The Anatomy of *Westlothiana lizziae* and a Novel Phylogenetic Analysis of Early Amniotes

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This thesis is submitted for the degree of

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Declaration of Authorship

The contents of the thesis presented here are entirely my own work, unless otherwise stated. Micro-CT scanning of the holotype of *Westlothiana lizziae* was carried out by Dr. Vincent Fernandez at the European Synchotron Radiation Facility, and so Dr. Fernandez provided details of the scanning parameters, indicated in Chapter 4 of the thesis.

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Abstract

Amniotes (reptiles, birds and mammals) first evolved by the late Carboniferous, around 318 million years ago. Ecologically diverse members of the amniote total-group are known from the Carboniferous and early Permian. However, the interrelationships of these groups and the timing of their deep divergences remain uncertain due to a scarcity of relevant fossils during the early Carboniferous and the incomplete knowledge and uncertain affinities of many of those that are known.

Here I use phase-contrast synchrotron computed-tomography to reveal considerable new data on the enigmatic early Carboniferous stem-amniote *Westlothiana lizziae*, which was originally described as a "reptiliomorph". *Westlothiana* has been recovered in various phylogenetic positions, including as a sister taxon to amniotes, to lepospondyls, or to a lepospondyl-amniote clade. I present new anatomical data of this key taxon, including detailed anatomy of the snout, temporal series, mandible and palate, atlas-axis complex, humerus, femur and pes. I show that *Westlothiana* possesses a mosaic of primitive and derived traits, including a plesiomorphic, extensive palatal dentition, an amniote-like temporal region and a microsaur-like circumorbital series.

I produce a new, comprehensive phylogenetic dataset by compiling and editing the characters of previous analyses focussed on both early tetrapods and early amniotes. Mine is the first analysis to include substantial, and near equal, representation of taxa typically considered both stem and crown amniotes. I find *Westlothiana* as the earliest diverging member of a monophyletic Lepospondyli, therefore occupying an important position at the divergence of amniotes and their closest relatives (diadectomorphs, captorhinids, protorothyrids) from other groups. I also recover araeoscelids, recognised in most previous analyses as stem reptiles, as stem mammals. My results show that substantial diversification of stem amniotes had occurred by the early Viséan or Tournasian stages of the early Carboniferous, during "Romer's Gap". This substantially increases the age of the tetrapod crown group, and changes our understanding of the origin of vertebrates on land.

Chapter 1: A Review of the Systematics of Stem Amniotes

Amniotes make up 78% of all land vertebrates today (Iucn 2020), ranging from dwarf chameleons just millimeters long and weighing less than a gram (Glaw, Köhler et al. 2021) to elephants weighing more than six tons (Laursen and Bekoff 1978), adapted to habitats ranging from Antarctica (Kooyman, Hunke et al. 2000) to the Sahara (Young and Morain 2002). The great diversity of amniotes today can be traced back to the evolutionary transition to a terrestrial lifestyle, made possible by key anatomical innovations related to living on land. These innovations include the amniotic egg (Romer 1957, Clack 2012), rib-based lung ventilation (Janis and Keller 2001), as well as innovations relating to feeding on land (Frazzetta 1968, Lauder and Gillis 1997) including the first terrestrial vertebrates to evolve adaptations for herbivory (Hotton, Olson et al. 1997, Berman, Henrici et al. 2004, Clack, Ruta et al. 2019). However, our understanding of amniote origins is impeded by uncertainties about the anatomy and the phylogenetic relationships of important fossil taxa, which obscures key aspects of the anatomical changes involved in amniote origins, and the divergence times of both stem and early crown amniotes.

Crown amniotes are defined by the mammal-reptile split, and so are characterised by a basal dichotomy between the mammalian total group, Synapsida, and the reptile total group, Reptilia (Laurin and Reisz 1995, Modesto and Anderson 2004). This divergence had occurred by the late Carboniferous, based on the appearance of the earliest probable synapsids in the mid-Pennsylvanian, approximately 309 Ma (Mann and Paterson 2020), and the earliest potential reptiles in the lower-Pennsylvanian, approximately 318 Ma (Carroll 1964, Benton, Donoghue et al. 2015). Some Carboniferous and Permian fossil groups are confidently placed on the stem of amniotes, including large-bodied terrestrial taxa such as the seymouriamorphs and the herbivorous diadectamorphs. Nonetheless, other groups have proved more difficult to resolve. For example, lepospondyls are a morphologically varied assemblage of mostly amphibious taxa, with some terrestrial forms (Carroll 2000). The group includes large terrestrial taxa with robust limbs such as the microsaurs *Pantylus cordatus* and *Cardiocephalus peabodyi* (Carroll and Gaskill 1978), as well as entirely limbless aquatic

taxa such as the aïstopods *Lethiscus stocki* (Anderson, Carroll et al. 2003) and *Phlegethontia linearis* (Anderson 2002). Lepospondyls have sometimes been assigned to the amniote stem (Ruta, Jeffery et al. 2003, Ruta and Coates 2007), but have also been considered to be more closely related to lissamphibians (frogs, salamanders, caecillians) than they are to amniotes (Panchen and Smithson 1988, Marjanović and Laurin 2019). Furthermore, some authors have argued that lepospondyls are a polyphyletic grouping of taxa that have been united by features that evolved convergently due to the small body size of lepospondyls (Milner 1993, Clack 2012), and they have been recovered as a polyphyletic group in multiple phylogenetic analyses (Gardiner 1982, Panchen and Smithson 1988, Clack, Ruta et al. 2019). Some recent studies have recovered a polyphyletic Lepospondyli in which one group of lepospondyls, the aïstopods, are recovered as stem tetrapods and another group, microsaurs, are recovered as crown amniotes (Pardo, Szostakiwskyj et al. 2017).

Other groups that have frequently been proposed to have a close relationship with amniotes include the large-bodied, predatory and superficially crocodile-like embolomeres, which are sometimes recovered as stem-tetrapods depending on the phylogenetic position of lissamphibians (Laurin, Reisz et al. 1997, Pardo, Szostakiwskyj et al. 2017, Pardo 2023) relative to lepospondyls. Additionally, multiple groups traditionally considered as stem reptiles, and therefore within the amniote crown (Laurin and Reisz 1995), have instead been recovered as crownward stem amniotes by some recent analyses, specifically araeoscelids and captorhinids (Simões, Kammerer et al. 2022). Araeoscelids have also been recovered as stem-reptiles stemwards of parareptiles, contrasting their previous position as the sister-group to diapsid reptiles (Ford and Benson 2020).

The main groups that have often been assigned to the amniote stem since the advent of synapomorphy based phylogenetic analyses in the 1980s (Gardiner 1982, Løvtrup 1985, Panchen and Smithson 1988) include “anthracosaurs” (which generally overlaps with embolomeres, see discussion below), Gephyrostegidae, Chroniosuchia, Seymouriamorpha, Diadectamorpha, and an array of groups that were classically referred to Lepospondyli — Microsauria, Nectridea, Aïstopoda, Lysorophia, Adelospondylii and Acherontiscidae. Diadectamorpha is typically considered as the sister-clade to amniotes (Ruta, Jeffery et al. 2003, Ruta and Coates 2007, Ford and Benson 2020), and Lepospondyli is considered the sister-clade to Amniota+Diadectamorpha (Ruta, Jeffery et al. 2003, Ruta and Coates

2007). “Anthracosaurs” are also usually considered to be amongst the earliest diverging stem amniotes, and Seymouriamorpha, Gephyrostegidae and Chroniosuchia are recovered in between “anthracosaurs” and lepospondyls (Ruta, Jeffery et al. 2003, Vallin and Laurin 2004, Ruta and Coates 2007, Marjanović and Laurin 2019). However, all of these relationships remain debated, and alternative hypotheses continue to be recovered (Laurin, Reisz et al. 1997, Pardo, Szostakiwskyj et al. 2017, Clack, Ruta et al. 2019). In the following review, I summarise the history and anatomy of these clades, and review the various phylogenetic hypotheses concerning the amniote stem, considering the current state of these hypotheses in the literature (Fig. 1).

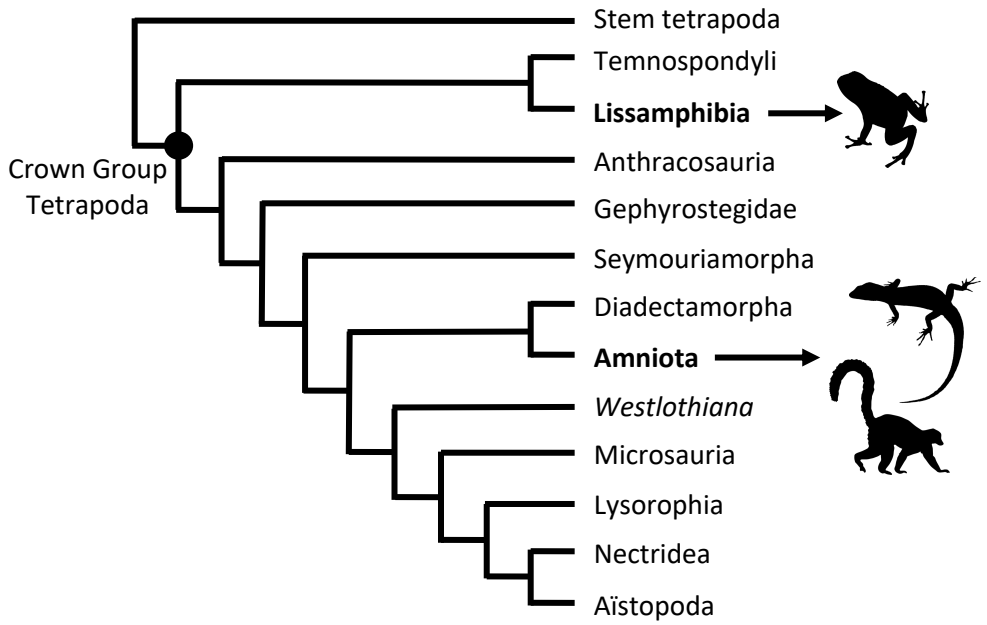


Figure 1: A summarised phylogenetic hypothesis of the relationships of the major groups of early tetrapods, based on Ruta and Coates (2007).

1.1 Clades that are contenders for stem amniotes

1.1.1 “Anthracosaurs”

Anthracosaurs, as currently understood (Ruta and Clack 2006, Ruta and Coates 2007) include various taxa from the base of the Viséan, approximately 331 Ma (Holmes 1984) to the lower Permian (Holmes 1989). They are predominantly known from the UK (Panchen 1975, Panchen 1977,

Smithson 1985, Clack 1987), with some specimens discovered in the USA, in West Virginia (Holmes 1984) and Texas (Holmes 1989). Amongst the best known taxa are *Anthracosaurus russeli* (Huxley 1863, Panchen 1977) and *Archeria crassidisca* (Cope 1884, Romer 1957, Holmes 1989). Anthracosaurs were large, predatory taxa that typically had an aquatic or semi-aquatic lifestyle. Many anthracosaurs had large skulls that could reach tens of centimeters in length, with conical or recurved sharp marginal teeth, and sizable palatal fangs. An aquatic lifestyle has been presumed based on the presence of lateral line canals and tails with long, overlapping neural spines and haemal arches (Holmes 1984, Holmes 1989). An elongate vertebral column with a high number of presacral vertebrae (Romer 1957, Holmes 1989) has also been considered as evidence of an aquatic habit for anthracosaurs (Panchen 1970). One clade of anthracosaurs, the embolomeres, has been described in particular to be crocodile-like predators, with long snouts (Clack 1987). Embolomeres also typically have short posterior projections of the tabular bones, forming a tabular horn. Anthracosaurs retain a full series of temporal bones, including the intertemporal, supratemporal and aforementioned tabular. Anthracosaurs have also been characterised by a contact between the tabular and parietal (Panchen 1980), which differs from stem-tetrapods in which the supratemporal contacts the postparietal (Smithson 1982). However, a tabular - parietal contact is not unique and is retained in other clades of stem amniotes closer to the amniote crown (Klembara 1997, Danto, Witzmann et al. 2012). Anthracosaurs are most clearly united by their vertebral morphology. Anthracosaur vertebrae are embolomerous or near embolomerous, meaning that the pleurocentrum is always fully cylindrical (Danto, Witzmann et al. 2017). The intercentrum is anteroposteriorly shorter than the pleurocentrum, and is also disc-like but ranges in levels of ossification; in Embolomeri the intercentrum forms a complete disc but this is incomplete in other anthracosaur taxa (Smithson 1985).

The term “anthracosaur”, has been used informally to refer to members of Anthracosauria (Säve-Söderbergh 1934) and Anthracosauroidea (Smithson 1985), which themselves have had various diagnoses and intended contents from different authors (Watson 1917, Romer 1956, Heaton 1980, Panchen 1980, Smithson 1985, Laurin, Reisz et al. 1997). Therefore, although there is a general consensus on what is meant by “anthracosaurs”, this term has not been used consistently to refer to a

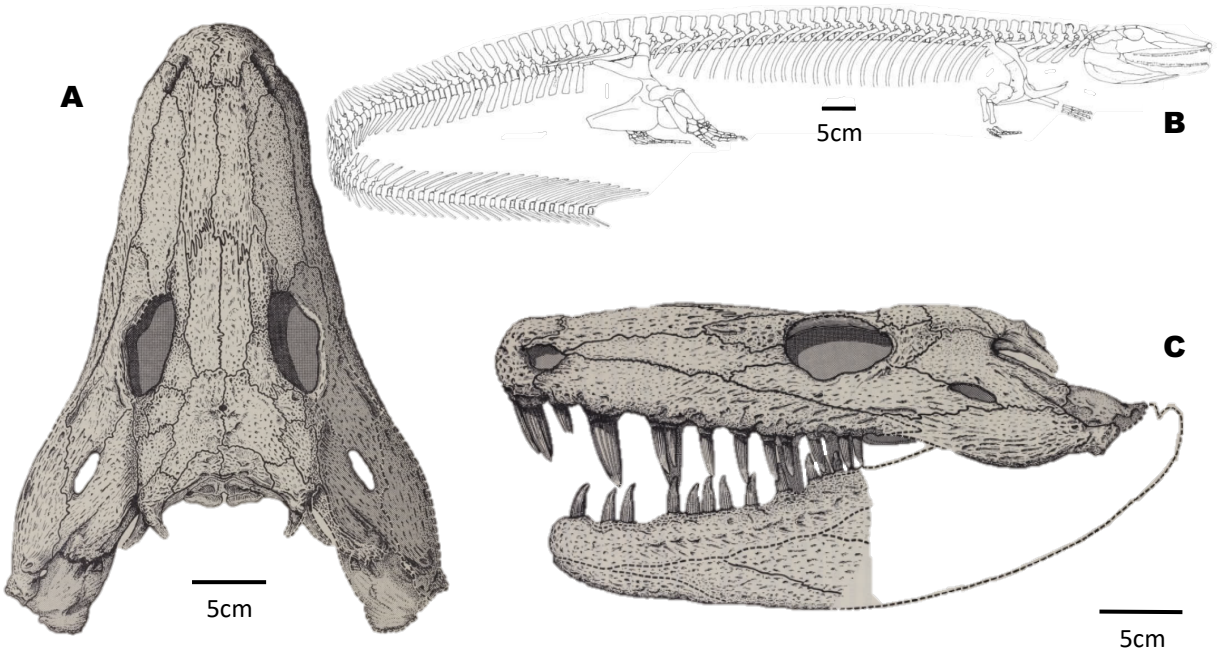


Figure 2: Examples of the morphology of some anthracosaurs. A, C, the skull of *Anthracosaurus russelli*, in dorsal and left lateral views respectively, from Panchen (1977). B, the skeleton of *Archeria crassidisca* in right lateral view, from Holmes (1989).

particular monophyletic group, or even for a paraphyletic grade. Various terminology has been used to describe anthracosaurs, and a large variety of taxa have been included or excluded from the clade.

Watson (1917, 1926) provided one of the earliest definitions of anthracosaurs. He defined a grade of amphibians called Embolomeri within the suborder Labyrinthodonta. Embolomeri, according to Watson (1917), included the family Anthracosauridae (Cope 1875) alongside the families Loxommidae (Watson 1917) and the monogeneric Pholidogasteridae, including only *Pholidogaster pisciformes*. Watson's Anthracosauridae included the embolomerous taxa *Anthracosaurus russelli* and *Pholiderpeton scutigerum*, as well as *Pteroplax cornutus*, from which only highly fragmentary material is known.

Säve-Södenbergh (1934) corroborated the hypothesis that *Anthracosaurus* and *Pholiderpeton* formed a group, though he referred to this group as Anthracosauria, rather than Anthracosauridae as in Watson's work (1917). He did this to distinguish his hypothesis from that of Watson (1917), because, while Säve-Sövenbergh (1934) agreed that *Anthracosaurus* and *Pholiderpeton* formed a group, he considered this group to have a different evolutionary origin to that of Watson (1917). Säve-

Sövenbergh (1934) did not consider Anthracosauria to be related to Loxommidae as Watson (1917) did when he grouped these two families together in Embolomeri. Säve-Sövenbergh (1934), instead, considered Anthracosauria to be relatives of amniotes, and considered Loxommidae to be relatives of amphibians. Thus, while Säve-Sövenbergh (1934) concurred with Watson (1917) that there was a real group incorporating *Anthracosaurus* and *Pholiderpeton*, the two authors referred to this very same group by different names, Anthracosauria and Anthracosauridae respectively, due to its different supposed phylogenetic position, introducing a source of confusion.

In 1947, Romer expanded the Anthracosauria to include the clade Seymouriamorpha. Following this, Anthracosauria and Embolomeri were used somewhat interchangeably (Panchen 1970) to refer to broadly the same set of taxa. *Anthracosaurus russelli*, *Pholiderpeton scutigerum* and *Archeria crassidisca* were grouped together, with no consensus emerging on whether Anthracosauria or Embolomeri should be used as the name for this group (Panchen 1970).

However, following the publication of Panchen (1970), more anthracosaur-like taxa were discovered that lacked fully embolomerous vertebrae, namely *Proterogyrinus scheelei* (Romer 1970) and *Eoherpeton watsoni* (Panchen 1975). They were nonetheless demonstrated to be closely related to Embolomeri on the basis of cranial characters, for example, well developed tabular horns and otic notches, as well as disc-like pleurocentra (Panchen 1980).

This necessitated a distinction between the group names “Anthracosauria” and “Embolomeri”. Panchen (1975) defined the group Batrachosauria. He considered this clade to consist of Anthracosauria and Seymouriamorpha, thus separating these two clades once again, whilst recognising the close relationship between them. He divided Anthracosauria into three infraorders; Herpetospondyli, Embolomeri and Gephyrostegoidea. Herpetospondyli (sensu Panchen 1975) consisted of *Proterogyrinus* and *Eoherpeton*. Gephyrostegoidea, including *Gephyrostegus bohemicus*, and the poorly known *Eusauropleura digitata* (Carroll 1970) and *Bruktererpeton fiebigi* (Boy and Bandel 1973), is a clade not always included within anthracosaurs or embolomeres today. Panchen (1975) further subdivided Embolomeri into three families; Anthracosauridae, Archeridae and Eogyrinidae, each known primarily from a single genus (*Anthracosaurus russelli* in Anthracosauridae, *Archeria crassidisca* in Archeridae) or two genera (*Eogyrinus* and *Pholiderpeton* in Eogyrinidae).

Panchen (1975) believed *Eoherpeton* could be a basal gephyrostegoid, and not a herpetospondyl, although under this classification *Eoherpeton* would still be considered an "anthracosaur". He did, however, acknowledge that it was also possible that *Eoherpeton* could be more closely related to seymouriamorphs and not an anthracosaur at all.

Thus, two distinct classifications had been proposed, both considering embolomeres and their relatives (which, at the time, included gephyrostegids) to be closely related to seymouriamorphs. Panchen's classification (Panchen 1970, Panchen 1975) referred to embolomeres and their closest relatives exclusively as Anthracosauria, excluding the seymouriamorphs, and using Batrachosauria to denote Anthracosauria + Seymouriamorpha. However, Romer's classification (Romer 1947, Romer 1956, Romer 1972) referred to this whole group as Anthracosauria, encompassing Seymouriamorpha. Romer deemed usage of the term Batrachosauria to encompass Embolomeri, as used by Panchen (Panchen 1970, Panchen 1975) as "highly improper" (Romer 1972) as the term was intended to refer to terrestrial forms related to *Seymouria* (Fig. 3a, b).

Panchen also commented that there was uncertainty over the relationships of seymouriamorphs, and that they may be more closely related to Diadectamorpha than to anthracosaurs (Panchen 1980), a view that was corroborated by other authors at the time (Heaton 1980). This hypothesis would mean that any usage of the term Anthracosauria that included seymouriamorphs, as in Romer (Romer 1947, Romer 1956, Romer 1972) would be referring to a polyphyletic group. However, to further complicate matters, Panchen (1980) expanded Batrachosauria to include *Crassigyrinus* and Loxommatoidea, and expanded Anthracosauria to now include Seymouriamorpha, as he considered gephyrostegids (including *Eoherpeton*) and seymouriamorphs to form a monophyletic group. Therefore, his use of terminology was brought more in line with that of Romer (Romer 1947, Romer 1956, Romer 1972) when considering taxa included within "Anthracosauria", but not in the usage of "Batrachosauria", which Panchen continued to use broadly (Fig. 3c).

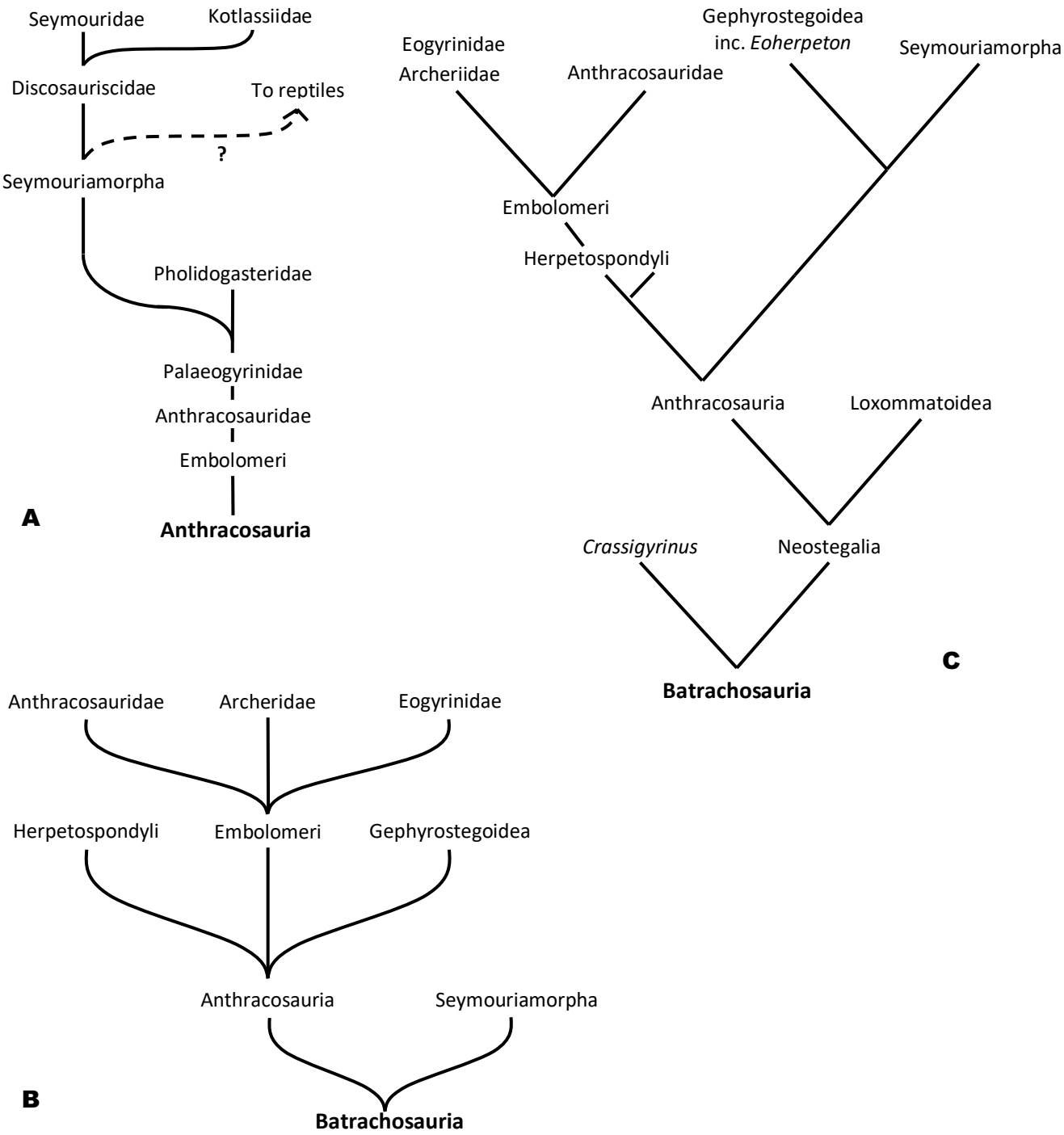


Figure 3: A selection of summarised phylogenetic hypotheses of anthracosaurs and their relatives. A, phylogeny proposed by Romer (1947). B, phylogeny proposed by Panchen (1970, 1975). C, phylogeny proposed by Panchen (1980).

Smithson (1985) corroborated Panchen's (1980) topology linking Seymouriamorpha with other anthracosaurs, but suggested a new internal topology. He considered *Proterogyrinus* to be part of Embolomeri because, although *Proterogyrinus* has crescentic intercentra, these were likely

continued by cartilage to form a complete embolomerous disc. Crucially, Smithson (1985) coined Anthracosauroidea to refer to the clade comprising Embolomeri, *Eoherpeton* (now moved to a monogeneric clade, Eoherpetontidae) and Gephyrostegidae. Anthracosauroidea and Seymouriamorpha together formed a monophyletic group, named Anthracosauria, according to Smithson (1985), who did not use the terms Batrachosauria or Herpetospondyli.

The modern usage of the term "anthracosaur" coincided with the advent of computerised phylogenetic analyses. Modern phylogenetic techniques have comprehensively shown that eoherpetontids and embolomeres form a clade, but that they do not form a clade with seymouriamorphs or gephyrostegids (Laurin, Reisz et al. 1997, Ruta and Coates 2007). Therefore, while Anthracosauroidea (sensu Smithson, 1985) remains a clade, Anthracosauria (sensu Panchen 1980, Smithson 1985) is a polyphyletic assemblage.

To complicate the terminology still further, several early computerised analyses (Gauthier, Kluge et al. 1988, Laurin and Reisz 1999) used Anthracosauroidea to refer to the clade encompassing embolomeres and eoherpetontids, and used Anthracosauria to refer to total-group Amniota, defining Anthracosauria as "amniotes and all extinct groups that are more closely related to amniotes than to lissamphibians" (Laurin and Reisz 1999). "Anthracosauria", under this usage, refers to taxa crownwards of, and including, anthracosauroids, and therefore includes seymouriamorphs, diadectamorphs and the entire amniote crown group, provided anthracosauroids are recovered as stem amniotes (Gauthier, Kluge et al. 1988). However, Laurin & Reisz (1999) found anthracosauroids to be stem-tetrapods, so under this naming scheme seymouriamorphs, diadectamorphs and crown amniotes are considered to be members of Anthracosauria, but anthracosauroids themselves are not. Nonetheless, following both Gauthier et al. (1988) and Laurin & Reisz (1999), synapsids and even *Homo sapiens* are anthracosaurs, but they are not anthracosauroids (Fig. 4).

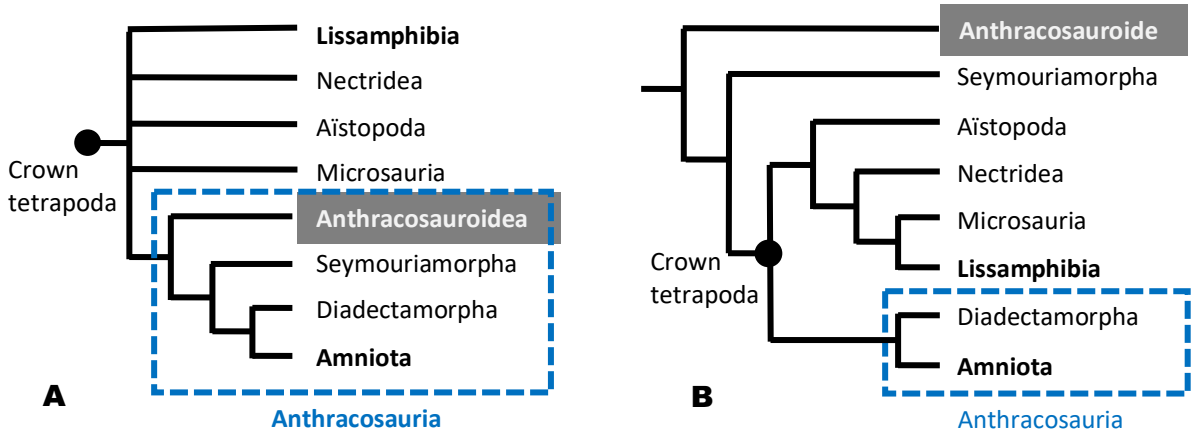


Figure 4: Early computerised phylogenetic hypotheses, demonstrating the different usage of the terms, and different taxa included within, "Anthracosauria" and "Anthracosauroidea". A, summarised phylogeny from Gauthier et al. (1988). B, summarised phylogeny from Laurin and Reisz (1999).

Two new anthracosaur-like taxa were described in 1993. *Eldeceeon* (Smithson 1993) was described as a primitive anthracosaur of uncertain affinity, and *Silvanerpeton* (Clack 1993) was described as an unequivocal anthracosauroid. Both are from the East Kirkton locality of the Viséan, considerably earlier than other anthracosaur taxa. Ruta et al., (2003) referred to both as 'anthracosaurs', using the term informally, but did not include them in their analysis.

Ruta & Clack (2006) redescribed *Silvanerpeton* as a basal anthracosaur. In this analysis, they once again use the term 'anthracosaur' informally, likely referring to Anthracosauroidea (sensu Smithson, 1985). "Anthracosaurs" in this analysis consists of Eoherpetontidae as the sister clade to Embolomeri, which itself consists of Anthracosauridae, Archeriidae, Eogyrinidae and Proterogyrinidae, although the internal relationships of these five clades remained unstable. Ruta & Clack (2006) carried out a phylogenetic analysis. They recovered "anthracosaurs" (referring to Eoherpetontidae and Embolomeri) as the sister-group to more derived amniotes, and they recovered *Silvanerpeton* as the sister taxon to this clade. Therefore, although it was described as an anthracosaur, *Silvanerpeton* was not recovered within the clade "anthracosaurs" as defined in their study. They also found *Gephyrostegus* to be crownwards of "anthracosaurs", and therefore not forming a monophyletic group with them.

The hypothesis that "anthracosaurs" encompasses Embolomeri and Eoherpetontidae has become the general consensus, although a consensus in the terminology has been lacking. More recent

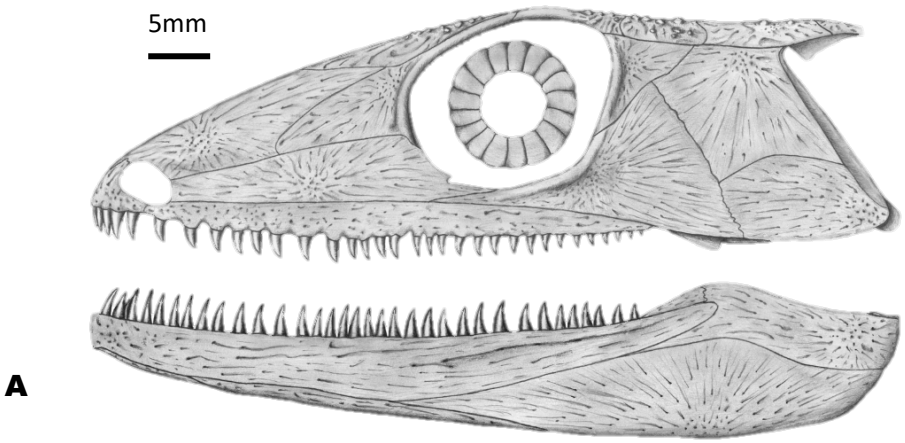
work has considered Anthracosauria to be a monophyletic group that excludes seymouriamorphs and gephyrostegids and broadly corresponds to Anthracosauroidea (sensu Smithson, 1985, incorporating eoherpetontids, eogyrinids, archeriids and *Anthracosaurus russelli*), differing only in the placement of *Silvanerpeton*, which shows an unstable phylogenetic position (Ruta and Coates 2007, Marjanović and Laurin 2019). When *Silvanerpeton* does not form a clade with taxa that are typically considered anthracosaurs (i.e. the taxa referred to in Anthracosauroidea, Smithson, 1985), then the clade consisting of anthracosauroids alone is referred to as Anthracosauria, and *Silvanerpeton* is therefore excluded from Anthracosauria (Marjanović and Laurin 2019). When *Silvanerpeton* does form a monophyletic group with the taxa that are referred to Anthracosauroidea (Smithson 1985), this group is also referred to as Anthracosauria (Ruta and Coates 2007). Thus, even today, usage of the term Anthracosauria is unclear as it certainly encompasses Embolomeri and *Eoherpeton*, but it is unclear if this clade includes *Silvanerpeton* or *Eldeceeon*.

In this review, we recommend the name Anthracosauria to refer to the most expansive group of taxa including *Anthracosaurus russelli*, but not *Seymouria sanjuanensis*, *Gephyrostegus bohemicus*, *Solenodonsaurus janenschi* or *Chroniosaurus dongusensis*.

1.1.2 Gephyrostegidae

Gephyrostegids are primarily known from the Nýřany locality, Czech Republic, from the Asturian, Late Carboniferous. The clade includes *Gephyrostegus bohemicus* (Jaekel 1902), as well as the poorly known taxa *Eusauropleura digitata* (Cope 1868, Romer 1930) and *Bruktererpeton fiebigi* (Boy and Bandel 1973). They were small, lightly built tetrapods with skulls ranging from 25 to 58 mm in anteroposterior length (Fig. 5). Gephyrostegids have tall skulls with large orbits and many sharp, recurved marginal teeth. They share many cranial similarities with anthracosaurs including a plesiomorphic temporal region in which an intertemporal, supratemporal and tabular are all retained (Carroll 1970). As in anthracosaurs and seymouriamorphs, the parietal contacts the tabular. The palate is extensively covered with denticles (Klembara, Clack et al. 2014), and has fang pairs on the vomer, palatine and ectopteryoid, similar to anthracosaurs. Unlike anthracosaurs, the denticles of

gephyrostegids are arranged in distinct rows and there are raised ridges on the anterior palate (Holmes 1989, Klembara, Clack et al. 2014). Gephyrostegids also possess a short, rectangular, laterally projecting transverse process of the pterygoid (Klembara, Clack et al. 2014). This is very similar to the condition in seymouriamorphs (Klembara 1997), but contrasts with anthracosaurs (Panchen 1977, Holmes 1989), which lack such a process. A transverse process on the pterygoid is also present in crown amniotes (Romer, Price et al. 1940, Reisz 1977). However, unlike in crown amniotes, the process in gephyrostegids is shorter and more horizontal, and lacks a tooth row (Klembara, Clack et al. 2014).



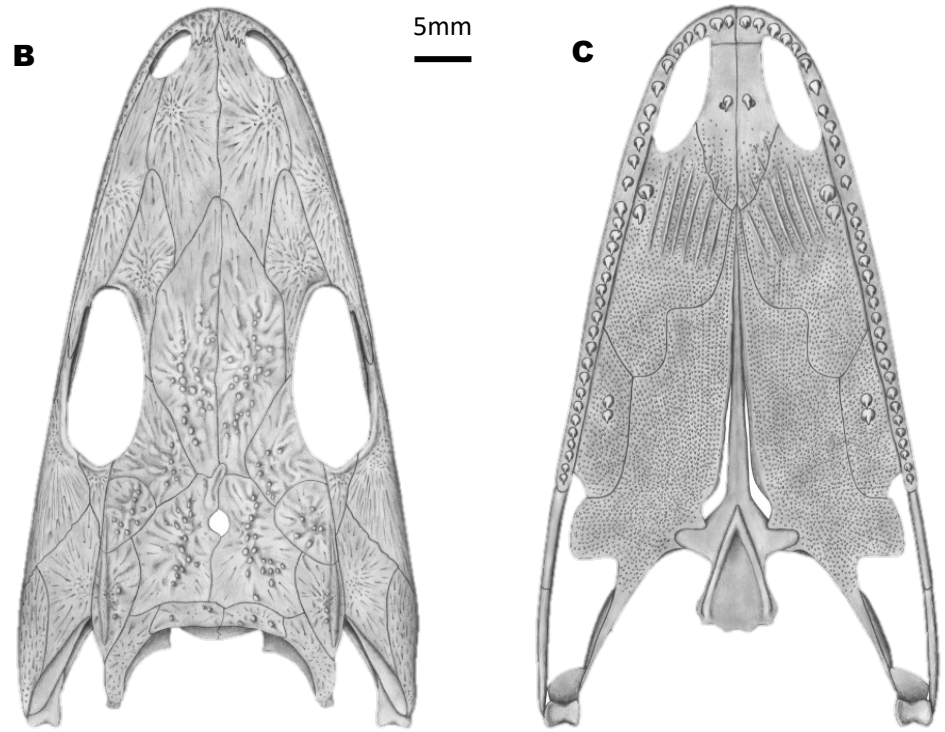


Figure 5 (previous page): The skull of *Gephyrostegus bohemicus* in: A, left lateral view; B, dorsal view; C, palatal view. All images from Klembara et al. (2014).

Gephyrostegids have gastrocentrous vertebrae, with a completely ossified, disc-like pleurocentrum, and a crescent shaped intercentrum (Carroll 1970, Godfrey and Reisz 1991). They have a robustly ossified postcranium with elongate, somewhat flattened ribs and relatively long, gracile limbs, which contrasts with anthracosaurs and potentially indicates that gephyrostegids had a more terrestrial lifestyle than anthracosaurs (Romer 1947, Carroll 1970, Holmes 1989, Clack 2012).

Gephyrostegids have not been as extensively described as other tetrapod taxa. *Gephyrostegus* was first described by Jaeckel (1902). The most substantial published work is Carroll (1970), but his research on the main specimens in Prague was cut short after two days by the Russian invasion, so his work was based on limited other material (Klembara, Clack et al. 2014). Other than a short publication on the vertebrae of *Gephyrostegus* (Godfrey and Reisz 1991), the only published information is a cranial description by Klembara et al. (2014). Another gephyrostegid taxon, *Brukererpeton fiebigi*, but it is known only from a single, partial skeleton and has not been extensively described (Boy and Bandel 1973).

Gephyrostegus was originally described as an anthracosaur (Jaekel 1902). Carroll (1970, p.286) considered gephyrostegids as a "relict" of an earlier stage of anthracosaur evolution, primitive relative to anthracosaurs and seymouriamorphs. He also described *Gephyrostegus* as an "almost ideal morphological antecedent to the reptiles", based on the fact it is proportionally similar to seymouriamorphs but lacks non-reptilian autapomorphies of seymouriamorphs, such as the exaggerated otic notch, and due to similarities of the morphology of the squamosal to captorhinomorphs. Therefore, Carroll (1970) considered *Gephyrostegus* to be a potential ancestor to reptiles as well. Computerised phylogenetic analyses typically recover *Gephyrostegus* as a stem amniote, crownwards of anthracosaurs and stemwards of seymouriamorphs (Vallin and Laurin 2004, Ruta and Coates 2007, Clack and Klembara 2009). In this review, we recommend the name Gephyrostegidae to refer to all taxa more closely related to *Gephyrostegus bohemicus* than to *Seymouria baylorensis* or *Anthracosaurus russelli*.

1.1.3 Chroniosuchia

Chroniosuchians are a poorly known clade from the Upper Permian to Middle Triassic (Clack and Klembara 2009), notable for their characteristic dermal armoured scutes (Golubev 1998). They are known almost exclusively from Russia (Novikov, Shishkin et al. 2000), and from a small amount of material from China (Young 1979). More recent discoveries include specimens from Germany, including isolated scutes of the Late Permian *Hassiacoscutum munki* (Witzmann and Schoch 2018) and isolated scutes and vertebrae of the Triassic *Bystrowiella schumanni* (Witzmann, Schoch et al. 2008), and a single partial skull of *Laosuchus naga* from the Permo-Triassic boundary of Laos (Arbez, Sidor et al. 2019). By far the best known chroniosuchian is *Chroniosaurus dongusensis* (Tverdokhlebova 1972), the only taxon for which a nearly complete, articulated skeleton is known (Clack and Klembara 2009); almost all other taxa are represented by isolated dermal scutes and some limited cranial material (Novikov, Shishkin et al. 2000).

A potential relationship between chroniosuchians and anthracosaurs or seymouriamorphs has long been recognized (Novikov, Shishkin et al. 2000), and they have been described as “relict” anthracosaurs (Golubev 1998) despite the fact that chroniosuchians are separated significantly in space and time from *Archeria*, the latest known embolomere from the Lower Permian of the USA (Holmes 1989). Chroniosuchians were first recognized as a group by Vjushkov (1957), who assigned them to Kotlassiomorpha, within seymouriamorphs. Tatarinov (1972) coined the name Chroniosuchia, although he used this name to include taxa that are today assigned to one of the two families of chroniosuchians, Chroniosuchidae (Buchwitz, Foth et al. 2012), the other family being Bystrowianidae (see below). Nonethless, Tatarinov (1972), assigned both Chroniosuchidae and Bystrowianidae to seymouriamorphs, who he considered to be within anthracosaurs. Ivakhenko & Tverdokhlebova (1980) expanded Chroniosuchia to incorporate both Chroniosuchidae and

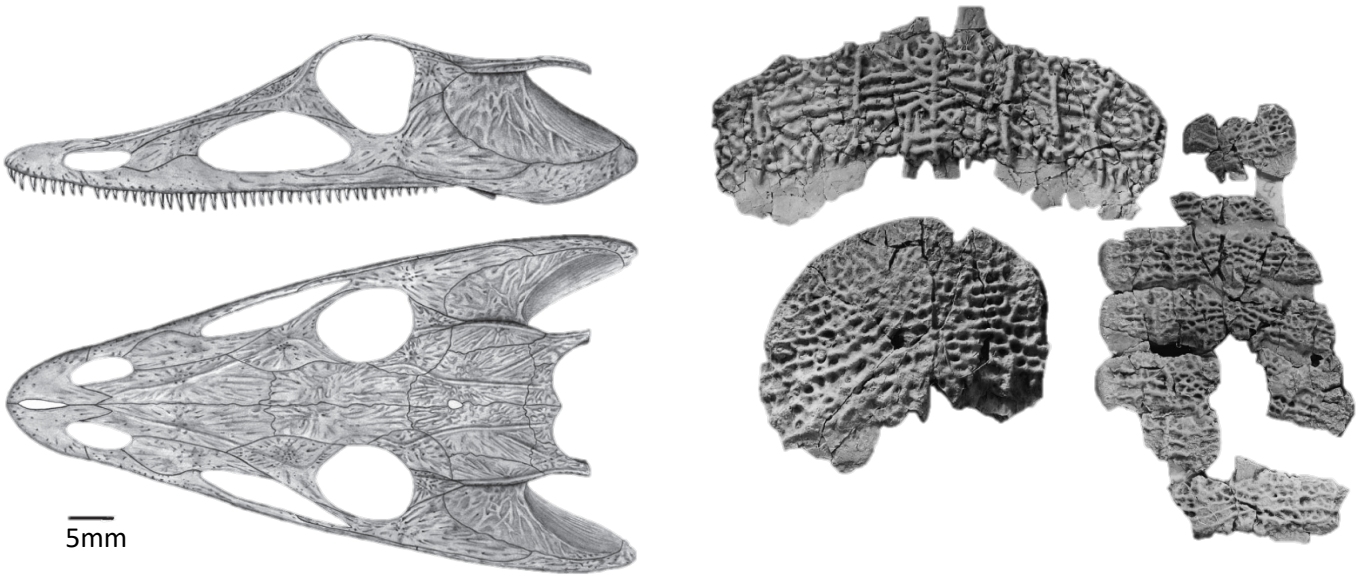


Figure 6: The skull and scutes of selected chroniosuchians. A, the skull of *Chroniosaurus dongusensis* in left lateral and dorsal view, from Clack and Klembara (2009). B, Scutes of multiple species of chroniosuchians, from Golubev (1997).

Bystrowianidae, and united chroniosuchians with anthracosaurs to form a clade referred to as Anthracosauromorpha.

Recent phylogenetic analyses that include chroniosuchians have generally recovered them as stem amniotes, in a polytomy with *Silvanerpeton*, anthracosaurs and more derived amniotes including seymouriamorphs and gephyrostegids (Clack and Klembara 2009, Buchwitz, Foth et al. 2012, Witzmann and Schoch 2018). However, they have also been recovered as the sister-clade to *Asaphestera intermedia* and diadectamorphs, crownwards of anthracosaurs (Arbez, Sidor et al. 2019).

Two families of chroniosuchians have been proposed; Chroniosuchidae and Bystrowianidae (Tatarinov 1972, Ivakhnenko and Tverdokhlebova 1980, Novikov, Shishkin et al. 2000). This has, however, been primarily based on limited evidence concerning the morphology of the armoured scutes, and the temporal distributions of the families. Chroniosuchids are restricted to the Permian, whilst bystrowianids are known only from the Triassic (Arbez, Sidor et al. 2019). The scutes of chroniosuchids are also wider than those of bystrowianids, and are attached to each other and to the neural arches differently to those of bystrowianids (Witzmann and Schoch 2018). There are also some differences in the cranium, but these are difficult to assess due to the highly limited cranial material of bystrowianids (Witzmann and Schoch 2018, Arbez, Sidor et al. 2019). Some authors have suggested

the limited evidence in support of the separation of chroniosuchids and bystrowianids is insufficient, and there is not enough anatomical data in the literature to evaluate this dichotomy (Clack and Klembara 2009). Recent phylogenetic analyses have found both chroniosuchids to be paraphyletic relative to bystrowianids (Buchwitz, Foth et al. 2012), and bystrowianids to be paraphyletic relative to chroniosuchids (Arbez, Sidor et al. 2019).

A large amount of material is known of chroniosuchians, but there are few articulated specimens and descriptions, particularly of bystrowianids (Arbez, Sidor et al. 2019). The skull of chroniosuchians shares features with those of anthracosaurs, particularly in the temporal region, in which the tabular displays small tabular horns like those of embolomeres (Holmes 1989). The palate bears many rows of denticles (Klembara, Clack et al. 2010), resembling the condition in *Gephyrostegus* (Klembara, Clack et al. 2014) and seymouriamorphs (Klembara 1997, Klembara, Ruta et al. 2005), and the pterygoid has a short, rectangular, laterally projecting transverse flange (Klembara, Clack et al. 2010), also like that of seymouriamorphs (Klembara 1997, Klembara, Ruta et al. 2005). Chroniosuchian skulls are otherwise highly unique, and have been compared to crocodiles. The cheek and skull table are not well sutured, resulting in a 'kinetic-line' (Clack and Klembara 2009). Chroniosuchids also possess a distinctive, large anterior fenestra in the snout (Novikov, Shishkin et al. 2000). Ribs are not well preserved in any chroniosuchian specimens (Clack and Klembara 2009).

All chroniosuchians are also united by the morphology of their vertebrae, and armoured scutes (Witzmann and Schoch 2018). The vertebrae of chroniosuchians are fully embolomerous (Clack and Klembara 2009). The vertebrae also possess a unique morphology in which the intercentrum and pleurocentrum form a ball-and-socket joint (Witzmann and Schoch 2018). The postcrania of chroniosuchians are also unique in possessing a single, large and broad dorsal osteoderm at the apex of every neural spine (Golubev 1998, Clack and Klembara 2009). Together, the vertebrae and osteoderms likely stabilised the vertebral column against torsion, assisting in terrestrial locomotion (Witzmann and Schoch 2018). However, it is overall unclear whether or not chroniosuchians would have had a terrestrial or semi-aquatic mode of life. Regarding chroniosuchids, even juvenile chroniosuchid skulls lacked lateral line canals, yet the limb morphology of

chroniosuchids is fairly simple and limb articulating surfaces are poorly developed, which has been associated with aquatic environments (Clack and Klembara 2009). However, no presumably adult limbs of chroniosuchids have been found and so the poor development could be associated with the age of the specimens (Clack and Klembara 2009). Some cranial material of bystrowianids has been found to possess lateral line canals (Novikov, Shishkin et al. 2000) but it is hard to assess the lifestyle of bystrowianids further due to the lack of postcranial material (Witzmann and Schoch 2018).

In this review, we recommend the name Chroniosuchia to refer to all taxa more closely related to *Chroniosaurus dongusensis* than to *Anthracosaurus russelli*, *Gephyrostegus bohemicus* or *Seymouria baylorensis*.

1.1.4 Seymouriamorpha

Seymouriamorphs were a clade of well ossified terrestrial tetrapods (Fig. 7) known from a wide range of localities across much of the northern hemisphere, including North America (Berman, Reisz et al. 1987, Laurin and Waggoner 1998), Europe (Klembara 1997, Berman, Henrici et al. 2000), Tajikistan (Klembara and Ruta 2005), Kazakhstan (Klembara and Ruta 2003) and China (Bulanov 2003). The best known and most complete seymouriamorphs include *Discosauriscus austriacus* Makowsky, 1876 (Kuhn 1933), *Ariekanerpeton sigalovi* Tatarinov, 1968 (Ivakhnenko 1981) and the genus *Seymouria*. *Seymouria* is primarily known from two species, *Seymouria baylorensis* Broili, 1904 from North America (Laurin and Waggoner 1998) and *Seymouria sanjuanensis* (Vaughn 1966), from North America (Berman, Reisz et al. 1987) and Europe (Berman, Henrici et al. 2000).

Seymouriamorphs were mostly restricted to the Permian, but for most of the history of study of the group it was unknown if seymouriamorphs extended into the Carboniferous (Bulanov 2003). One seymouriamorph, *Utegenia shpinari* (Ivakhnenko 1981), is known from horizons that are possibly from the latest Carboniferous, but there is no reliable dating of these sediments (Klembara and Ruta 2003). However, recent work has suggested that some specimens of *Discosauriscus pulcherrimus* Frič, 1883 are from the latest Upper Carboniferous (Klembara, Werneburg et al. 2023). Nonetheless, most well-known seymouriamorph specimens are known from the Early Permian



Figure 7: Photographs of the so-called "Tambach Lovers", *Seymouria sanjuanensis*, MNG 10553 and MNG 10554, displayed in the Museum of Nature, Gotha, Germany. Photographed by the author.

(Klembara 1997, Berman, Henrici et al. 2000, Klembara and Ruta 2005). Fragmentary remains are also known throughout the entire Permian (Bulanov 2003).

The skulls of seymouriamorphs retain a full series of temporal bones (Laurin and Waggoner 1998), as in anthracosaurs (Panchen 1977, Holmes 1989), gephyrostegids (Carroll 1970) and chroniosuchians (Clack and Klembara 2009). They also retain other plesiomorphic conditions, for example, a parietal-tabular contact, a shagreen of denticles and fangs on the palate, three separately ossified coronoids and two separately ossified splenials in the mandible (Laurin and Waggoner 1998, Klembara, Berman et al. 2005, Klembara and Ruta 2005). Juvenile specimens of the seymouriamorph *Discosauriscus* have been noted to possess external gills and a lateral line system, suggesting at least an aquatic larval stage (Klembara 1997). Like gephyrostegids, seymouriamorphs possess a short,

rectangular transverse process of the pterygoid (Klembara, Berman et al. 2005, Klembara, Clack et al. 2014).

Seymouriamorphs also possessed several distinctive features. The skulls have very large otic notches (Bulanov 2003, Klembara, Berman et al. 2005), proportionally larger, even, than otic notches of anthracosaurs (Panchen 1977, Holmes 1989), and differing from the closed skulls of lepospondyls (Carroll 2000) and early amniotes (Carroll 1964, Fox and Bowman 1966, Carroll 1969). The presence of distinctly swollen, domed neural arches on the presacral vertebrae has been used to unite seymouriamorphs (Heaton 1980) although some microsaurs possess similarly domed neural arches (Carroll and Gaskill 1978). Most notably, seymouriamorphs had moderately elongate trunks with short but robust and well ossified limbs, indicating a terrestrial mode of life for adults (Klembara and Bartík 1999, Berman, Henrici et al. 2000).

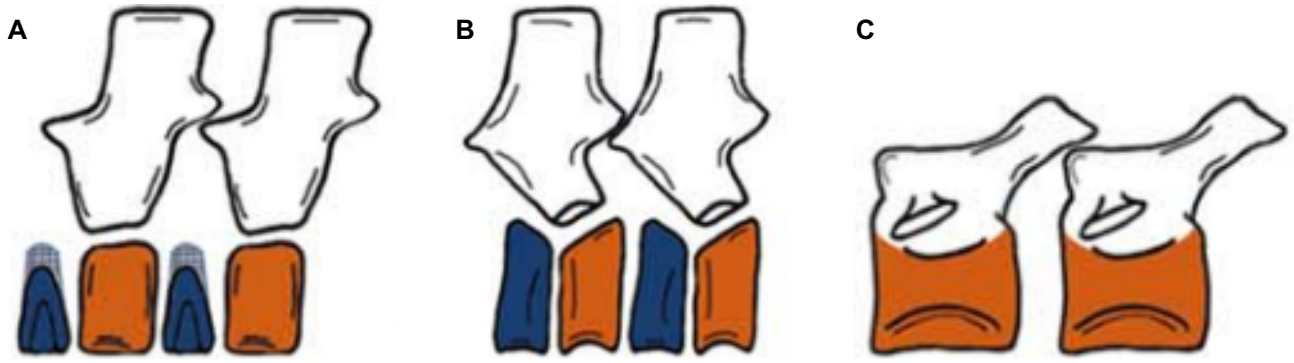


Figure 8: Vertebral morphologies of early tetrapods. A, the gastrocentrous vertebrae of *Chroniosaurus*. B, the embolomerous vertebrae of *Archeria*. C, the monospondylous vertebrae of microsaurs. All images from Danto et al. (2017).

Up to ten species of seymouriamorphs, from seven genera and three families have been described (Bulanov 2003). However, specimens of most taxa are not well described or complete, and are stored in the Palaeontological Institute, Russian Academy of Sciences in Moscow (PIN), making further observations complicated. Bulanov (2003) divided seymouriamorphs into two superfamilies, Kotlassoidea and Seymouriidae, although he distinguished the two families by fairly minor skull characters including the presence of denticles on the rostrum of the parasphenoid and on the pterygoid quadrate rami.

Discosauriscids were the first family of seymouriamorphs to be discovered. *Discosauriscus austriacus* was described in 1876, although it was originally assigned to the genus *Archegosaurus* Makowsky, 1876, and only later assigned to its own genus and renamed *Discosauricsus* Kuhn, 1933. However, discosauriscids have not always been considered to be seymouriamorphs (Heaton, 1980). Heaton (1980) noted that discosauriscids lack a transverse flange of the pterygoid and swollen neural arches, and thus considered them instead to be gephyrostegids. However, Smithson (1985) noted that a transverse flange of the pterygoid is present in discosauriscids but is usually obscured due to post-mortem compression during preservation. He also described that, as all known discosauriscid specimens are juvenile, they would not be expected to possess swollen neural arches. Thus, Smithson (1985) deemed that the criteria with which Heaton (1980) separated discosauriscids from other seymouriamorphs were invalid. The suggestion that discosauriscids are not part of seymouriamorphs has never been widely accepted, and they have been recovered with other seymouriamorphs in recent phylogenetic analyses (Ruta and Coates 2007, Marjanović and Laurin 2019). It has also been suggested that *Discosauriscus* could represent juvenile examples of *Seymouria* (Laurin and Waggoner 1998), but similarly sized skulls of *Discosauriscus* and *Seymouria* have been shown to have very different proportions (Klembara, Berman et al. 2006), indicating that they are indeed separate species.

In this review, we recommend the name Seymouriamorpha to refer to all taxa more closely related to *Seymouria baylorensis* than to *Gephyrostegus bohemicus*, *Chroniosaurus dongusensis* or *Anthracosaurus russelli*.

1.1.5 *Solenodonsaurus*

Solenodonsaurus janenschi Broili, 1904, from the Late Moscovian (Carboniferous) Nýřany locality in the Czech Republic, was first described by Broili (1904) and was suggested by Pearson (1924) to be a seymouriamorph. The holotype specimen was divided, with the part stored in the Palaeontological Institute in Munich (BSPG) and the counterpart, MB. Am. 989.1, stored in the Berlin Museum of Natural History (MB). A second, juvenile specimen, UMZC T.693 is stored in the University Museum of Zoology, Cambridge (UMZC). Unfortunately, the part of the holotype

specimen was destroyed by an Allied bombing raid during World War II. Brough & Brough (1967) suggested that *Solenodonsaurus* was not distinct from *Gephyrostegus*, but differences between the taxa were demonstrated comprehensively by Carroll (1970).

Solenodonsaurus was a small taxon with a skull of just over 10 cm (Danto, Witzmann et al. 2012). The skull resembles that of crown amniotes in several ways, for example, the intertemporal has been lost, although unlike crown amniotes the supratemporal remained on the skull table and did not contribute to the occiput (Carroll 1964, Carroll 1969, Reisz 1977, Danto, Witzmann et al. 2012). *Solenodonsaurus* had a very distinctive groove at the base of the maxillary teeth (Carroll, 1970) which has been used as evidence that MB. Am. 989.1 and UMZC T 693 can both be attributed to *Solenodonsaurus* (Danto, Witzmann et al. 2012). The palate is not exposed in either specimen of *Solenodonsaurus*, and has not been described (Laurin and Reisz 1999). The vertebrae resemble those of crown amniotes, with a well ossified pleurocentrum and a small, wedge-like intercentrum (Carroll, 1970). Like most crown amniotes, the ribs were slender, long and curved, which suggests that *Solenodonsaurus* could have performed some degree of costal ventilation (Danto, Witzmann et al. 2012). The limbs were gracile, with a high degree of torsion in the humerus, suggesting a taxon that was well adapted for terrestrial life (Carroll 1970, Danto, Witzmann et al. 2012).

1.1.6 Lepospondyli

Lepospondyli is a clade that was proposed to include a large assemblage of amphibious taxa of the Palaeozoic (Romer 1966, Carroll 2000). Several groups have been included within lepospondyls, including Nectridea, Lysorophia, Aïstopoda, Adelospondyli and Microsauria, united by their small bodies and characteristic vertebrae lacking intercentra (Carroll 2000, Clack 2012, Schoch 2014). This assemblage of taxa ranges from the Lower Carboniferous (Pardo, Szostakiwskyj et al. 2017) to the base of the Upper Permian (Harris, Lucas et al. 2005). It includes superficially reptile-like terrestrial forms such as large microsaurs including *Micraroter erythrogeois* (Daly 1973), burrowers such as recumbirostran microsaurs (Huttenlocker, Pardo et al. 2013), and obligate aquatic forms such as aïstopods (Anderson, Carroll et al. 2003). The number of presacral vertebrae could vary

from seventeen or fewer in diplocaulid nectrideans (Douthitt 1917, Milner 2018) to in excess of almost 100 in lysorophians (Wellstead 1991, Carroll 2000). Apart from a single nectridean, *Diplocaulus minimus* from Africa (Germain 2010), all lepospondyls are known from the Northern Hemisphere of Europe and North America, from deposits that broadly correspond with the Late Palaeozoic palaeotropics (Carroll 2000). Historically, lepospondyls have been referred to as a single group, implying that they were considered to be monophyletic (Colbert 1955, Romer 1966), a result corroborated by many phylogenetic analyses that recovered lepospondyls as either monophyletic, or paraphyletic including lissamphibians (Laurin, Reisz et al. 1997, Vallin and Laurin 2004, Ruta and Coates 2007). However, lepospondyl monophyly has been challenged on the grounds that the characters deemed to unite the group can be attributed to convergent evolution due to small body size (Milner 1993, Carroll 2000, Clack 2012, Pardo, Szostakiwskyj et al. 2017). Several phylogenetic studies have not recovered lepospondyls as monophyletic (Gardiner 1982, Panchen and Smithson 1988, Pardo, Szostakiwskyj et al. 2017, Clack, Ruta et al. 2019). The most recent of these phylogenetic analyses have suggested that one group of lepospondyls, microsaurs, show a particularly close relationship to reptiles and are crown-amniotes, but another group, aïstopods, are stem-tetrapods (Pardo, Szostakiwskyj et al. 2017, Clack, Ruta et al. 2019).

Some phylogenetic studies have suggested that Lissamphibia may have originated within Lepospondyli, or within certain groups of lepospondyls, known as the "lepospondyl hypothesis" (discussed further in Chapter 1, 1.2.3). Gardiner (1982) suggested that aïstopods and nectrideans may be stem-lissamphibians, whilst Laurin and Reisz (1997) recovered lissamphibians as originating within a monophyletic lepospondyls. McGowan (2002) recovered a close relationship between certain clades of lepospondyls (microsaurs and lysorophians) and caecilians, a clade of lissamphibians.

Lepospondyls are named for their characteristic lepospondylous vertebrae, a synapomorphy shared across the clade, in which the pleurocentrum is the dominant element forming the centrum (Colbert 1955, Romer 1966, Danto, Witzmann et al. 2017) (Fig. 8). The intercentrum is typically lost entirely, although could be ossified as a vestigial, superficial element. The vertebrae are also fully ossified even at extremely small sizes. In addition, lepospondyls typically lack a pterygoid transverse flange, an otic embayment, have a jaw articulation parallel to the occiput, lack labyrinthine infolding

of the teeth, and tend to have a very reduced series of dermal skull roof bones (Carroll 2000). This is particularly true of the temporal series, of which the intertemporal is absent in all lepospondyls (Carroll 2000), and the supratemporal is absent in all lepospondyls other than some aïstopods (Carroll 1998, Carroll 2000, Anderson 2002, Anderson, Carroll et al. 2003).

1.1.6.1 Nectridea

Nectrideans first appeared during the Bashkirian, Pennsylvanian (Carroll 2000), represented by *Keraterpeton galvani*, from 319 Ma (Milner 2018). They persevered until the Leonardian in the Late Permian, represented by the genus *Diplocaulus,* of which *Diplocaulus parvus* is known from latest Leonardian, approximately 270 Ma (Harris, Lucas et al. 2005). They are primarily known from coal swamp deposits in North America and Europe (Carroll 2000, Milner 2018), but a small number of specimens of *Diplocaulus minimus* are known from northern Africa as well (Germain 2010).

Although the boomerang-shaped head of the derived diplocaulid nectridean genera *Diplocaulus* Cope, 1877 and *Diploceraspis* Romer, 1952 is by far the most obvious and well known feature of the clade, Nectridea are actually united by highly distinct vertebrae that were deeply amphicoelous, hourglass shaped in cross section and perforated for the notochord, and always lacked intercentra (Carroll 2000). The atlas was always unipartite with a solidly fused arch and no ribs or proatlantes (Beerbower 1963). The zygapophyses were nearly flat, and widely spaced, which facilitated lateral undulation and resisted rotation. The neural spines were particularly distinctive; they were fused to the centrum, and were rectangular, extending for the full length of the arch (Milner 2018). The neural spines also formed accessory articulations between neural arches above the zygapophyses. All nectrideans also shared the condition of the haemal arches being fused without sutures to caudal centra. Nectrideans had a relatively low number of presacral vertebrae; no nectridean specimens are known with more than 26 presacral vertebrae (Carroll 2000), and most had fewer than

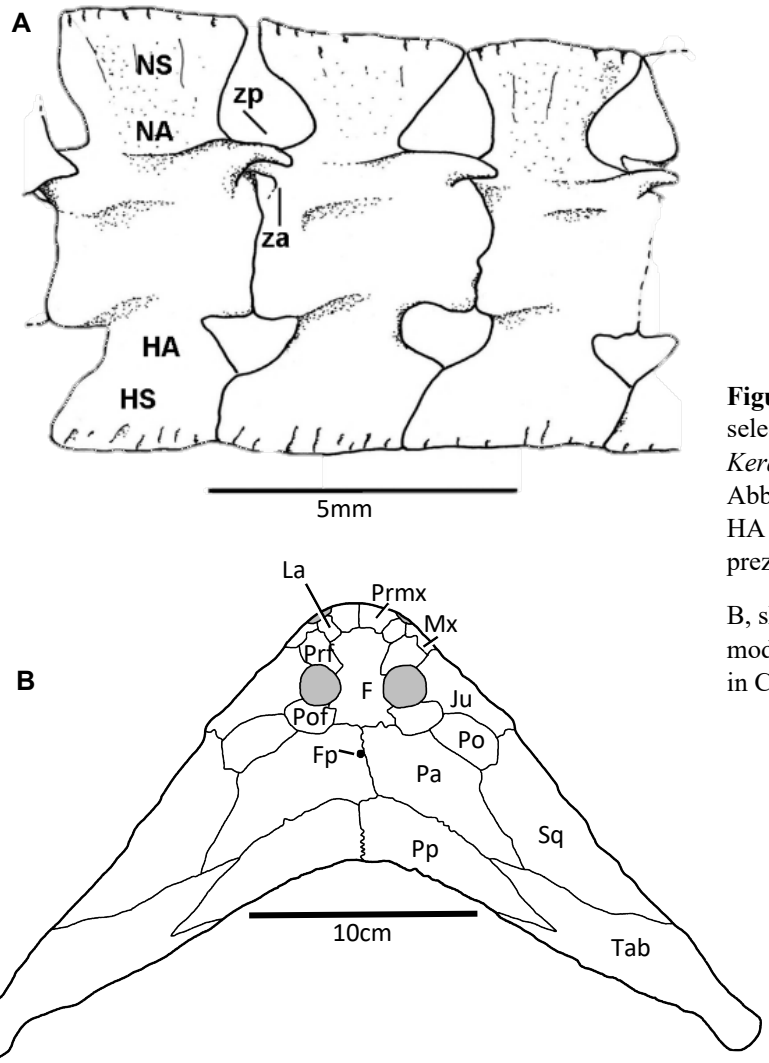


Figure 9: Vertebral and cranial morphology of selected nectridean taxa. A, caudal vertebrae of *Keraterpeton galvani*, from Milner (2018). Abbreviations: NS – neural spine, NA – neural arch, HA – haemal arch, HS – haemal spine, za – prezygapophyses, zp – postzygapophyses.

B, skull of *Diplocaulus magnicornis* in dorsal view, modified from Douthitt (1917). Abbreviations are as in Chapter 2 Figure 2.

20 (Douthitt 1917, Milner 2018). This differs from many other lepospondyls in which axial elongation is common, and presacral vertebral number typically exceeds 30 (Carroll and Gaskill 1978) and can reach numbers greater than 60 (Carroll 1998, Anderson 2002). All nectrideans had scales, at least ventrally. Despite the fact that most nectrideans were aquatic, no gills are known in any specimens, although no larval forms are known (Carroll 2000).

Nectridea is divided into three clades, Diplocaulidae, Scincosauridae and Urocordylidae. Urocordylids are primarily known from genera including *Urocordylus* Huxley, 1871 and *Sauropleura* Cope, 1868, though other species are known from fragmentary material. Urocordylids have the most plesiomorphic skull morphology of all nectrideans. With the exception of one taxon, *Sauropleura*, urocordylids retain paired skull table elements such as the frontals, and retain a supratemporal, unlike more derived nectrideans (Carroll 2000). As in anthracosaurs (Panchen 1977, Holmes 1989),

seymouriamorphs (Klembara 1997, Klembara and Ruta 2005) and gephyrostegids (Klembara, Clack et al. 2014) the tabular contacts the parietal. Urocordylids also lack the strong sutural attachment between the skull table and cheek of more derived nectrideans, and thus they were able to undergo some degree of cranial kinesis (Carroll 2000). Urocordylids are small taxa, reaching a maximum size of 30 cm in skull-trunk length. They possess laterally compressed tails with large neural and haemal arches, and are therefore clearly obligate aquatic taxa, although they lacked lateral line canals (Carroll 2000).

Scincosaurids are known from just two genera, the monospecific *Scincosaurus crassus* Fritsch, 1876 and *Sauravus* Thévenin, 1906, which is known from multiple species but lacks detailed descriptions. Scincosaurids have shorter neural and haemal spines than other nectridean taxa (Carroll 2000). Their skulls are small, measuring up to just 20% of the length of the trunk (Milner and Ruta 2009). The presacral vertebrae have weaker accessory articulations than other nectrideans, and short, anteriorly positioned transverse processes. Although no nectrideans have significant degrees of limb reduction, the limbs in scincosaurids are also more extensively ossified than other nectrideans (Milner and Ruta, 2009). These features all suggest a degree of terrestriality, but scincosaurids also have lateral line canals (Carroll 2000).

Diplocaulids are the best known nectrideans. By far the best known genus is *Diplocaulus*, which ranged from the Late Carboniferous to the middle of the Permian (Harris, Lucas et al. 2005). Some authors have suggested that there may be as many as six species of *Diplocaulus* (Harris, Lucas et al. 2005). *Diploceraspis burkei* (Romer 1952) and *Keraterpeton galvani* Wright & Huxley, 1866 represent the other well-known diplocaulid taxa (Beerbower 1963, Milner 2018). Diplocaulids have highly derived skulls that aere dorsoventrally flattened (Douthitt 1917). In the most plesiomorphic diplocaulid, *Keraterpeton*, the tabulars alone extend as posterior processes (Milner 2018), but in more derived diplocaulids the whole cheek is drawn out to give the skull an overall boomerang shape (Douthitt 1917, Beerbower, 1963). The frontal is single, not paired, the postorbital is displaced from the orbital margin, and major palatal changes occurred, including the exposure of the quadratojugal on the palate (Carroll 2000). Diplocaulid skulls are large, reaching up to 40% of the anteroposterior length of the trunk. In derived diplocaulids, the entire body has become dorsoventrally flattened,

suggesting some degree of dorsoventral undulation during an aquatic lifestyle, and their tails were laterally flattened (Carroll 2000) (Fig. 9).

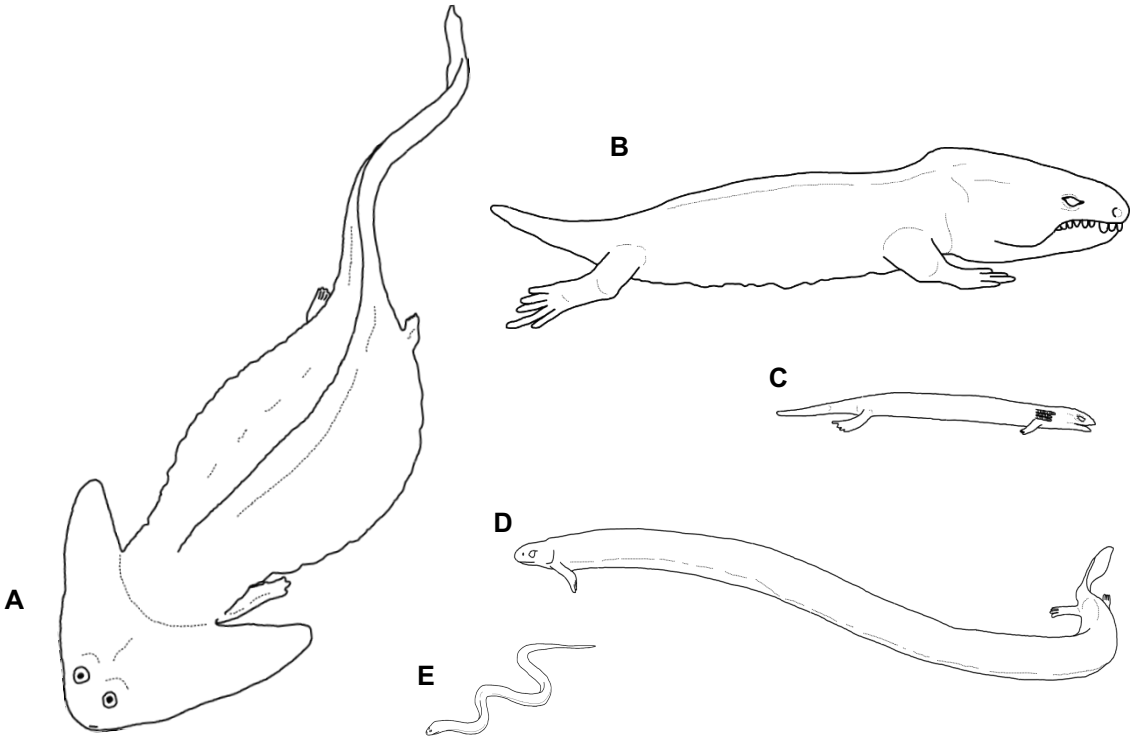


Figure 10: The great variety of body forms of lepospondyls, approximately to scale with each other. A, *Diplocaulus*, B, *Pantylus*, C, *Microbrachis*, D, *Brachydectes*, E, *Lethiscus*.

1.1.6.2 Lysorophia

Lysorophians were elongate taxa with highly reduced limbs and girdles (Pardo and Anderson 2016), known from just four genera (Wellstead 1991); *Brachydectes newberryi* Cope, 1868 and *Brachydectes elongatus* (Wellstead 1991), *Lysorophus tricarinatus* Cope, 1877 and *Lysorophus dunkardensis* (Romer 1952) and the monospecific *Pleuroptyx clavatus* Cope, 1875 and *Molgophis macrurus* Cope, 1868. The best known taxon is *Brachydectes newberryi*, for which detailed cranial descriptions based on micro-CT data have been recently published (Pardo and Anderson 2016). They ranged from the Middle Pennsylvanian to the Lower Permian of the British Isles and the USA (Carroll 2000). Lysorophians could range from just a few centimeters to over a meter in length. Nonetheless, both the cranial and postcranial morphology is highly conserved throughout all members of the group,

although a major change did occur in the presacral vertebral number, which increased from approximately 69 to 97 between the early and late members of the group respectively (Carroll 2000).

Lysorophians are united by a highly reduced skull with a massive orbitotemporal fenestration, a far anterior jaw articulation, and a premaxilla and maxilla only loosely attached to the rest of the skull (Wellstead 1991, Pardo & Anderson, 2016). This has been suggested to have allowed lysorophians to undergo a snake-like cranial kinesis (Bolt and Wassersug 1975). They lack a pineal opening, and have a low tooth count (approximately 5-10, Wellstead 1991) and highly reduced palatal dentition, with the only palatal teeth on the vomer (Pardo and Anderson 2016). The braincase was well ossified, but not highly sutured or fused with gaps in between the elements, unlike the highly co-ossified braincase in the superficially similar aïstopod lepospondyls (Carroll 2000, Pardo and Anderson 2016).

The mandible of lysorophians is extremely reduced. Just one splenial is retained, and all coronoid elements are lost. They also possess a well ossified hyobranchial skeleton which has been argued to have allowed suction feeding of small, aquatic prey (Wellstead 1991).

The presacrals of lysorophians are fully lepospondylous with no trace of intercentra. Neural arches are paired and only loosely attached to the centra (Wellstead 1991). Haemal arches are present, and like in microsaurs, are sutured to the caudal vertebrae, rather than fused. The vertebrae of lysorophians are unique in that they are pitted, with longitudinal carinae on the lateral and ventral surfaces forming rib attachment surfaces (Carroll 2000). Lysorophians retained girdles and limbs, although they are highly reduced and the distal portions of the limb elements remained unossified (Wellstead 1991) (Fig. 10).

1.1.6.3 Aïstopoda

Aïstopods were by far the earliest lepospondyls to appear. The earliest aïstopod, *Lethiscus stocki*, is known from the Mid-Viséan of Scotland (Anderson, Carroll et al. 2003). However, even by this time they were highly derived, considered to be “the most highly derived of all Palaeozoic amphibians” (Carroll 2000). Aïstopods were extremely small and elongate, snake-like taxa, lacking any trace of an appendicular skeleton (Anderson, Carroll et al. 2003).

Aïstopods have been classically divided into two distinct families (Carroll 1998). The first is the Ophiderpetontidae Schwartz, 1908, ranging from the Upper Viséan to the Stephanian (Carroll 2000) and including *Ophiderpeton brownriggi* Wright & Huxley, 1866, *Oestocephalus amphiuminus* Cope, 1868 and *Coloraderpeton brilli* Vaughn, 1969. Anderson (2003) united *Oestocephalus* and *Coloraderpeton* into a new family, Oestocephalidae, excluding *Ophiderpeton*. The other traditionally described family (Carroll 1998) is the Phlegethontiidae Cope, 1875, ranging from the Middle Westphalian A to the Lower Permian (Carroll 2000), including *Pseudophlegethontia mazonensis* (Anderson 2003) and the two species of the genus *Phlegethontia* Cope, 1871, *Phlegethontia linearis* Cope, 1871 and *Phlegethontia longissimi* Frič, 1875. Aïstopoda also includes the monogeneric Lethiscidae, containing only the aforementioned *Lethiscus stocki* (Wellstead 1982), which had previously been considered a specimen of *Ophiderpeton* (Anderson 2003).

Lethiscus stocki is known from a single specimen (Carroll 2000), preserved in a relatively hard matrix. It was therefore poorly known until micro-CT scans of the cranial region were described by Pardo et al. (2017). *Lethiscus* has an open cheek region, a single, fused parietal and lacks an intertemporal (Pardo, Szostakiwskyj et al. 2017). It has more than 78 vertebrae with no trace of intercentra, and completely fused neural arches (Carroll 2000).

Ophiderpetontidae have more plesiomorphic skulls than *Lethiscus* and retain paired parietals (Carroll 2000, Pardo, Szostakiwskyj et al. 2017), despite occurring more than 30 million years later, during the Moscovian in the Late Carboniferous (Carroll 1998). The ribs are more derived, though, and have developed a distinctive K-shaped head with an additional articulating projection (Carroll 2000).

Phlegethontiidae are also known from the Moscovian (Anderson 2002). Phlegethontids have an even greater reduction in the skull bones than other aïstopods (Anderson 2002), and the most complete specimens are known to have 214 vertebrae (Carroll 2000). They share K-shaped rib heads with ophiderpetontids (Anderson 2002).

1.1.6.4 Adelospondyli

Adelospondyls (Andrews and Carroll 1991) are known from just one family, Adelogyrinidae, that consists of four monotypic genera. These are *Adelogyrinus simorhynchus* Watson, 1929, *Palaeomolgophis scoticus* Brough & Brough, 1967, *Dolichopareias disjectus* Watson, 1929 and *Adelospondylis watsoni* Carroll, 1967. All adelospondyls are from a restricted geographic region in the Scottish Midland Valley, limited to just the Viséan and Namurian of the Carboniferous (Carroll 2000). Adelospondyls were elongate, long bodied lepospondyls with many typically lepospondyl associated features including the lack of palatal fangs, lack of labyrinthine tooth infolding, and the presence of fully lepospondylous vertebrae (Andrews and Carroll 1991). However, they have a very unique skull pattern. The whole cheek region is fused into a single ossification, termed the tabular-squamosal, which possesses a posterior projection like the tabular horn of embolomeres (Carroll 2000). As is the case in diplocaulid nectrideans, the postorbital does not enter the orbit margin. The teeth, too, are very distinctive; they are close set and cylindrical with oblique chisel-shaped tips, and a dimple on the labial and lingual sides. Adelospondyls have a high number of teeth, but conserved within a small range, from 45 to 49 (Andrews and Carroll, 1991). They possess an odontoid process on the atlas, as also seen in microsaurs (Carroll 2000).

The dermal portion of the pectoral girdle of adelospondyls is well ossified (Carroll 2000). However, it is the only known part of the entire appendicular skeleton, and adelospondyls are completely limbless (Andrews and Carroll 1991). In addition, the remains are always associated with fish, and distinct lateral line canals are present, so it therefore seems likely that adelopsondyls were aquatic (Carroll 2000).

Adelospondyls are not universally recovered as lepospondyls, and have been recovered as deep stem tetrapods in a small number of analyses (Ruta and Coates 2007). One additional taxon has been considered to be an adelospondyl too, *Acherontiscus caledoniae* Carroll, 1969. This taxon is known from a single specimen and is small, limbless and elongate, with a skull just 15 mm in anteroposterior length, and although its age is uncertain it is most likely dated to the Serpukhovian (Clack, Ruta et al. 2019). *Acherontiscus caledoniae* represents the earliest known fossil example of

durophagous and heterodont dentition (Clack, Ruta et al. 2019). It has been recovered as the sister clade to adelogyrinids (Clack, Ruta et al. 2019) but has also been considered to be a juvenile colosteid (Clack 2012).

1.1.6.5 Microsauria

Microsaurs were amongst the most diverse and longest ranging lepospondyls, exhibiting a great range of sizes and morphologies, ranging from taxa with skulls that were just millimeters long in the case of *Odonterpeton triangulare* (Carroll and Gaskill 1978) to in excess of 60cm in *Micraroter erythrogeois* (Daly 1973). They are known only from Europe and North America, ranging from the Serpukhovian to the base of the Upper Permian (Carroll 2000). Carroll and Gaskill (1978) produced the most extensive work on microsaurs, describing almost all known taxa, encompassing as many as 30 genera. They divided microsaurs into two suborders, encompassing eleven families (Carroll and Gaskill 1978, discussed further below). Whilst Carroll and Gaskill's (1978) work provides detailed descriptions of almost all known microsaurs, a small number of microsaur taxa have been described since this work, including *Carrolla craddocki* (Langston and Olson 1986), *Utaherpeton franklini* (Carroll, Bybee et al. 1991) and *Huskerpeton englehorni* (Huttenlocker, Pardo et al. 2013). Recent studies, utilising micro-CT data, have produced new, more detailed descriptions of some of the best known microsaurs, notably *Llistrofus pricei* (Gee, Bevitt et al. 2019) and *Euryodus dalyae* (Gee, Bevitt et al. 2021).

Microsaurs are united by a distinctive temporal region, and by a particular atlas-axis morphology. The temporal region shows a clear pattern of reduction; microsaurs have lost both the supratemporal and intertemporal, and retain only the tabular. An atlas intercentrum is never present, but the atlas is multipartite, unlike most other lepospondyls. The anterior articular surface of the atlas is widely expanded to approximately twice the transverse width of the posterior articular surface. Proatlantes are also generally absent and an odontoid process was present like some other lepospondyls, so lateral bending of the neck would have been very limited.

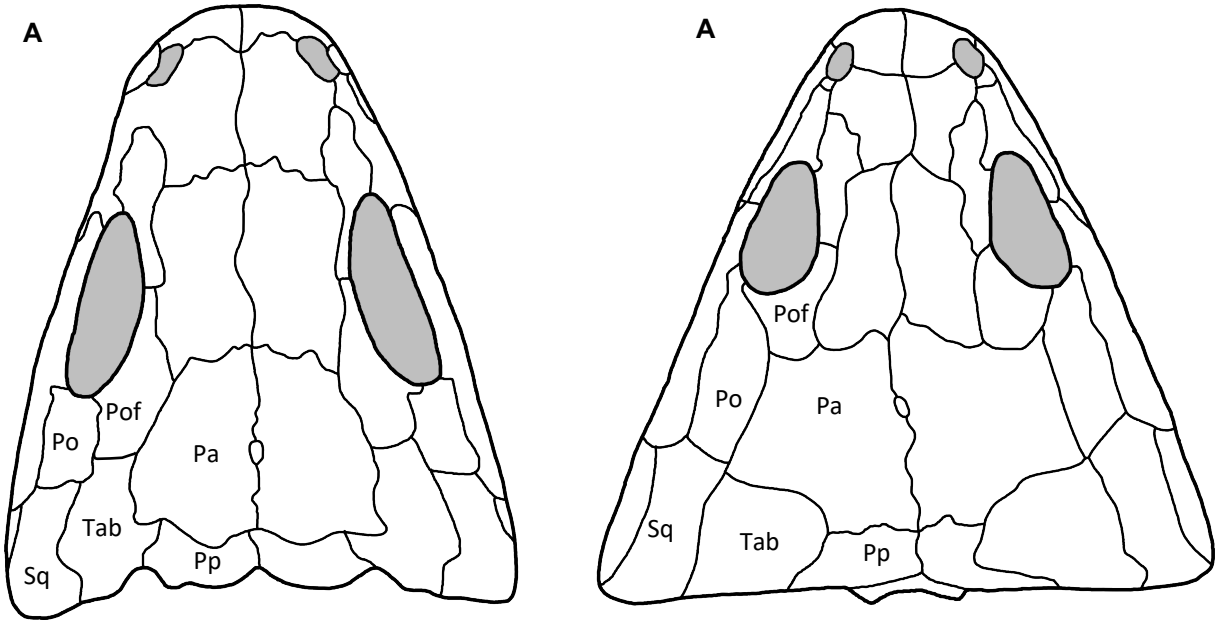


Figure 11: Schematics of a typical configuration of skull roofing bones for the two suborders of microsaurs, modified from Carroll & Gaskill (1978). A, typical skull of a tuditanomorph microsaur. B, typical skull of a microbracomorph microsaur. Abbreviations are as in Chapter 2 Figure 2.

Microsaurs have been divided into two suborders based on the pattern of the temporal bones (Carroll and Gaskill 1978). Tuditanomorpha (Carroll and Gaskill 1978) have a more conservative temporal pattern in which the tabular extends forward to contact the postorbital and postfrontal. In Microbracomorpha (Carroll and Gaskill 1978), the parietal extends laterally to contact the postorbital. According to Carroll & Gaskill (1978) Tuditanomorpha encompasses the families Tuditanidae Cope, 1875, Hapsidopareiontidae Daly, 1973, Pantylidae Case, 1911, Gymnarthridae Case, 1910, Ostodolepidae Romer, 1945, Trihecatontidae Vaughn, 1972 and Goniorhynchidae Carroll and Gaskill 1978. Microbracomorpha encompasses the families Microbrachidae Frič, 1883, Hyloplesiontidae Carroll and Gaskill, 1978, Brachystelechidae Carroll and Gaskill, 1978 and Odonterpetontidae Carroll and Gaskill, 1978.

Tuditanomorpha ranged from the Lower Pennsylvanian to the Lower Permain (Carroll and Gaskill 1978) and show a great variety of morphologies. The earliest member of the suborder, *Utaherpeton franklini* from the Serpukhovian, has a relatively plesiomorphic morphology (Carroll, Bybee et al. 1991). *Asaphestera intermedia* Steen, 1934 from the Late Bashkirian of Joggins, Nova Scotia (Carroll and Gaskill 1978), referred to Tuditanidae (Carroll and Gaskill 1978), has a similar

cranial morphology but reach five times the anteroposterior length of *Utaherpeton* (Carroll and Gaskill 1978). One family, Hapsidopareidontidae, possess extensive ventral emargination of the cheek (Carroll and Gaskill 1978) which is clearly seen in the well preserved skull of *Llistrofus pricei* (Gee, Bevitt et al. 2019).

Gymnarthrids, the largest family of tuditanomorphs, were the most common and diverse of the Lower Permian microsaurs, consisting of five species in three genera, *Cardiocephalus sternbergi* Broili, 1904 and *Cardiocephalus peabodyi* (Carroll and Gaskill 1978), *Euryodus primus* Olson, 1939 and *Euryodus dalyae* (Carroll and Gaskill 1978) and the monospecific *Pariotichus brachyops* Cope, 1878. The best known is *Euryodus dalyae*, for which cranial descriptions based on micro-CT data have been published (Gee, Bevitt et al. 2021). Gymnarthrids have a long trunk, and some taxa possess intercentra (Carroll and Gaskill 1978). Unlike other taxa that retain intercentra, including embolomeres or early crown amniotes, the intercentra occupy a superficial position, ventral to and surrounding the pleurocentra, rather than being positioned in between them (Carroll and Gaskill 1978).

Tuditanomorphs also includes relatively large bodied taxa; *Pantylus cordatus* Cope, 1881, a member of the family Pantylidae from the Lower Permian of Texas (Carroll and Gaskill 1978), is amongst the largest tuditanomorphs and has a skull that exceeded 10 cm with proportionally massive blunt teeth, as well as robust, proportionally large limbs and a highly reduced, short tail suggesting a fully terrestrial lifestyle (Carroll and Gaskill 1978). Ostodolepids, however, are the largest tuditanomorphs, and the largest microsaurs; *Micraroter erythrogeios* could reach more than 60 cm in length. They have a triangular, recumbent snout and a broad occipital surface for strong skull-neck muscle attachments, and were most likely burrowers (Carroll and Gaskill 1978).

Microbracomorphs have more variable skull morphologies than tuditanomorphs (Carroll and Gaskill 1978). They are smaller than tuditanomorphs, and could reach extremely small sizes; the skulls of the smallest specimens are just 6.7 mm long. No microbracomorphs show any trace of intercentra. *Microbrachis pelikani* Frič, 1875, the taxon for which the clade was named, possess bony gill rakers and a lateral line, as well as relatively tiny limbs, so was certainly obligatorily aquatic (Carroll and Gaskill 1978). Nonetheless, not all microbracomorphs were necessarily aquatic.

Odonterpeton triangulare, of the microbracomorph family Odonterpetontidae, which is even smaller than *Microbrachis* and amongst the very smallest microsaurs, has relatively massive and well ossified limbs (Carroll and Gaskill 1978). Whilst many lepospondyls possess four instead of the five manual digits that is typical for stem and early crown amniotes, *Hyloplesion longicostatum* Frič, 1883, of the microbracomorph family Hyloplesiontidae, has a manus with just three digits (Carroll and Gaskill 1978).

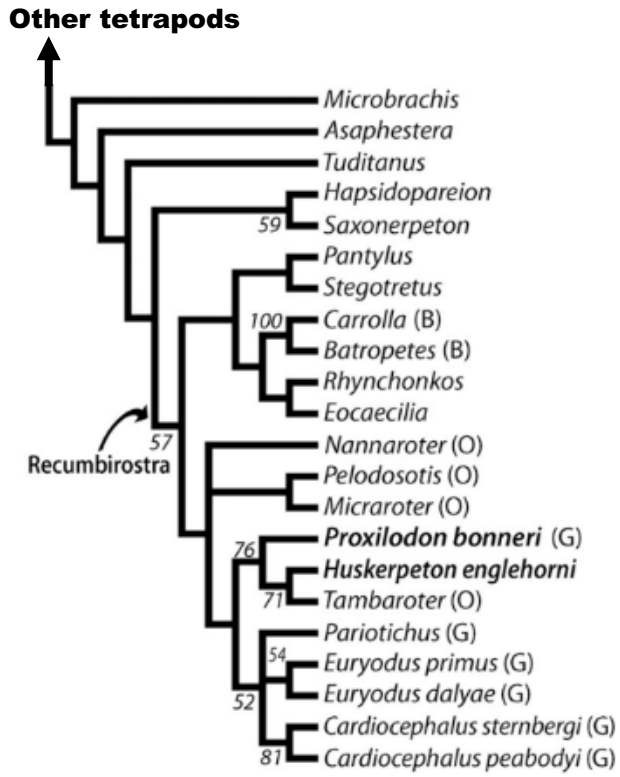


Figure 12: The phylogeny of microsaurs, modified from Huttenlocker et al (2013), demonstrating the clade of Recumbirostra.

More recently, a novel grouping of microsaurs has been suggested; Recumbirostra (Anderson 2007). This clade is united by a recumbent snout, and are presumed to be adapted for fossoriality (Huttenlocker, Pardo et al. 2013). It is formed of all microsaurs excluding *Microbrachis pelikani*, Tuditanidae and Hapsidopareiontidae (Fig. 12, Huttenlocker, Pardo et al. 2013). Recumbirostra has been recovered in multiple phylogenetic analyses since the clade was first defined by Anderson (2007), including Huttenlocker, Pardo et al. (2013), Pardo et al. (2017) and Mann & Maddin (2019). However, these phylogenetic analyses have lacked inclusion of taxa that were defined by Carroll & Gaskill (1978) as microbracomorphs, other than Huttenlocker, Pardo et al. (2013), who included

Microbrachis pelikani and found it to be the earliest diverging microsaur. Further phylogenetic analyses will likely provide further clarity on the position of Recumbirostra.

1.1.7 Diadectamorpha

Diadectamorphs are known from the Late Pennsylvanian to the Early Permian (Berman, Sumida et al. 1998, Berman, Henrici et al. 2004, Kennedy 2010) of primarily North America (Berman, Sumida et al. 1992) with some specimens also known from Germany (Berman, Henrici et al. 2004). It includes the genera and species *Diadectes* Cope, 1878 of which many species are known from across the USA (Berman, Sumida et al. 1992) and from the Kungurian, Permian of Germany (Berman, Henrici et al. 2004), *Orobates pabsti* (Berman, Henrici et al. 2004) from the same locality as *Diadectes abistus* (Berman, Henrici et al. 2004), *Tseajaia campi* Vaughn, 1964 and *Limnoscelis paludis* Williston, 1911 and *Limnoscelis dynatus* (Berman and Sumida, 1990). Diadectamorphs are grouped into three families (see below for further discussion). Diadectamorphs were large, terrestrial taxa with relatively massive skulls, and robust, well ossified limbs (Berman, Sumida et al. 1992, Kennedy 2010).

The skulls of diadectamorphs are short, broad and moderately high (Berman, Sumida et al. 1992). The jaw articulation is far forward of the occiput and below the level of the toothrow (Berman, Sumida et al. 1998). They lack an intertemporal and have lost the postparietal-tabular contact that characterises anthracosaurs and seymouriamorphs (Berman, Henrici et al. 2004). The supratemporal is greatly enlarged, and the tabular is reduced in size, but both elements contribute to the occiput as is often the case in crown amniotes (Berman, Sumida et al. 1992, Berman, Sumida et al. 1998, Berman, Henrici et al. 2004).

With the exception of *Diadectes* itself, the taxa included within diadectamorphs have varied through the history of study (Berman, Sumida et al. 1992). Watson (1917), who coined the term Diadectamorpha, did not include the Limnoscelidae, instead placing them within Captorhinidae. However, he did include both Diadectamorpha and Captorhinomorpha within the same order, the Cotylosauria, so obviously recognised a close relationship between all the taxa concerned.



Figure 13: The diadectamorph *Orobates pabsti*, on display at the Museum of Nature, Gotha, Germany. Photographed by the author.

In modern analyses, the clade generally includes three families: Diadectidae, Limnoscelidae and Tseajaiidae (Berman, Sumida et al. 1992, Ruta and Coates 2007). Diadectidae was, until recently, considered monogeneric with multiple species; *sideropelicus*, Cope, 1878; *lentus*, Marsh, 1878; *tenuitectus*, Cope, 1896; *carinatus*, Case & Williston, 1912; *sanmiguelensis*, Lewis & Vaughn, 1965. The several species of *Diadectes*, however, were generally distinguished from one another on size, proportions and distributions, and these distinctions have been considered dubious (Berman, Sumida et al. 1998). In 2004, a second diadectid, *Orobates*, was discovered with several well preserved, articulated specimens from the Tambach formation of the Kungurian, Permian of Germany (Berman, Henrici et al. 2004). Diadectidae possess distinctive features that relate to herbivory, making them the first tetrapods to be specialised for a high fiber herbivorous diet. They have heterodont dentition including chisel-like incisors and molar-like cheek teeth, as well as a large and barrel-shaped torso (Berman, Sumida et al. 1998, Berman, Henrici et al. 2004).

Tseajaiidae is known from a single species, *Tseajaia campi*, of the Permian of North America with just one detailed description (Moss 1972), but this description has several misinterpretations (Berman, Sumida et al. 1992). Limnoscelidae is also represented primarily by a single species, *Limnoscelis paludis* from the Upper Pennsylvanian of the USA (Kennedy 2010), as another species, *Limnoscelis dynatus*, has been described but is based on highly fragmentary specimens (Berman and Sumida 1990).

Berman et al. (1992) was the first in depth phylogenetic analysis of the relationships within diadectamorphs. They recovered *Limnoscelis* as the most basal diadectamorph, with *Diadectes* and *Tseajaia* forming a clade. However, they recovered diadectamorphs as the sister clade to synapsids, within crown amniotes, a result not recovered in most other phylogenetic analyses, which generally return diadectamorphs as the sister-clade to crown Amniota (Ruta, Jeffery et al. 2003, Ruta and Coates 2007). No clear consensus of the ingroup relationships of diadectamorphs has been reached.

1.2 The phylogenetic relationships of Stem Amniotes

1.2.1 Pre-cladistic hypotheses of relationships

Since the late 19th Century, certain fossil taxa have been recognised to have a somewhat close relationship to extant amniotes. As early as 1880, Cope suggested that there was a close relationship between embolomeres and amniotes. He observed that the embolomere *Cricotus*, today referred to the embolomere taxon *Archeria* (Holmes 1989), had an occipital condyle similar to that of reptiles. Over a long series of publications, Watson (1926) further developed the argument that there was an association between anthracosaurs and modern taxa by proposing that anthracosaurs were the most primitive group linking tetrapods with lobe-finned fish, and noting that they had several reptilian characteristics. This particular argument would be superseded by the discovery of aquatic stem-tetrapods including *Acanthostega gunnari* Jarvik, 1952 and the genus *Ichthyostega* Säve-Södenbergh, 1932, both from the Famennian of East Greenland (Coates 1996, Porro, Rayfield et al. 2015). *Achanthostega* and *Ichthyostega* possess well-developed limbs with digits, but also retain bony fin-

rays in the tail that would have restricted them to an aquatic habitat (Clack 2012). Nonetheless the relationship between anthracosaurs and amniotes became well established.

Multiple groups other than anthracosaurs have also been considered to be close relatives of crown amniotes, including seymouriamorphs and diadectamorphs. *Seymouria* was first described by Broili (1904), who initially described it as a reptile. Diadectamorphs were also observed to have a close relationship with amniotes by Watson (1917), who also supported the association of seymouriamorphs with amniotes. He coined the names Seymouriamorpha and Diadectamorpha, and considered both of these clades to be part of the super-order Cotylosauria. Watson (1917) placed Cotylosauria within Reptilia, a clade also encompassing reptiles and mammals (termed Anamodontia by Watson, 1917), although he was ambiguous about any internal relationships. Watson (1917) also considered the group Limnoscelidae, a group now considered part of Diadectamorpha, to be part of Captorhinidae. Captorhinidae, which is not generally found to include *Limnoscelis* in recent studies (Laurin and Reisz 1995, Ruta, Jeffery et al. 2003, Ruta and Coates 2007, Marjanović and Laurin 2019), is a group that has generally been found as a clade of stem, or crown, reptiles (Laurin and Reisz 1995, Ruta, Jeffery et al. 2003, Ruta and Coates 2007, Marjanović and Laurin 2019, Ford and Benson 2020), although they have also been recovered recently as stem amniotes (Simões, Kammerer et al. 2022). Therefore, whether Limnoscelidae are recovered as members of Diadectamorpha or Captorhinidae, diadectamorphs including limnoscelids have been thought to be close relatives of amniotes.

Säve-Södenbergh (1934) corroborated the earlier ideas of Cope and Watson relating anthracosaurs to amniotes. He described anthracosaurs as a clade in their own right, and named them the Anthracosauria. He also considered Diadectamorphs to be members of the Reptilia. Säve-Södenbergh (1934) stated that “a primitive Reptile like *Diadectes* belongs, in regard to the pattern of dermal bones, to the same line of evolution as Anthracosauria”. ‘Reptilia’, in Säve-Södenbergh (1934), refers to total-group amniotes, including mammals.

Anthracosaurs, seymouriamorphs and diadectamorphs continued to be the fossil clades considered to have a close relationship with amniotes, or various clades thereof. *Seymouria* was described as one of the earliest reptiles by White (1939). Olson (1947) considered that

diadectamorphs might be relatives of turtles, although such a view never gained popularity (Romer, 1956). Romer (1956) once again considered anthracosaurs as potential amniote ancestors, but included gephyrostegids within anthracosaurs. He also proposed that *Solenodonsaurus* could represent a plausible amniote ancestor. Romer (1956) also classified a group Anapsida as representing the reptilian stem, including both seymouriamorphs and diadectamorphs within this clade, and including *Limnoscelis* within captorhinomorphs. Carroll (1969) deemed that *Limnoscelis* was more primitive than captorhinomorph reptiles on the basis that *Limnoscelis* retained four proximal tarsals, but nonetheless observed that *Limnoscelis* had distinctly reptilian features such as the palatal structure and lack of an intertemporal, and continued to recognise it as an early relative of reptiles. He also described that *Gephyrostegus* was a potential reptilian ancestor, and that *Limnoscelis*, *Solenodonsaurus* and all reptiles evolved from anthracosaurian ancestors, particularly noting that *Solenodonsaurus* belonged to a "primitive reptilian lineage" (Fig. 14). Carroll (1970, p.268) further supported these arguments in following publications, stating that "among the [Palaeozoic 'amphibians'] only the anthracosaurs have the cranial and vertebral anatomy consistent with close relationships to the reptiles". He observed that within (what he considered to be) anthracosaurs, seymouriamorphs most closely resembled reptiles.

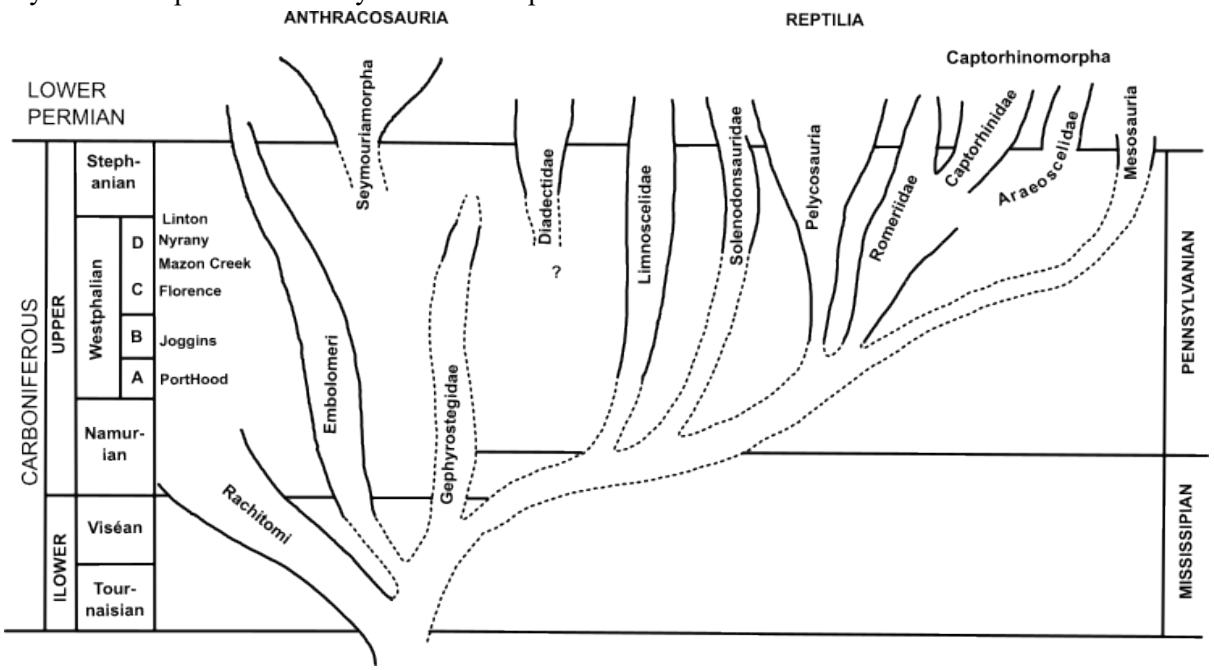


Figure 14: One hypothesis for the relationship of early tetrapods, modified from Carroll (1969).

Simultaneously, particular fossil groups have long been recognised as having a close association with lissamphibians. The suggestion of a relationship between temnospondyls and frogs was first recognised by Cope (1882), a view supported by Säve-Södenbergh (1934). Watson (1940) was the first to present a formal analysis recognising this relationship, and described synapomorphies that the temnospondyl *Amphibamus* shared with frogs. He suggested that *Amphibamus*, through some other fossil forms, could possibly be ancestral to Triassic frogs. More recently, lissamphibians have been considered to be nested within temnospondyls, and particularly close relationships have been suggested between amphibians and the temnospondyl clade Dissorophoidea (Bolt 1969, Bolt 1977, Bolt and Lombard 1985, Milner 1988). Not all studies have agreed, however, and a small number of publications have instead suggested that amphibians may have a close relationship with lepospondyls (Gregory 1965, Carroll and Currie 1975, Carroll and Holmes 1980). Carroll & Currie (1975) and Carroll & Holmes (1980), specifically, suggested a relationship between microsaurs and the amphibian clades of caecilians and salamanders respectively, although neither of these views have gained widespread acceptance. Nonetheless, in a substantial review of Palaeozoic lissamphibian relatives, Milner (1993) asserted that both a monophyletic Lissamphibia, and an ancestral relationship between microsaurs and caecilians, remained viable possibilities. However, since the introduction of molecular phylogenetic analyses, analyses that incorporate or solely utilise molecular data have exclusively recovered that Lissamphibia is monophyletic with respect to Amniota (Feller and Hedges 1998, Zardoya and Meyer 2001, Zhang, Chen et al. 2003, San Mauro, Gower et al. 2004). This strongly supports any morphological hypotheses that recover a monophyletic Lissamphibia, and renders it highly unlikely that any solely morphological analysis that recovers a polyphyletic Lissamphibia, originating from within both temnospondyls and lepospondyls, is correct (Anderson, Reisz et al. 2008).

The overwhelming majority of pre-cladistic analyses considered the origins of amphibians and amniotes separately. Later studies, close to the advent of computerised phylogenetic analyses,

began to suggest that global studies were necessary to understand whether or not each fossil clade were stem amphibians, stem amniotes or stem tetrapods (Gauthier et al., 1988).

1.2.2 Synapomorphy based analyses

In the later half of the 20th Century, many phylogenetic studies used synapomorphy based analyses to decipher phylogenetic relationships, by counting the numbers of synapomorphies that united certain clades. One of the largest of these was Gardiner (1982), who described the process of using synapomorphies as a technique to build a "character-state tree". Gardiner (1982) hypothesised that microsaurs represented the sister-clade to amniotes based on the loss of an otic notch, the reduction of the intercentrum and the morphology of the stapes. He also considered anthracosaurs as the sister-group to the Amniota+Microsauria clade. He considered nectrideans and aïstopods to be sister taxa to Lissamphibia based on a unipartite atlas and the vertebral morphology, resulting in a polyphyletic lepospondyls. Temnospondyls were recovered as stem tetrapods, not as more closely related to amphibians than amniotes. This analysis also recovered birds and mammals as a sister clade to the exclusion of other reptiles (Gardiner 1982), a result not corroborated by any modern analyses or molecular evidence (Fig. 15).

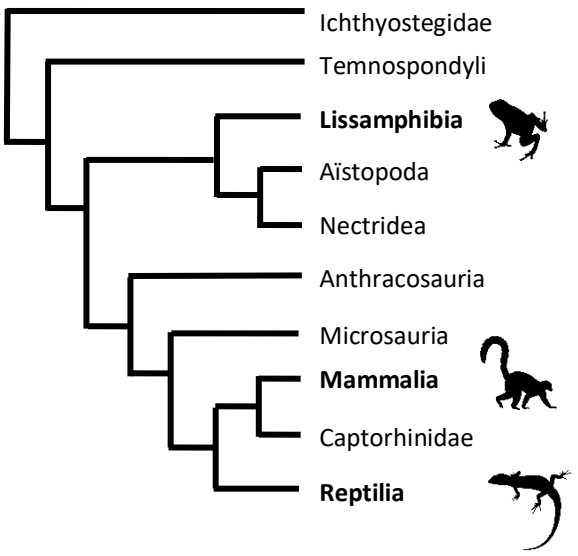


Figure 15: The phylogenetic hypothesis proposed by Gardiner (1982).

Løvtrup (1985) published another synapomorphy analysis that agreed with, and built upon, the results of Gardiner (1982), and further supported this topology by adding additional synapomorphies. However, this study clearly demonstrated the drawback of synapomorphy based

analyses of this time; they did not list the number of synapomorphies of any alternative phylogenetic hypotheses. Instead, these studies fit character states to a predetermined tree and can only compare a small number of tree options, owing to the limited computational power of carrying out such analyses manually. This approach searches for synapomorphies to support a relationship, rather than determining relationships by comparing the number of shared synapomorphies.

Nonetheless, synapomorphy based analyses made significant progress towards recovering many of the relationships that have achieved consensus today. Another significant analysis of this type was Panchen & Smithson (1988). This analysis considered *Limnoscelis* to be a part of Diadectamorpha, which they recovered to be the sister clade to amniotes. They also recovered both seymouriamorphs and anthracosaurs as closely related to amniotes, although noted that it was uncertain if these clades formed a monophyletic group with each other, or represented a grade in which anthracosaurs and then seymouriamorphs were progressively closely related to amniotes, as each of these alternative topologies would be supported by a single synapomorphy.

1.2.3 Computerised phylogenetic analyses

Computerised phylogenetic analyses, based on shared characters and the number of steps required in alternative tree topologies, began to become widespread, following the introduction of the computer program PAUP in 1984 (Swofford and Sullivan 2003). The earliest computerised phylogenetic analyses supported the hypothesis that Diadectamorpha was closely related to amniotes, and recovered diadectamorphs as the sister clade of all amniotes (Gauthier et al. 1988; Laurin and Reisz, 1995). *Solenodonsaurus* had a less stable phylogenetic position, but was still consistently recovered as a stem amniote. It was recovered as the sister taxon to Diadectamorpha+Amniota (Gauthier et al. 1988), but was also recovered as a basal relative of lepospondyls, in an analysis in which lepospondyls where placed on the amniote stem (Laurin and Reisz, 1999). Gauthier et al. (1988) also recovered Seymouriamorpha and Anthracosauroidea as successive sister clades to

amniotes, corroborating traditional hypotheses about close associations between these clades and amniotes.

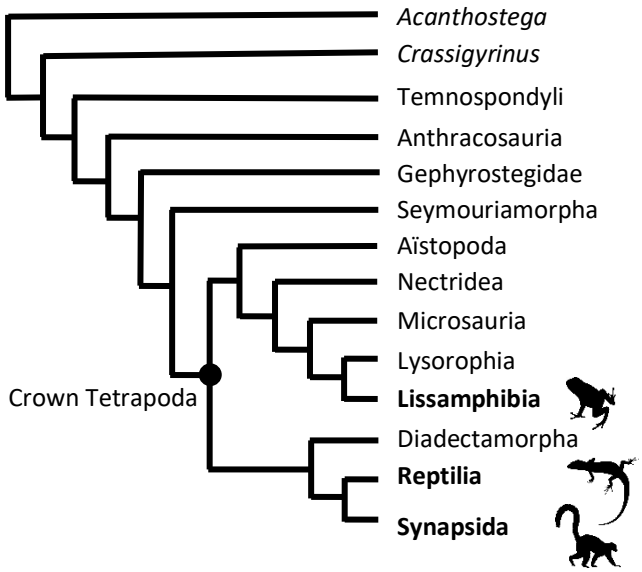


Figure 16: The phylogenetic hypothesis proposed by Laurin, Reisz et al. (1997)

The earliest computerised analyses of lissamphibian origins corroborated the hypothesis that they were closely related to dissorophoid temnospondyls (Trueb and Cloutier 1991). However, many of these early analyses did not consider both amphibian and amniote origins.

The first large scale computerised analysis that included both amniotes and lissamphibians was carried out by Laurin and Reisz (1997). This analysis uncovered an entirely novel hypothesis, that is, an origin of lissamphibians within a monophyletic lepospondyls. This was the first analysis in a series of modern phylogenetic analyses that would reignite a debate that has yet to achieve true consensus, the three hypotheses of lissamphibian origins; the lepospondyl hypothesis, the temnospondyl hypothesis and the polyphyletic hypothesis (Marjanović and Laurin 2013). Which of these hypotheses is considered has significant implications for which clades are considered to be stem amniotes, stem amphibians or stem tetrapods (Fig. 16, Fig. 17).

Some analyses of the early 2000s recovered a polyphyletic Lissamphibia (Anderson 2001, McGowan 2002). Anderson (2001) recovered a microsaurian origin for caecilians but did not include any other amphibians, so while it is possible that this analysis would support amphibian polyphyly, it cannot be said with certainty. However, polyphyletic hypotheses of Lissamphibia have never gained widespread acceptance. All molecular analyses, even though they have differed on their hypotheses of the internal lissamphibian topology, have unequivocally recovered lissamphibians as monophyletic

with relation to amniotes (Feller and Hedges 1998, Zardoya and Meyer 2001, Zhang, Chen et al. 2003, San Mauro, Gower et al. 2004). Schoch & Milner (2004) have suggested that similarities between caecilians and microsaurs were due to small size convergence, and the homoplasy that resulted from this.

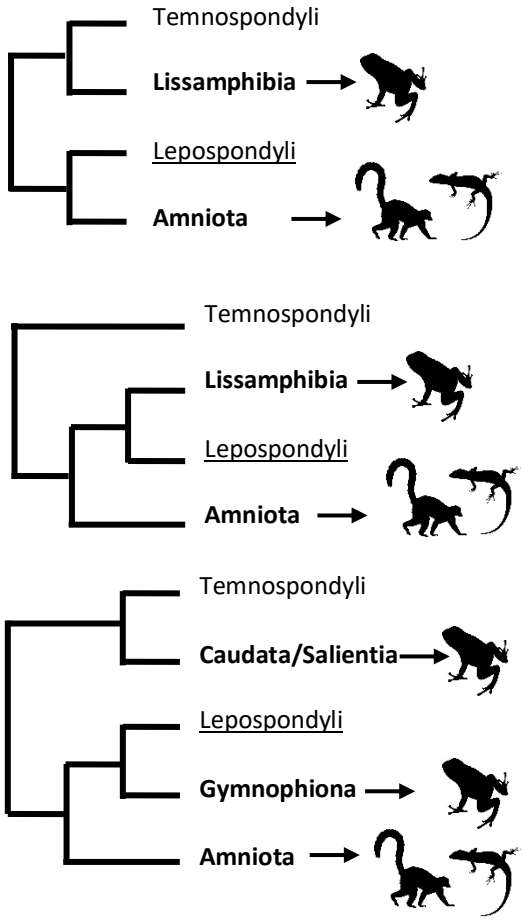


Figure 17: The three prevailing phylogenetic hypotheses concerning the origin of lissamphibians: A, the temnospondyl hypothesis, B, the lepospondyl hypothesis, C, the polyphyly hypothesis.

Several key phylogenetic analyses of this time recovered the more traditional hypothesis that Lissamphibia originated from within Temnospondylii. In particular, these included Ruta et al. (2003) and Ruta and Coates (2007), which were the largest analyses of the 2000s in terms of both character and taxonomic inclusion. These analyses recovered a monophyletic Anthracosauria, *Gephyrostegus*, a paraphyletic Seymouriamorpha, a monophyletic Lepospondyli and a paraphyletic Diadectamorpha as successively related sister-clades to Amniota. *Westlothiana* was recovered as the most basal relative of lepospondyls (Fig. 1).

The various hypotheses of the origin of Lissamphibia have implications to understanding which clades are members of the amniote stem, and thus the patterns of character acquisition that led

to the amniote morphology. An origin of Lissamphibia within lepospondyls (e.g. Laurin and Reisz 1997) results in many clades traditionally associated with amniotes, notably anthracosaurs and seymouriamorphs, to move onto the tetrapod stem and be considered as equally closely related to amniotes and amphibians (see Fig. 14). Solving the origin of lissamphibians is therefore essential to understanding which clades belong to the amniote stem.

1.2.5 Recent analyses and novel hypotheses

The discovery of new fossil specimens, and ever more expansive phylogenetic analyses, has resulted in novel, never before considered topologies.

A new probable stem amphibian, *Gerobatrachus hottoni*, from the Early Permian, was described in 2008 (Anderson, Reisz et al. 2008). Although the phylogenetic analysis in this publication initially recovered a polyphyletic Lissamphibia, this has not been supported by molecular evidence, which strongly supports a monophyletic Lissamphibia (Feller and Hedges 1998, Zardoya and Meyer 2001, Zhang, Chen et al. 2003, San Mauro, Gower et al. 2004). Once constrained for lissamphibian monophyly, a temnospondyl origin for amphibians was found to be more likely than a lepospondyl origin.

Eocaecilia micropodia Jenkins and Walsh, 1993, a stem-caecilian from the Early Jurassic, has helped to resolve the uncertainty about the morphological condition of early caecilians and has been recovered within temnospondyls alongside other amphibians (Maddin, Jenkins Jr et al. 2012). Pardo et al. (2017) reported a new possible stem caecilian, *Chinlostegophis jenkinsi*. Based on a phylogenetic analysis including this new taxon, he recovered a temnospondyl origin for caecilians, although not within dissorophoid temnospondyls (Pardo, Small et al. 2017). A further possible stem caecilian has been described recently, *Funcusvermis gilmorei* Kligman et al. 2023. *Funcusvermis* was described to bridge the morphological gap between dissorophoid temnospondyls and caecilians. Kligman et al. (2023) carried out a phylogenetic analysis including both *Funcusvermis* and *Chinlestegophis*, and recovered a monophyletic Lissamphibia, including caecilians, originating within dissorophoid temnospondyls (Kligman, Gee et al. 2023). They also did not recover *Chinlestegophis* as

a stem caecilian, but within a different group of temnospondyls: Stereospondylomorpha (Kligman, Gee et al. 2023). Nonetheless, whilst the hypotheses of Pardo et al. (2017) and Kligman et al. (2023) differ with regards to the phylogenetic position of *Chinlestegophis* and caecilians within temnospondyls, they are both consistent with a monophyletic Lissamphibia with respect to Amniota.

Another relatively novel hypothesis has been the recovery of a clade within Microsauria formed by the grouping of microsaurian taxa in which the snout has a recumbent morphology. This clade has been termed Recumbirostra and has been recovered in multiple analyses (Huttenlocker, Pardo et al. 2013, Pardo, Szostakiwskyj et al. 2017). Pardo et al. (2017) recovered an entirely novel topology that had major implications for the identity of various fossil clades. As well as recovering Recumbirostra, this analysis found all microsaurs to be the sister clade to Reptilia, within the amniote crown, the first time microsaurs had been recovered as crown amniotes. Moreover, it recovered aïstopods as very deep stem amniotes, stemwards of whatcheeriids and only one step crownwards of *Acanthostega*, based primarily on novel braincase characters that they introduced, and resulting in a polyphyletic lepospondyls. Amphibians were recovered within temnospondyls, and this clade represented the sister-clade to Amniota + Diadectamorpha + Seymouriamorpha (Fig. 18).

The findings of a polyphyletic lepospondyls, and a phylogenetic position for aïstopods as stem tetrapod, found by Pardo et al. (2017), have gained some support. Another phylogenetic analysis by Mann et al. (2019), based on the matrix of Pardo et al. (2017), recovered lepospondyls as polyphyletic, with microsaurs recovered as crown amniotes, and aïstopods recovered as part of a monophyletic group with stem tetrapods including *Acanthostega* and *Tiktaalik*. Another phylogenetic analysis by Clack et al. (2019), based on the matrix of Clack et al. (2016) also recovered lepospondyls as polyphyletic, with microsaurs closely related to amniotes, and all other lepospondyls, including aïstopods, as stem tetrapods.

However, certain cautions must be noted. No lepospondyls were included in the analysis of Pardo et al. (2017) other than aïstopods and microsaurs. The authors state that they were excluded due to the lack of substantial data relating to the braincase. Additionally, aïstopods lack an appendicular

skeleton and thus are inapplicable for many postcranial characters. This, combined with the proportionally very high number of braincase characters, somewhat biases the results of Pardo et al. (2017), and any analyses based on the matrix of Pardo et al. (2017), towards the characters relating to the braincase. Moreover, synapsids were represented by just *Ophiacodon* and *Dimetrodon*, both of which are substantially morphologically derived. Reptiles are represented by just *Petrolacosaurus*, *Captorhinus* and *Opisthodontosaurus*, an extremely poorly known captorhinid that has also been specifically noted to show mandibular convergence with microsaurs (Reisz, LeBlanc et al. 2015). *Opisthodontosaurus* lacks virtually all information about the braincase, and is scored as unknown for 55/57 of the characters relating to the braincase in this analysis (Pardo et al. 2017). Further work with greater taxonomic coverage is needed to address these issues.

Another interesting result from more recent phylogenetic analyses is the finding that certain clades of taxa that have always been considered to be crown amniotes, on the reptile stem, could possibly be stem amniotes. Simões et al., (2022) recovered captorhinids and araeoscelids as stem amniotes. Ford and Benson (2020) recovered araeoscelids as stem reptiles, but stemwards of parareptiles, and therefore not as diapsid reptiles, as they have typically been considered in previous studies (Laurin and Reisz 1995). These analyses demonstrate that the topology of early crown amniotes is far from certain, even today, and that there is currently no consensus about membership of the amniote stem lineage. The various taxa and groups included in many different phylogenetic analyses is presented in Table 1.

1.2 Aims of the Thesis

In this thesis, I aim to present substantial new anatomical data on *Westlothiana* using propagation phase-contrast synchrotron X-ray micro-computed tomography, and to test the phylogenetic affinities of *Westlothiana* in a novel phylogenetic analysis.

In the second chapter, I report novel anatomical information of the skull of *Westlothiana*. In particular, I reveal the ventral surface of the palate, the temporal region and the circumorbital bones,

all of which were previously poorly known. I then discuss then implications of the cranial material for the phylogenetic relationships of *Westlothiana*.

In the third chapter, I report novel anatomical information of the postcranial skeleton of *Westlothiana*. I reveal the atlas-axis complex for the first time, as well as providing updated descriptions of the humerus, femur and pes. I also discuss the previously referred second specimen of *Westlothiana*, on which previous descriptions of the postcranial information of the taxon are based (Smithson, Carroll et al. 1993), highlight the differences between the holotype and second specimens of *Westlothiana*, and suggest a new taxonomic identity from the second specimen.

In the fourth chapter, I present a novel phylogenetic analysis of early tetrapods, stem amniotes and early crown amniotes, including characters assembled from descriptive accounts and phylogenetic character lists of the last 30 years. My analysis is the first to include substantial representation of both stem and crown amniote taxa, in approximately equal sampling intensity, and thus provides a broad framework for testing contentious phylogenetic hypotheses of deep amniote divergences. I find support for a monophyletic Lepospondyli of which *Westlothiana* is the earliest representative, and a previously unrecovered topology of crown and late stem amniotes, and find early divergence times for the amniote crown.

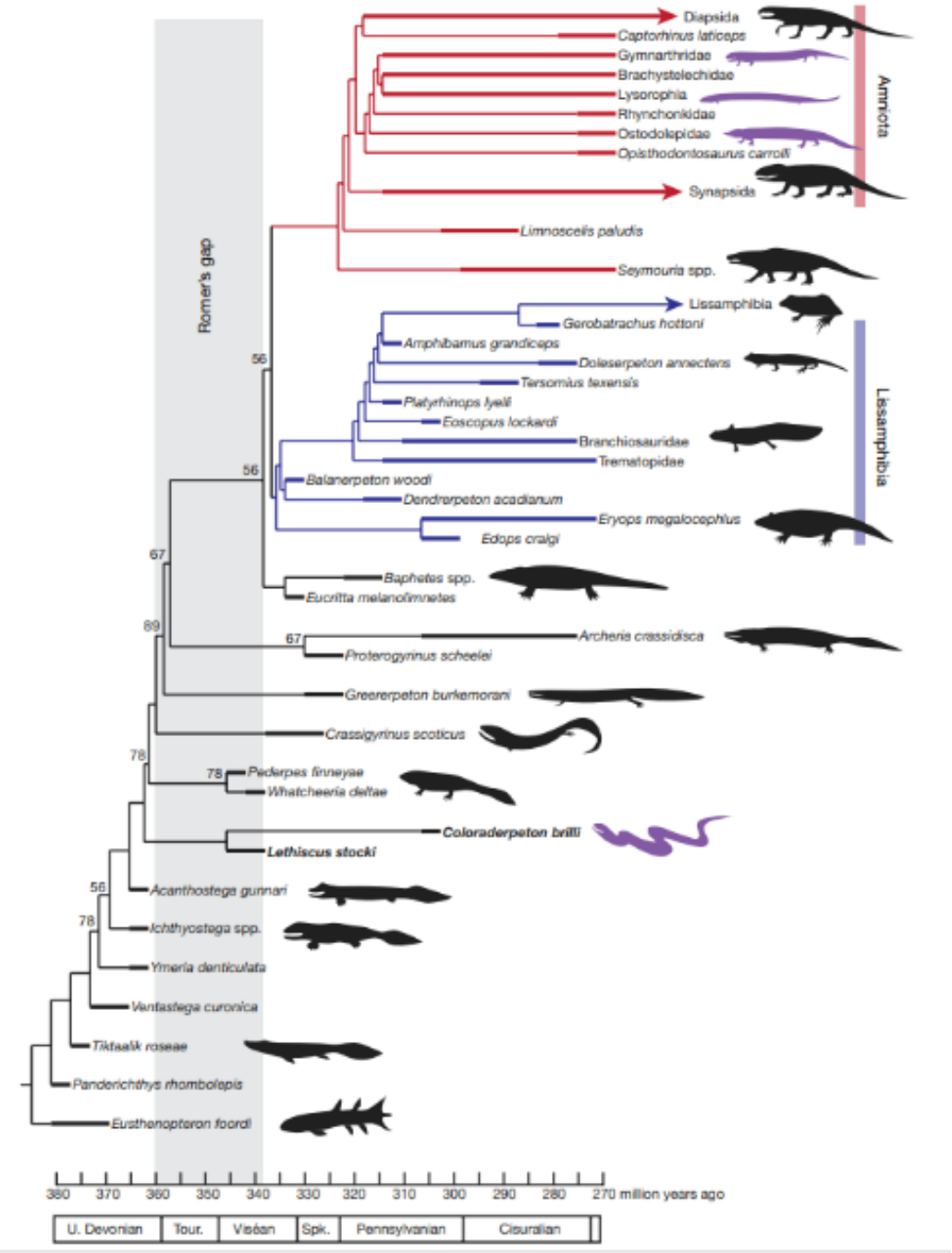


Figure 18: The phylogenetic hypothesis proposed by Pardo et al. (2017).

Table 1, Across the Following Pages: The inclusion of selected groups and taxa in previous phylogenetic analyses between 1995 and the present. If a group or taxon was not included in a particular analysis, this is shown by N/A. For each analysis, it is also indicated whether it recovered the Temnospondyl Hypothesis for Lissamphiabian origins (TH), the Lepospondyl Hypothesis (LH), or if these hypotheses could not be tested as insufficient representatives of lissamphibians were included (N/A). See Chapter 1 for further explanation of these hypotheses.

Analysis	Data Matrix Based On	No. taxa	No. Char	Lepospondyl Origin Hypothesis	Anthracosaurs	Seymouriamorphs	Lepospondyls	Gephyrostegids	Chroniosuchids	Diadectamorphs	*Solenodonsaurus*	*Westlothiana*
Laurin & Reisz, 1995	Novel	13	124	N/A	N/A	Stem-Amniotes	N/A	N/A	N/A	Stem-Amniotes	N/A	N/A
Laurin et al. 1997	Novel	38	157	LH	Stem-tetrapods	Stem-tetrapods	Paraphyletic, stem-amphibians	Stem-tetrapods	N/A	Stem-Amniotes	N/A	N/A
Laurin, 1998	Laurin et al. 1997	43	155	LH	Stem-tetrapods	Stem-tetrapods	Paraphyletic, stem-amphibians	Stem-tetrapods	N/A	Stem-Amniotes	N/A	Stem-tetrapod, sister to tetrapod crown
Berman et al., 2000	Novel	9	8	N/A	Stem-Amniotes	N/A	Monophyletic	N/A	N/A	Crown-amniotes, stem-synapsids	N/A	N/A
Vallin & Laurin, 2004	Laurin & Reisz, 1999	49	161	LH	Stem-tetrapods	Stem-tetrapods	Paraphyletic, stem-amphibians	Stem-tetrapods	N/A	Stem-Amniotes	Stem-Amniotes	Crown tetrapod, polytomy with total-clade Lissamphibia and total-clade Amniota

Analysis	Data Matrix Based On	No. taxa	No. Char	Lepospondyl Origin Hypothesis	Anthracosaurs	Seymouriamorphs	Lepospondyls	Gephyrostegids	Chroniosuchids	Diadectamorphs	*Solenodonsaurus*	*Westlothiana*
Muller & Reisz, 2006	Novel	25	90	N/A	N/A	Stem-Amniotes	N/A	N/A	N/A	Stem-Amniotes	N/A	N/A
Ruta et al., 2003	Novel	90	319	**TH**	Stem-Amniotes	Stem-Amniotes	Monophyletic, stem-amniotes	Stem-Amniotes	N/A	Stem-Amniotes	Stem-Amniotes	Sister to Lepospondyls
Ruta & Coates, 2007	Ruta et al., 2003	102	339	TH	Stem-amniotes	Stem-amniotes	Monophyletic, stem-amniotes	Stem-Amniotes	N/A	Stem-Amniotes	Stem-Amniotes	Sister to Lepospondyls
Marjanovic & Laurin, 2019	Ruta & Coates, 2007	158	277	LH	Stem-tetrapods	Stem-tetrapods	Paraphyletic, stem-amphibians	N/A	Stem-tetrapod	Crown-amniotes, stem-synapsids	Stem-Amniotes	Stem-amphibian, earliest diverging and sister to lepospondyls

Analysis	Data Matrix Based On	No. taxa	No. Char	Lepospondyl Origin Hypothesis	Anthracosaurs	Seymouriamorphs	Lepospondyls	Gephyrostegids	Chroniosuchids	Diadectamorphs	*Solenodonsaurus*	*Westlothiana*
Anderson, 2001	Novel	42	182	N/A	N/A	N/A	Monophyletic	N/A	N/A	N/A	N/A	N/A
Huttenlocker et al., 2013	Anderson, 2001	60	227	TH	Stem-amniotes	Stem-amniotes	Monophyletic, most microsaurs grouped into Recumbirostra. Stem-amniotes	N/A	N/A	N/A	N/A	N/A
Pardo et al., 2017	Novel, partially on Huttenlocker et al. 2013	58	370	TH	Stem-tetrapods	Stem-amniotes	Polyphyletic, aistopods are stem tetrapods, microsaurs are crown amniotes and stem reptiles	N/A	N/A	Stem-Amniotes	N/A	N/A
Gee et al., 2021	Pardo et al., 2017	68	370	TH	Stem-tetrapods	Stem-amniotes	Polyphyletic, aistopods are stem tetrapods, microsaurs are crown amniotes and stem reptiles	N/A	N/A	Stem-Amniotes	N/A	N/A

Analysis	Data Matrix Based On	No. taxa	No. Char	Lepospondyl Origin Hypothesis	Anthracosaurs	Seymouriamorphs	Lepospondyls	Gephyrostegids	Chroniosuchids	Diadectamorphs	*Solenodonsaurus*	*Westlothiana*
Ruta & Clack, 2006	Novel	33	314	TH	Stem-amniotes	Stem-amniotes	Polyphyletic, microsaurs are stem amniotes, *Adelogyrinus* is a stem amphibian	Stem-amniote	N/A	N/A	N/A	Sister to microsaurs
Clack & Klembara, 2008	Ruta & Clack, 2006	34	327	N/A	Stem-amniotes	Stem-amniotes	Monophyletic, stem-amniotes	Stem-Amniotes	Stem-Amniotes	N/A	N/A	Sister to Lepospondyls
Klembara et al., 2014	Assorted previous Klembara analyses	37	156	N/A	Stem-tetrapods	Stem-amniotes	Paraphyletic, stem-amniotes	Stem-amniotes	N/A	N/A	N/A	N/A
Ruta et al., 2020	Klembara et al., 2014, 2020	54	291	TH	Stem-amniotes	Stem-amniotes	N/A	Stem-Amniotes	Stem-Amniotes	Crown-amniotes, stem-synapsids	Stem-Amniotes	Sister to crown amniotes
Klembara et al., 2021	Klembara et al., 2014, 2020	55	294	TH	Stem-Amniotes	Stem-Amniotes	N/A	Stem-Amniotes	Stem-Amniotes	Crown-amniotes, stem-synapsids	Stem-Amniotes	Sister to crown amniotes

Analysis	Data Matrix Based On	No. taxa	No. Char	Lepospondyl Origin Hypothesis	Anthracosaurs	Seymouriamorphs	Lepospondyls	Gephyrostegids	Chroniosuchids	Diadectamorphs	*Solenodonsaurus*	*Westlothiana*
Clack et al., 2016	Novel	45	213	TH	Stem-Amniotes	Stem-Amniotes	Monophyletic, stem-amniotes	Stem-Amniotes	N/A	N/A	N/A	Sister to Lepospondyls
Clack et al., 2019	Clack et al., 2016	57	260	TH	Stem-amniotes	Stem-amniotes	Polyphyletic, microsaurs are stem amniotes, all other lepospondyls are a monophyletic stem-tetrapod clade	Stem-amniote	N/A	N/A	N/A	Sister to microsaurs
Ford & Benson, 2020	Novel	70	294	N/A	N/A	Stem-amniotes	N/A	Stem-amniote	N/A	Stem-amniotes	N/A	N/A

Chapter 2: The Cranial Skeleton of *Westlothiana*

2.1 Introduction

2.1.1 The East Kirkton Locality

The Carboniferous East Kirkton limestone is represented at a remarkable locality that has yielded some of the most important specimens pertinent to the origin of terrestrial vertebrates. It sits within the West-Lothian Oil-Shale Formation, which can be assigned to the Asbian-Brigantian ages within the Viséan, ranging from 337 to 329 million years ago (Smith, Monro et al. 1993). It has been known for a long time to preserve many tetrapod specimens (Wood, Panchen et al. 1985). Many of the preserved tetrapods do not have lateral line systems, and possess well-developed and intact limbs, indicating that terrestriality was possible in these taxa (Clarkson, Coates et al. 1993). Additionally, many terrestrial arthropods are known, including myriapods and scorpions (Jeram 1993, Jeram and Selden 1993, Shear 1993), but fish are conspicuously absent (Wood, Panchen et al. 1985). Thus, the East Kirkton Limestone has long been thought to represent a shallow, terrestrial lake in a richly vegetated region of volcanic soil. The tetrapod fauna recovered from East Kirkton was observed from early in its excavation to include probable members of both the lissamphibian stem-lineages (Wood, Panchen et al. 1985), including the temnospondyl *Balanerpeton woodi* (Milner and Sequeira 1993), and members of the amniote stem-lineage (Wood, Panchen et al. 1985) including the basal anthracosaur *Silvanerpeton miripedes* (Clack 1993) and the reptiliomorph *Westlothiana lizziae* (Smithson et al., 1993).

2.1.2 The lithology of East Kirkton

The East Kirkton limestone is a very localised lithology, found primarily in the East Kirkton Quarry near Bathgate, Lothian, Scotland (Wood, Panchen et al. 1985). There is currently no evidence that the depositional area of the lithology extends substantially beyond the boundaries of the quarry (Wood, Panchen et al. 1985). The limestone has been known for many years to have unusual sedimentary characteristics (Muir and Walton 1957), with large amounts of volcaniclastic material

represented (Clarkson, Coates et al. 1993). In 1985, Stan Wood described the discovery of a new assemblage of tetrapod fossils from the locality and highlighted their importance, including the discovery of the "earliest well-preserved amphibian skeleton ever discovered" (Wood et al 1985, p.355), later described as *Balanerpeton woodi* (Milner and Sequeira, 1993). The National Museums of Scotland (NMS) carried out a series of excavations between 1985 and 1992 (Rolfe, Baird et al. 1993).

The outcrop in the East Kirkton quarry spans approximately 14.7 metres and can be divided into a series of three separate lithologies, from bottom to top; the East Kirkton Limestone, the Little Cliff Shale and the Giekie Tuff (Rolfe, Baird et al. 1993), though tetrapod remains are only known from the East Kirkton Limestone (Wood, Panchen et al. 1985). The entire sequence is divided into 88 units, with the East Kirkton Limestone comprising units 39 through 88, with units 36-39 representing a transitional series between the East Kirkton Limestone and the overlying Little Cliff Shale (Rolfe, Baird et al. 1993).

The East Kirkton limestone has been identified as having been deposited in a freshwater lacustrine environment, based on the presence of the freshwater ostracod genus *Carbonita* throughout much of the sequence (Clarkson, Coates et al. 1993, Rolfe, Baird et al. 1993). Some units also preserve evidence of the evaporite mineral gypsum, which suggests that the lake was shallow, and that substantial evaporation occurred (Rolfe, Baird et al. 1993). It is thought that the lake is likely to have only existed for a few tens of thousands of years (Clarkson, Coates et al. 1993). Despite the presence of volcaniclastic material, there is no evidence of volcanic eruptions during the lifetime of the lake, and it is therefore likely that this material was washed into the lake from the surrounding sediment (Clarkson, Coates et al., 1993).

A significant quantity of plant material is preserved in the limestone (Scott, Brown et al. 1993). This material shows that the vegetation surrounding the lake was dominated by gymnosperms and pteridosperms (Scott, Brown et al. 1993). This suggests that the region was dominated by dense forests, but that the conditions were fairly dry as these conditions are preferred by gymnosperms (Clarkson, Coates et al., 1993). This is further supported by the presence of fusainised charcoal in several horizons (Scott, Brown et al. 1993), which suggests that forest fires were prevalent (Clarkson, Coates et al. 1993).

Lake bottom sediments in much of the sequence show evidence of photosynthetic life. This includes cyanobacteria and even some evidence of stromatolites. This suggests that, for the majority of the lifetime of the lake, the lake bottom waters were oxygenated (Clarkson, Coates et al. 1993). Isolated tetrapod bones are also known from the lower half of the sequence, ranging from Units 82-56 (Wood, Panchen et al. 1985). Terrestrial invertebrates are known from an even greater range of units, spanning Units 82 to 35 (Clarkson, Coates et al. 1993). Fish remains are known from the Little Cliff Shale that overlies the East Kirkton Limestone but, within the East Kirkton Limestone itself, the only unambiguously aquatic taxa are restricted to the uppermost units, units 37 and 36, which show a transitional lithology with the Little Cliff Shale (Rolfe, Baird et al. 1993).

Articulated tetrapod skeletons are almost exclusively found in Unit 82, towards the base of the East Kirkton Limestone (Clarkson, Coates et al. 1993). Unit 82 is a black shale, the lithology of which indicates that it was deposited below a thermocline within a low oxygen hypolimnion, suggesting that at the time of deposition of Unit 82 the lake was deeper than it was for much of the rest of its existence (Clarkson, Coates et al. 1993, Rolfe, Baird et al. 1993).

2.1.3 The History of the East Kirkton Lake

Clarkson et al. (1993) compiled a possible history of the East Kirkton Lake, based on the above sedimentological information. According to Clarkson et al. (1993), when the lake initially formed, it was a freshwater lake, but one that was geographically isolated from the nearby larger body of water, Lake Caldwell. It is possible that this is the reason that fish were absent from the East Kirkton Lake (Clarkson, Coates et al. 1993). The lake formed in the region of a tetrapod-rich forest. The lake was deepest for a period early in its history, during which the black shale of Unit 82 was deposited (Clarkson, Coates et al. 1993). During this time the waters of the lake were favourable for terrestrial tetrapods, such as *Westlothiana lizziae* (Smithson et al., 1993), to swim in. Although the East Kirkton tetrapods are predominantly terrestrial (Wood, Panchen et al. 1985), it is possible that aquatic larval forms of tetrapods such as *Balanerpeton woodi* were also present in the lake at this time (Milner and Sequeira, 1993). After this time the lake became shallower, maybe being represented by

just shallow pools with high levels of evaporation, although the surrounding environment remained forested and rich in terrestrial taxa (Clarkson, Coates et al. 1993). During this time the lake became less hospitable to swimming vertebrates. Tetrapods still lived in the surrounding forest, but entered the lake less often, and are therefore represented by just isolated remains (Clarkson, Coates et al. 1993). After the time period corresponding with Units 32-39, the lake became connected with the nearby larger lake Lake Caldwell, and fish were able to enter the lake for the first time (Clarkson, Coates et al. 1993, Rolfe, Baird et al. 1993).

2.1.4 *Westlothiana lizziae*

One of the most important and unique taxa discovered at East Kirkton is *Westlothiana lizziae*, first named by Smithson and Rolfe (1990). *Westlothiana* is known from a mostly articulated holotype specimen preserving the skull and postcrania. There is also a referred second specimen that lacks the skull and is considerably larger than the holotype. It was referred to *Westlothiana* based on morphological similarities in the vertebrae, pelvis, hindlimbs and scales, and on the basis of similar limb proportions; both specimens are notable for having proportionally small limbs (Smithson, Carroll et al. 1993). However, due to the size differences and lack of cranial material it can only moderately confidently be referred to *Westlothiana*. *Westlothiana* was recognised from its initial discovery to be important with regard to the origin of amniotes (Smithson 1989) and was originally described as a reptile (Smithson 1989, Smithson and Rolfe 1990), and later as a reptiliomorph (Smithson, Carroll et al. 1993). It was also observed to be considerably older than most other taxa associated with the origin of reptiles, being "substantially older than the oldest accepted amniotes" in the first, and to date only, detailed description of the taxon (Smithson, Carroll et al. 1993**,** p384). In fact, the skull table was initially reported to be most similar to that of primitive pelycosaurs (Smithson, Carroll et al. 1993). *Westlothiana* was deemed by Smithson et al., (1993) to be a stem amniote, crownwards of seymouriamorphs but stemwards of diadectomorphs and the amniote crown group, following the synapomorphy-scheme outlined in Panchen & Smithson (1988).

Westlothiana was observed in its initial descriptions to share traits with early amniotes (Smithson and Rolfe 1990, Smithson, Carroll et al. 1993). It has large parietals that extend the full width of the skull table and, in this respect, is similar to those of protorothyrids (Carroll 1964, Carroll 1969). It was also observed to have gastrocentrous trunk vertebrae, and a pedal phalangeal count that is the same as early amniotes, being 2, 3, 4, 5, 4 (Smithson, Carroll et al. 1993). It was noted to lack plesiomorphic characters associated with more primitive stem amniotes; *Westlothiana* was originally observed to lack a separately ossified intertemporal, a squamosal notch, palatal fangs and labyrinthine infolding of the tooth enamel (Smithson, Carroll et al. 1993).

Westlothiana also retains plesiomorphic character states. It lacks a transverse flange of the pterygoid, and therefore the tooth-row on the transverse flange of the pterygoid (Smithson, Carroll et al. 1993), like that is present in the earliest amniotes (e.g. Carroll 1969, Resiz 1977). *Westlothiana* retains three proximal tarsals (Smithson, Carroll et al. 1993), and in this respect differs from the amniote condition of having just two proximal tarsals, an astragalus and calcaneum (Carroll 1969, Reisz 1981). *Westlothiana* also possesses massive, oblong dorsal and ventral scales similar to those present in the probable stem amniote *Solenodonsaurus janenschi* (Laurin and Reisz 1999).

Some traits of *Westlothiana* suggest a potential relationship with microsaurs and other lepospondyls, and *Westlothiana* was noted in the original description to somewhat resemble microsaurs (Smithson, Carroll et al. 1993). Although amniotes have a pterygoid transverse flange that bears teeth comparable in size to the marginal teeth (Carroll 1969, Reisz 1977), stem amniotes such as seymouriamorphs and *Gephyrostegus* also possess a pterygoid transverse flange, but one that is short, projects laterally, and lacks any teeth other than denticles, which are far smaller than the marginal teeth (Klembara, Berman et al. 2005, Klembara, Clack et al. 2014). *Westlothiana* and lepospondyls, including microsaurs, lack the pterygoid transverse flange entirely (Carroll and Gaskill 1978, Smithson, Carroll et al. 1993, Gee, Bevitt et al. 2019, Gee, Bevitt et al. 2021). However, *Westlothiana* retains a supratemporal (Smithson, Carroll et al. 1993), unlike microsaurs (Carroll and Gaskill 1978), and as such does not possess the distinctly microsaurian temporal region. It also retains clear intercentra (Smithson, Carroll et al. 1993), unlike the majority of microsaurs and all other

lepospondyls (Carroll and Gaskill 1978, Andrews and Carroll 1991, Wellstead 1991, Anderson 2002, Milner 2018).

Smithson et al., (1993) produced a phylogeny, based on a synapomorphy scheme, in which *Westlothiana* was recovered as the sister-taxon to a clade consisting of amniotes + diadectomorphs, immediately crownwards of seymouriamorphs. Three synapomorphies were considered to unite *Westlothiana* with Amniota + Diadectamorpha: (1) Loss of an intertemporal, (2) a vertically positioned quadrate, (3) the supratemporal forms the corner of the skull table. Diadectamorpha + Amniota, excluding *Westlothiana*, were united by the following synapomorphies: (1) A tooth-row on the pterygoid transverse flange (which was reversed in *Diadectes*, Berman et al., 1998), (2) Separately ossified scapula and coracoid.

Following its discovery, *Westlothiana* has been included in a number of phylogenetic analyses, and has occupied a wide range of phylogenetic positions (Laurin, Reisz et al. 1997, Ruta, Jeffery et al. 2003, Ruta and Clack 2006, Marjanović and Laurin 2019, Klembara, Ruta et al. 2021). Although a broad pattern of affinities has emerged, *Westlothiana* has continued to demonstrate a close relationship with both lepospondyls (Ruta, Jeffery et al. 2003, Clack, Bennett et al. 2016, Clack, Ruta et al. 2019) and amniotes (Vallin and Laurin 2004, Ruta, Clack et al. 2020, Klembara, Ruta et al. 2021), and no clear consensus has been reached as to its relationships and evolutionary importance.

Several analyses have recovered *Westlothiana* as the sister taxon to a monophyletic or paraphyletic Lepospondyli that has typically been recovered on the amniote stem (Ruta, Jeffery et al. 2003, Ruta and Coates 2007, Clack and Klembara 2009, Clack, Bennett et al. 2016). Marjanovic & Laurin (2019) recovered Lissamphibia within Lepospondyli, a phylogenetic hypothesis in which lepospondyls would then represent the lissamphibian stem-lineage. Under this hypothesis, *Westlothiana* was still recovered as the sister-taxon to lepospondyls, making it the earliest diverging stem-amphibian.

In analyses where lepospondyls have been recovered as polyphyletic, *Westlothiana* has been recovered as the sister-taxon to microsaurs (Ruta and Clack 2006, Clack, Ruta et al. 2019). It has also been recovered as the sister-taxon to the amniote crown, although it must be noted that this occurred in analyses that did not include lepospondyls (Ruta, Clack et al. 2020, Klembara, Ruta et al. 2021).

Westlothiana has also been recovered in a more plesiomorphic position as the sister-taxon to crown Tetrapoda (Laurin 1998), or as a potential stem or crown tetrapod in a polytomy with total-clade Lissamphibia and total-clade Amniota (Vallin and Laurin 2004).

Here, I present a redescription of the cranial anatomy of *Westlothiana lizziae* based on data from synchrotron phase-contrast micro-computed tomography of the holotype specimen, NMS 1990.72.1. I identify various previously unrecognised cranial features of relevance to the phylogenetic position of *Westlothiana lizziae*. I reveal new features of the previously unknown circumorbital bones, reconstruct the temporal region, and reveal new features of the ventral surface of the palate.

2.2 Methods

2.2.1 Computed Tomography

Phase-contrast micro-computed tomography of the holotype specimen of *Westlothiana lizziae* was carried out by Dr. Vincent Fernandez at the European Synchotron Radiation Facility (ESRF). The following methods paragraphs, marked in quotation marks, were provided by Dr. Fernandez to detail the process by which these scans were carried out.

"NMS_1990.72.1 was imaged at the ID19 beamline of the European Synchrotron Radiation Facility (Grenoble, France) using propagation phase contrast synchrotron radiation X-ray micro-computed tomography. Given the orientation of the specimen on the block, two regions were imaged independently: region-1 consisted of the skull and anterior half of the postcrania; region-2 consisted of the posterior half of the postcrania. The beamline was setup for filtered white beam(W150-B wiggler gap 39 mm; filtered with Cu 10 mm and W 0.5 mm) resulting in a total integrated detected energy of ca 170 keV. Images were recorded with an indirect detector comprising a LuAG 500 µm scintillator, a set of two Hasselblad lenses (100 and 150 mm; Victor Hasselblad AB, Gothenburg, Sweden) set for a 0.67x magnification, and a PCO.edge 4.2 sCMOS camera (PCO, Kelheim, Germany), resulting in a measure pixel size of 8.96 µm. The sample-detector distance was set to 13.2 m for propagation phase contrast. Parameters for the two regions were slightly different, adjusting the

parameters region-2 for time constrain reasons. Parameters for region-1: 6000 projections over a 360° rotation, exposure time of 100 msec per projection (5 frames of 20 msec averaged); 41 flatfield images (radiograph with beam and no sample); 40 darkfield images (radiograph with no beam). Parameters for region-2: 5000 projections over a 360° rotation, exposure time of 60 msec per projection (3 frames of 20 msec averaged); 41 flatfield images; 40 darkfield images.

The recorded field of view in this configuration was 8.89 mm vertically and 18.35 mm horizontally (992 x 2048 pixels). To compensate for the limited field of view: 1) vertically, several acquisitions were performed, moving the specimen on the vertical axis (overlap between consecutive acquisition: 50% for region-1; 20% for region-2); 2) horizontally, the center of rotation was shifted by ca. 8 mm (corresponding to 900 pixels on the detector), effectively allowing to reconstruct tomograms of 34.59 x 34.59 mm (3861x3861 pixels). For region-2, we performed 2 adjacent vertical series, shifted laterally by 22.76 mm (2540 pixels), that were stitched together later in post-processing. Processing of the data was handled slightly differently: for region-1, tomographic reconstruction was performed independently for each acquisition using PyHST2 with the single distance phase retrieval approach (Mirone et al. 2014[FV1] , Paganin et al 2002[FV2]); then the post processing included a ring artefact correction (Lyckegaard [FV3] et al 2011), change of dynamic range from 32-bits to 16-bits using the maximum and minimum 0.001% histogram clipping values of all the datasets of the series, weighted averaging of duplicated tomograms resulting from the 50% overlap on the vertical axis. For region-2, as the vertical overlap between consecutive acquisition was limited to 20%, detector artefacts would not be as buffered as with a 50% overlap and weighted averaging. To compensate for this, radiographs were stitched vertically before the tomographic reconstruction (see Benoit [FV4] et al 2019 for details of the process), including a high frequency 1D vertical filter to correct for the noise pattern of the PCO.edge 4.2 (not completely eliminated with the darkfield correction). The newly created set of radiographs were reconstructed similarly with PyHST2 and the single distance phase retrieval approach. Post processing was also similar, ensuring that the 0.001% histogram clipping values would encompass the two laterally adjacent dataset. Finally, the two laterally adjacent 16-bits datasets were stitched using a weighted averaged in the overlapping part.

Both final datasets for region-1 and region-2 were cropped and a 2x2x2 binning version was also generated to allow for faster inspection if necessary.”

2.2.2 Processing the micro-CT scans

I segmented the data using Materialise Mimics v19.0 to produce three-dimensional models of the specimen, producing separate reconstructions of both the slab and counterslab.

I produced renderings and articulated reconstructions using Blender v2.93. Initially, I exported all models in situ from each of the reconstructions of the slab and counterslab. I then combined these two sets of models in Blender to produce a reconstruction of how the specimen would have resided, in situ, before the slab and counterslab were separated from one another. I then used this as the basis to reconstruct the skull. I moved different elements into the positions that they would have occupied to produce a full skull reconstruction, and duplicated and mirrored the right premaxilla in order to complete the reconstruction, as no left premaxilla was preserved. I also constructed a composite left mandible using the most complete elements from the left and right mandible, mirroring elements from the right mandible.

2.3 Anatomical Descriptions

2.4.1 Preservation.

The skull of NMS.1990.72.1 has been flattened dorsoventrally, so that most elements are preserved in almost the same plane. The right side of the skull has been displaced laterally, so elements of the right cheek and right mandible are visible in lateral view to the right of the skull roof bones, but the right articular and quadrate remain in articulation with each other. Most bones of the skull roof, palate and mandible are preserved, at least on one side. The left mandible is preserved beneath the elements exposed at the surface, and has become displaced laterally to lie diagonally across most other bones of the skull. (Fig. 1) Nothing of the occipital region, and very little of the braincase, can be identified.

2.2.2 General aspect (size, shape, proportions).

The skull of NMS.1990.72.1 is proportionally short compared to its transverse width (Fig. 2a, d), with a short rostrum that slopes strongly posterodorsally (Fig. 2b, e). The skull is slightly shorter than originally reconstructed (20 mm long anteroposteriorly and 130 mm wide mediolaterally; (Smithson, Carroll et al. 1993) at approximately 17 mm anteroposterioly, with a maximum mediolateral width of about 9.5 mm, as estimated from my digital reconstruction. The skull height, which could not previously be estimated due to the incompleteness and disarticulation of the specimen, is estimated to be 6.5 mm based on the height of the cheek bones, as oriented in the digital reconstruction (Fig. 2b, e).

The orbit is large, approximately 7mm long anteroposteriorly, which is 37% of the skull length (Fig. 2b, e). This is the largest orbit relative to skull length amongst all the taxa included in my phylogenetic analysis (see chapter 4). However, this large size is approached in araeoscelids (approximately 32-36%; Reisz 1977, Reisz and Dilkes 2003), and *Diadectes abistus* (approximately 33%; Berman et al. 1998). The orbit of NMS.1990.72.1 is also unusually long relative to its dorsoventral height, which is less than half of the anteroposterior length. Such a large ratio between the height and length is not observed in any of the other included taxa in my phylogenetic analysis (see chapter 4). It is possible that the particularly high anteroposterior length of the orbit in NMS.1990.72.1 is due to flattening and crushing of the specimen, although no crushing of any of the individual circumorbital bones is evident.

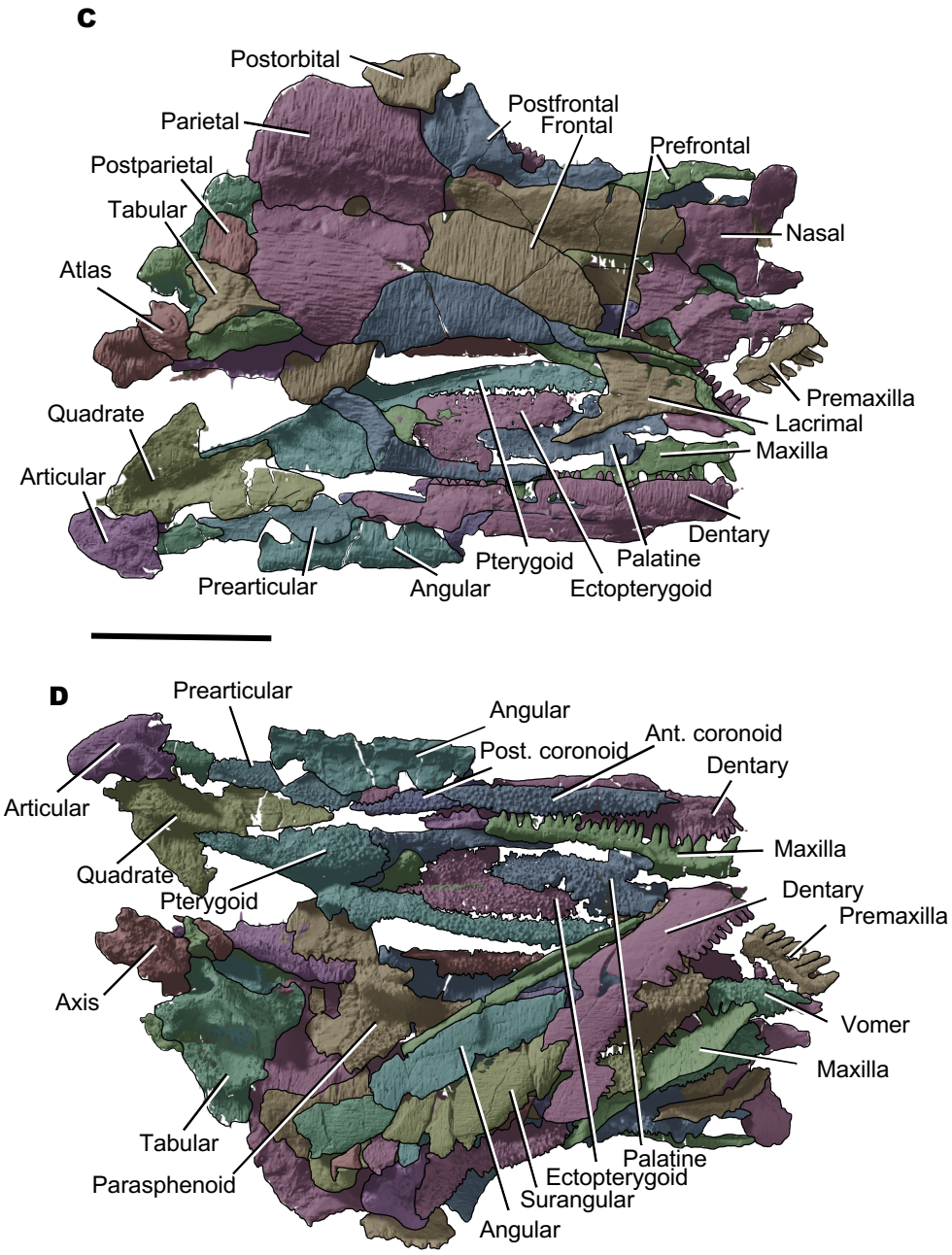


A



B

Figure 1: The skull of *Westlothiana lizziae*, NMS.1997.72.1. Previous page: A, Part, B, Counterpart, photographed by Becca Harry. Below: C, Compiled skull in dorsal view. D, compiled skull in ventral view. Scale bar = 5mm.



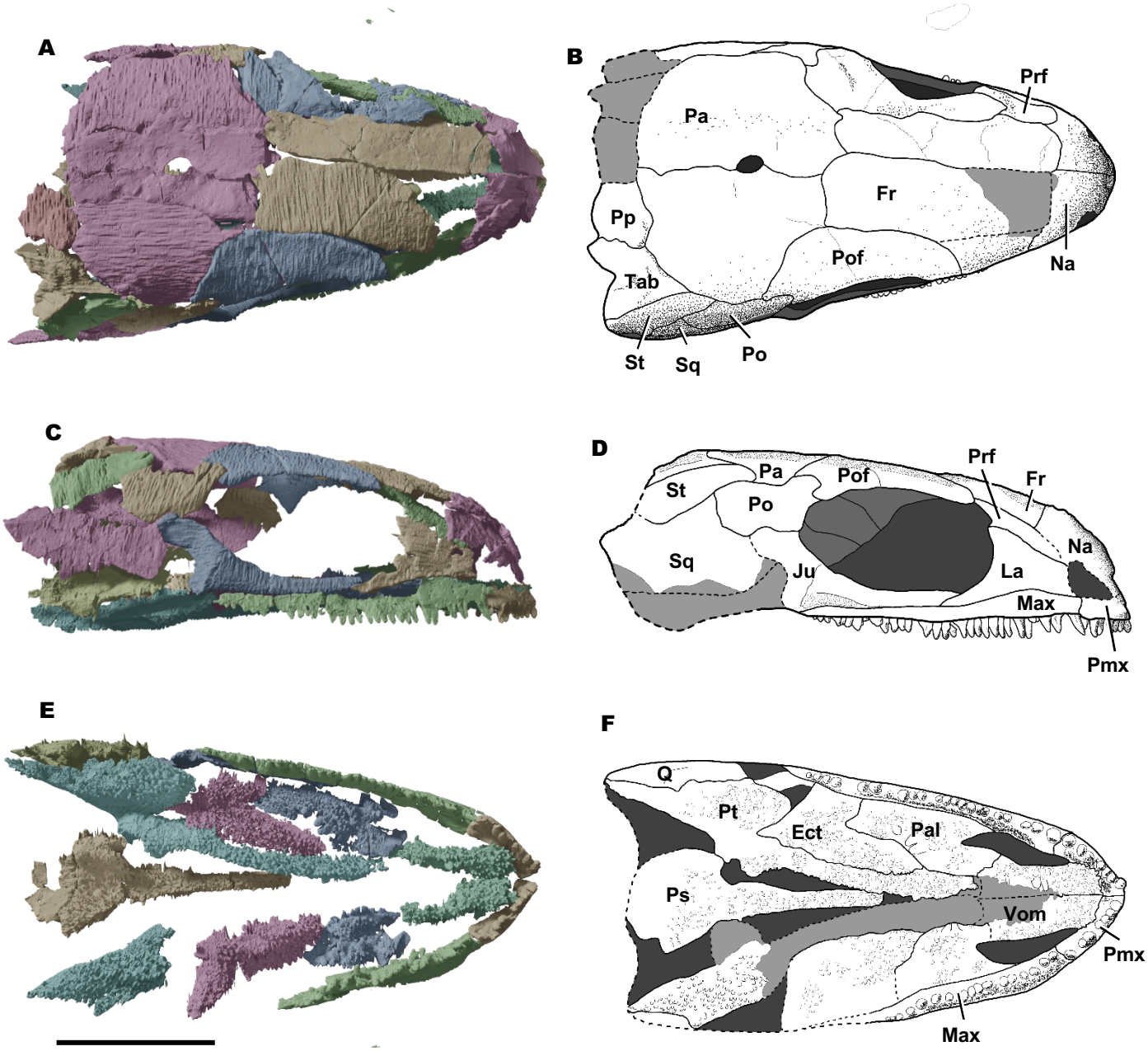


Figure 2: Renderings of the composite skull of *Westlothiana* based on the part and counterpart of NMS.1997.72.1, and reconstructions of the skull in A, B, dorsal view; C, D, right lateral view; E, F, palatal view. Abbreviations: Ectopterygoid (Ect), Frontal (Fr), Jugal (Ju), Lacrimal (La), Maxilla (Max), Nasal (Na), Palatine (Pal), Parasphenoid (Ps), Parietal (Pa), Postfrontal (Pof), Postparietal (Pp), Prefrontal (Prf), Premaxilla (Pmx), Pterygoid (Pt), Quadrate (Q), Squamosal (Sq), Supratemporal (St), Tabular (Tab), Vomer (Vom). Scale bar = 5mm.

2.2.3 Skull Roof

Most of the skull roof is preserved on the surface of the part or counterpart of NMS.1990.72.1, with some of the preserved skull roof bones split across the two slabs (Fig. 1). The left postorbital and postfrontal, both frontals, and both nasals are exposed in the part, although all elements show damage, particularly the nasals and anterior region of the frontals. Each of the parietals

is split between the part and counterpart along the anteroposterior axis of each bone, with the medial half of each parietal, closest to the skull midline, preserved in the part and the lateral half of each parietal preserved in the counterpart. The counterpart also preserves the right postfrontal, postorbital, postparietal and tabular on the surface. In the part, the left lacrimal, prefrontal and maxilla have become displaced ventrally and medially relative to the skull roof, and are preserved underneath the left frontal. The right prefrontal and lacrimal are preserved below the surface in the counterpart. The bone surfaces are generally unsculptured and smooth.

2.2.3.1 Premaxilla. Only the right premaxilla is preserved in NMS.1990.72.1. It is incomplete, and the dorsal ramus is not preserved. The palatal ramus forms a shelf which is short anteroposteriorly and wide mediolaterally, as in the stem amniote clades of seymouriamorphs (Klembara 1997, Klembara and Ruta 2005) and gephyrostegids (Klembara, Clack et al. 2014). It differs from most crown amniotes in that is not extended posteriorly into an elongate vomerine process (Reisz 1977, Laurin 1993, Berman, Reisz et al. 1995). Instead, it bears a shallow concavity along its posterior edge that receives the rounded anterior margin of the vomer (Fig. 4c). The orientation of the contact between the vomer and the premaxilla indicates that this contact would have been in the horizontal plane, and this, combined with the preserved morphology of the premaxilla, suggests that the premaxilla would have been oriented with its anterior surface vertically (Fig. 2b, e). This is different to the recumbent (anterodorsally inclined) position seen in many microsaurs (Huttenlocker, Pardo et al. 2013), as well as some diadectomorphs (Romer 1946, Berman, Henrici et al. 2004), captorhinids (Fox and Bowman 1966, Reisz, LeBlanc et al. 2015) and caseasaurs (Olson, Nash et al. 1968, Reisz, Godfrey et al. 2009). Instead, the vertical orientation of the premaxilla anterior margin in *Westlothiana* is similar to that seen in seymouriamorphs (Klembara 1997 Berman et al. 2000, Klembara and Ruta 2005), *Gephyrostegus* (Klembara et al. 2014) and protorothyrids (Carroll 1964, Carroll 1969). There are nine premaxillary alveoli (containing seven preserved teeth; Fig. 4a). This is more than any amniotes crownwards of lepospondyls including diadectomorphs, which have just three or four (e.g. Berman et al. 1998), captorhinids, which have four or five (Reisz, Haridy et al. 2016) or early crown amniotes, which have no more than six (e.g. Berman et al. 1995, Reisz and Dilkes 2003), but a similar number to some lepospondyls, including some nectrideans,

which range from five to eleven (Beerbower 1963, Milner 2018) and the microsaurs *Asaphestera* and *Microbrachis*, which possess seven (Carroll and Gaskill, 1978).

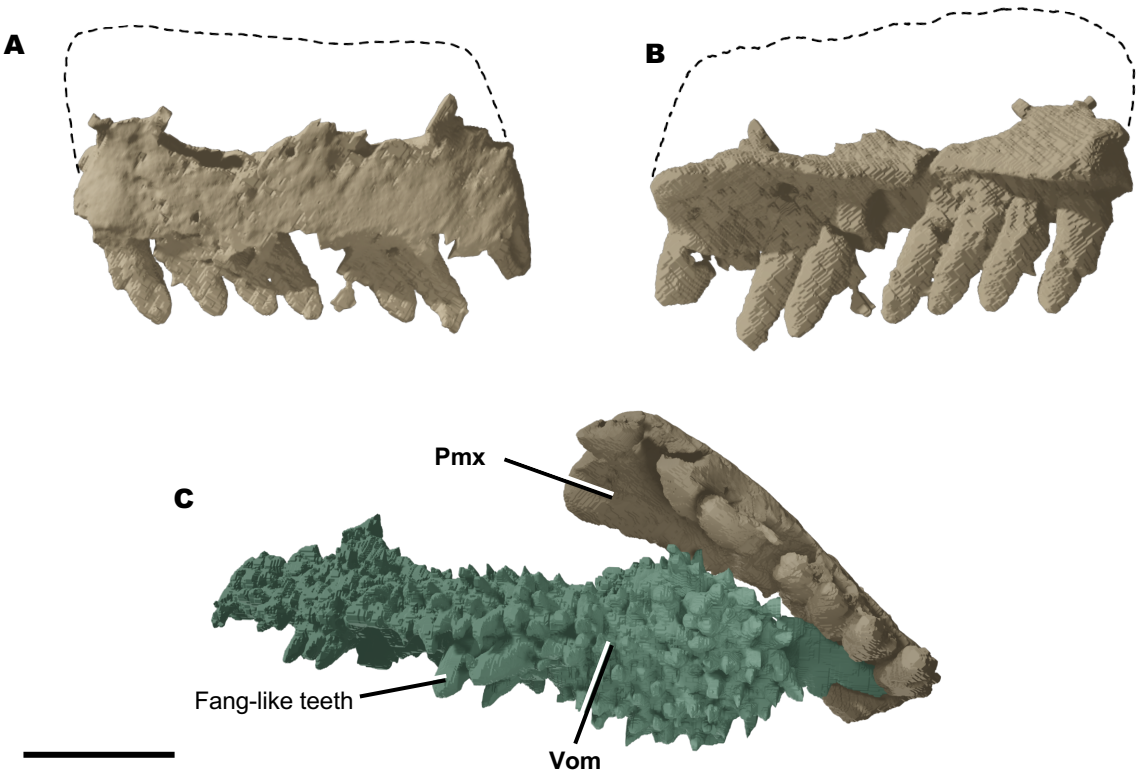


Figure 3: Renderings of the premaxilla and vomer of *Westlothiana*, NMS.1997.72.1. A, premaxilla in anterior view. B, premaxilla in posterior view. C, premaxilla and vomer in palatal view, illustrating contact between them. Scale bar = 1mm. Abbreviations as in Fig. 2.

2.2.3.2 Maxilla. Both maxillae are preserved. The right maxilla is exposed at the surface and the bone surface is significantly damaged, but the full extent of the bone is present. The left maxilla shows less damage anteriorly, and clearly preserves the bone surface, but it appears shorter than the right maxilla as preserved (Fig. 4). It is unclear whether this is due to the fact that the left maxilla is missing its posterior portion, or whether it represents a natural asymmetry between the left and right maxillae in the holotype specimen of *Westlothiana*.

The maxilla is the longest bone in the skull. Anteriorly it has a short, low contact with the premaxilla. Immediately posterior to this, the maxilla expands dorsoventrally to reach its greatest height at about

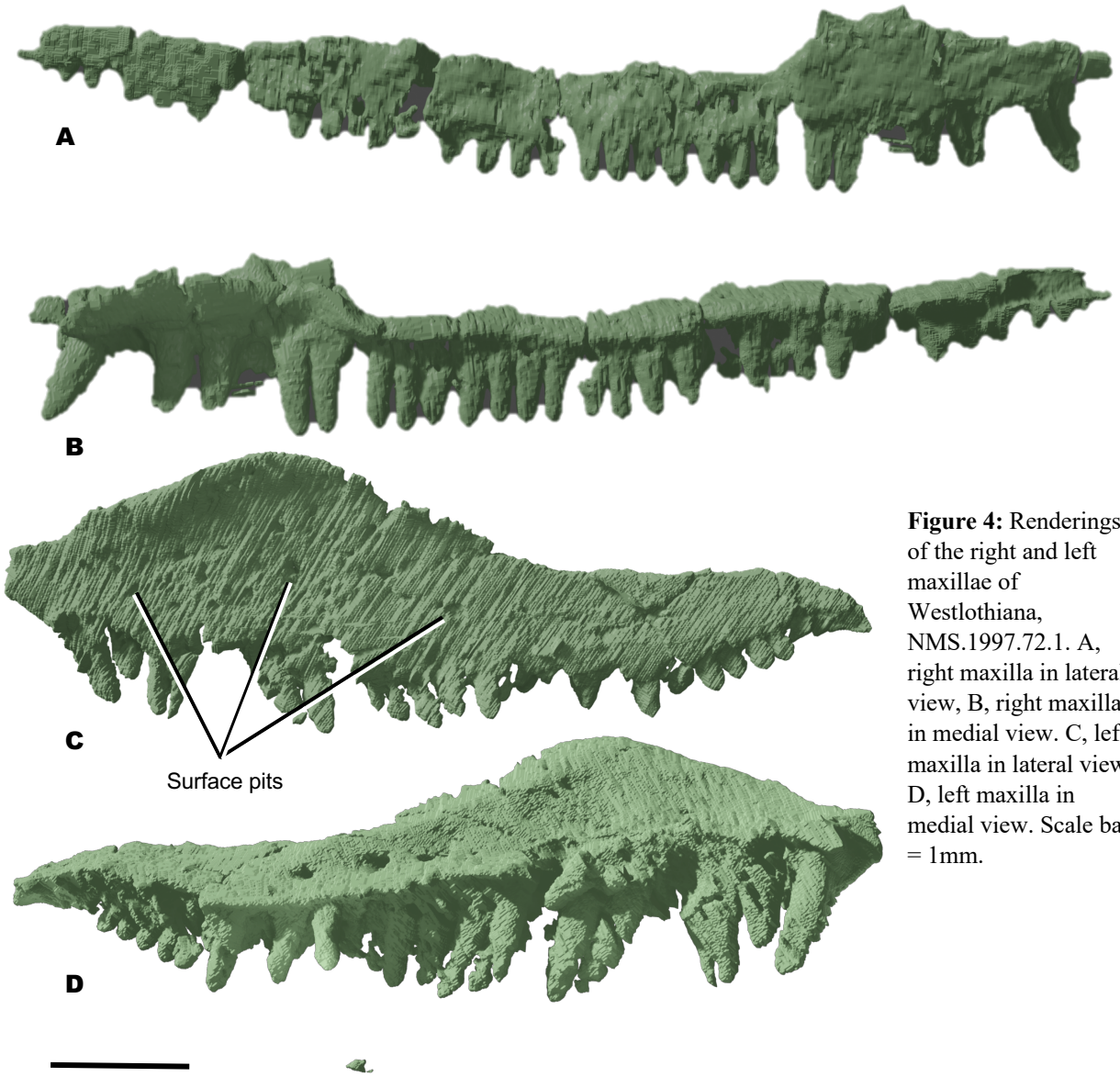


Figure 4: Renderings of the right and left maxillae of Westlothiana, NMS.1997.72.1. A, right maxilla in lateral view, B, right maxilla in medial view. C, left maxilla in lateral view, D, left maxilla in medial view. Scale bar = 1mm.

20% along the anteroposterior length (Fig. 2b, e), as is the case widely across stem tetrapods (Smithson 1982, Rawson, Porro et al. 2021) and stem amniotes including anthracosaurs (Panchen 1977, Holmes 1989) and seymouriamorphs (Klembara 1997, Klembara and Ruta 2005). This contrasts with most microsaurs, in which the peak of dorsoventral height is positioned more posteriorly, closer to the midpoint (Carroll and Gaskill, 1978). The maximum height of the maxilla is relatively low, at just under one quarter of the skull height at the same point. The maxilla of NMS.1990.72.1 is not expanded into the distinct dorsal process present in the microsaur *Pantylus* (Carroll and Gaskill, 1978) and a small number of early crown amniotes (e.g. Romer et al. 1940, Olson et al. 1968, Langston & Reisz 1981, Reisz et al. 2009). Posterior to the dorsal peak, the maxilla tapers gradually to its

posterior point, which is approximately at the level of the posterior margin of the orbit. The ventral margin of the maxilla is approximately straight.

The medial surface of the maxilla is slightly expanded into a narrow alveolar shelf. Thirty two to thirty four tooth alveoli are present on the right maxilla, with twenty-six blunt, conical, peg-like teeth preserved which steadily decrease in size towards the posterior end of the bone. There are just twenty eight teeth on the left maxilla, but it is possible that this count is incomplete if the posterior portion of this bone is missing (Fig. 5a, b). This count of at least thirty-two maxillary alveoli in NMS.1990.72.1 is considerably greater than in most lepospondyls (Clack 2012). Microsaurs typically have 19 to 24 teeth, although a small number, including *Pantylus cordatus* and *Euryodus dalyae*, possess approximately 10 (Carroll and Gaskill, 1978, Gee et al. 2021). Nectrideans possess between eight and 20 teeth (Douthitt 1917, Beerbower 1963, Milner and Ruta 2009, Milner 2018). Aïstopods possess a more comparable number of teeth to *Westlothiana*, approximately 30 maxillary teeth, although this is still smaller than the tooth count in NMS.1990.72.1. The tooth count in NMS.1990.72.1 is also considerably higher than the tooth count in diadectomorphs, in which the greatest observed number, in *Orobates pabsti*, is 20 (Berman et al. 2004). The tooth count in NMS.1990.72.1 is instead more similar in number to *Silvanerpeton miripedes*, which possesses about 35 teeth (Ruta and Clack 2006), or the protorothyrids *Hylonomus lyelli* (35; Carroll, 1964) and *Paleothyris acadiana* (35 to 41; Carroll, 1969).

The left maxilla shows approximately eight small, irregularly arranged, shallow pits on its lateral surface (Fig. 5c). This morphology is unlike most of the bones in the skull of NMS.1990.72.1, and is only observed in the maxilla and the dentary. Shallow pits, but no grooves, is similar to the condition seen in some anthracosaurs, particularly *Anthracosaurus russelli* (Panchen, 1977), but in these taxa the pits are far more extensive and numerous, covering most of the skull. It is also similar to *Captorhinus kierani* (DeBraga, Bevitt et al. 2019) in which shallow pits of a similar nature are also observed, but are restricted to the premaxilla.

2.2.3.3 Lacrimal. The right lacrimal is almost complete. Its anterodorsal and orbital margins are partially damaged, but the overall morphology can be discerned. Only the ventral portion of the left lacrimal is preserved.

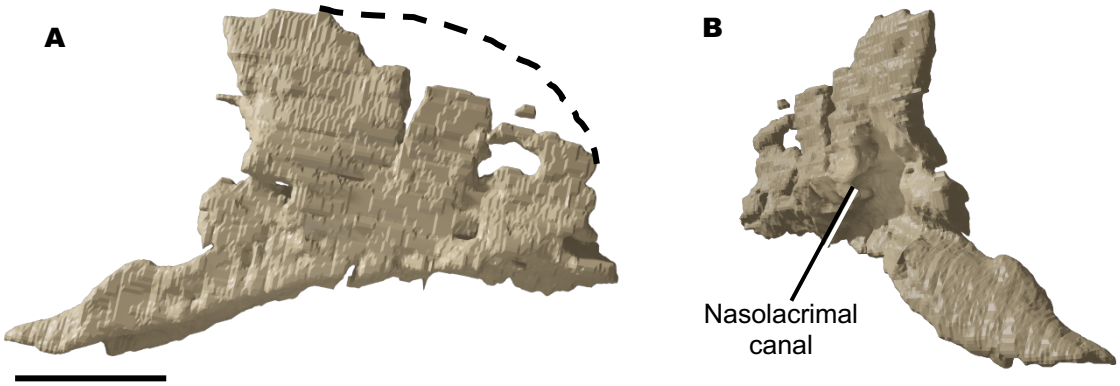


Figure 5: Renderings of the right lacrimal of Westlothiana, NMS.1990.72.1. A, lateral view, B, posteromedial view. Scale bar = 1mm.

The anterior portion of the lacrimal consists of a sheet of bone that is dorsoventrally broad and extends anteriorly to the external naris. This anterior part of the lacrimal consists of a thin sheet of bone dorsally, that is thickened ventrally to enclose the anterior portion of the nasolacrimal canal. The orbital margin of the medial surface is incomplete, and it is unknown if the nasolacrimal canal bifurcated posteriorly as it does in crownward stem amniotes and early crown amniotes (e.g. Carroll, 1964; Ford and Benson, 2019) (Fig. 5b).

The posteroventral part of the lacrimal is expanded into a long ventral orbital ramus that contributes to around one quarter of the ventral orbital margin. The ventral surface of this ramus articulates with the dorsal surface of the maxilla. The entire ventral ramus is thickened transversely, reaching twice the mediolateral thickness of the nasolacrimal canal (Fig. 5b). Posterodorsally, the main body of the lacrimal tapers to form a short but distinct dorsal orbital ramus, triangular in shape and much shorter than the ventral orbital ramus. A ventral orbital ramus of the kind observed in *Westlothiana* is widespread, and is present in temnospondyls (Milner & Sequeira, 1993; Arbez et al., 2022), *Silvanerpeton miripedes* (Ruta and Clack 2006), captorhinids (Fox and Bowman 1966, Reisz et al. 2016), protorothyrids (Carroll 1964, Carroll 1969), some reptiles (Reisz et al. 2007, Modesto et al. 2015), seymouriamorphs (Klembara 1997, Klembara and Ruta, 2005) and most lepospondyls (e.g. Carroll and Gaskill 1978, Pardo et al. 2017). A dorsal orbital process, however, is far less widespread but is present widely across microsaurs (Carroll & Gaskill 1978, Andrews and Carroll, 1991, Gee et

al. 2019), and a small number of crownward stem amniotes including *Paleothyris acadiana* (Carroll 1969) and captorhinids (Fox and Bowman 1966, Reisz et al. 2016).

2.2.3.4 Prefrontal. Both prefrontals are relatively well preserved in NMS.1990.72.1. The prefrontal is subrectangular in shape with its anteroposterior length roughly four times longer than its maximum transverse width. It contacts the nasal anteriorly, the lacrimal anteroventrally, the frontal dorsally and the postfrontal at its posterior tip. The prefrontal forms one quarter of the dorsal margin of the orbit. It gently narrows in transverse width towards both the anterior and posterior ends, but does not widen into a distinct flange on either end. This relatively simple prefrontal morphology, lacking any distinct flanges or expansions, is very similar to some microsaurs including *Cardiocephalus sternbergi* (Carroll and Gaskill 1978), as well as diadectomorphs (Berman et al. 1998, 2004), captorhinids (e.g. Fox and Bowman 1966, Reisz et al. 2016) and protorothyrids (Carroll 1964, 1969). The ratio of the anteroposterior length and dorsoventral width of the prefrontal in microsaurs (Carroll and Gaskill 1978), captorhinids (e.g. Fox and Bowman 1966, Reisz et al. 2016) and protorothyrids (Carroll 1964, 1969) is also similar to the ratio of these dimensions in the prefrontal of NMS.1990.72.1. However, the prefrontal of diadectomorphs is considerably wider relative to its length, and the prefrontal also makes a larger contribution to the orbit in diadectomorphs (Berman et al. 1998, 2004).

The dorsal margin of the prefrontal in NMS.1990.72.1 is thickened posteriorly to form a triangular shelf. This shelf articulates with the postfrontal, obscuring the frontal from making an orbital contribution (Fig. 2b, e). A contact between the prefrontal and postfrontal is also present in seymouriamorphs (Klembara 1997, Klembara & Ruta, 2005) and diadectomorphs (Berman et al. 1998, 2004). However, this contact is not present, and instead the frontal contributes to the orbital margin, in amniote taxa crownwards of diadectomorphs (e.g. Carroll 1969, Berman et al. 1995, Reisz & Dilkes 2003).

2.2.3.5 Nasal. Parts of both nasals are present. However, both nasals have undergone extensive damage and are very fragmentary (Fig. 2a, d), and detailed descriptions are not possible. The arrangement of bones in the snout suggests that the nasals would have been relatively large, quadrangular elements, approximately twice as long anteroposteriorly as wide mediolaterally. The

preserved material shows a small amount of curvature, and indicates that the nasals would have been oriented almost vertically at the anterior tip of the snout but curved posteriorly so that they were oriented almost horizontally at their articulation with the frontals (Fig. 2b, e).

2.2.3.6 Frontal. Both frontals are almost completely preserved. The left frontal has some minor cracks, and is missing a small portion posteriorly. The right frontal also shows some small amounts of damage, and the anteromedial one-third is missing. The right frontal is also somewhat wider than the left frontal. This may be a result of crushing during the preservation of the left frontal, or represent the genuine morphological condition. This, combined with the missing portion of the right frontal, result in the two frontal bones appearing asymmetrical. A full reconstruction of the frontal is nonetheless possible, with the description of the anterior third of the bone based solely on the left frontal.

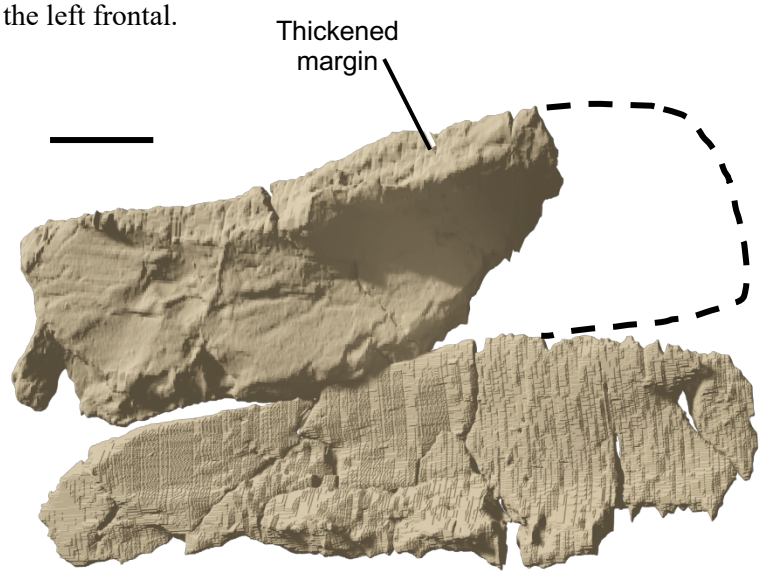


Figure 6: Renderings of the frontals of Westlothiana, NMS.1990.72.1 in ventral view. Anterior is oriented towards the right. Scale bar = 1mm.

The frontals are the longest bones of the skull roof, slightly anteroposteriorly longer than the parietals and several times longer than the nasals. They are subrectangular in shape, with their maximum anteroposterior length approximately three times greater than their maximum transverse width. The frontals contact the nasals along the anterior margin, the prefrontal for the anterior one-third of the lateral margin, the postfrontal for the remainder of the lateral margin, and the parietals posteriorly. The right frontal slightly overlaps the left frontal at the interfrontal suture. It is unclear if this is due to disarticulation of the specimen or represents the anatomical condition as it would have been in life.

The anterolateral ventral margin of the right frontal is thickened slightly, and the ventral surface of the right frontal is very gently concave. The left frontal shows no curvature, although it is damaged.

2.2.3.7 Parietal. Both parietals are well preserved, although they are divided between the part and counterpart slabs. The parietals are the widest elements in the skull, together making up the entire transverse width of the skull at their widest point, having expanded laterally to fill the space that would be occupied by the intertemporal and supratemporal in early diverging stem amniotes such as anthracosaurs (Panchen 1977, Holmes, 1989), *Gephyrostegus bohemicus* (Klembara et al. 2014) and seymouriamorphs (Klembara 1997, Berman et al. 2000, Klembara and Ruta 2005), in all of which the parietals are mediolaterally narrower than in *Westlothiana*. The parietals in *Westlothiana*, based on NMS.1990.72.1, are approximately one-and-a-half times longer anteroposteriorly than they are transversely wide. They reach their maximum width in their posterior two-thirds. The lateral margins of the parietals turn anteromedially anterior to their maximum width, from where their transverse width decreases to the same width as the frontals by the point of contact with the frontals. This anteromedially turned margin is concave along its suture with the postfrontals.

Transversely wide parietals, similar to those of NMS.1990.72.1, are also present in most amniotes crownwards of seymouriamorphs, in which the temporal series is also reduced, as the intertemporal is lost and the supratemporal occupies a posterior position. The parietals also extend transversely across the whole skull width, as in *Westlothiana*, in most crownward stem amniotes and early crown amniotes including captorhinids (Fox and Bowman 1966, Reisz et al. 2015, 2016), protorothyrids, (Carroll 1964, 1969) basal synapsids (e.g. Berman et al. 1995, Reisz et al. 2009) and parareptiles including *Belebey vegrandis* (Reisz et al. 2007). The width of the parietals of *Westlothiana* is also similar to the tranversely expanded parietals of microbrachomorph microsaurs (Carroll and Gaskill 1978).

The narrowing of the anterior portion of the parietals seen in *Westlothiana* is also similar to some basal amniotes including *Petrolacosaurus kansensis* (Reisz 1977), *Archaeovenator hamiltonensis* (Reisz and Dilkes 2003) and *Varanosaurus acutirostris* (Berman et al. 1995). It is less similar to microsaurs. In non-microbrachomorph microsaurs the parietals narrow in transverse width

in the anterior one-third, but less sharply than in *Westlothiana* (Carroll and Gaskill 1978, Gee et al. 2019, 2021) and in microbrachomorph microsaurs the parietals do not narrow in the anterior third (Carroll and Gaskill 1978).

A small pineal foramen is present. It is considerably smaller than the proportional size of the pineal foramen in diadectomorphs (Berman et al. 1998, 2004) and many synapsids (Reisz et al. 2009, Brocklehurst et al. 2016, Mann & Paterson 2020), in which the pineal foramen can be more than 25% of the interparietal suture length (Gauthier et al. 1988, Ford & Benson 2019). Instead, the pineal foramen in NMS.1990.72.1 is approximately 15% of the anteroposterior length of the interparietal suture. The condition in *Westlothiana* is similar to that of most lepospondyls (Carroll and Gaskill 1978, Pardo et al. 2017, Milner 2018) as well as stem amniotes including seymouriamorphs (Klembara 1997, Klembara and Ruta 2005), *Gephyrostegus bohemicus* (Klembara et al. 2014), *Chroniosaurus dongusensis* (Clack and Klembara 2009) and anthracosaurs (Panchen 1977, Holmes 1989). The pineal foramen is positioned anterior to the midpoint of the interparietal suture, with the posterior margin being slightly anterior to the midpoint, as is the case in captorhinids (Fox and Bowman 1966, Reisz et al. 2016) as well as seymouriamorphs (Klembara 1997, Klembara and Ruta 2005) and most lepospondyls (Beerbower 1963, Carroll and Gaskill 1978, Gee et al. 2019) apart from aistopods (e.g. Pardo et al. 2017).

2.2.3.8 Postparietal. The right postparietal is well preserved. The left postparietal is not identified. The postparietal is close to square in shape, and is only slightly anteroposteriorly shorter than it is transversely wide (Fig. 2a, d). It is a simple, dorsoventrally thin sheet of bone and is flat along its entire surface. It is therefore restricted entirely to the skull roof, and lacks any contribution to the occipital region. This is the case in most stem tetrapods (Smithson 1982, Rawson et al. 2021) and early stem amniotes including seymouriamorphs (Klembara 1997, Klembara et al. 2005), anthracosaurs (Panchen 1977, Holmes, 1989) and *Gephyrostegus bohemicus* (Klembara et al. 2014). It contrasts, however, with the condition in diadectomorphs (Berman et al. 1998, 2004), many basal crown amniotes (e.g. Berman et al. 1995, Reisz & Dilkes, 2003), and most microsaurs (Carroll and Gaskill 1978) in which the postparietal contributes strongly to the occiput.

2.2.3.9 Supratemporal. NMS.1990.72.1 clearly retains a separately ossified supratemporal. Only the right supratemporal is preserved, and has been rotated transversely so that it is not articulated with the adjacent tabular, and the lateral edge faces slightly ventrally. However, it shows no other damage and the margins are well formed. The presence of a supratemporal in NMS.1990.72.1 contrasts with the absence of a supratemporal in most lepospondyls (Clack 2012, Schoch 2014) including microsaurs (Carroll and Gaskill 1978, Gee et al. 2019, 2021) and nectrideans (Douthitt 1917, Beerbower 1963, Milner and Ruta 2009, Milner 2018). The aïstopods *Lethiscus stocki* (Pardo et al. 2017) and *Oestocephalus* (Carroll 1998) are the only lepospondyls in which the supratemporal is also present. Similarly to *Westlothiana*, a supratemporal is also present in earlier stem amniotes, including seymouriamorphs (Klembara 1997, Klembara and Ruta 2005), anthracosaurs (Panchen 1977, Holmes 1989), *Chroniosaurus dongusensis* (Clack and Klembara 2009) and *Gephyrostegus bohemicus* (Klembara et al. 2014), as well as crownward stem amniotes and early crown amniotes, including protorothyrids (Carroll 1964, 1969) and captorhinids (Fox and Bowman 1966, Reisz et al. 2016).

The supratemporal is a subrectangular, anteroposteriorly elongate element in *Westlothiana*. It maintains a relatively constant transverse width along its anteroposterior length, being only slightly wider in the posterior half. It is almost three and a half times anteroposteriorly longer than mediolaterally wide, and in this respect is similar to many crownward stem amniotes and basal synapsids, including the captorhinid *Euconcordia cunninghami* (Reisz et al. 2016), protorothyrids (Carroll 1964, 1969), *Petrolacosaurus kansensis* (Reisz 1977), *Varanosaurus acutirostris* (Berman et al. 1995) and *Haptodus garnettensis* (Laurin 1993). It is also similar to the condition in aistopods, in which the supratemporal is similarly elongate (Carroll 1998, Pardo et al. 2017).

The supratemporal of NMS.1990.72.1 is restricted entirely to the skull roof and does not contribute at all to the occiput, resembling the plesiomorphic condition observed in anthracosaurs (Panchen 1977, Holmes 1989), *Chroniosaurus dongusensis* (Clack and Klembara 2009), *Gephyrostegus bohemicus* (Klembara et al. 2014) and seymouriamorphs (Klembara 1997, Klembara and Ruta 2005). This contrasts with the condition in amniotes and crownard stem amniotes, including diadectomorphs (Berman et al. 1998, 2004), captorhinids (Fox and Bowman 1966, Reisz et al. 2016),

protorothyrids (Carroll 1964, 1969) and crown amniotes including both synapsids (e.g. Berman et al. 1995, Reisz and Frobisch 2014) and some reptiles (e.g. Gow 1972, 1974) in which the supratemporal contributes at least partially to the occiput.

In *Westlothiana*, the supratemporal is positioned partially dorsally and partially laterally, being positioned at the junction between the dorsal skull roof and the lateral cheek, and thus contributing, along with the tabular, to the posterolateral corner of the skull table. The supratemporal occupies a similar lateral position along the posterior skull margin, at the corner of the skull table, in crownward stem amniotes and early crown amniotes including diadectomorphs (Berman et al. 1998, 2004), araeoscelids (Reisz 1977, Reisz et al. 1984), *Paleothyris acadiana* (Carroll 1969), *Archaeovenator hamiltonensis* (Reisz and Dilkes 2003) and many synapsids (e.g. Reisz et al. 2009, Brocklehurst et al. 2016). This is unlike deeper stem amniote taxa including seymouriamorphs (Klembara 1997, Klembara and Ruta 2005) and *Gephyrostegus bohemicus* (Klembara et al. 2014), in which the supratemporal is positioned more anteriorly, and is also unlike microsaurs, in which a large tabular occupies the entirety of the posterolateral corner of the skull (Carroll and Gaskill 1978, Carroll et al. 1991, Gee et al. 2019).

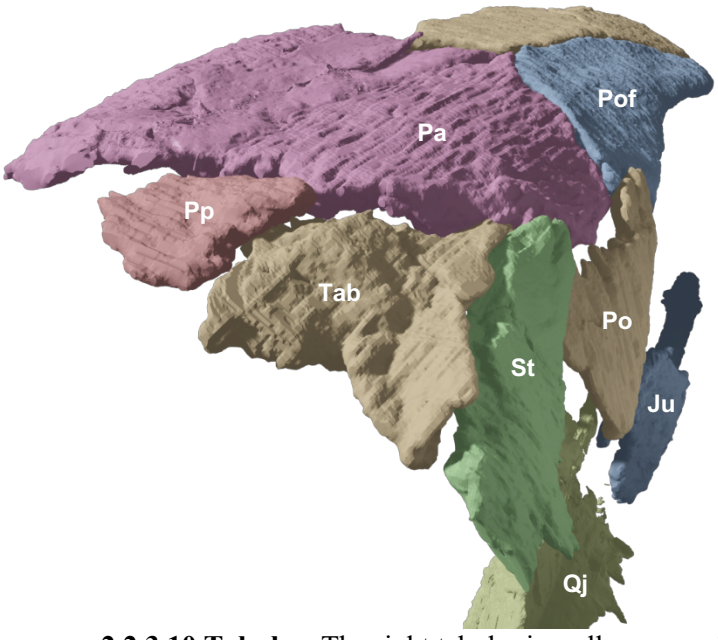


Figure 7: Rendering of the temporal region of Westlothiana, NMS.1990.72.1 in postero-dorso-lateral view (i.e. above and behind the back, right corner of the skull), demonstrating the relationship of the different bones of the temporal region. Abbreviations as in Fig. 2.

2.2.3.10 Tabular. The right tabular is well preserved and mostly intact, although it shows a small amount of damage to its posteromedial tip. The left tabular has not been identified. The tabular is an irregularly shaped element, but is overall squat and robust, and approximately as long anteroposteriorly as wide mediolaterally. Anteriorly it forms a rounded, semicircular process that fits

between the supratemporal and parietal. Medially, the tabular contacts the postparietal and laterally it contacts the supratemporal, where it contributes to the posterolateral corner of the skull table along its margin with the supratemporal (Fig. 2a, d).

The tabular is embayed posteriorly to form separate posterior and lateral processes. The lateral process articulates with the supratemporal. The posterior process is rounded posteriorly and forms a very short "tabular horn", which projects as a dorsoventrally thickened shelf dorsal to the occiput, in the same dorsoventral plane as the dorsal skull roof. These horns closely resemble those in some stem tetrapods, including *Baphetes* (Beaumont 1977) as well as some stem amniotes including anthracosaurs (Panchen 1977, Homes 1989), *Silvanerpeton miripedes* (Ruta and Clack 2006), and to a lesser extent, *Gephyrostegus bohemicus* (Klembara et al. 2014) in which the tabular horns are positioned similarly but extend further posteriorly. Diadectomorphs also possess a similar, very small posterior expansion (e.g. Berman et al. 1998), though these differ slightly as the tabular is positioned on the occipital surface. The tabular horns of *Westlothiana* are unlike the much larger horns in diplocaulid nectrideans (Douthitt 1917, Beerbower 1963, Milner 2018).

2.2.3.11 Postfrontal. Both postfrontals are preserved. The left postfrontal is complete posteriorly, but the anterior two thirds of the bone show extensive damage and the margins are incomplete. The right postfrontal is almost completely intact, and other than a single crack is fairly completely preserved.

The postfrontal is a relatively large bone in *Westlothiana*. It is anteroposteriorly long, at about 40% of the total anteroposterior skull length, and is also 40% as transversely wide as it is long. A large postfrontal, comparable to the size of the postfrontal in *Westlothiana*, is present in microsaurs (Carroll and Gaskill 1978). The postfrontal in *Westlothiana* is anteroposteriorly longer than the postfrontal in stem amniote taxa including *Gephyrostegus bohemicus* (Klembara et al. 2014) and seymouriamorphs (Klembara 1997, Klembara and Ruta 2005), but the postfrontal in these taxa is similar in transverse width to the postfrontal in *Westlothiana*. The postfrontal in *Westlothiana* is larger than crownward stem amniotes including diadectomorphs (Berman et al. 1998, 2004) and captorhinids (Fox and Bowman 1966, Reisz et al. 2016). It is gently crescentic, comprising most of

the dorsal margin of the orbit, and contacting the prefrontal anteriorly, the frontal and parietal laterally, and the postorbital posteriorly.

The posteriormost margin of the postfrontal is embayed along its contact with the postorbital, forming a large, concave notch. A similar notch in the postfrontal along its contact with the postorbital is present in most synapsids (e.g. Berman et al. 1995, Reisz et al. 2009, Brocklehurst et al. 2016). A notch very similar to the condition in *Westlothiana* is also present in the basal microsaurs *Tuditanus punctulatus*, *Asaphestera intermedia*, *Hapsidopareion lepton* (Carroll and Gaskill 1978) and *Llistrofus pricei* (Gee et al. 2019) although in these taxa the concavity is broader than in *Westlothiana*.

2.2.3.12 Postorbital. Both postorbitals are preserved. Neither shows extensive damage, but both show a small amount of damage around the margins.

The postorbital is a small, quadrangular element that contacts the postfrontal and parietal dorsally, the supratemporal posterodorsally, the squamosal posteriorly and posteroventrally, and the jugal ventrally. It also contributes to the orbit along its anterior margin, taking up around a quarter of the dorsal half of the orbit margin. The postorbital is approximately twice as anteroposteriorly long as tall dorsoventrally.

The anterodorsal corner of the postorbital is raised into a short, rounded process that is received by the notch in the postfrontal (Fig. 2b, e). As such, moving anteriorly, the dorsal margin becomes directed somewhat dorsally, before curving anteroventrally towards the orbit, resulting in an overall sinusoidal anterodorsal margin. A sinusoidal dorsal margin of the postorbital has been associated with microsaurs (Carroll and Gaskill 1978) and is present widely across them. However, a similarly shaped margin is also widely present across most synapsids (e.g. Romer et al. 1940, Berman et al. 1995, Modesto 1995, Brocklehurst et al. 2016). A similarly shaped anterodorsal margin is present in *Petrolacosaurus kansensis*, in which the margin extends into a distinct process, but in *Petrolacosaurus* it is positioned in between the postfrontal and parietal, instead of articulating within a concavity in the postfrontal (Reisz 1977) as it does in *Westlothiana*.

2.2.3.13 Jugal. The right jugal is completely preserved and realtively undamaged. The left jugal has not been identified. The jugal consists of a main body that is relatively dorsoventrally deep,

consisting of approximately one-third of the skull height. Projecting from the main body of the jugal are an anterior suborbital ramus, and a posterodorsally projecting ramus. The suborbital ramus is anteroposteriorly long, comprising most of the ventral orbit margin, and articulates at a short contact with the lacrimal, preventing the maxilla from contributing to the orbit margin. The suborbital ramus is dorsoventrally shallow, and is approximately six times longer than it is dorsoventrally tall. It remains a consistent height along almost the entire length, and only tapers to a point at its anterior tip.

Posterior to the suborbital ramus, the jugal expands significantly in dorsoventral depth. A large, rounded process extends posterodorsally from the expanded region, and thus the posteroventral margin of the jugal is strongly concave along its contact with the squamosal and quadratojugal, with the overall slope of the margin oriented posterodorsally to anteroventrally. This is an unusual morphology, and is different from the triradiate posterior jugal margin that is widespread across early crown amniotes (e.g. Reisz 1977, Reisz et al. 2009, Ford and Benson 2019), or the relatively straight margin that is either vertical or gently sloping anterodorsally to posteroventrally, in captorhinids (Fox and Bowman 1966, Reisz et al. 2016) and protorothyrids (Carroll 1964, 1969), most diadectomorphs (Romer 1946, Berman et al. 1998), and many early diverging stem amniotes including anthracosaurs (Panchen 1977, Holmes 1989), *Gephyrostegus bohemicus* (Klembara et al. 2014) and seymouriamorphs (Klembara 1997, Klembara and Ruta 2005). The condition in *Westlothiana* is more similar to the condition in the microsaurs *Hapsidopareion lepton*, *Cardiocephalus sternbergi* (Carroll and Gaskill 1978) and *Euryodus dalyae* (Gee et al. 2021) in which the posterior margin of the jugal slopes anteroventrally to posterodorsally. However, in these microsaurs, the posterior margin is relatively straight or even slightly convex, quite unlike the strongly concave margin of *Westlothiana*.

2.2.3.14 Squamosal. Both squamosals are partially preserved, but neither is well preserved or complete. The left squamosal is very poorly preserved, and is only identified as a few fragmentary bone pieces. The right squamosal is better preserved. It is broken into two parts, a smaller dorsal part and a larger ventral part. The dorsal part is mostly complete. The ventral part, however, is incomplete along its ventral margin, and much of the ventral portion of the bone is lost. As such, descriptions of the relationship of the squamosal and quadratojugal are not possible.

What remains of the squamosal is a large, plate-like element of thin bone that contributes to most of the cheek. Posteriorly it appears to taper towards a point, but it is likely that this is a result of preservation and does not represent the original morphology.

2.2.3.15 Quadratojugal. Neither quadratojugal has been identified in NMS.1990.72.1.

2.2.4 Palate

All palatal elements are at least partially preserved in NMS.1990.72.1, and only the left pterygoid shows significant damage, allowing for an almost complete palatal reconstruction. As noted in Smithson et al. (1993), the dorsal surface of part of the right side of the palate can be observed through the orbit on the surface of the part of NMS.1990.72.1, but the ventral surface of these elements is mostly embedded in matrix or covered by other bones in the physical specimen, as is the entirety of the vomers and the anterior portion of the palatines. The left side of the palate is preserved directly underneath the skull roof elements, and thus was not visible in the original study of the specimen.

The internal naris is elongate and is approximately four times longer than wide. It is enclosed by the premaxilla, maxilla, palatine and vomer. The anterior margins of the palatines are deeply embayed, enclosing the posterior one-third of the internal nares (Fig. 2c, f).

2.2.4.1 Vomer. Both vomers are preserved, but the right vomer is the more complete of the two. As such, this description will be primarily based on the right vomer. The vomer is an elongate element, more than three times longer than its maximum width. Overall the vomer is subrectangular, although it bulges in the anterior half, and the lateral margin of the posterior two-thirds is gently concave along its margin with the internal naris. The anterior one-quarter of the vomer is rounded and bulbous. The margin that contacts the premaxilla is convex and fits into the concave vomerine facet on the premaxilla medial shelf (Fig. 3c). The dorsoventral thickness of the vomer thins posteriorly from roughly its midlength, towards its contact with the palatine. Posteriorly to the anterior bulge, the vomer remains a consistent mediolateral width for most of the length of the bone. In the posterior one-fifth of the bone, the lateral margin is deflected posteromedially to contact the palatine along a short, straight margin, and therefore extends more posteriorly on the medial side, resulting in the posterior

fifth of the vomer tapering to a posterior point. The posterior portion of the lateral margins of both vomers are somewhat damaged, and thus the nature of their contact with the pterygoids cannot be completely discerned (see pterygoid for further discussion).

The entire ventral surface of the vomer is covered extensively in fine denticles. The vomer also bears a clear pair of enlarged fangs at the anteroposterior midpoint and close to the lateral margin, similar in size to the largest maxillary teeth but two to three times the height of the surrounding denticles (Fig. 8a). Such a fang pair is similar to the condition in seymouriamorphs (Klembara 1997, Klembara and Ruta 2005) and *Gephyrostegus bohemicus* (Klembara et al. 2014), but is not found in crown amniotes (e.g. Gow 1972, Reisz 1977, Modesto 1995). An absence of palatal fangs is also noted to be a synapomorphy of lepospondyls (Clack 2012, Schoch 2014).

2.2.4.2 Pterygoid. The right pterygoid is well preserved, and is complete, although it shows some damage in the region of the basal articulation and thus the exact nature of the contact between the pterygoid and the parasphenoid is unclear (Fig. 10b). Only a small part of the left pterygoid is preserved, consisting of the quadrate process and a small region anterior to this. Nothing of the basal articulation or palatal ramus of the left pterygoid is retained.

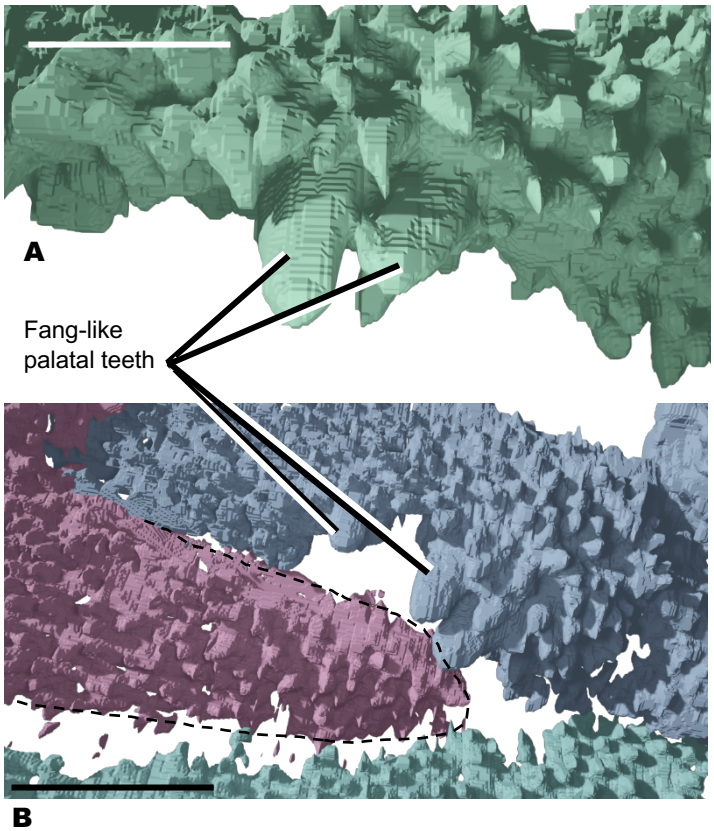
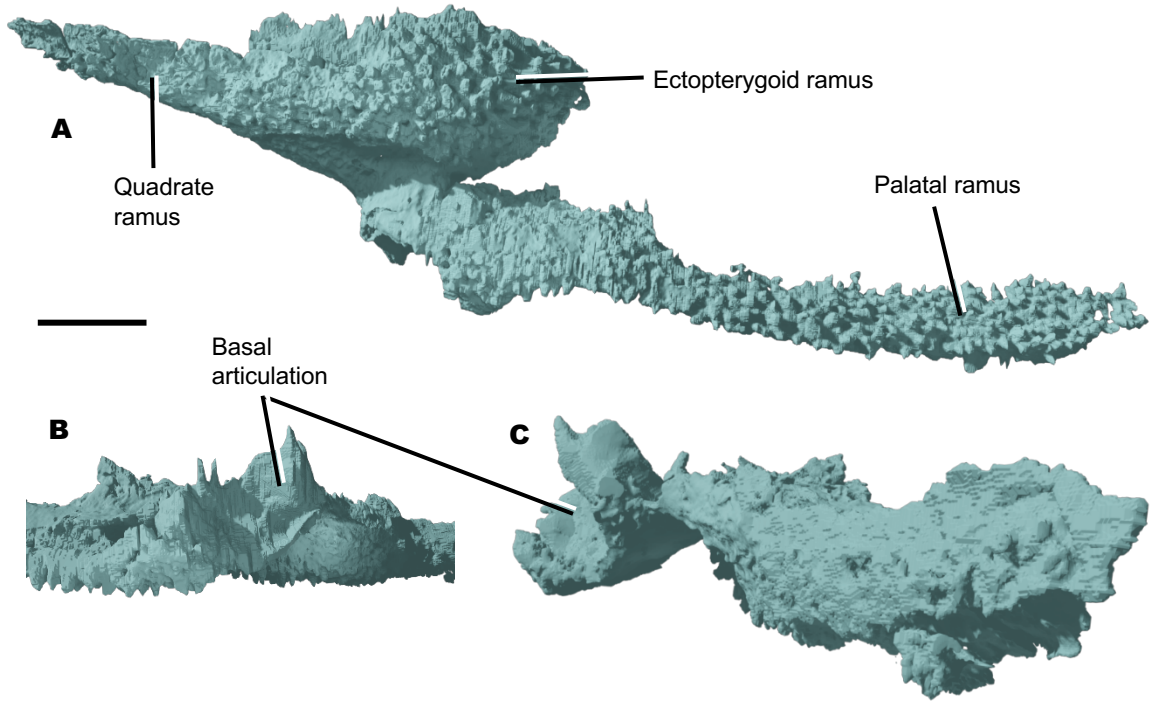


Figure 8 (left): Renderings of the palatal fangs of *Westlothiana*, NMS.1990.72.1. A, fangs of the vomer. B, fangs of the palatine. Dotted line indicates restored boundary of ectopterygoid. Scale bar = 0.5mm (A), 1mm (B).

Figure 9 (following page): Right pterygoid of *Westlothiana*, NMS.1990.72.1 A, ventral view, B, medial view in the region of the basal articulation, C, posterior view. Scale bar = 1mm (A), 0.5mm (B, C).



The pterygoid consists of a large, rounded, plate-like ectopterygoid ramus, a posteriorly directed quadrate ramus projecting from this plate, and an elongate palatal ramus projecting anteriorly from this plate. The size and orientation of the right palatal ramus indicates that the palatal rami would most likely have contacted their counterpart along the midline for a short distance anteriorly, as is also the case in most microsaurs (Carroll and Gaskill 1978, Gee et al. 2021), and many stem amniotes including seymouriamorphs (Klembara 1997, Berman et al. 2000) and *Gephyrostegus bohemicus* (Klembara et al. 2014), and diadectomorphs (Berman et al. 1998, 2004). The palatal ramus is also extremely narrow transversely, reaching one-eighth of the width of the palate at its widest point, comparable to most microsaurs (Carroll and Gaskill 1978) and diadectomorphs (Romer 1946, Berman et al. 2004) , but different to seymouriamorphs (Berman et al. 2000) and *Gephyrostegus bohemicus* (Klembara et al. 2014) in which the palatal ramus is substantially wider. The palatal ramus in NMS.1990.72.1 is also gently curved, with the concave surface facing laterally. The length of the palatal ramus indicates that it, at least, reached close to the posterior margins of the vomers, but the nature of the contact between the vomer and the pterygoid palatal ramus is uncertain and cannot be determined.

The pterygoid is deeply and sharply incised to accommodate the ectopterygoid, in between the anteromedial margin of the ectopterygoid ramus and the posterolateral margin of the palatal

ramus. The palatal ramus is inclined dorsolaterally-to-ventromedially, so that the ventral, tooth-bearing surface of the ramus is oriented partially laterally. The ventral surface of the ectopterygoid ramus is bulbous, bulging centrally. Therefore, the region between the palatal ramus and main body is V-shaped in anterior or posterior view, with the apex pointing dorsally (Fig. 9c).

Lateral to the posterior end of the palatal ramus, the ectopterygoid ramus is oval in shape and tapers posteriorly to form the quadrate process. The pterygoid lacks any kind of transverse flange and is therefore similar to lepospondyls (Carroll and Gaskill 1978, Pardo et al. 2017, Milner 2018) and anthracosaurs (Panchen 1977, Holmes 1989) that also lack a transverse flange of the pterygoid, unlike most crown and crownward stem amniotes including seymouriamorphs (Klembara 1997, Berman et al. 2000, Klembara and Ruta 2005), *Gephyrostegus bohemicus* (Klembara et al. 2014), diadectomorphs (Romer 1946, Berman et al. 1998, 2004), captorhinids (Fox and Bowman 1966, Reisz et al. 2015, 2016), protorothyrids (Carroll 1964, 1969), araeoscelids (Reisz 1977, Reisz et al. 1984), synapsids (e.g. Bolt & Scott 1995, Brocklehurst et al. 2016) and reptiles (e.g. Gow 1974, Reisz & Dilkes, 2003) in which a transverse, flange-like expansion extends from the lateral surface of the ectopterygoid ramus. The quadrate ramus projects posteriorly and slightly laterally from the posterolateral corner of the ectopterygoid ramus. It is long, and narrows to a point posteriorly. It is flattened dorsally into a thin, vertical shelf, but the medial surface is rounded and lacks the arcuate flange of more crownward stem and crown amniotes including the captorhinid *Euconcordia* (Reisz et al. 2016), the basal reptile *Orovenator* (Ford and Benson 2019) and the basal synapsid *Eothyris* (Reisz et al. 2009). Instead, the quadrate ramus in *Westlothiana* is more similar to the quadrate ramus in *Captorhinus* (deBraga et al. 2019) and *Paleothyris* (Carroll 1969), which lack an arcuate flange.

The ventral surface of the pterygoid is extensively covered in denticles. The entire palatal ramus and main body of the bone are covered. There is also a small patch of denticles as far back as the quadrate ramus, a condition that is only observed in *Caerorachis* (Ruta, Milner et al. 2001) amongst the taxa included in this analysis.

2.2.4.3 Palatine. The right palatine is completely preserved and shows very little damage. The left palatine is only partially preserved, and lacks most of its posterior half. It is a sub-triangular element in shape, widest close to the anterior margin, and gently tapering along the whole length of

the bone. The medial margin of the palatine contacts the pterygoid along the anterior one-third of its length and the ectopterygoid in the posterior two thirds. The palatine also contacts the ectopterygoid posteriorly, the maxilla laterally and the internal naris and vomer anteriorly.

The contact of the palatine with the vomer is short and straight. Immediately lateral to this contact, the palatine is deeply incised by almost one quarter of the length of the bone to accommodate the internal naris. The incision is strongly concave, with the two sides forming an acute angle at the posterior end of the internal naris so that the incision is V-shaped. The condition in NMS.1990.72.1 is similar to some early-diverging microsaurs (e.g. *Asaphestera*, Carroll and Gaskill 1978), and closely resembles that of crownward stem amniotes such as *Paleothyris* in shape and size (Carroll 1969), but is unlike the shallower concavities of *Gephyrostegus bohemicus* (Klembara et al. 2014), seymouriamorphs (e.g. Klembara 1997), or the diadectamorph *Limnoscelis* (Romer 1946). Lateral to the posteriormost quarter of the internal naris the palatine forms a short maxillary ramus that is dorsoventrally deep in the area of its contact with the maxilla. A short canal runs anteroposteriorly along the entirety of this ramus, similar to that of *Orovenator* (Ford and Benson 2019) (Fig. 10b). Such a canal, considered to carry the maxillary artery and nerve (Evans 1980), may be widespread, but is infrequently documented as its observation requires exceptional preservation, and thus conclusions cannot be drawn about the presence of such a canal in a larger number of taxa. Unlike in *Orovenator*, the canal does not branch. The posterior half of the palatine is a dorsoventrally flat sheet of bone that gently tapers in ventral view towards its posterior end.

As with the other palatal elements, the entire ventral surface of the palatine is covered in denticles. There is also a pair of fang-like teeth, a little over twice the height of the surrounding denticles and similar in size to the vomerine fangs, located close to the medial margin, and approximately at the anteroposterior midlength of the palatine (Fig. 10a). A third tooth is present, posterior to the fang pair, separated by a gap of roughly the diameter of one tooth. Dentition of this kind is similar to the condition in stem amniotes stemwards of lepospondyls, including seymouriamorphs (Klembara 1997, Klembara and Ruta 2005) and *Gephyrostegus bohemicus* (Klembara et al. 2014). Dentition of this kind also somewhat resembles the condition in anthracosaurs, in which a similar number of fangs are present in similar positions. However, unlike in

NMS.1990.72.1, *Gephyrostegus bohemicus* and seymouriamorphs, in which the fangs are equivalent in size to the marginal dentition, the fangs in anthracosaurs are far larger than the marginal dentition (Panchen 1977, Holmes 1989). Fangs on the palatine are not present in any lepospondyls (e.g. Carroll and Gaskill 1978, Pardo et al. 2017, Milner 2018, Gee et al. 2019, 2021) or crownward stem and early crown amniotes (e.g. Romer 1946, Fox and Bowman 1966, Carroll 1969, Reisz 1977, Bolt and Scott 1995, Ford and Benson 2019).

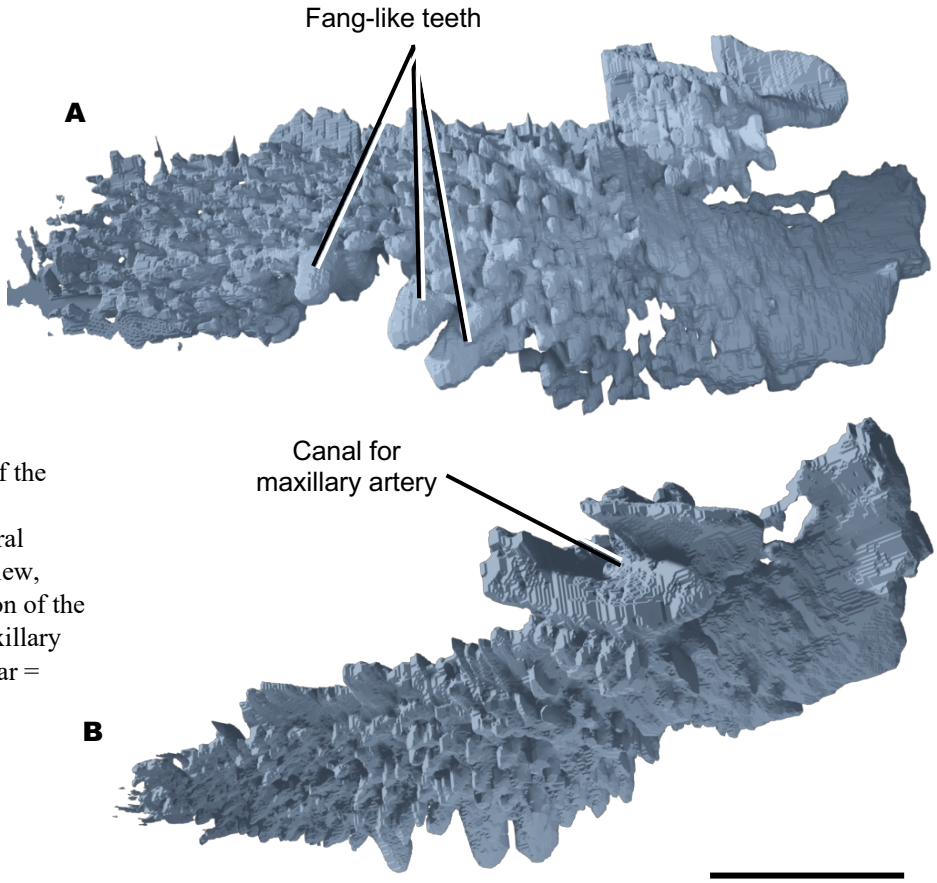


Figure 10: Renderings of the palatine of *Westlothiana*, NMS.1990.72.1. A, ventral view; B, posterolateral view, demonstrating the position of the canal that carries the maxillary artery and nerve. Scale bar = 1mm.

2.2.4.4 Ectopterygoid. The right ectopterygoid is the better preserved of the two elements. It is nearly completely preserved and has only a small amount of damage to the posterior margin. The left ectopterygoid is also well preserved and nearly complete, with some damage close to the midpoint of the lateral margin.

The ectopterygoid is broadly L-shaped, with a larger anterior ramus and a shorter, robust lateral ramus. It is a simple, dorsoventrally thin, sheet-like element and its anterior process slopes gently ventrally towards the medial margin, giving the ventral surface an overall concave shape. As with the other palatal elements, the ectopterygoid is entirely covered in denticles. However, no fangs or larger teeth of any kind are present on the ectopterygoid, as is the case in seymouriamorphs (Klembara and Ruta 2005, Klembara 1997) or anthracosaurs (Panchen 1977, Holmes 1989) but not in *Gephyrostegus bohemicus*, which possesses a pair of fangs on the ectopterygoid (Klembara et al. 2014).

2.2.5 Braincase

2.2.5.1 Parasphenoid. The parasphenoid is well preserved and is mostly complete. The cultriform process is intact, as is the anterior portion of the parasphenoid plate. There is, however, damage laterally on both sides in the area of the basal articulation, at the intersection of the cultriform process and parasphenoid plate. The posterior half of the parasphenoid plate is also incomplete, with some fragmentary material preserved on the right side in ventral view, but the posterior margins are not discernable.

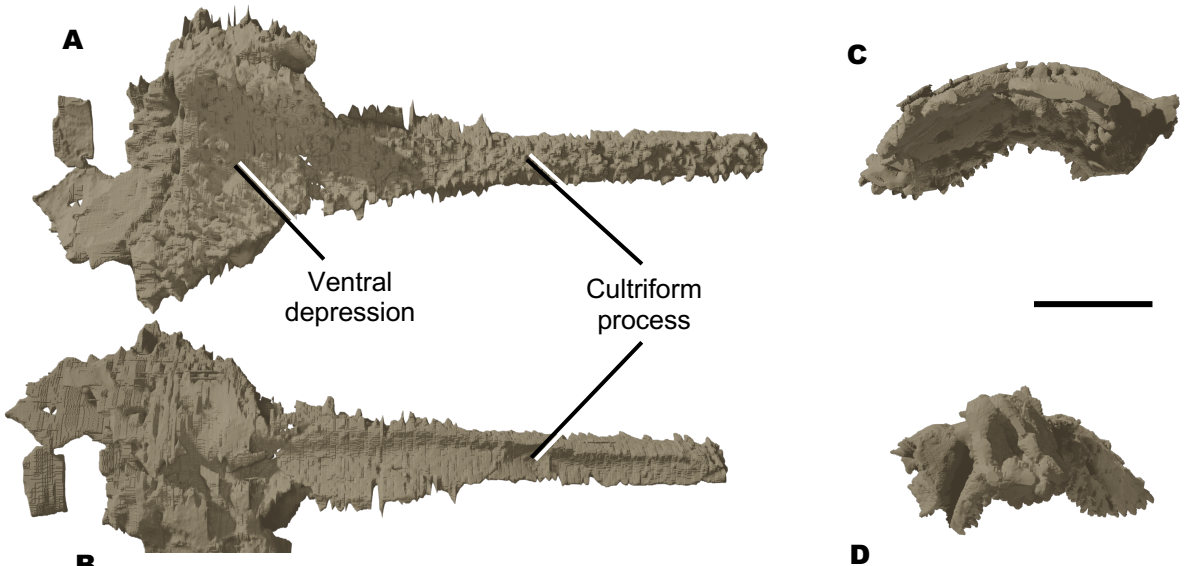


Figure 10: Renderings of the parasphenoid of *Westlothiana*, NMS.1990.72.1. A, ventral view; B, dorsal view; C, posterior view; D, anterior view. Scale bar = 1mm.

The cultriform process is fairly thick both dorsoventrally and transversely, and is anteroposteriorly short, reaching just halfway along the anteroposterior length of the skull and not approaching the vomers. The posterior quarter is mediolaterally expanded, but otherwise the process is parallel sided and ends in a rounded tip. It therefore lacks the distinctly tapering triangular shape that is present in *Gephyrostegus bohemicus* (Klembara et al. 2014), seymouriamorphs (Klembara 1997, Klembara and Ruta 2005) and some early-diverging microsaurs (Carroll & Gaskill 1978, Huttenlocker et al. 2013, Gee et al. 2019). Immediately posterior to the cultriform process the parasphenoid plate expands transversely in width gently, so that the anterior portion of the plate is triangular in shape, but the shape of the whole plate cannot be observed due to damage to the posterior portion of the plate.

The ventral surface of the parasphenoid plate is concave, resulting in a single, median depression, similar to the kind that is observed in most stem and crown amniotes including *Anthracosaurus* (Panchen 1977), *Silvanerpeton* (Ruta and Clack 2006), the seymouriamorph *Discosauriscus* (Klembara 1997), diadectomorphs (Romer 1946) and several crown amniotes (e.g. Gow 1974, Laurin 1993, Berman et al. 1995), but not lepospondyls, in which this surface is flat. (e.g. Carroll and Gaskill 1978, Pardo et al. 2017, Milner 2018).

The entire ventral surface of the parasphenoid is covered in a shagreen of denticles, including the whole cultriform process, and what can be observed of the parasphenoid plate. Denticles on the cultriform process are widespread across stem tetrapods (e.g. Smithson 1982) including temnospondyls (Romer and Witter 1942, Arbez, Atkins et al. 2022) and many amniotes (Fox and Bowman 1966, Olson et al. 1968, Carroll 1969), but denticles on the parasphenoid plate are typically absent. *Westlothiana* has an unusually extensive covering of denticles, and such an extensive covering, with denticles on the parasphenoid plate, is only noted to be present although they are present in *Caerorachis* (Ruta et al. 2001) amongst the taxa included in this analysis.

2.2.5.2 Sphenethmoid. A small amount of fragmentary bone can be observed, preserved in NMS.1990.72.1 immediately below the skull roof. It is likely that this represents braincase material, indicating that *Westlothiana* had an ossified sphenethmoid. However, none of the morphology of the bone can be discerned.

2.2.5.3 Quadrate. Both quadrates are preserved in NMS.1990.72.1. The right quadrate preserves the overall morphology more completely, but has been heavily damaged and little of the original margins of the bone are present. The left quadrate is preserved in articulation with the left articular, and what remains is well preserved, but the dorsal and anterior portions are absent.

The posteroventral corner of the quadrate forms a bulbous condyle that articulates with the articular in the mandible (Fig. 13). Both anterior and anterodorsal to the condyle that quadrate is expanded into a sheet like plate that forms two distinct processes. It is unclear if these processes would have been separate, though, or if this is due to damage.

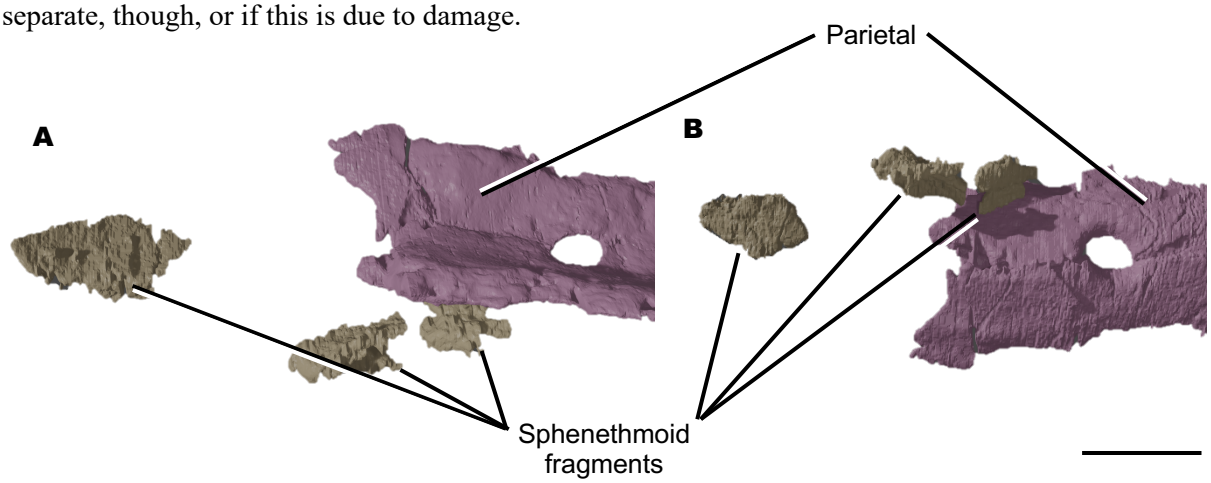
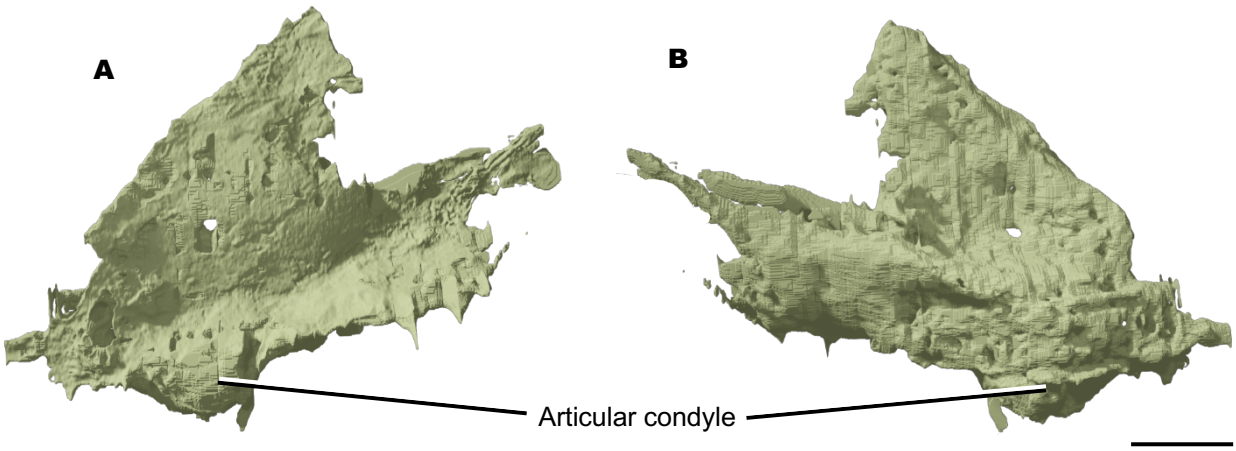


Figure 12 (Above): Renderings of the sphenethmoid fragments, and parietals, in the slab of the part of *Westlothiana*, NMS.1990.72.1, with all other bones removed to aid in visualisation of the sphenethmoid elements. A, dorsal view, B, ventral view. Scale bar = 1mm.

Figure 13 (Below): Rendering of the right quadrate of *Westlothiana*, NMS.1990.72.1. A, lateral view; B, medial view. Scale bar = 1mm.



2.2.6 Mandible

As described by Smithson et al. (1993), the right mandible is exposed in lateral view, although this exposed surface shows considerable damage. Smithson et al. (1993) noted the partial exposure of a single, denticulate coronoid. The full coronoid series is preserved in the right mandible, and the medial surface is revealed here for the first time through tomography. Smithson et al. (1993) also noted the exposure of the anterior end of the left dentary, but nothing else of the left lower jaw. The majority of the left mandible is present and complete, preserved below the plane of the skull roof, although the coronoid series is absent.

Contrary to Smithson et al. (1993), the ventral margin of the mandible is convexly curved along its entire length. This is unlike many later amniotes including *Paleothyris* (Carroll 1969), which has a straight ventral margin of the mandible and is the taxon that the mandible of *Westlothiana* was originally compared to. This overall shape seen in NMS.1990.72.1 closely resembles the mandible in anthracosaurs including *Archeria* (Holmes 1989), but is unlike most microsaurs in which the ventral margin is also often straight (Carroll and Gaskill 1978). In the posterior half of the jaw, there is a low but clear surangular crest. There is too much damage to the medial surface of both mandibles to determine if Meckelian fenestrae were present, as is the case in most stem and crown amniote taxa including anthracosaurs (Panchen 1977, Holmes 1989), seymouriamorphs (e.g. Berman et al. 2000) and diadectomorphs (e.g. Berman et al. 1998), or if Meckelian fenestrae were absent, as is the case in most microsaurs (Carroll and Gaskill 1978).

2.2.6.1 Dentary. The description of the dentary is based primarily on the left dentary, which is the more complete of the two. There is damage across a lot of the bone, particularly towards the ventral margin, and many fragments are missing, but the overall morphology can nonetheless be observed. The dentary is a relatively short element, comprising 56% of the length of the jaw. The dentary is relatively proportionally short and dorsoventrally deep, fewer than six times as long anteroposterioly as its dorsoventral depth, proportions that are very similar to most microsaurs (Carroll and Gaskill 1978). The dentary terminates posteriorly towards the anterior end of the surangular crest, and does not contribute to the peak of the surangular crest. In a unique condition, the

anterior part of the ventral margin is notched to accommodate the splenial. The ventral margin is not well preserved, but what remains, along with the shape of the angular, suggest that the ventral margin of the dentary of *Westlothiana* was not smooth. Instead, it appears to ascend posteriorly in distinct steps along its articulation with the angular, as is also the case in many lepospondyls (e.g. Carroll and Gaskill 1978, Andrews and Carroll 1991, Pardo et al. 2017) and in some captorhinids (Fox and Bowman 1966).

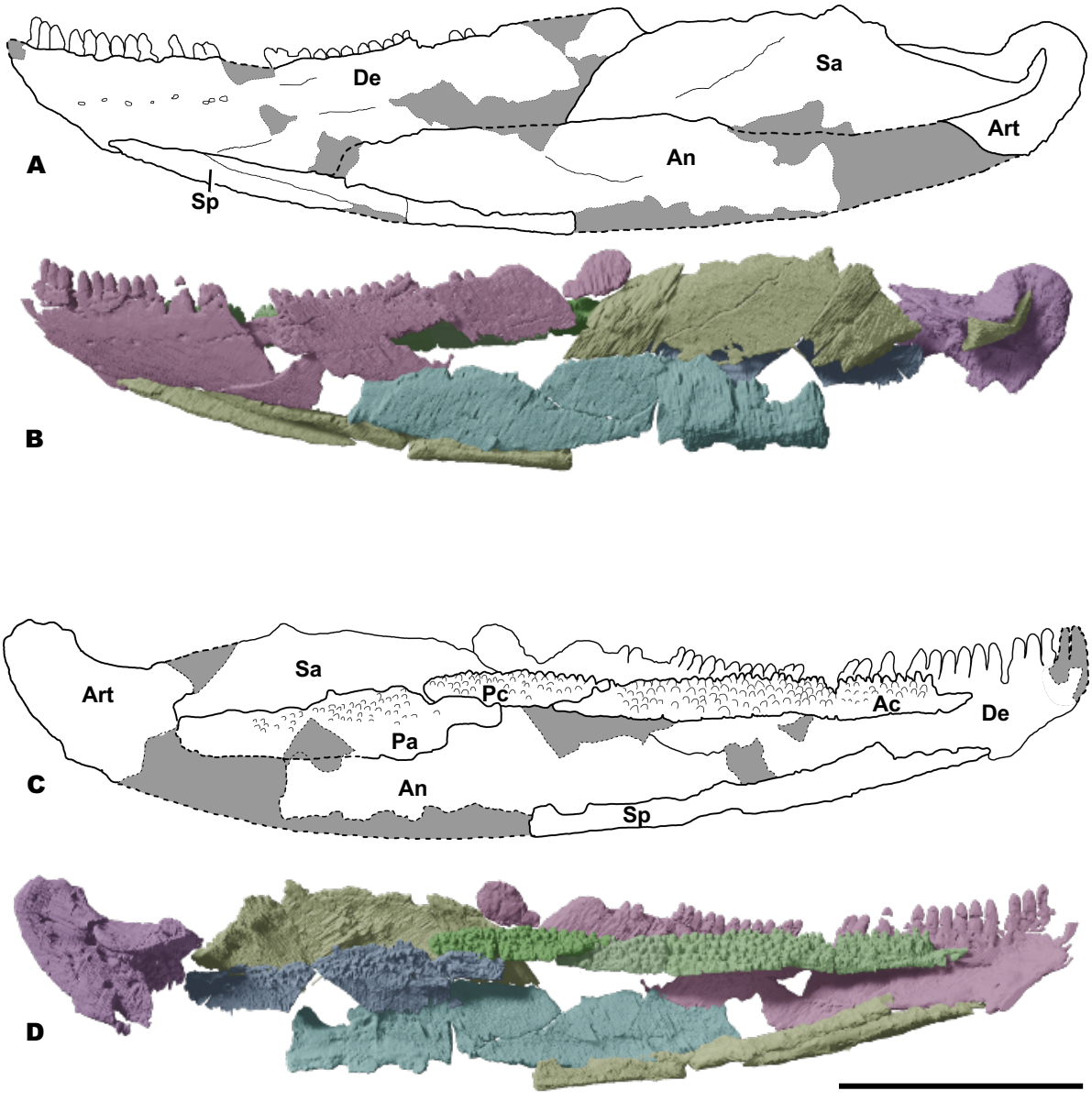


Figure 14: Composite mandible of *Westlothiana lizziae*, based on combining elements of the left and right mandibles of NMS.1990.72.1. A, reconstruction of mandible in lateral view; B, rendering of mandible in lateral view. C, reconstruction in medial view; D, rendering in lateral view. Abbreviations: Angular (An), Anterior Coronoid (Ac), Articular (Art), Dentary (De), Posterior Coronoid (Pc), Prearticular (Pa), Splenial (Sp), Surangular (Sa). Scale bar = 5mm.

On the lateral surface of the dentary, in the anterior half, are approximately seven or eight small foramina arranged in a single line (Fig. 14b). A small number of shallow sensory pits, extremely similar to those observed in NMS.1990.72.1 are also observed in the early diverging tuditanomorph microsaurs *Tuditanus* and *Asaphestera.* The limited number of foramina in NMS.1990.72.1 somewhat resemble, but are less extensive than, the larger pits in the microsaurs *Microbrachis* and *Hyloplesion* (Carroll and Gaskill 1978). The foramina in NMS.1990.72.1 are not as extensive as aquatic taxa in which an extensive mandibular covering of foramina are observed, including the anthracosaur *Archeria* (Holmes 1989), or taxa in which full lateral line canals are observed, including adelogyrinids (Andrews and Carroll 1991, Clack et al. 2019), and stem tetrapods including *Whatcheeria* (Rawson et al. 2021), *Pederpes* (Clack and Finney 2005) and *Greererpeton* (Smithson 1982). There are at least 33 alveoli preserved in the dentary, and there are 25 clearly preserved, blunt, conical, peg-like teeth on the dentary. The toothrow makes up roughly 80% of the dentary. The teeth steadily decrease in size from the anterior to the posterior ends of the toothrow.

2.2.6.2 Splenial/postsplenial. Only the left splenial is well preserved. It is heavily damaged. There is a crack between the anterior two thirds and posterior third, perpendicular to the long axis of the bone. There is also a crack running along the long axis of the bone for most of the anterior two thirds, so that the entire element is divided into three parts.

The splenial is a long element, extending from around the level of the sixth dentary alveolus almost to the posterior margin of the dentary. It does not participate in the mandibular symphysis. It is dorsoventrally narrow and broadly cylindrical in shape. The splenial also has a substantial lateral exposure. Smithson et al. (1993) described a single splenial element in *Westlothiana*, although this is uncertain. Due to the nature of the cracks, it is uncertain if the posterior third of the splenial documented here was a separate postsplenial like that of seymouriamorphs (e.g. Klembara 1997, Klembara and Ruta 2005) and some microsaurs including *Euryodus dalyae* (Gee et al. 2021), or if it is a fragment of the splenial separated by damage. A single splenial is present in crownward stem and early crown amniotes, including diadectomorphs (Romer 1946, Berman et al. 1998, 2004) *Paleothyris* (Carroll 1969), *Archaeovenator* (Reisz and Dilkes 2003) and *Varanosaurus* (Bolt and Scott 1995).

2.2.6.3 Angular. Both the left and right angular are preserved, although both also show substantial damage. As such, the overall morphology can be determined but the exact nature of the sutural surfaces remain uncertain. The angular is a sheet-like bone that maintains the same transverse thickness along its length. It is elongate and subrectangular in shape, and it is approximately five to seven times anteroposteriorly longer than dorsoventrally tall, depending on the uncertain posterior extent. It is deepest close to the midpoint, where it reaches marginally over half of the jaw depth, but does not significantly taper towards either end. It is a shorter element than as reconstructed in Smithson et al. (1993) at just 42% of the jaw length, as it was originally reconstructed at over half of the jaw length, but otherwise differs little from the original description.

Anteriorly, the angular extends to approximately the midpoint of the dentary tooth row. An angular extending to approximately the midpoint of the dentary tooth row is also present in many microsaurs (Carroll and Gaskill 1978), some other lepospondyls including *Acherontiscus* (Clack et al. 2019) and *Brachydectes* (Pardo and Anderson 2016), the stem amniote *Gephyrostegus bohemicus* (Klembara et al. 2014), the anthracosaur *Archeria* (Holmes 1989), and in sphenacodontid (Romer et al. 1940, Laurin 1993, Spindler 2016) and edaphosaurid (Modesto 1995) synapsids. The angular does not, however, extend as far anteriorly in seymouriamorphs (Klembara 1997, Berman et al. 2000, Klembara and Ruta 2005).

The angular does not reach the posterior end of the mandible, as it is prevented from doing so by a ventral projection of the articular (Fig. 14a, c). In most stem and early diverging crown amniotes, the angular reaches the posterior end of the mandible. However, the condition in *Westlothiana* is also observed in a small number of lepospondyls, including the microsaurs *Hapsidopareion* and *Llistrofus* (Carroll and Gaskill 1978, Gee et al. 2019) and the nectrideans *Diploceraspis* (Beerbower 1963) and *Keraterpeton* (Milner 2018), in the diadectomorphs *Diadectes abistus* (Berman et al. 1998) and *Orobates pabsti* (Berman et al. 2004), as well as in stem tetrapods (Smithson 1982, Clack and Finney 2005, Rawson et al. 2021).

2.2.6.4 Prearticular. The right prearticular is preserved, but is exposed laterally on the surface of the specimen, and has been damaged significantly. There is no trace of the left prearticular. Due to the level of damage, it is not possible to discern the dimensions or contacts of the prearticular.

Along the dorsal edge of the medial surface of the anterior two thirds of the prearticular, as preserved, is a row of denticles. Denticles on the prearticular are uncommon across stem and crown amniotes, temnospondyls and stem tetrapods, but are only observed in a small number of taxa including in the stem tetrapod *Whatcheeria* (Rawson et al. 2021), the stem amniote *Caerorachis* (Ruta et al. 2001) and the synapsid *Edaphosaurus* (Modesto 1995).

2.2.6.5 Coronoids. Nothing of the coronoid elements on the left lower jaw is preserved in articulation. A disarticulated element that may represent the left anterior coronoid is observed close to the left splenial. However, the entire coronoid series is well preserved in the right mandible, and shows little damage.

There are two coronoids present in NMS.1990.72.1 consisting of an anterior and posterior coronoid. A separately ossified middle coronoid is absent, although approximately one-third along the length of the anterior coronoid the bone narrows for a short section, which may indicate that the middle coronoid has become fused to the anterior coronoid. The absence of a separate middle coronoid is also observed in *Diadectes abistus* (Berman et al. 1998) and amniotes crownwards of diadectomorphs, including *Captorhinus* (Fox and Bowman 1966), *Araeoscelis* (Reisz et al. 1984), synapsids (e.g. Romer et al. 1940, Berman et al. 1995, Brocklehurst et al. 2016) and reptiles (e.g. Gow 1972, Reisz et al. 2007, Ford and Benson 2019). This is unlike earlier diverging stem amniotes, which retain three separately ossified coronoids, including anthracosaurs (Panchen 1977, Holmes 1989) and seymouriamorphs (Klembara 1997, Berman et al. 2000, Klembara and Ruta 2005).

Both coronoids are anteroposteriorly elongate, rod-like elements with gently tapered anterior and posterior ends. They are positioned dorsally in the mandible. They are a similar dorsoventral depth, and the anterior coronoid is considerably longer than the posterior coronoid. The anterior coronoid is ten times longer anteroposteriorly than dorsoventrally deep, and the posterior coronoid is approximately six times longer than it is deep. Such a dorsal position, combined with the narrow depth of the coronoids, results in the absence of a contact between the coronoids and the splenial, an unusual morphology that is observed only in *Westlothiana* and the lepospondyl *Acherontiscus* (Clack et al. 2019) amongst the taxa included in this analysis.

The medial surfaces of both coronoids are completely covered in a shagreen of denticles. Denticles on the coronoid series are observed in most stem amniotes including *Caerorachis* (Ruta et al. 2001), *Anthracosaurus* (Panchen 1977), seymouriamorphs (Klembara 1997, Berman et al. 2000, Klembara and Ruta 2005) and *Gephyrostegus bohemicus* (Klembara et al. 2014), as well as *Captorhinus* (Fox and Bowman 1966) and the diadectamorph *Limnoscelis* (Romer 1946). Denticles on the coronoids are absent, however, in most lepospondyls (e.g. Beerbower 1963, Carroll and Gaskill 1978).

2.2.6.6 Articular. Both articulars are present and are relatively well preserved. The left articular, in particular, shows very little damage, and is preserved in articulation with the quadrate and so is of very certain affinity.

The anterior portion of the articular forms the articulation with the quadrate. The anterior surface is expanded broadly to form a shallowly concave, dorsally facing cotyle. This surface is transversely wider than the posterior portion, and so expands both laterally and medially to the posterior portion to form two ridges that overhang the ventrolateral and ventromedial surfaces of the articular, and laterally the posteriormost portion of the surangular, where the surangular articulates with the ventral surface of the lateral ridge.

Posterior to the articulating surface, for about the same anteroposterior length as this surface, the articular forms a short, rounded retroarticular process. A retroarticular process is not present in stem amniote taxa that are stemwards of *Westlothiana* including anthracosaurs (Panchen 1977, Holmes 1989) and seymouriamorphs (Klembara 1997, Klembara and Ruta 2005) but is present widely across lepospondyls (Carroll and Gaskill 1978, Andrews and Carroll 1991, Milner 2018) and many amniotes (Fox and Bowman, 1966, Gow 1972, Berman et al. 1995). The retroarticular process is directed posterodorsally in *Westlothiana*.

2.3 Discussion

High-resolution propagation phase contrast synchrotron X-ray micro-computed tomography of the holotype specimen of *Westlothiana* has revealed substantial novel anatomical information of

previously poorly known or unknown regions of the skull, especially the circumorbital series, skull table, temporal region and palate. This has allowed for a significantly extended description of this important taxon, demonstrating anatomical features that are associated with various derived or plesiomorphic clades, particularly in the region of the circumorbital bones, the temporal region and the palate, all of which were previously poorly described. *Westlothiana* shows an unusual and enigmatic combination of plesiomorphic and derived traits, suggesting potential affinities with each of early amniotes, microsaurs, and stem amniotes including seymouriamorphs.

2.3.1 Potential synapomorphies of the circumorbital series

Certain aspects of the circumorbital bones that had phylogenetic significance were already known. In particular, it had been previously described that the prefrontal and postfrontal contacted above the orbit, in which *Westlothiana* resembles stem amniotes (e.g. Klembara 1997, Klembara and Ruta 2005) but not early crown amniotes (Carroll 1969, Berman et al. 1995, Reisz and Dilkes 2003). However, other anatomical areas of importance were unknown. The nature of the contact between the postorbital and postfrontal was unknown, as was the entire anterior part of the circumorbital series.

Presence of a lacrimal dorsal orbital process

The posterodorsal part of the lacrimal, along its contact with the orbit, is drawn out into a short but distinct process that tapers to a point. This is a synapomorphy of microsaurs (Carroll and Gaskill 1978). However, such as process is also present in the early diverging amniotes *Paleothyris* (Carroll 1969) and *Captorhinus* (Fox and Bowman 1966). The size and shape of the process in *Westlothiana* closely resembles the shape of the same process in these early amniotes.

The morphology of the postfrontal – postorbital contact

The morphology of this contact is described in my analysis by two characters, the presence or absence of a sigmoid dorsal margin of the postorbital, and the presence or absence of a distinct notch

in the posteroventral margin of the postfrontal to receive the sigmoid dorsal margin of the postorbital. The morphology of these two characters is closely related, and cannot be discussed separately.
In taxa that possess a sigmoid dorsal postorbital margin, the dorsal margin displays a distinct hump. Moving from posterior to anterior, the dorsal margin increases in dorsal height, then clearly curves ventrally towards the orbit. Often, as is the case in microsaurs, the curved margin of the postorbital is received by a concave margin of the postfrontal (Carroll and Gaskill 1978). However, in certain early amniote taxa, such as *Petrolacosaurus*, whilst the postorbital shows a sigmoid dorsal margin the peak of the curve is posterior to the postfrontal, and thus the postfrontal does not display a notch (Reisz 1977). Thus, the nature of the contact between the postorbital and postfrontal, as with the morphology of the lacrimal, result in a morphology of the circumorbital series of *Westlothiana* that strongly resembles that of microsaurs.

2.3.2 Potential synapomorphies of the skull table and temporal region

Much of the skull table of *Westlothiana* had been previously described, and many of the observations can be corroborated here. The great relative width of the parietals, which may indicate an affinity with amniotes (Smithson, Carroll et al. 1993), is supported by my reconstruction. I also corroborate the absence of an intertemporal, and the absence of an otic notch, both of which closely resemble and are indicative of an affinity to early amniotes (Fox and Bowman 1966, Carroll 1969, Reisz 1977), and a position crownwards of seymouriamorphs, anthracosaurs and *Gephyrostegus* (e.g. Panchen 1977, Holmes 1989, Klembara 1997, Klembara et al. 2005, 2014), in which an intertemporal and otic notch are present. I also corroborate the retention of a supratemporal. This contrasts microsaurs (Carroll and Gaskill 1978) and the majority of other lepospondyls, only excluding *Lethiscus* (Pardo et al. 2017) and *Oestocephalus* (Carroll 1998).

The temporal region of *Westlothiana* was originally described as being “advanced towards the amniote condition” (Smithson, Carroll et al. 1993). However, it was not known in great detail. I have revealed the temporal region more clearly than it was previously described, and thus several new anatomical features can be described that are of phylogenetic significance.

Supratemporal and tabular both contributing to skull table corner

In this condition, observed in *Westlothiana*, both the tabular and supratemporal make small and roughly equal contributions to the posterior margin of the skull, very close to the junction between the skull table and the cheek. This condition is associated with the clade consisting of amniotes and diadectomorphs. Amongst the taxa I have observed for this analysis, this condition is found exclusively in amniotes and diadectomorphs (e.g. Carroll 1964, Reisz 1977, Reisz et al. 1984, Berman et al. 1998).

Morphology of the supratemporal

Westlothiana possessed a particularly elongate supratemporal, in which the anteroposterior length was greater than three times the transverse width. This was previously suggested by the text in the original description (Smithson, Carroll et al. 1993), but the supratemporal was only exposed in section, and Smithson et al. **(**1993**)** acknowledged that it could be wider, reconstructing the bone as only just over twice as long as wide. Such an elongate supratemporal morphology is generally present in taxa that are commonly thought to be early crown amniotes, including many synapsids (e.g. Laurin 1993, Bolt and Scott 1995), *Petrolacosaurus* (Reisz 1977), the captorhinid *Euconcordia* (Reisz et al. 2016) and protorothyrids (Carroll 1964, 1969). However, it is not unique to these taxa and such an elongate supratemporal is also observed in aïstopods (Carroll 1998, Anderson 2002, Pardo et al. 2017) and *Discosauriscus* (Klembara 1997). Therefore, whilst the supratemporal morphology may indicate an affinity with amniotes this is certainly a trait that shows a degree of homoplasy. Nonetheless, the morphology of the supratemporal of *Westlothiana* is unlike that of stem amniotes including seymouriamorphs, *Gephyrostegus* and anthracosaurs. In these groups and taxa, the supratemporal is less anteroposteriorly elongate relative to the transverse width, and is typically no more than twice as long as wide (Panchen 1977, Holmes 1989, Klembara 1997, Klembara et al. 2005, 2014). This suggests that, if *Westlothiana* is a stem amniote, it is likely to be closely related to the amniote crown group.

Supratemporal contribution to occiput

When originally described, it was unclear if the supratemporal in *Westlothiana* had an occipital contribution (Smithson, Carroll et al. 1993). Here I show that the supratemporal was clearly restricted to the skull table in its entirety. Thus, the condition in *Westlothiana* is plesiomorphic relative to amniotes. A supratemporal contribution to the occiput is a synapomorphy of amniotes including and crownwards of diadectomorphs (e.g. Fox and Bowman 1966, Reisz et al. 1984, Laurin 1993, Reisz and Dilkes 2003, Berman et al. 2004). Although there are a small number of reversals in some synapsids (e.g. Campione and Reisz 2010, Brocklehurst et al. 2016) and parareptiles (e.g. Modesto et al. 2015), a supratemporal contribution to the occiput is exclusively found in amniotes and diadectomorphs.

Postparietal contribution to occiput

The original description of *Westlothiana* suggested that it was most likely that the postparietals were restricted to the skull table, but this was not certain (Smithson, Carroll et al. 1993). My reconstructions clearly demonstrate that the postparietals did not contribute to the occiput at all. A postparietal contribution to the occiput is found widely across both lepospondyls (e.g. Carroll and Gaskill 1978, Carroll 1998, Gee et al. 2019) and crown amniotes (e.g. Gow 1974, Reisz 1977, Bolt and Scott 1995, Berman et al. 2004) so *Westlothiana* is plesiomorphic relative to both of those clades in this regard.

2.3.3 Potential synapomorphies of the palatal region

The palate was previously poorly known in *Westlothiana*. This was particularly true of the anterior region of the palate, that was completely unknown. Many features of the palate of phylogenetic significance are newly revealed here. Overall, the palate shows a remarkably plesiomorphic morphology and is similar to some of the earliest diverging stem amniotes or even stem tetrapods.

The size of the ectopterygoid relative to the palatine

The ectopterygoid in *Westlothiana* is roughly equivalent in anteroposterior length to the palatine. This is extremely plesiomorphic, and most closely resembles the conditions found in stem-tetrapods, including taxa such as *Acanthostega* (Clack 1994, Porro, Rayfield et al. 2015) in which the ectopterygoid is the larger element, or stem-tetrapod taxa such as *Greererpeton* (Smithson 1982) in which the ectopterygoid and palatine are equivalent in length. This is also seen in temnospondyls (e.g. Milner and Sequiera 1993, Arbez et al. 2022). However, even the earliest diverging stem amniotes, the ectopterygoid is smaller than the palatine. This includes embolomeres (Panchen 1977, Holmes 1989), seymouriamorphs (Klembara 1997, Berman et al. 2000, Klembara and Ruta 2005) and *Gephyrostegus* (Klembara et al. 2014), a trend that was continued into both lepospondyls (e.g. Carroll and Gaskill 1978, Gee et al. 2019) and early amniotes (e.g. Modesto 1995, Reisz and Dilkes 2003, Reisz et al. 2007). Thus, the ectopterygoid of *Westlothiana* is curiously plesiomorphic for the derived position it tends to occupy in phylogenetic analyses and this may represent a reversal.

Absence of a pterygoid transverse flange

The lateral margin of the ectopterygoid ramus of the pterygoid in *Westlothiana* is smooth, and is not expanded into any kind of flange at all. A transverse flange of the pterygoid is present in most stem amniotes and crown amniotes, crownwards of anthracosaurs (e.g. Reisz 1977, Klembara 1997, Berman et al. 1998, 2004, Clack and Klembara 2009). Moreover, a tooth row on the pterygoid transverse flange is a distinctive synapomorphy of amniotes crownwards of diadectamorphs (Smithson, Carroll et al. 1993). In many stem amniotes, including seymouriamorphs and *Gephyrostegus*, a short, rounded flange is present in the same position (Klembara 1997, Berman 2000, Klembara and Ruta 2005). This flange differs from that of crown amniotes; it is not as large as the flange in amniotes, it is not in the same orientation as it is in amniotes, nor is it toothed, but a flange in the area is clearly present. Lepospondyls, however, all lack any kind of pterygoid transverse flange (Beerbower 1963, Carroll and Gaskill, 1978, Carroll 2000, Pardo and Anderson 2016). The lack of a flange of any kind in *Westlothiana* suggests that it may have a close phylogenetic relationship with lepospondyls.

Presence of palatal fangs and denticles

Westlothiana possesses palatal fangs on the vomer and palatine. In this respect, the dentition of *Westlothiana* does not resemble the dentition in lepospondyls. Lepospondyls have long been known to lack any kind of palatal fangs (Carroll 2000), and this absence is a key synapomorphy of the clade.

Palatal fangs are plesiomorphic, and are known in stem tetrapods including *Greererpeton* (Smithson 1982), and stem amniotes including embolomeres (Panchen 1977, Holmes 1989) and *Gephyrostegus* (Klembara et al. 2014), seymouriamorphs (Klembara 1997, Berman et al. 2000, Klembara and Ruta 2005) and *Chroniosaurus* (Clack and Klembara 2009).

However, in *Westlothiana,* palatal fangs were absent on the ectopterygoid. Amongst stem amniotes in which palatal fangs are retained on the vomer and palatine, the absence of palatal fangs on the ectopterygoid is only present in seymouriamorphs (Klembara 1997; Berman et al. 2000, Klembara and Ruta 2005) and *Chroniosaurus* (Clack and Klembara 2009).

Westlothiana also has a very extensive covering of denticles on the palate. Although denticles are known across a wide variety of taxa and do not show a particularly clear phylogenetic pattern, the extent of denticles on the palate of *Westlothiana* is more extensive than in almost any taxa examined in this analysis, and is only similar to *Caerorachis* (Ruta et al. 2001). *Westlothiana* even possessed denticles on the quadrate ramii of the pterygoid. Unfortunately the quadrate ramii are unknown in *Caerorachis*, but otherwise *Westlothiana* can be considered autapomorphic for this trait.

2.3.4 Conclusion

Westlothiana appears to occupy a somewhat transitional morphology, demonstrating traits of earlier stem amniotes, lepospondyls, and amniotes crownwards of diadectomorphs. The circumorbital bones resemble those of microsaurs, particularly the lacrimal, which has a dorsal process like that of most microsaurs, but is uncommon in other early tetrapod taxa. The prefrontal and postfrontal contact each other above the orbit, which is plesiomorphic relative to amniotes. The temporal region and skull

table, however, share key features with early amniotes. The parietals are extremely wide, and a supratemporal is retained, unlike in microsaurs. The supratemporal is elongate, and the supratemporal and tabular contact each other at the corner of the skull table, as in early amniotes. Neither the supratemporal or tabular, or the postparietal, contribute to the occiput, in a condition that is plesiomorphic relative to amniotes. The palate, too, is highly plesiomorphic relative to amniotes. The ectopterygoid is large, the pterygoid lacks a transverse flange, and palatal fangs are observed on the vomer and palatine, like those observed in seymouriamorphs and gephyrostegids. The palate is also highly denticulate, including denticles on the quadrate rami of the pterygoid, a condition not observed in other stem-amniotes or early crown amniotes.

Chapter 3: The postcranial skeleton of *Westlothiana*

4.1 Introduction

4.1.1 The specimens of *Westlothiana*

The holotype specimen of *Westlothiana lizziae* (NMS 1990.72.1) is relatively complete and mostly articulated, lacking only the posterior part of the tail. Unfortunately, the manner of cleavage between the part and counterpart in the holotype has resulted in all of the bones in the postcranial skeleton being split between the part and counterpart, so that no original bone surface is exposed in the specimen. The bone surface of one short series of vertebrae was revealed by preparation, but no other external bone surfaces are exposed.

A second specimen has been referred to *Westlothiana lizziae* (NMS G 1991.47.1). It was collected from unit 76 at the East Kirkton Quarry (Smithson, Carroll et al. 1993), separated by six units from the holotype (collected from unit 82; Smithson, Carroll et al. 1993). NMS G 1991.47.1 is hereafter referred to as the second specimen. It is more disarticulated than the holotype, and it is also approximately 50% larger than the holotype, based on the elements that can be directly compared (Table 1 in Smithson, Carroll et al. 1993). Unfortunately, the second specimen does not preserve any cranial material.

The second specimen was assigned to *Westlothiana* (Smithson, Carroll et al. 1993) on the basis of similarities in the structure of the vertebrae, which in both specimens are gastrocentrous with large, wedge-shaped intercentra and fused neural arches, and similarities in the pelvis in that the puboischiadic plate is notably long in both specimens. The second specimen was also assigned to *Westlothiana* due to similarities in the pes; both specimens were described to have five distal tarsals and a phalangeal formula of 2, 3, 4, 5, 4 (Smithson, Carroll et al. 1993). Smithson et al. (1993) also noted similarities in the highly distinctive, elongate and oval-shaped morphology of the scales between the type and second specimen. The limb proportions of the second specimen are also similar to the holotype, including the unusually small size of the forelimbs and hindlimbs relative to the body (Table 2 in Smithson, Carroll et al. 1993), and the proportionally small size of the forelimb relative to

the hindlimb, in which the forelimb is only approximately half the length of the hindlimb. Almost the entire postcrania is present in the second specimen, and it exposes far more details of the surface of the individual elements than can be observed in the holotype.

The second specimen provides the basis for most of the original descriptions of the postcrania of *Westlothiana lizziae* (Smithson, Carroll et al. 1993). However, it is important to acknowledge that it is a possibility that the two specimens assigned to *Westlothiana* do not belong to the same taxon. They were preserved in different units, and the vertebral count was at least four vertebrae higher in the second specimen than the type, as described by Smithson et al. (1993). Following the novel anatomical descriptions of the postcranium of the holotype that I present below, based on micro-CT scan data, more differences between the specimens have been revealed (see below for further discussion). As such, it is possible that not all of the information in the original descriptions of the postcrania of *Westlothiana* can be attributed with confidence to the taxon represented by the holotype specimen.

Many features of the postcrania of *Westlothiana lizziae* were noted by Smithson et al. (1993) to be of particular importance in deciphering the phylogenetic relationships of the taxon. Smithson et al. (1993) described that most features of the vertebrae "closely resemble those of Upper Carboniferous and Lower Permian amniotes", and they observed that the vertebrae were most similar to protorothyrids, and to *Captorhinus* (Smithson, Carroll et al. 1993). They also observed, however, that a presacral vertebral count of 36 in *Westlothiana* (see description below for details) is higher than in the earliest amniotes. The slender morphology of the humeri and femora (see description below for details) was also described to most closely resemble protorothyrids such as *Hylonomus* (Carroll 1964) and *Paleothyris* (Carroll 1969).

Amniotes are united by the synapomorphy of having just two proximal tarsal elements, an astragalus and a calcaneum (Laurin 1998). When first reported, the holotype of *Westlothiana* was suggested to be an amniote as it was thought to have just two proximal tarsals in the relatively well-preserved right pes (Smithson 1989). The second specimen, however, was conclusively observed to have three proximal tarsals (Smithson, Carroll et al. 1993). It was noted in the full description (Smithson, Carroll et al. 1993) that, following further study of the holotype, it was possible that there

was a small bone representing a third tarsal, but its identity could not be confirmed with confidence, and whether or not the type possessed two or three proximal tarsals has thus far not been clearly resolved.

Another key region in uncovering phylogenetic relationships that could not previously be observed was the atlas-axis complex. The morphology of the atlas-axis complex plays a particularly important role in defining microsaurs. Two synapomorphies of the atlas-axis define the group; an odontoid process, and a lateral expansion of the anterior articulating surface (Carroll and Gaskill 1978). *Westlothiana* was noted to have a potentially close phylogenetic relationship with microsaurs in the original description (Smithson, Carroll et al. 1993), and some later phylogenetic analyses (e.g. Clack et al. 2019) have also recovered *Westlothiana* as a close relative of microsaurs. However, so far, this crucial region of *Westlothiana* has not been visible.

Here, I provide a novel description of the postcranial anatomy of the holotype specimen of *Westlothiana lizziae*, NMS.1990.72.1, based on micro-CT data, and present a three-dimensional reconstruction of many aspects of the postcranial skeleton. I provide updated, and expanded, descriptions of the appendicular skeleton of the holotype, particularly concerning the humerus, femur and pes, and I reveal the atlas-axis complex of *Westlothiana lizziae* for the first time. Newly observed anatomical features shed new light on the phylogenetic relationships of *Westlothiana*.

3.2 Anatomical Descriptions

3.2.1 Preservation. As described by Smithson et al. (1993), most of the postcranial skeleton of NMS.1990.72.1 is preserved in articulation, although only the first nine caudal vertebrae are preserved, and the rest of the tail is missing. However, all the preserved bones are split between the part and counterpart, and no original bone surfaces are visible in the specimen (Fig. 1). Micro-tomography therefore reveals substantial new information concerning the atlas-axis complex, forelimb and hindlimb.





Figure 1: The holotype specimen of *Westlothiana*, NMS.1990.72.1. A, counterpart; B, part. Scale bar = 1cm. Following page, drawing of the part, reproduced from Smithson et al. (1993). Abbreviations: Angular (a), Articular (art), Caudal vertebrae (c1-5), Clavicle (CL), Caudal Rib (CR), Dentary (d), Ectopterygoid (ect), Femur (F), Frontal (f), Fibula (FI), Humerus (H), Haemal arch (He3-6), Intercentrum (IC), Ilium (IL), Ischium (IS), Jugal (j), Lacrimal (l), Maxilla (m), Nasal (n), Parietal (p), Postfrontal (pf), Premaxilla (pm), Postorbital (po), Postparietal (pp), Prefrontal (prf), Pubis (PU), Quadrate (q), Quadratojugal (qj), Radius ®, Surangular (sa), Scapulocoracoid (SC), Splenial (sp), Squamosal (sq), Supratemporal (st), Tabular (t), Tibia (T), Ulna (U), Vomer (v). Photographs by Rebecca Harry.



3.2.2 Axial skeleton.

The cervical and trunk vertebrae are extensively preserved in both specimens referred to *Westlothiana lizziae*, and although many individual vertebrae show damage, almost the entire presacral vertebral column is preserved in both specimens. The cervical vertebrae were observed by Smithson et al., (1993) to be present but they are poorly exposed in the type specimen. Due to poor preservation of the anterior vertebral column, it is unclear how many cervicals were present. Nonetheless, based on the articulated type specimen, Smithson et al., (1993) estimated a total presacral count of 36, including the atlas-axis complex. We confirm this count here, as, even with the poor exposure of some of the vertebrae, all of the presacral vertebrae can be counted and there are no gaps in the vertebral column (Fig. 1c). This contrasts with a count of at least 40 presacral vertebrae in the second specimen (Smithson, Carroll et al. 1993).

The vertebral column is elongate in *Westlothiana*. The presacral vertebral count is most similar to the elongate anthracosaur *Archeria* (38 presacral vertebrae, Romer 1957), and to the elongate microsaurs *Cardiocephalus* and *Microbrachis* (37 and 38 presacral vertebrae respectively, Carroll and Gaskill 1978). The presacral vertebral count in *Westlothiana* is considerably higher than that of most stem-amniotes, including *Gephyrostegus* (Carroll, 1970), seymouriamorphs (Berman et al., 1987, Klembara and Bartik 1999, Klembara and Ruta 2005) and diadectomorphs (Berman et al. 1998, 2004, Kennedy, 2010), all of which possess between 24 and 27 vertebrae. The presacral vertebral count in *Westlothiana* is also at least four higher than in taxa crownwards of diadectamorphs; *Paleothyris* has a vertebral count of 32 (Carroll 1969) and other amniotes had a presacral vertebral count even lower than this, including, *Petrolacosaurus* (26, Reisz 1981), *Milleretta* (24, Gow 1972) and synapsids, which typically had a presacral vertebral count of 27 (e.g. Romer et al. 1940, Modesto 1995, Mann and Paterson 2020), as well as *Captorhinus* (25, Fox and Bowman 1966) and *Hylonomus* (26, Carroll 1964).

The morphology of the individual vertebrae is consistent between both the holotype, and the second specimen, as was noted in Smithson et al., (1993).

3.2.2.1 Cervical vertebrae. The poor exposure of the cervical vertebrae prevented any anatomical descriptions in Smithson et al., (1993). The atlas-axis complex is split between the slabs, with the dorsal part preserved in the counterslab and the ventral part preserved in the slab. Nonetheless, some elements of the atlas-axis complex are revealed by micro-tomography, allowing for some anatomical descriptions (Fig. 2). The atlas centrum is broken into two parts, which are divided between the slab and counterslab, but between these two parts it is mostly complete. A partial atlantal neural arch is preserved dorsal to the atlas within the counterslab. The dorsal half of the axis centrum is preserved in articulation with the atlas in the counterslab, but the ventral half is not preserved. All the atlas-axis elements are partially distorted along the anteroposterior axis, with the right half having been sheared anteriorly relative to the left half.

The atlantal centrum is a single, fused element. The atlantal centrum is close to cylindrical, and the dorsal part of the anterior articulating surface is almost flat, being only very gently convex. The ventral quarter of the anterior articulating surface is deflected to incline posteriorly, which may

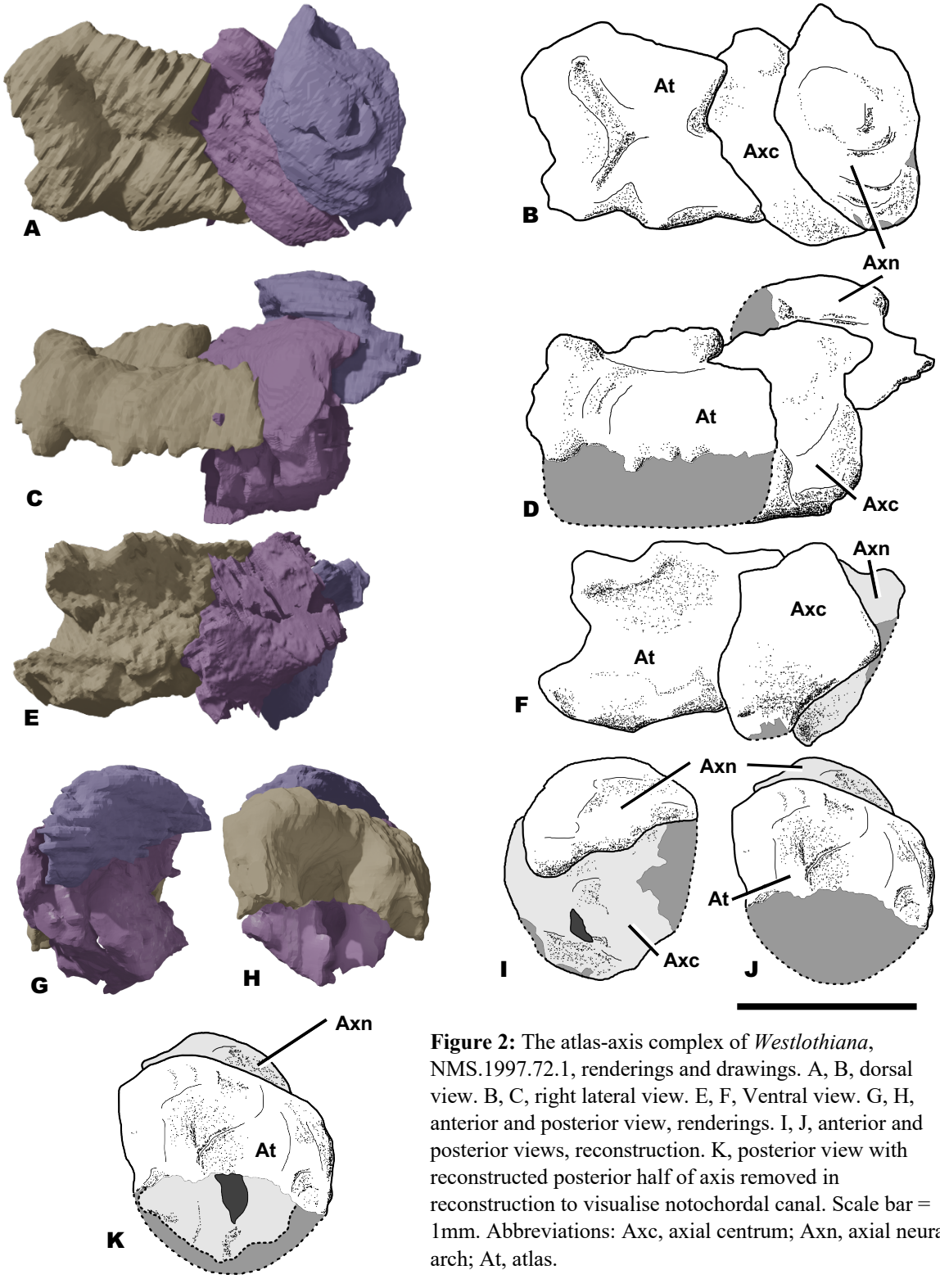


Figure 2: The atlas-axis complex of *Westlothiana*, NMS.1997.72.1, renderings and drawings. A, B, dorsal view. B, C, right lateral view. E, F, Ventral view. G, H, anterior and posterior view, renderings. I, J, anterior and posterior views, reconstruction. K, posterior view with reconstructed posterior half of axis removed in reconstruction to visualise notochordal canal. Scale bar = 1mm. Abbreviations: Axc, axial centrum; Axn, axial neural arch; At, atlas.

represent a facet for an atlantal intercentrum. There is no evidence preserved of a separate atlantal intercentrum, but it is possible that an atlantal intercentrum would have been present and is not preserved. A notochordal canal passes through the anteroposterior length of the centrum, and is positioned close to the ventral surface. It is narrowest at the anterior end, where it is approximately

one-seventh of the maximum transverse width of the centrum, but the canal expands in width posteriorly to almost double its initial transverse width by the posterior end of the centrum (Fig. 2d). The atlantal centrum and atlantal neural arch are articulated via a distinct suture, and are only loosely attached to one another. The atlantal neural arch is low, approximately half the dorsoventral height of the centrum, and the dorsal surface is gently rounded (Fig. 2c). Similar to the condition in *Westlothiana*, the atlantal centrum and neural arch are visibly sutured, rather than indistinguishably fused, in stem amniotes stemwards of lepospondyls, including *Caerorachis* (Ruta et al. 2001), anthracosaurs (Holmes 1989), seymouriamorphs (Klembara 1997, Berman et al. 2000, Klembara and Ruta 2005), as well as some diadectomorphs (Romer 1946, Berman et al. 2004) and a small number of microsaurs including *Hapsidopareion* and *Microbrachis* (Carroll and Gaskill 1978). However, in most other lepospondyls (Douthitt 1917, Beerbower 1963, Carroll and Gaskill 1978), *Diadectes* (Berman et al. 1998), and most stem and amniotes crownwards of diadectomorphs, including protorothyrids (Carroll 1964, 1969) and araeoscelids (Reisz 1981), the atlantal centrum and atlantal arch are indistinguishably fused.

The anterior and posterior articulating surfaces of the atlantal centrum have equal mediolateral widths (Fig. 2b). In this respect, *Westlothiana* resembles stem-tetrapods including *Greererpeton* (Godfrey 1989) and *Whatcheeria* (Otoo et al. 2021), temnospondyls including *Balanerpeton* (Milner and Sequeira 1993) and *Doleserpeton* (Sigurdsen and Bolt 2010), stem-amniotes including *Archeria* (Romer 1957), *Gephyrostegus* (Carroll 1970), seymouriamorphs (Berman et al. 1987, Klembara and Bartik 1999), diadectomorphs (Sumida and Lombard 1999, Berman et al. 2004, Kennedy 2010), and early-diverging amniotes including *Captorhinus* (Fox and Bowman 1966), protorothyrids (Carroll 1964, 1969) and araeoscelids (Reisz 1981, Reisz et al. 1984), and synapsids including *Dimetrodon* (Romer et al. 1940) and *Haptodus* (Laurin 1993). The atlas of *Westlothiana* does not resemble microsaurs, however, in this respect, as the anterior articulating surface in microsaurs is laterally expanded to approximately twice the width of the posterior articulating surface, including *Tuditanus*, *Hapsidopareion* and *Llistrofus* (Carroll and Gaskill 1978).

There is also no odontoid process projecting anteriorly from the ventral surface of the atlantal centrum. Therefore, *Westlothiana* resembles both stem-amniotes including seymouriamorphs

(Klembara 1997, Berman et al. 2000, Klembara and Ruta 2005) and early amniotes including protorothyrids (Carroll 1964, 1969) and araeoscelids (Reisz 1981). *Westlothiana* differs, however, from microsaurs including *Hapsidopareion*, *Tuditanus* and *Euryodus* (Carroll and Gaskill 1978), as well as other lepospondyls including aïstopods (Anderson 2002, Anderson et al. 2003), *Adelogyrinus* (Andrews and Carroll 1991) and the lysorophian *Brachydectes* (Wellstead 1991) in which an odontoid process is present.

In the second specimen, a relatively large intercentrum is present between the second and third pleurocentra in the cervical series (Smithson, Carroll et al. 1993). However, no atlantal intercentrum can be observed in the second specimen (Smithson, Carroll et al. 1993).

3.2.2.2 Trunk and caudal vertebrae

The trunk vertebrae are morphologically similar in both NMS.1990.72.1 and NMS.1991.47.1 (Smithson, Carroll et al. 1993). Many of the individual trunk vertebrae show substantial damage in both specimens, but enough are well preserved across both specimens to fully reconstruct the vertebral morphology. As such, Smithson et al. (1993) were able to provide a complete and accurate description of the morphology of these elements.

Crescentic intercentra are present throughout the entire vertebral column, resembling stem amniotes including seymouriamorphs (Klembara and Bartik 1999, Klembara and Ruta 2005) and diadectomorphs (Berman et al. 1998, 2004, Kennedy 2010), and some early-divering amniotes including captorhinids (Fox and Bowman 1966), protorothyrids (Carroll 1964, 1969) and araeoscelids (Reisz 1981, Reisz et al. 1984). The intercentra are comparable in size to those of seymouriamorphs (Klembara and Bartik 1999, Klembara and Ruta 2005), *Chroniosaurus* (Clack and Klembara 2009) and *Gephyrostegus* (Carroll 1970), being about one-third as long as the pleurocentra in anteroposterior length, and encompassing the entire ventral half of the pleurocentra. The intercentra in *Westlothiana*, whilst similar in their crescentic shape, are larger in anteroposterior length than those of early crown amniotes (Fox and Bowman 1966, Carroll 1969, Reisz 1981). The morphology of the intercentra in *Westlothiana* contrasts anthracosaurs, in which the intercentra and pleurocentra are roughly equal in size (Panchen 1977, Holmes 1989). It also contrasts the morphology in stem

tetrapods, in which the intercentrum is larger than the pleurocentrum, such as *Whatcheeria* (Otoo et al. 2021) and *Greererpeton* (Godfrey 1989). This is also the case in temnospondyls, such as *Balanerpeton* (Milner and Sequeira 1993) and *Doleserpeton* (Sigurdsen and Bolt 2010).

The presence of intercentra in *Westlothiana* contrasts with lepospondyls, including aïstopods (Carroll 1998, Anderson 2002, Anderson et al. 2003), *Adelogyrinus* (Andrews & Carroll 1991), lysorophians (Wellstead 1991) and nectrideans (Douthitt 1917, Beerbower 1963; Milner and Ruta 2009, Milner 2018). It also contrasts with microsaurs, most of which lacked intercentra entirely. In the microsaur taxa that did possess intercentra (e.g. *Euryodus*; Carroll and Gaskill 1978), they were superficial and did not play a structural role in the vertebral column, instead occupying a position lateral to the pleurocentrum, and therefore does not resemble the morphology of the intercentra in *Westlothiana*.

The pleurocentra are cylindrical throughout the vertebral column, and are mostly fused to the neural arches; faint sutures can only be observed in some of the vertebrae. A notochordal canal passes through the pleurocentra, but as the centra are flattened the width cannot be accurately estimated in the type. Smithson et al. (1993) estimated that the notochordal canal is approximately 30% of the width of the centrum, based on the second specimen.

Short transverse processes are present at the posterodorsal corners of the centra. The neural spines are triangular and positioned towards the posterior end of the centrum, closely resembling those of *Captorhinus* (Fox and Bowman 1966). The neural spines are considerably shorter than stem-amniotes including *Gephyrostegus* (Carroll 1970), anthracosaurs such as *Archeria* (Holmes 1989) and seymouriamorphs such as *Discosauriscus* (Klembara and Bartik 1999) and *Ariekanerpeton* (Klembara and Ruta 2005), and *Chroniosaurus* (Clack and Klembara 2009). The neural spines are more similar in height to the neural spines in microsaurs such as *Tuditanus* and *Pantylus* (Carroll and Gaskill 1978), and to those of late-diverging stem amniotes and the earliest diverging crown amniotes, including *Diadectes* (Berman et al. 1998), *Captorhinus* (Fox and Bowman 1966) and *Paleothyris* (Carroll 1969), although the neural spines in *Westlothiana* are shorter, even, than these taxa.

As noted by Smithson et al. (1993), lateral and ventral lamellae are present on many of the vertebrae, extending along most of the anteroposterior length of the centrum. Unfortunately, the

preservation of the vertebrae in both specimens does not allow for a full assessment of the distribution of such lamellae throughout the column. Ventral lamellae similar to those in *Westlothiana* are present in some pelycosaurs, such as *Dimetrodon* (Romer et al. 1940), but are absent in stem amniotes including *Gephyrostegus* (Carroll 1970) and seymouriamorphs (Berman et al. 1987, Klembara and Bartik 1999, Klembara and Ruta 2005), and are also absent in diadectamorphs (Berman et al. 1998, 2004, Kennedy 2010), captorhinids (Fox and Bowman 1966, Reisz et al. 2016), araeoscelids (Reisz 1981, Reisz et al. 1984) and protorothyrids (Carroll 1964, 1969).

No vertebrae can be confidently identified as sacral vertebrae in either specimen of *Westlothiana* (Smithson, Carroll et al. 1993).

Nine caudal vertebrae are preserved in articulation in the slab of the type. In the counterslab, the same nine caudal vertebrae are exposed, and evidence of an additional 18 are preserved posterior to this, bringing the total count to 27 (Fig. 1b). Most of these additional 18 vertebrae are either poorly exposed, or are just impressions, and so little morphological information can be gained from them. Just one disarticulated caudal vertebra is preserved in the second specimen.

The first nine caudal vertebrae closely resemble those of the trunk; the neural spines are low, and indistinguishably fused to the pleurocentra. Large, crescentic intercentra are present in between the pleurocentra. As noted by Smithson et al. (1993), the caudal vertebrae do not noticeably reduce in size, even up to caudal 27. This suggests that the original tail of *Westlothiana* was considerably longer than preserved.

Haemal arches are known from the second caudal vertebra to the end of the caudal vertebral series as preserved. There is also a haemal arch associated with the single caudal vertebra in the second specimen (Smithson, Carroll et al. 1993). The haemal arches appear to be fairly long and triangular in shape, but they are poorly preserved and little about the morphology can be determined.

3.2.2.3 Ribs. The ribs in *Westlothiana* were accurately described in Smithson et al., (1993). Poor preservation in the cervical region prevents any morphological description of the cervical ribs (Smithson, Carroll et al. 1993). The trunk ribs are relatively long and curved, and are relatively consistent in length along the majority of the vertebral column, shortening only immediately anterior

to the sacral region. The ribs therefore resemble those of stem-amniotes including *Archeria* (Romer 1957), diadectomorphs (Berman et al. 1998, 2004, Kennedy 2010), seymouriamorphs (Klembara and Bartik 1999, Klembara and Ruta 2005) and microsaurs (Carroll and Gaskill 1978). The ribs also resemble those of early diverging crown amniotes such as araeoscelids (Reisz 1981, Reisz et al. 1984), and resemble the ribs of captorhinids (Fox and Bowman 1966) and protorothyrids (Carroll 1964, 1969) too. This differs from the shorter and mostly straight ribs of stem tetrapods such as *Greererpeton* (Godfrey 1989), temnospondyls including *Balanerpeton* (Milner and Sequeira 1993), and *Dendrerpeton* (Holmes, Carroll et al. 1998), and many lepospondyls including aïstopods (Carroll 1998, Anderson 2002, Anderson et al. 2003) and some nectrideans, such as *Scincosaurus* (Milner and Ruta 2009) and *Keraterpeton* (Milner 2018).

3.2.2 Appendicular skeleton

3.2.2.1 Forelimb. Parts of both forelimbs are preserved in the part. Both forelimbs are displaced laterally and are preserved on the same side, on the left of the vertebral column (Fig. 1a, c). The left humerus is well preserved in the part, although it is split between the part and counterpart, with a small amount preserved in the counterpart. The right ulna and radius are well preserved, although the proximal part of the anterior margin of the right ulna is not well defined. Of the left ulna, only the proximal end is preserved, but the margins of the bone are clearer than for the right ulna. Only a fragment of the proximal end of the left radius is preserved (Fig. 3)

The limbs in *Westlothiana* are proportionally short relative to the trunk, and the humerus is particularly short relative to the femur as well, a feature that was noted by Smithson et al. (1993); the femur is equal in length to approximately four trunk vertebrae and the humerus is a little more than half of this length. The humerus is slightly less than the length of two and a half dorsal centra along its long axis. This is comparable in relative size to those of the microsaurs *Hyloplesion* and *Microbrachis*, (Carroll and Gaskill 1978), and to the lysorophian *Brachydectes*, (Wellstead 1991), all taxa noted to have distinctly small limbs. The humeral length in *Westlothiana* is also slightly shorter than those of the aquatic nectrideans *Scincosaurus* (Milner and Ruta 2009) and *Keraterpeton* (Milner

2018), in which the humeri measure approximately three centra in length, and it is also similar to the seymouriamorphs *Discosauriscus* (Klembara 1997) and *Ariekanerpeton* (Klembara and Ruta 2005), in which the humeri are also approximately as long as three dorsal centra. The humeri in *Westlothiana* are considerably shorter than the humeri of anthracosaurs (as long as six dorsal vertebrae, Holmes 1989), *Gephyrostegus bohemicus* (as long as five dorsal vertebrae, Klembara et al. 2014), diadectomorphs (as long as 3-6 dorsal vertebrae, Berman et al. 1998, 2004, Kennedy 2010), protorothyrids (as long as 4-5 dorsal vertebrae, Carroll 1964, 1969) and araeoscelids (as long as 5-6 dorsal vertebrae, Reisz 1981, Reisz et al. 1984).

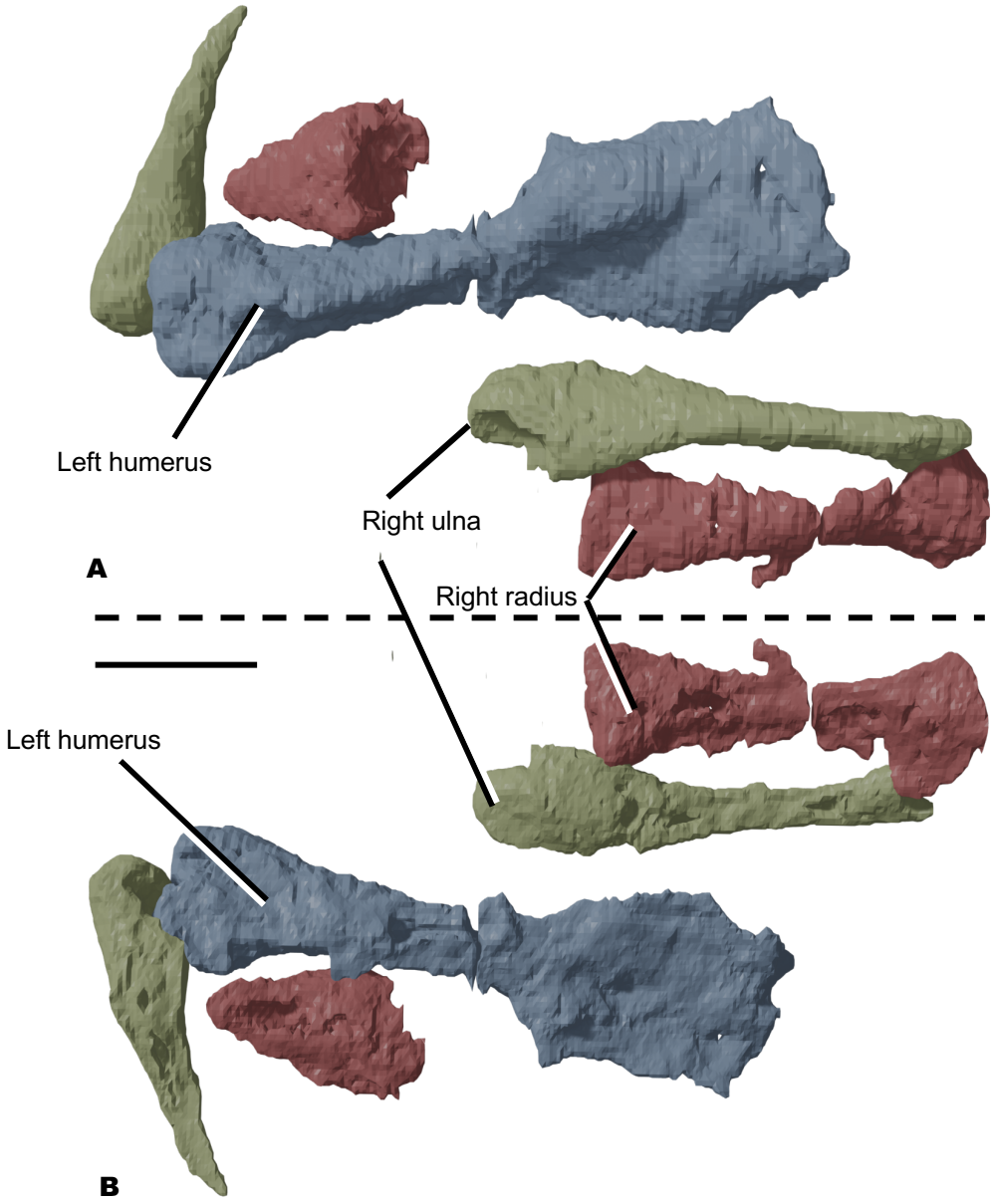
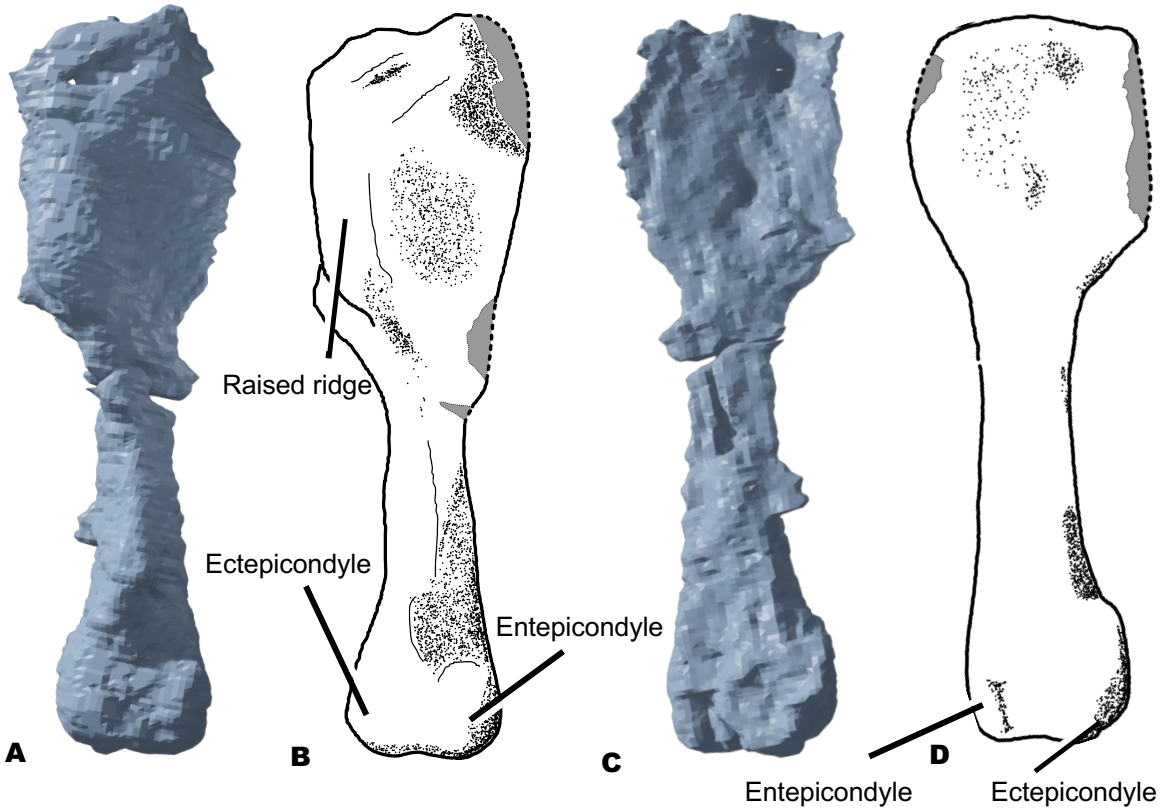


Figure 3 (Previous Page): The forelimbs of *Westlothiana*, NMS.1990.72.1, as preserved. Both forelimbs have been displaced relative to the trunk, and are preserved in opposite orientations. A, left forelimb in dorsal view, right forelimb in ventral view. B, left forelimb in ventral view, right forelimb in dorsal view. Scale bar = 1mm.



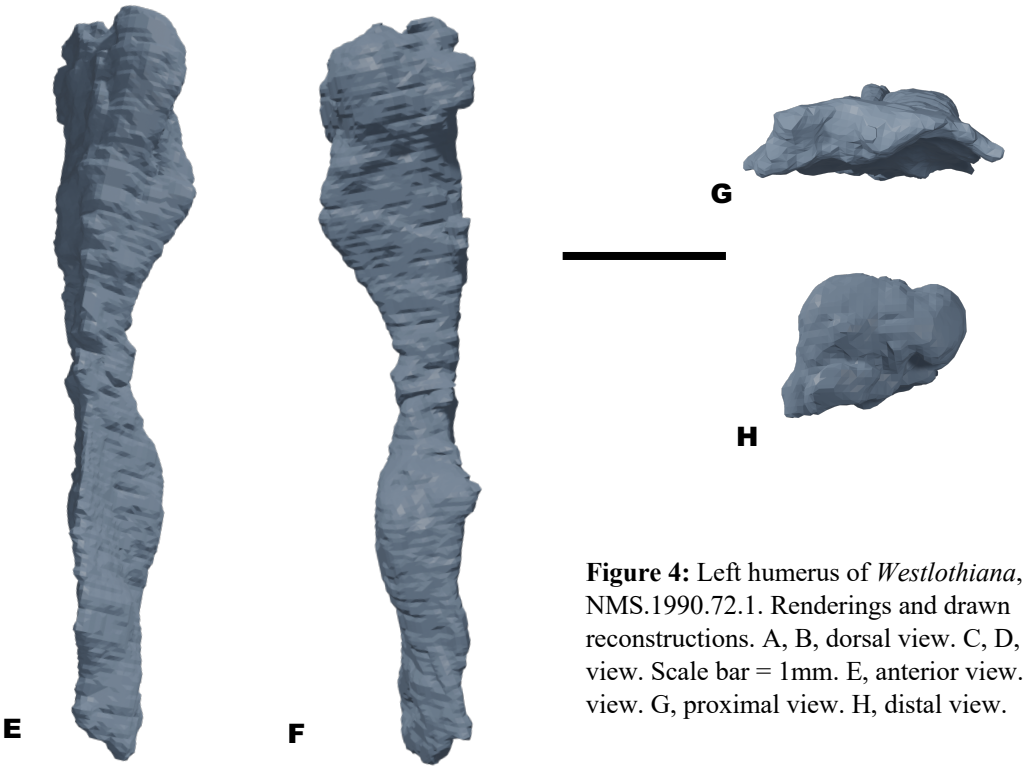


Figure 4: Left humerus of *Westlothiana*, NMS.1990.72.1. Renderings and drawn reconstructions. A, B, dorsal view. C, D, ventral view. Scale bar = 1mm. E, anterior view. F, posterior view. G, proximal view. H, distal view.

The humerus of NMS.1990.72.1 is relatively slender compared to its proximodistal length. It consists of a narrow shaft, with only very modestly expanded proximal and distal ends (Fig. 4). The maximum width of the proximal end is just one-quarter of the humeral length, and the maximum width of the distal end is one-fifth of the humeral length. These overall proportions are most similar to the slender humeri in protorothyrids (Carroll 1964, 1969) and araeoscelids (Reisz 1981, Reisz et al. 1984), as well as the microsaur *Cardiocephalus* (Carroll and Gaskill 1978). The humeri in other microsaurs tend to be relatively slender, but are nonetheless more widely expanded at the proximal and distal ends than the humerus in *Westlothiana* and so are only somewhat comparable (Carroll and Gaskill 1978). The similarity of the slender shape of the humerus in *Westlothiana* to that of protorothyrids was noted in Smithson et al., (1993), and they suggested that this was one of the features that indicated that *Westlothiana* had affinities to early diverging reptiles. The humerus, and forelimb as a whole, are nevertheless much shorter proportionally in *Westlothiana* than in the aforementioned taxa with slender humeri, when compared to the overall length of the body.

The humerus in *Westlothiana* is unlike the humeri of stem amniotes stemwards of lepospondyls, including anthracosaurs (Romer 1957), *Silvanerpeton* (Ruta and Clack 2006), that of diadectomorphs (Kennedy 2010), and in temnospondyls including *Dendrerpeton* (Holmes 1998) and *Doleserpeton* (Sigurdsen and Bolt 2010) in which the proximal and distal ends are considerably more expanded. The humerus in *Westlothiana* also differs from stem tetrapods including *Greererpeton* (Godfrey 1989) and *Whatcheeria* (Otoo et al. 2021) in which the humerus is L-shaped, rather than straight (Shubin, Daeschler et al. 2004).

The anterior margin of the proximal end of the humerus is thickened to form a distinct ridge on the dorsal surface, immediately proximal to where the humerus narrows to form a shaft. The dorsal surface of the proximal half of the humerus is gently concave. The proximal end is somewhat rounded, but the margins of the bone at the proximal end are poorly preserved, preventing further description (Fig. 4a, b).

The distal end of the humerus is only narrowly expanded relative to the shaft, and so both the entepicondyle and ectepicondyle are particularly low, consistent with the slender humeri described in the previous paragraph. There is no entepicondylar foramen, contrasting with the humerus of the

second specimen (Smithson, Carroll et al. 1993). The lack of an entepicondylar foramen is also observed in a small number of lepospondyls that have reduced limbs, including *Brachydectes* (Wellstead 1991), *Keraterpeton* (Milner 2018), and the microsaurs *Cardiocephalus* and *Euryodus* (Carroll and Gaskill 1978). This contrasts with the vast majority of early tetrapod taxa, in which an entepicondylar foramen is present. This includes stem tetrapods such as *Greererpeton* (Godfrey 1989), *Whatcheeria* (Otoo et al. 2021) and *Pederpes* (Clack and Finney 2005), temnospondyls including *Balanerpeton* (Milner and Sequeira, 1993) and *Dendrerpeton* (Holmes 1998), and many stem amniotes including the anthracosaur *Archeria* (Romer 1957), seymouriamorphs (Berman et al. 1987, Klembara and Bartik 1999, Klembara and Ruta 2005), *Gephyrostegus* (Carroll 1970), *Solenodonsaurus* (Danto et al. 2012) and diadectomorphs (Berman et al. 1998, 2004, Kennedy 2010). An entepicondylar foramen is also present in most early diverging amniotes including protorothyrids (Carroll 1964, 1969), araeoscelids (Reisz 1981, Reisz et al. 1984), captorhinids (Fox and Bowman 1966, Reisz et al. 2016), synapsids including *Echinerpeton* (Mann and Paterson 2020), *Varanops* (Campione and Reisz 2010) and *Dimetrodon* (Romer et al. 1940), and reptiles including *Milleretta* (Gow 1972) and *Youngina* (Gow 1974).

The radius appears to have been flattened dorsoventrally during preservation. The radius is a gently waisted bone, with a narrow shaft and both the proximal and distal ends expanded to 35% and 28% of the length respectively. The proximal articulating surface forms a relatively flat surface, but the posterior half is marginally concave where the radius articulates with the humerus. The distal end is expanded to form a point on both the anterior and posterior sides, with the anterior point positioned more distally. The distal articulating surface is smoothly curved between these points. Both the anterior and posterior margins of the shaft are concave, but the posterior margin is more strongly concave. The shaft of the radius appears oblong in cross section but it is possible that this is due to the dorsoventral flattening. The radius is approximately 63% of the length of the humerus (Fig. 3). This is proportionally similar to some stem amniotes including some seymouriamorphs (Klembara 1997, Berman et al. 2000), anthracosaurs (Holmes 1989) and *Solenodonsaurus* (Danto et al. 2012), and some late diverging stem and early crown amniotes including captorhinids (Fox and Bowman 1966, Reisz et al. 2016) and *Paleothyris* (Carroll 1969).

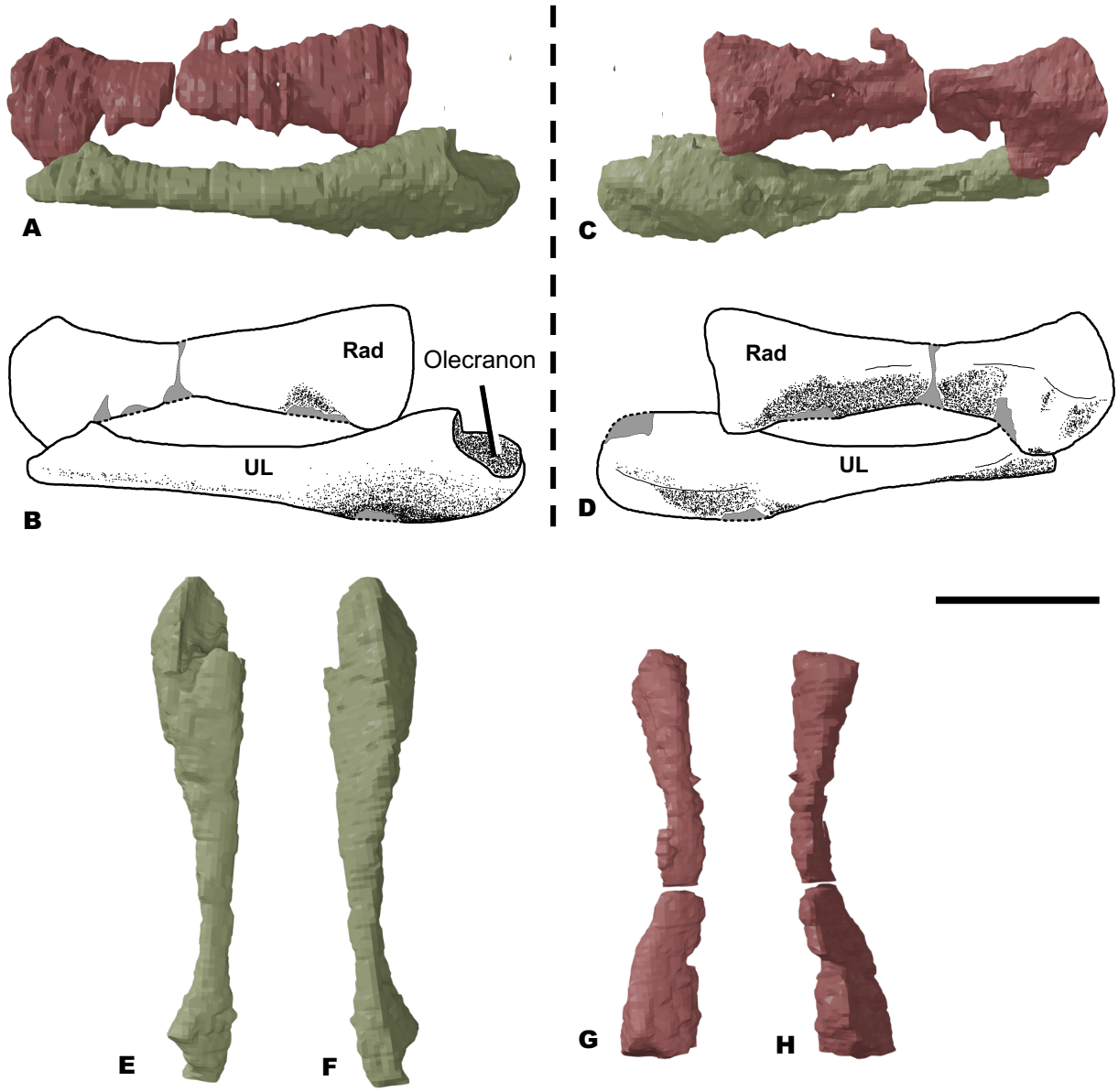


Figure 5: Right radius and right ulna of *Westlothiana*, NMS.1990.72.1. Renderings and drawn reconstructions. A, B, right forelimb in dorsal view. C, D, right forelimb in ventral view. E, ulna in anterior view; F, ulna in posterior view. G, radius in anterior view; H, radius in posterior view. Scale bar = 1mm. Abbreviations: Rad = Radius, UL = Ulna

The right ulna is relatively well exposed on the surface of NMS.1990.72.1, and therefore the description in Smithson et al., (1993) is extensive and accurate. The ulna measures approximately 50% of the length of the humerus, and possesses a well-ossified olecranon process that extends for approximately one-fifth of the length of the ulna. The proximal surface of the olecranon process is smooth and, as noted by Smithson et al. (1993), there is no evidence of any muscle attachment. The ulna is slender and gracile, resembling the ulna in early amniotes including *Paleothyris* (Carroll 1969)

and *Petrolacosaurus* (Reisz 1981), but is unlike the more robust, distally expanded ulna in stem-amniotes including *Silvanerpeton* (Ruta and Clack 2006), seymouriamorphs (Berman et al. 2000, Klembara and Ruta 2005) and *Gephyrostegus* (Carroll 1970). At the distal end, the anterior surface shows a small, triangular expansion which results in the anterior margin of the ulna being concave. The posterior margin is almost straight, and the distal end is not expanded posteriorly, resembling microsaurs including *Pantylus* and *Tuditanus* (Carroll and Gaskill 1978).

Nothing of the manus can be observed in the type specimen.

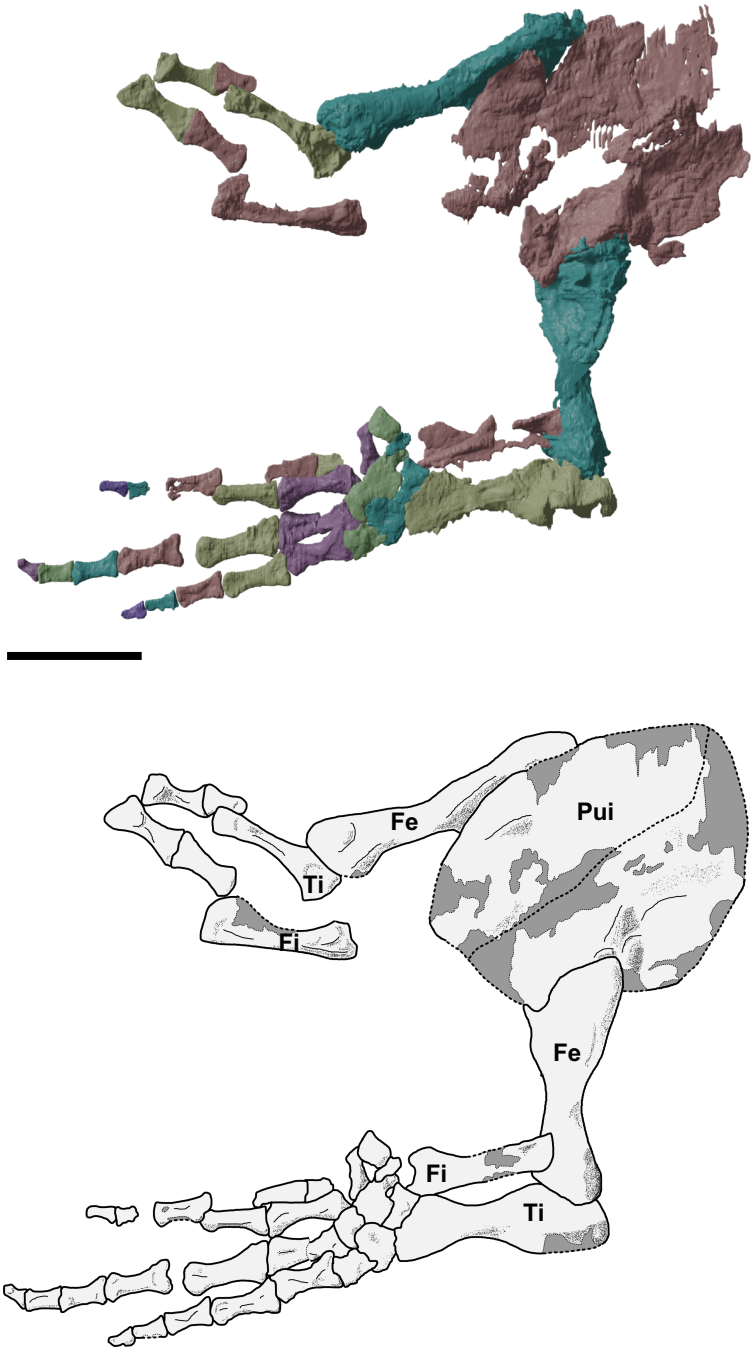


Figure 6: Pelvis and hindlimbs, as preserved in *Westlothiana*, NMS.1990.72.1, dorsal view. A, composite rendering of pelvis and hindlimb elements from both the slab and counterslab. B, drawn reconstruction. Dark grey indicates damage, and missing bone.

Abbreviations: Puboischiadic plate (Pui), Femur (Fe), Tibia (Ti), Fibula (Fi).

Scale bar = 5mm.

3.2.2.2 Pelvic girdle. A large amount of pelvic material is present, but it is not well preserved, and is dorsoventrally flattened, preventing detailed anatomical descriptions. The overall outline of the puboischidaic plate can be traced (Fig. 6), but the margins are not well finished, and no evidence of the ilium is observed, suggesting that the ilium may be disarticulated from the rest of the pelvis, a condition that has also occurred in the second specimen of *Westlothiana* (Smithson, Carroll et al. 1993). The anteroposterior length of the puboischiadic plate is approximately the same as five trunk vertebrae, based on the preserved material. Due to the poor quality of the preservation of the pelvic bone, it is possible that this is a slight underestimate. This estimate is shorter than the 6.7 vertebrae in length that the pelvis was estimated to be in Smithson et al., (1993), which they noted to be a "great length". Smithson et al. (1993) further observed that the pelvis in *Westlothiana* was proportionally long relative to the stem tetrapod *Acanthostega* (Coates 1996), and the protorothyrids *Hylonomus* (4.5 vertebrae in length, Carroll 1964) and *Paleothyris* (5.1 vertebrae in length, Carroll 1969).

The estimate of Smithson et al., (1993) is based on the second specimen of *Westlothiana*, which shows a proportionally longer pelvis. Nonetheless, the length of the pelvis in NMS.1990.72.1 (the holotype) is still a considerable length amongst stem and early crown amniotes, and the puboischiadic plate in NMS.1990.72.1 is most similar in length to *Hylonomus* (Carroll 1964) and *Paleothyris* (Carroll 1969). Although the puboischiadic plate of NMS.1990.72.1 is anteroposteriorly shorter than that of the second specimen, it is nonetheless larger than those of seymouriamorphs (approximately four vertebrae in length, Klembara 1997, Berman et al. 2000), and considerably longer than in all lepospondyls, including microsaurs such as *Tuditanus* and *Hapsidopareion* (three to four vertebrae in length, Carroll and Gaskill 1978), nectrideans (four vertebrae in length, Milner and Ruta 2009, Milner 2018) and *Brachydectes* (fewer than three vertebrae in length, Wellstead 1991).

The suture line between the two halves of the pelvis remains visible in NMS.1990.72.1, but no suture line is visible within the puboischiadic plate that would mark the boundary between the pubis and the ischium, on either side. However, due to the poor quality of preservation of the puboischiadic plate, it is unclear if the sutures remained visible, as in anthracosaurs (Holmes 1989), *Chroniosaurus* (Clack and Klembara 2009), seymouriamorphs (Klembara and Ruta 2005), araeoscelids (Reisz et al. 1984), protorothyrids (Carroll 1964, 1969) and most microsaurs (Carroll and

Gaskill 1978), or if the elements were indistinguishably fused as in captorhinids (Fox and Bowman 1966, Reisz et al. 2016) and some nectrideans (Milner and Ruta 2009). However, the apparent disarticulation of the ilium in NMS.1990.72.1, whilst the rest of the pelvis is present (Fig. 5), suggests that the sutures in the pelvis in *Westlothiana* remained visible, and that the ilium, at least, was loosely attached to the rest of the pelvis. This concurs with the observations of Smithson et al., (1993) of the second specimen, in which all elements of the pelvis appear to be disarticulated from one another.

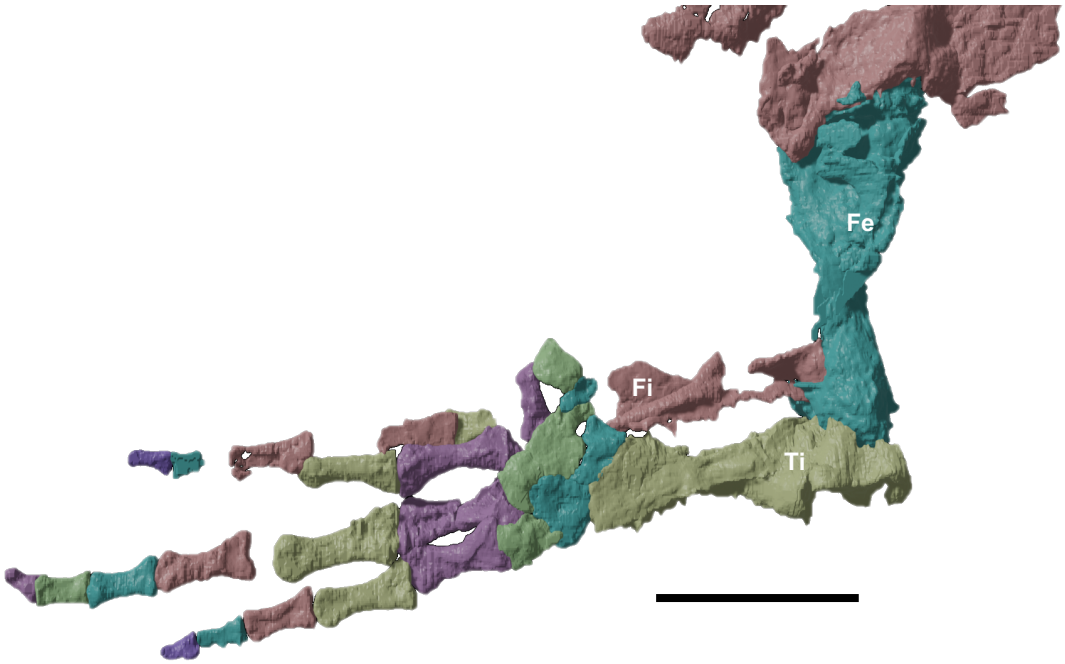


Figure 7: Rendering of the right hindlimb of *Westlothiana*, NMS.1990.72.1. Dorsal view. Composite rendering based on elements in both the slab and counterslab. Abbreviations as in Figure 6. Scale bar = 5mm. Abbreviations as in Fig. 6.

3.2.2.3 Hindlimb. The right hindlimb is almost completely preserved, including the femur, tibia, fibula, and almost all bones of the foot (Figs. 6, 7, 8, 9). The femur, tibia and fibula are split along their long axes, and are partially preserved in each of the slab and counterslab. The foot bones are entirely preserved in the counterslab. The left hindlimb is partially preserved, consisting of a femur, partial tibia and partial fibula, and a small number of foot bones (Fig. 7). The left femur is entirely preserved within the counterslab, and thus descriptions of the femur are based on this element.

The femur is well ossified in NMS.1990.72.1, and the margins of the bone are well defined. It is similar in morphology to the descriptions of the femur of the second specimen in Smithson et al. (1993), with a relatively long shaft and moderately expanded proximal and distal ends. This differs

from the femora of *Hylonomus* (Carroll 1964) and *Paleothyris* (Carroll 1969) in which the overall morphology is more slender. As described in Smithson et al. (1993) there is no fourth trochanter. This is similar to many early amniotes, including *Paleothyris* (Carroll 1969) and araeoscelids (Reisz 1981, Reisz et al. 1984), and lepospondyls including nectrideans (Milner and Ruta 2009, Milner 2018) and microsaurs such as *Tuditanus*, *Pantylus* and *Euryodus* (Carroll and Gaskill 1978). This differs from diadectomorphs (Berman et al. 1998, Kennedy 2010), captorhinids (Fox and Bowman 1966; Reisz et al. 2015) and synapsids (Campione and Reisz 2010, Brocklehurst et al. 2016), which have a fourth trochanter.

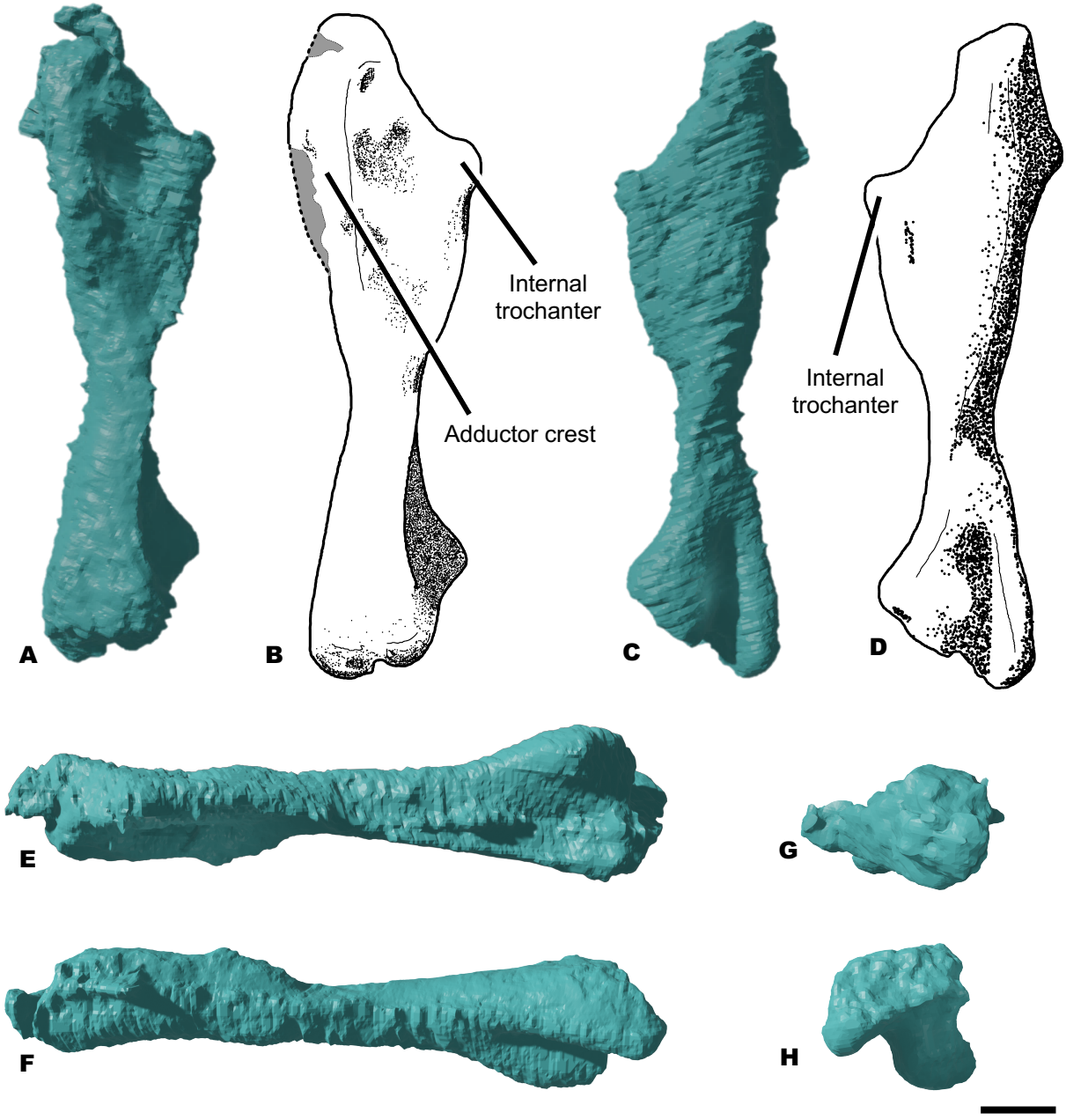


Figure 8 (Previous page): Renderings and reconstructions of the left femur of *Westlothiana*, NMS.1990.72.1. A, rendering in dorsal view, B, drawn reconstruction in dorsal view. C, rendering in ventral view, D, drawn reconstruction in ventral view. E, anterior view, F, posterior view, anterior is oriented towards the left. G, proximal view, H, distal view, dorsal is oriented upwards. Scale bar = 1mm.

Some additional observations can be added to the descriptions of Smithson et al. (1993). The femur is approximately the length, along its long axis, of four trunk vertebrae (Fig. 8). This is a very similar relative length to the femur in the elongate microsaur *Hyloplesion* (Carroll and Gaskill 1978), to that of *Paleothyris* (Carroll 1969) and to that of stem amniotes including seymouriamorphs (Klembara 1997, Berman et al. 2000) and *Silvanerpeton* (Clack and Ruta 2006). It is longer that of most other microsaurs, including *Pantylus*, *Euryodus* and *Micraroter* in which the femur does not exceed three-and-a-half vertebrae in length (Carroll and Gaskill 1978), and *Diadectes abistus*, in which the femur is as long as just three vertebrae (Berman et al. 1998). The femur in *Westlothiana* is shorter, however, than in many other stem and crown amniotes, including most diadectomorphs (five to seven vertebrae, Berman et al. 1998, Kennedy 2010), araeoscelids (four to six vertebrae, Reisz 1981, Reisz et al. 1984) and the microsaur *Tuditanus*, in which the femur exceeds six vertebrae in length (Carroll and Gaskill 1978).

The femur is a very slender element, and micro-tomography of the complete femur reveals it to be more slender than that of the second specimen as reconstructed by Smithson et al. (1993), with a narrow shaft and only moderately expanded proximal and distal ends (Fig. 8). The proximodistal length of the femur is 5.4 times the maximum width of the femoral head. Such a slender femur is uncommon amongst lepospondyls, and is only observed in the lysorophian *Brachydectes* (Wellstead 1991), and in the microsaur *Tuditanus* (Carroll and Gaskill 1978). A slender humerus comparable to that of *Westlothiana* is also observed in *Paleothyris* (Carroll 1969) and *Youngina* (Gow 1972). In most stem amniotes the femur is more widely expanded at the proximal and distal ends, including some temnospondyls such as *Balanerpeton* (length is three times maximum width, Milner and Sequeira 1993) and *Dendrerpeton* (length is three times maximum width, Holmes 1998), anthracosaurs such as *Archeria* (length is three times maximum width, Romer 1957), seymouriamorphs (length is four to five times maximum width Klembara and Bartik 1999, Berman et al. 2000) diadectomorphs (length is less than four times maximum width, Berman et al. 1998, 2004)

and synapsids including *Dimetrodon* (length is three to four times maximum width, Romer et al. 1940) and *Vaughnitis* (length is three times maximum width, Brocklehurst et al. 2016). The femur in *Westlothiana* was described in Smithson et al., (1993) to generally resemble that of protorothyrids, but differ in that it was less slender, an observation which contrasts with our descriptions.

A clear, well developed internal trochanter is present on the posterior surface of the bone (Fig. 8). It is low, and consists of a short, stubby projection proximally which expands into a low, dorsoventrally narrow adductor crest distally that terminates just proximal to the midpoint of the femoral length. The posterior edge of the femoral head curves gently to form the internal trochanter, and does not form a trough-like space. In this respect, the femoral head of *Westlothiana* is similar to most microsaurs, in which an internal trochanter is present but is only gently separated from the femoral head (Carroll and Gaskill 1978). A similar condition is also observed in many stem and crown amniote taxa crownwards of lepospondyls, including *Hylonomus* (Carroll 1964), *Petrolacosaurus* (Reisz 1981), most synapsids (e.g. Romer et al. 1940; Modesto 1995, Campione and Reisz 2010, Brocklehurst et al. 2016), and reptiles including *Youngina* and parareptiles (Gow 1972, 1974, Modesto et al. 2015).

The femur of *Westlothiana* also has a thickened adductor crest along the anteroventral edge of the proximal half, which reaches almost to the midpoint of the femoral length. Distal to the midpoint of the femoral length there is an additional portion of adductor crest that is extremely low, and reaches to the distal end of the femur, as described in Smithson et al. (1993), and as in early amniotes including protorothyrids (Carroll 1964, 1969) and *Petrolacosaurus* (Reisz et al. 1981).

The tibia and fibula are relatively poorly preserved, and no bones are complete. Nonetheless, the morphology that can be observed broadly matches the descriptions of the second specimen in Smithson et al., (1993). The tibia and fibula are approximately equal in length to each other, and approximately half the length of the femur. The tibia has expanded proximal and distal ends, and the proximal end is expanded approximately 50% more than the distal end. Smithson et al., (1993) noted than the second specimen lacks a cnemial crest, but due to the level of preservation it is unclear whether or not this would have been the case in NMS.1990.72.1. Distally there is a fairly large, flat articulating surface. No other observations can be added to those outlined in Smithson et al., (1993).

The fibula also has expanded proximal and distal ends, but these are roughly equal in transverse width to one another. As noted in Smithson et al., (1993) the distal articulating surface is long and curved.

The left foot is bent at the ankle and has become disarticulated. However, the right foot is well preserved, with almost all elements preserved and mostly articulated (Fig. 9). The posterior edge of the foot is slightly disarticulated, so that one proximal tarsal, one or two distal tarsals, and the posteriormost metatarsal and digit are partially disarticulated (Fig. 9). The right foot, as noted in Smithson et al., (1993) is preserved closely overlapping with the anterior caudal vertebrae. This results in the right foot being somewhat distorted when viewed on the surface of the original specimen, which made the descriptions difficult in Smithson et al., (1993). However, the use of micro-CT scanning has allowed the right foot to be virtually separated from the anterior caudal vertebrae, and thus viewed separately.

Three proximal tarsals are preserved in *Westlothiana*. The anterior two, the fibulare and intermedium, are considerably larger than the third, the tibiale, but nonetheless a separate tibiale is clearly retained. Three proximal tarsals are also observed in diadectomorphs (Berman et al. 2004, Kennedy 2010). Moreover, the tibiale in *Westlothiana* resembles those in diadectomorphs as, in diadectomorphs, the tibiale is also reduced in size relative to the other tarsals (Berman et al. 2004, Kennedy 2010). This differs from earlier diverging stem amniotes in which three or four proximal tarsals of approximately equal size are retained, including *Caerorachis* (Ruta et al. 2001) and *Gephyrostegus* (Carroll 1970).

The presence of three tarsals in *Westlothiana* demonstrates that the intermedium and tibiale of *Westlothiana* have not become fused into a single element, the astragalus. This differs from amniote taxa more derived than diadectomorphs in which the intermedium and tibiale are fused into a single astragalus, including captorhinids (Fox and Bowman 1966, Reisz et al. 2015), protorothyrids (Carroll 1964, 1969); araeoscelids (Reisz 1981, Reisz et al. 1984), synapsids (Romer et al. 1940, Langston & Reisz 1981, Laurin 1993) and reptiles (Gow 1972, 1974, Reisz and Dilkes 2003, Modesto et al. 2015).

Only four distal tarsal elements can be identified in articulation in the articulated right pes of NMS.1990.72.1. This differs from the account of the pes in the holotype given by Smithson et al., (1993), who stated that eight tarsal bones could be identified in each pes; three proximal tarsals and

five distal tarsals, although Smithson et al. (figure 11b, 1993) acknowledges there is some degree of uncertainty in the identification of the tarsal elements. This is further corroborated by the second specimen, which is described to have five distal tarsals (Smithson et al., 1993). However, due to the disarticulation that has occurred at the posterior edge of the foot in NMS.1990.72.1, it is entirely possible that one distal tarsal has been lost, as the distal tarsals do not form a clearly articulated series (Fig. 9).

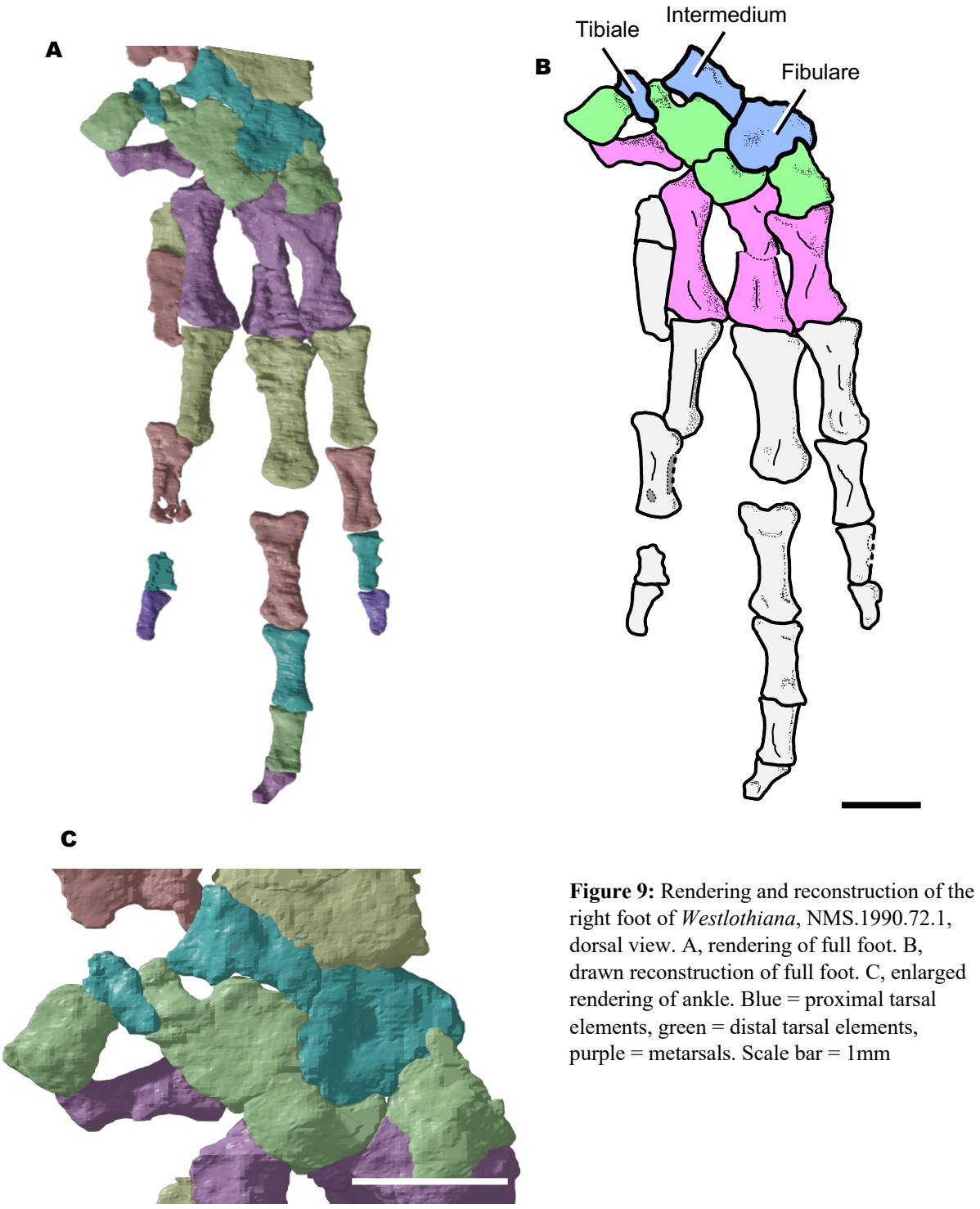


Figure 9: Rendering and reconstruction of the right foot of *Westlothiana*, NMS.1990.72.1, dorsal view. A, rendering of full foot. B, drawn reconstruction of full foot. C, enlarged rendering of ankle. Blue = proximal tarsal elements, green = distal tarsal elements, purple = metarsals. Scale bar = 1mm

In the right foot of NMS.1990.72.1, there appear to be only four digits preserved. This contrasts with the descriptions in Smithson et al. (1993) who described that five digits could be identified in the right foot of the type with "reasonable confidence", and also identified five digits in the second specimen. However, as discussed above, the right foot overlies the anterior caudal vertebrae, and the outer digit on the medially facing side is partially disarticulated. Only four digits can be accounted for based on the micro-CT data. Although it is possible that a digit has been lost through disarticulation, there are also only four metatarsals preserved, and the phalanges of the four preserved digits remain mostly in articulation. The total width of the metatarsus is similar to the full width of the foot as preserved, and thus it does seem likely that four digits represents the true morphology of NMS.1990.72.1. If this is the case, it would represent a unique morphology amongst early tetrapods including *Whatcheeria* (Otoo et al. 2021) and *Greererpeton* (Godfrey 1989), stem amniotes including anthracosaurs (Romer 1957), *Silvanerpeton* (Ruta and Clack 2006), seymouriamorphs (Klembara 1997, Berman et al. 2000), *Gephyrostegus* (Carroll 1970), and early diverging amniotes including protorothyrids (Carroll 1964, 1969) and araeoscelids (Reisz 1981, Reisz et al. 1984), all of which retain five digits on the pes. Microbracomorph microsaurs are specifically observed to have reduced limbs, and just three digits on the forelimb (Carroll and Gaskill 1978), but even these taxa still retain five hindlimb digits.

The best estimate of the pedal phalangeal formula of NMS.1990.72.1 is ?-?2?-4-5-4. This is based on the phalangeal formula of 4-5-4 of the distal-most three digits, which are presumed to be digits III-IV-V. This matches the phalangeal formula of the second specimen (Smithson, Carroll et al. 1993) and better matches the phalangeal formulae in other stem-amniotes and early diverging crown amniotes (see below) than if these digits were identified as digits II-III-IV. There appear to be two phalanges on digit II, but this digit is disarticulated, and thus it is unclear if a phalanx could have been lost (Fig. 9).

The phalangeal formula of digits III-IV-V is the same as in almost all stem and crown amniotes crownwards of lepospondyls including *Petrolacosaurus* (2, 3, 4, 5, 4, Reisz 1981), *Archaeovenator* (2, 3, 4, 5, 4, Reisz and Dilkes 2003), *Limnoscelis* (2, 3, 4, 5, 4) and *Eocasea* (2, 3, 4, 5, 4, Reisz and Fröbisch 2014), as well as *Silvanerpeton* (2, 3, 4, 5, 4, Ruta and Clack 2006) and the

seymouriamorph *Ariekanerpeton* (2, 3, 4, 5, 4, Klembara and Ruta 2005). The phalangeal count contrasts, however, with some earlier diverging stem tetrapods and stem amniotes, including *Whatcheeria* (2, 3, 4, 4, 4, Otoo et al. 2021) and *Gephyrostegus* (2, 3, 4, 5, 5, Carroll 1970), and from temnospondyls such as *Balanerpeton*, which had fewer phalanges (2, 2, 3, 4, 3, Milner and Sequeira 1993). It also differs from most lepospondyls, in which the number of phalanges in digit V is reduced relative to NMS.1990.72.1 by one or two (Carroll and Gaskill 1978, Wellstead 1991, Milner and Ruta 2009, Milner 2018).

3.3 Discussion

Phase contrast synchrotron micro-computed tomography of the holotype of *Westlothiana* reveals significant new information about the postcranial skeleton. For the first time, I describe the morphology of the atlas-axis complex. Well preserved humeri, femora and an articulated tarsus allow for an updated description of the appendicular skeleton.

This novel information demonstrates differences between the morphology of the holotype and NMS.1991.47.1, previously referred as a second potential specimen of *Westlothiana*. Unlike the NMS.1991.47.1 (Smithson, Carroll et al. 1993), the holotype lacks an entepicondylar foramen, the puboischiadic plate is shorter (comparable to five trunk vertebrae in anteroposterior length rather than 6.5 as in the second specimen), and the femur is more slender. The holotype also possesses just four distal tarsals and four digits, contrasting the five distal tarsals and five digits that are present in the second specimen (Smithson, Carroll et al. 1993), and has four fewer presacral vertebrae than NMS.1991.47.1.

The possible second specimen, additionally, is significantly larger than the holotype (Smithson, Carroll et al. 1993). This is possibly due to the fact that the two specimens represent separate taxa. It has also been thought that the holotype could represent a younger individual, and that the second specimen is simply an older individual of *Westlothiana*. If this were the case, then the differences between the two specimens would necessarily be due to ontogeny, or due to intraspecific variation.

However, many of these differing features are highly unlikely to change during the development of an individual of an individual of a species, or vary between different individuals of a species. This is particularly the case for the different numbers of presacral vertebrae between the two specimens, and the different complement of ossifications making up the pes. Therefore, I deem that these differences are sufficient to conclude that NMS.1991.47.1 does not belong to the same taxon as the holotype specimen of *Westlothiana*. No other taxa are present in the East Kirkton limestone with a morphology similar to NMS.1991.47.1 (Clarkson et al. 1993), and therefore this specimen must be defined as a new species (see Systematic Palaeontology, 3.4, later in this chapter).

Nonetheless, the new anatomical information of the holotype of *Westlothiana* has shed additional light on the possible affinities of the taxon. Many of the newly observed traits in the holotype specimen are shared with microsaurs, particularly associated with the relative reduction in size of the forelimbs and hindlimbs, a pattern of body proportions that is widespread across microsaurs (Carroll and Gaskill 1978). These traits include a humerus that is comparable in size to the microsaurs *Microbrachis* and *Hyloplesion* (Carroll and Gaskill 1978), the absence of an entepicondylar foramen in the humerus, shared with the microsaurs *Cardiocephalus* and *Euryodus* (Carroll and Gaskill 1978), the absence of a trough separating the internal trochanter from the proximal end of the humerus, and the absence of a fourth trochanter on the femur, both of which are absent in all microsaurs (Carroll and Gaskill 1978).

However, overall the postcranial skeleton closely resembles that of early amniotes and shares a large number of features with late-diverging stem amniotes and early-diverging crown amniotes. The presence of three proximal tarsals, including a tibiale that is highly reduced in size, closely resembles the condition in diadectomorphs (Berman et al. 2004, Kennedy 2010). NMS.1990.72.1 also resembles early-diverging amniotes in the equal width of the anterior articulating surface of the atlas to the posterior articular surface, the absence of an odontoid process, a slender humerus that specifically resembles that of protorothyrids (Carroll 1964, 1969) and araeoscelids (Reisz 1981, Reisz et al. 1984), a radius that is considerably shorter than the humerus, similar to captorhinids (Fox and Bowman 1966) and *Paleothyris* (Carroll 1969), a slender ulna, a puboischiadic plate equal to approximately five vertebrae, and a phalangeal formula of 2, 3, 4, 5, 4 (see descriptions for

comparisons). As reported by Smithson et al. (1993) the vertebral morphology also resembles that of stem-amniotes and early crown-amniotes, rather than microsaurs, in possessing wedge-shaped intercentra that reside between the pleurocentra.

3.3.2 Axial skeleton

Of the axial skeleton, micro-CT data has only revealed new information about the atlas-axis complex. However, within the atlas-axis, an atlantal centrum, atlantal neural arch and axial centrum are all at least partially preserved, revealing substantial information and potential synapomorphies.

3.3.2.1 Potential synapomorphies of the atlas-axis complex

Absence of lateral expansion of the anterior articulating surface of the atlas centrum

A laterally expanded anterior articulating surface of the atlantal centrum is found in all microsaurs for which it can be observed, including *Tuditanus* and *Pantylus* (Carroll and Gaskill 1978). However, this is lacking in *Westlothiana*, and the anterior articulating surface shows no lateral expansion at all. This suggests that, despite the features of the forelimbs and hindlimbs in *Westlothiana* which resemble microsaurs (see above), *Westlothiana* is not phylogenetically within microsaurs, should they form a monophyletic group (Ruta et al. 2003, Ruta and Coates 2007).

Absence of an odontoid process on the atlas centrum

An anterior projection from the ventral part of the anterior surface of the atlas centrum, the odontoid process, is present in almost all lepospondyls, including microsaurs such as *Hapsidopareion*, *Tuditanus* and *Euryodus* (Carroll and Gaskill 1978), *Adelogyrinus* (Andrews and Carroll 1991) and aïstopods such as *Lethiscus* (Anderson et al. 2003) and *Phlegethontia* (Anderson 2002). The only lepospondyls lacking an odontoid process are nectrideans, including *Diploceraspis* (Beerbower 1963) and *Keraterpeton* (Milner 2018). The absence of this feature in *Westlothiana* suggests that *Westlothiana* is not a member of a monophyletic Lepospondyli.

3.3.3 Appendicular skeleton

New information concerning the appendicular skeleton of *Westlothiana* comes primarily from the very well preserved right humerus and left femur. Both elements are significantly more slender than they were originally reconstructed (Smithson, Carroll et al. 1993). However, these original descriptions were primarily based on the second specimen.

3.3.3.1 Potential synapomorphies of the appendicular skeleton

Slender humerus, more than three times longer than distal width

A slender humerus, more than three times as long along its long axis as its maximum transverse width at the distal end, is found sporadically in a variety of early tetrapod taxa. In most taxa included in my phylogenetic analysis (see Chapter 4), the humerus is proportionally shorter than in *Westlothiana* and is less than three times as long as its maximum transverse width at the distal end, including temnospondyls such as *Balanerpeton* (Milner and Sequeira 1993) and *Edops* (Romer and Witter 1942), stem amniotes including seymouriamorphs (Klembara and Bartik 1999, Berman et al. 2000) and diadectomorphs (Berman et al. 1998, 2004, Kennedy 2010), and in many synapsids, including *Dimetrodon* (Romer et al. 1940) and *Haptodus* (Laurin 1993). In these taxa the humerus has a less slender appearance with more expanded distal ends. In stem tetrapod taxa such as *Greererpeton* (Godfrey 1989) and *Whatcheeria* (Otoo et al. 2021), in anthracosaurs such as *Archeria* (Romer 1957), and in *Silvanerpeton* (Ruta and Clack 2006), the humerus is L-shaped and lacks a well-defined shaft, giving it a particularly squat appearance.

However, amongst the taxa that are often recovered in a phylogenetic position close to *Westlothiana*, a slender humerus is present in many of the earliest-diverging amniotes crownwards of diadectomorphs, particularly araeoscelids (Reisz et al. 1981, 1984) and protorothyrids (Carroll 1964, 1969). This suggests a possible close phylogenetic relationship between *Westlothiana* and early-diverging amniotes.

Absence of entepicondylar foramen

An entepicondylar foramen is present in most stem amniotes and early crown amniotes, including *Archeria* (Romer 1957), seymouriamorphs such as *Seymouria* (Berman et al. 1987) and *Discosauriscus* (Klembara and Bartik 1999), diadectomorphs including *Diadectes* (Berman et al. 1998), protorothyrids (Carroll 1964, 1969), captorhinids (Fox and Bowman 1966, Reisz et al. 2016) and araeoscelids (Reisz 1981, Reisz et al. 1984). An entepicondylar foramen is absent, however, in a large number of lepospondyls. For example, the foramen is absent in several microsaurs including *Cardiocephalus* (Carroll and Gaskill 1978) and *Huskerpeton* (Huttenlocker et al. 2013), as well as the lysorophian *Brachydectes* (Wellstead 1991) and the nectridean *Keraterpeton* (Milner 2018). This indicates that there could be some tendency within lepospondyls to lose the entepicondylar foramen in those taxa that have relatively reduced limbs, which could suggest a close phylogenetic relationship of *Westlothiana* to lepospondyls.

Internal trochanter not separated from the shaft by trough-like space

In the original reconstruction of the femur in *Westlothiana*, the internal trochanter was reconstructed as being separated from the main shaft of the femur by a distinct trough (Smithson, Carroll et al. 1993), based on the second specimen. However, while the holotype shows a distinct internal trochanter, it is smoothly associated with the shaft, and there is no evidence of a trough. Moreover, in the original reconstruction it is clear from the figures that there was substantial damage in this region of the second specimen (Smithson, Carroll et al. 1993). The absence of such a trough, and a smooth intersection between the internal trochanter and proximal end of the femur, is very similar to most microsaurs (Carroll and Gaskill 1978), early amniotes such as *Hylonomus* (Carroll 1964) and *Petrolacosaurus* (Reisz 1981), and many crown amniotes including both synapsids (e.g. *Dimetrodon*, Romer et al. 1940, *Edaphosaurus* Modesto 1995) and reptiles (*Youngina*, Gow 1974, *Milleretta*, Gow 1972).

Presence of three proximal tarsal elements

The second specimen of *Westlothiana* was described to have three proximal tarsal elements. This is most similar to diadectomorphs, in which three proximal tarsal elements are present (Berman et al. 2004, Kennedy 2010). However, it represents the plesiomorphic condition relative to the earliest diverging amniotes, in which just two proximal tarsals are present, including in captorhinids (Fox and Bowman 1966, Reisz et al. 2015), protorothyrids (Carroll 1964, 1969) and araeoscelids (Reisz 1981, Reisz et al. 1984). The tibiale in the holotype of *Westlothiana* is also substantially reduced in size, as it is in diadectomorphs (Berman et al. 2004, Kennedy 2010). The number of tarsals in *Westlothiana*, nonetheless, is more derived than earlier diverging stem amniotes, in which three or four proximal tarsals of equal size are present including *Caerorachis* (Ruta et al. 2001), *Seymouria* (Berman et al. 2000) and *Gephyrostegus* (Carroll 1970), as well as stem tetrapods such as *Greererpeton* (Godfrey 1989), and temnospondyls such as *Balanerpeton* (Milner and Sequeira 1993), in which three or more large proximal tarsals are present.

Previously, it was unknown whether or not the holotype specimen of *Westlothiana* had two or three proximal tarsals. I reveal here that it is clear that the holotype of *Westlothiana* possessed three proximal tarsals, corroborating the described (but now unreffered) morphology of the second specimen (Smithson, Carroll et al. 1993) and therefore confirming that *Westlothiana*, in this respect, it is plesiomorphic relative to early amniotes, and most similar to diadectomorphs, regardless of whether or not the two specimens belong to the same taxon.

3.4 Systematic Palaeontology

AMNIOTA Haeckel, 1866

Genus *WESTLOTHIANA* Smithson & Rolfe, 1990

Type species. *Westlothiana lizziae* Smithson & Rolfe, 1990

Holotype. National Museums of Scotland NMS.1990.72.1, slab and counterslab. A nearly complete, mostly articulated skeleton.

Locality and Horizon. From Unit 82 of the East Kirkton Limestone (Smithson, Carroll et al. 1993), of the East Kirkton Quarry, near Bathgate, West Lothian, 17 miles west of Edinburgh, Scotland (Rolfe, Baird et al. 1993). The East Kirkton Limestone is within the West-Lothian Oil-Shale Formation, which can be assigned to Asbian-Brigantian age (Smith et al, 1993).

Revised Diagnosis. Overall length under 200mm. Skull table and temporal region amniote-like: skull has wide parietal bones, intertemporal absent, tabular and supratemporal form posterolateral corner of orbit. Postparietal, tabular and supratemporal all restricted to skull table. Orbits are large and anteroposteriorly elongate, encompassing ring of sclerotic plates, postfrontal large and extends almost to front of orbit, contacting prefrontal. Lacrimal has dorsal orbital process. Vomer elongate and bulbous anteriorly. Palatine deeply incised to accommodate internal naris. Plesiomorphic palatal dentition; palate is almost entirely denticulate, including parasphenoid plate and quadrate ramus of pterygoid. Fang pairs present on vomer and palatine but not ectopterygoid. Ectopterygoid is large, so near equal in size to palatine. Pterygoid lacks amniote-like transverse flange. Quadrate large and vertical. Atlas lacks odontoid process, atlas anterior and posterior articulating surfaces equal in width, atlas neural arch unfused to centrum. 36 gastrocentrous presacral vertebrae. Neural arches fused to centra, wedge-shaped intercentra, ribs extend for length of presacral vertebral column. Limbs particularly small relative to trunk. Forelimbs approximately half the size of hindlimbs, humerus clearly waisted and with supinator process, large pelvis with long puboischiadic plate, slender femur with only very moderately expanded proximal and distal ends. Three proximal tarsals in which the tibiale is significantly smaller than the rest, four distal tarsals, and four digits on the pes. Pes phalangeal formula 2, 4, 5, 4. Thick, overlapping dorsal scales and thin, narrow, oblong ventral scales.

Westlothiana species sp. nov.

Holotype. NMS.1991.47.1, slab and counterslab. A skeleton preserving an almost complete, but disarticulated post-cranium, and no cranial material.

Locality and Horizon. From Unit 76 of the East Kirkton Limestone (Smithson, Carroll et al. 1993), of the East Kirkton Quarry, detail of which is given above.

Revised Diagnosis. Diagnosis the same as the holotype specimen in the morphology of individual vertebrae, the rib morphology, the size of the puboischiadic plate, the proportions of the limbs relative to both the trunk, most features of the humerus and femur, the proportions of the forelimbs relative to the hindlimbs, and the presence of three proximal tarsals. Differs from the holotype in the following ways: larger size, overall length up to 300mm, widely expanded distal end of humerus, entepicondylar foramen present on humerus, the presence of 40 rather than 36 presacral vertebrae, widely expanded proximal and distal ends of the femur, two centralia and five distal tarsals, and five digits on the pes with a phalangeal formula of 2-3-4-5-4.

Remarks. When originally described, NMS.1991.47.1 was referred to *Westlothiana lizziae.* Here, I unrefer this specimen to the taxon *Westlothiana lizziae*, and instead determine that it should be referred to a novel species, *Westlothiana sp.nov.* The two specimens are from different units of the East Kirkton Limestone. However, during the original research little was known about the postcranial morphology of the holotype. Now that more detail of the holotype is known, substantial differences can be noted between the two specimens, including the differing numbers of vertebrae, and the differing components making up the foot. I deem that these features are highly unlikely to be ontogenetic, and therefore sufficient to refer NMS.1991.47.1 to a new taxon.

3.5 Conclusion

Many features of the postcranial skeleton of *Westlothiana* provide possible evidence for its phylogenetic relationships. As with the cranial skeleton, *Westlothiana* demonstrates traits of earlier stem amniotes, lepospondyls, and amniotes crownwards of diadectomorphs. Many aspects of the appendicular skeleton are more similar to lepospondyls, and especially microsaurs. These traits include the small size of both the forelimbs and hindlimbs, the absence of an entepicondylar foramen in the humerus, and, in the femur, the absence of a fourth trochanter and a trough between the first trochanter and the shaft. In contrast, the atlas-axis complex lacks key features that are observed in

lepospondyls, including the expanded anterior articulating surface that is present in microsaurs, and the anteriorly projecting odontoid process that is present widely across lepospondyls.

The vertebrae of *Westlothiana* are similar to those of stem-amniotes and early crown amniotes in the presence of large pleurocentra and moderately sized, wedge-shaped intercentra in between the pleurocentra. The ribs, too, are fairly long and gently curved like those of early amniotes. The proportions of the bones of the limbs are similar to those of some of the earliest diverging amniotes. In particular, the very slender proportions of the humerus and femur are most similar to protorothyrids and araeoscelids amongst late-diverging stem amniotes and early-diverging crown amniotes. Despite this, the tarsus is plesiomorphic with respect to crown amniotes in that it retains three proximal tarsal elements and does not possess the astragalus and calcaneum of early amniotes. Instead, the presence of three proximal tarsals, of which the tibiale is highly reduced in size, closely resembles the condition in diadectomorphs. There appear to be four distal tarsals and four digits in the pes, at least of the holotype specimen, a unique morphology amongst stem tetrapods, stem amniotes and early crown amniotes.

NMS.1991.47.1, a specimen which was originally referred to *Westlothiana lizziae*, is shown to be more different to the holotype specimen of *Westlothiana* than originally believed. In additional to the previously described 40 presacral vertberae (contrasting 36 presacral vertebrae in the holotype), the morphology of the humeri and femora are different, and NMS.1991.47.1 has a larger puboischiadic plate, and a larger number of tarsal bones. These differences are sufficient to conclude that NMS.1991.47.1 represents a new taxon.

Chapter 4: A Novel Phylogenetic Analysis of Stem Amniotes

4.1 Introduction

Tetrapoda consists of amphibians, mammals, birds and reptiles and includes all living terrestrial vertebrates. The tetrapod crown group is defined by the basal divergence between Lissamphibia (frogs, salamanders and caecilians) and Amniota (mammals, and reptiles including birds) (Laurin and Anderson 2004). Today, amniotes include 78% of all tetrapod species (IUCN 2020). Amniotes are characterised by key anatomical innovations that allow them to live on land; eggs with an amniotic membrane (Romer 1957, Packard and Seymour 1997, Clack 2012), rib-based lung ventilation, epaxial muscles for postural support and the differentiation into separate pterygoideus and temporalis jaw adductor muscles allowing for static pressure in the jaws (Janis and Keller 2001), as well as multiple osteological correlates with terrestrial locomotion, such as the progressively more gracile humerus (Sumida and Martin 1997).

Palaeontologists have debated which fossil clades are most closely related to amniotes since the latter half of the 19th Century (Huxley 1863, Cope 1880). Generally, several groups are considered to be related to amniotes, including anthracosaurs, seymouriamorphs, gephyrostegids, chroniosuchians, lepospondyls and diadectamorphs (Ruta et al. 2003, Ruta and Coates 2007). However, to this day, contrasting hypotheses exist that find a stem tetrapod position for anthracosaurs and seymouriamorphs, or some lepospondyls (Laurin, Reisz et al. 1997, Pardo, Szostakiwskyj et al. 2017), or stem amphibian position for lepospondyls (Laurin, Reisz et al. 1997, Marjanović and Laurin 2019), and there are also doubts about the monophyly of lepospondyls (Pardo, Szostakiwskyj et al. 2017, Clack, Ruta et al. 2019). Key uncertainties remain, particularly regarding the monophyly and phylogenetic position of lepospondyls. As such, no truly universal consensus has emerged about which fossil clades are more closely related to amniotes than to amphibians, or about the topology of the amniote stem and early amniote crown.

4.1.1 The phylogenetic relationships of stem amniotes

Several fossil clades are typically recovered on the amniote stem in most modern phylogenetic analyses. These clades include anthracosaurs, seymouriamorphs, gephyrostegids, lepospondyls and Diadectomorphs (Ruta et al. 2003, Ruta and Clack 2006, Ruta and Coates 2007, Clack and Klembara 2008, Huttenlocker et al. 2013, Clack et al. 2016, 2019, Ruta et al. 2020, Klembara et al. 2021, see also Chap. 1 Table. 1). Diadectomorphs, in particular, are usually recovered as the sister-clade to the amniote crown (Laurin and Reisz, 1995, Laurin, Reisz et al. 1997, Laurin 1998; Ruta et al. 2003, Vallin and Laurin 2004, Ruta and Coates 2007, Pardo et al. 2017, Ford and Benson, 2020). The origin of the amniote crown node is characterised, further, by the division between the mammalian total group, Synapsida, and the reptile total group, Reptilia (Laurin and Reisz 1995, Modesto & Anderson, 2004). Nonetheless, the phylogenetic identity and position of several clades has remained difficult and enigmatic, with new hypotheses emerging in the last decade to challenge older phylogenetic topologies.

4.1.2 The position of lissamphibians and lepospondyls

The identity of certain clades as either stem tetrapods or as stem amniotes can change depending on the supposed affinities of Lissamphibia. Many phylogenetic analyses have recovered lissamphibians completely within Lepospondyli (Laurin, Reisz et al. 1997, Laurin 1998, Vallin and Laurin 2004, Marjanovic and Laurin 2019). Lissamphibians may also be only partially recovered within lepospondyls, due to the stem-caecilian *Eocaecilia* sometimes showing an affinity to long bodied lepospondyls (McGowan 2002, Huttenlocker et al. 2013). Notwithstanding the position of lissamphibians, lepospondyls, themselves, have proved a particularly difficult clade to resolve, which has further complicated the situation (see below for further discussion). In the cases in which lepospondyls are considered monophyletic, they are usually recovered as more being closely related to amniotes than several other fossil groups, including anthracosaurs and seymouriamorphs (e.g. Laurin, Reisz et al. 1997). Therefore, when lissamphians are found within lepospondyls, this has the effect of pushing clades such as seymouriamorphs and anthracosaurs onto the tetrapod stem lineage.

Nevertheless, whilst it is still not universally accepted, a consensus appears to be emerging that lissamphibians are not lepospondyls, but instead belong within temnospondyls. This has been recovered in the majority of modern phylogenetic analyses (Ruta et al. 2003, Ruta and Clack 2006, Ruta and Coates 2007, Huttenlocker et al. 2013, Clack et al. 2016, Pardo et al. 2017, Clack et al. 2019, Ruta et al. 2020, Gee et al. 2021, Klembara et al. 2021), and has received increasing support in recent years due to the discovery of new fossils that support a close relationship between amphibians and one particular clade of temnospondyls, Dissorophoidea, including the key taxon *Gerobatrachus*, (Anderson et al. 2008). A recently discovered, possible stem caecilian, *Funcusvermis*, has also helped to bridge the morphological gap between caecilians and dissorophoids (Kligman et al. 2023). Other recent phylogenetic analyses have recovered non-caecilian lissamphibians within dissorophoid temnospondyls, and have recovered caecilians within non-dissorophoid temnospondyls (Pardo et al. 2017). This is, nevertheless, consistent with a monophyletic Lissamphibia (with respect to amniotes) having originated within temnospondyls.

4.1.3 Problematic clades of stem amniotes

The monophyly of lepospondyls, generally accepted for many years (Carroll 2000, Clack 2012) has recently been doubted. This is due to the placement of two clades that are commonly referred to Lepospondyli: Microsauria and Aïstopoda. Microsaurs, an anatomically diverse group, are often regarded as lepospondyls (e.g. Ruta et al. 2003, Ruta and Coates 2007). However, in recent years, they have also been suggested as phylogenetically separate from other lepospondyls, as close to (Clack et al. 2019) or within (Pardo et al. 2017) the amniote crown, based on similarities between themselves and the captorhinid *Opisthodontosaurus* (Reisz et al. 2015). The aïstopod *Lethiscus stocki*, from the Mid-Viséan of Scotland (Anderson et al. 2003), is also often regarded as a lepospondyl (Carroll 2000, Clack 2012), and therefore the earliest occurring probable stem amniote. It has also, however, been considered a stem tetrapod due to a plesiomorphic braincase anatomy (Pardo et al. 2017), which suggests that aïstopods do not form a monophyletic group with other lepospondyls.

Diadectomorphs, the clade most often considered to form the sister-clade to crown amniotes, also lacks a universal phylogenetic consensus. In a small number of analyses, they are recovered as crown amniotes, as the sister-clade to Synapsida (Berman et al. 2000, Marjanovic and Laurin 2019, Ruta et al. 2020, Klembara et al. 2021).

The reptile groups traditionally recovered as the sister-clades to diapsid reptiles, Araeoscelidia and Captorhinida (e.g. Laurin and Reisz 1995), have also not held a stable phylogenetic position in recent analyses. Ford and Benson (2020) recovered a novel topology of stem reptiles that found parareptiles close to the reptilian crown. This suggested that araeoscelids and captorhinomorphs were not the sister-clades to diapsid reptiles. Moreover, it also indicated that the evolution of a morphologically diapsid temporal fenestration showed homoplasy. Other recent analyses have recovered captorhinids and araeoscelids as stem amniotes, and not members of total group Reptilia at all (Simões, Kammerer et al. 2022).

4.1.4 Romer's gap

Different phylogenetic topologies of early tetrapods, amphibians and amniotes have different implications for the timing of the divergences of these various clades. As such, substantial disparities exist within the hypothesised divergences of total group amphibians and total group reptiles. In particular, this relates to the extent of evolution and diversification that occurred during a period known as Romer's gap.

Romer's gap is a period of scarcity of terrestrial tetrapod fossils following the End Devonian Mass Extinction, first observed by Romer (1956). The gap was originally thought to last for approximately 30 million years, but fossil discoveries of terrestrial tetrapods in the later half of the 20th Century, such as those of East Kirkton (see Chapter 2), narrowed the gap to 15 million years (Smithson, Wood et al. 2012).

Romer's gap has been widely regarded as a gap in the fossil record, during which we are missing sufficient evidence of terrestrial tetrapod evolution (Coates and Clack 1995, Clack 2002). Nonetheless, some authors have suggested that this was a genuine period marked by a rarity of

tetrapods in terrestrial ecosystems due to low oxygen levels (Ward, Labandeira et al. 2006). Other authors have suggested that it was simply a period in which terrestrial tetrapod specimens are rare due to lack of sampling (Smithson, Wood et al. 2012), and recent fossil discoveries have continued to further populate the gap with evidence of terrestrial tetrapods (Smithson, Wood et al. 2012, Clack, Ruta et al. 2019).

Time-calibration of the novel topology recovered by Pardo et al. (2017) finds the origin of the tetrapod crown, after which followed a substantial period of diversification, to be approximately 337 Ma, just after Romer's gap, with very little diversification during the gap. Thus, this phylogenetic topology is entirely consistent with the hypothesis that Romer's gap represented a genuine lull in terrestrial vertebrate evolution. However, this finding is contingent on the phylogenetic position of *Lethiscus stocki* from the early Viséan of Scotland, which Pardo et al. (2017) recovered as a stem tetrapod, a result not found in any previous phylogenetic analyses (Ruta et al. 2003, Ruta and Coates 2007). Moreover, Pardo et al. (2017) did not include *Westlothiana lizziae* in their analysis. *Westlothiana* is from the late Viséan of Scotland and has long been considered to have a close relationship with amniotes (Smithson et al. 1993, Ruta et al. 2003, Ruta and Coates 2007).

Here, I seek to evaluate phylogenetic hypotheses of early terrestrial vertebrates, with a focus on taxa that are typically regarded as stem amniotes or early crown amniotes. I present a novel phylogenetic analysis with a character list compiled following an extensive review of existing phylogenetic analyses in the literature. Mine is the first phylogenetic analysis to include substantial, and near equal, representation of taxa that are traditionally considered as both stem and crown amniotes, allowing contradicting hypotheses of the phylogenetic relationships of lepospondyls to be robustly tested.

4.2 Methods

4.2.1 Character List and Data Matrix

I compiled a taxon list with a focus on extensive taxonomic representation of both stem and traditionally recognised crown amniotes. 77 taxa were included in total. This included seven stem tetrapods, representing two separate potential outgroups (see below), four temnospondyls, the stem amphibian *Gerobatrachus*, 36 taxa typically recognised as stem amniotes and 27 taxa typically recognised as crown amniotes. *Whatcheeria* and *Pederpes* were selected as the outgroup (see below). Additionally, *Eusthenopteron*, *Tiktaalik* and *Acanthostega* were selected as a more expansive outgroup to test the impact of the outgroup on the topology.

I constructed a novel character list of 328 characters (313 of which are parsimony informative for this selection of taxa), following a comprehensive review of major previous phylogenetic analyses of stem tetrapods, stem amniotes and crown amniotes (Laurin and Reisz 1995, Laurin, Reisz et al. 1997, Laurin 1998, Berman et al. 2000, Anderson 2001, Ruta et al. 2003, Ruta and Coates 2007, Benson 2012, Huttenlocker et al. 2013, Klembara et al. 2014, Clack et al. 2016, Pardo et al. 2017, Clack et al. 2019, Marjanovic and Laurin 2019, Ford and Benson 2020, Simões et al. 2022). My analysis includes 28 novel characters, 23 of which concern the sutural contacts within the skull, and five of which are based on observations of the anatomy of specimens and within the literature. Taxa were scored following a combination of observations of specimens, and consulting the relevant literature. I completed first hand observations of specimens for 23% of included taxa. All specimens and literature used for this purpose are outlined in Appendix 1. A complete character list, including additional explanatory comments on their usage in previous analyses are provided in Appendix 2.

4.2.2 Phylogenetic Analysis.

4.2.2.1 Maximum Parsimony Analysis. I performed maximum parsimony phylogenetic analyses using Paup* 4.0a169. All characters were equally weighted and unordered. All analyses were performed using the heuristic algorithm using 100,000 random addition replicates with a tree bisection reconnection (TBR) branch swapping algorithm, holding one tree in memory at each replicate. Following this, the trees stored in memory were subjected to multiple rounds of the same search algorithm, but with the save multiple trees option enforced, until no additional Most Parsimonious Trees (MPTs) were obtained.

The initial analysis resulted in 174 MPTs of length 2074 steps after the first search, with an additional three MPTs obtained following the repeated searches, resulting in a total of 177 MPTs. In order to improve the resolution, the Strict and Adams consensuses were compared to identify 'wildcard taxa' that occupy multiple positions in different MPTs, following the approach of Ketchum & Benson (2010). *Archaeothyris*, *Echinerpeton* and *Carrolla* were identified as 'wildcard taxa'. Pruning these taxa resulted in 150 trees being discarded due to redundancy, and as such these taxa were excluded. In order to assess the statistical support for the results, I calculated the Bremer support and performed a Bootstrap analysis, both of which were carried out in Paup* 4.0a169. The Bootstrap analysis consisted of a full heuristic search following the parameters outlined above, and 100 replicates.

To ensure that the choice of outgroup was not biasing the topology, I performed a second phylogenetic analysis with a more expansive outgroup consisting of *Eusthenopteron*, *Tiktaalik* and *Acanthostega*, with *Whatcheeria* and *Pederpes* included in the ingroup. The choice of outgroup in a maximum parsimony phylogenetic analysis determines the relative polarity of characters (Farris 1982, Lyons-Weiler, Hoelzer et al. 1998). Topology can therefore vary depending on the choice of outgroup (Lyons-Weiler, Hoelzer et al. 1998, Wilberg 2015).

In the phylogenetic analysis with the expanded outgroup, 30 MPTs were obtained, and the resolution was improved following the above methodology. *Baphetes* and *Echinerpeton* were identified as wildcard taxa. Once removed, three MPTs were obtained. The topology did not differ at

all from the results using the initial outgroup. The tree resulting from the MP analysis was calibrated to geological time using the timePaleoPhy function in the R package Paleotree v3.4.5 (Bapst 2012).

4.2.2.2 Bayesian Analysis. I performed a non-time calibrated Bayesian phylogenetic analysis on the same dataset twice, once with *Whatcheeria* defined as the outgroup and once with *Eusthenopteron* defined as the outgroup. The parameters of each analysis were the same. Rates were set to 'gamma' and coding was set to 'informative'. The analysis was allowed to run for up to 100,000,000 generations, and was run until the standard deviation of split frequencies had a value of <0.01, the stop value, ensuring convergence was reached.

I also performed a time-calibrated Bayesian phylogenetic analysis using the Fossilised Birth-Death (FBD) model, with an igr clock model on the taxon sample with the outgroup *Whatcheeria*, with rates set to 'gamma' and coding set to 'informative'. The ages of all the OTUs were specified using a uniform distribution between the maximum and minimum possible numerical ages of the taxa, following an assessment of the estimates of rock ages in the literature (Appendix 3). The treeage prior was set to uniform between the age of the oldest fossil (*Whatcheeria*, 341Ma), and the base of the Carboniferous Period, the beginning of Romer's gap, as no evidence of terrestrial vertebrates is known before this time. The other parameters for the analysis were as in the non-time calibrated Bayesian analysis.

4.3 Results

4.3.1 Phylogenetic topologies

4.3.1.1 Maximum Parsimony. (Fig. 1a) *Greererpeton* is recovered as the earliest diverging ingroup taxon. It is therefore here recovered as a stem tetrapod. *Caerorachis* and *Baphetes* are recovered in a basal polytomy with the total groups Lissamphibia and Amniota (assuming that the position of Lissamphibia is marked by the position of temnospondyls, including *Gerobatrachus*). However, this polytomy is due to the uncertain position of *Baphetes*, which is recovered either as the sister taxon to the crown tetrapod group, or as an early diverging stem amniote, one step crownwards of *Caerorachis*. *Caerorachis* itself is invariably recovered as the earliest diverging stem amniote, as

shown by the Adams consensus (Fig. 1b). Temnospondyls are recovered as a monophyletic group, with *Edops* as the earliest diverging temnospondyl. *Doleserpeton* is found to be the sister taxon to *Gerobatrachus*, a result that is consistent with a dissorophoid temnospondyl origin for Lissamphibia, as is found in most recent phylogenetic analyses (Pardo et al. 2017, Kligman et al. 2023).

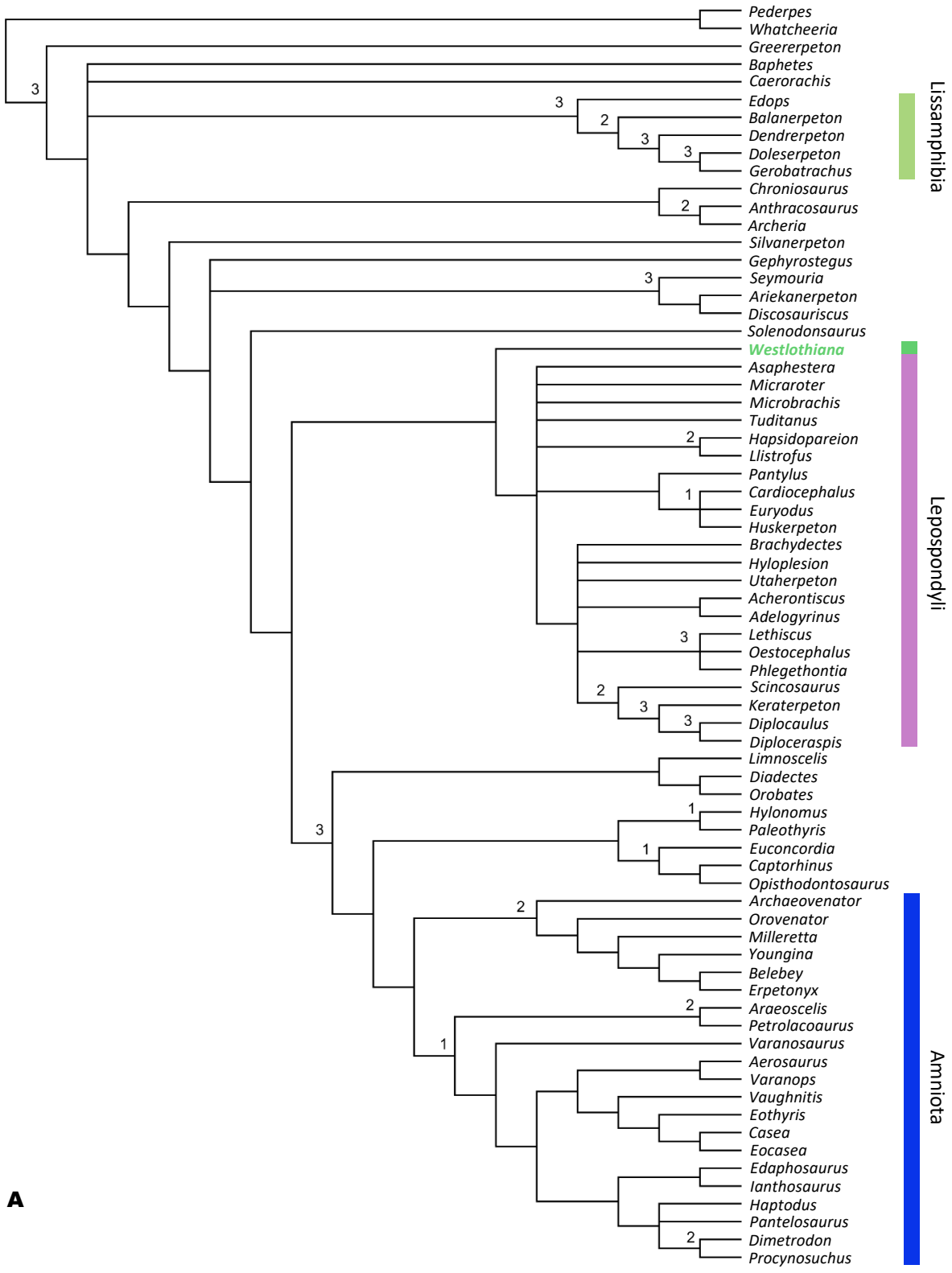
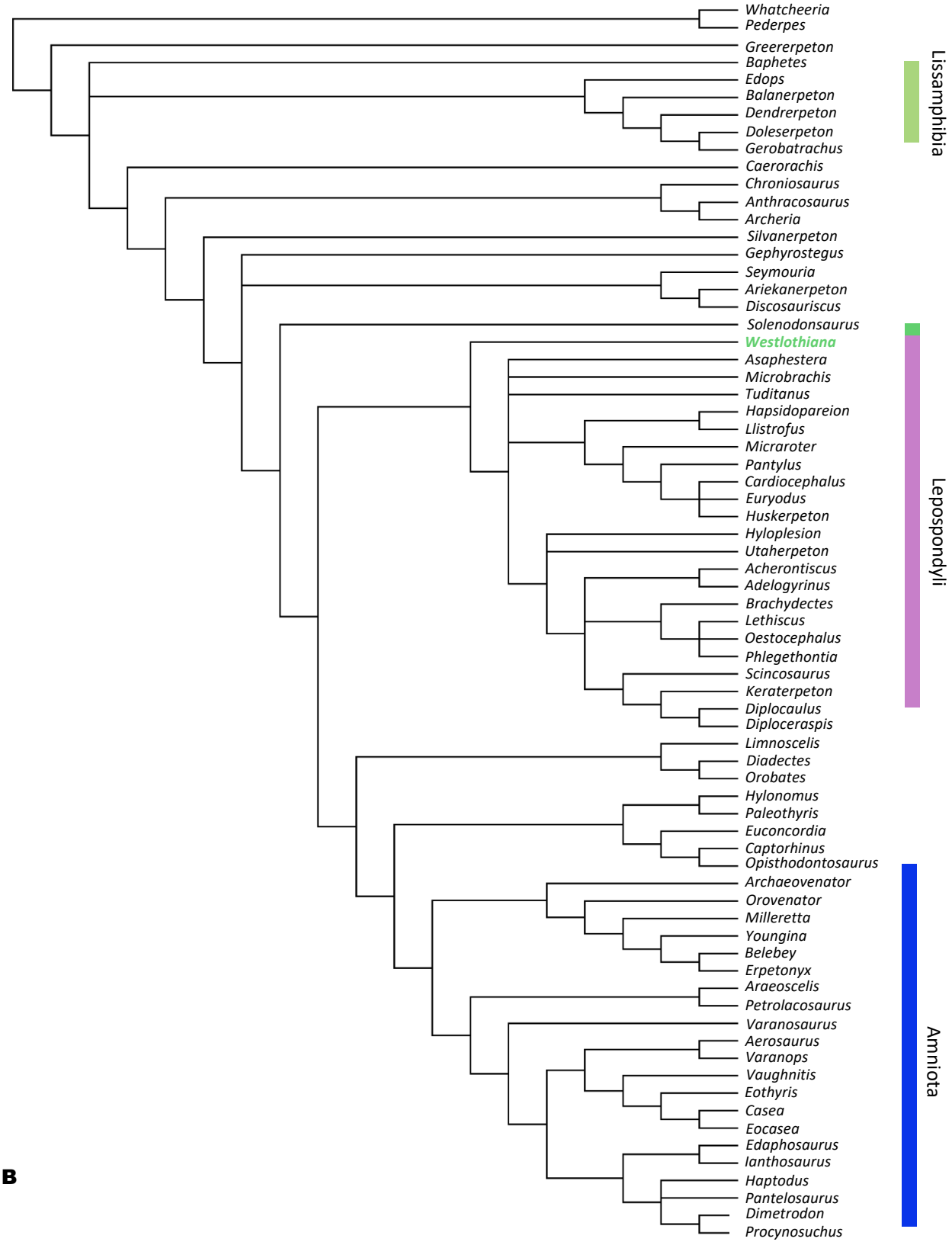


Fig. 1 (Across the following and previous pages):

A (previous page), Strict Consensus Tree, numbers indicate Bremer support values. B (this page), Adams Consensus Tree. C, Bootstrap Tree with all taxa included. D, Bootstrap Tree with adelospondyls removed. E, Strict Consensus Tree with expanded outgroup including *Eusthenopteron*, *Tiktaalik* and *Acanthostega*.



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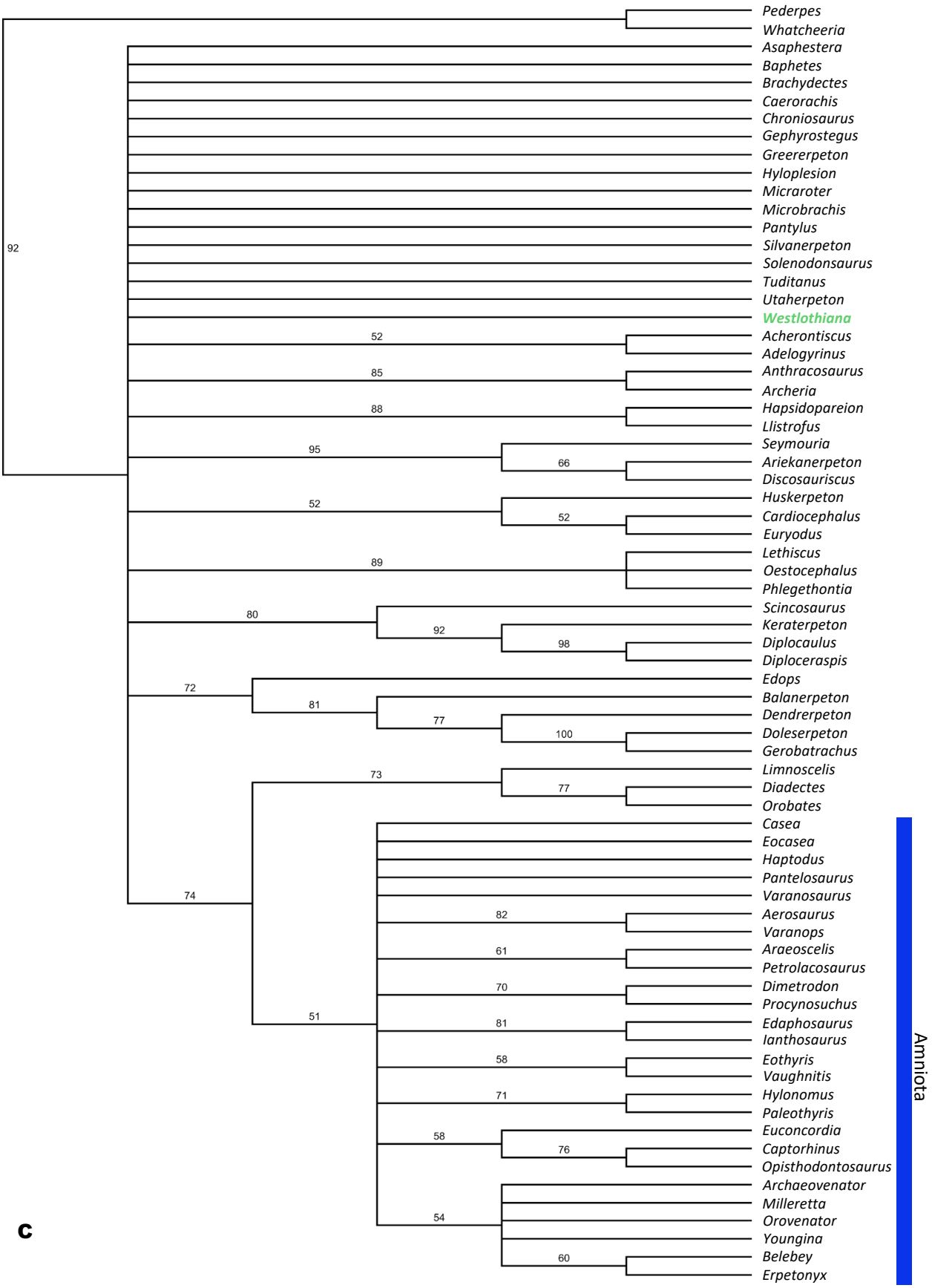
Pederpes
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Asaphestera
Baphetes
Brachydectes
Caerorachis
Chroniosaurus
Gephyrostegus
Greererpeton
Hyloplesion
Micraroter
Microbrachis
Pantylus
Silvanerpeton
Solenodonsaurus
Tuditanus
Utaherpeton
Westlothiana
Acherontiscus
Adelogyrinus
Anthracosaurus
Archeria
Hapsidopareion
Llistrofus
Seymouria
Ariekanerpeton
Discosauriscus
Huskerpeton
Cardiocephalus
Euryodus
Lethiscus
Oestocephalus
Phlegethontia
Scincosaurus
Keraterpeton
Diplocaulus
Diploceraspis
Edops
Balanerpeton
Dendrerpeton
Doleserpeton
Gerobatrachus
Limnoscelis
Diadectes
Orobates
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Eocasea
Haptodus
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Varanosaurus
Aerosaurus
Varanops
Araeoscelis
Petrolacosaurus
Dimetrodon
Procynosuchus
Edaphosaurus
Ianthosaurus
Eothyris
Vaughnitis
Hylonomus
Paleothyris
Euconcordia
Captorhinus
Opisthodontosaurus
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Orovenator
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Erpetonyx
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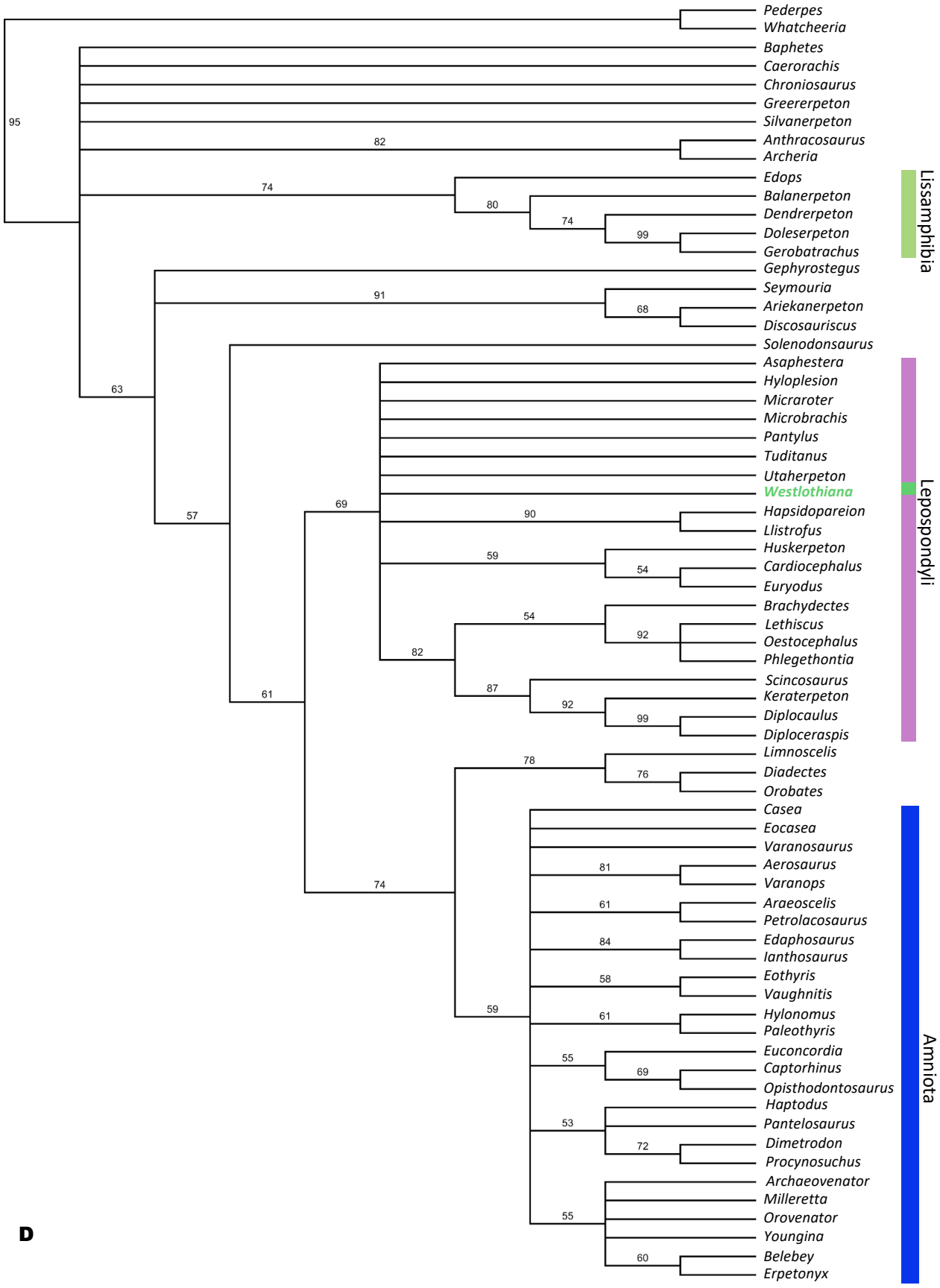
Pederpes
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Baphetes
Caerorachis
Chroniosaurus
Greererpeton
Silvanerpeton
Anthracosaurus
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Dendrerpeton
Doleserpeton
Gerobatrachus
Gephyrostegus
Seymouria
Ariekanerpeton
Discosauriscus
Solenodonsaurus
Asaphestera
Hyloplesion
Micraroter
Microbrachis
Pantylus
Tuditanus
Utaherpeton
Westlothiana
Hapsidopareion
Llistrofus
Huskerpeton
Cardiocephalus
Euryodus
Brachydectes
Lethiscus
Oestocephalus
Phlegethontia
Scincosaurus
Keraterpeton
Diplocaulus
Diploceraspis
Limnoscelis
Diadectes
Orobates
Casea
Eocasea
Varanosaurus
Aerosaurus
Varanops
Araeoscelis
Petrolacosaurus
Edaphosaurus
Ianthosaurus
Eothyris
Vaughnitis
Hylonomus
Paleothyris
Euconcordia
Captorhinus
Opisthodontosaurus
Haptodus
Pantelosaurus
Dimetrodon
Procynosuchus
Archaeovenator
Milleretta
Orovenator
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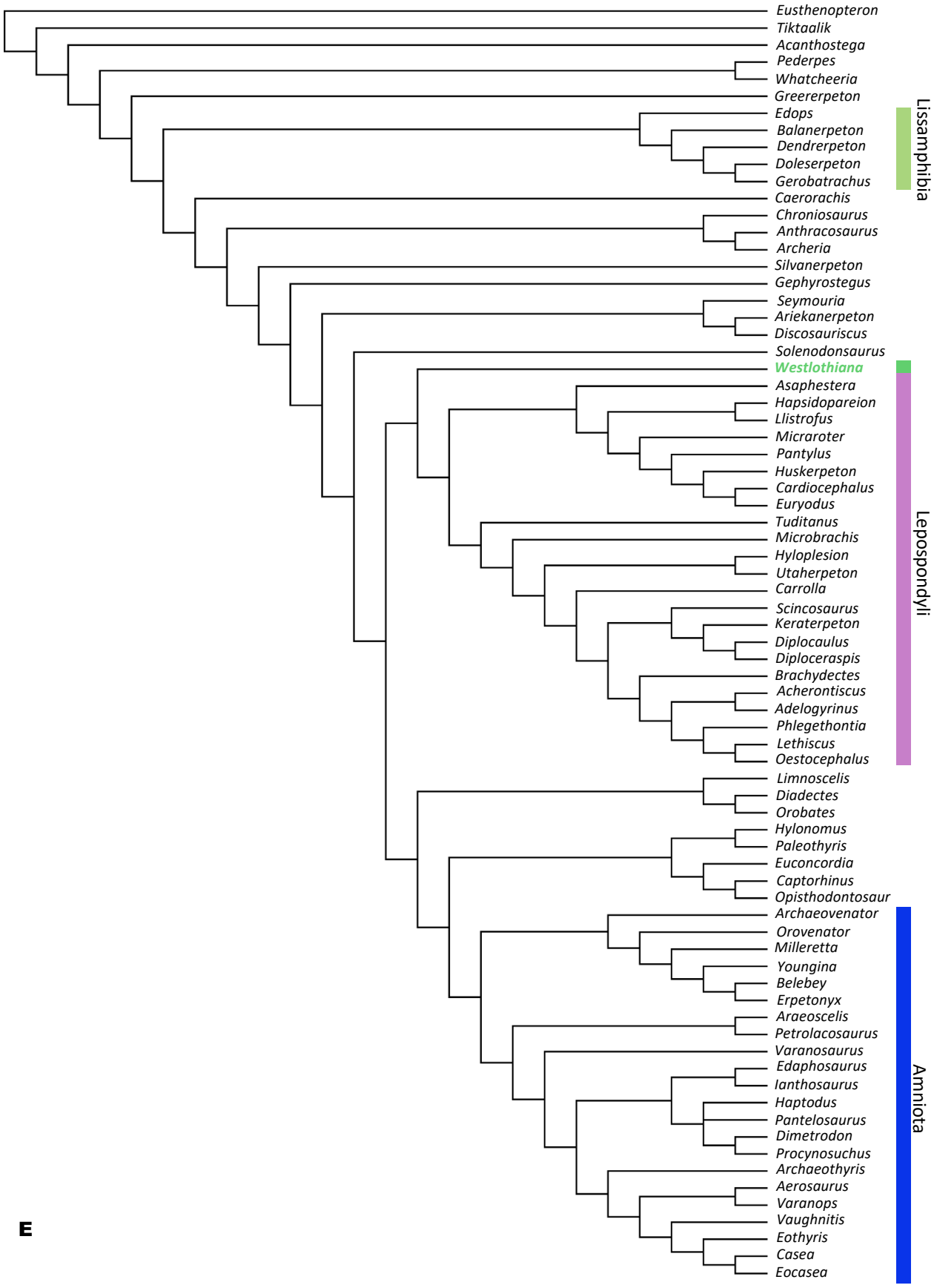
Lissamphibia
Lepospondyli
Amniota

D


Eusthenopteron
Tiktaalik
Acanthostega
Pederpes
Whatcheeria
Greererpeton
Edops
Balanerpeton
Dendrerpeton
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Caerorachis
Chroniosaurus
Anthracosaurus
Archeria
Silvanerpeton
Gephyrostegus
Seymouria
Ariekanerpeton
Discosauriscus
Solenodonsaurus
Westlothiana
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Hapsidopareion
Llistrofus
Micraroter
Pantylus
Huskerpeton
Cardiocephalus
Euryodus
Tuditanus
Microbrachis
Hyloplesion
Utaherpeton
Carrolla
Scincosaurus
Keraterpeton
Diplocaulus
Diploceraspis
Brachydectes
Acherontiscus
Adelogyrinus
Phlegethontia
Lethiscus
Oestocephalus
Limnoscelis
Diadectes
Orobates
Hylonomus
Paleothyris
Euconcordia
Captorhinus
Opisthodontosaur
Archaeovenator
Orovenator
Milleretta
Youngina
Belebey
Erpetonyx
Araeoscelis
Petrolacosaurus
Varanosaurus
Edaphosaurus
Ianthosaurus
Haptodus
Pantelosaurus
Dimetrodon
Procynosuchus
Archaeothyris
Aerosaurus
Varanops
Vaughnitis
Eothyris
Casea
Eocasea
Lissamphibia
Lepospondyli
Amniota

E

The earliest diverging group that is definitively on the amniote stem is *Chroniosaurus* + anthracosaurs including *Archeria* and *Anthracosaurus*. This is followed successively by *Silvanerpeton*, seymouriamorphs + *Gephyrostegus*, and *Solenodonsaurus*, as sequentially closer divergences to crown amniotes. *Solenodonsaurus* is recovered as the sister taxon to a clade consisting of lepospondyls, and diadectomorphs + amniotes. Thus, seymouriamorphs, gephyrostegids and anthracosaurs are all recovered as stem amniotes, contrasting the stem-tetrapod position of anthracosaurs returned by Pardo et al. (2017).

Lepospondyli is recovered as a monophyletic, consisting of microsaurs, nectrideans, lysorophians, adelospondyls and aïstopods. *Westlothiana* is recovered as the sister taxon to a monophyletic Lepospondyli. Most microsaurs are recovered as a basal polytomy comprising the earliest diverging positions within lepospondyls. All taxa typically considered to be microsaurs are recovered within this polytomy, either monophyletic or paraphyletic with respect to all other lepospondyls, apart from *Utaherpeton* and *Hyloplesion*, which are found to be in a polytomy with adelogyrinids, *Brachydectes*, aïstopods and nectrideans. Aïstopods form a clade, as do nectrideans. The clade encompassing lepospondyls, and *Westlothiana*, is recovered as the sister clade to a clade comprising diadectomorphs (which themselves form a monophyletic group) plus all more crownward lineages. Captorhinids and protorothyrids form a clade of crownward stem amniotes, as the immediate sister to crown amniotes. A crownward stem amniote position of captorhinids and protorothyrids was also recovered by Simões et al (2023).

Within Amniota, *Archaeovenator* and *Orovenator* are recovered as the respectively earliest diverging members of total group Reptilia, forming a paraphyletic grade. *Youngina* is recovered as nested within the three parareptiles included in this analysis, with *Milleretta* forming the sister taxon to a *Youngina* + (*Belebey* + *Erpetonyx*) clade. Araeoscelids, traditionally recovered as and widely hypothesised to be the earliest diapsid reptiles (Reisz 1977, Gauthier et al. 1988, Laurin and Reisz 1995), are here recovered as the earliest diverging group of total group Synapsida. This is a completely novel result that has not been recovered elsewhere previously. *Varanosaurus* is recovered as the next earliest diverging synapsid. All other included synapsids are characterised by a basal

dichotomy. Edaphosaurids and sphenacodontids form one branch, and varanopids and caseids form the other.

There are no significant changes to the topology of the tree recovered by Maximum Parsimony Analysis in which *Eusthenopteron*, *Tiktaalik* and *Acanthostega* are added to form an outgroup (Fig 1c).

4.3.1.2 Non-time calibrated Bayesian Phylogenetic Analysis. I carried out two Bayesian phylogenetic analyses, one analysis without *Eusthenopteron*, *Tiktaalik* and *Acanthostega*, in which *Whatcheeria* is specified as the outgroup (hereafter referred to as Bayesian analysis A), and one where the aforementioned taxa are all included and *Eusthenopteron* is specified as the outgroup (hereafter referred to as Bayesian analysis B). Convergence was achieved in both analyses, with an average PSRF of 1, and a maximum PSRF of 1.006 and 1.008 and average ESS of 4656.75 and 4083.05 (for the TL parameter) in analyses A and B respectively.

The results of both of these analyses are very similar to each other. The results of the Bayesian phylogenetic analyses are also broadly similar to the results of the Maximum Parsimony analyses, with no substantial topological differences. Nonetheless, a small number of minor differences are recovered.

In Bayesian analysis A (Fig. 2a), *Greererpeton* and *Baphetes* are recovered as sequentially closer sister taxa to crown group tetrapods. However, in Bayesian analysis B (Fig. 2b) *Greererpeton* and *Baphetes* form a polytomy with the tetrapod crown group. In both Bayesian analyses, *Gephyrostegus* is not recovered as the sister taxon to seymouriamorphs, but rather as the sister taxon to a clade formed of seymouriamorphs and all more crownward lineages.

In both analyses, lepospondyls continue to be recovered as a monophyletic group, and *Westlothiana* continues to be recovered as the earliest diverging lepospondyl. Moreover, in both analyses, lepospondyls, reptiles and synapsids all have less internal resolution than in the Maximum Parsimony analyses. This is particularly the case for synapsids and for lepospondyls; within both clades just a few small clades are recovered, but the majority of taxa and clades form a single, large polytomy.

Within lepospondyls, aïstopods, nectrideans and adelogyrinids are still recovered as monophyletic. Some groups of microsaurs form clades with each other: *Llistrofus* and *Hapsidopareion* form a clade, *Tuditanus* and *Asaphestera* form a clade, and a clade consisting of *Micraroter*, *Pantylus*, *Huskerpeton*, *Euryodus* and *Cardiocephalus* is alos recovered. Nonetheless, each of these clades, and all other microsaurs, form a polytomy with other lepospondyls.

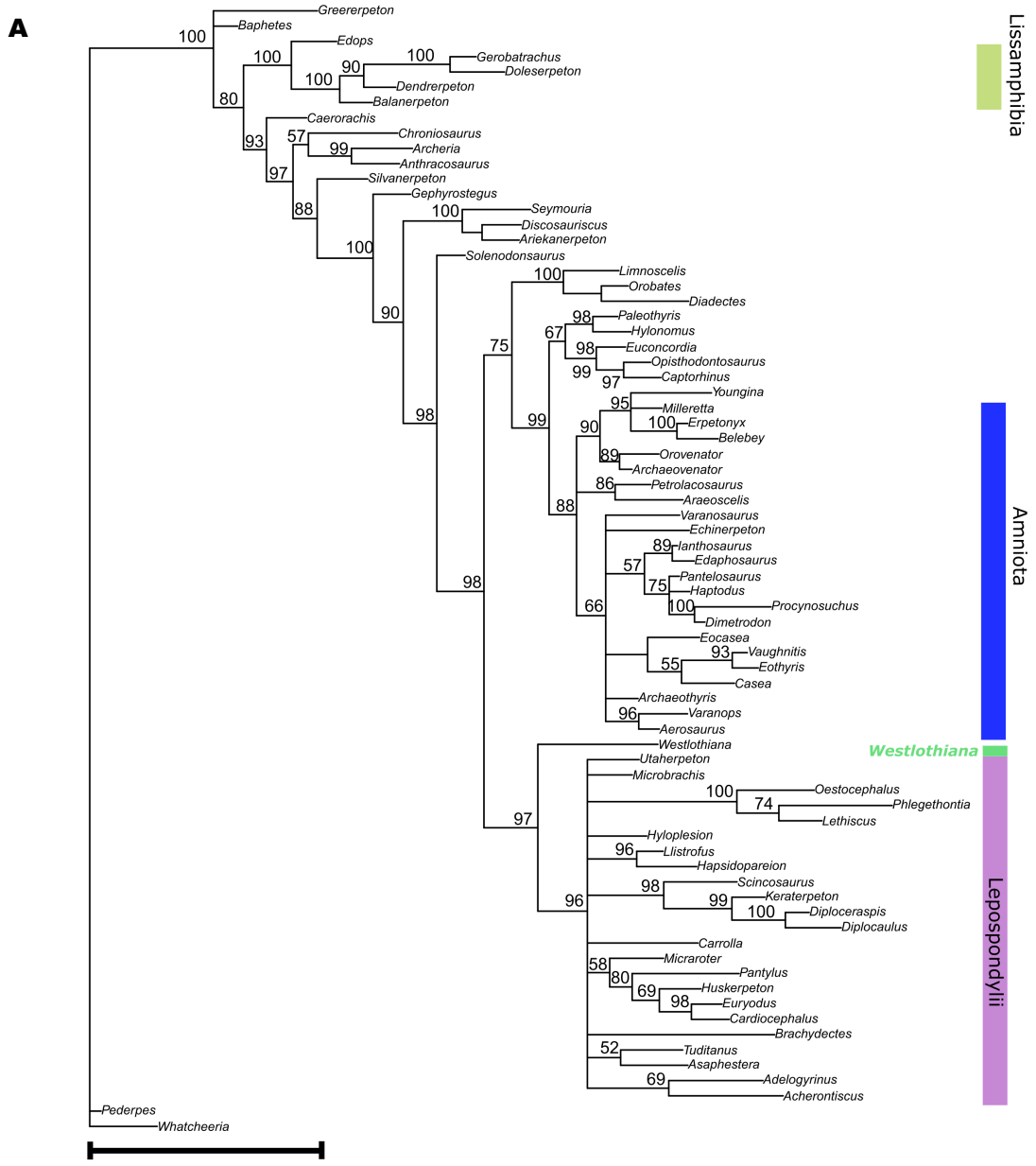
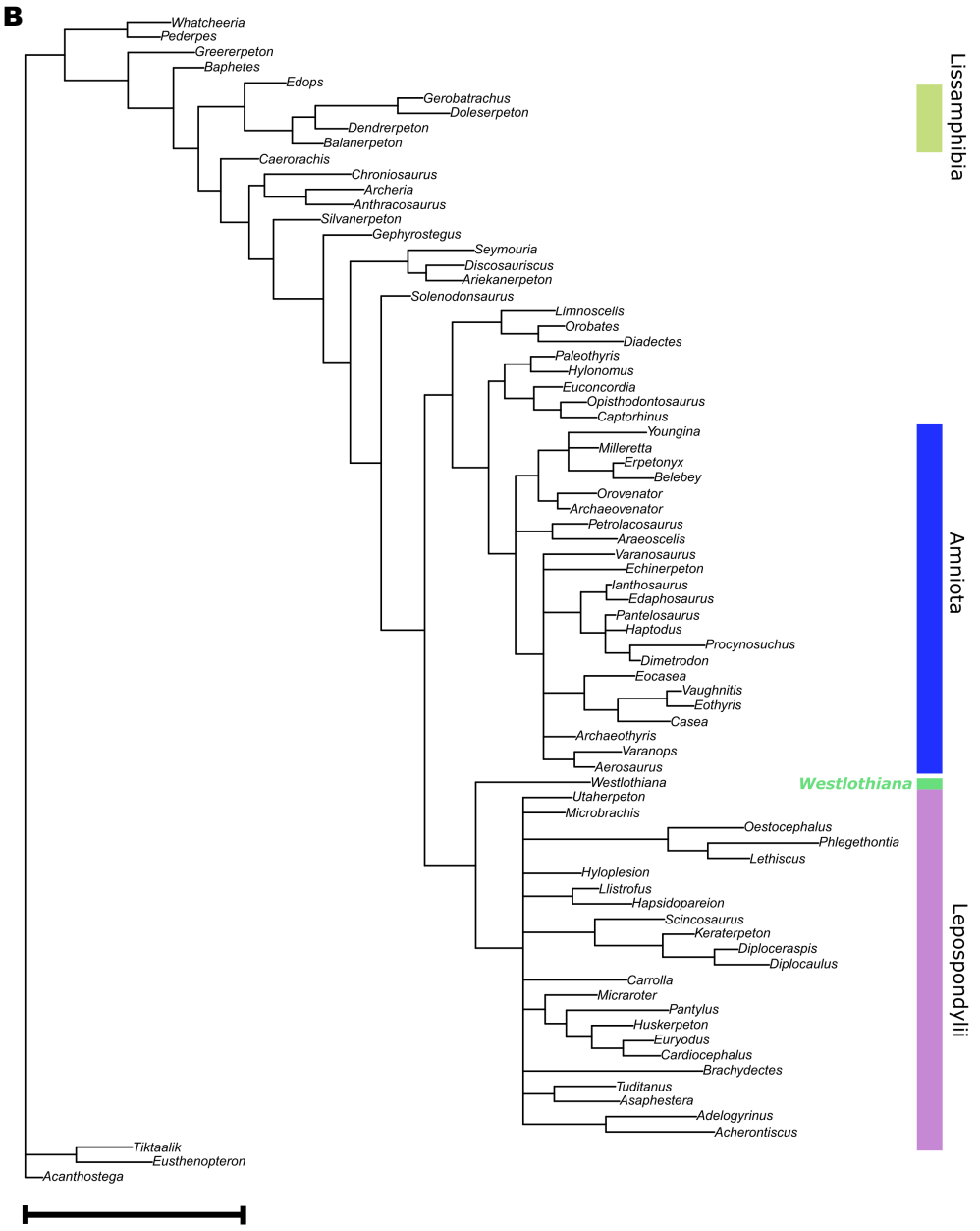


Fig. 2:

Non-time calibrated Bayesian phylogenetic analyses. A (this page), non-time calibrated Bayesian phylogenetic analysis. Numbers indicate posterior probability values. B (following page), non-time calibrated Bayesian phylogenetic analysis with an expanded outgroup including *Eusthenopteron*, *Tiktaalik* and *Acanthostega*. Scale bar indicates 0.500 expected changes per site.



In both Bayesian analyses, captorhinids and protorothyrids form a clade together that is positioned on the amniote stem. However, the position of araeoscelids is recovered as an unresolved polytomy with synapsids and reptiles.

4.3.1.3 Time-calibrated Bayesian analysis. Convergence was reached in the time-calibrated Bayesian analysis, using the FBD model, with an average PSRF of 1.001 and a maximum PSRF of 1.021, and an average ESS value of 1901.15 (for the TL parameter).

The topology of the time-calibrated Bayesian analysis (Fig. 3 – Majority rule tree, 4b – Fully resolved tree) is mostly consistent with the results of the Maximum Parsimony and non-time

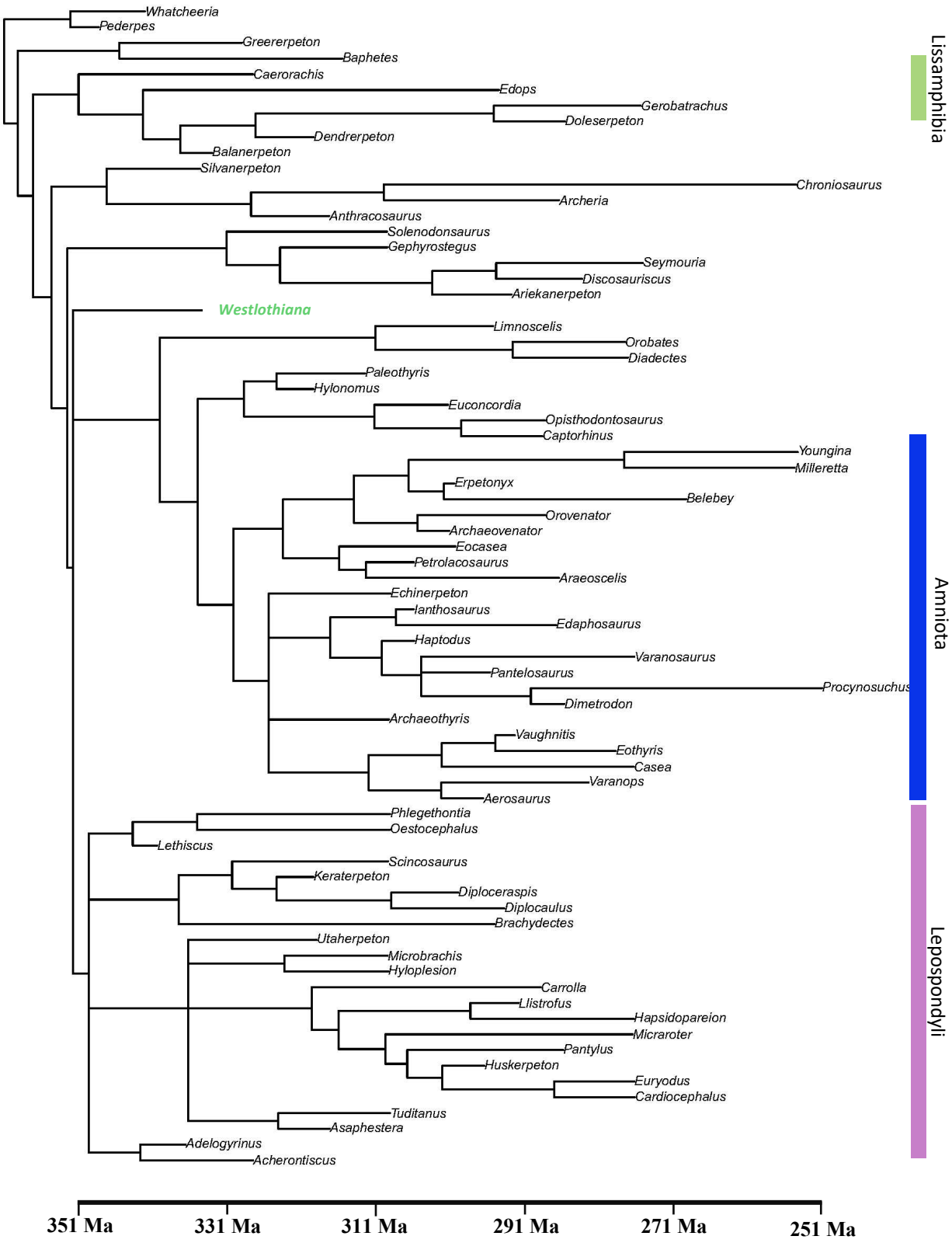
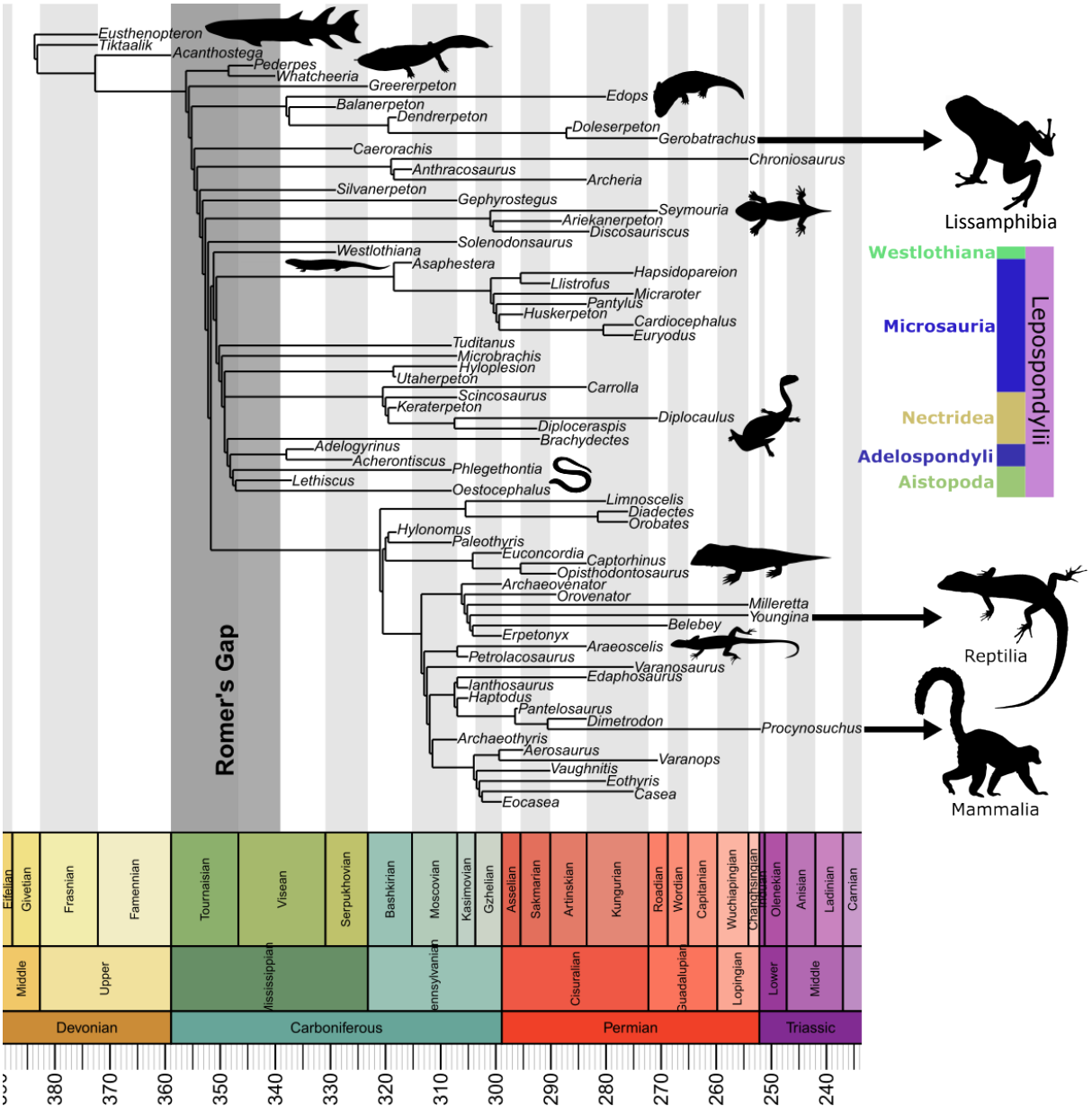


Fig. 3:

50% majority rule tree of the FBD model timed Bayesian phylogenetic analysis. Scale bar represents real time of the phylogeny in millions of years ago. Detailed representation of the geological timescale is not included to improve readability of the phylogenetic topology.

calibrated Bayesian analyses, though there are a few differences. *Caerorachis* is recovered as the earliest diverging temnospondyl, as per its original description (Holmes and Carroll 1977). *Silvanerpeton* is recovered as the earliest diverging anthracosaur, and *Chroniosaurus* is the sister taxon to *Archeria*, within anthracosaurs. Microsaurs, form a monophyletic group, as do aïstopods, nectrideans and adelogyrinids. These four clades together are recovered as a polytomy at the base of Lepospondyli. Protorothyrids and captorhinids still form a stem-amniote clade, but araeoscelids are recovered as stem-reptiles in the same position as in Ford and Benson (2020), as the sister-clade to parareptiles and diapsid reptiles. *Eocasea* is recovered as the sister-taxon to araeoscelids.



A

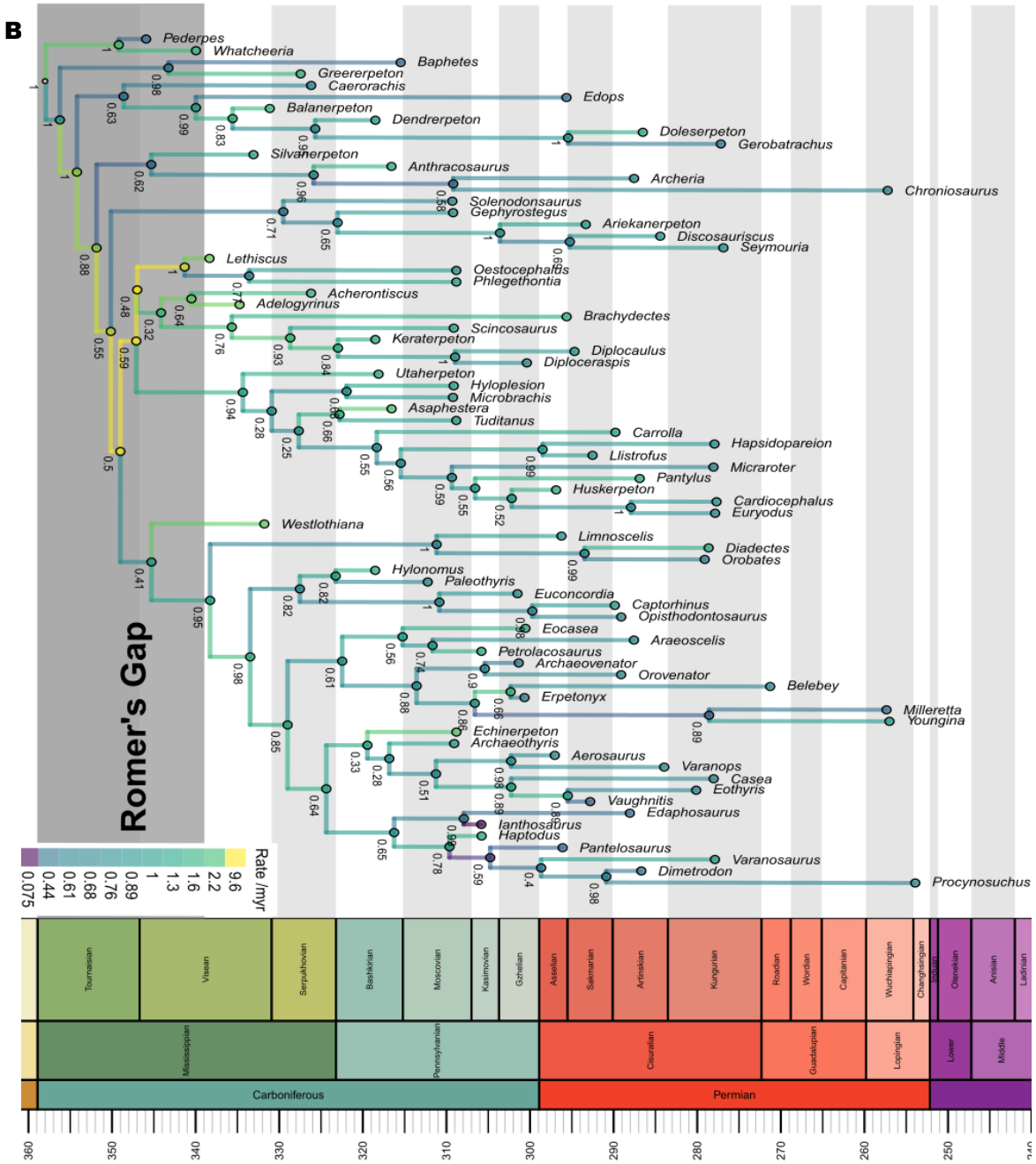


Fig. 4:

Time calibrated phylogenetic analyses on geological timescales. A (previous page) Time-calibrated Maximum Parsimony analysis, including the expanded outgroup of *Eusthenopteron*, *Tiktaalik* and *Acanthostega* to provide visualisation of the time-calibration of nodes earlier than Romer's Gap. B (above), Fully resolved time-calibrated Bayesian phylogenetic analysis.

Notably, unlike all other analyses, *Westlothiana* is not unambiguously recovered as the earliest diverging lepospondyl. It is instead recovered in an unresolved polytomy with Lepospondyli, and amniotes crownwards of and including diadectamorphs. When the topology is resolved fully, *Westlothiana* is recovered as the sister taxon to Amniota + Diadectamorpha, with a posterior probability of 41%.

4.3.2 Support for selected clades and novel groupings

4.3.2.1 Monophyletic Lepospondyli + *Westlothiana.*

A monophyletic Lepospondyli, and *Westlothiana* as the sister taxon to the clade, is well supported by 10 synapomorphies. These are (Appendix 5**)**:

1. Anterposterior skull length less than 30mm (ch. 1, state 0)
2. Antorbital region of skull mediolaterally narrow (ch. 7, state 1)
3. Marginal teeth blunt and peg-like (ch. 29, state 0)
4. Lacrimal dorsal orbital process present (ch. 44, state 1)
5. Large, concave notch present in posteroventral margin of postfrontal to accommodate the postorbital (ch. 61, state 1)
6. Postorbital irregular, without a clearly defined shape (ch. 66, state 0)
7. Anterodorsal margin of postorbital has distinct sigmoid shape (ch. 69, state 1)
8. Retroarticular process present (ch. 202, state 1)
9. Anteroposterior length of dentary toothrow is less than 50% of jaw length (ch. 209, state 0)
10. Internal trochanter not separated from the general surface of the femur by a trough (ch. 311, state 0)

Some studies have suggested that lepospondyls may be polyphyletic, and that the synapomorphies uniting them are convergent reduction of features due to small body size (Clack 2012, Pardo et al. 2017). However, several of the synapomorphies that here unite lepospondyls, and *Westlothiana*, cannot be directly attributed to size. These include, in particular, the tooth morphology (synapomorphy 3), a lacrimal dorsal orbital process (synapomorphy 4), those concerning the morphology of the postorbital and its contact with the postfrontal (synapomorphies 5, 6 and 7), the presence of a retroarticular process (synapomorphy 8) and a relatively shortened dentary toothrow (synapomorphy 9). A monophyletic Lepospondyli + *Westlothiana* is also well supported by a posterior probability of 97% in the Bayesian analysis.

A monophyletic Lepospondyli + *Westlothiana* is not recovered in the Bootstrap analysis (i.e. it receives bootstrap support of <50%). However, this is not due to a possible position for aïstopods as

stem tetrapods (see Pardo et al. 2017). Instead, it results from ambiguity about the position of adelospondyls: a monophyletic lepospondyls is recovered in a Bootstrap analysis in this analysis if adelospondyls are removed. Adelospondyls have, in multiple phylogenetic analyses, been recovered as relatives of anthracosaurs or colosteids (e.g. Ruta and Coates 2007) and thus occupy a fairly unstable phylogenetic position. The finding of a monophyletic Lepospondyli in the Bootstrap analysis if adelospondyls are removed shows that we can be more confident of the finding of aïstopods within Lepospondyli than expected.

The position of aïstopods as deeply nested within lepospondyls is also well supported. The clade of non-microsaur lepospondyls (which includes aïstopods) is recovered in the Bootstrap analysis following the removal of adelospondyls, with a support of 82%, and is supported by a further 10 synapomorphies. These are:

1. Posteriormost extent of maxilla extends posterior to orbit posterior margin (ch. 24, state 1)
2. Anterodorsal margin of postorbital smooth and lacks sigmoid shape (ch. 69, state 0)
3. Posterior margin of jugal slopes anterodorsally to posteroventrally (ch. 82, state 2)
4. Parietal-parietal total width shorter than the distance between the orbit posterior margin and skull posterior margin (ch. 101, state 0)
5. Pineal foramen postitioned posterior to midpoint of interparietal suture (ch. 104, state 0)
6. Denticle shagreen on ectopterygoid absent (ch. 187, state 0)
7. More than 29 dentary teeth (ch. 207, state 3)
8. Atlantal neural arch halves fused into single arch (ch. 243, state 1)
9. Anterior articulating surface of atlas equal in diameter to posterior articulating surface (ch. 248, state 0)
10. Carpals unossified (ch. 303, state 0)

Additionally, the early diverging position of *Westlothiana* within lepospondyls is extremely well supported in the maximum parsimony analyses. The clade consisting of Lepospondyli, excluding *Westlothiana*, has a posterior probability of 96% in the Bayesian analysis, and is also supported by a further 10 synapomorphies (Appendix 5). These are:

1. Interorbital distance larger than maximum anteroposterior orbit diameter (ch. 4, state 2)
2. Posterior margin of the jugal is straight and vertical (ch. 82, state 1)
3. Separately ossified supratemporal absent (ch. 112, state 0)
4. No ventral depression in body of parasphenoid (ch. 148, state 0)
5. Vomers separated by pterygoids for more than half of vomer length (ch. 153, state 2)
6. Dentary is only element forming adductor crest (ch. 199, state 2)
7. Between 20 and 29 teeth on dentary (ch. 207, state 2)
8. Anterior articulating surface of the atlas laterally expanded relative to posterior articulating surface (ch. 248, state 1)
9. Loss of ossified intercentra (ch. 252, state 0)
10. Haemal arches parallel sided (ch. 260, state 1)

However, it must be noted that this result is not recovered in all of my analyses, and *Westlothiana* is recovered in a polytomy with Diadectamorpha + Amniota, and Lepospondyli, in the time-calibrated Bayesian analysis. The fully resolved time-calibrated Bayesian tree demonstrates that *Westlothiana* is recovered as the sister taxon to Amniota + Diadectamorpha in the highest proportion of trees, though this is not a particularly well supported result, and has a Bayesian posterior probably of 41%.

4.3.2.2 Lepospondyli/*Westlothiana* as the sister clade to Diadectomorpha + Amniota.

This clade is moderately well supported by five synapomorphies (Appendix 5), including the loss of posterior emargination of the cheek, a large parietal width, and a parietal-postorbital contact. This clade also has a posterior probability of 98% in the Bayesian analysis. This clade is also recovered in the Bootstrap analysis in which adelospondyls are removed, with a support value of 61.

4.3.2.3 Captorhinidae and Protorothyridae as stem amniotes. The position of captorhinids and protorothyrids as stem amniotes is relatively robustly supported. The crown amniote clade, which excludes captorhinids and protorothyrids, has a posterior probability of 88% in the Bayesian analysis and is rejected with one additional step. The crown amniote clade excluding captorhinids and protorothyrids is also supported by seven synapomorphies. These are:

1. Jugal has free posterior margin (ch. 73, state 1)
2. Jugal triradiate, with posterodorsal margin sloping anterodorsally to posteroventrally and posteriorly forming a distinct process (ch. 82, state 3)
3. Pineal foramen positioned posterior to midpoint of interparietal suture anteroposterior length (ch. 104, state 0)
4. Tooth row present on pterygoid transverse flange (ch. 181, state 1)
5. Radius more than 71% of length of humerus (ch. 300, state 2)
6. Puboischiadic plate equivalent in anteroposterior length to four trunk vertebrae (ch. 309, state 1)
7. Internal trochanter not separated from general surface of femur by trough-like space (ch. 311, state 0)

The monophyly of captorhinids and protorothyrids with each other is less well supported. Captorhinidae + Protorothyridae is rejected with one additional step, and is united by just two synapomorphies; a parietal – squamosal contact (ch. 106, state 1), and the presence of a denticle shagreen of the pterygoid transverse flange (ch. 180, state 1).

4.3.2.4 Araeoscelidae as stem synapsids. The position of *Petrolacosaurus* and *Araeoscelis* as synapsids, rather than reptiles, is moderately well supported. Two additional steps are also required for this clade to not be recovered. However, the position of araeoscelids as stem synapsids is not recovered in the Bayesian analysis, and instead araeoscelids are recovered in a polytomy with mammals and reptiles. The position of araeoscelids as stem synapsids is, nonetheless, supported by five synapomorphies. These are:

1. Posterior margin of skull bilaterally embayed (ch. 13, state 1)
2. Anteriormost premaxillary teeth larger than posterior premaxillary teeth, forming conspicuous peak (ch. 19, state 1)
3. Ventral temporal bar dorsoventrally deep, occupying more than 20% of skull height (ch. 75, state 1)

4. Anterior extent of cultriform process terminates posterior to sphenethmoid anterior margin (ch. 130, state 0)
5. Supraglenoid foramen located on or anterior to the apex of the supraglenoid buttress (ch. 278, state 1)

4.4 Discussion

4.4.1 Taxonomic Representation

My analysis samples taxa of both the amniote stem and crown more extensively than any previous phylogenetic analyses. Previous analyses of early tetrapods have generally included a very small sample of taxa to 'represent' the amniote crown. These taxa typically include *Captorhinus*, *Paleothyris* and *Petrolacosaurus* to represent reptiles, though not even always all three (Ruta and Coates 2007, Clack et al. 2016, Pardo et al. 2017, Marjanovic and Laurin 2019; Klembara et al. 2021). Taxa representing synapsids are included in even fewer numbers, with some analyses selecting taxa such as the highly derived *Dimetrodon* and *Ophiacodon* (Pardo et al. 2017) or Caseasauria, along with *Archaeovenator* (Marjanovic and Laurin, 2019) and other analyses having no taxa to represent synapsids at all (Ruta and Coates 2007, Clack et al. 2016). Likewise, analyses that have focussed on early amniotes have typically included just a small sample of stem amniote taxa stemwards of diadectomorphs (e.g. Laurin and Reisz 1995, Ford and Benson 2020). Crown groups are, by definition, designated by taxa that are extant, not by morphology (Laurin and Anderson 2004). Therefore, there is no particular morphological reason for this sampling dichotomy. The lack of taxonomic sampling on either the amniote stem, or within the early crown, prevents detailed testing of character changes, which is essential to resolving the position of problematic clades that were previously considered to be stem amniotes but have been recovered recently in the amniote crown, and vice versa (Pardo et al. 2017, Ford and Benson 2020, Simões et al., 2022).

My phylogenetic analysis is also the first to include substantial taxonomic sampling of taxa typically considered to be both stem and crown amniotes, and to have near equal representation of characters and taxa concerning both the amniote stem and crown. Indeed, I attempted comprehensive representation of the character state variation proposed by previous studies for these groups. Whilst

much of my topology concurs with previous analyses, the differences, including the potential stem mammal position of araeosceids in the Maximum Parsimony analysis, may be at least partially explained by this increased taxonomic representation.

4.4.2 Phylogenetic topological results of particular interest

4.4.2.1 The position of araeoscelids. The placement of captorhinids and protorothyrids as stem amniotes rather than stem reptiles, whilst unusual, is not completely unprecedented and was recovered in the recent phylogenetic analysis by Simões et al., (2022). However, the placement of araeoscelids on the mammalian stem, as recovered in my Maximum Parsimony analysis, has never been found before. Much of the significant work suggesting an affinity between araeoscelids and reptiles follows the work of Gauthier et al. (1988) and Laurin and Reisz (1995), the earliest computerised phylogenetic analyses of early amniotes. In both of these analyses, overall taxon sampling was poor, encompassing just 29 and 13 taxa respectively. The single outgroup OTUs were representative of whole clades. In particular, Laurin & Reisz (1995) recovered synapsids as the sister-clade to all other amniotes, but they "reconstructed a primitive morphotype… instead of coding all variations occurring in the clade" (Laurin and Reisz 1995, p. 170), making assumptions based on the prior phylogeny of Reisz (1986). This prevented detailed testing of alternative phylogenetic hypotheses to the synapsid topology outlined in Reisz (1986). My more extensive sampling, combined with novel characters, allows for more detailed investigation of the position of araeoscelids, and suggests that their position as reptiles as not as definitive as previously thought.

Nonetheless, the finding that araeoscelids may not be the earliest diverging diapsid reptiles is not new, and builds on the results in recent analyses which have recovered them as stem amniotes (Simões et al., 2022) or as stem reptiles rootwards of parareptiles (Ford and Benson 2020). My character list utilised characters from a wide range of analyses, including novel characters introduced in the two analyses mentioned above. In particular, Ford and Benson (2020) introduced several novel characters concerning temporal fenestration, designed to remove any assumptions of the homology of temporal fenestration that were implicit to the characters used; the presence of an "upper temporal

fenestra" and a "lower temporal fenestra" being considered two of the synapomorphies that were previously considered to unite araeoscelids with diapsid reptiles (Laurin and Reisz 1995). Ford & Benson (2020), instead, chose their characters to reflect the skull bone margins contributing to any temporal fenestrae, rather than the fenestrae themselves.

In their analysis, with assumptions of homology of removed, the topology Ford & Benson (2020) recovered araeoscelids on the reptile stem, but stemwards of parareptiles, which lack temporal fenestration (Gow 1972, Reisz et al. 2007, Modesto et al. 2015). This suggests that temporal fenestration showed substantial homoplasy in early amniotes. Without assumptions of homology, the affinity of araeoscelids to diapsid reptiles is weakened by the removal of two synapomorphies. Recent work (Ford and Benson 2020, Simões et al. 2022; My analysis) has demonstrated the position of araeoscelids to be uncertain and lacking consensus, and further work over the coming years will be required to resolve the position of this clade.

4.4.2.2 Lepospondyls.

Lepospondyls have traditionally been viewed as monophyletic throughout much of the 20th Century (Colbert 1955, Romer 1966), including microsaurs, nectrideans, the long-bodied lysorophians, the long-bodied, limbless aïstopods and adelospondyls (Carroll 2000, Clack 2012, Schoch 2014). This result has been found in almost all modern phylogenetic analyses (e.g. Anderson 2001, Ruta and Coates 2007, Huttenlocker et al. 2013), with the exception of adelospondyls, which are only sometimes recovered as lepospondyls (Ruta and Coates 2007).

However, a small number of analyses have disputed lepospondyl monophyly (Milner 1993, Clack et al. 2019). In particular, Pardo et al. (2017) published a phylogenetic analysis that proposed the novel result that microsaurs are stem reptiles, and recovered aïstopods stemwards of whatcheeriids, and so outside of crown tetrapods. Their analysis incorporated a greater focus on the braincase than previous analyses, introducing 59 novel braincase characters, totalling 69 braincase characters, and consisting of nearly 20% of their total characters. They also described and incorporated new data of the braincase of the aïstopods *Lethiscus* and *Coloraderpeton*. This analysis

has gained traction in recent years and formed the basis of several subsequent phylogenetic analyses (e.g. Mann et al. 2019, Gee et al. 2021, Pardo 2023).

In my analysis, I find strong support for monophyly of lepospondyls across both Maximum Parsimony and Bayesian phylogenetic analyses. This contrasts the recent findings of Pardo et al. (2017). However, the poor taxonomic representation of lepospondyls in Pardo et al. (2017) prevented their monophyly from being thoroughly tested. Pardo et al. (2017) included a very limited taxon sample; no lepospondyls were included other than two aïstopods and thirteen microsaurs. Nectrideans and adelospondyls were completely omitted. Within aïstopods, they included no representative of phlegethontiids, one of the traditionally recognised aïstopod families (Carroll 1998), despite the phylogenetic position of aïstopods being the principal focus of their analysis. In light of their finding that microsaurs were crown amniotes, it must also be noted that a detailed testing of the topology of early crown amniotes was precluded by the equally limited taxonomic sampling of the amniote crown. The highly derived *Dimetrodon* and *Ophiacodon* were the only representatives of synapsids included by Pardo et al. (2017), and just three taxa were included to represent the total group of reptiles. The uncertainty over the finding of microsaurs as stem reptiles is exacerbated by the inclusion of *Opisthodontosaurus* as one of the three reptile taxa. *Opisthodontosaurus* is a captorhinid reptile specifically noted to have dental and mandibular convergence with microsaurs (Reisz et al. 2015).

Pardo et al. (2017) introduced, as discussed previously, a large number of novel characters concerning the braincase. However, aspects of their taxonomic inclusion have the effect of increasing the effect of their braincase characters on the outcome of their topology, potentially partly explaining the differences in topology between that analysis and the topology I recover. As well as the great number of braincase characters, they also stated that they only included taxa for which a complete braincase was known and well described. As such, nectrideans and adelospondyls were excluded from their analysis, preventing a true, complete test of lepospondyl monophyly. Moreover, aïstopods lack limbs and girdles, so are inapplicable for the majority of postcranial characters, further increasing the significance of cranial characters, and therefore braincase characters, in determining their phylogenetic affinities. Given their finding of microsaurs as stem-reptiles, and the supposed exclusion of taxa without a well described braincase, it is also particularly curious that the microsaur-like reptile

Opisthodontosaurus is included in their analysis despite the fact it does not have a preserved braincase, contrary to the authors claims about taxonomic inclusion in their analysis.

In addition to the greater taxonomic inclusion of lepospondyls in my analysis relative to that of Pardo et al. (2017), I incorporated sixteen of the novel braincase characters of Pardo et al. (2017) into my analysis. I specifically included all characters that varied within my taxon sample, and in which the wording of the character was sufficiently clear to allow it to be understood anatomically. Despite the inclusion of these characters, I still find very strong support for the traditional hypothesis of lepospondyl monophyly. This suggests that plesiomorphic features of the braincase that are present in aïstopods (Pardo et al. 2017) are not sufficient to recover araeoscelids as stem tetrapods, compared to the weight of evidence from other anatomical regions, and the features that are shared between aïstopods and other lepospondyls that were not included by Pardo et al. (2017), notably nectrideans.

A relationship of *Westlothiana* to lepospondyls, and a close relationship of lepospondyls to amniotes and diadectomorphs, has been recovered by some previous analyses that had access to much less information on the anatomy of *Westlothiana* (Ruta et al. 2003, Ruta and Coates 2007, Clack et al. 2016). My new anatomical data demonstrates that *Westlothiana* shares traits with lepospondyls, deeper stem amniotes, and early crown amniotes, and while the phylogenetic position of *Westlothiana* is not clearly resolved between Maximum Parsimony, Bayesian, and time-calibrated Bayesian analyses, *Westlothiana* clearly occupies a crucial phylogenetic position close to the divergence of amniotes from lepospondyls, and the origin amniotes.

4.4.3 The Timing of the Divergences of Major Clades

Time-calibration of my topology indicates an early origin of crown tetrapods. The amniote-amphibian divergence occurred at roughly the midpoint of the Tournasian (354.5 Ma) comfortably having occurred by the earliest part of the Viséan (346.7Ma), following both the time-calibrated Maximum Parsimony analysis, and the time-calibrated Bayesian analysis. This is primarily due to the phylogenetic position of the aïstopod *Lethiscus* within a monophyletic Lepospondyli. *Lethiscus* is the oldest known lepospondyl, from the early Viséan (Anderson 2002), and thus has strong implications

for the time of the origin of the trapod crown, depending on whether *Lethiscus* is recovered as a crown tetrapod (as in this analysis), or as a stem tetrapod (as in Pardo et al. 2017).

Our results, therefore, contrast with the recent findings of Pardo et al. (2017), who found that crown tetrapods originated considerably later, in the mid-Viséan, approximately 338 Ma, some 15 million years later than the origin of crown tetrapods in my analysis. Furthermore, Pardo et al. (2017) did not include *Westlothiana* in their analyses. However, the occurrence of *Westlothiana* by the mid-Viséan, and the close relationship between *Westlothiana* and amniotes, implies that the tetrapod crown group was well established by this time. Therefore, major stem amniote linages including anthracosaurs and seymouriamorphs must have diverged no later than this. This remains the case even if aïstopods are found outside the tetrapod crown group in future studies.

4.4.3.1 Romer's Gap. If we are confident in the position of *Lethiscus* as a stem amniote, a result I find considerable support for, then it indicates that all major lepospondyl lineages had also been established by the early Viséan. *Westlothiana*, too, can be dated to immediately following the very end of Romer's gap (Smithson et al. 1993, 2012). This suggests a major episode of phenotypic evolution and lineage diversification among lepospondyls and stem amniotes during Romer's gap in the earliest part of the Carboniferous.

Romer's gap has been proposed as both a sampling artefact (Smithson et al. 2012) or as a genuine lull in tetrapod evolution (Ward et al., 2006). The ages and phylogenetic position of both *Westlothiana* and *Lethiscus* in my analysis, crownwards of the stem amniotes anthracosaurs, seymouriamorphs and *Solenodonsaurus*, implies that several diversification events of stem amniotes had happened by the appearance of *Westlothiana* at the end of Romer's gap. Moreover, calculation of the rates of phenotypic evolution in my time-calibrated Bayesian analysis demonstrate that the highest rates of phenotypic evolution occurred close to the divergence of lepospondyls from more derived amniotes, and in the very earliest lepospondyls. This is likely due to the unique morphology of aïstopods, alongside their well supported position as lepospondyls. This further suggests high rates of evolution of terrestrial tetrapods during the earliest Carboniferous.

My results suggest that Romer's gap was, in fact, an important and active period in the evolution of stem amniotes and terrestrial tetrapods. This indicates that the lack of fossil evidence of terrestrial

tetrapods during this time is indeed a sampling artefact, as hypothesised by Smithson et al. (2012), and that fieldwork will continue to reveal a greater number of specimens and taxa from this time, building on the work of Smithson et al. (2012) and Clack et al. (2016). My results provide strong evidence against the hypothesis that terrestrial tetrapods were absent during the earliest stages of the Carboniferous.

4.5 Conclusion

I carried out a novel phylogenetic analysis of 328 characters and 77 taxa, incorporating a large number of taxa typically regarded as both stem and crown amniotes.

In this analysis, temnospondyls were recovered as a monophyletic group that included *Gerobatrachus* as the closest relative of *Doleserpeton*, supporting a dissorophoid temnospondyl origin of Lissamphia, as is recovered in many of the most recent phylogenetic analyses (Pardo et al. 2017, Kligman et al. 2023). Anthracosaurs, seymouriamorphs, *Chroniosaurus*, *Gephyrostegus* and *Solenodonsurus* are all recovered as stem amniotes, consistent with the majority of recent phylogenetic analyses (Ruta et al. 2003, Ruta and Coates 2007) but contrasting the results of some analyses, which have placed these groups as stem tetrapods (Laurin and Reisz, 1995).

Lepospondyli is recovered as a monophyletic group, contrasting the recent hypothesis that it may represent a polyphyletic group (Pardo et al. 2017, Clack et al. 2019). *Westlothiana* is generally recovered as the sister taxon to this clade, although in the time-calibrated Bayesian analysis it is recovered as the sister taxon to Diadectamorpha + Amniota, demonstrating the key phylogenetic position of this enigmatic taxon.

Captorhinids and protorothyrids are recovered as stem amniotes, as they have been in other recent phylogenetic analyses (Simões et al., 2022) but contrasting longstanding hypotheses over their phylogentic position (Gauthier et al. 1988, Laurin and Reisz 1995). Araeoscelids are recovered in maximum parsimony analyses as stem synapsids, a completely novel result.

The afforementioned phylogenetic results result in an early origin for the divergence of Amniota and Lissamphibia, forming the tetrapod crown group, during the early stages of the

Carboniferous, and suggesting substantial evolution and diversification of terrestrial tetrapods had occurred during Romer's gap.

Chapter 5: Conclusions and Direction of Future Research

5.1 Summary of Conclusions

In the first chapter of my thesis, I introduced the major groups that are often considered to be stem amniotes, and summarised the current phylogenetic hypotheses concerning the phylogeny of the origin of amniotes, amphibians, and the amniote stem.

In chapter 2, I introduced the enigmatic Carboniferous taxon *Westlothiana*, which has been hypothesised to have a close phylogenetic relationship to amniotes. I described the cranial morphology of *Westlothiana* using visualisation of data from synchrotron phase-contrast micro-CT scans of the holotype specimen of *Westlothiana*. I demonstrated that the cranial morphology of *Westlothiana* demonstrates traits of earlier stem amniotes, lepospondyls, and crown amniotes. The circumorbital bones resemble those of microsaurs, particularly in the possession of a dorsal process. The prefrontal and postfrontal contact each other above the orbit, which is plesiomorphic relative to amniotes. Unlike microsaurs, the parietals are extremely wide, and a supratemporal is retained. The temporal region resembles that of early amniotes; the supratemporal and tabular contact each other at the corner of the skull table. However, the intersection of the temporal region and the occiput is plesiomorphic relative to amniotes; neither the supratemporal or tabular, or the postparietal, have an occipital contribution.

I showed that the palate of *Westlothiana* is extremely denticulate, more so than almost any other early amniote or amphibian, and showed that the palate is highly plesiomorphic relative to amniotes. The ectopterygoid is large and the pterygoid lacks a transverse flange. I showed that palatal fangs can be observed on the vomer and palatine, similar to stem amniotes such as seymouriamorphs.

In chapter 3 I described the postcranial morphology of *Westlothiana* based on the holotype skeleton. I highlighted differences between the holotype and supposed second specimen of *Westlothiana*, proposed that the second specimen represents a new species, and suggested what the postcranial skeleton could demonstrate about the phylogenetic relationships of *Westlothiana*.

As with the cranial skeleton, the postcranial skeleton of *Westlothiana* demonstrates traits of earlier stem amniotes, lepospondyls, and amniotes crownwards of diadectomorphs. The small size of both the forelimbs and hindlimbs, the absence of an entepicondylar foramen in the humerus, and, in the femur, the absence of a fourth trochanter and a trough between the first trochanter and the shaft all resemble the appendicular skeleton of microsaurs. However, the atlas-axis complex lacks key features that are observed in lepospondyls, including the expanded anterior articulating surface that is present in microsaurs, and the anteriorly projecting odontoid process that is present widely across lepospondyls.

I showed that the tarsus of *Westlothiana* is plesiomorphic with respect to crown amniotes. It retains three proximal tarsal elements and does not possess the astragalus and calcaneum of early amniotes. Instead, the presence of three proximal tarsals, of which the tibiale is highly reduced in size, closely resembles the condition in diadectomorphs. There appears to be four distal tarsals and four digits in the pes, at least of the holotype specimen, a unique morphology amongst stem tetrapods, stem amniotes and early crown amniotes.

In chapter 4, I described the results of my novel phylogenetic analysis of 328 characters and 77 taxa, incorporating a large number of taxa typically regarded as both stem and crown amniotes.

I showed that temnospondyls formed a clade including *Gerobatrachus* as the closest relative of *Doleserpeton*, supporting an origin of Lissamphia within dissorophoid temnospondyls. I showed that anthracosaurs, seymouriamorphs, *Chroniosaurus*, *Gephyrostegus* and *Solenodonsurus* are all recovered as stem amniotes, and Lepospondyli is recovered as a monophyletic group. I generally recovered *Westlothiana* as the sister taxon to this clade, although in the time-calibrated Bayesian analysis it is recovered as the sister taxon to Diadectamorpha + Amniota. Thus, in chapter 4, I demonstrated the important and transitional role, close to the origin of amniotes, that *Westlothiana* occupies.

I also showed that I found a novel topology of amniotes crownwards of diadectamorphs. I recovered captorhinids and protorothyrids as stem amniotes, and recovered araeoscelids as stem synapsids in the maximum parsimony analysis, a completely novel result. I also discussed the implications of my topology on the divergence times of the amniote crown and tetrapod crown

groups, as my results suggest an origin for the divergence of Amniota and Lissamphibia, forming the tetrapod crown group, during the early stages of the Carboniferous. I discussed Romer's gap, and suggested substantial evolution and diversification of terrestrial tetrapods had occurred during this time.

5.2 Direction of Future Research

My analysis continues to demonstrate that a consensus has yet to be reached concerning the phylogenetic positions of multiple groups of both stem and early crown amniotes. Groups such as lepospondyls and caecilians have not held stable phylogenetic positions throughout the entire history of computerised phylogenetic analyses, and groups such as aïstopods, microsaurs, araeoscelids and captorhinids have all been recovered in novel positions in recent phylogenetic analyses. We have moved further away from a consensus, not closer. Clearly, more work is needed to resolve the phylogenetic position of these enigmatic groups, and to reach a consensus on the phylogenetic relationships of the earliest amniotes and amphibians. I believe this work will consist of two strands.

5.2.1 Novel anatomical data

In any area of palaeontology, more fieldwork yielding more specimens is highly desirable. However, the last decade has demonstrated the vast ability of micro-CT scanning to reveal novel anatomical data hidden by matrix in existing specimens. This technique has allowed for extensive and updated redescriptions of many early amniotes and amphibians, but a great many more specimens remain to be scanned and studied in this way. Amongst these many specimens, for example, I am most familiar with those in the UMZC, including specimens of *Silvanerpeton* (UMZC T. 1251, 1317 and 1351) and *Gephyrostegus* (UMZC T. 1337), and I believe that these specimens would represent ideal candidates for future scanning. However, there are hundreds of specimens in museums all over the world that could potentially yield new anatomical data if scans are produced.

5.2.2 Expansion of phylogenetic data matrices

Recent analyses have demonstrated that substantial expansion of either characters or taxa included in phylogenetic analyses is enough to substantially change the resulting phylogenetic

topology. Pardo et al. (2017)s significant expansion of characters relating to the braincase resulted in a topology with a novel result, that of aïstopods as stem tetrapods and microsaurs as crown amniotes. My own expansion of taxonomic inclusion, being the first phylogenetic analysis to include substantial, near equal numbers of taxa traditionally regarded as both stem and crown amniotes, has resulted in the novel finding of araeoscelids as stem synapsids.

Therefore, future phylogenetic data matrices must continue to expand taxonomic sampling, and character sampling, across all relevant taxa in order to truly test phylogenetic hypotheses. I believe that, for my own analysis, the next step must be to expand my taxonomic and character sampling to include a large number of temnospondyls and early lissamphibians. This would allow for a more detailed, robust test of the hypothesis of a dissorophoid origin of lissamphibians, and test the potential affinities of lepospondyls to amphibians in more detail.

As more taxa and characters are added to phylogenetic analyses, and anatomical data of more taxa are revealed, we will inch ever closer to truly understanding the origin of vertebrate life on land.

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Appendix 1: Specimens and literature examined

Taxon name	Specimens studied	Reference(s)
Acherontiscus caledoniae		Carroll, 1969; Clack et al, 2019
Adelogyrinus simorhynchus		Andrews & Carroll, 1991
Aerosaurus wellesi		Langston & Reisz, 1981
Anthracosaurus russelli		Panchen, 1977
Araeoscelis gracilis	MCZ 4380	Reisz et al, 1984
Archaeovenator hamiltonensis		Reisz & Dilkes, 2003
Archeria crassidisca	MCZ 2045, 2047	Holmes, 1989
Ariekanerpeton sigalovi		Klembara & Ruta, 2005
Asaphestera intermedia		Carroll & Gaskill, 1978
Balanerpeton woodi		Milner & Sequeira, 1993
Baphetes sp.		Beaumont, 1977; Milner & Lindsay, 1998
Belebey vegrandis		Reisz et al, 2007
Brachydectes newberryi		Pardo & Anderson, 2016; Wellstead, 1991
Caerorachis bairdi		Ruta et al, 2001
Captorhinus aguti		Fox & Bowman, 1966
Cardiocephalus sp.		Carroll & Gaskill, 1978
Casea broilii		Olson et al, 1968
Chroniosaurus dongusensis		Clack & Klembara, 2009
Dendrerpeton helogenes		Arbez et al, 2022
Diadectes abistus	FM UC 1075/675	Berman et al, 1998
Dimetrodon sp.		Romer et al, 1940
Discosauriscus austriacus	UMZC 2000.11 R37612	Klembara, 1997; Klembara & Bartik, 1999
Diplocaulus sp.		Douthitt, 1917
Diploceraspis sp	MCZ3009	Beerbower, 1963
Doleserpeton annectens		Sigurdsen & Bolt, 2010
Echinerpeton intermedium		Mann & Paterson, 2020
Edaphosaurus boanerges		Modesto, 1995
Edops craigi		Romer & Witter, 1942
Eocasea martini		Reisz & Fröbisch, 2014
Eothyris parkeyi	MCZ1161	Reisz et al, 2009
Erpetonyx arsenaultorum		Modesto et al, 2015
Euconcordia cunninghami		Reisz et al, 2016
Euryodus sp.		Carroll & Gaskill, 1978; Gee et al, 2021
Gephyrostegus bohemicus	UMZC T. 1337	Klembara et al. 2014
Gerobatrachus hottoni		Anderson et al, 2008
Greererpeton burkemorani		Smithson, 1981; Godfrey, 1989
Hapsidopareion lepton		Carroll & Gaskill, 1978
Haptodus garnettensis		Laurin, 1993
Huskerpeton englehorni		Huttenlocker et al, 2013
Hylonomus lyelli		Carroll, 1964
Hyloplesion longicostatum	NMS 1899.32.3	Carroll & Gaskill, 1978
Ianthosaurus hardestii		Reisz & Berman, 1986
Keraterpeton galvani	PV R 8452/8457	Milner, 2018
Lethiscus stocki		Pardo et al, 2017; Anderson et al, 2003
Limnoscelis paludis	MCZ1948	Romer, 1946; Kennedy, 2010

Llistrofus pricei		Gee et al, 2019
Micraroter erythrogeois		Carroll & Gaskill, 1978
Microbrachis pelikani	NMS 1898.105.26/27	Carroll & Gaskill, 1978
Milleretta sp.		Gow, 1972
Oestocephalus sp.	NMW 1899.IX.13b	Carroll, 1998
Opisthodontosaurus carrolli		Reisz et al, 2015
Orobates pabsti	MNG 8760 MNG 14257 MNG 8980	Berman et al, 2004
Orovenator mayorum		Ford & Benson, 2019
Paleothyris acadiana		Carroll, 1969
Pantelosaurus saxonicus		Spindler, 2016
Pantylus cordatus	FMUC 1075 FMUC 675	Carroll & Gaskill, 1978
Pederpes finneyae		Clack & Finney, 2005
Petrolacosaurus kansensis		Reisz, 1977
Phlegethontia linearis	NMW.1899.IX.13b MCZ2038 (skull/vert) MCZ2204(skull/vert)	Anderson 2002, Anderson 2007
Procynosuchus delaharpeae		Kemp, 1979; Kemp & Parrington, 1980
Seymouria sp.	MNG - 7727	
Scincosaurus crassus		Milner & Ruta, 2009
Silvanerpeton miripedes	UMZC T.1317 UMCZ T.1251 UMZC T.1351	Ruta & Clack, 2006
Solenodonsaurus janenschi		Danto et al, 2012
Tuditanus punctulatus		Carroll & Gaskill, 1978
Utaherpeton franklini		Carroll et al, 1991
Varanops brevirostris		Campione & Reisz, 2010
Varanosaurus acutirostris		Bolt & Scott, 1995
Vaughnitis smithae	MCZ 2985	Brocklehurst et al, 2016
Westlothiana lizziae	NMS.1990.72.1, NMS.1991.47.1	Smithson et al, 1993
Whatcheeria deltae		Rawson et al, 2021
Youngina capensis		Gow, 1974

Appendix 2: Character List

The following character list has been created following the characters in a comprehensive list of existing phylogenetic analyses, with examples that focus both on stem tetrapods and stem amniotes, and on crown amniotes, representing the wide range of taxa included in this analysis. Some novel characters have also been introduced. Each character is listed with notes on its source, optimisation, and comments on the scoring, interpretive thoughts, and explanations as to the inclusion or modification of the character. Characters in this analysis are denoted by "ch.", while characters in previous analyses are referred to by "c."

The previous analyses from which characters have been taken and modified have been listed below, along with abbreviations that are used to summarise the analyses from this point forward:

Brinkman & Eberth, 1983 (**BE1983**), Heaton & Reisz, 1986 (**HR1986**), Reisz, 1986 (**R1986**), Gauthier et al., 1988 (**Gea1988**), Carroll & Currie, 1991 (**CC1991**), Laurin, 1991 (**L1991**), Reisz et al., 1992 (**Rea1992**), Laurin, 1993 (**L1993**), Modesto, 1994 (**M1994**), Berman et al., 1995 (**Bea1995**), Laurin & Reisz, 1995 (**LR1995**), DeBraga & Rieppel, 1997 (**DR1997**), Laurin & Reisz, 1997 (**LR1997**), Dilkes, 1998 (**D1998**), Laurin et al., 1998 (**Lea1998**), Reisz et al., 1998 (**Rea1998**), Sidor & Hopson, 1998 (**SH1998**), Rieppel, 1999 (**R1999**), Berman et al., 2000 (**Bea2000**), Anderson, 2001 (**A2001**), Reisz & Dilkes, 2003 (**RD2003**), Ruta et al., 2003 (**Rea2003**), Modesto et al., 2004 (Mea2004), Müller, 2004 (**M2004**), Maddin et al., 2006 (**Mea2006**), Müller & Reisz, 2006 (**MR2006**), Tsuji, 2006 (**T2006**), Modesto et al., 2007 (**Mea2007**), Reisz et al., 2007 (**Rea2007**), Ruta & Coates, 2007 (**RC2007**), Maddin et al., 2008 (**Mea2008**), Reisz et al., 2009 (**Rea2009**), Reisz et al., 2010 (**Rea2010**), Fröbisch et al., 2011 (**F2011**), Nesbitt, 2011 (**N2011**), Reisz et al., 2011 (**Rea2011**), Benson, 2012 (**B2012**), Tsuji et al., 2012 (**Tea2012**), Huttenlocker et al., 2013 (**Hea2013**), Ezcurra et al., 2014 (**Eea2014**), Klembara et al., 2014 (**Kea2014**), MacDougall & Reisz, 2014 (**MR2014**), Reisz & Fröbisch, 2014 (**RF2014**), Modesto et al., 2015 (**Mea2015**), Pritchard et al., 2015 (**Pea2015**), Schoch & Sues, 2015 (**SS2015**), Brocklehurst et al., 2016 (**Bea2016**), Clack et al., 2016 (**Cea2016**), Ezcurra, 2016 (**E2016**), Laurin & Piñeiro, 2017 (**LP2017**), Pardo et al., 2017 (**Pea2017**), Modesto et al., 2018 (**Mea2018**), Clack et al., 2019 (**Cea2019**), Marjanovic & Laurin, 2019 (**ML2019**), Ford & Benson, 2020 (**FB2020**), Simões et al., 2022 (**Sea2022**).

1. **Anteroposterior skull length: <30mm (0); 31-50mm (1); 51-70mm (2); >70mm (3).**

A2001 (c.181), Hea2013 (c.1), Pea2017 (c.1).

The anteroposterior skull length is measured as in the previous character.

Unambiguous: Lepospondyli (3 -> 0), *Adelogyrinus simorhynchus* (0 -> 1), *Brachydectes newberryi* (0 -> 1), *Lethiscus stocki* (0 -> 1), *Asaphestera intermedia* (0 -> 1), *Micraroter erythrogeois* (0 -> 1), *Eothyris parkeyi* (3to2), *Captorhinus aguti* (1to3), *Paleothyris acadiana* (1 -> 0), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (3 -> 1), *Silvanerpeton miripedes* (3 -> 1), *Caerorachis* (3to2), *Balanerpeton* (3 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (3 -> 0). ACCTRAN: *Diplocaulus sp.* + *Diploceraspis sp.* (0 -> 2), *Diplocaulus sp.* (2 -> 3), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (3 -> 1), Synapsida (1 -> 2), Synapsida except Araeoscelidia (2 -> 3), Parareptilia (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (0 -> 2). DELTRAN: *Diplocaulus sp.* (0to3), *Diploceraspis sp.* (0 -> 2), Araeoscelidia (3to2), Reptilia (3 -> 1), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (1 -> 2), *Milleretta sp.* (1 -> 2), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (3 -> 1).

2. **Skull length:width ratio: broader than long (0); as long as broad (1); longer than broad (2).**

Cea2016 (c.154), ML2019 (c.95), Cea2019 (c.154), Hea2013 (c.3), Pea2017 (c.3).

Almost all included taxa have a skull that is longer than broad, but some temnospondyls, nectrideans and seymouriamorphs have skulls that are relatively broad. Within temnospondyls, *Doleserpeton* has a skull that is as broad as long (Sigurdsen & Bolt, 2010) and *Gerobatrachus* even has a skull that is broader than long (Anderson et al., 2008). A skull that is broader than long is also present in the microsaur *Pantylus* (Carroll & Gaskill, 1978), diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963), as does *Seymouria* (Berman et al., 2000), whilst other seymouriamorphs have a skull that is as broad as long (Klembara, 1997; Klembara & Ruta, 2005).

Unambiguous: *Diplocaulus sp.* + *Diploceraspis sp.* (2 -> 0), *Scincosaurus crassus* (2 -> 1), *Pantylus cordatus* (2 -> 0). ACCTRAN: Seymouriamorpha (2 -> 0), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (2 -> 0), *Doleserpeton annectens* (0 -> 1). DELTRAN: *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (2 -> 1), *Seymouria sanjuanensis* (2 -> 0), *Doleserpeton annectens* (2 -> 1), *Gerobatrachus hottoni* (2 -> 0).

3. **Ratio of anteroposterior skull length:trunk length: <0.2 (0); 0.2-0.29 (1); 0.3 - 0.45 (2); >0.45 (3).**

A2001 (c.182), Hea2013 (c.2), Pea2017 (c.2)

The skull length is measured along the midline from the tip of the premaxillae to the posterior point of the occiput or midline skull table, depending on which occupies the posterior most position, in dorsal view.

Unambiguous: Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Westlothiana lizzae* (1 -> 0), Sphenacodontia (1 -> 2), *Edaphosaurus boanerges* (1 -> 0), *Diadectes abistus* (1 -> 2), Seymouriamorpha + *Gephyrostegus bohemicus* (1to3), *Seymouria sanjuanensis* (3 -> 2), *Chroniosaurus dongusensis* (1to3), *Dendrerpeton helogenes* (2 -> 3). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (3 -> 1), Tetrapoda + *Baphetes sp.* (1 -> 2), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (2 -> 1), Diplocaulidae (0 -> 1), *Diplocaulus sp.* + *Diploceraspis sp.* (1 -> 3), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (1 -> 2), Captorhinidae (2 -> 3). DELTRAN: Tetrapoda (3 -> 2), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (2 -> 1), *Diplocaulus sp.* (0to3), *Keraterpeton galvani* (0 -> 1), *Captorhinus aguti* (1to3), *Hylonomus lyelli* + *Paleothyris acadiana* (1 -> 2), *Greererpeton burkemorani* (3 -> 1).

4. **Interorbital distance (at narrowest point) relative to maximum anteroposterior orbit diameter: interorbital distance smaller (0); interorbital distance equal (1); interorbital distance larger (2).**

Cea2016 (c.158), Cea2019 (c.158). Modified from Rea2003 (c.103, c.104), RC2007 (c.106, c.107), ML2019 (c.86, c.87).

The minimum distance separating the medial (in dorsal aspect) margins of the orbits is measured.

Unambiguous: Lepospondyli except *Westlothiana lizzae* (0 -> 2), *Adelogyrinus symorhynchus* (2 -> 1), *Utaherpeton franklini* (2 -> 0), *Diplocaulus sp.* + *Diploceraspis sp.* (2 -> 1), Aïstopoda (2 -> 0), *Microbrachis pelikani* (2 -> 0), Diadectamorpha (0 -> 2), *Dendrerpeton helogenes* (0 -> 1), *Edops craigi* (0 -> 2), *Baphetes sp.* (0 -> 1), *Greererpeton burkemorani* (0 -> 2). ACCTRAN: Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), Edaphosauridae + Sphenacodontia (1 -> 2), *Haptodus garnettensis* (2 -> 0), Seymouriamorpha (0 -> 2), *Discosauriscus austriacus* (2 -> 0). DELTRAN: *Eothyris parkeyi* (0 -> 1), Sphenacodontidae (0 -> 2), *Edaphosaurus boanerges* (0 -> 2), *Ariekanerpeton sigalovi* (0 -> 2), *Seymouria sanjuanensis* (0 -> 2).

5. **Interorbital distance (at narrowest point) relative to half of maximum skull table width: interorbital distance smaller (0); interorbital distance equal (1); interorbital distance larger (2).**

Rea2003 (c.103), RC2007 (c.106), ML2019 (c.86).

The interorbital distance is measured as the shortest straight line between the orbits perpendicular to the anteroposterior axis of the skull. A particularly large interorbital distance is present widely in *Westlothiana* many lepospondyls including *Brachydectes* (Pardo et al., 2016) and several microsaurs (Carroll & Gaskill, 1978), diadectamorphs (Romer, 1946; Berman et al., 1998; 2004), seymouriamorphs (Klembara, 1997; Berman et al., 2000; Klembara & Ruta, 2005), *Milleretta* (Gow, 1972) and *Edaphosaurus* (Modesto, 1995).

Unambiguous: *Brachydectes newberryi* (0 -> 2), *Tuditanus punctulatus* (0 -> 1), *Asaphestera intermedia* (0 -> 1), *Micraroter erythrogeois* (0 -> 1), *Hapsidopareion lepton* (0 -> 2), *Westlothiana lizzae* (0 -> 2), *Milleretta sp.* (0 -> 1), Diadectamorpha (0 -> 2), *Seymouria sanjuanensis* (0 -> 2). ACCTRAN: Edaphosauridae (0 -> 2). DELTRAN: *Edaphosaurus boanerges* (0 -> 2).

6. **Preorbital region of skull length:width ratio (preorbital region is defined as the region anterior to a straight line perpendicular to the long axis of the skull, in line with the anteriormost tip of orbits): less than twice as wide as long (0); twice as wide as long (1).**

Cea2016 (c.155), Cea2019 (c.155), A2001 (c.27), LR1997 (c.4), Lea1998 (c.4), Hea2013 (c.36), Pea2017 (c.32).

The preorbital region of the skull becomes relatively short and wide, so that it measures twice as wide as long, in many lepospondyls, including the microsaurs *Hyloplesion*, *Microbrachis* and *Pantylus* (Carroll & Gaskill, 1978), nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018), *Brachydectes* (Pardo et al., 2016) and adelospondyls (Andrews & Carroll, 1991; Clack et al., 2019). This state is also observed in seymouriamorphs (Klembara, 1997; Berman et al., 2000; Klembara & Ruta, 2005), the temnospondyls *Balanerpeton* (Milner & Sequeira, 1993) and *Doleserpeton* (Sigurdsen & Bolt, 2010) and *Gerobatrachus* (Anderson et al., 2008).

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondylii + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (0 -> 1), *Utaherpeton franklini* (1 -> 0), Aïstopoda (1 -> 0), *Pantylus cordatus* (0 -> 1), Seymouriamorpha (0 -> 1). ACCTRAN:

Temnospondyli except *Edops craigi* (0 -> 1), *Dendrerpeton helogenes* (1 -> 0). DELTRAN: *Balanerpeton woodi* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (0 -> 1).

7. **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).**

FB2020 (c.2), M1994 (c.9), Rea1998 (c.12), RD2003 (c.12), Mea2006 (c.43), Rea2010 (c.5), B2012 (c.3), Sea2018 (c.4).

A dorsoventrally tall snout, resulting in a predominantly lateral contribution of the nasal to the snout, is present particularly in most synapsids (Romer et al., 1940; Laurin, 1993; Bolt & Scott, 1995; Modesto, 1995; Campione & Reisz, 2010; Spindler, 2016), although the condition is not found in Caseasaurs, in which the skull is not dorsoventrally tall (Olson et al., 1968; Reisz et al., 2009; Brocklehurst et al., 2016). A tall snout is, however, observed in a variety of other disparate taxa including *Whatcheeria* (Rawson et al., 2021), and the nasal is positioned quite vertically in microsaurs (Carroll & Gaskill, 1978).

Unambiguous: Lepospondyli (0 -> 1), *Acherontiscus caledoniae* (1 -> 0), Nectridea + Lysorophia (1 -> 0), Synapsida (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0), *Archaeovenator hamiltonensis* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0). DELTRAN: *Whatcheeria deltae* (0 -> 1).

8. **Nature of dermal sculpturing: no ornamentation or sculpture (0); sculpturing in pits or grooves (1).**

LR1997 (c.3), Lea1998 (c.3), A2001 (c.47), Cea2016 (c.170), Cea2019 (c.170), Hea2013 (c.65). Modified from Pea2017 (c.59, c.344 and c.345)

A variety of taxa from across various clades show different levels of dermal sculpture. In order to score as state 1, the dermal sculpturing must consist of clear pits or grooves across most of the dermal skull elements. For example, whilst there are a small number of pits on the dentary of *Westlothiana*, as these are restricted to the anterior tip of the mandible it is scored as state 0.

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondylii + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0), Nectridea (0 -> 1), *Oestocephalus sp.* (0 -> 1), *Huskerpeton englehorni* (1 -> 0), Caseidae (0 -> 1), *Euconcordia cunninghami* (0 -> 1), *Diadectes abistus* (1 -> 0),

Whatcheeria deltae (1 -> 0), *Discosauriscus austriacus* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), Lepospondyli except *Westlothiana lizziae* (0 -> 1), Diadectamorpha (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). DELTRAN: *Westlothiana lizziae* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (1 -> 0), *Solenodonsaurus janenschi* (1 -> 0), *Doleserpeton annectens* (1 -> 0).

9. **Lateral line canals in adults: absent (0); present (1).**

A2001 (c.46), Hea2013 (c.64), Pea2017 (c.58). Modified from a division of LR1997 (c.1), Lea1998 (c.1), Rea2003 (c.115), RC2007 (c.120), ML2019 (c.100).

Lateral line sensory canals are present in stem tetrapods (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021) in a small number of disparate taxa within the ingroup, including *Anthracosaurus* (Panchen, 1977), the microsaurs *Asaphestera* and *Microbrachis* (Carroll & Gaskill, 1978) and diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963; Milner, 2018).

Unambiguous: Tetrapoda (1 -> 0), Adelospondyli (0 -> 1), Diplocaulidae (0 -> 1), *Microbrachis pelikani* (0 -> 1), *Asaphestera intermedia* (0 -> 1), *Anthracosaurus russelli* (0 -> 1).

10. **Lateral line canal enclosure: entirely within grooves (0); partially in grooves, partially enclosed (1); entirely enclosed (2); lateral line canals absent (inapplicable).**

Modified from a division of LR1997 (c.1), Lea1998 (c.1), Rea2003 (c.115), RC2007 (c.120), ML2019 (c.100).

Unambiguous: *Diplocaulus sp.* + *Diploceraspis sp.* (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* (1 -> 0), Lepospondyli (0 -> 1), Adelospondylii + *Utaherpeton franklini* (1 -> 2), Embolomeri + *Chroniosaurus dongusensis* (0 -> 2). DELTRAN: *Acherontiscus caledoniae* (1 -> 2), Synapsida (1 -> 0), *Anthracosaurus russelli* (1 -> 2), *Baphetes sp.* (1 -> 0).

11. **Mandibular sensory canal: absent (0); present (1).**

Cea2016 (c.134), Cea2019 (c.134), Pea2017 (c.306).

A mandibular sensory canal is present in the outgroup (Clack & Finney, 2005; Rawson et al., 2021) and other stem tetrapod taxa (Smithson, 1981), along with the microsaur *Microbrachis* (Carroll & Gaskill, 1978) and the nectridean *Diplocaulus* (Douthitt, 1917).

Unambiguous: Adelospondyli (0 -> 1), *Diplocaulus sp.* (0 -> 1), *Microbrachis pelikani* (0 -> 1), *Asaphestera intermedia* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* (1 -> 0), Embolomeri + *Chroniosaurus dongusensis* (0 -> 1). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 0), Temnospondyli (1 -> 0).

12. Posterior skull margin: concave (0); straight (1); convex (2); undulating (3).

ML2019 (c.43, c.69), Hea2013 (c.34), Pea2017 (c.30). Modified from FB2020 (c.5)

There is a wide and complicated distribution of states of this character, although scoring is straightforward and done in dorsal view. This character does not incorporate Ford and Benson (2020) c.5, which concerns a bilateral embayment of the skull, and is considered to be a reptile synapomorphy. A reptile-like bilateral embayment is only scored as state 3 if it gives the skull an overall undulating margin, as it does in *Petrolacosaurus*, in which the posterior peak of the midline skull, in between the embayment, approaches a similar distance posteriorly as the lateral corners of the skull (Reisz, 1977). There are, however, taxa in which there is a small bilateral embayment, but the overall dominant shape of the posterior margin is concave, and as such should be scored as state 0, such as *Archaeovenator* (Reisz & Dilkes, 2003) and *Orovenator* (Ford & Benson, 2019). This is covered further in ch.120.

Unambiguous: Tetrapoda + *Baphetes sp.* (3 -> 0), *Cardiocephalus sp.* (1 -> 2), *Micraroter erythrogeois* (1 -> 2), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 2), *Procynosuchus delaharpeae* (0 -> 3), Araeoscelidia (0 -> 3), *Ariekanerpeton sigalovi* (0 -> 1), *Silvanerpeton miripedes* (0 -> 1). ACCTRAN: Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 3), *Acherontiscus caledoniae* (3 -> 2), Nectridea (3 -> 0), *Scincosaurus crassus* (0 -> 1), *Lethiscus stocki* + *Phlegethontia linearis* (3 -> 1), *Tuditanus punctulatus* (1 -> 0), *Asaphestera intermedia* (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (0 -> 3), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (3 -> 0), *Hylonomus lyelli* (3 -> 1), Temnospondyli except *Edops craigi* (0 -> 1), *Dendrerpeton helogenes* (1 -> 0).. DELTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (0 -> 1), *Acherontiscus caledoniae* (1 -> 2), *Adelogyrinus simorhynchus* (1 -> 3),

Brachydectes newberryi (1to3), Diplocaulidae (1 -> 0), *Oestocephalus sp.* (1 -> 3), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (0 -> 1), *Westlothiana lizziae* (0 -> 1), *Belebey vegrandis* (0 -> 1), *Euconcordia cunninghami* (0 -> 3), *Hylonomus lyelli* (0 -> 1), *Paleothyris acadiana* (0 -> 3), *Balanerpeton woodi* (0 -> 1), *Doleserpeton annectens* (0 -> 1).

13. Bilateral embayment: absent (0); present (1).

From Sea2022 (c.93), FB2020 (c.5)

This distribution of states in this character is related to ch.12, but they are not co-dependent and are therefore retained as separate characters, as is discussed in more detail in ch.12. In cases where there is a reptile-like central bilateral embayment, even if it is small, such as that of *Aerosaurus* (Langston & Reisz, 1981) then this character is scored as 1, regardless of the overall shape of the posterior margin of the skull.

Unambiguous: *Asaphestera intermedia* (0 -> 1), Synapsida + Araeoscelidia (0 -> 1), *Varanops brevirostris* (1 -> 0), Edaphosauridae + Sphenacodontia (1 -> 0), *Euconcordia cunninghami* (0 -> 1), *Paleothyris acadiana* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1).

14. Alary process of premaxilla: absent (0); present (1).

A2001 (c.19), RC2007 (c.1), Cea2016 (c.56), Cea2019 (c.56), Hea2013 (c.26), Pea2017 (c.23). Modified from a division of ML2019 (c.1).

The alary process is a subtriangular bony lappet that originates from the posterodorsal margin of the dorsal ramus of the premaxilla and extends posteriorly, overlapping the nasal. It is a character associated with temnospondyls (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022) but a similar condition is also present in *Chroniosaurus* (Clack & Klembara, 2009).

Unambiguous: *Chroniosaurus dongusensis* (0 -> 1). ACCTRAN: Temnospondyli (0 -> 1). DELTRAN: Temnospondyli except *Edops craigi* (0 -> 1).

15. Premaxilla anterior margin: vertical (0); overturned (1).

A2001 (c.48), Hea2013 (c.66), Pea2017 (c.60), RC2007 (c.6), ML2019 (c.4).

The derived condition of this feature refers to the oblique anteroventral surface of the premaxillae, which results in a distinct slope in some taxa and a subterminal mouth opening. It is found in captorhinids (Fox & Bowman, 1966; Reisz et al, 2015), some diadectamorphs (Romer, 1946; Berman et al., 2004), and a number of microsaurs (e.g. Carroll & Gaskill, 1978; Gee et al., 2021) that have previously been grouped together as "recumbirostrans" (Huttenlocker et al, 2013).

Unambiguous: *Hyloplesion longicostatum* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1), *Orovenator mayorum* (0 -> 1), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (0 -> 1). ACCTRAN: *Casea*sauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (0 -> 1), Diadectamorpha (0 -> 1), *Diadectes abistus* (1 -> 0). DELTRAN: *Casea*sauria (0 -> 1), *Orobates pabsti* (0 -> 1), *Limnoscelis paludis* (0 -> 1).

16. **Ratio of maximum width of both premaxillae together to maximum width of skull roof: <0.2 (0); 0.21-0.3 (1); 0.31-0.4 (2); 0.41-0.5 (3); >0.5 (4).**

RC2007 (c.5), ML2019 (c.3).

The total width of the conjoined premaxillae is measured as the distance between their lateralmost extremities (in dorsal view), the total skull table width is between the lateral extremities of the suspensorium. There is no particularly distinct phylogenetic distribution to this character.

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (0 -> 1), *Brachydectes newberryi* (2 -> 4), *Asaphestera intermedia* (0 -> 2), *Hapsidopareion lepton* (0 -> 1), *Westlothiana lizziae* (0 -> 4), *Hylonomus lyelli* + *Paleothyris acadiana* (0 -> 1), Embolomeri (2 -> 1), *Dendrerpeton helogenes* (2 -> 4), *Greererpeton burkemorani* (2 -> 3), *Whatcheeria deltae* (2 -> 3). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (2 -> 0), Adelospondyli (1 -> 4), Nectridea + Lysorophia + Aïstopoda (1 -> 2), *Diplocaulus sp.* + *Diploceraspis sp.* (2 -> 0), *Scincosaurus crassus* (2 -> 1), *Phlegethontia linearis* (2 -> 3), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (0 -> 1), Edaphosauridae (0 -> 1), Araeoscelidia (0 -> 1), *Diadectes abistus* + *Orobates pabsti* (0 -> 2), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (0 -> 1), *Gephyrostegus bohemicus* (0 -> 2), Temnospondyli (2 -> 3), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (3 -> 2). DELTRAN: Amniota + Diadectamorpha + Lepospondyli (2 -> 0), *Acherontiscus caledoniae* (1 -> 4), *Diplocaulus sp.* + *Diploceraspis sp.* (1 -> 0), *Keraterpeton galvani* (1 -> 2), *Lethiscus stocki* (1 -> 2), *Phlegethontia linearis* (1to3), *Eothyris parkeyi* (0 -> 1), *Edaphosaurus boanerges* (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), *Diadectes abistus* (0 -> 2), *Ariekanerpeton*

sigalovi + *Discosauriscus austriacus* (2 -> 1), *Seymouria sanjuanensis* (2 -> 0), *Balanerpeton woodi* (2 -> 3), *Edops craigi* (2 -> 3).

17. **Number of premaxillary teeth: fewer than 4 (0); 4-6 (1); more than 6 (2).**

A2001 (c.56), Cea2016 (c.105), Cea2019 (c.105), Hea2013 (c.74), Pea2017 (c.67).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (2 -> 1), Diplocaulidae (1 -> 2), *Microbrachis pelikani* (1 -> 2), *Asaphestera intermedia* (1 -> 2), *Pantylus cordatus* (1 -> 0), *Westlothiana lizziae* (1 -> 2), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0), *Dimetrodon sp.* (1 -> 0), Parareptilia (1 -> 0), Embolomeri (2 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 2), Adelospondyli + *Utaherpeton franklini* (1 -> 2), *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 2), Diadectamorpha (1 -> 0), *Diadectes abistus* (0 -> 1). DELTRAN: *Acherontiscus caledoniae* (1 -> 2), *Phlegethontia linearis* (1 -> 2), *Orobates pabsti* (1 -> 0), *Limnoscelis paludis* (1 -> 0), Embolomeri (2 -> 0), *Whatcheeria deltae* (2 -> 1).

18. **Premaxilla, tooth size compared to marginal maxillary teeth: small or subequal to (non-caniniform) maxillary teeth (0); premaxillary teeth larger (1)**

FB2020 (c.20). Modified from Gea1988 (c.114), Rea1992 (c.60), L1993 (c.6), M1994 (c.2), Mea2007 (c.34), Rea2011 (c.36), B2012 (c.18).

Enlarged premaxillary teeth are present in some crownward stem amniotes such as *Hylonomus* (Carroll, 1964) and *Captorhinus* (Fox & Bowman, 1966). They are also present in *Petrolacosaurus* (Reisz, 1977) and many synapsids (e.g. Romer et al., 1940; Bolt & Scott, 1995; Reisz et al., 2009) although they are absent in *Casea* (Olston et al, 1968) and edaphosaurids (Modesto, 1995). Enlarged premaxillary teeth are also known in diadectamorphs (Romer, 1946; Berman et al., 2004) and anthracosaurs (Panchen, 1977; Holmes, 1989), and in the stem tetrapod *Whatcheeria* (Rawson et al., 2021).

Unambiguous: *Procynosuchus delaharpeae* (1 -> 0), *Captorhinus aguti* (0 -> 1), *Hylonomus lyelli* (0 -> 1), Diadectamorpha (0 -> 1), Embolomeri (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Synapsida + Araeoscelidia (0 -> 1), Caseidae (1 -> 0), Edaphosauridae (1 -> 0), *Araeoscelis gracilis* (1 -> 0). DELTRAN: Synapsida (0 -> 1), *Casea broilii* (1 -> 0), *Edaphosaurus boanerges* (1 -> 0), *Petrolacosaurus kansensis* (0 -> 1), *Whatcheeria deltae* (0 -> 1).

19. **Relative proportions of premaxillary teeth: all teeth are approximately equal in size (0); anterior teeth are enlarged, forming conspicuous peak (1).**

Cea2016 (c.104), Cea2019 (c.104), Pea2017 (c.289).

The anteriormost teeth in many synapsids are enlarged relative to the more posterior teeth in the premaxilla, such as *Varanosaurus* (Bolt & Scott, 1995), *Varanops* (Campione & Reisz, 2010), *Casea* (Olson et al., 1968) and *Dimetrodon* (Romer et al., 1940). The condition is also present in araeoscelids (Reisz, 1977; Langston & Reisz, 1981), as well as *Captorhinus* (Fox & Bowman, 1966), *Limnoscelis* (Romer, 1946) and the microsaurs *Llistrofus* (Gee et al., 2019) and *Pantylus* (Carroll & Gaskill, 1978). The condition is absent in the synapsids *Eothyris* (Reisz et al., 2009) and *Edaphosaurus* (Modesto, 1995) in which the premaxillary teeth are roughly equal in size.

Unambiguous: *Pantylus cordatus* (0 -> 1), *Llistrofus pricei* (0 -> 1), Synapsida (0 -> 1), *Eothyris parkeyi* (1 -> 0), *Limnoscelis paludis* (0 -> 1). ACCTRAN: Edaphosauridae (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (0 -> 1). DELTRAN: *Edaphosaurus boanerges* (1 -> 0), *Captorhinus aguti* (0 -> 1).

20. **Distinctly ossified septomaxilla: absent (0); present (1).**

A2001 (c.20), Rea2003 (c.10), Hea2013 (c.28), Pea2017 (c.24).

Unambiguous: *Discosauriscus austriacus* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (1 -> 0), Embolomeri + *Chroniosaurus dongusensis* (1 -> 0). DELTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Anthracosaurus russelli* (1 -> 0).

21. **Position of highest point of maxilla dorsal margin along length of maxilla: in anterior third (0); at midlength (1); in posterior half (2).**

Cea2016 (c.28), Cea2019 (c.28).

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0), *Asaphestera intermedia* (1 -> 0), *Huskerpeton englehorni* (1 -> 2), *Pantylus cordatus* (1 -> 0), *Llistrofus pricei* (1 -> 0), *Westlothiana lizziae* (1 -> 0), *Varanops brevirostris* (1 -> 0), Caseasauria (1 -> 0), Sphenacodontidae + *Pantelosaurus saxonicus* (1 -> 0),

Belebey vegrandis + *Erpetonyx arsenaultorum* + *Youngina capensis* (0 -> 1), *Hylonomus lyelli* (1 -> 0), *Archeria crassidisca* (1 -> 2), *Balanerpeton* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), Amniota (1 -> 0), Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), *Araeoscelis gracilis* (0 -> 1), Seymouriamorpha (1 -> 0), Embolomeri (0 -> 1). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (0 -> 1), *Varanosaurus acutirostris* (1 -> 0), *Petrolacosaurus* (1 -> 0), Reptilia (1 -> 0), *Gephyrostegus bohemicus* (0 -> 1), *Anthracosaurus* (0 -> 1).

22. **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).**

FB2020 (c.24). Modified from L1993 (c.29), Bea1995 (c.34), RD2003 (c.5), B2012 (c.25), Sea2018 (c.21).

This character is taken from Ford & Benson (2020). An enlarged, relatively deep anterior region of the maxilla is found the stem tetrapod *Greererpeton* (Smithson et al, 1981), the microsaur *Hyloplesion* (Carroll & Gaskill, 1978) and a variety of crown amniote taxa (Langston & Reisz, 1981; Bolt & Scott, 1995; Ford & Benson, 2019), as well as in *Westlothiana*. A further enlarged, particularly deep maxilla anterior region (state 2) is found in sphenacodontids (Romer et al., 1940) and the microsaur *Pantylus* (Carroll & Gaskill, 1978). It is included to help differentiate between different crown amniote groups.

Unambiguous: *Hyloplesion longicostatum* (0 -> 1), *Pantylus cordatus* (0 -> 2), *Westlothiana lizziae* (0 -> 1), Synapsida (0 -> 1), *Varanops brevirostris* (1 -> 2), Caseasauria (1 -> 0), Sphenacodontidae (1 -> 2), *Youngina capensis* (0 -> 2), *Orovenator mayorum* (0 -> 1), *Seymouria sanjuanensis* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1), *Greererpeton burkemorani* (0 -> 1). ACCTRAN: Captorhinidae (0 -> 1). DELTRAN: *Captorhinus aguti* (0 -> 1).

23. **Maxilla length relative to palatine: shorter than palatine (0); longer than palatine (1).**

A2001 (c.52), Hea2013 (c.70), Pea2017 (c.63).

A maxilla that has become stout and is shorter than the palatine is present in nectrideans (Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018), and is also seen in the microsaur *Hyloplesion* (Carroll & Gaskill, 1978).

Unambiguous: Nectridea (1 -> 0), *Hyloplesion longicostatum* (1 -> 0).

24. Posterior extent of maxilla relative to posterior margin of orbit: maxilla does not extend posterior to orbit (0); maxilla extends posterior to orbit (1).

Cea2016 (c.29), ML2019 (c.21), Cea2019 (c.29), Pea2017 (c.267). Modified from Rea2003 (c.28, c.33), RC2007 (c.27, c.32).

State 0 of this character, in which the posterior end of maxilla is restricted anteriorly, is observed in most lepospondyls, including microsaurs (Carroll & Gaskill, 1978) and nectrideans (Beerbower, 1963; Milner & Ruta, 2009), but in aïstopods (Anderson, 2002; Pardo et al, 2017) the plesiomorphic condition is observed, in which the maxilla terminates posterior to the posterior margin of the orbit. The derived condition, state 0, also occurs in several stem and basal crown amniotes including captorhinids (Fox & Bowman, 1966; Reisz et al, 2016), araeoscelids (Reisz, 1977; Reisz et al, 1984), some synapsids (e.g. Laurin, 1993; Bolt & Scott, 1995), parareptiles (Gow, 1972; Reisz et al, 2007) and *Youngina* (Gow, 1974). and also occurs in some other stem amniotes such as *Archeria* (Holmes, 1989) and *Solenodonsaurus* (Danto et al, 2012).

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (0 -> 1), Nectridea (1 -> 0), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), *Archeria crassidisca* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* (0 -> 1), *Gephyrostegus bohemicus* (0 -> 1). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), *Euryodus sp.* (0 -> 1), Seymouriamorpha (1 -> 0).

25. 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).

FB2020 (c.36), Rea1998 (c.10), RD2003 (c.10), Mea2006 (c.11), Rea2009 (c.13), B2012 (c.36), Bea2016 (c.25), Sea2018 (c.24).

A lateral swelling of the maxilla, above the caniniform teeth, is associated with several synapsids (e.g. Laurin, 1993; Modesto, 1995; Mann & Paterson, 2020).

Unambiguous: *Varanops brevirostris* (0 -> 1), *Eothyris parkeyi* (0 -> 1), Sphenacodontidae (0 -> 1), *Varanosaurus acutirostris* (0 -> 1).

26. **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).**

FB2020 (c.37). Modified from Rea1992 (c.27), L1993 (c.28 c.70), Bea1995 (c.33), Fea2011 (c.21,c.56), B2012 (c.37), Sea2018 (c.25).

A medial swelling of the maxilla, like the previous character, is seen in some synapsids (e.g. Bolt & Scott, 1995; Mann & Paterson, 2020), but is also noted in *Youngina capensis* (Gow, 1974) and the reptile taxa that have been previously found (e.g. Ford & Benson, 2019) to be varanopids, namely *Archaeovenator* (Reisz & Dilkes, 2003) and *Orovenator* (Ford & Benson, 2019).

Unambiguous: *Echinerpeton intermedium* (0 -> 1), Sphenacodontia (0 -> 1), *Varanosaurus acutirostris* (0 -> 1). ACCTRAN: Reptilia (0 -> 1), Parareptilia (1 -> 0). DELTRAN: *Archaeovenator* (0 -> 1), *Orovenator* (0 -> 1).

27. **Maxilla, ventral surface in lateral view: straight or weakly convex (0); pronounced convexity (1).**

FB2020 (c.44). Modified from Gea1988 (c.30), Rea1992 (c.25), Bea1995 (c.31), RD2003 (c.52), Mea2008 (c.12), B2012 (c.27).

A pronounced convexity in the ventral surface of the maxilla is primarily associated with the skull shape of sphenacodontids (Romer et al., 1940; Laurin, 1993), but is also found in *Acherontiscus* (Clack et al., 2019), *Lethiscus* (Pardo et al., 2017) and *Varanosaurus* (Bolt & Scott, 1995).

Unambiguous: *Acherontiscus caledoniae* (0 -> 1), *Lethiscus stocki* (0 -> 1), Sphenacodontia (0 -> 1), *Varanosaurus acutirostris* (0 -> 1).

28. **Number of maxillary teeth: fewer than 13 (0); 14-29 (1); 30-40 (2); greater than 40 (3) (ordered).**

A2001 (c.57), RC2007 (c.235), Cea2016 (c.96), ML2019 (c.189), Cea2019 (c.96), Hea2013 (c.75), Pea2017 (c.68).

The states for this character are taken from Marjanovic & Laurin (2019 c189). The states used in that analysis were chosen to better represent phylogenetic distributions, according to the authors of that

study, as opposed to previous analyses where state distribution arbitrarily followed multiples of 10, a decision we concur with here. Most stem and crown amniotes crownwards of lepospondyls range from approximately 15 to 30 teeth (e.g. Romer et al., 1940; Gow, 1972; 1974; Reisz, 1977; Modesto, 1995; Reisz et al., 2009), with just a few exceptions including protorothyrids, which possess around 35 teeth (Carroll, 1964; 1969), *Varanosaurus* which has around 56 teeth (Bolt & Scott, 1995), and the parareptile *Belebey* which possesses just 10 teeth (Reisz et al., 2007). Temnospondyls mostly have in excess of 30 teeth (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010). Many microsaurs are characterised by a particularly low tooth number, often lower than 14, such as *Pantylus*, *Cardiocephalus* (Carroll & Gaskill, 1978) and *Euryodus* (Gee et al., 2021).

Unambiguous: *Adelogyrinus simorhynchus* (1 -> 2), Nectridea + Lysorophia (1 -> 0), *Diplocaulus sp.* + *Diploceraspis sp.* (0 -> 1), *Oestocephalus sp.* (1 -> 2), *Westlothiana lizziae* (1 -> 2), *Varanosaurus acutirostris* (1 -> 3), *Belebey vegrandis* (1 -> 0), *Opisthodontosaurus carrolli* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* (1 -> 2), *Diadectes abistus* + *Orobates pabsti* (1 -> 0), *Gephyrostegus bohemicus* (1 -> 2), *Silvanerpeton miripedes* (1 -> 2), *Archeria crassidisca* (1 -> 3), *Chroniosaurus dongusensis* (1 -> 2), *Caerorachis bairdi* (1to3), *Balanerpeton woodi* (1 -> 2), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 3), *Baphetes sp.* (1 -> 2), *Greererpeton burkemorani* (1to3). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0), *Huskerpeton englehorni* (0 -> 1), Caseidae (1 -> 0). DELTRAN: *Cardiocephalus sp.* + *Euryodus sp.* (1 -> 0), *Pantylus cordatus* (1 -> 0), *Casea broilii* (1 -> 0).

29. Shape of marginal teeth: blunt and peg-like (0); sharp, conical and straight (1); sharp and recurved (2); chisel tipped (3).

Modified from A2001 (c.55, c.58), Rea2003 (c.222, c.224), RC2007 (c.232, c.234), ML2019 (c.186, c.187, c.188), Hea2013 (c.73, c.76), Pea2017 (c.66, c.69).

The states in this character are combined from multiple different characters in previous analyses, in order to incorporate most possible tooth shapes into a single, relatively simple character. Many microsaurs are possess by blunt, peg like teeth with a rounded tip (Carroll & Gaskill, 1978). Sharp and recurved teeth are common across amniotes (Bolt & Scott, 1995; Modesto, 1995; Campione & Reisz, 2010; Brocklehurst et al., 2016).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 2), Lepospondyli (2 -> 0), *Adelogyrinus simorhynchus* (0 -> 3), Nectridea + Lysorophia + Aïstopoda (0 -> 1), *Scincosaurus crassus* (1 -> 3), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (0 -> 1), Caseasauria + *Echinerpeton intermedium* (2 -> 1), Araeoscelidia (2 -> 1), *Captorhinus aguti* +

Opisthodontosaurus carrolli (2 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* (2 -> 1), *Ariekanerpeton sigalovi* (1 -> 2), *Archeria crassidisca* (1 -> 3), *Chroniosaurus dongusensis* (1 -> 2). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (2 -> 1), Sphenacodontidae + *Pantelosaurus saxonicus* (2 -> 1), *Diadectes abistus* + *Orobates pabsti* (2 -> 3). DELTRAN: *Pantelosaurus saxonicus* (2 -> 1), *Diadectes abistus* (2 -> 3), *Whatcheeria deltae* (1 -> 2).

30. Marginal tooth morphology: single cusps (0); multiple cusps (1).

A2001 (c.60), Rea2003 (c.219), Hea2013 (c.78), Pea2017 (c.71). Modified from LR1997 (c.97), Lea1998 (c.93), ML2019 (c.183, c.190).

In stem tetrapods (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021) the teeth possess a single cusp, a condition that is almost ubiquitous across the crown tetrapods included in this analysis. A small number of taxa including some diadectamorphs (Berman et al., 1998; 2004), synapsids (Olson et al., 1968; Kemp, 1979), the parareptile *Belebey* (Reisz et al., 2007) and the temnospondyl *Doleserpeton* (Sigurdsen & Bolt, 2010) possess multiple cusps.

Unambiguous: *Casea broilii* (0 -> 1), *Procynosuchus delaharpeae* (0 -> 1), *Belebey vegrandis* (0 -> 1), *Diadectes abistus* + *Orobates pabsti* (0 -> 1), *Doleserpeton annectens* (0 -> 1).

31. Orientation of multiple tooth cusps: labiolingual (0); anteroposterior (1).

A2001 (c.61), Rea2003 (c.220), RC2007 (c.229), Hea2013 (c.79), Pea2017 (c.72).

In *Casea* the multiple tooth cusps are arranged anteroposteriorly (Olson et al, 1968).

ACCTRAN: Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1). DELTRAN: *Casea broilii* (0 -> 1).

32. Dimple on marginal teeth: absent (0); present (1).

Rea2003 (c.223), RC2007 (c.233), Cea2019 (c.235).

A small dimple on the marginal teeth is present in *Adelogyrinus* (Andrews & Carroll, 1991).

Unambiguous: *Adelogyrinus simorhynchus* (0 -> 1).

33. **Marginal teeth pedicelly: teeth are non-pedicellate (0); teeth are pedicellate (1).**

Hea2013 (c.134), LR1997 (c.98), Lea1998 (c.94), Rea2003 (c.218), RC2007 (c.228), ML2019 (c.182), Pea2017 (c.80).

Tooth pedicelly is a feature of dissorophoid temnospondyls (Sigurdsen & Bolt, 2010) and *Gerobatrachus* (Anderson et al., 2008). In these taxa, the teeth bear a base, or pedicel, upon which the apical portion of the tooth crown sits.

Unambiguous: *Doleserpeton annectens* + *Gerobatrachus hottoni* (0 -> 1).

34. **Labyrinthine infolding of teeth: absent (0); present (1).**

LR1997 (c.100), Lea1998 (c.96), A2001 (c.63), Hea2013 (c.81), Pea2017 (c.74).

Layrinthine infolding of the teeth is present in stem tetrapods (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021), as well as basally diverging temnospondyls (Milner & Sequeira, 1993; Arbez et al., 2021). Labyrinthine infolding of the teeth is absent in all stem and crown amniote taxa, including *Caerorachis* (Ruta et al., 2001), the taxon recovered here as the most basally diverging stem amniote. Labyrinthine infolding is, however, present in the diadectamorph *Limnoscelis* (Romer, 1946).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (1 -> 0), *Limnoscelis paludis* (0 -> 1). ACCTRAN: *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). DELTRAN: *Doleserpeton annectens* (1 -> 0).

35. **Marginal tooth size along row, excluding caniniform teeth: consistent along row (0); decrease in size posteriorly along row (1).**

A2001 (c.54), Hea2013 (c.72), Pea2017 (c.65) Modified from Hea2013 (c.77), A2001 (c.59).

In stem tetrapods (Beaumont, 1977; Smithson, 1981; Rawson et al., 2021) the teeth are approximately uniform in size along the anteroposterior length of the tooth row, a condition also observed in early diverging stem amniotes such as anthracosaurs (Panchen, 1977; Holmes, 1989) and *Silvanerpeton* (Ruta & Clack, 2006). In most stem and crown amniote taxa more derived than lepospondyls, the marginal dentition decreases in size steadily towards the posterior end of the tothrow, including

protorothyrids (Carroll, 1964; 1969), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015; 2016), *Petrolacosaurus* (Reisz, 1977; many synapsids (e.g. Langston & Reisz, 1981; Bolt & Scott, 1995; Reisz et al., 2009), parareptiles (Gow, 1972; Modesto et al., 2015) and *Youngina* (Gow, 1974). This condition is also present in some lepospondyls, namely the aïstopod *Phlegethontia* (Anderson, 2002) and some microsaurs (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2019; 2021) but not in other aïstopods (Carroll, 1998; Pardo et al., 2017), diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009) and other microsaurs (Carroll & Gaskill, 1978; Carroll et al., 1991).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (1 -> 0), *Phlegethontia linearis* (0 -> 1), *Cardiocephalus sp.* (1 -> 0), *Micraroter erythrogeois* (1 -> 0), *Hapsidopareion* (1 -> 0), *Varanops brevirostris* (1 -> 0), *Echinerpeton intermedium* (1 -> 0), *Araeoscelis gracilis* (1 -> 0), *Edops craigi* (0 -> 1).

36. Caniniform teeth, identified by forming conspicuous peak in the middle or the marginal tooth row: absent, tooth size is consistent along row or change size gradationally along whole row (0); present (1).

Hea2013 (c.77), A2001 (c.59), Cea2016 (c.97), Cea2019 (c.97).

Distinct caniniform teeth, clearly larger than the adjacent marginal teeth, are present and are a prominent feature of captorhinids (Fox & Bowman, 1966; Reisz et al., 2015), protorothyrids (Carroll, 1964; 1969), araeoscelids (Reisz, 1977; Reisz et al., 1984) and most synapsids (e.g. Laurin, 1993; Reisz et al., 2009; Campione & Reisz, 2010). They are also present in a a small number of microsaurs (Carroll & Gaskill, 1978; Gee et al., 2021) and diadectamorphs (Romer, 1946; Berman et al., 1998; 2004).

Unambiguous: *Hyloplesion longicostatum* (0 -> 1), *Euryodus sp.* (0 -> 1), *Pantylus cordatus* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), Edaphosauridae (1 -> 0), Reptilia (1 -> 0), *Anthracosaurus russelli* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0), *Eothyris parkeyi* (0 -> 1). DELTRAN: *Casea* broili (1 -> 0), *Echinerpeton intermedium* (1 -> 0), *Whatcheeria deltae* (0 -> 1).

37. **Position of external naris ventral rim relative to naris height: ventral rim closer to jaw margin than height of naris (0); ventral rim further from jaw margin than height of naris (1).**

LR1997 (c.9), L1998 (c.9), Cea2016 (c.160), Cea2019 (c.160).

In nectrideans, the flattened skull results in a relatively dorsal position of the external naris so that it is further from the ventral rim of the skull than the height of the naris (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018). The naris of *Limnoscelis* is dorsoventrally shallow, and is positioned relatively dorsally on the deep snout (Romer, 1946) so this taxon also scores state 1 for this character, as do *Anthracosaurus* (Panchen, 1977) and *Dendrerpeton* (Arbez et al, 2022).

Unambiguous: Nectridea (0 -> 1), *Limnoscelis paludis* (0 -> 1), *Anthracosaurus russelli* (0 -> 1), *Dendrerpeton helogenes* (0 -> 1).

38. **External naris exposed in dorsal view: not exposed (0); exposed (1).**

A2001 (c.22), Hea2013 (c.30), Pea2017 (c.26).

The external naris is exposed in dorsal view in most ingroup taxa. However, in some taxa, the snout can be relatively narrow and deep, resulting in a laterally facing naris, such as *Oestocephalus* (Carroll, 1998), and *Archeria* (Holmes, 1989) and diadectamorphs (Berman et al, 1998; Berman et al, 2004) in which the nasals are transversely broad and take up the entire dorsal roof of the snout. The recumbent snout in several microsaurs (Carroll & Gaskill, 1978; Gee et al, 2021) restricts the naris to a ventrolateral orientation.

Unambiguous: Tetrapoda + *Baphetes sp.* (0 -> 1), *Oestocephalus sp.* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0), *Westlothiana lizziae* (1 -> 0), Diadectamorpha (1 -> 0), *Archeria crassidisca* (1 -> 0), *Pederpes finneyae* (0 -> 1). ACCTRAN: Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0). DELTRAN: *Eothyris parkeyi* (1 -> 0).

39. **External naris, posterodorsal expansion: absent (0); present (1).**

FB2020 (c.45). Modified from RD2003 (c.43), Mea2006 (c.42), Rea2009 (c.9), Rea2010 (c.21), B2012 (c.4), Sea2018 (c.5).

A distinct expansion of the external naris is present in the varanopids, a clade reconstructed previously as monophyletic (Ford & Benson, 2020). This includes includes *Archaeovenator* (Reisz & Dilkes, 2003) and *Orovenator* (Ford & Benson, 2019), recovered in this analysis as reptiles, and the synapsid *Varanops* (Campione & Reisz, 2010).

Unambiguous: *Varanops brevirostris* (0 -> 1), *Edops craigi* (0 -> 1). ACCTRAN: Reptilia (0 -> 1), Parareptilia (1 -> 0). DELTRAN: *Archaeovenator hamiltonensis* (0 -> 1), *Orovenator mayorum* (0 -> 1).

40. Separately ossified nasals: entirely absent (0); present (1).

A2001 (c.18), Hea2013 (c.24), Pea2017 (c.21). Modified from a division of Rea2003 (c.12), RC2007 (c.10), ML2019 (c.8).

The nasals are lost in derived diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963). In the taxa studied, these are also the only taxa in which the premaxilla contacts the frontals, and as such a character for the latter condition is not included.

Unambiguous: *Diplocaulus sp. + Diploceraspis sp.* (1 -> 0).

41. Paired nasals present: no, nasals fused into single median element (0); yes (1); nasals entirely absent (inapplicable).

Modified from division of Rea2003 (c.12), RC2007 (c.10), ML2019 (c.8).

This character does not vary amongst taxa included in this analysis, but the character is retained to allow future expansion of the data matrix to panderichthyids or even more stemward stem tetrapods, in which paired nasals are absent (Ruta et al., 2003).

42. Separately ossified lacrimal: absent (0); present (1).

A2001 (c.9), Rea2003 (c.23), RC2007 (c.22), ML2019 (c.18), Hea2013 (c.13), Pea2017 (c.10).

A separately ossified lacrimal is absent in some lepospondyls, including *Diploceraspis* (Beerbower, 1963) and *Phlegethontia* (NMW.1899.IX.13b; Anderson, 2002) from the current dataset.

Unambiguous: *Diploceraspis sp.* (1 -> 0), *Phlegethontia* (1 -> 0).

43. Lacrimal ventral orbital process: absent (0); present (1).

A2001 (c.9), Rea2003 (c.23), RC2007 (c.22), ML2019 (c.18), Hea2013 (c.13), Pea2017 (c.10)

This, and the following character, describe a process of the lacrimal that curves round the anteroventral orbit margin and is clearly and distinctly separate from the main body of the bone, as seen clearly in *Petrolacosaurus* (Reisz, 1977) and *Llistrofus* (Gee et al, 2019), for example. A ventral process is present in almost all microsaurs (Carroll & Gaskill, 1978) and other lepospondyls (Anderson, 2002; Pardo et al, 2017). It also present in many amniote taxa, including crown ward stem amniotes such as captorhinids and protorothyrids (Fox & Bowman, 1966; Carroll, 1969), edaphosaurids (Reisz & Berman, 1986; Modesto, 1995), varanopids (Langston & Reisz, 1981; Campione & Reisz, 2010) and some basal parareptiles (Reisz et al, 2007; Modesto et al, 2015) but is absent in most other synapsids (e.g. Bolt & Scott, 1995; Reisz et al, 2009), *Milleretta* (Gow, 1972) and *Youngina* (Gow, 1974).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (0 -> 1), Adelospondyli (1 -> 0), Nectridea (1 -> 0), Temnospondyli except *Edops craigi* (0 -> 1). ACCTRAN: Synapsida (1 -> 0), Varanopidae (0 -> 1), Edaphosauridae (0 -> 1), Parareptilia (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (0 -> 1), Diadectamorpha (1 -> 0), *Orobates pabsti* (0 -> 1). DELTRAN: Caseasauria (1 -> 0), Sphenacodontia (1 -> 0), *Varanosaurus acutirostris* (1 -> 0), *Youngina capensis* (1 -> 0), *Milleretta sp.* (1 -> 0), *Diadectes abistus* (1 -> 0), *Limnoscelis paludis* (1 -> 0).

44. Lacrimal dorsal orbital process: absent (0); present (1).

Modified from A2001 (c.12), Hea2013 (c.16), Pea2017 (c.14).

Unlike the previous character, a dorsal process of the lacrimal is less widespread. A dorsal process is primarily associated with microsaurs, where it is present in all taxa apart from *Hyloplesion* and *Hapsidopareion* (Carroll & Gaskill, 1978). It is also noted in a small selection of amniote taxa.

Unambiguous: Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0), *Utaherpeton franklini* (0 -> 1), *Hapsidopareion lepton* (1 -> 0). ACCTRAN: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (0 -> 1), *Hylonomus lyelli* (1 -> 0). DELTRAN: Captorhinidae (0 -> 1), *Paleothyris acadiana* (0 -> 1).

45. **Distinct dorsal process on maxilla dorsal margin forming a distinct dorsal 'step': absent, dorsal margin of maxilla is smooth (0); present (1).**

ML2019 (c.25), Rea2003 (c.32), RC2007 (c.31).

This character described a condition in which a raised section of the dorsal margin of the maxilla is present, defined by sharp angles of close to 90 degrees from the rest of the dorsal margin. It is most clearly seen and recognised in *Pantylus* (FM UC 1075; Carroll & Gaskill, 1978), which is a good example of this state, but is also observed in other taxa including *Eothyris* (Reisz et al, 2009) and *Casea* (Olson et al, 1968).

Unambiguous: *Utaherpeton franklini* (0 -> 1), *Pantylus cordatus* (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), *Dimetrodon sp.* (0 -> 1). ACCTRAN: *Doleserpeton annectens* + *Gerobatrachus hottoni* (0 -> 1). DELTRAN: *Doleserpeton annectens* (0 -> 1).

46. **Jugal - lacrimal contact: absent, maxilla makes contribution to orbit margin (0); present, excluding maxilla from orbit margin (1).**

Novel

Unambiguous: *Diplocaulus sp.* + *Diploceraspis sp.* (1 -> 0), *Micraroter erythrogeois* (1 -> 0), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), Nectridea + Lysorophia (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* (1 -> 0). DELTRAN: Adelospondyli + *Utaherpeton franklini* (1 -> 0), Aïstopoda (1 -> 0), *Euryodus sp.* (1 -> 0).

47. **Prefrontal maximum length along long axis relative to maximum width perpendicular to long axis: less than three times longer than wide (0); at least three times longer than wide (1).**

Rea2003 (c.16), RC2007 (c.15), Cea2016 (c.53), ML2019 (c.13), Cea2019 (c.53), Pea2017 (c.270).

The length is calculated, in dorsal or lateral aspect as appropriate, as the distance between the anterior and posterior extremities of the bone. Elongation of the prefrontals occurs in a disparate selection of

taxa, such as sphenacodontids (e.g. Romer et al, 1940), *Petrolacosaurus* (Reisz, 1977), *Greererpeton* (Smithson, 1981) and many microsaurs (Carroll & Gaskill, 1978).

Unambiguous: Nectridea (1 -> 0), *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 0), *Tuditanus punctulatus* (1 -> 0), *Pantylus cordatus* (1 -> 0), *Hapsidopareion lepton* (1 -> 0), Sphenacodontia (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), *Euconcordia cunninghami* (0 -> 1), *Paleothyris acadiana* (0 -> 1), *Diadectes abistus* (0 -> 1), *Greererpeton burkemorani* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), Adelospondyli (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0), Seymouriamorpha (1 -> 0). DELTRAN: Lepospondyli (0 -> 1), *Adelogyrinus simorhynchus* (1 -> 0), *Solenodonsaurus janenschi* (0 -> 1), *Gephyrostegus bohemicus* (0 -> 1).

48. Prefrontal - postfrontal contact: absent, frontal makes contribution to orbit margin (0); present, excluding frontal from orbit margin (1).

Novel

When the postfrontal and prefrontal contact, they obscure the frontal from making a contribution to the orbit. The frontal contribution to the orbit margin is a character of crown amniotes (e.g. Gow, 1974; Bolt & Scott, 1995; Brocklehurst et al., 2016) and their closest relatives, captorhinids (Fox & Bowman, 1966; Reisz et al., 2016), *Hylonomus* (Carroll, 1964) and *Paleothyris* (Carroll, 1969). There are, however, other cases where the frontal contacts the orbit in a number of lepospondyls (Beerbower, 1963; Anderson, 2002; Pardo et al., 2016; 2017), *Chroniosaurus* (Clack & Klembara, 2009) and dissorophoid temnospondyls (Anderson et al., 2008; Sigurdsen & Bolt, 2010).

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Diplocaulus sp.* + *Diploceraspis sp.* (1 -> 0), *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 0), *Llistrofus pricei* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (1 -> 0), *Procynosuchus delaharpeae* (0 -> 1), *Opisthodontosaurus carrolli* (0 -> 1), *Chroniosaurus dongusensis* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0).

49. Separately ossified frontals: absent (0); present (1).

Cea2019 (c.224), Pea2017 (c.266).

This character does not vary within the taxon sample in this analysis. However, it is retained to allow for future expansion of the taxon sample towards deeper stem taxa, such as the addition of osteolepiforms, which may lack frontals (Zhang & Yu, 1997).

50. **Paired frontals: absent, frontals fused into single median element (0); present, frontals are separately-ossified paired elements with a midline contact (1); no ossified frontals (inapplicable).**

A2001 (c.16), Rea (c.34), RC2007 (c.33), ML2019 (c.26), Hea2013 (c.21), Pea2017 (c.18).

Fusion of the frontals into a single, median element occurs in derived diplocaulid nectrideans (MCZ3009; Douthitt, 1917; Beerbower, 1963), and also in the aïstopod *Phlegethontia* (MCZ 2038; Anderson, 2002).

Unambiguous: *Diplocaulus sp.* + *Diploceraspis sp.* (1 -> 0), *Phlegethontia linearis* (1 -> 0).

51. **Frontal anterior margin wedged between nasals: absent (0), present (1).**

Rea2003 (c.38), RC2007 (c.37), Cea2017 (c.11), Cea2019 (c.11), ML2019 (c.30)

This character describes a condition in which the anterior margin of the frontals extends distinctly between the nasals, forming a roughly triangular anterior process, with the nasals and frontals overlapping considerably along the anterior-posterior axis. State 1 is present in a widespread selection of disparate taxa.

Unambiguous: Adelospondyli (0 -> 1), *Phlegethontia linearis* (0 -> 1), *Varanosaurus acutirostris* (0 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (0 -> 1), *Limnoscelis paludis* (0 -> 1), *Discosauriscus austriacus* (0 -> 1), *Gephyrostegus bohemicus* (0 -> 1), Embolomeri (0 -> 1), *Greererpeton burkemorani* (0 -> 1), *Whatcheeria deltae* (0 -> 1)

52. **Frontal length:nasal length ratio: nasals longer than frontals (0), frontals approximately equal in length to, or longer than, nasals (1).**

Cea2016 (c.12), Cea2019 (c.12).

Most ingroup taxa possess frontals that are at least as long as the nasals, and usually longer. However, some clades show an elongation of the nasals, notably sphenacodontids (Romer et al, 1940),

anthracosaurs (Panchen, 1977; Holmes, 1989), some parareptiles (Reisz et al, 2007) and *Youngina* (Gow, 1974).

Unambiguous: *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (1 -> 0), Embolomeri (1 -> 0), *Baphetes sp.* (1 -> 0). ACCTRAN: Sphenacodontidae + *Pantelosaurus saxonicus* (1 -> 0). DELTRAN: Sphenacodontidae (1 -> 0)

53. **Anteroposterior length of frontals in relation to anteroposterior length of parietals: parietals shorter (0); frontals and parietals approximately equal in length (1); parietals longer (2).**

Rea2003 (c.35), RC2007 (c.34), Cea2016 (c.10), Cea2019 (c.10), ML2019 (c.27)

The left and right elements of both of these paired bones tend to be similar in length, but where there was a small disparity the larger was chosen to take measurements. The distribution of character states does not appear to be congruent either between or within groups. Microsaurs, in particular, show a large variety of states. For example, the parietals are shorter (state 0) in *Tuditanus* and *Hapsidopareion* (Carroll & Gaskill, 1978), approximately equivalent (state 1) in *Pantylus* (Carroll & Gaskill, 1978) and *Huskerpeton* (Huttenlocker et al., 2013), and the parietals are longer (state 2) in *Cardiocephalus* (Carroll & Gaskill, 1978) and *Euryodus* (Gee et al., 2021).

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (0 -> 2), *Utaherpeton franklini* (2 -> 1), *Brachydectes newberryi* (2 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* (1 -> 2), *Llistrofus pricei* (0 -> 2), *Varanosaurus acutirostris* (0 -> 1), *Hylonomus lyelli* (0 -> 1), *Ariekanerpeton sigalovi* (0 -> 1), *Dendrerpeton helogenes* (0 -> 2). ACCTRAN: *Lethiscus stocki* + *Phlegethontia linearis* (2 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (0 -> 2). DELTRAN: *Lethiscus stocki* (2 -> 1), *Eothyris parkeyi* (0 -> 2)

54. **Frontal, contribution to orbital margin: narrow (0); broad, >1/4 of maximum orbital length (1); inapplicable, frontal does not contribute to orbital margin (inapplicable).**

FB2020 (c63). Modified from RRea1992 (c.11), Rea1998 (c.13), RD2003 (c.13), Mea2006 (c.18), Rea2009 (c.19), Rea2010 (c.26), B2012 (c.60), Sea2018 (c.40).

The frontal makes a particularly small contribution to the orbit, in taxa where it still makes a contribution, in captorhinids (Fox & Bowman, 1966; Reisz et al., 2016) and the caseasaurs *Eothyris* (Reisz et al., 2009) and *Casea* (Olson et al., 1968).

Unambiguous: Captorhinidae (1 -> 0). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (1 -> 0), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0), Embolomeri + *Chroniosaurus dongusensis* (1 -> 0). DELTRAN: *Llistrofus pricei* (1 -> 0), Caseasauria (1 -> 0), *Chroniosaurus dongusensis* (1 -> 0).

55. Ossifications within the orbit: absent (0); present (1).

Hea2013 (c.49). Modified from a division of Pea2017 (c.45).

Ossifications within the orbit, whether that is a single ossification, as in *Huskerpeton* (Huttenlocker et al, 2013) or multiple sclerotic plates as in the crown amniote *Orovenator* (Ford & Benson, 2019), occur in a widespread but limited selection of disparate taxa. As well as these taxa, they are present in a range of other taxa from lepospondyls such as *Hapsidopareion* and *Microbrachis* (Carroll & Gaskill, 1978), other stem amniotes such as *Gephyrostegus* (Klembara et al., 2014) and even stem tetrapods such as *Baphetes* (Beaumont, 1977).

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0), *Scincosaurus crassus* (0 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (0 -> 1), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (1 -> 0), *Orobates pabsti* (0 -> 1), *Ariekanerpeton sigalovi* (0 -> 1), *Baphetes sp.* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0), *Huskerpeton englehorni* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0), Seymouriamorpha (1 -> 0), Temnospondyli except *Edops craigi* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). DELTRAN: Lepospondyli (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* (1 -> 0), *Pantylus cordatus* (1 -> 0), *Solenodonsaurus janenschi* (0 -> 1), *Gephyrostegus bohemicus* (0 -> 1), *Balanerpeton woodi* (0 -> 1), *Dendrerpeton helogenes* (0 -> 1).

56. Ossifications within orbit: single large plate (0); mosaic of bony plates (1), no orbital ossifications (inapplicable).

Modified from a division of Pea2017 (c.45).

Unambiguous: *Gephyrostegus bohemicus* (1 -> 0). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0). DELTRAN: *Huskerpeton englehorni* (1 -> 0).

57. Raised orbital rim: absent (0); present (1).

A2001 (c.30), Hea2013 (c.44), Pea2017 (c.40).

A raised orbital rim describes a condition in which at least some of the circumorbital bones are transversely thickened immediately adjacent to the orbit, and is very clearly evident in *Gephyrostegus* (Klembara et al., 2014). A raised rim is present in a variety of taxa, but primarily within microsaurs (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2021) and seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005).

Unambiguous: *Hyloplesion longicostatum* (0 -> 1), Sphenacodontia (0 -> 1), *Procynosuchus delaharpeae* (1 -> 0), *Varanosaurus acutirostris* (0 -> 1), *Milleretta sp.* (0 -> 1), Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1), *Edops craigi* (0 -> 1). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1), *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0). DELTRAN: *Asaphestera intermedia* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1).

58. Ratio of length and depth of orbit: orbit deeper than long (0); orbit longer than deep (1).

RC2007 (c.109), ML2019 (c.89). Modified from a division of Cea2016 (c.163), Cea2019 (c.163), LR1997 (c.5), Lea1998 (c.5).

The depth of the orbit is greater than its maximum anteroposterior length in the outgroup, in *Whatcheeria* (Rawson et al, 2021) and *Pederpes* (Clack & Finney, 2005). A small number of ingroup taxa show a reversal to this condition, such as *Discosauriscus* (Klembara, 1997), *Chroniosaurus* (Clack & Klembara, 2009) and edaphosaurids (Modesto, 1995).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), Edaphosauridae (1 -> 0), *Discosauriscus austriacus* (1 -> 0), *Chroniosaurus dongusensis* (1 -> 0).

59. **Orbit maximum anteroposterior length relative to anteroposterior distance between posterior orbit margin and posterior skull margin: orbit length is shorter than this distance (0); orbit length is at least as long as this distance (1).**

RC2007 (c.110), ML2019 (c.90).

The distribution of different states of this character is irregular and shows several instances of parallel developments. A particularly large orbit is noted in taxa ranging from temnospondyls (Anderson et al, 2008; Sigurdsen & Bolt, 2010) to stem amniotes such as *Silvanerpeton* (UMZC T.1317; Ruta & Clack, 2006), lepospondyls (Carroll & Gaskill, 1978), *Diadectes* (Berman et al, 1998) and some crown amniotes (Laurin, 1993; Reisz et al, 2007).

Unambiguous: *Asaphestera intermedia* (0 -> 1), *Westlothiana lizziae* (0 -> 1), *Haptodus garnettensis* (0 -> 1), *Diadectes abistus* (0 -> 1), *Silvanerpeton miripedes* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (0 -> 1). ACCTRAN: *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (0 -> 1). DELTRAN: *Belebey vegrandis* (0 -> 1).

60. **Separately ossified postfrontal: absent (0); present (1).**

Lea1998 (c.27), Rea2003 (c.57), RC2007 (c.56), ML2019 (c.45).

Lack of an ossified postfrontal is recorded in lysorophians (Pardo et al., 2016). Aïstopods show a single bone where postorbital and postfrontal would be expected (NMW1899.II.34; Carroll, 1998; Anderson, 2002; Pardo et al., 2017). Here, we follow Pardo et al., (2017), the only micro-CT reconstruction of an aïstopod, and Marjanovic & Laurin (2019), one of the most recent and most extensive tetrapod phylogenies, in considering that single bone to be a postorbital. Therefore, aïstopods are scored as absent for a postfrontal.

ACCTRAN: Nectridea + Lysorophia + Aïstopoda (1 -> 0), Nectridea (0 -> 1). DELTRAN: *Brachydectes newberryi* (1 -> 0), *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 0).

61. **Large, concave notch in posterior/ventral margin of postfrontal to accommodate the postorbital: absent, posterior margin is smooth (0); present (1).**

Hea2013 (c.9), Pea2017 (c.7).

A clear concavity in the posteroventral margin of the postfrontal is widespread across microsaurs (Carroll & Gaskill, 1978; Gee et al., 2019), many synapsids (Laurin, 1993; Bolt & Scott, 1995; Reisz et al., 2009), and is present in *Westlothiana*. As it is inherently connected to the shape of the anterodorsal margin of the postorbital, it is closely related to the presence of a sigmoid anterodorsal margin of the postorbital (ch.59), which is a character that has traditionally been associated with microsaurs (Carroll & Gaskill, 1978). However, the two characters are not entirely co-distributed; a notch in the postfrontal is not always necessary for a sinusoidal margin of the postorbital, such as in microbracomorph microsaurs (Carroll & Gaskill, 1978). There are other cases, too, where the two characters are not co-distributed; as such they are retained as two separate characters, and see ch.69 for further discussion.

Unambiguous: Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (1 -> 0), *Scincosaurus crassus* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (1 -> 0), Synapsida (0 -> 1), Varanopidae (1 -> 0), *Opisthodontosaurus carrolli* (0 -> 1), *Silvanerpeton miripedes* (0 -> 1).

62. Position of posteriormost extent of postfrontal relative to posteriormost extent of jugal: postfrontal posterior extent is anterior to jugal posterior extent (0); postfrontal posterior extent is approximately in line with, or posterior to, jugal posteriormost extent (1).

Rea2003 (c.59), RC2007 (c.58), ML2019 (c.46).

The distribution of the derived state of this character, in which the postfrontal extends proportionally significantly posteriorly appears to be incongruent as it is observed in a wide selection of taxa in multiple clades. A large postfrontal is associated with tuditanomorph microsaurs in which the postfrontal incorporates much of the temporal region (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2019; Gee et al., 2021). It is also present in some seymouriamorphs (Klembara, 1997; Berman et al., 2000), the nectridean *Diploceraspis* (Beerbower, 1963) and many stem and crown amniotes (e.g. Carroll, 1969; Gow, 1974; Reisz, 1977). This character, while related to the size of the jugal (ch.15, ch.16), the two are not entirely co-dependent. For example, in *Haptodus* the postorbital region of the jugal is short, at less than one-third of the cheek (Laurin, 1993) but in *Dimetrodon* the postorbital region of the jugal is almost half of the cheek (Romer et al., 1940). However, in both these taxa the postfrontal is small enough that it doesn't approach the posterior margin of the jugal, regardless of the size of the jugal itself. As such, these are retained as separate characters.

Unambiguous: *Diploceraspis sp.* (0 -> 1), Araeoscelidia (0 -> 1), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (0 -> 1), *Paleothyris acadiana* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Aïstopoda (0 -> 1), *Lethiscus stocki* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (0 -> 1), *Pantylus cordatus* (1 -> 0), Seymouriamorpha (0 -> 1), *Ariekanerpeton sigalovi* (1 -> 0). DELTRAN: *Phlegethontia linearis* (0 -> 1), *Oestocephalus sp.* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (0 -> 1), *Hapsidopareion lepton* + *Llistrofus pricei* (0 -> 1), *Discosauriscus austriacus* (0 -> 1), *Seymouria sanjuanensis* (0 -> 1), *Whatcheeria deltae* (0 -> 1).

63. **Postfrontal - tabular contact: absent, parietal contacts postorbital or supratemporal is present (0); present (1).**

Novel

A contact between the postfrontal and the tabular is absent in all taxa in which a supratemporal is present. Amongst those in which a supratemporal is lost, most microsaurs have a contact between the postfrontal and the tabular (Carroll & Gaskill, 1978).

Unambiguous: *Scincosaurus crassus* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1).

64. **Postfrontal - jugal contact: absent, postorbital contributes to orbit margin (0); present, excluding postorbital from orbit margin (1).**

Novel

In a small number of taxa, including some nectridean lepospondyls (Douthitt, 1917; Beerbower, 1963), the postfrontal and jugal obscure the postorbital from contacting the orbit margin.

Unambiguous: *Adelogyrinus simorhynchus* (0 -> 1), *Diplocaulus sp.* + *Diploceraspis sp.* (0 -> 1), *Oestocephalus sp.* (0 -> 1), *Araeoscelis gracilis* (0 -> 1).

65. **Separately ossified postorbital: absent (0); present (1).**

A2001 (c.31), Rea2003 (c.75), RC2007 (c.77), ML2019 (c.60), Hea2013 (c.45), Pea2017 (c.41). Modified from a division of LR1997 (c.28), Lea1998 (c.28)

The single bone in the position of the postfrontal and postorbital in aïstopods (Carroll, 1998; Anderson, 2002; Pardo et al., 2017) is considered to be a postorbital, as per Pardo et al., (2017) and Marjanovic & Laurin (2019), and so they are scored as state 1 for this character. See ch.60 for further discussion.

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Procynosuchus delaharpeae* (1 -> 0).

66. Postorbital shape: irregularly polygonal, without a clearly defined shape (0); broadly triangular shape, narrowing to a distinct point posteriorly/anteroposteriorly (1).

Modified from Rea2003 (c.78), RC2007 (c.80), Cea2016 (c.47), Cea2019 (c.47), ML2019 (c.63), Hea2013 (c.48), Pea2017 (c.44).

The shape of the postorbital may appear irregular in many deeper stem tetrapod taxa such as Pederpes (Clack & Finney, 2005) and *Greererpeton* (Smithson, 1981).In most crown tetrapods, the postorbital is more triangular in shape, and tapers posteriorly or posterodorsally to a very clearly defined point, including temnospondyls (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022), anthracosaurs (Panchen, 1977; Holmes, 1989) and seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005). Within a small number crown amniotes and some diadectamorphs and lepospondyls, the clearly defined shape is subsequently lost and the postorbital is irregular in shape, such as *Petrolacosaurus* (Reisz, 1977), *Casea* (Olson et al, 1968), and *Diadectes* (Berman et al, 1998), most nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009) and some microsaurs (Carroll & Gaskill, 1978).

Unambiguous: Lepospondyli (0 -> 1), *Keraterpeton galvani* (0 -> 1), *Phlegethontia linearis* (0 -> 1), *Tuditanus punctulatus* (0 -> 1), *Llistrofus pricei* (0 -> 1), *Casea broilii* (1 -> 0), *Haptodus garnettensis* (1 -> 0), *Petrolacosaurus kansensis* (1 -> 0), *Diadectes abistus* + *Orobates pabsti* (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* (0 -> 1), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (1 -> 0), Captorhinidae (1 -> 0). DELTRAN: Tetrapoda (0 -> 1), *Youngina capensis* (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 0).

67. Postorbital width (measured as maximum dorsal to ventral distance) relative to maximum anteroposterior orbit width: postorbital smaller (0); postorbital larger (1).

Modified from Rea2003 (c.80), RC2007 (c.82), Cea2016 (c.48), Cea2019 (c.48), ML2019 (c.65).

This and the following character are modified from the same characters in previous analyses, combining them and then dividing them in a different way. Previously these characters were ambiguous as they did not define the specific dimensions of the postorbital that they were referring to. As such, this and the following character have been rewritten for clarity of scoring. A relatively tall postorbital (state 1) occurs in the stem tetrapods *Baphetes* (Beaumont, 1977) and *Greererpeton* (Smithson, 1981), the temnospondyl *Edops* (Romer & Witter, 1942) and the lepospondyls *Pantylus* (Carroll & Gaskill, 1978), *Scincosaurus* (Milner & Ruta, 2009) and *Diplocaulus* (Douthitt, 1917). Most the lepospondyls in which this occurs are nectrideans.

Unambiguous: *Diplocaulus sp.* (0 -> 1), *Scincosaurus crassus* (0 -> 1), *Pantylus cordatus* (0 -> 1), *Edops craigi* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), Tetrapoda (1 -> 0). DELTRAN: *Baphetes sp.* (0 -> 1), *Greererpeton burkemorani* (0 -> 1).

68. Postorbital length (measured as maximum anterior to posterior distance) relative to maximum anteroposterior orbit width: postorbital smaller or equal (0); postorbital larger (1).

Modified from Rea2003 (c.80), RC2007 (c.82), Cea2016 (c.48), Cea2019 (c.48), ML2019 (c.65).

The distribution of this character is similar to that of the previous character, as both are characters concerning the size of the postorbital. However, there are some differences, and anterior-posterior elongation of the postorbital (which is covered in this character) occurs with a somewhat different distribution as dorsal-ventral elongation of the postorbital (which is covered in the previous character). Some taxa, such as *Baphetes* (Beaumont, 1977), *Greererpeton* (Smithson, 1981), *Edops* (Romer & Witter, 1942) and *Diplocaulus* (Douthitt, 1917) demonstrate a general enlargement of the postorbital, and therefore are scored as state 1 in both this and the previous character. Other taxa, such as the microsaur *Microbrachis* (Carroll & Gaskill, 1978), the diadectamorph *Limnoscelis* (Romer, 1946) and the varanopid *Aerosaurus* (MCZ4380; Langston & Reisz, 1981) show an anteroposterior elongation of the postorbital (state 1), but the postorbital is not sufficiently dorsoventrally tall to score state 1 in the previous character.

Unambiguous: *Diplocaulus sp.* (0 -> 1), *Microbrachis pelikani* (0 -> 1), *Aerosaurus wellesi* (0 -> 1), *Youngina capensis* (0 -> 1), *Limnoscelis paludis* (0 -> 1), *Edops craigi* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), Tetrapoda (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1).

DELTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (0 -> 1), *Baphetes sp.* (0 -> 1), *Greererpeton burkemorani* (0 -> 1).

69. Anterodorsal margin of postorbital: smooth, straight or gently curved margin (0); distinct sigmoid shape (1).

Rea2003 (c.82), RC2007 (c.84), ML2019 (c.67).

This character describes a curve observed in the anteromedial margin of the postorbital to produce a somewhat S-shaped profile. It consist of a clear dorsal or anterodorsally directed bump, then the margin descends anteriorly towards the orbit. This character is traditionally associated with microsaurs (Carroll & Gaskill, 1978), as described in ch.61, but it is also present in araeoscelids (Reisz, 1977; Reisz et al., 1984) and in most synapsids (e.g. Laurin, 1993; Bolt & Scott, 1995; Reisz et al., 2009; Campione & Reisz, 2010). This character is somewhat correlated with ch.61, which describes a concave notch in the postfrontal for the postorbital, as the sigmoid margin of the postorbital (state 1 of this character) must be accommodated somewhere. However, there are cases where a sigmoid margin (state 1 of this character) can occur without a notch in the postfrontal. This is most clearly demonstrated in *Petrolacosaurus* (Reisz, 1977), in which the postorbital shows a dorsal sigmoid margin, but the raised portion of the margin is not encompassed by the postfrontal, but instead is interspersed in between the postfrontal and the parietal.

Unambiguous: Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Youngina capensis* (0 -> 1), *Opisthodontosaurus carrolli* (0 -> 1).
ACCTRAN: Amniota (0 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (1 -> 0).
DELTRAN: Synapsida + Araeoscelidia (0 -> 1), *Archaeovenator hamiltonensis* (0 -> 1).

70. Postorbital - supratemporal contact: absent (0); present (1); supratemporal absent (inapplicable).

Novel

This contact occurs in anthracosaurs (Panchen, 1977; Holmes, 1989) and diadectamorphs (Romer, 1946; Berman et al, 1998; 2004), amongst a large variety of taxa. Amongst those that retain a supratemporal that doesn't contact the postorbital, it can be because of a parietal-squamosal contact, such as in *Captorhinus* (Fox & Bowman, 1966), temporal fenestration such as in *Petrolacosaurus* (Reisz, 1977), or the presence of an intertemporal blocking the contact, such as in seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), Nectridea + Lysorophia + Aïstopoda (1 -> 0), Seymouriamorpha + *Gephyrostegus bohemicus* (1 -> 0), *Dendrerpeton helogenes* (1 -> 0). ACCTRAN: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (1 -> 0), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), Sphenacodontidae (0 -> 1), Reptilia (0 -> 1), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (1 -> 0). DELTRAN: Edaphosauridae + Sphenacodontia (1 -> 0), *Dimetrodon sp.* (0 -> 1), Araeoscelidia (1 -> 0), *Youngina capensis* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (1 -> 0).

71. Postorbital - tabular contact: supratemporal absent and contact absent (0); contact present (1); supratemporal present (inapplicable).

Novel

A contact between the postorbital and tabular is never present when a supratemporal is present. Amongst taxa in which a supratemporal is absent, in most microsaurs, the postorbital extends posteriorly to contact the tabular (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 22019; 021). In most other lepospondyls, including a small number of microsaurs such as *Hyloplesion* and *Microbrachis* (Carroll & Gaskill, 1978), as well as diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963; Milner, 2018), the parietal contacts the squamosal anterior to the tabular, preventing the postorbital from extending posteriorly. As such, when a supratemporal is present, this character is scored as inapplicable so that this character distinguishes only between the condition in most microsaurs and the condition in nectrideans.

Unambiguous: *Scincosaurus crassus* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1), *Hapsidopareion lepton* (1 -> 0), *Youngina capensis* (0 -> 1).

72. Postorbital, free dorsal margin: absent (0); present (1).

FB2020 (c.75).

This character is one of several novel characters introduced by Ford & Benson (2020) to tackle the scoring of characters relating to temporal fenestration, and in particular the presumed homology of fenestrae in distantly related taxa. In previous analyses, temporal fenestration has been typically scored by characters relating to the presence or absence of both an upper and lower temporal fenestra

separately (e.g. Gauthier et al, 1988; Laurin & Reisz, 1995). Here, we follow the characters of Ford & Benson (2020). A free dorsal margin of the postorbital, associated with the presence of two temporal fenestrae, is found most taxa that are traditionally recognised as diapsids Laurin & Reisz, 1995), including araeoscelids (Reisz, 1977; Reisz et al, 1984) and *Youngina* (Gow, 1974) in the current dataset.

Unambiguous: Araeoscelidia (0 -> 1), *Youngina capensis* (0 -> 1).

73. Jugal, free posterior margin: absent (0); present (1)

FB2020 (c.76).

This is the second character from Ford & Benson (2020) relating to temporal fenestration (see ch.72). A free posterior margin of the jugal is associated with the presence of the lower temporal fenestra, and is widespread across crown amniotes, including all included synapsids (e.g. Romer et al, 1940; Bolt & Scott, 1995; Modesto, 1995), parareptiles (Gow, 1972; Reisz et al, 2007; Modesto et al, 2015), and *Youngina* (God, 1974). The condition is present in the araeoscelid *Petrolacosaurus* (Reisz, 1977) but not *Araeoscelis* (Reisz et al, 1984; MCZ4380) in which the single temporal fenestra occupies a particularly dorsal position. It is also present in aïstopods, and the microsaurs *Hapsidopareion* (Carroll & Gaskill, 1978) and *Llistrofus* (Gee et al, 2019).

Unambiguous: Aïstopoda (0 -> 1), *Hapsidopareion lepton* + *Llistrofus pricei* (0 -> 1), Amniota (0 -> 1), *Araeoscelis gracilis* (1 -> 0).

74. Parietal, free lateral margin: absent (0); present (1).

FB2020 (c.95).

This is the third character from Ford & Benson (2020) relating to temporal fenestration (also see ch.72 and ch.73). A free lateral margin of the parietal is associated with the presence of an upper temporal fenestra, such as in *Petrolacosaurus* (Reisz, 1977) and neodiapsids such as *Youngina* (Gow, 1974) but is also present in other amniote taxa that have an enlarged single temporal fenestra, such as *Edaphosaurus* (Romer & Price, 1940; Modesto, 1995). State 1 is also present in the aïstopod and lysorophian lepospondyls, which are characterised by skulls with reduced ossification (Pardo et al, 2016; Pardo et al, 2017).

Unambiguous: *Edaphosaurus boanerges* (0 -> 1), Araeoscelidia (0 -> 1), *Youngina capensis* (0 -> 1), *Orovenator mayorum* (0 -> 1). ACCTRAN: Nectridea + Aïstopoda + Lysorophia (0 -> 1), Nectridea (1 -> 0). DELTRAN: *Brachydectes newberryi* (0 -> 1), *Lethiscus stocki* + *Phlegethontia linearis* (0 -> 1).

75. Height of ventral temporal (=zygomatic) bar (complete or partially complete): dorsoventrally narrow, occupying less than 20% of postorbital skull height (0); dorsoventrally deep, occupying more than 20% of skull height (1); ventral temporal bar absent (inapplicable).

FB2020 (c.74). Modified from L1991 (c.B4), D1998 (c.32), RD2003 (c.18), M2004 (c.91), Rea2010 (c.41), Eea2014 (c.40).

This character is taken from Ford & Benson (2020) to help distinguish between different clades traditionally recognised as crown amniotes, or close to the amniote crown. State 1, a dorsoventrally deep ventral temporal bar, is generally present across synapsids (e.g. Romer & Price 1940; Brocklehurst et al, 2016; Mann & Paterson, 2020) and in *Petrolacosaurus* (Reisz, 1977), with a small number of reversals. Total-clade reptilian tend to show a narrower ventral temporal bar (state 0), although *Milleretta* shows state 1 (Gow, 1972). Within aïstopods, *Lethiscus* has a less open postorbital skull than other aïstopods (Pardo et al, 2017) and is therefore scored as state 1.

Unambiguous: *Lethiscus stocki* (0 -> 1), Synapsida + Araeoscelidia (0 -> 1), Varanopidae (1 -> 0), *Haptodus garnettensis* (1 -> 0), *Milleretta sp.* (0 -> 1).

76. Jugal, anteroposterior thickness of dorsal ramus (forming postorbital bar): narrow (0); broad, temporal fenestra only weakly emarginates the jugal (1); inapplicable, temporal fenestration absent or jugal lacks dorsal ramus (inapplicable).

B2012 (c.73), FB2020 (c.81). Modified from Mea2008 (c.20).

This character describes the condition in caseasaurs and closely related taxa, in which the jugal dorsal ramus is thick anteroposteriorly, relative to the size of the temporal fenestra. In other taxa, it tends to narrow to a splinter-like thickness. State 1 also occurs in *Milleretta* (Gow, 1972).

Unambiguous: Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (0 -> 1), *Milleretta sp.* (0 -> 1). ACCTRAN: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0). DELTRAN: Amniota (1 -> 0).

77. **Squamosal contribution to postemporal fenestra: absent (0); present (1); posttemporal fenestra absent (inapplicable).**

FB2020 (c.94), LR1995 (c.26), DR1997 (c.36), MR2006 (c.49), T2006 (c.26), Tea2012 (c.25), LP2017 (c.25).

In captorhinids (Fox & Bowman, 1966), *Paleothyris* (Carroll, 1969) and *Hylonomus* (Carroll, 1964), as well as several crown amniotes, such as the synapsid *Varanosaurus* (Bolt & Scott, 1995), and the reptiles *Youngina* (Gow, 1974) and *Belebey* (Reisz et al., 2007), the squamosal extends onto the occiput and contributes to part of the margin of the posttemporal fenestra.

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (1 -> 0), *Milleretta sp.* (1 -> 0). ACCTRAN: *Hapsidopareion lepton* + *Llistrofus pricei* (0 -> 1). DELTRAN: *Hapsidopareion lepton* (0 -> 1).

78. **Squamosal - jugal contact beneath temporal fenestra: absent, quadratojugal contributes to margin of fenestra (0); present (1); temporal fenestra absent (inapplicable).**

Modified from FB2020 (c.90)

In Ford & Benson (2020) there are two characters concerning the contact of the squamosal and jugal. They scored separately whether or not the squamosal contacted the posterodorsal margin of the jugal (FB2020 c.89) and whether or not the squamosal contacted the posteroventral margin of the jugal (FB2020 c.90). The latter of these characters also describes whether or not the quadratojugal enters the temporal fenestra. Here, the wording is simplified for the sake of clarity, and the character is specified to describe whether or not the quadratojugal entered the temporal fenestra.

Unambiguous: *Lethiscus stocki* + *Phlegethontia linearis* (0 -> 1), Synapsida (0 -> 1), *Milleretta sp.* (0 -> 1). ACCTRAN: Varanopidae (1 -> 0), Caseidae (1 -> 0). DELTRAN: *Aerosaurus wellesi* (1 -> 0), *Casea broilii* (1 -> 0).

79. **Separately ossified jugal: absent (0); present (1).**

Rea2003 (c.88), RC2007 (c.90), ML2019 (c.71). Modified from a division of LR1997 (c.30), Lea1998 (c.30).

Loss of a separately ossified jugal occurs within lysorophians (Wellstead, 1991; Pardo & Anderson, 2016).

Unambiguous: *Brachydectes newberryi* (1 -> 0).

80. Maximum depth of jugal measured beneath orbit midpoint, relative to maximum anteroposterior orbit diameter: smaller than one-third of orbit diameter, tapers to a point beneath orbit (0); between one-third and one-half of orbit diameter (1); equal to or larger than one-half of orbit diameter (2).

Rea2003 (c.91), Cea2019 (c.17), RC2007 (c.93), ML2019 (c.74), Cea2016 (c.17), Kea2014 (c.34)

The suborbital process of the jugal tapers to a point anteriorly in most ingroup taxa, and therefore the maximum dorsoventral depth of the jugal (from the margin of the orbit to its ventral edge) is smaller than 1/3 of the maximum diameter of the stem tetrapods, the jugal can extend anterior to the orbit (see ch.84), and therefore the jugal does not typically taper to a point below the orbit, but the suborbital ramus exhibits different depths in anthracosaurs and stem tetrapods, and therefore states 1 and 2 are included here to differentiate between them. In anthracosaurs (Panchen, 1977; Holmes, 1989), the jugal extends anterior to the orbit, but the suborbital process remains relatively narrow, being between 1/3 and 1/2 of the orbit diameter in height (state 1). This contrasts the condition in deeper stem taxa such as *Baphetes* (Beaumont, 1977) and *Greererpeton* (Smithson, 1981), in which the jugal suborbital process is larger than half of the orbit diameter (state 2).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 2), *Pantylus cordatus* (0 -> 1), Sphenacodontidae (0 -> 2), *Varanosaurus acutirostris* (0 -> 1), *Limnoscelis paludis* (0 -> 1), *Solenodonsaurus janenschi* (0 -> 1). ACCTRAN: Tetrapoda (2 -> 0), Nectridea + Lysorophia (0 -> 1), Embolomeri + *Chroniosaurus dongusensis* (0 -> 1), *Edops craigi* (0 -> 2). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (2 -> 0), Diplocaulidae (0 -> 1), Embolomeri + *Chroniosaurus dongusensis* (2 -> 1), Temnospondyli except *Edops craigi* (2 -> 0).

81. Length of postorbital region of jugal relative to suborbital region of jugal: postorbital region is shorter (0); suborbital region is shorter (1).

Novel

The suborbital and postorbital regions are measured from a vertical line tangential to the posteriormost point of the orbit. In taxa in which there is a substantial suborbital ramus of the jugal (ch.84), the suborbital region is often longer than the postorbital region, such as is the case in *Anthracosaurus* (Panchen, 1977) or *Ariekanerpeton* (Klembara & Ruta, 2005). Conversely, in taxa in which the jugal forms a substantial portion of the cheek and therefore extends posterior to the postorbital (ch.83), the postorbital region is often longer than the suborbital region, such as in the temnospondyl *Dendrerpeton* (Arbez et al., 2022). However, these characters are not completely codependent on each other. For example, in microsaurs, the jugal typically forms a substantial part of the cheek, and the postorbital region is longer than the suborbital region, but the postorbital is also expanded more posteriorly than most other taxa, and thus the jugal does not extend more posteriorly than the postorbital, such as in *Huskerpeton* (Huttenlocker et al., 2013) or *Euryodus* (Gee et al., 2021). As such, this character, ch.83 and ch.84 are retained as separate characters.

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), *Limnoscelis paludis* (0 -> 1), *Solenodonsaurus janenschi* (0 -> 1), *Greererpeton burkemorani* (0 -> 1).
ACCTRAN: *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (0 -> 1).
DELTRAN: *Dendrerpeton helogenes* (0 -> 1).

82. Shape of posterior margin of jugal: sloping anteroventrally to posterodorsally, whether concave or straight (0); straight, vertical margin (1); margin slopes anterodorsally to posteroventrally, whether concave or straight, but ventrally does not form a distinct posterior process (2); distinctly triradiate, with an anterodorsal to posteroventrally sloping concave margin, but ventrally forms a distinct posterior process (3).

Novel

State 3 describes the condition observed in many derived amniotes, in which there is a concave posterior margin that slopes anterodorsally to posteroventrally (e.g. Reisz, 1977; Bolt & Scott, 1995; Reisz & Dilkes, 2003; Reisz et al., 2009), but unlike in other taxa showing a similarly concave margin (e.g. *Ariekanerpeton*, Klembara & Ruta, 2005; *Silvanerpeton*, Ruta & Clack, 2006), the concavity is restricted to the dorsal part of the posterior margin, and ventral to this the posterior margin is stretched out into a thick, distinct posterior process that does not taper. As such, state 3 is generally correlated with having a free posterodorsal margin of the jugal that opens into a temporal fenestra. However, this state is retained separately to scoring of temporal fenestration as there are two taxa noted in this study

that have a triradiate, amniote-like jugal but do not have temporal fenestration, namely *Orobates* (MNG 8760, 14257) and *Opisthodontosaurus* (Reisz et al, 2015).

Unambigous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 2), *Hapsidopareion lepton* (1 -> 0), Amniota (2 -> 3), *Milleretta sp.* (3 -> 1), *Orobates pabsti* (2 -> 3), *Discosauriscus austriacus* (2 -> 1), *Archeria crassidisca* (2 -> 1), *Dendrerpeton helogenes* (2 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 2), Lepospondyli (2 -> 0), Lepospondyli except *Westlothiana lizziae* (0 -> 1), *Lethiscus stocki* + *Phlegethontia linearis* (2 -> 3), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (3 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (2 -> 1), *Lethiscus stocki* (2 -> 3), *Westlothiana lizziae* (2 -> 0), *Belebey vegrandis* (3 -> 0), *Whatcheeria deltae* (2 -> 1).

83. Posteriormost extent of the jugal relative to posteriormost extent of the postorbital: Not posterior or in line with posterior margin of postorbital (0), extending clearly beyond level of postorbital (1), jugal absent (inapplicable).

Modified from Cea2019 (c.243).

This character has a wide, disparate distribution. The character has been completely reworded from Clack et al. (2019 c.243) so that it is clearer how to score this character if the posterior extension is similar in both bones. In most included taxa, the scores for this character are consistent with the scores for ch.83, as a jugal that takes up a large proportion of the cheek is also likely to extend more posteriorly, relative to the postorbital. However, in some taxa such as *Adelogyrinus* (Andrews & Carroll, 1991), *Dimetrodon* (Romer et al., 1940) and many microsaurs (Carroll & Gaskill, 1978) the jugal is large but the postorbital is also large, and so the jugal does not terminate posteriorly to the postorbital. In the seymouriamorphs *Discosauriscus* (Klembara, 1997) and *Ariekanerpeton* (Klembara & Ruta, 2005) both the jugal and postorbital are short, so the jugal does not extend to more than one-third of the cheek length, but still terminates posterior to the postorbital.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli (1 -> 0). *Acherontiscus caledoniae* (0 -> 1), *Keraterpeton galvani* (0 -> 1), *Lethiscus stocki* (0 -> 1), *Varanops brevirostris* (0 -> 1), *Haptodus garnettensis* (0 -> 1), *Edaphosaurus boanerges* (0 -> 1), *Varanosaurus acutirostris* (0 -> 1), *Opisthodontosaurus carrolli* (0 -> 1), *Limnoscelis paludis* (0 -> 1), *Seymouria sanjuanensis* (1 -> 0), *Archeria crassidisca* (1 -> 0), *Balanerpeton woodi* (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1). DELTRAN: Tetrapoda + *Baphetes sp.* (0 -> 1).

84. Jugal anteriormost extent beneath orbital margin: jugal terminates posterior to or at orbit midlength (0); jugal terminates anterior to orbit midlength but posterior to anteriormost extent of orbit (1); jugal terminates anterior to orbit (2) (ordered).

Modified from Cea2016 (c.18), Cea2019 (c.18)

This replaces a character concerning whether or not the jugal contributed more than a third or not to the orbital margin (Clack et al., 2016 c.18; Clack et al., 2019 c.18). The first two states in the version of the character used here are almost perfectly co-distributed with the original character as in almost every case where the jugal contributes less than a third of the orbital margin, it also terminates posterior to the orbit midlength. However, this further distinction of states accounts for more division amongst those taxa with large jugals contributing large portions of the orbit margin, and specifically accounts for the condition in anthracosaurs in which the jugal extends far anterior to the orbit (Panchen, 1977; Holmes, 1989). As stated previously, although the distribution is related to ch.80 (the dorsoventral depth of the jugal ventral to orbit midlength), but this character and ch.80 are not perfectly co-distributed, and so are retained as separate characters.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (2 -> 1), *Diplocaulus sp.* (1 -> 2), *Scincosaurus crassus* (1 -> 2), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0), *Pantylus cordatus* (1 -> 2), Sphenacodontia (1 -> 2), *Varanosaurus acutirostris* (1 -> 2), Temnospondyli except *Edops craigi* (2 -> 1). ACCTRAN: Nectridea + Lysorophia (0 -> 1), *Diplocaulus sp.* (1 -> 2), Caseasauria + *Echinerpeton intermedium* (1 -> 0). DELTRAN: Diplocaulidae (0 -> 1), *Echinerpeton intermedium* (1 -> 0).

85. Jugal - squamosal contact: absent, typically due to ventral emargination or temporal fenestration (0); present (1).

Novel

A lack of a contact between the jugal and the squamosal is observed where there is some degree of ventral emargination in the microsaurs *Llistrofus* (Gee et al, 2019) and *Hapsidopareion* (Carroll & Gaskill, 1978), or a temporal fenestra such as in *Lethiscus* (Pardo et al, 2017) or *Petrolacosaurus* (Reisz, 1977).

Unambiguous: *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), Caseidae (1 -> 0), *Petrolacosaurus kansensis* (1 -> 0), *Youngina capensis* (1 -> 0). ACCTRAN: Aïstopoda (1 -> 0), *Phlegethontia*

linearis (0 -> 1), Varanopidae (1 -> 0), Edaphosauridae (1 -> 0). DELTRAN: *Lethiscus stocki* (1 -> 0), *Oestocephalus sp.* (1 -> 0), *Aerosaurus wellesi* (1 -> 0), *Edaphosaurus boanerges* (1 -> 0).

86. Maxilla - quadratojugal contact: absent, jugal makes contribution to ventral skull margin (0); present, excluding jugal from ventral skull margin (1).

Rea2003 (c.89), RC2007 (c.91), Cea2016 (c.22), Cea2019 (c.22).

In several taxa, particularly stem tetrapods such as *Greererpeton* (Smithson, 1981), stem amniotes such as anthracosaurs (Panchen, 1977; Holmes, 1989, and temnospondyls such as *Doleserpeton* (Sigurdsen & Bolt, 2010), the maxilla extends posteriorly sufficiently to contact the quadratojugal.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 0), Adelospondyli (0 -> 1), *Oestocephalus sp.* (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), Caseidae (1 -> 0), *Captorhinus aguti* (0 -> 1). ACCTRAN: *Belebey vegrandis* + *Erpetonyx arsenaultorum* (0 -> 1). DELTRAN: *Belebey vegrandis* (0 -> 1).

87. Jugal - prefrontal contact: absent, lacrimal makes contribution to orbit margin (0); present, excluding lacrimal from orbit margin (1); jugal and lacrimal do not contact, maxilla enters orbit (inapplicable).

Novel

There are no cases where the maxilla enters the orbit and the jugal still contacts the prefrontal. As such, if the maxilla enters the orbit then this character is scored as inapplicable, so that the scoring of this character is kept separate from ch.46.

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), *Diplocaulus sp.* (0 -> 1), *Edops craigi* (0 -> 1). ACCTRAN: Embolomeri + *Chroniosaurus dongusensis* (0 -> 1), *Anthracosaurus russelli* (1 -> 0). DELTRAN: *Archeria crassidisca* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1).

88. Jugal - quadratojugal contact: absent, due to ventral emargination of the cheek (0); present (1).

Rea2003 (c.112), RC2007 (c.117), ML2019 (c.98), Hea2013 (c.225), Pea2017 (c.183).

This distribution of states in this character is related to the distribution of states in ch.85. There are, however, some differences and so they are scored separately. Ch.85, a contact between the jugal and squamosal, is sometimes absent due to ventral emargination, as seen in the microsaurs *Llistrofus* (Gee et al, 2019) and *Hapsidopareion* (Carroll & Gaskill, 1978). However, an absence of a contact between the jugal and squamosal is also sometimes due to temporal fenestration, but such temporal fenestration does not prevent a jugal-quadratojugal contact (this character). In addition, in edaphosaurids and sphenacodontids (Romer et al., 1940; Laurin, 1993; Modesto, 1995), there is a partial ventral emargination in addition to the temporal fenestra which prevents the jugal from contacting the quadratojugal.

Unambiguous: *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 0), Edaphosauridae + Sphenacodontia (1 -> 0). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0). *Micraroter erythrogeois* (1 -> 0), *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0).

89. **Separately ossified quadratojugal: absent (0); present (1).**

LR1997 (c.35), Lea1998 (c.35), A2001 (c.13), Rea2003 (c.95), RC2007 (c.97), ML2019 (c.77), Hea2013 (c.18), Pea2017 (c.15).

A lack of a quadratojugal is observed in lysorophian lepospondyls (Pardo et al., 2016). It is also missing in the microsaur *Hapsidopareion* (Carroll & Gaskill, 1978). The element in that could be considered a squamosal of *Phlegethontia* is better considered to be a quadratojugal by comparison with other aïstopod taxa (Anderson, 2002).

Unambiguous: *Procynosuchus delaharpeae* (1 -> 0). ACCTRAN: Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0). DELTRAN: Varanopidae (0 -> 1), Edaphosauridae + Sphenacodontia (0 -> 1).

90. **Maximum dorsoventral depth of quadratojugal relative to 1/4 of the maximum dorsoventral depth of squamosal: quadratojugal is smaller than 1/4 of squamosal (0); quadratojugal is larger than 1/4 of squamosal (1).**

RC2007 (c.98), ML2019 (c.78). Modified from Rea2003 (c.96), which was improved in RC2007.

The depth of the bones is measured, in lateral aspect, between their ventral edge and the dorsal most part of their external surface. A dorsoventrally narrow quadratojugal is present in all synapsids included in this analysis in which it can be discerned (e.g. Olson et al., 1968; Bolt & Scott, 1995; Modesto, 1995), and is also known in seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005) and derived temnospondyls (Anderson et al., 2008; Sigurdsen & Bolt, 2010; Arbez et al., 2022). Some lepospondyls, including the nectridean *Diploceraspis* (Beerbower, 1963) and some microsaurs (Carroll & Gaskill, 1978), also show a narrow quadratojugal.

Unambiguous: Synapsida (1 -> 0), *Opisthodontosaurus carrolli* (1 -> 0), Seymouriamorpha (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (1 -> 0). ACCTRAN: *Diplocaulus sp.* + *Diploceraspis sp.* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* (1 -> 0). DELTRAN: *Diploceraspis sp.* (1 -> 0), *Cardiocephalus sp.* (1 -> 0).

91. Dorsalmost extent of quadratojugal relative to dorsalmost extent of maxilla: lower than dorsalmost extent of maxilla (0); higher than dorsal most extent of maxilla (1).

Novel

In stem tetrapods, the quadratojugal extends dorsally to a point at least as high as the dorsal margin of the maxilla (Beaumont, 1977; Smithson, 1981; Rawson et al., 2021). A large number of stem tetrapods across many disparate clades show a dorsal extent of the maxilla that exceeds the dorsal extent of the quadratojugal including temnospondyls (e.g. Sigurdsen & Bolt, 2010; Arbez et al., 2022), *Anthracosaurus* (Panchen, 1977), seymouriamorphs (Klembara, 1977; Klembara & Ruta, 2005), lepospondyls (e.g. Beerbower, 1963; Carroll & Gaskill, 1978), diadectamorphs (Romer, 1946; Berman et al., 1998) and many crownward stem and crown amniotes (e.g. Fox & Bowman, 1966; Carroll, 1969; Gow, 1972; Gow, 1974; Laurin, 1993; Brocklehurst et al., 2016).

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0), *Aerosaurus wellesi* (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), Seymouriamorpha (1 -> 0), *Anthracosaurus russelli* (1 -> 0), Temnospondyli (1 -> 0). ACCTRAN: Nectridea + Lysorophia (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (1 -> 0), *Huskerpeton englehorni* (0 -> 1). DELTRAN: Diplocaulidae (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* (1 -> 0), *Pantylus cordatus* (1 -> 0).

92. Quadratojugal anteriormost extent: not reaching level of posteriormost margin of orbit (0); reaching posteriormost margin of orbit (1).

LR1995 (c.23).

This character is one of several characters included in Laurin & Reisz (1995) that defined various amniote clades in their included taxa. It is included here as some traditional groups recovered in that study are not recovered here. Laurin & Reisz (1995) comment that the quadratojugal of diadectamorphs is short, as is the case in eureptilia, a clade encompassing captorhinids, araeoscelids and younginiforms. We do not recover this clade here. However, Laurin & Reisz note that this character is of uncertain polarity, due to the presence of a longer quadratojugal that reaches the orbit, in seymouriamorphs, most synapsids, and many parareptiles.

Unambiguous: *Varanosaurus acutirostris* (0 -> 1), *Diadectes abistus* + *Orobates pabsti* (0 -> 1), *Seymouria sanjuanensis* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1), *Gerobatrachus hottoni* (0 -> 1). ACCTRAN: *Belebey vegrandis* + *Erpetonyx arsenaultorum* (0 -> 1). DELTRAN: *Belebey vegrandis* (0 -> 1).

93. Squamosal posterodorsal margin shape: concave (0); sigmoid or approximately straight (1); convex (2).

Cea2016 (c.59), Cea2019 (c.59).

A clearly concave posterior margin of the squamosal is present in many taxa that have a posterior emargination of the skull, such as some temnospondyls (Milner & Sequeira, 1993; Arbez et al., 2022) or *Silvanerpeton* (Ruta & Clack, 2006). Embolomeres (Panchen, 1977; Holmes, 1989) and seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005), due to posterior emargination, have a short, shallowly concave section right at the dorsal end of the posterior margin of the squamosal. However, as this represents only a short section and most the posterior margin is straight, they are scored as having a straight margin (state 1).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli (0 -> 1), *Brachydectes newberryi* (1 -> 0), *Keraterpeton galvani* (1 -> 0), *Phlegethontia linearis* (1 -> 0), *Westlothiana lizziae* (1 -> 2), *Diadectes abistus* (1 -> 0), *Gephyrostegus bohemicus* (0 -> 1), Embolomeri + *Chroniosaurus dongusensis* (0 -> 1), *Greererpeton burkemorani* (0 -> 2). ACCTRAN: Adelospondyli (1 -> 0), *Adelogyrinus* (0 -> 2), *Doleserpeton annectens* + *Gerobatrachus hottoni* (0 -> 2). DELTRAN: *Acherontiscus caledoniae* (1 -> 0), *Adelogyrinus simorhynchus* (1 -> 2), *Doleserpeton annectens* (0 -> 2).

94. **Posterior margin of squamosal sloping anteroventrally to posterodorsally: not sloping, oriented vertically or sloping anterodorsally to posteroventrally (0); sloping anteroventrally to posterodorsally (1).**

Rea2003 (c.84), RC2007 (c.86).

An overturned posterior squamosal margin, so that it slopes in the opposite direction than is typical for most tetrapods, is found in the lysorophian lepospondyl *Brachydectes* (Pardo & Anderson, 2016), the microsaurs *Cardiocephalus* (Carroll & Gaskill, 1978) and *Euryodus* (Gee et al, 2021) and the synapsid *Procynosuchus* (Kemp, 1979).

Unambiguous: *Brachydectes newberryi* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* (0 -> 1), *Procynosuchus delaharpeae* (0 -> 1).

95. **Anteriormost extent of the squamosal position relative to parietal mid-length, measured along anteroposterior axis of skull: posterior to parietal mid-length (0); level with or anterior to parietal mid-length (1).**

Rea2003 (c.83), RC2007 (c.85), Cea2016 (c.62), ML2019 (c.68), Cea2019 (c.62).

In most ingroup taxa, the anteriormost part of the squamosal lies well in front of the midlength of the parietals. However, some lepospondyls (e.g. Carroll & Gaskill, 1978; Pardo et al., 2017) and many synapsids (Olson et al., 1968; Laurin, 1993; Reisz & Fröbisch, 2014) show a posterior shift in the position of the anterior margin of the squamosal.

Unambiguous: *Tuditanus punctulatus* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (1 -> 0), *Haptodus garnettensis* (1 -> 0), *Archaeovenator hamiltonensis* (1 -> 0), *Greererpeton burkemorani* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), Nectridea + Lysorophia (0 -> 1). DELTRAN: *Acherontiscus caledoniae* (1 -> 0), Aïstopoda (1 -> 0).

96. **Internal shelf of squamosal along which the quadrate articulates: absent (0); present (1).**

Rea2003 (c.87), RC2007 (c.89), ML2019 (c.70), Hea2013 (c.37).

In nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018), the ventral side of the squamosal sends a bony sheet, or strut, which provides support and buttressing for the quadrate. Amniotes and diadectamorphs, some of which show a more sheet like occipital exposure of the squamosal, are scored as state 0 as the squamosal does not buttress robustly against the quadrate as it does in nectrideans.

Unambiguous: Nectridea (0 -> 1).

97. Squamosal making contact with posterior corner of skull table: absent, posterior emargination present (0); present, squamosal contacts tabular, or supratemporal if this is forming posterior corner of skull table (1).

Novel

A contact between the squamosal and whichever elements make up the posterior corner of the skull table does not occur where there is a posterior embayment to the posterior margin of the skull, such as that in anthracosaurs (Panchen, 1977; Holmes, 1989) and seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (0 -> 1), *Edops craigi* (0 -> 1), *Greererpeton burkemorani* (0 -> 1).

98. Parietal anterior margin position relative to orbit midlength: posterior to orbit midlength (0); level with orbit midlength (1); anterior to orbit midlength (2).

Rea2003 (c.41), RC2007 (c.40), Cea2016 (c.40), Ml2019 (c.33), Cea2019 (c.40).

The position of the midlength of the orbit is measured along its greatest anteroposterior diameter.

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), *Oestocephalus sp.* (0 -> 2).

99. Parietal length relative to width: less than two and a half times longer than wide (0); at least two and a half times longer than wide (1).

Rea2003 (c.43), RC2007 (c.42), ML2019 (c.35), Cea2019 (c.224).

The greatest anteroposterior length is measured, and the greatest lateral width. Ruta & Coates (2007) stated that the metric cut-off points used to discriminate between the two states are based upon the pattern of parietal elongation in the outgroup. Certain lepospondyls, as well as colosteids, show a return to plesiomorphic condition.

Unambiguous: *Adelogyrinus simorhynchus* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1), *Greererpeton burkemorani* (0 -> 1). ACCTRAN: Nectridea + Lysorophia + Aïstopoda (0 -> 1), Nectridea (1 -> 0). DELTRAN: *Brachydectes newberryi* (0 -> 1), Aïstopoda (0 -> 1).

100. Parietal width relative to frontal width: parietals narrower than frontals or equal in width (0); parietals wider than frontals (1).

Hea2013 (c.227), Pea2017 (c.185).

Unambiguous: *Adelogyrinus simorhynchus* (1 -> 0), *Tuditanus punctulatus* (1 -> 0), *Hapsidopareion lepton* (1 -> 0), *Procynosuchus delaharpeae* (1 -> 0), *Silvanerpeton miripedes* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0), *Edops craigi* (1 -> 0).

101. Parietal - parietal total width: shorter than the distance between the orbit posterior margin and skull posterior margin, measured along skull midline (0); longer than this distance (1).

Rea2003 (c.73), RC2007 (c.73), ML2019 (c.57), Cea2019 (c.231).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Diplocaulus sp.* + *Diploceraspis sp.* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0), *Llistrofus pricei* (1 -> 0), *Eothyris parkeyi* (1 -> 0), *Procynosuchus delaharpeae* (1 -> 0), *Varanosaurus acutirostris* (1 -> 0), *Seymouria sanjuanensis* (0 -> 1). ACCTRAN: Edaphosauridae (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (1 -> 0), *Euconcordia cunninghami* (0 -> 1). DELTRAN: *Edaphosaurus* (1 -> 0), *Captorhinus aguti* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* (1 -> 0).

102. Width of anteriormost third of parietals: narrow anteriorly so that the width is not wider than frontals at the level of the frontal-parietal contact (0); do not narrow anteriorly, wider than frontals at this level (1).

Rea2003 (c.42), RC2007 (c.41), Cea2016 (c.41), ML2019 (c.34), Cea2019 (c.41).

State 0 of this character describes a particular condition in which the parietals narrow in their anterior third, towards the anterior contact with the frontals, so that they reach the same width as the frontals by their contact with the frontals. State 1 describes the case in which the parietals remain a relatively constant width along their entire length. Generally, within the ingroup taxa, the parietals narrow anteriorly (state 0), such as in *Westlothiana* or *Gephyrostegus* (Klembara et al, 2014), but there are several reversals to state 1, particularly within lepospondyls, such as *Hyloplesion* (Carroll & Gaskill, 1978), *Lethiscus* (Pardo et al., 2017) and *Acherontiscus* (Clack et al., 2019) and temnospondyls (Romer & Witter, 1942; Sigurdsen & Bolt, 2010; Arbez et al., 2022).

Unambiguous: *Acherontiscus caledoniae* (0 -> 1), *Brachydectes newberryi* (0 -> 1), *Milleretta sp.* (0 -> 1), Diadectamorpha (0 -> 1), *Anthracosaurus russelli* (0 -> 1). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Diplocaulus sp.* + *Diploceraspis sp.* (0 -> 1), Temnospondyli (0 -> 1), *Balanerpeton woodi* (1 -> 0), *Gerobatrachus hottoni* (1 -> 0). DELTRAN: *Diplocaulus sp.* (0 -> 1), *Lethiscus stocki* (0 -> 1), *Hyloplesion longicostatum* (0 -> 1), *Microbrachis pelikani* (0 -> 1), *Dendrerpeton helogenes* (0 -> 1), *Doleserpeton annectens* (0 -> 1), *Edops craigi* (0 -> 1).

103. Pineal foramen: absent (0); present (1).

Hea2013 (c.54), Anderson2001 (c.38), LR1997 (c.15), L1998 (c.15), Rea2003 (c.106), ML2019 (c.91), Pea2017 (c.48).

A pineal foramen is present widely across the included taxa. However, it is absent in many lepospondyls, including the aïstopods *Oestocephalus* (Carroll, 1998) and *Phlegethontia* (NMW1899.IX.13b; Anderson, 2002), the lysorophian *Brachydectes* (Pardo et al., 2016), and the microsaurs *Pantylus* (Carroll & Gaskill, 1978) and *Huskerpeton* (Huttenlocker et al., 2013). A pineal foramen is absent in some, but not all, specimens of the microsaurs *Cardiocephalus* (Carroll & Gaskill, 1978) and *Euryodus* (Carroll & Gaskill, 1978; Gee et al., 2021).

Unambiguous: *Acherontiscus caledoniae* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda (1 -> 0), Nectridea (0 -> 1), *Lethiscus stocki* (0 -> 1). DELTRAN: *Brachydectes newberryi* (1 -> 0), *Phlegethontia linearis* (1 -> 0), *Oestocephalus sp.* (1 -> 0).

104. Position of pineal foramen along anteroposterior length of parietals: posterior to midpoint (0); at midpoint (1); anterior to midpoint (2).

Rea2003 (c.107), RC2007 (c.111), Cea2016 (c.166), Cea2019 (c.166), ML2019 (c.92). Modified from Pea2017 (c.249, c.250).

The position of the pineal foramen relative to the midpoint of the parietals is determined by comparing the length from the anterior tip of the foramen to the anterior tip of the parietals, and the posterior tip of the foramen to the posterior tip of the parietals. In those taxa in which these lengths are approximately equivalent, the pineal foramen is deemed to be at the midpoint. In stem tetrapods the pineal foramen occupies a relatively posterior position (Smithson, 1981; Rawson et al., 2021). In some temnospondyls, the pineal foramen is positioned more anteriorly, at the midpoint in *Dendrerpeton* (Arbez et al., 2022) and anterior to the midpoint in *Balanerpeton* (Milner & Sequeira, 1993). Some stem amniotes also have a more anterior position; the pineal foramen is at the midpoint in anthracosaurs (Panchen, 1977; Holmes, 1989) and *Chroniosaurus* (Clack & Klembara, 2009), and the pineal foramen is anterior to the midpoint in seymouriamorphs (Klembara et al., 1997; Klembara & Ruta, 2005). Lepospondyls typically show a more anterior position than the outgroup as well, with some taxa having a pineal foramen at the midpoint such as *Lethiscus* (Pardo et al., 2017), *Diploceraspis* (Beerbower, 1963) and *Utaherpeton* (Carroll et al., 1991), or anterior to the midpoint as in *Cardiocephalus* (Carroll & Gaskill, 1978), *Keraterpeton* (Milner, 2018) and *Diplocaulus* (Douthitt, 1917). Crownward stem amniotes and crown amniotes show a similar variety of states, with the pineal foramen positioned anterior to the midpoint in captorhinomorphs (Fox & Bowman, 1966; Reisz et al., 2016), at the midpoint in *Petrolacosaurus* (Reisz, 1977) and some synapsids (Olson et al., 1968; Reisz et al., 2009), and even posterior to the midpoint in most synapsids (e.g. Laurin, 1993; Bolt & Scott, 1995; Brocklehurst et al., 2016) and some parareptiles (Gow, 1972; Reisz et al, 2007).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 2), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (2 -> 0), *Utaherpeton franklini* (0 -> 1), Diplocaulidae (0 -> 2), *Diploceraspis sp.* (2 -> 1), *Asaphestera intermedia* (2 -> 1), *Micraroter erythrogeois* (2 -> 1), Amniota (2 -> 0), *Procynosuchus delaharpeae* (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), *Youngina capensis* (0 -> 2), Diadectamorpha (2 -> 1), Embolomeri + *Chroniosaurus dongusensis* (0 -> 1). ACCTRAN: *Lethiscus stocki* + *Phlegethontia linearis* (0 -> 1), Caseasauria + *Echinerpeton intermedium* (0 -> 1), Temnospondyli except *Edops craigi* (0 -> 1), *Balanerpeton woodi* (1 -> 2), *Doleserpeton annectens* (1 -> 0). DELTRAN: *Lethiscus stocki* (0 -> 1), Caseasauria (0 -> 1), *Balanerpeton woodi* (0 -> 2), *Dendrerpeton helogenes* (0 -> 1), *Gerobatrachus hottoni* (0 -> 1).

105. Size of the pineal foramen: small, less than 25% of mid-parietal length (0); large, at least 25% of mid-parietal length (1); pineal foramen absent (inapplicable).

FB2020 (c96). Modified from Gea1988 (c.17), Rea1992 (c.17), Bea1995 (c.22), M2004 (c.12), Rea2009 (c.84), Rea2010 (c.31), B2012 (c.35), Sea2018 (c.52).

An enlarged pineal foramen is present various clades of crown amniotes. It is present in synapsids including caseasaurs (Olson et al., 1968; Reisz et al., 2009; Brocklehurst et al., 2016), *Varanosaurus* (Bolt & Scott, 1995) and the varanopid *Aerosaurus* (Langston & Reisz, 1981), as well as the parareptile *Belebey* (Reisz et al., 2007). It is also present in the diadectamorphs *Diadectes* (Berman et al., 1998) and *Orobates* (Berman et al., 2004).

Unambiguous: *Pantelosaurus saxonicus* (0 -> 1), *Diadectes abistus* + *Orobates pabsti* (0 -> 1). ACCTRAN: Synapsida (0 -> 1), *Varanops brevirostris* (1 -> 0), Edaphosauridae + Sphenacodontia (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (0 -> 1). DELTRAN: *Aerosaurus wellesi* (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (0 -> 1), *Varanosaurus acutirostris* (0 -> 1), *Belebey vegrandis* (0 -> 1).

106. Parietal - squamosal contact: absent (0); present (1).

Novel

There are several instances in which the parietal and squamosal contact each other. In nectrideans (e.g. Beerbower, 1963; Milner, 2018) both bones are part of the posterior extension of the skull that forms the tabular horn. In *Captorhinus* (Fox & Bowman, 1966), contact is allowed by the loss of the tabular. In *Dimetrodon* (Romer et al, 1940) and *Belebey* (Reisz et al, 2007), the postorbital is restricted to an anterior position and so does not contact any bones of the temporal series, allowing a contact between the parietal and the squamosal.

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (0 -> 1), *Scincosaurus crassus* (1 -> 0), Aïstopoda (1 -> 0), Edaphosauridae + Sphenacodontia (0 -> 1), *Dimetrodon sp.* (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (0 -> 1).

107. Parietal - postorbital contact: absent (0); present (1).

Novel

Often, the parietal and postorbital contact each other, such as in diadectamorphs (Berman et al., 1998; 2004) and most amniotes crownwards of diadectamorphs (e.g. Carroll, 1964; 1969; Reisz, 1977; Bolt & Scott, 1995; Reisz et al., 2007; Campione & Reisz, 2010; Modesto et al., 2015), but this isn't always the case. This could be because of the presence of an intertemporal (e.g. Panchen, 1977; Klembara, 1997), and in microsaurs it is because of a backwards extension of the postfrontal (Carroll & Gaskill, 1978).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli (0 -> 1), *Scincosaurus crassus* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (1 -> 0), *Youngina capensis* (1 -> 0), *Greererpeton burkemorani* (0 -> 1).

108. Parietal - tabular contact: absent, postparietal contacts supratemporal (0); present (1).

Novel

Most taxa show a contact between the parietal and the tabular, regardless of the presence of a supratemporal, including in *Archeria* (Holmes, 1989), Seymouria (Berman et al. 1987) and *Gephyrostegus* (Klembara et al, 2014) which all retain an intertemporal and a supratemporal. In the outgroup taxa (Clack & Finney, 2005; Rawson et al., 2021), other stem tetrapods (Beaumont, 1977; Smithson, 1981) and temnospondyls (e.g. Romer & Witter, 1942; Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010) there is a contact instead between the postparietal and the supratemporal.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (0 -> 1), *Acherontiscus caledoniae* (1 -> 0), *Brachydectes newberryi* (1 -> 0), *Diadectes abistus* (1 -> 0).

109. Separately ossified intertemporal: absent (0); present (1).

LR1997 (c.16), Lea1998 (c.16), Rea2003 (c.60), RC2007 (c.59), Kea2014 (c.23), Cea2016 (c.13), Cea2019 (c.13), Hea2013 (c.4). Modified from Pea2017 (c.4).

An absence of an ossified intertemporal occurs in many crown tetrapods, resulting from multiple independent evolutionary losses on the lissamphibian stem and amniote stem (Clack & Klembara,

2009; Sigurdsen & Bolt, 2010; Danto et al, 2012). Hence, the intertemporal is present in early-diverging stem amniotes such as embolomeres (Panchen, 1977; Holmes, 1989) and seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005), and in early-diverging temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993). Within temnospondyls, in the taxon set studied here, it is only known to be absent in *Doleserpeton* (Sigurdsen & Bolt, 2010).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), *Chroniosaurus dongusensis* (1 -> 0). ACCTRAN: *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). DELTRAN: *Doleserpeton annectens* (1 -> 0).

110. Intertemporal size relative to supratemporal size: smaller than supratemporal (0); equal or larger than supratemporal (1), supratemporal or intertemporal absent (inapplicable).

Kea2014 (c.24), Cea2016 (c.14), ML2019 (c.49), Cea2019 (c.14)

This character exhibits a clear dichotomy in the states. In some stem tetrapods, such as *Greererpeton*, the intertemporal is a tiny element, particularly when compared to the supratemporal (Smithson, 1981), and in temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993) and seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005), the intertemporal is still substantially smaller than the supratemporal, and approaches a maximum of half the size of the supratemporal in area. In anthracosaurs (Panchen, 1977; Holmes, 1989) and *Gephyrostegus* (Klembara et al., 2014) the two elements are roughly equivalent in area. Such a dichotomy has been previously noted in Marjanovic & Laurin (2019).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (0 -> 1); Seymouriamorpha (1 -> 0)

111. Intertemporal - squamosal contact: absent (0); present (1); intertemporal absent (inapplicable).

Novel

In taxa where this contact is absent, such as anthracosaurs (Panchen, 1977; Holmes, 1989), the postorbital contacts the supratemporal instead.

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (0 -> 1). DELTRAN: Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1), *Dendrerpeton helogenes* (0 -> 1).

112. Separately ossified supratemporal: absent (0); present (1).

LR1997 (c.17), Lea1998 (c.17), A2001 (c.2), RC2003 (c.63), Rea2007 (c.63), Hea2013 (c.5), Cea2016 (c.65), Pea2017 (c.5), Cea2019 (c.65).

A supratemporal is lost in lepospondyls (e.g. Carroll & Gaskill, 1978; Pardo et al., 2016; Milner, 2018), which have a particularly reduced temporal series. It is also lost in a small number of other taxa including the synapsid *Procynosuchus* (Kemp, 1979) and *Belebey* (Reisz et al., 2007).

Unambiguous: Lepospondyli except *Westlothiana lizziae* (1 -> 0), *Acherontiscus caledoniae* (0 -> 1), *Procynosuchus delaharpeae* (1 -> 0), *Belebey vegrandis* (1 -> 0).

113. Supratemporal exposure on occiput: absent, supratemporal restricted entirely to skull table (0); present (1).

A2001 (c.3), Hea2013 (c.6), Pea2017 (c.6).

The supratemporal makes at least a partial contribution to the occiput in many crown amniotes (e.g. Gow, 1972; Gow, 1974; Bolt & Scott, 1995; Reisz & Fröbisch, 2014), captorhinids, *Hylonomus* (Carroll, 1964) and *Paleothyris* (Carroll, 1969).

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (1 -> 0), Caseidae (0 -> 1). ACCTRAN: *Belebey vegrandis* + *Erpetonyx arsenaultorum* (1 -> 0). DELTRAN: *Erpetonyx arsenaultorum* (1 -> 0).

114. Supratemporal length relative to width: length is less than three times longer than wide (0); more than three times longer than wide, supratemporal is narrow and strap-like (1).

RC2007 (c.65), ML2019 (c.51), Cea2019 (c.221)

The derived condition of this character is based on metric cut off points observed in the strap-like supratemporal of aïstopods (Anderson, 2002; Pardo et al., 2017). A similar, elongate supratemporal is present in *Westlothiana*, the seymouriamorphs *Discosauriscus* (Klembara, 1997), the diadectamorph *Orobates* (Berman et al., 2004), protorothyrids (Carroll, 1964; 1969), *Petrolacosaurus* (Reisz, 1977) and a small number of synapsids (e.g. Romer et al., 1940; Bolt & Scott, 1995; Laurin, 1993)

Unambiguous: Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0), *Orobates pabsti* (0 -> 1), *Discosauriscus austriacus* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli (0 -> 1), Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Araeoscelis gracilis* (1 -> 0), Reptilia (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 0), Diadectamorpha (1 -> 0). DELTRAN: Aïstopoda (0 -> 1), *Westlothiana lizziae* (0 -> 1), Synapsida (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), *Euconcordia cunninghami* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* (0 -> 1).

115. Separately ossified tabular: absent (0); present (1).

LR1997 (c.18), Lea1998 (c.18), A2001 (c.42), Rea2003 (c.67), RC2007 (c.67), ML2019 (c.53), Hea2013 (c.59), Pea2017 (c.53).

Unambiguous: *Adelogyrinus simorhynchus* (1 -> 0), *Phlegethontia linearis* (1 -> 0), Captorhinidae (1 -> 0), *Discosauriscus austriacus* (1 -> 0).

116. 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); tabular absent (inapplicable).

FB2020 (c104). Modified from DR1997 (c.55), SH1998 (c.54), RD2003 (c46), Mea2006 (c.29), Rea2009 (c.51), Bea1995 (c.55), B2012 (c.86), SSS2015 (c.55), Sea2018 (c.64, c.65).

Within amniotes, edaphosaurids (Modesto, 1995) and sphenacodontids (Romer et al., 1940) both possess a tabular that participates significantly in the margin of the posttemporal fenestra.

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), Synapsida except Araeoscelidia (1 -> 0), Varanopidae (0 -> 2), Edaphosauridae + Sphenacodontia (0to3), *Araeoscelis gracilis* (1 -> 2), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (1 -> 2).

117. Tabular horns: absent (0); present (1).

LR1997 (c.20), Lea1998 (c.20), Rea2003 (c.72), RC2007 (c.68), A2001 (c.43), Bea2000 (c.5), Hea2013 (c61), Pea2017 (c55), Cea2016 (c67), Cea2019 (c67).

A tabular horn is defined here as a posterior extension of the tabular beyond the occiput and the rest of the posterior margin of the skull. Small tabular horns, consisting of short and narrow extensions, are sporadically present across a variety of stem tetrapod and stem amniote taxa, including *Baphetes* (Beaumont, 1977) and anthracosaurs (Panchen, 1977; Holmes, 1989). A very enlarged posterior extension of the tabular, resulting in a skull that is enlarged posteriorly and has a boomerang shape, is distinctly present in diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963; Milner, 2018), but this is distinguished from other tabular horns in the following character (ch.118).

Unambiguous: *Adelogyrinus simorhynchus* (0 -> 1), *Diadectes abistus* + *Orobates pabsti* (0 -> 1), Temnospondyli (1 -> 0), *Gerobatrachus hottoni* (0 -> 1), *Greererpeton burkemorani* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (1 -> 0), Nectridea + Lysorophia (0 -> 1), *Scincosaurus crassus* (1 -> 0), *Gephyrostegus bohemicus* (0 -> 1). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), *Brachydectes newberryi* (0 -> 1), Diplocaulidae (0 -> 1), Seymouriamorpha (1 -> 0).

118. Squamosal forms base of tabular horn: absent (0); present (1).

A2001 (c.45), Hea2013 (c.63), Pea2017 (c.53).

As mentioned in ch.117, the tabular horn of diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963; Milner, 2018) is larger than most other taxa, and changes the overall shape of the skull to resemble a boomerang. As such, the squamosal forms a considerable ventral contribution to the tabular horn.

ACCTRAN: Nectridea (0 -> 1). DELTRAN: Diplocaulidae (0 -> 1).

119. Elements contributing to posterolateral corner of skull table: tabular (0); supratemporal and tabular (1); parietal and supratemporal (2); large supratemporal (3).

Modified from Bea2000 (c.7).

In some taxa scoring state 2 and 3, the tabular has become occipital in its position, such as *Doleserpeton* (Sigurdsen & Bolt, 2010) and *Haptodus* (Laurin, 1993). In captorhinids the tabular is a tiny element (*Captorhinus*; Fox & Bowman, 1966) or lost completely (*Euconcordia*; Reisz et al., 2016), so while it may be situated at the posterolateral corner of the skull, it doesn't contribute significantly. In parareptiles (Gow, 1972; Reisz et al., 2007; Modesto et al., 2015), the supratemporal is expanded and covers the entire posterolateral corner of the skull.

Unambiguous: *Oestocephalus sp.* (0 -> 1), *Haptodus garnettensis* (1 -> 2), *Youngina capensis* (3to2), Captorhinidae (1 -> 2), *Doleserpeton annectens* (0 -> 2). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli (0 -> 1), Lepospondyli except *Westlothiana lizziae* (1 -> 0), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (1to3). DELTRAN: *Westlothiana lizziae* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), Parareptilia (1to3).

120. Separately ossified postparietals: absent (0); present (1).

Rea2003 (c.47), RC2007 (c.46). Modified from a division of LR1997 (c.22), Lea1998 (c.22), A2001 (c.37), ML2019 (c.39), Cea2019 (c.256), Hea2013 (c.53), Pea2017 (c.47).

Absence of postparietals occurs in a small number of lepospondyls, namely the nectridean *Scincosaurus* (Milner & Ruta, 2009) and the aïstopod *Phlegethontia* (Anderson, 2002).

Unambiguous: *Scincosaurus crassus* (1 -> 0), *Phlegethontia linearis* (1 -> 0).

121. Postparietals paired: absent, postparietals are fused into single median element (0); present (1); postparietals absent (inapplicable).

Rea2003 (c.48), RC2007 (c.47). Modified from a division of LR1997 (c.22), Lea1998 (c.22), A2001 (c.37), ML2019 (c.39), Cea2019 (c.256), Hea2013 (c.53), Pea2017 (c.47).

A single, central postparietal is observed in some synapsids including edaphosaurids (Modesto, 1995) and sphenacodontids (Romer et al., 1940), and *Varanosaurus* (Campione & Reisz, 2010). The condition is also observed in *Diadectes* (Berman et al., 1998) and some microsaurs (Carroll & Gaskill, 1978). It has been referred to previously as the interparietal (e.g. Romer et al, 1940).

Unambiguous: *Pantylus cordatus* (1 -> 0), *Hapsidopareion lepton* (1 -> 0), *Diadectes abistus* (1 -> 0). ACCTRAN: Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (1 -> 0), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (0 -> 1), *Procynosuchus delaharpae* (0 -> 1), Seymouriamorpha (1 -> 0), *Ariekanerpeton sigalovi* (0 -> 1). DELTRAN: *Varanops brevirostris* (1 -> 0), *Dimetrodon sp.* (1 -> 0), *Edaphosaurus boanerges* (1 -> 0), *Discosauriscus austriacus* (1 -> 0), *Seymouria sanjuanensis* (1 -> 0).

122. Postparietal size: each postparietal less than 75% of the area of each parietal (0); each postparietal more than 75% of the area of each parietal (1).

A2001 (c.39), Hea2013 (c.55), Pea2017 (c.49).

The choice of 75% of of the area of the parietals as a distinction between states 0 and 1 for this character is based on the choice of 75% in previous analyses. Enlarged postparietals are common within lepospondyls (e.g. Douthitt, 1917; Beerbower, 1963; Carroll & Gaskill, 1978; Pardo et al., 2017; Gee et al., 2021), as well as some stem tetrapods such as *Whatcheeria* (Rawson et al., 2021) and *Greererpeton* (Smithson, 1981).

Unambiguous: *Euryodus sp.* (0 -> 1), *Micraroter erythrogeois* (0 -> 1), *Caerorachis bairdi* (0 -> 1), *Greererpeton burkemorani* (0 -> 1), *Whatcheeria deltae* (0 -> 1). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (0 -> 1), *Adelogyrinus simorhynchus* (1 -> 0), *Keraterpeton galvani* (1 -> 0), *Oestocephalus sp.* (1 -> 0). DELTRAN: *Acherontiscus caledoniae* (0 -> 1), *Brachydectes newberryi* (0 -> 1), *Diplocaulus sp.* + *Diploceraspis sp.* (0 -> 1), *Lethiscus stocki* (0 -> 1).

123. Postparietal posteroventrally sloping occipital exposure: absent, postparietals restricted to skull table (0); present (1).

Rea2003 (c.53), RC2007 (c.52), ML2019 (c.42).

In lysorophians (Pardo et al., 2016), most microsaurs (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2021) and many crownward stem and crown amniotes (e.g. Carroll, 1969; Gow, 1974; Modesto, 1995; Reisz et al., 2009; Modesto et al., 2015), the surface of the postparietals bends abruptly posteroventrally, exhibiting a slope that continues onto the occipital surface of the skull. In some cases, the postparietals are found entirely, or almost entirely, on the occipital surface and do not even have a dorsal contribution, therefore these postparietals lack a bend but can still be scored as state 1. *Petrolacosaurus*, for example, shows this condition (Reisz, 1977).

Unambiguous: *Hylonomus lyelli* (1 -> 0), *Ariekanerpeton sigalovi* (0 -> 1), *Doleserpeton annectens* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Brachydectes newberryi* (0 -> 1), *Oestocephalus* (0 -> 1), *Westlothiana lizziae* (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (0 -> 1), Adelospondyli (1 -> 0), Diplocaulidae (1 -> 0), *Lethiscus stocki* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), *Captorhinus aguti* (1 -> 0).

124. Postparietal - tabular contact: absent, tabular restricted to posterior position contacted only by supratemporal (0); present (1).

Novel

In *Diadectes* (Berman et al, 1998) the tabular is extremely reduced, and is only attached to the supratemporal. In *Hyloplesion*, the parietal and squamosal contact each other posterior to the tabular (Carroll & Gaskill, 1978).

Unambiguous: *Hyloplesion longicostatum* (1 -> 0), *Diadectes abistus* (1 -> 0).

125. Supraoccipital, lateral expansion providing dorsal margin of posttemporal fenestra: absent (0); present (1); posttemporal fenestra absent (inapplicable).

FB2020 (c107). Modified from BE1983 (c.15), HR1986 (C), L1993 (c.43), B2012 (c.92)

The supraoccipital makes a contribution to the margin of the posttemporal fenestra in varanopids (Langston & Reisz, 1981; Campione & Reisz, 2010), other synapsids including edaphosaurids (Reisz & Berman, 1986; Modesto, 1995) and sphenacodontids (Romer et al., 1940; Laurin, 1993), and the araeoscelid *Araeoscelis* (Reisz et al, 1984).

Unambiguous: *Procynosuchus delaharpeae* (1 -> 0). ACCTRAN: Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0). DELTRAN: Varanopidae (0 -> 1), Edaphosauridae + Sphenacodontia (0 -> 1).

126. Exoccipital - postparietal contact: absent (0); present (1).

Novel

This, and all subsequent characters concerning contacts in the skull, are novel and were created from scratch. They will, inevitably, resemble or overlap with previous characters concerning contacts. However, given the potential redundancy with different bone contact characters, all such characters in this paper are not directly based on any other characters. In certain taxa such as *Diadectes* (Berman et al, 1998), the opisthotics and/or supraoccipital obscure the exoccipitals from the postparietals. In *Doleserpeton* (Sigurdsen & Bolt, 2010) the exoccipitals are obscured in the normal position, but a flange of the postparietals contacts the exoccipitals anyway.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (1 -> 0), *Diploceraspis sp.* (0 -> 1), *Llistrofus pricei* (1 -> 0). ACCTRAN: Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0). DELTRAN: *Microbrachis* pelinaki (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1).

127. Exoccipital - pterygoid contact: absent (0); present (1).

Novel

The exoccipitals contact the pterygoid ventrally in derived diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963).

Unambiguous: *Diplocaulus sp.* + *Diploceraspis sp.* (0 -> 1).

128. Dorsal trabeculae morphology: absent or incomplete, no dorsolateral bridge between sphenoid region and nasal capsule (0); dorsal trabeculae provide dorsolateral bridge between sphenoid region and nasal capsule (1).

Pea2017 (c.187).

This is the first of a series of characters from Pardo et al. (2017) that concern the braincase. The braincase was one of the principal focusses of Pardo et al. (2017), and their matrix introduced many completely novel characters concerning the braincase. Here, we use those characters from Pardo et al. (2017) that were clear and vary within the taxa included in this analysis.

Unambiguous: *Huskerpeton englehorni* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1). ACCTRAN: Nectridea + Lysorophia (0 -> 1), Temnospondyli except *Edops craigi* (0 -> 1). DELTRAN: *Brachydectes newberryi* (0 -> 1), *Doleserpeton annectens* (0 -> 1).

129. Ossification within columella ethmoidalis: absent (0); present (1).

Pea2017 (c.189).

The columella ethmoidalis is the space between the olfactory nerves, in the anterior braincase. There may be a presphenoid ossification which can fill this space. It is absent in several lepospondyls including the aïstopods *Lethiscus* (Pardo et al., 2017) and *Phlegethontia* (Anderson, 2002) and several microsaurs (Carroll & Gaskill, 1978), but is ossified in the lysorophian *Brachydectes* (Pardo et al., 2016). There is also an ossification in *Dimetrodon* (Romer et al. 1940), and *Petrolacosaurus* (Reisz et al, 1977).

Unambiguous: *Archeria crassidisca* (0 -> 1), *Edops craigi* (0 -> 1). ACCTRAN: Nectridea + Lysorophia (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (1 -> 0). DELTRAN: *Brachydectes newberryi* (0 -> 1), Synapsida + Araeoscelidia (0 -> 1), *Limnoscelis paludis* (0 -> 1).

130. Anterior extent of cultriform process of parasphenoid relative to sphenethmoid ossification: terminates posterior to sphenethmoid anterior margin (0); terminates in line with sphenethmoid anterior margin (1); terminates clearly anterior to sphenethmoid anterior margin (2); sphenethmoid absent or unossified (inapplicable).

Pea2017 (c.193).

A short cultriform process that terminates posterior to the sphenethmoid anterior margin is found in some temnospondyls (Sigurdsen & Bolt, 2010; Arbez et al., 2022), and in the synapsids *Petrolacosaurus* (Pardo et al, 2017) and *Casea* (Olson et al, 1968), although *Dimetrodon* (Romer et al, 1940) possesses a more elongate cultriform process.

Unambiguous: *Oestocephalus sp.* (1 -> 2), *Microbrachis pelikani* (1 -> 2), *Pantylus cordatus* (1 -> 2), Synapsida + Araeoscelidia (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton*

helogenes (2 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (2 -> 1), Edaphosauridae + Sphenacodontia (0 -> 2), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (1 -> 2), *Anthracosaurus russelli* (1 -> 2). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (2 -> 1), *Dimetrodon sp.* (0 -> 2), *Captorhinus aguti* (1 -> 2), *Archeria crassidisca* (2 -> 1).

131. Olfactory bulbs size: narrow (0); endocasts swollen, leaving considerable impressions in lateral and ventral wall of sphenoid region and in ventral surface of frontal (1).

Pea2017 (c.194).

Enlarged olfactory bulbs that leave impressions in the frontals are found in *Doleserpeton* (Sigurdsen & Bolt, 2010), the synapsid *Procynosuchus* (Kemp, 1979), and in the microsaur *Pantylus* (Carroll & Gaskill, 1978) and *Huskerpeton* (Huttenlocker et al., 2013).

Unambiguous: *Procynosuchus delaharpeae* (0 -> 1). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (0 -> 1), Temnospondyli except *Edops craigi* (0 -> 1). DELTRAN: *Huskerpeton englehorni* (0 -> 1), *Pantylus cordatus* (0 -> 1), *Captorhinus aguti* (0 -> 1), *Doleserpeton annectens* (0 -> 1).

132. Sphenethmoid forms interorbital septum: no (0); yes (1); sphenethmoid absent or unossified (inapplicable).

Pea2017 (c.200).

The sphenethmoid does not form an interorbital septum in *Greererpeton* (Smithson, 1981), temnospondyls (Romer & Witter, 1942; Sigurdsen & Bolt, 2010), most lepospondyls (Carroll & Gaskill, 1978; Pardo et al., 2017; Gee et al., 2019), or diadectamorphs (Romer, 1946). The sphenethmoid does, however, form an interorbital septum in many amniotes crownwards of diadectamorphs (e.g. Romer et al., 1940; Reisz, 1977; Laurin, 1993; Modesto, 1995), and in *Anthracosaurus* (Panchen, 1977) and the lepospondyls *Phlegethontia* (Anderson, 2002) and *Brachydectes* (Pardo et al., 2016).

Unambiguous: *Anthracosaurus russelli* (0 -> 1). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (0 -> 1), *Lethiscus stocki* (1 -> 0), Amniota (0 -> 1). DELTRAN: *Brachydectes newberryi* (0 -> 1), *Phlegethontia linearis* (0 -> 1), Synapsida + Araeoscelidia (0 -> 1).

133. Posterior extent of parasphenoid beneath braincase: floors sphenoid region only (0); floors sphenoid and otic region (1); floor sphenoid, otic and occipital regions (2).

Pea2017 (c.200).

The parasphenoid is restricted to an anterior position, flooring only the sphenoid region (state 0), in the stem tetrapod *Whatcheeria* (Rawson et al., 2021) and in the aïstopod *Lethiscus* (Pardo et al., 2017). State 1, in which the parasphenoid floors the otic region but not the occipital region, is observed in a variety of taxa from many clades including the stem tetrapods *Greererpeton* (Smithson, 1981) and *Baphetes* (Beaumont, 1977), the temnospondyls *Dendrerpeton* (Arbez et al., 2022) and *Edops* (Romer & Witter, 1942), anthracosaurs (Panchen, 1977; Holmes, 1989), captorhinomorphs (Fox & Bowman, 1966; Reisz et al., 2016), synapsids (e.g. Romer et al., 1940; Modesto, 1995) and reptiles such as *Youngina* (Gow, 1974), nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018) and some microsaurs such as *Micraroter*, *Microbrachis* (Carroll & Gaskill, 1978) and *Llistrofus* (Gee et al., 2019). A similarly wide selection of taxa possess state 2 in which the parasphenoid floors the occipital region including the aïstopod *Oestocephalus* (Carroll, 1998), the temnospondyl *Doleserpeton* (Sigurdsen & Bolt, 2010), *Petrolacosaurus* (Reisz, 1977), the diadectamorph *Limnoscelis* (Romer, 1946), the seymouriamorph Seymouria (Berman et al., 2000) and the microsaur *Pantylus* (Carroll & Gaskill, 1978).

Unambiguous: *Pantylus cordatus* (1 -> 2). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 2), Nectridea (2 -> 1), *Lethiscus stocki* + *Phlegethontia linearis* (2 -> 0), Araeoscelidia (1 -> 2), Diadectamorpha (1 -> 2), Seymouriamorpha + *Gephyrostegus bohemicus* (1 -> 2), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 2). DELTRAN: *Brachydectes newberryi* (1 -> 2), *Lethiscus stocki* (1 -> 0), *Oestocephalus sp.* (1 -> 2), *Petrolacosaurus kansensis* (1 -> 2), *Limnoscelis paludis* (1 -> 2), *Seymouria sanjuanensis* (1 -> 2), *Doleserpeton annectens* (1 -> 2), *Whatcheeria deltae* (1 -> 0).

134. Basal tubera: absent (0); present (1).

Modified from a division of Pea2017 (c.206).

Basal tubera are widely present across the included taxa, including some stem tetrapods (Smithson, 1981), temnospondyls (Romer & Witter, 1942; Sigurdsen & Bolt, 2010), the stem amniote *Silvanerpeton* (Ruta & Clack, 2006), and many synapsids (e.g. Romer et al., 1940; Langston & Reisz, 1981; Modesto, 1995). However, they are generally lacking in certain clades such as microsaurs (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2021) and reptiles (Gow, 1974; Ford & Benson, 2019). This character and the following character are a division of Pardo et al (2017) c.206 to allow taxa that retain a basal tubera to be scored together, regardless of the elements that contribute to the basal tubera.

Unambiguous: *Lethiscus stocki* (0 -> 1), *Silvanerpeton miripedes* (0 -> 1), *Archeria crassidisca* (0 -> 1), *Greererpeton burkemorani* (0 -> 1). ACCTRAN: *Hapsidopareion lepton* + *Llistrofus pricei* (0 -> 1), Synapsida (0 -> 1), Temnospondyli (0 -> 1), *Dendrerpeton helogenes* (1 -> 0). DELTRAN: *Llistrofus pricei* (0 -> 1), Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), *Doleserpeton annectens* (0 -> 1), *Edops craigi* (0 -> 1).

135. Elements contributing to basal tubera: contribution of parasphenoid only (0); significant endochondral contribution (1); basal tubera absent (inapplicable).

Modified from a division of Pea2017 (c206).

ACCTRAN: Tetrapoda + *Baphetes sp.* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0), Varanopidae (0 -> 1). DELTRAN: Tetrapoda (0 -> 1), *Casea broilii* (1 -> 0), *Dimetrodon sp.* (1 -> 0).

136. Pila antotica morphology: pila antotica is a thin broad sheet (0), pila antotica is a robust dorsoventral pillar bracing the skull roof against the palate (1), pila antotica absent (inapplicable).

Pea2017 (c.209).

A small number of lepospondyls (Pardo et al., 2016) and diadectamorphs (Romer, 1946) have a robust pila antotica.

ACCTRAN: Nectridea + Lysorophia (0 -> 1), Diadectamorpha (0 -> 1). DELTRAN: *Brachydectes newberryi* (0 -> 1), *Limnoscelis paludis* (0 -> 1).

137. Epipterygoid laterally contributing to basal articulation: no, basal articulation is entirely within the pterygoid and epipterygoid does not contact the basipterygoid process of the parasphenoid, or caps the joint (0); yes (1).

Pea2017 (c.212).

In most taxa included in this analysis, the epipterygoid articulates at least partially laterally with the parasphenoid, as can be observed in the anthracosaur *Archeria* (Holmes, 1989) or the lysorophian lepospondyl *Brachydectes* (Pardo et al., 2016). In reptiles, the epipterygoid does not have a lateral contribution to the basal articulation, which is made up entirely of the parasphenoid and pterygoid. Instead, it sits entirely dorsal to the contact between the parasphenoid and pterygoid, and caps the joint between them. This is particularly clear in *Orovenator* (Ford & Benson, 2019), but is also present in *Archaeovenator* (Reisz & Dilkes, 2003); *Milleretta* (Gow, 1972) and *Youngina* (Gow, 1974) and separately in the diadectamorph *Limnoscelis* (Romer, 1946).

Unambiguous: Reptilia (1 -> 0), *Limnoscelis paludis* (1 -> 0).

138. Sphenethmoid ossification: unossified (0), ossified (1).

Pea2017 (c.216)

An ossified sphenethmoid is absent in the outgroup (Clack & Finney, 2005; Rawson et al., 2021) but is present across most ingroup taxa, although it is subsequently lost in a small number of disparate taxa including *Oestocephalus* (Anderson, 2002), *Microbrachis* (Carroll & Gaskill, 1978) and Seymouria (Berman et al., 2000).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), *Oestocephalus sp.* (1 -> 0), *Microbrachis pelikani* (1 -> 0), *Procynosuchus delaharpeae* (1 -> 0), *Seymouria sanjuanensis* (1 -> 0).

139. Elements contributing to margin of fenestra vestibuli: parasphenoid excluded by neurocranial elements (basisphenoid and basioccipital) (0), parasphenoid contributes to anteroventral margin of fenestra vestibuli (1), parasphenoid floors entire fenestra vestibuli (2), ossification of otic capsule surrounds entire fenestra vestibuli (3).

Pea2017 (c.220)

ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 2), Aïstopoda (2 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* (2 -> 3), *Hapsidopareion lepton* + *Llistrofus pricei* (2 -> 0), Edaphosauridae + Sphenacodontia (2 -> 3). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (1 -> 2), *Lethiscus stocki* (2 -> 0), *Euryodus sp.* (2 -> 3), *Llistrofus pricei* (2 -> 0), *Dimetrodon sp.* (2 -> 3), *Whatcheeria deltae* (1 -> 0).

140. Opisthotic, paraoccipital process attachment: contacts skull laterally (0); ends freely (1).

FB2020 (c.115).

In stem tetrapods (Beaumont, 1977; Smithson, 1981), temnospondyls (e.g. *Doleserpeton*; Sigurdsen & Bolt, 2010), and most stem amniotes (e.g. Panchen, 1977; Berman et al., 2000; Berman et al., 2004), the paraoccipital process contacts the dorsal or lateral bones of the skull. In captorhinids (Fox & Bowman, 1966; Reisz et al., 2016) and *Paleothyris* (Carroll, 1969), *Petrolacosaurus* (Reisz, 1977), the basal synapsid *Varanosaurus* (Campione & Reisz, 2010) and in parareptiles (Gow, 1972; Reisz et al., 2007) and *Youngina* (Gow, 1974) the paraoccipital process ends freely and does not contact the dermal skull bones distally. In *Araeoscelis* (Reisz et al., 1984) and all other synapsids, the plesiomorphic condition of the paraoccipital process contacting the skull distally is present (e.g. Olson et al., 1968; Modesto, 1995; Reisz et al., 2009).

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (1 -> 0), *Araeoscelis gracilis* (1 -> 0).

141. Opisthotic obscures occipital in lateral view: no, occipital is visible in lateral view (0); yes, occipital is not visible in lateral view (1).

Pea2017 (c.231)

The only included taxon in which the occipital is obscured in lateral view is *Dimetrodon* (Romer et al, 1940; Pardo et al, 2017).

ACCTRAN: Edaphosauridae + Sphenacodontia (0 -> 1). DELTRAN: Sphenacodontidae (0 -> 1).

142. Occipital condyle shape: round, concave (0); round, convex (1); paired (2).

Modified from Hea2013 (c.84, c.85), Pea2017 (c.238).

The wording of this character has been slightly modified from previous studies. Huttenlocker et al. (2013) had two characters, one concerning whether or not the shape of the occipital condyle was concave or convex (c.84) and whether the occipital condyle was single or double (c.85). However, this wording has some redundancy because a paired condyle can be concave. Pardo et al. (2017) had a single character (c.238) with three states, being round, U-shaped, or paired. This wording is unclear because round is vague, and a variety of shapes can be considered round. The new wording here provides greater clarity. A paired condyle specifically, which can be concave in between the posterior projections, is distinguished from a concave condyle in that a paired condyle possesses two posteriorly projecting processes that project beyond the posterior skull margin, with a concavity in between. A concave condyle is considered to be one in which the shape of the condyle is concave, but these projections are lacking. In particular, most microsaurs show a paired condyle (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2021), which articulates with the odontoid process present on the atlas. Nectrideans also possess a paired condyle (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018).

Unambiuous: Aïstopoda (2 -> 0), *Cardiocephalus sp.* (2 -> 0), *Balanerpeton woodi* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), Lepospondyli (1 -> 2), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0), Araeoscelidia (1 -> 2), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 0), Diadectamorpha (1 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (0 -> 2), Amniota (0 -> 1), *Casea broilii* (1 -> 0), *Petrolacosaurus kansensis* (1 -> 2), *Euconcordia cunninghami* (0 -> 1), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (0 -> 1).

143. Ossification of the median wall of the otic capsule: completely unossified (0); ossification of opisthotic (1); ossification of supra occipital and basioccipital (2).

Pea2017 (c.251).

The ossification of the otic capsule shows a variety of conditions across the included taxa. For example, in synapsids the opisthotic predominantly makes up the otic capsule (e.g. Romer et al., 1940; Laurin, 1993; Modesto, 1995), whereas in lepospondyls there is a greater variety of conditions,

with states 0, 1 and 2 all represented within microsaurs, for example in *Llistrofus* (Gee et al., 2019), *Euryodus* (Gee et al., 2021) and *Cardiocephalus* (Carroll & Gaskill, 1978) respectively.

Unambiguous: Tetrapoda + *Baphetes sp.* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (0 -> 2), *Euryodus sp.* (2 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 2), Lepospondyli (2 -> 0), *Microbrachis pelikani* (0 -> 1), Synapsida except Araeoscelidia (2 -> 1), *Gephyrostegus bohemicus* (2 -> 1). DELTRAN: Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 2), Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (2 -> 1), *Seymouria sanjuanensis* (1 -> 2).

144. Semicircular canals separated from utricular region by bone: not separated (0); separated (1).

Pea2017 (c.253).

ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (0 -> 1), Aïstopoda (0 -> 1), *Pantylus cordatus* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0). DELTRAN: *Brachydectes newberryi* (0 -> 1), *Huskerpeton englehorni* (0 -> 1), *Llistrofus pricei* (0 -> 1), *Archeria crassidisca* (0 -> 1).

145. Elongate, broad posterolateral processes on parasphenoid: absent (0); present (1).

Modified from a division of RC2007 (c.179), ML2019 (c.139).

The posterior margins of the parasphenoid plate are drawn out into wide, elongate processes that project laterally in several taxa. They are best demonstrated in seymouriamorphs such as *Discosauriscus* (Klembara, 1997) and *Ariekanerpeton* (Klembara & Ruta, 2005).

Unambiguous: *Brachydectes newberryi* (0 -> 1), *Micraroter erythrogeois* (0 -> 1), Seymouriamorpha (0 -> 1), *Balanerpeton woodi* (0 -> 1).

146. Shape of basal plate of parasphenoid: triangular (0); rectangular (1).

RC2007 (c.186), ML2019 (c.145), Hea2013 (c.105), Pea2017 (c.215).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (0 -> 1), Adelospondyli + *Utaherpeton franklini* (1 -> 0), Temnospondyli (0 -> 1). ACCTRAN: Caseasauria (0 -> 1), Seymouriamorpha (0 -> 1), *Ariekanerpeton sigalovi* (1 -> 0). DELTRAN: *Eothyris parkeyi* (0 -> 1), *Discosauriscus austriacus* (0 -> 1), *Seymouria sanjuanensis* (0 -> 1).

147. Parasphenoid much wider than long immediately posterior to level of basal articulation: absent (0); present (1).

Rea2003 (c.176), RC2007 (c.185), ML2019 (c.144).

In temnospondyls and *Gerobatrachus*, the parasphenoid plate is extremely wide. The anterior margin of the plate, immediately posterior to the basal articulation, expands rapidly to reach the maximum width of the plate, which is wider than it is long (Romer & Witter, 1942; Milner & Sequeira, 1993; Anderson et al., 2008; Sigurdsen & Bolt, 2010; Arbez et al., 2022).

Unambiguous: Temnospondyli (0 -> 1).

148. Depression in body of parasphenoid: absent (0); single, median depression (1); paired lateral depressions (2).

Rea2003 (c.171), RC2007 (c.180), Cea2016 (c.77), ML2019 (c.140), Cea2019 (c.77).

Most amniotes (e.g. Romer et al., 1940; Gow, 1974; Reisz & Dilkes, 2003; Bolt & Scott, 1995) and stem amniotes (e.g. Fox & Bowman, 1966; Panchen, 1977; Clack & Ruta, 2006) have a single, central depression in the parasphenoid. Temnospondyls lack any depression (e.g. Romer & Witter, 1942; Milner & Sequeira, 1993; Arbez et al., 2022), as do lepospondyls (e.g. Beerbower, 1963; Carroll & Gaskill, 1978; Pardo et al., 2016; 2017), with the exception of *Westlothiana* which retains a single, central depression.

Unambiguous: Lepospondyli except *Westlothiana lizziae* (1 -> 0), *Procynosuchus delaharpeae* (1 -> 2), *Seymouria sanjuanensis* (1 -> 0), *Archeria crassidisca* (1 -> 0). Tetrapoda + *Baphetes sp.* +

Greererpeton burkemorani (1 -> 2), Tetrapoda (2 -> 0), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (0 -> 1). DELTRAN: Temnospondyli (1 -> 0), *Baphetes sp.* (1 -> 2), *Greererpeton burkemorani* (1 -> 2).

149. Parasphenoid cultriform process: tapering along most of length (0); parallel sided for most of length (1).

Rea2003 (c.169), RC2007 (c.176), Cea2016 (c.76), ML2019 (c.136), Cea2019 (c.76).

Generally, the cultriform process is parallel sided, or close to parallel sided, such as in the aïstopod *Lethiscus* (Pardo et al., 2017), the diadectamorph *Orobates* (Berman et al., 2004), or in *Petrolacosaurus* (Reisz, 1977). However, in several taxa the cultriform process tapers to a degree significant enough to consider the shape of the cultriform process as distinctly triangular. Examples include *Ariekanerpeton* (Klembara & Ruta, 2005) or *Silvanerpeton* (Ruta & Clack, 2006).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), *Tuditanus punctulatus* (1 -> 0), *Huskerpeton englehorni* (1 -> 0), *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 0), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (0 -> 1), Adelospondyli + *Utaherpeton franklini* (1 -> 0). DELTRAN: *Acherontiscus caledoniae* (1 -> 0), Seymouriamorpha + *Gephyrostegus bohemicus* (1 -> 0), *Silvanerpeton miripedes* (1 -> 0).

150. Cultriform process of parasphenoid contacting vomers: absent (0); present (1).

Novel

This character is related to ch.169, which describes whether or not the pterygoids contact on the midline, as previously described. The distribution of states is related, as those taxa in which the cultriform process of the parasphenoid contacts the vomers also lack a midline contact of the pterygoids, a condition clearly demonstrated, for example, in *Doleserpeton* (Sigurdsen & Bolt, 2010). However, as discussed in ch.169, not all taxa that lack a pterygoid midline contact possess a contact between the cultriform process and vomers, and as such they are retained as separate characters. Temnospondyls (see ch.69), nectrideans (e.g. Beerbower, 1963; Milner, 2018) and lysorophians (Pardo et al., 2016) have a cultifrom process that contacts the vomers.

Unambiguous: Nectridea + Lysorophia (0 -> 1), *Hyloplesion longicostatum* (0 -> 1), Temnospondyli except *Edops craigi* (0 -> 1).

151. Denticle shagreen on parasphenoid: absent (0); present (1).

LR1997 (c.60), Lea1998 (c.58), A2001 (c.79), RC2007 (c.184), Cea2016 (c.101), Cea2019 (c.101), Hea2013 (c.102), Pea2017 (c.281), Cea2016 (c.102), Cea2019 (c.102), Kea2014 (c.55).

Denticles are present on the parasphenoid, typically at the posterior end of the cultriform process and the anterior end of the parasphenoid plate, in most stem tetrapods (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005). They are also present widely across crown tetrapods in many disparate clades, including temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022) and *Gerobatrachus* (Anderson et al., 2008), *Silvanerpeton* (Ruta & Clack, 2006), *Solenodonsaurus* (Danto et al., 2012), most seymouriamorphs (Klembara, 1997; Berman et al., 2000), Westlothaina, some microsaurs (Carroll & Gaskill, 1978; Gee et al., 2019), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015; 2016), protorothyrids (Carroll, 1964; 1969), *Petrolacosaurus* (Reisz, 1977), *Orovenator* (Ford & Benson, 2019) and *Casea* (Olson et al., 1968).

Unambiguous: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0), *Petrolacosaurus kansensis* (0 -> 1), *Orovenator mayorum* (0 -> 1), *Ariekanerpeton sigalovi* (1 -> 0), *Gephyrostegus bohemicus* (1 -> 0), Embolomeri (1 -> 0), *Whatcheeria deltae* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (1 -> 0), *Hyloplesion longicostatum* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0), Caseidae (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (0 -> 1). DELTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Tuditanus punctulatus* (1 -> 0), Amniota (1 -> 0), *Casea* broili (0 -> 1), Diadectamorpha (1 -> 0).

152. Vomer anteroposterior length relative to transverse width: shorter than or equal to twice as long as wide (0); longer than twice as long as wide (1).

Rea2003 (c.117), Cea2016 (c.91), Pea2017 (c.275), Cea2019 (c.91), ML2019 (c.102). Modified from a division of RC2007 (c.122, c.132).

In stem tetrapods (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021) the vomers are relatively anteroposteriorly short and transversely wide. This is particularly pronounced in temnospondyls, the vomers are particularly, and distinctly transversely wide (Romer & Witter, 1942; Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022). In most stem and crown amniote taxa, however, the vomers are considerably more elongate and measure more than twice the anteroposterior length as the transverse width. This includes anthracosaurs (Panchen, 1977) and *Silvanerpeton* (Ruta & Clack, 2006), seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015; 2016), synapsids (e.g. Bolt & Scott, 1995; Modesto, 1995), parareptiles (Gow, 1972; Reisz et al., 2007; Modesto et al., 2015) and *Youngina* (Gow, 1974). Nectrideans (Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018), *Hylonomus* (Carroll, 1964) and *Diadectes* (Berman et al, 1998) show anteroposteriorly shorter vomers, and are thus scored as state 0.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (0 -> 1), Nectridea (1 -> 0), *Hylonomus lyelli* (1 -> 0). ACCTRAN: *Diadectes abistus* + *Orobates pabsti* (1 -> 0). DELTRAN: *Diadectes abistus* (1 -> 0).

153. Vomer separation by pterygoids relative to length: not separated at all by pterygoids (0); separated for less than half of anteroposterior length of vomers (1); separated for more than half of anteroposterior length of vomers (2).

Cea2019 (c.88), Cea2016 (c.88), Pea2017 (c.274).

Where the pterygoids partially overlap with the vomers, and contact them medially so that the interrupt the midline suture of the vomers, then state 1 or 2 is present. There is a great variety of the extent of contact between the vomers and the pterygoids in ingroup taxa. For example, state 1, in which the overlap is less than half of the anteroposterior length of the vomers, is present in the stem tetrapod *Greererpeton* (Smithson, 1981), the stem amniote *Silvanerpeton* (Ruta & Clack, 2006), and in *Youngina* (Gow, 1974). A degree of overlap reaching more than half the anteroposterior length of the vomers is present in seymouriamorphs (Klembara, 1997; Berman et al., 2000; Klembara & Ruta, 2005) and some microsaurs (Carroll & Gaskill, 1978).

Unambiguous: Lepospondyli except *Westlothiana lizziae* (1 -> 2), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (2 -> 0), *Pantylus cordatus* (2 -> 1), *Youngina capensis* (0 -> 1), *Orovenator mayorum* (0 -> 1), *Euconcordia cunninghami* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* (1 -> 0), Lepospondyli (0 -> 1),

Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (0 -> 1), Araeoscelidia (0 -> 1), Seymouriamorpha (0 -> 2), *Silvanerpeton miripedes* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 2), *Caerorachis bairdi* (0 -> 1), *Edops craigi* (0 -> 1). DELTRAN: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0), *Casea* broili (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), Seymouriamorpha (1 -> 2), *Gephyrostegus bohemicus* (1 -> 0), *Anthracosaurus russelli* (1 -> 0), *Chroniosaurus dongusensis* (1 -> 2), Temnospondyli except *Edops craigi* (1 -> 0), *Baphetes sp.* (1 -> 0).

154. Vomer, asymmetric bifurcated anterior processes: absent (0); present, vomer terminates anteriorly in short lateral and elongate medial projections (1).

FB2020 (c134).

A division of the anterior margin of the vomer into two distinct processes, as described in Ford & Benson (2020), is present in *Paleothyris* (Carroll, 1969), the araeoscelid *Petrolacosaurus* (Reisz, 1977), and *Archaeovenator* (Reisz & Dilkes, 2003) and *Orovenator* (Ford & Benson, 2019), identified by Ford & Benson (2020) as varanopids and recovered here as basal stem reptiles. It is also present in the parareptile *Erpetonyx* (Modesto et al., 2015), as well as the diadectamorph *Limnoscelis* (Romer, 1946) and the microsaur *Euryodus* (Gee et al., 2021). It is absent, however, in *Youngina* (Gow, 1974) and synapsids (e.g. Romer et al., 1940; Laurin, 1993; Bolt & Scott, 1995)

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), Synapsida (1 -> 0). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (0 -> 1), Parareptilia (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (0 -> 1), Captorhinidae (1 -> 0). DELTRAN: *Euryodus sp.* (0 -> 1), *Youngina capensis* (1 -> 0), *Milleretta sp.* (1 -> 0), *Captorhinus aguti* (1 -> 0).

155. Anterior palatal fenestra: absent (0); present, single (1); present, double (2).

Cea2016 (c.156), Cea2019 (c.156), Pea2017 (c.340).

A vacuity in the anterior palate, in addition to the choanae, is present in *Greererpeton* (Smithson, 1981) and some aïstopods (Anderson, 2002; PArdo et al., 2017).

Unambiguous: *Greererpeton burkemorani* (0 -> 1). ACCTRAN: Aïstopoda (0 -> 1). DELTRAN: *Lethiscus stocki* + *Phlegethontia linearis* (0 -> 1).

156. Choana transversely wider in anterior half than posterior half: no, anterior half is equal in transverse width or narrower than posterior half (0); wider in anterior half (1).

Rea2003 (c.157), RC2007 (c.164), ML2019 (c.130).

The choana is transversely wider in the anterior half, giving a distinct teardrop shape, in derived temnospondyls (Sigurdsen & Bolt, 2010; Arbez et al., 2022) and *Gerobatrachus* (Anderson et al., 2008).

Unambiguous: *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (0 -> 1).

157. Fangs on vomer: absent (0); present (1).

LR1997 (c.42), Lea1998 (c.40), Rea2003 (c.118), RC2007 (c.183), Cea2016 (c.106), ML2019 (c.103), Cea2019 (c.106), Pea2017 (c.290).

Fangs on the vomer are present in stem tetrapods (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021). They are absent, however, in a variety of taxa from clades across crown tetrapods, including *Lethiscus* (Pardo et al., 2017), *Doleserpeton* (Sigurdsen & Bolt, 2010) and *Gerobatrachus* (Anderson et al., 2008), synapsids (e.g. Laurin, 1993; Bolt & Scott, 1995; Brocklehurst et al., 2016), protorothyrids (Carroll, 1964; 1969), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015; 2016), diadectamorphs (Romer, 1946; Berman et al., 1998; 2004), nectrideans (Douthitt, 1917, Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018) and microsaurs (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2019; 2021).

Unambiguous: Embolomeri + *Chroniosaurus dongusensis* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), *Westlothiana lizziae* (0 -> 1), Parareptilia (0 -> 1), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (1 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0), *Youngina capensis* (0 -> 1), *Milleretta* (0 -> 1).

158. Denticle shagreen on vomer: absent (0); present (1).

LR1997 (c.43), Lea1998 (c.41), A2001 (c.77), Rea2003 (c.119), RC2007 (c.124, c.130), Cea2016 (c.110, c.111), ML2019 (c.104), Cea2019 (c.110, c.111), Hea2013 (c.100), Pea2017 (c.294).

Unambiguous: Tetrapoda + *Baphetes sp.* (0 -> 1), Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Cardiocephalus sp.* (1 -> 0), *Hapsidopareion lepton* (1 -> 0), *Vaughnitis smithae* (1 -> 0), Sphenacodontidae (1 -> 0), *Varanosaurus acutirostris* (1 -> 0), Parareptilia (1 -> 0), *Captorhinus aguti* (1 -> 0), *Paleothyris acadiana* (1 -> 0), *Diadectes abistus* + *Orobates pabsti* (1 -> 0), *Pederpes finneyae* (0 -> 1). ACCTRAN: Embolomeri (1 -> 0). DELTRAN: *Anthracosaurus russelli* (1 -> 0).

159. Row of at least three teeth on vomer, comparable in size to marginal teeth: absent (0); present (1).

ML2019 (c.107). Modified from LR1997 (c.40), Lea1998 (c.38), Cea2016 (c.108), Cea2019 (c.109), Pea2017 (c.293). Modified from a division of Kea2014 (c.60).

A toothrow on the vomer is present in the outgroup (Clack & Finney, 2005; Rawson et al., 2021) but is absent in the stem tetrapods *Greererpeton* (Smithson, 1981) and *Baphetes* (Beaumont, 1977). A toothrow is absent in most crown tetrapods included in this analysis, but it present in many taxa in clades from across crown tetrapods, including *Lethiscus* (Pardo et al., 2017), *Doleserpeton* (Sigurdsen & Bolt, 2010), the synapsids *Vaughnitis* (Brocklehurst et al., 2016) and *Varanosaurus* (Bolt & Scott, 1995), *Youngina* (Gow, 1974), *Orobates* (Berman et al., 2004), diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963; Milner, 2018), *Brachydectes* (Pardo et al., 2016) and a small number of microsaurs, namely *Cardiocephalus* (Carroll & Gaskill, 1978), *Euryodus* (Gee et al., 2021) and *Huskerpeton* (Huttenlocker et al., 2013).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0). Nectridea + Lysorophia + Aïstopoda (0 -> 1), *Scincosaurus crassus* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (0 -> 1), *Vaughnitis smithae* (0 -> 1), *Varanosaurus acutirostris* (0 -> 1), *Youngina capensis* (0 -> 1), *Diadectes abistus* + *Orobates pabsti* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1), *Doleserpeton annectens* (0 -> 1), *Edops craigi* (0 -> 1).

160. Vomerine fangs noticeably smaller than other palatal fangs: no, fangs are equal in size to other palatal fangs (0); yes (1), vomerine fangs absent (inapplicable).

Cea2016 (c.107), Cea2019 (c.107), Pea2017 (c.291).

The vomerine fangs are substantially smaller than the other palatal fangs in the outgroup (Clack & Finney, 2005; Rawson et al., 2021), and the stem tetrapod *Greererpeton* (Smithson, 1981). The

condition is also observed in the temnospondyls *Edops* (Romer & Witter, 1942) and *Dendrerpeton* (Arbez et al., 2022), as well as the *Gephyrostegus* (Klembara et al, 2014).

Unambiguous: *Gephyrostegus bohemicus* (0 -> 1), *Balanerpeton woodi* (1 -> 0), *Baphetes sp.* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (1 -> 0). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 0).

161. Separately ossified palatine: absent (0); present (1).

LR1997 (c.44), Lea1998 (c.42), RC2007 (c.139), ML2019 (c.114)

A separately ossified palatine is lost in the aïstopod *Phlegethontia* (Anderson, 2002).

Unambiguous: *Phlegethontia linearis* (1 -> 0).

162. Ectopterygoid - palatine exposure: narrow, approximately confined to tooth row (0); broad medial exposure additional to tooth row (1).

Cea2016 (c.73), Cea2019 (c.73), Pea2017 (c.258).

A small number of disparate taxa show a reduction in the width of the ectopterygoid and palatine. In these taxa, the palatine and ectopterygoid are only approximately as wide as the row of teeth on these elements. This condition is observed in some lepospondyls (Carroll & Gaskill, 1978; Milner, 2018; Clack et al., 2019), dissorophoid temnospondyls and *Gerobatrachus* (Anderson et al., 2008; Sigurdsen & Bolt, 2010) and in *Whatcheeria* (Rawson et al., 2021).

Unambiguous: *Acherontiscus caledoniae* (1 -> 0), *Keraterpeton galvani* (1 -> 0), *Micraroter erythrogeois* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0), *Whatcheeria deltae* (1 -> 0).

163. Ectopterygoid - palatine width: narrower than maxilla (0); wider than maxilla (1).

Hea2013 (c.122, Pea2017 (c.86).

This character is somewhat related to the previous character, and as such some taxa score the narrower condition for both, such as *Keraterpeton* (Milner, 2018) and dissorophoid temnospondyls and *Gerobatrachus* (Anderson et al., 2008; Sigurdsen & Bolt, 2010). However, several taxa demonstrate a palatine that is narrower than the maxilla but not so narrow and width as to be confined to the width of the toothrow, such as *Brachydectes* (Pardo et al., 2016) and parareptiles (Gow, 1972; Reisz et al., 2007), and as such the characters are scored separately.

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Keraterpeton galvani* (1 -> 0). ACCTRAN: Parareptilia (1 -> 0), *Youngina capensis* (0 -> 1), *Diadectes abistus* + *Orobates pabsti* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). DELTRAN: *Belebey vegrandis* (1 -> 0), *Milleretta sp.* (1 -> 0), *Diadectes abistus* (1 -> 0), *Gerobatrachus hottoni* (1 -> 0).

164. Fangs on palatine: absent (0); present (1).

LR1997 (c.46), Lea1998 (c.44), Rea2003 (c.127), RC2007 (c.133), Cea2016 (c.98), ML2019 (c.110), Cea2019 (c.98).

Fangs on the palatine follow a similar distribution to fangs on the ectopterygoid (ch.186), and are present in all taxa that possess ectopterygoid fangs. However, they are present in some taxa that lack ectopterygoid fangs, such as *Lethiscus* (Pardo et al., 2017) and seymouriamorphs (Klembara, 1997; Berman et al., 2000; Klembara & Ruta, 2005).

Unambiguous: *Chroniosaurus dongusensis* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), *Lethiscus stocki* + *Phlegethontia linearis* (0 -> 1). DELTRAN: Amniota + Diadectamorpha + Lepospondyli (1 -> 0), *Lethiscus stocki* (0 -> 1).

165. Denticle shagreen on palatine: absent (0); present (1).

LR1997 (c.47), Lea1998 (c.45), A2001 (c.78), Rea2003 (c.128), RC2007 (c.134), Cea2016 (c.100), ML2019 (c.111), Cea2019 (c.100), Hea2013 (c.101)

A denticle shagreen on the palatine occurs in most of the same taxa as a denticle shagreen on the ectopterygoid (ch.187). However, there are a small number of taxa in which this is not the case. *Acherontiscus* is considered to have denticles on the palatine but a tooth row on the ectopterygoid (Clack et al., 2019). In *Archaeovenator*, the denticles extend across the pterygoid and palatine but not the ectopterygoid (Reisz et al., 1984), and palatal denticles are restricted only to the palatine in

Scincosaurus (Milner & Ruta, 2009). Conversely, *Llistrofus* possesses a small patch of denticles restricted only to the ectopterygoid and thus lacks denticles on the palatine (Gee et al., 2019).

Unambiguous: Tetrapoda + *Baphetes sp.* (0 -> 1), Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Scincosaurus crassus* (0 -> 1), *Vaughnitis smithae* (1 -> 0), *Procynosuchus delaharpeae* (1 -> 0), *Varanosaurus acutirostris* (1 -> 0), Parareptilia (1 -> 0), *Diadectes abistus* + *Orobates pabsti* (1 -> 0), *Doleserpeton annectens* (1 -> 0), *Pederpes finneyae* (0 -> 1). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Euryodus sp.* (0 -> 1), *Micraroter erythrogeois* (0 -> 1), Embolomeri (1 -> 0). DELTRAN: *Cardiocephalus sp.* (1 -> 0), *Pantylus cordatus* (1 -> 0), *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Anthracosaurus russelli* (1 -> 0).

166. Row of at least three teeth on palatine, comparable in size to marginal teeth: absent (0); present (1).

Rea2003 (c.130), RC2007 (c.135), Cea2016 (c.99), ML2019 (c.112), Cea2019 (c.99), Pea2017 (c.86). Modified from a division of LR1997 (c.39), Lea1998 (c.37).

A row of teeth on the palatine is present in the outgroup (Clack & Finney, 2005; Rawson et al., 2021) and the stem tetrapod *Greererpeton* (Smithson, 1981) but is absent in most taxa crownwards of this. A toothrow is nonetheless present in a small number of taxa, particularly within diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963; Milner, 2018) and most microsaurs (Carroll & Gaskill, 1978; Gee et al., 2019; 2021). In *Westlothiana*, there are three teeth on the palatine larger than the denticles and therefore this is scored as a toothrow rather than fangs.

Unambiguous: Tetrapoda + *Baphetes sp.* (1 -> 0), Diplocaulidae (0 -> 1), *Oestocephalus sp.* (0 -> 1), *Vaughnitis smithae* (0 -> 1), *Youngina capensis* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1), *Doleserpeton annectens* (0 -> 1). ACCTRAN: Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (1 -> 0). DELTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (0 -> 1), *Westlothiana lizziae* (0 -> 1).

167. Size of palatal teeth relative to marginals: palatal teeth are smaller than marginals (0); palatal teeth are equal in size to marginals (1); palatal teeth are larger than marginals (2).

A2001 (c.80), Hea2013 (c.103), Pea2017 (c.81).

In most included taxa, even those with palatal fangs or toothrows, the palatal teeth are either roughly equivalent or smaller than the marginal teeth. However, in the stem tetrapods *Greererpeton* (Smithson, 1981) and *Baphetes* (Beaumont, 1977) and in temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010), the palatal fangs are clearly larger than the marginal teeth.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (2 -> 0), *Asaphestera intermedia* (0 -> 2), *Westlothiana lizziae* (0 -> 1), Seymouriamorpha (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 2), Diplocaulidae (0 -> 1), *Lethiscus stocki* + *Phlegethontia linearis* (0 -> 1). DELTRAN: *Diplocaulus sp.* + *Diploceraspis sp.* (0 -> 1), *Lethiscus stocki* (0 -> 1), *Whatcheeria deltae* (2 -> 0).

168. Transverse flange of pterygoid: absent (0); present (1).

LR1997 (c.52), Lea1998 (c.49), Rea2003 (c.141), RC2007 (c.147), ML2019 (c.119).

A transverse flange of the pterygoid is found in all stem amniotes (Carroll, 1964; Fox & Bowman, 1966; Carroll, 1969) and amniotes (e.g. Reisz & Dilkes, 2003; Campione & Reisz, 2010; Reisz & Fröbisch, 2014) crownwards of *Silvanerpeton* (Ruta & Clack, 2006), although it is not present in lepospondyls (e.g. Carroll & Gaskill, 1978; Pardo et al., 2017; Milner, 2018; Gee et al., 2019), including being absent in *Westlothiana*.

Unambiguous: *Chroniosaurus dongusensis* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), Lepospondyli (1 -> 0). DELTRAN: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1).

169. Pterygoids contact each other anteriorly along midline: do not contact (0); contact each other (1).

A2001 (c.90), Cea2016 (c.83), Cea2019 (c.83), Hea2013 (c.116).

In many ingroup taxa, the pterygoids meet along the midline, from the stem tetrapods *Greererpeton* (Smithson, 1981) and *Baphetes* (Beaumont, 1977) to stem amniotes such as anthracosaurs (Panchen, 1977) and *Silvanerpeton* (Ruta & Clack, 2005), seymouriamorphs (e.g. Klembara & Ruta, 2005),

diadectamorphs (e.g. Berman et al., 2004), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015; 2016) and many crown amniotes (e.g. Bolt & Scott, 1995, Ford & Benson, 2019). In temnospondyls more derived than *Edops*, including *Gerobatrachus*, the cultriform process contacts the vomers and prevents contact between the pterygoids (Milner & Sequeira, 1993; Anderson et al., 2008; Sigurdsen & Bolt, 2010; Arbez et al., 2022). In some lepospondyls, such as *Lethiscus* (Pardo et al, 2017) and *Westlothiana* the pterygoids are widely separated, despite the cultriform process not reaching forward sufficiently to contact the vomers.

Unambiguous: *Llistrofus pricei* (1 -> 0), *Westlothiana* (1 -> 0), Temnospondyli except *Edops craigi* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0), Adelospondyli + *Utaherpeton franklini* (0 -> 1), *Oestocephalus sp.* (0 -> 1). DELTRAN: Nectridea + Lysorophia (1 -> 0), *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 0), *Hyloplesion longicostatum* (1 -> 0).

170. Pterygoid quadrate ramus orientation: mostly caudally (0); or mostly laterally in ventral aspect (1).

Rea2003 (c.143), RC2007 (c.148), ML2019 (c.120).

In nectrideans, the quadrate ramus of the pterygoid has become rotated forwards so that they face more lateral than caudal, with the dominant direction more than 45 degrees from the midline of the skull (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018). A similar condition is observed in the aïstopod *Phlegethontia* (Anderson, 2002).

Unambiguous: Nectridea (0 -> 1), *Phlegethontia linearis* (0 -> 1).

171. Quadrate ramus of pterygoid breadth: shorter than or equal to twice as long as maximum width (0); more than twice as long as maximum width (1).

Rea2003 (c.149), RC2007 (c.154).

In nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018), lysorophians (Pardo et al., 2016), and a small number of other, disparate taxa from across the phylogeny, including *Phlegethontia* (Anderson, 2002) and *Silvanerpeton* (Clack & Ruta, 2006), the quadate ramus of the pterygoid is more robust than is typical for most taxa, and has become at least half as broad as it is long. In these taxa it is less clearly separated from the rest of the pterygoid.

Unambiguous: Nectridea + Lysorophia (1 -> 0), *Phlegethontia linearis* (1 -> 0), *Orobates pabsti* (1 -> 0), *Silvanerpeton miripedes* (1 -> 0).

172. Pterygoid quadrate ramus margin in adductor fossa: concave (0), with some convex component (1).

Cea2016 (c.85), Cea2019 (c.85), Pea2017 (c.273).

Unambiguous: Tetrapoda (0 -> 1), *Huskerpeton englehorni* (1 -> 0), *Hapsidopareion lepton* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (0 -> 1), *Captorhinus aguti* (0 -> 1), *Ariekanerpeton sigalovi* (1 -> 0), *Gephyrostegus bohemicus* (1 -> 0), *Doleserpeton annectens* (1 -> 0).

173. Pterygoid, quadrate ramus, median shelf (='posteromedian flange'; 'tympanic flange';'arcuate flange'): absent (0); present (1).

FB2020 (c.146). Modified from B2012 (c.120), BE1983 (c.14), Rea1992 (c.37), L1993 (c.40), Bea1995 (c.46), Fea2011 (c.102), MR2014 (c.65), Mea2015 (c.65).

An arcuate flange is present in several synapsids including caseasaurs (Olson et al., 1968; Reisz et al., 2009) and varanopids (Bolt & Scott, 1995; Langston & Reisz, 1981) but not edaphosaurids (Modesto, 1995) or sphenacodontids (Laurin, 1993, Romer et al., 1940). It is also present in *Orovenator* (Ford & Benson, 2019), a taxon recognised here as a stem-reptile but by Ford & Benson (2019) as a varanopid, but it is not present in *Archaeovenator* (Reisz & Dilkes, 2003), a taxon grouped both here and in Ford & Benson (2020) with *Orovenator*. and in the parareptiles *Belebey* (Reisz et al., 2007) and *Milleretta* (Gow, 1972), but not in *Youngina* (Gow, 1974). It is also present in a small number of stem amniote taxa including diadectamorphs (Romer, 1946; Berman et al., 1998; 2004) and *Chroniosaurus* (Clack & Klembara, 2009).

Unambiguous: Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), *Araeoscelis gracilis* (0 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (0 -> 1), *Youngina capensis* (1 -> 0), *Euconcordia cunninghami* (0 -> 1), Diadectamorpha (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1).

174. Pterygoid, ascending dorsal lamina of the anterior (palatal) ramus: absent or low (0); tall (1).

FB2020 (c.148), Rea1992 (c.36), Bea1995 (c.45), Fea2011 (c.101), B2012 (c.116), Sea2018 (c.71).

An ascending lamina of the palatal ramus of the pterygoid is present in edaphosaurids (Reisz & Berman, 1986; Modesto, 1995) and sphenacodontids (Romer et al., 1940; Laurin, 1993), although due to the difficult nature of scoring the character it is unknown in many other synapsid taxa.

ACCTRAN: Synapsida (0 -> 1). DELTRAN: Edaphosauridae + Sphenacodontia (0 -> 1).

175. Interpterygoid vacuities: absent (0); present (1).

Rea2003 (c.153), RC2007 (c.160), Hea2013 (c.115), LR1997 (c.56), Lea1998 (c.54), A2001 (c.89), Cea2016 (c.159), Cea2019 (c.159). Modified from a division of Pea2017 (c.342, c.83).

Most ingroup taxa possess at least small interpterygoid vacuities, including the stem tetrapods Pederpes (Clack & Finney, 2005) and *Greererpeton* (Smithson, 1981), temnospondyls (e.g. Milner & Sequeira, Sigurdsen & Bolt, 2010), and microsaurs (Carroll & Gaskill, 1978) amongst others. However, a large number of taxa across a variety of clades have a closed palate, such as *Brachydectes* (Pardo et al., 2016), some seymouriamorphs (Berman et al., 2000; Kelmbara & Ruta, 2005) and anthracosaurs (Panchen, 1977; Holmes, 1989).

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Phlegethontia linearis* (1 -> 0), *Vaughnitis smithae* (1 -> 0), *Dimetrodon sp.* (1 -> 0), *Varanosaurus acutirostris* (1 -> 0), *Ariekanerpeton sigalovi* (0 -> 1), *Baphetes sp.* (1 -> 0), *Whatcheeria deltae* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (1 -> 0), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (0 -> 1), Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (1 -> 0), *Chroniosaurus dongusensis* (0 -> 1). DELTRAN: *Acherontiscus caledoniae* (1 -> 0), *Belebey vegrandis* (1 -> 0), Seymouriamorpha + *Gephyrostegus bohemicus* (1 -> 0), *Silvanerpeton miripedes* (1 -> 0), Embolomeri (1 -> 0).

176. Total transverse width of interpterygoid vacuities, excluding cultriform process of parasphenoid, measured at widest extent of interpterygoid vacuities: less than half of total transverse palatal width at same level (0); at least half of total palatal transverse palatal width at same level (1).

Rea2003 (c.154), RC2007 (c.161), ML2019 (c.127).

In all temnospondyls more derived than *Edops* (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022) and *Gerobatrachus* (Anderson et al., 2008), as well as the nectridean *Diploceraspis* (Beerbower, 1963), the palatal vacuities are distinctly wide relative to all other taxa, and are together at least half as wide as the whole palate at the same transverse level as their maximum width.

Unambiguous: *Diploceraspis sp.* (0 -> 1), Temnospondyli except *Edops craigi* (0 -> 1).

177. Interpterygoid vacuities concave along whole margins: no, at least partially convex (0); completely concave (1).

Rea2003 (c.155), RC2007 (c.162), ML2019 (c.128).

Unambiguous: *Westlothiana lizziae* (1 -> 0), *Petrolacosaurus kansensis* (1 -> 0), *Captorhinus aguti* (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* (0 -> 1), *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 0), Parareptilia (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* (1 -> 0), Seymouriamorpha + *Gephyrostegus bohemicus* (1 -> 0). DELTRAN: Tetrapoda (0 -> 1), *Lethiscus stocki* (1 -> 0), *Youngina capensis* (1 -> 0), *Paleothyris acadiana* (1 -> 0), *Ariekanerpeton sigalovi* (1 -> 0).

178. Maxilla - pterygoid contact: absent (0); present (1).

Novel

Unambiguous: *Oestocephalus sp.* (0 -> 1), *Tuditanus punctulatus* (0 -> 1), *Doleserpeton annectens* (0 -> 1).

179. Denticle shagreen on palatal process of pterygoid: absent (0); present (1).

LR1997 (c.53), Lea1998 (c.51), A2001 (c.75), Cea2016 (c.103), Cea2019 (c.103), Hea2013 (c.97), Pea2017 (c.287).

Denticles on the palatal process of the pterygoid are present in stem tetrapods (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021) and are present in the majority of ingroup taxa. However, they are absent in many taxa from various clades, including *Gerobatrachus* (Anderson et al., 2008), *Anthracosaurus* (Panchen, 1977), *Vaughnitis* (Brocklehurst et al., 2016), *Varanops* (Campione & Reisz, 2010), parareptiles and *Youngina* (Got, 1972; 1974; Reisz et al., 2007)

and *Orobates* (Berman et al., 2004). Within lepospondyls, they are also absent in the microsaurs *Cardiocephalus* (Carroll & Gaskill, 1978) and *Huskerpeton* (Huttenlocker et al., 2013), nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018) and aïstopods (Carroll, 1998; Anderson, 2002; Pardo et al., 2017).

Unambiguous: Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Varanops brevirostris* (1 -> 0), *Vaughnitis smithae* (1 -> 0), *Procynosuchus delaharpeae* (1 -> 0), Parareptilia (1 -> 0), *Orobates pabsti* (1 -> 0), *Anthracosaurus russelli* (1 -> 0), *Gerobatrachus hottoni* (1 -> 0). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (1 -> 0), *Euryodus sp.* (0 -> 1). DELTRAN: *Cardiocephalus sp.* (1 -> 0), *Huskerpeton englehorni* (1 -> 0).

180. Denticle shagreen on transverse process of pterygoid: absent (0); present (1); transverse flange of pterygoid absent (inapplicable).

Modified from a division of Pea2017 (c.288).

The presence of denticles on the transverse flange of the pterygoid is present in some seymouriamorphs (Klembara, 1997; Berman et al., 2000), as well as captorhinids (Fox & Bowman, 1966; Reisz et al., 2015; 2016) and protorothyrids (Carroll, 1964; 1969). They are also present in a small number of crown amniotes such as *Casea* (Olson et al., 1968), *Edaphosaurus* (Modesto, 1995) and *Haptodus* (Laurin, 1993).

Unambiguous: *Erpetonyx arsenaultorum* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (0 -> 1), *Orobates pabsti* (0 -> 1), *Ariekanerpeton sigalovi* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), Caseidae (0 -> 1), Edaphosauridae + Sphenacodontia (0 -> 1), Sphenacodontidae + *Pantelosaurus saxonicus* (1 -> 0). DELTRAN: Amniota + Diadectamorpha + Lepospondyli (1 -> 0), *Casea broilii* (0 -> 1), *Haptodus garnettensis* (0 -> 1), *Edaphosaurus boanerges* (0 -> 1).

181. Tooth row on transverse flange of pterygoid: absent (0); present (1); transverse flange of pterygoid absent (inapplicable).

Lea1998 (c.50, Rea2003 (c.142). Modified from a division of Pea2017 (c.288).

This character was considered by Laurin & Reisz (1995) to be a synapomorphy of crown amniotes, a result with which I concur. However, they considered captorhinids to be crown amniotes. Laurin & Reisz (1995) stated that in captorhinids there is a reversal to the primitive condition of denticles.

Petrolacosaurus (Reisz, 1977) is considered to have a toothrow rather than denticles due to the large dentition at the posterior point of the flange, and the arrangement of the smaller dentition in rows on the flange. As both this analysis and Laurin & Reisz (1995) recover araeoscelids as crown amniotes, and they note a reversal to denticles in captorhinomorphs, the scores in this analysis are entirely consistent with Laurin & Reisz (1995) despite a different topology.

Unambiguous: Amniota (0 -> 1), *Procynosuchus delaharpeae* (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (1 -> 0), *Limnoscelis paludis* (0 -> 1). ACCTRAN: Caseidae (1 -> 0), Edaphosauridae (1 -> 0), *Casea broilii* (1 -> 0), *Edaphosaurus boanerges* (1 -> 0).

182. Separately ossified ectopterygoid: absent (0); present (1).

LR1997 (c.48), Lea1998 (c.46), A2001 (c.92), Rea2003 (c.134), RC2007 (c.140), Pea2017 (c.259).

An ossified ectopterygoid is absent in a number of lepospondyls including the microsaur *Pantylus* (Carroll & Gaskill, 1978), the nectridean *Scincosaurus* (Milner & Ruta, 2009) and the aïstopod *Lethiscus* (Pardo et al, 2017). It is also lost in captorhinids (Fox & Bowman, 1966; Reisz et al, 2016).

Unambiguous: *Pantylus cordatus* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Scincosaurus crassus* (0 -> 1), *Lethiscus stocki* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (1 -> 0). DELTRAN: *Brachydectes newberryi* (1 -> 0), Diplocaulidae (1 -> 0), *Phlegethontia linearis* (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 0).

183. Ectopterygoid narrowly wedged between palatine and pterygoid: no (0); yes (1).

Rea2003 (c.140), RC2007 (c.146).

This character describes a specific condition in which the palatine, pterygoid and maxilla entirely and tightly surround the ectopterygoid. The shape of the pterygoid and palatine are concave to fully encompass the ectopterygoid. This condition is observed in sphenacodontids (Romer & Price, 1940; Laurin, 1993) and *Edaphosaurus* (Modesto, 1995).

ACCTRAN: Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1). DELTRAN: Edaphosauridae + Sphenacodontia (0 -> 1).

184. Ectopterygoid maximum length (measured along long axis of element) relative to maximum length of palatine (measured along long axis of element): ectopterygoid shorter than palatine (0); ectopterygoid equal in length or longer than palatine (1).

Rea2003 (c.137), RC2007 (c.143), Cea2016 (c.71), ML2019 (c.115), Cea2019 (c.71), Pea2017 (c.260).

In the outgroup (Clack & Finney, 2005; Rawson et al., 2021) and some other stem tetrapods (*Baphetes*, Beaumont, 1977), the ectopterygoid is a larger element than the palatine, or at least as big as the ectopterygoid as in *Greererpeton* (Smithson, 1981). This is also the condition present in temnospondyls (Milner & Sequeira, 1993; Arbez et al., 2022). In most crown amniotes and crownward stem amniotes (e.g. Romer et al., 1940; Gow, 1974; Reisz, 1977; Bolt & Scott, 1995; Ford & Benson, 2019), diadectamorphs (Romer, 1946; Berman et al., 1998; 2004), and several microsaurs (Carroll & Gaskill, 1978) the ectopterygoid has become substantially reduced in size.

Unambiguous: *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (1 -> 0), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (0 -> 1), Nectridea + Lysorophia (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (1 -> 0), *Acherontiscus caledoniae* (0 -> 1), *Lethiscus stocki* (0 -> 1), *Euryodus sp.* (0 -> 1), *Gerobatrachus hottoni* (1 -> 0).

185. Ectopterygoid - maxilla contact: absent (0); present (1).

Novel

In *Archaeovenator* (Reisz & Dilkes, 2003) and *Orovenator* (Ford & Benson, 2019), there is no contact between the ectopterygoid and maxilla, and instead there is a contact between the ectopterygoid and the jugal. These taxa, recovered here as basal reptiles but as varanopids in Ford & Benson (2020), share this condition with *Youngina* (Gow, 1974) but not parareptiles (Gow, 1972; Reisz et al., 2007; Modesto et al., 2015). A small number of other taxa also lack this contact, namely *Procynosuchus* (Kemp, 1979) and the lepospondyls *Scincosaurus* (Milner, 2018) and *Hyloplesion* (Carroll & Gaskill, 1978).

Unambiguous: *Hyloplesion longicostatum* (1 -> 0), *Procynosuchus* (1 -> 0), *Youngina capensis* (1 -> 0). ACCTRAN: Nectridea + Lysorophia (1 -> 0), Reptilia (1 -> 0), Parareptilia (0 -> 1). DELTRAN: *Scincosaurus crassus* (1 -> 0), *Archaeovenator hamiltonensis* (1 -> 0), *Orovenator mayorum* (1 -> 0).

186. Fangs on ectopterygoid: absent (0); present (1).

LR1997 (c.49), Lea1998 (c.47), Rea2003 (c.135), RC2007 (c.141), Cea2016 (c.92), ML2019 (c.116), Cea2019 (c.92), Pea2017 (c.283).

Fangs on the ectopterygoid, comparable in size or larger than the marginal dentition but significantly larger than the surrounding denticles, are present widely across stem tetrapods (Beaumont, 1977; Smithson, 1981). They are present in temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993; Arbez et al., 2022), and stem amniotes such as *Gephyrostegus* (Klembara et al, 2014), seymouriamorphs (and anthracosaurs (Panchen, 1977; Holmes, 1989). They are absent in all lepospondyls (e.g. Carroll & Gaskill, 1978; Pardo et al., 2017; Milner, 2018) and amniotes crownwards of lepospondyls (e.g. Reisz, 1977; Bolt & Scott, 1995; Ford & Benson, 2019), but are retained in *Westlothiana*.

ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (1 -> 0), *Gephyrostegus bohemicus* (0 -> 1), Embolomeri (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). DELTRAN: Amniota + Diadectamorpha + Lepospondyli (1 -> 0), Seymouriamorpha (1 -> 0), *Chroniosaurus dongusensis* (1 -> 0), *Gerobatrachus hottoni* (1 -> 0).

187. Denticle shagreen on ectopterygoid: absent (0); present (1).

LR1997 (c.50), Lea1998 (c.48), Rea2003 (c.136), RC2007 (c.142), Kea2014 (c.67, c.69, c.72), Cea2016 (c.94, c.95), ML2019 (c.117), Cea2019 (c.94, c.95), Pea2017 (c.285).

Denticles on the ectopterygoid are widely present in several disparate clades from across the included taxa, including some stem tetrapods (Smithson, 1981; Clack & Finney, 2005), some temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993), edaphosaurids (Modesto, 1995) and sphenacodontids (Romer et al., 1940), and *Orovenator* (Ford & Benson, 2019).

Unambiguous: Tetrapoda + *Baphetes sp.* (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Cardiocephalus sp.* (1 -> 0), *Hapsidopareion lepton* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -

> 0), *Araeoscelis gracilis* (0 -> 1), *Orovenator mayorum* (0 -> 1), Embolomeri (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (1 -> 0), *Pederpes finneyae* (0 -> 1). ACCTRAN: Edaphosauridae + Sphenacodontia (0 -> 1), *Procynosuchus delaharpeae* (1 -> 0). DELTRAN: *Dimetrodon sp.* (0 -> 1), *Edaphosaurus boanerges* (0 -> 1).

188. Row of at least three teeth on ectopterygoid, comparable in size to marginal teeth: absent (0); present (1).

Rea2003 (c.138), RC2007 (c.144), ML2019 (c.118), Cea2016 (c.93), Cea2019 (c.93), Pea2017 (c.284).

A row of teeth, larger than any surrounding denticles and more comparable in size to the marginal teeth, is present in the outgroup (Clack & Finney, 2005; Rawson et al., 2021) and the stem tetrapod *Greererpeton* (Smithson, 1981), but also in the lepospondyls *Acherontiscus* (Clack et al, 2019) and *Euryodus* (Gee et al, 2019), *Micraroter* and *Cardiocephalus* (Carroll & Gaskill, 1978), all of which are microsarus.

Unambiguous: Tetrapoda + *Baphetes sp.* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1). ACCTRAN: Adelospondyli + *Utaherpeton franklini* (0 -> 1). DELTRAN: *Acherontiscus caledoniae* (0 -> 1).

189. Suborbital opening: absent (0); present (1).

FB2020 (c153), L1991 (c.A3), CC1991 (c.3), LR1995 (c.49), R1999 (c.43), M2004 (c.32), Rea2010 (c.48), Kea2014 (c.83), Mea2015 (c.79).

A suborbital opening in the palate, between the lateral skull bones, palatine and ectopterygoid, is a character noted in previous analyses to have united reptiles (Laurin & Reisz, 1995; Ford & Benson, 2019), a clade consisting of at least captorhinids, protorothyrids, araeoscelids, younginiforms, and most parareptiles. It is present in parareptiles (Gow, 1972; Reisz et al., 2007), *Youngina* (Gow, 1972), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015; 2016) and araeoscelids (Reisz, 1977; Reisz et al., 1984). It is also present in *Orovenator* (Ford & Benson, 2019), but not in *Archaeovenator* (Reisz & Dilkes, 2003).

Unambiguous: *Phlegethontia linearis* (0 -> 1), Araeoscelidia (0 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (0 -> 1), Captorhinidae (0 -> 1), Seymouriamorpha (0 -> 1).

190. Anteroposterior position of jaw joint relative to occiput: jaw joint posterior to occiput (0); in line with occiput (1); anterior to occiput (2).

LR1997 (c.6), Lea1998 (c.6), A2001 (c.70), Rea2003 (c.177), RC2007 (c.187), ML2019 (c.146), Cea2019 (c.222), Hea2013 (c.87), Pea2017 (c.75).

In most taxa, the position of the articulation between the mandible and the quadrate lies roughly in line with the occiput. Some clades, however, show a distinctly different position. In the outgroup and other stem tetrapods (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021), temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993; Arbez et al., 2022) and some diadectamorphs (Romer, 1946; Berman et al., 2004) the jaw articulation is posterior to the occiput, with the posterior skull margin sloping somewhat anterodorsally to posteroventrally. In nectrideans, the jaw articulation is anterior to the occiput (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018).

Unambiguous: *Cardiocephalus sp.* (1 -> 2), Varanopidae (1 -> 0), *Varanosaurus acutirostris* (1 -> 0), *Diadectes abistus* (0 -> 1), Seymouriamorpha (0 -> 1), *Archeria crassidisca* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda (1 -> 0), Nectridea + Lysorophia (0 -> 2), *Phlegethontia linearis* (0 -> 1), Diadectamorpha (1 -> 0). DELTRAN: Lepospondyli (0 -> 1), Nectridea + Lysorophia (1 -> 2), *Lethiscus stocki* (1 -> 0), *Oestocephalus sp.* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1).

191. Dorsoventral position of jaw joint relative to toothrow: below (0); in line with (1); above (2).

Pea2017 (c.98).

The jaw articulation is positioned ventrally to sit below the average level of the toothrow in a small number of basal microsaurs, namely *Tuditanus* and *Hyloplesion* (Carroll & Gaskill, 1978), some diadectamorphs (Romer, 1946; Berman et al., 2004), the seymouriamorph *Discosauriscus* (Klembara, 1997) and in edaphosaurids (Reisz et al., 1986; Modesto, 1995) and sphenacodontids (Romer et al., 1940; Laurin, 1993). When the toothrow is not straight, the average position is considered.

Unambiguous: *Lethiscus stocki* (1 -> 2), *Hyloplesion longicostatum* (1 -> 0), *Tuditanus punctulatus* (1 -> 0), *Pantylus cordatus* (1 -> 0), Edaphosauridae + Sphenacodontia (1 -> 0), *Varanosaurus*

acutirostris (1 -> 2), *Araeoscelis gracilis* (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 0), *Discosauriscus austriacus* (1 -> 0), Temnospondyli (1 -> 2). ACCTRAN: Caseidae (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (1 -> 0), Diadectamorpha (1 -> 0), *Diadectes abistus* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (2 -> 1). DELTRAN: *Casea* broili ((1 -> 0), *Belebey vegrandis* (1 -> 0), *Orobates pabsti* (1 -> 0), *Limnoscelis paludis* (1 -> 0), *Doleserpeton annectens* (2 -> 1).

192. Quadrate dorsal process: absent, quadrate lacks dorsal process (0); present (1).

Rea2003 (c.98), RC2007 (c.100), ML2019 (c.80).

The process in question is recorded in dissorophoids (Ruta et al., 2003) and is hypothesised to have supported a cartilaginous tympanum in life. We observe that an ossified dorsal portion of the quadrate, expanding dorsally as a sheet or rod-like process from the ventral portion of the quadrate forming the jaw articulation, is not limited to temnospondyls, however, and is also found many other taxa including *Westlothiana* and many microsaurs (Carroll & Gaskill, 1978) and many amniotes crownwards of, and including, diadectamorphs (Romer, 1946; Berman et al., 1998) including captorhinids (Fox & Bowman, 1966; Reisz et al., 2016), parareptiles (Gow, 1972; Reisz et al., 2007) and some synapsids (Laurin, 1993; Modesto, 1995).

Unambiguous: *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0). DELTRAN: Amniota + Diadectamorpha + Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda (1 -> 0).

193. Length of quadrate anterior process along articulation with pterygoid quadrate ramus: short, contacts pterygoid quadrate ramus along less than 55% of the length of the pterygoid quadrate ramus (0); long, contacts pterygoid quadrate ramus along more than 55% of the pterygoid quadrate ramus (1).

LR1995 (c.35).

This character was defined by Laurin & Reisz (1995) as if the quadrate anterior process is more or less than 55% of the quadrate ramus of the pterygoid. It is often difficult to score with confidence as this region has been reconstructed with some interpretation in many taxa, and is not often clearly preserved. Nonetheless, it was included here and scored where possible as it is a character stated to

unite eureptilia in Laurin & Reisz (1995), where eureptilia are united by a quadrate anterior process (state 0). However, Laurin & Reisz (1995) included very few outgroup taxa, and so the basal condition was not well determined. In particular, their analysis defined synapsids as a single, functional taxonomic unit. A long quadrate anterior process is found in a small number of synapsids such as *Casea* (Olson et al., 1968) and *Dimetrodon* (Romer et al., 1940), as well as *Gephyrostegus* (Klembara et al., 2014) and seymouriamorphs (Klembara, 1997; Berman et al., 2000; Klembara & Ruta, 2005).

Unambiguous: Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1), *Edops craigi* (0 -> 1). ACCTRAN: Synapsida (0 -> 1), Edaphosauridae (1 -> 0). DELTRAN: *Casea broilii* (0 -> 1), *Dimetrodon sp.* (0 -> 1).

194. Stapes dorsal process: absent (0); present (1).

LR1997 (c.79), Lea1998 (c.76), A2001 (c.85), Hea2013 (c.111), Pea2017 (c.223).

Unambiguous: *Procynosuchus delaharpeae* (1 -> 0), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (1 -> 0), *Micraroter erythrogeois* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (0 -> 1), Nectridea + Lysorophia (0 -> 1), Araeoscelidia (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (1 -> 0). DELTRAN: *Brachydectes newberryi* (0 -> 1), *Araeoscelis gracilis* (1 -> 0), *Youngina capensis* (1 -> 0), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1).

195. Shape of proximal stapedial footplate: oval (0); round (1).

LR1997 (c.80), L1998 (c.77), A2001 (c.84), Hea2013 (c.110), Pea2017 (c.243).

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (0 -> 1), *Euryodus sp.* (0 -> 1), Sphenacodontia (0 -> 1). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), Synapsida (1 -> 0). DELTRAN: *Micraroter erythrogeois* (0 -> 1), *Hapsidopareion lepton* + *Llistrofus pricei* (0 -> 1),

Parareptilia + *Youngina capensis* + *Orovenator mayorum* (0 -> 1), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (0 -> 1).

196. Stapes columella perforated by stapedial foramen: no, stapes is imperforate (0); yes (1).

LR1997 (c.81), Lea1998 (c.78), A2001 (c.83), Hea2013 (c.108), Pea2017 (c.241)

Unambiguous: *Microbrachis pelikani* (0 -> 1), *Euryodus sp.* (0 -> 1), *Micraroter erythrogeois* (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (1 -> 0). ACCTRAN: Nectridea + Lysorophia (0 -> 1), Lepospondyli (1 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (1 -> 0), *Brachydectes newberryi* (0 -> 1).

197. Stapes orientation: dorsal, towards tabular or posterior emargination (0); anteroventral, towards quadrate (1).

Hea2013 (c.109), Pea2017 (c.242)

Unambiguous: *Edops craigi* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (0 -> 1). DELTRAN: Amniota + Diadectamorpha + Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Doleserpeton annectens* (0 -> 1).

198. Adductor crest on mandible: absent, dorsal margin of mandible is smooth (0); present (1).

Pea2017 (c.296).

The dorsal margin of the jaw is smooth in the outgroup (Clack & Finney, 2005; Rawson et al., 2021) and in other stem tetrapods (Beaumont, 1977; Smithson, 1981). In the anthracosaur *Archeria* (Holmes, 1989) and the stem amniote *Silvanerpeton* (Ruta & Clack, 2006), the dorsal margin forms a distinct, raised adductor crest. This condition is present in most amniote taxa crownwards of this including most lepospondyls (Beerbower, 1963; Carroll & Gaskill, 1978; Andrews & Carroll, 1991; Milner & Ruta, 2009), diadectamorphs (Romer, 1946; Berman et al., 1998; 2004), *Paleothyris* (Carroll, 1969), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015) and most crown amniotes

(e.g. Gow, 1972; Laurin, 1993; Bolt & Scott, 1995; Modesto, 1995; Spindler, 2016; Ford & Benson, 2019) This is absent in aïstopods (Carroll, 1998; Anderson, 2002; Pardo et al., 2017), which have a reduced mandible with a small number of ossifications. An adductor crest is also gained in a small number of other taxa.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (0 -> 1), Aïstopoda (1 -> 0), *Varanops brevirostris* (1 -> 0), *Eothyris parkeyi* (1 -> 0), *Archeria crassidisca* (0 -> 1), *Balanerpeton woodi* (0 -> 1).

199. Elements forming adductor crest: surangular only (0); posterior coronoid and surangular (1); dentary (2).

Novel

This character describes the elements that, in lateral view, are the dominant contribution to the dorsalmost point of the adductor crest. Where multiple elements meet at the dorsalmost point of the crest, and contribute relatively equally, such taxa have been scored as multistate. In the majority of microsaurs (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2019; 2021) and diplocaulid nectrideans (Douthitt, 1917; Beerbower, 1963) the dentary is the dominant element forming the adductor crest. This contrasts with *Westlothiana*, in which the surangular forms the adductor crest. There is no clear phylogenetic signal within amniotes more crownwards of lepospondyls.

Unambiguous: Lepospondyli except *Westlothiana lizziae* (0 -> 2), *Brachydectes newberryi* (2 -> 1), *Pantylus cordatus* (2 -> 1), Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (1 -> 2), *Araeoscelis gracilis* (1 -> 2). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), Lepospondyli (1 -> 0), Adelospondyli + *Utaherpeton franklini* (2 -> 0), Varanopidae (2 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* (1 -> 2), *Limnoscelis paludis* (1 -> 0), *Ariekanerpeton sigalovi* (1to(0 2)), Temnospondyli (0 -> 2). DELTRAN: *Acherontiscus caledoniae* (2 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), *Aerosaurus wellesi* (2 -> 0), *Paleothyris acadiana* (1 -> 2), *Diadectes abistus* + *Orobates pabsti* (0 -> 1), *Discosauriscus austriacus* (0 -> 1), *Gephyrostegus bohemicus* (0 -> 1), *Balanerpeton woodi* (0 -> 2).

200. Elements contributing to mandibular symphysis: dentary alone (0); dentary and splenial (1).

Hea2013 (c.139), A2001 (c.109), Pea2017 (c.101).

Unambiguous: *Pantylus cordatus* (0 -> 1), Varanopidae (1 -> 0), Temnospondyli except *Edops craigi* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 0), Nectridea (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), Amniota (1 -> 0), Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), *Seymouria sanjuanensis* (0 -> 1). DELTRAN: Lepospondyli (1 -> 0), Diplocaulidae (0 -> 1), *Varanosaurus acutirostris* (1 -> 0), *Araeoscelis gracilis* (1 -> 0), Reptilia (1 -> 0), *Discosauriscus austriacus* (1 -> 0), *Gephyrostegus bohemicus* (1 -> 0).

201. Number of Meckelian fossae: none (0); one (1); two or more (2) (ordered).

Pea2017 (c.94), A2001 (c.100), Hea2013 (c.130).

Most included taxa show a single meckelian fossa on the medial surface of the mandible (e.g. Fox & Bowman, 1966; Gow, 1972; Smithson, 1981; Bolt & Scott, 1995; Berman et al., 2004; Sigurdsen & Bolt, 2010; Pardo et al., 2017). An absence of any meckelian fossae is seen in some microsaurs (Carroll & Gaskill, 1978; Huttenlocker et al., 2013), and sphenacodontids (Romer et al., 1940; Laurin, 1993), as well as a small number of other taxa including the aïstopod *Phlegethontia* (Anderson, 2002) and the parareptile *Belebey* (Reisz et al., 2007). A small number of disparate taxa including *Archeria* (Holmes, 1989), *Caerorachis* (Ruta et al, 2001) and *Orovenator* (Ford & Benson, 2019) show two fossae.

Unambiguous: *Diplocaulus sp.* (1 -> 2), *Phlegethontia linearis* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (1 -> 0), *Hapsidopareion lepton* (1 -> 0), Sphenacodontia (1 -> 0), *Orovenator mayorum* (1 -> 2), *Archeria crassidisca* (1 -> 2), *Caerorachis* (1 -> 2), *Balanerpeton woodi* (1 -> 2). ACCTRAN: *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (1 -> 0), Seymouriamorpha + *Gephyrostegus bohemicus* (1 -> 2), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (2 -> 1). DELTRAN: *Belebey vegrandis* (1 -> 0), *Seymouria sanjuanensis* (1 -> 2), *Gephyrostegus bohemicus* (1 -> 2).

202. Retroarticular process: absent (0); present (1).

A2001 (c.102), Hea2013 (c.132), Pea2017 (c.96).

A retroarticular process, extending posteriorly from the articular articulation with the quadrate, is present in a variety of clades including *Hylonomus* (Carroll, 1964), *Captorhinus* (Fox & Bowman, 1966), the parareptiles *Erpetonyx* (Modesto et al., 2015) and *Belebey* (Reisz et al., 2007), and many synapsids (e.g. Bolt & Scott, 1995; Campione & Reisz, 2010; Spindler, 2016). A retroarticular process is also found widely across lepospondyls, including adelogyrinids (Andrews & Carroll, 1991; Clack et al., 2019), some nectrideans (Beerbower, 1963; Milner & Ruta, 2009), and some microsaurs such as *Tuditanus*, *Pantylus*, *Microbrachis* (Carroll & Gaskill, 1978) and *Llistrofus* (Gee et al., 2019).

Unambiguous: Lepospondyli (0 -> 1), *Utaherpeton franklini* (1 -> 0), *Diplocaulus sp.* (1 -> 0), Aïstopoda (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (1 -> 0), *Hapsidopareion lepton* (1 -> 0), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0), *Belebey vegrandis* (1 -> 0), *Captorhinus aguti* (0 -> 1), *Hylonomus lyelli* (0 -> 1), *Diadectes abistus* (0 -> 1). ACCTRAN: Amniota (0 -> 1), Araeoscelidia (1 -> 0). DELTRAN: Synapsida except Araeoscelidia (0 -> 1), Reptilia (0 -> 1).

203. Mandible, retroarticular process, orientation: posteriorly directed (0); upturned posterodorsally (1); curves posteroventrally (2) inapplicable process is absent (inapplicable).

FB2020 (c173). Modified from Gea1988 (c.105), D1998 (c.75), M2004 (c.101), B2012 (c.133).

A posteroventrally curving retroarticular process is distinctly present in sphenacodontids (Romer et al., 1940; Laurin, 1993; Ford & Benson, 2019).

Unambiguous: *Scincosaurus crassus* (0 -> 1), *Westlothiana lizziae* (0 -> 1), *Varanops* (0 -> 1), Sphenacodontia (0 -> 2).

204. 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).

FB2020 (c.165).

A distinct curvature of the dorsal margin of the mandible is distinctly present in derived sphenacodontids (Romer et al., 1940; Spindler, 2016; Ford & Benson, 2019), in which it corresponds with a large ventral curvature of the maxilla. A similar condition is present in a variety of other taxa including *Whatcheeria* (Rawson et al., 2021), *Archeria* (Holmes, 1989), some other synapsids (e.g.

Bolt & Scott, 1995; Mann & Paterson, 2020), *Hylonomus* (Carroll, 1964), *Gephyrostegus* (Klembara et al., 2014), *Seymouria* (Berman et al., 2000), *Brachydectes* (Pardo et al., 2016) and *Westlothiana*.

Unambiguous: *Brachydectes newberryi* (0 -> 1), *Westlothiana lizziae* (0 -> 1), *Echinerpeton intermedium* (0 -> 1), Sphenacodontia (0 -> 1), *Varanosaurus acutirostris* (0 -> 1), *Hylonomus lyelli* (0 -> 1), *Archeria crassidisca* (0 -> 1), *Caerorachis bairdi* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (1 -> 0). DELTRAN: *Seymouria sanjuanensis* (0 -> 1), *Gephyrostegus bohemicus* (0 -> 1), *Whatcheeria deltae* (0 -> 1).

205. Dentary ventral edge shape: smooth continuous line (0); abruptly tapering or "stepped" margin (1).

Cea2016 (c.133), Cea2019 (c.133), Pea2017 (c.304).

This character describes a condition in which the ventral margin of the dentary turns upwards with a sharp angle, rather than a smooth curve. A sharp angle is present sporadically in *Adelogyrinus* (Andrews & Carroll, 1991), *Lethiscus* (Pardo et al, 2017), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015; 2016), nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009) and some microsaurs including *Tuditanus*, *Pantylus*, and *Microbrachis* (Carroll & Gaskill, 1978).

Unambiguous: *Acherontiscus caledoniae* (1 -> 0), *Oestocephalus sp.* (1 -> 0), *Hyloplesion longicostatum* (1 -> 0), Captorhinidae (0 -> 1), *Balanerpeton woodi* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Lepospondyli (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (1 -> 0), *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), Caseasauria (0 -> 1), Seymouriamorpha (0 -> 1), Embolomeri + *Chroniosaurus dongusensis* (0 -> 1). DELTRAN: Lepospondyli except *Westlothiana lizziae* (0 -> 1), *Cardiocephalus sp.* (1 -> 0), *Hapsidopareion lepton* (1 -> 0), *Eothyris parkeyi* (0 -> 1), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (0 -> 1), *Archeria crassidisca* (0 -> 1), *Whatcheeria deltae* (0 -> 1).

206. Teeth on the dentary: absent (0); present (1).

Rea2003 (c.186), RC2007 (c.196), ML2019 (c.154).

There are no taxa in this analysis in which dentary teeth are absent. However, due to the inclusion of this character in the large matrices of Ruta & Coates (2007) and Marjanovic & Laurin (2019) this character is retained to allow for future inclusion of taxa in which dentary teeth are absent,

particularly for further expansion into amphibians, as teeth are absent on the dentary in salientians (Ruta et al., 2003).

207. Number of dentary teeth: fewer than 14 (0); 15-19 (1); 20-29 (2); more than 29 (3).

Cea2016 (c.130), Cea2019 (c.130).

The states for this character were chosen to represent phylogenetic distributions. Most stem tetrapods (Beaumont, 1977, Smithson, 1981) and stem amniotes including *Archeria* (Holmes, 1989) and *Silvanerpeton* (Ruta & Clack, 2006), *Gephyrostegus* (Klembara et al., 2014) and seymouriamorphs (Klembara, 1997; Berman et al., 2000; Klembara & Ruta, 2005) possess at least of 29 teeth. Protorothyrids possess at least 35 teeth (Carroll, 1964; 1969), and within araeoscelids *Petrolacosaurus* possesses around 29 (Reisz, 1977) but *Araeoscelis* has just 18 (Reisz et al., 1984). Captorhinids, similarly, show a variety, with more than 30 in *Captorhinus* (Fox & Bowman, 1966), *Euconcordia* has 17 (Reisz et al., 2016) and *Opisthodontosaurus* has just 10 (Reisz et al., 2015). Most synapsids crownwards of this have between 20 and 30 dentary teeth (e.g. Romer et al., 1940; Modesto, 1995; Reisz et al., 2009), although there are exceptions with both more and less, such as *Varanosaurus* with as many as 60 teeth (Bolt & Scott, 1995) or *Casea* with 12 teeth (Olson et al., 1968). Varanopids (Langston & Reisz, 1981; Campione & Reisz, 2010) along with *Archaeovenator* (Reisz & Dilkes, 2003) and *Orovenator* (Ford & Benson, 2019), have at least 30 teeth Temnospondyls possess a very high number of dentary teeth, ranging from 35 to upwards of 60 (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022). The choice of 14 as the lower bound was chosen to differentiate diadectamorphs and nectrideans. No diadectamorphs have fewer than 15 teeth (Romer, 1946; Berman et al., 1998; 2004), and typically nectrideans have more than 14 (Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018), although *Diplocaulus* has in excess of 30 (Douthitt, 1917).

Unambiguous: Lepospondyli except *Westlothiana lizziae* (3 -> 2), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (2 -> 3), *Acherontiscus caledoniae* (3 -> 1), Nectridea + Lysorophia (3 -> 0), *Diplocaulus sp.* (0 -> 3), *Phlegethontia linearis* (3 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (2 -> 1), *Procynosuchus delaharpeae* (2 -> 1), Araescelis gracilis (3 -> 1), Parareptilia (3 -> 0), *Opisthodontosaurus carrolli* (3 -> 0), *Euconcordia cunninghami* (3 -> 1), Diadectamorpha (3 -> 1), *Solenodonsaurus janenschi* (3to2). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (2 -> 3), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0), *Huskerpeton englehorni* (0 -> 1), Sphenacodontia + Edaphosauridae + Caseasauria + *Echinerpeton intermedium* + *Vaughnitis*

smithae + Varanopidae (3to2), Varanopidae (2 -> 3), Caseidae (2 -> 0). DELTRAN: Tetrapoda + *Baphetes sp.* (2 -> 3), *Cardiocephalus sp.* + *Euryodus sp.* (1 -> 0), *Pantylus cordatus* (1 -> 0), Caseasauria + *Echinerpeton intermedium* (3to2), *Casea broilii* (2 -> 0), Edaphosauridae + Sphenacodontia (3 -> 2).

208. Dentary accessory tooth row: absent, dentary has no teeth or just a single tooth row (0); present (1).

Rea2003 (c.182), RC2007 (c.192).

More than one row of teeth on the dentary, in parallel with each other for at least part of the length of the dentary, is classically associated with *Captorhinus* (Fox & Bowman, 1966). However, it is also noted in some nectrideans and the microsaur *Euryodus* (Gee at al, 2019).

Unambiguous: *Diplocaulus sp.* (0 -> 1), *Scincosaurus crassus* (0 -> 1), *Euryodus sp.* (0 -> 1), *Captorhinus aguti* (0 -> 1).

209. Anteroposterior length of dentary tooth row relative to total anteroposterior length of jaw: tooth row is under 50% of jaw (0); tooth row is more than 50% of jaw (1).

Pea2017 (c.88).

A short toothrow on the dentary is present in *Captorhinus* (Fox & Bowman, 1966) and *Euconcordia* (Reisz et al., 2016) but is also widespread across lepospondyls, being present in *Brachydectes* (Pardo et al., 2016), the nectrideans *Diploceraspis* (Beerbower, 1963) and *Keraterpeton* (Milner & Ruta, 2009) and most microsaurs (Carroll & Gaskill, 1978, Gee et al., 2019).

Unambiguous: Lepospondyli (1 -> 0), *Diplocaulus sp.* (0 -> 1). *Limnoscelis paludis* (1 -> 0). Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (0 -> 1), Nectridea + Lysorophia (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (0 -> 1), *Cardiocephalus sp.* (1 -> 0), Captorhinidae (1 -> 0), *Opisthodontosaurus carrolli* (0 -> 1). DELTRAN: *Adelogyrinus simorhynchus* (0 -> 1), Aïstopoda (0 -> 1), *Euryodus sp.* (0 -> 1), *Huskerpeton englehorni* (0 -> 1), *Captorhinus aguti* (1 -> 0), *Euconcordia* (1 -> 0).

210. Dentary fangs lingual to marginal dentary tooth row: absent (0); present (1).

Rea2003 (c.183). Modified from a division of RC2007 (c.193), Cea2016 (c.129), ML2019 (c.151), Cea2019 (c.129), Pea2017 (c.332).

Stem tetrapods (Beaumont, 1977; Smithson, 1981; Rawson et al., 2021) and temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022) possess symphyseal fangs on the dentary, close to the anterior margin of the jaw, and lingual to the toothrow. A similar condition is also observed in *Limnoscelis* (Romer, 1946).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (1 -> 0), *Limnoscelis paludis* (0 -> 1).

211. Size of dentary teeth relative to maxillary teeth: dentary teeth are smaller or equal in size to maxillary teeth (0); dentary teeth are larger than maxillary teeth (1).

Rea2003 (c.221), RC2007 (c.231), ML2019 (c.185). Modified from Cea2019 (c.250), Pea2017 (c.333).

Large dentary teeth, larger in height than the teeth on the maxilla, occur in many temnospondyls (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022), and a small number of other taxa including *Araeoscelis* (Reisz et al., 1984), *Captorhinus* (Fox & Bowman, 1966) and the microsaur *Micraroter* (Carroll & Gaskill, 1978).

Unambiguous: *Micraroter erythrogeois* (0 -> 1), *Araeoscelis gracilis* (0 -> 1), *Captorhinus aguti* (0 -> 1). ACCTRAN: Temnospondyli (0 -> 1), Temnospondyli except *Edops craigi* (0 -> 1).

212. Separately ossified postsplenial: absent (0); present (1).

LR1997 (c.87), Lea1998 (c.84), Rea2003 (c.191), RC2007 (c.201), ML2019 (c.157).

Two separately ossified splenial elements are present in the outgroup (Clack & Finney, 2005; Rawson et al., 2021), other stem tetrapods (Beaumont, 1977; Smithson, 1981), temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022), and most microsaurs (Carroll & Gaskill, 1978; Gee et al., 2021). A second splenial, the postsplenial, is lost in most non-microsaur lepospondyls (e.g. Milner & Ruta, 2009; Pardo et al., 2017), and all stem and crown amniotes crownwards of lepospondyls including diadectamorphs (e.g. Romer, 1946; Fox & Bowman, 1966; Carroll, 1969; Reisz, 1977; Bolt & Scott, 1995; Berman et al., 1998; 2004; Campione & Reisz, 2010; Ford & Benson, 2019).

Unambiguous: Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Diplocaulus sp.* (0 -> 1), *Huskerpeton englehorni* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0). ACCTRAN: *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0). DELTRAN: *Hapsidopareion lepton* (1 -> 0).

213. Splenial exposed in lateral view: no (0); yes (1).

Hea2013 (c.129), Pea2017 (c.93), A2001 (c.98).

A lateral exposure of the splenial and/or postsplenial occurs in the outgroup (Clack & Finney, 2005; Rawson et al., 2021) and in most other stem tetrapods (Beaumont, 1977; Smithson, 1981) and stem amniotes including, and stewards of, diadectamorphs (Romer, 1946; Berman et al., 1998; 2004; Ruta & Clack, 2006). The splenial lateral exposure is absent in some temnospondyls (Arbez et al., 2022), some lepospondyls (Beerbower, 1963; Carroll & Gaskill, 1978; Carroll, 1998; Pardo et al., 2017), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015), some synapsids (Bolt & Scott, 1995; Brocklehurst et al., 2016), and reptiles including parareptiles (Gow, 1972; Reisz & Dilkes, 2003; Reisz et al., 2007; Modesto et al., 2015; Ford & Benson, 2019).

Unambiguous: Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Diploceraspis sp.* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Aerosaurus wellesi* (1 -> 0), *Vaughnitis smithae* (1 -> 0), *Varanosaurus acutirostris* (1 -> 0). ACCTRAN: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (1 -> 0), Synapsida (0 -> 1), *Euconcordia cunninghami* (0 -> 1), Embolomeri + *Chroniosaurus dongusensis* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (1 -> 0). DELTRAN: Reptilia (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 0), *Paleothyris acadiana* (1 -> 0), *Archeria crassidisca* (1 -> 0), *Dendrerpeton helogenes* (1 -> 0).

214. Separately ossified anterior coronoid: absent (0); present (1).

LR1997 (c.83), Lea1998 (c.80), Rea2003 (c.202), RC2007 (c.212), ML2019 (c.167).

The absence of an anterior coronoid is observed in captorhinids (Fox & Bowman, 1966; Reisz et al., 2015), the basal reptiles *Archaeovenator* (Reisz & Dilkes, 2003) and *Orovenator* (Ford & Benson, 2019), parareptiles (Gow, 1972; Reisz et al., 2007) and *Petrolacosaurus* (Reisz, 1977). In these taxa,

the number of coronoids is reduced to one, which is considered here to be the posterior coronoid based on its position.

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Phlegethontia linearis* (1 -> 0), *Procynosuchus delaharpeae* (1 -> 0). ACCTRAN: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1 -> 0), Synapsida except Araeoscelidia (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* (0 -> 1), *Limnoscelis paludis* (0 -> 1). DELTRAN: *Petrolacosaurus kansensis* (1 -> 0), Reptilia (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 0), *Diadectes abistus* (1 -> 0).

215. Separately ossified middle coronoid: absent (0); present (1).

LR1997 (c.84), Lea1998 (c.81), Rea2003 (c.206), RC2007 (c.216), ML2019 (c.171).

A middle coronoid is lost in most reptiles, captorhinids and *Petrolacosaurus* as these taxa retain just one coronoid (see ch.180). However, a middle coronoid is also lost in synapsids (e.g. Bolt & Scott, 1995; Campione & Reisz, 2010; Brocklehurst et al., 2016), which retain two coronoids, considered to be anterior and posterior based on position. It is also lost in *Westlothiana*.

Unambiguous: Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Huskerpeton englehorni* (1 -> 0), *Greererpeton burkemorani* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), Lepospondyli except *Westlothiana lizziae* (0 -> 1), *Limnoscelis paludis* (0 -> 1). DELTRAN: *Westlothiana lizziae* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (1 -> 0), *Diadectes abistus* (1 -> 0).

216. Separately ossified posterior coronoid: absent (0); present (1).

LR1997 (c.85), Lea1998 (c.82), Rea2003 (c.210), RC2007 (c.220), ML2019 (c.175).

A posterior coronoid is lost in the aïstopods *Lethiscus* (Pardo et al, 2017) and *Phlegethontia* (Anderson, 2002), in which the mandible is reduced to a small number of ossifications.

ACCTRAN: Aïstopoda (1 -> 0). DELTRAN: *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 0).

217. Posterodorsal process on posterior coronoid: absent (0); present (1).

Rea2003 (c.214), RC2007 (c.224), Cea2016 (c.120), Cea2019 (c.121), Pea2017 (c.301). Modified from a division of ML2019 (c.179).

The posterior coronoid sends a backward process detaching immediately posterolateral to its main (sometimes dentigerous) part and contributing in various degrees to the anterolateral portion of the adductor fossa in the majority of stem and crown amniotes crownwards of *Silvanerpeton*, including seymouriamorphs (Klembara, 1997; Berman et al., 2000; Klembara & Ruta, 2006), most lepospondyls (e.g. Beerbower, 1973; Carroll & Gaskill, 1978), most diadectamorphs (Romer, 1946, Berman et al, 1998) and crown amniotes (e.g. Reisz, 1977; Bolt & Scott, 1995; Reisz & Dilkes, 2003). However, it is absent in *Westlothiana* and *Orobates* (Berman et al., 2004). It is also noted to be present in *Caerorachis* (Ruta et al., 2001) and *Dendrerpeton* (Arbez et al., 2022).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), *Westlothiana lizziae* (1 -> 0), *Orobates pabsti* (1 -> 0), *Caerorachis bairdi* (0 -> 1), *Dendrerpeton helogenes* (0 -> 1).

218. Posterodorsal process of posterior coronoid contributing to tallest point of lateral margin of adductor fossa: no (0), yes (1).

Rea2003 (c.216), RC2007 (c.226). Modified from a division of ML2019 (c.179).

This refers to the extension, backward and dorsalward, of the process referred to in ch.217. In some taxa, the latter forms part of the tallest point of the lateral margin of the adductor fossa, regardless of the presence of absence, in the surangular, of a 'crest' (that is, a peak in the dorsal margin of the surangular) such as in temnospondyls (Romer & Witter, 1942; Arbez et al., 2021), synapsids (e.g. Bolt & Scott, 1995; Campione & Reisz, 2010) and reptiles (Gow, 1972; Ford & Benson, 2019).

Unambiguous: Temnospondyli (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (0 -> 1), *Microbrachis pelikani* (1 -> 0), *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Limnoscelis paludis* (1 -> 0), *Ariekanerpeton sigalovi* (1 -> 0), *Gephyrostegus bohemicus* (1 -> 0). DELTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), *Diadectes abistus* (0 -> 1), *Discosauriscus austriacus* (0 -> 1), *Seymouria sanjuanensis* (0 -> 1).

219. Posterior coronoid exposed in lateral view: no (0); yes (1).

Rea2003 (c.215), RC2007 (c.225), Cea2016 (c.122), ML2019 (c.180), Cea2019 (c.122), Pea2017 (c.302).

In some taxa, the posterior coronoid is visible in lateral view as either a sliver or a more substantial lappet of bone tightly appressed against the surangular and posterodorsal to the posterior ramus of the dentary, including *Brachydectes* (Pardo et al., 2016), *Petrolacosaurus* (Reisz, 1977), *Diadectes* (Berman et al., 1998) and *Gephyrostegus* (Klembara et al., 2014).

Unambiguous: *Brachydectes newberryi* (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), *Diadectes abistus* (0 -> 1), Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1), *Ariekanerpeton sigalovi* (1 -> 0). ACCTRAN: Reptilia (0 -> 1), *Milleretta sp.* (1 -> 0), Embolomeri + *Chroniosaurus dongusensis* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (0 -> 1). DELTRAN: *Belebey vegrandis* (0 -> 1), *Orovenator mayorum* (0 -> 1), *Archeria crassidisca* (0 -> 1), *Dendrerpeton helogenes* (0 -> 1).

220. Anterior coronoid - splenial contact: absent (0); present (1); anterior coronoid absent (inapplicable).

Novel

In almost all taxa included in this analysis, the anterior coronoid and the splenial make contact. In *Westlothiana*, the splenial is a narrow, rod-like element restricted to a ventral postion, and the anterior coronoid is also narrow and restricted to a particularly dorsal position. A similar condition is observed in *Acherontiscus* (Clack et al, 2019).

Unambiguous: *Westlothiana lizziae* (1 -> 0). ACCTRAN: Adelospondyli + *Utaherpeton franklini* (1 -> 0). DELTRAN: *Acherontiscus caledoniae* (1 -> 0).

221. Middle coronoid - splenial contact: absent (0); present (1); middle coronoid absent (inapplicable).

Novel

In some taxa, as discussed in ch.220, the splenial possesses a ventral position and the coronoids are dorsoventrally narrow and dorsally located. However, in several taxa, such as *Gephyrostegus* (Klembara et al, 2014), the splenial is taller and extends dorsally to contact the middle coronoid. Such

a condition is also observed in *Greererpeton* (Smithson, 1981), the temnospondyls *Balanerpeton* (Milner & Sequeira, 1993) and *Dendrerpeton* (Arbez et al., 2022), the anthracosaur *Archeria* (Holmes, 1989), the seymouriamorph *Discosauriscus* (Klembara, 1997) and the microsaurs *Pantylus* (Carroll & Gaskill, 1978) and *Euryodus* (Gee et al., 2021).

Unambiguous: Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1), *Archeria crassidisca* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1). DELTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (0 -> 1), Temnospondyli except *Edops craigi* (0 -> 1), *Greererpeton burkemorani* (0 -> 1).

222. Fangs on anterior coronoid (recognisable as at least twice the height of coronoid teeth): absent (0); present (1); anterior coronoid absent (inapplicable).

Rea2003 (c.203), RC2007 (c.213), ML2019 (c.168). Modified from a division of LR1997 (c.92), Lea1998 (c.88), Cea2016 (c.123), Cea2019 (c.124), Pea2017 (c.326, c.327).

In the included taxa, *Gephyrostegus* is noted to have a large fang, clearly larger than the surrounding denticles and comparable in size to the marginal teeth, on both the anterior and middle coronoids (Klembara et al., 2014).

Unambiguous: *Gephyrostegus bohemicus* (0 -> 1).

223. Fangs on middle coronoid (recognisable as at least twice the height of coronoid teeth): absent (0); present (1); middle coronoid absent (inapplicable).

Rea2003 (c.207), RC2007 (c.217), ML2019 (c.172).

See ch. 222.

Unambiguous: *Gephyrostegus bohemicus* (0 -> 1).

224. Fangs on posterior coronoid (recognisable as at least twice the height of coronoid teeth): absent (0); present (1); posterior coronoid absent (inapplicable).

Rea2003 (c.211), RC2007 (c.221), ML2019 (c.176).

No taxa other than *Eusthenopteron* in the current analysis posses fangs on the posterior coronoid, but the character is retained in order to allow for expansion of the future analysis to include deeper stem tetrapod taxa including more panderichthyids, some of which possess posterior coronoid fangs (Ruta et al., 2003).

225. Denticles forming shagreen or discrete patches on anterior coronoid: absent (0); present (1); anterior coronoid absent (inapplicable).

Rea2003 (c.204), RC2007 (c.214), ML2019 (c.169). Modified from a division of LR1997 (c.93), Lea1998 (c.89), Cea2016 (c.126, c.127), Cea2019 (c.127, c.127), Pea2017 (c.329).

A small number of disparate taxa possess a denticle shagreen on the anterior coronoid. While present in temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1993; Arbez et al., 2022) or stem amniotes such as anthracosaurs (Panchen, 1977; Holmes, 1989), seymouriamorphs (Kelmbara, 1997; Berman et al., 2000; Klembara & Ruta, 2005) and *Limnoscelis* (Romer, 1946), such a shagreen is largely absent in lepospondyls or crown amniotes, with the exception of *Westlothiana*, *Microbrachis* (Carroll & Gaskill, 1978) and *Edaphosaurus* (Modesto, 1995).

ACCTRAN: Tetrapoda + *Baphetes sp.* (0 -> 1), Lepospondyli except *Westlothiana lizziae* (1 -> 0), *Microbrachis pelikani* (0 -> 1), Amniota (1 -> 0), Edaphosauridae (0 -> 1). DELTRAN: Tetrapoda (0 -> 1), Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (1 -> 0), Synapsida except Araeoscelidia (1 -> 0), *Edaphosaurus boanerges* (0 -> 1).

226. Denticles forming shagreen or discrete patches on middle coronoid: absent (0); present (1); middle coronoid absent (inapplicable).

Rea2003 (c.208), RC2007 (c.215), ML2019 (c.173). Modified from a division of LR1997 (c.93), Lea1998 (c.89), Cea2016 (c.126, c.127), Cea2019 (c.127, c.127), Pea2017 (c.329).

As is the case for ch.225, denticles on the middle coronoid have a scattered distribution across a number of disparate tetrapods. They are present in *Greererpeton* (Smithson, 1981), temnospondyls (Romer & Witter, 1940; Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022), anthracosaurs (Panchen, 1977; Holmes, 1989) seymouriamorphs (Klembara, 1997; Berman et al.,

2000; Klembara & Ruta, 2005), *Gephyrostegus* (Klembara et al., 2014), *Limnoscelis* (Romer, 1946) and *Westlothiana*.

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), Adelospondyli + *Utaherpeton franklini* (0 -> 1), Diadectamorpha (0 -> 1). DELTRAN: Lepospondyli except *Westlothiana lizziae* (1 -> 0), *Acherontiscus caledoniae* (0 -> 1), *Vaughnitis smithae* (1 -> 0).

227. Denticles forming shagreen or discrete patches on posterior coronoid: absent (0); present (1); posterior coronoid absent (inapplicable).

Rea 2003 (c.212), RC2007 (c.222), ML2019 (c.177). Modified from a division of LR1997 (c.93), Lea1998 (c.89), Cea2016 (c.126, c.127), Cea2019 (c.127, c.127), Pea2017 (c.329).

The distribution of states in this character is almost exactly co-distributed with ch.226. However, there are a small number of differences. *Doleserpeton* possesses denticles on the middle coronoid but not the posterior coronoid (Sigurdsen & Bolt, 2010). *Edaphosaurus* (Modesto, 1995) and *Haptodus* (Laurin, 1993) both have denticles on the posterior coronoid but lack a middle coronoid altogether.

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), Adelospondyli + *Utaherpeton franklini* (0 -> 1), *Westlothiana lizziae* (0 -> 1), Edaphosauridae + Sphenacodontia (0 -> 1), Sphenacodontidae + *Pantelosaurus saxonicus* (1 -> 0), *Limnoscelis paludis* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (1 -> 0), *Acherontiscus caledoniae* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (1 -> 0), *Haptodus garnettensis* (0 -> 1), *Edaphosaurus boanerges* (0 -> 1), *Diadectes abistus* (1 -> 0), *Doleserpeton annectens* (1 -> 0).

228. Tooth row on anterior coronoid: absent (0); present (1); anterior coronoid absent (inapplicable).

RC2007 (c.215), Rea2003 (c.205), ML2019 (c.170). Modified from a division of Cea2016 (c.125), Cea2019 (c.125), Pea2017 (c.328).

Greererpeton (Smithson, 1981), *Diploceraspis* (Beerbower, 1963) and most microsaurs (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2021) have a toothrow of teeth clearly larger than any surrounding denticles, and comparable to the marginal teeth, on the anterior coronoid.

ACCTRAN: Tetrapoda + *Baphetes sp.* (1 -> 0), Nectridea + Lysorophia (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1). DELTRAN: Tetrapoda (1 -> 0), *Diploceraspis sp.* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1).

229. Tooth row on middle coronoid: absent (0); present (1); middle coronoid absent (inapplicable).

Rea2003 (c.209), RC2007 (c.219), ML2019 (c.174). Modified from a division of Cea2016 (c.125), Cea2019 (c.125), Pea2017 (c.328).

A toothrow on the middle coronoid is noted in the outgroup (Clack & Finney, 2005; Rawson et al., 2021), and the microsaurs *Pantylus* (Carroll & Gaskill, 1978) and *Euryodus* (Gee et al., 2021).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1). DELTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (0 -> 1).

230. Tooth row on posterior coronoid: absent (0); present (1); posterior coronoid absent (inapplicable).

Rea2003 (c.213), RC2007 (c.223), ML2019 (c.178). Modified from a division of Cea2016 (c.125), Cea2019 (c.125), Pea2017 (c.328).

The distribution of a toothrow on the posterior coronoid is almost identical to ch.229. However, there are some differences noted, and as such these are retained as separate characters. Araeoscelids (Reisz, 1977; Reisz et al., 1984), *Captorhinus* (Fox & Bowman, 1966), some parareptiles (Gow, 1972; Reisz et al., 2007) and most synapsids (Romer et al., 1940; Laurin, 1993; Bolt & Scott, 1995; Modesto, 1995) lack a tooth row on the posterior coronoid, but they lack a middle coronoid altogether. *Vaughnitis* has a tooth row on the posterior coronoid (Brocklehurst et al., 2016).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), *Vaughnitis smithae* (0 -> 1). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus*

+ *Micraroter erythrogeois* (0 -> 1), *Huskerpeton englehorni* (1 -> 0). DELTRAN: *Euryodus sp.* (0 -> 1), *Pantylus cordatus* (0 -> 1).

231. Coronoid tooth size relative to marginal teeth: smaller (0); equal in size or larger (1).

A2001 (c.108), Cea2016 (c.128), Cea2019 (c.128), Hea2013 (c.138), Pea2017 (c.330).

Particularly large coronoid teeth are noted in *Pantylus* (Carroll & Gaskill, 1978) and *Diploceraspis* (Beerbower, 1963).

Unambiguous: *Pantylus cordatus* (0 -> 1). ACCTRAN: Nectridea + Lysorophia + Aïstopoda (0 -> 1). DELTRTAN: *Diploceraspis sp.* (0 -> 1).

232. Separately ossified angular: absent (0); present (1).

LR1997 (c.89), Lea1998 (c.85), Rea2003 (c.194), RC2007 (c.204), ML2019 (c.160).

A separately ossified angular is lost in the aïstopod *Phlegethontia* (Anderson, 2002), where the mandible is simplified to only two ossifications.

Unambiguous: *Phlegethontia linearis* (1 -> 0).

233. Angular dorsoventral depth as a proportion of dorsoventral jaw depth, at the point of deepest dorsoventral extent of angular: less deep than half of jaw (0); deeper than half of jaw (1).

A2001 (c.97), Hea2013 (c.127), Pea2017 (c.91).

The angular is measured, in lateral view, at its deepest point, compared to the dorsoventral height of the jaw at the same point. There is no obvious phylogenetic signal to this character. Taxa as disparate as stem tetrapods such as *Greererpeton* (Smithson, 1981), temnospondyls such as *Dendrerpeton* (Arbez et al., 2022), lepospondyls such as the microsaur *Hapsidopareion* (Carroll & Gaskill, 1978) and crown amniotes such as *Orovenator* (Ford & Benson, 2019) possess an angular that is dorsoventrally shallower than half of the dorsoventral jaw depth. However, there are stem tetrapods such as *Baphetes* (Beaumont, 1977), temnospondyls such as *Balanerpeton* (Milner & Sequeira, 1993),

crown amniotes such as most synapsids (e.g. Bolt & Scott, 1995) and the lepospondyl microsaur *Tuditanus* (Carroll & Gaskill, 1978) all possess a dorsoventrally deeper angular.

Unambiguous: *Diploceraspis sp.* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Euryodus sp.* (0 -> 1), *Pantylus cordatus* (0 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (1 -> 0), *Balanerpeton woodi* (0 -> 1), *Baphetes sp.* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0), *Acherontiscus caledoniae* (0 -> 1), Diadectamorpha (1 -> 0), *Orobates pabsti* (0 -> 1). DELTRAN: *Adelogyrinus simorhynchus* (1 -> 0), Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Diadectes abistus* (1 -> 0), *Limnoscelis paludis* (1 -> 0).

234. Anteriormost extent of the angular in lateral view: posterior to mid-point of tooth row (0); in line with or anterior to mid-point of tooth row (1).

A2001 (c.105), Hea2013 (c.135), Pea2017 (c.99).

The angular extends anteriorly at least to the mid-point of the toothrow in variety of taxa, including multiple lepospondyls such as *Brachydectes* (Pardo et al., 2016), *Acherontiscus* (Clack et al., 2019) and *Diploceraspis* (Beerbower, 1963), but particularly within microsaurs (Carroll & Gaskill, 1978; Gee et al., 2019). The condition is also observed in edaphosaurids (Modesto, 1995) and sphenacodontids (Romer et al., 1940; Laurin, 1993; Spindler, 2016), and the stem amniotes *Archeria* (Holmes, 1989) and *Silvanerpeton* (Ruta & Clack, 2006).

Unambiguous: *Brachydectes newberryi* (0 -> 1), *Diploceraspis sp.* (0 -> 1), *Tuditanus punctulatus* (0 -> 1), *Hapsidopareion lepton* + *Llistrofus pricei* (0 -> 1), *Westlothiana lizziae* (0 -> 1), Edaphosauridae + Sphenacodontia (0 -> 1), *Procynosuchus delaharpeae* (1 -> 0), *Gephyrostegus bohemicus* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (0 -> 1), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (1 -> 0), Adelospondyli + *Utaherpeton franklini* (0 -> 1), *Adelogyrinus simorhynchus* (1 -> 0). DELTRAN: *Acherontiscus caledoniae* (0 -> 1), *Utaherpeton franklini* (0 -> 1), *Silvanerpeton miripedes* (0 -> 1), *Archeria crassidisca* (0 -> 1).

235. Angular reaching or not reaching posteriormost extent of lower jaw: does not reach posteriormost point (0); reaches posteriormost point (1).

Rea2003 (c.197), RC2007 (c.207), Kea2014 (c.93), Cea2016 (c.116), ML2019 (c.162), Cea2019 (c.116).

In most ingroup taxa, the angular participates in the posterior margin of the mandible in lateral view, including taxa ranging as widely as *Baphetes* (Beaumont, 1977), *Seymouria* (Berman et al., 2000), *Tuditanus* (Carroll & Gaskill, 1978) and *Petrolacosaurus* (Reisz, 1977). Even when the mandible is sloping anteroventrally to posterodorsally, if the angular forms part of this margin then that is considered to be state 1, such as in *Paleothyris* (Carroll, 1969). However, in several taxa, such as parareptiles (Gow, 1972; Reisz et al., 2007; Modesto et al., 2015) and *Diadectes* (Berman et al, 1998), the articular extends to the ventral margin of the jaw and prevents the angular reaching the posterior margin.

Unambiguous: Tetrapoda + *Baphetes sp.* (0 -> 1), *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Westlothiana lizziae* (1 -> 0), *Aerosaurus wellesi* (1 -> 0), Reptilia (1 -> 0), *Diadectes abistus* + *Orobates pabsti* (1 -> 0). ACCTRAN: Nectridea (1 -> 0), *Diplocaulus sp.* (0 -> 1), Sphenacodontidae + *Pantelosaurus saxonicus* (1 -> 0). DELTRAN: *Diploceraspis sp.* (1 -> 0), *Keraterpeton galvani* (1 -> 0), Sphenacodontidae (1 -> 0).

236. Medially-projecting flange on dorsal edge along posterior border of adductor fossa on prearticular: absent (0); present (1).

Pea2017 (c.322).

A medial flange on the prearticular is present in anthracosaurs (Panchen, 1977; Holmes, 1989), as well as a small number of other taxa, namely *Pantylus* (Carroll & Gaskill, 1978) and *Orovenator* (Ford & Benson, 2019).

Unambiguous: *Pantylus cordatus* (0 -> 1), *Orovenator mayorum* (0 -> 1). ACCTRAN: Embolomeri + *Chroniosaurus dongusensis* (0 -> 1). DELTRAN: Embolomeri (0 -> 1).

237. Longtidunal ridge below coronoids present on prearticular: absent (0); present (1).

Cea2016 (c.150), Cea2019 (c.150), Pea2017 (c.321).

A medial ridge on the prearticular, anterior to that of ch.236 and below the coronoids, is present in *Archeria* (Holmes, 1989).

ACCTRAN: Embolomeri + *Chroniosaurus dongusensis* (0 -> 1). DELTRAN: *Archeria crassidisca* (0 -> 1).

238. Prearticular - splenial contact: absent (0); present (1).

Novel

A contact between the splenial and prearticular is almost ubiquitous across the taxa included in this analysis, but is absent in a small number of taxa such a contact is absent. In *Huskerpeton* (Huttenlocker et al, 2013), for example the coronoid series is present between them, preventing contact. An absence of a contact between the splenial and prearticular is also observed in *Llistrofus* (Gee et al., 2019), *Anthracosaurus* (Panchen, 1977) and *Belebey* (Reisz et al., 2007).

Unambiguous: *Huskerpeton englehorni* (1 -> 0), *Llistrofus pricei* (1 -> 0), *Anthracosaurus russelli* (1 -> 0). ACCTRAN: *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (1 -> 0). DELTRAN: *Belebey vegrandis* (1 -> 0).

239. Prearticular - surangular contact: absent (0); present (1).

Novel

Unambiguous: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (1 -> 0), Edaphosauridae + Sphenacodontia (1 -> 0), Diadectamorpha (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* (0 -> 1), Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 0), *Balanerpeton woodi* (1 -> 0). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (0 -> 1), *Acherontiscus caledoniae* (1 -> 0), *Lethiscus* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (0 -> 1).

240. Denticle shagreen on prearticular: absent (0); present (1).

Modified from a division of Cea2016 (c.148), Cea2019 (c.148), Pea2017 (c.339).

A denticle shagreen on the prearticular is present in the outgroup taxon *Whatcheeria* (Rawson et al, 2021) and a small number of other, distantly related ingroup taxa, namely *Westlothiana*, *Caerorachis* (Ruta et al., 2001) and *Edaphosaurus* (Modesto, 1995).

Unambiguous: *Westlothiana lizziae* (0 -> 1), *Caerorachis bairdi* (0 -> 1), *Whatcheeria deltae* (0 -> 1). ACCTRAN: Edaphosauridae (0 -> 1). DELTRAN: *Edaphosaurus boanerges* (0 -> 1).

241. Separately ossified proatles: absent (0); present (1).

A2001 (c.139), Hea2013 (c.174), Pea2017 (c.136).

ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (1 -> 0), Nectridea + Lysorophia + Aïstopoda (0 -> 1). DELTRAN: *Adelogyrinus simorhynchus* (1 -> 0), *Microbrachis pelikani* (1 -> 0).

242. Articulation of atlantal neural arch to atlantal centrum: sutured (0); indistinguishably fused (1).

LR1997 (c.108), Lea1998 (c.104), A2001 (c.137), Rea2003 (c.284), RC2007 (c.302), Cea2016 (c.199), ML2019 (c.251), Cea2019 (c.199), Hea2013 (c.172), Pea2017 (c.134).

In most lepospondyls, there is no visible trace of a suture between the atlantal centrum and atlantal neural arch, including aïstopods (Carroll, 1998; Anderson, 2002), nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018) and most microsaurs (Carroll & Gaskill, 1978; Gee et al., 2021). This condition is also observed in *Doleserpeton* (Sigurdsen & Bolt, 2010), protorothyrids (Carroll, 1964; 1969), araeoscelids (Reisz, 1977; Langston & Reisz, 1981), *Diadectes* (Berman et al., 1998)

Unambiguous: *Tuditanus punctulatus* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* (0 -> 1), *Diadectes abistus* (0 -> 1). ACCTRAN: Nectridea + Lysorophia + Aïstopoda (0 -> 1), *Brachydectes newberryi* (1 -> 0), Synapsida (0 -> 1), Edaphosauridae + Sphenacodontia (1 -> 0), Temnospondyli (0 -> 1). DELTRAN: Nectridea (0 -> 1), Aïstopoda (0 -> 1), *Aerosaurus wellesi* (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), *Doleserpeton annectens* (0 -> 1).

243. Atlantal neural arch halves: paired, sutured to each other (0); fused into single arch (1).

A2001 (c.135), Hea2013 (c.170), Pea2017 (c.132).

In the stem tetrapod *Greererpeton* (Smithson, 1981), the atlantal neural arch consists of two laterally paired ossifications that suture along the midline, a condition that is present across almost all included taxa. In most lepospondyls, however, the two lateral halves of the neural arch are indistinguishably fused with no visible trace of a suture, including *Adelogyrinus* (Andrews & Carroll, 1991), the aïstopod *Phlegethontia* (Anderson, 2002), nectrideans (Douthitt, 1917; Beerbower, 1963; Milner, 2018), and the microsaur *Cardiocephalus* (Carroll & Gaskill, 1978). The condition is also present in *Seymouria* (Berman et al., 2000) and *Caerorachis* (Ruta et al., 2001).

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (0 -> 1), *Brachydectes newberryi* (1 -> 0), *Cardiocephalus sp.* (0 -> 1), *Seymouria sanjuanensis* (0 -> 1), *Caerorachis bairdi* (0 -> 1).

244. Atlas parapophyses: absent (0); present (1).

Modified from a division of A2001 (c.136), Hea2013 (c.171), Pea2017 (c.133).

ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (0 -> 1), Lepospondyli (1 -> 0), *Microbrachis pelikani* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (1 -> 0). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (0 -> 1), Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Westlothiana lizziae* (1 -> 0), *Milleretta sp.* (1 -> 0).

245. Atlas parapophyses position: on centrum (0); on transverse process (1); absent (inapplicable).

Modified from a division of A2001 (c.136), Hea2013 (c.171), Pea2017 (c.133).

ACCTRAN: *Diadectes abistus* + *Orobates pabsti* (1 -> 0). DELTRAN: *Orobates pabsti* (1 -> 0).

246. Articulation of axial neural arch to axial centrum: sutured (0); indistinguishably fused (1).

Rea2003 (c.285), RC2007 (c.303), ML2019 (c.252).

In stem tetrapods, the axis arch and centrum are joined with a visible suture between them, such as in *Greererpeton* (Smithson, 1981). Fusion between the arch and the centrum of the axis, thus erasing any visible trace of a suture, is present in aïstopods (Carroll, 1998; Anderson, 2002), the temnospondyl *Balanerpeton* (Milner & Sequeira, 1993), *Captorhinus* (Fox & Bowman, 1966), protorothyrids (Carroll, 1964; 1969), araeoscelids (Reisz, 1977; Langston & Reisz, 1981), some synapsids (Romer et al., 1940; Laurin, 1993; Campione & Reisz, 2010), *Archaeovenator* and *Orovenator* (Reisz et al., 1984; Ford & Benson, 2019), diadectamorphs (Romer, 1946; Berman et al., 1998; 2004), nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018) and some microsaurs (Carroll & Gaskill, 1978; Gee et al., 2021).

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), *Procynosuchus delaharpeae* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda (0 -> 1), *Brachydectes newberryi* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (0 -> 1), *Pantylus cordatus* (1 -> 0), Parareptilia (1 -> 0), Temnospondyli (0 -> 1). DELTRAN: Nectridea (0 -> 1), Aïstopoda (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* (0 -> 1), *Micraroter erythrogeois* (0 -> 1), *Milleretta sp.* (1 -> 0), *Balanerpeton woodi* (0 -> 1).

247. Axial neural arch anteroposterior length relative to more posterior neural arches: anteroposteriorly shorter than more posterior arches (0); equal in size to more posterior arches (1); anteroposteriorly longer than posterior arches (2).

Hea2013 (c.175), Pea2017 (c.137).

In some taxa, the axial neural arch is expanded anteroposteriorly in length, so that is is clearly and distinctly longer along its anteroposterior axis than the arches immediately posterior to it. This condition is observed in the diadectamorph *Orobates* (Berman et al., 2004) and almost all amniotes crownwards of diadectamorphs, including *Captorhinus* (Fox & Bowman, 1966), protorothyrids (Carroll, 1964; 1969), araeoscelids (Reisz, 1977; Langston & Reisz, 1981), reptiles (Gow, 1972; 1974; Reisz et al., 1984; Ford & Benson, 2019) and most synapsids included in this analysis (e.g. Romer et al., 1940; Bolt & Scott, 1995; Modesto, 1995) with the exception of *Eocasea* (Reisz & Fröbisch, 2014) and *Varanops* (Campione & Reisz, 2010). The condition is also observed in

Greererpeton (Smithson, 1981), *Balanerpeton* (Milner & Sequiera, 1993), *Gephyrostegus* (Klembara et al., 2014), *Seymouria* (Berman et al., 2000), *Diplocaulus* (Douthitt, 1917) and a small number of microsaurs (Carroll & Gaskill, 1978).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 2), *Euryodus sp.* (1 -> 2), *Varanops brevirostris* (2 -> 0), *Diadectes abistus* (2 -> 1), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (2 -> 1), Embolomeri + *Chroniosaurus dongusensis* (2 -> 0). ACCTRAN: Lepospondyli (2 -> 1), *Diplocaulus sp.* + *Diploceraspis sp.* (1 -> 2), *Microbrachis pelikani* (1 -> 2), Caseasauria (2 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (2 -> 1). DELTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (2 -> 1), *Diplocaulus sp.* (1 -> 2), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* (2 -> 1), *Eocasea martini* (2 -> 0), *Doleserpeton annectens* (2 -> 1).

248. Anterior articulating surface of atlas: equal in diameter to posterior articulating surface (0); laterally expanded relative to posterior articulating surface (1).

Hea2013 (c.168), Pea2017 (c.130), LR1997 (c.110), Lea1998 (c.106), A2001 (c.133).

In microsaurs, the antlantal intercentrum has a somewhat trapezium-like shape in ventral view. The centrum expands towards the anterior end, so that the anterior surface approaches twice as wide, laterally, as the posterior surface (Carroll & Gaskill, 1978; Huttenlocker et al., 2013; Gee et al., 2019). A similar condition is also observed in *Diplocaulus* (Douthitt, 1917).

Unambiguous: Lepospondyli except *Westlothiana lizziae* (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Diplocaulus sp.* (0 -> 1).

249. Odontoid process on atlas: absent (0); present (1).

RC2007 (c.304), ML2019 (c.253), Cea2019 (c.217). Modified from a division of LR1997 (c.109), Lea1998 (c.105).

An odontoid process on the atlas describes an anteriorly protruding, stout process of the atlas body fitting into a variously deep recess or pit in the occiput (Anderson, 2001; Ruta & Coates, 2007). It is present in most lepospondyls (Carroll & Gaskill, 1978; Andrews & Carroll, 1991; Carroll, 1998; Anderson, 2002; Anderson et al., 2003; Huttenlocker et al., 2013) apart from nectrideans (Douthitt,

1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018), and in *Gerobatrachus* (Anderson et al, 2008).

Unambiguous: Nectridea (1 -> 0), *Gerobatrachus hottoni* (0 -> 1). ACCTRAN: Lepospondyli (0 -> 1), Lepospondyli except *Westlothiana lizziae* (0 -> 1).

250. 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).

FB2020 (c207). Modified from Gea1988 (c.139), L1991 (c.H2), Rea1992 (c.69), L1993 (c.92), DR1997 (c.103), Rea2010 (c.70), N2011 (c.190), B2012 (c.154), Pea2015 (c.108), E2016 (c.327), Sea2018 (c.109).

The size and shape of ventral of keel varies between various clades of crown amniotes. State 1, a low keep or ridge, is present in *Haptodus* (Laurin 1993), varanopids (Langston & Reisz, 1981; Campione & Reisz, 2010) and captorhinids (Fox & Bowman, 1966). It is also present in *Orovenator* (Ford & Benson, 2019) and araeoscelids (Reisz, 1977; Reisz et al., 1984). Derived sphenacodontids posses a dorsoventrally deeper and sheet-like keel (state 2, Romer et al., 1940), while in caseids there is no keel, and they possess a rounded ventral surface (state 0)(Olson et al., 1968; Reisz & Fröbisch, 2014).

Unambiguous: Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Diplocaulus sp.* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (0 -> 1), Caseasauria (1 -> 0), Sphenacodontidae + *Pantelosaurus saxonicus* (1 -> 2), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (1 -> 0), Diadectamorpha (1 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), *Eocasea martini* (1 -> 0), *Dimetrodon sp.* (1 -> 2), *Youngina capensis* (1 -> 0).

251. Separately ossified atlantal intercentrum: absent (0); present (1).

LR1997 (c.113), Lea1998 (c.109), A2001 (c.116), Hea2013 (c.167), Pea2017 (c.129).

In lepospondyls more derived than *Westlothiana*, the intercentrum is entirely lost (ch.267) (Douthitt, 1917; Beerbower, 1963; Carroll & Gaskill, 1978; Andrews & Carroll, 1991; Carroll et al., 1991; Carroll; 1998; Anderson, 2002; Anderson et al., 2003; Huttenlocker et al., 2013; Pardo et al., 2016; Milner & Ruta, 2009; Clack et al., 2019; Gee et al., 2019). This includes the atlantal intercentrum. Westlothaina retains intercentra in the trunk, but it is unclear if the cervical centra are retained as well.

An atlantal intercentrum is also lost in the temnospondyl *Doleserpeton* (Sigurdsen & Bolt, 2010) and the synapsid *Echinerpeton* (Mann & Paterson, 2020).

Unambiguous: *Echinerpeton intermedium* (1 -> 0). ACCTRAN: Lepospondyli (1 -> 0), Temnospondyli (1 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (1 -> 0), *Doleserpeton annectens* (1 -> 0).

252. Elements making up trunk vertebrae: intercentrum absent, pleurocentrum is only element (0); intercentrum present but pleurocentrum is dominant element (1); intercentrum and pleurocentrum make roughly equal contribution to centrum (2); intercentrum is dominant (3).

Modified from A2001 (c.115), Cea2016 (c.171), Cea2019 (c.171), Hea2013 (c.148), Lea1998 (c.98), LR1997 (c.102), ML2019 (c.259), Pea2017 (c.110), RC2007 (c.316), Rea2003 (c.299).

A variety of conditions of the elements making up centra appears across tetrapods (Danto et al, 2012). In most stem tetrapods, temnospondyls, and *Gerobatrachus* the rachitomous condition is present where the intercentrum is the dominant element (state 3)(Romer & Witter, 1942; Smithson, 1981; Milner & Sequeira, 1993; Clack & Finney, 2005; Anderson et al., 2008; Sigurdsen & Bolt, 2010; Rawson et al., 2021; Arbez et al., 2022). Embolomeres, so named for their embolomerous centra, possess an intercentrum and pleurocentrum that are roughly equivalent in size (Holmes, 1989). In most amniotes crownwards of anthracosaurs, including *Silvanerpeton* (Ruta & Clack, 2006), the pleurocentrum is the dominant element, and they retain a small, wedge shaped intercentrum, including seymouriamorphs, diadectamorphs, protorothyrids, captorhinids and crown amniotes (e.g. Romer et al., 1940; Romer, 1946; Fox & Bowman, 1966; Carroll, 1969; Gow, 1972; Reisz et al., 1984; Berman et al., 2000; 2004), a condition which is also present in *Westlothiana*. However, in derived caseasaurs, intercentra are almost completely lost (Olson et al., 1968; Brocklehurst et al., 2016). This is state 0, the 'lepospondylous' condition, and is present in lepospondyls as well (Carroll & Gaskill, 1978; Andrews & Carroll, 1991; Wellstead, 1991; Carroll, 1998; Anderson, 2002; Anderson et al., 2003; Milner & Ruta, 2009; Milner, 2018). However, in a small number of microsaurs, such as *Euryodus* and *Cardiocephalus*, a small number of trunk intercentra are retained, although they occupy a more superficial position relative to the pleurocentra than in other taxa, and are positioned more distally relative to the pleurocentra (Carroll & Gaskill, 1978).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (3 -> 1), Lepospondyli except *Westlothiana lizziae* (1 -> 0), *Acherontiscus caledoniae* (0 -> 2), *Casea broilii* (1

-> 0), *Vaughnitis smithae* (1 -> 0), *Procynosuchus delaharpeae* (1 -> 0). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (0 -> 1), Embolomeri + *Chroniosaurus dongusensis* (1 -> 2). DELTRAN: *Cardiocephalus sp.* + *Euryodus sp.* (0 -> 1), *Archeria crassidisca* (1 -> 2).

253. Capitular facets on posterior rim of mid trunk centra: absent (0); present (1).

Rea2003 (c.311), RC2007 (c.328), ML2019 (c.271).

Capitular facets on the posterior rim of the mid trunk vertebrae are found in a small number of lepospondyls including *Adelogyrinus* (Andrews & Carroll, 1991), *Brachydectes* (Wellstead, 1991), *Scincosaurus* (Milner & Ruta, 2009) and *Microbrachis* (Carroll & Gaskill, 1978).

Unambiguous: *Microbrachis pelikani* (0 -> 1). ACCTRAN: Adelospondyli (0 -> 1), Nectridea + Lysorophia (0 -> 1), Diplocaulidae (1 -> 0). DELTRAN: *Adelogyrinus simorhynchus* (0 -> 1), *Brachydectes newberryi* (0 -> 1), *Scincosaurus crassus* (0 -> 1).

254. Number of presacrals: <20 (0); 20-24 (1); 25-35 (2); >35 (3).

LR1997 (c.118), Lea1998 (c.114), A2001 (c.180), Hea2013 (c.145), Pea2017 (c.107).

The division of states across this taxa is consistent with the previous analyses of Anderson (2001), Huttenlocker et al. (2013) and Pardo et al. (2017) which include similar taxon samples to the taxa of focus in this analyses. Anderson (2001) suggested that above and below 35 as a top cut off was intended to capture general elongation while avoiding the issue of limbless ecomorph long branch attraction. Many synapsids are characterised by 27 vertebrae (Romer et al., 1940; Modesto, 1995; Campione & Reisz, 2010; Reisz & Fröbisch, 2014; Mann & Paterson, 2020), and a similar number, ranging from around 24 to 27 is widespread across crownward stem and early crown amniotes including in *Hylonomus* (26 vertebrae, Carroll, 1964), *Petrolacosaurus* (26 vertebrae, Reisz, 2918), *Captorhinus* (27 vertebrae, Fox & Bowman, 1966) and in reptiles (Now, 1972; 1974; Modesto et al., 2015). Lepospondyls show a great variety of presacral number, from fewer than 18 in *Diplocaulus* (Douthitt, 1917) to at least 69 in *Brachydectes* (Wellstead, 1991).

Unambiguous: *Microbrachis pelikani* (2 -> 3), *Casea broilii* (2 -> 1), *Diadectes abistus* (2 -> 1), Seymouriamorpha + *Gephyrostegus bohemicus* (2 -> 1), *Gerobatrachus hottoni* (1 -> 0), *Greererpeton burkemorani* (2 -> 3). ACCTRAN: Lepospondyli (2 -> 3), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (3to2), Nectridea + Lysorophia + Aïstopoda (2 -> 3), Nectridea (3 ->

0), *Scincosaurus crassus* (0 -> 1), *Pantylus cordatus* (3 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (2 -> 1), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (1 -> 2), Embolomeri (2 -> 3), Temnospondyli (2 -> 1). DELTRAN: Nectridea + Lysorophia + Aïstopoda (2 -> 3), Diplocaulidae (3 -> 0), *Scincosaurus crassus* (3 -> 1), *Cardiocephalus sp.* (2 -> 3), *Pantylus cordatus* (2 -> 1), *Westlothiana lizziae* (2 -> 3), *Youngina capensis* (2 -> 1), *Milleretta sp.* (2 -> 1), *Archeria crassidisca* (2 -> 3), Temnospondyli except *Edops craigi* (2 -> 1).

255. Number of sacral vertebrae: none (0); one (1); two (2); three (3).

LR1997 (c.119), Lea1998 (c.115), A2001 (c.145), Hea2013 (c.181), Pea2017 (c.143).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli (1 -> 2), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (2 -> 1), *Seymouria sanjuanensis* (1 -> 2). ACCTRAN: Adelospondyli + *Utaherpeton franklini* (1 -> 2), Synapsida except Araeoscelidia (2 -> 3), *Varanops brevirostris* (3to2), *Eocasea martini* (3to2), *Belebey vegrandis* + *Erpetonyx arsenaultorum* (2 -> 3). DELTRAN: *Utaherpeton franklini* (1 -> 2), *Aerosaurus wellesi* (2 -> 3), *Casea broilii* (2 -> 3), Edaphosauridae + Sphenacodontia (2 -> 3), *Erpetonyx arsenaultorum* (2 -> 3).

256. Accessory articulations above zygapophyses present in at least some trunk and caudal vertebrae: absent (0); present (1).

A2001 (c.112), Rea2003 (c.286), RC2007 (c.305), ML2019 (c.254), Cea2019 (c.218).

State 1 of this character describes interdigitating projections of neural arches dorsal to the zygapophyses. Such accessory articulations are present in nectrideans (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018) and the aïstopod *Oestocephalus* (Carroll, 1998).

Unambiguous: Nectridea (0 -> 1), *Oestocephalus sp.* (0 -> 1), *Youngina capensis* (0 -> 1).

257. Haemal arches: absent (0); present (1).

A2001 (c.123), Hea2013 (c.156), Pea2017 (c.118).

Heamal arches are observed to be absent in aïstopods (Carroll, 1998; Anderson, 2002) and araeoscelids (Langston & Reisz, 1981; Reisz, 1981) and the microsaur *Tuditanus* (Carroll & Gaskill, 1978). However, they are unknown in many other taxa as they are often lost during preservation.

Unambiguous: Aïstopoda (1 -> 0), *Tuditanus punctulatus* (1 -> 0), Araeoscelidia (1 -> 0).

258. Articulation of heamal arches to caudal centra: loosely articulated or sutured (0); fused (1); haemal arches absent (inapplicable).

A2001 (c.124), Rea2003 (c.289), RC2007 (c.308), ML2019 (c.257), Hea2013 (c.157), Pea2017 (c.119).

Haemal arches are fused to the caudal centra in nectrideans (Douthitt, 1917; Beerbower, 1963; Milner, 2018), a feature which is characteristic of the robustly ossified tails of the clade (Ruta et al., 2003). The condition is also observed here in *Doleserpeton* (Sigurdsen & Bolt, 2010), and is unknown in the basal nectridean *Scincosaurus* (Milner & Ruta, 2009).

ACCTRAN: Nectridea (0 -> 1), Temnospondyli (0 -> 1). DELTRAN: Diplocaulidae (0 -> 1), *Doleserpeton annectens* (0 -> 1).

259. Heamal arch size: shorter than neural spines on same vertebrae (0); equal or longer than neural spines on same vertebrae (1).

A2001 (c.125), Hea2013 (c.158), Pea2017 (c.120).

Small neural spines in the tail are noted in a small number of taxa, including the amniotes *Eocasea* (Reisz & Fröbisch, 2014) and *Archaeovenator* (Reisz & Dilkes, 2003) and the stem amniote *Caerorachis* (Ruta et al, 2001).

Unambiguous: *Eocasea martini* (1 -> 0), *Caerorachis bairdi* (1 -> 0). ACCTRAN: Reptilia (1 -> 0). DELTRAN: *Archaeovenator hamiltonensis* (1 -> 0).

260. Haemal arch shape: non-parallel (triangular) (0); parallel (rectangular) (1).

A2001 (c.127), Hea2013 (c.160), Pea2017 (c.122).

Parallel-sided, rectangularly shaped haemal arches are present in some lepospondyls, including *Brachydectes* (Pardo et al., 2016) and *Pantylus* (Carroll & Gaskill, 1978), and particularly in nectrideans where they form a robust, rectangular shape contributing to the well ossified nature of the

nectridean tail (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Milner, 2018). *Doleserpeton* (Sigurdsen & Bolt, 2010) is also noted to have haemal arches of this shape.

Unambiguous: Lepospondyli except *Westlothiana lizziae* (0 -> 1). ACCTRAN: *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (0 -> 1). DELTRAN: *Doleserpeton annectens* (0 -> 1).

261. Rib curvature: ribs straight (0); ribs curved in at least part of the trunk (1).

LR1997 (c.120), Rea2003 (c.280), RC2007 (c.297), Cea2016 (c.203), ML2019 (c.246), Cea2019 (c.203), Hea2013 (c.179), Pea2017 (c.141).

Straight ribs are present in the stem tetrapods Pederpes (Clack & Finney, 2005) and *Baphetes* (Beaumont, 1977) as well as a small number of in-group taxa, namely *Lethiscus* (Pardo et al., 2017), temnospondyls and *Gerobatrachus* (Milner & Sequeira, 1993; Anderson et al., 2008; Sigurdsen & Bolt, 2010; Arbez et al., 2022) and the seymouriamorphs *Discosauriscus* (UMZC2000.11; Klembara, 1997) and *Ariekanerpeton* (Klembara & Ruta, 2005).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (0 -> 1), *Lethiscus stocki* (1 -> 0), *Limnoscelis paludis* (1 -> 0), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (1 -> 0), *Greererpeton burkemorani* (0 -> 1), *Whatcheeria deltae* (0 -> 1).

262. Costal process at head of rib giving rib distinctive "k-shape": absent (0); present (1).

Cea2019 (c.237), Hea2013 (c.180), Pea2017 (c.142), A2001 (c.144), RC2007 (c.295).

This process, found in aïstopods (Carroll, 1998; Anderson, 2002; Pardo et al., 2017), gives the rib head a distinctive "k-shape".

Unambiguous: Aïstopoda (0 -> 1).

263. Length of longest trunk ribs: less than two and a half times the maximum height of neural arch plus centrum of largest trunk vertebrae (0); more than two and a half times this height (1).

Lea1998 (c.116), Cea2016 (c.204), ML2019 (c.250), Cea2019 (c.204), Hea2013 (c.178), Pea2017 (c.140).

This character applies to the longest ribs in the spine. Measured vertebrae and ribs were chosen from the same section of trunk.

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (0 -> 1), *Discosauriscus austriacus* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Brachydectes newberryi* (0 -> 1), *Diplocaulus sp.* + *Diploceraspis sp.* (0 -> 1). DELTRAN: *Keraterpeton galvani* (1 -> 0), *Scincosaurus crassus* (1 -> 0), Aïstopoda (1 -> 0).

264. Number of sacral rib pairs: none (0); one (1); two or more (2).

Novel

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (2 -> 1), *Brachydectes newberryi* (1 -> 0), *Eocasea martini* (2 -> 1), *Solenodonsaurus janenschi* (2 -> 1), *Ariekanerpeton sigalovi* (2 -> 1), *Gephyrostegus bohemicus* (2 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* (1 -> 2), Embolomeri + *Chroniosaurus dongusensis* (2 -> 0). DELTRAN: Tetrapoda (1 -> 2), *Archeria crassidisca* (2 -> 0).

265. Morphology of first sacral rib: subequal to or only slightly larger than the second sacral rib (0); greatly enlarged in comparison with the second sacral rib (1).

FB2020 (c228). Modified from Bea1995 (c.76), Mea2008 (c.76, c.77), RD2003 (c.48), Mea2006 (c.53), Rea2009 (c.63), B2012 (c.173), E2016 (c.372), Sea2018 (c.122).

A greatly enlarged first sacral rib is present in some seymouriamorphs (Berman et al., 2000) and diadectamorphs (Kennedy, 2010), as well as captorhinids (Fox & Bowman, 1966) and araeoscelids (Reisz et al., 1984). It is also present in some synapsids including varanopids (Langston & Reisz, 1981; Campione & Reisz, 2010), *Varanosaurus* (Bolt & Scott) & *Eocasea* (Reisz & Fröbisch, 2014) and is also present in *Youngina* (Gow, 1974). It is absent, however, in parareptiles (Modesto et al., 2015) and *Archaeovenator* (Reisz & Dilkes, 2003).

Unambiguous: *Casea broilii* (1 -> 0), Edaphosauridae + Sphenacodontia (1 -> 0). ACCTRAN: Reptilia (1 -> 0), *Youngina capensis* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* (1 -> 0). DELTRAN: *Archaeovenator hamiltonensis* (1 -> 0), *Erpetonyx arsenaultorum* (1 -> 0), *Paleothyris acadiana* (1 -> 0).

266. Number of pairs of caudal ribs: two or fewer (0); three (1); four (2); five or more (3).

A2001 (c.147), Hea2013 (c.183), Pea2017 (c.145).

Unambiguous: Nectridea + Lysorophia (3 -> 0), *Hyloplesion longicostatum* (3 -> 1), *Microbrachis pelikani* (3 -> 2), *Araeoscelis gracilis* (3 -> 0), *Seymouria sanjuanensis* (3 -> 2), *Caerorachis bairdi* (3to2). ACCTRAN: Reptilia (3to2), Captorhinidae (3 -> 1), *Diadectes abistus* + *Orobates pabsti* (3 -> 1), Embolomeri + *Chroniosaurus dongusensis* (3 -> 0), *Chroniosaurus dongusensis* (0 -> 1). DELTRAN: *Erpetonyx arsenaultorum* (3 -> 2), *Captorhinus aguti* (3 -> 1), *Orobates pabsti* (3 -> 1), *Archeria crassidisca* (3 -> 0), *Chroniosaurus dongusensis* (3 -> 1).

267. Gastralia: absent (0); present (1).

Modified from Cea2016 (c.211), Cea2019 (c.211).

Unambiguous: Aïstopoda (0 -> 1), *Araeoscelis gracilis* (1 -> 0), *Whatcheeria deltae* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0), Embolomeri + *Chroniosaurus dongusensis* (1 -> 0). DELTRAN: Lepospondyli (1 -> 0), *Eocasea martini* (1 -> 0), Diadectamorpha (1 -> 0), *Archeria crassidisca* (1 -> 0).

268. Tail length: shorter than trunk (0); at least as long as trunk (1).

Hea2013 (c.162), Pea2017 (c.124).

Some taxa, such as nectrideans and some aïstopods, are characterised by particularly long tails relative to the trunks.

Unambiguous: Nectridea (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1). ACCTRAN: *Lethiscus stocki* + *Phlegethontia linearis* (0 -> 1),

Ariekanerpeton sigalovi + *Discosauriscus austriacus* (0 -> 1). DELTRAN: *Phlegethontia* (0 -> 1), *Discosauriscus* (0 -> 1).

269. Separately ossified clavicle: absent (0); present (1).

LR1997 (c.125), Lea1998 (c.121).

A separately ossified clavicle is absent in aïstopods (Carroll, 1998; Anderson, 2002; Anderson et al., 2003), in which the entire appendicular skeleton is absent.

Unambiguous: Aïstopoda (1 -> 0).

270. Clavicles meet anteriorly: absent, clavicles are separate anteriorly (0); clavicles contact (1).

Rea2003 (c.228), RC2007 (c.239), Cea2016 (c.176), ML2019 (c.194), Cea2019 (c.176), A2001 (c.156), Hea2013 (c.195), Pea2017 (c.157).

In state 0, the anteroventral plates of the clavicles fail to contact each other and a strip of the ventral side of the interclavicle is interposed between them. On both sides of this strip, the impressions of the clavicular plates are discernible and the morphology of the interclavicle provides clues to the degree of separation between them. This condition is present in the stem tetrapod Pederpes (Clack & Finney, 2005), in *Adelogyrinus* (Andrews & Carroll, 1991), some temnospondyls (Sigurdsen & Bolt, 2010; Arbez et al., 2022), *Silvanerpeton* (UMZC T.1317; Ruta & Clack, 2006) and amniotes crownwards of lepospondyls (e.g. Romer et al., 1940; Olson et al., 1968; Reisz et al., 1984; Reisz & Dilkes, 2003). In state 1, however, the clavicles make a contact along the midline.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (1 -> 0), *Greererpeton burkemorani* (0 -> 1), *Whatcheeria deltae* (0 -> 1). ACCTRAN: Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Adelogyrinus simorhynchus* (1 -> 0).

271. Posterior stem on interclavicle: absent (0); present (1); interclavicle absent (inapplicable).

LR1997 (c.124), Lea1998 (c.120), Rea2003 (c.229). Modified from a division of RC2007 (c.240), A2001 (c.148), Pea2017 (c.354).

A posterior stem on the interclavicle, an anteroposteriorly elongate section of bone distinctly and clearly projecting posteriorly from the interclavicle plate, is present in the outgroup (Clack & Finney, 2005; Rawson et al., 2021). It is retained widely across the included taxa, but it is absent in some other stem tetrapods (Beaumont, 1977; Smithson, 1981), temnospondyls (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022) and some lepospondyls (Douthitt, 1917; Beerbower, 1963; Milner & Ruta, 2009; Andrews & Carroll, 1991; Carroll et al., 1991; Pardo et al., 2016; Clack et al., 2019).

Unambiguous: *Keraterpeton galvani* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0). DELTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), Temnospondyli except *Edops craigi* (1 -> 0), *Greererpeton burkemorani* (1 -> 0).

272. Interclavicle posterior stem morphology: tapering along most of length (0); parallel sided along most of length, tapering abruptly towards the posterior end (1); interclavicle absent or lacking posterior stem (inapplicable).

RC2007 (c.240), Cea2019 (c.197), ML2019 (c.195), Cea2016 (c.197), Rea2003 (c.230).

In *Whatcheeria*, the posterior stem of the interclavicle is approximately parallel sided, and tapers to a point only at the posterior end, forming a blunt, rounded tip. In *Silvanerpeton* (Ruta & Clack, 2006) and seymouriamorphs (Klembara, 1997; Berman et al., 2000) the posterior stem tapers along almost its entire length, resulting in a slight but clear triangular shape to the stem. A tapering posterior stem such as this is also present in microsaurs (Carroll & Gaskill, 1978), and some crownward stem and early crown amniotes such as *Paleothyris* (Carroll, 1969), *Aerosaurus* (Langston & Reisz, 1981), *Archaeovenator* (Reisz & Dilkes, 2003) and *Milleretta* (Gow, 1972).

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (0 -> 1), Reptilia (1 -> 0), *Paleothyris acadiana* (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Varanopidae (1 -> 0). DELTRAN: *Aerosaurus wellesi* (1 -> 0), *Whatcheeria deltae* (0 -> 1).

273. Interclavicle plate morphology anteroposterior length to transverse with ratio: longer than wide (0); wider than long (1).

Rea2003 (c.231), ML2019 (c.196), RC2007 (c.241).

Where a posterior stem of the interclavicle is present, the anteroposterior length of the interclavicle is measured from the anteriormost extremity to where the posterolateral margins are deflected medially towards the posterior stem. Seymouriamorphs (Berman et al., 2000; Klembara & Ruta, 2005), most microsaurs (Carroll & Gaskill, 1978), and stem and crown amniotes crownwards of lepospondyls possess a transversely wide interclavicle plate, including *Paleothyris* (Carroll, 1969), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015), *Araeoscelis* (Reisz et al., 1984), most synapsids (e.g. Romer et al., 1940; Olson et al., 1968; Mann & Paterson, 2020), *Archaeovenator* (Reisz & Dilkes, 2003), parareptiles (Gow, 1972; Modesto et al., 2015) and *Youngina* (Gow, 1974). An interclavicular plate that is anteroposteriorly longer than it is transversely wide, however, is present in non-microsaur lepospondyls such as adelospondyls (Andrews & Carroll, 1991; Clack et al., 2019) and nectrideans (Beerbower, 1963; Milner, 2018) and temnospondyls (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022).

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (0 -> 1), *Haptodus garnettensis* (1 -> 0), *Whatcheeria deltae* (0 -> 1). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* (1 -> 0). DELTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0).

274. Caudal part of interclavicle anteroposterior length relative to cranial part length: caudal part anteroposteriorly shorter (0); cranial part anteroposteriorly shorter (1).

Rea2003 (c.232), RC2007 (c.242), ML2019 (c.197).

The boundary between the two parts is measured along mediolateral line along which the interclavicle is at its greatest transverse width. Differing states exist across a variety of clades, with no large phylogenetic signal evident. For example, an anteroposteriorly longer caudal part is present in temnospondyls (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022) and seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005). An anteroposteriorly longer cranial part exists in taxa as disparate as *Greererpeton* (Smithson, 1981), *Silvanerpeton* (Ruta & Clack, 2006) and *Haptodus* (Laurin, 1993).

Unambiguous: Adelospondyli (1 -> 0), *Diploceraspis sp.* (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* (0 -> 1), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 0), Lepospondyli (0 -> 1), Synapsida (0 -> 1), *Haptodus garnettensis* (1 -> 0), Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1). DELTRAN: Lepospondyli except *Westlothiana lizziae* (0 -> 1), Caseasauria + *Echinerpeton intermedium* (0 -> 1), *Dimetrodon sp.* (0 -> 1), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (0 -> 1), *Chroniosaurus dongusensis* (0 -> 1), Temnospondyli except *Edops craigi* (0 -> 1).

275. Sternum, not mineralised (0); mineralised (1).

FB2020 (c.246), LR1995 (c.100).

This character was considered by Laurin & Reisz (1995) to be a synapomorphy of diapsid reptiles. In this taxon sample, it is noted only in *Araeoscelis* (Reisz et al, 1984) and *Youngina* (Gow, 1974). It is very difficult to score the absence of a sternum with any confidence as lack of preservation is not good evidence of the absence of mineralisation. As such, this character is scored as unknown in many taxa.

Unambiguous: *Araeoscelis gracilis* (0 -> 1). ACCTRAN: *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (0 -> 1). DELTRAN: *Youngina capensis* (0 -> 1).

276. Scapulocoracoid ossification: single ossification (0); divided into multiple ossifications (1).

LR1997 (c.131), Lea1998 (c.128), A2001 (c.159), Rea2003 (c.233), RC2007 (c.244), Cea2016 (c.210), ML2019 (c.199), Cea2019 (c.210), Hea2013 (c.198), Pea2017 (c.160).

In many disparate taxa from clades across the included taxa, including the stem tetrapod Pederpes (Clack & Finney, 2005) and crown amniotes *Varanops* (Campione & Reisz, 2010) and *Araeoscelis* (Reisz et al, 1984), the scapulocoracoid is fused into a single ossification with no trace of sutures.

Unambiguous: *Varanops brevirostris* (0 -> 1), *Araeoscelis gracilis* (0 -> 1), Seymouriamorpha (0 -> 1), *Pederpes finneyae* (0 -> 1). ACCTRAN: Diplocaulidae (0 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (0 -> 1). DELTRAN: *Diplocaulus sp.* (0 -> 1), *Milleretta sp.* (0 -> 1).

277. Supraglenoid foramen: absent (0); present (1).

A2001 (c.157), Rea2003 (c.235), RC2007 (c.246), ML2019 (c.201), Hea2013 (c.196), Pea2017 (c.158)

A distinct supraglenoid foramen is present in the outgroup (Clack & Finney, 2005; Rawson et al., 2021), temnospondyls (Sigurdsen & Bolt, 2010; Arbez et al., 2022), stem amniotes such as *Archeria* (Holmes, 1989), seymouriamorphs (Klembara, 1997; Berman et al., 2000) and diadectamorphs (Kennedy, 2010). Absence of a distinct glenoid foramen occurs sporadically in *Greererpeton* (Smithson, 1981) and a small number of crown amniotes including *Casea* (Olson et al., 1968), *Archaeovenator* (Reisz & Dilkes, 2003) and *Milleretta* (Gow, 1972).

Unambiguous: *Pantylus cordatus* (0 -> 1), *Procynosuchus delaharpeae* (1 -> 0), Reptilia (1 -> 0), *Greererpeton burkemorani* (1 -> 0). ACCTRAN: Lepospondyli (1 -> 0), Nectridea (0 -> 1), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* (1 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (1 -> 0), Diplocaulidae (0 -> 1), *Casea broilii* (1 -> 0).

278. Supraglenoid foramen location: posterior to the apex of the spuraglenoid buttress (0); located on or anterior to the apex of the buttress (1); supraglenoid foramen absent (inapplicable).

FB2020 (c240). Modified from B2012 (c.180), Rea1992 (c.82), Fea2011 (c.112) Sea2018 (c.129).

The plesiomorphic condition (state 0) in which the supraglenoid is located posterior to the dorsal apex of the supraglenoid buttress is present in stem amniote taxa, such as seymouriamorphs (Klembara, 1997; Berman et al., 2000), diadectamorphs (Kennedy, 2010) and captorhinomorphs (Fox & Bowman, 1966). The supraglenoid foramen is located anterior to the apex of the glenoid buttress (state 1) in sphenacodontids (Romer et al., 1940; Laurin, 1993), protorothyrids (Carroll, 1969), and araeoscelids (Reisz, 1981; Reisz et al., 1984).

Unambiguous: Synapsida (0 -> 1). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1), Edaphosauridae (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* (0 -> 1). DELTRAN: *Pantylus cordatus* (0 -> 1), *Edaphosaurus boanerges* (1 -> 0), *Paleothyris acadiana* (0 -> 1).

279. Number of coracoid foramina: none (0); one (1); two (2).

A2001 (c.158), Hea2013 (c.197), Pea2017 (c.159).

Most taxa included in this analyses possess a single coracoid foramen. A small number of taxa possess no coracoid foramina, such as *Edaphosaurus* (Modesto, 1995), *Aerosaurus* (Langston & Reisz, 1981), *Archaeovenator* (Reisz & Dilkes, 2003), *Brachydectes* (Pardo et al., 2016) and *Whatcheeria* (Rawson et al., 2021). Two foramina are present in *Greererpeton* (Smithson, 1981) and *Seymouria* (Berman et al., 2000).

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Asaphestera intermedia* (1 -> 2), *Aerosaurus wellesi* (1 -> 0), *Archaeovenator hamiltonensis* (1 -> 0), *Seymouria sanjuanensis* (1 -> 2). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), Edaphosauridae (1 -> 0), *Greererpeton burkemorani* (1 -> 2). DELTRAN: Tetrapoda (0 -> 1), *Edaphosaurus boanerges* (1 -> 0), *Greererpeton burkemorani* (0 -> 2).

280. Scapulocoracoid dorsal blade: transversely narrow (0); large, broad plate (1).

Pea2017 (c.360).

Lysorophian lepospondyls (Pardo et al., 2016) possess a distinctly transversely narrow scapulocoracoid blade, which is still present but highly reduced in ossification.

Unambiguous: *Brachydectes newberryi* (1 -> 0).

281. Number of coracoids: one (0); two (1).

FB2020 (c.244), Gea1988 (c.148), LR1995 (c.95), Mea2008 (c.85), B2012 (c.184), Sea2018 (c.133).

Stem amniotes such as seymouriamorphs (Klembara, 1997; Berman et al., 2000; Klembara & Ruta, 2005) and diadectamorphs (Kennedy, 2010) have a single ossified element in the position of the coracoid. Most early amniotes crownwards of diadectamorphs have two ossifications in the same position, thus regarded as two coracoids (Ford & Benson, 2020), such as captorhinids (Fox & Bowman, 1966; Reisz et al., 2015), *Araeoscelis* (Reisz et al., 1984), and synapsids (e.g. Romer et al., 1940; Bolt & Scott, 1995; Campione & Reisz, 2010). In many taxa the anterior and posterior ossifications of the coracoid fuse in mature specimens and the suture is lost. 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*. A single coracoid is also present in the reptiles *Youngina* (Gow, 1974) and *Milleretta* (Gow, 1972).

ACCTRAN: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), *Petrolacosaurus kansensis* (1 -> 0), Reptilia (1 -> 0). DELTRAN: Synapsida except Araeoscelidia (0 -> 1), *Araeoscelis gracilis* (0 -> 1), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (0 -> 1).

282. Separately ossified cleithrum: absent (0); present (1).

Hea2013 (c.193), Pea2017 (c.155).

Unambiguous: *Archaeovenator hamiltonensis* (1 -> 0). ACCTRAN: Aïstopoda (1 -> 0), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (1 -> 0). DELTRAN: *Lethiscus stocki* + *Phlegethontia linearis* (1 -> 0), Varanopidae (1 -> 0).

283. Cleithrum dorsal expansion: absent, cleithrum is simple rod without dorsal expansion (0); present (1).

LR1997 (c.127), Lea1998 (c.123), Hea2013 (c.192), Pea2017 (c.154).

Most stem tetrapod taxa that possess a cleithrum have a dorsal expansion (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021). A dorsal expansion is also observed in the temnospondyls *Balanerpeton* (Milner & Sequeira, 1993) and *Dendrerpeton* (Arbez et al., 2022), and in *Gerobatrachus* (Anderson et al., 2008), as well as the anthracosaur *Archeria* (Holmes, 1989), some nectrideans (Douthitt, 1917; Milner, 2018) and the microsaur *Tuditanus* (Carroll & Gaskill, 1978). In some other taxa, particularly seymouriamorphs (Klembara, 1997; Berman et al., 2000), diadectamorphs (Berman et al., 1998; 2004; Kennedy, 2010), and within lepospondyls (Carroll & Gaskill, 1978; Milner & Ruta, 2009), the cleithrum is still present but it has become reduced in size to a simple, rod-like shape.

Unambiguous: Diplocaulidae (0 -> 1), *Tuditanus punctulatus* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 0), Adelospondyli + *Utaherpeton franklini* (0 -> 1). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (1 -> 0), *Adelogyrinus simorhynchus* (0 -> 1).

284. Postbranchial laminae on cleithrum: absent (0); present (1).

Rea2003 (c.226), RC2007 (c.237), ML2019 (c.192), Cea2019 (c.242), Pea2017 (c.348), Lea1998 (c.124).

Postbrachial laminae are plesiomorphically present in a number of Carboniferous and Devonian stem tetrapods such as *Whatcheeria* (Rawson et al, 2021) and *Greererpeton* (Smithon, 1981). The lamina is a narrow sheet of bone projecting anteriorly from the anterior edge of the cleithrum.

Unambiguous: *Greererpeton burkemorani* (0 -> 1), *Whatcheeria deltae* (0 -> 1).

285. Humerus length along long axis relative to midtrunk vertebral length: shorter than four times the anteroposterior length of the anteroposteriorly longest midtrunk vertebra (0); equal to or longer than four times the length of the longest midtrunk vertebra (1).

A2001 (c.164), Rea2003 (c.249, c.255), RC2007 (c.260, c.266), Hea2013 (c.203), Pea2017 (c.164), ML2019 (c.219).

The cutoff for the states of this character are based on the states in the previous analyses referenced above. The longest measurement along the long axis of the humerus, from the proximal to the distal extremities, are taken. Almost all included taxa in this analysis have a humerus that is at least four times the length of the anteroposteriorly longest vertebra. However, many lepospondyls show a reduction in the relative length of the humerus, including *Westlothiana*, most microsaurs (Carroll & Gaskill, 1978; Carroll et al., 1991), *Brachydectes* (Wellstead, 1991)and nectrideans (Douthitt, 1917; Milner & Ruta, 2009; Milner, 2018). Some seymouriamorphs also show a relatively short humerus (Klembara, 1997; Klembara & Ruta, 2005).

Unambiguous: *Araeoscelis gracilis* (1 -> 0), *Diadectes abistus* (1 -> 0), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (1 -> 0), *Silvanerpeton miripedes* (1 -> 0), *Chroniosaurus dongusensis* (1 -> 0), *Pederpes finneyae* (1 -> 0). ACCTRAN: Lepospondyli (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (1 -> 0). DELTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* (1 -> 0), *Westlothiana lizziae* (1 -> 0).

286. Humerus length relative to maximum diameter of distal end: less than three times longer than maximum distal end width (0); more than three times longer than distal end width (1).

RC2007 (c.260).

The metric cut off point is selected following the source of this character, Ruta & Coates (2007), who describe a survey of humerus proportions in all taxa. State 1 describes a slender humerus, and is observed in *Doleserpeton* (Sigurdsen & Bolt, 2010) and *Gerobatrachus* (Anderson et al., 2008), *Paleothyris* (Carroll, 1969), araeoscelids (Reisz, 1981; Reisz et al., 1984), *Erpetonyx* (Modesto et al., 2015), *Brachydectes* (Pardo et al., 2016) and *Westlothiana*.

Unambiguous: *Brachydectes newberryi* (0 -> 1), *Cardiocephalus sp.* (0 -> 1), *Westlothiana lizziae* (0 -> 1), Araeoscelidia (0 -> 1). ACCTRAN: *Belebey vegrandis* + *Erpetonyx arsenaultorum* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* + *Dendrerpeton helogenes* (0 -> 1). DELTRAN: *Erpetonyx arsenaultorum* (0 -> 1), *Paleothyris acadiana* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (0 -> 1).

287. Portion of humeral shaft length along long axis proximal to entepicondyle relative to humeral head width: length of portion of shaft smaller than humeral head width (0); portion of shaft longer than humeral head width (1).

RC2007 (c.264), ML2019 (c.217).

The humeral head width is the maximum distance between the anterior and posterior margins in the plane of its dorsoventral flattening. The shaft length is the longest possible measurement of length along the long axis of the humerus. Stem tetrapods are possess short, robust humeri (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021). In most ingroup taxa, the humerus is relatively elongate and slender when compared to the outgroup, but is nonetheless sufficiently robust to be scored as state 1 for this character in a small number taxa. These include *Diadectes* (Berman et al, 1998; MNG 10553, 10554) and seymouriamorphs (Berman et al., 2000; Klembara & Ruta, 2005), which have robustly ossified skeletons.

Unambiguous: Tetrapoda (0 -> 1), *Keraterpeton galvani* (1 -> 0), *Diadectes abistus* (1 -> 0). ACCTRAN: Seymouriamorpha + *Gephyrostegus bohemicus* (1 -> 0), *Discosauriscus austriacus* (0 -> 1). DELTRAN: *Ariekanerpeton sigalovi* (1 -> 0), *Seymouria sanjuanensis* (1 -> 0).

288. Degree of torsion in humerus: less than 80 degrees (0); more than 80 degrees (1).

A2001 (c.161), Cea2016 (c.180), Cea2019 (c.180), Hea2013 (c.200), Pea2017 (c.161).

Stem tetrapods have a low degree of tension between the proximal and distal ends of the humerus (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021). This is measured by comparison of the orientation of the plane of the proximal and distal ends. A high degree of tension in the humerus is widely present across the ingroup taxa. However, many ingroup taxa have a lower degree of torsion, such as the stem amniotes *Archeria* (Holmes, 1989) or *Silvanerpeton* (Ruta & Clack, 2006), which have around 20 to 30 degrees of torsion, *Casea* (Olson et al., 1968), which lacks significant torsion, *Dimetrodon* (Romer et al., 1940), which has around 35 to 60 degrees of torsion, or diplocaulid nectrideans (Douthitt, 1917; Milner, 2018) which range from very little torsion to a maximum torsion of approximately 45 degrees.

Unambiguous: Sphenacodontidae (1 -> 0), Temnospondyli (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), Nectridea + Lysorophia + Aïstopoda (1 -> 0), *Scincosaurus crassus* (0 -> 1), Caseasauria (1 -> 0), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (1 -> 0). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (0 -> 1), *Brachydectes* nweberryi (1 -> 0), Diplocaulidae (1 -> 0), *Casea broilii* (1 -> 0), *Seymouria sanjuanensis* (0 -> 1).

289. Latissimus dorsi process position relative to ectepicondyle: aligned with ectepicondyle (0); offset anteriorly relative to ectepicondyle (1).

Rea2003 (c.238), RC2007 (c.249), Cea2016 (c.185), ML2019 (c.204), Cea2019 (c.185).

If the greater axis of the entepicondyle is extended proximally, it can be aligned with the latissimus dorsi process, in those taxa where both structures are readily indistinguishable.

ACCTRAN: Tetrapoda + *Baphetes sp.* (0 -> 1), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 0), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (0 -> 1), Edaphosauridae + Sphenacodontia (0 -> 1), Diadectamorpha (0 -> 1). DELTRAN: *Scincosaurus crassus* (0 -> 1), *Dimetrodon sp.* (0 -> 1), *Diadectes abistus* + *Orobates pabsti* (0 -> 1), *Archeria crassidisca* (0 -> 1), *Baphetes sp.* (0 -> 1).

290. Humerus shaft shape: straight (0); L-shaped (1).

Modified from Cea2016 (c.181), ML2019 (c.214).

Stem tetrapods possess a distinctly L-shaped humerus (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021), in which the distal end of the humerus is expanded largely asymmetrically relative to the position of the shaft. In almost all crown tetrapods, the proximal and distal ends are roughly symmetrically expanded relative to the shaft, so the main anteroposterior axis of the humerus passes roughly through the midpoint of both the proximal and distal ends. *Archeria* (Holmes, 1989) and *Silvanerpeton* (Ruta & Clack, 2006), however, do possess a stem-tetrapod like L-shaped humerus.

Unambiguous: Temnospondyli (1 -> 0); Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (1 -> 0).

291. Humerus shaft waisting: not waisted (0); waisted (1).

Rea2003 (c.247), RC2007 (c.258), Cea2016 (c.181), ML2019 (c.212, c.214).

A waisted humerus describes the condition in which the proximal and distal ends of the humerus are both expanded, and the shaft is narrowed, so that the anterior and posterior margins of the shaft are concave in shape. The distribution of states of this character is almost identical to that of ch.290, as humeri tend to be straight and waisted, or L-shaped and not waisted. However, the humerus of *Keraterpeton* (Milner, 2018), the humerus is both straight and not waisted, and as such these are retained as two separate characters.

Unambiguous: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (0 -> 1), *Keraterpeton galvani* (1 -> 0), Temnospondyli (0 -> 1).

292. Distinct supinator process on humerus: absent (0); present (1).

LR1997 (c.133), Lea1998 (c.131), A2001 (c.163), Rea2003 (c.239), RC2007 (c.250), Cea2016 (c.190), ML2019 (c.205), Cea2019 (c.190), Hea2013 (c.202), Pea2017 (c.163).

The supinator process us situated proximal to the ectepicondyle and projects from the main body of the distal end of the humers (Romer, 1956). The supinator attachment area may be represented by faint rugosities, or be a conspicuous blunt process detaching from the distal part of the anterior surface of the humerus. A supinator process is present in most included taxa but is absent in temnospondyls and *Gerobatrachus* (Milner & Sequeira, 1993; Anderson et al., 2008; Sigurdsen & Bolt, 2010; Arbez et al., 2022), most lepospondyls including *Brachydectes* (Pardo et al., 2016), nectrideans (Douthitt, 1917; Milner & Ruta, 2009; Milner, 2018) and microsaurs (Carroll & Gaskill, 1978), as well as

Discosauriscus (Klembara, 1997), *Hylonomus* (Carroll, 1964), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015), *Milleretta* (Gow, 1972) and *Youngina* (Gow, 1974).

Unambiguous: *Echinerpeton intermedium* (1 -> 0), *Discosauriscus austriacus* (1 -> 0), Temnospondyli except *Edops craigi* (1 -> 0), *Pederpes finneyae* (1 -> 0). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* (1 -> 0), *Westlothiana lizziae* (0 -> 1), Synapsida (0 -> 1), *Paleothyris acadiana* (0 -> 1), Diadectamorpha (0 -> 1). DELTRAN: Lepospondyli except *Westlothiana lizziae* (1 -> 0), Parareptilia (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 0), *Hylonomus lyelli* (1 -> 0), *Solenodonsaurus janenschi* (1 -> 0).

293. 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 (inapplicable).

FB2020 (c254). Modified from LR1995 (c.101), DR1997 (c.126), Rea2007 (c.101), SS2015 (c.125), Mea2015 (c.143), Mea2018 (c.72).

A supinator process that is confluent with the humeral shaft has previously been considered a character that unites diapsid reptiles (Laurin & Reisz, 1995; Ford & Benson, 2020) and as such as included in this analysis. It is observed in this analysis in araeoscelids (Reisz, 1981; Reisz et al., 1984) and parareptiles including *Youngina* (Gow, 1972; 1974).

ACCTRAN: Amniota (0 -> 1), Synapsida (1 -> 0). DELTRAN: Araeoscelidia (0 -> 1), Parareptilia (0 -> 1).

294. Distinct ectepicondyle on humerus: ectepicondyle is absent, low or indistinct (0); ectepicondyle is high and well defined (1).

LR1997 (c.134), Lea1998 (c.133), Rea2003 (c.244), RC2007 (c.255), Cea2016 (c.192), Cea2019 (c.192). Modified from a division of ML2019 (c.210).

The ectepicondyle is a ridge that runs on the extensor surface of the humerus and may resemble a thick keel, but varies in shape and size across various taxa. It is present in most taxa, although it is absent in *Brachydectes* (Wellstead, 1991) which has a very reduced appendicular skeleton, as well as dissorophoid temnospondyls (Sigurdsen & Bolt, 2010) and *Gerobatrachus* (Anderson et al., 2008).

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Echinerpeton intermedium* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). ACCTRAN: *Hylonomus lyelli* + *Paleothyris acadiana* (1 -> 0). DELTRAN: *Paleothyris acadiana* (1 -> 0).

295. Entepicondyle width relative to humeral length: less than half of humeral length (0); more than half of humeral length along long axis (1).

LR1997 (c.136), Lea1998 (c.135), Rea2003 (c.252), Cea2016 (c.195), RC2007 (c.263). Modified from Cea2019 (c.194, c.195).

The entepidondyle width is measured in the plane of the surface of the entepicondyle. The humerus length is the maximum distance between its proximal and distal extremities. A large entepicondyle relative to the humerus size is present in stem tetrapods (Beaumont, 1977; Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021) and *Silvanerpeton* (Ruta & Clack, 2006).

Unambiguous: Tetrapoda (1 -> 0), *Silvanerpeton miripedes* (0 -> 1).

296. Ectepicondylar foramen: absent (0); present (1).

RC2007 (c.254), LR1997 (c.137), Lea1998 (c.136), ML2019 (c.209), Rea2003 (c.242).

A foramen in the entepicondyle is present in *Edaphosaurus* (Modesto, 1995) and *Araeoscelis* (Reisz et al., 1984).

Unambiguous: *Araeoscelis gracilis* (0 -> 1). ACCTRAN: Edaphosauridae (0 -> 1). DELTRAN: *Edaphosaurus* boangerges (0 -> 1).

297. Entepicondylar foramen: absent (0); present (1).

LR1997 (c.138), Lea1998 (c.137), A2001 (c.160), Rea2003 (c.243), RC2007 (c.253), ML2019 (c.208), Hea2013 (c.199).

An entepicondylar foramen is present in almost all included taxa. It is absent in a variety of both lepospondyl (e.g. Carroll & Gaskill, 1978; Pardo et al., 2016; Milner, 2018) and temnospondyl (Romer & Witter, 1942; Sigurdsen & Bolt, 2010) taxa. It is also absent in *Orobates* (Berman et al., 2004).

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Keraterpeton galvani* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (1 -> 0), *Westlothiana lizziae* (1 -> 0), *Orobates pabsti* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0), *Edops craigi* (1 -> 0).

298. Olecranon process: unossified (0); ossified (1).

LR1997 (c.140), Lea1998 (c.139), A2001 (c.166), Rea2003 (c.258), RC2007 (c.271), ML2019 (c.224), Cea2019 (c.240), Hea2013 (c.205), Pea2017 (c.166), Hea2013 (c.142).

A hook like process projecting from the proximal end of the ulna is present in most stem tetrapods (Smithson, 1981; Rawson et al., 2021). It is also present in almost all of the ingroup taxa in this analysis. It is absent, however, in a number of disparate taxa in multiple separate clades, including the stem amniotes *Silvanerpeton* (Ruta & Clack, 2006) and *Solenodonsaurus* (Danto et al., 2012), the seymouriamorphs *Ariekanerpeton* and *Discosauriscus* (Klembara, 1997; Klembara & Ruta, 2005), *Diadectes* (Berman et al., 1998), the microsaurs *Microbrachis* and *Cardiocephalus* (Carroll & Gaskill, 1978), *Petrolacosaurus* (Reisz, 1981), and the synapsids *Varanops* (Campione & Reisz, 2010) and *Pantelosaurus* (Spindler, 2016).

Unambiguous: *Microbrachis pelikani* (1 -> 0), *Cardiocephalus sp.* (1 -> 0), *Varanops brevirostris* (1 -> 0), *Pantelosaurus saxonicus* (1 -> 0), *Petrolacosaurus kansensis* (1 -> 0), *Diadectes abistus* (1 -> 0), *Solenodonsaurus janenschi* (1 -> 0), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (1 -> 0), *Silvanerpeton miripedes* (1 -> 0), *Pederpes finneyae* (1 -> 0).

299. Length of ulna along long axis in relation to length of radius along long axis: ulna shorter than radius (0); ulna and radius equivalent in length (1); ulna longer than radius (2).

Lea1998 (c.140), Rea2003 (c.257), ML2019 (c.222), Cea2019 (c.202), RC2007 (c.269), Cea2016 (c.202), Pea2017 (c.357).

Unambiguous: *Brachydectes newberryi* (2 -> 0), *Microbrachis pelikani* (2 -> 1), *Youngina capensis* (2 -> 0), *Limnoscelis paludis* (2 -> 1), *Pederpes finneyae* (2 -> 1). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* (2 -> 1), Edaphosauridae (2 -> 0), Araeoscelidia (2 -> 1). DELTRAN: *Cardiocephalus sp.* + *Euryodus sp.* (2 -> 1), *Edaphosaurus boanerges* (2 -> 0), *Petrolacosaurus kansensis* (2 -> 1).

300. Ratio of radius length along long axis:humerus length along long axis: <0.5 (0); 0.51-0.7 (1); 0.71-1 (2).

A2001 (c.165), Hea2013 (c.204), Rea2003 (c.256), RC2007 (c.268), Pea2017 (c.165), ML2019 (c.221).

The division of states in this character is based on those in the previous analyses referenced above. In the outgroup and most other stem tetrapods, the radius is large in size to the humerus, reaching roughly one half to 70% of humerus length (Smithson, 1981; Clack & Finney, 2005; Rawson et al., 2021). In some clades, such as diplocaulid nectrideans (Douthitt, 1917; Milner, 2018) and some crown amniotes (e.g. Romer et al., 1940; Gow, 1972; 1974; Reisz, 1981), the radius is almost as long as the humerus. In many microsaurs, the radius is less than half of the length of the humerus (Carroll & Gaskill, 1978).

Unambiguous: Diplocaulidae (1 -> 2), *Hyloplesion longicostatum* (1 -> 0), Amniota (1 -> 2), *Ariekanerpeton sigalovi* (1 -> 2), *Gephyrostegus bohemicus* (1 -> 0), *Silvanerpeton miripedes* (1 -> 2), *Baphetes sp.* (1 -> 0). ACCTRAN: Adelospondyli + *Utaherpeton franklini* (1 -> 2), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (1 -> 0), *Euryodus sp.* (0 -> 1), Edaphosauridae (2 -> 1). DELTRAN: *Utaherpeton franklini* (1 -> 2), *Cardiocephalus sp.* (1 -> 0), *Pantylus cordatus* (1 -> 0), *Edaphosaurus boanerges* (2 -> 1).

301. Digits present on manus: absent (0); present (1); manus or entire forelimb absent (inapplicable).

Rea2003 (c.313), RC2007 (c.333).

This character does not vary among the ingroup taxa included in this analysis, and digits are only absent in *Eusthenopteron* and *Tiktaalik* amongst the taxa included here. The limbs are lost completely in aïstopods (Carroll, 1998; Anderson, 2002; Anderson et al., 2003) and adelospondyls (Andrews & Carroll, 1991) and they are therefore scored as inapplicable. However, it is retained to allow for future inclusion of deeper stem tetrapod taxa at the level of panderichthyiids in which the digits on the manus are absent (Ruta et al., 2003).

302. Number of digits on manus: three (0); four (1); five (2); manus or entire forelimb absent (inapplicable).

ML2019 (c.276), LR1997 (c.141), Lea1998 (c.141), A2001 (c.168), Cea2019 (c.226), Hea2013 (c.208), Pea2017 (c.169). Modified from Rea2003 (c.314, c.315, c.316), RC2007 (c.334, c.335, c.336).

Almost all taxa included in this analysis have five manual digits. Temnospondyls have four digits on the manus (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Arbez et al., 2022), as does *Diadectes* (Berman et al., 1998). Many lepospondyls have a lower number of manual digits as well, including *Brachydectes* (Pardo et al., 2016), *Scincosaurus* (Milner & Ruta, 2009) and non-microbracomorph microsaurs (Carroll & Gaskill, 1978) have four manual digits. Microbrachomorph microsaurs have just three digits on the hand (Carroll & Gaskill, 1978).

Unambiguous: *Diadectes abistus* (2 -> 1). ACCTRAN: Lepospondyli (2 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (1 -> 0), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (0 -> 1), Diplocaulidae (1 -> 2), Temnospondyli (2 -> 1). DELTRAN: Lepospondyli except *Westlothiana lizziae* (2 -> 1), *Keraterpeton galvani* (1 -> 2), *Hyloplesion longicostatum* (1 -> 0), *Microbrachis pelikani* (1 -> 0), Temnospondyli except *Edops craigi* (2 -> 1).

303. Ossification of carpals: completely unossified (0); at least partially ossified (1).

A2001 (c.167), Hea2013 (c.206), Pea2017 (c.167).

The outgroup taxa lack ossified carpals (Clack & Finney, 2005; Rawson et al., 2021), but almost all ingroup taxa have at least some ossified carpals. Some seymouriamorphs (Klembara, 1997; Klembara & Ruta, 2005), *Silvanerpeton* (Ruta & Clack, 2006; UMZC T.1317), *Brachydectes* (Wellstead, 1991), diplocaulid nectrideans (Douthitt, 1917; Milner, 2018) and a small number of microsaurs (Carroll & Gaskill, 1978; Carroll et al., 1991) have carpals that are completely unossified, despite have a well ossified limb and manus.

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Scincosaurus crassus* (0 -> 1), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (1 -> 0), *Silvanerpeton miripedes* (1 -> 0).

304. Shape of manual terminal phalanges: lacking distal ventral curvature (0); taper distally to a point and curve ventrally (1).

FB2020 (c266).

This character was a novel character in Ford & Benson (2020). It describes a keratinous claw, which sheaths the ungual (terminal) phalanx of the manus. In amniotes more derived than lepospondyls, the ungual tapers to a point distally with a distinct ventral curvature (state 1) (e.g. Romer et al., 1940; Fox & Bowman, 1966; Olson et al., 1968; Carroll, 1969; Gow, 1972; 1974; Campione & Reisz, 2010). In stem amniote taxa such as seymouriamorphs (Klembara, 1997; Berman et al., 2000; Klembara & Ruta, 2005) and diadectomorphs (Berman et al., 2004; Kennedy, 2010) the ungual phalanx is hoof-like.

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1).

305. Pelvis ossification: poorly ossified or absent (0); elements sutured (1); elements fused into single ossification (2).

A2001 (c.169), Cea2016 (c.212), Cea2019 (c.212), Hea2013 (c.209), Pea2017 (c.170), LR1997 (c.142), Lea1998 (c.142).

The pelvis is completely absent in adelogyrinids (Andrews & Carroll, 1991; Clack et al., 2019), and it is absent along with the whole appendicular skeleton in aïstopods (Carroll, 1998; Anderson, 2002; Anderson et al., 2003). Generally, across almost most taxa included in this analysis sutures are visible. However, a small number of disparate taxa show a fused pelvis with no sutures visible, such as *Doleserpeton* (Sigurdsen & Bolt, 2010), *Petrolacosaurus* (Reisz, 1981), *Captorhinus* (Fox & Bowman, 1966) and *Scincosaurus* (Milner & Ruta, 2009).

Unambiguous: Adelospondyli (1 -> 0), *Scincosaurus crassus* (1 -> 2), Aïstopoda (1 -> 0), *Petrolacosaurus kansensis* (1 -> 2), *Discosauriscus* sp. (1 -> 0), *Doleserpeton annectens* (1 -> 2), *Whatcheeria deltae* (1 -> 2). ACCTRAN: *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), Captorhinidae (1 -> 2). DELTRAN: *Hapsidopareion lepton* (1 -> 0), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (1 -> 2).

306. Number of pelvic obturator foramina: none (0); one (1); two or more (2).

RC2007 (c.279), ML2019 (c.230).

In the outgroup, in *Whatcheeria* (Rawson et al, 2021), three obturator foramina on the pelvis are observed. In almost all ingroup taxa, there is a single obturator foramen. However, a small number of taxa, primarily lepospondyls and amniotes stemwards of lepospondyls have no obturator foramina,

namely *Eocasea* (Reisz & Fröbisch, 2014), *Hylonomus* (Carroll, Carroll, 1964), *Scincosaurus* (Milner & Ruta, 2009) and *Brachydectes* (Pardo et al., 2016).

Unambiguous: *Eocasea martini* (1 -> 0), *Hylonomus lyelli* (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (2 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (1 -> 0). DELTRAN: Nectridea + Lysorophia (1 -> 0), *Whatcheeria deltae* (1 -> 2).

307. Dorsal iliac blade: single blade (0); bifurcated into two dorsal processes (1).

LR1997 (c.143), Lea1998 (c.143), A2001 (c.170), Rea2003 (c.259), RC2007 (c.272), Cea2016 (c.213), ML2019 (c.255), Cea2019 (c.213), Hea2013 (c.211), Pea2017 (c.172).

In the outgroup (Clack & Finney, 2005; Rawson et al., 2021) and the stem tetrapod *Baphetes* (Beaumont, 1977), the iliac blade is divide into two processes; a more dorsally projecting process, and a more posteriorly projecting process. This character is also present in a sporadic set of other taxa, including, *Gephyrostegus* (Klembara et al, 2014), the microsaur *Tuditanus* (Carroll & Gaskill, 1978), the diadectamorph *Orobates* (Berman et al., 2004) and the anthracosaur *Archeria* (Holmes, 1989).

Unambiguous: *Tuditanus punctulatus* (0 -> 1), *Asaphestera intermedia* (0 -> 1), *Gephyrostegus bohemicus* (0 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), *Diadectes abistus* + *Orobates pabsti* (0 -> 1), Embolomeri (0 -> 1), *Baphetes sp.* (0 -> 1). DELTRAN: Tetrapoda (1 -> 0), *Orobates pabsti* (0 -> 1), *Archeria crassidisca* (0 -> 1), *Greererpeton burkemorani* (1 -> 0).

308. Transverse pelvic ridge: absent (0); present (1).

Rea2003 (c.261), RC2007 (c.275), ML2019 (c.228).

State 1 of this character describes a transverse ridge sweeping from immediately dorsal to acetabulum, and running obliquely in posterodorsal direction. It is found in diadectamorphs (Berman et al., 2004; Kennedy, 2010) and seymouriamorphs (Klembara, 1997; Berman et al., 2000), as well as the microsaur *Tuditanus* (Carroll & Gaskill, 1978) and the temnospondyl *Dendrerpeton* (Arbez et al, 2022).

Unambiguous: *Tuditanus punctulatus* (0 -> 1), Diadectamorpha (0 -> 1), *Dendrerpeton helogenes* (0 -> 1). ACCTRAN: Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1). DELTRAN: Seymouriamorpha (0 -> 1).

309. Length of puboischiadic plate in relation to length of trunk vertebrae: three (0); four (1); five (2); six (3).

A2001 (c.171).

Unambiguous: *Brachydectes newberryi* (1 -> 0), Amniota (3 -> 1), Edaphosauridae + Sphenacodontia (1 -> 3), *Hylonomus lyelli* + *Paleothyris acadiana* (3to2), *Diadectes abistus* (3 -> 1), *Greererpeton burkemorani* (3 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (3 -> 1), *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Westlothiana lizziae* (1 -> 2), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota + Diadectamorpha (1to3), Varanopidae (1 -> 0). DELTRAN: Lepospondyli except *Westlothiana lizziae* (3 -> 1), *Hapsidopareion lepton* (1 -> 0), *Westlothiana lizziae* (3 -> 2), *Varanops brevirostris* (1 -> 0), Seymouriamorpha (3 -> 1).

310. Distinct internal trochanter: absent (0); present (1).

Rea2003 (c.265), RC2007 (c.280). Modified from a division of LR1997 (c.144), Lea1998 (c.144), A2001 (c.172), Hea2013 (c.212), Pea2017 (c.173).

The internal trochanter may appear as either a weakly developed indistinct area, or a projection, on the anterior surface of the femur (Romer, 1956). An internal trochanter is absent in the outgroup (Clack & Finney, 2005; Rawson et al., 2021) but is present in almost all ingroup taxa with the exception of *Keraterpeton* (Milner, 2018).

Unambiguous: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (0 -> 1). ACCTRAN: Diplocaulidae (1 -> 0). DELTRAN: *Keraterpeton galvani* (1 -> 0).

311. Internal trochanter separated from the general surface of the femur shaft by a distinct, trough-like space: absent (0); present (1).

Rea2003 (c.266), RC2007 (c.281), ML2019 (c.231). Modified from a division of LR1997 (c.144), Lea1998 (c.144).

In some taxa, the internal trochanter and the part of the shaft of the femur that is originates from are separated by a deeply notched web of bone. This condition is present in *Greererpeton* (Smithson, 1981), temnospondyls (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010; Holmes et al., 1998), *Casea* (Olson et al., 1968), *Paleothyris* (Carroll, 1969), captorhinids (Fox & Bowman, 1966; Reisz et al., 2015), diadectamorphs (Berman et al., 1998; 2004; Kennedy, 2010), seymouriamorphs (Klembara, 1997; Berman et al., 2000) and some lepospondyls including *Brachydectes* (Wellstead, 1991), *Scincosaurus* (Milner & Ruta, 2009) and some microsaurs (Carroll & Gaskill, 1978).

Unambiguous: Lepospondyli (1 -> 0), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (0 -> 1), Amniota (1 -> 0), *Hylonomus lyelli* (1 -> 0). ACCTRAN: Diplocaulidae (1 -> 0), Caseasauria + *Echinerpeton intermedium* (0 -> 1), Embolomeri + *Chroniosaurus dongusensis* (1 -> 0). DELTRAN: *Keraterpeton galvani* (1 -> 0), *Casea broilii* (0 -> 1), *Archeria crassidisca* (1 -> 0).

312. Maximum extent of femur adductor crest along length of femur: does not reach mid-shaft length (0); reaches mid-shaft length (1).

Rea2003 (c.268), RC2007 (c.283), ML2019 (c.233). Modified from a division of Lea1998 (c.146).

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Westlothiana lizziae* (1 -> 0), *Araeoscelis gracilis* (1 -> 0), *Seymouria sanjuanensis* (1 -> 0). ACCTRAN: Varanopidae (1 -> 0), Reptilia (1 -> 0), *Milleretta sp.* (0 -> 1). DELTRAN: *Varanops brevirostris* (1 -> 0), *Archaeovenator hamiltonensis* (1 -> 0), *Erpetonyx arsenaultorum* (1 -> 0).

313. Length of femur along long axis relative to maximum width of femoral head: length is less than 5 times the width (0); length is more than 5 times the width (1).

A2001 (c.173), Hea2013 (c.213), Pea2017 (c.174).

The femur is measured as the maximum length along the long axis. The femoral head width is measured as the maximum transverse width from the anterior to posterior extremity of the femoral head. A particularly slender femur (state 1) is present across a small number of taxa from many clades, including *Greererpeton* (Smithson, 1981), *Doleserpeton* (Sigurdsen & Bolt, 2010), *Paleothyris* (Carroll, 1969), *Youngina* (Gow, 1972), *Brachydectes* (Wellstead, 1991), Westlothaina and *Tuditanus* (Carroll & Gaskill, 1978).

Unambiguous: *Brachydectes newberryi* (0 -> 1), *Paleothyris acadiana* (0 -> 1), *Greererpeton burkemorani* (0 -> 1). ACCTRAN: Lepospondyli (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (1 -> 0), *Belebey vegrandis* + *Erpetonyx arsenaultorum* + *Youngina capensis* (0 -> 1), *Doleserpeton annectens* + *Gerobatrachus hottoni* (0 -> 1). DELTRAN: *Tuditanus punctulatus* (0 -> 1), *Westlothiana lizziae* (0 -> 1), *Youngina capensis* (0 -> 1), *Doleserpeton annectens* (0 -> 1).

314. Femur length along long axis relative to midtrunk vertebral anteroposterior length: shorter than four times the length of the longest midtrunk vertebra (0); equal to or longer than four times the length of the longest midtrunk vertebra (1).

A2001 (c.174), Rea2003 (c.269), RC2007 (c.284), ML2019 (c.234), Hea2013 (c.214), Pea2017 (c.175).

A “long” femur (state 1) is defined following the distribution of states in Anderson (2001). The femur is substantial in size across most taxa, but shows a smaller size across a variety of clades, particularly within lepospondyls, in which most microsaurs (Carroll & Gaskill, 1978) and nectrideans (Douthitt, 1917; Milner, 2018) possess a shorter humerus. A short humerus (state 0) is also present in *Discosauriscus* (Klembara, 1997), *Doleserpeton* (Sigurdsen & Bolt, 2010) and *Silvanerpeton* (Ruta & Clack, 2006).

Unambiguous: *Diadectes abistus* (1 -> 0), *Silvanerpeton miripedes* (1 -> 0), *Chroniosaurus dongusensis* (1 -> 0), *Pederpes finneyae* (1 -> 0). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (1 -> 0), *Hyloplesion longicostatum* (0 -> 1), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* (1 -> 0), *Ariekanerpeton sigalovi* + *Discosauriscus austriacus* (1 -> 0), *Doleserpeton annectens* + *Gerobatrachus hottoni* (1 -> 0). DELTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* (1 -> 0), *Microbrachis pelikani* (1 -> 0), *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* (1 -> 0), *Discosauriscus austriacus* (1 -> 0), *Doleserpeton annectens* (1 -> 0).

315. Distinct rugose area on fourth trochanter of femur: absent, fourth trochanter lacks rugose area or is absent (0); present (1).

Rea2003 (c.267), RC2007 (c.282), ML2019 (c.232).

A rough, textured area on the fourth trochanter is present in a small number of disparate taxa, namely *Greererpeton* (Smithson, 1981), *Dimetrodon* (Romer et al., 1940) and *Captorhinus* (Fox & Bowman, 1966).

Unambiguous: *Greererpeton burkemorani* (0 -> 1). ACCTRAN: Sphenacodontia (0 -> 1), Captorhinidae (0 -> 1). DELTRAN: *Dimetrodon sp.* (0 -> 1), *Captorhinus aguti* (0 -> 1).

316. 4th trochanter of the femur: absent (0); present as a raised ridge on the ventral surface of the femoral shaft (1).

FB2020 (c279), Gea1988 (c.193). Modified from N2011 (c.315, c.316), B2012 (c.228), E2016 (c.504).

Close to the distal margin of the intertrochanteric fossa the adductor ridge of the femur may increase in height to form a projection called the 4th trochanter (Romer 1956). A fourth trochanter is present in a number of disparate taxa including stem tetrapods such as *Whatcheeria* (Rawson et al., 2021) and *Greererpeton* (Smithson, 1981), the temnospondyl Dendererpeton (Holmes et al., 1998), the synapsids *Vaughnitis* (Brocklehurst et al., 2016) and *Varanops* (Campione & Reisz, 2010), *Captorhinus* (Fox & Bowman, 1966) and most diadectamorphs (Berman et al., 1998; Kennedy, 2010).

ACCTRAN: Tetrapoda + *Baphetes sp.* (1 -> 0), Caseasauria + *Echinerpeton intermedium* + *Vaughnitis smithae* + Varanopidae (0 -> 1), Caseasauria + *Echinerpeton intermedium* (1 -> 0), Captorhinidae (0 -> 1), Diadectamorpha (0 -> 1), *Orobates pabsti* (1 -> 0), Embolomeri + *Chroniosaurus dongusensis* (0 -> 1), *Dendrerpeton helogenes* (0 -> 1). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (1 -> 0), *Varanops brevirostris* (0 -> 1), *Vaughnitis smithae* (0 -> 1), *Captorhinus aguti* + *Opisthodontosaurus carrolli* (0 -> 1), *Diadectes abistus* (0 -> 1), *Limnoscelis paludis* (0 -> 1), *Caerorachis bairdi* (1 -> 0), *Doleserpeton annectens* (1 -> 0).

317. Rows of tubercles near posterior edge of fibula flexor surface: absent (0); present (1).

Rea2003 (c.273), RC2007 (c.290), ML2019 (c.239).

A row of tubercles near the posterior edge of the surface of the fibula is present in the outgroup, and in the stem tetrapod *Baphetes* (Beaumont, 1977).

ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), *Baphetes sp.* (0 -> 1). DELTRAN: Tetrapoda (1 -> 0), *Greererpeton burkemorani* (1 -> 0).

318. Fibula waisted: no (0); yes (1).

Rea2003 (c.271), RC2007 (c.288), ML2019 (c.237).

As in the case of other limb bones, a waisted shaft implies the presence of a distinct constriction of the shaft of the element, with expanded proximal and distal ends. Almost all included taxa possess a waisted fibula, but *Araeoscelis* (Reisz et al., 1984) and *Utaherpeton* (Carroll et al., 1991) lack a waisted fibula.

Unambiguous: *Araeoscelis gracilis* (1 -> 0). ACCTRAN: Adelospondyli + *Utaherpeton franklini* (1 -> 0). DELTRAN: *Utaherpeton franklini* (1 -> 0).

319. Flange along posterior edge of tibia: absent (0); present (1).

Rea2003 (c.270), RC2007 (c.287), ML2019 (c.236).

Unambiguous: Tetrapoda (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* (0 -> 1). ACCTRAN: *Diadectes abistus* + *Orobates pabsti* (0 -> 1). DELTRAN: *Orobates pabsti* (0 -> 1).

320. Number of proximal tarsal elements: two, with tibiale, intermedium and proximal centrale fused into astragalus (0); three (1); four or more (2).

Rea2003 (c.275), RC2007 (c.291), LR1997 (c.148), Lea1998 (c.148), A2001 (c.178), Hea2013 (c.218), Pea2017 (c.179), ML2019 (c.240).

The fusion of the proximal tarsal elements into an astragalus and calcaneum, with a total of two elements, is seen in all amniote taxa more derived than diadectamorphs (e.g. Romer et al., 1940; Fox & Bowman, 1966; Gow, 1972; 1974; Reisz, 1981). A similar condition is observed in the microsaur *Tuditanus* (Carroll & Gaskill, 1978). The stem tetrapod *Greererpeton* (Smithson, 1981) and the stem amnitoe *Gephyrostegus* (Klembara et al, 2014) are noted to have more than three ossified tarsals.

Unambiguous: *Hyloplesion longicostatum* (1 -> 2), *Tuditanus punctulatus* (1 -> 0), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (1 -> 0), *Gephyrostegus bohemicus* (1 -> 2).

ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri (2 -> 1). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (2 -> 1).

321. L-shaped proximal tarsal element: absent (0); present (1).

RC2007 (c.292), ML2019 (c.241), Cea2019 (c.232), Rea2003 (c.276).

In several stem and crown amniotes (e.g. Romer et al., 1940; Carroll, 1969; Gow, 1972; 1974; Reisz, 1981; Modesto, 1995; Reisz & Dilkes, 2003) the proximal tarsal element, either the intermedium or astragalus depending on the level of fusion, carries a shall proximal notch or evacuation. Sometimes this is pronounced, distinctly angular and confers a vaguely L-shaped outline to this tarsal element. This condition is also observed in *Silvanerpeton* (Ruta & Clack, 2006), *Diadectes* (Berman et al., 1998) and *Tuditanus* (Carroll & Gaskill, 1978).

Unambiguous: *Tuditanus punctulatus* (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1), *Eocasea martini* (1 -> 0), *Araeoscelis gracilis* (1 -> 0), *Diadectes abistus* (0 -> 1). ACCTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (0 -> 1), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha (1 -> 0). DELTRAN: *Silvanerpeton miripedes* (0 -> 1), *Caerorachis bairdi* (0 -> 1).

322. Number of distal tarsal elements: five or fewer (0); six (1).

Modified from RC2007 (c.293, c.294), A2001 (c.177), Rea2003 (c.277, c.278), ML2019 (c.242, c.243), Hea2013 (c.217), Pea2017 (c.178).

Unambiguous: Seymouriamorpha + *Gephyrostegus bohemicus* (0 -> 1). ACCTRAN: Lepospondyli except *Westlothiana lizziae* (0 -> 1), Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (1 -> 0), Araeoscelidia (0 -> 1), Captorhinidae (0 -> 1), Temnospondyli (0 -> 1). DELTRAN: *Tuditanus punctulatus* (0 -> 1), *Pantylus cordatus* (0 -> 1), *Petrolacosaurus kansensis* (0 -> 1), *Captorhinus aguti* (0 -> 1), *Balanerpeton woodi* (0 -> 1).

323. Number of phalanges in third pedal digit: three (0); four (1); more than four.

LR1997 (c.152), Lea1998 (c.152).

Most in-group taxa have four pedal digits. This includes stem and crown amniotes, including *Westlothiana* (e.g. Romer & Price, 1940; Carroll, 1969; Gow, 1974; Klembara, 1997; Ruta & Clack, 2006; Reisz & Fröbisch, 2014) and most lepospondyls (e.g. Carroll & Gaskill, 1978; Milner & Ruta, 2009; Milner, 2018). However, the lepospondyl *Brachydectes* (Wellstead, 1991) has three pedal digits, which accompanies its poorly ossified appendicular skeleton, as do Seymouria (Berman et al., 2000) and temnospondyls (Milner & Sequeira, 1993; Sigurdsen & Bolt, 2010).

Unambiguous: *Brachydectes newberryi* (1 -> 0), *Seymouria sanjuanensis* (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (1 -> 0), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (0 -> 1), *Whatcheeria deltae* (1 -> 2). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (0 -> 1), *Pederpes finneyae* (0 -> 1), *Whatcheeria deltae* (0 -> 2).

324. Number of phalanges in fourth pedal digit: three (0); four (1); five (2).

LR1997 (c.153), Lea1998 (c.153).

Unambiguous: *Microbrachis pelikani* (2 -> 1), *Seymouria sanjuanensis* (2 -> 1), *Doleserpeton annectens* (1 -> 0). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (2 -> 1), Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* + Embolomeri + *Caerorachis bairdi* (1 -> 2), Nectridea + Lysorophia + Aïstopoda (2 -> 0). DELTRAN: Amniota + Diadectamorpha + Lepospondyli + *Solenodonsaurus janenschi* + Seymouriamorpha + *Silvanerpeton miripedes* (1 -> 2), Nectridea + Lysorophia (2 -> 0), *Whatcheeria deltae* (1 -> 2).

325. Number of phalanges in fifth pedal digit: two (0); three (1); four (2); five (3).

LR1997 (c.154), Lea1998 (c.154).

Unambiguous: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* (2 -> 1), *Haptodus garnettensis* (2 -> 1). ACCTRAN: Tetrapoda + *Baphetes sp.* + *Greererpeton burkemorani* (3 -> 2), Nectridea + Lysorophia + Aïstopoda (1 -> 0), Diplocaulidae (0 -> 1), *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae (2 -> 1), Seymouriamorpha + *Gephyrostegus bohemicus* (2 -> 1), *Ariekanerpeton*

sigalovi (1 -> 2), *Gephyrostegus bohemicus* (1to3), Temnospondyli (2 -> 1). DELTRAN: *Brachydectes newberryi* (1 -> 0), *Scincosaurus crassus* (1 -> 0), *Paleothyris acadiana* (2 -> 1), *Discosauriscus austriacus* (2 -> 1), *Seymouria sanjuanensis* (2 -> 1), *Gephyrostegus bohemicus* (2 -> 3), Temnospondyli except *Edops craigi* (2 -> 1), *Whatcheeria deltae* (2 -> 3).

326. Tarsus, tibio-astragalar joint: flat (0); tibial ridge fits into astragalar groove (1); inapplicable, astragalus absent (inapplicable).

FB2020 (c284), Gea1988 (c.195), L1991 (c.J9), LR1995 (c.116), Rea2010 (c.107).

A complex tibio-astragular joint was indicated by Laurin & Reisz (1995) as a character that unites diapsid reptiles, which incorporated younginiforms and araeoscelids. In Ford & Benson (2020), where parareptiles are recovered as the sister clade to younginiforms and closer to the reptile crown than araeoscelids, state 1 of this character was described to have been independently acquired in araeoscelids and younginiforms, a result that concurs with the results in this analysis.

Unambiguous: Araeoscelidia (0 -> 1), *Youngina capensis* (0 -> 1).

327. Tarsus, number of centralia: two centralia present (0); only one centrale is present (1).

FB2020 (c291). Modified from DR1997 (c.158), M2004 (c.151), Eea2014 (c.214), Mea2015 (c.162).

Sphenacodontids and edaphosaurids are noted to have two centralia in the tarsus (Romer et al., 1940; Modesto, 1995; Ford & Benson, 2020).

Unambiguous: *Hylonomus lyelli* + *Paleothyris acadiana* + Captorhinidae + Amniota (0 -> 1). ACCTRAN: Nectridea + Lysorophia + Aïstopoda + Adelospondyli + *Utaherpeton franklini* + *Hyloplesion longicostatum* + *Microbrachis pelikani* + *Tuditanus punctulatus* (0 -> 1), Synapsida except Araeoscelidia (1 -> 0). DELTRAN: *Tuditanus punctulatus* (0 -> 1), Edaphosauridae + Sphenacodontia (1 -> 0).

328. Metatarsus, ratio of lengths of metatarsals I and IV: equal or greater than 0.42 (0); less than 0.42 (1).

FB2020 (c292). Modified from Eea2014 (c.216), D1998 (c.123), M2004 (c.173), MS2004 (c.123).

Sphenacodontids possess a short fourth metatarsal, which is less than 42% of the length of the first metatarsal (Romer et al., 1940; Laurin, 1993).

Unambiguous: Sphenacodontia (0 -> 1), *Seymouria sanjuanensis* (0 -> 1). ACCTRAN: *Cardiocephalus sp.* + *Euryodus sp.* + *Huskerpeton englehorni* + *Pantylus cordatus* + *Micraroter erythrogeois* + *Hapsidopareion lepton* + *Llistrofus pricei* + *Asaphestera intermedia* (0 -> 1), Parareptilia + *Youngina capensis* + *Orovenator mayorum* (0 -> 1). DELTRAN: *Pantylus cordatus* (0 -> 1), *Youngina capensis* (0 -> 1).

Appendix 3: Ages of included taxa

Taxon	Source	FAD	LAD	ICS stage(s)	Comments
Whatcheeria	Rawson et al, 2021. Lombard & Bolt, 1995	340	340	Viséan	Specimens from Hiemstra Quarry, Iowa (Rawson et al, 2021). The horizons are Viséan V3b in age, c. 340Ma (Lombard & Bolt, 1995).
Pederpes	Clack, 2002. Clack & Finney, 2005.	348	344	Tournasian/ Viséan	From a site in Auchenreoch Glen, north of Dumbarton, Scotland. The site is within the Ballagan Formation, part of the Cementstone Group (Clack & Finney, 2005). Clack (2002) gives a more specific age of 348-344Ma.
Greererpeton	Smithson, 1982. Busanus & Hoare, 1991.	333	323.2	Upper Viséan/ Serpukhovian	From the Bickett Shale of the Bluefield Formation, Mauch Chunk Group, at Greer Limestone Quarry, Monongalia County, West Virginia (Smithson, 1982). The Bickett Shale dates entirely within the North American Chesterian series (Busanus & Hoare, 1991).
Baphetes	Beaumont, 1977	318	308	Westphalian B to D	Material from multiple localities, listed in Beaumont (1977): Albion Mine, Stellarton, Nova Scotia. Part of the Stellarton Group, corresponds to Westphalian C. Earl David's Parrot Coal, Middle Coal Measures of East Fifeshire, Scotland, Westphalian B. Bradford Coal Group, Lancashire, Westphalian C. Upper Freeport Coal, Linton Diamond Mine, Ohio. Westphalian C. Specimens also known from Nyrany, Westphalian D.

Edops	Romer & Witter, 1942. Yang & Kominz, 1999.	298.9	280	Cisuralian	Known from the Moran and Pueblo formations of Texas (Romer & Witter, 1942). These sit after the start of the Permian, within the Wolfcampain North American Stage, but before the start of the Leonardian North American Stage (Yang & Kominz, 1999).
Balanerpeton	Milner & Sequeira, 1993	337	329	Late Viséan	From the East Kirkton Quarry (Milner & Sequeira, 1993). See Westlothiana for further discussion of age.
Dendrerpeton	Arbez et al, 2021.	319	318	Bashkirian	Division 4 of Joggins Formation, Joggins, Nova Scotia, Canada. Langsettian (= Westphalian A) (Arbez et al, 2021). See Hylonomus for discussion of age of Joggins material.
Doleserpeton	Sigurdsen & Bolt, 2010. MacDougall et al, 2016.	286.7	286.2	Artinskian	Numerus specimens from Lower Permian Fissure Fills of Richards Spur, Fort Sill, Oklahoma (Sigurdsen & Bolt, 2010). Precisely dated to the ages shown by MacDougall et al (2016).
Gerobatrachus	Anderson et al, 2008	280	270.6	Kungurian/ Roadian	From Don's Dump Fish Quarry, Clear Fork Group, Baylor County, Texas, Leonardian in age (Anderson et al, 2008).
Adelogyrinus	Andrews & Carroll, 1991	337.5	333	Viséan	Dunnet Shale, Upper Oil Shale Group. Part of the regional Asbian Stage of the Viséan (Andrews & Carroll, 1991)
Acherontiscus	Clack et al, 2019	326.4	326		The only known specimen lacks field or locality data. However, recent work has refined the age to the Pendleian, early Serpukhovian (Clack et al, 2019)
Anthracosaurus	Panchen, 1977	318	315.2	Late Bashkirian	From the Airdrie or Mushet's Black Band Ironstone, Lanarkshire, Scotland, which correlates with the

					Westphalian B (Panchen, 1977)
Archeria	Holmes, 1989	290.1	283.5	Artinskian	Geraldine bone beds, part of the Admiral Formation (Holmes, 1989). See Dimetrodon for further discussion of age of this formation.
Silvanerpeton	Ruta & Clack, 2006	337	329	Late Viséan	From the East Kirkton Quarry (Ruta & Clack, 2006) See Westlothiana for further discussion of age.
Gephyrostegus	Klembara et al, 2014. Ford & Benson, 2020.	311	307	Late Moscovian	Plattenkhole of Humboldt Mine, Nýřany, Plzeň-Manětín Basin, Czech Republic, Asturian (Klembara *et al.* 2014). The Asturian is equal to the Westphalian D, synchronous with the Late Moscovian (Ford and Benson, 2020).
Seymouria	Berman et al, 2000. Laurin, 1996. Stemmerik et al, 2000.	281	270.6	Kungurian	S. Baylorensis is from the Clear Fork Group, within the Leonardian period (Laurin, 1996). European specimens are from the Bromacker locality (Berman et al, 2000) which falls most reliably within the range of 281-276Ma (Stemmerik et al, 2000).
Ariekanerpeton	Klembara & Ruta, 2005	300	288		Sarytaypan locality, Leninabad province, Kuramin Ridge, Adrasman district, Tajikistan. These beds are most likely coeval with the Lower Rotliegende of central Europe but this is somewhat uncertain (Klembara & Ruta, 2005). The range of the Lower Rotliegende is given as 288-300Ma (Stemmerik et al, 2000).
Discosauriscus	Klembara, 1997. Werneburg & Schneider, 2006.	285.5	283		Materail from the Bacov Horizon, Boskovice Furrow, Letovice, Czech Republic (Klembara, 1997). The Discosauriscus bearing horizon of Letowice can

					be dated to 285.5-283Ma (Werneburg & Schneider, 2006).
Solenodonsaurus	Danto et al, 2012	311	307	Late Moscovian	Nyrany, Czech Republic (Danto et al, 2012). Nyrany specimens are from the Westphalian D, see Gephyrostegus.
Westlothiana	Smithson et al, 1994. Smith et al, 1993.	337	329	Late Viséan	From the East Kirkton Quarry (Smithson et al, 1994). The East Kirkton outcrop sits within the West-Lothian Oil-Shale Formation, which can be assigned to Asbian-Brigantian age (Smith et al, 1993).
Tuditanus	Carroll & Gaskill, 1978	309.5	308	Moscovian	From the Canneloid Shale underlying Upper Freeport Coal, Allegheny Group, from Diamond Mine, Linton, Ohio, equivalent to Westphalian D of Europe (Carroll & Gaskill, 1978)
Microbrachis	Carroll & Gaskill, 1978	311	307	Late Moscovian	From the Nyrany location, Czech Republic (Carroll & Gaskill, 1978). See Gephyrostegus for further discussion.
Hapsidopareion	Carroll & Gaskill, 1978	280	275	Kungurian	Hennessey Formation, part of the Arroyo Formation (Carroll & Gaskill, 1978). See Varanosaurus for further discussion of the age of the Arroyo Formation.
Llistrofus	Gee et al, 2019	295	290.1	Sakmarian	Karst infills, Dolese Brothers Limestone Quarry, Sakmarian (Gee et al, 2019)
Micraroter	Carroll & Gaskill, 1978	280	275	Kungurian	Hennessey Formation, same locality as Hapsidopareion (Carroll & Gaskill, 1978). See Hapsidopareion for further discussion.
Pantylus	Carroll & Gaskill, 1978	290.1	283.5	Artkinskian	Many specimens from Moran, Putnam, Belle Plains and Clyde Formations, all part of the Wichita Group (Carroll & Gaskill,

					1978). See Dimetrodon for further discussion of Wichita group.
Huskerpeton	Huttenlocker et al, 2013	298.9	295	Asselian	Mayer Farm locality, lower half of the Eskridge formation, Richardson County, Nebraska, Asselian (Huttenlocker et al, 2013)
Cardiocephalus	Carroll & Gaskill, 1978	280	275	Kungurian	There is some difficulty determining the exact horizons that specimens are from, but they are all presumed to come from the Arroyo Formation, Lower Clear Fork Group (Carroll & Gaskill, 1978). See Varanosaurus for further discussion of the age of the Arroyo formation.
Euryodus	Carroll & Gaskill, 1978	280	275	Kungurian	Arroyo Formation, Clear Fork Group (Carroll & Gaskill, 1978). See Varanosaurus.
Hyloplesion	Carroll & Gaskill, 1978	311	307	Moscovian	Known from two Middle Pennsylvanian localities, from near Pilzen, Nyrany and Tremosna, Czech Republic (Carroll & Gaskill, 1978).
Utaherpeton	Carroll et al, 1991	318.1	318.1	Bashkirian	Uppermost Manning Canyon Shale Formation. From a horizon between beds containing taxa from the North American Chesterian Age below, and Morrowan age taxa above. Thus it sits precisely at the Chesterian-Morrowan boundary, within the ICS Bashkirian stage (Carroll et al, 1991).
Carrolla	Maddin et al, 2011	295	283.5	Artinskian/Sakmarian	From the Petrol Formation, Wichita Group, Artinskian/Sakmarian (Maddin et al, 2011).

Brachydectes	Boardman II et al, 2009. Pardo et al, 2016.	298.9	292	Asselian/Sakmarian	Specimens from the Council Grove Group of Kansas, which includes the Eskridge Shale, representing the whole Asselian (Pardo et al, 2016), and the Spieser Shale, from the earliest Sakmarian
Lethiscus	Anderson et al, 2003	346.7	337	Viséan	From the Wardie Shales of Scotland, which are Viséan in age and predate the East Kirkton deposits (Anderson et al, 2003), which have an oldest age of 337Ma
Phlegethontia	Anderson, 2002	309.5	308	Moscovian	Linton, Jefferson County, Ohio. Canneloid shale below Upper Freeport Coal, Allegheny Group from Westphalian D (Anderson, 2002).
Oestocephalus	Carroll, 1998	309.5	308	Moscovian	From various locations including Nyrany, Linton, Ohio, and Mazon Creek, Illinois. These range from the Westphalian C/D boundary to the latest Westphalian D in age (Carroll, 1998)
Scincosaurus	Milner & Ruta, 2009	311	307	Moscovian	Nyrany 'Gaskohle', Czech Republic. See Gephyrostegus for age of Nyrany specimens.
Keraterpeton	Milner, 2018	319	318	Bashkirian	From the Jarrow Coal Formation, Kilkenny, Republic of Ireland, which is dated to the Langsettian (Westphalian A) in age
Diplocaulus	Harris et al, 2005	306.5	270.6	Kasimovian to Roadian	Diplocaulus is known from many localities and has an extremely broad temporal distribution, ranging, in the North American system, from the early Missourian to the end of the Leonardian (Harris et al, 2005).

Diploceraspis	Beerbower, 1963. Hembree & Bowen, 2017.	307	292.5	Kasimovian to Sakmarian	Most specimens are from the Dunkard group, but the earliest specimens come from a Conemaugh locality (Beerbower, 1963). The Dunkard group is from the Asselian and first half of the Sakmarian, while the Conemaugh group, which stretches back to the start of the Kasimovian (Hembree & Bowen, 2017)
Limnoscelis	Kennedy, 2010. Lucas et al, 2010.	305	280	Late Carboniferous-Early Permian	Specimens from El Cobre Canyon Formation, Cutler Group, El Cobre Canyon, Rio Arriba County, northern New Mexico (Kennedy, 2010). This is Virgilian-Wolfcampian age in North American Stratigraphy (Lucas et al, 2010)
Diadectes	Berman et al, 1998	281	276	Kungurian	Uppermost level of the Tambach Sandstone of the Tambach Formation (Berman et al, 1998). See Seymouria for geological details and age of this locality.
Orobates	Berman et al, 2004. Stemmerik et al, 2000.	281	276	Kungurian	Tambach formation, Upper Rotliegend, Bromacker quarry, see Seymouria for geological details of this locality.
Hylonomus	Carroll, 1964. Benton et al, 2015.	319	318	Bashkirian	All specimens come from the Joggins formation (Carroll, 1964). Carroll assigned this to the Westphalian B, but later work has suggested an age of Westphalian A (= Langsettian) for all Joggins material, with an age of 319-318Ma (Benton et al 2015).
Paleothyris	Carroll, 1969.	315.2	308	Moscovian	Morien Group, equivalent to the Westphalian C and D (Carroll, 1969).

Euconcordia	Reisz et al, 2016. Heckel & Clayton, 2006	303.7	298.9	Gzhelian	Calhoun Shale, Shawnee Group, Hamilton Quarry near Hamilton, Greenwood County, Kansas. Locality from the Virgilian series (Reisz et al, 2016) which correlates with the Gzhelian (Heckel & Clayton, 2006).
Captorhinus	Fox & Bowman, 1966.	295	283.5	Sakmarian/ Artinskian	Primarily known from Dolese Brothers Limestone Quarry Richards Spur, which is Sakmarian (see Llistrofus), and from Bally Mountain Cave Deposit, which is early Artinskian (Fox & Bowman, 1966).
Opisthodontosaurus	Reisz et al, 2015	289	289	Artinskian	From the Dolese Brothers Limestone Quarry, Oklahoma, and specifically dated to 289Ma (Reisz et al, 2015)
Archaeovenator	Reisz & Dilkes, 2003	303.7	298.9	Gzhelian	Calhoun Shale, Shawnee Group, Hamilton Quarry near Hamilton, Greenwood County, Kansas. (Reisz & Dilkes, 2003). See Euconcordia for discussion of age.
Orovenator	Ford & Benson, 2019	289	289	Artinskian	From Claystone Fissure Fills within the Dolese Brothers Limestone Quarry, Richards Spur, Oklahoma. The fills have been dated to 289Ma (Ford & Benson, 2019)
Milleretta	Gow, 1972. Gastaldo et al, 2017.	259.1	254.1	Wuchiapingian	Multiple South African localities, all outlined within Gow (1972). The ages of these localities fall within the Wuchiapingian (Gastaldo et al, 2017).
Youngina	Gow, 1975.	259.1	254.1	Wuchiapingian	Multiple South African localities, co-occuring with Milleretta, localities are outlined in Gow (1975). See Milleretta for discussion of age.

Erpetonyx	Modesto et al, 2015	303.7	298.9	Gzhelian	Cape Egmont, Prince Edward Island, Canada. The fossil is Gzhelian in age (Modesto et al, 2015).
Belebey	Reisz et al, 2007	273	268.8	Roadian	Bashkortostan and Orenburg regions, southern Russia. Upper Kaznian (Reisz et al, 2007). The Kaznian (European) overlaps with the Guadalupian, therefore the Upper Kaznian is roughly equivalent to the Roadian
Petrolacosaurus	Peabody, 1952	306.5	305	Kasimovian	Fossiliferous shales of the Garnett locality, Kansas. They are considered to be Missourian, which are part of the middle Upper Pennsylvanian, according to Peabody (1952). Missourian falls within the Kasimovian, which correlates with middle Upper Pennsylvanian stated by Peabody.
Araeoscelis	Reisz et al, 1984	290.1	283.5	Artkinskian	Collected from the Admiral Formation, Wichita Group. Other specimens have been collected from overlying strata but have not been included in the descriptions followed here, and there has been some debate as to whether they belong to the same species (Reisz et al, 1984). As such, the Admiral Formation, Whichita Group is used to denote the age, which is Artinskian (see Dimetrodon).
Varanosaurus	Berman et al, 1995. Johnnelson et al, 2013. Chaney & DeMichele, 2007.	280	275	Kungurian	Arroyo Formation, Clear Fork Group, Lower Permian, Baylor County, Texas (Berman et al, 1995). Biostragraphers agree the Clear Fork Group sits within the Leonardian stage of North America (Johhnelson et al,

					2013). The Arroyo Formation is in the lower part of the Clear Fork Group (Carroll & Gaskill, 1978) which sits comfortably within the first half of the Leonardian (Chaney & DiMichele, 2007).
Edaphosaurus	Modesto, 1995	290.1	283.5	Artinskian	Geraldine bone beds in Archer County, Texas, part of the Wichita Group (Modesto, 1995). See Dimetrodon for discussion of the age.
Ianthosaurus	Reisz & Berman, 1986	306.5	305	Kasimovian	Rock Lake Member, Stanton Formation, Lansing Group, Kansas, part of the Missourian series of the Upper Pennsylvanian (Reisz & Berman, 1986). See Haptodus or Petrolacosaurus for further explanation of age
Haptodus	Laurin, 1993	306.5	305	Kasimovian	All specimens collected from the Rock Lake Shale member, Lansing group, of North American Missourian age (Laurin, 1993).
Dimetrodon	Ford & Benson, 2020. Romer & Price, 1940.	290.1	283.5	Artinskian	Several taxa are known for Dimetrodon, but most of the data studied here comes from the earlier taxa described in Romer and Price (1940), which Ford and Benson (2020) note are from the Admiral Formation of the Wichita Group, Artinskian.
Pantelosaurus	Spindler, 2016.	296	296	Asselian	Top of the youngest hard coal seam of the Döhlen formation, Saxony, Germany. Asselian in age, matching dating of 296Ma, plus or minus 3Ma (Spindler, 2016)

Varanops	Campione & Reisz, 2010	289	270.6	Artinskian to Roadian	Cacops bonebed, Arroyo formation, Clear Fork Group, Baylor County Texas, Leonardian in age. Specimens also from Mud Hill Locality, Clear Fork Group, Taylor County Texas, Leonardian in age, and from Dolese Brothers Limestone Quarry, Oklahoma, Lower Permian (Campione & Reisz, 2010). See Varanosaurus for discussion of age of Clear Fork Group.
Aerosaurus	Langston & Reisz, 1981	298.9	295	Asselian	From the Abo/Cutler formation of Rio Arriba, New Mexico (Langston & Reisz, 1981). This is deemed to be Asselian in age (Ford & Benson, 2020).
Vaughnitis	Brocklehurst et al, 2016	298.9	290.1	Asselian/Sakmarian	An age of Asselian/Sakmarian is reasonable for the Placerville area, where Vaughnitis is from (Brocklehurst et al, 2016).
Eothyris	Reisz et al, 2009. Hotton III et al, 2002.	280	280	Artinskian to early Kungarian	From the Wichita group (Reisz et al, 2009) which corresponds to the earliest Leonardian (Hotton III et al, 2002).
Echinerpeton	Mann & Paterson, 2020.	309.5	308	Westphalian D (Asturian)	Morien Group, above the Lloyd Cove Coal Seam, equivalent to the Westphalian D of Europe (Mann & Paterson, 2020)
Eocasea	Reisz & Frobisch, 2014.	302	298.9	Late Gzhelian	From Hamilton Quarry, Greenwood County, Kansas, USA, part of the Virgilian series (Reisz & Frobisch, 2014) which places Eocasea in the Late Gzhelian (Ford & Benson, 2020; supplementary information).
Casea	LeBlanc & Reisz, 2014.	280	275	Kungurian	Cacops bonebed of Baylor County, Texas (LeBlanc & Reisz, 2014). The Cacops bonebeds are part of the Arroyo formation, see

					Varanosaurus for further discussion.
Procynosuchus	Kemp, 1979. Viglietti, 2020.	255.2	251.9	Wuchiapingian/Changhsingian	Collected from Madumabisa Mudstones of the Middle Luangwa Valley of Zambia, regarded equivalent to the Daptocephalus zone of the Beaufort beds of the South African Karoo (Kemp, 1979). The base of the Daptocephalus zone is 255.2Ma, and overlaps with the Changhsingian epoch (Viglietti, 2020).
Caerorachis	Ruta et al, 2001	326.4	326	Pendleian stage, Serpukhovian	Most likely Upper Limestone Coal Group; Loanhead No.2 Ironstone, which matches the lithology of the specimen, although the original locality is unknown (Ruta et al, 2001)
Chroniosaurus	Clack & Klembara, 2009	259.1	254.1	Wuchiapingian	Commonest in the Poldarsa formation, from the upper Tartian stage (Clack & Klembara, 2009) which corresponds with the Wuchiapingian
Asaphestera	Carroll & Gaskill, 1978	318	315.2	Late Bashkirian	Lower Pennsylvanian, equivalent to the Westphalian B of Europe (Carroll & Gaskill, 1978)
Acanthostega	Clack, 2002	372.2	358.9	Fammenian	From the middle Fammenian, Stage 2b
Tiktaalik	Daeschler, Shubin & Jenkins, 2006	382.7	372.2	Early Frasnian	From the Fram Formation of the early and middle Frasnian stage of the Late Devonian
Eusthenopteron	Downs et al., 2018	382.7	372.2	Early Frasnian	From the Fram Formation of the early and middle Frasnian stage of the Late Devonian
Archaeothyris	Reisz et al., 1972	311	307		Westphalian D

Appendix 4: Nexus file for Maximim Parsimony and time-calibrated Bayesian Phylogenetic Analyses

#NEXUS

BEGIN TAXA;

TITLE Taxa;

DIMENSIONS NTAX=77;

TAXLABELS

Acanthostega Acherontiscus Adelogyrinus Aerosaurus Anthracosaurus Araeoscelis Archaeothyris Archaeovenator Archeria Ariekanerpeton Asaphestera Balanerpeton Baphetes Belebey Brachydectes Caerorachis Captorhinus Cardiocephalus Carrolla Casea Chroniosaurus Dendrerpeton Diadectes Dimetrodon Diplocaulus Diploceraspis Discosauriscus Doleserpeton Echinerpeton Edaphosaurus Edops Eocasea Eothyris Erpetonyx Euconcordia Euryodus Eusthenopteron Gephyrostegus Gerobatrachus Greererpeton Hapsidopareion Haptodus Huskerpeton Hylonomus Hyloplesion Ianthosaurus Keraterpeton Lethiscus Limnoscelis Llistrofus Micraroter Microbrachis Milleretta Oestocephalus Opisthodontosaurus Orobates Orovenator Paleothyris Pantelosaurus Pantylus Pederpes Petrolacosaurus Phlegethontia Procynosuchus Scincosaurus Seymouria Silvanerpeton Solenodonsaurus Tiktaalik Tuditanus Utaherpeton Varanops Varanosaurus Vaughnitis Westlothiana Whatcheeria Youngina

;

END;

BEGIN CHARACTERS;

TITLE Character_Matrix;

DIMENSIONS NCHAR=328;

FORMAT DATATYPE = STANDARD RESPECTCASE GAP = - MISSING = ? SYMBOLS = " 0 1 2 3 4";

MATRIX

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Acherontiscus 02?1010?12120004200??0110?1100-00000010111000?111112-0-
010???00100001-000--?-10121011-1111000001001010--?100--1001?0-01?101-
???????????1?????000?000?????????10(0 1)010001010??0--01--
1011001?11?????10?11000110(0 1)0(0
1)11?1111?00?00?11?0001111??100?0????????02????????10??????1?0-
00?????????????????????????????0?????????????????????

Adelogyrinus 12?1011?1?13?00????000?10?0230-10000?1011?00000111112-0-
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?0?????????????????????????????010-11?????0???????????--????????11??????1(0
2)0?100113010011?????0?????????????1001????001??0101?001???????101???0?100-00?------
110----------0----------

Aerosaurus 3?1??0100-03100?(0 1)1??1111000120-000110101111011001 1???10-0(0
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2)11???20011?0001?00?0?????????????1????1?????101????????01??1?01100110001301000
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Anthracosaurus 32?0000112?000010100101 10?0110-000011101110001011 1100-0-
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00?02?110???1?0?01?0001?0010?00000-111100-01011??0--00--10?1100001??????0-
?1??0?1?0?001?111???10000111000 01???1?0?0?????????????????????????????????????
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Araeoscelis 22?0?000000 3100?101?10?00?0110-000010?01111001001101010-0(0
1)110101110010-101-??0100301100111001010100 1??1000110--110120-111011-
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001101010 1?011101-0-0?-00-0-1101??1?0??????2??1?1?2200---
?0?2100?10111?1111111000111?0111?0111?2121?110011?001-000000????110

Archaeothyris ???????10-??1???????01???10110-00011???1?1??11?0110?010-0(0
1)0100001?0011-0101??110030110-110?1101?1?01??101???0--10?1?0-
?11001???1?11??
????1?120?0?00???????-
??????????1?????????????12??1?1022?????1012??????1?????????????10101011010 01?????
??110?????01?????0????????

Archaeovenator 1?1???100-000000100100100 10120-000100111111 00?001101010-0(0
1)(0 1)10000110011-01000?0100301?0-111?0100?1001101000110--110110-
11?01?????????????0???????0001??0??1??????1110100 1?0100?10101011000000011??????1(
1 2)0?1000130100000?111??-?-0?-0?-0-1100001101001?120011102201 00?10??0???101010?00-
01?0--?????????????????1???110011?0010001?010122?10

Archeria 321000010-10000101 0?20?00?0330-000000001110001011 1100-0-
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00?1??????01011?110101011 01?1001211???1?1??1010101 0???????????

Ariekanerpeton 11?201010-010001(1 2)00100100?0120-00?100101111001011 1011-
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00?????????????????1??100?000120001100111111011?0100?100010010110101111??????1(0 2)??0-
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???1?1011?110?10100000 0?011010010221200 1?0?????????????????122???

Asaphestera 12?210(0 1)11?10100220?00100?0100-000100101111101111101 0-111(0 1)11101010001-1000--0-100(1 2)0110011110101010011011000 10--0--100-011011010??????????????0?2????????????0?????1???1?20?011??10??1-- 1????1?011????????????011200?0?1??????????????????110????????????????????0???0????10 1?????111011?00-210???1011?010?10010??1?????1??????1?????????????

Balanerpeton 122001010-010103200?10110??210-00100?1011110010111(0 1)10- 110101(0 1)000110001-000--?-1002011?0111?000100001001200001001001 00-011001- 10??2???????1???1??111011100000110011111020001107?11101--10111100020000101202 0-011(2 3)011111111??0110001110000110100100 1?0??12000?301101??00002-31?1?0- 01?0???1?110101??010-1001121111017?0031110 1??010201011-00

Baphetes 32?1000110?(0 1)0002200100110?0210-00100010111000101110 00- 11010100001(0 1)1101-000--?-1202121(0 1)011110(0 2)0100001001000001001001010011001- ?0?????10-01?10001?0002101000001100111110201010??0--01--1011110001????00-1?0- 0013011011???0?0?????????????1101?????????????????????????1???00????1?1????????????110 ?0001101?1101??01???1?10????????111?????????

Belebey 22?000000-01?000000?10100?0021(0 1)000?0??01111001001110010- 011101001?000-00100-10100001110?1101101010011010111 10--0--120- 311011??0?????????????1?1??0001?0010?00000-110000-11011100--0000100100011010????1(1 2)000-0?10010000001111----0--0--0- 100000010???1???????????1???????? ???????????????

Brachydectes 120221000-030004(0 1)00?-0110?0010-0000001011110 0?101101110- 0100----0------??10-??0--------10--?01101011010--1-00--0--10100111110001110120- 1112?02011100?1010000001-1-0000000000??0--000-0------0210?111011011-111000000-001111--- -0--0--0-101100-101000-0101000131010111010-0001?0--??00-00?1000110?010-0- 000011100100001101000?1?10?000-??

Caerorachis 222?0??1???(0 3)0????????0?11?0?310-00000?1?11??????111???-0- 01010?00110?01-000--?-1??2???????1????????00100???000100100101001110 1?00????10- ?????????0?01??101000110111111020107?10?101?1--10111100????????(0 1)0120- 1?1301101?11110?1000011100001??1001?1101????????102?0100?100??21?1?????????????? ????????????1??1???1?(0 1)0311(0 1)0100?1?21???????

Captorhinus 323000000-000010(0 1)1111110000100-000110101111101001101000- 01010000100000-000--1-10020(1 2)1101110010101001001201 1-0--1100-0-21100--001021010- 0112100200001?011000?000-111010011011001000110 0------ 1101011111111100113100100001110 1-0-01-00-0- 1101001?010???12001?102201?1?1012111?10111000101111???10110010- 1001121121121003111011101001 1???010

Cardiocephalus 021200110-020010100?101(0 1)0?0010-00000000111110(0 1)1111012- 0-1101011010011-1000--0-101(0 1)0110011000111010010 0(0 1)200010--0--100-011011- 10?????1????1?0002?0(0 1)0010012?00001-1110010010110?10?00--10(0 1)1001021??100112000- 00100000?0?????0????????????1001001?0?11??111?1?1?320????1012??0??????????0- ?1?1000111?010-1000010????110?1?????????????????

Carrolla 00?200100-0100101?01??100?1000- 0000001?1111101001101201001010 1?011101-?000--?-1(0 1)0101?00????0???0100110120?1?0-- 0--????00---?-??1011020-?112?02??01101?0100000?0-1110?00001010011110-- 11010?00211?10111(0 2)010-

0110000?00??????????????????10000011O?????????1?????????????????????????????????
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Chroniosaurus 32300001???0110220??0111000220-0000001011100O?001101000-
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2)02??10??10???1??101?01??????????0010?1(0 1)??1001???1???1?0??1??00???1??????????

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00130111101111111 1000111000-100100110???????????301?01???000??31?100-
01?01011?1101?11?010-100112111101101311101?1010?????????

Diadectes 322220000-0000021?011010000031000011??011100011111010-0-
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00????????????0?0??000??0000?00001-
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1)0102?111?11??111?00-101??1????-0?

Dimetrodon 322200100-000000011?02101111(1 2)0-000110101110011101100010-1(0
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2)1012101201000(0 1)1011101-0-00-00-0-
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0110010010122001

Diplocaulus 303101011010000020 0??0000?0110-000001100-1000000100-210-0(0
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1?1101101100010?010-10010221?0?1??????10000010?????????

Diploceraspis 20?10101100000000200??0000?0110-00000?100-0--0000100-210-
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00??

Discosauriscus 113001000-000001100000100?0110-000100101111100101111 10-0-
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Doleserpeton 012001000-01010220010011O??3-10010000101111011001101010-01110000110001-000--0-10(0 1)21111011000201000000011000-00--100100-211011-10100102110?1100??0011011100001011-10-001?000100?11111--10-----0011000010-?10-??1301111??110-????00?10?0001??????10?100-?10000301?01111000?????100-0??01?11?1??1111?010-000012111102100311110000010???00????

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Edops 32?200010-000?0320010?110??110-00?10011111000101110l0-0-11010000111101-000--0-12(0 1)(1 2)121?111?0000101000011000-0100100100-011001-10012001110111?00??0110101010?011111111102010110?10101--10111100020100l1??110-0?13011(0 1)1?111?1???000111000l1???00??0???????????3?????????0?????????????????????????011?01101000?21????????????1?????10?????????

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Eothyris 22?10000000310110l0?00?11?0110-000110001110010001101200-01011000110011-010110110130(0 1)11-11000100010010011101l0--100100-11101100?????????????0?????1????0?????????????????1????1??????01???????011??????0-1?0-0112?(0 1)0001?????0?????????????1101???

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Euryodus 02?200110-010010(0 1)00?10110?0010-000110001111100111101l-0-1(0 1)01011010011-1000--0-101(0 1)011(0 1)011(0 1)001110100100(0 1)200010--0--100-011111-1000100(1 2)0-01130021?0(0 1)0010(0 1)?(1 2)100011-1110110010110010101--

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Gephyrostegus 323000010-000002100110110?0210-000100101111001111111O-
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Gerobatrachus 0020010?0-0(0 1)01022001?0110??3(0 1)0-
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??????????????????011??1100001010-100010?00(0 1)110?11100--100100000????????0-
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Greererpeton 3212000111130003200?01110?0310-0010000011100011111110-0-
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001(2 3)011011101000110000111000100000100l000-020001303101010100l-310110-00?00-
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Hapsidopareion 02?220110-0100011001101O0?0100-000000101111001011101O-110(0
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Haptodus 322000100-0000001111111001l1(2 3)0-000110101110001101101010-1(0
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2)?0031(0 1)101?00100101?10?1

Huskerpeton 02?20(0 1)100-010010??0120100?01(1 2)0-000100001111101111101l-
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Hylonomus 122000000-?1000111??0010000210-000110101111001001101110-0(0
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1?????01???110?????????11??1?1?????1?10130?00??1???????0??1??0??01????????11?1?120
0?1102?01?1?101??31?1?11??0??????????1?11?010-?0?1???12??10002101O?0?011010????1?

Hyloplesion 021201100-01001110?01000?01(0 1)0-000010101111001111012-0-1(0 1)01000010001-0000--?-10110010011110101010011112011 10--0--100-011010-??????????????????2??01001111 0?00010-11101000001 00?10101--1000010010???10?1?????00120(0 1)0011?????0?????????????1?01???????0??01111000210 1???1011-100???????0???1????00???01??1???1201010(0 1)?0011111010001020 0121-?0

Ianthosaurus 321??0?00-??????????11?00?0120-000100?0??1100100?????10-00(0 1)110?011001??01010?1100301?0001???10??1???????0?????-??????????????1???1?????????????10?????1???1?0?1?0?000?????????????????????1???00?????????????????2??????101?????1????0???11???101??01?????????1???1100?????????????????????

Keraterpeton (0 1)21201011100000220000000?0010-000001101110001011 1012-0-010100001100000000--0-11121110011100001110010012011 10--0--1011011001-?0?????1????????2??0?0011000000001-100001(0 1)00(0 1)0???101000-0------021??????1?111001100000000?????????????????????1000??????11??1100000000?11111100??001111?0???1011?1100000?000-?0000221200??0010010000?10---101--0

Lethiscus 120000100-010002?00?00110?1110-000000101111000001101110-0100-000100000001111?110131000-01110(1 2)0001011011100110--101100-01?1010??0010001101100000000100100 1?01?001-1?1100100010 0?10000--1011000002000?000-010-011(2 3)010000100---1-0--0--0---1001001001???????100003??????010???1?0-----?------0----------0----------

Limnoscelis 32?220010-0000100111(0 1)0100?0120-00111100111000101111 10-0-01010000110101-000--0-11121110011100101010011111100110--110100-111011-001110020-10120002000011001010 0010-111010011(0 1)111?10101011001000000 10????10110-00110010011111100100001110000100100100100111?00?1102201??000121301 1?111?0010110100 1011?011010011111210110131110 1?101010?122-?0

Llistrofus 02?200110-0100?01?1100100?0100-000100101111101101101201101011110 11(0 1)01-10100-?0100101000011101000100100120001 0--0--100-011011000001001110?10?020100000?11?000010-1110010000110010101--100?0100?11?11011201100(0 1)110000?0??1100????0??0??0-101000010??00-0?11100????????101???

Micraroter 12?210110-020010100?10100?0100-000000101111100111101 1-111(0 1)010?101????-1000--??101????0-01??0100010011011000 10--0--100-011111-10??????1??????002??1(0 1)001?11??00010-10101100?0110?10?01--100101101 1??0111120?1001110(0 1)01101????01?0??0??1??0100(0 1)001?0?101?11111000??0?????0??????111?1???

Microbrachis 0(1 2)1001111111000020 0?101(0 1)0?01(0 1)0-000000101111101111101 2-110(0 1)01000010011-0000--?-10110110011110101010 01(0 1)1120?110--0--100-011011-10??2?-1????0???21?010010?12000010-11101000101 10?10101--100101001111?001112011001120000111111001000010000001101001?00001?021110013101???1011-2001?101???0-?1?1000011?010-?00?01110(0 1)0(0 1)?(0 1)??11?0000010???111??0

Milleretta 021010000-00000?00?100100?0120-00010??0111000?001111011111101000011000 1-010110110010110011100101010011111000110--110110-311011000?????1???0?2101??000110010000100-1100000110101?10?000110010001111011111(1 2)011000100100000011 10----0--0--0-

1000001?01000-02001110120????1012??1?101010010-110100101l?0101100102221?111?0?(0
1)10101000100l0???01?

Oestocephalus (0 1)20000110-03000?1?0000?10?0210-000000001111000111l012-0-
010??101?????0-01?01-01012?001-111(0 1)0100012110000000?10--101100-1110110????20-
2????0?0?00?0100100?????????1?100100101001?10110--???????00100?1?00-010-
0013010000?????0?????????????1001001101l?0-110100003?10---110??3100-----?------???----------
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Opisthodontosaurus 12???0000-0?0?1??0?11?100000(0 1)0-000110????11?01?111???-0-
0?0110?0100010-000-??-10021(1 2)1001100010101001?01?011?0--???0-0-?????--
?0?????????????????0001??11??00010-111010011010??101?1100------1101011111(1 2)1?0-
0110010000001110----0--0--
001?0?????0?????????????????????0??????101?10?0??1?1????011?010-
100112112l?2?0??11?0??1???0????????

Orobates 3212?0010-00001?010110100?00(2 3)10000110001111001011101O-
1?0101000010000?-000--0-100301100111?110101001111110110--1111010111011-
00?????????1??000???00?100?????001-11?000011001l?101?010100?000000?0?0??11110-
00110?0001??10?0????0?????0-
11?0001?0100101200?1102201010101l?10111?????????1?100101110110100012112101111311l
0100011100122-00

Orovenator 12?000000-00001010010110010(1 2)20-00010011111100(0
1)0011110111O1?10000??????-?1100??1003?1?001???0????1001?0100??10--
110?????????????????????0-?0???????000110111100010-
111010011010101010101100001011l1??1?11(1 2)02??0013010000001111----0--0--0-
100?101?0?????12??1???
??????????????????

Paleothyris 022000000-031001100?101(0 1)000210-000110101111101101101010-0(0
1)010100110000-000--1-100201100111001010100100120111O--111110-111011-
00????????????1????000?10110100000011101O-1101000100011O?0?????011?01?1112??0-
0013010000?????0?????????????1101????0110111200l?10220????101203??1?101?00111?????
111??0110000112112111100211111000110l0121010

Pantelosaurus 322??0100-0?0???(0 1)1??01?00?1110-
000110?0111???110110?01??1??1?00?110010?010?0?11003?2100?1??0(1
2)0101001101011l???-??????????????1?????????????????????????0?10?00010-
??????0110????10?????????????10??????1???1?1?120100O?????????????????111???????
?????2?????0230????1012??111?1???00???1110?1011?011?100102212111100З???01??01001?
??????

Pantylus 001201110-0100100011021(0 1)0?0000-000110001111111010111011-0-
1101(0 1)01010111-1000--0-111102100111001000100l000--0010--0--100-010011-100021020-
?11200200000010011000010-111001(0 1)010110?10101--0------
0101?100111111001100000l????11?1100000011111l?1101101l?1?0111100?1?010?1101???001
1101??01111?10010110010-100112011101?0??101?000??0101???-01

Pederpes 323000?1111(1 3)0002????00110001?0-001??01?111000101110l0-0-
00010?00100000-000--?-110??21?1111?000?0010100???000111100101001l-??????-
?????0??????010?0010???01111111111(0 2)0101???10?01--1011111001??0?100-??0-
??1201?01?111?????000000111010?0???00??????0??0?30210????0011-
?1?101?00?11??1?1100000(0 1)100-110101112001?1??0-10001111?---1??--?

Petrolacosaurus 221000000-031001111?0010000110-000110101111001101101010-01110100100010-111101010030100011111(0 1)10101001101100110--111110-1110110??1100120--1121022000011011110 0???1110100110100010001011001000111?0????111?0-00130100010?11?1????0??0??0-110100??011011120011102200---1012?3111????00?1?10100111?01111?0101212 1?2100?101010001001112211 0

Phlegethontia 020000100-010003200000-(0 1)0?0110-00010010110--00001011?10-0100-10011000-001101?110(0 1)(2 3)0010-00--?00?0-?----0--01-0--0--0-0--0----0??00?01?0-?11??000?0-0?100--?1?----0------00100??0--00--0------1110?01000-000-0?1101000-000----------0-------0111??110100003?00---110???110-----?------0----------0----------

Procynosuchus 322200100-03000010110210 1?11(1 2 3)10000110101110001(0 1)111000-0-0101-00?0-------1?10011203?210001?00(1 2)1101000001101??0--0--130-?11011000??-1?1??010?01(1 2)100002?0010000000-111000-11010011010000110000000 10??011112-012101101000?001110----0--0--0-110000?0010?110200?10023010 1?10120???1??????00-111???1010?01??10011??121?1?00?10?01?0010?????????

Scincosaurus 010201010-?10001100??0000??030-000?01101110 0?10111012-1101011?10101(0 1)0-1000--0-1?1??210011??0101110010010000 10--0--100-00-----?0?????1????????2??010011000000000-111010000100??10100--1000000021-??????????10?101?00??????????????????????????0?1???11000?011111??11001-001110-?1?0?????10000111010-100112111102000111????0010100100-?0

Seymouria 302221010-?0000010010110 0?0110-000100101111001011 1010-0-110101001100000000--?-100201100110010010000011012000110110010 0-010001-?0?01??20-?10200?2?11000011200011001111101110110?0--0110100101011 1?1???01?12?01?130100111111111?000111000011010011 0?01??0200?11012010??101212?01?10??011021010010010011010011212101101111001 0?010101011-01

Silvanerpeton 121000010-010002200?00110?0210-000000101111001011 1010-0-01111000110001-000--?-100211100111100010000000 1000-11101001010011001-????????1???????0??000100111?0?11001??11020100 1??0--01--???????001??????1(0 2)??0-0013010011?110-0?0?00?11?0001011?????????????????1?2?01???101???1?10101 0?????????0010?1010110102 21200??0?????00???1?110122-?0

Solenodonsaurus 32?000000-?0?????????1??00?0120-00010???11110011111?10-110101000011000?-000--?-11121110011?10001010010?1200010--100100-01?001-??????????????????????00???1??01??????????????120?00???10?10????1011-???1?1?10?0???1?1001011?010-10010?11?????????????????????????

Tiktaalik 32300001???00?????????????????????????110??100?11111??0-0-01011100101111-000--??1200021?011??0?00?0200011000000--100100-011101???11000011011-?0?????????????????????????0?????????????????????0????????0-1?10(0 1)011011?1111100011 1??000111011?0001?????????????????3??????0?0?????0-----00??11?111?000?100-11000020-?-2?1?????????????????????

Tuditanus 021210110-0000001001 10?00?01(0 1)0-000100101111101011 1010-1??(0 1)01100011001-0000--?-10110110011111010001000(0 1)01?01110--0--100-011011-??????????????????010?000??0?????????????01(0 1)100?10111--???????010??000?????10011??0?011?????0????????????1111??????1????1110002200---1012??0?1?101????????110001??01??100112111101111110111000 10011122?10

Utaherpeton 021000100-0?00?1????????0?0100-00000?1?11111101111011-0-0(0 1)0100001000???000--?-101??010-11??010?01?0100110?1???????100???????-

?0??????????????2??00????????????????111010???01???????1????????011??????1???0-
011?0?00?1?????0????????????1?11?????????????1002201O??101??3??1?0-
01??????????00?1?010-1001122110O1?0?????000?000---121??0

Varanops 32??00100-0?000011110211100120-00001??1111101l?01101010-
01010000110011-010000?101311?1011?00100?1001101000110--101120-
1100?11?????????????1??0?1?????????????????????????????1????1?????001??????001??????0-
0111001301000110111O1-0-00-00-0-
110100110?????1000111022010???0??131?1?1???01111110--
1011001101001022121111000100010l?10010???0??

Varanosaurus 32?000100000100011110110111320-000110101110001001111110-
1101100011001?-0101011110312100110(0 1)110101001001O1?110--111100-
111011000???????????1?1????00011001?000001-111000-1101?0?0--
0101100100000l??10111101l?10130100001O111?1-0-00-00-0-
1101001?0??????????1?????????????????1?????????0?????1?????????????????????????????????
?????????????0??

Vaughnitis ??????00??0?????01?????1????20-0001??????1???0?011????0-
01011000110011-01011?11013?111-11??0??0??001?01010110--1001?0-
1????1?????????????????????????????0?????001-??1001(0 1)11?????0--
?001?????0??11???????1(1 2)1?0-
001?0??0001011101?000000??10110100??0???????????0???0????101?????????????????????
??????????????????????????????10101?1????????????

Westlothiana 020020100-01000420O?01100?0200-000100001111101111101O-
1101111000100011-000--?-100001100111(0 1)020101001101200110--101100-111001-?????0??0-
??12?????000110111O?0110011101110001100100O1--10(0
1)10100111?????100?111?130000?11010-00?0-01-10-001110????1?0?0-
0?0???103?010?01012??0?1??????0????????0111?01101000121l?1?11002100110001010012 2-
??

Whatcheeria 32300010111300031101001100012O-00101000111000101111l0-0-
00010100100000-000--?-11010211111110001001010010000011110010100111O1-
???????0????00?0???0101000010001011101101001010O?0--01--101110100l????1?0-110-
111201101111100010000000111010000010l?0?0-000001302101010101l-
30?111110?01001?1111000(0 1)10101101121120022l?30-101?1111---223--0

Youngina 22(1 2)000000-?00000000?12100?0120-000100101110001001110011l0(0
1)(0 1)10100100110111100101003010001110010101001101201010--110110-211011000?????10-
00?210(0 1)20000110011000101-11100101?01100100000110000001111001111?????00?1(0
1)0100?????????????????????????????????????2??0?101211??010121???1?1?1?1??01?0---
1011?0101100100212111100(0 1)10?11?????010122111

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END;

Bayesian Phylogenetic Analysis nexus file begins on next page.

[Mr.Bayes script without the expanded outgroup, and with dates, for fossilised birth/death prior run. Run date 01.11.23]

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#NEXUS

Begin data;

	Dimensions ntax=74 nchar=328;

	Format datatype=standard gap=- missing=? [symbols = "0 1 2 3 4"];


	MATRIX

	Acherontiscus	02?2010?12120004200??0110?1100-0000001011100000?111112-0-
010???00100001-000--?-10121011-1111000001001010--?100--1001?0-01?101-
????????????1??????000?000?????????10(0 1)010001010??0--01--
1011001?11??????10?11000110(0 1)0(0
1)11?1111?00?00?11?0001111??100?0????????02????????10??????1?0-
00??????????????????????????????0????????????????????

	Adelogyrinus	12?1011?1?13?00????000?10?0230-10000?1011?00000111112-0-
0101?0?110000-?000--?-101?0111-11??020(0 1)01010001001110--0--0?1?011001-
?0??????????????????????????????010-11?????0???????????--????????11??????1(0
2)0?100113010011?????0?????????????1001?????001??0101?001???????101???0?100-00?------
110----------0----------

	Aerosaurus	3?1??0100-03100?(0 1)1??1111000120-000110101111011001 1???10-0(0
1)010000110111-010000010(0 1)30101011?10?00??001101010110--101120-1?????1?0??-??(1
2)11???20011?0001?00?0?????????????????1????1?????101????????01??1?01100110001301000
01?????1????????????1(0 1)00?0?10110??12001?10230????1012131?1?101?00110?10--
10?1?0110???112212111?00?10?010?0100?0???0??

	Anthracosaurus	32?0000112?000010100101l0?0110-000011101110001011 1100-0-
01010000110001-000-1--1102121101110?10100001011100011101001010011001-
00?02?110???1?0?01?0001?0010?00000-111100-01011??0--00--10?1100001??????0-
?1??0?1?0?001?111???10000111000011???1?0?0?????????????????????????????????????????
????????????????????????????????????????????

	Araeoscelis	22?0?000000310O?101?10?00?0110-000010?01111001001101010-0(0
1)110101110010-101-??0100301100111001010100l??1000110--110120-111011-
?????????????0????0001?00?????????1??0?0011010l?101?10110?10101101?0?1(0 1)12010-
0011010101?011101-0-0?-00-0-1101??1?0??????2??1?1?2200---
?0?2100?10111?11111111000111?0111?0111?2121?110011?001-000000????110

	Archaeothyris	???????10-??1???????01???10110-00011???1?1??11?0110?010-0(0
1)0100001?0011-0101??110030110-110?1101?1?01??101???0--10?1?0-
?11001?????????????????????????????????????????????????????????????????????????1?11??
????1?120?0?00???????-
??????????1?????????????12??1?1022?????1012??????1?????????????10101011010O1?????
??110?????01?????0????????

	Archaeovenator	1?1???100-000000100100100l0120-000100111111100?001101010-0(0
1)(0 1)10000110011-01000?0100301?0-111?0100?1001101000110--110110-
11?01?????????????0???????0001??0??1??????1110100l?0100?10101011000000011??????1(


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1 2)0?10001301000000?111??-?-0?-0?-0-1100001101001?120011102201 00?10??0???101010?00-01?0--?????????????????1???110011?0010001?010122?10

Archeria 321000010-10000101 0?20?00?0330-000000001110001011 1100-0-01010000110001-000----1101021111111010100001001100011101001010011001-0001100111011100 0?10000??0????????????????0?0110?0-??1--10?1100011??????10120-1113010010111001110001110000101111110?0011000012?31010??1010-00?1??????01011?1101010110 1?10011211???1?1??10101010???????????

Ariekanerpeton 11?201010-010001(1 2)00100100?0120-00?1001011110010111011-1111010000110000-000--?-10021110011000001000010012000110110010000110 11-00????????????????1??100?000120001100111110 11?0100?10001001011010111??????1(0 2)??0-0113010011111100??000111000011 01????0100??01000?10110????0011-???1?1011?110?10100000 0?0110100102212001?0??????????????????122???

Asaphestera 12?210(0 1)11?10100220 0?00100?0100-000100101111101111101 0-111(0 1)11101010001-1000--0-100(1 2)0110011110101010011011000 10--0--100-011011010????????????0?2????????????0?????1???1?20?011??10??1--1????1?011?????????????011200?0?1??????????????????????110????????????????????0???0????101?????111011?00-210???1011?010?10010??1?????1??????1?????????????

Balanerpeton 122001010-010103200?10110??210-00100?1011110010111(0 1)10-110101(0 1)000110001-000--?-1002011?0111?000100001001200001001001 00-011001-10??2????????1???1??111011100000110011111020001 10?11101--10111100020000101202 0-011(2 3)011111111??0110001110000110100100 1?0??12000?301101??00002-31?1?0-01?0???1?110101??010-100112111101?00311101??010201011-00

Baphetes 32?1000110?(0 1)0002200100110?0210-00100010111000101110 00-11010100001(0 1)1101-000--?-1202121(0 1)011110(0 2)0100001001000001001001010011001-?0?????10-01?10001?000210100000110011111020101 0??0--01--1011110001?????00-1?0-0013011011???0?0?????????????1101?????????????????????????1???00????1?1?????????????110?0001101?1101??01???1?10????????111?????????

Belebey 22?000000-01?000000?10100?0021(0 1)000?0??01111001001110010-011101001?000-00100-1010000111 0?1101101010011010111 10--0--120-311011??0?????????????1?1??0001?0010?00000-110000-11011100--0000100100011010????1(12)000-0?10010000001111----0--0--0-10000001 0???1??????????1????????????????????

Brachydectes 120221000-030004(0 1)00?-0110?0010-0000001011110 0?101101110-0100----0------??10-??0--------10--?01101011010--1-00--0--1010011111000111012 0-1112?02011100?1010000001-1-0000000000??0--000-0------0210?111011011-111000000-001111-----0--0--0-101100-101000-0101000131010111010-0001?0--??00-00?1000110?010-0-0000111001000011010 00?1?10?000-??

Caerorachis 222?0??1???(0 3)0???????0?11?0?310-00000?1?11?????111???-0-01010?00110?01-000--?-1??2???????1????????00100???000100100101001110 1?00?????-??????????0?01??1010001101111110201 0?10?101?1--10111100????????(0 1)0120-1?1301101?11110?1000011100001??1001?1101????????102?0100?100??21?1?????????????????????????????1??1???1?(0 1)0311(0 1)0100?1?21???????

Captorhinus 323000000-000010(0 1)1111110000100-000110101111101001101000-01010000100000-000--1-10020(1 2)1101110010101001001 2011-0--1100-0-21100--001021010-0112100200001?011000?000-111010011011001 0001100------1101011111111100113100100001 1101-0-01-00-0-

1101001?010???12001?102201?1?1012111?10111000101111???10110010-
1001121121121003111011101001 1???010

Cardiocephalus 021200110-020010100?101(0 1)0?0010-00000000111110(0 1)1111012-
0-1101011010011-1000--0-101(0 1)011001100011101001 00(0 1)200010--0--100-011011-
10?????1????1?0002?0(0 1)0010012?00001-11100100101 10?10?00--10(0
1)1001021??100112000-
00100000?0?????0?????????????1001001?0?11??111?1?1?320????1012??0?????????0-
?1?1000111?010-1000010????110?1??????????????????

Carrolla 00?200100-0100101?01??100?1000-
0000001?1111101001101201001010 1?011101-?000--?-1(0 1)0101?00????0???0100110120?1?0--
0--????00---?-??1011020-?112?02??01101?0100000?0-1110?00001010011110--
11010?00211?10111(0 2)010-
0110000?00?????????????????????10000011 0?????????1?????????????????????????????????????
??

Casea 321???010-0?101?001100110000?11000100?0111001 0?011???00-
0101?0001000?1-01011?01013?(0 1)000110001000 1?011?1110110--1101?0-
111011?001?0?1?10??1?0?01?0?0?10111?00010-
1?1010011011?1?10101101??????010111?011(1 2)1?0-0?1001000?1011101-0-00-00-0-
1101001?0???????00(0 1)100130101?101203?1101111000-?11???1010?0110100112212111100(1
2)11?01?0?10010??20?0

Chroniosaurus 32300001???0110220??0111000220-0000001011100 0?001101000-
00010000110001-000--?-11(0 1)2121111111110100011001100010--
1001010011001?????????????1??0???000110112000011-
111011?110111?10101101 0?1011001??????0-
?1????1?????????????????????????????????????10?1100?0?1(1
2)02??10??10???1??101?01??????????0010?1(0 1)??1001???1???1?0??1??00???1??????????

Dendrerpeton 323100010-000104200100110?0110-00100110111100 10111012-
1101010000110000-000--?-10111111011000001000010111000010 1100100-011001-10?00??10-
??11?0010?1101110000111011111102000110?11101--10111000021000000-010-
00130111101111111 1000111000-10010011 0????????????301?01???000??31?100-
01?01011?1101?11?010-1001121111011013111 01?1010?????????

Diadectes 322220000-0000021?011010000031000011??011100011111010-0-
01110000100001-000--0-1002011001110100101001111110100--1101010110010-
00?????????????0?0??000??0000?00001-
110000?1101?1?101?10010010000111010 1?111100011010001001111----0--0--0-
100000100110??1100011012 01?10101?????1??????0???1?1000001101101(0
1)0102?111?11??111?00-101??1????-0?

Dimetrodon 322200100-000000011?02101111(1 2)0-000110101110011101100010-1(0
1)011000110(0 1)11-0101001120302100 01??0(1 2)0101001101000110--111130-
110011100?1201110?1130111000 01?0010000000-1110100110100 10--0101110101001011111111(1
2)1012101201000(0 1)1011101-0-00-00-0-
1110001001?0111200211023 01?1?10120311101111001 1?11???10101011010011221211 1?00310?
0110010010122001

Diplocaulus 303101011010000020 0??0000?0110-000001100-1000000100-210-0(0
1)01000110110-0000--0-11(0 1)(2 3)0210111?00101110011112011 0--0--1011011101-
01?????1????1???2??0100110?00?0001-1110011001 00??10100--0------021??????12120-
0113110010?????0????????????1001001?0?110-1210100001111111011-001110--
1?1101101100010?010-10010221?0?1??????10000010?????????

Diploceraspis 20?10101100000000200??0000?0110-00000?100-0--0000100-210-0101010110000-0000--0-11120110011000101111100?1?1101110--0--1011011101-11?????1?????????2??010011000000001-11100110010???11100--?0?????021-?????12111001100000011?11101?000000100111100011011101-1?000000?111111????-???110-00???

Discosauriscus 113001000-0000011000001007?0110-000100101111001011111 0-0-100101001100000000--?-10011110011000001000010012001-1101101000-010001-00??????????1???1??1101(0 1)01120001100111110111011 0?0--01101011010110?11?1?11010-?113010011111111110001110000110100110100 1?0100011011010 1?0002-31111101 1?1101101000010001 0-100102112000101111100000 10???121??0

Doleserpeton 012001000-010102200100110??3-100100001011110110011010 10-01110000110001-000--0-10(0 1)2111101100020100000011000-00--100100-211011-10100102110?1100??001101110000101 1-10-001?000100?11111--10-----0011000010-?10-??1301111??110-????00?10?0001??????10?100-?10000301?01111000?????100-0??01?11?1??1111?010-000012111102100311110000 10???00????

Echinerpeton ???????00-0?????????11?1?10110-00000????????(0 1)0?011????0-0??1???01???1??01?????101??0??-???????????????1???000???0???121???10120100???????0?????????????????????????????2??101?2????????0????????1111?????1????1?11?010-0001???1?????????????????01??1???????

Edaphosaurus 320220100-0000011001111000(0 1)120-000100101111001001101 0(0 1)0-00011000110010-011100110(0 1)3110000100010101001001001110--111130-110011100???111??11?0?11?0001?0010?00010-111010011011011010110110101001010101 11(1 2)11100012010001101110 1-0-01-10-001111001011?0???200?1102301???10120?111?????00100111?01011?011010111011211110031010100010 01?122000

Edops 32?200010-000?0320010?110??110-00?100111110001011101 0-0-11010000111101-000--0-12(0 1)(1 2)121?111?0000101000011000-0100100100-011001-10012001110111?00??011010101 0?011111111102010110?10101--10111100020100 11??110-0?13011(0 1)1?111?1???000111000 01???00??0???????????3?????????0?????????????????????????011?01101000?21????????????1?????10?????????

Eocasea ???????100?31???????????????10-000?????????????????????????????0011??1?-?10?1??1??30?00?11??0??001???1?1???110--1101?0-1110110???1?????????????????1?????????0-?????????????????0????????????11?????????????0??0?1?220100?10111?0?????????????????????????????1???10001???01???1?00?122??0

Eothyris 22?10000000310110 10?00?11?0110-000110001110010001101200-01011000110011-010110110130(0 1)11-11000100010010011101 10--100100-11101100?????????????0?????1????0?????????????????1????1??????01???????011??????0-1?0-0112?(0 1)0001?????0?????????????1101???

Erpetonyx ?2?????00-0?????????????1??00120-00010???11110??0011???10-0??10?001?000?-?1?????1???????0?1???10?01????????1110--100120-3110?10?0??1?????????????0?01?00101??????1????01?011?????0?10???????????1?????1?

0?1?????????00?????????????????????1??000??01???????????0230????101202??1?1?1??????? ????1111?01??????022121?1?00?100(0 1)100010010???0??

Euconcordia 12?000010-03100010011(0 1)100?0120-0001?0?01111101101101000-0(0 1)?100-01?0000-000--1-10?20(1 2)10011???101?10011012011-0--1110-0-21101-- 0??????1?????1012?000110111?0?010-11101001101011010110???????1?1101?11????0-01110000?1?????????????????????1??1?? ??

Euryodus 02?200110-010010(0 1)00?10110?0010-000110001111100111101 2-0-1(0 1)01011010011-1000--0-101(0 1)011(0 1)011(0 1)001110100100(0 1)200010--0--100-011111-1000100(1 2)0-01130021?0(0 1)0010(0 1)?(1 2)100011-1110110010110010101-- 10110110111?11111200(0 1)-0(0 1)10110010111110110000001110110(0 1)00100?101?12111?10??0????10????0???1?1??0???1????0011?010-10001111?1?1???11???0?0010?????????

Gephyrostegus 323000010-000002100110110?0210-000100101111001111111 0-1011010000110000-000--?-10021110011110101000010012000111111001010011001-??????????????????1?000100010?001101111110011010??0--011010011100010 1????11020-10130100111111011111011100001111001101 00??0200?11?11?????1010????1?1????01????1001?????1??1?0112012 1?1?1??????1??0102?1123-??

Gerobatrachus 0020010?0-0(0 1)01022001?0110??3(0 1)0-01???010111???1001101010-011100001?00???000--0-10??1111?11001?010000000111???????100101001?001-??????????????????011??1100001010-100010?00(0 1)110?11100--100100000????????????0-??13?????????????????????????1???0???0????????1??3?0??????000?????1?????????????110 1111?010-00001??1???1?00?????????????????011??0

Greererpeton 3212000111130003200?01110?0310-00100000111000111111110-0-01010000101101-000----1212(0 1)211011110200010110010001 0(0 1)00100100-011101-1000200110-1110000?000210101010100111111012010100?10001--10(0 1)11010010000100-110-001(2 3)011011101000110000111000100000100100 0-020001303101010100 1-310110-00?00-21?111100001010110112111?1?110011111111011200012-00

Hapsidopareion 02?220110-010001100110100?0100-000000101111001011101 0-110(0 1)01111010001-00100-1010000100000--010001000101200010--0--100-010011010?????????????????2??000000112000000-111001001010 0?10101--100100001111?110112000-0011000000????00?????????????1010001?0?000-0?111000?2??????0?2??0??????????????????????????????????02???1?0?000?????????????????? ??

Haptodus 322000100-0000001111111001 11(2 3)0-000110101110001101101010-1(0 1)111000100010-0100001100312100010001000100011010 0011?0--111????21????100????1???011?0??1?0001?0010000010-11101001101001101011111101???0101?11111(1 2)10121012010001101 1101-?-0?-1?-00111100 1?0100??12001110??01?10101??3??10110000111?11???1011?011010011221211(1 2)?0031(0 1)101?00100101?10?1

Huskerpeton 02?20(0 1)100-010010??0120100?01(1 2)0-000100001111101111101 1-101101(0 1)1101(0 1)(0 1)11-1000--?-10110110011110101010 01(0 1)00--0010--0--100-011011-101011010-0112?022100000001(1 2)?000?1-1?10??00(0 1)010??101?0--???????011??????12000-0(0 1)110100001011 1?1-0-00-01-00100100000????????1??0??

Hylonomus 122000000-?1000111??0010000210-000110101111001001101110-0(0
1)010000110000-000--?-100201100111?0101?100100??01110--1?1110-111001-
??????????????????????000???10????010-1??010-
1?????01???110????????11??1?1?????1?10130?00??1???????0??1??0??01????????11?1?120
0?1102?01?1?101??31?1?11??0?????????1?11?010-?0?1???12??10002101?0?011010????1?

Hyloplesion 021201100-01001110?01000?01(0 1)0-000010101111001111012-0-1(0
1)01000010001-0000--?-101100100111101010100111120111 0--100-011010-
??????????????????2??01001111 0?00010-111010000100?10101--
100001001 0???10?1?????00120(0
1)0011?????0?????????????1?01???????0??01111000 2101???1011-
100???????0???1????00???01??1???1201010(0 1)?0011111 0100010200121-?0

Ianthosaurus 321??0?00-??????????11?00?0120-000100?0??1100100?????10-00(0
1)110?011001??01010?1100301?0001???10??1???????0?????-
??????????????1???1???????????????10?
?????1???1?0?1?0?000?????????????????????1???00?????????????????2??????101?????1????
??0???11???101??01?????????1???1100?????????????????????

Keraterpeton (0 1)21201011100000220000000?0010-000001101110001011 1012-0-
010100001100000000--0-111211100111000011100100120111 0--0--1011011001-
?0??????1????????2??0?0011000000001-100001(0 1)00(0 1)0???101000-0------
021??????1?1110011000000??????????????????1000??????11??1100000000?11111100??0011
11?0???1011?1100000?000-?0000221200??0010010000?10---101--0

Lethiscus 120000100-010002?00?00110?1110-000000101111000001101110-0100-
000100000001111?110131000-01110(1 2)0001011011100110--101100-
01?1010??0010001101100000001001001?01?001-1?11001000100?10000--1011000002000?000-
010-011(2 3)010000100---1-0--0--0---100100100 1???????100003??????010???1?0-----?------0-------
----------0----------

Limnoscelis 32?220010-0000100111(0 1)0100?0120-00111100111000101111 10-0-
01010000110101-000--0-111211100111001010100111 1100110--110100-111011-001110020-
101200020000110010100010-111010011(0 1)111?101010110010000010????10110-
00110010011111100100001110000100100100100111?00?1102201??000121301 1?111?0010110100
1011?011010011111210110131110 1?101010?122-?0

Llistrofus 02?200110-0100?01?1100100?0100-
000100101111101101101201101011110 11(0 1)01-10100-?0100101000011101000100100120001 0--
0--100-011011000001001110?10?020100000?11?000010-111001000011001 0101--
100?0100?11?11011201100(0 1)110000?0??1100????0??0??0-101000010??00-
0?11100????????101???
??

Micraroter 12?210110-020010100?10100?0100-000000101111100111101 1-111(0
1)010?101????-1000--??101????0-01??0100010011011000 10--0--100-011111-
10??????1??????002??1(0 1)001?11??00010-10101100?0110?10?01--
100101101 1??0111120?1001110(0 1)01101????01?0??0??1??0100(0
1)001?0?101?11111000??0?????0??????111?1???
?????????????

Microbrachis 0(1 2)1001111111000020 0?101(0 1)0?01(0 1)0-
000000101111101111101 2-110(0 1)01000010011-0000--?-101101100111101010100 1(0
1)1120?110--0--100-011011-10??2?-1????0???21?010010?12000010-111010001011 0?10101--
100101001111?001112011001120000111111001000010000001101001?00001?021110013101???10
11-2001?101???0-?1?1000011?010-?00?01110(0 1)0(0 1)?(0 1)??11?0000010???111??0

Milleretta 021010000-00000?00?100100?0120-
00010??0111000?00111101111101000011000 1-0101101100101100111001010100111100011 0--
110110-311011000?????1???0?2101??000110010000100-
1100000110101?10?000110010001111011111(1 2)0110001001000000111 0----0--0--0-
1000001?01000-020011101 20????1012??1?101010010-110100101 1?0101100102 21?111?0?(0
1)10101000100 10???01?

Oestocephalus (0 1)20000110-03000?1?0000?10?0210-000000001111000111101 2-0-
010??101?????0-01?01-01012?001-111(0 1)0100012110000000?10--101100-1110110????20-
2????0?0?00?0100100?????????1?100100101 00?10110--???????00100?1?00-010-
0013010000?????0????????????????100100111011?0-110100003?10---110??3100-----?------???----------
----------0----------

Opisthodontosaurus 12???0000-0?0?1??0?11?100000(0 1)0-000110????11?01?111???-0-
0?0110?0100010-000-??-10021(1 2)1001100010101001?01?011?0--???0-0-?????--
?0??????????????????0001??11??00010-111010011010??101?1100------1101011111(1 2)1?0-
0110010000001110----0--0--
001?0?????0?????????????????????????0??????101?10?0??1?1????011?010-
100112112 1?2?0??11?0??1???0????????

Orobates 3212?0010-00001?010110100?00(2 3)1000011000111100101110 10-
1?0101000010000?-000--0-100301100111?110101001111110110--1111010111011-
00?????????1??000???00?100?????001-11?000011001 1?101?010100?000000?0?0??11110-
00110?0001??10?0????0?????0-
11?0001?0100101200?1102201010101 2?10111?????????1?1001011101101000121121011113111
0100011100122-00

Orovenator 12?000000-00001010010110010(1 2)20-00010011111100(0
1)0011110111 01?10000??????-?1100??1003?1?001???0????1001?0100??10--
110?????????????????????0-?0????????000110111100010-
1110100110101010101011000010111 1??1?11(1 2)02??0013010000000111 1----0--0--0-
100?101?0?????12??1???
??????????????

Paleothyris 022000000-031001100?101(0 1)000210-000110101111101101101010-0(0
1)010100110000-000--1-100201100111001010100100120 1110--111110-111011-
00????????????1????000?10110100000011101 0-1101000100011 0?0?????011?01?1112??0-
0013010000?????0?????????????1101????0110111200 1?10220????101203??1?101?00111?????
111??0110000112112111100211111000110 10121010

Pantelosaurus 322??0100-0?0???(0 1)1??01?00?1110-
000110?0111???110110?01??1??1?00?110010?010?0?11003?2100?1??0(1
2)0101001101011 1???-?????????????1?????????????????????????0?10?00010-
??????0110????10?????????????10??????1???1?1?120100??????????????????111???????
?????2?????0230????1012??111?1???00???1110?1011?011?100102212111 1003???01??01001?
??????

Pantylus 001201110-0100100011021(0 1)0?0000-000110001111111010111011-0-
1101(0 1)01010111-1000--0-111102100111001000100 1000--0010--0--100-010011-100021020-
?11200200000010011000010-111001(0 1)010110?10101--0------
0101?100111111001100000 1???11?1100000011111 1?1101101 1?1?0111100?1?010?1101???001
1101??01111?10010110010-100112011101?0??101?000??0101???-01

Pederpes 323000?1111(1 3)0002????00110001?0-001??01?111000101110 10-0-
00010?00100000-000--?-110??21?1111?000?0010100???000111100101001 1001-??????-
?????0??????010?0010???01111111111(0 2)0101???10?01--1011111001??0?100-??0-

??1201?01?111????000000111010?0???00??????0??0?30210????0011-
?1?101?00?11??1?1100000(0 1)100-110101112001?1??0-1000111?---1??--?

Petrolacosaurus 221000000-031001111?0010000110-000110101111001101101010-
01110100100010-111101010030100011111(0 1)10101001101100110--111110-1110110??1100120--
11210220000110111100????11010011010001000101100100011 1?0????111?0-
00130100010?11?1????0??0??0-110100??011011120011102200---
1012?3111?????00?1?10100111 1?01111?0101212 1?2100?101010001 0011122110

Phlegethontia 020000100-010003200000-(0 1)0?0110-00010010110--00001011?10-
0100-10011000-001101?110(0 1)(2 3)0010-00--?00?0-?----0--01-0--0--0-0--0----0??00?01?0-
?11??000?0-0?100--?1?----0------00100??0--00--0------1110?01000-000-0?1101000-000----------
0-------0111??110100003?00---110???110-----?------0----------0----------

Procynosuchus 322200100-030000101102101?11(1 2 3)10000110101110001(0
1)111000-0-0101-00?0-------1?10011203?210001?00(1 2)1101000001101??0--0--130-?11011000??-
1?1??010?01(1 2)100002?0010000000-111000-1101001101000011000000 10??011112-
012101101000?001110----0--0--0-110000?0010?110200?10023010 1?10120???1??????00-
111???1010?01??10011??121?1?00?10?01?0010?????????

Scincosaurus 010201010-?10001100??0000??030-000?011011100?10111012-
1101011?10101(0 1)0-1000--0-1?1??210011??0101110010010000 10--0--100-00-----
?0?????1????????2??010011000000000-111010000100??10100--1000000021-
??????????10?101?00??????????????????????????????0?1???11000?011111??11001-001110-
?1?0?????10000111010-100112111102000111????0010100100-?0

Seymouria 302221010-?0000010010110 0?0110-000100101111001011 1010-0-
110101001100000000--?-100201100110010010000110120001101100100-010001-?0?01??20-
?10200?2?11000011200011001111101110110?0--
011010010101111?1???01?12?01?1301001111111111?000111000011010011 0?01??0200?11012010
??101212?01?10??011021010010010011010011211210110111110010?010101011-01

Silvanerpeton 121000010-010002200?00110?0210-000000101111001011 1010-0-
01111000110001-000--?-100211100111100010000000 1000-11101001010011001-
????????1???????0??000100111?0?11001??1102010 01??0--01--???????001??????1(0 2)??0-
0013010011?110-
0?0?00?11?0001011?????????????????1?2?01???101???1?101010?0????????0010?1010110102
21200??0?????00???1?110122-?0

Solenodonsaurus 32?000000-?0?????????1??00?0120-00010???11110011111?10-
110101000011000?-000--?-11121110011?10001010010?1200010--100100-01?001-
??????????????????????00???1?????????????????????????????????????01?????????????1
20?00???10?10????1011-
???1?1?10?0???1?1001011?010-10010?11?????????????????????????

Tuditanus 021210110-000000100110?00?01(0 1)0-000100101111110101110 10-1??(0
1)01100011001-0000--?-101101100111101000 1000(0 1)01?01110--0--100-011011-
??????????????????010?000??0?????????????01(0 1)100?10111--
???????010??000?????10011??0?011?????0?????????????1111??????1?????1110002200---
1012??0?1?101????????110001??01??100112111101111110111000 10011122?10

Utaherpeton 021000100-0?00?1????????0?0100-00000?1?11111101111011-0-0(0
1)0100001000???000--?-101??010-11??010?01?0100110?1???????100???????-
?0?????????????????2??00?????????????????111010???01???????1?????????011??????1???0-
011?0?00?1?????0?????????????1?11?????????????????10002201 0??101??3??1?0-
01??????????00?1?010-100112211001?0?????000?000---121??0

Varanops 32??00100-0?000011110211100120-00001??1111011?01101010-
01010000110011-010000?101311?1011?00100?1001101000110--101120-
1100?11?????????????1??0?1?????????????????????????????1????1?????001??????001??????0-
011100130100011011101-0-00-00-0-
11010011 0?????100011102201 0???0??131?1?1???01111110--
10110011010010221211110001000101?10010???0??

Varanosaurus 32?000100000100011110110111320-000110101110001001111110-
1101100011001?-010101111031210011 0(0 1)11010100100101?110--111100-
111011000???????????1?1????00011001?000001-111000-1101?0?0--
01011001000002??10111101 1?10130100001011 1?1-0-00-00-0-
1101001?0?????????1?????????????????1?????????0?????1?????????????????????????????????
??????????????0??

Vaughnitis ??????00??0?????01?????1????20-0001??????1???0?011????0-
01011000110011-01011?11013?111-11??0??0??001?01010110--1001?0-
1????1?????????????????????????????0?????001-??1001(0 1)11?????0--
?001?????0??11??????1(1 2)1?0-
001?0??000101110 1?000000??10110100??0???????????0???0????101?????????????????????
??????????????????????????10101?1????????????

Westlothiana 020020100-010004200?01100?0200-000100001111101111101 0-
1101111000100011-000--?-100001100111(0 1)020101001101200110--101100-111001-?????0??0-
??12?????000110111 0?011001110111000110010001--10(0
1)10100111?????100?111?130000?11010-00?0-01-10-001110????1?0?0-
0?0???103?010?01012??0?1??????0????????0111?011010001211?1?11002100110001010012 2-
??

Whatcheeria 32300010111300031101001100012 0-00101000111000101111 10-0-
00010100100000-000--?-11010211111110001001010010000011111001010011101-
???????0????00?0???0101000010001011101101001010 0?0--01--10111010012????1?0-110-
11120110111110001000000011101000001 01?0?0-0000013021010101011-
30?111110?01001?1111000(0 1)10101101121120022 1?30-101?1111---223--0

Youngina 22(1 2)000000-?00000000?12100?0120-000100101110001001110011 10(0
1)(0 1)10100100110111100101003010001110010101001101201010--110110-211011000?????10-
00?210(0 1)20000110011000101-11100101?011001000001100000011110011 1?????00?1(0
1)0100?????????????????????????????????????2??0?101211??010121???1?1?1?1??01?0---
1011?010110010021211 1100(0 1)10?11?????010122111

;

END;

begin trees;

translate

1 Acherontiscus,
2 Adelogyrinus,
3 Aerosaurus,
4 Anthracosaurus,

Araeoscelis,
Archaeothyris,
Archaeovenator,
Archeria,
Ariekanerpeton,
Asaphestera,
Balanerpeton,
Baphetes,
Belebey,
Brachydectes,
Caerorachis,
Captorhinus,
Cardiocephalus,
Carrolla,
Casea,
Chroniosaurus,
Dendrerpeton,
Diadectes,
Dimetrodon,
Diplocaulus,
Diploceraspis,
Discosauriscus,
Doleserpeton,
Echinerpeton,
Edaphosaurus,
Edops,
Eocasea,
Eothyris,
Erpetonyx,
Euconcordia,
Euryodus,
Gephyrostegus,
Gerobatrachus,
Greererpeton,
Hapsidopareion,
Haptodus,
Huskerpeton,
Hylonomus,
Hyloplesion,
Ianthosaurus,
Keraterpeton,
Lethiscus,
Limnoscelis,
Llistrofus,
Micraroter,
Microbrachis,
Milleretta,
Oestocephalus,
Opisthodontosaurus,
Orobates,
Orovenator,
Paleothyris,

```
        57      Pantelosaurus,
        58      Pantylus,
        59      Pederpes,
        60      Petrolacosaurus,
        61      Phlegethontia,
        62      Procynosuchus,
        63      Scincosaurus,
        64      Seymouria,
        65      Silvanerpeton,
        66      Solenodonsaurus,
        67      Tuditanus,
        68      Utaherpeton,
        69      Varanops,
        70      Varanosaurus,
        71      Vaughnitis,
        72      Westlothiana,
        73      Whatcheeria,
        74      Youngina
;

Begin MrBayes;

outgroup Whatcheeria;

[defining ingroup excluding Whatcheeria and Pederpes]
constraint ingroup1 -1 = 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 60 61
62 63 64 65 66 67 68 69 70 71 72 74;
[defining ingroup excluding Whatcheeria, Pederpes, Greererpeton and Baphetes. Baphetes and
Greererpeton are recovered as monophyletic, paraphyletic or a polytomy so I will leave the topology
of the two of them unconstrained]
constraint ingroup2 -1 = 1 2 3 4 5 6 7 8 9 10 11 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29
30 31 32 33 34 35 36 37 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 60 61 62 63
64 65 66 67 68 69 70 71 72 74;

log start filename=Mr_Bayes_FBD09model_uniformtreeagepr_codinginformative_21.11.23.txt;

lset rates = gamma coding=informative;

CALIBRATE   Acherontiscus   = uniform (326.0,326.4);
CALIBRATE   Adelogyrinus    = uniform (333,337.5);
CALIBRATE   Aerosaurus      = uniform (295,298.9);
CALIBRATE   Anthracosaurus  = uniform (315.2,318);
CALIBRATE   Araeoscelis     = uniform (283.5,290.1);
CALIBRATE   Archaeothyris   = uniform (307,311);
CALIBRATE   Archaeovenator  = uniform (298.9,303.7);
CALIBRATE   Archeria        = uniform (283.5,290.1);
CALIBRATE   Ariekanerpeton  = uniform (288,300);
CALIBRATE   Asaphestera     = uniform (315.2,318);
CALIBRATE   Balanerpeton    = uniform (329,337);
CALIBRATE   Baphetes        = uniform (308,318);
CALIBRATE   Belebey                 = uniform (268.8,272.95);
```

```
CALIBRATE Brachydectes = uniform (292,298.9);
CALIBRATE Caerorachis = uniform (326,326.4);
CALIBRATE Captorhinus = uniform (283.5,295);
CALIBRATE Cardiocephalus = uniform (275,280);
CALIBRATE Carrolla = uniform (283.5,295);
CALIBRATE Casea = uniform (275,280);
CALIBRATE Chroniosaurus = uniform (254.14,259.1);
CALIBRATE Dendrerpeton = uniform (318,319);
CALIBRATE Diadectes = uniform (276,281);
CALIBRATE Dimetrodon = uniform (283.5,290.1);
CALIBRATE Diplocaulus = uniform (270.6,306.5);
CALIBRATE Diploceraspis = uniform (292.5,307);
CALIBRATE Discosauriscus = uniform (283,285.5);
CALIBRATE Doleserpeton = uniform (286.2,286.7);
CALIBRATE Echinerpeton = uniform (308,309.5);
CALIBRATE Edaphosaurus = uniform (283.5,290.1);
CALIBRATE Edops = uniform (280,298.9);
CALIBRATE Eocasea = uniform (298.9,302);
CALIBRATE Eothyris = uniform (280,280.01);
CALIBRATE Erpetonyx = uniform (298.9,303.7);
CALIBRATE Euconcordia = uniform (298.9,303.7);
CALIBRATE Euryodus = uniform (275,280);
CALIBRATE Gephyrostegus = uniform (307,311);
CALIBRATE Gerobatrachus = uniform (270.6,280);
CALIBRATE Greererpeton = uniform (323.2,333);
CALIBRATE Hapsidopareion = uniform (275,280);
CALIBRATE Haptodus = uniform (305,306.5);
CALIBRATE Huskerpeton = uniform (295,298.9);
CALIBRATE Hylonomus = uniform (318,319);
CALIBRATE Hyloplesion = uniform (307,311);
CALIBRATE Ianthosaurus = uniform (305,306.5);
CALIBRATE Keraterpeton = uniform (318,319);
CALIBRATE Lethiscus = uniform (337,346.7);
CALIBRATE Limnoscelis = uniform (280,305);
CALIBRATE Llistrofus = uniform (290.1,295);
CALIBRATE Micraroter = uniform (275,280);
CALIBRATE Microbrachis = uniform (307,311);
CALIBRATE Milleretta = uniform (254.14,259.1);
CALIBRATE Oestocephalus = uniform (308,309.5);
CALIBRATE Opisthodontosaurus = uniform (289,289.01);
CALIBRATE Orobates = uniform (276,281);
CALIBRATE Orovenator = uniform (289,289.01);
CALIBRATE Paleothyris = uniform (308,315.2);
CALIBRATE Pantelosaurus = uniform (296,296.01);
CALIBRATE Pantylus = uniform (283.5,290.1);
CALIBRATE Pederpes = uniform (344,348);
CALIBRATE Petrolacosaurus = uniform (305, 306.5);
CALIBRATE Phlegethontia = uniform (308,309.5);
CALIBRATE Procynosuchus = uniform (251.9,255.2);
CALIBRATE Scincosaurus = uniform (307,311);
CALIBRATE Seymouria = uniform (270.6,281);
CALIBRATE Silvanerpeton = uniform (329,337);
```

```
CALIBRATE    Solenodonsaurus        = uniform (307,311);
CALIBRATE    Tuditanus        = uniform (308,309.5);
CALIBRATE    Utaherpeton      = uniform (318.1,318.11);
CALIBRATE    Varanops         = uniform (270.6,289);
CALIBRATE    Varanosaurus     = uniform (275,280);
CALIBRATE    Vaughnitis       = uniform (290.1,298.9);
CALIBRATE    Westlothiana     = uniform (329,337);
CALIBRATE    Whatcheeria      = uniform (340,340.01);
CALIBRATE    Youngina         = uniform (254.14,259.1);

PRSET nodeagepr = calibrated; [enforces 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 up clock to use a FBD process]
PRSET samplestrat = fossilTip;

PRSET speciationpr = exponential(10);
PRSET extinctionpr = beta(1,1);
PRSET fossilizationpr = beta(1,1);

PRSET treeagepr = uniform(341,358.9);

mcmcp  nrun = 2 nchain = 4 temp = 0.09 ngen=100000000 samplefreq=500 printfreq=500
diagnfr=5000 savebrlens=yes relburnin=yes burninfrac=0.25 stoprule=y stopval=0.01 app=n
filename=unconstrained ;
mcmc;


sumt contype = allcompat conformat = Figtree relburnin=yes burninfrac=0.25;
sump relburnin=yes burninfrac=0.25;

end;
```

Appendix 5: Synapomorphies of Selected Clades

Crown Group Tetrapods – Node 113

Unambiguous: 9(1->0), 172(0->1), 287(0->1), 295(1->0), 319(1->0); ACCTRAN: 67(1->0), 68(1->0), 80(2->0), 148(2->0); DELTRAN: 3(3->2), 66(0->1), 135(0->1), 177(0->1), 225(0->1), 228(1->0), 264(1->2), 279(0->1), 307(1->0), 317(1->0).

9 Lateral line canals are absent in adults

172 Pterygoid quadrate ramus margin in adductor fossa has some convex component

287 The portion of humeral shaft proximal to the entepicondyle is longer than the width of the humeral head

295 Width of the entepicondyle is more than half of the humeral length

319 A flange is present along the posterior edge of the tibia

Temnospondyls – Node 109

Unambiguous: 91(1->0), 117(1->0),146(0->1), 147(0->1), 191(1->2), 218(0->1), 288(0->1), 290(1->0), 291 (0->1); ACCTRAN: 14(0->1), 16(2->3), 102(0->1), 134(0->1), 199(0->2), 211(0->1), 242(0->1), 246(0->1), 251(1->0), 254(2->1), 258(0->1), 302(2->1), 322(0->1),325(2->1); DELTRAN: 11(1->0), 148(1->0).

91 Dorsalmost extent of the quadratojugal is lower than the dorsalmost extent of the maxilla

117 Tabular horns absent

146 Parasphenoid basal plate is triangular in shape

147 Parasphenoid is much wider than long immediately posterior to the level of the basal articulation

191 Dorsoventral position of jaw joint is above the toothrow

218 Posterodorsal process of posterior coronoid contributes to tallest point of lateral margin of adductor fossa

288 Degree of torsion in the humerus is more than 80 degrees

290 Humerus shaft is straight

291 Humerus shaft is waisted

Dissorophoid temnospondyls (including *Gerobatrachus*) – Node 106

Unambiguous: 1(3->0), 28(1->3), 33(0->1), 48(1->0), 59(0->1), 100(1->0), 157(1->0), 162(1->0), 164(1->0), 294(1->0), 297(1->0); ACCTRAN: 2(2->0), 8(1->0), 34(1->0), 45(0->1), 55(1->0), 93(0->2), 109(1->0), 133(1->2), 163(1->0), 184(1->0), 186(1->0), 191(2->1), 197(0->1), 227(1->0), 313(0->1), 314(1->0); DELTRAN: 6(0->1), 286(0->1).

1 Anteroposterior skull length less than 30mm

28 Number of maxillary teeth greater than 40

33 Marginal teeth are pedicellate

48 Frontal makes a contribution to the orbital margin, prefrontal and postfrontal do not contact each other

59 Orbit maximum anteroposterior length at least as long as the distance between the posterior orbit margin and the posterior skull margin

100 Parietals are not wider than frontals

157 Fangs absent on vomer

162 Ectopterygoid-palatine width not significantly wider than width of toothrow

164 Fangs absent on palatine

294 Ectepicondyle absent or low on humerus

297 Entepicondylar foramen absent on humerus

Total group amniotes – Node 114

Unambiguous: 34(1->0), 126(1->0), 252(1->0), 261(0->1); ACCTRAN: 130(2->1), 144(0->1), 148(0->1), 194(0->1), 221(1->0), 234(0->1), 244(0->1), 271(0->1), 321(0->1), 323(0->1), 324(1->2).

34 Labyrinthine infolding of teeth absent

126 Contact between the exoccipital and postparietal absent

252 Pleurocentrum is the dominant element in the centra, although intercentra are retained

261 Ribs are curved in at least part of the trunk

Anthracosaurs + *Chroniosaurus* – Node 105

Unambiguous: 93(0->1), 104(0->1), 157(1->0), 247(2->0); ACCTRAN: 10(0->2), 11(0->1), 20(1->0), 54(1->0), 80(2->1), 87(0->1), 205(0->1), 213(1->0), 219(0->1), 236(0->1), 237(0->1), 252(1->2), 264(2->0), 266(3->0), 267(1->0), 311(1->0), 316(0->1); DELTRAN: 80(0->1).

80 Maximum depth of the jugal beneath orbit midpoint between one-third and one-half of orbit diameter

93 Squamosal posterodorsal margin convex

104 Pineal foramen at midpoint of interparietal suture

157 Fangs absent on vomer

247 Axial neural arch anteroposteriorly shorter than more posterior arches

Anthracosaurs – Node 104

Unambiguous: 16(2->1), 17(2->0), 18(0->1), 51(0->1), 52(1->0), 151(1->0), 187(1->0); ACCTRAN: 21(0->1), 158(1->0), 165(1->0), 186(0->1), 254(2->3), 307(0->1); DELTRAN: 175(1->0), 236(0->1).

16 Total width of premaxillae between 21% and 30% of total skull width

17 Fewer than 4 teeth on the premaxillary

18 Premaxillary teeth are larger than maxillary teeth

51 Frontal anterior margin is wedged between nasals

52 Nasals are longer than frontals

151 Denticle shagreen absent on parasphenoid

187 Denticle shagreen absent on ectopterygoid

Amniotes crownwards of anthracosaurs – Node 116

Unambiguous: 43(0->1), 84(2->1), 86(1->0), 198(0->1), 273(0->1); ACCTRAN: 139(1->2), 143(1->2), 149(1->0), 200(1->0), 218(0->1), 274(1->0), 283(1->0), 289(1->0); DELTRAN: 11(1->0), 80(2->0), 160(1->0), 320(2->1), 323(0->1), 324(1->2).

43 Lacrimal ventral orbital process present

84 Jugal anteriormost extent terminates anterior to anterior margin of orbit

86 Jugal contributes to ventral skull margin

198 Adductor crest is present on dorsal margin of mandible

273 Interclavicle plate is wider than long

Seymouriamorphs + *Gephyrostegus* Node 119

Unambiguous: 3(1->3), 57(0->1), 70(1->0), 193(0->1), 219(0->1), 221(0->1), 254(2->1), 322(0->1); ACCTRAN: 133(1->2), 177(1->0), 201(1->2), 204(0->1), 274(0->1), 287(1->0), 308(0->1), 325(2->1); DELTRAN: 111(0->1), 149(1->0), 168(0->1), 175(1->0).

3 Anteroposterior skull length is more than 45% of anteroposterior trunk length

57 Orbital rim is thickened

70 Postorbital and supratemporal contact absent

193 Quadrate contacts pterygoid quadrate ramus along more than 55% of length of pterygoid quadrate ramus

219 Posterior coronoid exposed in lateral view

221 Contact present between the middle coronoid and splenial

254 Between 20 and 24 presacral vertebrae

322 Six distal tarsal elements

Seymouriamorphs – 118

Unambiguous: 6(0->1), 90(1->0), 91(1->0), 110(1->0), 145(0->1), 167(0->1), 189(0->1), 190(0->1), 276(0->1); ACCTRAN: 2(2->0), 4(0->2), 21(1->0), 47(1->0), 55(1->0), 62(0->1), 121(1->0), 146(0->1), 153(0->2), 205(0->1); DELTRAN: 24(1->0), 117(1->0), 153(1->2), 186(1->0), 308(0->1), 309(3->1).

6 Preorbital region of skull more than twice as wide as long

90 Quadratojugal depth is smaller than one-quarter of squamosal depth

91 Dorsalmost extent of quadratojugal is lower than dorsalmost extent of maxilla

110 Intertemporal smaller in area than supratemporal

145 Elongate, broad posterolateral processes present on parasphenoid

153 Vomers separated by pterygoid for more than half of anteroposterior length of vomers

167 Palatal teeth equal in size to marginal teeth

189 Suborbital opening in palate present

190 Jaw joint positioned in line with occiput along anteroposterior skull length

276 Scapulocoracoid consists of multiple ossifications

Amniotes including, and crownwards of, lepospondyls – Node 122

Unambiguous: 83(1->0), 93(0->1), 101(0->1), 107(0->1), 255(1->2); ACCTRAN: 114(0->1), 119(0->1), 123(0->1), 190(0->1); DELTRAN: 16(2->0), 164(1->0), 180(1->0), 186(1->0), 192(0->1), 197(0->1).

83 Posteriormost extent of the jugal is not posterior to the posterior margin of the postorbital

93 Squamosal posterodorsal margin is approximately straight

101 Parietal-parietal total width larger than the distance between the orbit posterior margin and posterior skull margin

107 Parietal – postorbital contact present

255 Between 25 and 35 presacral vertebrae

Lepospondyls including *Westlothiana* – Node 123

Unambiguous: 1(3->0), 7(0->1), 29(2->0), 44(0->1), 61(0->1), 66(1->0), 69(0->1), 202(0->1), 209(1->0), 311(1->0); ACCTRAN: 10(0->1), 12(0->1), 82(2->0), 126(0->1), 142(1->2), 143(2->0), 153(0->1), 166(0->1), 168(1->0), 196(1->0), 199(1->0), 205(0->1), 244(1->0), 247(2->1), 249(0->1), 251(1->0), 254(2->3), 274(0->1), 277(1->0), 285(1->0), 302(2->1), 313(0->1); DELTRAN: 47(0->1), 55(0->1), 190(0->1), 200(1->0), 267(1->0).

1 Anteroposterior skull length less than 30mm

7 Antorbital region of skull mediolaterally narrow

29 Marginal teeth blunt and peg-like

44 Lacrimal dorsal orbital process present

61 Large, concave notch present in posteroventral margin of postfrontal to accommodate the postorbital

66 Postorbital irregular, without a clearly defined shape

69 Anterodorsal margin of postorbital has distinct sigmoid shape

202 Retroarticular process present

209 Anteroposterior length of dentary toothrow is less than 50% of jaw length

311 Internal trochanter not separated from the general surface of the femur by a trough

Lepospondyls more derived than *Westlothiana* – Node 131

Unambiguous: 4(0->2), 112(1->0), 148(1->0), 153(1->2), 199(0->2), 207(3->2), 248(0->1), 252(1->0), 260(0->1); ACCTRAN: 8(0->1), 82(2->1), 119(1->0), 215(0->1), 225(1->0), 322(0->1); DELTRAN: 82(0->1), 123(0->1), 142(0->2), 157(1->0), 196(1->0), 205(0->1), 226(1->0), 227(1->0), 249(0->1), 250(0->1), 251(1->0), 274(0->1), 277(1->0), 292(1->0), 302(2->1), 309(3->1).

4 Interorbital distance larger than maximum anteroposterior orbit diameter

82 Posterior margin of the jugal is straight and vertical

112 Separately ossified supratemporal absent

148 No ventral depression in body of parasphenoid

153 Vomers separated by pterygoids for more than half of vomer length

199 Dentary is only element forming adductor crest

207 Between 20 and 29 teeth on dentary

248 Anterior articulating surface of the atlas laterally expanded relative to posterior articulating surface

252 Loss of ossified intercentra

260 Haemal arches parallel sided

Non-microsaur lepospondyls (but including *Utaherpeton*) – Node 142

Unambiguous: 24(0->1), 69(1->0), 82(1->2), 101(1->0), 104(2->0), 187(1->0), 207(2->3), 243(0->1), 248(1->0), 303(1->0); ACCTRAN: 12(1->3), 46(1->0), 95(1->0), 102(1->0), 122(0->1). 123(1->0), 184(0->1), 302(0->1); DELTRAN: 20(1->0), 151(1->0), 218(0->1), 271(1->0), 273(1->0), 314(1->0).

24 Posteriormost extent of maxilla extends posterior to orbit posterior margin

69 Anterodorsal margin of postorbital smooth and lacks sigmoid shape

82 Posterior margin of jugal slopes anterodorsally to posteroventrally

101 Parietal-parietal total width shorter than the distance between the orbit posterior margin and skull posterior margin

104 Pineal foramen positioned posterior to midpoint of interparietal suture

187 Denticle shagreen on ectopterygoid absent

207 More than 29 dentary teeth

243 Atlantal neural arch halves fused into single arch

248 Anterior articulating surface of atlas equal in diameter to posterior articulating surface

303 Carpals unossified

Nectrideans – Node 137

Unambiguous: 8(0->1), 23(1->0), 24(1->0), 37(0->1), 43(1->0), 47(1->0), 96(0->1), 152(1->0), 170(0->1), 249(1->0), 256(0->1), 268(0->1); ACCTRAN: 12(3->0), 60(0->1), 74(1->0), 99(1->0), 103(0->1), 118(0->1), 133(2->1), 200(0->1), 235(1->0), 254(3->0), 258(0->1), 277(0->1); DELTRAN: 242(0->1), 246(0->1).

8 Dermal sculpturing in pits and grooves present

23 Maxilla is shorter than palatine

24 Maxilla does not extend posteriorly to orbit

37 External naris positioned further from jaw margin than height of naris

43 Lacrimal ventral orbital process absent

47 Prefrontal less than three times longer than wide

96 Internal shelf of squamosal articulates with quadrate

152 Vomer anteroposterior length less than twice as mediolaterally wide

170 Pterygoid quadrate ramus oriented mostly laterally in ventral aspect

249 Odontoid process on atlas absent

256 Accessory articulations present above zygapophyses on at least some vertebrae

268 Tail at least as long as trunk

Aïstopods – Node 140

Unambiguous: 4(2->0), 6(1->0), 73(0->1), 106(1->0), 142(2->0), 198(1->0), 202(1->0), 257(1->0), 262(0->1), 267(0->1), 269(1->0), 305(1->0); ACCTRAN: 62(0->1), 85(1->0), 112(0->1), 139(2->0), 144(1->0), 155(0->1), 216(1->0), 282(1->0); DELTRAN: 46(1->0), 95(1->0), 99(0->1), 114(0->1), 209(0->1), 242(0->1), 246(0->1), 263(1->0).

4 Interorbital distance smaller than maximum anteroposterior orbit diameter

6 Preorbital region of skull less than twice as wide as long

73 Jugal free posterior margin present

106 Parietal – squamosal contact absent

142 Occipital condyle is round in shape

198 Adductor crest on mandible absent, dorsal mandibular margin is smooth

202 Retroarticular process is absent

257 Haemal arches absent

262 Costal (K-shaped) processes at head of rib

267 Gastralia present

269 Separately ossified clavicle absent

305 Pelvis is absent

Amniotes crownwards of lepospondyls – Node 103

Unambiguous: 36(0->1), 91(1->0), 113(0->1), 128(0->1), 154(0->1), 187(1->0), 212(1->0), 246(0->1), 268(0->1), 272(0->1); ACCTRAN: 47(1->0), 55(1->0), 76(1->0), 129(0->1), 135(1->0), 144(1->0), 151(1->0), 200(0->1), 214(1->0), 309(1->3); DELTRAN: 119(0->1), 123(0->1), 143(1->2), 153(1->0), 157(1->0), 168(0->1).

36 Caniniform teeth present in marginal dentition

91 Dorsalmost extent of quadratojugal lower than dorsalmost extent of maxilla

113 Supratemporal makes contribution to occiput

128 Dorsal trabeculae present

154 Vomer asymmetrically bifurcated anteriorly

187 Denticle shagreen on ectopterygoid absent

212 Separately ossified postsplenial absent

246 Axial neural arch and axial neural centrum indistinguishably fused

268 Tail at least as long as trunk

272 Interclavicle posterior stem parallel sided along most of length

Diadectamorphs – Node 102

Unambiguous: 4(0->2), 5(0->2), 18(0->1), 38(1->0), 102(0->1), 104(2->1), 173(0->1), 207(3->1), 239(1->0), 308(0->1); ACCTRAN: 8(0->1), 15(0->1), 17(1->0), 43(1->0), 114(1->0), 133(1->2), 136(0->1), 142(1->0), 190(1->0), 191(1->0), 226(0->1), 233(1->0), 250(1->0), 289(0->1), 292(0->1), 316(0->1); DELTRAN: 151(1->0), 267(1->0).

4 Interorbital distance larger than maximum anteroposterior orbit diameter

5 Interorbital distance larger than half of maximum skull width

18 Premaxillary teeth larger than maxillary teeth

38 External naris not exposed in dorsal view

102 Anteriormost third of the parietals do not narrow and remains wider than frontals

104 Pineal foramen positioned at midpoint along interparietal suture anteroposterior length

173 Arcuate flange on quadrate ramus of pterygoid

207 15 to 19 teeth in dentary

239 Prearticular – surangular contact absent

308 Transverse pelvic ridge present

Amniotes crownwards of diadectamorphs – Node 100

Unambiguous: 48(1->0), 77(0->1), 116(0->1), 140(0->1), 172(1->0), 270(1->0), 304(0->1), 320(1->0), 321(0->1), 327(0->1); ACCTRAN: 1(3->1), 70(1->0), 195(0->1), 213(1->0), 267(0->1), 281(0->1); DELTRAN: 8(1->0), 190(0->1), 199(0->1), 215(1->0), 218(0->1), 227(1->0), 250(0->1).

48 Prefrontal – postfrontal contact absent, frontal contributes to orbital margin

77 Squamosal contributes to posttemporal fenestra

116 Tabular is small and wedge-shaped, located dorsal to the posttemporal fenestra

140 Paraoccipital process on the opisthotic ends freely and does not contact lateral skull

172 Pterygoid quadrate ramus margin in adductor fossa completely concave

270 Clavicles meet anteriorly

304 Manual phalanges taper distally to a point and curve ventrally

320 Tibiale, intermedium and proximal centrale fused into astragalus, just two proximal tarsal elements present

321 Proximal tarsal element L-shaped

327 Only one centrale present in the tarsus

Captorhinids + protorothyrids – Node 99

Unambiguous: 106(0->1), 180(0->1); ACCTRAN: 3(1->2), 12(0->3), 44(0->1), 101(1->0), 129(1->0), 130(1->2), 131(0->1), 151(0->1), 182(1->0), 325(2->1); DELTRAN: 1(3->1), 70(1->0).

106 Parietal – squamosal contact present

180 Denticle shagreen present on transverse flange of pterygoid

Crown amniotes – Node 95

Unambiguous: 73(0->1), 82(2->3), 104(2->0), 181(0->1), 300(1->2), 309(3->1), 311(1->0); ACCTRAN: 21(1->0), 69(0->1), 132(0->1), 200(1->0), 202(0->1), 225(1->0), 293(0->1); DELTRAN: 76(1->0), 142(0->1), 151(1->0).

73 Jugal has free posterior margin

82 Jugal triradiate, with posterodorsal margin sloping anterodorsally to posteroventrally and posteriorly forming a distinct process

104 Pineal foramen positioned posterior to midpoint of interparietal suture anteroposterior length

181 Tooth row present on transverse flange of pterygoid

300 Radius more than 71% of length of humerus

309 Puboischiadic plate equivalent in anteroposterior length to four trunk vertebrae

311 Internal trochanter not separated from general surface of femur by trough-like space

Total group reptiles – Node 94

Unambiguous: 36(1->0), 137(1->0), 235(1->0), 272(1->0), 277(1->0); ACCTRAN: 26(0->1), 39(0->1), 70(0->1), 114(1->0), 185(1->0), 219(0->1), 259(1->0), 265(1->0), 266(3->2), 281(1->0), 298(1->0), 312(1->0); DELTRAN: 1(3->1), 21(1->0), 200(1->0), 202(0->1), 213(1->0), 214(1->0).

36 Maxillary caniniform teeth absent

137 Epipterygoid caps basal articulation and does not contribute laterally

235 Angular does not reach posteriormost extent of lower jaw

272 Interclavicle posterior stem tapers along most of length

277 Supraglenoid foramen absent

Parareptiles + *Youngina* – Node 92

Unambiguous: 17(1->0), 158(1->0), 165(1->0), 179(1->0), 207(3->0); ACCTRAN: 1(1->0), 26(1->0), 39(1->0), 43(1->0), 154(1->0), 157(0->1), 163(1->0), 177(1->0), 185(0->1), 246(1->0); DELTRAN: 119(1->3), 292(1->0), 293(0->1), 298(1->0).

17 Fewer than 4 premaxillary teeth

158 Denticle shagreen absent on vomer

165 Denticle shagreen absent on palatine

179 Denticle shagreen absent on palatal ramus of pterygoid

207 Fewer than 14 dentary teeth

Total group Mammalia (i.e. synapsids + araeoscelids) – Node 89

Unambiguous: 13(0->1), 19(0->1), 75(0->1), 130(1->0), 278(0->1); ACCTRAN: 1(1->2), 18(0->1), 195(1->0), 213(0->1), 242(0->1), 274(0->1), 292(0->1); DELTRAN: 10(1->0), 69(0->1), 129(0->1), 132(0->1).

13 Posterior margin of skull bilaterally embayed

19 Anteriormost premaxillary teeth larger than posterior premaxillary teeth, forming conspicuous peak

75 Ventral temporal bar dorsoventrally deep, occupying more than 20% of skull height

130 Anterior extent of cultriform process terminates posterior to sphenethmoid anterior margin

278 Supraglenoid foramen located on or anterior to the apex of the supraglenoid buttress

Synapsids – Node 87

Unambiguous: 7(0->1), 22(0->1), 61(0->1), 78(0->1), 90(1->0), 116(1->0), 154(1->0); ACCTRAN: 1(2->3), 43(1->0), 105(0->1), 134(0->1), 143(2->1), 174(0->1), 193(0->1), 214(0->1), 255(2->3), 293 (1->0), 327(1->0); DELTRAN: 18(0->1), 114(0->1), 202(0->1), 225(1->0), 281(0->1).

7 Skull antorbital region is mediolaterally narrow and dorsoventrally tall

22 Maxilla preorbital ascending process more than 1.5 times the height of the maxilla at the point of the anterior orbital margin

61 Large, concave notch present in posteroventral margin of postfrontal to accommodate postorbital dorsal margin

78 Squamosal and jugal contact beneath temporal fenestra

90 Quadratojugal maximum depth is smaller than one-quarter of the maximum depth of the squamosal

116 Tabular is broad, sub-rectangular sheet located dorsal to the posttemporal fenestra

154 Vomer is not bifurcated anteriorly

Araeoscelids – Node 88

Unambiguous: 12(0->3), 29(2->1), 59(0->1), 62(0->1), 72(0->1), 74(0->1), 189(0->1), 257(1->0), 286(0->1), 326(0->1); ACCTRAN: 16(0->1), 133(1->2), 142(1->2), 153(0->1), 194(1->0), 202(1->0), 299(2->1), 322(0->1); DELTRAN: 1(3->2), 70(1->0), 293(0->1).

12 Posterior skull margin is undulating

29 Marginal teeth are sharp and conical

59 Orbit maximum anteroposterior length greater than distance between orbit posterior margin and skull posterior margin

62 Position of posteriormost extent of postfrontal is posterior to posteriormost extent of jugal

72 Postorbital has free dorsal margin

74 Parietal has free lateral margin

189 Suborbital opening on palate present

257 Heamal arches absent

286 Humerus length is more than 3 times greater than the width of the distal end

326 Tibio-astragalar joint is complex; tibial ridge fits into astragalar groove