta	2	0	0	0	0	1	1	0	1	0	?	?	?	?	0	1	0	0	1
Proterosuchus	2	1	0	0	?	1	1	0	1	1	?	?	?	?	0	1	0	0	?
Thuringothyris	?	?	?	?	?	0	-	-	-	?	?	?	?	?	0	0	?	0	0
Captorhinus	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0
Protocaptorhinus	0	0	1	0	?	1	0	?	?	0	?	?	?	?	0	?	?	?	?
Romeria	0	0	1	0	0	0	-	-	-	0	?	?	?	?	0	1	1	0	0
Euconcordia	?	0	?	?	?	0	-	-	-	0	?	?	?	?	0	0	0	?	1
Reiszorhinus	0	0	1	0	0	0	-	-	-	0	0	1	0	0	1	0	1	0	0
Eudibamus	?	?	?	3	1	0	-	-	-	?	0	?	?	?	?	?	?	?	?
Mesosaurus	2	0	0	0	?	1	1	0	0	0	1	-	-	-	0	0	2	1	0
Erpetonyx	?	?	?	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	1
Belebey	0	0	0	3	1	0	-	-	-	0	0	0	1	1	1	0	1	0	1
Macroleter	?	?	?	?	?	1	0	?	0	0	0	1	0	1	?	?	?	?	1
Milleretta	0	0	0	0	1	1	0	1	0	0	0	1	0	1	0	0	0	0	?
Acleistorhinus	0	?	?	?	?	1	0	1	?	0	?	?	?	?	?	?	?	0	1
Colobomycter	0	0	0	0	?	1	0	?	?	0	0	1	1	0	0	0	1	0	1
Procolophon	1	0	1	3	0	1	1	0	?	0	0	1	1	1	0	1	0	0	1
Owenetta	2	0	1	3	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1

Character/Taxon	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195
Gephyrostegus	?	0	0	0	0	0	?	0	?	?	0	0	0	-	?	0	1	?	0
Seymouria	?	0	0	0	0	0	3	0	?	?	?	?	1	0	?	0	1	?	0
Tseajaia	?	1	0	1	1	0	0	0	0	0	0	0	?	?	0	0	1	0	0
Limnoscelis	1	1	0	1	1	0	0	0	?	?	0	0	0	-	0	0	1	0	0
Oedaleops	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eothyris	?	1	?	1	?	?	0	0	0	0	0	0	0	-	?	?	?	?	?
Vaughnictis	?	?	?	?	1	0	?	0	?	?	?	?	0	-	?	?	?	?	?
Eocasea	?	?	?	?	?	?	0	0	?	?	0	0	?	?	?	0	0	0	?
Euromycter	1	0	?	?	?	0	?	1	0	0	?	?	?	?	?	0	?	0	0
Casea	0	1	?	1	1	0	0	1	0	0	0	0	?	?	0	0	1	0	0
Ennatosaurus	1	0	?	1	1	0	0	1	?	?	0	0	0	?	0	?	?	?	?
Echinerpeton	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Archaeothyris	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Varanosaurus	?	1	1	1	?	1	1	1	?	?	0	0	1	0	?	?	0	0	0
Ophiacodon	0	1	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0
Haptodus	0	0	?	1	1	0	1	1	?	?	0	0	0	-	1	?	0	?	0
Secodontosaurus	0	0	1	1	1	1	2	1	?	?	0	0	?	-	1	0	?	0	1
Dimetrodon	0	0	0	1	1	1	2	1	?	?	0	0	0	-	1	?	0	0	1
Ianthasaurus	?	?	?	1	?	?	1	?	?	?	0	0	?	?	1	?	0	?	?
Edaphosaurus	0	0	0	1	1	0	1	1	?	?	0	0	0	-	1	?	?	?	?
Hylonomus	?	?	?	?	1	0	?	?	?	?	?	?	?	?	0	0	0	0	0
Anthracodromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?
Paleothyris	0	1	?	1	2	1	3	1	0	0	0	0	0	-	0	0	0	0	0
Protorothyris	0	1	?	1	?	?	0	0	?	?	0	0	0	-	0	0	?	?	?
Petrolacosaurus	0	1	1	0	2	1	0	0	0	0	0	0	0	-	0	0	1	0	0
Araeoscelis	0	0	0	1	1	1	0	1	0	0	0	?	0	-	?	0	0	?	?
Orovenator	0	1	0	1	2	1	0	0	0	0	1	0	1	1	0	0	?	?	?
Archaeovenator	0	1	0	1	2	1	0	0	0	0	0	0	?	?	0	0	0	?	?
Ascendonanus	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	?	?
Aerosaurus	?	1	?	?	?	?	3	0	0	0	1	0	1	1	0	0	0	0	?
Apsisaurus	?	?	?	?	?	?	0	0	0	0	1	0	1	1	?	0	?	?	?
Heleosaurus	?	1	?	1	?	?	3	1	0	0	?	?	?	?	?	?	?	?	?
Mesenosaurus	0	1	1	1	2	1	3	0	0	0	0	0	1	1	0	0	0	?	?
Mycterosaurus	?	?	?	1	?	1	?	1	0	0	1	0	1	1	?	0	?	?	?
Elliotsmithia	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Varanops	?	1	0	1	1	1	3	0	?	0	1	0	1	1	0	0	0	?	?
Varanodon	?	?	?	?	?	?	3	?	?	0	1	0	?	?	?	0	0	?	1
Watongia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	?	1	?	1	?	?	3	?	0	0	?	?	0	-	?	0	1	?	?
Acerosodont.	?	?	?	1	2	1	?	?	?	?	1	0	?	?	?	0	1	0	0
Lanthanolania	?	?	?	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Claudiosaurus	0	1	0	1	2	1	?	1	?	?	?	?	0	-	?	?	1	1	?
Prolacerta	0	1	1	1	2	1	3	0	1	1	?	?	0	-	?	1	1	1	?
Proterosuchus	?	1	?	1	2	1	?	0	1	1	?	?	0	-	?	1	?	1	?
Thuringothyris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?
Captorhinus	0	1	1	1	2	1	3	1	0	0	0	0	1	0	0	0	1	0	0
Protocaptorhinus	?	1	?	1	2	?	3	?	?	?	?	?	?	?	?	?	?	0	?
Romeria	?	1	?	1	2	1	?	1	?	?	?	?	0	-	?	?	?	?	?
Euconcordia	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Reiszorhinus	?	1	1	1	2	1	0	1	0	0	0	0	1	0	?	?	?	?	?
Eudibamus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Mesosaurus	?	0	?	1	2	1	?	0	0	0	0	0	0	-	?	?	0	0	?
Erpetonyx	?	?	?	?	?	?	?	0	?	?	0	0	?	?	?	?	0	?	?
Belebey	0	1	0	1	2	1	?	1	0	0	0	1	0	-	?	?	?	?	?
Macroleter	?	1	?	1	2	?	?	1	0	0	0	1	?	?	?	?	?	?	?
Milleretta	0	1	1	1	2	1	?	0	?	1	?	?	0	-	?	1	1	?	0
Acleistorhinus	?	1	?	1	?	?	0	1	0	0	?	?	?	?	?	?	?	?	?
Colobomycter	?	?	?	1	?	?	0	?	0	0	0	0	?	?	?	?	?	?	?
Procolophon	0	1	1	1	2	1	?	1	0	0	0	1	0	-	?	?	0	0	0
Owenetta	0	1	1	1	2	1	?	1	0	0	0	0	0	-	?	?	0	?	?

Character/Taxon	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213
Gephyrostegus	0	0	0	?	?	0	1	0	0	0	0	0	0	0	0	-	0	0
Seymouria	?	?	0	0	?	0	[01]	0	1	0	?	0	1	?	0	-	0	0
Tseajaia	0	0	?	?	1	0	1	0	0	0	0	1	0	?	?	?	0	0
Limnoscelis	0	0	?	?	?	0	1	?	0	?	0	0	0	0	0	-	0	0
Oedaleops	?	?	?	?	?	?	?	?	?	?	0	?	?	1	?	?	0	?
Eothyris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Vaughnictis	?	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?	?	?
Eocasea	2	0	?	0	0	0	1	?	?	0	0	0	0	?	0	-	0	0
Euromycter	2	0	?	?	0	0	1	0	1	?	?	?	?	?	?	?	?	?
Casea	0	0	?	0	0	0	1	0	1	0	0	0	1	1	0	-	0	0
Ennatosaurus	2	0	?	0	0	?	?	?	1	?	0	0	1	?	?	?	0	0
Echinerpeton	0	0	?	?	1	0	1	?	?	0	1	1	?	1	?	?	0	0
Archaeothyris	0	1	0	0	1	0	1	?	?	0	1	1	1	1	0	-	0	0
Varanosaurus	0	0	?	0	1	?	?	?	?	?	0	1	1	1	0	-	0	0
Ophiacodon	0	1	0	0	1	0	1	0	1	0	0	3	1	1	0	-	1	0
Haptodus	0	1	0	0	1	0	1	0	0	0	0	0	1	1	0	-	1	0
Secodontosaurus	1	1	?	1	2	0	1	?	?	0	1	2	?	1	0	-	2	0
Dimetrodon	1	2	?	[01]	2	1	1	0	1	0	[01]	2	1	2	0	-	2	0
Ianthasaurus	2	2	?	0	?	?	?	?	0	?	1	1	0	2	2	-	2	1
Edaphosaurus	2	0	?	0	?	0	?	?	1	?	1	0	1	2	2	-	2	1
Hylonomus	0	1	0	?	?	0	?	0	0	0	?	?	?	0	0	-	0	0
Anthracodromeus	0	1	0	0	?	0	1	0	1	0	0	1	1	1	?	?	0	0
Paleothyris	0	1	0	0	1	0	1	0	1	0	0	1	0	0	?	?	0	0
Protorothyris	0	1	0	0	?	0	1	0	1	0	1	?	0	[01]	?	?	0	0
Petrolacosaurus	0	0	0	1	1	1	1	1	1	1	0	1	0	1	0	-	0	0
Araeoscelis	1	0	0	1	1	1	1	1	0	1	1	1	0	1	0	-	0	0
Orovenator	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?
Archaeovenator	0	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0	0	0
Ascendonanus	?	0	?	0	?	?	?	?	?	?	?	1	0	1	?	?	0	0
Aerosaurus	0	1	0	[01]	1	1	1	0	1	0	0	1	0	1	?	?	1	0
Apsisaurus	?	?	?	0	1	0	1	?	?	0	?	1	0	1	?	?	0	?
Heleosaurus	0	?	0	0	1	1	1	0	0	0	1	3	0	1	?	?	0	0
Mesenosaurus	?	?	?	?	1	1	1	0	?	0	?	1	0	1	?	?	0	0
Mycterosaurus	?	?	?	0	1	1	1	0	0	0	0	1	0	1	1	0	1	0
Elliotsmithia	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Varanops	0	1	?	1	1	1	1	0	?	0	0	1	0	1	1	1	1	0
Varanodon	0	1	?	1	1	1	1	0	1	0	?	1	0	1	1	1	1	0
Watongia	?	?	?	?	1	?	1	0	?	0	0	1	0	1	?	?	1	0
Youngina	?	?	0	0	?	0	1	0	0	0	0	?	0	1	0	-	0	0
Acerosodont.	?	?	?	0	1	?	1	?	?	0	0	?	0	1	?	?	[01]	0
Lanthanolania	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Claudiosaurus	0	0	0	0	?	0	1	0	1	0	1	?	0	1	0	-	0	0
Prolacerta	0	0	1	1	1	0	1	1	?	1	0	[01]	1	1	0	-	0	0
Proterosuchus	?	?	1	1	1	1	1	1	0	1	0	0	1	1	?	?	?	0
Thuringothyris	?	0	0	?	1	0	?	?	1	0	1	1	0	?	?	?	0	0
Captorhinus	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	-	0	0
Protocaptorhinus	?	?	?	?	1	0	0	?	1	?	?	?	?	0	?	?	?	0
Romeria	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euconcordia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Reisaurhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eudibamus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Mesosaurus	?	?	0	0	[01]	0	?	?	0	0	1	0	0	[01]	0	-	1	0
Erpetonyx	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Belebey	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macroleter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Milleretta	0	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?	0	0
Acleistorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Colobomycter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Procolophon	0	1	?	0	1	0	1	0	1	0	?	3	?	?	0	-	1	0
Owenetta	?	?	?	0	?	0	1	0	1	0	?	?	0	0	0	-	0	0

Character/Taxon	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231
Gephyrostegus	?	?	?	?	?	0	0	?	?	?	?	?	?	0	?	?	?	-
Seymouria	1	0	1	0	0	0	0	0	0	0	0	0	1	2	0	1	0	-
Tseajaia	1	0	1	0	1	0	0	0	0	0	1	?	0	0	?	1	2	0
Limnoscelis	1	0	1	0	1	0	0	0	?	0	2	?	0	1	1	0	2	0
Oedaleops	?	?	0	?	?	?	?	?	?	?	?	?	0	0	0	0	2	0
Eothyris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Vaughnictis	?	?	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Eocasea	0	?	0	?	?	0	0	0	0	0	1	?	?	?	?	?	?	?
Euromycter	?	?	?	?	?	?	0	?	?	?	?	?	0	0	0	?	2	0
Casea	0	0	0	0	0	1	0	1	0	1	1	0	?	?	0	0	2	0
Ennatosaurus	?	0	?	0	?	1	0	1	?	?	?	?	?	?	0	0	2	0
Echinerpeton	?	1	0	0	?	0	?	?	?	?	?	?	?	?	0	1	2	0
Archaeothyris	0	?	0	?	0	0	?	?	?	0	?	0	?	?	?	?	?	?
Varanosaurus	1	1	1	0	?	?	0	0	?	0	1	?	?	?	?	?	?	?
Ophiacodon	0	1	0	1	0	0	0	0	0	0	3	0	0	0	0	1	[12]	1
Haptodus	0	0	2	0	0	0	0	?	?	1	1	?	1	0	0	1	2	-
Secodontosaurus	0	0	2	1	0	?	0	1	?	?	?	?	?	?	?	?	?	?
Dimetrodon	0	0	2	1	0	0	0	1	?	1	3	0	1	3	0	[01]	1	-
Ianthasaurus	0	0	2	0	0	0	0	?	?	0	?	?	?	?	?	?	?	?
Edaphosaurus	0	0	0	1	0	1	0	1	?	1	3	1	1	3	0	?	1	?
Hylonomus	0	?	0	?	0	?	0	?	?	0	?	?	1	0	?	?	?	?
Anthracodromeus	0	?	0	?	0	0	0	0	?	0	?	?	?	?	?	?	?	?
Paleothyris	?	0	0	0	0	0	0	1	?	0	?	?	1	0	1	?	2	0
Protorothyris	?	?	0	0	0	0	0	1	?	0	?	?	1	2	0	0	2	1
Petrolacosaurus	1	1	2	?	0	0	0	?	0	0	0	1	0	2	1	1	2	1
Araeoscelis	1	0	2	?	0	0	0	0	0	0	0	1	?	?	0	0	2	1
Orovenator	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Archaeovenator	0	?	0	?	1	0	0	1	0	0	0	0	0	0	1	0	2	1
Ascendonanus	?	?	0	0	1	0	0	0	0	0	?	?	?	0	?	0	2	1
Aerosaurus	0	?	2	?	0	0	0	0	0	1	?	?	?	2	?	0	2	0
Apsisaurus	?	1	2	?	0	?	?	?	?	0	0	?	?	0	?	?	?	?
Heleosaurus	0	?	?	?	1	0	1	?	?	0	?	?	?	0	?	0	?	?
Mesenosaurus	0	?	?	?	1	0	0	?	?	0	?	?	?	?	?	?	?	?
Mycterosaurus	0	?	2	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Elliotsmithia	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
Varanops	0	?	2	0	0	0	0	0	?	0	?	?	0	2	0	1	1	-
Varanodon	0	1	2	1	0	0	0	0	0	0	2	?	0	0	?	?	?	?
Watongia	0	1	2	1	?	?	?	?	?	?	?	?	0	0	?	?	?	?
Youngina	0	1	0	0	1	0	1	?	0	0	1	2	1	0	0	?	2	0
Acerosodont.	0	1	0	?	1	0	0	?	?	0	?	?	?	?	?	?	?	?
Lanthanolania	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Claudiosaurus	0	?	0	?	1	0	0	1	0	0	0	?	?	0	0	?	2	1
Prolacerta	1	1	2	1	1	0	0	1	1	0	0	2	?	?	1	1	2	0
Proterosuchus	0	1	2	?	1	0	0	1	1	0	[02]	2	?	?	1	0	2	0
Thuringothyris	?	?	?	?	0	0	0	?	?	?	?	?	?	?	0	0	2	1
Captorhinus	1	0	1	0	0	0	0	0	0	0	?	1	1	1	0	0	2	0
Protocaptorhinus	1	?	1	0	?	0	0	?	?	?	?	?	?	?	?	0	2	1
Romeria	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euconcordia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Reiszorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eudibamus	?	?	1	0	?	-	0	0	0	0	?	?	?	?	?	?	?	?
Mesosaurus	0	0	1	0	1	0	0	1	0	0	0	1	0	2	0	1	2	0
Erpetonyx	?	?	2	0	1	0	0	1	?	1	?	?	?	?	?	?	?	0
Belebey	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macroleter	?	?	1	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0
Milleretta	0	?	0	0	1	0	0	?	?	0	?	?	?	?	0	0	2	1
Acleistorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Colobomycter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Procolophon	0	?	1	?	1	0	0	?	0	1	?	?	?	0	0	1	2	0
Owenetta	0	?	1	0	0	?	0	1	0	1	?	?	?	0	0	?	2	0

Character/Taxon	232	233	234	235	236	237	238	239	240	241	242	243	244	245	246	247	248	249
Gephyrostegus	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?
Seymouria	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
Tseajaia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Limnoscelis	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
Oedaleops	1	-	1	0	?	?	?	0	?	1	0	0	0	0	?	?	0	0
Eothyris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Vaughnictis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eocasea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euromycter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
Casea	1	-	0	?	1	0	0	0	0	1	0	0	0	2	0	0	?	0
Ennatosaurus	1	-	0	?	?	0	0	0	0	?	?	0	0	2	0	?	?	?
Echinerpeton	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?	?	?	?
Archaeothyris	?	?	?	?	?	?	?	0	?	1	0	0	0	0	0	?	?	?
Varanosaurus	?	?	?	?	1	0	0	?	1	?	?	?	?	?	?	1	?	?
Ophiacodon	0	0	0	1	1	0	0	0	1	1	0	0	2	0	0	1	1	0
Haptodus	0	1	0	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0
Secodontosaurus	0	1	0	0	1	1	0	?	1	1	?	0	0	0	?	?	?	?
Dimetrodon	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	[12]	1	0
Ianthasaurus	?	?	?	?	1	?	?	?	?	1	0	0	0	0	?	?	?	?
Edaphosaurus	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	0
Hylonomus	?	?	?	?	?	?	0	0	?	1	1	0	?	3	-	?	?	?
Anthracodromeus	?	?	?	?	?	?	?	?	?	1	1	0	1	0	?	0	0	0
Paleothyris	0	1	0	?	?	0	0	0	?	1	1	0	0	0	0	0	0	0
Protorothyris	0	1	0	0	?	1	0	?	?	?	?	0	0	3	-	?	?	?
Petrolacosaurus	0	1	1	0	1	1	0	0	1	1	1	0	0	0	1	2	1	0
Araeoscelis	0	1	1	0	1	1	1	0	1	1	1	0	0	1	1	2	?	0
Orovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Archaeovenator	1	-	0	0	?	[01]	?	?	?	?	?	?	?	?	?	?	?	?
Ascendonanus	?	?	?	?	?	0	?	?	?	?	1	?	1	1	?	0	?	0
Aerosaurus	0	1	?	1	1	[01]	0	1	0	1	0	0	0	0	0	1	1	0
Apsisaurus	1	?	0	?	?	0	0	?	?	1	1	0	1	0	1	1	1	0
Heleosaurus	1	-	0	?	?	0	0	?	?	?	1	?	1	1	1	2	1	0
Mesenosaurus	?	?	?	?	?	0	0	?	?	?	?	0	?	?	?	?	?	0
Mycterosaurus	1	-	0	0	?	?	0	?	?	?	?	0	?	0	?	?	?	0
Elliotsmithia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Varanops	[01]	1	0	1	1	0	0	1	0	1	0	0	0	0	0	2	?	0
Varanodon	?	?	0	?	?	?	?	?	?	1	0	0	0	?	?	0	1	0
Watongia	?	?	0	?	?	?	?	?	0	1	0	0	0	0	?	1	0	0
Youngina	1	-	0	1	0	0	1	1	?	1	1	0	1	0	1	1	1	1
Acerosodont.	?	?	?	?	?	?	?	1	?	?	?	0	0	1	1	?	1	1
Lanthanolania	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Claudiosaurus	?	?	?	?	0	0	0	1	?	1	1	0	0	0	1	0	1	?
Prolacerta	1	-	0	1	0	0	?	2	?	1	1	1	1	0	1	2	1	0
Proterosuchus	1	-	0	0	0	0	?	2	?	?	?	1	?	?	?	2	1	0
Thuringothyris	?	?	?	?	?	?	?	1	?	1	0	0	0	3	-	2	0	0
Captorhinus	0	0	0	0	1	0	0	0	0	1	0	0	0	3	-	0	?	0
Protocaptorhinus	?	?	?	?	?	?	?	?	?	1	?	?	0	3	-	?	?	?
Romeria	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euconcordia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Reiszorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eudibamus	1	?	?	?	?	?	0	?	?	1	0	?	?	0	1	?	?	?
Mesosaurus	1	-	1	1	0	0	0	2	?	1	1	0	1	1	1	0	1	0
Erpetonyx	?	?	?	?	?	?	?	1	?	1	?	0	?	1	?	1	1	0
Belebey	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?
Macroleter	1	?	?	?	?	?	0	?	?	?	?	0	?	1	1	?	?	?
Milleretta	1	-	?	?	0	?	0	?	?	1	0	0	?	1	1	?	0	?
Acleistorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Colobomycter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Procolophon	1	-	0	?	1	0	0	1	?	1	0	0	2	0	1	0	0	0
Owenetta	1	-	?	?	1	?	0	?	?	1	?	1	?	?	1	1	?	0

Character/Taxon	250	251	252	253	254	255	256	257	258	259	260	261	262	263	264	265	266	267
Gephyrostegus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Seymouria	?	1	1	0	0	0	0	0	0	0	0	0	1	0	?	0	?	0
Tseajaia	1	1	1	0	0	0	0	0	0	0	1	0	?	?	0	2	0	0
Limnoscelis	1	1	1	?	1	0	0	0	0	0	1	0	1	1	0	1	0	0
Oedaleops	2	?	?	?	?	?	?	?	?	0	0	0	?	?	1	0	0	?
Eothyris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Vaughnictis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eocasea	?	?	?	?	?	?	?	?	?	?	0	0	1	1	[01]	0	0	0
Euromycter	2	1	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?
Casea	1	0	1	0	0	0	0	0	1	0	0	?	2	0	1	0	0	0
Ennatosaurus	1	?	1	?	?	?	0	0	1	?	?	?	?	?	1	0	0	?
Echinerpeton	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Archaeothyris	?	?	?	?	?	?	0	?	?	?	0	0	2	?	?	?	0	?
Varanosaurus	?	?	?	?	?	?	?	?	?	0	0	0	2	1	0	1	?	?
Ophiacodon	2	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0
Haptodus	1	0	0	0	?	0	0	1	1	0	0	?	?	0	1	0	1	?
Secodontosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?
Dimetrodon	2	0	0	0	1	0	0	1	1	0	0	1	1	0	1	0	1	0
Ianthasaurus	?	?	?	?	?	?	?	?	?	0	?	?	?	?	1	0	1	?
Edaphosaurus	2	0	1	0	1	?	0	1	1	0	0	0	3	0	1	0	1	0
Hylonomus	?	?	?	?	?	?	?	?	?	0	0	0	?	1	0	0	0	0
Anthracodromeus	?	?	?	?	?	?	?	?	1	?	?	?	?	?	0	?	?	0
Paleothyris	2	1	0	1	0	1	?	?	1	0	?	?	1	1	0	2	0	0
Protorothyris	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Petrolacosaurus	2	1	0	1	0	0	1	?	?	0	1	1	1	1	0	1	0	1
Araeoscelis	2	?	0	1	0	0	?	?	?	0	0	1	1	0	0	2	0	1
Orovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Archaeovenator	?	?	?	?	?	?	?	?	?	?	1	?	1	?	0	2	0	?
Ascendonanus	0	1	1	1	?	1	1	1	1	?	?	?	0	0	?	?	?	0
Aerosaurus	1	1	1	0	?	1	1	0	1	0	?	?	?	?	0	2	0	1
Apsisaurus	0	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?
Heleosaurus	0	1	1	1	?	0	1	?	?	0	0	1	[12]	?	0	?	0	?
Mesenosaurus	1	1	1	?	?	?	1	0	1	0	?	0	?	0	0	2	?	1
Mycterosaurus	?	?	?	?	?	?	?	?	?	0	0	1	2	?	0	2	0	?
Elliotsmithia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Varanops	1	1	1	0	1	1	?	0	1	0	0	1	1	1	0	0	0	1
Varanodon	0	?	1	?	?	1	1	0	1	0	?	?	?	?	?	?	?	?
Watongia	0	1	1	0	1	1	0	?	1	?	?	?	?	?	?	?	?	?
Youngina	0	?	1	1	?	1	1	?	1	0	1	0	1	0	0	0	0	1
Acerosodont.	0	1	1	0	0	0	0	?	?	1	1	0	1	?	0	0	?	?
Lanthanolania	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Claudiosaurus	0	1	1	0	1	0	[01]	0	1	1	?	?	1	?	0	?	?	1
Prolacerta	0	?	?	1	?	0	?	?	1	1	1	0	1	0	0	0	0	1
Proterosuchus	0	?	?	?	?	?	?	?	1	1	0	?	1	?	0	?	0	?
Thuringothyris	1	?	1	0	0	1	1	?	1	?	?	?	?	?	?	?	?	?
Captorhinus	2	1	1	0	0	0	0	?	1	0	1	0	2	1	0	2	0	0
Protocaptorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Romeria	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Euconcordia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Reiszorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eudibamus	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	2	?	1
Mesosaurus	0	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0
Erpetonyx	0	1	0	?	0	1	?	?	?	?	?	0	?	0	0	2	?	?
Belebey	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Macroleter	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Milleretta	?	?	?	0	?	?	?	?	1	?	?	?	?	?	2	?	?	?
Acleistorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Colobomycter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Procolophon	1	?	1	0	?	0	0	1	1	1	0	0	1	0	2	0	0	0
Owenetta	0	?	?	?	?	?	?	?	1	?	?	?	?	?	0	0	?	?

Character/Taxon	268	269	270	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285	286
Gephyrostegus	?	?	0	?	?	?	?	?	-	?	?	-	0	-	?	?	?	?	?
Seymouria	0	?	0	?	0	1	1	?	-	0	0	-	0	-	0	0	1	0	0
Tseajaia	0	0	0	0	0	?	?	0	-	0	0	-	0	-	?	?	?	0	?
Limnoscelis	0	0	0	0	0	0	1	0	-	?	0	-	0	-	?	?	0	0	1
Oedaleops	1	?	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Eothyris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Vaughnictis	1	?	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Eocasea	1	?	0	?	?	0	?	?	?	?	1	?	0	?	?	?	0	?	?
Euromycter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Casea	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	?	0	0	0
Ennatosaurus	?	?	0	?	?	?	?	?	0	0	1	0	1	0	0	?	0	0	0
Echinerpeton	0	?	?	?	1	?	?	?	?	?	1	1	?	?	?	?	?	?	?
Archaeothyris	?	0	0	?	1	?	?	?	?	?	?	?	1	?	?	?	?	?	?
Varanosaurus	0	?	0	?	1	0	0	1	0	0	1	0	1	1	?	?	?	?	1
Ophiacodon	0	[01]	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1
Haptodus	0	0	0	0	1	?	?	?	0	?	1	1	1	1	0	?	0	?	1
Secodontosaur.	0	?	1	0	1	0	1	?	?	?	1	?	1	?	?	?	?	?	?
Dimetrodon	0	0	[01]	0	1	0	1	0	0	0	1	1	1	1	?	0	1	1	1
Ianthasaurus	0	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?
Edaphosaurus	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	1
Hylonomus	0	0	?	?	1	1	1	?	?	?	1	0	0	0	0	1	?	?	?
Anthracodrom.	?	0	1	?	?	?	?	?	?	1	1	?	0	?	?	1	?	0	0
Paleothyris	0	0	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	0
Protorothyris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Petrolacosaurus	0	0	1	1	2	?	1	0	1	1	1	1	1	1	0	1	0	1	1
Araeoscelis	0	0	1	1	2	0	1	0	1	1	1	0	0	1	0	1	0	1	1
Orovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Archaeovenator	0	?	1	1	2	?	?	1	?	1	1	1	1	1	0	1	0	1	1
Ascendonanus	?	0	1	?	?	?	?	1	?	1	1	0	1	0	?	?	1	0	0
Aerosaurus	0	0	0	?	?	?	?	0	0	0	1	0	1	1	0	?	?	1	1
Apsisaurus	1	1	1	1	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Heleosaurus	?	?	1	1	?	?	?	?	0	?	1	0	?	?	?	?	?	1	?
Mesenosaurus	?	?	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	1	?
Mycterosaurus	0	?	1	1	2	0	?	?	0	?	1	0	?	0	0	?	?	?	?
Elliotsmithia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Varanops	0	1	0	0	2	0	0	0	0	0	1	0	0	1	0	?	?	1	1
Varanodon	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	1	1
Watongia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Youngina	1	1	1	?	?	0	0	1	1	1	1	0	0	?	0	1	1	1	1
Acerosodont.	1	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Lanthanolania	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Claudiosaurus	1	0	1	1	2	0	0	1	0	1	1	0	0	1	0	1	0	1	1
Prolacerta	0	1	1	1	2	?	0	0	1	1	1	0	?	1	1	1	?	1	1
Proterosuchus	1	?	1	1	2	0	0	?	?	?	1	0	?	?	1	1	0	1	?
Thuringothyris	0	1	0	?	1	0	?	?	?	0	1	?	1	0	0	1	1	0	?
Captorhinus	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	0	?
Protocaptorhin.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Romeria	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euconcordia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Reiszorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eudibamus	1	1	1	1	1	?	0	0	0	?	1	1	1	-	?	1	1	1	0
Mesosaurus	1	?	1	1	2	0	0	1	0	0	1	0	0	1	0	1	0	0	0
Erpetonyx	0	0	1	1	1	0	0	1	0	?	1	1	1	0	?	?	?	?	0
Belebey	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macroleter	?	?	?	?	1	?	?	?	0	?	?	?	?	?	?	1	?	0	?
Milleretta	1	1	1	1	2	0	?	?	0	0	1	?	?	?	?	1	?	?	?
Acleistorhinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Colobomycter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Procolophon	0	0	1	1	0	0	1	?	?	0	1	1	1	?	0	1	?	0	?
Owenetta	?	1	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 3 - Additional data to Chapter 2

A) A virtual reconstruction of the scleral ring and orbit of *Orovenator mayorum* and the measurement of dimensions.

The orbit of *Orovenator* was reconstructed using the *in situ* articulated left maxilla, lacrimal and prefrontal of OMNH 74606, and the left frontal and postfrontal of OMNH 74607 reduced in scale by 33% to achieve best fit with the prefrontal of OMNH 74606. The right jugal of OMNH 74606 was mirror-imaged and articulated with the left maxilla. The position of the postorbital, missing in both specimens, was estimated from the articular surfaces of the ventral process of the postorbital and the dorsal process of the jugal (Fig.1A)

The degree of arc of the internal margin in a series of four articulated scleral plates in OMNH 74606 was measured at approximately 75°. This was extrapolated to calculate the total number of plates required to produce a circular scleral ring (360/75*4=19.2). The ring was assembled using four groups of the articulated quartet of plates to produce a 300°array of scleral plates with equal internal degrees of arc for each quartet. Three additional articulated plates from the quartet, making 19 plates in total, were chosen to complete the ring with an internal arc of approximately 60°(Fig. 1B).

Based on the relative actual measurements of the inner margin of the scleral plates and the length of the maxilla, the anteroposterior length of the orbit (orbital length=ol), the maximum internal diameter (int) and external diameter (ext) of the scleral ring were measured. The geometric mean ($\sqrt[3]{ol * int * ext}$) of all three data points and the optical ratio (int^2/ext*ol) were calculated as follows:
ol: 8.20 mm

int: 4.29 mm

ext: 6.70 mm

mean: 6.1758 mm

optical ratio: 0.334985

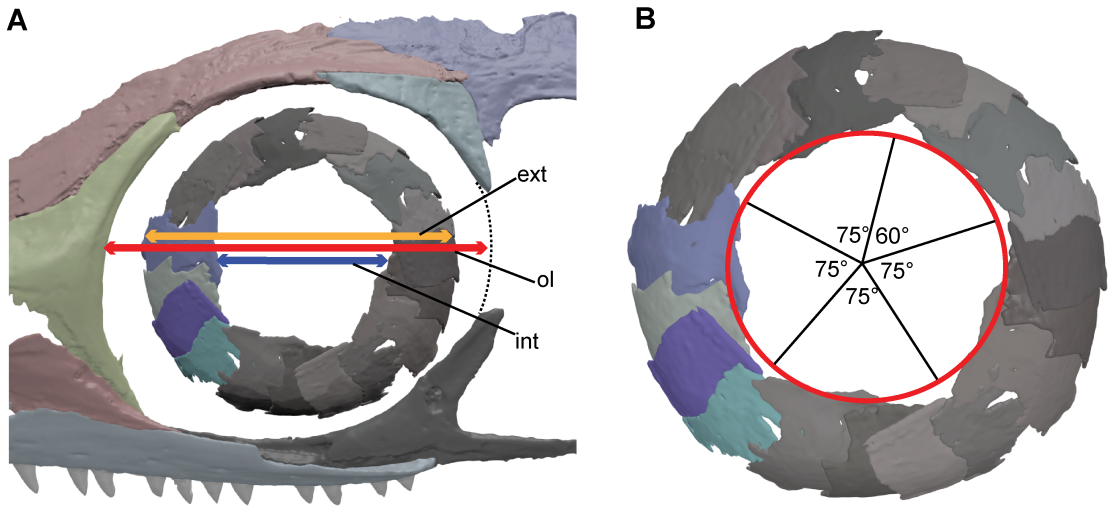


Figure 1: Reconstruction of the circumorbital elements and scleral ring of *Orovenator mayorum*. A, orbit and scleral ring, with dotted line denoting estimated position of the orbital margin of postorbital. B, ring of 19 scleral plates, articulated in situ plates in blue, duplicated plates in grey. Abbreviations; ext (yellow bar), maximum external diameter of scleral ring; ol (red bar), maximum orbital length; int (blue bar), maximum internal diameter of scleral ring.

These data were added to the scleral ring and orbital morphology dataset of Angielczyk and Schmitz (2014), and *Orovenator* was inserted into the accompanying time calibrated phylogeny as the sister taxon to the 'pelycosaur'- grade synapsids. Both the datasets are available to download from the Dryad Digital Repository as follows:

ANGIELCZYK K. D., SCHMITZ L. 2014. Data from: Nocturnality in Synapsids predates the origin of mammals by over 100 million years. Dryad Digital Repository. https://doi.org/10.5061/dyrad.1v8kj

The analysis was performed using R studio (RStudio Team 2015) based on a script available online from L. Schmitz - 'phylo.fda/phylo.fda.v0.2.R' (http://schmitzlab.info/phylo.fda.tutorial.html)

The posterior probability results for *Orovenator* were as follows:

Cathemeral: 0.0008071

Diurnal: 0.01301778

Nocturnal: 0.98617512

Additional references:

RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

B) Phylogenetic analysis

a) Scoring for *Orovenator mayorum* for the character list of Reisz *et al.* (2010)

01000 10011 11101 0-?10 10000 12100 1000? ???11 2 2 30??? ??102
11??0 2???1 00??0 0?0?1 0???? ????? ????? ????? ????? ????? ?????
????? ???

b) Notes on scoring of *Orovenator mayorum* for the character list of Reisz *et al.* (2010)

Character 18 - Septomaxilla shape: pillar-like (0); curled sheet (1); flat sheet (2)
State (1) is applied to all scored sauropsids in the matrix of Reisz *et al.* (2010). The shape of the septomaxilla in *Orovenator* is not applicable to any of the states described for this character, consequently *Orovenator* is scored as (?).

Character 40- Lateral temporal fenestra: absent (0); present, quadratojugal excluded (1); present, quadratojugal enters or is absent (2)
Since the quadratojugal is not preserved in *Orovenator*, this character is scored as (1 2) , i.e. partial uncertainty.

Character 41- Ventral temporal bar (zygomatic arch): absent (no fenestra) (0); tall, occupying more than 20% of skull height (1); narrow but complete, occupying less that 20% of postorbital skull height (2); incomplete (3); absent (with fenestra) (4).
Since both the squamosal and quadratojugal are not preserved in *Orovenator* this character is scored as (2 3), partial uncertainty.

Character 50 - parasphenoid dentition posterior to level of transverse flange: absent (0); along edges (1); on edges and posterior body (2).

This is scored as state (2) for *Orovenator*, based on examination of the parasphenoid by SEM (Reisz *et al.* 2011).

C) Specimen measurements

All measurements of length are anteroposterior, of height dorsoventral and of width lateromedial unless otherwise stated. All measurements are in millimetres.

OMNH 74606

Premaxilla		**Parabasisphenoid**	
max. length	4.2	max. length	17.0
max. length of maxillary process	1.9	length of cultriform process	12.0
max. width of subnarial process	1.1	width across basipterygoids	4.8
length of vomerine process	0.4	length of basipterygoid process	1.6
Septomaxilla		width of basipterygoid process	1.0
max. length	2.0	length of pituitary fossa	1.2
max. height	1.4	width of pituitary fossa	0.7
max. width	1.2	width across dorsum sellae	1.8
Nasal		**Pterygoid**	
max. length from frontonasal suture to tip of anterolateral process	10.0	length from basal articulation to anterior tip	15.4
max. length anterolateral process	2.5	width of transverse process from basal articulation	3.6
max. width	1.4	**Ectopterygoid**	
Lacrimal		max. length	3.6
max. length	11.0	max. width	3.5
max. length dorsal process	6.8	**Epipterygoid**	
max. height ventral process	6.4	length of base	3.0
max. width dorsal process	1.5	max. height	4.3
Prefrontal		width of columella	0.5
max. height ventral process	4.3	**Quadrate**	
max. length dorsal process	6.5	max. height	4.0
max. width dorsal process	2.0	max. length	3.0
Maxilla		**Stapes**	
max. length	20.0	max. length of footplate	1.8
max. height	2.7	max. width of footplate	1.3
Scleral ossicles		**Dentary**	
radial length	2.5	max. length	24.0
circumferential width	1.6	max. height	2.0
Jugal		**Surangular**	
max. length	10.3	max. length	14.3
height of dorsal process	3.7	max. height	2.5
max. height of subtemporal process	0.7	**Angular**	
Vomer		max. length	16.3
max. length	12.7	max. height	1.7
max. width	2.1		

Palatine		**Prearticular**	
max. length	10.2	max. length	15.0
max. width of palatal ramus	2.8	max. height	1.4
length of maxillary ramus	3.4	**Splenial**	
Coronoid		max. length	19.2
max. length	6.3	max. height	1.5
max. width	1.0		

OMNH 74607

Frontal		**Parietal**	
max. length	18.6	max. length	13.2
max. intraorbital width	2.5	length of posterolateral process	4.2
Prefrontal		length at midline	9.0
max. height	6.8	length of embayment for upper temporal fenestra	4.5
Lacrimal		diameter of pineal foramen	1.5
max. length	14.0	width at level of pineal foramen	4.0
max. height ventral process	8.3	**Cervical vertebrae**	
Postfrontal		length of centrum	5.0
max. length	5.8	height of centrum	3.4
max. height	4.2		

Appendix 4 - Nexus file and MrBayes script

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[Mr.Bayes script for fossilised birth/death prior run: 60 fossil amniotes. Heat 09. Run date
6.12.18]

#NEXUS

BEGIN DATA;
       DIMENSIONS  NTAX=60 NCHAR=286;
       FORMAT DATATYPE = STANDARD GAP = - MISSING = ? [SYMBOLS = "0 1 2 3"];
       MATRIX

Gephyrostegus_bohemicus
00030000000000-000000?00000-30----0??0000200-000000?010??000--10000?0-000-0--0000010-?0?
000-0000000?0000?????????????0000??00??00?0-000000000?1?00000-?0?1????701010????00111000l??00000?0??
000-?01?0000??0100000000-00?????00??????0???-???????????0?0?????????????????????????0?????-??-0-?????

Seymouria_spp
00000000?00000-000000001200-1110000??0001-00-010000?00010000--000000?0-000-(0 2)--0000110-00?00(1
2)-000000000000?1000????000000000000001100010000100?000?10000??1?1-0101010000011110000?0000030????
10?01?0??00?0(0 1)010?01?0-0010100000000012010-00000000?000000000?1100000000010?0?00?0?
011?-00-0-00100

Tseajaia_campi
001-10000001?10001?10?00000-1111000???011-10-01000000100??00--11000001-000-0-10000110-1??
012-000102000(0 1)01?001-000002000??000101?0-111000000?0?00100-10010000?000000---0011001??0?
10110000000??0010000??10100001O???00101010000001?00?1200000000000000001001110000000010??02000000??
0-00-0-???0?

Limnoscelis_plaudis
001-1001?00110-001011200000-1100000???011-10-010000001100??
00--11011001-000-1-10000110-000001-000100000100000000??0002?00??000111011010001017107001007000000?0?
000000---0011010010111011000??000-0010000???01?0?00000-0010101000?02?01102000000000?000000000111?
1000001011010000000010-?0-0-??001

Oedaleops_campi
100?21-0000111000??11?00100-11111000-1001-00-00100000010-0000101011101010?-01100001010007011-00?
10???01000?????????????????????????????????????????????????0???0????0???????????
0?????????????????????????????????????0??1??0???0?????????0000201-10???0?10000??002????????000??100?1?
00001????????????

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Eothyris_parkeyi
10??21-0000111000101l?00100-1111101??1000100-00100001-10-0000101011001010110010000010100?
0011-0001000000000l300??1?001????000??1??????0010??10?????0-000100???001000---0????00?0???1?1??
0000000-????????????????????????????????????????????????????????????????????????????????????????
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Vaughnictis_smithae
?01-?0000001????????11?????????????????????01????????0?1-1????0???101110101010000?0001011???011-00?
10?????????????????????01??????01???01?000????0?????????????????0?00????0????00????????10?0????
0-??????????????100???????0??0?????????????????????????????????????????????1?00001???????????

Eocasea_martini
??012???0?????????????????????????????????0?????????????????????????1100l?10???00?0?????????0??-00110??
000010?????????0?????????????????????????????????0100?0????000---0?????????????00??00???000?20?
0001??0000?0-000?0??000001?????????????????????????????????0011(0 1)0001?0??0????1?0???0??

Euromycter_rutena
100121-0001110-001000200201010----00-1000100-0110000001??0000100011101010110000000100000010-00110?
00010011300??1011111?00000????01?0001?010??0??0-000100100010???0---0??????1??010???0?100?????0?0020??
00101?????????????????0????000?20?????????????????012100000001?????????????????????????

Casea_broilii
100121-0001110-000000?00100-10----00-1000100-011?000?-1??0000?0?01??0101011000000?00000?010-00110?
0?010001300??10111010000??01?0-012000100l0?0???0-00?100100001000---0001?11??001?110010000??00100000?
000101000110-00000001010110??00201-0?100001000200?0101000000100?2010000000011100101107000

Ennatosaurus_tecton
100221-0001110-000011200201000----00-1000100-001000?0110-?0010000111110101101000000?0?
0010-001101??00001131-??1011??1??00??0110-01?00110110010010-2001?0???101000---0001111000l0?11001??
000?0????20?00???1?001???00?0?0?101?????00201-0??0000??0020???1?1???001?????100???0?????00101007000

Echinerpeton_intermedium
?????1-?000???????????011???111100?1000???0?????0?????????????????????
10?????????????????????????????????????????????????????????????????????????????????????????21????????????
0?1?????????????????????00??101??011?1??00?100?0????????0120?????????100?????????????????????0???0???
1?????11???????

Archaeothyris_florensis
0?0?200?100??0-???????011???211100?10??0??0?-0?0????011?????1?120????10100-1??0000l011?0?012-0??
1????01?????????1?????????????????????????????????????????0??0?21???????1????0?0???1?????????????0???
0100101??011110-000?0?00???0?0?????????????0?100000?????????0???002???0??00?1????????1??????

Varanosaurus_acutirostris
01022000000020-110111301100-3111011110001-10-020010?
0110-0111012011010100-11101001011001012-0101000000000021-??0100200010011011??11200200100?
10100-1001?0000210000---1001100001?111?111??0010??00000?01?????01110-001110??00?01????????????100?
1??????1?????????????0002101??0?0?100100101l????1

Ophiacodon_spp
011-2000(0 1)00020-100011?02100-3100010110001-10-02000?
00110-0111112011010100-11101001011001012-0101000001000020-0001002000110l0?110-1120020?110110?
00-100100001210000---1001100001010111110000100000001001010100311O-100101000000300001(1
2)1000110001100200110200010001000010100O(0 1)00000000100100111
```

Haptodus_garnettensis
01021000000000-001011301100-1111010100001-10-00001000110-01011110001011100-1100010-010000002-01010?
01????0?00???00?20000100100110-0120010010011101?0-0100000010001110020l---1010000?11011??000-1?0?
0010010100000110-100020000??11?10012-0101110011000001001000?001100??0101?00001???0?11110?0?1

Secodontosaurus_obtusidens
011-1001000000-001011302100-1111010100001-10-0201-000110-01011200001010110-1100010-01000011200101030
1010000100??0002?00011101011??012002001001101O0-0000000012101111120l---0010100111121??00?-10?01111?
1201??012?10-2000210?01??????????0100110?11?000?????????????????????101?0?10101???1?1??????

Dimetrodon_spp
011-1001110100-001011302100-1111001100001-10-0201-000110-01011200111010110-1110010-010000002-0101030
1010000100??000200001101011111012002001001100O0-0100000010101111120l---1000000011121??000-1?00112?(0
1)211010(0 1)2120-2000210001?130130(0 1)1-010011001100000(1 2)1020001001100110101000(0
1)0101000111?0111

Ianthasaurus_hardestiorum
0???11-1?00??0-???????01100-311(0 1)0(0 1)0??0001-00-0?000000110-00?11110001?11100-0100010-010?0?
002-01?10?0??????????????0???????????1???????00????01????????11?00???0001?????0????101?0???1??1???
00??1?0??22?0????0?11022-210020000??0?????????????1????10000?????????????0????101?0??????????1???????

Edaphosaurus_boanerges
011-11-1100000-000000301100-10----00-0011-00-000000?
011100001101000101111O-0100010-0100001020010103017100011002?00100000100000l?0-012?00?
0000110010-011000001101101000001111110000011011??000-1????20?0?0??1?10122-2100010101?131130?1?
000010001100010010201017011000301010000001100011010010l

Archaeovenator_hamiltonensis
011-2000000100-000100201101120----01?0101-01100000101-1??001101201117111OO-0100000101017?002-00?
101??00?0??????????0010???0000?101?01100201?10000110-?0?000???2000010?0000110011101012100000??000??
000010100011011000?0?100100000010211-00?(0 1)??????????????????????1?1?020?0?112??1?1111101011

Ascendonanus_nestleri
0?1-200000000??????00?0110??1110?000-0001-0??0(0 1)?0?10001???0?0??20010?11100-0100000101017?002-01?
101??0000???????????11????0?00????01?002????0??0????0001?????2000?10??0????000????????0?????????0???
0?0???????101??00??00100000???0?021?????0????1?11?0?00111?1111???00???0?01????1?11010??100

Aerosaurus_spp
011-2011010110-000101?01101011000000-0?00200-0?0000200l??00?10?2?????11101001017001000??0012-010?02?
1?????000?000000111??0100?????????02???10????????0?200?00200??100000011000017?1????300010110000?010(0
1)1110100101??100?2?000001????2?02001?11(0 1)0101000001101110?11010????0201000???00010110??11

Apsisaurus_witteri
?????000000?????????????????????????????1?????????????????????????????????1100-?10100010l?10????????
1?????????????????????1????00?????????????0010??100?01?0?????0?????????????0?????????????????000010117
0??????0101??0?101??0??12?0????00??0????1?0??00??1101011100?????????????1?????111120?????????????

Heleosaurus_scholtzi
011-2011?10000-000?00?021111111100?0?-0001-0100101-1????1??00?10121110?11100-01110001010110012-01?
102100000?00???????0111??000101???0110020???00?0??0-00?1?0???2000?100?0????00????1?1??3100?????????
0?0011100013017?000???101??0???0?0??1-0??00???1?1112100111?01??001(1 2)?0?0???11????0?10??????1?

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Mesenosaurus_romeri
011-2011110000-100100?021110111000??0001-0100101-111-11000110121010111100-01110001010110012-01?
10210000000??????0000111??0101010110110011010000100-00010001-2000010000????
000110111213000001100??????1110?0?101??000???100??0?????????????00????0?????0111???1010?0?002?1??
1????1?????????1?

Mycterosaurus_longiceps
011-2011?10100-?0010??02111?1100000?000000100101-11??11000110?21?111111010011100010101??012-01?1???
0010000?????0???11100000101???01?0010???0???????00?00000020000????0?????0?1????1?1?1001011?0??????
011100001011010?2?1?????????????1-00??0????0?0???0?????????0012?020?0?1120??0?10?00????

Elliotsmithia_longiceps
0?1-2011110?????????????????1???11?00???0?000????????1??-110?0110?2111111111011011100010101101 12-010102?
00?????0?????????????????????1?????0020???0??0????00?100????0???100?0????0?1?????????0????????????
00?????????????????????1?????????????????????????????????????????????????????????????????????

Varanops_brevirostris
011-?011010010-000001312101011100110-000020110100000010-00110120101011101001?
10001100100002-010102010 1?0???0000?100111?00000?1???????01???10?????0-1002000002002-100100011000?1?
1011130?01011000??01?11110?00101111100?200000?0??02011-(0 1)10110010100000 2?0111011?
0100111000101002000001001 0??11

Varanodon_agilis
111-(1 2)011010000-0?0?01?1210??1110011??0000201101000020010-00110121?0?0111010010000011001 0?0?2-01?
1???10????0000?????????????????1???????02????0???????10?200???2002-10010????0?0????????3??010???00?
101?1111010?10111100121000000 2?00??????0??????1000??0100?1??11010?????????????0????????????11

Watongia_meieri
????011010??0-??????????????????????????????????????????????
21??????????????????????????????????????????????????????????????????????????????????????????????????
??????????????????????????????????????1?10?00101??100121????????00??????0?????010000?1000110110?
1?????????????????????????????

Hylonomus_lyelli
001-01-0000000-00001??00100-31100000-0001-00-0000000001??0001000000001-000-0--0000010-0??00?-???
101??0000?????????????0011???0?001???010000????00??????00????00?21?????????????0?0?1????10????????
00000010??0?000??700-000?0?0?0??0??10???????????00?110?3-????????????000?1000000??111???100001???

Anthracodromeus_longipes
0?002?????????????????????????????????0?????????????????????????????00001-000-?--??00110-00?
000-0101010000000021-??00?????????????????????????????????
0-?????????????????????????????????????????????????000?0100?0101001 11??000?0?0000?0?????????????????11010?
000????????1?????0??0?01??????11?0??1?00

Paleothyris_acadiana
000221-0000000-000000?00100-31110100-0000100-00000000010-00?1010000001-000-0--0000111-001002-01?
101000000???1-??10000(0 1)1??0000010??0100010?000000??0-00?10000?2000?0---0????0000?01?
1213100000-000000100101010010 0??00?0000001?0??101?20010??000?11000000021010 1??10??
110200001111110111110 1000
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Protorothyris_archeri
000021-0000(0 1)00-000?01?00100-2111010??0000000-0000000001???00101(1
2)000001-000-0--0000111-001001-01?1010000000??1-??10000????000001110010002010000?000?0-0000?0?0?
200000---0010100001017?1??00??000-00???0100?01010?0(0 1)??00??000001?0??120021010?10????
003-?????????????0?????????????????????????

Petrolacosaurus_kansensis
00022000000000-000011?0010103111010O-0001-00-0000000001??000101100010101O0-0100000?
000101101001010100000000001-000000011??000001011010001110000000110000000000?200000---0????001?
10110210000000-0010000011111111010-00112?000?000102112101101100111000121021010012??011110101001127
1011111101011

Araeoscelis_spp
001-21-0000000-1?0000200100-1111000??0001-00-00000000010-00010?2001101-000-0??
0000111-1001010010102000000000200??000?000000000?1??????0011?010?000010010000000000010---01---001?
1000111010000?0-?00??100111110111010-00102?00000001??002101101110111001127?02?0100???
0011002010011201011100101011

Orovenator_mayorum
001-2000000010-101100201101120----0110101-01000001101-1100011012?????11100-01?00???0?????102001?
1?????????????????????001100000001011011001011100000110?00?0?01-20000????
000110011101012100001011007???????10?????????????????
0?????????????????????????????????????????????????????????????????????

Youngina_capensis
001-1000000100-000000?02110-20-----??0001-00-0101-0?0010-10010120011011100-0100000100017
1102101010100001O?0001011000(0 1)000000?001111010002O?0100001110000000001-20???????0????000?1?1?1??3?
00??0-?01???00?010000?010-000100101?0012100?201-010011?1101011110?11?11?101010000111??001111007
01111

Acerosodontosaurus_piveteaui
0????000000?????????????0211??3????????00?1-??????1-?10010-??010?2??11??1100-010?010?000??????????
1?????????????????????????????????1?????????????????????????00??????00107?1?????????????121????10???
0100???01?1??00?01??(0 1)0010?100??0?????????????????1???0011?1101100000??1101?00??1?????0????????????

Lanthanolania_ivakhnenkoi
00???00???0??0-???????02101O?0----0??000000?????1-0?001??10010??0??101-100-01-0010?00???????????
1?????????????????????00100?????1?????????????1???0?????????????0?0?????????????0?????
121?????????????????????????????????????????????????????????????????????????????????????????????????
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Claudiosaurus_germaini
001-11-?000000-100000?01200-30----0??0001-00-1001-1?1-1??00011?20011?1-100-01-0010-00010?
111101-11--?1----001-??000?000??000001111010000117107001110?00000???200000---000110000101012171????
0-??11?0000?010101?010-000?0?1001000??00?21????0001?1100010107011010(0 1)011??1?0??
11011200101100101011

Prolacerta_broomi
001-1011010001100100020220111O----0110001-00-1201-110010-10010120001011100-0100010-0001101(0
2)1101-11--01----0001111000100000O(1 2)0011110100020121000011100000101l-200001101O????
0100101112130117?0-?111?00111011?10(0 1)110-0011211001100277112O1-0100?2?111101210077170??
11101000010111270011107111?11
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Proterosuchus_spp
001-10111100011103000202101 1(1 2)0----0??0?00100-1201-1?001??11?102(0 1 2)0011001100-11100(0
1)0-00011?1(0 2)1101-11--?0100???0?11?0???0000??2001111011002012?00?0111010?11011-2100?11011????
0100??1?121?011??0-?1?1???111111010011???0012?100110(0 2)2??10201-0000?2???1???2100???????110?1?0?0?
1?11200???10??1101?

Thuringothyris_mahlendorffae
001-21-0000100-000001?00100-10----0??0?00100-000000?
0110-0000000000101-000-1-0000011?-001000-0101010000 10???1-??00?00000??0??1111?01?0000?0?0?10?1??0??
0?0000?????0---?????00?00?????????????????10??00?10??10110???00????000???????0021???????1?10003-2001?
10011?1?????????010?10???01?100110?

Captorhinus_spp
100011-0000(0 1)00-01201110(0 1)100-11110000-0011-00-00000000110-000000(0
1)000001-000-1-00000010-001000-01-11--00010000(0 1)-???
0020010000001111101200001000001--1100000000000100100000101011000111213100001000100000010000010000-00
1010000000?1110020000010000010003-0?02110000?10102102000000011000101101 00?

Protocaptorhinus_pricei
100011-0000000-012011101100-1111000??0010100-000000?011??
0000000000001-000-0-00000111-001000-01-11--000100001-???00???????????1??????0000????0?01--1100?00000?
0010?10??0????0??????1?12?3??????????0?????100?1????0???01?10?00????????021?????????1??
03-??????????????????????????????????????

Romeria_spp
100021-?000(0 1)00-0(0 1)2011100100-1111000??0010000-000000?011??00001(0 1)(0
1)000001-000-0-10000010-001000-01-11--000100??1-???00200???????11?100120000 1000?01--1100?0?
0000001000---0????01100?1?121?1????0-?????????????????????
0?????????????????????????????????????????1?????????????????????????

Euconcordia_cunninghami
?00021-1000000-010?10?00100-1100000???001-00-00000000110-0000000000001-000-1-000???
1?-001000-01-11--000100?1-????7001100000001???0100000101 0?0???11000??0001?0???0---0????000?1????
2??????????????????????????????????????????????????????????????????????????????????????????????????
??????

Reiszorhinus_olsoni
00021000?10000-012011100100-11100000??
1011-00-00000000110-0000010000001-000-1-10000110-001000-01-11--000000???-????????????????????????
???????????0000?0???001000---0010010100?
1112101000010??????????????????????????????????????????????????????????????????????????????????????
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Eudibamus_cursoris
??1-01-00001?????0??????????1?0----?????????????0??????111???10?????0??110??0???000?11??01????
1--1??????????0??????????00????0?11???11?11-2???0??01???0????0??????310---?0??????????????????????
1?????????????????????0??10?-0000????????1?????0???10??01?????????0?????????2?111111?000?111-?1110
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Mesosaurus_tenuidens
001-11-0000000-000-00001?00-10----00-0?01000-0200-110010-0000012000?
01-000-1--0000111-101011-001101000001?001-??00?2100??000101?1101000000111001--0?1000?0?0?2000?
110001---00210?0?121?000000-??00???00(0 1)0??00100(0 1)0-10001010010001020120 1-11000?1101110100?10?
0000?000000001?11200100100101000

Erpetonyx_arsenaultorum
??1-?000000???????????0?????10----?0-??0??0???????????1????010?2????????10??????0???????0?????
001102??00?1?00????0??????????0???0?????01?0????0?????????1?????????0?11?????????????1???????0??00????
0?????0??????????????????20100 1?1???????0???????1?1?0?1?110010?01?????0?002??00111001 0?1110????0

Belebey_vegrandis
001-01-0000100-000000?00100100----0??0001-00-01000010111100010000?
1001110110-000001111001012-1--1020?00?1?0?1-??01?0000010?0?11?0-11211-20110010101100 00?0???
000310---000111010101012 1?100010-??????????????????????????1?????????????????????????????1???????????
1??????????1???????????????

Macroleter_poezicus
00031001000000-000001?01201111000000-0001-00-0001-1?00111000000111100111011100000 01101??
0012-00-111000(0 1)01???0-??11?2000???00001?1101000200110010111120???1?1-?????10?000101????1?1?12??
10001?????????????????????????????1??????1???????01?????0????0?11???1?????????????????????1???0??????
1?0?

Milleretta_rubidgei
000310000?0100-?0100?200100110----0??0001-00-00000?1-111?
0010120011010100-000000000001000002-001101000000??01-??000?0111-???2011??01?0010??10?00101120 00?
001-000011010001010000?011121?0?1??0-?11?00?????????0??0??000?00100??0????00211-??0?0??100?11?0????
0????1?????2???111120??001????1???

Acleistorhinus_pteroticus
000110000001?0-0?1000201210110----0??0000100-0001-01001??
000010101100011010000000001100101001-000101??0100?1?01??00???11????000111101000 10?010?001?112010?00??
0????101?0???????01?1?1??
0100?????????????????????????????????????????????????????????????????????????????????????????????????
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Colobomycter_pholeter
000111-1000100-000011211110111110000-0000000-0011-10(0 1)-11100011010?1001110110000000 01000?0?
001-00-11--?0001????-?????2011???0??0111101000100011?1010??20?300???0000?10??00110001010???1??0?
0000?????????????????????????????????????????????????????????????????????????????????????????????????
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Procolophon_trigoniceps
001-01-000011110000030010010 0----00-0011-00-0011-00001110000002010?
01-010-1--0001100-000010-00-11--01---1000-??00020?01-0?200111101001-1001000010112113 01?1-10130110?
0011101001011121?100010-??00001?0101010?3??0-100?1?100?01???001201-0?1001?1002010001?10?
0011100102000001100 1??0111?01?0?

Owenetta_kitchingorum
001-0000000000-000000?0220011100000??0001-00-0001-0000111?
000012010000-100-0--0011100-000010-00-11--000010100-??0102000??00000111101001-10010000 1?1120030 1???
20130110000100010010111121?100000-??0?????0?01010??000-000?100?0101???00?201-??1?0??1?1??11?00???????
1?????00???11???0????????????;
```

```
[begin trees;

translate
              1     Gephyrostegus_bohemicus,
              2     Seymouria_spp,
              3     Tseajaia_campi,
              4     Limnoscelis_plaudis,
              5     Oedaleops_campi,
              6     Eothyris_parkeyi,
              7     Vaughnictis_smithae,
              8     Eocasea_martini,
              9     Euromycter_rutena,
              10    Casea_broilii,
              11    Ennatosaurus_tecton,
              12    Echinerpeton_intermedium,
              13    Archaeothyris_florensis,
              14    Varanosaurus_acutirostris,
              15    Ophiacodon_spp,
              16    Haptodus_garnettensis,
              17    Secodontosaurus_obtusidens,
              18    Dimetrodon_spp,
              19    Ianthasaurus_hardestiorum,
              20    Edaphosaurus_boanerges,
              21    Archaeovenator_hamiltonensis,
              22    Ascendonanus_nestleri,
              23    Aerosaurus_spp,
              24    Apsisaurus_witteri,
              25    Heleosaurus_scholtzi,
              26    Mesenosaurus_romeri,
              27    Mycterosaurus_longiceps,
              28    Elliotsmithia_longiceps,
              29    Varanops_brevirostris,
              30    Varanodon_agilis,
              31    Watongia_meieri,
              32     Hylonomus_lyelli,
              33     Anthracodromeus_longipes,
              34     Paleothyris_acadiana,
              35     Protorothyris_archeri,
              36    Petrolacosaurus_kansensis,
              37    Araeoscelis_spp,
              38    Orovenator_mayorum,
              39    Youngina_capensis,
              40    Acerosodontosaurus_piveteaui,
              41     Lanthanolania_ivakhnenkoi
              42    Claudiosaurus_germaini,
              43    Prolacerta_broomi,
              44    Proterosuchus_spp,
              45    Thuringothyris_mahlendorffae,
              46    Captorhinus_spp,
              47    Protocaptorhinus_pricei,
              48    Romeria_spp,
              49    Euconcordia_cunninghami,
```

```
                50      Reiszorhinus_olsoni,
                51      Eudibamus_cursoris,
                52      Mesosaurus_tenuidens,
                53      Erpetonyx_arsenaultorum,
                54      Belebey_vegrandis,
                55      Macroleter_poezicus,
                56      Milleretta_rubidgei,
                57      Acleistorhinus_pteroticus,
                58      Colobomycter_pholeter,
                59      Procolophon_trigoniceps,
                60       Owenetta_kitchingorum
;


begin mrbayes;

outgroup Gephyrostegus_bohemicus;

constraint ingroup1 = 2-60;

constraint ingroup2 = 3-60;

log start filename=Mr_Bayes_60taxa_FBD09_286_final.txt;

lset rates=gamma coding=variable;

[constraint root = 1-. ;] [root constraints are usually required for dating analyses, but since the
outgroup is constrained I have omitted this command]

[prset topologypr constraints(root)][this would enforce the root prior if included]

[uniform priors are used for fossils]

CALIBRATE     Gephyrostegus_bohemicus       = uniform (306.95,311.45);
CALIBRATE     Seymouria_spp               = uniform (272.5,279.5);
CALIBRATE     Tseajaia_campi                    = uniform (284,290);
CALIBRATE     Limnoscelis_plaudis           = uniform (295,303.4);
CALIBRATE     Oedaleops_campi                   = uniform (280.0,299);
CALIBRATE     Eothyris_parkeyi              = uniform (270.6,280);
CALIBRATE     Vaughnictis_smithae           = uniform (290,299);
CALIBRATE     Eocasea_martini                   = uniform (299,305);
CALIBRATE     Euromycter_rutena             = uniform (257,290);
CALIBRATE     Casea_broilii               = uniform (275.2,279.2);
CALIBRATE     Ennatosaurus_tecton           = uniform (257,263);
CALIBRATE     Echinerpeton_intermedium      = uniform (306.95,311.45);
CALIBRATE     Archaeothyris_florensis       = uniform (306.95,311.45 );
CALIBRATE     Varanosaurus_acutirostris     = uniform (272.95,279.2);
CALIBRATE     Ophiacodon_spp                    = uniform (279.5,295);
CALIBRATE     Haptodus_garnettensis         = uniform (303.4,305.9);
CALIBRATE     Secodontosaurus_obtusidens    = uniform (272.9,290.1);
CALIBRATE     Dimetrodon_spp                    = uniform (272.5,290.1);
CALIBRATE     Ianthasaurus_hardestiorum     = uniform (303.4,305.9);
CALIBRATE     Edaphosaurus_boanerges            = uniform (290,299);
```

```
CALIBRATE     Archaeovenator_hamiltonensis  = uniform (295,303.4);
CALIBRATE     Ascendonanus_nestleri            = uniform (288.2,291.8);
CALIBRATE     Aerosaurus_spp                    = uniform (295,303.4);
CALIBRATE     Apsisaurus_witteri          = uniform (280,290);
CALIBRATE     Heleosaurus_scholtzi        = uniform (259,265);
CALIBRATE     Mesenosaurus_romeri         = uniform (257,260.4);
CALIBRATE     Mycterosaurus_longiceps           = uniform (270.6,280);
CALIBRATE     Elliotsmithia_longiceps           = uniform (259,265);
CALIBRATE     Varanops_brevirostris             = uniform (270.6,290);
CALIBRATE     Varanodon_agilis               = uniform (265,272.5);
CALIBRATE     Watongia_meieri                    = uniform (265,272.5);
CALIBRATE     Hylonomus_lyelli            = uniform (314.6,318.1);
CALIBRATE     Anthracodromeus_longipes       = uniform (306.95, 311.45);
CALIBRATE     Paleothyris_acadiana           = uniform (306.95,314.6);
CALIBRATE     Protorothyris_archeri             = uniform (290,299);
CALIBRATE     Petrolacosaurus_kansensis      = uniform (303.4,305.9);
CALIBRATE     Araeoscelis_spp                    = uniform (270.6,290);
CALIBRATE     Orovenator_mayorum          = uniform (288.32,289.68);
CALIBRATE     Youngina_capensis           = uniform (254,259);
CALIBRATE     Acerosodontosaurus_piveteaui  = uniform (254.14,261.1);
CALIBRATE     Lanthanolania_ivakhnenkoi      = uniform (257,260.4);
CALIBRATE     Claudiosaurus_germaini            = uniform (254.14,261.1);
CALIBRATE     Prolacerta_broomi           = uniform (247.2,261.1);
CALIBRATE     Proterosuchus_spp           = uniform (247.2,252.3);
CALIBRATE     Thuringothyris_mahlendorffae  = uniform (270.5,290.1);
CALIBRATE     Captorhinus_spp                    = uniform (272.95,288.32);
CALIBRATE     Protocaptorhinus_pricei        = uniform (279.5,290.1);
CALIBRATE     Romeria_spp                  = uniform (295,296.4);
CALIBRATE     Euconcordia_cunninghami        = uniform (295,303.4);
CALIBRATE     Reiszorhinus_olsoni            = uniform (272.5,290.1);
CALIBRATE     Eudibamus_cursoris          = uniform (279.5,290.1);
CALIBRATE     Mesosaurus_tenuidens        = uniform (279.5,290.1);
CALIBRATE     Erpetonyx_arsenaultorum           = uniform (298.9,303.4);
CALIBRATE     Belebey_vegrandis           = uniform (260.4,265);
CALIBRATE     Macroleter_poezicus         = uniform (258,265);
CALIBRATE     Milleretta_rubidgei         = uniform (252.3,254);
CALIBRATE     Acleistorhinus_pteroticus      = uniform (272.5,279.5);
CALIBRATE     Colobomycter_pholeter             = uniform (288.32,289.68);
CALIBRATE     Procolophon_trigoniceps        = uniform (247.2,251.3);
CALIBRATE     Owenetta_kitchingorum          = uniform (251.3, 252.3);

PRSET nodeagepr = calibrated; [enforces the above calibrations]
       prset clockvarpr=igr;
       prset igrvarpr=exp(10);
       prset clockratepr = normal(0.001,0.01);

prset topologypr = constraints (ingroup1,ingroup2);

[Following sets up FBD parameters]

PRSET brlenspr = clock:fossilization; [Sets the clock to use a FBD process]
[PRSET sampleprob = 0;] [this normally represents a fraction of extant species that are sampled in
the analysis, but since this analysis contains only fossil taxa, this prior is omitted]
PRSET samplestrat = fossilTip;
```

```
[setting prior values for speciation rate (lambda), extinction rate (mu) and sampling rate (psi)]

PRSET speciationpr = exponential(10)      ;
PRSET extinctionpr = beta(1,1);
PRSET fossilizationpr = beta(1,1) ;

[Following sets the root age of the tree; comment: specifies the prior probability distribution on
the tree age when a uniform or fossilization prior is used on the branch lengths of a clock tree --
offset exponential distribution with minimal age, which in this dataset is Hylonomus_lyelli (first
value) and mean density of the exponential curve (second value)calculated using a Cumulative Density
Function, and a absolute maximum age for amniote origins set at the start of the Carboniferous 358.8
Ma]

PRSET treeagepr = offsetexponential(318.1,327.54);

[next commands set up the mcmc and runs it]

mcmcp nrun = 2 nchain = 4  temp = 0.09  ngen=50000000 samplefreq=500 printfreq=500 diagnfr = 5000
savebrlens=yes relburnin=yes burninfrac=0.25;
mcmc;

[define outputs]

sumt contype = allcompat conformat = Figtree relburnin=yes burninfrac=0.25;
sump relburnin=yes burninfrac=0.25;

end;

[this is the code for the Mkv run - MrBayes script for Mkv run. 60 fossil amniotes Mkv run.Run date
5.12.18]

begin mrbayes;

[comment: log screen output]
log start filename=60taxa_Mkv_286_Mkv_final.txt;

lset rates=gamma coding=variable;

outgroup Gephyrostegus_bohemicus;

constraint ingroup1 = 2-60;

constraint ingroup2 = 3-60;

prset topologypr = constraints (ingroup1,ingroup2);

mcmcp nrun = 2 nchain = 4 temp = 0.10 ngen=50000000 samplefreq=500 printfreq=500 diagnfr = 5000
savebrlens=yes relburnin=yes burninfrac=0.25;
mcmc;

[define outputs]
```

```
[define outputs]

sumt contype = allcompat conformat = Figtree relburnin=yes burninfrac=0.25;
sump relburnin=yes burninfrac=0.25;
end;

[This is the script for the Mkv run - MrBayes script for Mkv run. 60 fossil amniotes  Mkv run.Run
date 5.12.18]


begin mrbayes;

[comment: log screen output]
log start filename=60taxa_Mkv_286_Mkv_final.txt;

lset rates=gamma coding=variable;

outgroup Gephyrostegus_bohemicus;

constraint ingroup1 = 2-60;

constraint ingroup2 = 3-60;

prset topologypr = constraints (ingroup1,ingroup2);

mcmcp nrun = 2 nchain = 4 temp = 0.10 ngen=50000000 samplefreq=500 printfreq=500 diagnfr = 5000
savebrlens=yes relburnin=yes burninfrac=0.25;
mcmc;

[define outputs]

sumt contype = allcompat conformat = Figtree relburnin=yes burninfrac=0.25;
sump relburnin=yes burninfrac=0.25;

end;
```

Appendix 5 - Taxon Date Ranges

TAXON	RANGE EARLY	RANGE LATE	SOURCE	PBDB range	COMMENTS
Gephyrostegus	311.45	306.95	Klembara et al. 2014	311.45/306.95	Plattenkohle of Humboldt Mine, Nyrany, Plzen-Manetın Basin, Czech Republic, Asturian (Upper Moscovian), Late Carboniferous (Nemejc, 1952). Moscovian (315-307), Middle Pennsylvanian, (Westphalian D - Godfrey and Reisz 1991)
Seymouria	299	270.6	Berman et al. 2000, Laurin 1996,	279.5/272.5	*S.sanjuanensis*: Bromacker quarry, Lower Permian Tambach Formation (Wolfcampian - Vaughn 1966) and Cutler Formation, New Mexiaco. *S. baylorensis* Baylor County, Clear Fork Group (Leonardian). The North American Stages: Wolfcampian (299-280), Leonardian (280-270.6)
Tseajaia	290	284	Vaughn 1955, Sumida et al. 1992	296.4/268.0	Organ Rock Shale, Utah and Cutler Formation, New Mexico. Permo-Pennsylvanian(Sumida et al. 1992). The Organ Rock Formation is Permian in age (see' Geology of the Pennsylvanian and Permian Cutler Group and Permian Kaibab Limestone in the Paradox Basin, Southeastern Utah and Southwestern Colorado' Condon 2000.
Limnoscelis	305	280	Romer 1946, Berman et al. 2010	303.4/295.0	Cañion del Cobre, Rio Arriba County, New Mexico. Cutler Group, late Pennsylvanian-early Permian (Virgilian 305 to 299-Wolfcampian 299 to 280) from 'Summary of Geology of Canon del Cobre, Rio Arriba County, New Mexico' Lucas et al. 2010
Oedaleops	299	280	Langston 1965, Reisz et al. 2009	303.4/268.0	Camp quarry, Arroyo del Agua, Rio Arriba County,Cutler Formation, Wolfcampian(299-280)
Eothyris	280	270.6	Reisz et al. 2009	290.1/279.5	Petrolia Formation, Wichita Group, Leonardian (280 -270.6), Lower Permian, from Tit Mountain, near Dundee, Archer County, Texas, USA.

Vaughnictis	299	290	Brocklehurst et al. (2016)	296.4/268.0	San Miguel County, Colorada, Cutler Group (Asselian - Sakmarian)
Eocasea	305	299	Reisz and Frobish 2014	303.4/295.0	Hamilton Quarry, Greenwood County, Kansas; Calhoun Shale, Shawnee Group, Virgilian Series(305-299), (Stephanian of Europe), Upper Pennsylvanian
Euromycter	290	257	Sigogneau-Russell and Russell 1974	295/254	Gres Rouge Red Sandstone. Authors only note 'Saxonian - with reservations' - roughly lower Permian, underlying the Thuringian 270-250 (see The Permian of Northern Pangea: vol . 2). However, Reisz et al. (2014) assign the Saxonian group to a range from the late Sakmarian to early Lopingian (i.e 290-257)
*Casea_*	280	270.6	LeBlanc and Reisz 2014	279.2/275.2	*Cacops* bone bed, Baylor County, Texas (Leonardian 280- 270.6)
Ennatosaurus	263	257	Maddin et al. 2008	272.5/265	The Moroznitsa locality , near the towns of Pinega and Karpoga, on the Pinega River, northwestern Russia, whose strata are assigned to the earliest early Tatarian age (late Guadalupian) of the Middle Permian. Tartarian 260.4- 251. Guadalupian 270.6 - 260.4
Echinerpeton	311.45	306.95	Reisz 1972	314.6/306.95	Morien Group, Florence, Nova Scotia (Westphalian D)
Archaeothyris	311.45	306.95	Reisz 1972	314.6/306.95	Morien Group, Florence, Nova Scotia - Westphalian D
Varanosaurus	280	270.6	Berman et al. 1995	279.2/275.2	Arroyo Formation, Clear Fork Group, Baylor County, Texas. Also Wellington Formation, Garvin County, Oklahoma.(Leonardian 280 -270.6)

Ophiacodon	305	280	Vaughn 1963, Romer and Price 1940	295/279.5	El Cobre Canyon, Cutler Formation,New Mexico-Virgilian 305-299 (*O. navajovicus*), Abo Formation, New Mexico, Wolfcampian 299-280 (*O.mirus*) Wichita Group, Wolfcampian (*O.uniformis, O. retroversus*). Clyde Formation, Clear Fork Group, Texas/Oklahoma (*O. major*)
Haptodus	305	304.5	Laurin 1993, Reisz et al. 1982	305.9/303.4	Rock Lake Shale Member, Stanton Formation, Anderson County, near Garnett , Kansas (late Missourian 306.5 -305). Latest Kasimovian per Mazierski and Reisz 2010, i.e between 305-304
Secodontosaurus	290.1	272.95	Reisz et al. 1992	279.5/272.5	Admiral and Belle Plains Formations, Wichita Group, Texas (Artinskian). Arroyo Formation, Clear Fork Group, Baylor County, Texas (Kungurian).
Dimetrodon	290.1	272.95	Romer and Price 1940	290.1/272.5	Putnam Formation (*D. milleri*), Belle Plains Formation (*D. booneorum*), Admiral Formation (*D.limbatus, D. natalis*), all Wichita Group. Arroyo Formation, Clear Fork Group (*D.grandis*. Artinskian-Kungurian.
Ianthasaurus	305	304.5	Mazierski and Reisz 2010	305.9/303.4	Rock Lake Shale Member, Stanton Formation, Anderson County, near Garnett , Kansas (late Missourian 306.5 -305). Latest Kasimovian per Mazierski and Reisz 2010, i.e between 305-304
Edaphosaurus	299	290	Modesto 1995	290.1/279.5	Admiral Formation, Wichita Group, Texas (Wolfcampian)

Archaeovenator	305	299	Reisz and Dilkes 2003	303.4/295	Hamilton Quarry, Greenwood County, Kansas; Calhoun Shale, Shawnee Group, Virgilian Series (305-299), (Stephanian of Europe), Upper Pennsylvanian
Ascendonanus	291.8	288.2	Splindler et al. 2018	not in database	Zeisigwald Tuff, upper Leukerdorf Formation, Germany. Dated to 290 +/- 1.8 by U=Pb dating of zircon grains. Sakmarian/ Artinskian boundary
Aerosaurus	305	299	Langston and Reisz 1981	303.4/295	El Cobre Canyon, Cutler Formation,New Mexico (Virgilian 305-299) *(A.greenleeorum*). Camp quarry , Arroyo del Agua, Rio Arriba County, New Mexicao, Abo/Cutler Formation (Wolfcampian 299-280)(*A.Wellesi*)
Apsisaurus	290	280	Laurin 1991	296.4/268	Archer City Formation, Wichita Group, Texas (Wolfcampian)
Heleosaurus	265	260.4	Botha-Brink and Modesto 2007, Reisz and Modesto 2007	265/259	Tapinocephalus AZ, Abrahamskraal Formation, Beaufort Group, South Africa (late Guadalupian - see Day et al 2015)
Mesenosaurus	260.4	257	Reisz and Berman 2001	272.5/265	Mezen River Basin, Russia. Lower Tatarian
Mycterosaurus	280	270.6	Berman and Reisz 1982	290.1/272.5	Baylor County, Clyde Formation, Clear Fork Group, Texas. (Leonardian). Fort Sill, Comanche County, Oklahoma (Leonardian)
Elliotsmithia	265	260.4	Dilkes and Reisz 1996	265/259	Tapinocephalus AZ, Abrahamskraal Formation, Beaufort Group, South Africa (late Guadalupian - see Day et al 2015)

Varanops	290	270.6	Campione and Reisz 2010	279.5/272.5	*Cacops* bonebed, Arroyo Formation, Clear Fork Group, (Leonardian), Baylor County, Texas. Vale Formation, Clear Fork Group, (Leonardian), Taylor County, Texas. Dolese Brothers Limestone Quarry, near Richards Spur Comanche County, Oklahoma (Wolfcampian/Leonardian)
Varanodon	272.95	262.8	Olson 1965	272.5/265	Flowerpot Shale, Chickasha Formation, Oklahoma (Roadian) see Reisz and Laurin 2002 in response to Lucas 2002
Watongia	272.95	262.8	Reisz and Laurin 2004	272.5/265	Flowerpot Shale, Chickasha Formation, Oklahoma (Roadian) see Reisz and Laurin 2002 in response to Lucas 2002
Hylonomus	319	318	Carroll 1964, Benton et al. 2015	318.1/314.6	Joggins, Nova Scotia. Benton et al. (2015) argue for a minimum age of the Joggins fauna as 318 (Westphalian A - Lansettian or late Bashkirian)
Anthracodrom.	309	306.95	Carroll and Baird 1972	311.45/306.95	Allegheny Group, Linton, Ohio (middle Pennsylvanian - latest Westphalian D)
Paleothyris	311.45	306.95	Carroll 1969	314,6/306.95	Morien Group, Florence, Nova Scotia - Westphalian D
Protorothyris	299	290	Clark and Carroll 1973	298.9/295	Archer County, Moran Formation,Wichita Group (Wolfcampian)
Petrolacosaurus	305	304.5	Reisz 1977, Reisz et al. 1982	305.9/303.4	Rock Lake Shale Member, Stanton Formation, Anderson County, near Garnett , Kansas (late Missourian 306.5 -305). Latest Kasimovian per Mazierski and Reisz 2010, i.e between 305-304

Araeoscelis	290	270.6	Vaughn 1955	279.5/272.5	Belle Plains and Admiral Formation, Witchta Group, Texas (Wolfcampian). Arroyo Formation, Clear Fork Group, Texas (Leonardian)
Orovenator	289.68	288.32	Reisz et al. 2011	290.1/268	Dolese quarry, Richards Spur, Oklahoma.See Woodhead et al. 2010 for U-Pb dating of speleothems
Youngina	259	252.3	Gow 1975	259/254	Daptocephalus AZ, New Bethesda, Graaf-Reinet and Beeldhouersfontein, Murraysburg, South Africa (Wuchiapingian)
Acerosodont.	261.1	254.14	Bickelmann et al. 2009	259/252.3	Sakamena River Valley, Madagascar. Lower Sakamena Formation (Capitanian/Wuchiapingian)
Lanthanolania	260.4	257	Modesto and Reisz 2003	272.5/265	Mezen River basin, Russia. Upper Kazanian/lower Tatarian
Claudiosaurus	261.1	254.14	Carroll 1981, Smith 2000	259/252.3	Sakamena River Valley, Madagascar. Lower Sakamena Formation (Capitanian/Wuchiapingian)
Prolacerta	251.9	247.2	Modesto and Sues 2004	252.3/251.3	Lystrosaurus AZ, Beaufort Group, South Africa. Fremouw Formation, Antarctica - Lower Triassic
Proterosuchus	251.9	247.2	Ezcurra and Butler 2015	252.3/247.2	Lystrosaurus AZ, Beaufort Group, South Africa - Lower Triassic
Thuringothyris	299	280	Muller et al. 2006	290.1/279.5	Bromacker quarry, Thuringian Forest, Tambach Formation, Lower Permian of central Germany (Wolfcampian)

Captorhinus	288.32	272.95	Fox and Bowman 1966, Heaton 1979	279.5/254	Craddock bone bed, Arroyo Formation, Texas (Kungurian). Dolese quarry, Richards Spur. Oklahoma (Artinskian) - *C. aguti*. Waggoner Ranch Formation, Texas (Artinskian-Kungurian) - *C.laticeps*
Protocaptorhinus	290.1	283.5	Clark and Carroll 1973	290.1/279.5	Rattlesnake Canyon, Archer County, Witchita Group, Texas.Uppermost Admiral Formation (Artinskian)
Romeria	299	280	Clark and Carroll 1973	296.4/295	Archer City bone bed, Putnam Formation, Wichita Group , Texas (*R.texana*). Moran Formation, Witchita Group, Texas (*R.primus*)
Euconcordia	305	299	Reisz et al. 2016	303.4/295	Hamilton Quarry , Greenwood County, Calhoun Shale, Virgilian Series, Greenwood County, Kansas
Reiszorhinus	290.1	272.95	Sumida et al. 2010	290.1/272.5	Waggoner Ranch Formation, Lower Permian, Baylor County, Texas (Artinskian-Kungurian)
Eudibamus	299	280	Berman et al. 2000	290.1/279.5	Bromacker quarry, Lower Permian Tambach Formation (Wolfcampian)
Mesosaurus	293.52	290.1	Modesto et al. 2006, Pinero et al. 2012	290.1/279.5	Whitehill Formation, Ecca Group, South Africa. Irati Formation, Passa Dois Group, Brazil. Mangrullo Formation, Tacuarembo and Cerro Largo Counties, Uruguay -latest Sakmarian per Oelofsen & Araújo (1987)
Erpetonyx	303.7	298.9	Modesto et al. 2015	303.4/298.9	Egmont Bay Formation, Prince Edward Island, Newfoundland. Gzhelian (303.7 to 298.9 Ma)