The Early Evolution of Synapsida (Vertebrata, Amniota) and the Quality of their Fossil Record

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Erklärung

Hiermit versichere ich, dass ich diese Dissertation eigenständig und nur unter Verwendung der angegebenen Quellen und Hilfsmittel angefertigt habe.

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Abstracts

Abstract in English

Synapsids (the clade containing mammals and all taxa more closely related to them than to other vertebrates) first appear in the fossil record during the late Pennsylvanian, and dominated the terrestrial realm until the end of the Palaeozoic. Their early evolution includes some of the first amniotes to evolve large size, herbivory, and macrocarnivory. However, much of the research into their macroevolutionary patterns during the Palaeozoic has focussed on therapsids, the clade containing mammals. Very little work has been done on the more basal pelycosaurian-grade synapsids, a paraphyletic assemblage of six families which were particularly diverse and abundant during the Late Carboniferous and Early Permian. This thesis provides the first detailed examination of the earliest evolution of synapsids. First, new material is incorporated into a phylogenetic analysis of basal synapsids, including the eothyridid “Mycterosaurus” smithae, re-described herein. The phylogeny produced is integrated into an examination of the completeness of the fossil record of pelycosaurian-grade synapsids. Modifications of previously published metrics are used to assess the completeness of their specimens, and a variety of methods are employed to measure the fit of the fossil record to the phylogeny. An assessment of species richness is undertaken, with multiple sampling correction methods used to provide a detailed picture of how the diversity of pelycosaurian-grade synapsids has changed through time. Finally, analysis of tree topology is used to investigate the timing and location within the phylogeny of significant shifts in the rate of diversification, and to investigate the link between these shifts and potential “key” morphological innovations. The analysis into the completeness of pelycosaurian-grade specimens reveals a negative correlation between diversity and the Skeletal Completeness Metric, assessing the bulk of material preserved, suggesting a tendency to name many species based on poor material. The lack of correlation between the Character Completeness Metric (assessing the proportion of phylogenetic characters that can be scored) and diversity is attributed to the history of discovery in the group: the majority of pelycosaurian-grade species were named between the 1930s and 1960s, when assignments were often based on size, location and stratigraphy rather than morphological characters. A strong correspondence between the phylogeny and stratigraphy implies a reliable phylogenetic hypothesis, but the low Relative Completeness Index score suggests that a great deal of the fossil record is missing. Despite this, and evidence of anthropogenic sampling bias affecting richness estimates throughout history, the different methods of assessing diversity provide very similar results. The initial diversification of synapsids in the Late Pennsylvanian and early Cisuralian was followed by an extinction event during the Sakmarian. A second extinction event occurred across the Kungurian/Roadian boundary. Despite the large number of morphological innovations occurring in early synapsids, the tree topology analysis found no significant increases in diversification rate occurring in pelycosaurian-grade taxa relative to their contemporaries. A broader examination of diversification patterns in Palaeozoic and Triassic amniotes reveals a possible explanation; diversification rate shifts within early amniotes tend to occur during periods of elevated extinction. While there are diversification rate shifts coinciding with the evolution of innovations, the elevation of origination rates occur during times of elevated extinction, rather than at the first appearance of such novelties. The fact that pelycosaurian-grade synapsids were so innovative did not translate into great increases in their diversification rate.
Abstract in German

Chapter 1
Introduction and Literature Reviews
Introduction to the Pelycosaurian-grade Synapsids

Synapsida is the clade including mammals and all taxa more closely related to them than to other modern vertebrates. The earliest unambiguous members of this clade appear in the fossil record during the Moscovian (Middle Pennsylvanian) after which they rapidly diversified, dominating terrestrial ecosystems during the Late Carboniferous and Permian. Their early evolution includes some of the earliest amniotes to show large body size, high-fibre herbivory, macro-carnivory, evidence of group-living, and possibly a return to a semi-aquatic lifestyle. They are defined by the following synapomorphies: presence of a lower temporal fenestra (Romer and Price, 1940); five or more cervical vertebrae (Benson, 2012); posterior shaft of the humerus convex around the exit of the entepicondylar foramen (Benson, 2012); postparietals fused to form an interparietal (Hill, 2005); craniomandibular joint positioned posterior to the occiput (Hill, 2005).

![Composite phylogeny showing relationships of major amniote clades. Synapsid relationships based on Reisz and Fröbisch (2014) and Sidor and Hopson (1998). Sauropsid relationships based on Bickelmann et al. (2009). Pelycosaurian-grade synapsids are highlighted in red.](image)

Synapsids belong to the clade Amniota, the fully terrestrial vertebrates which possess the amniotic egg, giving their reproduction independence from water (Reisz, 1997). The amniotes are split into two clades (Figure 1): Synapsida (including extant mammals) and Sauropsida (including extant reptiles and birds). The earliest examples of amniotes in the fossil record are found in the Joggins Formation of Canada, of late Bashkirian age (Benton and Donoghue, 2007). This formation also includes the earliest putative synapsid,
Protoclepsydrops haplous (Carroll, 1964; Reisz, 1972), although this assignment is debated; the characters previously linking it to synapsids have now been observed in basal sauropsids (Reisz, 1980; 1986). The earliest undisputed synapsids are Archaeothyris florensis and Echinerpeton intermedium, both from the Morien Group of Nova Scotia, of late Moscovian age (Reisz, 1972).

During the Late Carboniferous and Early Permian, six synapsid families were particularly diverse and abundant in the terrestrial realm: Ophiacodontidae, Edaphosauridae, Varanopidae, Sphenacodontidae, Caseidae and Eothyrididae (shown in order of their appearance in the fossil record). These families have historically been united into a group known as “Pelycosauria” (Cope, 1878a; Case, 1907; Romer and Price, 1940; Reisz, 1986). Pelycosauria are now known to be a paraphyletic grade (Figure 1) including all synapsids not belonging to the monophyletic clade Therapsida, the clade from which mammals originate.

Palaeozoic Synapsids

Ophiacodontidae

The earliest synapsid family to appear in the fossil record is Ophiacodontidae. Archaeothyris florensis, one of the earliest synapsids from the Morien group (see above) was assigned to this family (Reisz, 1972), an assignment supported by numerous phylogenetic analyses (Berman et al., 1995; Maddin et al., 2006; Reisz et al., 2009; Reisz et al., 2010; Benson, 2012). Ophiacodontidae is defined by a dorsally projecting pubic tubercle anteroventral to the acetabulum (Berman, 1995) and a dorsoventrally narrow temporal fenestra with a deep temporal bar (Benson, 2012). Their skulls are elongated and narrow, particularly in the facial region (Romer and Price, 1940). All species for which dentition is preserved are inferred to be carnivorous. Their teeth are numerous, but the caniniform region is weakly developed (Romer and Price 1940). Ophiacodontidae are known from North America and western Europe from the Middle Pennsylvanian until the end of the Early Permian.

One genus of this family, Ophiacodon, has been interpreted as a semi-aquatic piscivore. This was first suggested by Case (1907) in his review of pelycosaurs, although this monograph provided no evidence. The hypothesis was challenged by Williston and Case (1913), citing the slender tail as poorly adapted for swimming. However, other anatomical features have provided support for an aquatic lifestyle, including flattened unguals (Romer and Price 1940), longer hind limbs than forelimbs (Romer and Price, 1940;
Kemp, 1982), and the poorly ossified appendicular skeleton, slow ossification being widespread among secondarily aquatic tetrapods (Reisz, 1986). The skull morphology has also been cited as being indicative of a piscivorous diet. The tall, narrow skull with slender jaws and thin bone would be mechanically weak, unsuited for large terrestrial prey (Romer and Price, 1940). The small, numerous, unserrated conical teeth are also suggestive of a fish-based diet (Romer and Price, 1940). Conversely, Thomson and Russell (1986) argued against the mechanical weakness of the skull, pointing out that the large palatines would brace the snout against bending and torsion. The significance of the flat unguals has also been challenged, having been found in other terrestrial amniotes (Maddin and Reisz, 2007). Felice and Angielczyk (2014) argued the morphology of the manus and pes is mostly inconsistent with other secondarily aquatic amniotes. They also used morphometrics to show the morphology of the vertebrae was closer to that of a terrestrial animal. Analysis of bone microstructure has proven inconclusive: the high bone density of *Ophiacodon*, whilst suggesting an aquatic lifestyle, is outside the range of any extant species, aquatic or otherwise (Germain and Laurin, 2005).

*Varanopidae*

Varanopidae is a clade of small to medium-sized carnivores. As their name suggests, their skulls strongly resemble those of varanid lizards, with a long, narrow rostrum and strongly recurved and serrated teeth (Romer and Price, 1940). Other defining features include an elongated external naris (Reisz and Dilkes, 2003), a large, sheet-like septomaxilla (Reisz and Dilkes, 2003), absence of the supraglenoid foramen (Maddin et al., 2006), reduction of the occipital flange of the squamosal (Maddin et al., 2006), a short anterior process of the jugal (Benson, 2012), separation of the atlantal and axial intercentra (Benson, 2012), anterior orientation of posterior dorsal neural spines (Benson, 2012), a strongly concave ventral surface of the pubic apron (Benson, 2012) and a straight anterior margin of the interclavicle (Benson, 2012). Most known varanopid species are small carnivores, but three species, *Varanodon agilis* ( Olson 1965) and *Watongia meieri* ( Olson, 1974; Reisz and Laurin, 2004) from the Chickasha Formation of Oklahoma, and *Tambacarnifex unguifalcatus* from the Tambach Formation of Germany (Berman et al., 2014), reached lengths of over 1.2 meters, possibly approaching two meters (Reisz and Laurin, 2004). The large macro-carnivores in most Lower Permian terrestrial ecosystems are sphenacodontid synapsids (see below). However, the Tambach Formation has yielded only small sphenacodontid specimens ( Berman et al., 2001; Berman et al., 2004), whilst the Chickasha Formation has yielded none. Berman
et al. (2014) theorised that in the dry upland areas represented by these formations, large varanopids replaced sphenacodontids as the dominant carnivores.

The earliest and most basal member of Varanopidae, *Archaeovenator hamiltonensis*, appears in the Virgilian (late Kazimovian-Gzhelian) aged Hamilton Quarry of Kansas (Reisz and Dilkes, 2003). *Milosaurus mccordi*, from the earlier Missourian (Kazimovian) sediments of Illinois, was originally described as a varanopid (DeMar 1970), but the fragmentary nature of this specimen makes a reliable assignment difficult (Reisz, 1986). The varanopids are the longest-lived and geographically most widespread clade of pelycosaurian-grade synapsids, having been found in North America, western Europe, European Russia and South Africa as late as the Middle Permian. The youngest known pelycosaur is an unnamed varanopid from the *Pristerognathus* Assemblage Zone (late Capitanian-early Wuchiapingian) of South Africa (Modesto et al., 2011). The South African varanopid *Heleosaurus scholtzi* has provided the earliest evidence of group-living and parental care in amniotes. A group assemblage of specimens includes an adult and four juveniles possibly living together in a burrow (Botha-Brink and Modesto, 2007; 2009).

**Edaphosauridae**

Edaphosauridae are ecologically an extremely important clade. The genus *Edaphosaurus* represents one of the earliest terrestrial herbivores to appear in the fossil record, along with diadectid amphibians which appeared at a similar time (Vaughn, 1968; Kissel, 2010). Prior to the appearance of *Edaphosaurus* in the Gzhelian (Williston and Case, 1913; Lucas et al., 2005), and possibly earlier in the Kazimovian of Kansas and the Czech Republic (Fritsch, 1895; Peabody, 1957), most primary consumers in terrestrial ecosystems were arthropod detritivores (Shear and Sheldon 2001). *Edaphosaurus* and the diadectid amphibians are the earliest examples of vertebrates feeding directly on living plants. *Edaphosaurus* itself possesses several adaptations related to its dietary specialisation. Its palatal and dentary teeth form occluding tooth plates which, combined with a propalineal motion of the lower jaw, allow it to grind vegetation (Modesto, 1995). They also possess a large, barrel-shaped trunk presumably housing the large digestive system required to digest plants (Romer and Price, 1940).

Edaphosaurids other than *Edaphosaurus* have varied diets. The basalmost member of the clade, *Ianthosaurus hardestiourm* from the late Kazimovian Garnett Quarry of Kansas, is a small insectivore (Modesto and Reisz, 1990; Mazierski and Reisz, 2010). Two other species appear in the later Early Permian in the USA: *Glaucosaurus megalops* (Williston, 1915;
Modesto, 1994) and _Lupeosaurus kayi_ (Romer, 1936; Sumida, 1989). Both of these species are problematic. _Lupeosaurus_ does not preserve a skull or dentition, so no reliable inferences about its diet may be made. However the large size and morphology of the ribs (recalling the barrel-like trunk of _Edaphosaurus_) do suggest an herbivorous animal (Sumida, 1989). _Glaucosaurus_, meanwhile, is only represented by juveniles, and is therefore difficult to interpret. Although the conical teeth suggest an insectivorous or omnivorous diet, other features thought to correlate with herbivory are present, such as isodonty, loss of the transverse flange of the pterygoid, and the shortened snout (Modesto, 1994). It is possible that its diet varied through ontogeny; the consumption of herbivorous insects as a juvenile may have provided amniotes with the bacteria necessary for fermentation of plant material in adulthood (Sues and Reisz, 1998).

Edaphosaurids are characterised by spatulate, slightly bulbous teeth which lack recurvature (Modesto, 1994), a long and broad postfrontal (Modesto, 1994), dorsal neural spines being subcircular and rod-like for most of the spine’s length (Modesto, 1994), strongly posteriorly inclined posterior dorsal neural spines (Modesto, 1994), the quadrate condyles being confluent rather than distinctly separate (Modesto, 1995), a short frontal process (Benson, 2012), anterior inclination of the axial neural spine (Benson, 2012) and dorsal transverse processes located anterior to the midlength of the neural arch (Benson, 2012). All members of Edaphosauridae for which postcranial information is available possess elongated neural spines (Romer and Price, 1940; Reisz and Berman, 1986). These structures, sometimes up to three times the height of the animal, have also appeared numerous times in sphenacodontid synapsids (Romer and Price, 1940; Hook and Hotton, 1991), as well as in dinosaurs (Benton, 1979; Sereno et al., 1996), crurotarsan archosaurs (Butler et al., 2011b) and amphibians (Lewis and Vaughn, 1965; Vaughn, 1971). Most workers believe them to have supported a sail formed from skin webbing, although defensive spines (Jackel, 1910) or a fatty hump as found in bison (Bailey, 1997) have also been suggested. With the exception of _Lupeosaurus_, the spines of edaphosaurids possess lateral tubercles which would have protruded from the sail (Romer and Price, 1940; Reisz and Berman, 1986).

The function of such sails is debated, with sexual display (Bakker, 1986) and thermoregulation (Romer and Price, 1940) having been suggested. Under the thermoregulatory hypothesis, large animals such as _Dimetrodon_ and edaphosaurids would use the sails to increase their surface area, allowing them to heat up more quickly in the sun and become active faster than their predators or prey. Experiments on airflow and heat flow over a model edaphosaurid (Bennett, 1996) suggest that the turbulent airflow over the sail caused by
the lateral tubercles causes the sail to be a more efficient radiator. On the other hand, Tomkins et al. (2010) opposed a thermoregulatory function. These authors argued that if sails had such a purpose, then they should scale allometrically with size, since smaller animals heat up more rapidly and have less need of a large heating surface. This is not seen in \textit{Dimetrodon}, and several small species of synapsids such as the enigmatic \textit{Xyrospodylus eocordi} and the edaphosaurid \textit{Ianthisaurus} carry sails larger than they would need for thermoregulation. This, as well as evidence of sexual dimorphism in sail height (Romer and Price, 1940) lead Tomkins et al. (2010) to support display as their function.

\textit{Sphenacodontidae}

Sphenacodontidae, as mentioned above, were the most abundant large carnivores during the Early Permian, and represent the earliest evolution of macro-carnivory (feeding on large vertebrate prey) in amniotes. Sphenacodontids have a morphology ideally suited for feeding on large animals. The skulls of most species are tall and strongly built, with the exception of \textit{Secodontosaurus}, which has a long, narrow rostrum (Romer and Price, 1940). The teeth are laterally compressed and serrated. The genera \textit{Dimetrodon} and \textit{Secodontosaurus} demonstrate the earliest known example of serrations possessing denticles with a dentine core, a condition known as ziphodonty (Brink and Reisz, 2014). The dentition is strongly heterodont, with enlarged anterior teeth. There is a step in the upper jaw into which the anterior teeth of the lower jaw fit, presumably to grip prey (Romer and Price, 1940). Other defining characters include extreme elongation of the frontal (Benson 2012) and the lateral centrale proximally overlapping the third distal carpal (Benson 2012).

Sphenacodontidae first appears in fossil record in the late Pennsylvanian. A number of possible sphenacodontid specimens have been identified from the Kazimovian aged Rakonitz Coal Basin of the Czech Republic (Romer, 1945), but all are highly fragmentary and their affinity cannot be determined with confidence. The earliest unambiguous species are of Gzhelian age: \textit{Sphenacodon ferox} from the El Cobre Canyon Formation of New Mexico (Case, 1907), and \textit{Cryptovenator hirschbergeri} from the Remiguisberg Formation of Germany (Fröbisch et al., 2010). Many species appear in the Early Permian, most of which are assigned to the genus \textit{Dimetrodon} (although this genus has not undergone substantial revision since the comprehensive review of Romer and Price in 1940). Only one species is known from the Middle Permian: \textit{Dimetrodon angelensis} from the San Angelo Formation of Oklahoma, of early Roadian age (Olson, 1962).
**Caseidae**

Caseids reflect the second independent evolution of herbivory in synapsids. Their morphology is very different to that of *Edaphosaurus*; instead of the grinding tooth plates, caseid teeth are leaf-shaped with serrated tips, presumably for the shredding of plant material (Olson, 1968). The fore-limbs are robust, with large claws suitable for digging (Sues and Reisz, 1998). Similar to *Edaphosaurus*, the rostrum is short and the ribs form a barrel-shaped trunk, again presumably to house a large gut (Olson, 1968). Other defining features include a large external naris (Maddin et al., 2008), a maxillary tooth count of less than 15 (Maddin et al., 2008) and a deep depression on the anterior process of the lacrimal (Maddin et al., 2008). There is considerable size variation within caseids, but extremely large sizes were obtained, including the largest known pelycosaur-grade synapsid at 6.5 meters: *Cotylorhynchus romeri* (Romer and Price, 1940; Olson, 1968).

Until very recently, caseids were known only from the Permian. The earliest caseids identified before 2014 were from the Richard’s Spur locality of Oklahoma (Reisz, 2005) and the Bromacker Quarry of Germany (Sumida et al., 2002; Berman et al., 2004). Richard’s Spur has been dated radiometrically to 289 Ma (Woodhead et al., 2010) and a similar Artinskian age has been suggested for Bromacker (Lucas et al., 2005). It was not until description of *Eocasea martini* from the Late Pennsylvanian Hamilton Quarry (Reisz and Fröbisch, 2014) that a record for the early evolution of this clade was available. This specimen shows that early caseids were small insectivores with sharp conical teeth (Reisz and Fröbisch, 2014).

Like varanopids, caseids were a long-lived and geographically widespread clade. During the Early Permian they are known from the USA, France and Germany (Olson, 1968; Sumida et al., 2002; Berman et al., 2004). Middle Permian deposits in the Russian Mezen Group have produced the species *Ennatosaurus tecton* (Efremov, 1956; Maddin et al., 2008). Specimens thought to belong to *Cotylorhynchus* are known from the Lodève group of France (Lucas et al., 2006) and a specimen recently named *Alierasaurus ronchii* has been found at the Cala del Vino Formation of Sardinia (Ronchi et al., 2011, Romano & Nocosia, 2014). Both of these last formation are of uncertain age but are thought to be Middle Permian.

**Eothyrididae**

For a long time after this family was erected by Romer and Price (1940), Eothyrididae was treated very much as a “wastebasket taxon”, containing any small, carnivorous, primitive-looking pelycosaur-grade synapsids that could not be assigned to any other clades. Nine genera were included within the family in the review of Langston (1965), but with the
introduction of a classification based on cladistics, Reisz (1986) assigned most of these taxa to other families, either within Synapsida or in some cases more distant clades. Only two species were retained in the Eothyrididae: *Eothyris parkeyi* and *Oedaleops campi*. The monophyletic grouping of these two species was later confirmed by phylogenetic analysis (Maddin et al., 2008; Reisz et al., 2009; Benson, 2012). These species share a secondary caniniform region posterior to the primary caniniform teeth (Maddin et al., 2008), nasals shorter than the frontals (Reisz et al., 2009) and an elongated subnarial process of the premaxilla (Reisz et al., 2009).

A number of authors have commented on the seemingly primitive morphology of Eothyrididae (Romer, 1937; Romer and Price, 1940; Langston, 1965; Sumida et al., 2014). However, despite the highly plesiomorphic skulls, Eothyrididae appears in the fossil record comparatively late. The oldest species, *Oedaleops campi* (Langston, 1965), was found in the Camp Quarry of the upper El Cobre Canyon Formation. This formation spans the Pennsylvanian-Permian boundary, and the internal biostratigraphy is uncertain, but the upper part of the formation is likely to represent the earliest Permian, possibly Asselian-early Sakmarian (Lucas et al., 2005), leaving Eothyrididae with no Carboniferous representatives. *Eothyris parkeyi* (Romer, 1937) appears in the younger Belle Plains Formation, of early Kungurian age.

**Therapsida**

Therapsids are the more derived synapsids that survive to the present day as mammals (Kemp, 1982). The Palaeozoic therapsids include an increased number of mammal-like features of the anatomy, such as the loss of several skull elements (Sidor, 2001) and the acquisition of a femoral head, which allows a more upright posture (Kemp, 1978). The heterodont dentition that first appeared in pelycosaurian-grade synapsids has further advanced. Carnivorous clades like Biarmosuchia, Therocephalia and Gorgonopsia have greatly enlarged canine teeth in the upper and lower jaws (Rubidge and Sidor, 2001). The Dinocephalia (a clade containing both carnivorous and herbivorous species) possess intermeshing incisors with a lingual heel forming a grinding surface (King, 1988). The herbivorous clade Anomodontia and their diverse subclade Dicynodontia show reduction and eventual loss of teeth, replacing them with a keratinous beak (King, 1988). Therapsids also possess an elongated choana and later develop a secondary palate independently in multiple lineages (Sidor, 2003), allowing more efficient ventilation. The more effective food processing and ventilation allowed a higher metabolic rate, permitting greater environmental
tolerance and a more active foraging mode (Kemp, 2006; Hopson, 2012). Therapsids replaced the pelycosaurian-grade synapsids in their ecological roles during the earliest Middle Permian, and were particularly diverse and abundant during the Middle and Late Permian. Their diversity was greatly reduced by the end-Permian mass extinction, although anomodonts, therocephalians and cynodonts survived into the Triassic (Fröbisch, 2008; Sahney and Benton, 2008; Fröbisch, 2013; Irmis et al., 2013; Fröbisch, 2014).

Some studies have suggested *Tetraceratops insignis*, from the late Kungurian Arroyo Formation of Texas, is the earliest and basalmost therapsid (Laurin and Reisz, 1990; 1996; Amson and Laurin, 2011). Unfortunately there is only one poorly preserved specimen of this species, and its assignment to Therapsida is disputed (Conrad and Sidor, 2001; Liu et al., 2009a). The earliest unambiguous therapsids appear in the fossil record during the Roadian in the Golyusherma Group of Russia (Ivakhnenko, 1995; Benton, 2012). Olson (1962) described a large number of putative therapsid species from the San Angelo formation in Oklahoma, of similar age to the Russian material, but all were extremely fragmentary and most have been reinterpreted as sphenacodontid or caseid synapsids (Sidor and Hopson, 1995; Battail, 2000; Kammerer, 2011).

**Introduction to the Study of Diversity**

The investigation of diversity patterns through time is an important aspect of the study of macroevolutionary processes occurring in organisms. It enables palaeontologists to deduce the major events in the history of the group under study and is also relevant to broader questions, such as the impact and recovery from mass extinctions, the processes underlying evolutionary radiations and the importance of competition and co-evolution.

As would be expected for such an important aspect of palaeontological research, there has been considerable debate throughout its history regarding suitable methods. Much of this debate has concerned the completeness of the fossil record and its adequacy for inferring biological signals (Raup, 1975; Sepkoski et al., 1981; Maxwell and Benton, 1990; Sepkoski, 1993; Benton, 1999; Benton et al., 2000; Fara and Benton, 2000; Alroy et al., 2001; Fountaine et al., 2005; Dyke et al., 2007; Smith and McGowan, 2007; Alroy et al., 2008; Fröbisch, 2008; Barrett et al., 2009; Alroy, 2010b; Benton et al., 2011b; Mannion et al., 2011; Benton, 2012; Brocklehurst et al., 2012; Benson and Upchurch, 2013; Fröbisch, 2013; Pearson et al., 2013; Fröbisch, 2014). Other debates have concerned suitable methods to estimate species richness
and correct for sampling biases (Alroy et al., 2001; Lane et al., 2005; Smith and McGowan, 2007; Alroy et al., 2008; Alroy, 2010b; Benton and Ruta, 2011; Mannion et al., 2011).

Biases in the Fossil Record

The incompleteness of the fossil record has long been acknowledged, but it wasn’t until the seminal paper of Raup (1972) that consideration was given towards how the incompleteness of the fossil record may be impacting on our interpretations of it in a systematic and, more importantly, correctable manner. Raup identified seven sources of error which may be influencing estimates of species richness:

1: Range charts. Early estimates of diversity were based on compendia giving range data of the taxa rather than details of specific occurrences. For example, if a species is listed as being present from the Asselian until the Artinskian, its range will pass through the Sakmarian stage, even if no specimens of that species have been discovered in Sakmarian strata. Such counting methods lead to phenomena known as edge effects, resulting from the fact that the first and last appearances of a taxon in the fossil record are unlikely to be the true first and last appearances; the ranges will actually be truncated at either end (Raup, 1972). This leads to diversity being artificially lowered during the earliest time slices, as taxa which were actually present in these time slices may not have their ranges extended back into them. If the time period under study does not extend to the recent, then the latest time slices will also have lowered diversity.

Mass extinctions can produce a specific edge effect for the same reason (Signor and Lipps, 1982); many taxa may have died out in a single event, but not all their ranges will be observed as extending to this event. Therefore, many taxa (particularly rare taxa with a lower probability of preservation and discovery) will appear to have died out before the event, and the mass extinction will appear to be a gradual decline (Signor and Lipps, 1982). This effect has been dubbed the Signor-Lipps effect.

2: Influence of extant records. Since our knowledge of extant taxa is better than that of the fossil record, fossil taxa with living representatives will most probably have their ranges extended to the recent (Cutbill and Funnel, 1967). As such the truncation of ranges mentioned above is considerably less likely for taxa surviving to the present. This leads to a specific edge effect dubbed “The Pull of the Recent” (Raup, 1972): since a higher number if late Mesozoic
and Cenozoic taxa have living representatives and will have their ranges extended to the recent, estimates of diversity during the late Mesozoic and Cenozoic will be raised relative to the Palaeozoic.

Alroy et al. (2008) demonstrated that the Pull of the Recent has a large effect on global diversity patterns. Two curves were produced, the ranges of recent taxa in one extended to the recent, and ranges in the other extended only to the last fossil occurrence. There was little difference between the two curves during the Palaeozoic, since few Palaeozoic species have survived until the present day. However, during the Late Jurassic and Cretaceous the curve not including recent occurrences is noticeably lower than the other (Figure 2). During the Palaeogene and the Neogene, the curve incorporating recent occurrences shows a considerable increase in diversity from less than 1000 to almost 2500 genera. However, the curve only based on fossil occurrences shows a much more modest increase to less than 1500. Alroy et al. (2008) argued that the Cenozoic increase which has been supported in previous diversity curves of Valentine (1970) and Sepkoski (1982; 1993) was in fact an artefact of the Pull of the Recent.

Figure 2: Diversity curves illustrating the impact of the Pull of the Recent, from Alroy et al. (2008). The thick line represents the diversity estimate when the ranges of genera are extended to the recent. The thin line represents the diversity estimate when the ranges of genera are extended to the last fossil occurrence.

3: Duration of geological time units. The time bins employed in diversity studies are usually the geological time units, whether stages, epochs or periods. Raup (1972) argued that this is problematic, since longer time intervals will show a higher diversity. Foote (1994)
supported this opinion, arguing that more taxa would come and go during a long interval, raising that interval’s diversity. Miller and Foote (1996) added that during a longer time interval, there would be more sedimentation, leading to a higher probability of preservation. On the other hand, Fastovsky et al. (2004), in their study on dinosaur diversity, found no correlation between generic richness and the length of the stages and argued that the richness patterns they observed were not related to stage length. It is important to note that the geological time units are based on biostratigraphy, and the length of these units is therefore not independent of species turnover through time.

4: Monographic effects. Raup (1972) suggested that the level of interest in a particular group or geographic area will affect diversity estimates, as will the quality of the taxonomic research into a group. As an example of this, Raup cited a single monograph (Cooper, 1958) which alone shifted a diversity peak in brachiopods from the Devonian to the Ordovician. The tendency for workers to examine particular areas more thoroughly is well documented (e.g. Fastovsky et al., 2004; Brocklehurst et al., 2012; Cleary et al., 2015), with many groups showing a bias towards North America, Europe and Asia and the southern landmasses being considerably less well sampled. Interest in particular clades, either for reasons of popularity e.g. dinosaurs, or usefulness e.g. ammonites for biostratigraphy, will lead to substantially more work being done on those clades and potentially more species being named (Raup, 1972). A time dependant aspect was also noted by Raup: if a fossil clade has living representative, more complete morphological information is available for that clade, which will affect taxonomic revisions.

5: Lagerstätten. Areas of exceptional preservation, such as the Burgess Shale, Solnhofen, and the Messel Shale, produce large numbers of nearly complete fossils. The quantity of material will obviously produce a high diversity, and the quality of the preservation will increase the amount of information available for taxonomic revisions. This correlation between Lagerstätten and peaks in diversity has been noted in multiple studies (e.g. Brocklehurst et al., 2012; Friedman and Sallan, 2012; Cleary et al., 2015). Raup (1972) pointed out that Lagerstätten appear to be more common in younger rocks, possibly raising recent diversity estimates. At the very least, they add noise to the data (Raup, 1972).

6: Area-diversity relationships. Taxa tend to be geographically restricted due to barriers to their dispersal. As such, when a new area is explored, a high rate of discovery of new taxa
inevitably follows (Raup, 1972). Raup suggested that this problem should be particularly severe in the marine realm; only a small fraction of the ocean area at any point in the geological past is available for study since, with the exception of deep ocean cores, palaeontologists are limited to studying rocks on continents and islands. Therefore the apparent diversity of any group is limited to the taxa restricted to the areas available for sampling. This problem is exacerbated by the fact that diversity has been shown to be area dependant (Preston, 1962). Our diversity estimates depend not only on outcrop exposure, but also on the distribution of the exposure. Moreover if geographic coverage improves towards the recent, as Raup (1972) suggests, this is yet another bias towards higher diversity in younger rocks.

![Figure 3: The relationship between estimates of diversity and the volume of sedimentary rock. From Raup (1972)](image)

7: Sediment volume. Raup (1972) was the first to note a correlation between sediment volume and diversity estimates (Figure 3). Since then such a correlation, as well correlations with similar proxies such as number of formations in each time interval and rock outcrop area, has been verified both globally and within individual clades and areas (Smith, 2001; Crampton et al., 2003; Fröbisch, 2008; Smith and McGowan, 2008; Wall et al., 2009; Benson et al., 2010; Mannion et al., 2011; Benson and Upchurch, 2013; Fröbisch, 2013; 2014). It is
intuitive that a higher availability of rock of a particular age would lead to a higher observed
diversity in that particular time bin. Unfortunately the strength of the correlations between
observed diversity and proxies for rock availability seem to be suggesting that our diversity
estimates are merely showing how much rock is available from each time bin rather than
diversity. Rocks are continuously being destroyed by erosion or subduction, or overlain by
other layers. Moreover, rates of sedimentation have varied through time, and a higher rate of
sedimentation increases the probability of preservation (Raup, 1972).

Since this leading paper, other influences have been shown to affect the quality of the
fossil record. The impact of the size of the organisms, for example, has been shown to be
important but also complicated. It is natural to think that smaller animals, more easily
destroyed by taphonomic processes, would have a worse fossil record than larger, more robust
species. Indeed, it has been shown in studies of dinosaurs in the Dinosaur Park Formation
(Brown et al., 2013) and in comparing sauropod dinosaurs to Mesozoic birds (Brocklehurst et
al., 2012) that smaller animals tend to leave more incomplete skeletons. However, Fara and
Benton (2000), assessing the proportion of Lazarus taxa relative to observed lineages in
Cretaceous tetrapods, found the fossil record of small bodied animals is no less complete than
that of larger ones. Cleary et al. (2015), in their study on ichthyosaurs, found an unusual
result: both small and large ichthyosaurs were poorly preserved relative to those of
intermediate size. Complicating factors may include the influence of Lagerstätten; smaller
animals may be easier to destroy, but are also easier to rapidly bury and preserve whole
(Brocklehurst et al., 2012). Historical factors are also important; during the early days of
palaeontological collection, a desire for large articulated specimens for museum displays may
create the impression that smaller animals are less likely to be preserved (Brown et al., 2013).

The environment in which an organism lived unsurprisingly has a great effect on the
probability of its preservation, as well as the quality of the fossil preserved. For example,
Brocklehurst et al. (2012) showed that Mesozoic birds from fluvial and lacustrine localities
were better preserved than those from marine localities (where the high energy would destroy
skeletons) or terrestrial localities (in which sedimentation rates are lower). Cleary et al.
(2015), meanwhile, found ichthyosaurs to be better preserved in marine muds and sands than
carbonates. They suggested this is due to the larger number of benthic scavengers in marine
carbonates. However, again, this issue is shown to be more complicated by further study.
Benson and Butler (2010) showed that the influences of sampling biases on the record of
marine tetrapods differ in shallow marine and open ocean formations; the open ocean record
is heavily influenced by the quantity of rock known from each time interval, suggesting a strong influence of bias due to temporal heterogeneity of fossil sampling. The shallow marine record, meanwhile, showed a stronger relationship with continental flooding, demonstrating that it was the environment directly influencing diversity: the Common Cause hypothesis (Benson and Butler, 2010). Uneven sampling of different lithologies will affect the fossil record: taxa limited in the proportion of environments in which they live will not be sampled if their preferred environment is not sampled (Rook et al., 2013). This biases the marine and non-marine realms differently; marine vertebrate diversity correlates strongly with the evenness of sampling of different lithologies, but marine invertebrates and continental taxa do not (Rook et al. 2013).

The influence of lithification (consolidation of sediments) on the fossil record has recently begun to receive attention. Lithified rock units produce about half of the diversity of unlithified units (Alroy et al., 2008; Hendy, 2009) since fossils are more likely to be destroyed during lithification or during the mechanical breaking required to examine such sediments (Kowaleski et al., 2006). Small specimens are particularly vulnerable to being destroyed, or simply overlooked (Kowaleski et al., 2006). Meanwhile, unlithified rocks may be examined by sieving, increasing the likelihood of finding smaller specimens undamaged (Kowaleski et al., 2006). Unlithified sediments are more common in more recent sediments (Hendy 2009), yet another bias towards higher observed diversity in the Cenozoic. For invertebrate workers, there is a bias towards organisms with calcite shells in lithified sediments, since aragonite is more easily destroyed during diagenesis (Hendy, 2009).

With these complications surrounding the interaction between diversity and sampling biases, it is unsurprising that debate exists concerning the quality of the fossil record, and whether the signal of our diversity curves represents biases or an actual biological signal. As might be predicted, investigation into the completeness of the fossil record of different clades produces different results. Tarver et al. (2011) suggested that systematic datasets of palaeontological data should be investigated individually for the quality of their record if they are to be used to derive macroevolutionary patterns.

**Creation of Diversity Curves**

The simplest method of producing curves of species richness through time is the taxic diversity estimate. This is a raw count of the number of species in each time bin. Whilst this method is simple and requires minimal information, it is, as discussed above, heavily
influenced by the vagaries of sampling and other sources of error in the fossil record, and may not accurately reflect the true palaeodiversity. As such, several methods have been proposed in order to create diversity estimates which more closely represent actual historical trends.

The Use of Compendia and Databases in Diversity Estimates

Early estimates of diversity (species richness) were produced using extremely basic methods. In fact the earliest published curve (Philips, 1860), based on a compendium of British fossil data, was a hand drawn estimate of diversity, with no scale or indications of time binning. Later studies (e.g. Valentine, 1969; Sepkoski et al., 1981; Raup and Sepkoski, 1982) used the more objective method of assigning taxa to bins and creating a curve representing the changing diversity between bins to produce family-level curves. These diversity estimates showed many of the signals found in later diversity estimates, such as the “Big Five” mass extinctions (Raup and Sepkoski, 1982), the three evolutionary faunas (Sepkoski, 1981) and the large increase in diversity during the Cenozoic (Valentine, 1969). All of these early studies were based on compendia of marine taxa detailing first and last appearances in the fossil record, several updates of which were published by Sepkoski, along with diversity curves and extinction estimates over the following years (Sepkoski, 1984; 1993; 1996; 2002). However, diversity estimates based on compendia are problematic. These supply age range data for taxa, but little or no information on collections, localities, geography, environment, or collection method. As such, the possible counting methods available to researchers are limited, as well as the possibility of correcting for sample size or examining local patterns or biases. The need for such information has led to the introduction of databases into diversity studies.

The Paleobiology Database (hereafter PBDB, recently renamed Fossilworks) was created to address these issues. This database not only lists taxa at the genus and species level, but also collections, references, localities, formations, and information on lithology and ecology. Such data allows not only the generation of diversity curves at both global and local levels, but furthermore allows investigation into ecological changes through time and space in the fossil record and also into sample size. The PBDB is a user-updated database, and as such is not fully complete and may contain errors due to failure to update changes in taxonomy or the ages of formations. However, for a well-sampled, numerous, and comprehensively updated clade, such rare errors in the database should not have a large effect on diversity estimates. The PBDB has been used to investigate global diversity through time by Alroy et al. (2001; 2008) as well as in other investigations into local and clade-specific
diversity patterns, sampling biases and ecological changes through geological time (see PBDB official publication list)

Because datasets in the terrestrial fossil record tend to be smaller than those in the marine realm, the impact of missing or incorrect data becomes greater. Many studies of terrestrial clades have therefore not taken data from the PBDB, but instead used up-to-date databases generated specifically for their chosen time and clade. One such database is the Early Tetrapod Database, used in several studies on the diversity of tetrapods from the Middle Devonian until the Early Jurassic (Sahney and Benton, 2008; Sahney et al., 2010; Benton, 2012; Benton et al., 2013). A local database details the contents of localities belonging to the Beaufort Group of the Karoo Supergroup of South Africa, spanning the Middle Permian until the Early Triassic (Nicolas & Rubidge, 2009; 2010). This has been instrumental in investigations of diversity and sampling bias in South Africa across the Permian-Triassic boundary (Fröbisch, 2013; Irmis et al., 2013; Fröbisch, 2014).

**Counting Methods**

Simple modifications to counting methods may produce more accurate diversity estimates. The earliest diversity estimates, based on range data of species (e.g. Valentine, 1969; Raup and Sepkoski, 1982) are afflicted by edge effects (Figure 4A). Foote (1999; 2000) suggested that one should only count taxa sampled in the time bin and ignoring Lazarus taxa (taxa sampled before and after a particular time bin, and so inferred to be present within the bin). This so-called “sampled in bin” diversity estimate reduces issues such as edge effects, but does not remove another set of biases known as rate effects. Periods of high species turnover would lead to many species being present for only a short period of time. This reduces the probability of their preservation and discovery in the present day (Foote, 1999; Alroy, 2010a). As such our diversity estimates would be lower for times of high species turnover, particularly in time bins where sampling is poor. Alternatively, if turnover rates are high within a long, well-sampled time bin, the number of species counted within that time bin will be considerably higher than the standing diversity (the actual diversity at any one point in time) (Foote, 1999). It has been suggested that a possible solution to rate effects might be to remove taxa known only from a single interval (singletons) from diversity estimates (Harper, 1996). To do so would also reduce the effect of Lagerstätten by eliminating taxa only found in areas of exceptional preservation. However, removing singletons artificially reduces the diversity estimated for the most recent time bins (Figure 4B): any species which first appears in the latest time bin can only be a singleton (Foote, 2000).
Figure 4: Illustration of the impact of different counting methods on a time period of constant diversity. From Foote (2000). A) All observed species counted; B) All observed species except singletons (taxa known only from one time bin) counted; C) Singletons only counted; D) Taxa which cross the boundaries between time bins counted.

Alroy (1996) and Alroy et al. (2001) suggested counting taxa at the boundaries between time bins, including only the taxa which crossed the boundary. This method automatically eliminates singletons, which by definition do not cross the boundaries, and is independent of interval length. The smoothness of the diversity curve was interpreted as the curve containing less “noise” (Alroy et al., 2001). However, Foote (2000) suggests that this method is heavily biased by edge effects (Figure 4D). Alroy (2010a) argued that, although sampled in bin diversity estimates are not completely reliable due to rate effects, the heavy impact of edge effects on boundary crosser and range through diversity estimates makes it the best method to use.

Sampling proxies

One of the most frequently used methods to investigate the impact of sampling biases on the fossil record is to investigate the strength of the correlation between diversity estimates and various proxies for biases. Such proxies endeavour to quantify a particular aspect of the
bias through geological time. For example, one can use the area of sedimentary rock outcrop available from each time bin as a proxy for geological biases (Smith, 2001; Crampton et al., 2003; Smith and McGowan, 2007; 2008; Wall et al., 2009; Fröbisch, 2013; 2014). An alternative quantification of rock availability is the number of fossil-bearing rock formations (Fröbisch, 2008; Barrett et al., 2009; Butler et al., 2009; Benson et al., 2010; Mannion et al., 2011; Benton, 2012; Benson and Upchurch, 2013). Quantification of human sampling effort is more difficult, but the development of the PBDB allows the use of fossil-bearing collections. Each of these collections represents an event in which a fossil-bearing locality of a particular age was sampled, and so can provide a quantification of the amount of effort workers have put into sampling rocks of a different ages. Some studies have used the number of fossil-bearing collections as a proxy for anthropogenic sampling biases (Crampton et al., 2003; Butler et al., 2011a; Brocklehurst et al., 2012).

Many of the above studies have cited a significant correlation between such sampling proxies and the diversity estimates of the clades under study as evidence that the signal from the diversity curves is predominantly that of sampling rather than a biological signal. However, such inferences have been criticised. Benton et al. (2011) argued that the sampling proxies used may well be redundant with the diversity signal; if the diversity of a particular clade decreases, one would expect the number of formations or collections bearing fossils of that clade to decrease as well. It was also argued that using the number of formations or collections bearing fossils of a particular clade as a sampling proxy for that clade does not take into account times when workers have studied rocks of a particular age, but have not found fossils of the clade of interest (Benton et al., 2011). Benson and colleagues (Benson et al., 2010; Benson and Mannion, 2012) supported the use of such proxies, but argued against the simplistic view that presence of a significant correlation indicates a strong influence of sampling biases and absence of a significant correlation indicates the fossil record is good. The observed fossil record is a product of both the biological signal and sampling, and one should only expect a perfect correlation between sampling and observed diversity if the actual diversity was constant through time (Benson and Mannion, 2012). It was shown that multivariate models incorporating both sampling bias and an underlying biological signal fit marine reptile data (Benson et al., 2010) and sauropodomorph data (Benson and Mannion, 2012) best.

As well as these more general issues, problems with specific proxies have been identified. Formation counts have been criticised as being extremely arbitrarily defined, with formations varying by up to eight orders of magnitude in volume (Peters, 2006; Peters and
Heim, 2010; Dunhill, 2012). Crampton et al. (2003) demonstrated that the number of formations poorly represents sedimentary outcrop area. In fact, rock outcrop area measured from geological maps may not necessarily correlate with the area of rock that is exposed and available for study due to factors such as soil coverage (Dunhill, 2012). Benton et al. (2013) provided a detailed comparison of various proxies for the quality of the rock record, including formation counts from various sources, rock outcrop area, and counts of rock units from the Macrostrat database (units representing hiatus bound sedimentary rock packages [Peters and Heim, 2010]). These different proxies, supposedly assessing similar biases, showed great variation in the strength of their correlation to each other and to tetrapod diversity.

Another extensively-discussed issue with the use of such proxies is the possibility that both diversity and proxies such as rock outcrop area or number of formations may be under the control of an external factor: the Common Cause hypothesis. The most frequently cited external cause is sea-level change, the impact of which is complex and has received much attention in the literature. It is logical that fluctuations in sea level will affect the preservation potential in certain environments. Positive correlations have been found between sea level and the raw diversity of marine organisms, suggesting that increased formation and preservation of coastal deposits have resulted in a higher quality fossil record (e.g. Benson and Butler, 2010; Rook et al., 2013). It has also been suggested that increased sea level increases preservation potential for terrestrial organisms, as more will be washed into environments with high preservation quality such as deltas, estuaries and lagoons (Haubold, 1990). Conversely, a negative correlation between sea level and the quality of the terrestrial fossil record has been found (Mannion and Upchurch, 2010; Upchurch et al., 2011), as higher sea level reduces the amount of terrestrial sedimentary rock (Smith, 2001; Smith and McGowan, 2007). The Common Cause hypothesis further complicates the relationship between sea level and diversity. In the marine realm, it has been argued that rises in sea level not only increase the quantity of coastal deposits, but also marine diversity itself due to the expansion of near shore environments (Benton and Emerson, 2007; Butler et al., 2009; Benson and Butler, 2010; Hannisdal and Peters, 2011). On land it is possible that rises in sea level result in fragmentation of terrestrial land areas, promoting an increase in speciation rates (Bakker, 1977; Upchurch and Barrett, 2005; Benton, 2009). Conversely, higher sea level reduces available land area, maybe resulting in decreases in the diversity of terrestrial clades (Weishampel and Horner, 1987; Dodson, 1990; Benton and Emerson, 2007). A final alternative is that sea level may have little impact on either preservation potential or diversity.
in the terrestrial fossil record. Butler et al. (2009) demonstrated that sea level does not show significant positive or negative correlation with the diversity of dinosaurs.

**Sampling correction**

While different counting methods are able to reduce the impact of certain errors such as edge effects, they do not solve the problems of heterogeneous sampling by palaeontologist, or variations in rock availability. Raup (1972) suggested two methods to deal with this issue: modelling and subsampling. Later a third method was introduced: the phylogenetic diversity estimate (Norrell, 1992; Smith, 1994).

Diversity analyses, both in palaeontology and neontology, depend heavily on sample size (Sanders, 1968; Raup, 1972). If only one specimen from a locality is sampled, the dataset will contain only one species. Increasing the number of specimens will increase the number of species, although the amount by which the number of species increases depends upon the relative abundances of individual species. If the locality is dominated by a few very abundant species and all other species are rare, sampling more specimens will lead to a very slow increase in the number of species since most new specimens sampled are more likely to belong to the abundant species rather than a new species.

Subsampling standardises the size of all samples to the size of the smallest sample. The method which has been most commonly used in palaeontology is rarefaction (Sanders, 1968). The technique, originally proposed for ecological study, was to draw specimens from a locality at random until the number of specimens reached the chosen sample size, and to count the number of species present in the subsample. This would be repeated multiple times in order to converge on a mean expected number of species. When applied to palaeodiversity, one wishes to standardise the sample size of each time bin instead of each locality. As such, instead of drawing specimens from each locality at random, one may draw either individual taxonomic occurrences (Miller and Foote, 1996) or entire collections (Smith et al., 1985; Alroy et al., 2001) at random from each time bin. The former weights each taxonomic occurrence equally, assuming that the number of occurrences is directly proportional to the number of species (Alroy et al., 2001). This is a problematic assumption to make, as the relationship between occurrences and taxa will vary depending on how widespread individual taxa are: widespread taxa are found in more localities, and so will be represented by more occurrences. On the other hand, to draw collections assumes that the number of species is proportional to the number of collections. This is again a problematic assumption if different collections within a single time period have produced very different numbers of species.
Figure 5: Three species accumulation curves representing the mean number of species observed over 1000 random sets samplings from three collections of specimens. Each collection has identical numbers of species and identical numbers of individuals, but different relative abundances of species. The red curve represents a collection in which all species have the same frequency; the black curve represents a collection in which all species have a different frequency; the blue curve represents a collection in which one species has a high abundance, and all other species have equal lower abundance.

In short, rarefaction makes assumptions that are only valid if taxon abundance and distribution do not vary. The consequences of these assumptions of rarefaction may be seen when one examines taxon accumulation curves (Figure 5). These curves represent the relationship between the number of samples drawn (either occurrences or collections) and the mean number of species sampled. Such curves show a rapid initial increase as each new draw has a large potential to uncover a new species, before reaching a plateau when most of the species have been found and drawing a new sample is less likely to add a new taxon. For rarefaction to give an accurate representation of the relative diversity difference between two time bins, the rarefaction curve for both time bins should be identical if they contain the same number of species. However this is not always the case: the curves may vary because of different relative abundances and range sizes of different species. If one were to subsample
the three time bins represented by the rarefaction curves in Figure 5, drawing for example 50 samples from each, one would obtain different diversity values despite the fact that the actual number of species in all three collections is the same.

Alroy (2010b) presents an alternative subsampling method as a solution to this problem: Shareholder Quorum Subsampling (SQS). The name comes from the fact that each taxon is treated as a “shareholder”, whose share is its number of occurrences. As in rarefaction, occurrences are sampled at random. A taxon’s full share is considered represented if it is sampled at least once. Unlike rarefaction, the sampling does not continue until a specific number of occurrences have been drawn, but instead continues until a certain proportion of shares (the “quorum”) are represented (Alroy, 2010b). Alroy (2010a) provided a hypothetical example demonstrating the advantages of the SQS method over rarefaction. One time bin contains 10 species, each of equal frequency making up 0.1 of occurrences. If two samples are drawn, on average 1.9 species will be observed, since the second sample will be a different species from the first 90% of the time. A second time bin has 20 species again of equal frequency, so each species will have a frequency of 0.05. Thus, if two samples are drawn again, the mean number of species counted will be 1.95. Rarefaction has failed to show that the second time bin is twice as diverse as the first. If, however, SQS is used with a quorum of 0.2, the correct relative diversity is recovered. Since every species in the first time bin has a frequency of 0.1, the quorum is reached when two species have been drawn. In the second time bin, in which each species has a frequency of 0.05, the quorum is reached when four species have been drawn. SQS therefore shows that the second time bin is twice as diverse as the first.

Subsampling methods are only appropriate when the sample sizes in all time bins are reasonably large. One ideally would not reduce the sample size to the point on the species accumulation curve before the plateau (Hammer and Harper, 2006). When the curve is beginning to plateau, this implies that the subsample contains all but the rarest taxa. However, if one time bin contains a particularly small sample, then one is faced with two options: either reducing the sample size of all time bins to a point where subsampling becomes unreliable, or removing this bin from the analysis and potentially missing a key event. Neither of these options is ideal, and so researchers working on clades or time periods where sample sizes are small are forced to use different methods to correct for sampling bias.

Raup (1972) suggested modelling as an alternative to subsampling, but this was not explored in great detail until Smith and McGowan (2007) introduced the residual diversity estimate. This approach requires a proxy for sampling bias such as number of collections or
formations or outcrop area in each time bin. A model diversity estimate, based on a perfect linear relationship between diversity and the chosen sampling proxy, is produced by sorting both diversity and proxy data from low to high and fitting a linear model. The model diversity estimate is then subtracted from the observed diversity, leaving the residual diversity estimate. The thinking behind this method is that the observed diversity estimate is a signal of both sampling and the actual diversity. Subtracting the model diversity estimate in theory removes the signal from sampling, leaving only the biological signal (Smith and McGowan, 2007). This method has proven popular, particularly in analyses of terrestrial datasets where sample sizes are often small (Smith and McGowan, 2008; Barrett et al., 2009; Butler et al., 2009; Wall et al., 2009; Benson et al., 2010; Butler et al., 2011a; Benson and Upchurch, 2013; Fröbisch, 2013; Pearson et al., 2013; Fröbisch, 2014).

There have been controversies surrounding this method. Benton et al. (2011) has subjected it to the same criticism of using proxies to test for sampling bias: the problem of redundancy. It should also be noted that it only takes into account a single sampling bias, and assumes sampling has a perfect linear relationship with diversity, an assumption only true if diversity never varied (Benson and Mannion, 2012). Lloyd (2012) refined the method, allowing for non-linear relationships between the sampling proxy and diversity, and also introducing confidence intervals to show which peaks and troughs are significant. However, Pearson et al. (2013) argued against using this method, finding no reason why there would be a polynomial relationship between sampling and diversity.

The final method of sampling correction is the phylogenetic diversity estimate (Smith, 1994). This method incorporates ghost lineages into a diversity estimate: lineages not sampled from the fossil record but inferred from a phylogeny under the assumption that two sister taxa must have split from their common ancestor at the same time (Norrell, 1992). Incorporating these lineages into a phylogeny allows the inclusion of as-yet unsampled portions of the fossil record. Use of this method is obviously limited to clades for which a comprehensive phylogeny exists, and as such it has been most widely applied to vertebrates (Upchurch and Barrett, 2005; Barrett et al., 2009; Benson et al., 2010; Mannion et al., 2011; Ruta et al., 2011; Walther and Fröbisch, 2013).

As with all other sampling correction methods, flaws have been identified with the phylogenetic diversity estimate. The sampling correction is one-directional: lineages may only be extended back in time, not forward, causing higher diversity earlier in time (Wagner, 2000; Lane et al., 2005) and exaggerating the Signor-Lipps effect (Lane et al., 2005). Polytomies in the phylogeny will also create an error, biasing towards higher diversity as all
taxa in the polytomy will have ghost lineages extending back as far as the oldest taxon (Upchurch and Barrett, 2005). Another issue surrounds ancestor-descendant relationships. The cladograms produced by current cladistic methods assume bifurcating speciation from hypothetical ancestors (Norrell, 1992; Smith; 1994; Wagner and Erwin, 1995). If ancestors are sampled in the fossil record, cladistic analysis will resolve them either in a polytomy with or as the sister to the descendants (Lane et al., 2005; Bapst, 2013). While previous studies have tried to sidestep this issue by assuming that the probability of sampling an ancestor is low enough to be negligible (e.g. Norrell, 1993), it has been shown that such assumptions are invalid (Funk and Omland, 2003). If ancestors are included in a phylogeny and are not identified as such, they will lead to the inference of an incorrect ghost lineage and raise the phylogenetic diversity estimate (Lane et al., 2005). Despite these issues, the simulations of Lane et al. (2005) suggest that the phylogenetic diversity estimate is more accurate than the raw data, although these simulations assumed a correct phylogeny.

No method of estimating species richness through time is without flaws or biases. While some methods are more appropriate for certain datasets than others, none may be considered perfect. As such it is advisable to use multiple methods to estimate species diversity. Where the methods agree, one may assume that the estimated diversity trends are reflecting an accurate biological signal. Where they disagree, one must examine the biases affecting each method and deduce which diversity estimate is most reliable in the particular instance.

**New Research Areas**

Studies into the diversity and the completeness of the fossil record during the time period occupied by pelycosaurian-grade synapsids have been extremely limited. There have been no studies dedicated to the detailed examination of the changes in species richness in synapsids during the Late Carboniferous and Early Permian. Examinations of the wider tetrapod and amniote clades have produced differing opinions, for example regarding the diversification of herbivores, Olson’s extinction and the impact of sampling biases on the fossil record. The use of sampling correction has been patchy, and restricted to the use of the residual diversity estimate. Investigations onto the quality of the fossil record have included correlation tests with sampling proxies and an examination of the completeness of specimens using the arbitrary and coarse grading system, but little else.
This thesis will present a thorough evaluation of the evolution of basal synapsids. The investigation will begin with a study of the phylogeny of pelycosaurian-grade synapsids, which will form the basis of further analyses. This part of the thesis also includes the redescription of the poorly-known basal synapsid “Mycterosaurs” smithae. In addition, an examination of the quality of the fossil record of pelycosaur-grade synapsids will be undertaken, including the completeness of their specimens using both the character and skeletal completeness metrics, the fit of the fossil record to phylogeny, and also examination of the history of discovery in order to ascertain whether the influence of biases has changed through time and how the taxonomic practices may affect diversity estimates. Synapsid diversity will be investigated at both the genus and the species level. Global diversity curves will be generated, as well as diversity curves for each family of pelycosaurian-grade synapsids in order to examine the changes in faunal composition occurring at this time. Sampling correction will be carried out using the phylogenetic and residual diversity estimates.

Moreover, since synapsids represent the earliest appearance of many morphological innovations, such as herbivory, macro-carnivory and possibly a semi-aquatic lifestyle, the impact of such innovations on the patterns of cladogenesis, origination and extinction will be studied. This examination will be extended to all amniotes until the end of the Triassic, in order that the more general patterns can be identified and compared to those found in pelycosaurian-grade synapsids. Tree topology analysis will be used to identify areas in the amniote phylogeny in which significant shifts in the rate of cladogenesis occur. These shifts will be examined for correlation with events such as mass extinctions and the evolution of “key innovations”. To further test the impact of innovations such as herbivory and an aquatic lifestyle, origination rates of those with such innovations will be compared to those without, to see if the timing of increases in origination rate of those with “key innovations” coincides with the timing of diversification shifts identified by tree topology analysis.
Chapter 2
Phylogenetic Analysis of Pelycosaurian-Grade Synapsids
Hypotheses of the Relationships of Pelycosaurian-grade Synapsids

Romer and Price (1940) provided the first review of relationships of pelycosaurian-grade synapsids incorporating information from all specimens known at the time. This review proposed that basal synapsids were divided into three suborders: Ophiacodontia, Edaphosauria and Sphenacodontia (Figure 6). Ophiacodontia were considered the basalmost group from which the other clades evolved, and contained Ophiacodontidae and Eothyrididae. Edaphosauria was a grouping of the two herbivorous clades, Edaphosauridae and Caseidae. The Sphenacodontia contained Varanopidae (supposedly basal within this clade), Sphenacodontidae and Therapsida. Since this review by Romer and Price (1940), the sister-group relationship between sphenacodontids and therapsids has been largely accepted, whereas the relationships of all other basal synapsid clades have undergone many revisions.

Figure 6: The relationships of pelycosaurian-grade synapsids suggested by Romer and Price (1940)

Reisz (1980) was the first to employ phylogenetic treatment of characters to decipher the relationships of pelycosaurian-grade synapsids. Unlike Romer and Price (1940), who focused mostly on the postcranium, 20 out of the 24 characters used by Reisz (1980) were cranial characters. This analysis supported a basal split between the Caseasauria (a clade containing caseids and eothyridids) and Eupelycosauria (all other synapsids). Romer and
Price’s Sphenacodontia was still supported, with Varanopidae, Edaphosauridae, Ophiacodontidae, and Caseasauria as successive outgroups (Figure 7A). Brinkman and Eberth (1983) also used a phylogenetic approach, but employed a different character list compiled through study of six well-known species representing the major clades. For the first time a sister-group relationship between Edaphosauridae and the clade containing sphenacodontids and therapsids was suggested, a grouping named Sphenacomorpha (Ivakhnenko, 2003; Spindler et al., 2015), that is also considered valid in the most recent phylogenetic analyses of basal synapsids. Ophiacodontidae was suggested to represent the sister taxon to Sphenacomorpha, whereas Varanopidae were found to be the sister to Caseidae (Figure 7B).

Reisz (1986), in the volume of the Handbook of Paleoherpetology dedicated to Pelycosauria, used a set of 26 characters to infer the relationships that have since become the widely accepted consensus (Figure 7C). The basal split between Caseasauria and Eupelycosauria was supported and Edaphosauridae, Ophiacodontidae and Varanopidae were found to be successive outgroups to Sphenacodontia (the clade containing sphenacodontids and therapsids). These relationships have been sustained by the introduction of computer
algorithms for phylogenetic analysis (Gauthier et al., 1988; Modesto, 1994; Berman et al., 1995; DeBraga and Rieppel, 1997; Reisz and Fröbisch, 2014).

Most recent phylogenetic analyses of pelycosaurian-grade synapsids have examined the relationships within clades. Varanopidae has been a particular focus, not only with the description of new taxa and specimens (Reisz and Dilkes, 2003; Anderson and Reisz, 2004; Maddin et al., 2006; Campione and Reisz, 2010; Modesto et al., 2011; Berman et al., 2014) but also the reassignment to this clade of several species previously thought to be diapsids or therapsids (Reisz et al., 1998; Reisz and Laurin, 2004; Reisz and Modesto, 2007; Reisz et al., 2010). Sphenacodontidae has also come under scrutiny (Reisz et al., 1992; Laurin, 1993; Kissel and Reisz, 2004; Fröbisch et al., 2011; Spindler et al., 2015), leading to the realisation that one of the subfamilies traditionally included within this clade, the Haptodontinae (Romer and Price, 1940), are in fact a paraphyletic grade outside Sphenacodontidae. Other analyses have examined the relationships within Ophicacoacodontidae (Berman et al., 1995), Caseidae (Maddin et al., 2008; Reisz and Fröbisch, 2014), and Edaphosauridae (Modesto, 1994; 1995; Mazierski and Reisz, 2010).

Recently, Benson (2012) reviewed the relationships of pelycosaurian-grade synapsids with a global phylogenetic analysis of 53 taxa. This analysis included evaluation of all characters from analyses published prior to that date, as well as the addition of new characters. Recognising that the majority of phylogenetic analyses thus far had been heavily biased towards the cranium, Benson (2012) added large numbers of new postcranial characters. The relationships obtained by this analysis did not recover the basal split between Caseasauria and Eupelycosauria. Instead, Caseasauria was found to be the sister to Sphenacomorpha, while Ophiacodontidae and Varanopidae formed a monophyletic grouping that was the sister to all other synapsids (Figure 7D). It was the postcranial characters which forced this set of relationships; when these characters are removed, Caseasauria is returned to a basal position. However, Benson (2012) acknowledged that the lack of information on the early evolution of both caseids and eothyridids was a problem. At that time, no postcranial information was available on either Eothyris or Oedaleops, and caseids earlier than the latter part of the Early Permian were unknown. The discovery of the Late Carboniferous caseid Eocasea provided fresh information on the postcranial anatomy of caseids early in their evolution (Reisz and Fröbisch, 2014) and re-analysis of Benson’s matrix with Eocasea included found Caseasauria in their more “traditional” position as the sister to all other synapsid clades (Reisz and Fröbisch, 2014).
Expanding Phylogenetic Analysis of Pelycosaurian-grade Synapsids

Institutional Abbreviations
FMNH – Field Museum of Natural History, Chicago
USNM – National Museum of Natural History, Washington DC

Many of the analyses undertaken in this thesis required an up-to-date and comprehensive phylogeny of pelycosaurian-grade synapsids. As such, the data matrix of Benson (2012) was expanded by the addition both of new material and new characters. The new material includes four previously described species as well as the postcranial material of *Oedaleops campi* (Sumida et al., 2014), unpublished at the time of Benson’s original analysis. The four species newly added to the matrix are:

1: *Apsisaurus witteri* (MCZ 1474) includes a partial skull and lower jaw, a string of vertebrae from the posterior cervicals to the anterior caudals, several ribs and parts of both limbs. This specimen from Archer City Formation of Texas was first described as a diapsid by Laurin (1991), and so was not included in most subsequent phylogenetic analyses of pelycosaurian-grade synapsids. However, in more recent years, knowledge of basal synapsid morphology and relationships, in particular that of varanopids (Reisz and Dilkes, 2003; Anderson and Reisz, 2004; Maddin et al., 2006), has increased. With the benefit of this knowledge, Reisz et al. (2010) re-assigned *Apsisaurus* to Varanopidae, an assignment supported by a phylogenetic analysis including both varanopids and eureptiles. Reisz et al. (2010) noted that several of the previously considered synapomorphies of diapsids were in fact present in varanopids, such as the short quadratejugal. *Apsisaurus* did lack the recurved, laterally compressed teeth thought characteristic of varanopids, but the discovery of *Archaeovenator* (Reisz and Dilkes, 2003) showed that conical teeth are the primitive condition for varanopids. The presence of a tubercle on the jugal and similarities of the mandible to that of *Archaeovenator* confirmed the varanopid affinities of *Apsisaurus*. However, this specimen was not included in the global analysis of Benson (2012). Due to its importance as a basal member of the varanopids it was added to the analysis presented herein.

2: *Casea nicholsi* is a large caseid represented by two specimens (FMNH UR 85 and 86) from the late Kungurian Upper Vale Formation of Texas (Olson, 1954). The specimens
include partial vertebral columns, fragments of the skull roof, partial pelvic girdles, a forelimb, a pes, and a distal femur. The specimen was re-examined by Olson in his review of the family Caseidae (Olson, 1968), but has never been included in a phylogenetic analysis. Such an analysis is required to confirm the monophyly of the genus *Casea*. Four species were included in this genus in the review of Reisz (1986), but the analyses of Maddin et al. (2006) and Benson (2012) confirmed that “*Casea*” *rutena* did not form a monophyletic clade with the type, *Casea broilii*; this species has since been assigned to a new genus, *Euromycter* (Reisz et al., 2011). Further examination of this genus is required in order to produce reliable estimates of diversity. For this purpose, *Casea nicholsi* was included in the analysis presented here.

3: *Eocasea martini* is currently the earliest known caseid, represented by a fairly complete skeleton found in the Upper Pennsylvanian Hamilton Quarry (Reisz and Fröbisch, 2014). This is a crucial species for understanding the earliest evolution of caseids. Not only is it the earliest, and also the most basal member of the clade (Reisz and Fröbisch, 2014), but it is also not a medium-large sized herbivore, as are the other members of Caseidae. Instead, it is small, and was thought to be an insectivore (although unfortunately the sharp conical teeth were lost in preparation) (Reisz and Fröbisch, 2014). Moreover, a phylogenetic analysis presented in the supplementary materials of the description suggested that this specimen lacked many of the characters which Benson (2012) had used to unite Caseasauria with the clade containing Sphenacodontidae and Edaphosauridae, returning Caseasauria to their basal position within synapsids. It is necessary to examine this material alongside the eothyridid postcranial material now available in order to confirm or reject this hypothesis.

4: *Mycterosaurus smithae* was described very briefly in a catalogue of the vertebrate fauna found at the Placerville Localities of southwestern Colorado (Lewis and Vaughn, 1965). Two specimens were assigned to this species. The holotype MCZ 2985 (Figure 8) consisted of a partial skull, five vertebrae and ribs and a proximal femur and tibia, while the referred specimen USNM 22098 was a partial femur and a string of seven vertebrae. The type species of *Mycterosaurus*, *M. longiceps* (Williston, 1915), has been included in numerous cladistic analyses which have supported its assignment to the varanopid subfamily Mycterosaurinae (Maddin et al., 2006; Botha-Brink and Modesto, 2009; Campione and Reisz, 2010; Benson, 2012). However *Mycterosaurus smithae* has received comparatively little attention since its original description. In order to incorporate it into the phylogeny presented herein, the holotype underwent further preparation to reveal more details of its morphology. The new
material exposed, as well as the improved knowledge of basal synapsid anatomy since its original description, allowed the re-assignment of this species to Eothyrididae. This makes “Mycterosaurus” smithae an extremely important taxon. It is only the third known eothyridid species, and the second with postcranial material. It is also one of the earliest members of this family (see geological setting below), and as such can potentially provide a great deal of information on the earliest evolution of Caseasauria. The new information obtained from this specimen is presented here in a re-description of the type specimen, MCZ 2985.

Geological Setting

The Cutler Group spans the late Pennsylvanian and most of the Early Permian (Lucas, 2006), outcropping across New Mexico, Utah and Colorado. The Placerville Area, from which MCZ 2985 originates, is a locality where the sediments of the Cutler Group are exposed in the San Miguel Canyon (Lewis and Vaughn, 1964). Unfortunately, the biostratigraphy of the Cutler Group in Colorado is not as well established as in other areas. Lewis and Vaughn (1964) considered the localities to represent the upper portion of the Cutler Group, equivalent to the late Sakmarian-Artinskian aged Moran, Putnam and Admiral Formations (Lucas, 2006). However, they also drew comparisons with the Dunkard Group of Ohio. Most of the taxa from Placerville which are shared with the Dunkard Group are found in the lower layers of the latter: the lower Washington Formation (Lucas, 2013), implying an earlier age, possibly Asselian-Sakmarian. Baars (1962; 1974) also supported an earlier age of the Cutler Group in southwest Colorado, suggesting equivalence with the Halgaito Tongue and lower Supai Formation of Utah and lower Abo Formation of New Mexico. These formations are considered earliest Early Permian (Asselian-Sakmarian) or possibly latest Carboniferous in the case of the Halgaito Tongue (Lucas, 2006). Since MCZ 2985 was found in the uppermost 200ms of the section, an Asselian-Sakmarian age seems best supported.

List of Abbreviations in Figures

Figure 8: MCZ 2985, after preparation.
Systematic Palaeontology

Synapsida (Osborn, 1903)
Caseasauria (Wiliston, 1912)
Eothyrididae (Romer and Price, 1940)
“Mycterosaurus” smithae (Lewis and Vaughn, 1965)

Diagnosis: Distinguished from other members of Eothyrididae by the unusually small temporal fenestra and the large posttemporal region. Distinguished from other pelycosaurian-grade synapsids by the extension of the posterior ramus of the maxilla beyond the posterior margin of the temporal fenestra.

Holotype: MCZ 2985 (Museum of Comparative Zoology, University of Harvard), a partial skull; a string of six dorsal vertebrae; several ribs; a left femur and tibia; other fragments.

Locality and Horizon: Placerville Localities 11-13, San Miguel County, Colorado (38.0° N, 108.0° W). Cutler Group, Asselian-Sakmarian.

Description

The specimen MCZ 2985 consists of a previously articulated block bearing a skull and several postcranial fragments, including five vertebrae, ribs and a proximal femur and tibia (Figure 8). During the course of preparation, the skull has been separated from the block bearing postcranial material, and the postcranial block has been separated into multiple blocks in order to better expose the postcranial material, although these fragments still articulate.

Skull

The skull (Figures 9-11) is laterally compressed and slightly distorted, but preserved in three dimensions. The preservation quality of the skull roof makes defining sutures problematic. The sutures on the lateral sides of the skull are considerably clearer, particularly on the right (Figure 9). Most of the occiput and palate is not exposed. The orbit is relatively large, but the temporal fenestra is extremely small compared to other pelycosaurian-grade taxa, less than a quarter of the length of the orbit. Its dorsoventral height is greater than the anteroposterior length. The fenestra is oblong in shape, rather than being narrower ventrally
as in ophiacodontids or dorsally as in most other pelycosaurian-grade synapsids, including *Oedaleops*. Its shape is instead more similar to that of *Eothyris* and some mycterosaurine varanopids.

The antorbital region is missing except for a separate fragment, representing a counterpart and preserving a part of the left maxilla and premaxilla with teeth as well an internal view of the tip of the right mandible (Figure 10).
Only a small part of the premaxilla is preserved in medial view on the small separate fragment, which fits as a counterpart and extends the anteriormost preserved part of the skull. Nothing can be said about the anatomy of the premaxilla, except for details about its teeth (see Dentition below). The septomaxillae and the nasals are not present.

The frontal is the anteriormost preserved element of the skull roof. Its anterior margin is not preserved, so it is impossible to ascertain its length. The bones around the dorsal margin of the orbits are damaged, so it is unclear whether there is a lateral lappet of the frontal.
contacting the orbit. If there is one it would have to be extremely narrow, as seen in caseasaurids. The posterior process of the frontal is only visible on the right hand side. It is a short triangle of bone intruding between the parietal and the postfrontal but still leaving a substantial contact between the two, unlike in varanopids and ophiacodontids where the contact is limited.

Figure 11: Skull of MCZ 2985 in dorsal view

The parietals have been displaced so that the posterior end of the right one overlies that of the left. Despite this, one can see that the pineal foramen is large and positioned at about midlength of the parietal, as in eothyridids.
The maxilla is only fragmentarily preserved, but better on the right than the left side. The posterior process of the maxilla is a narrow splint extending beyond the level of the temporal fenestra, and contributes to the lower orbital margin.

A fragment of the lacrimal is preserved at the anterior edge of the right orbit. A ventral process of the prefrontal incises the lacrimal and limits its contribution to the orbital margin in lateral view, a feature of eothyridids, sphenacodontids and some varanopids. A lacrimal foramen cannot be identified.

The lateral surface of the prefrontal is flat, lacking the concavity observed in sphenacodontids and ophiacodontids. In dorsal view the prefrontal has a long, narrow posterior process forming about a third of the upper margin of the orbit.

The postfrontal, best preserved on the right side, is a transversely narrow triangular element with a flat surface. It contacts the parietal posteriorly but is separated from it anteriorly by the posterior process of the frontal. The posterior margin of the postfrontal is incised by an anterior protrusion of the postorbital, a feature shared with *Eothyris* and sphenacodontids.

The postorbital is a robust element with a broad posterior process. It has a posterior contact with a squamosal, but this contact does not extend far back over the temporal region as in some sphenacodontids and mycterosaurine varanopids. The ventral process of the postorbital and the dorsal process of the jugal form a thick postorbital bar, similar to those of *Eothyris* and *Eocasea*.

The jugals are also robust elements: both the anterior and posterior rami are dorsoventrally thick. The anterior ramus is short, not reaching beyond the orbital midline, but the posterior ramus extends well beyond the posterior margin of the temporal fenestra reaching at least halfway along the posttemporal region (the erosion of the lateral surface of this region makes identifying the full extent impossible).

The supratemporal is preserved on the right, but eroded away on the left. It is a large element set in the parietal, more similar in proportions to that of caseasaurids than to the splint of bone seen in varanopids and sphenacodontids. It is oblong in shape.

The squamosal is broad, flat and has a lateral exposure similar to that seen in ophiacodontids: the length of the posttemporal region is considerably greater than the breadth of the temporal fenestra. The temporal fenestra itself is bordered anteriorly by the jugal and dorsally by the postorbital and squamosal; there is no anterior process of the squamosal contacting the jugal dorsally.
On both sides of the skull a narrow splint of bone excludes the jugal from the ventral margin of the skull, formed from both the posterior process of the maxilla and the anterior process of the quadratojugal. The contribution of the quadratojugal to the exclusion of the jugal to the ventral margin of the skull, visible on the left side (Figure 11) is reduced relative to other caseasurs, wherein the anterior ramus reached anteriorly beyond the temporal fenestra. “Mycterosaurus” smithae shows the condition found in mycterosaurine and varanodontine varanopids with the posterior ramus of the maxilla having the greatest contribution. In “Mycterosaurus” smithae, in fact, the posterior ramus of the maxilla extends further posteriorly than in any other pelycosaurian-grade synapsid, reaching beyond the posterior margin of the temporal fenestra.

The occipital and ventral sides of the skull of MCZ 2985 are almost entirely covered my matrix. However, a small portion of the pterygoid is exposed in left lateral view between the left maxilla and mandible. Not much can be said about the morphology of the pterygoid, but it bears a few teeth. Unfortunately not enough is exposed to say anything about their arrangement and distribution, although they are obviously large.

*Mandible*

Both left and right mandibles are preserved, the right as a counterpart showing the lingual sutures. The left mandible is preserved throughout most of its length, although the tip is missing. The counterpart of the right mandible is preserved throughout its entire length, although the tip is on the separate fragment also bearing the premaxilla. The mandible is a gracile element with slight curvature, narrowing distally. The coronoid eminence is only a slight prominence, positioned more posteriorly than that of *Eothyris*. It is formed laterally by the posterior coronoid.

The dentary is the largest element in lateral view, although it does not quite reach two thirds of the length of the mandible. The splenial does not appear to have lateral exposure seen in caseids, edaphosaurids and sphenacodontids. On the lingual surface, the splenial covers about half the length of the mandible, not reaching posteriorly enough to contact the posterior coronoid. The angular is visible in both labial and lingual views. On the lingual side it extends anteriorly about halfway along the length of the mandible. There is no keel on its ventral surface. The prearticular covers a similar length.
**Dentition**

One premaxillary tooth is preserved with space for two more behind it. This tooth is enlarged relative to the maxillary teeth, implying that it is the anteriormost tooth (this tooth is also enlarged in *Eothyris*).

Four maxillary teeth are preserved on each side of the skull. Two of those preserved on the right side are larger and more robust than the others. From their position (under the anterior margin of the orbit) it might be suggested that these represent the secondary caniniform region seen in *Eothyris* and *Oedaleops*. The maxillary teeth are conical, with no serrations and only slight recurvature.

Four teeth are preserved on the right dentary and two on the left. Some poorly preserved teeth are visible in the dentary tip on the separate fragment. These are identical in morphology to the maxillary teeth: conical and only slightly recurved. Those preserved are uniform in size.

**Axial skeleton**

Preparation has exposed a series of six dorsal vertebrae in dorsal view (Figure 12), three of which are mostly uninformative. Two of these vertebrae are also exposed ventrally (Figure 13). The vertebrae are plesiomorphic in anatomy, very similar to those described for *Oedaleops*. The ventral surface is rounded, without the keel present in varanopids and sphenacodontids, and no longitudinal troughs as in ophiacodontids. The neural spines have been slightly eroded dorsally so that no information is available on their exact height, but the bases indicate a blade-like morphology. The neural arches are again plesiomorphic, with no swelling or buttressing. The prezygapophyses show a flat morphology, without the concave surface seen in some caseids. The postzygapophyses are widely spaced with no hyposphene visible. The transverse processes are positioned far anteriorly on the vertebrae, a feature seen in some caseids and edaphosaurusids. They are broad and flat and project slightly anteriorly; whether this is distortion or a feature of their morphology is unclear.

Fragments of at least 14 dorsal ribs are preserved on various postcranial blocks (Figures 14-15). The ribs are curved only proximally, in contrast to those of herbivorous pelycosaurian-grade synapsids, which are curved throughout their length to form a barrel-like chest. In proportions, however, they are very thick compared to the vertebrae, more similar to derived caseids than those of *Oedaleops* and *Eocasea*. 


Figure 12: Dorsal vertebrae of MCZ 2985 in dorsal view.

Appendicular skeleton

Preparation has revealed the right femur fully in dorsal (Figure 14) and ventral (Figure 13) views. It is very plesiomorphic in its anatomy and agrees in most details with that of *Oedaleops*. However, the femoral shaft of MCZ 2985 is considerably more robust, the proportions being more similar to those of sphenacodontids. The head of the femur is short relative to its total length. The shaft is almost straight, and is oval rather than circular in cross section. The internal trochanter has been eroded away, but the prominent fourth trochanter is preserved. The internal fossa is enclosed posteriorly by a ventral ridge, the plesiomorphic
condition absent in caseids and *Dimetrodon*. A low longitudinal ridge extends proximodistally across the ventral surface of the femur. There is no longitudinal mound on the proximodorsal surface, a condition independently evolved in several clades, but unfortunately not visible in *Oedaleops*. The distal end of the femur is damaged, so less information can be derived. The condyles are separated with virtually no difference in distal expansion, as in *Oedaleops* and *Eocasea* but unlike in more derived caseids. Also similar to *Oedaleops* and *Eocasea* but different to more derived caseids is the lack of compression of the anterior condyle. The dorsal surface of the posterior condyle is not concave as in some varanopids.

![Figure 13: Postcranial material of MCZ 2985, including two dorsal vertebrae, left femur and left tibia, all in ventral view](image)

The right tibia has been exposed completely in ventral view (Figure 13), whereas only the proximal part is visible in dorsal view (Figure 14A). Like the femur, its morphology is very similar to *Oedaleops* in its characteristics. It is almost straight with a low ridge along the ventral surface and a prominent cnemial crest. However, again, the proportions of the tibia of “*Mycterosaurus*” *smithae* are different to that of *Oedaleops* in that it is shorter but considerably thicker throughout.
Figure 14: Two articulating rock fragments bearing postcranial material of MCZ 2985, including a left femur and tibia in dorsal view, a phalanx of unclear origin and rib fragments. A) The first of these fragments, fully exposing the proximal part of the left tibia in dorsal view; B) The two fragments in articulation, covering part of the proximal part of the tibia but showing the almost complete right femur in dorsal view; C) drawing incorporating information from both of these views.

Another element is preserved which could be the distal end of the ulna or fibula; it is a flattened concave fragment of bone with part of a cylindrical shaft visible (Figure 15).
Eothyridid Affinities of MCZ 2985

Since its original description, the type specimen of "Mycterosaurus" smithae has received only limited attention in the literature. Berman and Reisz (1982), in their re-description of *M. longiceps*, tentatively kept this species assigned to the genus *Mycterosaurus* within Varanopidae, though noting that no characters of either were visible. Reisz (1986), in his thorough review of pelycosaurian-grade synapsid species undertaken for the Handbook of Paleoherpetology, also noted the lack of varanopid synapomorphies in "Mycterosaurus" smithae, and suggested the assignment should be considered provisional.
This detailed re-examination of MCZ 2985 and new features revealed in preparation allow the rejection of an affinity with *Mycterosaurus*, Mycterosaurinae and Varanopidae. “*Mycterosaurus*” smithae has a ventral ridge system on the femur, the lack of which was considered an autapomorphy of *Mycterosaurus* (Berman and Reisz, 1982). Most unambiguous varanopid and mycterosaurine synapomorphies that could be compared reject a varanopid affinity for MCZ 2985: the femur is not slender, the teeth are not serrated and there is no lateral boss on the postorbital. The long posterior ramus of the jugal is a feature of Mycterosaurinae, but this is a variable character within pelycosaurian-grade synapsids and is also present in eothyridids. Other characters that “*Mycterosaurus*” smithae shares with varanopids are those that are extremely variable within basal synapsids, such as the short anterior process of the jugal (also seen in caseasaurids) and the reduced lacrimal contribution to the orbital margin (also in eothyridids and sphenacodontids).

The large supratemporal is set in the parietal and in contact with the postorbital, supporting the assignment of “*Mycterosaurus*” smithae to Caseasauria, the clade containing the families Caseidae and Eothyrididae. Further evidence includes the short dentary relative to the rest of the lower jaw and the large size of the pineal foramen. An affinity with Eothyrididae is suggested based on the reduced contribution of the lacrimal to the orbital margin, the extension of the posterior ramus of the jugal beyond the temporal fenestra and the position of the pineal foramen midway along the midline of the parietal. Eothyrididae thus far contains only two other species of small carnivorous basal synapsids: *Eothyris parkeyi* and *Oedaleops campi*. Of the two, “*Mycterosaurus*” smithae is most similar to *Eothyris*, sharing with this species the thick postorbital bar, the incision of the postfrontal by the postorbital and the small temporal fenestra with an oblong rather than trapezoid or triangular shape. The separate fragment bearing the dentary tip, premaxilla and maxilla indicate a large overbite, another similarity with *Eothyris*.

It is unlikely that *Eothyris parkeyi* and “*Mycterosaurus*” smithae represent two specimens of the same species; “*Mycterosaurus*” smithae has a shorter posterior process of the postorbital, a more posteriorly placed coronoid eminence, a smaller temporal fenestra and a greatly expanded lateral surface of the squamosal (more similar in extent to Ophiacodontidae). There could, meanwhile, be justification for assigning them to the same genus. “*Mycterosaurus*” smithae shares with *Eothyris* the contribution of the maxilla to the margin of the orbit, a character Reisz et al. (2009) considered definitive of *Eothyris*. However, this is an extremely variable character, also seen in some derived caseids and varanopids. Other autapomorphies of *Eothyris* could not be compared with the less complete skull of
“Mycterosaurus” smithae. Therefore, in this study it is considered more conservative to regard them as separate genera, implying the need for a new generic name for “Mycterosaurus” smithae, which will be given elsewhere.

Eothyrididae is widely considered to consist of small, agile carnivores or insectivores (Romer and Price 1940, Langston 1965, Benton 2005, Reisz et al. 2009). The recent description of new material of Oedaleops campi (Sumida et al., 2014), including the first postcranium, supports this ecological hypothesis, illustrating generalised tooth structure, long gracile limbs and ribs with only proximal curvature unlike those of herbivorous caseids. The lower dentition of “Mycterosaurus” smithae is of the same conical shape, with little recurvature and no visible serrations, possibly indicating a similar diet. Unfortunately very little information is available on the upper dentition; the robust caniniform teeth seen in Oedaleops and Eothyris are not preserved, and the presence of a secondary caniniform region cannot be confirmed with certainty. An important difference between Oedaleops and “Mycterosaurus” smithae is in the robusticity of the limbs and the skull; although Oedaleops has a longer femur and tibia, those of “Mycterosaurus” smithae are considerably broader, both at the distal ends and at the mid-shaft. The postorbital and subtemporal bars are also thicker than their equivalents in Oedaleops. It appears that “Mycterosaurus” smithae may not have led the lifestyle of an agile insectivore that is inferred for Oedaleops, but may have been a more robust carnivore. Alternatively, it is possible that the differences in proportions were ontogenetic; the small size and large orbit of “Mycterosaurus” smithae could indicate a young individual. However the state of ossification of the limb bones suggests otherwise; all condyles and trochanters of the femur and the cnemial crest of the tibia are well ossified. Alternative explanations must be sought for the unusual morphology of “Mycterosaurus” smithae. It is clear from this specimen that there was a greater morphological diversity and potentially greater ecological diversity within eothyridids than has previously been suspected.

Comparison with USNM 22098

USNM 22098 is another specimen found at Placerville, although much lower in the section than MCZ 2985, the holotype of “Mycterosaurus” smithae (Lewis and Vaughn, 1965). This specimen consists of seven poorly preserved dorsal vertebrae, a proximal right femur and shaft, and other rather undiagnostic fragments. Lewis and Vaughn (1965) concluded that this was a second specimen of “Mycterosaurus” smithae, although they acknowledged that the preservation was too poor to properly compare it with the type. Their
justification for assigning the two specimens to the same species was the similar size of the vertebrae and the occurrence in the same formation and area. They also favourably compared the proportions of the femur of USNM 22098 with that of “Mycterosaurus” longiceps. The additional preparation of MCZ 2985 in the framework of this study has revealed a complete femur, permitting comparison between these two specimens. Based on this it is clear that they cannot be assigned to the same species. The femur of “Mycterosaurus” smithae is considerably more robust, with a much thicker shaft than that of USNM 22098. Moreover, the femoral head of USNM 22098 is proportionately much longer relative to its width than that of “Mycterosaurus” smithae. The gracile nature of the USNM 22098 femur hints at a varanopid affinity, although the preservation and current state of preparation of this specimen prevent reliable assignment. Unfortunately no diagnostic characters are visible on the vertebrae.

Phylogenetic Analysis

The four species noted above, as well as the postcranial material of Oedaleops campi were added to the matrix of Benson (2012). Also added were two extra characters. The first of these represents the shape of the temporal fenestra and has three character states: 0 – temporal fenestra is narrower dorsally than ventrally; 1 – temporal fenestra is narrower ventrally than dorsally; 2 – temporal fenestra is oblong, dorsal and ventral margins are of similar length. While most pelycosaurian-grade synapsids have a temporal fenestra narrower dorsally than ventrally, the eothyridids Eothyris parkeyi and “Mycterosaurus” smithae both share an oblong temporal fenestra, with a dorsal margin of a similar length to the ventral margin. This feature is also seen in the varanopids Mycterosaurus longiceps and Mesenosaurus romeri. Meanwhile, the ventrally narrow temporal fenestra has been noted for the members of Ophiacodontidae which preserve skulls (Romer and Price, 1940; Berman, 1995). The second character added refers to the webbing under the transverse processes of the vertebrae, and also has three character states: 0 – Webbing absent; 1 – webbing slight, does not extend further ventrally than the tip of the transverse process; 3 – webbing extensive, reaches ventrally beyond the transverse process. This character was introduced in the hope of resolving the relationships of Echinerpeton intermedium, which was found to be a wildcard taxon in the analysis of Benson (2012), but shares the extensive webbing with some members of Ophiacodontidae. The character scores of these new characters for all taxa, the character scores for the new specimens added to the matrix, and details of all changes made to the codings of Benson (2012), are available in Appendix A.
The matrix was analysed with parsimony in the Willi Hennig Society edition of TNT version 1.1 (Goloboff et al., 2008). The new technology driven search at level 100 was used, incorporating the drift, sectorial search and fusion algorithms. The minimum tree length was searched for 100 times. *Limnoscelis* was set as the outgroup. 756 most parsimonious trees (MPTs) were identified, with a length of 759, a retention index of 0.74 and a consistency index of 0.43. Support values for individual nodes were calculated using bootstrap resampling (10,000 replicates) and relative fit difference (Goloboff and Farris, 2001), again calculated in TNT.

**Figure 16:** Strict consensus phylogenies produced by parsimony analyses A) All taxa included; B) The wildcard taxa *Angelosaurus dolani, Caseopsis agilis, Ctenorhachis jacksoni* and *Basicranodon fortissensis* excluded.
In all most parsimonious trees (Figure 16A), “Mycterosaurus” smithae was found to be the sister to Eothyris parkeyi, with Oedaleops campi the sister to these two eothyridids. The monophyly of Eothyrididae is fairly poorly supported, but the sister-taxon relationship between “Mycterosaurus” smithae and Eothyris receives better support. The position of Eocasea as the basalmost caseid and that of Apsisaurus as a basal varanopid were confirmed. “Casea” nicholsi was not found to form a monophyletic grouping with Casea broilii, but was instead found in a polytomy with Euromycter rutenus and the clade containing Ennatosaurus, Cotylorhynchus and Angelosaurus. Relationships elsewhere in the phylogeny were identical to those found in the original analysis by Benson (2012), with two exceptions. In the original analysis Echinerpeton intermedium was found in three equally parsimonious positions: as basalmost synapsid, as ophiacodontid and as sister taxon to a clade containing caseasaurids, edaphosaurids and sphenacodontians. In this analysis it is found to be a caseid. This position has never before been suggested in previous examinations of this taxon (Reisz, 1972; Reisz, 1986; Benson 2012), and is only supported here by three characters: the short anteroposterior length of the dorsal centra, the lack of recurvature of the teeth, and the flattened medial surface of the ilium. Both the monophyly of and the relationships within Caseidae are extremely poorly supported, particularly near the base where Echinerpeton is found.

The second difference between the results presented here and those found by Benson (2012) is the position of Caseasauria (the clade containing Eothyrididae and Caseidae). Since the review of Reisz (1986), caseasaurids have been considered the sister clade to all other synapsids (the Eupelycosauria), a position based primarily on cranial characters. Benson (2012) introduced a larger number of postcranial characters into the analysis and found caseasaurids to be more derived, as sister group to Sphenacomorpha. However, Benson (2012) did note the lack of postcranial material available for eothyridids, and predicted that the discovery of such material could return caseasaurids to their position as sister to all other synapsids.

After the modifications to the original matrix presented here, the prediction of Benson is borne out. As argued by Reisz and Fröbisch (2014), it is here suggested that the result observed by Benson (2012) was due to the lack at the time of postcranial material of eothyridids and of a well-preserved basal caseid, provided by Eocasea. Many of the characters that were put forward by Benson (2012) as synapomorphies of a clade containing Caseasauria, Edaphosauridae and Sphenacodontia are found to be absent in Eocasea and the new eothyridid material (Table 1). However, once again the monophyly of Eupelycosauria is extremely poorly supported both by bootstrapping and relative fit.
Table 1: Nine characters used by Benson (2012) to support the relationship between Caseasauria, Edaphosauridae and Sphenacodontia, and the new information on these characters provided by Eocasea, Oedaleops and “Mycterosaurus” smithae.
provided greater resolution. Meanwhile, scored characters may be examined by comparing the length of the character when the score for the unstable taxon is replaced by a missing entry. If the change in length differs between different MPTs, this character is supporting conflicting positions for that taxon. These analyses were carried out in TNT.

<table>
<thead>
<tr>
<th>Wildcard Taxon</th>
<th>Unscored characters which could better resolve its position</th>
<th>Characters supporting conflicting topologies</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Caseopsis agilis</strong></td>
<td>1, 2, 5, 9, 23, 24, 25, 29, 34, 57, 73, 85, 92, 93, 98, 101, 110, 111, 115, 119, 122, 126, 129, 131, 139, 142, 148, 151, 157, 158, 159, 160, 161, 162, 166, 172, 173, 176, 179, 182, 187, 189, 190, 191, 193, 194, 195, 197, 198, 201, 205, 206, 208, 209, 210, 213, 238, 239 (Total = 58)</td>
<td>171, 233</td>
</tr>
<tr>
<td><strong>Ctenorhachis jacksoni</strong></td>
<td>2, 7, 8, 17, 18, 19, 22, 27, 28, 32, 33, 35, 43, 51, 56, 58, 59, 63, 65, 66, 68, 69, 75, 85, 98, 104, 106, 123, 125, 126, 127, 131, 135, 136, 138, 140, 151, 152, 162, 180, 185, 187, 200, 202, 230, 194, 195, 197, 198, 201, 205, 206, 208, 209, 210, 213, 238, 239 (Total = 40)</td>
<td>None</td>
</tr>
<tr>
<td><strong>Angelosaurus dolani</strong></td>
<td>25, 29, 44, 102, 110, 148, 171, 176, 182, 189, 205 (Total = 11)</td>
<td>None</td>
</tr>
</tbody>
</table>

Table 2: Characters with missing scores which could provide better resolution in the wildcard taxa, and characters supporting conflicting topologies in the wildcard taxa.

It was found that missing data is mostly responsible for the instability of the wildcard taxa (Table 2). In Basicranodon, Angelosaurus dolani and Ctenorhachis, no character conflict was found, while multiple unscored characters were found to be potentially relevant missing entries (40 characters for Basicranodon, 11 for A. dolani and 40 for Ctenorhachis). Two
scored characters in *Caseopsis* were found to support conflicting topologies, but 58 unscored characters were found to be important missing data. The character conflict in *Caseopsis* is between character 171 and 233. The cup-like articular facet of the dorsal rib tuberculum of *Caseopsis* (Character 171, state 2) is characteristic of the caseid clade containing the genera *Angelosaurus* and *Cotylorhynchus*. However, the anterior condyle of the femur of *Caseopsis* is not compressed (character 233, state 0), which supports a more basal position within Caseidae; all caseids more derived than *Casea* have a compressed anterior condyle.

Due to the poorly supported relationships and lack of resolution provided by parsimony analysis, alternative methods were used to assess phylogenetic relationships in order to compare the results. The first was Bayesian analysis, a model based approach that has been widely used in analyses of molecular data as it can incorporate information on the probabilities of different mutations (Lanave et al., 1984; Tavaré, 1986). Its use in analyses of morphology is controversial (Spencer and Wilberg, 2013), but some morphological systematists have suggested its use should be preferred over parsimony (Lee and Worthy, 2010; Wright and Hillis, 2014). One reason cited is that Bayesian analysis, which takes into account branch lengths, is less affected by issues such as long-branch attraction (Felsenstein, 1978); longer branches are more likely to convergently evolve characters and therefore cluster together under parsimony.

The second alternative method used was an implied weights analysis (Goloboff, 1993). This method is a modification of maximum parsimony: after a single round of tree searches, characters found to be homoplasies are downweighted for a subsequent round of searches. Again, the use of this method has been controversial, mainly due to a sentiment that the weighting of characters is unparsimonious (Kluge, 1997a; b; 2005; Källersjö et al., 1999). Nevertheless, it has been shown that using such weighting schemes produces better supported relationships (Goloboff et al., 2008).

The Bayesian analysis was carried out in MrBayes version 3.2.2 (Ronquist et al., 2012) using the Markov model (Lewis, 2001) with a gamma distributed rate parameter. Two analyses were carried out: the first with the same matrix used in the parsimony analysis, and the second including 109 autapomorphous characters; since Bayesian analysis takes into account branch lengths, autapomorphies are necessary information (Müller and Reisz, 2006). The autapomorphies are available in Appendix B. For both analyses a majority rule consensus was constructed from the probability distribution of trees. The Implied Weights analysis was undertaken in TNT, using the same settings as in the parsimony analysis. Homoplasicous
characters were downweighted with a concavity constant of 3.0. 18 most parsimonious trees were found by the implied weights analysis (Figure 17B).

Figure 17: Comparison of the results of the phylogenetic analysis using A) Parsimony, and B) Implied Weights.

The implied weights and Bayesian analyses (Figures 17-18) show broadly similar results to the parsimony analysis. The biggest difference is that in both *Echinerpeton* is found to be the sister taxon to the clade containing Edaphosauridae and Sphenacodontia rather than as a caseid, a position supported by the increased number of precanine maxillary teeth, the elongation of neural spines and the flattened medial surface of the ilium. The support values for the phylogeny produced by implied weights analysis are higher than those found in the parsimony analysis, although still low. The clade credibility values found in the Bayesian analyses are considerably higher, with most being over 80% and many being over 90%.
The positions of the wildcard taxa are better resolved in both the implied weights and Bayesian analyses; Basicranodon is found to be a mycterosaurine varanopid, Caseopsis is resolved within the clade containing Cotylorhynchus and Angelosaurus, and Ctenorhachis is found in a basal position within Sphenacodontidae. However, in some areas resolution is worsened. The relationships of basal varanopids are not so well resolved in both Bayesian analyses. Moreover, when autapomorphies are not included in the Bayesian analysis, the monophyly of Eothyrididae could also not be resolved; Oedaleops is found in a polytomy with Caseidae and the clade containing Eothyris and “Mycterosaurus” smithae.

Figure 18: Phylogenies produced by the Bayesian analyses. Numbers at nodes represent clade credibility values. A) Autapomorphies included; B) Autapomorphies not included.
While these analyses and comparisons provide much to consider in future phylogenetic examinations of pelycosaurian-grade synapsids, it is encouraging that, with the exception of the placement of *Echinerpeton*, the relationships obtained with the different methods are remarkably stable. The eothyridid affinity of "Mycterosaurus" smithae is consistent in all analyses. However, low resolution and poor support for relationships within caseasaurids are also consistent. Considerably more work is needed before firm conclusions may be drawn about caseasaurian relationships. It is regrettable that the lack of resolution in the parsimony analyses is due to missing data rather than conflicting characters. The issue of conflicting characters may be resolved by the addition of more characters or species to provide further information on character polarities. There is unfortunately little that can be done to resolve the issue of incomplete data, at least until more specimens are found. However, the increased resolution provided by the implied weights and Bayesian analyses provide working hypotheses which may be kept in mind during future examinations of these taxa.
Chapter 3

Data
A comprehensive database of synapsid taxa, both pelycosaurian-grade and therapsid, from their earliest occurrence in the late Westphalian of Nova Scotia (Reisz 1972) until the latest occurrence of pelycosaurian-grade taxa named to species level from the *Tapinocephalus* Assemblage Zone of South Africa (Dilkes and Reisz, 1996; Reisz and Modesto, 2007; Botha-Brink and Modesto, 2009), was assembled for this study. This list was scrutinised for synonyms and nomina dubia. *Protoclepsyrops haplous* (Carroll, 1964), from earlier in time but of dubious synapsid affinity (Reisz, 1986), was not included. The youngest record of pelycosaurian-grade synapsids, a varanopid from the middle Permian *Pristerognathus* Assemblage Zone of South Africa (Modesto et al., 2011) was excluded, as this specimen is only identifiable to subfamily level. The database may be regarded as complete until April 2014, and is available in Appendix C, indicating the age range of the species and the country of origin. The timescale was obtained by splitting the international stages into two equal substages (early and late), which were used as time bins. The boundary between each substage was set as the middle of the international stage. The timescale used was that of Gradstein et al. (2012). The time interval under study stretched from the late Moscovian until the late Capitanian.

If a taxon’s age could not be constrained, it was included in the full range of possible time bins. While this method does lead to less resolution i.e. certain taxa known from a single specimen or locality will be found in more than one time bin, it has been demonstrated that, as long as the stratigraphic uncertainties are randomly distributed, the diversity signal will not be false, but merely “dampened” (peaks and troughs become less extreme) (Raup, 1991; Smith, 2001). This is preferable over attempting to provide resolution to the data and potentially crating a false signal. In order to assess the impact of stratigraphic uncertainty, a more resolved dataset was created, in which each locality is constrained to no more than two substages.

As part of the analysis into the completeness of the fossil record of pelycosaurian-grade synapsids, further data was added to the taxonomic entries in this database. A list of all specimens recorded in the published literature was created and details of these specimens, including number and material preserved, were added. The data from the published literature was supplemented by personal observations in museum collections. This database includes details of the locality from which each specimen is known and may be found in Appendix D.
Supertree

A Review of Supertree Methods and Uses

Although macroevolutionary studies require phylogenies to be as inclusive as possible, such phylogenies are not always available. Workers very rarely include all known species in a phylogenetic analysis, either because poor specimens lead to a lack of resolution, because they do not feel a species is relevant to the study they are undertaking, or in some cases simply because a specimen was not available for study at the time of their analysis. Continual updating of molecular phylogenetic analyses is easier, since sequence data may be constantly added to databases such as Genbank. Morphological characters, on the other hand, are subject to constant revision and disagreement. The practical difficulties of examining first-hand the necessary specimens limit the possible scope of morphological analyses. At the moment of writing, the largest trees produced using morphological data are limited to 192 taxa (Gauthier et al., 2014) and 4541 characters (O’Leary et al., 2013). Palaeozoic synapsids provide an excellent example of the dearth of comprehensive phylogenies. The vast majority of phylogenetic analyses focus on a single family or clade. There are not analyses that include large samples of taxa from both pelycosaurian-grade and therapsid synapsids; even the more comprehensive studies focus on one or the other (Liu et al., 2009a; Cisneros et al., 2011; Benson, 2012). As a result, in order to elucidate the evolutionary history of a clade, one must attempt to combine these hypotheses. Some workers have created composite trees by simply ‘grafting’ trees together and adding missing species in their preferred position, and have used these trees in studies of macroevolutionary patterns (e.g. Laurin, 2004; Ruta et al., 2011). However, such methods of tree building are highly subjective, and the author feels that they should not be used in quantitative macroevolutionary analyses.

Supertree and supermatrix methods allow one to combine phylogenetic hypotheses into a more quantitative way. These are two very different concepts. Supermatrix methods use the primary character data; data matrices from the phylogenetic hypotheses are combined into one supermatrix with taxa coded as missing for all characters in the matrices in which they are not present. The supermatrix may be analysed using parsimony, as in morphological analyses.

Supertree methods instead use the tree topologies rather than the characters as the source data, with a variety of methods available for combining these topologies. If all trees are compatible, with no conflict suggested, the procedure is simple: a ‘backbone’ tree may be constructed from the shared taxa, and then each branch of the backbone tree may be compared
to corresponding branches in the source trees to ascertain if any taxa unique to any source tree should be added. Steel (1992) has provided an algorithm suitable for this task. More usually, some phylogenetic hypotheses will conflict, and more complex methods are needed to reconcile them. The earliest suggested, and most commonly used, is ‘Matrix Representation with Parsimony’ (MRP), independently proposed by Baum (1992) and Regan (1992). This method combines source trees in such a way that no tree has the power of veto over another; where conflict occurs, the most commonly occurring topology will be chosen, or a polytomy will be formed from the conflicting taxa. The method (Figure 19) constructs a matrix in which characters refer to the nodes within source trees rather than morphology. Each node on each source tree is represented by one character. Each taxon descended from that node is scored ‘1’. Taxa present in the source tree but not descended from that node are scored ‘0’. Taxa not present in that particular source tree are scored ‘?’. The resulting matrix may be analysed using parsimony, rooted on a hypothetical outgroup taxon with all ‘characters’ scored as ‘0’.

Figure 19: A hypothetical example illustrating the Matrix Representation with Parsimony method. A) Two source trees with nodes numbered. Conflict is present regarding the position of taxon D. B) The MRP matrix representing the presence or absence of each taxon within each node. C) The supertree produced from the MRP matrix.
Purvis (1995) suggested a modification to the Baum and Ragan method. He pointed out that their method is biased in favour of the topologies of larger source trees, since these trees will contain more nodes and therefore be represented by more characters, a bias later confirmed in simulations (Beninda-Emonds and Bryant, 1998). The modification suggested was to base the coding on sister group relationships rather than inclusion within clades. In the Purvis method, each node is again represented by a character, and taxa descended from that node are scored ‘1’. However, it is only the sister taxa to that node which are scored ‘0’. All other taxa, whether included in the source tree or not, are scored ‘?’.

The performance of the Purvis method compared to the Baum and Ragan method has been examined (Purvis and Webster, 1998), using primates as an example. It was found that of 160 resolved nodes obtained using the Purvis method, only 12 conflicted with the tree produced using the Baum and Ragan method (Purvis and Webster 1998). The Baum and Ragan tree was also better resolved (Purvis and Webster, 1998). It was suggested that greater conflict between the source trees would lead to greater conflict between the two methods (Purvis and Webster, 1998).

The Purvis method has been criticised in that it fails to weight the source trees equally, since larger trees now contribute more missing data (Ronquist, 1996), but a further criticism is warranted. The reasoning behind the modification suggested by Purvis (1995) was that the Baum and Ragan method provides greater weight to larger source trees. However, it could be argued that it is right that this should occur. More inclusive phylogenetic analyses are more reliable (Gauthier et al., 1988; Pollock et al., 2002; Zwickl and Hillis, 2002; Conrad, 2008) since the addition of more taxa can provide information on the polarity of characters and will thus affect tree topology. As such, the additional weight given towards larger trees in the Baum and Ragan method is providing additional weight towards more reliable trees. In any case, the bias appears to be minimal (Beninda-Emonds et al., 2002). Another criticism against MRP was put forward by Wilkinson et al. (2001; 2005a), who analysed tree-shape related biases and found MRP would favour topologies suggested by an unbalanced tree. Moreover, it has been demonstrated that unsupported clades, not suggested by any of the input source trees, can be recovered by the MRP method (Beninda-Emonds and Bryant, 1998). This is obviously undesirable; the supertree is supposed to summarise existing hypotheses, not suggest new relationships. However, such clades are extremely rare (Beninda-Emonds and Bryant, 1998; Pisani et al., 2002; Beninda-Emonds, 2003).

Other methods have been proposed to produce supertrees. The BUILD algorithm (similar to the Adam’s consensus) organises taxa into clusters, excluding each cluster’s outgroup taxa one at a time (Aho et al., 1981). This method often produces more resolution,
but at the cost of ignoring certain possible relationship combinations (Beninda-Emonds et al., 2002). It is also not able to include incompatible source trees. The MinCut algorithm (Semple and Steel, 2000) expanded on this method, allowing incompatible trees to be included. When clusters cannot be separated due to conflicting source trees, the minimum number of branches needed to create an agreed outgroup are removed. The MinFlip method (Chen et al., 2003) uses a similar matrix representation method to MRP, but resolves conflict by ‘flipping’ matrix cells from 0 to 1 or 1 to 0. The supertree with the minimum number of flips necessary is selected. MRP has a large advantage over these methods, in that it has been extensively tested with regard to various biases and potential methodological problems. There are also practical advantages: it is simple, computationally easy and there are a large number of computer programs capable of performing the analysis quickly.

Some workers (e.g. Gatesy et al., 2002; Gatesy et al., 2004; Gatesy and Springer, 2004) have criticised the use of supertrees over supermatrices as they are removed from the primary data i.e. the morphological or molecular character list. These authors have suggested that using the character data in a supermatrix is more reliable than using the trees themselves as a source. Gatesy et al. (2004) also argued that the supermatrix may produce novel clades, supported by ‘hidden character support’; two sets of characters on their own may indicate two different relationships, but together they may favour one or the other, or even suggest entirely new relationships. However, supermatrix methods do have their drawbacks. Firstly, supermatrices contain a large amount of missing data, which can lead to poorly resolved phylogenies (Beninda-Emonds, 2004). While one should most certainly not choose a method purely because it provides more resolution, taxa that have been included in only one phylogenetic analysis may become ‘wildcard taxa’, even if the original analysis was able to constrain their position. This problem is exacerbated if fewer taxa are shared between analyses (Sanderson et al., 1998). Simulations have shown that supertree methods can produce no less accurate representations of the source trees than supermatrix methods (Beninda-Edmonds and Sanderson, 2001; Chen et al., 2003; Levasseur and Lapointe, 2003; Piaggio-Talice et al., 2004). Supermatrix methods are also computationally demanding and time consuming. A further issue with supermatrix methods mentioned by Beninda-Emonds (2004) is that data of different sorts e.g. molecular and morphological, cannot be combined. This concern is irrelevant to this particular study, limited to morphological data as it is, but is still worth noting. For these reasons, supertree methods have been used in this study.

There are a number of supertree analyses that have included phylogenies based on fossils. Some have been used to investigate the topologies recovered when source trees are
combined (Pisani et al., 2002; Ruta et al., 2003; Bronzati et al., 2012). Others have also been produced to compare methods of supertree formation or to compare supertree methods to supermatrix methods (Gatesy et al., 2004; Lefebvre, 2005; Hone and Benton, 2008). More recently they have been applied to analytical palaeontology: supertrees have been used by Marjanović and Laurin (2007) to investigate the fit of fossils to stratigraphy and molecular clock dates, by Ruta et al. (2007) and Lloyd et al. (2008) to investigate shifts in rates of diversification, and by Ruta et al. (2008; 2011) to create phylogenetic diversity estimates.

Supertree Generation

The results of phylogenetic analysis of pelycosaurian-grade synapsids produced in the previous chapter were not entirely satisfactory for the further analyses intended for this thesis. Since the different analyses found *Echinerpeton* to be in greatly different positions, one cannot use the consensus of all trees produced in subsequent analyses; the lack of resolution would greatly affect the results. Moreover, the analyses of diversity through time requires phylogenies not only of pelycosaurian-grade synapsids, but also of therapsids in order to compare the diversity curves. Currently a combined phylogeny of pelycosaurian-grade and therapsid synapsids does not exist, and such an analysis is beyond the scope of this study. In order to alleviate these issues a supertree of all synapsids from their first appearance in the late Moscovian until the end of the Capitanian (the last appearance of all named pelycosaurian-grade synapsids) was generated using MRP. All hypotheses of phylogenetic relationships published before April 2014, produced using computer algorithms, rather than manually generated, and containing three or more taxa from the time period under study were considered as source trees. The phylogenies produced in Chapter 2 were also included.

In order that the supertree input data was “accountable” (a concern raised by Gatesy et al., 2002), publications that did not include full details of their method e.g. not including a character matrix, details of algorithms or outgroups used, were rejected. In order to reduce instances of tree non-independence (another issue raised by Gatesy et al., 2002; including many trees based on the same character list would bias the supertree towards topologies suggested by those characters) the following procedure was followed (modified from Beninda-Emonds et al., 2004): (1) if one study uses a character list and a taxon list that is identical to or a subset of another analysis, then only the more inclusive study was included as a source tree; (2) if one study uses a character list which is identical to, or a subset of, another analysis, but the taxon lists are not identical nor is one a subset of the other, then a mini
supertree (using the MRP method) was constructed from the two or more trees. This mini supertree was included as a source tree; (3) if a study uses different methods to analyse the same dataset e.g. analysing the dataset using both parsimony and Bayesian methods, a mini-supertree was constructed from the results of each analysis to be used as a source tree.

After pruning the list of published phylogenetic analyses in this way, 29 phylogenetic hypotheses and four mini supertrees remained (Appendix E). These trees then needed to be standardised with respect to the taxonomic level. Different phylogenetic analyses study phylogeny at different levels: the family, genus or species level. This is a problem when combining trees, and has in the past led to a supertree with, for example, Lepidosauromorpha, Squamata and two rhynchocephalian species included as terminal taxa (Hone and Benton, 2008) despite the fact that squamates and rhynchocephalians are contained within Lepidosauromorpha. The following procedures were carried out to standardise the level of the source trees: (1) If a taxon is not studied at species level in any included analysis, then it is included at the genus level in all source trees e.g., *Sphenacodon* spp. (2) If the paper specifies that their coding for a higher level taxon above the level of species is based primarily on a particular species, then that species is used to replace the higher-level taxon in the source tree. (3) If a taxon is included at the genus level or higher in one or more studies, and one or more different studies use more than one different species of that taxon, then a single representative of the higher taxon is chosen to replace it (the type if possible) e.g. if Ophiacodontidae is used as a terminal taxon in a source tree, it is replaced in this analysis with *Ophiacodon mirus*. The taxon specified as the outgroup in the original analyses were removed, as their position is assumed rather than tested. The MRP matrix was generated from the source trees using the program Supertree0.85b (Salamin et al., 2002). The Baum and Regan method was applied. All trees and nodes within trees were given equal weight. The matrix was input into the Willi Hennig Society edition of TNT (Goloboff et al., 2008). A new technology search was applied, using the tree fusing, drift and sectorial search algorithms.

**Time Calibration**

Time calibration of a phylogeny can be a complex issue with many potential problems. For example, if a taxon is only known from a single occurrence and its sister taxon is younger, the younger taxon will have a ghost lineage extended only as far back as the older. The length of the branch representing the older taxon will be zero e.g. taxa V and W in Figure 20C. This would imply instantaneous character evolution from the states of the common
ancestor to those of the older taxon. Zero-length branches may also imply instantaneous speciation events; if three taxa X, Y and Z (Z being the oldest), have relationships (X,(Y,Z)), then the ghost lineages of X and Y will only be extended as far back as Z (Figure 20C). This would imply that the cladogenic event splitting X and (Y,Z), and the cladogenic event splitting Y and Z, occurred simultaneously. These implications of zero-length branches are unrealistic, and will affect analyses of diversification and morphological evolution.

Figure 20: Time calibration of phylogenies using different methods. A) The observed fossil record of five taxa. Black dots indicate single occurrences, black lines indicate ranges. B) The uncalibrated phylogeny of the five taxa. C) The most basic time calibration of the phylogeny, with no correction for zero-length branches. Ghost lineages in red. D) Time calibration of the phylogeny, with a minimum branch length of T0.5 enforced, as in Laurin (2004). E) Time calibration of the phylogeny using the branch-sharing method of Brusatte et al. (2008). F) Time calibration using the method proposed herein.
A variety of methods exist to eliminate these zero-length branches. The majority involve selecting an arbitrary length of time, and adding this to all branches (Ruta et al., 2011) or to zero-length branches only (Hunt and Carrano, 2010), or extending the length of branches until all reach an arbitrary minimum length (Laurin, 2004), the latter illustrated in Figure 20D. These methods suffer from being highly subjective, with the results of phylogeny-based analyses depending greatly on the length of time selected. Two less arbitrary methods have been proposed. Both involve extending zero-length branches back in time along the non-zero-length branch immediately ancestral to them, sharing this ancestral branch’s length among the zero-length branches descended from it. The zero-length branches may be shared equally among the ancestral branch (Brusatte et al., 2008) as illustrated in Figure 20E or, if a morphological character matrix exists, adjusting branch lengths to represent the proportion of morphological change occurring along each branch (Ruta et al., 2006). While these methods are more objective, they do make assumptions: Brusatte et al.’s method assumes equal speciation rate, while Ruta et al.’s method assumes equal rates of morphological change. Since this thesis is investigating patterns of diversification and species richness, employing a method that biases towards equal rates of speciation is circular and inappropriate. Ruta et al.’s method is more appropriate (its bias towards equal rates of character change is irrelevant to the analyses herein) but since it is a supertree being analysed, there is no matrix of morphological characters to deduce character evolution along any branch.

In this study, a new method of time calibration is used, working on the assumption that the majority of speciation and extinction occurs at the boundaries between the geological time intervals, an assumption that is both supported by previous studies (Foote, 1994; Alroy et al., 2008; Alroy, 2010a) and intuitive (the geological timescale is based on biostratigraphy). The range of each terminal taxon is extended to include the entirety of any substage in which it has been found (Figure 20F), concentrating speciation and extinction events at the boundaries between substages. The zero-length branches are regarded as zero-length; adding values, whether arbitrarily determined or not, will push the origination rates away from the boundaries. Instead it is assumed that the length of time between the speciation events concentrated at the boundaries between substages is short enough to become negligible. This produces similar results to the basic time calibration shown in Figure 20C, but one important difference is that the hypothetical ancestors of nodes implied by the phylogeny (ghost taxa) are never present in the same time bin as their descendants. Under the basic time calibration method these would be counted as separate taxa in a phylogenetic diversity estimate, pushing the in-bin diversity higher than the maximum standing-diversity (the diversity counted from
the record at a single point in time rather than in the whole bin. For example in Figure 20C, the most recent common ancestor of V and W would be counted as an additional taxon in the same time bin as X and the ghost lineage of W. Under the new time calibration method presented here, ghost taxa are only counted in time bins not shared with their descendants (Figure 20F), and so in-bin diversity is never pushed above maximum standing diversity.

Relationships suggested by the Supertree

It should be emphasised that the supertree does not incorporate any new information, and the raw data are previously-proposed phylogenetic relationships rather than characters. As such the supertree should not suggest any relationships that have not been previously suggested. However, the relationships of basal synapsids are still not fully resolved, and conflicting topologies have been produced in cladistic analysis. The selection of a particular topology by the supertree can provide insights into the characteristics of the method used. It is worth examining some of the relationships produced by the supertree analysis.

Caseasauria

As discussed in Chapter 2, since the review by Reisz (1986), Synapsida has been thought to be split into two clades: Caseasauria (Eothyrididae and Caseidae) and Eupelycosauria. This relationship was supported by the cladistic analyses that examined phylogenetic relationships between amniote clades (e.g. Gauthier et al. 1988, Hill 2005), although these analyses were characterised by poor within-clade sampling. Phylogenetic analyses of pelycosaurian-grade synapsid clades have used caseasaurians as outgroups, assuming rather than testing a basal position (e.g. Modesto, 1994; Berman et al., 1995; Reisz et al., 1998; Modesto et al., 2001; Anderson and Reisz, 2004; Maddin et al., 2006; Maddin et al., 2008; Botha-Brink and Modesto, 2009; Reisz et al., 2009; Campione and Reisz, 2010).

The first global analysis by Benson (2012) in fact challenged the basal position of Caseasauria. In this analysis, Caseasauria were found to be the sister to the clade containing Edaphosauridae and Sphenacodontia, while Ophiacodontidae and Varanopidae formed a clade, which was the sister taxon to all other synapsids. These relationships are supported by the fact that Ophiacodontidae are the earliest clade to appear in the fossil record (Reisz, 1972) while Caseasauria does not appear until the latest Carboniferous (Reisz and Fröbisch, 2014). If the relationships advocated by Reisz (1986) are correct, they would imply a long ghost lineage of Caseasauria.
Figure 21: The portion of the time calibrated supertree showing the relationships of pelycosaurian-grade synapsids. Black lineages indicate best supported observed range, grey lineages indicate uncertainty surrounding the age ranges, red lineages indicate ghost lineages.

The supertree, however, does not include the analysis of Benson (2012) as a source tree, since this analysis was expanded in Chapter 2. Therefore the supertree recovered Caseasauria as the sister to other synapsids (Figure 21). The other source trees supporting this relationship included Modesto (1994) and Hill (2005), although it should be noted that these latter analyses have extremely poor within-clade taxon sampling. Despite this and the poor
support for the split between Caseasauria and Eupelycosauria found in Chapter 2, the basal position of Caseasauria is assumed in all subsequent analyses of this thesis.

*Elliotsmithia longiceps*

*Elliotsmithia* is a varanopid from the Abrahamskraal Farm in South Africa. It is an important species in studying the later evolution of pelycosaurian-grade synapsids. Along with *Heleosaurus scholtzi* it is the youngest pelycosaurian-grade synapsid named to species level (both species are known from the *Tapinocephalus* Assemblage zone of South Africa), and one of the two varanopid species known from South Africa. The holotype, some fragmentary skull material and cervical vertebrae, was originally described as a therapsid (Broom, 1937), but was reassessed as a pelycosaurian-grade synapsid (Romer and Price, 1940) and later a varanopid (Olson, 1965; Langston and Reisz, 1981). Reisz et al. (1998) provided the first cladistic analysis of *Elliotsmithia*, which was shown to belong to the varanodontine subfamily. Modesto et al. (2001) described a second specimen, supposedly of *Elliotsmithia*, which was incorporated into cladistic analysis and suggested *Elliotsmithia* was a mycterosaurine varanopid. This debate has great implications for varanopid evolution. A varanodontine affinity for *Elliotsmithia* would imply that two invasions of South Africa were made by varanopids since the other South African genus, *Heleosaurus*, is unquestionably a mycterosaurine (Botha-Brink and Modesto, 2009; Benson, 2012). A mycterosaurine affinity of *Elliotsmithia*, however, would not only imply a single invasion of South Africa, but also that only the mycterosaurine varanopids survived until the Capitanian; the Varanodontinae would have died out in Olson’s Extinction (See Chapter 5).

The interpretation of *Elliotsmithia* as a mycterosaurine is based on the assumption that the second specimen (BP/1/5678) does in fact belong to this genus. This assignment has been questioned (Reisz and Dilkes, 2003). Later analyses not using this specimen in coding *Elliotsmithia* (Maddin et al., 2006; Reisz et al 2010) supported varanodontine affinities, while that of Botha-Brink and Modesto (2009), adding two characters to the Maddin et al. matrix shows *Elliotsmithia* to be a mycterosaurine. Campione and Reisz (2010) found that the morphological data alone supported varanodontine relationships, but a stratocladistic analysis found *Elliotsmithia* to be a mycterosaurine. This analysis added an ordered character representing the stratigraphic position of each taxon. The most parsimonious tree implied by the stratigraphic character is that which minimises the length of ghost lineages (each time bin covered by a ghost lineage is represented by a character state change).
That the supertree supports varanodontine affinities of *Elliotsmithia* (Figure 21) is due to the procedure used to select which phylogenetic hypotheses to include. Two of the source trees include *Elliotsmithia*: Reisz et al. (2010) and mini supertree 1. Both show varanodontine relationships. The Modesto et al. (2001) analysis was not included as its character and taxon list is a subset of the Botha-Brink and Modesto (2009) analysis. The Botha-Brink and Modesto analysis, which also supported mycterosaurine affinities, was included in mini supertree 1 along with the Maddin et al. analysis and the Campione and Reisz analysis. Since these latter two analyses support varanodontine relationships, the mini supertree does also. Some might criticise the inclusion of the Maddin et al. (2006) analysis in the mini supertree. Its character list is a subset of that of Botha-Brink and Modesto (2009), but Maddin et al. includes *Archaothyris* and *Ophiacodon*, while Botha-Brink and Modesto score Ophiacodontidae as a single terminal taxon (replaced with *Ophiacodon mirus* when forming the supertree; see above). Thus the taxon list of Maddin et al. is not a subset of that of Botha-Brink and Modesto, and it is included in the mini supertree. One might argue that the inclusion of *Archaeothyris* should not force the inclusion of the Maddin et al. phylogeny, since it is not a species, which belongs to the group that was under focus in the analysis (Varanopidae). Such questions as these do indicate that the guidelines of Bininda-Emonds et al. (2004), though refined for this study, are still worth further examination.

It should also be noted that the stratocladistic analysis of Campione and Reisz (2010) was not included as a source tree. The reason is that the supertree is used to investigate the fit of the fossil record to stratigraphy in Chapter 4; to incorporate a source tree produced using stratigraphic data would be circular. Nevertheless it has been suggested that the combination of stratigraphy and morphology should be preferred over morphology alone (Clyde and Fisher, 1997; Fox et al., 1999). While the analysis based solely on morphology supported a varanodontine affinity of *Elliotsmithia*, the stratocladistic analysis found it to be the sister of the contemporary *Heleosaurus*, a mycterosaurine (Campione and Reisz, 2010). Both specimens referred to *Elliotsmithia* require redescription to resolve such inconsistencies.

*Tetraceratops insignis*

*Tetraceratops* is an enigmatic synapsid represented by a single, incomplete and severely crushed skull from the Big Witchita locality of Texas. When first described, it was thought to be closely related to *Dimetrodon* (Matthew, 1908). However, in their Review of the Pelycosaurs, Romer and Price (1940) argued that it belonged to Eothyrididae, at that time a wastebasket group containing several small carnivores now known to be unrelated.
(Langston, 1965; Reisz, 1986; Reisz et al., 2009). More recently, arguments have been put forward that *Tetraceratops* is in fact the basalmost therapsid (Laurin and Reisz 1990, 1996), a hypothesis supported by phylogenetic analysis (Laurin and Reisz 1990, Amson and Laurin 2011, Cisneros et al. 2011). However, this association has been disputed; Conrad and Sidor (2001) argued that *Tetraceratops* is actually a sphenacodontid. Liu et al. (2009a) were unable to resolve the position of *Tetraceratops* in their cladistic analysis (it formed a polytomy with therapsids and sphenacodontids) but the authors considered sphenactodontid affinities more likely. Amson and Laurin (2011) reassessed the Liu et al. analysis. By adding seven characters and modifying the coding of three others, Amson and Laurin were able to resolve this polytomy, and again demonstrated therapsid affinities for *Tetraceratops*.

The supertree shows *Tetraceratops* to be the basalmost therapsid (Figure 22). Although arguments have been put forward for its sphenacodontid affinities, no published phylogenetic analyses have demonstrated this relationship. The only cladistic analysis that has cast doubt on the therapsid affinities is that of Liu et al (2009), which was not included as a source tree as the character list is a subset of that of Amson and Laurin (2011). Two of the three analyses containing *Tetraceratops* were included as source trees (Amson and Laurin, 2011; Cisneros et al., 2011) and all support its position as a basal therapsid. The third, that of Laurin and Reisz (1990) also supports a therapsid affinity, but was not included as a source tree due to the fact that a character list and matrix were not published along with the analysis. This does highlight one issue with the supertree; the position of an uncertain taxon will depend on what taxa it has been tested against. Thus far, no one has tested the relationships of *Tetraceratops* against a comprehensive set of pelycosaurian-grade synapsids. Benson (2012) unfortunately did not include it in their wide-ranging analysis due to the material not being available for study. The poor quality of the single specimen is also unfortunate. The fact that one poor specimen has been found at a heavily sampled locality lead to the suggestion that it might be allochtonous (Amson and Laurin 2011). This is regrettable, as it would make the discovery of more material unlikely.

**Therapsid relationships**

Although this study is primarily concerned with pelycosaurian-grade synapsids, the relationships of therapsids will strongly influence the phylogenetic diversity curve of synapsids during the Guadalupian. As such it is worth discussing the phylogeny of therapsids used in this diversity estimate.
Figure 22: The portion of the time calibrated supertree showing the relationships of therapsids.
The ‘traditional’ view of therapsid relationships, put forth by Romer (1956) was that they were split into two clades: 1) Anomodontia, which contained the taxa currently referred to as anomodonts, and also those belonging to Dinocephalia; 2) Theriodontia containing Biarmosuchia, Gorgonopsia, Therocephalia and Cynodontia. More recent cladistic analyses have overturned these ideas, although there is still considerable disagreement. Many analyses have suggested that Biarmosuchia are the sister to all other therapsid clades (Hopson and Barghusen, 1986; Rowe, 1986; Gauthier et al., 1988; Sidor and Hopson, 1998). However, the analysis of Liu et al. (2009) and its subsequent modification by Amson and Laurin (2012) found Biarmosuchia to be more closely related to Gorgonopsia (a return to the traditional relationship), while Dinocephalia were the basalmost therapsid clade. It has also been suggested that Biarmosuchia are paraphyletic (Kemp, 2009; Cisneros et al., 2011). Dinocephalia are usually not found to be more closely related to Anomodonts than to other therapsid taxa (Hopson and Barghusen, 1986; Rowe, 1986; Gauthier et al., 1988; Laurin and Reisz, 1990; Liu et al 2009a; Amson and Laurin, 2011; but see Liu et al, 2009b; Cisneros et al., 2011). The placement of Gorgonopsia is controversial; they have been variously placed within Theriodontia as the sister to Therocephalia and Cynodontia (Hopson and Barghusen, 1986; Sidor and Hopson, 1998), the sister to Biarmosuchia (Liu et al, 2009b; Amson and Laurin, 2011), and the sister to a clade containing Anomodontia, Therocephalia and Cynodontia (Rowe, 1986; Gauthier et al., 1988; Laurin and Reisz, 1990).

A final controversy is found in the relationships between Therocephalia and Cynodontia. While there has been little doubt that these taxa form a clade to the exclusion of other therapsids (Kemp, 1978; Kemp, 1982; Hopson and Barghusen, 1986; Sidor and Hopson, 1998), the exact nature of their relationship is unclear. Some cladistic analyses have suggested that Therocephalia are in fact paraphyletic, with Cynodontia nested within (Abdala, 2007; Botha et al., 2007; Oliveira et al., 2010), while others suggest that Therocephalia is the monophyletic sister taxon of Cynodontia (Huttenlocker, 2009; Huttenlocker et al., 2011).

The supertree supports Biarmosuchia and Dinocephalia being successive outgroups to other therapsid clades (Figure 22). This is unsurprising; it is the most commonly suggested topology among the source trees (Sidor and Hopson, 1998; Sidor and Welman, 2003; Hill, 2005; Sidor and Rubidge, 2006). Gorgonopsia are not well represented; only three species are present. No published analyses of gorgonopsian relationships have been undertaken, and usually a single taxon (typically Gorgonops) is used as an outgroup to studies of other taxa (e.g. that of Fröbisch and Reisz, 2011 on Anomodontia; Huttenlocker et al., 2011 on Therocephalia; Sidor and Rubidge, 2006 on Biamosuchia). Only two studies have tested the
relationships of multiple gorgonopsians against the other therapsid clades: Liu et al. (2009a) and the modification by Amson and Laurin (2011). Amson and Laurin (2011), included as a source tree, showed Gorgonopsia to be the sister to Biarmosuchia. However this relationship is not recovered in the supertree. Instead, Gorgonopsia occupy a position as the sister to Anomodontia, Therocephalia and Cynodontia (Figure 22), as supported by the analysis of Hill (2005). However it should be noted that this analysis only included a composite coding of Gorgonopsia (replaced by *Gorgonops torvus* when forming the supertree). The clade containing anomodonts, therocephalians and cynodonts to the exclusion of Gorgonopsia and other therapsids is not well supported, demonstrating the urgent need for work on gorgonopsian relationships. Preliminary work on a global phylogeny of early therapsids, including a greater sampling of gorgonopsians and a number of new early dinocephalians, is in fact suggesting a topology similar to that proposed by Romer in 1956: dinocephalians were found to be the sister to the anomodonts, while gorgonopsians, therocephalians and cynodonts were found within a paraphyletic Biarmosuchia (Kammerer et al., 2014). However, this analysis is as yet unpublished and so was not included in the supertree.

The supertree suggests that Therocephalia is the monophyletic sister taxon to Cynodontia (Figure 22). Why this relationship is supported over a paraphyletic Therocephalia becomes apparent when one examines the source trees. Those analyses that suggest cynodonts are a clade within therocephalians are mostly analyses focussing of cynodont relationships (Abdala, 2007; Botha et al., 2007; Oliveira et al., 2010). They contain few therocephalians, and as cynodonts are only known from the latest Permian, none of these studies contain the four taxa from the time period under study. As such none were included as source trees. The two analyses that support a monophyletic Therocephalia (Huttenlocker, 2009; Huttenlocker et al., 2011) focus on Therocephalian relationships, and contain several taxa from the time period under study, although only three cynodonts. The more inclusive study of Huttenlocker et al. (2011) was included as a source tree, and the sister group relationship between Cynodontia and Therocephalia is the one recovered in the supertree and is well supported. This implies a ghost lineage of Cynodontia extending back into the Guadalupian

This particular controversy demonstrates the need for an inclusive phylogeny containing large samples of taxa from both Cynodontia and Therocephalia. The existing studies focus on one or the other, and as such vital information on character polarities may be missed. This also highlights the dangers of being too selective when choosing source trees; when a wider selection of trees is included (those containing three or more taxa from the late Moscovian until the end of the Triassic), a paraphyletic Therocephalia is recovered, and no
cynodont ghost lineage extends into the Guadalupian (see Chapter 6). One can justify restricting the number of source trees; the more inclusive analyses may confuse the relationships of the taxa present during the time period under study. The most obvious example of this is the analysis of Abdala (2007), which included Prorubidgea. This taxon is not used in any other analysis, and even the analysis of Abdala (2007) shows little about its relationships other than it being outside Therocephalia. As such becomes a wildcard taxon in the supertree, obscuring the relationships of other clades. Finally, if one chooses to include as source trees phylogenetic analyses containing no taxa within the time period under study one has to ask where one should stop. What effect would including analyses containing three or more taxa from just the Permian, but including the Lopingian, have? What would be the effect of including only those phylogenies containing five or more taxa from the time period under study instead of just four? Such questions are beyond the scope of this thesis, but are worth bearing in mind.
Chapter 4
The Completeness of the Fossil Record of Pelycosaurian-Grade Synapsids
Quantifying the Completeness of the Fossil Record

When one considers the multitude of issues which can affect the fossil record, the difficulty of assessing its quality becomes apparent. An enormous variety of metrics and methods have been proposed, each using different raw data and investigating a different aspect of the completeness of a clade’s fossil record.

Fit of Phylogenies to Stratigraphy

A widely-explored branch of methods used to examine the quality of the fossil record incorporates stratigraphic ranges of species and phylogenetic hypotheses of their relationships. Phylogenies are usually produced using data independent of stratigraphy, and so stratigraphy can be used to test these phylogenetic hypotheses, or a phylogenetic hypothesis can be used to test for gaps in the fossil record. In theory, given a complete record and a correct phylogeny, taxa should appear in the stratigraphic column in the order implied by the splitting of the nodes in the phylogeny, and ghost lineages (lineages not observed in the fossil record but inferred from the phylogeny on the assumption that sister taxa should diverge from their common ancestor at the same time) should be absent. If species appear in the fossil record at a time which defies the sequence suggested by the phylogeny, one may infer either there are gaps in the record or the phylogenetic hypothesis is erroneous.

There exist a large number of methods to show to what extent a phylogeny fits the stratigraphic ranges of the taxa. Many of these have been examined in simulations or in case studies, investigating biases such as tree balance (Siddall, 1996; Hitchin and Benton, 1997a; b; Siddall, 1997; 1998; Wills, 1998; 1999; Pol et al., 2004; Wills et al., 2008), tree size (Benton and Storrs, 1994; Hitchin and Benton, 1997a) and the length of time represented by the phylogenetic analysis (Benton and Storrs, 1994; Hitchin and Benton, 1997a; b; Finarelli and Clyde, 2002; Pol et al., 2004), as well as studying the completeness of the record and the reliability of phylogenies of various clades (Gauthier et al., 1988; Norrell and Novacek, 1992; Benton and Storrs, 1994; Huelsenbeck, 1994; Smith and Littlewood, 1994; Hitchin and Benton, 1997a; Benton et al., 2000; Angielczyk, 2002).

Stratigraphic Rank Correlation

The Stratigraphic Rank Correlation (SRC) measures the correlation between two sets of ranks applied to each species in the phylogeny: a stratigraphic rank based on their relative
position in the stratigraphic column, and a phylogenetic rank based on the number of nodes the taxa are removed from the root. These two ranks can be subjected to tests for correlation. The first study of this sort used the Product Moment Correlation Coefficient (Gauthier et al., 1988), although later it was suggested that the Spearman’s Rank is more appropriate (Norrell and Novacek, 1992). The latter authors also pointed out that, while stratigraphic data is linear, the phylogenetic data are not unless a fully pectinate tree is used. It was suggested that the phylogenies should be reduced to all possible fully pectinate topologies, each of which should be subjected to separate examination (Norrell and Novacek, 1992). This creates a second problem: how to combine tests on different pectinate trajectories; simply averaging the Spearman’s rho value is problematic as the nodes within separate analyses are not independent (Siddall, 1998). Furthermore, the rank correlation tends to increase in larger (Benton and Storrs, 1994) and more resolved (Hitchin and Benton, 1997a) trees. Another concern is that this metric does not account for the length of the gaps implied by the phylogeny, instead only measuring the clade rank (Norrell and Novacek, 1992). In fact, simulations suggest that the SRC shows little relationship with sampling, and is more strongly affected by the accuracy and resolution of the phylogeny (Wagner and Sidor, 2000).

**Stratigraphic Consistency Index**

The Stratigraphic Consistency Index (SCI) counts the number of stratigraphically consistent nodes relative to the total number of nodes in a phylogeny (Siddall, 1997). A node is considered consistent if it appears in the same or a later time bin than its sister (Figure 23A). This method has been criticised most frequently for tree-shape related biases (Siddall, 1996; 1997; 1998). In any tree that is not fully pectinate, there will be at least one node inconsistent by virtue of the fact that its sister is consistent (Siddall, 1998). This also leads to the phenomenon that in a completely balanced tree the minimum score is 50%, not 0. The exact nature of the bias of tree balance on results is debateable. Hitchin and Benton (1997 a; b) argued that it has no effect, finding no correlation with metrics of balance and the SCI. However, their analysis included cladograms containing recent taxa, biased towards higher SCI scores; all nodes containing only modern taxa are consistent (Siddall, 1997). Simulations suggest that there is a correlation between SCI and tree balance, but both positive (Siddall, 1997) and negative (Pol et al., 2004) relationships have been supported. Another problem is that one taxon can have a large effect on the result (Hitchin and Benton, 1997a); a single long lived derived taxon can render many nodes inconsistent. Despite these issues, simulations suggest that an accurate phylogeny should score reasonably well (Wagner and Sidor, 2000).
Figure 23: Methods of comparing the consistency of a phylogeny to the fossil record. From Wills (1999). A) Stratigraphic consistency index (SCI); B) Observed tree and stratigraphic ranges. Relative completeness index (RCI calculated by dividing the minimum implied gap (MIG; length of inferred ghost lineages) by the simple range length (SRL; observed ranges). Gap excess ratio (GER) is derived from the MIG, normalised for the maximum and minimum possible gap inferred in C and D. Observed lineages in black, ghost lineages in grey; C) tree with the smallest possible MIG; D) tree with the largest possible MIG.
**Gap Excess Ratio**

The Gap Excess Ratio (GER) was introduced by Wills (1999) to correct for problems with the SCI such as tree balance and size bias. This metric compares the length of the “gaps” (ghost lineages) implied by the phylogeny (Figure 23B) to the maximum and minimum gap possible with the stratigraphic ranges observed (Figure 23C, D). Like the SCI, it ranges from 0 to 100%. As well as correcting for problems with balance, this method takes into account the length of the implied gaps, rather than just the stratigraphic rank as in the SRC, or whether a node is consistent as in the SCI. There is still a tree shape bias (simulations suggest the GER is higher in balanced trees), but it is less pronounced than in the SCI (Pol et al., 2004). However, the same simulations also suggested that a higher GER would be seen when the length of time observed was higher.

**Relative Completeness Index**

The above three metrics all measure the fit of a phylogeny to the fossil record. Although they may be affected by both inaccuracy of the phylogeny and an incomplete fossil record, if all taxa appear in the fossil record in the order implied by the phylogeny, the phylogeny should receive a perfect score (notwithstanding the issues of tree balance affecting the SCI). On the other hand, the Relative Completeness index (RCI) is more a measure of completeness than of fit (Benton and Storrs, 1994). It will be affected by inaccuracies in the cladogram (Wagner, 2000), but it is possible for a phylogeny to have perfect consistency with the stratigraphy, and thus perfect SRC, SCI and GER scores, but to have a poor RCI score. The RCI measures the gap implied by the phylogeny relative to the length of observed lineages but, unlike the GER, does not normalise for the maximum and minimum possible gap implied by the stratigraphic ranges presented (Figure 23B). Thus the score has a maximum value of 100% (no gaps implied), but a theoretically infinite lower limit; values can be negative if the ghost lineages implied by the phylogeny cover more time than observed lineages (Benton and Storrs, 1994). This metric does not appear to be affected by the same tree balance biases as the other metrics discussed (Hitchin and Benton, 1997 a; b), but different problems have been identified. Firstly, the taxonomic level of the cladograms under study will have an effect: high level groups e.g. families, with long stratigraphic ranges will mask gaps within the families (Benton and Storrs, 1994). Secondly, unless ancestors are included in phylogenetic hypotheses, the maximum score of 100% may never be reached.
Other Methods

The four metrics described above have been used most extensively in studying the fit of the fossil record, having been applied to many clades from multiple time periods. Other methods do exist, but have been less widely applied either due to methodological concerns or practical issues e.g. lack of readily available automation. These will therefore be discussed only briefly.

The Stratigraphic Retention Index (Clyde and Fischer, 1997) quantifies how well a matrix of stratigraphic characters (wherein each character refers to a time interval crossed by a taxon) fits a phylogeny. Although the performance and assumptions of this method have been examined (Clyde and Fischer, 1997; Finarelli and Clyde, 2002), this has never been applied to empirical data. Problems identified with this method include the fact that the stratigraphic character matrix includes no way of taking into account periods where no fossils at all are found (Finarelli and Clyde, 2002). The method also only takes into account the length of ghost lineages in an indirect way: the number of stratigraphic character changes rather than the actual length of time (Clyde and Fischer, 1997). The Implied Gap (Smith and Littlewood, 1994) is similar to the RCI, but simply divides the length of ghost lineages by the total length (observed and ghost). This method is subject to similar biases to the RCI, but has a lower and upper limit (0-1). It has been applied to empirical data only once to compare phylogenies of echinoids (Smith and Littlewood, 1994). Finally, the Character Consistency Ratio (Angielczyk, 2002) employs a character list to examine how consistent with stratigraphy the character changes inferred from the phylogeny are. A character change is inconsistent if the more derived state appears in the record before the plesiomorphic state. This method was tested on the therapsid clade Anomodontia (Angielczyk, 2002), but several issues were raised: different character optimisations and different character lists can produce different results for the same phylogeny. A lack of readily available automation has also limited its application.

Completeness of Specimens

An aspect of the completeness of the fossil record which received little attention during early discussions of sampling bias, but has been considered more in recent years, is the completeness of the specimens themselves. This may provide information not only on the impact of taphonomic processes on our interpretations of the fossil record, but also on how reliable our taxonomic assignments may be; their accuracy depends on enough of the
organism being preserved to display the relevant characters. Early investigations into the completeness of fossil specimens were based on grading specimens. For example, in their study on Mesozoic birds, Fountaine et al. (2005) assigned each bird species a grade from 1-4 whereby a species given a grade of 1 was represented by a single bone, 2 by more than one bone, 3 by a single nearly complete specimen and 4 by more than one nearly complete specimen. Similar systems have been used in studies on early tetrapods (Benton et al., 2004), echinoids (Smith, 2007) and dinosaurs (Benton, 2008). Such studies are subjective and provide only coarse quantifications of specimen quality. For example, where exactly is the boundary between a collection of associated skeletal elements (scored as ‘2’ in Fountaine et al.’s scheme) and a nearly complete skeleton (scored as ‘3’)? Different workers may assign different completeness scores to the same specimens, making it difficult to reproduce the results of the analyses. Also, the coarse nature of completeness metrics based on just four or five categories means that important fluctuations in fossil record quality might be obscured.

Mannion and Upchurch (2010), in their study on Sauropodomorpha, attempted to remedy these issues with two new completeness metrics: the Skeletal Completeness Metric (SCM) and the Character Completeness Metric (CCM). Both these metrics assign a percentage completeness score to each species. In the SCM, the percentage is based on the relative bulk and number of elements preserved, while in the CCM it is based on the portion of phylogenetic characters that may be scored. As well as the initial study on sauropodomorph dinosaurs, the Character Completeness Metric has also been applied to Mesozoic birds (Brocklehurst et al., 2012), anomodont therapsids (Walther and Fröbisch, 2013) and expanded to include all dinosaurs (Bell et al., 2013). The Skeletal Completeness Metric has been used globally in the original study on sauropodomorphs and most recently ichthyosaurs (Cleary et al., 2015), but also at a more local level to examine body size bias in the Dinosaur Park Formation (Brown et al., 2013).

A variety of methods have been used to implement the CCM. In the original study, Mannion and Upchurch (2010) examined four published character lists from phylogenetic analyses of sauropodomorphs and counted what percentage of characters from each referred to each bone. A score for each bone was assigned to each bone by finding the average percentage across the four character lists. If a species preserves a particular bone, it receives the relevant percentage score. Brocklehurst et al. (2012) modified this method, assembling a single list of over 500 characters, and calculating what proportion of the characters related to each bone. This method has two advantages over other implementations. Firstly, it allows the inclusion of all species; the methods discussed below only allow the inclusion of species,
which have been incorporated into phylogenetic analysis. Moreover, different specimens of the same species may be scored separately e.g. if appearing in different time bins or in different localities. However it does have one flaw in that it over-estimates the completeness of specimens. It assumes that if a bone is preserved, all characters referring to the bone may be coded and that the specimens should receive the full percentage score for that bone; it does not take into account issues such as surface weathering or damage which may obscure characters.

Walther and Fröbisch (2013) took a different approach, using what was then the most comprehensive phylogenetic analysis of anomodonts and calculating what percentage of characters that had been scored for each species within. This method can calculate completeness only for specimens included in that phylogeny, and so is only appropriate when applied to a clade for which such a comprehensive phylogeny exists. Bell et al. (2013), in a study of dinosaurs, expanded this method so that all phylogenetic analyses of the clade in question would be taken into account. Again, this method does not include species which have not been included in phylogenetic analyses, but it allows the analysis of clades for which a single comprehensive phylogeny does not exist. Unlike the Brocklehurst et al. method, both the Walther and Fröbisch and the Bell et al. methods are based directly on the character scorings rather than the presence or absence of bones and are therefore less likely to over-estimate completeness. In fact, it is possible that completeness may be underestimated since characters referring to a portion of the anatomy not possessed by a particular species are scored as unknown and so are deducted from the completeness score. However, since individual specimens are not scored separately in phylogenetic analyses, the Walther and Fröbisch and Bell et al. methods do not allow different specimens from the same taxon found in different time bins or environments to be scored separately.

The Completeness of the Fossil Record of Palaeozoic Synapsids

Thus far, there has never been a dedicated study examining the completeness of the fossil record of pelycosaurian-grade synapsids. Such studies on contemporary organisms have been more general, focusing on wider groups like amniotes and tetrapods. In this chapter, I present the first examination of the quality of the basal synapsid record as a precursor to the examinations of diversity and diversification patterns in the following chapters.Completeness metrics are used to examine the record through geological time, including modifications of previously proposed methods to examine the completeness of the fossil specimens (Mannion
and Upchurch, 2010). Four methods are used to examine the fit of the fossil record to phylogeny to investigate the reliability of cladistic hypotheses and the possibility that large portions of the record may be missing. Finally a historic approach is used to examine whether new discoveries are altering our interpretations of the evolution of pelycosaurian-grade synapsids.

**Materials and Methods**

**Completeness Metrics**

An investigation into the completeness of basal synapsid specimens was undertaken using the Character and Skeletal completeness metrics of Mannion and Upchurch (2010). The Character Completeness Metric (CCM) was undertaken using the method applied by Brocklehurst et al. (2012) to the avian fossil record. This method was selected over those proposed by Walther and Fröbisch (2014) and Bell et al. (2013) due to its ability to score all species, not just those included in phylogenetic analyses. The specimens incorporated into this analysis were those included in the database described in Chapter 3, based on the published literature prior to April 2014 and personal observations from museum specimens.

The Character Completeness Metric requires a list of phylogenetic characters relevant to the group under study. Five character lists were selected for the present study: one of amniotes (Reisz et al., 2010), two of pelycosaurian-grade synapsids (Mazierski and Reisz, 2010; Benson, 2012), and two of therapsids (Huttenlocker, 2009; Amson and Laurin, 2011), relevant as therapsids overlap in time with pelycosaurian-grade synapsids and so it is necessary to include characters which may distinguish them. These character lists were combined, and duplicate characters were removed, creating a list of 503 characters (see Appendix F). Scores were then assigned to each region of the skeleton based on the number of characters pertaining to that region. If a species preserves a particular region of the skeleton, then it received the relevant CCM percentage score. The percentage scores assigned to each region of the skeleton may be viewed in Appendix G.

For the Skeletal Completeness Metric (SCM), Mannion and Upchurch (2010) did not propose a quantitative way to assess the bulk of particular regions of the skeleton and assign a percentage score to each region. In this study we propose that if the various regions of the skeleton were modelled as cones, cylinders and prisms, percentage scores for each bone may be derived from the volume of each region. While such a model is clearly not a perfect
measure of the volume of the bones, it does allow a more objective measure of the bulk of skeletal elements than the estimates provided by Mannion and Upchurch (2010). Obviously the proportions of the various bones in a skeleton vary from species to species. As such, four specimens, each from a different family of pelycosaurian-grade synapsids, were selected as representatives, and the final percentages assigned to each region were based on the mean volume of each element from each species. The specimens used were AMNH FAR 7517 (Cotylorhynchus romeri), MCZ 1365 (Dimetrodon milleri), MCZ 1366 (Ophiacodon uniformis) and FMNH UR 34 (Varanops brevirostris). Edaphosaurids and eothyridids were represented due to a lack of nearly complete specimens. Eothyris, Oedaleops and “Mycterosaurus” smithae are known from limited material; the former from a skull and the latter two by partial skulls and few postcranial elements. There are more complete edaphosaurid specimens, but the most complete skeletons are mostly composites. The percentage scores assigned to each region of the skeleton, and details of the shapes used to model the skeleton for the SCM may be viewed in Appendix H, and a condensed overview of the percentages assigned to the CCM and SCM is shown in Table 3.

<table>
<thead>
<tr>
<th>Character Completeness</th>
<th>Metric</th>
<th>Skeletal Completeness</th>
<th>Metric</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skull</td>
<td>69.98%</td>
<td>18.13%</td>
<td></td>
</tr>
<tr>
<td>Pectoral girdle</td>
<td>4.37%</td>
<td>7.19%</td>
<td></td>
</tr>
<tr>
<td>Forelimb</td>
<td>6.19%</td>
<td>10.94%</td>
<td></td>
</tr>
<tr>
<td>Pelvic girdle</td>
<td>3.20%</td>
<td>3.26%</td>
<td></td>
</tr>
<tr>
<td>Hindlimb</td>
<td>5.37%</td>
<td>18.30%</td>
<td></td>
</tr>
<tr>
<td>Vertebral column</td>
<td>9.58%</td>
<td>42.18%</td>
<td></td>
</tr>
</tbody>
</table>

Table 3: A comparison of the percentage scores assigned to different regions of the skeleton (see Appendices G and H for the more detailed breakdown of the scores)

As in the CCM, a species preserving a particular element received the relevant percentage score for that element. A species for which only part of an element is preserved will receive only a part of the relevant score e.g. a single femur will receive an SCM score of 4.08%, while if only proximal end of a femur is preserved it will receive a one third of this score: 1.36%. For a region of the vertebral column, the completeness of a specimen is based on the number of vertebrae preserved compared to the number of vertebrae the species is thought to have had e.g. the dorsal column is worth 7.67%. If a species had 22 dorsal
vertebrae, but one specimen preserves only 11 of these, that specimen will receive only half the SCM score: 3.84%. Where the total number of vertebrae of a species is not known for certain, it is inferred from closely related species. The same system is used for digits; the SCM score is based on then number of phalanges preserved relative to the number the species is thought to have had.

A CCM and SCM score is calculated for each time bin by assigning a score to each species present within that bin, and then calculating the mean score of all species (see Appendix I). If different specimens of the same species were known from different time bins, they were scored separately. Where there is uncertainty over the age of a specimen, it is assigned to the full range of possible ages. These mean scores were plotted through time to create CCM and SCM curves. The correlation between these two curves, and between each curve and the taxic diversity, was tested using Kendall’s Tau and Spearman’s Rank correlation coefficients, implemented using R version 3.0.0 (R Core Team, 2013) after applying generalised differencing to correct for autocorrelation (McKinney, 1990).

It should be noted that Mannion and Upchurch (2010) proposed two methods to implement both of these metrics. SCM1 and CCM1 estimate the completeness of the most complete specimen of each species, while SCM2 and CCM2 assess the completeness based on the combined information from all known specimens. Mannion and Upchurch (2010) and Brocklehurst et al. (2012) considered the second of these metrics to be more meaningful, not only because it includes all available information, but also because the SCM1 and CCM1 both require some species to be omitted from an analysis in cases where associations of disarticulated bones make it difficult to recognise ‘the most complete individual’. As such, in this study only the SCM2 and CCM2 are applied.

Fit of the Phylogeny to the Fossil Record

The fit of the phylogeny of pelycosaurian-grade synapsids to the stratigraphic record was assessed to examine both the completeness of the fossil record and to provide an independent test of the accuracy of the phylogeny. The metrics used were the Stratigraphic Rank Correlation (SRC), the Stratigraphic Consistency Index (SCI), the Gap Excess Ratio (GER) and the Relative Completeness Index (RCI). These have been used widely, including on contemporary taxa closely related to pelycosaurian-grade synapsids, e.g. Palaeozoic amniotes and other synapsid clades (Norrell and Novacek, 1992; Benton and Storrs, 1994; Hitchin and Benton 1997; Benton 2000, Angielczyk, 2001). It is important that this be the
case: the completeness of the fossil record is a relative concept, and so the results of this study need to be compared to previous analyses. The Character Consistency Index (Angielczyk, 2002), despite having been applied to the closely related Palaeozoic synapsid group Anomodontia, was not used due to methodological concerns. This index assesses whether the time of character transitions implied by the phylogeny agrees with the appearance of a particular character state in the fossil record. However, this method introduces further uncertainties into the study. A poor result could mean a poor phylogeny or an incomplete record, as in other metrics, but could also mean a poor choice of characters or incorrect character optimization.

The four metrics were applied to a time calibrated version of the supertree produced in chapter 3. Only the portion representing pelycosaurian-grade synapsids was included. Therapsids were collapsed into a single lineage. In implementing the SRC the tree was reduced to all possible fully pectinate phylogenies, following the recommendations of Norrell and Novacek (1992). All phylogenies containing four or less taxa were removed from the analysis, since it is impossible for such small phylogenies to show a significant correlation (Hitchin and Benton, 1997a). Stratigraphic and clade ranks were inferred from all others and were subjected to the Spearman’s Rank Correlation Coefficient using R (R Core team, 2013). The SCI, GER and RCI were all implemented using R (R Core team, 2013) using custom scripts based on functions in the Paleotree package (Bapst, 2013). In order to test the significance of the obtained values, R was also used to generate 10,000 random tree topologies, onto which the observed age ranges were overlain. The resultant values were compared to the values observed, in order to assess the probability of obtaining the observed results by chance.

Collector Curves

Collector curves (Cain, 1938) show changes in the rate of discovery through historical time and allow examination of the pattern of knowledge accumulation. The numbers of taxa known can be plotted against any measure of effort, in palaeontology usually the number of years of study. One use of such curves is to investigate whether the number of species found from a certain taxonomic group is reaching saturation, or whether there are likely to be many more yet to be discovered. In a clade in which discovery is approaching saturation, one expects a sigmoid-shaped curve, with low initial rates of discovery, followed by a rapid acceleration in the number of species found per year, and then eventually a slowing in the rate
of discovery, as the curve approaches an asymptote representing the maximum ‘knowable’ record (Benton et al., 2011). Collector curves formed for different clades have shown different signals, with some e.g., mammals (Alroy, 2002), birds (Fountaine et al., 2005) dinosaurs (Benton, 2008) and amphibians (Bernard et al., 2010) showing no sign of having reached an asymptote, while others e.g., tetrapods as a whole (Maxwell and Benton, 1990), echinoderms (Smith, 2007) and trilobites (Tarver et al., 2007) indicate that the rate of discovery is slowing.

A collector curve was formed to illustrate discoveries of pelycosaurian-grade synapsids since 1854, when *Bathygnathus borealis* (Leidy, 1854), was described. New discoveries were added in annual intervals until 2014. This curve represents “now valid” species, as opposed to “then valid”, as distinguished by Alroy (2002), meaning that the curve represents when species considered valid in the present dataset were discovered, whether or not they were originally recognised as pelycosaurian-grade synapsids, and does not include taxa which after their original description were synonymised, declared *nomina dubia* or assigned to other clades. The ‘now valid’ curve is considered more relevant to this study on the current state of the record.

The polynomial model function in Past (Hammer et al., 2001) was applied to the collector curve. The function fits several polynomial curves to the data, and the best-fitting model was chosen based on the Akaike Information Criterion. This reveals the long-term trends in the curve, enabling identification of the point at which the stepwise increase in the number of species shows a genuine rather than temporary slowing of the rate of discovery.

**Investigating the Influence of New Discoveries**

A taxic (raw, without sampling correction) diversity estimate of pelycosaurian-grade synapsids was used for an examination of the degree to which new discoveries change the shape of diversity curves and our interpretations of major events within the evolution of pelycosaurian-grade synapsids. A “current” diversity curve, representing the state of knowledge in 2014, was produced by counting the number of basal synapsid species known in each substage. Taxa were pruned from the diversity curve going back in time in decade-long intervals from 2014. A new diversity curve was formed only from the taxa remaining in the dataset after the pruning. This was done as far back as 1864, at which point only one taxon (*Bathygnathus borealis*) was present in the dataset. The correlation between the past diversity curves and the 2014 diversity curve was tested with the Kendall’s Tau and Spearman’s Rank
Correlation Coefficients using R, after transforming the data with generalised differencing to correct for autocorrelation.

This study did not take into account changing opinions on the stratigraphic ages of formations. It is difficult to ascertain what the ‘widely-held opinion’ of the age of a particular formation was during history, particularly when the age of sediments are even now subject of debate. Previous databases could give an idea of how these opinions have changed, but the two previously published databases of pelycosaurian-grade synapsids (Romer and Price, 1940; Reisz, 1986) do not provide ages giving enough temporal resolution to form diversity curves. As such, the ages assigned to species in the past diversity curves are the same as those assigned to the species in the 2014 diversity curve. However changes in the known stratigraphic ranges of species are taken into account. If a species was named one year, but a specimen was discovered later which extended the range, the full range will only be used in the more recent diversity curve.

The Relative Completeness Index was used to investigate how the completeness of the fossil record has changed through history, and to answer the question: are new discoveries filling gaps or creating more? The RCI of the basal synapsid record was calculated for the supertree to give a value for 2014. Values for each preceding year were calculated by pruning taxa not named before that year. The tree topology of the remaining taxa was retained after the pruning. The RCI was calculated for each year back in time until 1878, when the first pelycosaurian-grade species subjected to phylogenetic analysis were described. As described above, changes in the opinion on the age of formations was not taken into account, but new discoveries which changed the stratigraphic range of a species were.

**Results**

**Completeness Metrics**

The Character Completeness Metric (Figure 24A) starts on a peak in the late Moscovian of 42.52%, higher than in any other Carboniferous time bin, before falling to its lowest trough (17.94%) in the Kasimovian. After this initial fluctuation, the CCM curve remains extremely stable for the next ten time bins with only small variations between 28.00 and 36.12%. This consistency lasts until the late Kungurian, when there is a peak CCM score of 45.79%, and then another trough in the early Roadian of 29.05%. The score then rises to an overall peak in the Wordian of 67.16%, before dropping slightly to 60.38% in the Capitanian.
Figure 24: A) Character Completeness Metric Curve (solid line) and one standard deviation either side (dashed line). B) Skeletal Completeness Metric curve (solid line) and one standard deviation either side (dashed line). Timescale representing millions of years ago shown at the bottom.

The Skeletal Completeness Metric (Figure 24B) shows a significant positive correlation with the Character Completeness Metric (Table 4). The same trends and peaks appearing in the CCM curve are mostly visible in the SCM curve as well. The biggest difference between the two appears in the first two substages. Whereas the CCM curve indicates a fall from a late Moscovian peak to an early Kasimovian trough, the SCM scores increase from 30.35 to 35.15% between these substages. Between the late Kasimovian and early Kungurian, the SCM shows the same stability as the CCM, although the SCM values are consistently lower (ranging from 26.11 to 35.29%). As in the CCM, the SCM curve shows a late Kungurian peak, an early Roadian trough, and a Wordian overall peak.
Table 4: The correlations between the Character Completeness Metric curve (CCM), the Skeletal Completeness Metric curve (SCM) and the taxic diversity curve (TDE) of pelycosaurian-grade synapsids. Significant correlations (p<0.05) are highlighted with an asterix.

<table>
<thead>
<tr>
<th></th>
<th>Kendall’s tau</th>
<th>Spearmann’s rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCM vs SCM</td>
<td>0.503268 (p=0.002986)*</td>
<td>0.6594427 (p=0.093701)*</td>
</tr>
<tr>
<td>CCM vs TDE</td>
<td>-0.254902 (p=0.1519)</td>
<td>-0.3828689 (p=0.1177)</td>
</tr>
<tr>
<td>SCM vs TDE</td>
<td>-0.3856209 (p=0.02643)*</td>
<td>-0.504544 (p=0.03456)*</td>
</tr>
</tbody>
</table>

Both the CCM and the SCM show a negative relationship with the diversity of the pelycosaurian-grade synapsids (Figure 25), according to the Spearman’s rank and Kendall’s tau correlation coefficients. Only the correlation with the SCM is significant (Table 4).

Figure 25: A comparison of the Character Completeness Metric curve, the Skeletal Completeness Metric curve and the taxic diversity curve of pelycosaurian-grade synapsids. Timescale representing millions of years ago shown at the bottom.

Fit of the Phylogeny to the Fossil Record

When the supertree is reduced to all its fully pectinate component trees, and all those containing four or less taxa were removed, 107 trees remained. Of these, 36% showed a significant (p<0.05) Spearmann’s rank correlation between the phylogenetic rank and stratigraphic rank of the taxa. The mean Spearmann’s rank score was 0.57. The largest fully pectinate trees (13 terminal taxa) all show significant correlation, with values ranging from 0.56 to 0.74 (p= 0.031936–0.0038814).
The other three metrics of fit were applied to the entire supertree and so produced one value each: the Stratigraphic Consistency Index = 54%; the Gap Excess Ratio = 58% (P-value obtained from random permutations = 0.0169); the Relative Completeness Index = 2% (P-value = 0.0159).

Collector’s Curve

The collector’s curve (Figure 26) shows that the rate of discovery of pelycosaurian-grade synapsids remained low between 1854 and 1877, during which only 5 species were described. There was a brief and rapid increase in the number of known species to 11 in 1878, following five papers by Cope (Cope, 1877b; a; 1878a; b; c). After this year the gradual increase in the rate of discovery continued, with 9 new species named between 1879 and 1906. During the 1900s and 1910s, the rate of discovery again intensified. The Revision of the Pelycosauria of North America by Case (1907) and the papers of Williston (Williston, 1910; 1911; 1913; Williston and Case, 1913; Williston, 1915), among others, contributed to the naming of 11 new species in an interval of 7 years.

![Collector’s Curve](image)

Figure 26: The collectors curve representing descriptions of pelycosaurian-grade synapsid taxa through historical time (solid line) and the polynomial model fitted using Past (dashed line).
The biggest leap in the number of known species occurred in 1937, when 13 new species were described, 11 erected by Romer (1937). A further 4 species were named over the next four years, but after 1940, no new descriptions were made until 1952. It is unclear why there was such a long period without discovery. Benton (2008) observed a slower rate of discovery of dinosaurs at a similar time and attributed it to the Second World War.

Discoveries since 1952 do not follow the stepwise pattern described for the preceding years. Instead there is a consistent rate of increase in known species until 1991. During these 39 years, 35 species were named. Many of those found in the 1950s and 1960s were named in papers by Olson (Olson and Beerbower, 1953; Olson, 1954; 1962; Olson and Barghusen, 1962; Olson, 1965). After 1991, there was again a plateau which has lasted until the present day, with no new species named for the next 10 years, and only 7 named in the 20 years between 1991 and 2011.

The polynomial model function in Past suggests that, according to the Akaike information criterion, a fifth order model best fits the collector’s curve. This model indicates the sigmoid pattern expected for a clade whose discovery is reaching saturation. After a low initial rate of discovery, the rate accelerates between the 1920s and 1980s. During the 1980s, the rate of discovery slows, reaching a plateau after the year 2000.

**Historical RCI Analysis**

The Relative Completeness Index has fluctuated greatly through historical time (Figure 27). It was at its highest during the early years of discovery; when the supertree is pruned to include only taxa known in 1878, the RCI is 30% (although it should be noted that this value is based on a supertree pruned to only 3 pelycosaurian-grade taxa and a lineage representing Therapsida). Early discoveries caused large changes in the RCI; as there were so few taxa, a single discovery can have a large effect. Most of the changes are decreases. The discovery of *Varanosaurus acutirostris* (Broili, 1904) produced a long ghost lineage from the Kungurian to the Sakmarian, and the RCI decreased from 32 to 15%. Further discoveries in 1907 and 1908 led to additional gaps in the record, causing the RCI to fall to its lowest point: -57%.

After this trough, the RCI rose following the descriptions of Williston (Williston, 1910, 1911, 1913; Williston and Case, 1913; Williston, 1915) to a peak of -6% in 1913. It fell again to -13% in 1915, and remained between -13 and -11% for the next 21 years. Between 1936 and 1938, 9 species now included in the supertree were described, 5 of them in Romer
These discoveries again created more gaps than they filled, causing the RCI to fall to -38%. This trough lasted only until 1940, when the new taxa described in Romer and Price (1940), and the expansion of ranges of known species by the identification of new specimens in the same volume, pushed the RCI up to -24%.

Discoveries between the early 1940s and early 1960s have very little impact on the RCI, which remains between -24 and -22%. It is not until 1965 that there is a noticeable increase to -14%. This increase is in part due to the discovery of *Oedaleops campi* (Langston, 1965), which partially fills a caseasaur ghost lineage stretching from the Kungurian to the late Carboniferous. In 1972 the earliest known synapsid, *Archaeothyris floresiensis* (Reisz, 1972) was described. This late Moscovian ophiacodontid caused ghost lineages from Caseasauria, Varanopidae, and the clade containing Edaphosauridae and Sphenacodontia to be drawn back into the late Moscovian, decreasing the RCI to -21%. During the late 1970s and early 1980s the RCI rose again, reaching -1% in 1983. Thereafter, the RCI fluctuates between -3% and 3% with no large excursions, either positive or negative.
Historical Diversity Curves

The current diversity curve of pelycosaurian-grade synapsids correlates significantly with each of the historical diversity curves as far back as 1914 (Table 5). Unsurprisingly, the correlation becomes weaker further back in time. The 1874 curve shows a significant correlation when Spearman’s rank is used, but not Kendall’s tau. However, in 1874 only two taxa were known, so it is likely that this significant correlation is an artefact of this.

<table>
<thead>
<tr>
<th></th>
<th>Kendall’s tau</th>
<th>Spearmann’s rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>2014 vs 2004</td>
<td>0.8823529 (p=8.282x10^{-10}) *</td>
<td>0.9628483 (p=6.54x10^{-8}) *</td>
</tr>
<tr>
<td>2014 vs 1994</td>
<td>0.8823529 (p=8.282x10^{-10}) *</td>
<td>0.9690402 (p=7.434x10^{-6}) *</td>
</tr>
<tr>
<td>2014 vs 1984</td>
<td>0.8300654 (p=2.713x10^{-5}) *</td>
<td>0.9484004 (p=3.235x10^{-6}) *</td>
</tr>
<tr>
<td>2014 vs 1974</td>
<td>0.7908497 (p=2.295x10^{-7}) *</td>
<td>0.9360165 (p=2.2x10^{-16}) *</td>
</tr>
<tr>
<td>2014 vs 1964</td>
<td>0.7385621 (p=2.522x10^{-6}) *</td>
<td>0.9029928 (p=2.2x10^{-16}) *</td>
</tr>
<tr>
<td>2014 vs 1954</td>
<td>0.5947712 (p=0.0003246) *</td>
<td>0.7121063 (p=0.01265) *</td>
</tr>
<tr>
<td>2014 vs 1944</td>
<td>0.503268 (p=0.002986) *</td>
<td>0.5768834 (p=0.01374) *</td>
</tr>
<tr>
<td>2014 vs 1934</td>
<td>0.5163399 (p=0.002244) *</td>
<td>0.5727554 (p=0.01455) *</td>
</tr>
<tr>
<td>2014 vs 1924</td>
<td>0.4901961 (p=0.003935) *</td>
<td>0.5438596 (p=0.0214) *</td>
</tr>
<tr>
<td>2014 vs 1914</td>
<td>0.503268 (p=0.002986) *</td>
<td>0.5706914 (p=0.01497) *</td>
</tr>
<tr>
<td>2014 vs 1904</td>
<td>0.254902 (p=0.1519)</td>
<td>0.3601651 (p=0.1425)</td>
</tr>
<tr>
<td>2014 vs 1894</td>
<td>0.254902 (p=0.1519)</td>
<td>0.370485 (p=0.1308)</td>
</tr>
<tr>
<td>2014 vs 1884</td>
<td>0.2287582 (p=0.2008)</td>
<td>0.3168215 (p=0.1999)</td>
</tr>
<tr>
<td>2014 vs 1874</td>
<td>0.3333333 (p=0.05736)</td>
<td>0.4901961 (p=0.04076) *</td>
</tr>
<tr>
<td>2014 vs 1864</td>
<td>-0.1111111 (p=0.5498)</td>
<td>-0.124871 (p=6.208)</td>
</tr>
</tbody>
</table>

Table 5: The correlations between the current (2014) taxic diversity curve of pelycosaurian-grade synapsids and pruned diversity curves, with taxa described after the specified year removed. Significant correlations (p<0.05) highlighted with an asterix.

The Quality of the Fossil Record of Pelycosaurian-Grade Synapsids – Current Perspectives

Completeness of Specimens Through Geological Time

The two methods employed for assessing the completeness of pelycosaurian-grade synapsid specimens, the Character Completeness Metric (CCM) and the Skeletal
Completeness Metric (SCM), are assessing different aspects of the fossil record. The CCM is a measure of how much information may be obtained from the fossils, since it is based on phylogenetically relevant characters. However, it should not be considered a representation of taphonomic bias, since it is possible for a species to receive a complete CCM score with less than half the skeleton preserved; each paired bone can be scored if only one is present, and only one vertebra and neural spine from each region of the column is needed. The SCM, however, requires all regions to be preserved to achieve a perfect score. For example, if two femora are preserved, the SCM score will be 8.15%, but if only one is preserved, the score will be 4.08%. The SCM more closely represents the amount of material, rather than information, that is preserved and so is a better proxy for taphonomic biases.

With all that said, Mannion and Upchurch (2010) found a significant correlation between the two metrics, implying that the choice of metric may not have been important. However, the SCM and CCM percentage scores assigned to each region, when applied to Sauropodomorpha, were reasonably similar. When applied to pelycosaurian-grade synapsids, they are very different (Table 3). The CCM shows a great emphasis towards the skull, which is the basis for 69.98% of characters. In the SCM, however, the skull is responsible for only 18.13% of the skeleton by volume. The SCM instead shows a large emphasis on the axial skeleton (vertebrae, neural spines and ribs): 42.18%.

Given these differences, it is surprising that there is a significant correlation between the two metrics (Figure 25, Table 4). The two curves show extremely similar scores and trends, including a peak in the late Kungurian and an overall peak in the Wordian (Figure 25). The only noticeable difference is found in the early Kazimovian, in which four species are represented by mostly postcranial material and only poor skulls. As such, the CCM of this period is extremely low, while the SCM is similar to the following substages. The SCM curve shows lower values for most substages (Figure 25). This should not be surprising; as mentioned, a species needs considerably less of its skeleton preserved to achieve the same CCM score. The same can be observed in the curves of Mannion and Upchurch (2010: Fig 2).

For most of the period under study, both the mean SCM and CCM vary between about 25 and 35%, although the confidence intervals are wide, indicating a great range of individual values for species (Figure 24). As mentioned, the completeness of the fossil record is a relative concept, and it is necessary to compare these results to others in order to judge whether the fossil record of pelycosaurian-grade synapsids can be called “good” or “bad”. Unfortunately, these recently proposed methods have been applied to very few clades, and so comparison is difficult. The range of values is similar to those observed in Sauropodomorpha.
(Mannion and Upchurch, 2010), but a much larger range of values was observed in the mean CCM of Mesozoic birds, which ranged from 1.53% to 75.72% (Brocklehurst et al., 2012). This was thought to result from the effect of Lagerstätten, which would more strongly influence the record of small delicate animals as they can be more easily buried and preserved whole than large animals, but also can more easily be completely destroyed (Brocklehurst et al., 2012). There are no Carboniferous and Lower Permian formations containing pelycosaurian-grade synapsids that could be described as areas of exceptional preservation. However during the Middle Permian the Mezen faunal assemblage produces abundant fossils, although with varying degrees of articulation and preservation (Efremov, 1940; Olson, 1957). The overall peak of both the SCM and CCM is in the Wordian (Middle Permian), during which time all known pelycosaurian-grade synapsid species are from this assemblage. There are only three species known from this area, but two of them (*Mesenosaurus romeri* and *Ennatosaurus tecton*) are represented by numerous, in some cases fully articulated specimens. These species are also smaller than many of their relatives in the Early Permian. It is possible that the Wordian peak in the SCM and CCM is due to a similar Lagerstätten effect to that which caused peaks in the CCM curve of Mesozoic birds.

The only attempt to apply the CCM to a group from a similar time period to that occupied by the pelycosaurian-grade synapsids is the study of Walther and Fröbisch (2013) on anomodont therapsids. The mean CCM of Anomodontia in all but one time bin is consistently higher than 60%, considerably higher than the values obtained for pelycosaurian-grade synapsids. However, it should be noted that the periods in which the pelycosaurian CCM is at its highest are in the latest time slices, during which they overlapped temporarily and spatially with anomodonts. Walther and Fröbisch (2013) suggested that the exceptional completeness of known anomodonts may be the result of the unrivalled fossil record of Permian–Triassic terrestrial tetrapods in the South African Karoo Basin. One might therefore suggest that the Mid–Late Permian record is better than that of the Early Permian and Pennsylvanian. However, as noted, very few studies using these metrics have been undertaken, and further work is necessary before such conclusions can be firmly supported.

**Completeness Metrics and Diversity**

It has been suggested that the completeness of specimens may have an influence on diversity estimates (Benton et al., 2004; Mannion and Upchurch, 2010; Benton et al., 2011a; Brocklehurst et al., 2012; Walther and Fröbisch, 2013). A time period containing many poorly
preserved specimens may have a lower number of taxa named to species level, as it is more difficult to identify diagnostic characters. Such a mechanism has been proposed to explain the significant positive correlation observed between various completeness metrics and taxic diversity of sauropodomorphs (Mannion and Upchurch, 2010), Permian tetrapods (Benton et al., 2011) and Mesozoic birds (Brocklehurst et al., 2012). It has even been suggested that the CCM and the SCM could be used as sampling proxies in order to implement sampling correction on diversity curves (Mannion and Upchurch, 2010). Alternative reasons for a strong positive correlation between diversity and completeness score might be that an absolutely greater number of fossil discoveries in a particular time period leads not only to more species being discovered, but also more taxa being represented by more specimens and receiving a higher completeness score. A final possibility suggested by Brocklehurst et al. (2012) is that in a time period in which the clade was more abundant and diverse, there is a higher probability of specimens being preserved.

Surprisingly, the SCM of pelycosaurian-grade synapsids show a significant negative correlation with the taxic diversity curve (Figure 25, Table 4). In contrast to previous studies, it seems that as the quality of the preserved specimens gets worse, the estimates of diversity increase. Such a result has never been observed in previous studies although the possibility has been discussed (Mannion and Upchurch, 2010; Brocklehurst et al., 2012). The hypothesised scenario is that basal synapsid workers have diagnosed a large number of species based on poorly preserved, non-overlapping material which could potentially have belonged to a single species, thus raising the diversity estimate.

The correlation between diversity and the character completeness metric, while also negative, is not significant. This is again surprising; one might expect it to be the number of characters preserved in a specimen that affects the number of taxa identified, as has been seen in sauropodomorphs and Mesozoic birds (Mannion and Upchurch, 2010; Brocklehurst et al., 2012). Both these studies showed significant correlation between the CCM and taxic diversity. The lack of such a correlation in pelycosaurian-grade synapsids may reflect the history of discovery. The period of greatest discovery in basal synapsids was between the 1930s and 1960s (Figure 26). At this time, classifications were based to a large extent on stratigraphy, location and body size (e.g. Romer and Price, 1940). While there have been some recent taxonomic revisions using phylogenetic methods, this has mostly focussed on a single family: the Varanopidae (Reisz and Dilkes, 2003; Anderson and Reisz, 2004; Maddin et al., 2006; Reisz et al. 2010). Meanwhile, the rate of discovery of dinosaur (including avian) species has increased alongside the introduction and refinement of phylogenetic methods.
between the late 80s and the present day (Fountaine et al., 2005; Benton, 2008). As such, phylogenetic methods have been much more important in the classification of dinosaur species. This may be why sauropodomorph and bird diversity is much more closely linked to the CCM, a metric based on phylogenetic characters. Anomodontia, a clade subjected to many recent cladistics analyses (for summary see Kammerer et al., 2011), also show a strong relationship between diversity and the CCM (Walther and Fröbisch, 2013). The classification of pelycosaurian-grade synapsids is not so closely linked to methods based on characters, and correlates more closely to the measure of absolute completeness provided by the SCM.

The Fit of the Phylogeny to Stratigraphy

Previous studies comparing the fossil record to phylogeny have suggested a good fit when examining phylogenies of Palaeozoic organisms. Benton et al. (2000), examining how the quality of the fossil record changes through time, found that the Gap Excess Ratio (GER) and Stratigraphic Consistency Index (SCI) of phylogenies containing Palaeozoic organisms were 52.9% and 61.8 % respectively: the same as, or little worse than, those of more recent time periods. In fact the Relative Completeness Index (RCI) of phylogenies of Palaeozoic organisms was 62.064%, considerably higher than those of other time periods. Benton et al. (2000) concluded that the Palaeozoic record, while incomplete, was adequate for study.

Other results, focussing on amniotes and tetrapods in general (clades containing pelycosaurian-grade synapsids) have again found a strong correspondence between phylogenies and stratigraphy. The first such study, performed by Gauthier et al. (1988) using the Stratigraphic Rank Correlation (SRC) coefficient between a taxon’s stratigraphic rank and its clade rank, found a significant correspondence for Amniota: 0.679. When the Speamann’s rank correlation coefficient method was applied to the same phylogeny, including a reduction of the phylogeny to its various fully pectinate components, a much lower score was obtained (a mean of 0.376) (Norrell and Novacek, 1992). However, when the analysis is limited to synapsids, this is raised to 0.978 (Norrell and Novacek, 1992), suggesting that synapsids have a much better record than that of other amniotes. The SCI of this same phylogeny was found to be 0.74 (Huelsenbeck, 1994). Hitchin and Benton (1997a) applied the SCI, SRC and RCI to a large number of phylogenies of tetrapods, finding a mean SCI of 0.618, mean SRC of 0.58 and mean RCI of 49.8 %. This RCI value was lower than for echinoderms and fish, implying more of the tetrapod record is missing, but the other two metrics were higher than those of fish, indicating a better fit of phylogeny to stratigraphy (Hitchin and Benton, 1997a).
The GER produced in this study from the supertree of pelycosaurian-grade synapsids is 57%, higher than the mean GER of Palaeozoic organisms (Benton et al., 2000). This result is strongly significant according to the randomisation test, in which only 1.69% of randomly permuted trees achieved a higher GER value. The mean SRC of the pectinate components of the supertree was 0.56, only slightly lower than that of other tetrapod phylogenies (Hitchin and Benton, 1997a). While only 36% out of all 107 fully pectinate trees produced from the supertree showed a significant correlation between the record and stratigraphy, it should also be noted that reducing the supertree to all its pectinate components means a large number of very small phylogenies are included in this analysis, which are less likely to show a significant fit. The largest fully pectinate trees that can be obtained from the supertree produce SRC values ranging from 0.56 (p=0.046411) to 0.74 (p=0.0038814), implying a highly significant fit. The SCI of pelycosaurian-grade synapsids is 0.54, less than that produced for phylogenies of amniotes, tetrapods, and Palaeozoic organisms (Huelsenbeck, 1994; Hitchin and Benton, 1997a; Benton et al., 2000). However, the difference between the results for basal synapsids produced here and those of Hitchin and Benton (1997a) is not great. One should also note the SRC and SCI can only indicate what proportion of nodes is inconsistent, not how inconsistent they are. That information can only be obtained from the GER, which we consider to be a more reliable measure of fit.

The Relative Completeness Index provides a different view of the fossil record of pelycosaurian-grade synapsids. The RCI of the supertree is only 2%. This value, close to 0, implies that the many ghost lineages inferred from the phylogeny cover almost as much time as observed lineages. Comparing the RCI of these basal synapsids to values obtained by other studies is not encouraging. The mean RCI for phylogenies of Palaeozoic organisms is 62.064% (Benton et al., 2000), while that of tetrapods is 49.8% (Hitchin and Benton, 1997a). Despite this, only 1.59% of the randomly permuted trees had a higher RCI value than the supertree.

One can reconcile the disparity in results by looking at the differences in what each of the metrics measure. The SRC, SCI and GER are measures of congruence between a phylogeny and stratigraphy, while the RCI is a measure of completeness. A low value of the former measures can mean either a poor fossil record or an incorrect phylogeny. The poor fossil record may not even be indicated by the SRC and SCI: the simulations of Wagner and Sidor (2000) suggest that these metrics are inappropriate as measures of sampling and that an accurate phylogeny should score reasonably well even if the fossil record is poor. The RCI, however, measures the amount of missing data compared to the amount of observed data, and
does not normalise the implied gap relative to the maximum and minimum possible gap (as does the GER). It is entirely possible for a tree to be perfectly consistent with the fossil record, to have perfect scores in the SRC, SCI and GER, but to have a low RCI score.

Simulations suggest that a low RCI may be a result of an incorrect phylogeny as well as an incomplete fossil record (Wagner, 2000). However the SRC, SCI and GER all suggest that the congruence of the phylogeny to stratigraphy is no worse than in other tetrapod groups, or other clades from the Palaeozoic. This implies that the result of the phylogeny is of no worse quality than others it has been compared to. Therefore in this case it seems more likely that the gaps in the fossil record are to blame for the low RCI score. The completeness of the record of pelycosaurian-grade synapsids is not only low, it is considerably worse than most of the other clades to which the RCI has been applied. The significant p-value obtained from the RCI should not be taken to indicate a significantly complete fossil record; the random permutations used the same age ranges as the observed data. As such, what they are testing is what happens when a fossil record of similar quality is applied to different tree topologies.

It appears that relationships of pelycosaurian-grade synapsids are reasonably well understood. Their phylogeny shows a good congruence with the stratigraphy, comparable to many other clades that have been tested. However it is obvious that there are large gaps in the record, leading to an extremely low Relative Completeness Index. It has not escaped the notice of previous workers on this taxonomic group that the earliest evolution of synapsids is not clear (Romer and Price, 1940; Benson, 2012). With such gaps in our record, it needs to be asked: is the fossil record improving? Or is this record as good as it is going to get?

**The Quality of the Fossil Record of Pelycosaurian-Grade Synapsids – Historical Perspectives**

The observation that new discoveries do not appear to change the shape of diversity curves has been made before. Maxwell and Benton (1990) compared six databases of vertebrates formed between 1900 and 1987, and found that all databases showed the same global diversity signal, with most of the major events appearing in all six curves. Sepkoski (1993) compared diversity curves formed from his 1982 compendium of marine fossils to those from the next edition in 1992. Despite the addition of over 800 new families, the deletion of nearly 200 invalid families, and more than 2000 stratigraphic alterations, the two curves correlated significantly. Irmis et al. (2013) examined the effect of using different datasets on diversity estimates in the Karoo, including datasets based on collection records
from museums (likely to contain misidentifications and obsolete taxonomy), and datasets updated by different researchers with different interests. Again, all datasets produced a similar diversity signal (although see Bernard et al., 2010, who found noticeable historical changes when examining early tetrapod datasets, and Lloyd and Friedman, 2013, who found fish datasets show highly variable correlations, with some even being negative).

Such a result is supported in pelycosaurian-grade synapsids. Examining the diversity curve pruned to species known 100 years ago (Figure 28), one can still see the events present in the current diversity curve: the rise to an early Sakmarian peak, the trough in the late Sakmarian, a second peak in the early Kungurian, and a decline during the Roadian. The similarities of the present curve with the diversity curve produced from taxa known 50 years ago are striking, with even minor, short-term changes being picked up, such as the brief Gzhelian plateau during the initial radiation. The present diversity curve correlates significantly with the signal obtained including only the taxa known in 1914, 100 years ago. It is only once the dataset has been reduced to taxa known 110 years ago that the correlation becomes insignificant, and by that time the dataset contains only 19 species (Table 4).

Figure 28: A comparison of the current (2014) taxic diversity curve with pruned taxic diversity curves representing species known in 50-year intervals.

Both Maxwell and Benton (1990) and Sepkoski (1993) concluded that the similarity of the curves produced by databases of different age was an indication that the events shown are genuine; that despite the gaps in our knowledge, real macroevolutionary events are still visible with an incomplete dataset. This cannot be supported when one examines
pelycosaurian-grade synapsids. The extremely low relative completeness index implies an extremely poor record. Moreover evidence for extensive sampling bias, both temporal and geographical, has already been noted for the Early Permian (Benson and Upchurch, 2013). The strong correlation between the number of amniote-bearing formations and diversity (Benson and Upchurch, 2013) suggests that the signal that has been visible for the last 150 years is the signal of sampling biases. There are two explanations for the strong correlation seen between older datasets and the current one: 1) workers have continued to sample well-known collections rather than finding new collections from less well-sampled time periods, or 2) the number of collecting opportunities in the time periods which have, over the decades, continued to produce fewer taxa, are limited by a low number of fossiliferous formations.

While new discoveries may not be altering the shape of diversity curves, it does not necessarily imply new discoveries have no effect on our interpretations of the fossil record. New discoveries can both create and fill gaps in the fossil record. It has been asserted that the fossil record is improving, and that new discoveries are filling gaps, rather than creating them (Benton and Storrs, 1994; Fara and Benton, 2000; but see Tarver et al., 2011). When one examines the RCI curve of pelycosaurian-grade synapsids through historical time, the issue appears to be more complicated. The curve constantly fluctuates, particularly during the earliest years of discovery. The RCI values range from 37% in 1881 to -57% in 1908 (Figure 27).

When making a judgement on whether discoveries are creating or filling gaps, it is unreasonable to include these earliest years of discovery in our examination. While the RCI of the supertree pruned to taxa known in the late 1800s is consistently higher than it is today, and remains so until 1908, this is likely to be an artefact of the low number of known taxa. At the time of peak RCI (1881), only 12 pelycosaurian-grade species were known, of which only 5 have been included in phylogenetic analyses. Moreover, the time period in which these taxa lived was much shorter than the range occupied by taxa known today. As such there was considerably less potential for long ghost lineages, resulting in the much higher RCI values.

It is more sensible to limit the examination to the RCI values since 1914, the time at which enough species were known to produce a diversity curve similar to that of the present day (see above). When one examines the historical RCI curve from this year onward, one can see there has been a trend towards an increase in the RCI from -6% to 2% (Figure 27). Even then, the statement that new discoveries tend to fill gaps in our knowledge should still be considered an oversimplification. Despite the 11 new species discovered in the last 30 years (Figure 28), there has been very little change in the RCI, which has remained between -3 and
3%. This implies that the recent discoveries are creating just as many gaps as they are filling. Periods of great discovery and great increase in the number of species known can fill gaps, such as the discoveries of the late 70s and early 80s which coincide with a rapid increase in RCI. However, such periods of great discovery can also create gaps, such as during the late 1930s, when large increases in the number of species coincide with troughs in the RCI. It should also be noted that it is not only the description of large numbers of species that can cause great change in the RCI; single species can have a large effect. The most obvious example of this is *Archaeothyris florensis*, described in 1972, which extended the age of synapsids back into the Moscovian (Reisz, 1972). This drew back ghost lineages of other clades to this time, causing the RCI to fall from -14 to -21%.

When one considers that the RCI has reached only 2%, it is worrying that the polynomial model applied to the collector’s curve appears to suggest that the curve is levelling off, and has been doing so since 1990 (Figure 26). In the past 20 years, only 9 new pelycosaurian-grade synapsid species have been found, compared to 12 in the preceding 20 years and 23 in the 20 before that. The fact that the collector’s curve is approaching an asymptote may imply that the limit of what the fossil record has to offer is close to being reached. The RCI indicates that this limit may be extremely low. Alternatively, the asymptote may reflect the current lack of fieldwork in Lower Permian terrestrial sites, limiting most recent discoveries to description of specimens from museum collections (e.g. Reisz and Dilkes, 2003; Reisz 2005; Mazierski and Reisz, 2010; Reisz et al., 2010; Reisz and Fröbisch 2014). It is mostly in the Middle Permian of South Africa, Sardinia and Russia that fieldwork is still producing new specimens of pelycosaurian-grade synapsids (e.g. Botha-Brink and Modesto, 2009; Modesto et al., 2011, Romano & Nicosia, 2014).

**Conclusions**

While this chapter may present a bleak picture of the basal synapsid fossil record, it is not intended to indicate that the evolutionary history is unknowable. Rather it is meant to highlight the need for sampling correction when examining the patterns of diversity. The results presented in the following chapters need to be examined with the quality of the fossil record kept in mind. The fossil record may be poor, and the events it indicates may be artifacts of bias and incompleteness, but there is a biological signal present in the data. It is simply necessary to apply the required methods to tease out this signal.
Chapter 5
Diversity of Early Synapsids and the Influence of Sampling on their Fossil Record
The identification of diversity patterns through time is an important aspect of the investigation into the macroevolutionary processes occurring in organisms. It enables palaeontologists to determine the major events in the history of the group under study and is also relevant to broader questions, such as the impact and recovery from mass extinctions, the processes underlying evolutionary radiations and the importance of competition and co-evolution. Because of their importance in the establishment of terrestrial ecosystems, several studies have been made of changes in species richness though time in both basal synapsids and other early amniotes. Much of this study has focussed on the later Permian and Triassic, in particular the changes across the Permian-Triassic boundary and the impact of the great mass extinction occurring at this time on amniote evolution (e.g., Sidor and Smith, 2004; Fröbisch, 2008; 2009; Fröbisch et al., 2010; Huttenlocker et al., 2011; Fröbisch, 2013; Irmis et al., 2013). The diversity of tetrapods during the Late Carboniferous and Early Permian has been less well studied, and thus far no study has examined species richness in pelycosaurian-grade synapsids in detail.

**Previous Studies into the Diversity of Early Amniotes**

The first examination of the changes in diversity of tetrapods including the Early and Middle Permian was by Sahney and Benton (2008). This paper included a diversity curve of tetrapods at the family level from the Artinskian (late Early Permian) until the Early Triassic. No method of sampling correction was used, and there was no examination of the individual clades, although the relative diversity of families of different body sizes and ecologies was examined. While the main focus of this study was the end-Permian mass extinction, there was discussion of the changes in diversity during the late Early Permian and Middle Permian, including the first description of an extinction event at the end of the Early Permian, coinciding with the transition from the pelycosaur-dominated Early Permian fauna to the therapsid-dominated Late Permian fauna (Sahney and Benton, 2008), an event they dubbed Olson’s extinction.

The transition between these two faunas has been an issue of some debate. Part of the reason for this has been the argument for a gap in the fossil-bearing rock record of terrestrial vertebrates during the Roadian, dubbed Olson’s gap (Lucas and Heckert, 2001; Lucas, 2004; 2006). This gap supposedly separates the pelycosaur-dominated formations in North America from the therapsid-dominated formations in Russia and South Africa, giving very little idea of the timing and causes of the transition. However, this interpretation of the biostratigraphy has
been disputed (Reisz and Laurin, 2001; 2002; Lozovsky, 2005; Liu et al., 2009a; Benton, 2012). Reisz and Laurin (2001) argued that the presence of the parareptile *Macroletter* in both North American and Russian deposits suggested that there was temporal overlap between these formations. These authors argued for a Roadian age for the Chikasha and San Angelo formations in North America, and the Mezen assemblage of Russia. The link between these faunas was supported by Lozovsky (2005), who argued for a “bridge” between Russia and North America at this time, allowing easy dispersal between the two. Liu et al. (2009a) maintained that the presence of basal therapsids in the Xidagou Formation of China supported a Roadian age for this fauna.

Kemp (2006) put forward a biogeographic hypothesis for the transition. He pointed out that the Lower Permian pelycosaur-dominated fauna is known almost entirely from North America and western Europe, then in equatorial positions, while the Middle Permian therapsid-dominated fauna is known almost entirely from the palaeotemperate localities of Russia and South Africa. Attention was also drawn to the climate changes occurring at the time of the transition: the equatorial tropical everwet biome which had sustained the pelycosaur-dominated fauna disappeared, to be replaced with a desert belt (Rees et al., 2002). Kemp (2006) hypothesised that the elimination of the tropical everwet biome forced terrestrial ecosystems to move towards the temperate latitudes, where the therapsids, with their advanced physiology and metabolism, were better able to survive in this more seasonal environment. However, doubt is cast on the idea that the Middle and Upper Permian faunas were restricted to palaeotemperate regions by the recent work on the Moradi Formation of Niger, which has yielded a diverse Upper Permian palaeoequatorial fauna (Sidor et al., 2003; O'Keefe et al., 2005; Sidor et al., 2005; Damiani et al., 2006; Steyer et al., 2006; Smiley et al., 2008; Sidor, 2013; Tsuji et al., 2013).

Sahney and Benton (2008) were the first to recognise that transition between the two faunas may have been a period of mass extinction amongst tetrapods, dubbed Olson’s extinction (Figure 29B). During the Artinskian and Kungurian, they found two thirds of families were lost, along with a loss in the number of occupied ecological guilds. Recovery began almost immediately, but was interrupted by a second extinction event at the end of the Middle Permian (Sahney and Benton, 2008). Both these extinctions changed the Permian faunas, both in terms of clades and ecological guilds present, and also the degree of endemism; the Upper Permian and Lower Triassic faunas were considerably more provincial than those at the end of the Early Permian (Sahney and Benton, 2008).
Sahney et al. (2010) expanded on this earlier study, examining family-level tetrapod diversity during the Carboniferous and Early Permian (Figure 29A). This study focused on the impact of the collapse of rainforests on the diversity of tetrapods. During the Pennsylvanian, North America and Europe were positioned at the equator and covered in tropical rainforest (DiMichele et al., 2006). It was in these “Coal Forests” that the earliest amphibians and basal amniotes diversified. However, towards the end of the Carboniferous, the aridification of the climate led to the decline and fragmentation of these rainforests and the development of more seasonal ecosystem based on ferns and tree-ferns (DiMichele and Philips, 1996; DiMichele et al., 2006). The diversity curve of tetrapod families shows that, while family richness increased gradually during the Late Carboniferous and Early Permian, the diversity within each locality (alpha diversity) drops sharply during the Kazimovian and Gzhelian (Sahney et al., 2010). A drop in alpha diversity, with no substantial change in global diversity (Figure 29A), was interpreted as an increase in endemism following the fragmentation of the rainforest (Sahney et al., 2010). Amphibians suffered widespread extinction, while amniotes, and in particular synapsids, diversified (Sahney et al., 2010). The relative success of amniotes was assumed to result from the amniotic egg and scales, both of which allowed water retention in the drier, more seasonal environment (Sahney et al., 2010).

In 2012, Benton undertook a thorough re-examination of Permian biostatigraphy and geological biases affecting the terrestrial fossil record at this time (Benton 2012). This study also included the first genus-level diversity curve of Permian amphibians and amniotes. Benton (2012) argued that geological biases were not substantially affecting the diversity
estimates of tetrapods during the Permian. No evidence of Olson’s gap was found, and no significant correlation was seen between the number of tetrapod-bearing formations and the genus-level diversity. As such, it was argued that the raw data was adequate for inferring diversity patterns. Benson and Upchurch (2013) opposed this interpretation of the record. By fitting multivariate models to the observed diversity data (this time at the species level), it was found that tetrapod diversity was best explained as being a composite of sampling and genuine diversity change. A strong relationship between the sampling proxy and observed diversity was found (Benson and Upchurch, 2013). The lack of a significant correlation between diversity and number of formations found in Benton (2012) was judged to be due to the use of inappropriate measures to correct for autocorrelation.

Figure 30: Diversity estimates of tetrapods, from Benson and Upchurch (2013). A) Taxic diversity estimates of tetrapods, amniotes and amphibians, and sampling represented by number of formations; B) Residual diversity estimate of tetrapods; C) Residual diversity estimate of amphibians; D) Residual diversity estimate of amniotes.

The raw diversity data in Benton (2012) and Benson and Upchurch (2013) both show evidence of a diversity decrease across the Kungurian/Roadian boundary (Figure 30A), providing further support for Olson’s extinction. When examining the raw data, it is only the amphibians which suffer in the extinction; amniotes in fact increase in diversity throughout the latest Early Permian and Middle Permian. Benson and Upchurch (2013) also presented a sampling-corrected diversity estimate using the residual diversity estimate (see Chapter 1), which supports a significant diversity decrease across the Kungurian/Roadian boundary.
affecting both amphibians and amniotes (Figure 30C, D). However, these authors still argued against Olson’s extinction being a genuine event, reasoning that the observed decrease in diversity is an artefact of the geographic shift in the fossil-bearing localities. As mentioned above, our knowledge of the terrestrial realm during the Early Permian is restricted to the then equatorial localities in North America and western Europe, while during the Middle Permian, the record abruptly shifts to the palaeotemperate localities of South Africa, South America, Russia, and China. It is possible that the apparent extinction merely reflects a latitudinal biodiversity gradient: prior to the Kungurian/Roadian boundary diverse equatorial faunas are sampled, while after the boundary the more species-poor temperate localities are sampled (Benson and Upchurch, 2013). The residual diversity estimate would not correct for such a bias, as it assumes a linear relationship between sampling and number of species found, an assumption violated by spatial variations in diversity.

The evolution of herbivores during this early stage in amniote evolution has been a point of considerable interest, due to their importance in the establishment of early terrestrial ecosystems and the morphological innovations with which this new diet was explored (Olson, 1966; Sues and Reisz, 1998; Reisz and Sues, 2000). A recent study examined the changes in the global diversity of early herbivores, as well as the changing patterns within individual herbivorous clades (Pearson et al., 2013). Sampling correction was carried out using residuals, with tetrapod bearing formations as a sampling proxy. The earliest appearance of herbivores in the fossil record coincided with the collapse of rainforests described by Sahney et al. (2010). However no massive increase in the diversity of herbivores is found to have occurred at this time in either the raw or sampling corrected diversity curves (Pearson et al., 2013). Sahney et al. (2010) had argued that the fragmentation of the rainforest into isolated “islands” had resulted in the simultaneous independent evolution of herbivory. This hypothesis was rejected by Pearson et al. (2013), who demonstrated that the diversity of herbivores increased gradually during the late Pennsylvanian and Early Permian, with new herbivorous clades appearing throughout this time. This study also found little evidence for Olson’s extinction; neither the raw nor sampling corrected diversity estimates show a significant decline in diversity across the Kungurian/Roadian boundary. Following Benson and Upchurch (2013) in arguing that any apparent extinction is an artefact of the latitudinal shift in the record, Pearson et al. (2013) suggested that the hypothesised latitudinal biodiversity gradient was less pronounced in herbivores. Alternatively they suggested that differences in the timescale used might have affected the results. Benson and Upchurch (2013) used substages as the time bins, whilst Pearson et al. (2013) used the Land Vertebrate Faunachrons (time bins defined by
terrestrial vertebrate biostratigraphy). Interestingly, the taxic diversity estimate of herbivorous tetrapods does not correlate significantly with the number of tetrapod-bearing formations (Pearson et al., 2013) leading the authors to suggest that a strong biological signal was present in the dataset. They still argued that sampling correction was necessary; although the signal from the data contains a large “genuine” diversity signal, this did not mean that sampling has had no effect on the fossil record. The differences between the taxic diversity estimate and residual diversity estimate were small but were potentially important (Pearson et al., 2013).

The most recent global examination of changes in species richness among tetrapods during the Late Carboniferous and Early Permian was that of Benton et al. (2013), compiled using the early tetrapod database. Taxic diversity estimates at the genus level were compiled for tetrapods as a whole, as well as for amniotes and amphibians, from their earliest appearance in the Middle Devonian until the Early Jurassic. This study also included extensive discussion into the use of sampling proxies such as number of formations to assess and correct for sampling biases. During the period under study in this thesis (Late Carboniferous-Middle Permian), two major extinction events were identified. The first is a major drop in amphibian diversity at the end of the Moscovian as identified by Sahney et al. (2010), coinciding with the breakdown of rainforests and increased seasonality of the climate. The second, Olson’s extinction, was recovered as a gradual decline in diversity throughout the Early Permian rather than the single mass extinction event recovered by previous studies (Sahney and Benton, 2008; Benson and Upchurch, 2013). There was also no evidence of a decline found in amniotes, whose diversity rose gradually to a Wordian peak (Benton et al., 2013). Amphibian diversity remained low and reasonably constant for the rest of the Permian, while the diversity of amniotes fluctuated greatly, with peaks in the Wordian and mid Capitanian separated by a substantial trough.

No attempt was made to correct for sampling biases in this study, although significant correlations were found between the diversity of tetrapods and the number of tetrapod-bearing formations. Investigation was made into the completeness of the tetrapod fossils using a grading system from 1-4: a grade of 1 was represented by a single bone, 2 by more than one bone, 3 by a single nearly complete specimen and 4 by more than one nearly complete specimen. A mean completeness score was calculated for each time bin, and also a ratio of good material (number of taxa graded 2-4) to the total amount of material. The completeness score was found to correlate significantly with amniote diversity but not with tetrapod diversity as a whole or the diversity of amphibians (Benton et al., 2013), possibly indicating that the different environments in which amphibians and amniotes lived affected the quality
of the preservation. On the whole, the mean completeness of tetrapod specimens was high, remaining above 3 for most of the Carboniferous and Permian, with more than 50% of fossils classed as “good” in most time bin throughout this period.

As has been seen, considerable debate surrounds many areas of early amniote evolution. As one of the most diverse and abundant clades during the Late Carboniferous and Early Permian, a detailed examination of the changes in species richness of synapsids during the time period occupied by the pelycosaurian-grade synapsids would be a vital addition to discussions of tetrapod evolution at this time. Moreover, although a few of the previous studies have employed sampling correction, its use has been patchy and limited to the residual diversity estimate. The analyses described in Chapter 4 give clear indications that the fossil record of basal synapsids is incomplete and that correction for sampling bias is necessary. Moreover, as mentioned in the introduction, all methods of sampling correction have their advantages and disadvantages. Here multiple methods are used and compared in order to provide as thorough an assessment of synapsid diversity as possible.

**Materials and Methods**

**Raw Data and the Taxic Diversity Estimate**

The comprehensive database of all synapsid species, both pelycosaurian-grade and therapsid, from the late Moscovian until the late Capitanian described in Chapter 3 was employed in this study. A taxic diversity estimate was generated by counting the number of species and genera present in each time bin (including Lazarus taxa). Such diversity curves were compiled for all synapsids, pelycosaurian-grade synapsids, therapsids, Caseasauria, Ophiacodontidae, Sphenacodontidae, Varanopidae and Edaphosauridae. As mentioned in Chapter 3, two sets of ages had been applied to each taxon: one in which, if a taxon’s age could not be constrained, it was included in the full range of possible time bins; one in which each locality was restricted to two substages or less. While the former method does lead to less resolution (certain taxa known from a single specimen or locality will be found in more than one time bin), it has been demonstrated that, as long as the stratigraphic uncertainties are randomly distributed, the diversity signal will not be false, but merely “dampened” (peaks and troughs become less extreme) (Raup, 1991; Smith, 2001). A second taxic diversity curve was produced from the second set of ages. However, for the reasons given, this curve is
considered less reliable and, though the differences between the two curves will be noted, the curve that takes into account the uncertainty will form the basis of the discussion.

The Residual Diversity Estimate

The residual diversity estimate, the modelling approach to sampling correction described in Chapter 1, was calculated using the recent update of the method proposed by Lloyd (2012) which allows non-linear relationships between sampling the sampling proxy and the observed diversity to be taken into account, and allows confidence intervals to be placed around the data to indicate which peaks and troughs are significant. The sampling proxy used was the number of amniote-bearing collections (sensu Benton et al., 2011) in each time bin, collections being considered to be a proxy for human sampling effort (Alroy et al., 2001; Crampton et al., 2003; Alroy et al., 2008; Butler et al., 2011a). Data on this proxy was downloaded from the Paleobiology Database (http://paleodb.org) in June 2012 and was supplemented with data from the published literature. The Spearman’s rank and Kendall’s Tau correlation coefficients, implemented in R, were used to compare the taxic diversity estimate of synapsids to the proxy, to ascertain the impact of biases on the fossil record, after transforming the time series using generalised differencing. Amniote-bearing collections were used instead of synapsid-bearing collections to mitigate the concerns reported by Benton et al (2011): redundancy and non-occurrences (see Chapter 1). This proxy includes instances where searches have been made in rocks producing closely related taxa, but not synapsids have been found, thus taking into account non-occurrences. This method also deals with the issue of redundancy: if the diversity of synapsids decreased, one would expect there to be less synapsid-bearing collection, but not necessarily less amniote-bearing collections.

Residual diversity curves were generated in R, using the functions made available online by Lloyd (2012), for Synapsida, Caseasauria, Varanopidae, Ophiacodontidae, Sphenacodontidae, Edaphosauridae and Therapsida. Geological influences on sampling were not tested; while it is possible that the area of rock outcrop of a particular age may influence opportunities to find fossils (Smith, 2001; Crampton et al., 2003; Smith and McGowan, 2008; Wall et al., 2009), there is little data on this proxy from this time period (but see Fröbisch, 2013; 2014, for a regional perspective on the South African Karoo Basin). An alternative might be to use the number of formations (Fröbisch, 2008; Barrett et al., 2009; Butler et al., 2009; Benson et al., 2010; Mannion et al., 2011; Benson and Upchurch, 2013). However, formations are very much artificial subdivisions, and it is somewhat arbitrary where one
begins and the other ends. The impact of the length of time bin was also examined; in a longer
interval, there is more time for sediment to be laid down and a higher probability of
preservation (Miller and Foote, 1996). In this case, no significant correlation was found
between the length of the substages and the diversity (Table 6), so no correction was made for
this.

The Phylogenetic Diversity Estimate

The second method used to correct for sampling bias was the phylogenetic diversity
estimate. As described in Chapter 1, this method incorporates ghost lineages inferred from a
phylogeny into the diversity estimate in order to take into account missing portions of the
fossil record. The supertree produced in Chapter 3 was used to infer a phylogenetic diversity
estimate for synapsids as a whole, and also for Caseasauria, Varanopidae and Edaphosauridae
(none was constructed for Ophiacodontidae or Sphenacodontidae as too few species from
these families have been tested in a phylogenetic context). A second phylogenetic diversity
estimate for all synapsids was generated using the second set of ages, where localities of
uncertain age were restricted to two or less substages. As noted above, this curve is
considered less reliable and the discussion will primarily be based on the curve produced from
the set of ages taking into account uncertainty in dating.

One caveat should be noted when generating phylogenetic diversity curves: the
presence of unresolved polytomies in the phylogeny can affect these curves. Moreover, the
polytomies do not produce a random error, but instead a bias towards higher diversity, since
all taxa in the polytomy will have ghost lineages extending back as far as the oldest taxon
(Upchurch and Barrett 2005). Several options exist on how to deal with polytomies. The first
is to produce separate diversity curves for all possible trees to ascertain if they differ. For this
study this is clearly an unrealistic option, as the analysis produced hundreds of most-
parsimonious trees. Alternatively one can select a preferred most-parsimonious tree and base
the phylogenetic diversity estimate on that. This decision suffers from being highly arbitrary,
depending on the personal preferences of the researcher. Finally, one could prune taxa from
the tree until a fully resolved tree remains. However, when polytomies contain many taxa or
even entire families, removing them will greatly reduce the number of taxa, and therefore the
reliability of the phylogenetic diversity estimate. It was decided to keep polytomies in the
supertree and include the relevant ghost lineages in the phylogenetic diversity curve. Time
intervals where this may have affected the results will be noted.
**Results**

**Sampling Bias in the Early Synapsid Fossil Record**

The taxic diversity estimate shows very close correlation with the number of amniote-bearing collections (Table 6). If collections are accepted as a proxy for sampling effort, then there is a clear bias in temporal sampling, which is affecting the taxic diversity curve. For example, the early Capitanian is the most extensively sampled substage (239 amniote-bearing collections), and has produced the most synapsid taxa (63 species in 59 genera). There is also significant spatial bias. Of those species known from the Pennsylvanian and Cisuralian, only 17% were found outside North America, and all of those 17% are from Europe. In the Guadalupian, by contrast, 79% of known species have been found in South Africa and Russia (the remainder from the USA, Brazil and China). These spatial biases indicate huge gaps in our knowledge of synapsid diversity, although whether this is due more to biases in sampling (a preference for looking in rocks where amniotes of a particular age are known to be found) or a lack of fossiliferous rocks of a particular age in a particular area is yet to be seen. Nevertheless, it is clear that correction for sampling is necessary in this study.

<table>
<thead>
<tr>
<th>Statistical Test</th>
<th>Spearman’s $\rho$</th>
<th>Kendall’s $\tau$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of synapsid species vs Number of amniote-bearing collections.</td>
<td>0.76667 ($p=0.0012867$)*</td>
<td>0.60234 ($p=0.0031394$)*</td>
</tr>
<tr>
<td>Number of synapsid species vs Length of time bin.</td>
<td>-0.10526 ($p=0.66801$)</td>
<td>-0.099415 ($p=0.55201$)</td>
</tr>
<tr>
<td>Number of synapsid species (total dataset) vs Number of synapsid species (pruned dataset containing only taxa present in the supertree).</td>
<td>0.75263 ($p=0.00020063$)*</td>
<td>0.60234 ($p=0.00031394$)*</td>
</tr>
</tbody>
</table>

Table 6: The correlations between selected variables, tested by Spearmann’s $\rho$ and Kendall’s $\tau$. Significant correlations ($p=0.05$) are highlighted with an asterix

**Taxic Diversity Estimates**

The earliest synapsid family to appear in the fossil record, and the only family present in the late Moscovian, was Ophiacodontidae, represented by *Archaeothyris florensis* (Reisz
Echinerpeton intermedium (Reisz, 1972) is from the same time interval, but cannot be constrained phylogenetically (see Chapter 2). Ophiacodontidae is also the only family present in the early Kasimovian. Varanopidae, Edaphosauridae and Sphenacodontidae appeared in the late Kasimovian (Romer, 1945; Reisz and Dilkes, 2003; Mazierski and Reisz, 2010) and diversified during the early Gzhelian. The earliest caseid caseasaur (Eocasea martini) first appears in the fossil record at a similar time, but later members do not appear until later in the Cisuralian, producing a long ghost lineage within this clade. The earliest member of Eothyrididae (one of the two families within Caseasauria) is “Mycterosaurus” smithae (see Chapter 2), found in sediments of uncertain age but probably Asselian or Sakmarian.

Figure 31: Taxic diversity curves of Synapsida, Therapsida and pelycosaurian-grade synapsids at A) the species level, and B) the genus level.
The taxic diversity estimate (Figure 31) shows these Carboniferous radiations with a continuous rise from two species in the late Moscovian to 16 by the end of the Gzhelian. The most diverse families during the Carboniferous are Ophiacodontidae, with a maximum diversity of four species in as many genera present during the late Gzhelian, and Varanopidae, with four species in three genera in the same substage (Figure 32A, B). Caseasaurids and varanopids both have considerably higher phylogenetic diversity estimates than taxic diversity estimates at this time, indicating many unsampled ghost lineages at this time (Figure 32B, E).

Figure 32: Species and genus-level taxic diversity curves and phylogenetic diversity curves (grey dashed-dotted) of: (A) Ophiacodontidae, (B) Varanopidae, (C) Edaphosauridae, (D) Sphenacodontidae and (E) Caseasauria.

The taxic diversity curve indicates that this radiation continues into the early Cisuralian, reaching a peak in the early Sakmarian of 23 species in 17 genera. Between the early and late Sakmarian, diversity falls to just 13 species in 11 genera. This fall in diversity is visible in all families with the exception of Edaphosauridae, whose diversity actually continues to increase between the two substages (Figure 32C).

The diversity of all clades recovers during the early Artinskian. Sphenacodontidae became considerably more diverse (Figure 32D), particularly with the radiation of the genus
*Dimetrodon* (five new species of this genus originate in the Artinskian). The herbivorous caseid caseasaursa also appear at this time, with three species known from the Artinskian. *Euromycter rutenus* and *Ruthenosaurus russelorum* (Sigogneau-Russell and Russell, 1974; Reisz et al., 2011) have been found in the Grès Rouge group of France. The age of this group is debated (Rolando et al. 1988), but is thought to be Artinskian-Kungurian. Meanwhile the age of the Richards Spur Locality, Oklahoma, which has produced the basal caseid *Oromycter dolesorum* (Reisz, 2005), has been radiometrically dated to the earliest Artinskian: 289 ± 0.68 Mya (Woodhead et al., 2010).

The taxic diversity of synapsids continues to rise to an early Kungurian peak of 29 species in 16 genera, but the composition of the faunas begins to change. Ophiacodontidae, Edaphosauridae, Varanopidae and Sphenacodontidae begin to decline between the early and late Kungurian, although Sphenacodontidae remain the most diverse synapsid family, with 12 species known from the early Kungurian and nine from the late. The diversity of Caseidae increases to a peak of seven species in the late Kungurian (Figure 32B, E). The earliest therapsid, *Tetraceratops insignis* (Matthew, 1908; Laurin and Reisz, 1990; 1996; Amson and Laurin, 2011), appears in the late Kungurian. It should be mentioned that the youngest species of Eothyrididae, *Eothyris parkeyi* (Romer, 1937), is found in early Kungurian sediments. After this time bin, the diversity curves of Caseasauria relate only to Caseidae.

Across the Kungurian/roadian boundary, an interval of extinction is visible, and diversity falls from 26 synapsid species in the late Kungurian to 16 in the early Roadian (Figure 31A). Interestingly the number of genera only falls by one (Figure 31B), possibly due to the large number of polyspecific genera from the Kungurian. Ophiacodontidae and Edaphosauridae disappear from the record across this boundary, and the number of sphenacodontid species falls to one (Figure 32B). The number of caseid and varanopid species does not decrease, remaining at seven and two respectively (Figure 32D, E). There is no extinction visible in therapsids, whose diversity increases from one species in the late Kungurian to five in the early Roadian (Figure 31). Between the early and late Roadian, there is further extinction among the pelycosaurian-grade synapsids. Sphenacodontidae die out, and the number of caseid species falls to three. However, Varanopidae show no decline (Figure 32B) and the number of therapsid species continues to increase (Figure 32). The total diversity of synapsids increases to 19 species (Figure 31).

Thereafter, synapsid diversity rises rapidly and continuously to an overall peak in the early Capitanian of 59 species in 55 genera, before the number of species drops to 52 in the late Capitanian. During this period, the number of therapsids increases to a peak of 57 species
in the early Capitanian, but the number of pelycosaurian-grade synapsid species falls to two. No caseids are known after the Wordian, but varanopids survive beyond the study interval.

Figure 33: The diversity curves produced when taxa of uncertain age are assigned to the full possible stratigraphic range (dashed-dotted lines) compared to the diversity curves produced when each locality of uncertain ages is restricted to two or less time bins (solid line). A) Taxic diversity curves. B) Phylogenetic diversity curves. Timescale representing millions of years ago appears at the bottom.

The taxic diversity estimate produced using the dataset in which localities of uncertain age are restricted to two or less time bins (Figure 33) shows an extremely similar signal to the curve already discussed, which incorporates the uncertain ages and is thus considered more reliable. Both show a diversity increase during the Late Carboniferous, a trough during the late Sakmarian, recovery from this trough during the Artinskian, a decline across the
Kungurian/Roadian boundary and a peak during the Capitanian. There are, however, noticeable differences. The Late Carboniferous rise occurs in a more step-wise fashion, with a decline in the early Gzhelian (many localities dated as Gzhelian in the dataset incorporating uncertain ages are restricted to the late Gzhelian when the greater temporal resolution is applied). Also the decline to the late Sakmarian trough occurs more gradually when the greater resolution is applied as a number of localities are removed from the late Sakmarian.

**Phylogenetic Diversity Estimate**

The reliability of the phylogenetic diversity estimate depends on the phylogeny containing a high enough proportion of taxa to be representative of the whole. It also requires that taxa missing from the phylogeny be randomly distributed, rather than concentrated in a particular time bin. In order to test that these requirements are not violated, a pruned taxic diversity estimate was produced, including only taxa present in the supertree. This correlates significantly with the complete taxic diversity estimate (Table 6), indicating that a representative sample of taxa is present in the supertree.

![Figure 34: A comparison of the phylogenetic and species-level taxic diversity estimates of Synapsida.](image)

The phylogenetic diversity estimate (Figure 34) begins with a slight decline from five lineages in the late Moscovian to four in the early Kasimovian, due to the lack of phylogenetically tested Kasimovian species, after which there is a rapid rise, reaching 30 lineages in the late Gzhelian. This Gzhelian peak coincides with a peak in the phylogenetic
diversity of Varanopidae (nine lineages) and Edaphosauridae (five lineages) (Figure 32B, C). During the early Cisuralian, the phylogenetic diversity curve indicates a slight but steady decline to a late Sakmarian trough of 20 lineages. As in the taxic diversity estimate, the recovery occurs during the early Artinskian, and for the rest of the Cisuralian diversity remains between 23 and 25 lineages. It is, however, possible that the lack of species-level phylogenies of the two most speciose genera (*Dimetrodon* and *Ophiacodon*) has lowered the phylogenetic diversity during the Artinskian and Kungurian, the time that most of these species are known from. The diversity of Caseasauria increases to six lineages in the early Artinskian (Figure 32E), as the position of *Euromycter rutenus* in the supertree causes several caseid ghost lineages to be drawn back into this bin. Caseidae reach their highest phylogenetic diversity of eight lineages in the Late Kungurian.

Like the taxic diversity curve, the phylogenetic diversity curve indicates that diversity declined across the Kungurian/Roadian boundary from 23 to 18 lineages (Figure 34). Declines in diversity are experienced by Caseidae and Varanopidae, while Edaphosauridae go extinct as indicated by the taxic diversity curve (the phylogenetic diversity estimate cannot extend the ranges of lineages forward from their last occurrence, so the possibility that these families survived beyond their last appearance cannot be tested). Meanwhile, the presence of *Microsyodon orlovi* (Ivakhnenko, 1995) in Roadian sediments draws several therapsid ghost lineages back into the Roadian. However, unlike the taxic diversity curve, the extinction continues into the late Roadian, when the number of lineages falls to 16.

As in the taxic diversity estimate, the phylogenetic diversity estimate rises to a peak in the early Capitanian of 49 lineages, before declining in the late Capitanian to 47 (Figure 34). During this time, both Varanopidae and Caseidae decrease in diversity; Caseidae decline from three lineages in the late Roadian, to one in the Wordian, and none in the Capitanian, while Varanopidae decline from six lineages to four and two in the same intervals (Figure 32B, E).

The phylogenetic diversity curve produced when the ages of localities are restricted to two less time bins (Figure 33) is extremely similar to the estimate in which temporal uncertainty is taken into account. The only noticeable difference between the two is that rapid rise in phylogenetic diversity occurs in the late Gzhelian when greater temporal resolution is applied. As mentioned previously, when greater temporal resolution is applied, localities previously dated as Gzhelian are restricted to the late Gzhelian.
Residual Diversity Estimate

The residual diversity estimate (Figure 35) indicates a rise from an early Kasimovian trough to a significant peak in the late Kasimovian. Ophiacodontidae and Varanopidae both show significant increases (Figure 36A, B). A second peak in the residual diversity curve occurs in the early Sakmarian, immediately followed by a decline to a significant trough in the late Sakmarian. This extinction event affects all clades with the exception of Edaphosauridae, which, as shown in the taxic diversity curve, increase in diversity between the early and late Sakmarian (Figure 36C). Residual diversity recovers during the Artinskian. The variation in residual diversity remains within confidence limits between the late Artinskian and late Kungurian, indicating no substantial changes in diversity of synapsids, although the residual diversity of Caseasauria increases significantly (Figure 36E).

![Figure 35: The residual diversity estimate of Synapsida (solid black) with 95% confidence intervals based on the standard deviation of the model (dashed-dotted lines). 3: A comparison of the phylogenetic diversity estimate and species-level taxic diversity estimate of Synapsida.](image)

A significant decrease in residual diversity occurs across the Kungurian and Roadian boundary (Figure 35). The residual diversity of Sphenacodontidae shows a similar decline (Figure 36D), but that of Caseidae and Therapsida reach their peak diversity during the early Roadian (Figure 36E, F). No significant change is seen in the diversity of Varanopidae (Figure 36B). Unlike the taxic diversity, residual diversity does not recover during the late Roadian, instead decreasing to its lowest value in the interval under study (Figure 35). After
this time, the residual diversity estimate contains signals from only therapsids, caseids and varanopids.

The residual diversity of synapsids increases between the Roadian and Wordian (Figure 35), after which no significant change is seen. The diversity of Caseidae falls from their early Roadian peak until their last appearance in the fossil record during the late Wordian, while that of Varanopidae also reaches its lowest point during the Wordian and the Capitanian (Figure 36B, E).

Figure 36: The residual diversity estimates (solid black) of (A) Ophiacodontidae, (B) Varanopidae, (C) Edaphosauridae, (D) Sphenacodontidae, (E) Caseasauria and (F) Therapsida, with 95% confidence intervals based on the standard deviation of the model (dashed-dotted lines).

**The Effect of Sampling Bias on Synapsid Diversity**

There has been considerable discussion in recent years concerning the quality of the Permian terrestrial fossil record, much of which has focussed on potential geological factors influencing our assessment of diversity. For example, Lucas and Heckert (2001) and Lucas (2004; 2006) have argued for a significant gap in the record during the Roadian, dubbed Olson’s gap, but this has been disputed (Reisz and Laurin, 2001; Lozovsky, 2005; Liu et al.,
Other discussions have concerned possible correlations between numbers of fossiliferous formations and diversity. Fröbisch (2008) found that the diversity of Anomodontia correlated strongly with the number of anomodont-bearing formations, and used this correlation to argue for significant sampling bias in the continental Permian. On the other hand Benton (2012) observed no such correlation between formations and family-level diversity of tetrapods during the Permian, and concluded that the Permian fossil record was adequate for macroevolutionary analyses. In fact the studies of Sahney and Benton (2008) and Sahney et al. (2010) assessing tetrapod diversity during the Carboniferous, Permian and Triassic, made no attempt to correct for sampling. Benson and Upchurch (2012) disputed the suggestion that geological biases have not been affecting the terrestrial Permian record. In fact they found a significant correlation between tetrapod diversity and the number of tetrapod formations. The discrepancy between these results and the findings of Benton (2012) were put down to the different methods used to correct for autocorrelation (McKinney, 1990). Significant geological influences on vertebrate diversity were also found at a regional scale in the Karoo Basin of South Africa (Fröbisch, 2013; 2014)

There has, however, been no discussion of potential global anthropogenic bias, caused by workers investigating formations of a particular age more frequently than those of other ages. Such biases have been examined at a regional scale in the later Permian and Triassic of the South African Karoo Basin and the fore-Ural Region of Russia (Irmis et al., 2013; Fröbisch, 2013) and found to be significant. The global study presented here also finds anthropogenic sampling biases to be an important factor affecting the Late Carboniferous and Permian fossil record of Synapsida. The strong correlation between the number of amniote-bearing collections within each time interval and the number of synapsid species indicates that this factor is strongly influencing our interpretations of diversity. As such, one has to treat the taxic diversity estimate with extreme caution, as a large part of the signal may have been overprinted by the sampling bias. There is also a clear geographical bias in the diversity of terrestrial tetrapods during the Carboniferous and Permian. As described above, while the Carboniferous and Cisuralian are dominated by collections from North America and western Europe, the Guadalupian is dominated by those from South Africa and Russia. It is unclear whether this is due to an anthropogenic sampling bias (the relevant formations have not yet been found) or a geological bias (there are no fossil-bearing rocks of relevant age), but whatever the cause, this is an obvious gap in our understanding of the Carboniferous and Permian; data from entire continents is missing from certain time intervals.
It has been suggested that this spatial bias may represent, at least in part, a genuine biogeographic signal. The shift in spatial sampling coincides with an environmental change: the disappearance of the palaeoequatorial tropical everwet biome, which had supported the pelycosaur-dominated fauna (Rees et al., 2002). It is possible that these environmental changes restricted Middle Permian tetrapods to the higher palaeolatitudes (Sidor et al., 2005; Kemp, 2006). However, the discovery of mid-Late Permian palaeoequatorial localities (Jalil, 1999; Sidor et al., 2005) does indicate that there is an equatorial fauna at this time. This is yet another reason why sampling correction is necessary. For example, the supertree (Figure 21) indicates that several Russian taxa, such as *Pyozia mesenensis* (Anderson and Reisz, 2004), *Mesenosaurus romeri* (Efremov, 1938), and *Ennatosaurus tecton* (Efremov, 1956) have ghost lineages extending into the Cisuralian, and in the case of *Pyozia* into the Carboniferous (although see Maddin et al., 2006, who cast doubt on *Pyozia*’s synapsid affinities; also note that the ghost lineage of *Mesenosaurus* may have been extended by the polytomy present in the mycterosaurine varanopids in the supertree), allowing the inference of a possible Russian fauna not yet sampled. Such inferences are vital for biogeographic studies.

Benton’s (2012) assertion that the fossil record is adequate cannot be supported with the available data. While he may have shown a lack of geological bias, there is clearly an anthropogenic bias in sampling, as well as a geographical bias, both of which will affect diversity estimates. Therefore the taxic diversity estimate must be questioned, and the phylogenetic and residual diversity estimates probably represent true diversity more closely.

**Diversity Trends in Early Synapsids**

The Effect of Environmental Change on Early Synapsid Diversification

The Late Carboniferous and early Cisuralian was a period of considerable environmental change. This is an interval in which significant warming and drying of the climate occurred (Kessler et al., 2001; Rees et al., 2002; Tarbor and Poulsen, 2008; Izart et al., 2012) and the coal swamps and forests in North America and Europe transitioned to a savannah-like biome (Rees et al., 2002; Tarbour and Poulsen, 2008). During the Kasimovian, the coal forests had been reduced to islands of rainforest surrounded by more arid habitats (DiMichele et al., 2006; DiMichele et al., 2009). Later, during the early Cisuralian, alkanes from European sediments indicate that the climate there transitioned to a seasonal tropical climate (Izart et al., 2012). The tropical belt across the equator narrowed, and the arid zones
surrounding it expanded (Rees et al., 2002; Tarbor and Poulsen, 2008). The family-level taxic diversity curve of tetrapods (Sahney and Benton, 2010) indicates a rapid increase in diversity during the Late Carboniferous, coinciding with the aridification and fragmentation of the rainforest habitats. This was explained by the diversification of Amniota, whose amniotic egg allowed them to cope in the drier climate (Sahney and Benton, 2010).

This study supports a Late Carboniferous radiation in synapsids. The taxic, phylogenetic and residual diversity curves all show increases during the Kasimovan and Gzhelian. Varanopidae and Ophiacodontidae were particularly successful during this early radiation; they are the only families that show significant increases in residual diversity (Figure 36A, B). In fact, both the residual and phylogenetic diversity estimates indicate that the Kasimovian was the time of greatest varanopid diversity (Figure 36B, 32B). The first amniote herbivores also appear during the Kasimovian, not only in synapsids (Edaphosaurus) but also independently in other tetrapod clades (Sues and Reisz, 1998).

Both the taxic and residual diversity curves presented in this study show an early Sakmarian peak in diversity followed by significant extinction of synapsids (Figure 31, 35). This event had not previously been discussed in studies of Permian tetrapod diversity. The curve of Sahney and Benton (2010) does not show any evidence of increased extinction during the Cisuralian, possibly due to their diversity being calculated at the family level. Species level taxic diversity curves of Permian tetrapods produced by Benson and Upchurch (2013) do indicate a trough in diversity during the late Sakmarian (Figure 29), but when the residual method of sampling correction is applied, the event no longer appears to affect amniotes, although it does affect amphibians (Figure 29). Interestingly the extinction event is still visible in synapsids even after sampling correction is applied (Figure 35). Although the number of synapsid species declines from 23 species to 13, no families become extinct. All synapsid families are affected, however, except for Edaphosauridae, whose taxic, residual and phylogenetic diversity increases between the early and late Sakmarian (Figure 36C, 32C).

It is interesting to note that the phylogenetic diversity curve presented in this study does not show a sudden extinction event during the Sakmarian as seen in the taxic and residual curves. Instead a gradual decline from a late Gzhelian peak is indicated (Figure 34). The disagreement of the phylogenetic diversity curve with the others is probably due to the unidirectional correction of the phylogenetic diversity curve; observed lineages may only be extended backwards in time, not forwards. This has the effect of “smearing” extinction events over a longer period of time, causing a bias towards higher diversity earlier in time and exaggerating the Signor-Lipps effect (Signor and Lipps, 1982; Lane et al., 2005).
The reasons for this Sakmarian extinction can only be speculative at the moment, but it is possible that environmental change may have had an influence. The changes in the Late Carboniferous climate mentioned before continued into the Cisuralian (Rees et al., 2002; Tarbour and Poulsen, 2008; Izart et al., 2012) with further expansion of arid areas. During the Sakmarian, there was a sudden spike in CO$_2$ levels, an abrupt shift to a higher temperature, and rapid deglaciation occurring at the south pole (Montanez et al., 2007). These environmental changes may have had an adverse effect on synapsids. The recovery from the extinction during the Artinskian and Kungurian included the radiation of large carnivores such as *Ophiacodon major*, *Ctenospondylus casei*, *Secodontosaurus obtusidens* and many of the largest species of *Dimetrodon*, as well as large herbivores such as Caseidae (which include the largest pelycosaurian-grade synapsids known) and the largest species of *Edaphosaurus* (Romer and Price, 1940; Reisz, 1986). It is possible that the evolution of larger animals was a result of the decline of the closed forests and transition to a more open habitat.

**The Evolution of Synapsid Herbivores**

One of the key innovations that appeared in terrestrial tetrapods during the Late Carboniferous and Permian is the evolution of high-fibre herbivory. This appeared several times independently in clades such as diadectomorphs, captorhinids and several lineages within parareptiles. Among synapsids, two pelycosaurian-grade families have produced herbivorous species. Edaphosauridae include the genus *Edaphosaurus*, possessing large tooth plates on their palate and the lingual surface of their lower jaw which, together with an anteroposterior motion of the lower jaw, allowed it to crush vegetation (Modesto, 1995). Caseidae possess a particularly wide ribcage, robust forelimbs with large claws, possibly for digging, as well as spatulate teeth suitable for shredding plant material (Sues and Reisz, 1998).

It is interesting to compare the trends in diversity of these two families. During the Late Carboniferous and early Cisuralian, the only synapsid herbivores known from the fossil record are several species of *Edaphosaurus*; although the insectivorous *Eocasea* is present in the Carboniferous, herbivorous members of the clade do not appear until the Artinskian. During the Artinskian and the Kungurian, Caseidae increased in diversity (Figure 32E, 36E), while the diversity of Edaphosauridae remained high until the early Kungurian, before declining to extinction in the early Roadian (Figure 32C, 36C).
Reisz (2005) discussed the possibility of competitive exclusion of edaphosaurids from the herbivorous niche by caseids. He came to the tentative conclusion that extinction of edaphosaurids, followed by the occupation of the freed ecospace by caseids, was more likely, since direct competition would require co-existence of the two families. It is true that there has been little evidence found of the two living side-by-side (only three localities have produced both edaphosaurid and caseid specimens). However, both groups were definitely present in southern North America during the Kungurian. The significant increases in taxic, residual and phylogenetic diversity of Caseidae during the late Kungurian occurs while there are still two species of the herbivorous genus *Edaphosaurus*, as well as *Glaucosaurus megalops* (Williston, 1915), which is represented by a juvenile and so is hard to interpret, but may have had a herbivorous component to its diet or a herbivorous ancestor (Modesto, 1994). There is little evidence of a substantial decline in Edaphosauridae prior to the radiation of Caseidae. Instead one sees the increase in the diversity of the caseids occurring contemporaneously with the decline in edaphosaurids (Figure 32, 36). While it is generally difficult to test competitive exclusion in the fossil record (Benton, 2008, Butler et al., 2009) the “inverse wedge” pattern displayed by the diversity curves of these two synapsid clades suggests that this possibility should not be rejected without further investigation.

**Olson’s Extinction and the Demise of “Pelycosaurs”**

The early Guadalupian was an interval of major turnover in terrestrial vertebrate faunas. It is at this time that the earlier Permian faunas, dominated by pelycosaurian-grade synapsids, are replaced by the therapsid-dominated faunas of the Late Permian. This changeover is accompanied by ecological changes, including increased complexity of ecosystems with more trophic levels (Olson, 1966). Unfortunately, our understanding of this turnover is hindered by a fossil record of doubtful quality.

One problem is the patchiness of fossil distribution during this time. As discussed above, the Cisuralian record of amniotes is almost entirely dominated by records from North America and western Europe, while that of the Guadalupian is dominated by records from Russia and South Africa (Lucas, 2006). The San Angelo and Chickasha formations of Texas are probably Roadian in age (Olson, 1962; Reisz and Laurin, 2001; Lozovsky, 2003; 2005; Benton, 2012), but this still leaves little idea of what was occurring in North America for the rest of the Guadalupian. Moreover, Lucas and Heckert (2001) and Lucas (2004; 2006) consider even these formations to be Kungurian rather than Roadian. For the same reasons,
there is little evidence of what occurred in Africa and Russia during the Cisuralian. As such it is not clear over what timescale the transition takes place and to what extent biogeographic factors play a role.

Another problem is that the Roadian synapsid record includes several species whose therapsid or “pelycosaurian” affinities are uncertain. Several taxa from the San Angelo formation e.g., Dimacrodon hottoni, Driveria ponderosa, Steppesaurus gurleyi (Olson and Beerbower, 1953), Gorgodon minutus, Knoxosaurus niteckii and Mastersonia driverensis (Olson 1962), were assigned to various therapsid groups, but have since been reinterpreted as indeterminate sphenacodontids or caseids (Sidor and Hopson, 1995; Kammerer, 2011). Various Russian taxa based on postcranial elements (e.g., Phreatosuchidae) also require study; although originally described as therapsids (Efremov, 1954), some may represent caseids (Olson, 1962). These taxa create further confusion over the timing and duration of the turnover.

The raw family-level diversity curve of tetrapods indicates an extinction event between the Kungurian and Roadian, dubbed Olson’s extinction (Sahney and Benton, 2008). This has since been supported by sampling corrected curves of tetrapods, temnospondyls and parareptiles (Ruta and Benton, 2008; Ruta et al., 2011; Benson and Upchurch, 2012). As such, it is worth assessing whether Olson’s extinction is visible in synapsids.

The taxic, residual and phylogenetic diversity curves all support an extinction event across the Kungurian/Roadian boundary. The number of synapsid species falls from the early Kungurian peak of 29 to 26 in the late Kungurian and 16 in the early Roadian. One might be tempted to assume this is a result of sampling bias; more amniote-bearing collections have been sampled from the late Kungurian than any other substage in the Cisuralian, and considerably less have been sampled from the late Roadian. However both methods used to correct for sampling bias have supported this extinction event, which coincides with the disappearance from the fossil record of Ophiacodontidae and Edaphosauridae. The taxic and residual diversity curves of Sphenacodontidae indicate a large decrease in the diversity of this family (Figure 32D, 36D).

The effects of this event are not consistent across clades. The taxic, phylogenetic and residual diversity curves indicate little significant change in the diversity of Varanopidae (Figure 32B, 36B). The phylogenetic diversity curve of Caseidae suggests a decline across the boundary (Figure 32E), but this curve is likely to have been influenced by a polytomy within the supertree, which draws several caseid ghost lineages into the late Kungurian, increasing the phylogenetic diversity of this substage relative to the Roadian. The residual diversity
curve for this clade shows that the early Roadian was actually the peak of their diversity (Figure 36E). Therapsids also increase in diversity across this boundary (Figure 31, 36F); 5 species are known from the early Roadian compared with 1 from the late Kungurian (not including several species of uncertain affinities; see above). The presence of Microxyodon orlovi (Ivakhnenko, 1995), an antosaurian therapsid, in Roadian sediments causes several therapsid ghost lineages to be drawn back into the early Roadian, indicating a large cryptic radiation in therapsids occurred at this time.

It is interesting that only a slight decline in genus-level diversity is observed (Figure 31B). The number of genera falls by only one across the Kungurian/Roadian boundary, from 15 to 14. However, this may be explained by the large number of polyspecific genera in the late Kungurian. Genera like Dimetrodon, with eight species known from the Kungurian, and Casea, with three, have a much greater impact on the species-level diversity curve. One must treat this genus-level curve with caution; many of the polyspecific pelycosaurian-grade genera are of untested monophyly; as demonstrated in Chapter 2, for example, the genus Casea is likely to be non-monophyletic as “Casea” nicholsi is more closely related to the genera Euromycter, Cotylorhynchus, Angelosaurus and Ennatosaurus than to Casea broili. Even at the genus level, it is clear that a significant event is occurring across the Kungurian/Roadian boundary: the diversity of pelycosaurian-grade synapsids declines from 14 genera to eight, while that of therapsids rises from one genus to six.

The biases relating to the completeness of specimens described in Chapter 4 should be remembered at this point. The results of that analysis indicated that, when an abundance of poor material was present, those who worked on pelycosaurian-grade synapsids have tended to name large numbers of species based on inadequate material. During the early Roadian, at the time of Olson’s extinction, there is a sharp drop in the completeness of specimens relative to the late Kungurian (Figure 24). The poor quality of the specimens at this time could have led to an oversplitting of the Roadian taxa. Indeed this has been observed; as mentioned above, large numbers of putative therapsids from the San Angelo Formation have been declared undiagnostic pelycosaurian-grade synapsids (Sidor and Hopson, 1995; Kammerer, 2011). There are, however, numerous poorly preserved taxa from the early Roadian which have not yet been subjected to re-examination. Therefore it is possible that the diversity of the early Roadian has been overestimated, and therefore the severity of the extinction has been underestimated.

The taxic diversity curve (Figure 31) indicates the recovery from this extinction event began during the Roadian, as the number of synapsid species increases to 19 in the late
Roadian. Again, however, the influence of sampling bias should be noted. More amniote-bearing collections have been sampled from the late than the early Roadian, and it is possible the apparent recovery visible in the taxic diversity curve is an artefact of the greater effort put into sampling rocks of this age. Both the phylogenetic and residual diversity curves (Figure 33, 35) indicate that the fall in diversity continues throughout the Roadian. Between the early and late Roadian, Sphenacodontidae disappear from the fossil record and Caseidae, which had been unaffected by the Kungurian/Roadian extinction, experience a fall in diversity from seven to three species, a decline supported by the phylogenetic and residual diversity curves (Figure 31E, 36E). Therapsid diversity, however, continues to increase (Figure 31), and again no significant change is visible in the diversity of Varanopidae (Figure 32B, 36B).

It has been suggested that the Roadian, unlike the sphenacodontid-dominated Artinskian and Kungurian and the therapsid-dominated later Permian, was a period with a distinct fauna of its own, dominated by varanopids and caseids (Reisz and Laurin, 2002). This study does indicate that in the early Roadian, pelycosaurian-grade synapsids were still more speciose relative to therapsids (although once again remember the cautionary note above about the affinities of many taxa) (Figure 31). Varanopid species present in North America at this time are larger predatory species such as *Watongia meieri* (Olson, 1974; Reisz and Laurin, 2004) and *Varanodon agilis* (Olson, 1962), possibly replacing the sphenacodontids as apex predators after the latter’s decline from an early Kungurian peak. Caseids, although suffering in the second phase of the Roadian extinction, were more speciose than any other synapsid clade during the early Roadian (Figure 32). However, while pelycosaurian-grade synapsids suffer extinctions during the Roadian, therapsids are unaffected, instead increasing in diversity. In the late Roadian, they outnumber pelycosaurian-grade synapsids. The mass extinction during the Roadian while therapsids are still rare does lend support to Sahney and Benton’s (2008) hypothesis that the changes between the Lower and Middle Permian communities are a result of Olson’s extinction.

**The Rise of Therapsids**

Taxic, phylogenetic and residual diversity curves support the recovery of synapsids from the Roadian extinction across the Roadian/Wordian boundary, with the radiation of therapsid groups such as anteosaurian dinocephalians and anomodonts. Pelycosaurian-grade synapsids are a very minor part of the fauna, and are extremely rare (Figure 31). There are three species of pelycosaurian-grade synapsid found in the late Roadian-Wordian sediments.
of the Russian Mezen group: the varanopids *Mesenosaurus romeri* (Efremov, 1938) and *Pyozia mesenensis* (Anderson and Reisz, 2004), and the caseid *Ennatosaurus tecton* (Efremov, 1956). Ghost lineages of the South African varanopids *Heleosaurus scholtzi* (Botha-Brink and Modesto, 2007; Reisz and Modesto, 2007) and *Elliotsmithia longiceps* (Dilkes and Reisz, 1996) are also present during these intervals. According to the residual and phylogenetic diversity curves, the Wordian is a period of decreasing varanopid and caseid diversity (Figure 36). Although varanopids survive into the Capitanian in South Africa (Dilkes and Reisz, 1996; Botha-Brink and Modesto, 2007), no caseids younger than *Ennatosaurus* are known, with the possible exception of an unnamed specimen from sediments of uncertain age in Lodève, France (Lucas et al., 2006).

While the taxic diversity curve indicates a continuous increase in synapsid diversity from the early Wordian until the early Capitanian, the phylogenetic diversity curve argues for a more stepwise increase (Figure 32). The first radiation, across the Roadian/Wordian boundary, includes Dinocephalia, basal Therocephalia and non-dicynodont Anomodontia. A second radiation occurs across the Wordian/Capitanian boundary. According to both the phylogenetic and taxic diversity estimates, the early Capitanian represents the overall peak in synapsid diversity during the Permian (Figure 31, 34). This is due to a burst of diversification in Dicynodontia (although the earliest members of this clade are known from the Wordian, most species appear during or after the Capitanian) and Biarmosuchia (there are only three species known from the Capitanian, but 9 ghost lineages are also present). Both curves indicate a decline in diversity between the early and late Capitanian. However, no higher level synapsid clades become extinct and the phylogenetic diversity estimate suggests a decrease in diversity of only two lineages.

The residual diversity curve conflicts with the taxic and phylogenetic diversity estimates. This curve indicates a decline between the late Wordian and the end of the Capitanian (Figure 35), due to the model’s correction for the enormous number of amniote-bearing collections from South Africa. It is difficult to reconcile this signal with any of the available data. All other indications are that the Wordian and the Capitanian were times of radiation not only of species, but of entire clades, including anomodonts and dinocephalians in the Wordian and dicynodonts and biarmosuchians in the Capitanian. While it is probable that the Capitanian peak from the taxic diversity curve contains a large signal from sampling, the idea of a decline directly conflicts with both the raw data and the supertree. The fact that all the residual values during the Capitanian change within the confidence intervals suggests that the apparent decrease in diversity is not significant. Another issue to note is the length of
the *Tapinocephalus* Assemblage Zone, which covers much of the Capitanian. While efforts are being made to subdivide it (Angielczyk and Rubidge 2012), the lack of radiometric dates is proving a hindrance (but see Rubidge et al., 2013 for radiometric dates of later assemblage zones). It is possible that greater resolution within the *Tapinocephalus* Assemblage Zone would lead to a different signal being observed.

The Capitanian is the last period containing pelycosaurian-grade synapsids named to species level. They are a very minor part of the fauna, with only 2 species present, compared to therapsids, with 60 and 53 species known from the early and late Capitanian respectively (Figure 31). Only Varanopidae survived until the end of the interval under study. A single varanopid specimen is known from after this interval, in the *Pristerognathus* Assemblage Zone of South Africa (Modesto et al., 2011), but this has not been assigned to a species, and so was not included in this analysis.

Unlike the varanopids present in the Roadian, all the Wordian and Capitanian species are small, having been replaced in the macro-predator niche by anteosaurian dinocephalians, biarmosuchians and early therocephalians. Despite their reduction in diversity and their smaller size compared to the Kungurian and Roadian varanodontine species, varanopids retained a role in the Middle Permian ecosystem as small predators until the appearance of small diapsid and eutherocephalian predators in the latest Capitanian. There may only be four species known from the Wordian and Capitanian, but they are present in both the northern and southern hemispheres. Caseids were replaced in the herbivorous niche by the new therapsid and pareiasaurian herbivores. The last caseid is only found in the Mezen group where such herbivores are not known (Reisz and Laurin, 2002).

**Conclusions**

The present study describes the major trends in early synapsid diversity, including two extinction events that influenced the evolution of pelycosaurian-grade synapsids. An initial radiation occurred during the Kasimovian, particularly among Ophiacodontidae and Varanopidae. An extinction during the Sakmarian interrupted the diversification of synapsids, possibly due to the changing climate at the time and the transition to a more open and arid habitat. This extinction was followed by the radiation of many larger species of synapsid, as well as the diversification of Caseidae. However, Sphenacodontidae, Ophiacodontidae and Edaphosauridae began to decline during the Kungurian, and Eothyrididae went extinct.
An extinction event across the Kungurian/Roadian boundary caused the demise of Ophiacodontidae and Edaphosauridae, whereas Caseidae and Therapsida diversified. The early Roadian fauna was still dominated by pelycosaurian-grade synapsids, but unlike the Artinskian and Kungurian, in which sphenacodontids were most speciose, the early Roadian fauna contained large predatory varanopids and large herbivorous caseids. Further extinctions occurred during the Roadian with Sphenacodontidae disappearing between the early and late Roadian, and Caseidae decreasing in diversity, while therapsids continued to diversify.

Synapsid diversity recovered from this extinction during the Wordian, but it was therapsid clades that radiated; no recovery is visible in the surviving pelycosaurian-grade families. They are a minor component of the Middle Permian fauna, with only 2 small varanopid species present in the Capitanian. Capitanian diversity is ambiguous due to conflicting diversity curves; the taxic and phylogenetic diversity curves indicate that this was the time of greatest diversity during the interval under study, but the residual diversity estimate shows no significant change from the late Wordian.

Debates surrounding the adequacy of the Permian terrestrial record have previously focussed on potential geological biases, with less attention paid to “human” factors, such as the greater effort put into sampling rocks of a particular age. The strong correlation between the number of amniote-bearing collection, as well as the geographically ‘patchy’ record indicates that the fossil record at this time is clearly inadequate for studying macroevolutionary patterns without correction for sampling.
Chapter 6

Clade Diversification and Key Innovations in Early Amniotes
Clade Diversification

Investigating Uneven Rates of Diversification

Diversification rate is the rate at which the diversity of a clade increases, and is thus a function of both origination and extinction (Foote, 1999). The asymmetric shape of the Tree of Life testifies to the fact that different clades have undergone different rates of diversification throughout their evolutionary history. If a clade is at any point in time more diverse than its sister, this is an indication that this clade has either experienced a higher rate of origination, a lower rate of extinction, or both. Particularly interesting are events in which the rates of diversification in a clade shift significantly relative to its contemporaries. The detection of shifts in diversification rates is central to investigations on clade dynamics and the interaction between originations and extinctions that ultimately shaped the Tree of Life.

Numerous methods have been devised to identify uneven rates of cladogenesis and extinction within a clade. One of the earliest studies of this issue (Raup et al., 1973) provided a template for many that have come since: a simple birth-death model was used to randomly generate phylogenies, in which each lineage had at any one time an equal probability of speciation (splitting into two lineages) or extinction. The diversity profiles of clades (Figure 37A-C) within model phylogenies was compared to the observed diversity profiles of reptile clades (Figure 37D), albeit visually rather than statistically. The similarities between the two indicated that the background pattern of diversification in reptiles follows the simple stochastic model. There were a number of time periods and clades which showed variation outside that which is observed in the model phylogenies e.g. the end-Cretaceous extinction, the rapid diversification of therapsids in the Permian, and the consistently low diversity of Rhynchocephalia since the Triassic; these were taken to indicate time periods and clades in which diversification rates were greatly different to background rates. This seminal study introduced much of the theory which underlies the methods used in this section of the thesis: the comparison of observed diversity patterns with the diversity patterns from an equal-rates model. This model, along with an alternative model in which an optimum clade size was specified, was tested against a larger selection of clades by Gould et al. (1977). In this study real clades showed greater fluctuations in diversity than modelled clades, indicating real clades experience variation in rates of origination and extinction beyond what would be expected from an equal-rates model, although the differences were not marked. Heard and Mooers (2002) further modified these models, incorporating parameters to simulate rapid initial radiations, wherein extinction rates were reduced until the clade reached a specific size, and mass extinction events. Although these models were not compared to empirical data, Heard and Mooers (2002) did model selective extinction based on a modelled trait to show that selective extinctions produce greater variation in clade size than random extinction.

Other methods investigating uneven rates of origination and extinction have eschewed a modelling approach. Roy et al. (2009) used matrix correlations to investigate selectivity in extinction between different families of bivalves. Two pairwise matrices of genera were created, one indicating whether each species pair belonged to the same family or not, one indication whether each species pair shares the same extinction fate (survival or extinction) in the time period under study. The matrix correlation between these two matrices provided a measure of whether the extinction is clustered in particular families or is random. The study showed that selectivity of extinction in bivalves varied; in most time bins studied, little
selectivity was observed. However in certain periods such as the Maastrichtian, Aptian and Toarcian, strong phylogenetic clustering of extinctions was observed (Figure 38).

![Figure 38: Temporal trend in phylogenetic clustering of extinctions. Shaded bars represent 95% confidence intervals around the expected value of R_{CL}. The intervals showing statistically significant phylogenetic clustering of extinctions are labeled in bold; an additional interval, the Campanian, is marginally significant. From Roy et al. (2009).](image)

### Tree Topology and Diversification Rates

The methods described above all employ a higher-level taxonomic framework; that is they are comparing diversification patterns within families or other higher taxa. This presents a problem, particularly when endeavouring to compare observed diversification patterns with a birth-death model in the manner of Raup et al. (1973) and Gould et al. (1977). As discussed previously, families are highly subjective groupings, and it is impossible to accurately overlay taxonomic practices over a phylogeny grown by a birth-death model. Raup et al. (1973) and Gould et al. (1977) defined the higher taxa in their model as monophyletic groupings which reached a particular size, but families vary hugely and have even been erected for single species.

Studies of diversification shifts that rely on tree topology have recently attracted much attention as a potential solution to the problem. These were first introduced by Rambaut et al. (1997) in the program End-Epi. This algorithm, and others similar, follows the ideas introduced by Raup et al. (1973): variation in diversity between different clades that is beyond
the variation produced in a stochastic birth-death model is an indication of significant
differences in diversification rate. End-Epi compares an ultrametric phylogeny of the clade of
interest, with branch lengths scaled to represent divergence times, to those created from
stochastic birth-death models in order to indicate points on the tree where diversification
events have been concentrated in time relative to what one expects from the models.

The program SymmeTREE (Chan and Moore, 2002) implements a slightly different
set of statistics which require no information on branch lengths. Once again, these statistics
not only deduce the presence of uneven diversification rates within a phylogeny, but can also
show at which nodes in the phylogeny shifts in diversification rate occur. The statistics used
in SymmeTREE, the $\Delta_1$ and $\Delta_2$ shift statistics (Moore et al., 2004), assess the likelihood that
the observed imbalance between two lineages descended from a particular node could have
appeared under two models: an equal rates Markov model (Chan and Moore, 2002) in which
speciation rate is constant and a lineage has equal probability of diverging at any time, and a
heterogeneous diversification model. Having calculated the difference in likelihoods under
the equal-rates and heterogeneous models, one then needs to ascertain whether any shift in
diversification rate occurred at the node being investigated, or at a higher node within the
more diverse descendant. Therefore, the likelihood of a diversification shift at a particular
node must be conditioned by the likelihood of a rate shift within the descendants of that node
(Moore et al. 2004). The $\Delta_1$ and $\Delta_2$ shift statistics differ in the way in which they correct for
this issue. The $\Delta_1$ simply calculates the difference between the likelihood of a shift occurring
at the node in question and the likelihood of a shift occurring within the node immediately
descending from its more diverse descendant (Moore et al., 2004). The $\Delta_2$ statistic is more
complicated. The diversity of the descendants of the node under study is adjusted by
removing tips which can be attributed to a rate shift along an internal node rather than the
node under examination (Moore et al., 2004). Under simulation studies, the $\Delta_2$ was found to
perform better (Moore et al., 2004).

Diversification Shifts and Key Innovations

Although analyses of rate shifts are primarily designed to assess variation in rates of
cladogenesis and extinction at different nodes in phylogenies, they have also been used to link
shifts to both extrinsic (e.g. physical) and intrinsic (e.g. biological) causes. For instance, the
timing of a shift may happen to coincide with that of a climatic or environmental change
(Wiens et al., 2007; Tolley et al., 2008; Steeman et al., 2009), occur in the aftermath of a
large-scale crisis such as a mass extinction (Ruta et al., 2007), or be associated with a “key” morphological, ecological, or behavioural feature (Cook and Lessa, 1998; Vences et al., 2002; Rüber et al., 2003; Kozak et al., 2005; Forest et al., 2007; McLeish et al., 2007; Kazancıoğlu et al., 2009). Potential links between a “key innovation” and a shift in diversification rate have received special interest: a particular innovation might provide access to a new resource or gives a clade a competitive advantage over other species, leading to rapid speciation (Cook and Lessa, 1998; Beninda-Edmonds et al., 1999; Benson and Choiniere, 2013). Innovations that have been correlated with diversification shifts, and a causal relationship suggested, have been morphological e.g. the first appearance of elaiosomes in milkworts (Forest et al., 2007) and the evolution of powered flight in birds (Benson and Choiniere, 2013); behavioural e.g. the change in breeding behaviour in gobies (Rüber et al., 2003) and Malagasy tree frogs (Vences et al., 2002); or ontogenetic e.g. a change in host in acacia thrips (McLeish et al., 2008).

It is obviously tempting to view a diversification shift occurring in a clade that also possesses an obvious evolutionary innovation as being causally linked to the novelty (Cook & Lessa, 1998; Vences et al., 2002; Ruber et al., 2003; Kozak et al., 2005; Forest et al., 2007; McLeish et al., 2008; Kazancıoğlu et al., 2009). This is an adaptive radiation model (Simpson, 1953): a key innovation gives a lineage a selective advantage or allows it to enter a new ecological niche, thus leading to a massive increase in the rate of speciation. However there are problems with viewing a diversification rate increase and an evolutionary novelty as being causally linked. Such inferences are often circumstantial, relying solely on the coincidence of the two events. Moreover, the inference makes an implicit assumption that the diversification shift is the result of an increase in the rate of cladogenesis, an assumption that is not always valid. Diversification is a function of both origination and extinction (Foote, 1999). A diversification rate shift in one clade could imply either that its origination rate has increased or the extinction rate of its sister has increased. Tree topology analyses alone cannot distinguish between these two instances. Finally, the analyses often focus on a limited temporal and taxonomic range. Such limited analyses force the researcher to focus on the small number of shifts occurring in the clade of interest and do not allow investigation into the more general patterns of origination and extinction behind the diversification rate shifts occurring in the larger clade. The analysis of McLeish et al. (2008), for example, suggested that a diversification rate shift at a particular node in a milkwort phylogeny was caused by the evolution of elaiosomes. This analysis, in fact, found several other diversification shifts within milkworts, but the authors did not attempt to find a common factor uniting these shifts.
and then look for possible exceptions to the general pattern. Instead the shift coinciding with the supposed “key innovation” was assumed to be an adaptive radiation.

Therefore, in the analysis of diversification rates presented herein, a much broader dataset is used. A supertree of all amniotes from the Pennsylvanian until the end of the Triassic was generated. This supertree maximizes the taxonomic scope and sample size of our investigation, and is used to address three major questions: (1) What portions of the Palaeozoic and early Mesozoic amniote tree underwent significant shifts in diversification? (2) Did shifts coincide with the acquisition of morphological innovations? (3) What is the influence of uneven rates of extinction on diversification rates? In order to address these questions, the supertree was subjected to analysis of tree topology-dependent shifts. Species richness, origination rates, and extinction rates were deduced from the supertree and compared to the timing of the shifts and the appearance of key innovations.

Amniote evolution in the late Palaeozoic and early Mesozoic offers a benchmark for analysing models of diversification and the influence of evolutionary innovation in a diverse and successful vertebrate radiation. Early amniotes evolved a large variety of morphologies and occupied a wide range of niches. They developed numerous ecological adaptations, such as herbivory (Sues and Reisz, 1998), fossoriality (Cox, 1972; Cluver, 1978), arboreality (Renesto, 1994; Spielmann, 2005; Fröbisch and Reisz, 2009), and secondarily aquatic lifestyles (DeBraga and Reisz, 1995; Modesto, 2006; 2010), and went through multiple radiations and extinctions, including the most catastrophic of all biological crises in Earth’s history at the Permian-Triassic boundary (Benton, 1989; 2003; Sahney and Benton, 2008; Benton et al., 2013; Fröbisch, 2013). Amniotes are used as a model group to infer general patterns of vertebrate diversification over an extensive time period, which can then be used to make inferences about possible factors responsible for individual shifts within the group on which this thesis focusses: the pelycosaurian-grade synapsids.

**Materials and Methods**

**Expansion of the Supertree**

An expanded supertree was generated using the methods described in Chapter 3. For this set of analyses the list of source trees was expanded to include all phylogenies containing three or more amniote taxa from the time period covering the late Moscovian until the end of the Triassic. Once again, the source trees were limited to those which included full details of
the method and data. Those that did not were rejected, as were those which had been superseded by more recent analyses (methods for judging this were identical to those presented in Chapter 3). After pruning the list of published phylogenetic analyses in this way, 177 phylogenies remained (Appendix J), which were standardised with respect to taxonomic level (see Chapter 3). The MRP matrix was again produced using Supertree0.85b (Salamin et al., 2002) and analysed in TNT under identical settings to those presented before. However at this point a modification to the method had to be made since the MRP matrix of all 177 trees could not be analysed using parsimony; more trees were produced in a single round of searches than could be stored in the memory of TNT. In order to deal with this problem, the list of source trees was divided into 8 categories: Synapsida, Parareptilia, Archosauromorpha, Lepidosauriformes, Sauropterygia, Ichthyopterygia, and “Basal” forms. The source trees were divided between these categories based on which clade they were representing the relationships of. Those in the “Basal” category include studies examining the relationships of multiple clades relative to each other and those including diadectomorphs and stem eureptiles. An MRP matrix was produced for each category, and a supertree created for each clade, using the procedure described above. Because of the uncertainty surrounding the position of turtles (either within parareptiles or lepidosauromorphs), the categories Parareptilia, Sauropterygia and “Basal” forms were combined, and a single supertree of the taxa in the categories produced in order to test which of these relationships was best supported. The supertrees produced in each of these separate analyses were combined, again with MRP. The final supertree, after collapsing all nodes containing no descendant taxa from the time interval under study and removing post hoc several taxa whose position could not be resolved (Appendix K), contained 686 species. The full time calibrated tree may be seen in Appendix L, and a summary version in Figure 39.

It should be noted that the lack of resolution of the position of those taxa was sometimes due to controversy surrounding their relationships, but it could also be due simply to the fact that a species had not been tested against a wide enough sample of taxa for the MRP method to resolve its position e.g. the assignment to *Nothosaurus* of *N. haasi*, *N. jagisteus*, *N. edingerae*, *N. marchicus*, *N. winterswijkensis*, *N. youngi*, *N. juvenilis*, *N. tchernovi*, *N. winkelhorsti*, *N. yangiuanensis* is not controversial and was supported in a recent study (Klein and Albers, 2009). However, since this study employed few outgroup taxa and no other has included any *Nothosaurus* species other than the type and *N. giganteus*, the MRP methods could not resolve the position of these species relative to other sauropterygians.
Figure 39: A summary version of the supertree (see Appendix L for the full tree). Red arrows indicate substantial diversification shifts, identified using the Ruta method of time slicing; black arrows indicate statistically significant shifts.
SymmeTREE Analysis

The supertree was subjected to analysis in SymmeTREE v. 1.1 (Chan and Moore, 2002, 2005) to infer diversification shifts. Random resolutions were used to resolve polytomies in the analysis: $10^6$ for the whole tree and $10^4$ for individual nodes. $10^6$ trees were simulated under the equal rates and heterogeneous models: the maximum allowed by SymmeTREE. The program outputs a value of $\Delta_1$ and $\Delta_2$ for each node, as well as a p-value for each indicating whether the departure from the equal rate model for that node is statistically significant. The $\Delta_2$ statistic was used to infer diversification shifts following recommendations in Moore et al. (2004). A p-value of less than 0.05 indicates that a lineage underwent a significant shift, whereas a p-value between 0.05 and 0.1 indicates a substantial shift (Ruta et al., 2007; Lloyd et al., 2008). A diversification shift was inferred to have occurred on the lineage leading to the more diverse of the two descendants of the node with a significant or substantial $\Delta_2$ (Chan and Moore, 2002). The timing and location within the tree of the diversification shifts may be seen in Appendix N. A plot of mean $\Delta_2$ values through time was produced to illustrate temporal trends in magnitude and frequency of shifts.

Sensitivity Analyses

Three analyses were carried out to test the impact of three possible sources of error: poorly supported relationships within the supertree, uncertain ages of specimens, and different methods of time slicing.

Method of time slicing

SymmeTREE does not incorporate any temporal information into the analysis. However the statistics employed assume that descendants of the node under analysis have had equal time to diversify (Ruta et al., 2007). This assumption is not valid if a tree includes fossils; lineages that die out before their sisters had less time to diversify. As such, Ruta et al. (2007) suggested that time slicing be employed for datasets containing extinct taxa. This has a further advantage in that it allows the researcher to ascertain the timing of a diversification shift as well as its location within the phylogeny. The period of time under study is split into bins and the phylogeny is pruned to include only taxa observed in a particular bin, as well as ghost lineages inferred from the phylogeny (Ruta et al., 2007). The phylogenies of each time slice are analysed individually (hereafter, this method is referred to as the “Ruta method”).
Tarver and Donoghue (2011) suggested a different method of time slicing (hereafter referred to as the “Tarver method”). They point out that the trees produced by the Ruta method are incomplete and therefore one cannot distinguish between extinction and speciation as causes of the imbalance of nodes. As such, they advocated “growing” the tree through time: every time slice, add in the new lineages which appear in this time interval, but retain those which became extinct (and would therefore be removed under the Ruta method).

Both methods of time slicing were implemented using the `timeSliceTree` function of the paleotree (Bapst, 2012) package in R (R Core Team 2013). For each substage, a phylogeny was derived from the supertree using both the Ruta and the Tarver methods. These phylogenies were analysed in SymmeTREE under the settings described above.

Support for relationships

It is important to remember that a supertree analysis should not be considered a unique morphological analysis. Rather it should be considered a summary of researchers’ opinions on the relationships of the clade under study. That the MRP analysis favoured a particular set of relationships does not necessarily mean that those relationships are supported by better morphological data. Moreover, although in theory an MRP supertree should not contain any relationships that have never before been suggested, unsupported relationships can appear, albeit rarely (Beninda-Emonds, 2003). For these reasons, it is necessary to provide a support measure indicating to what extent the source trees support the relationships shown in the supertree. Since the usual support measure for phylogenetic analysis, such as Bremer support and Bootstrapping, are inappropriate for supertrees (the input data of a supertree are source trees rather than characters), several alternative measures have been put forward.

In this study the V measure was used (Wilkinson et al., 2005b). Each node is assigned a value between -1 and 1, representing the proportion of source trees supporting that node relative to the source trees conflicting with it. A V of 1 indicates that all relevant source trees support the node, a V of 0 indicates equal numbers of trees supporting and conflicting with the node, and a V of -1 indicates none of the source trees support the node. Other measures of support for supertrees exist, such as the qualitative support (Beninda-Emonds, 2003) and input tree bootstrapping (Creevey et al., 2004), but these were rejected for the current study. The qualitative support measure has been criticised for being too harsh: Wilkinson et al. (2005b) showed an example of a supertree which did not conflict with any input trees, but the mean QS was only 0.028 (in a measure ranging from -1 to 1). Input tree bootstrapping was rejected, meanwhile, since it is inappropriate for datasets containing many non-overlapping...
trees (Moore et al. 2006). In order to ensure that poorly supported relationships do not unduly affect the inferences, the analyses with SymmeTREE were repeated with nodes having negative support collapsed into a polytomy. The nodes collapsed due to low support are marked in Appendix L.

**Uncertainty of ages of taxa**

As in the investigation of diversity, two sets of ages were assigned to each species. The first took into account uncertainty in the dating of certain formations; if a formation was of uncertain age, species within that formation were assigned to the full range of possible ages. The second set of ages restricted the age of formations of uncertain age to at most two substages based on examination of the recent literature. Data using both sets of ages were subjected to analyses in SymmeTREE to assess the effect of uncertain dates on results. The age ranges assigned to taxa may be viewed in Appendix N.

**Comparison of Rate Shifts with Diversity, Extinction Rates and Origination Rates**

A phylogenetic diversity estimate of amniotes from the late Moscovian until the end of the Triassic was calculated from the time-calibrated supertree. The supertree was also used to infer extinction and origination rates. Per-lineage extinction rates were calculated by dividing the number of lineages terminating in a time bin by the total number of lineages (observed and ghost) present in that bin. Per-lineage origination rates are calculated by dividing the total number of cladogenic events in each time bin by the total number of lineages present in that bin. Since inference of origination rates is affected by polytomies, these were randomly resolved 1000 times in order to provide a mean origination rate.

Origination rates were used to evaluate the impact of morphological innovation on diversification. Two such innovations within early amniotes were examined: herbivory and a secondarily aquatic lifestyle. Two binary characters were created, one representing the presence or absence of each innovation in all taxa in the supertree. These characters were optimised over the tree by deducing ancestral character states for all nodes with parsimony using the ancestral.pml function from the phangorn package in R. A set of per-lineage origination rates within all lineages descended from an herbivorous ancestor, and another for those descended from an aquatic ancestor.

The PDE and rate estimates were calculated from the supertree in R using custom scripts written from functions in paleotree. The origination and extinction rate estimates were
compared to the number of diversification shifts in each time bin using the Spearman’s rank and Kendall’s tau correlation coefficients, carried out in R, after implementing generalised differencing. Generalised least squares regression (GLS) was also used to investigate the relationship between diversification and origination and extinction rates. This method has an advantage over simple correlation tests in that it allows multivariate models to be compared as well as single variables. The curve of amniote $\Delta_2$ through time was compared using GLS to a null model (random variation around a mean of 0), to origination and extinction rates, and to a multivariate model of both origination and extinction.

**Results and Discussions**

**Sensitivity Analysis**

The analyses that tested the impact of uncertainty surrounding the age ranges of species and of poorly supported relationships both found that neither of these issues substantially affect the results. When nodes with negative support are collapsed into a polytomy, the timing and location of the substantial and significant diversification shifts identified by SymmeTree are unchanged from those found using the original supertree (Appendix M). There are minor differences in the analyses employing the two different sets of age ranges, however, this only affect four clades. In two clades the timing of the diversification shift changes: a diversification shift in the clade containing Pareiasauridae and Procolophonoiidea is found in the late Wuchiapingian when the restricted ages are used, but when uncertainty of ages is incorporated it is found in the early Wuchiapingian. A diversification shift in anomodonts more derived than *Wadiasaurus* is found in the early Ladinian when uncertainty of ages is taken into account, but is found in the late Anisian when ages are restricted. Two further clades are only found to experience a diversification shift only when using ages which account for uncertainty: Eucynodontia and Kannemeyeriiformes.

The use of different time-slicing methods has a greater effect (Appendix M). The Ruta method identified 21 clades experiencing substantial diversification shifts, while the Tarver method identified 26. Of these clades, only 16 were identified using both methods: Amniota, Ankyromorpha, anomodonts more derived than *Wadiasaurus*, Archosauromorpha, the clade containing Erythrosuchidae and archosauromorphs more derived, the clade containing Leptopleurinae and Procophoninae, the clade containing Pylaecephalidae and dicynodonts more derived, Dinosauriomorpha, Eucynodontia, Eutherocephalia, Paracrocodylomorpha,
Phytosauria, Sauria, Saurischia, Sauropterygia and Therapsida. With two exceptions, the timing of the shifts in these clades was identical: when using the Tarver method of time slicing, a diversification shift in Archosauromorpha occurs in the early Olenekian, but in the late Olenekian when using the Ruta method; when using the Tarver method of time slicing, a diversification shift in Eutherocephalia occurs in the late Ansian, but in the early Wuchiapingian when using the Ruta method. Five clades were found to experience shifts only when using the Ruta method: Archosauria, the clade containing Kayentatheridae and cynodonts more derived, the clades containing Protorosaurusia and all archosauromorphs more derived, Kannemeyeriiformes and Plateosaurus. Ten clades were found to experience shifts only when using the Tarver method: the clade containing Captorhinidae and Diapsida, the clade containing Dinocephalia, Therocephalia and Anomodontia, the clade containing Eutherocephalia and Scylacosauridae, the clade containing Millerettidae and all parareptiles more derived, the clade containing Traversodontidae and Trirachodontidae, the clade containing Venjukovoidea and all anomodonts more derived, Diapsida, Dinosauriformes, Protorosaurusia and Sphenacodontia.

The results presented in the main text are those using the ages that take into account uncertainties in dating, and time sliced using the Ruta method. The Tarver method, while allowing one to observe the relative effects of both speciation and extinction, does not resolve the issue that Ruta et al. (2007) were trying to solve: under the Tarver method, not all the lineages of the trees input into SymmeTree will have had equal time to diversify.

Extinction and Origination Rates Compared to Diversification Statistics

There is a significant correlation between the number of significant (those with a p value of less than 0.05 using the $\Delta_2$ statistic) and substantial (those with a p value of less than 0.1) shifts in the rate of diversification in each time bin and the per-lineage origination rate (Spearman’s $\rho = 0.4275418$, $p = 0.009835$; Kendall’s $\tau = 0.3047619$, $p = 0.008596$). $\Delta_2$ values depend both on the number and on the arrangement of taxa on the more speciose of the two branches subtended by a given internal node, such that a substantial shift allows us to infer increased cladogenesis. Interestingly, a significant (albeit weaker) correlation was also found between the number of shifts and per-lineage extinction rate ($\rho = 0.3840412$, $p =0.0214$; $\tau = 0.2666667$, $p = 0.02215$). This result implies that one cannot only explain shifts in diversification rate as increases in the rate of cladogenesis in the more diverse clades; increased extinction in the less diverse clades must also be considered.
Figure 40: A comparison of the phylogenetic diversity estimate (black solid) and mean Δ2 values (grey dashed) for A) Synapsida; B) Parareptilia and C) Eureptilia.
Figure 41: A comparison of per-lineage extinction rate (black solid) and mean Δ2 values (grey dashed) for a) Synapsida; b) Parareptilia and c) Eureptilia.
The coincidence of diversification shifts with periods of high extinction is clearly evident in plots of mean $\Delta_2$ through time (Figures 40, 41). Peaks in mean $\Delta_2$, representing both the magnitude and the number of shifts, tend to coincide with, or follow immediately after, large drops in diversity and peaks in extinction rate, the latter representing mass extinctions. Among synapsids (Figures 40A, 41A), the two largest peaks in mean $\Delta_2$ values occur immediately after two mass extinctions: Olson’s Extinction in the Kungurian and Roadian (Sahney and Benton, 2008; Benton 2012, see also Chapter 5) and the end-Permian event (Benton, 1989; 2003; Sahney and Benton, 2008; Benton et al., 2013; Fröbisch, 2013). The former extinction event, as discussed in Chapter 5, included the decline of pelycosaurian-grade synapsids, and was followed immediately by the radiation of therapsids. The extinction rates presented here support the fact that this was a severe extinction event in synapsids; per-lineage extinction rates at the end of the Kungurian are almost as high as those during the end-Permian mass extinction. Immediately following the extinction, there is a diversification shift found at the base of therapsids, which as discussed in Chapter 5 show a dramatic increase in diversity relative to their outgroups within pelycosaurian-grade synapsids. The diversification shift found here is both a product of the massive increase in therapsid diversity following Olson’s extinction, but also the high extinction rates within the pelycosaurian-grade outgroups.

The end-Permian mass extinction was the most severe extinction event in early synapsid evolution. The two curves of phylogenetic diversity estimate (PDE) and extinction rates point to a two-phase event, with synapsids showing peaks in extinction rate occurring at the end of the Changhsingian and at the end of the Induan (Figure 40A, 41A). The first peak coincides with the complete extinction of gorgonopsians and biarmosuchians, as well as large loss of diversity within anomodonts and therocephalians. The second phase of the extinction coincided with the extinction of the Induan post-extinction fauna, including the members of the genus *Lystrosaurus*. A further peak in $\Delta_2$ occurs in the early Ladinian, coinciding with another peak in synapsid extinction rate and a diversification shift in the anomodont clade containing *Wadiasaurus* and the more derived Kannemyeriiformes.

In parareptiles, an early Artinskian peak in mean $\Delta_2$ coincides with the sudden appearance of multiple lineages in the fossil record. Mesosauridae are an exclusively early Artinskian clade, and there are also several parareptiles known from the Richard’s Spur locality in Oklahoma, also of Early Artinskian age (MacDougal and Reisz, 2012). Finally, several bolosaurid specimens are known from the Artinskian aged Admiral Formation (Sander 1989). The appearance of these clades within a short space of time is represented by a
diversification shift within Ankyromorpha (the clade containing lanthanosuchoids and parareptiles more derived), identified by SymmeTREE at this time. This is a clear example of a diversification shift driven by increased rates of cladogenesis. However, the next two biggest peaks in mean parareptile $\Delta_2$ values follow the two largest extinction rate peaks in the Permian (Figure 41B), one at the end of the Wordian and one at the very end of the Permian. The extinction peak at the end of the Wordian is driven by the disappearance of bolosaurids and the decline of nycteroleterids, and is followed by a substantial shift in diversification rate within the clade containing Pareiasauridae and Procolophonoidia. The end-Permian mass extinction, in which Pareiasauridae, Nycteroleteridae and Millerettidae die out, is followed by a diversification shift within the procolophonid clade containing Leptopleurinae and Procolophininae. As in synapsids, one can observe shifts in diversification rate in parareptiles being driven not only by increased cladogenesis, but also selective extinction.

The largest peak in extinction rate of eureptiles occurs during Olson’s extinction; the rate of extinction in eureptiles at the end of the Early Permian is higher than during the end-Permian mass extinction. At this time, Captorhinidae, then the most diverse sauropod family in the Permian, suffered a massive decline in diversity. A peak in mean $\Delta_2$ follows immediately after Olson’s Extinction (Figure 40C, 41C). There is a second peak in extinction rate at the end of the Permian, again followed by a smaller peak in mean $\Delta_2$ (Figure 41C) and a shift in diversification rates in Sauria (the clade containing Lepidosauriformes and Archosauriformes). This shift represents the extinction of the more basal sauropod clades such as captorhinids and basal diapsids such as Younginiformes, but also cladogenesis within saurians. In the immediate aftermath of the extinction, Lepidosauromorpha such as Paliguana (Broom, 1903a), ichthyopterygians such as Utatsusaurus and Grippia (Shikama et al., 1978; Brinkman et al., 1992) and sauropterygians such as Placodus appear in the fossil record, along with Archosauromorpha such as Koilamasuchus (Ezcurra et al., 2010), Proterosuchus (Broom, 1903b), Osmolskina (Borsuk-Bialynicka and Evans, 2003) and the poposauroid Xilousuchus (Wu, 1981). This provides a further example of a selective extinction followed by increased cladogenesis within the survivors. However, as in parareptiles, the biggest peaks in eureptile $\Delta_2$ values occur during periods of radiation rather than extinction. The two largest peaks coincide with the appearance of eureptiles in the late Moscovian, and with the appearance of archosauromorphs in the Late Permian (Figure 40C). Nevertheless, the fact that the number and magnitude of substantial shifts increases during times of elevated extinction in all three amniote subclades indicates that the selectivity of extinction may be as important as uneven rates of origination in producing tree shape imbalance.
### Table 7: Results of the comparison between amniote $\Delta_2$ values through time with extinction and origination rates using generalised least squares regression.

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<th>Model</th>
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<th>Akaike Weights</th>
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<td>Extinction and Origination</td>
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<td>300.3195</td>
<td>0.1281</td>
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</tbody>
</table>

The generalised least squares regression analysis produced a surprising result. Based on the Akaike Weights (Table 7), it is overwhelmingly extinction that is found to best fit the $\Delta_2$ curve of amniotes, substantially better than the multivariate model incorporating both origination and extinction. This is indicating that many and large diversification rate shifts are tending to occur during periods of high extinction rate more than high origination rate. This serves to emphasise that one cannot simply assume increased cladogenesis as the driving force behind the diversification rate shifts when carrying out studies of this sort. In early amniotes at least, uneven rates of extinction are an extremely significant influence, perhaps even more so than uneven rates of origination.

#### Key Innovations Among Amniotes

There are several examples of diversification shifts in early amniotes coinciding with the emergence of key ecological and functional innovations. For instance, the highly significant diversification shift observed in therapsids coincides with several physiological and morphological innovations, which allowed more effective food processing, ventilation and environmental tolerance (Kemp 2006, Hopson 2012). Diversification shifts within Kannemeyeriiformes coincide with the evolution of large body size, and a shift at the very base of Amniota may be related to the amniotic egg, giving reproduction independence from water (although this shift from the very base of the tree should be interpreted with care; the absence of further outgroups makes it difficult to ascertain the precise location of the shift). There are further examples of diversification shifts coinciding with morphological novelties relating to the two case studies examined in more detail here: herbivory and a secondary return to an aquatic environment. The evolution of an aquatic lifestyle coincides with diversification shifts at the base of Sauropterygia and Phytosauria. Cranial and mandibular re-
modelling accompanying increased specializations towards herbivory are marked by shifts in distinct groups, such as dicynodonts (a keratinous beak combined with propalinal lower jaw movements, which evolved earlier in anomodonts) (Reisz and Sues, 2000; Rubidge and Sidor, 2001), Triassic procolophonids (chisel-shaped teeth for processing tough vegetation) (Reisz and Sues, 2000), and plateosaurian sauropodomorph dinosaurs (increase in body size and high browsing) (Sereno, 1999).

It is obviously tempting to view these diversification shifts as representing adaptive radiations: the evolutionary novelty provides a selective advantage and the entry into a new niche and causes increases in the rate of cladogenesis. However the previous analyses do cast doubt on this line of reasoning: one cannot assume increased cladogenesis as the driving force behind diversification rate shifts. Detailed analysis into two case studies (herbivory and an aquatic lifestyle) provided further evidence against this line of reasoning.

Although there were arthropod herbivores in the terrestrial realm before the appearance of amniotes, the vast majority of primary consumers in Carboniferous and earliest Permian terrestrial ecosystems were arthropod detritivores (Shear and Sheldon 2001). Those amniotes which first adopted a high-fibre herbivorous diet were therefore entering an extremely under-filled region of ecospace. However, we see no evidence of an adaptive radiation in these earliest herbivores such as Edaphosauridae, Caseidae and Diadectidae. SymmeTREE identifies no diversification rate shifts in these earliest herbivores. Instead, significant and substantial shifts are found in the later Permian and Triassic herbivore specialists such as Dicynodontia, Plateosauria and Triassic procolophonids. The origination rates of herbivores show that it is not during the Carboniferous and earliest Permian, but during the Middle and Late Permian and across the Permo-Triassic boundary that extinction rates of herbivores are consistently higher than those of other taxa (Figure 42A). This is not only the time when diversification shifts are observed in dicynodonts and Triassic procolophonids, but is also a time of consistently high extinction rates among amniotes (Figure 41). The timing of the shifts is also interesting. Despite dicynodonts and their evolutionary innovations first appearing in the Wordian, the shift in their diversification rate occurs in the late Capitanian. The first members of Plateosauria appear in the Carnian, but this clade does not experience a shift in diversification rate until the Rhaetian. Both the Capitanian and Rhaetian are periods of high extinction rate (Figure 41). One does not see an adaptive radiation of these herbivore specialists coincide with the appearance of their “key innovation”. Instead the diversification shift coincides with periods of high extinction rate, as was shown in the earlier analyses. It is therefore here suggested that these key innovations do not alone
cause an increase in the rate of cladogenesis, but instead buffer against extinction. It is the selective extinction of those without the innovation, and only then the subsequent radiation of survivors, that SymmeTREE is detecting.

Figure 42: A comparison of per-lineage origination rate of herbivorous (a), aquatic (b) and other lineages through geological time.

Unlike the example of herbivores, amniotes that evolved a secondarily aquatic lifestyle did not colonise under-filled ecospace. Aquatic or semi-aquatic taxa, such as mesosaurid parareptiles and various Late Permian diapsid species, would have faced competition from other medium and large-sized vertebrates (e.g. amphibians; fish). This may explain why those secondarily aquatic lineages show low origination rates during the Carboniferous and Early
Permian (Figure 42B), and no diversification rate increases were identified by Symmetree during this time. It was not until the earliest Triassic that origination rates in aquatic lineages exceeded those in other lineages. It is also not until the Triassic that SymmeTREE identifies diversification rate increases coinciding with the evolution of an aquatic bauplan: at the base of the Sauropterygia and the Phytosauria.

Once again one could infer the influence of extinction on these diversification shifts. The shift observed in sauropterygians, and the increase in origination rate of aquatic amniotes at the same time (Figure 42B), follows immediately after the end-Permian mass extinction, and was perhaps facilitated by the reduced diversity of potential competitors such as fish and marine archegosaurid amphibians (Friedman & Sallan 2012, Koot 2013, Ruta and Benton, 2008). The shift observed in phytosaurs occurs at the end of the Carnian, post-dating their first appearance, but coinciding with a period of high extinction rate and declining diversity not only amongst amniotes (Figure 40, 41) but also among temnospondyl amphibians (Ruta & Benton, 2008). As before we do not see an adaptive radiation of phytosaurs coinciding with the first appearance of their novel bauplan, but instead the diversification shift is deferred to a period of high extinction rate amongst their competitors.

**Diversification Rates Within Pelycosaurian-grade Synapsids**

As discussed in Chapter 1, pelycosaurian-grade synapsids represent the earliest appearance in terrestrial amniotes of several innovations, including large body size, macro-carnivory, herbivory, and possibly a return to an aquatic environment. Under an adaptive radiation model, such novelties might be expected to lead to great increases in diversification rate within some of the pelycosaurian clades. Indeed, pelycosaurian-grade synapsids were the most diverse amniotes for much of the Early Permian (Figure 40), and the large number of evolutionary novelties could have provided an explanation for this; pelycosaurian-grade synapsids were some of the earliest amniotes to enter these niches, and so would have had empty ecospace in which to diversify.

Curiously, however, SymmeTREE finds no significant or substantial shifts in diversification rate within any families of pelycosaurian-grade synapsids throughout the late Carboniferous and Early Permian, the time at which these evolutionary novelties appeared. There is also no shift found at the base of synapsids at this time, indicating that this highly innovative group is no more diverse compared to contemporary clades than is expected under an equal rates model. Mean $\Delta_2$ values of synapsids show no great peaks prior to the Middle
Permian; a single minor peak appears in the Gzhelian coinciding with a peak in synapsid diversity (see Chapter 5) but is considerably lower than later peaks and coincides with no shifts in diversification rate.

Why is it that the pelycosaurian-grade synapsids experience no great variations in their diversification rate beyond what may be expected from an equal-rates model? A possible explanation may lie in the link between evolutionary innovation, extinction events and diversification rate shifts. During the Late Carboniferous and Early Permian, there are no substantial extinction events. Despite the decline in diversity observed in the Sakmarian (see Chapter 5) the extinction rates of synapsids do not increase far above background rates during the Carboniferous and Early Permian. It is possible that this diversity decrease was driven more by a decrease in origination rate than by an increase in extinction rate. Under the model proposed in this chapter, innovations alone do cause increases in diversification rates during periods of background extinction. It is during the periods of environmental hardship and elevated extinction in which such innovations provide the impetus for an increase in diversification rates. Since pelycosaurian-grade synapsids, during the Late Carboniferous and Early Permian, experienced merely a background level of extinction rates, their evolutionary novelties did not translate to increases in diversification rate over those who lacked such innovations. The first mass extinction to occur during the time period occupied by the pelycosaurian-grade synapsids was Olson’s extinction, in which therapsids diversified at the expense of basal synapsids.

There are, however, alternative issues that should be discussed, one of which is the comprehensiveness of the supertree. Although the analyses in Chapter 5 show that the synapsid portion of the tree is inclusive enough to infer diversity patterns in synapsids as a whole, there are clearly clades that receive less attention than others, most noticeably Sphenacodontidae and Ophicaodontidae. Both of these clades have undergone very little phylogenetic or taxonomic re-evaluation. The two most diverse pelycosaurian-grade genera, *Ophiacodon* and *Dimetrodon* are only included at genus level in all phylogenetic analyses which are included as source trees in the supertree. Re-evaluation of Sphenacodontidae is a work in progress, and while the work of Brink and Reisz (2014) has increased the taxonomic scope of the phylogenetic analyses, most of the sphenacodontid species currently considered valid have not been examined since the work of Romer and Price (1940). *Ophiacodon*, meanwhile, has received no such revision since Romer and Price’s monograph. It is unclear how further examination of these taxa would alter the results presented here. The data presented in Chapter 4 would indicate that an abundance of fragmentary specimens may have
led to oversplitting of the taxa, and it is likely that many of the species in these two families are invalid. Therefore, increasing the scope of phylogenetic analyses would be unlikely to affect results substantially. It is probable that the inferences made from the analyses undertaken herein are still valid, in spite of these issues.

Conclusions

It is tempting to view simultaneously occurring diversification shifts and evolutionary novelties as being causally linked. Indeed a number of studies have made such a connection (Cook and Lessa, 1998; Vences et al., 2002; Rüber et al., 2003; Kozak et al, 2005; Forest et al., 2007; McLeish et al., 2007; Kazancıoğlu et al., 2009). However such analyses often focus on a limited temporal and taxonomic range and do not investigate other possible correlations. The broader scale analysis presented here indicates that the patterns of radiation within early amniotes are heavily connected to the extinction events occurring during this time. The strong correlation of extinction rate and the number of substantial diversification shifts illustrates that uneven extinction rates within amniotes have had just as significant effect on tree topology as the pattern of origination. Some previous studies have suggested that shifts co-occur with extinction events (Ruta et al., 2007) or other extrinsic factors such as climate or geographic changes (Kiessling and Baron-Szabo, 2004; Wiens et al., 2007; Tolley et al., 2008; Steeman et al., 2009). However, the present study indicates that, at least within early amniotes, there is a more complex relationship between the two factors. Extinction selectivity based on morphology and ecology has been documented in a number of clades (Smith and Jeffrey, 1988; Friedman, 2009; Moore and Donoghue, 2009; Roy et al., 2009; Friedman and Sallan, 2012). In early amniotes, the appearance of these novelties such as herbivory and an aquatic bodyplan and even the expansion into almost unoccupied ecospace (as in the earliest herbivores) did not on its own cause significant shifts in diversification rate. Instead, it appears that the diversification shifts identified by SymmeTREE represent selective elimination of taxa and subsequent radiation of survivors, in which those taxa with pre-existing innovations allowing the exploitation of new resources were buffered against extinction and experienced a deferred diversification. Hence, the phylogeny of Palaeozoic amniotes was shaped by the interaction between evolutionary innovation and extinction.
Chapter 7

Conclusions and Future Work
As the most diverse and abundant vertebrate taxa in the terrestrial realm during the Early Permian, understanding the evolution of pelycosaurian-grade synapsids is of vital importance if we are to comprehend the establishment of the earliest terrestrial ecosystems. Many of the ecologies and morphotypes found in terrestrial organisms first appear in the basal synapsids. They provide an ideal model organism for understanding not only macroevolutionary patterns in the earliest terrestrial vertebrates, but an excellent case study into the state of our knowledge and research practices when examining this crucial period in the evolution of life on earth.

Examination of the phylogeny of pelycosaurian-grade synapsids using a variety of methods has produced a consistent set of relationships, at least between higher-level taxa. The position of Caseasauria as the sister to all other synapsids is confirmed by the addition of a basal caseid and postcranial material from eothyridids. Unfortunately there is much work still to be done. Poor support and poor resolution are found in many areas of the tree, and much of this appears to be due to missing data. Simply adding new characters and taxa will not resolve the issue of un-scored characters in existing specimens. This requires either more complete specimens of these existing taxa, or detailed re-examinations of the existing specimens. Many of the wildcard taxa have not been examined in the literature since their original descriptions, often from the 1960s and 1970s. In particular, *Echinerpeton intermedium* is in urgent need of re-description. As one of the earliest synapsids it is vital to our understanding of character evolution at the base of the tree, and yet it has not been studied in detail since 1972 and phylogenetic analysis has produced conflicting opinions of its affinities.

The need for taxonomic revision was further highlighted by the analysis of the completeness of the fossil record of the basal synapsids. The negative correlation between the Skeletal Completeness Metric and the number of species named from a particular time bin shows that several species have been named based on very poor material. The most rapid period of discovery was in the three decades between 1940 and 1970, and many of these taxa were defined based on size, locality and stratigraphy. A detailed examination of the amount of morphological variation within speciose genera such as *Dimetrodon*, *Sphenacodon*, *Casea* and *Ophiacodon* is required in order to identify how many species within these genera may still be considered valid.

Despite these issues, and evidence of significant anthropogenic sampling bias, the pattern of species richness identified using multiple methods to correct for sampling is remarkably consistent. Events such as a rapid radiation at the end of the Carboniferous, a mid-Sakmarian trough and an extinction event at the end of the Early Permian are found
independent of which method is used to correct for sampling. This is greatly encouraging; it indicates that a genuine biological signal is visible despite the many issues with the fossil record. Further study is now necessary in order to better understand these events. Examinations of morphological evolution and diversity would supplement the information from species richness. Differences and similarities between diversity and disparity (morphological diversity) would greatly improve our understanding of these events and might provide information as to the causes. Study of Olson’s extinction during the Kungurian and Roadian in particular would benefit from such analyses. Patterns of morphological selectivity in the extinction and of morphological evolution during the recovery would be invaluable in understanding the replacement of pelycosaurian-grade synapsids by therapsids. However such an analysis would benefit from a more detailed understanding of early therapsid relationships.

The results observed in the analysis of tree topology provide an interesting insight into the interactions between morphological evolution and lineage diversification. It appears that the many morphological innovations occurring in early amniote clades did not immediately result in massive increases in the rate of cladogenesis in those clades, as would be expected in an adaptive radiation model. Instead, increases in diversification rate appear to occur during periods of high extinction rate, and in particular during mass extinctions. Diversification rate shifts do not temporally coincide with the first appearance of a “key” innovation, but are instead deferred to periods of high extinction rate among plesiomorphic taxa. This realisation would benefit greatly from further analyses, not only to see if such a signal is found in other clades, but also a more detailed examination of the pattern of diversification in the clades examined here. Detailed comparisons of the rates and modes of morphological changes in clades exploring new areas of ecospace, and comparisons with the rates of origination and extinction, both in times of environmental stability and in times of turbulence and mass extinction, would provide confirmation of the patterns observed here as well as a more thorough understanding of macroevolutionary processes.

This thesis provides the first detailed examination of the evolution of pelycosaurian-grade synapsids using a quantitative, and allows a much greater understanding of their period of dominance in Earth’s history. The investigation of the completeness of their fossil record also provides much information on the biases that are affecting our interpretations of the fossil record. Information on biases and completeness, as well as richness and diversification patterns, is a necessary starting point into macroevolutionary research, and will hopefully provide a basis for further study into this fascinating group of organisms.
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Appendix A

Changes made to the character matrix of Benson (2012) for the phylogenetic analysis undertaken herein. With these exceptions, the character scores are unchanged from the nexus file included in the electronic supplement of the original paper.

Scores Changed

Character 17: The specimen BP-1-5678 (?Elliotsmithia) was coded, despite the fact that no premaxilla is preserved on this specimen. This coding has been replaced with “?”.

Character 51: Both Eothyris parkeyi and Oedaleops campi both originally scored as state 0 (large contribution of the lacrimal to the orbit), but the observed morphology is no different to that of Sphenacodontidae which were scored as state 1 (contribution of the lacrimal restricted by a descending process of the prefrontal). Eothyrididae have both been re-scored as character state 1.

Character 59: The anterior process of the frontal was originally coded as long in both Eothyris parkeyi and Oedaleops campi (state 1) despite being shorter than the posterior process (Reisz et al., 2009). Both have been re-scored as state 0.

Character 119: Mesenosaurus romeri was originally coded as state 0 (posterolateral orientation of the transverse flange of the pterygoid), but the anterior orientation of the transverse flange was specifically noted by Reisz & Berman (2001). This taxon has been re-scored as state 1 (anterolateral orientation of the transverse flange of the pterygoid).

Character 228: Stereophallodon ciscoensis and Mycterosaurus longiceps were both originally scored as character state 0 (prominent ventral ridge system on the femur). However, the poorly developed ventral ridge system has been considered characteristic of both these taxa (Brinkman & Eberth 1986, Berman & Reisz 1982). Therefore both have been re-scored as state 1 (ventral ridge system low and feebly developed)
Characters Modified

Character 17 – This character refers to the premaxillary tooth count. Benson (2012) divided it into two character states: state 0 representing 2-4 premaxillary teeth; state 1 representing 5-6 premaxillary teeth. However, these states miss some of the evolutionary variation. Several of the outgroup taxa, as well as some of the more basal members of the clades have four premaxillary teeth. It is possible that four premaxillary teeth is the primitive condition. By including the possession of four premaxillary teeth in the character state representing fewer teeth, this character does not acknowledge reductions in tooth count from the primitive condition. Therefore the number of character states of character 17 have been increased to three: 0) 2-3 premaxillary teeth; 1) 4 premaxillary teeth; 2) 5-6 premaxillary teeth.

Characters Added

Character 240: Temporal fenestra morphology: 0) narrower dorsally than ventrally; 1) dorsal and ventral margins of similar length, fenestra has an oblong shape; 2) narrower ventrally than dorsally.

Character 241: Webbing under transverse processes of dorsal vertebrae: 0) webbing extensive, extends distally beyond the distal extent of the tips of the transverse processes and anteriorly to the forward edge of the vertebra; 1) webbing slight, does not extend distally beyond the distal extent of the tip of the transverse process; 2) webbing absent.
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Watongia meieri
Ruthiromia elcobriensis
Varanodon agilis
Varanops brevirostris
Aerosaurus wellesi
Aerosaurus greenleorum
Basicranodon fortsillensis
Archaeovenator
hamiltonensis
Mesenosaurus romeri
Mycterosaurus longiceps
Heleosaurus scholtzi
BP 1 5678 Elliotsmithia
Pyozia mesensis
Casea nicholsi
Eocasea martini
"Mycterosaurus" smithae
Apsisaurus witteri

Modified
Character 17
?
?
2
2
1
?
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New Character
240
0
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0
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New Character
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1
1
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0

1

1

2
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1

Added Material
Four species have been added to the matrix of Benson (2012): Casea nicholsi, Eocasea
martini, “Mycterosaurus” smithae and Apsisaurus witteri. New material was also considered
for Oedaleops campi. Here are presented the character scores for all five of these species:
Eocasea martini ?????110?010??????????????0?????????????000????????????????????000?100??000000000
001?201010000?12??00???????????????????????0????000????0?????0?0??1??200000?0000
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?0
Casea nicholsi ???????????????????????????????????????????????????????????????0????0?????????0???01
0??????????????????????????????????????????????????????????????11????????11?0000000
001?11???????????????????????????1001110011??1??1???????0000?0?0000????0?0

222


“Mycterosaurus” smithae -

Apsisaurus witteri -

Oedaleops campi -
Appendix B

Autapomorphies included in the Bayesian analysis of pelycosaurian-grade synapsids. Some of these autapomorphies represent specific characteristics within an already existing character. In these cases the relevant character was altered in the Bayesian analysis by adding an extra character state, and the autapomorphous taxon is the only taxon scored with this state. Such characters are noted below. In all other cases, an extra character was added to represent the autapomorphy, with the autapomorphous taxon coded as character state 1 and all others as character state 0, or “?” if the feature is not preserved.

*Oedaleops campi* – Parietal excludes postparietal from the posterior edge of the skull table (Reisz et al. 2009)

*Eothyris parkeyi* – No precanine teeth in maxilla (Reisz et al. 2009) (requires modification of character 32)

*Ennatosaurus tecton* – narrow parasphenoid body (Maddin et al. 2008)
  – two large conical premaxillary teeth (Maddin et al. 2008)
  – 5-7 apical serrations on marginal teeth arranged longitudinally
    (Maddin et al. 2008) (requires modification of character 44)

*Ianthasaurus hardestiorum* – elongate cross-barred dorsal process on axis (Reisz & Berman 1986)
  – at least 29 presacral vertebrae (requires modification of character 148) (Reisz & Berman 1986)
  – maximum of 8 lateral tubercles on each side of the neural spine
    (Reisz & Berman 1986)
  – proximal tubercles with ventral webbing (Reisz & Berman 1986)
  – lateral tubercles lacking on posterior neural spines (or modify character 169) (Reisz & Berman 1986)

*Glaucosaurus megalops* – prearticular extends to the jaw symphysis (Modesto 1994)
  – septomaxilla exposed facially (also in *Haptodus, Varanodon* and *Varanosaurus* and therapsids) (Modesto 1994)
*Edaphosaurus boanerges* – pterygoid tooth plate with 120-150 teeth (Modesto 1995)
  – deeply excavated dorsal jaw symphysis (Modesto 1995)
  – slender lateral tubercles (Modesto 1995)

*Lupeosaurus kayi* – transverse processes located high on the centrum (Sumida 1989)

*Edaphosaurus novomexicanus* – anisodont tooth plate (Modesto & Reisz 1992)
  – reduced number of lateral tubercles on anterior presacral neural spines (Modesto & Reisz 1992)

*Varanosaurus acutirostris* – step-like expansion of the ventral margin of the anterior maxilla (Berman 1995)
  – lateral and dorsal surface of snout separated by a sharp ridge (Berman 1995)
  – dorsal process of the premaxilla bifurcated (Berman 1995)
  – septomaxilla exposed facially (also in *Haptodus, Varanodon* and *Glaucosaurus*) (Berman 1995)
  – Posterior process of jugal dorsoventrally narrow (also in *Secodontosaurus*) (Berman 1995)
  – middorsal margin of the quadratojugal forms the lateral wall of a narrow, shallow, trough-like channel that is bounded medially by the jugal and opens dorsally (Berman 1995)
  – up to 56 maxillary teeth (requires modification of character 29) (Berman 1995)
  – basipterygoid fits into socket in the posteromedial flange of the quadrate ramus of the pterygoid (Berman 1995)
  – cultriform process long and narrow, reaches posterior boarder of the internal naris (Berman 1995)
  – cultriform process supported along its length by anterior ramus of pterygoid (Berman 1995)
  – dorsal process of stapes projects at right angle from the shaft (Berman 1995)
**Haptodus garnettensis** – nasal overlaps tongue-like process of lacrimal (Currie 1977)
- notched supratemporal (Laurin 1993)
- robust, chisel-shaped teeth (requires modification of character 40) (Laurin 1993)
- teeth on palatal ramus of the premaxilla (Laurin 1993)
- septomaxilla exposed facially (also in *Varanosaurus*, *Varanodon* and *Glaucosaurus*)

**Secodontosaurus obtusidens** – skull roof elements thin (Reisz et al. 1992)
- parietal contributes to dorsal margin of the temporal fenestra (Reisz et al. 1992)
- poorly developed supracanine buttress (requires modification of character 37) (Reisz et al. 1992)
- Posterolateral wing of parietal reduced and directed posteriorly (Reisz et al. 1992)
- Postparietal covers large area of supraoccipital (Reisz et al. 1992)
- reduction of dorsal and lateral processes of supraoccipital (Reisz et al. 1992)
- reduction of lateral exposure of prefrontal (Reisz et al. 1992)
- posterior ramus of jugal dorsoventrally narrow (also in *Varanosaurus*) (Reisz et al. 1992)
- transverse flange of pterygoid reduced in width (Reisz et al. 1992)
- Palatal exposure of palatine, vomer and ectopterygoid reduced (Reisz et al. 1992)
- dorsal process of quadrate tilted anterodorsally (Reisz et al. 1992)
- lateral condyle of quadrate extends beyond lateral edge of skull roof (Reisz et al. 1992)
- first dentary tooth directed forwards (Reisz et al. 1992)
- retroarticular process widely separated from reflected lamina of angular (Reisz et al. 1992)
Archaeothyris floresnsis – ectepicondyle angled at 85 degrees to the plane of the distal humerus (Reisz 1972)
  – Well developed pubic tubercle (Reisz 1972)

Pyozia mesenensis – contact between quadratojugal and maxilla unexposed laterally
  (Anderson & Reisz 2004)
  – basipterygoid process anteriorly directed (Anderson & Reisz 2004)
  – interpterygoid vacuity rounded anteriorly (Anderson & Reisz 2004)

Heleosaurus scholtzi – straight suture between premaxilla and nasal (Botha Brink & Modesto 2009)
  – ornamented angular and surangular (Botha Brink & Modesto 2009)

Varanops brevirostris – maxilla dorsal process has anterior and posterior depression of subequal size (Campione & Reisz 2010)
  – postorbital with smooth transition from lateral to dorsal surfaces (Campione & Reisz 2010)
  – basipterygoid process hypertrophies (Campione & Reisz 2010)
  – basipterygoid articular facets elongated mediollaterally (Campione & Reisz 2010)
  – posterior dorsal neural spines taper distally in lateral view (Campione & Reisz 2010)
  – presence of anterolateral excavation of femur proximal to fourth trochanter (Campione & Reisz 2010)

Archaeovenator hamiltonenesis – medial process of postorbital underlying parietal (Reisz & Dilkes 2003)
  – broadly expanded nasal process of premaxilla (Reisz & Dilkes 2003)

Watongia meieri – radius strongly curved (Reisz & Laurin 2004)
  – enlarged pisiform (Reisz & Laurin 2004)
  – reduced head of clavicle (Reisz & Laurin 2004)
**Mesenosaurus romeri** – premaxilla slender, forming a narrow rectangular snout in dorsal view (Reisz & Berman 2001)
- long dorsal process of premaxilla forms anterior half of dorsal margin of the external naris (Reisz & Berman 2001)
- lateral surface of premaxilla excavated, narrowing the base of the dorsal process and expanding the narial shelf to extend nearly to the snout tip (Reisz & Berman 2001)
- palatal process of premaxilla with elongated median suture (Reisz & Berman 2001)
- well-developed depression in the lateral surface of the nasal extending from narial border to the anterior end of the prefrontal (Reisz & Berman 2001)
- slight lateral swelling of the maxilla above the canine (also in
  - first premaxillary tooth shorter than second and third (Reisz & Berman 2001)
  - Vomerine teeth form a single median tooth row (Reisz & Berman 2001)
  - Postorbital bar with nearly vertical posterior margin (Reisz & Berman 2001)
- stapes rod-like with expanded quadrate process (requires modification of character 94) (Reisz & Berman 2001)

**Varanodon agilis** – suspensorium far posterior, well back of occipital condyle (Olson 1965)
- well-developed antorbital fenestra (Olson 1965)
- fourth manual digit elongated and robust (Olson 1965)
- septomaxilla exposed facially (also in *Haptodus, Varanosaurus* and *Glaucosaurus*)

**Ruthiromia elcobriensis** – posterior dorsal centra pinched laterally (hourglass shape in cross section) (Brinkman & Eberth 1983)

**Aerosaurus greenleeorum** – proximal face of deltopectoral crest on the humerus is a large triangular area (Romer 1937)
**Cotylorhynchus hancocki** – epicondyle of humerus broad, thin and platelike (Olson & Beerbower 1953)

– attachment of M. pectoralis forms broad concave triangle that flare to form a shelf-like ridge over surface of area of attachment of M. coracobrachialis and M. brachialis (Olson & Beerbower 1953)

– first sacral rib greatly enlarged (Olson 1962)

**Cotylorhynchus bransoni** – astragulus with large foramen (Olson & Barghusen 1962)

**Caseiopsis agilis** – deepened acetabulum (Olson 1962)

– thickened pubis (Olson 1962)

**Angelosaurus dolani** – Femur with internal trochanter and ridge extending to proximal end of intertrochantric fossa (Olson 1962)

**Mycterosaurus longiceps** – anterior ridge bordering intertrochateric fossa extends proximally nearly to the end of the femur (Berman & Reisz 1982)

**Casea broili** – supratemporal and tabular overhang squamosal to form a small but distinct notch (Olson 1968)

– posterior tuber on the parasphenoid (Olson 1968)

– basipterygoid process forms two laterally projecting spurs (Olson 1968)

– basicranial articulation is mobile (Olson 1968)

– palatal teeth separated by deep grooves (Olson 1968)

– absence of stapedial foramen (Olson 1968)

– dorsal processs of stapes positioned more distally (Olson 1968)

– quadrate articulation of the side of the stapes (Olson 1968)

**Euromycter rutenus** – expanded temporal fenestra (Reisz et al. 2011)

– supernumerary blade-like intranarial bone located posteromedially to the septomaxilla (Olson 1954)
Casea nicholsi – shafts of ribs expanded from the twelfth vertebra to the sacrum (Olson 1954)

Angelosaurus romeri – sacral ribs blade-like (Olson & Barghusen 1962)
  – sacral ribs separated at articulation with ilium (Olson & Barghusen 1962)

Lupeosaurus kayi – strong posterior curvature of dorsal blade of scapula (Romer & Price 1940)
  – ilium incised to receive sacral ribs (Romer & Price 1940)
  – articular surface of sacral ribs concave (Romer & Price 1940)
  – Puboischiadic plate broadened dorsoventrally (Romer & Price 1940)

Ianthodon schultzei – lingual fluting on marginal dentition (Kissel & Reisz 2004)
  – anterior dorsal bulging of lacrimal (Kissel & Reisz 2004)

Cutleria wilmarthi – jugal-squamosal suture is anteriorly concave

Pantelosaurus saxonicus – Posterior end of the dentary well below posterior edge of the jaw

Ctenorhachis jacksoni – tapering tips of neural spines (requires modification of character 166) (Hook & Hotton 1991)
  – posterior neural spines transversely compress posteriorly (Hook & Hotton 1991)

Dimetrodon – Level of jaw articulation below dentary tooth row (Brink & Reisz 2014)

Stereophallodon ciscoensis – labial surface of maxilla extends down almost covering the postcanine dentition (Romer & Price 1940)
  – dorsal centra subrectangular in cross section (Brinkman & Eberth 1986)
  – lumbar vertebrae trefoil-shaped in cross section (Brinkman & Eberth 1986)
  – proximal fibula triangular (Brinkman & Eberth 1986)
*Ophiacodon* – Canines do not project laterally from the tooth row (Romer & Price 1940)
  – Secondary adductor ridge on femur (Romer & Price 1940)

*Apsisaurus witteri* – anteroposteriorly elongate neural spines (Reisz et al. 2010)
  – ovoid suborbital fenestra (Laurin 1999)
  – interclavicle head broadened (Laurin 1991)

“*Mycterosaurus*” *smithae* – posterior process of the maxilla extends beyond the posterior margin of the temporal fenestra (observed)
### Appendix C

List of synapsid taxa used in the diversity estimates, their age ranges and provenance.

<table>
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<th>Genus</th>
<th>Species</th>
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<th>Age range (localities of uncertain age restricted to two or less time bins)</th>
<th>Country of origin</th>
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**Varanopidae**

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**Sphenacodontidae**

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<td>Age</td>
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Appendix D

A list of all specimens of pelycosaurian-grade synapsids incorporated into the analysis of the completeness of specimens

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Number</th>
<th>Affinities</th>
<th>Locality</th>
<th>Stage</th>
<th>Material</th>
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<td>Archaeothyris</td>
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<td>MCZ 4079</td>
<td>Ophiacodontidae</td>
<td>Florence, Nova Soctia</td>
<td>Late Moscovian</td>
<td>Partial skull, several vertebrae, humerus, cervical ribs</td>
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<td>Late Moscovian</td>
<td>Pelvis, sacral vertebra, axis</td>
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<td>florensis</td>
<td>MCZ 4081</td>
<td>Ophiacodontidae</td>
<td>Florence, Nova Soctia</td>
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<td>Caudal vertebra</td>
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<td>florensis</td>
<td>MCZ 4082</td>
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<td>Anterior dorsal vertebra</td>
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<td>Florence, Nova Soctia</td>
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<td>Ophiacodontidae</td>
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<td>Late Moscovian</td>
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<td>Florence, Nova Soctia</td>
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<td>Maxilla, dentary, presacral and caudal vertebrae, interclacivle, calcaneum</td>
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<td>MCZ 4091</td>
<td>Ophiacodontidae (?)</td>
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<td>Almost complete interclavicle, vertebral material</td>
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<td>Ophiacodontidae</td>
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<td>mccordi</td>
<td>FM PR 703</td>
<td>Sphenacodontidae (?), Varanopidae (?)</td>
<td>Newton locality, Jasper County, Illinois</td>
<td>Kazimovian</td>
<td>A presacral rib</td>
</tr>
<tr>
<td>Milosaurus</td>
<td>mccordi</td>
<td>FM PR 704</td>
<td>Sphenacodontidae (?), Varanopidae (?)</td>
<td>Newton locality, Jasper County, Illinois</td>
<td>Kazimovian</td>
<td>A lumbar vertebra</td>
</tr>
<tr>
<td>Milosaurus</td>
<td>mccordi</td>
<td>FM PR 705</td>
<td>Sphenacodontidae (?), Varanopidae (?)</td>
<td>Newton locality, Jasper County, Illinois</td>
<td>Kazimovian</td>
<td>A lumbar or dorsal nural spine</td>
</tr>
<tr>
<td>Haptodus</td>
<td>baylei</td>
<td>Geologisches Landesmuseum, Berlin</td>
<td>Sphenacodontia,</td>
<td>Nowa Ruda, Lower Silesia</td>
<td>Kasimovian-Gzhelian</td>
<td>Nearly complete skeleton</td>
</tr>
<tr>
<td>Xyrospondylus</td>
<td>ecordi</td>
<td>KUVP 9963</td>
<td>Pelycosaurs</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Posterior cervical vertebra</td>
</tr>
<tr>
<td>Haptodus</td>
<td>garnettensis</td>
<td>RM 14,156</td>
<td>Sphenacodontia,</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Partially articulated skeleton</td>
</tr>
<tr>
<td><strong>Haptodus</strong></td>
<td><strong>garnettensis</strong></td>
<td><strong>RM 14,157</strong></td>
<td><strong>Sphenacodontia, Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</strong></td>
<td><strong>Late Kazimovian</strong></td>
<td><strong>Partial skull</strong></td>
<td></td>
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</tr>
<tr>
<td><strong>Haptodus</strong></td>
<td><strong>garnettensis</strong></td>
<td><strong>RM 14,158</strong></td>
<td><strong>Sphenacodontia, Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</strong></td>
<td><strong>Late Kazimovian</strong></td>
<td><strong>Distal lower jaw</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Haptodus</strong></td>
<td><strong>garnettensis</strong></td>
<td><strong>RM 14,159</strong></td>
<td><strong>Sphenacodontia, Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</strong></td>
<td><strong>Late Kazimovian</strong></td>
<td><strong>Femur, tibia, fibula and tarsus</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Haptodus</strong></td>
<td><strong>garnettensis</strong></td>
<td><strong>RM 14,162</strong></td>
<td><strong>Sphenacodontia, Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</strong></td>
<td><strong>Late Kazimovian</strong></td>
<td><strong>Quadrate process of the pterygoid</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Haptodus</strong></td>
<td><strong>garnettensis</strong></td>
<td><strong>RM 14,223</strong></td>
<td><strong>Sphenacodontia, Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</strong></td>
<td><strong>Late Kazimovian</strong></td>
<td><strong>Ischium, neural arch</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Ianthosaurus</strong></td>
<td><strong>hardestiorum</strong></td>
<td><strong>KUVP 69035</strong></td>
<td><strong>Edaphosauridae, Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</strong></td>
<td><strong>Late Kazimovian</strong></td>
<td><strong>Portions of the cranial, axial and appendicular skeleton, including a nearly complete articulate series of 27 presacral neural arches</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Ianthosaurus</strong></td>
<td><strong>hardestiorum</strong></td>
<td><strong>ROM 29940</strong></td>
<td><strong>Edaphosauridae, Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</strong></td>
<td><strong>Late Kazimovian</strong></td>
<td><strong>Partial dorsal neural arch with nearly complete neural spine, 1st sacral, 7 caudal ribs</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Ianthosaurus</strong></td>
<td><strong>hardestiorum</strong></td>
<td><strong>ROM 29941</strong></td>
<td><strong>Edaphosauridae, Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</strong></td>
<td><strong>Late Kazimovian</strong></td>
<td><strong>1 cervical vertebra, one dorsal vertebra with right rib, 1 lumbar vertebra with attached rib</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Ianthosaurus</strong></td>
<td><strong>hardestiorum</strong></td>
<td><strong>ROM 29942</strong></td>
<td><strong>Edaphosauridae, Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</strong></td>
<td><strong>Late Kazimovian</strong></td>
<td><strong>Disarticulated and scattered elements of the skull and postcranial skeleton</strong></td>
<td></td>
</tr>
<tr>
<td><em>Ianthosaurus</em> hardestiorum</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>ROM 37751</td>
<td>ROM 59933</td>
<td>CM 34449</td>
<td>CM 34500</td>
<td>CM 34576</td>
<td>CM 34577</td>
<td>CM 34578</td>
</tr>
<tr>
<td>Ianthosaurus hardestiorum</td>
<td>ROM 37751</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Articulated skeleton</td>
<td></td>
</tr>
<tr>
<td>Ianthosaurus hardestiorum</td>
<td>ROM 59933</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Left maxilla quadrate, postorbital, pterygoid, mandibular ramus, 7 presacral vertebrae, 4 caudal vertebrae, 8 ribs, 7 phalanges</td>
<td></td>
</tr>
<tr>
<td>Ianthosaurus hardestiorum</td>
<td>CM 34449</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Partial right maxilla</td>
<td></td>
</tr>
<tr>
<td>Ianthosaurus hardestiorum</td>
<td>CM 34500</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Partial neural spine</td>
<td></td>
</tr>
<tr>
<td>Ianthosaurus hardestiorum</td>
<td>CM 34576</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Partial neural spine</td>
<td></td>
</tr>
<tr>
<td>Ianthosaurus hardestiorum</td>
<td>CM 34577</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Dorsal vertebra and base of neural spine</td>
<td></td>
</tr>
<tr>
<td>Ianthosaurus hardestiorum</td>
<td>CM 34578</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Dorsal portion of right scapula blade</td>
<td></td>
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<tr>
<td>Ianthosaurus hardestiorum</td>
<td>CM 34579</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Left femur</td>
<td></td>
</tr>
<tr>
<td>Ianthosaurus hardestiorum</td>
<td>CM 34580</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Left astragulus</td>
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</tr>
<tr>
<td>Genus</td>
<td>Species</td>
<td>Catalogue Number</td>
<td>Family</td>
<td>Location Details</td>
<td>Age</td>
<td>Description</td>
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<tr>
<td><em>Ianthosaurus</em></td>
<td><em>hardestiorum</em></td>
<td>CM 34581</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Partial right femur</td>
</tr>
<tr>
<td><em>Ianthosaurus</em></td>
<td><em>hardestiorum</em></td>
<td>CM 47700</td>
<td>Edaphosauridae</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Centra and neural spines</td>
</tr>
<tr>
<td><em>Ianthodon</em></td>
<td><em>schultzei</em></td>
<td>KUVP 133735</td>
<td>Sphenacodontida</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Nearly complete skull roof</td>
</tr>
<tr>
<td><em>Ianthodon</em></td>
<td><em>schultzei</em></td>
<td>KUVP 133736</td>
<td>Sphenacodontida</td>
<td>Garnett Quarry, 10km north of Garnett, Anderson County, Kansas</td>
<td>Late Kazimovian</td>
<td>Left maxilla</td>
</tr>
<tr>
<td><em>Clepsydrops</em></td>
<td>(?) <em>magnus</em></td>
<td>CMNH 13942</td>
<td>Ophiacodontida</td>
<td>McKnight Road at junction with Brown, Kounova, 35 miles northwest of Prague</td>
<td>Late Kasimovian-Early Gzhelian</td>
<td>Distal right humerus, proximal right scapula, proximal left ulna</td>
</tr>
<tr>
<td><em>Macromerion</em></td>
<td>(?) <em>schwarzenbergii</em></td>
<td></td>
<td>Sphenacodontida</td>
<td>Kounova, 35 miles northwest of Prague</td>
<td>Late Kazimovian-Early Gzhelian</td>
<td>Right maxilla,frontals, fragments of prefrontals and postfrontals, left pelvic girdle</td>
</tr>
<tr>
<td><em>Edaphosaurus</em></td>
<td>(?) <em>mirabilis</em></td>
<td>Praha Museum</td>
<td>Edaphosauridae</td>
<td>Kounova, 35 miles northwest of Prague</td>
<td>Late Kazimovian-Early Gzhelian</td>
<td>Fragment of a dorsal vertebra, with the centrum and a fragment of the neural spine</td>
</tr>
<tr>
<td><em>Archaeovenator</em></td>
<td><em>hamiltonensis</em></td>
<td>KUVP 12483</td>
<td>Varanopidae</td>
<td>Hamilton Quarry, near Hamilton, Greenwood County, Kansas</td>
<td>Late Kasimovian - Gzhelian</td>
<td>Nearly complete articulated specimen</td>
</tr>
<tr>
<td><em>Eocasea</em></td>
<td><em>martini</em></td>
<td>KUVP 9616b</td>
<td>Ccaseida</td>
<td>Hamilton Quarry, near Hamilton, Greenwood County, Kansas</td>
<td>Late Kasimovian - Gzhelian</td>
<td>Nearly complete articulated specimen</td>
</tr>
<tr>
<td><em>Ophiacodon</em></td>
<td><em>navajovicus</em></td>
<td>UCLA VP 1627</td>
<td>Ophiacodontida</td>
<td>Platyhystrix pocket, locality, Halgaito Tongue, San Juan County, Utah</td>
<td>Ghezelian</td>
<td>Dorsal vertebra</td>
</tr>
<tr>
<td><em>Ophiacodon</em></td>
<td><em>navajovicus</em></td>
<td>UCLA VP 1628</td>
<td>Ophiacodontida</td>
<td>Platyhystrix pocket, locality, Halgaito Tongue, San Juan County, Utah</td>
<td>Ghezelian</td>
<td>Dorsal vertebra</td>
</tr>
<tr>
<td>Species</td>
<td>Form</td>
<td>Location</td>
<td>Age</td>
<td>Description</td>
<td></td>
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<tr>
<td><strong>Ophiacodon navajovicus</strong></td>
<td>UCLA VP 1629</td>
<td>Ophiacodontidae</td>
<td>Ghezelian</td>
<td>Dorsal vertebra</td>
<td></td>
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<td></td>
<td></td>
<td>Platyhystrix pocket locality, Halgaito Tongue, San Juan County, Utah</td>
<td></td>
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<tr>
<td><strong>Ophiacodon navajovicus</strong></td>
<td>UCLA VP 1630</td>
<td>Ophiacodontidae</td>
<td>Ghezelian</td>
<td>Dorsal vertebra</td>
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<td></td>
<td></td>
<td>Platyhystrix pocket locality, Halgaito Tongue, San Juan County, Utah</td>
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<tr>
<td><strong>Ophiacodon navajovicus</strong></td>
<td>UCLA VP 1631</td>
<td>Ophiacodontidae</td>
<td>Ghezelian</td>
<td>Scapulocoracoid</td>
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<td></td>
<td></td>
<td>Platyhystrix pocket locality, Halgaito Tongue, San Juan County, Utah</td>
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<tr>
<td><strong>Ophiacodon navajovicus</strong></td>
<td>UCLA VP 1632</td>
<td>Ophiacodontidae</td>
<td>Ghezelian</td>
<td>Scapulocoracoid</td>
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<tr>
<td></td>
<td></td>
<td>Platyhystrix pocket locality, Halgaito Tongue, San Juan County, Utah</td>
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</tr>
<tr>
<td><strong>Ophiacodon navajovicus</strong></td>
<td>UCLA VP 1633</td>
<td>Ophiacodontidae</td>
<td>Ghezelian</td>
<td>Scapulocoracoid</td>
<td></td>
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<td></td>
<td></td>
<td>Platyhystrix pocket locality, Halgaito Tongue, San Juan County, Utah</td>
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<tr>
<td><strong>Ophiacodon navajovicus</strong></td>
<td>UCLA VP 1634</td>
<td>Ophiacodontidae</td>
<td>Ghezelian</td>
<td>Scapulocoracoid</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Platyhystrix pocket locality, Halgaito Tongue, San Juan County, Utah</td>
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<tr>
<td><strong>Ophiacodon navajovicus</strong></td>
<td>UCLA VP 1635</td>
<td>Ophiacodontidae</td>
<td>Ghezelian</td>
<td>Distal left humerus</td>
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<td></td>
<td></td>
<td>Platyhystrix pocket locality, Halgaito Tongue, San Juan County, Utah</td>
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<tr>
<td><strong>Aerosaurus greenlecorum</strong></td>
<td>FMNH 464</td>
<td>Varanopidae</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Fragmentary disarticulated postcranial skeleton</td>
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<tr>
<td></td>
<td></td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
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<td></td>
</tr>
<tr>
<td><strong>Ruthiromia elcobriensis</strong></td>
<td>MCZ 3150</td>
<td>Varanopidae</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Articulated partial vertebral column, pelvis and hind limbs, as well as other fragments</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
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<tr>
<td><strong>Nitosaurus jacksonorum</strong></td>
<td>AMNH 4782</td>
<td>Edaphosauridae? Nitosauridae? (Romer &amp; Price 1940); Chimera? (Reisz 1986)</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Fragments of limb and pelvic girdle; two proximal caudal centra, incomplete upper and lower jaws</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td></td>
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<tr>
<td>Species</td>
<td>Specimen</td>
<td>Family</td>
<td>Collection Site</td>
<td>Age Range</td>
<td>Description</td>
<td></td>
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<tr>
<td><em>Baldwinonus</em></td>
<td>trux</td>
<td>Ophiacodontidae</td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Maxilla, articular part of the quadrate, fragments of vertebrae and ribs</td>
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<tr>
<td><em>Sphenacodon</em></td>
<td>ferox</td>
<td>Sphenacodontidae</td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Partial maxilla, quadrate, presacral vertebrae</td>
<td></td>
</tr>
<tr>
<td><em>Ophiacodon</em></td>
<td>navajovicus</td>
<td>Ophiacodontidae</td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Dorsal (43) and caudal (29) vertebrae without spines, 14 neural spines and unguals, Teeth (maxillary and dentary ?), Proximal and distal radii, Humeri, Proximal and distal femora, 1 scapula, Fibulae (1 whole, one no shaft), Proximal and distal tibiae, Atlas/axis complex with spine</td>
<td></td>
</tr>
<tr>
<td><em>Ophiacodon</em></td>
<td>navajovicus</td>
<td>Ophiacodontidae</td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Ilium and acetabulum</td>
<td></td>
</tr>
<tr>
<td><em>Ophiacodon</em></td>
<td>navajovicus</td>
<td>Ophiacodontidae</td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Vertebrae</td>
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<tr>
<td><em>Ophiacodon</em></td>
<td>navajovicus</td>
<td>Ophiacodontidae</td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Manus: distal carpals, medial and proximal, metacarpals of digits 1-4, Phalanx 1 of digit 1-3, Phalanx 2 of 1 and 2, Ungula of 1, 2 and 5</td>
<td></td>
</tr>
<tr>
<td><em>Ophiacodon</em></td>
<td>navajovicus</td>
<td>Ophiacodontidae</td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Partial manus</td>
<td></td>
</tr>
<tr>
<td><em>Ophiacodon</em></td>
<td>navajovicus</td>
<td>Ophiacodontidae</td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Femur</td>
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<tr>
<td><em>Ophiacodon</em></td>
<td>navajovicus</td>
<td>Ophiacodontidae</td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Caudal centrum, cervical centrum Thoracic centrum, humerus, proximal humerus, fragment of proximal ischium</td>
<td></td>
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<tr>
<td><strong>Ophiacodon</strong></td>
<td><strong>navajovicus</strong></td>
<td><strong>AMNH 4781</strong></td>
<td><strong>Ophiacodontidae</strong></td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
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<td><strong>Ophiacodon</strong></td>
<td><strong>navajovicus</strong></td>
<td><strong>AMNH 4783</strong></td>
<td><strong>Ophiacodontidae</strong></td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
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<td><strong>WM 1101</strong></td>
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<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
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<td>Isolated fragments</td>
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<td><strong>navajovicus</strong></td>
<td><strong>YP 1383</strong></td>
<td><strong>Ophiacodontidae</strong></td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
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<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
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<td>Distal left humerus, calcaneum and astragulus, left carpus, left femur, pubis, axis spine, dorsal spine, right humerus, 2 dorsal vertebrae and spines, distal tibia and fibula</td>
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<tr>
<td><strong>Edaphosaurus</strong></td>
<td><strong>novomexicus</strong></td>
<td><strong>UCLA VP 1641</strong> (Transferred to CMNH? Berman et al 1993)</td>
<td><strong>Edaphosauridae</strong></td>
<td>El Cobre Canyon, near Abiquiu, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Several incomplete neural spines</td>
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<td><em>wellesi</em></td>
<td>UCMP 35762</td>
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<td>Ghezelian-Early Sakmarian</td>
<td>Isolated brain case</td>
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<td><em>wellesi</em></td>
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<td>Fragmentary disarticulated remains</td>
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<tr>
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<td><em>wellesi</em></td>
<td>UCMP 40095</td>
<td>Varanopidae</td>
<td>Camp Quarry, 440m south of New Mexico State Highway, 840m southeast of Rio Puerco Bridge at Arroyo del Agua, Rio Arriba County, New Mexico</td>
<td>Ghezelian-Early Sakmarian</td>
<td>Fragmentary disarticulated remains</td>
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<td>Ghezelian-Early Sakmarian</td>
<td>Nearly complete articulated specimen</td>
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<td>Eothyrididae</td>
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<td>Ghezelian-Early Sakmarian</td>
<td>Skull, missing palatals, braincase and some facial elements</td>
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<td>campi</td>
<td>UCMP 40095</td>
<td>Eothyrididae</td>
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<td>Ghezelian-Early Sakmarian</td>
<td>Isolated dentary bones</td>
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<td><strong>Species</strong></td>
<td><strong>Catalog Number</strong></td>
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<td><strong>Condition</strong></td>
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<td>Ghezelian-Early Sakmarian</td>
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<td>Ghezelian-Early Sakmarian</td>
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<td>Anderson quarry, Rio Arriba County, New Mexico</td>
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<td>Sphenacodontidae</td>
<td>Quarry Butte, Rio Arriba County, New Mexico</td>
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<td>Ophiacodontidae</td>
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<td>Miller Bonebed, Rio Arriba County, New Mexico</td>
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<td>OMNH 55210</td>
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<td>Right radius</td>
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<td>OMNH 55224</td>
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<td>Ophiacodon</td>
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<td>OMNH 55241</td>
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<td>OMNH V1005, North of the Canadian River, Seminole County, Oklahoma</td>
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<td>OMNH 55244</td>
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<td>OMNH 55252</td>
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<td>OMNH V1005, North of the Canadian River, Seminole County, Oklahoma</td>
<td>Late Gzhelian</td>
<td>Articulated series of 27 distal caudal vertebrae</td>
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<td>Specimen</td>
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<td>OMNH 55253</td>
<td>Ophiacodontidae</td>
<td>OMNH V1005, North of the Canadian River Seminole County, Oklahoma</td>
<td>Late Gzhelian</td>
<td>Articulated series of 4 lumbar vertebrae, lacking intercentra</td>
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<td>OMNH 55254</td>
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<td>OMNH V1005, North of the Canadian River Seminole County, Oklahoma</td>
<td>Late Gzhelian</td>
<td>Articulated series of 5 lumbar vertebrae</td>
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<td>Cervical vertebra</td>
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<td>Late Gzhelian</td>
<td>Dorsal vertebra, incomplete above the level of the transverse process</td>
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<td>Articulated series of 3 dorsal vertebrae, lacking neural arch above the transverse process</td>
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<td>Ophiacodontidae</td>
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<td>Late Gzhelian</td>
<td>Centrum of proximal caudal vertebra</td>
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<th>Age</th>
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<td>Koenigin-Carola-Schacht, Dohlen Basin, near Dresden Asselian 6 nearly complete skeletons</td>
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<td><em>cynodus</em></td>
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<td>Besancon, Moissey, Department of Jura Asselian-early Samarkian Left maxilla</td>
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<td>4 articulated mid-dorsal vertebrae, with 2 neural spines and 3 left ribs, scattered partial vertebrae and ribs</td>
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<td>Caseidae</td>
<td>Colline du Cayla, 1km west of the village of Saint-Christophe-Vallon, commune of Valady, Aveyron</td>
<td>Anterior postcranial skeleton</td>
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<td>Euromycter</td>
<td>rutena</td>
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<td>Caseidae</td>
<td>Colline du Cayla, 1km west of the village of Saint-Christophe-Vallon, commune of Valady, Aveyron</td>
<td>Complete skull, lower jaw, hyoid apparatus, six cervical vertebrae in articulation, posterior coracoid, clavicle, interclavicle, distal head of right humerus, radius, ulna, manus</td>
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<td>South of Fulda, north side of Godwin Creek</td>
<td>Early Kungurian</td>
<td>Femur</td>
</tr>
<tr>
<td><em>Dimetrodon</em></td>
<td>booneorum</td>
<td>WM 788</td>
<td>Sphenacodontidae</td>
<td>South of Fulda, north side of Godwin Creek</td>
<td>Early Kungurian</td>
<td>Femur</td>
</tr>
<tr>
<td><em>Ophiacodon</em></td>
<td>uniformis</td>
<td>MCZ 1443</td>
<td>Ophiacodontidae</td>
<td>Belle Plains, north of Godwin Creek, Baylor County, Texas</td>
<td>Early Kungurian</td>
<td>Tibia</td>
</tr>
<tr>
<td><em>Dimetrodon</em></td>
<td>natalis</td>
<td>MCZ</td>
<td>Sphenacodontidae</td>
<td>Military Crossing, north of Fulda, Texas</td>
<td>Early Kungurian</td>
<td></td>
</tr>
<tr>
<td><em>Dimetrodon</em></td>
<td>limbatus</td>
<td>WM 152</td>
<td>Sphenacodontidae</td>
<td>North of Fulda, east Baylor County, Texas</td>
<td>Early Kungurian</td>
<td>Scapulocoracoid</td>
</tr>
<tr>
<td><em>Ophiacodon</em></td>
<td>retroversus</td>
<td>MCZ 1204</td>
<td>Ophiacodontidae</td>
<td>North of Fulda, east Baylor County, Texas</td>
<td>Early Kungurian</td>
<td>Partial skeleton</td>
</tr>
<tr>
<td>Genus</td>
<td>Species</td>
<td>Specimen ID</td>
<td>Family</td>
<td>Location Description</td>
<td>Time Interval</td>
<td>Remarks</td>
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</tr>
<tr>
<td>Dimetrodon</td>
<td>dollovianus</td>
<td>WM 461</td>
<td>Sphenacodontidae</td>
<td>South of Electra, Western Wichita County, Texas</td>
<td>Early Kungurian</td>
<td>Intraclavicle</td>
</tr>
<tr>
<td>Edaphosaurus</td>
<td>cruciger (?)</td>
<td>Elmo, Kansas</td>
<td>Edaphosauridae</td>
<td>Early Kungurian</td>
<td></td>
<td>Fragments</td>
</tr>
<tr>
<td>Varanodon</td>
<td>acutirostris</td>
<td>FMNH PR 1760</td>
<td>Ophiacodontidae</td>
<td>South Pauls Valley Locality, Garvin County, Oklahoma</td>
<td>Early Kungurian</td>
<td>Nearly complete skull with atlas and axis attached</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>limbatas (?)</td>
<td>Waurika, Oklahoma</td>
<td>Sphenacodontidae</td>
<td>Waurika, Oklahoma</td>
<td>Early Kungurian</td>
<td>Fragments</td>
</tr>
<tr>
<td>Edaphosaurus</td>
<td>pogonias</td>
<td>Edaphosauridae</td>
<td>Edaphosauridae</td>
<td>Waurika, Oklahoma</td>
<td>Early Kungurian</td>
<td></td>
</tr>
<tr>
<td>Glaucosaurus</td>
<td>megalops</td>
<td>Coal Creek, Baylor County, Texas</td>
<td>Edaphosauridae</td>
<td></td>
<td>Early Kungurian</td>
<td></td>
</tr>
<tr>
<td>Glaucosaurus</td>
<td>megalops</td>
<td>Mitchell Creek, Northeast of Maybelle, Baylor County, Texas</td>
<td>Edaphosauridae</td>
<td></td>
<td>Kungurian</td>
<td>Skull, without roof and lower posterior portion</td>
</tr>
<tr>
<td>Varanodon</td>
<td>Witchitaensis</td>
<td>Mitchell Creek, Northeast of Maybelle, Baylor County, Texas</td>
<td>Ophiacodontidae</td>
<td></td>
<td>Kungurian</td>
<td>Scapula blade, distal humerus, distal femur, proximal tibia and fibula</td>
</tr>
<tr>
<td>Mycterosaurus</td>
<td>longiceps</td>
<td>AMNH 7002</td>
<td>Varanopidae</td>
<td>Mitchell Creek, Northeast of Maybelle, Baylor County, Texas</td>
<td>Kungurian</td>
<td>Nearly complete skull, scapulae, forelimbs, Pelvis, hindlimbs, vertebrae</td>
</tr>
<tr>
<td>Mycterosaurus</td>
<td>longiceps</td>
<td>FMNH UC 692</td>
<td>Varanopidae</td>
<td>Mitchell Creek, Northeast of Maybelle, Baylor County, Texas</td>
<td>Kungurian</td>
<td>Nearly complete skull, few postcranial fragments</td>
</tr>
<tr>
<td>Mycterosaurus</td>
<td>longiceps</td>
<td>FMNH UC 169</td>
<td>Varanopidae</td>
<td>Mitchell Creek, Northeast of Maybelle, Baylor County, Texas</td>
<td>Kungurian</td>
<td>Partial skull and postcranial remains</td>
</tr>
<tr>
<td>Mycterosaurus</td>
<td>longiceps</td>
<td>WM</td>
<td>Varanopidae</td>
<td>Mitchell Creek, Northeast of Maybelle, Baylor County, Texas</td>
<td>Kungurian</td>
<td>Pelvis, scapulocoracoid</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>dollovianus</td>
<td>WM 1201</td>
<td>Sphenacodontidae</td>
<td>Moonshine Creek, Bayor County, Texas</td>
<td>Kungurian</td>
<td>Radius ulna, partial carpus, tarsus</td>
</tr>
<tr>
<td>Edaphosaurus</td>
<td>cruciger</td>
<td>FMNH UC 658</td>
<td>Edaphosauridae</td>
<td>Moonshine Creek, Bayor County, Texas</td>
<td>Kungurian</td>
<td>Skull</td>
</tr>
<tr>
<td><strong>Ophiacodon major</strong></td>
<td>AM</td>
<td>Ophiacodontidae</td>
<td>Military Trail 32, Baylor County, Texas</td>
<td>Kungurian</td>
<td>Ilium</td>
<td></td>
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</tr>
<tr>
<td><strong>Dimetrodon limbatus</strong></td>
<td>AMNH 4001</td>
<td>Sphenacodontidae</td>
<td>Military Trail 32, Baylor County, Texas</td>
<td>Kungurian</td>
<td>Skull elements, pelvis, femur</td>
<td></td>
</tr>
<tr>
<td><strong>Secodontosaurus obtusidens</strong></td>
<td>WM 690</td>
<td>Sphenacodontidae</td>
<td>Military Trail 32, Baylor County, Texas</td>
<td>Kungurian</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Ophiacodon uniformis</strong></td>
<td>WM 690</td>
<td>Ophiacodontidae</td>
<td>Maybell, Baylor County, Texas</td>
<td>Kungurian</td>
<td>Skeleton in ventral view</td>
<td></td>
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<tr>
<td><strong>Ophiacodon major</strong></td>
<td>AM 4109</td>
<td>Ophiacodontidae</td>
<td>Maybell, Baylor County, Texas</td>
<td>Kungurian</td>
<td>10 vertebrae</td>
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<tr>
<td><strong>Dimetrodon macropodylus</strong></td>
<td>AMNH 4055</td>
<td>Sphenacodontidae</td>
<td>Deep Red Run</td>
<td>Late Kungurian</td>
<td>Axis, humerus</td>
<td></td>
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<tr>
<td><strong>Dimetrodon macropodylus</strong></td>
<td>AMNH 4065</td>
<td>Sphenacodontidae</td>
<td>Deep Red Run</td>
<td>Late Kungurian</td>
<td>Part of the axis and third cervical, 4 posterior dorsal and 2 lumbar vertebrae, with fragments of neural spines</td>
<td></td>
</tr>
<tr>
<td><strong>Dimetrodon macropodylus</strong></td>
<td>University of Chicago 1019</td>
<td>Sphenacodontidae</td>
<td>Deep Red Run</td>
<td>Late Kungurian</td>
<td>Dorsal vertebrae</td>
<td></td>
</tr>
<tr>
<td><strong>Dimetrodon gigashomogenes</strong></td>
<td>MCZ 1342</td>
<td>Sphenacodontidae</td>
<td>Pond Creek, Oklahoma</td>
<td>Late Kungurian</td>
<td>Vertebrae</td>
<td></td>
</tr>
<tr>
<td><strong>Dimetrodon gigashomogenes</strong></td>
<td>MCZ 1346</td>
<td>Sphenacodontidae</td>
<td>Pond Creek, Oklahoma</td>
<td>Late Kungurian</td>
<td>Scapulocoracoid</td>
<td></td>
</tr>
<tr>
<td><strong>Dimetrodon grandis (?)</strong></td>
<td>UM</td>
<td>Sphenacodontidae</td>
<td>Pond Creek, Oklahoma</td>
<td>Late Kungurian</td>
<td>Fragments</td>
<td></td>
</tr>
<tr>
<td><strong>Varanops brevirostris</strong></td>
<td>TMM 43628-1</td>
<td>Varanopidae</td>
<td>Mud Hill Locality, Southwest of Abilene, Taylor County, Texas</td>
<td>Late Kungurian</td>
<td>Partial skull, complete right and partial left rami of lower jaw, nearly complete series of dorsal vertebrae, 1 sacral vertebra, several caudal vertebrae, gastralia, partial pectroal and pelvic gridles and limbs</td>
<td></td>
</tr>
<tr>
<td><strong>Varanops brevirostris</strong></td>
<td>FMNH UC 644</td>
<td>Varanopidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Nearly complete skeleton</td>
<td></td>
</tr>
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</tr>
<tr>
<td><strong>Varanops brevirostris</strong></td>
<td>FMNH UR 2423</td>
<td>Varanopidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Nearly complete skull and lower jaw, atlas and axis</td>
<td></td>
</tr>
<tr>
<td><strong>Varanops brevirostris</strong></td>
<td>FMNH P 12841</td>
<td>Varanopidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Partial skeleton</td>
<td></td>
</tr>
<tr>
<td><strong>Varanops brevirostris</strong></td>
<td>MCZ 1926</td>
<td>Varanopidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Complete skull and lower jaw, girdle and limb bones</td>
<td></td>
</tr>
<tr>
<td><strong>Casea broilii</strong></td>
<td>FMNH UC 656</td>
<td>Caseidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Skull and skeleton</td>
<td></td>
</tr>
<tr>
<td><strong>Casea broilii</strong></td>
<td>FMNH UC 657</td>
<td>Caseidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Ribs (Williston 1911), Skeleton (Romer &amp; Price 1940), Right pes (Olson 1968)</td>
<td></td>
</tr>
<tr>
<td><strong>Casea broilii</strong></td>
<td>FMNH UC 698</td>
<td>Caseidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Skull</td>
<td></td>
</tr>
<tr>
<td><strong>Casea broilii</strong></td>
<td>FMNH UC 883</td>
<td>Caseidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Most of the presacral vertebrae, three sacral and some caudal vertebrae, pelvis, ribs, limb bones</td>
<td></td>
</tr>
<tr>
<td><strong>Casea broilii</strong></td>
<td>FMNH UC 901</td>
<td>Caseidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Manus, radii, humeri, shoulder girdle, some ribs and vertebrae</td>
<td></td>
</tr>
<tr>
<td><strong>Casea broilii</strong></td>
<td>FMNH UC 1011</td>
<td>Caseidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Basal skull and lower jaws</td>
<td></td>
</tr>
<tr>
<td><strong>Edaphosaurus pogonias</strong></td>
<td>FMNH UC 656</td>
<td>Edaphosauridae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Dimetrodon gigashomogenes</strong></td>
<td>AM 4138</td>
<td>Sphenacodontidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Scapulocoracoid</td>
<td></td>
</tr>
<tr>
<td><strong>Dimetrodon gigashomogenes</strong></td>
<td>AM 4173</td>
<td>Sphenacodontidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Cervical vertebrae</td>
<td></td>
</tr>
<tr>
<td><strong>Dimetrodon grandis</strong></td>
<td>AM 4138</td>
<td>Sphenacodontidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Scapulocoracoid</td>
<td></td>
</tr>
<tr>
<td><strong>Dimetrodon grandis</strong></td>
<td>AM 4173</td>
<td>Sphenacodontidae</td>
<td>Cacops Bonebed, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Cervical vertebrae</td>
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</tr>
<tr>
<td>Genus</td>
<td>Species</td>
<td>Catalog Number</td>
<td>Family</td>
<td>Location</td>
<td>Age</td>
<td>Type</td>
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<tr>
<td>Dimetrodon</td>
<td>loomsi</td>
<td>WM 411</td>
<td>Sphenacodontidae</td>
<td>Poney Creek, east of the Craddock Region</td>
<td>Late Kungurian</td>
<td>Cervical vertebrae</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>loomsi</td>
<td>WM 1140</td>
<td>Sphenacodontidae</td>
<td>Poney Creek, east of the Craddock Region</td>
<td>Late Kungurian</td>
<td>Humerus</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>kempae</td>
<td>WM 1139</td>
<td>Sphenacodontidae</td>
<td>Poney Creek, east of the Craddock Region</td>
<td>Late Kungurian</td>
<td>Humerus</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>gigashomogenes</td>
<td>WM 411</td>
<td>Sphenacodontidae</td>
<td>Poney Creek, east of the Craddock Region</td>
<td>Late Kungurian</td>
<td>Cervical vertebrae</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>WM 1131</td>
<td>Sphenacodontidae</td>
<td>Crooked Creek</td>
<td>Late Kungurian</td>
<td>Postcranial fragments</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>WM 1197</td>
<td>Sphenacodontidae</td>
<td>Crooked Creek</td>
<td>Late Kungurian</td>
<td>Fragments</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>loomsi</td>
<td>WM 214</td>
<td>Sphenacodontidae</td>
<td>Dead Man</td>
<td>Late Kungurian</td>
<td>Partial Skull</td>
</tr>
<tr>
<td>Edaphosaurus</td>
<td>pogonias</td>
<td>WM 1092</td>
<td>Edaphosauridae</td>
<td>Hog Creek, west of Table</td>
<td>Late Kungurian</td>
<td>Femur, tibia, fibula</td>
</tr>
<tr>
<td>Edaphosaurus</td>
<td>pogonias</td>
<td>AM 4015</td>
<td>Edaphosauridae</td>
<td>Hog Creek, west of Table</td>
<td>Late Kungurian</td>
<td>Presacral column, mounted</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>MCZ 1348</td>
<td>Sphenacodontidae</td>
<td>Hog Creek, west of Table</td>
<td>Late Kungurian</td>
<td>Jaw</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>MCZ 1345</td>
<td>Sphenacodontidae</td>
<td>Hog Creek, west of Table</td>
<td>Late Kungurian</td>
<td>Scapulocoracoid</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>loomsi</td>
<td>MCZ 1345</td>
<td>Sphenacodontidae</td>
<td>Hog Creek, west of Table</td>
<td>Late Kungurian</td>
<td>Scapulocoracoid</td>
</tr>
<tr>
<td>Varanosaurus</td>
<td>acutirostris</td>
<td>BSPHM 1901 XV 20</td>
<td>Ophiacodontidae</td>
<td>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Nearly complete skeleton</td>
</tr>
<tr>
<td><strong>Varanosaurus</strong></td>
<td><strong>acutirostris</strong></td>
<td><strong>NM 15562</strong></td>
<td><strong>Ophiacodontidae</strong></td>
<td><strong>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</strong></td>
<td><strong>Late Kungurian</strong></td>
<td><strong>Humerus</strong></td>
</tr>
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<tr>
<td><strong>Varanosaurus</strong></td>
<td><strong>acutirostris</strong></td>
<td><strong>NM 15563</strong></td>
<td><strong>Ophiacodontidae</strong></td>
<td><strong>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</strong></td>
<td><strong>Late Kungurian</strong></td>
<td><strong>Femur</strong></td>
</tr>
<tr>
<td><strong>Varanosaurus</strong></td>
<td><strong>acutirostris</strong></td>
<td><strong>NM 15564</strong></td>
<td><strong>Ophiacodontidae</strong></td>
<td><strong>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</strong></td>
<td><strong>Late Kungurian</strong></td>
<td><strong>Pubis</strong></td>
</tr>
<tr>
<td><strong>Varanosaurus</strong></td>
<td><strong>acutirostris</strong></td>
<td><strong>NM 15565</strong></td>
<td><strong>Ophiacodontidae</strong></td>
<td><strong>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</strong></td>
<td><strong>Late Kungurian</strong></td>
<td><strong>Ischium</strong></td>
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<tr>
<td><strong>Varanosaurus</strong></td>
<td><strong>witchitaensis</strong></td>
<td><strong>MCZ 6379</strong></td>
<td><strong>Ophiacodontidae</strong></td>
<td><strong>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</strong></td>
<td><strong>Late Kungurian</strong></td>
<td><strong>Astragulus, femur</strong></td>
</tr>
<tr>
<td><strong>Secodontosaurus</strong></td>
<td><strong>obtusidens</strong></td>
<td><strong>FMNH 754</strong></td>
<td><strong>Sphenacodontidae</strong></td>
<td><strong>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</strong></td>
<td><strong>Late Kungurian</strong></td>
<td><strong>Maxilla and dentary</strong></td>
</tr>
<tr>
<td><strong>Secodontosaurus</strong></td>
<td><strong>obtusidens</strong></td>
<td><strong>WM 772</strong></td>
<td><strong>Sphenacodontidae</strong></td>
<td><strong>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</strong></td>
<td><strong>Late Kungurian</strong></td>
<td><strong>Clavicle</strong></td>
</tr>
<tr>
<td><strong>Secodontosaurus</strong></td>
<td><strong>obtusidens</strong></td>
<td><strong>WM 1316</strong></td>
<td><strong>Sphenacodontidae</strong></td>
<td><strong>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</strong></td>
<td><strong>Late Kungurian</strong></td>
<td><strong>Scapulocoracoid</strong></td>
</tr>
<tr>
<td>Genus</td>
<td>Species</td>
<td>Specimen</td>
<td>Family</td>
<td>Locality</td>
<td>Age</td>
<td>Description</td>
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</tr>
<tr>
<td>Secodontosaurus</td>
<td>obtusidens</td>
<td>WM 752</td>
<td>Sphenacodontidae</td>
<td>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</td>
<td>Late Kungurian</td>
<td>Partial scapula</td>
</tr>
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<td>Vertebræ</td>
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<td>Dimetrodon, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</td>
<td>Nearly complete skull, lower jaw, vertebrae, ribs, thoracic girdle, humerus, ulna radius, femur tibia and pes</td>
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<td>Dimetrodon</td>
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<td>Femur</td>
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<td>Maxilla</td>
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<td>Radius, ulna</td>
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<td>Hind limb bones</td>
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322
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<th>Sphenacodontidae</th>
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<td>Craddock Bonebed, Brush Creek, Craddock Ranch, North of Seymour, Baylor County, Texas</td>
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<td>Pelvic material</td>
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<td><strong>Trichasaurus</strong></td>
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<td>FMNH UC 652</td>
<td>Caseidae (Romer &amp; Price 1940, Benson in press) (?), Edaphosauridae (Olson 1968) (?)</td>
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<td>Part of the vertebral column, pelvis, limb and foot elements</td>
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<td>Species</td>
<td>Catalog</td>
<td>Age</td>
<td>Location</td>
<td>Part</td>
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<td>MCZ 1117</td>
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<td>Skull, left humerus, scapulocoracoid</td>
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<td>AMNH 4174</td>
<td>Late Kungurian</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Incomplete skeleton, with posterior portion of the skull, thoracic girdle and forelimb missing</td>
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<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Facial portion of the skull</td>
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<td>Edaphosaurus</td>
<td>pogonias</td>
<td>NM 10461</td>
<td>Edaphosauridae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Vertebrae and spines</td>
</tr>
<tr>
<td>Secodontosaurus</td>
<td>obtusidens</td>
<td>WM 1100</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Pelvis and femur</td>
</tr>
<tr>
<td>Secodontosaurus</td>
<td>obtusidens</td>
<td>WM 25</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Pelvis</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>WM 1002</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Skull, most of the presacral column and spines, 14 caudals, scapulocoracoid, hind leg bones</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>UM VIlA</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Skull</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>AM 4036</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Partial skull</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>AM 4033</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Jaw</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>WM 1132</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Partial skull</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>AM 4169</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Dentary and head of ulna</td>
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<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>MCZ 1491</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Skeleton fragments</td>
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<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>AM 4644</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Cervicals, scapulocoracoid, clavice, partial interclavicle</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>grandis</td>
<td>AM 4147</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Axis</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>loomsi</td>
<td>AM 4037</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Fragments of skull and dentary</td>
</tr>
<tr>
<td>Dimetrodon</td>
<td>loomsi</td>
<td>WM 1260</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Fragments of skull and dentary</td>
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<tr>
<td>Dimetrodon</td>
<td>loomsi</td>
<td>WM 423</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Braincase</td>
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<tr>
<td>Dimetrodon</td>
<td>loomsi</td>
<td>WM 114</td>
<td>Sphenacodontidae</td>
<td>Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Skeleton</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>WM 112</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Pelvis, 2 cervical vertebrae, most posterior presacral vertebrae, some caudal vertebrae</td>
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<tr>
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<td>Dimetrodon gigashomogenes</td>
<td>MCZ 1283</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Most of the skeleton</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>WM 1134</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Jaw, braincase and postcranial material</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>AM 4035</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Mounted series of 19 vertebrae with nearly complete neural spines</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>WM 639</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Clavicle and interclavicle</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>MCZ 1340</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Centra, partial shoulder girdle, humerus</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>MCZ 1109</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Coracoid</td>
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<td>Dimetrodon gigashomogenes</td>
<td>WM 30</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Scapulocoracoid</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>YP 661</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Scapulocoracoid</td>
<td></td>
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<td>Dimetrodon gigashomogenes</td>
<td>AM 4149</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Humerus</td>
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<tr>
<td>Specimen</td>
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<td>Catalog Number</td>
<td>Family</td>
<td>Location</td>
<td>Age</td>
<td>Part/Region</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>AM 4037</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Humerus</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>UM 3410</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Femur</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>WM 8</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Femur</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>WM 465</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Pelvis</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>WM 1019</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>3 Lumbar vertebrae</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>Munich</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Pelvis</td>
<td></td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>AM 4103</td>
<td>Sphenacodontidae</td>
<td>Coffee Creek, Baylor/Willbarger County, Texas</td>
<td>Late Kungurian</td>
<td>Interclavicle</td>
<td></td>
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<tr>
<td>Dimetrodon loomsi</td>
<td>FM UR 2333</td>
<td>Sphenacodontidae</td>
<td>South Garfield, Tillman County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Axis</td>
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<tr>
<td>Dimetrodon loomsi</td>
<td>FM UR 2334</td>
<td>Sphenacodontidae</td>
<td>South Garfield, Tillman County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Dorsal vertebra without spine</td>
<td></td>
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<tr>
<td>Dimetrodon loomsi</td>
<td>FM UR 2332</td>
<td>Sphenacodontidae</td>
<td>South Garfield, Tillman County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Spine fragments, teeth, flat pieces of bone</td>
<td></td>
</tr>
<tr>
<td>Cotylorhynchus romeri</td>
<td>OUSM 4-0-S1</td>
<td>Caseidae</td>
<td>Ross Farm, 4.75 miles west of Navina, Logan County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Right side of the skull, portion of the interclavicle, one manus</td>
<td></td>
</tr>
<tr>
<td>Cotylorhynchus romeri</td>
<td>OUSM 4-0-S2</td>
<td>Caseidae</td>
<td>Pierce Farms, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Caudal vertebrae, pelvis, hindlimb</td>
<td></td>
</tr>
<tr>
<td>Specimen</td>
<td>Location</td>
<td>Age</td>
<td>Description</td>
<td></td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Pierce Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Anterior skeleton, first 19 vertebrae, ribs, humeri, scapulae</td>
<td></td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Partial skeleton</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Partial skeleton</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Foot, radius, humerus, tibia, fibula, femur, vertebrae, pelvis</td>
<td></td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Partial skull and lower jaws</td>
<td></td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Skull and jaws</td>
<td></td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Lumbar vertebrae</td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Scapula, humerus, radius, phalanges, foot</td>
<td></td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Fragments</td>
<td></td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Skeleton</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Skeleton lacking skull</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Skeleton lacking skull</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Skeleton lacking skull</td>
<td></td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>Near Norman, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Skeleton lacking skull</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S4</td>
<td>Caseidae</td>
<td>Polk Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>4 1/2 caudal vertebrae, pelvis</td>
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<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S5</td>
<td>Caseidae</td>
<td>Polk Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Radius, ulna, front foot, part of second foot</td>
<td></td>
</tr>
<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S21</td>
<td>Caseidae</td>
<td>Polk Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Mounted skeleton (Stovall museum 1251)</td>
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<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S21</td>
<td>Caseidae</td>
<td>Polk Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Rib, humerus, right pes and manus, part pelvis</td>
<td></td>
</tr>
<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S23</td>
<td>Caseidae</td>
<td>Polk Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Skull</td>
<td></td>
</tr>
<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S2</td>
<td>Caseidae</td>
<td>Polk Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Vertebral column</td>
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</tr>
<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S6</td>
<td>Caseidae</td>
<td>Boggs Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Part of foot</td>
<td></td>
</tr>
<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S10</td>
<td>Caseidae</td>
<td>Boggs Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Skeleton</td>
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<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S11</td>
<td>Caseidae</td>
<td>Boggs Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Foot, tarals, metatarsals, phalanges, 10 ribs, fragments of vertebrae pelvis, femur</td>
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<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S9</td>
<td>Caseidae</td>
<td>SW 1/4 Section 7, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Fragments, ribs</td>
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<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S14</td>
<td>Caseidae</td>
<td>Burton Farm, Oklahoma</td>
<td>Late Kungurian</td>
<td>Ribs, part of foot</td>
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<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S17</td>
<td>Caseidae</td>
<td>Burton Farm, Oklahoma</td>
<td>Late Kungurian</td>
<td>Fragments, mostly ribs</td>
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<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S18</td>
<td>Caseidae</td>
<td>Burgess Farm, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Partial skeleton</td>
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<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S20</td>
<td>Caseidae</td>
<td>South of Cedar Lane Golf Course, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Skull, shoulder girdle, left forelimb, foot</td>
<td></td>
</tr>
<tr>
<td><strong>Cotylorhynchus romeri</strong></td>
<td>OUSM 4-0-S21</td>
<td>Caseidae</td>
<td>South Oklahoma City, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Incomplete skeleton</td>
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<tr>
<td>Animal</td>
<td>Catalog Number</td>
<td>Family</td>
<td>Location Description</td>
<td>Age</td>
<td>Remarks</td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>OUSM 4-0-S24</td>
<td>Caseida</td>
<td>3 miles north of Norman on Highway 77, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Partial skeleton</td>
<td></td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>OUSM 4-0-S26</td>
<td>Caseida</td>
<td>Richardson farm, South of Highway 9, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Partial postcranial skeleton</td>
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<tr>
<td>Cotylorhynchus romeri</td>
<td>OUSM 4-0-S28</td>
<td>Caseida</td>
<td>Noble, Cleveland County, Oklahoma</td>
<td>Late Kungurian</td>
<td>Fragments</td>
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<td>Cotylorhynchus romeri</td>
<td>OUSM 4-1-S3</td>
<td>Caseida</td>
<td>NE 1/4 Section 15</td>
<td>Late Kungurian</td>
<td>Indeterminate bones</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>CNHM UR 123</td>
<td>Sphenacodontida</td>
<td>Locality BZ, Knox County, Texas</td>
<td>Late Kungurian</td>
<td>Maxilla and teeth</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>CNHM UR 30</td>
<td>Sphenacodontida</td>
<td>Locality KF, Knox County, Texas</td>
<td>Late Kungurian</td>
<td>Maxilla and teeth</td>
<td></td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>CMNH UR 33</td>
<td>Sphenacodontida</td>
<td>Locality KD, Knox County, Texas</td>
<td>Late Kungurian</td>
<td>Dorsal vertebrae, femur, skull fragments</td>
<td></td>
</tr>
<tr>
<td>Dimetrodon gigashomogenes</td>
<td>CMNH UR 34</td>
<td>Sphenacodontida</td>
<td>Locality KA, Knox County, Texas</td>
<td>Late Kungurian</td>
<td>Partial vertebral column, cervicals 4 and 5, presacras 20-27, three sacras and one caudal</td>
<td></td>
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<tr>
<td>Casea nicholsi</td>
<td>CNHM UR 85</td>
<td>Caseida</td>
<td>KC Locality, Knox County, Texas</td>
<td>Late Kungurian</td>
<td>Posterior portion of skull, pre-caudal vertebral column, partial shoulder girdle, pelvis, femure, proximal fibula</td>
<td></td>
</tr>
<tr>
<td>Casea nicholsi</td>
<td>CNHM UR 86</td>
<td>Caseida</td>
<td>KC Locality, Knox County, Texas</td>
<td>Late Kungurian</td>
<td>Partial basal skull, lower jaw, pre-caudal column, partial pelvic, forelimb, partial pes</td>
<td></td>
</tr>
<tr>
<td>Dimetrodon gigashomogenes</td>
<td>CMNH UR 128</td>
<td>Sphenacodontida</td>
<td>Locality FA, Foard County, Texas</td>
<td>Late Kungurian</td>
<td>14 vertebrae with spines (7-20), partial skull and lower jaw, pelvis, distal femur, other fragments</td>
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<tr>
<td>Dimetrodon gigashomogenes</td>
<td>CMNH UR 122</td>
<td>Sphenacodontida</td>
<td>Locality FA, Foard County, Texas</td>
<td>Late Kungurian</td>
<td>Dorsal vertebra</td>
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<tr>
<td>Casea halselli</td>
<td>FMNH UR 117</td>
<td>Caseida</td>
<td>FC Locality, Halsell Ranch, Foard County, Texas</td>
<td>Late Kungurian</td>
<td>Pelvic girdle, partial left femur and tibia, head of right femur, 5 caudal vertebrae lacking arches, fragments of lumbar vertebrae</td>
<td></td>
</tr>
<tr>
<td>Genus</td>
<td>Species</td>
<td>Catalog No.</td>
<td>Family</td>
<td>Locality Information</td>
<td>Age</td>
<td>Description</td>
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<tr>
<td><em>Caseopsis</em></td>
<td>agilis</td>
<td>FMNH UR 253</td>
<td>Caseidae</td>
<td>Locality KV, MacFayden Ranch, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Partial skull and lower jaw, lumbar vertebra, fragments of other vertebrae, partial left scapula, radius, ulna, pelvis, femur, partial tibia and fibula, parts of the pes</td>
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<tr>
<td><em>Cotylorhynchus</em></td>
<td>hancocki</td>
<td>CNHM UR 249</td>
<td>Caseidae</td>
<td>Locality KV, MacFayden Ranch, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Humerus and ulna</td>
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<tr>
<td><em>Cotylorhynchus</em></td>
<td>hancocki</td>
<td>CNHM UR 5250</td>
<td>Caseidae</td>
<td>Locality KV, MacFayden Ranch, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Six vertebrae and ribs</td>
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<tr>
<td><em>Dimetrodon</em></td>
<td>angelensis</td>
<td>CNHM UR 32</td>
<td>Sphenacodontidae</td>
<td>Locality KV, MacFayden Ranch, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Skull, lower jaw, 4 cervical vertebrae, ulna</td>
</tr>
<tr>
<td><em>Cotylorhynchus</em></td>
<td>hancocki</td>
<td>CNHM UR 144</td>
<td>Caseidae</td>
<td>Locality KN, Little Croton Creek, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Four ribs</td>
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<tr>
<td><em>Angelosaurus</em></td>
<td>dolani</td>
<td>FMNH UR 149</td>
<td>Caseidae</td>
<td>Locality KN, Little Croton Creek, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Posterior part of the skeleton, some anterior vertebrae, humerus, fragments of skull and jaws</td>
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<tr>
<td><em>Angelosaurus</em></td>
<td>dolani</td>
<td>FMNH UR 701</td>
<td>Caseidae</td>
<td>Locality KN, Little Croton Creek, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Fragmentary vertebrae</td>
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<tr>
<td><em>Caseoides</em></td>
<td>sanageloensis</td>
<td>FMNH UR 151</td>
<td>Caseidae</td>
<td>KP Locality, Little Croton Creek, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Right hindlimb, part of foot, left femur, humerus, fragments of vertebra</td>
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<tr>
<td><em>Caseoides</em></td>
<td>sanageloensis</td>
<td>FMNH UR 152</td>
<td>Caseidae</td>
<td>KP Locality, Little Croton Creek, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Left femur, dorsal ilium, symphysial region of pubish, centrum</td>
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<tr>
<td><em>Cotylorhynchus</em></td>
<td>hancocki</td>
<td>CNHM UR 480</td>
<td>Caseidae</td>
<td>KY Locality, Driver Ranch, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Ischium, parts of the pelvis, ribs, fragments of vertebra</td>
</tr>
<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 481</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KY Locality, Driver Ranch, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Distal humerus, lumbar vertebrae, fragments</strong></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 563</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KY Locality, Driver Ranch, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Humerus, ribs, partial pelvis</strong></td>
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<tr>
<td><strong>Dimetrodon angelensis</strong></td>
<td><strong>CMNH UR 482</strong></td>
<td><strong>Sphenacodontidae</strong></td>
<td><strong>KY Locality, Driver Ranch, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Vertebræ, scapula, fragments of skull and ribs</strong></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 487</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Two scapulocoracoids</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 488</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Two humeris, one femur</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 489</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Partial skull</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 490</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Partial skull and dentition</strong></td>
<td></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 491</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Lower jaw and dentition</strong></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 492</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Partial lower jaw and dentition</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 493</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Lower jaw and dentition</strong></td>
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<tr>
<td>Specimen ID</td>
<td>Locality, Quarry, County, Texas</td>
<td>Age</td>
<td>Description</td>
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<tr>
<td>Cotylorhynchus hancocki CNHM UR 494</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Partial lower jaw and dentition</td>
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<tr>
<td>Cotylorhynchus hancocki CNHM UR 500</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Fragment of jaw</td>
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<tr>
<td>Cotylorhynchus hancocki CNHM UR 504</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Caudal vertebrae</td>
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<td>Cotylorhynchus hancocki CNHM UR 506</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Humerus shaft</td>
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<tr>
<td>Cotylorhynchus hancocki CNHM UR 564</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Two dorsal vertebrae</td>
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<td>Cotylorhynchus hancocki CNHM UR 565</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Five vertebrae, limb bone</td>
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<td>Cotylorhynchus hancocki CNHM UR 567</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Right ulna</td>
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<tr>
<td>Cotylorhynchus hancocki CNHM UR 568</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Caudal vertebrae</td>
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<tr>
<td>Cotylorhynchus hancocki CNHM UR 569</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Dorsal vertebrae</td>
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<tr>
<td>Cotylorhynchus hancocki CNHM UR 571</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Third or fourth presacral vertebra, one caudal vertebra, ulna, partial femur, ribs</td>
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<tr>
<td>Specimen</td>
<td>Number</td>
<td>Locality</td>
<td>Age</td>
<td>Description</td>
<td></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 580</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Sacral vertebrae, four partial posterior presacral vertebrae, sacral rib</td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 581</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Nearly complete skeleton</td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 585</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Ulna</td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 586</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Tibia, partial femur</td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 621</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Partial skeleton and skull</td>
<td></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 622</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Partial skeleton, braincase and palate</td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 623</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Ulna</td>
<td></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 624</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Fragments of skull and teeth</td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 625</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Unguals</td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td>CNHM UR 626</td>
<td>KAC Locality, Kahn Quarry, Knox County, Texas</td>
<td>Early Roadian</td>
<td>Caudal vertebrae and limb bones</td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 703</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Vertebrae, caudal, sacral, lumbar and dorsal vertebrae, pelvis, femur, radius, ulna and ribs</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 704</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Phalanx</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 705</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Dorsal vertebra</strong></td>
<td></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 706</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Dorsal vertebra</strong></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 707</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Tibia</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 708</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Interclavicle</strong></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 709</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Vertebra</strong></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 710</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Vertebra</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 718</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Vertebrae and pedal phalanges</strong></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 719</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Cervical vertebrae and ribs</strong></td>
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337
<table>
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<th><strong>Cotylorhynchus hancocki</strong></th>
<th><strong>CNHM UR 720</strong></th>
<th><strong>Caseidae</strong></th>
<th><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></th>
<th><strong>Early Roadian</strong></th>
<th><strong>Vertebrae, ribs and clavicle</strong></th>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 821</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Vertebrae and ribs</strong></td>
</tr>
<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 822</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Humerus and scapulocoracoid</strong></td>
</tr>
<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>CNHM UR 823</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Humerus</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>FMNH UR 875</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Pelvis</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>FMNH UR 877</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Clavicle, rib, cervical vertebrae</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>FMNH UR 878</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Femur and fibula</strong></td>
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<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>FMNH UR 879</strong></td>
<td><strong>Caseidae</strong></td>
<td><strong>KAC Locality, Kahn Quarry, Knox County, Texas</strong></td>
<td><strong>Early Roadian</strong></td>
<td><strong>Humerus, clavicle, rib, radius m 8 vertebrae, chevron</strong></td>
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<tr>
<td><strong>Cotylorhynchus hancocki</strong></td>
<td><strong>FMNH UR 881</strong></td>
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<td>PIN 294-24</td>
<td>Caseidae (?) (Olson 1962), Phreatosuchidae, Dinocephalia (?) (Ivakhnenko 1991)</td>
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**Cotylorhynchus bransoni**

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<td><strong>Angelosaurus romeri</strong></td>
<td>FMNH UR 943</td>
<td>Caseidae</td>
<td>KF-1 Locality, Omega Quarry, Kingfisher County, Oklahoma</td>
<td>Roadian</td>
<td>Lower jaws</td>
</tr>
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<td><strong>Angelosaurus romeri</strong></td>
<td>FMNH UR 944</td>
<td>Caseidae</td>
<td>KF-1 Locality, Omega Quarry, Kingfisher County, Oklahoma</td>
<td>Roadian</td>
<td>2 dorsal ribs</td>
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<td><strong>Angelosaurus romeri</strong></td>
<td>FMNH UR 945</td>
<td>Caseidae</td>
<td>KF-1 Locality, Omega Quarry, Kingfisher County, Oklahoma</td>
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<td>Anterior dorsal ribs</td>
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<td><strong>Angelosaurus romeri</strong></td>
<td>FMNH UR 971</td>
<td>Caseidae</td>
<td>KF-1 Locality, Omega Quarry, Kingfisher County, Oklahoma</td>
<td>Roadian</td>
<td>20 caudal vertebrae with ribs on anterior ones</td>
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<td><strong>Angelosaurus romeri</strong></td>
<td>FMNH UR 978</td>
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<td>Pubis</td>
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<td>FMNH UR 979</td>
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<td>FMNH UR 980</td>
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<td>Roadian</td>
<td>Pelvis</td>
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<td><strong>Mesenosaurus romeri</strong></td>
<td>PIN 4660/7</td>
<td>Varanopidae</td>
<td>Dorogaya Gora</td>
<td>Late Roadian-Wordian</td>
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<td><strong>Mesenosaurus romeri</strong></td>
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<td>Varanopidae</td>
<td>Dorogaya Gora</td>
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<td>Dorogaya Gora</td>
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<td><strong>Mesenosaurus romeri</strong></td>
<td>PIN 4543/19</td>
<td>Varanopidae</td>
<td>Nysogora, Arkangel</td>
<td>Late Roadian-Wordian</td>
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<td><strong>Mesenosaurus romeri</strong></td>
<td>PIN 4543/21</td>
<td>Varanopidae</td>
<td>Nysogora, Arkangel</td>
<td>Late Roadian-Wordian</td>
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<td><strong>Ennatosaurus tecton</strong></td>
<td>PIN 4543/1</td>
<td>Caseidae</td>
<td>Nysogora, Arkangel</td>
<td>Late Roadian-Wordian</td>
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<td>Mesenosaurus romeri</td>
<td>PIN 4653/1</td>
<td>Varanopidae</td>
<td>Karashchelya, Arkangel</td>
<td>Late Roadian-Wordian</td>
<td>Skull</td>
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<td>PIN 4653/2</td>
<td>Caseidae</td>
<td>Karashchelya, Arkangel</td>
<td>Late Roadian-Wordian</td>
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<td>Ennatosaurus tecton</td>
<td>PIN 4543</td>
<td>Caseidae</td>
<td>Nyisagora locality, Mezen River near the junction with the Vashka River</td>
<td>Late Roadian-Wordian</td>
<td>Skull, lower jaw, fragment of cheek region and fragment of dentary</td>
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<tr>
<td>Mesenosaurus romeri</td>
<td>PIN 158/1</td>
<td>Varanopidae</td>
<td>Kiselicha, Arkangel</td>
<td>Late Roadian-Wordian</td>
<td>Partial skull, nearly complete right maxilla</td>
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<td>PIN 158/2</td>
<td>Varanopidae</td>
<td>Kiselicha, Arkangel</td>
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<td>Orbital region of the skull</td>
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<td>PIN 158/3</td>
<td>Varanopidae</td>
<td>Kiselicha, Arkangel</td>
<td>Late Roadian-Wordian</td>
<td>Lower jaw fragments</td>
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<td>PIN 158/18</td>
<td>Varanopidae</td>
<td>Kiselicha, Arkangel</td>
<td>Late Roadian-Wordian</td>
<td>Skull fragments and teeth</td>
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<td>PIN 158/19</td>
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<td>PIN 158/20</td>
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<td>Maxilla fragment</td>
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<td>PIN 3706/11</td>
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<td>Peza-1, Arkangel</td>
<td>Late Roadian-Wordian</td>
<td>Partial skull</td>
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<td>PIN 3706/15</td>
<td>Varanopidae</td>
<td>Peza-1, Arkangel</td>
<td>Late Roadian-Wordian</td>
<td>Partial skull roof</td>
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<td>PIN 3706/28</td>
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<td>Late Roadian-Wordian</td>
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<td>PIN 3706/48</td>
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<td>Late Roadian-Wordian</td>
<td>Partial skull</td>
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<tr>
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<td>PIN 162/3</td>
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<td>Glyadnaya Schel</td>
<td>Late Roadian-Wordian</td>
<td>Jaw fragments, skull missing snout and occiput</td>
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<td>PIN 162/4</td>
<td>Varanopidae</td>
<td>Glyadnaya Schel</td>
<td>Late Roadian-Wordian</td>
<td>Jaw, palate, teeth</td>
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<td>PIN 4654/1</td>
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<td>PIN 4541/8</td>
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<td>Ust-Vashka locality, Mezen River Basin, Arkhangel</td>
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<td>Skull and jaw fragments</td>
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<td>PIN 4541/15</td>
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<td>PIN 3586/38</td>
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<td>Late Roadian-Wordian</td>
<td>Anterior skull</td>
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<td>Ust Peza, Arkangelsk Province</td>
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<td>Varanopidae</td>
<td>Ust Peza, Arkangelsk Province</td>
<td>Late Roadian-Wordian</td>
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<td>PIN 4609/4</td>
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<td>PIN 4609/5</td>
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<td>PIN 4609/13</td>
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<td>Jaw fragments</td>
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<td><strong>Mesenosaurus romeri</strong></td>
<td>PIN 4609/14</td>
<td>Varanopidae</td>
<td>Leshikanskii, Arkangelsk Province</td>
<td>Late Roadian-Wordian</td>
<td>Jaw fragments</td>
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<td>PIN 4609/16</td>
<td>Varanopidae</td>
<td>Leshikanskii, Arkangelsk Province</td>
<td>Late Roadian-Wordian</td>
<td>Jaw fragments</td>
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<tr>
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<td>PIN 4609/18</td>
<td>Varanopidae</td>
<td>Leshikanskii, Arkangelsk Province</td>
<td>Late Roadian-Wordian</td>
<td>Jaw fragments</td>
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<td><strong>Mesenosaurus romeri</strong></td>
<td>PIN 4609/20</td>
<td>Varanopidae</td>
<td>Leshikanskii, Arkangelsk Province</td>
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<td>Jaw fragments</td>
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<td>Late Roadian-Wordian</td>
<td>Jaw fragments</td>
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<td>Leshikanskii, Arkangelsk Province</td>
<td>Late Roadian-Wordian</td>
<td>Jaw fragments</td>
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<td><strong>Mesenosaurus romeri</strong></td>
<td>PIN 4609/49</td>
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<td>Leshikanskii, Arkangelsk Province</td>
<td>Late Roadian-Wordian</td>
<td>Jaw fragments</td>
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<td><strong>Mesenosaurus romeri</strong></td>
<td>PIN 4659/3</td>
<td>Varanopidae</td>
<td>Kozmogorodskoe, Arkangelsk Province</td>
<td>Late Roadian-Wordian</td>
<td>Jaw fragments</td>
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<td><strong>Genus</strong></td>
<td><strong>Species</strong></td>
<td><strong>Catalog Number</strong></td>
<td><strong>Family</strong></td>
<td><strong>Location</strong></td>
<td><strong>Age</strong></td>
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<td><em>romeri</em></td>
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<td>Varanopidae</td>
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<td><em>romeri</em></td>
<td>PIN 4659/13</td>
<td>Varanopidae</td>
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<td><em>romeri</em></td>
<td>PIN 4659/16</td>
<td>Varanopidae</td>
<td>Kozmogorodskoe, Arkhangelsk Province</td>
<td>Late Roadian-Wordian</td>
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<td>PIN 4659/17</td>
<td>Varanopidae</td>
<td>Kozmogorodskoe, Arkhangelsk Province</td>
<td>Late Roadian-Wordian</td>
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<td><em>Ennatosaurus</em></td>
<td><em>tecton</em></td>
<td>PIN 1580/5</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
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<td><em>tecton</em></td>
<td>PIN 1580/6</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
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<td><em>tecton</em></td>
<td>PIN 1580/7</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
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<td><em>Ennatosaurus</em></td>
<td><em>tecton</em></td>
<td>PIN 1580/10</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
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<td><em>tecton</em></td>
<td>PIN 1580/11</td>
<td>Caseidae</td>
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<td>Late Roadian-Wordian</td>
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<td><em>tecton</em></td>
<td>PIN 1580/12</td>
<td>Caseidae</td>
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<td>Caseidae</td>
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<td>PIN 1580/17</td>
<td>Caseidae</td>
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<td>Late Roadian-Wordian</td>
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<td>PIN 1580/18</td>
<td>Caseidae</td>
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<td>Late Roadian-Wordian</td>
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<td>Caseidae</td>
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<td>Late Roadian-Wordian</td>
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<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/22</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Dorsal vertebrae</td>
</tr>
<tr>
<td>---------------------</td>
<td>-------------</td>
<td>----------</td>
<td>--------------------------------------</td>
<td>---------------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/23</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Ilium and sacral ribs</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/24</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Skull and lower jaw</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/101</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>16 vertebrae and ribs, part of the shoulder girdle, femur, ulna and radius</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/102</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Radius, ulna, carpus, scapula, part of the coracoid</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/103</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Ilium and sacral ribs</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/104</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>1 vertebra</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/105</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>4 vertebrae, part of an Indeterminate/ Undescribed limb bone, head of tibia</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/106</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>3 vertebrae</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/107</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>7 presacral and 8 caudal vertebrae, femur, ilium</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/108</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Humerus, part of radius and ulna, part of scapula, pedal bones</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/109</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Fragments of vertebrae, part of scapula, radius</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/110</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>2 radii, fibula, centrum, pedal phalanx, sacral rib</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/111</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>5 centra</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/112</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>2 partial maxillae</td>
</tr>
<tr>
<td>Ennatosaurus tecton</td>
<td>PIN 1580/113</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Interclavicale</td>
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351
<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Catalog Number</th>
<th>Family</th>
<th>Location</th>
<th>Age</th>
<th>Description</th>
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<tr>
<td>Ennatosaurus</td>
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<td>PIN 1580/114</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Part of ilium</td>
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<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/115</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>2 anterior dorsal vertebrae</td>
</tr>
<tr>
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<td>tecton</td>
<td>PIN 1580/117</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Scapulocoracoid, pterygoid</td>
</tr>
<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/118</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Part of pelvis, right femur, head of tibia</td>
</tr>
<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/119</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Fibula</td>
</tr>
<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/120</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Part of scapula, humerus, radius, ulna, part of clavicle, pedal bones</td>
</tr>
<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/121</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Ulna and part of humerus</td>
</tr>
<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/122</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Front part of left side of the skull and lower jaw</td>
</tr>
<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/123</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Scapula, 2 ribs, part of interclavicle</td>
</tr>
<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/124</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Ulna and interclavicle</td>
</tr>
<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/125</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Scapulocoracoid</td>
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<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/126</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Left pes</td>
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<tr>
<td>Ennatosaurus</td>
<td>tecton</td>
<td>PIN 1580/127</td>
<td>Caseidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td>Right dentary</td>
</tr>
<tr>
<td>Mesenosaurus</td>
<td>romeri</td>
<td>PIN 1580/1</td>
<td>Varanopidae</td>
<td>Moroznitsa, near Karpoga, Arkhangelsk</td>
<td>Late Roadian-Wordian</td>
<td></td>
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<tr>
<td>Mesenosaurus</td>
<td>romeri</td>
<td>PIN 4657/2</td>
<td>Varanopidae</td>
<td>Petrova Scheya, Arhangelsk</td>
<td>Late Roadian-Wordian</td>
<td></td>
</tr>
<tr>
<td>Heleosaurus</td>
<td>scholtzi</td>
<td>SAM-PK-1070</td>
<td>Varanopidae</td>
<td>Victorian West District</td>
<td>Capitanian</td>
<td>Skull, lower jaw, axial skeleton, pectoral and pelvic girdles and femur</td>
</tr>
<tr>
<td>Heleosaurus</td>
<td>scholtzi</td>
<td>SAM-PK-8305</td>
<td>Varanopidae</td>
<td>Beukesplass (Giannakraal 422), Fraserburg District, Northern Cape Province</td>
<td>Capitanian</td>
<td>Five individuals, with 4 skulls, anterior portions of the vertebral column, articulated ribs, gastralia, osteoderms, forelimbs, anterior caudal vertebrae</td>
</tr>
<tr>
<td>------------</td>
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<td>-------------------------------------------------------------------------</td>
<td>-----------</td>
<td>----------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Elliotsmithia</td>
<td>longiceps</td>
<td>TM 1483</td>
<td>Varanopidae</td>
<td>Abrahamskraal, Prince Albert, Western Cape Province</td>
<td>Capitanian</td>
<td>Postorbital skull and lower jaw, 4 anterior cervical vertebrae, rib fragments, dermal ossifications</td>
</tr>
</tbody>
</table>
Appendix E

A list of all scientific publications containing a phylogenetic analysis of Paleozoic synapsids incorporating at least 3 species from the time period under study. Indicates those which are incorporated into the supertree, and the reason for including those which are not.

<table>
<thead>
<tr>
<th>Phylogenetic Hypothesis</th>
<th>Status in the supertree</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reference</td>
<td>Status</td>
</tr>
<tr>
<td>--------------------------------------------------------------------------</td>
<td>-------------------------</td>
</tr>
<tr>
<td>Angielczyk, K. D. and Rubidge, B. S. 2010. A new pylaecephalid dicynodont (Therapsida, Anomodontia) from the <em>Tapinocephalus</em> Assemblage Zone, Karoo Basin, Middle Permian of South Africa</td>
<td>Removed; subset of Angielczyk &amp; Rubidge 2012</td>
</tr>
<tr>
<td>Angielczyk, K. D. and Rubidge B. S. 2012. Skeletal morphology, phylogenetic relationships and stratigraphic range of <em>Eosimops newtoni</em> Broom, 1921, a pylaecephalid dicynodont (Therapsida, Anomodontia) from the Middle Permian of South Africa. Journal of Systematic Palaeontology (in press)</td>
<td>Retained</td>
</tr>
<tr>
<td>Author(s)</td>
<td>Year</td>
</tr>
<tr>
<td>-----------</td>
<td>------</td>
</tr>
<tr>
<td>Damiani, R., Vasconcelos, C., Renaut, A., Hancox, J. and Yates, A.</td>
<td>2007</td>
</tr>
<tr>
<td>Fröbisch, J.</td>
<td>2007</td>
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<table>
<thead>
<tr>
<th>Author(s)</th>
<th>Title</th>
</tr>
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<tbody>
<tr>
<td>Kamerer, C. F., Angielczyk, K. D. and Fröbisch, J.</td>
<td>A comprehensive taxonomic revision of <em>Dicynodon</em> (Therapsida, Anomodontia) and its implications for dicynodont phylogeny, biogeography, and biostratigraphy. Journal of Vertebrate Paleontology 31 (S1):1-158</td>
</tr>
<tr>
<td>Lee, M.</td>
<td>Molecules, morphology and the monophyly of diapsid reptiles. Contributions to Zoology 70:<a href="http://dpc.uba.uva.nl/ctz/vol70/nr01/art01">http://dpc.uba.uva.nl/ctz/vol70/nr01/art01</a></td>
</tr>
<tr>
<td>Liu, J., Rubidge, B. S. and Li, J.</td>
<td>New basal synapsid supports Laurasian origin for therapsids. <em>Acta Palaeontologica Polonica</em> 54:393-400</td>
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<table>
<thead>
<tr>
<th>Reference</th>
<th>Citation</th>
<th>Status</th>
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<td>Author(s)</td>
<td>Title and Details</td>
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</tr>
<tr>
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</tr>
<tr>
<td>Reference</td>
<td>Note</td>
<td></td>
</tr>
<tr>
<td>---------------------------------------------------------------------------</td>
<td>-------------------------------</td>
<td></td>
</tr>
</tbody>
</table>
### Appendix F

Character list used in the Character Completeness Metric calculation, and the region of the skeleton required to accept that character as scored

<table>
<thead>
<tr>
<th>Region of the Skeleton</th>
<th>Other regions required</th>
<th>Character Description</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Requires prefrontal</td>
<td>Maxilla-prefrontal contact: absent (0); present (1).</td>
</tr>
<tr>
<td></td>
<td>Requires vomer</td>
<td>Palatal processes of the maxillae are absent (0), form a well-developed crista choanalis with a ridge extending posteriorly onto the palatine (1), contact or nearly contact the ventrally extending vomer with no sutural connection (2); bear a moderately long sutural connection with the lateral margins of the vomer (3), or meet at the midline, sharing a sutural connection and obscuring most of the vomer on the palatal surface (4).</td>
</tr>
<tr>
<td></td>
<td>Requires palatine</td>
<td>Formation of secondary palate occurs such that the posterior portion of the maxillae and palatines approach at the midline, but are slightly open anteriorly, thus creating an incipient incisive fissure or foramen (0), or the anterior portion is more closed than the posterior, leaving no indication of an incisive foramen (1).</td>
</tr>
<tr>
<td></td>
<td>Requires dentary</td>
<td>Maxilla and dentary, medial surface adjacent to alveoli: smooth (0): rugose, striated bone encloses tooth bases (1).</td>
</tr>
<tr>
<td>Maxilla</td>
<td>Requires upper canine</td>
<td>Upper dominant canine in adults large relative to maxillary height (0), medium (1) or extremely reduced (2).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maxilla, lateral buttress: absent (0); dorsally oriented buttress on lateral surface (1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maxilla, ascending process, morphology: smoothly curving posterior margin (0); angular emargination in posterior margin so apex of process is located anteriorly (1).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maxilla, supracanine buttress on medial surface: absent (0); present, may be expanded into lateral margin of internal naris [choana] (1).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maxilla, morphology of dorsal portion of supracanine buttress: anteroposteriorly broad region of thickened bone (0); narrow, strut-like ascending process (1); inapplicable, supracanine buttress absent (?).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maxilla, lateral surface orientation: vertical or slopes weakly dorsomedially (0); slopes dorsolaterally, overhanging tooth row (1).</td>
</tr>
<tr>
<td><strong>Maxilla</strong></td>
<td>Maxilla, ‘lacrimal facet’ at base of dorsal process: absent (0); present, distinct dorsoventral ridge present on ascending process divides anterior and posterior depressions (1).</td>
<td></td>
</tr>
<tr>
<td>-------------</td>
<td>------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maxilla, subnarial foramina: small or absent (0); present and large (1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maxillary facial plate high (0) or low with a height less than 40% its length (1).</td>
<td></td>
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<tr>
<td></td>
<td>Concave ventral step in maxillary facial plate between caniniform(s) (or anterior-most maxillary teeth) and incisors present (0) or absent (1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Broad excavation or pit in the maxilla immediately posterior to the dominant canine absent (0) or present (1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maxilla, ventral surface: straight or weakly convex (0); pronounced convexity (1); strongly convex with prominent ‘precanine step’ anteriorly (2).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Posterior region of the maxillary facial plate is folded inward onto the palatal region, so that the maxilla is well exposed ventrally just anterior to the orbit: absent (0) or present (1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maxilla, lateral surface of anterior process bears deep depression dorsally forming narial rim: no (0); yes (1).</td>
<td></td>
</tr>
<tr>
<td><strong>Septomaxilla</strong></td>
<td>Septomaxilla, shape: curled in external naris (0); forming a pillar which divides the external naris, septomaxillary foramen subequal in size to anterior part of external naris (1); septomaxilla large and sheet-like (2); anteroposteriorly broad septomaxilla resulting in reduced septomaxillary foramen (3); septomaxillary foramen absent (4).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Septomaxilla, posterodorsal extension on to lateral surface of skull [facial process]: absent (0); present (1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Septomaxilla: contained within external naris (0), escapes to have a short (1) or long facial exposure (2).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Septomaxilla lateral sheet-like exposure: absent (0); present (1).</td>
<td></td>
</tr>
<tr>
<td><strong>Naris</strong></td>
<td>External nares: terminal (0), retracted (1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>External nares are moderately large and face anterolaterally (0) or are extremely large, close-set and face more anteriorly (1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Naris posterodorsal expansion (ordered): absent (0); pinched between nasal and maxilla (1); greatly enlarged, between nasal and lacrimal (2).</td>
<td></td>
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<tr>
<td><strong>Nasal</strong></td>
<td>Requires Frontal</td>
<td>Nasal, length: distinctly shorter than the frontal (0); approximately equal to the frontal (1); longer than frontal (2).</td>
</tr>
<tr>
<td></td>
<td>Median fronto-nasal crest absent (0) or present (1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Requires</td>
<td>Nasal–lacral contact absent (0) or present (1).</td>
</tr>
<tr>
<td>----------</td>
<td>-----------</td>
<td>------------------------------------------------</td>
</tr>
<tr>
<td>Nasal</td>
<td>Lacrimal</td>
<td>Shape of dorsal surface of nasals: flat (0), with median boss (1).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nasal, premaxillary process: broad (0); narrow (1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>V-shaped, posterior border of nasals pointing towards the occiput absent (0) or present (1).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nasal, contribution to external naris: forms posterodorsal margin (0); extends anterovertrally as a blade-like process (‘external narial shelf’) bearing a lateral fossa (1).</td>
</tr>
<tr>
<td>Lacrimal</td>
<td>Requires</td>
<td>Lacral length: participates in margin of external naris (0); does not reach external naris (1).</td>
</tr>
<tr>
<td></td>
<td>naris</td>
<td>Lacral lateral surface of anterior process bears deep depression forming narial rim: no (0); yes (1).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lacrimal duct (ordered): opens on posterior edge of lacrimal (0); opens laterally near posterior edge of lacrimal (1); opens laterally on concave surface of lacrimal (2).</td>
</tr>
<tr>
<td>Frontal</td>
<td>Requires</td>
<td>Frontal, length: less than 1.5 times parietal length (0); greater than 1.6 times parietal length (1); greater than 2.5 times parietal length (2).</td>
</tr>
<tr>
<td></td>
<td>Parietal</td>
<td>Frontal, posterolateral process: short (0); long and narrow, matching length of postfrontal, and substantially separating parietal from postfrontal (1); completely absent (2).</td>
</tr>
<tr>
<td></td>
<td>Requires</td>
<td>Frontal width:length ratio: &lt;1, frontal narrow (0); &gt;1.5, frontal transversely broad (1).</td>
</tr>
<tr>
<td></td>
<td>postfrontal</td>
<td>Frontal, anterior process length: short (0); longer than posterior process (1); very long, forming at least 2/3 length of bone (2).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Frontal, anterior process: width equal to that of posterior process (0); narrower than posterior process (1).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Frontal posterolateral process (ordered): absent, fr-par suture forming right angle to parasagittal plane (0); absent or very short, fr-par suture forming obtuse angle to parasagittal plane (1); long, narrow, forming acute angle with parasagittal plane (2).</td>
</tr>
<tr>
<td>Preparietal</td>
<td></td>
<td>Preparietal: absent (0), present (1).</td>
</tr>
<tr>
<td>Parietal</td>
<td>Requires</td>
<td>Prefrontal-nasal suture: parasagittal, at least in its caudal third (0); anterolateral (1).</td>
</tr>
<tr>
<td></td>
<td>nasal</td>
<td>Size of pineal foramen (ordered): large, more than 25% of mid-parietal length (0); small, less than 25% of mid-parietal length (1); absent (2).</td>
</tr>
<tr>
<td><strong>Parietal</strong></td>
<td>Parietal, raised rim around pineal foramen: absent (0); surrounded by raised area forming a pineal ‘ridge’ or boss (1).</td>
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<td></td>
<td>Position of pineal foramen in dorsal view (ordered): parietal-parietal suture rostral to foramen longer than caudal to it (foramen caudal) (0); equal (foramen in middle) (1); rostral shorter than caudal (foramen rostral) (2); foramen in frontal-parietal suture (3).</td>
<td></td>
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<tr>
<td></td>
<td>Parietal expanded posteriorly on the midline behind the region of the parietal foramen absent (0) or present (1)</td>
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<tr>
<td></td>
<td>Parietal (= pineal) opening in adults present (0) or absent/extremely reduced (1).</td>
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<td></td>
<td>Parietal: width/length ratio lower than 0.8 (0); width/length ratio higher than 0.8 (1).</td>
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<td></td>
<td>Parietal, supratemporal notch: shallow (0); deep (1).</td>
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<td></td>
<td>Parietal: in dorsal aspect, the lateral margin is straight or convex (0) or concave (1)</td>
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<td></td>
<td>Parietal ventrolateral flange: absent (0); present (1).</td>
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<tr>
<td></td>
<td>Parietal crest located posteriorly (0) or extends forwards in adults to include the parietal foramen (1).</td>
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<tr>
<td></td>
<td>Sagittal crest on parietals: absent (0); present (1).</td>
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</tr>
<tr>
<td><strong>Prefrontal</strong></td>
<td>Requires jugal</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tuberous ornamentation on prefrontal and/or jugal: absent (0); present (1).</td>
<td></td>
</tr>
<tr>
<td>Requires maxilla</td>
<td>Prefrontal-maxilla contact: absent (0); present anterodorsal to lacrimal (1)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Prefrontal, ventral process: transversely narrow edge [‘tongue-like’] (0); expanded medially forming antorbital buttress (1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Prefrontal, lateral surface: approximately flat or convex (0); concave, forming antorbital recess [prefrontal pocket] (1).</td>
<td></td>
</tr>
<tr>
<td><strong>Postfrontal</strong></td>
<td>Requires postorbital</td>
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</tr>
<tr>
<td></td>
<td>Postorbital-postfrontal contact: overall trend approximately straight (0); incised by postorbital (1).</td>
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<tr>
<td></td>
<td>Adductor musculature originates on lateral surface of postorbital absent (0), present (1), originates on both postorbital and postfrontal (2).</td>
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</tr>
<tr>
<td></td>
<td>Postfrontal present (0) or absent (1).</td>
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<tr>
<td></td>
<td>Postfrontal: without (0) or with (1) posterior extension along its medial contact with the frontal.</td>
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</tr>
<tr>
<td></td>
<td>Prefrontal: ventral process tongue-like (0) or expanded medially (1)</td>
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</tr>
<tr>
<td>Postfrontal</td>
<td>Postfrontal morphology: small, occupies approximately one-third of dorsal orbit rim, not transversely broad, and has approximately flat or convex dorsolateral surface (0); dorsolateral surface concave (recessed between orbit and temporal fenestra) (1); long and broad forming prominent supraorbital shelf (2); strongly recessed posterolateral surface forming anterior part of fossa around temporal fenestra (3).</td>
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</tr>
<tr>
<td>Requires postorbital</td>
<td>Squamosal anterodorsal process: no or little underlap of posterior process of postorbital (0); extensive underlap of posterior process of postorbital (1). Scored as inapplicable in the absence of a lateral temporal fenestra.</td>
<td></td>
</tr>
<tr>
<td>Requires opisthotic</td>
<td>Mastoid process’ absent or poorly developed (0) or squamosal and paroccipital processes of the opisthotic form a distinct, posteriorly projecting ‘mastoid process’ (1).</td>
<td></td>
</tr>
<tr>
<td>Requires Pro-otic</td>
<td>Medially directed process of the squamosal contacting the pro-otic absent (0) or present, enclosing the pterygoparoccipital foramen (1).</td>
<td></td>
</tr>
<tr>
<td>Squamosal</td>
<td>Squamosal posterodorsal process: absent (0); present (1).</td>
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<tr>
<td></td>
<td>Posteroventral process of the squamosal absent (0) or present (1).</td>
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<tr>
<td></td>
<td>Squamosal occipital shelf (ordered): broad, contributes to occipital surface of skull (0); narrow, quadrate exposed in occipital view (1); absent, posterior edge of quadrate exposed in lateral view (2).</td>
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<td></td>
<td>Squamosal external auditory meatus groove: absent (0), present (1)</td>
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<td></td>
<td>Dorsal and lateral surfaces of postorbital: form smooth curve (or dorsal surface absent, postorbital not participating in skull roof) (0); sharply divided (meeting at edge) (1).</td>
<td></td>
</tr>
<tr>
<td>Requires supratemporal</td>
<td>Postorbital-supratemporal contact: present (0); absent, (1); inapplicable, supratemporal absent (?).</td>
<td></td>
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<tr>
<td>Requires temporal</td>
<td>Postorbital, posterior process, length: short (0); long, extending more than half of temporal length (1).</td>
<td></td>
</tr>
<tr>
<td>Requires jugal</td>
<td>Postorbital and jugal, medial orbital process (deep, dorsoventrally tall medial flange): absent (0); present (1).</td>
<td></td>
</tr>
<tr>
<td>Postorbital</td>
<td>Postorbital, posterior process, transverse width: broad (0); narrow (1)</td>
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<tr>
<td></td>
<td>Postorbital lateral boss at orbital margin: absent (0); present (1).</td>
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<tr>
<td></td>
<td>Postorbital-squamosal contact: anteroposteriorly short (0); extensive due to long posterior process of the postorbital that obliquely overlaps the squamosal in posterior half of temporal region (1).</td>
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</tr>
<tr>
<td>Component</td>
<td>Requires maxilla and quadratojugal</td>
<td>Requires maxilla and lacrimal</td>
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</tr>
<tr>
<td>Jugal</td>
<td>Jugal, contribution to ventral margin of skull: present (0); absent, jugal excluded from ventral margin by maxilla-quadratojugal contact achieved by a long posterior extension of the maxilla (1); maxilla-quadratojugal contact achieved by long anterior extension of the quadratojugal (2).</td>
<td>Jugal, length and dorsoventral expansion of anterior ramus: intermediate, contacts lacrimal but a distinct anterodorsal projection is absent (0); anterodorsal projection present, anterior process of jugal dorsoventrally deep (1); anterior process of jugal short, terminates ventral to orbital midlength as a tapering splint and maxilla partipates in orbit margin (2).</td>
</tr>
</tbody>
</table>
| **Parasphenoid** | Parasphenoid body, median longitudinal ridge on ventral surface: absent (0); present (1)  
Parasphenoid, expansion of body [ventral plate] posterior to basicranial articulation: gradual (0); abrupt (1)  
Requires palatine  
Vomeron median crest between palatines on posterior portion of vomer absent (0) or present (1).  
Vomer, internarial shape: widest posteriorly (0); widest near middle (1).  
Portion of vomer separating the choanae is slightly bulbous, narrowing towards its contact with the premaxilla (0), expands anteriorly and is widest at its contact with the premaxilla (1), or bears specialized transverse processes just behind the contact with the premaxilla overlapping vomeral processes of the crista choanalis (2).  
Interchoanal portion of vomer where it meets the postchoanal portion: broad (0), forms median ridge (1).  
Vomer ventral surface: flat to convex (0), lateral ridges and median trough (1).  
Vomer anterior vault present (0) or absent (1).  
Vomer, width of ventral surface: broad (0); narrow (1).  
Choanal and postchoanal portions of vomer: meet at similar level on palate (0), choanal portion is offset ventrally from postchoanal portion (1).  
Vomers paired (0), fused anteriorly (1) or completely fused (2). |
| **Pterygoid** | Basal articulation [basicranial joint]: present (0); absent (1)  
Requires basiptyerygoid process  
Basipterygoid articulation located: high above primary palate (0), just dorsal to basicranial ramus of pterygoid (1), at level basicranial ramus (i.e., suture visible in ventral view) (2).  
Parasagittal ridges running from medial posterior flare of transverse flanges to basioccipital absent (0) or present (1).  
Basal articulation, position: approximately level with transverse flange of pterygoid (0); anterior to transverse flange (1); posterior to transverse flange (2).  
Basicranial rami of pterygoids: broadly separated (0), narrowly separated with median trough formed (1), broadly contacting anterior to basicranium (2).  
Pterygoid bears no median tubercle/crest (0) or a ventromedian tubercle/crest is present anterior to the interpterygoid vacuity (1).  
Medial edge of pterygoid basicranial ramus forms parasagittal ridge on ventral surface: absent (0), present (1). |
<table>
<thead>
<tr>
<th><strong>Ptérygoid</strong></th>
<th><strong>Ptérygoid, ascending lamina/dorsal flange of the anterior ramus of the ptérygoid: low [?poorly ossified] (0); tall (1).</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><strong>Interptérygoid vacuity of adults present (0), absent/extremely reduced (1), enlarged and somewhat heart-shaped, with the anterior end positioned between the transverse flanges of the ptérygoids (2).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ptérygoids, interptérygoid vacuity: anteroposteriorly long (0); short (1).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ptérygoid, distinct transverse flange: present (0); absent (1).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ptérygoid, transverse flange, orientation of posterior margin: lateral or posterolateral (0); anterolateral (1).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ptérygoid flange expansion moderate (0), reduced (1) or sharp, posteriorly projecting wings with slight posterolateral expansion (2).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ventral rim of ptérygoid transverse flanges sweeps posteriorly at the midline vacuity (0) or does not sweep posteriorly at the vacuity (1).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ptérygoid at level of posterior edge of transverse flange: far from sagittal plane, leaving the interptérygoid vacuity posteriorly opened (0), interptérygoid vacuity closed or constricted posteriorly by median flange (1), or quadrate processes of ptérygoid medially appressed (2).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Interptérygoid vacuity: long (0) or short (1).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ptérygoid: without (0) or with (1) shelf posterior to its transverse flange.</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ptérygoid, distinct process projects medially from transverse flange: absent (0); present (1).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ptérygoid, palatal ramus length: two times longer or greater than two times the length of the quadrate ramus (0); palatal ramus less than two times length of quadrate ramus (1).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Ptérygoid, quadrate ramus, medial shelf (‘posteromedian flange’; ‘tympanic flange’): present (0); absent (1).</strong></td>
</tr>
<tr>
<td><strong>Epiphtérygoid</strong></td>
<td><strong>Requires Parietal</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Epiphtérygoid separate from parietal (0) or contacts parietal (1).</strong></td>
</tr>
<tr>
<td><strong>Requires Pro-otic</strong></td>
<td><strong>Posterior apophysis of the epiphtérygoid contacting or nearly contacting the pro-otic absent (0) or present, enclosing an aperture presumably for the trigeminal nerve (1).</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Trigeminal nerve exit exists between pro-otic incisure and epiphtérygoid (0), via a foramen between the pro-otic and epiphtérygoid (1), or via multiple foramina (2).</strong></td>
</tr>
<tr>
<td><strong>Requires Frontal</strong></td>
<td><strong>Epiphtérygoid–frontal contact absent (0) or present (1).</strong></td>
</tr>
<tr>
<td><strong>Epipterygoid</strong></td>
<td>Epipterygoid ascending process appears as a thin rod (0), is slightly expanded anteroposteriorly (1) or is extremely expanded (2). Epipterygoid ventral plate: large, part of basicranium (0) or small, excluded from basicranium (1).</td>
</tr>
<tr>
<td><strong>Pro-otic</strong></td>
<td>Laterally directed processes of the pro-otic participating in the pterygoparoccipital foramen absent (0) or present (1).</td>
</tr>
<tr>
<td><strong>Palatine</strong></td>
<td>Two palatines: separated by the vomer and pterygoid (0), join in midline (1) Palatine, width: broad (0); narrow (1).</td>
</tr>
<tr>
<td><strong>Basipterygoid process</strong></td>
<td>Basipterygoid processes (unordered): short, broad, with short articulating facets facing anterolaterally (0); long, wing-like, with long articulating facets facing anteriorly (1); long, with hemispherical articulating facets facing more or less anterolaterally (2). Basal articulation, morphology of articular surface of basipterygoid process: single, rounded articular surface (0); flat anterior facet (1); inapplicable, basal articulation absent (?)</td>
</tr>
<tr>
<td><strong>Supratemporal</strong></td>
<td>Supratemporal: present (0), absent (1). Supratemporal shape: broad, subrectangular, superficial bone that extends onto lateral surface of skull (0); large, elongate (subequal to parietal length), but placed in groove on parietal (1); long, slender, located in groove on parietal (2); supratemporal absent (3).</td>
</tr>
<tr>
<td><strong>Tabular</strong></td>
<td>Requires opisthotic Tabular: contacts paroccipital process of opisthotic (0), restricted dorsally (1). Tabular (ordered): large, sheet-like (with ventral expansion) (0); narrow, slender (1); absent (2). Tabular, posteromedial process that subdivides posttemporal fenestra and contacts the supratemporal: absent (0); present (1) Tabular morphology: subrectangular sheet located dorsal to posttemporal fenestra (0); large, sheet-like, L-shaped bone comprising suborthogonal ventral and medial processes that enclose posttemporal fenestra dorsally and laterally (1); reduced, displaced laterally, now located dorsolateral to posttemporal fenestra, medial portion tapering (2); tabular absent (3)</td>
</tr>
<tr>
<td><strong>Postparietal</strong></td>
<td>Postparietal size (ordered): sheet-like, both together not much smaller than suproccipital in state 59(1) (0); small, splint-like (1); absent (2). Shape of postparietal: wider than tall (0), approximately square (1), or taller than wide (2). Postparietals: unfused/paired (0); fused to form a midline element (1).</td>
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<tr>
<td>Bone</td>
<td>Requires occipital and squamosal</td>
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<tr>
<td><strong>Quadrate</strong></td>
<td>Quadrate contact: primarily paroccipital process (0), about equal paroccipital process and squamosal (1), mostly squamosal (2)</td>
</tr>
<tr>
<td></td>
<td>Posteroventral process on quadrate in posterior notch of squamosal absent (0) or present (1).</td>
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<tr>
<td></td>
<td>Quadrate shape (ordered): straight posteriorly (0); shallowly emarginated (1); with conch (2).</td>
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<td></td>
<td>Quadrate, condyles: distinct, separate (0); confluent, forming a saddle-shaped articular facet (1).</td>
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<td></td>
<td>Occipital margin of quadrate (ordered): anterior slope ≥ 80° (0); 80° &gt; anterior slope &gt; 50° (1); anterior slope ≤ 50° (2).</td>
</tr>
<tr>
<td><strong>Occiput</strong></td>
<td>Occiput, slope: approximately vertical (0); inclined anterodorsally by 10-50 degrees (1); strongly inclined anterodorsally by &gt;60 degrees (2); inclined posterodorsally (3)</td>
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<td></td>
<td>Basal tuber small (0) or large, approximately one-third the occipital breadth (1)</td>
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<td></td>
<td>Dorsal surface of the paroccipital process is relatively smooth or straight (0), or deeply hollowed (1) in the floor of the post-temporal fenestra.</td>
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<tr>
<td></td>
<td>Paroccipital process shape: vertical or nearly vertical sheet, height ≥ 0.5 transverse length (0); elliptical in cross-section, height &lt; 0.5 transverse length (1).</td>
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<tr>
<td></td>
<td>Paroccipital process orientation: strongly posteroventral and lateral (0), moderately posteroventral and lateral (1), transverse (2)</td>
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<tr>
<td></td>
<td>Paroccipital process attachment (ordered): ends freely (0); weak contact (1); strong contact (2).</td>
</tr>
<tr>
<td><strong>Supraoccipital</strong></td>
<td>Supraoccipital, prominent lateral processes forming dorsal margin of posttemporal fenestra: absent, fenestra bounded dorsally by tabular only (0); present (1)</td>
</tr>
<tr>
<td><strong>Exoccipital</strong></td>
<td>Exoccipital, lateral wing: tall and narrow (0); broad, extending ventral to paraoccipital process (1).</td>
</tr>
<tr>
<td><strong>Basioccipital</strong></td>
<td>Basioccipital, occipital condyle orientation: posteriorly directed (0); posteroventrally directed (1).</td>
</tr>
<tr>
<td>Opisthotic</td>
<td>Requires squamosals and supraoccipital</td>
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<tr>
<td></td>
<td>Opisthotic, morphology and orientation of paraoccipital process: robust, horizontal rod (0); slender rod, extends posterovertrally (1); dorsoventrally broad sheet, extends laterally (2).</td>
</tr>
<tr>
<td>Coronoid</td>
<td>Number of coronoids: two (0); one (1).</td>
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<tr>
<td></td>
<td>The posterodorsal terminal margin of the coronoid process is straight (0), more rounded (1) or comes to a sharp point (2).</td>
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<tr>
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<td>Mandible, shape of coronoid eminence: slightly convex (0); strongly convex (1); subhorizontal/flat (2).</td>
</tr>
<tr>
<td>Mandible</td>
<td>Mandible, position of coronoid eminence: posteriorly, within posterior 1/3 of total length (0); anteriorly, approximately 2/5 of total length from posterior end (1).</td>
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<tr>
<td></td>
<td>Mandible, bone forming dorsal margin of coronoid eminence laterally: coronoid or surangular (0); dentary (1).</td>
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<tr>
<td></td>
<td>Retroarticular process size (ordered): absent (0); small (1); large (2).</td>
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<tr>
<td></td>
<td>Mandible, retroarticular process: absent (0); present (1).</td>
</tr>
<tr>
<td></td>
<td>Mandible, composition of retroarticular process: formed by articular, angular and surangular (0); formed only by articular, large, and curved ventrally (1); inapplicable, retroarticular process absent (?).</td>
</tr>
<tr>
<td></td>
<td>Postdentary bones’ height relative to total dentary height equal (0), between one-half and equal (1) or much less than one-half (2).</td>
</tr>
<tr>
<td></td>
<td>Mandibular fenestra absent (0), penetrating the mandible and visible laterally (1), or surangular above and prearticular below a small fenestra on the medial surface of the mandible (2).</td>
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<tr>
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<td>Splenial overlaps angular: along complex suture (0); ventrally (1); dorsally (2); ventrally and dorsally (3).</td>
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<tr>
<td></td>
<td>Foramen between prearticular and angular (sometimes bordered by splenial as well) on medial surface of lower jaw: absent (0), present (1).</td>
</tr>
<tr>
<td>Distal</td>
<td>Mandibular symphysis: dorsoventrally low, mandible tapers anteriorly (0); dorsoventrally thick, almost as deep as mandible at midlength of the tooth row (1).</td>
</tr>
<tr>
<td>Distal</td>
<td>Mandible</td>
</tr>
<tr>
<td>Distal</td>
<td>Splenial</td>
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<tr>
<td>Distal</td>
<td>Splenial</td>
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<td>Whole</td>
<td>Dentary</td>
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<td>Whole</td>
<td>Mandible</td>
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<td>Whole</td>
<td>Splenial</td>
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<tr>
<td>Prearticular</td>
<td>Requires articular</td>
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<td>Prearticular</td>
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<td>Articular</td>
<td>Articular</td>
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<tr>
<td>Angular</td>
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<td>Angular</td>
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<tr>
<td>Angular</td>
<td>Reflected lamina shape and ventral extent: rounded, projecting below the ventral margin of the dentary at about the level of the second groove (0), slightly anteroposteriorly elongate (spade-shaped) and does not appear to extend below the dentary (1), or is extremely reduced and spoon-shaped (2).</td>
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<tr>
<td></td>
<td>Reflected lamina of angular (= tympanic) size: large (0) or reduced (1).</td>
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<td></td>
<td>Angular, reflected lamina: shallow (0); deep (1); not applicable, reflected lamina absent (?).</td>
</tr>
<tr>
<td></td>
<td>Angular with pattern of ridges and fossae on its lateral surface: absent (0), present (1).</td>
</tr>
<tr>
<td></td>
<td>Size of lateral exposure of angular: wide (0); narrow (1).</td>
</tr>
<tr>
<td>Surangular</td>
<td>Surangular, transverse expansion of dorsal surface: thin, sheet-like surangular, unexpanded (0); transversely expanded dorsally forming broad platform (1)</td>
</tr>
<tr>
<td></td>
<td>Surangular contribution to notch of reflected lamina: absent (0); small (1); large (2).</td>
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<tr>
<td></td>
<td>Posterior end of surangular: straight (0); strongly curved ventrally (1).</td>
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<tr>
<td></td>
<td>Dorsal edge of surangular just posterior to dentary with laterally projecting ridge: absent (0), or present (1).</td>
</tr>
<tr>
<td>Dentary</td>
<td>Requires angular</td>
</tr>
<tr>
<td></td>
<td>Lateral mandibular fenestra between dentary and angular: absent (0); present (1)</td>
</tr>
<tr>
<td></td>
<td>Ventral margins of angular and dentary confluent (0) or angular (= tympanic) positioned dorsal to ventral margin of dentary (1).</td>
</tr>
<tr>
<td></td>
<td>Dentary–angular suture: runs diagonally across lateral surface of mandible (0), posterior margin of dentary deeply incised (1).</td>
</tr>
<tr>
<td></td>
<td>Overall dentary shape is best described as deep/robust (0), short and banana-shaped (1), or long, slender, and relatively straight with a smooth ventral edge (2).</td>
</tr>
<tr>
<td></td>
<td>Dentary: coronoid eminence (0), coronoid process (1)</td>
</tr>
<tr>
<td></td>
<td>Dentary masseteric fossa in adults absent (0), present high on coronoid process (1) or enlarged, extending to the ventral border of the dentary (2).</td>
</tr>
<tr>
<td></td>
<td>Lateral sulcus along the ramus and coronoid process of the dentary, absent (0) or present (1).</td>
</tr>
<tr>
<td></td>
<td>Area between left and right dentaries widens greatly posteriorly (0) or remains relatively long and narrow (almost slit-like) just posterior to symphyseal region (1).</td>
</tr>
<tr>
<td><strong>Dentary</strong></td>
<td>Lateral surface of the dentary is relatively smooth (0) or bears a marked constriction behind the canine (1) in dorsal and ventral views.</td>
</tr>
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<tr>
<td></td>
<td>Dentary angle, lateral to the reflected lamina, is absent/rounded (0), moderate/sharp (1) or pronounced, protruding with an angle of &lt; 120° (2).</td>
</tr>
<tr>
<td></td>
<td>Dentary height in canine versus anterior postcanine regions: nearly equivalent (0), shows pronounced difference (1).</td>
</tr>
<tr>
<td><strong>Splenial</strong></td>
<td>Splenial, contact with posterior coronoid: absent (0); present (1); inapplicable, posterior coronoid absent (?).</td>
</tr>
<tr>
<td><strong>Stapes</strong></td>
<td>Stapes: robust, with thick shaft (0); slender, rod-like shaft (1).</td>
</tr>
<tr>
<td></td>
<td>Dorsal process of stapes present (0) or reduced/ absent (1)</td>
</tr>
<tr>
<td></td>
<td>Stapedial foramen oriented posteroventrally (0), dorsoventrally (1) or reduced/absent (2).</td>
</tr>
<tr>
<td><strong>Hyoid</strong></td>
<td>Hyoid: short, directed to quadrate region (0); long, directed posteriorly beyond skull (1).</td>
</tr>
<tr>
<td><strong>Vertebrae</strong></td>
<td>Vertebral centra, notochordal canal: present in adults (0); absent in adults (1).</td>
</tr>
<tr>
<td></td>
<td>Neural arches: arches possess lateral excavations (0) or no excavations (1).</td>
</tr>
<tr>
<td><strong>Presacral vertebral</strong></td>
<td>Presacral vertebrae, count: 27 or more (0); &lt;27 (1)</td>
</tr>
<tr>
<td></td>
<td>Cervicodorsal centra, ventral surface: low, rounded ridge (0); prominent, transversely narrow, sheet-like keel (1).</td>
</tr>
<tr>
<td><strong>Presacral and Sacral Vertebrae</strong></td>
<td>Presacral/sacral vertebrae, intercentra: present along entire series (0); present only in parts of series, cartilaginous intercentra may be present in places (1); absent (2).</td>
</tr>
<tr>
<td><strong>Cervical vertebrae</strong></td>
<td>Requires a caudal dorsal vertebra</td>
</tr>
<tr>
<td></td>
<td>Cervical centra length: no longer than caudal dorsals (0); longer than caudal dorsals (1).</td>
</tr>
<tr>
<td><strong>Requires all</strong></td>
<td>Cervical vertebrae, count: 3 or fewer (0); 5 or more (1)</td>
</tr>
<tr>
<td><strong>Requires anterior</strong></td>
<td>Atlas-axis complex, atlantal and axial intercentra: contact ventrally or in very close proximity (0); widely separated by ventral extension of the atlantal centrum (odontoid) (1).</td>
</tr>
<tr>
<td></td>
<td>Ventral surface of cervical centra: rounded (0); strongly keeled (1).</td>
</tr>
<tr>
<td><strong>Any</strong></td>
<td>Cervical neural arch excavation (ordered): absent (0); shallow (1); deep (2).</td>
</tr>
<tr>
<td><strong>Dorsal vertebrae</strong></td>
<td>Dorsal centra (anterior–middle dorsal centra), ventral surface: transversely rounded (0); ventral ridge (1); strongly pinched forming transversely narrow, sheetlike keel (2); ventrally raised platform or keel bearing longitudinal trough (3).</td>
</tr>
<tr>
<td>Dorsal vertebrae</td>
<td>Any</td>
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<tr>
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<td></td>
<td></td>
</tr>
<tr>
<td>Sacral vertebrae</td>
<td>All</td>
</tr>
<tr>
<td>Neural spines</td>
<td>Any Presacral</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td></td>
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</tr>
<tr>
<td></td>
<td>Anterior cervical</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cervical</td>
</tr>
<tr>
<td><strong>Neural spines</strong></td>
<td><strong>Caudal cervical and anterior dorsal</strong></td>
</tr>
<tr>
<td>-------------------</td>
<td>----------------------------------------</td>
</tr>
<tr>
<td><strong>Anterior dorsal</strong></td>
<td>Dorsal neural spines, anterior spines: slender, not expanded dorsally (0); expanded dorsally giving club-shaped appearance (1).</td>
</tr>
<tr>
<td><strong>Dorsal</strong></td>
<td>Dorsal neural spines, height: short, approximately 1.5 times centrum height or lower (0); intermediate, 2–3 times centrum height (1); very tall (2).</td>
</tr>
<tr>
<td></td>
<td>Dorsal neural spines, lateral tubercles: absent (0); present (1).</td>
</tr>
<tr>
<td></td>
<td>Dorsal neural spines, longitudinal grooves on anterior and posterior surfaces: absent (0); present (1).</td>
</tr>
<tr>
<td></td>
<td>Dorsal neural spines, when elongate: without ‘shoulders’ (0); with ‘shoulders’ (1).</td>
</tr>
<tr>
<td></td>
<td>Dorsal neural spines morphology: consistent along column (0); alternating (1).</td>
</tr>
<tr>
<td><strong>Mid dorsal</strong></td>
<td>Ratio of height of mid-dorsal neural spines from base of zygapophysis: ≤ 1.5 (0); &gt; 1.5 (1).</td>
</tr>
<tr>
<td><strong>Posterior dorsal</strong></td>
<td>Posterior dorsal neural spines, orientation: approximately vertical (0); posteriormost one or two dorsal neural spines anterodorsally inclined (1); several posterior neural spines anterodorsally inclined (2); strongly posterodorsally inclined (3).</td>
</tr>
<tr>
<td><strong>Dorsal or sacral</strong></td>
<td>Dorsal and sacral neural spines, cross section: transversely compressed, subrectangular, blade-like spines (0); subcircular, rod-like for most of spine length [except basally] (1).</td>
</tr>
<tr>
<td><strong>Sacral or caudal</strong></td>
<td>Sacral and caudal neural spines: smooth (0); rugose with longitudinal ridges on lateral surface and tapering apex ['leaf-shaped'] (1).</td>
</tr>
<tr>
<td></td>
<td>Sacral and caudal vertebrae: smooth sided spines (0) or spines with longitudinal ridges (1).</td>
</tr>
<tr>
<td><strong>Caudal</strong></td>
<td>Caudal vertebrae: neural spines are rectangular from the lateral aspect (0) or are wider at the tip (1).</td>
</tr>
<tr>
<td></td>
<td>Caudal vertebrae: neural spines are short and square (0) or tall and pointed (1).</td>
</tr>
<tr>
<td><strong>Any</strong></td>
<td>Neural spines: triangular (0); rectangular (1).</td>
</tr>
<tr>
<td><strong>Cervical ribs</strong></td>
<td>Accessory process on craniolateral surface of cranial cervical ribs: absent (0); present (1).</td>
</tr>
<tr>
<td></td>
<td>Cervical ribs: some or all holocephalous (0); all dichocephalous (1).</td>
</tr>
<tr>
<td><strong>Thoracic ribs</strong></td>
<td>Trunk ribs: dichocephalous (0); holocephalous (1).</td>
</tr>
</tbody>
</table>
| **Thoracic ribs** | Dorsal ribs, tuberculum (contacts diapophysis) morphology: well-developed and flange-like (0); reduced to low tuberosity (1); low tuberculum with expanded, concave, cup-like articular facet (2)  
Dorsal ribs, curvature: curved proximally, only weakly curved distally (0); strongly arched proximally, curved throughout length enclosing expanded, ‘barrelshaped’ trunk (1) |
| **Sacral ribs** | Sacral ribs (ordered): two unequal (0); two equal (1); three (2).  
Sacral ribs, morphology of first sacral rib: hugely enlarged and braces contact of second sacral rib with ilium (0); subequal to or only slightly larger than more posterior sacral ribs (1). |
| **Sternum** | Sternum: not mineralized (0); mineralized (bone or calcified cartilage) (1). |
| **Interclavicle** | Minimal interclavicle shaft width: ≤ 0.105 tip-to-tip width (0); ≥ 0.137 tip-to-tip width (1).  
Interclavicle shape: +-shaped (cranial process present) (0); T-shaped (cranial process absent) (1).  
Interclavicle, shape of posterior margin of head: distinctly offset from shaft by posterolateral emargination (0); grades gradually into shaft (1).  
Interclavicle, angle of head: low angle, interclavicle weakly curved in lateral view (0); head sharply upturned (1)  
Interclavicle, shape of anterior end: triangular, pointed anteriorly with ‘diamond-shaped’ appearance (0); truncated anteriorly (1); trapezoidal with narrow, straight anterior margin (2). |
| **Clavicle** | Clavicle, shape of ventromedial plate: narrow (0); deep (1); intermediate (2); narrow and short, but with additional anterior process (3).  
Clavicle, orientation of long axis of ventromedial plate relative to shaft: highly obtuse angle (0); almost perpendicular (1) |
| **Cleithrum** | Cleithrum, size and contacts: large, approximately two-thirds the height of the scapula and contacts clavicle (0); intermediate, approximately half the height of the scapula and contacts clavicle (1); reduced and does not contact clavicle (2).  
Cleithrum: present (0); absent (1). |
| **Scapula** | Cranial margin of scapula: straight, at least dorsally (0); convex along entire length (1).  
Scapula, anteroposterior breadth of proximal end (base): broad (0); pinched/narrow (1)  
Scapulocoracoid, glenoid shape: anteroposteriorly elongate and helical (0); short, faces posterolaterally (1) |
<table>
<thead>
<tr>
<th>Column</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scapula</td>
<td>Scapula, posterolateral surface of blade immediately dorsal to glenoid: weakly concave (0); deep, triangular concavity bounded anteriorly by prominent supraglenoid buttress (1); distinct supraglenoid buttress absent (2)</td>
</tr>
<tr>
<td></td>
<td>Supraglenoid foramen: absent (0); present (1).</td>
</tr>
<tr>
<td></td>
<td>Scapula, location of supraglenoid foramen: posterior to supraglenoid buttress (0); anterior to supraglenoid buttress (1); on apex of supraglenoid buttress (2); inapplicable, supraglenoid foramen absent (?) (Figure A6).</td>
</tr>
<tr>
<td>Shaft</td>
<td>Ventral surface of cervical centra: rounded (0); strongly keeled (1).</td>
</tr>
<tr>
<td>Distal</td>
<td>Scapula, anteroposterior breadth of distal end: broad (0); narrow (1).</td>
</tr>
<tr>
<td>Requires corocoid</td>
<td>Scapulocoracoid, notch in anterior margin on scapulocoracoid contact (scapulocoracoid notch): absent (0); present (1).</td>
</tr>
<tr>
<td>Coracoid</td>
<td>Triceps process on coracoid: small or absent (0); large (1).</td>
</tr>
<tr>
<td>Proximal</td>
<td>Coracoid, foramen on posterodorsal surface between glenoid and triceps process: absent (0); present (1).</td>
</tr>
<tr>
<td></td>
<td>Coracoids, number: two (0); one (1).</td>
</tr>
<tr>
<td>Humerus</td>
<td>Humerus, ridge connecting deltopectoral crest to head: double, paired ridge enclosing proximolateral fossa, deltopectoral crest anteroposteriorly expanded and ‘tuberous’ (0); single, fossa absent (1)</td>
</tr>
<tr>
<td>Proximal</td>
<td>Humerus, anterior surface of deltopectoral crest: weakly concave (0); strongly concave, bounded dorsally by a prominent, proximodistally elongate ridge (1).</td>
</tr>
<tr>
<td></td>
<td>Humerus, morphology of latissimus dorsi attachment: step-like transverse ridge or mound (0); prominent, posteriorly-directed tubercle (1).</td>
</tr>
<tr>
<td></td>
<td>Humerus, ventral surface of proximal end: extends proximally forming a low, anteroposteriorly oriented crest posteroverentral to head (0); extends far proximally, forming a prominent crest (1).</td>
</tr>
<tr>
<td>Shaft</td>
<td>Humerus, posterior surface of shaft around exit of entepicondylar foramen: convex (0); exit foramen very large and rimmed by a longitudinal depression, foramen only enclosed by a narrow strip of bone (1).</td>
</tr>
<tr>
<td></td>
<td>Humerus, ‘distinct shaft’: absent (0); present (1).</td>
</tr>
<tr>
<td>Distal end and shaft</td>
<td>Ratio of width of distal head of humerus to shaft length: ≥ 0.3 (0); &lt; 0.3 (1).</td>
</tr>
<tr>
<td>Distal</td>
<td>Entepicondyle: moderately large (0); strongly developed at maturity (1).</td>
</tr>
<tr>
<td>Anatomical Region</td>
<td>Proximal</td>
</tr>
<tr>
<td>Manual Phalanges</td>
<td>Digit 4</td>
</tr>
<tr>
<td>---</td>
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<tr>
<td>Ungual</td>
<td>Manus, ungual phalanges, height:width ratio: low, ratio &lt;1.1 and blood vessel grooves may be visible on the dorsolateral surfaces of the phalanx (0); high, ratio &gt;1.5, strongly recurved and blood vessel grooves are located on the lateral surfaces of the phalanx (1).</td>
</tr>
<tr>
<td>Any</td>
<td>Manus, ungual phalanges, flexor tubercle: single bulbous eminence (0); paired, medial and lateral eminences (1); absent (2)</td>
</tr>
<tr>
<td>Pelvic girdle</td>
<td>Whole</td>
</tr>
<tr>
<td>Pubis</td>
<td>Proximal</td>
</tr>
<tr>
<td>Distal and shaft</td>
<td>Lateral and distal pubic tubercles: small or absent (0); large (1)</td>
</tr>
<tr>
<td>Distal</td>
<td>Pubis, pectineal ridge: absent (0), present (1)</td>
</tr>
<tr>
<td>Requires Acetabulum</td>
<td>Pubis, midline symphysial contact: enlarged, dorsoventrally broad (0); subequal to height of ischial midline symphysis, restricted to peripheral margin of medial surface (1)</td>
</tr>
<tr>
<td>Requires Ischium</td>
<td>Pubis, ventral surface of pubic apron: flat or convex, pubes extend ventromedially (0); strongly concave, pubes extend approximately medially (1)</td>
</tr>
<tr>
<td>Acetabulum</td>
<td>Pubis, length relative to acetabulum: &gt;1.5 times (0); 1.0–1.5 times (1).</td>
</tr>
<tr>
<td>Obturator foramen size is small (0), moderately enlarged (1) or extremely enlarged (2).</td>
<td></td>
</tr>
<tr>
<td>Requires Ischium</td>
<td>Pubis and ischium orientation relatively vertical (0) or more horizontal, forming a broad puboischiatic plate (1).</td>
</tr>
<tr>
<td>Acetabulum: elongate (0); circular (1).</td>
<td></td>
</tr>
<tr>
<td>Ilium</td>
<td>Dorsal</td>
</tr>
<tr>
<td>Ilium, dorsal process morphology: long, tapering posterodorsal blade and anterodorsal blade small or absent (0); marked anterodorsal expansion present, dorsal process tall and plate-like (1)</td>
<td></td>
</tr>
<tr>
<td>Whole</td>
<td>Ilium, medial surface: weakly concave or flat (0); anteroventrally oriented ridge contacts pubic articulation (1).</td>
</tr>
<tr>
<td>Ilium, fossa on dorsal surface [dorsal groove], or external shelf: dorsal groove present (0); external shelf present (1); both absent, ilium plate-like (2).</td>
<td></td>
</tr>
<tr>
<td>Ischium</td>
<td>Distal</td>
</tr>
<tr>
<td>---------</td>
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</tr>
<tr>
<td></td>
<td>Shaft</td>
</tr>
<tr>
<td>Hindlimb and trunk</td>
<td>Hindlimb-trunk length ratio: hindlimb much shorter than trunk (0); hindlimb almost as long as trunk or longer (1).</td>
</tr>
<tr>
<td></td>
<td>Femur</td>
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<tr>
<td>Proximal</td>
<td>Femur</td>
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<tr>
<td></td>
<td>Distinct trochanter minor of the femur absent (0) or present (1).</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Femur</td>
<td>Shaft</td>
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<tr>
<td></td>
<td>Distal</td>
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<td></td>
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<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Whole</td>
<td></td>
</tr>
<tr>
<td>Requires humerus</td>
<td>Femur-humerus length ratio (ordered): &gt; 1.2 (0); 1 to 1.2 (1); &lt; 1 (2).</td>
</tr>
<tr>
<td>Shaft, requires humerus shaft</td>
<td>Femoral and humeral shaft diameters: femur = 150% humerus (0); more or less equal (up to 120%) (1).</td>
</tr>
<tr>
<td>Fibula</td>
<td>Fibula, distal head/shaft diameter: less than 3:1 (0); more than 3:1 (1).</td>
</tr>
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<td>------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Tibia</td>
<td>Tibia, cnemial crest: low (0); prominent and distinct (1)</td>
</tr>
<tr>
<td>Lower hindlimb</td>
<td>(106) Lower leg: foot length ratio: articulated tibia + tibiale/astragalus longer than articulated 4th metatarsal + digit (0); shorter (1).</td>
</tr>
<tr>
<td>Astragalus-calcanem articulation</td>
<td>Astragalus-calcanem articulation (unordered): flat (0); concave-convex (1); foramen on calcaneum, articulation expanded (2); sutured or fused (3).</td>
</tr>
<tr>
<td>Astragalus</td>
<td>Lepidosauriform ankle joint: absent (0); present (1).</td>
</tr>
<tr>
<td>Calcaneum</td>
<td>Lateral tuber on calcaneum: absent (0); present (1).</td>
</tr>
<tr>
<td>Calcaneum (fibulare), proportions: length approximately equal to width (0); length conspicuously greater than width (1).</td>
<td></td>
</tr>
<tr>
<td>Tarsals</td>
<td>Pes, lateral centrale: no larger than second or third distal tarsals (0); large than second or third distal tarsals (1); absent (2).</td>
</tr>
<tr>
<td>Fifth</td>
<td>Pes, distal tarsal V: present (0); absent (1).</td>
</tr>
<tr>
<td>Metatarsals</td>
<td>Fourth metatarsal: short (0); long (at least 40% of digit IV) (1).</td>
</tr>
<tr>
<td>Fifth</td>
<td>Fifth metatarsal: straight (0); hooked (1).</td>
</tr>
<tr>
<td>Metapodials</td>
<td>Metapodials overlapping proximally: no (0); yes (1).</td>
</tr>
<tr>
<td>Fore or Hind limbs</td>
<td>Appendicular skeleton, limb proportions: short and stout (0); long and slender (1).</td>
</tr>
</tbody>
</table>
## Appendix G

Percentages assigned to each region of the skeleton in calculating the Character Completeness Metric

<table>
<thead>
<tr>
<th>Element</th>
<th>Percentage score assigned</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Skull - 69.98%</strong></td>
<td></td>
</tr>
<tr>
<td>Premaxilla</td>
<td>1.99%</td>
</tr>
<tr>
<td>Maxilla</td>
<td>2.58%</td>
</tr>
<tr>
<td>Septomaxilla</td>
<td>0.80%</td>
</tr>
<tr>
<td>Naris</td>
<td>0.60%</td>
</tr>
<tr>
<td>Nasal</td>
<td>0.80%</td>
</tr>
<tr>
<td>Lacrimal</td>
<td>0.40%</td>
</tr>
<tr>
<td>Frontal</td>
<td>0.80%</td>
</tr>
<tr>
<td>Preparietal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Parietal</td>
<td>2.19%</td>
</tr>
<tr>
<td>Postparietal</td>
<td>0.60%</td>
</tr>
<tr>
<td>Prefrontal</td>
<td>0.40%</td>
</tr>
<tr>
<td>Postfrontal</td>
<td>0.80%</td>
</tr>
<tr>
<td>Squamosal</td>
<td>0.99%</td>
</tr>
<tr>
<td>Postorbital</td>
<td>0.60%</td>
</tr>
<tr>
<td>Jugal</td>
<td>0.40%</td>
</tr>
<tr>
<td>Quadratojugal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Basisphenoid</td>
<td>0.20%</td>
</tr>
<tr>
<td>Parasphenoid</td>
<td>0.99%</td>
</tr>
<tr>
<td>Vomer</td>
<td>1.59%</td>
</tr>
<tr>
<td>Pterygoid</td>
<td>3.18%</td>
</tr>
<tr>
<td>Epipterygoid</td>
<td>0.40%</td>
</tr>
<tr>
<td>Pro-otic</td>
<td>0.20%</td>
</tr>
<tr>
<td>Bone Name</td>
<td>Percentage</td>
</tr>
<tr>
<td>---------------------------</td>
<td>------------</td>
</tr>
<tr>
<td>Palatine</td>
<td>0.40%</td>
</tr>
<tr>
<td>Basipterygoid process</td>
<td>0.40%</td>
</tr>
<tr>
<td>Supratemporal</td>
<td>0.40%</td>
</tr>
<tr>
<td>Tabular</td>
<td>0.60%</td>
</tr>
<tr>
<td>Quadrat</td>
<td>0.80%</td>
</tr>
<tr>
<td>Supraoccipital</td>
<td>0.20%</td>
</tr>
<tr>
<td>Exoccipital</td>
<td>0.20%</td>
</tr>
<tr>
<td>Basioccipital</td>
<td>0.20%</td>
</tr>
<tr>
<td>Opisthotic</td>
<td>0.20%</td>
</tr>
<tr>
<td>Coronoid</td>
<td>0.60%</td>
</tr>
<tr>
<td>Prearticular</td>
<td>0.20%</td>
</tr>
<tr>
<td>Articular</td>
<td>0.20%</td>
</tr>
<tr>
<td>Angular</td>
<td>1.59%</td>
</tr>
<tr>
<td>Surangular</td>
<td>0.80%</td>
</tr>
<tr>
<td>Dentary</td>
<td>1.79%</td>
</tr>
<tr>
<td>Splenial</td>
<td>0.20%</td>
</tr>
<tr>
<td>Stapes</td>
<td>0.60%</td>
</tr>
<tr>
<td>Hyoid</td>
<td>0.20%</td>
</tr>
<tr>
<td>Maxilla and prefrontal</td>
<td>0.40%</td>
</tr>
<tr>
<td>Maxilla and vomer</td>
<td>0.20%</td>
</tr>
<tr>
<td>Maxilla and palatine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Maxilla and dentary</td>
<td>0.20%</td>
</tr>
<tr>
<td>Maxilla and upper canine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Nasal and frontal</td>
<td>0.40%</td>
</tr>
<tr>
<td>Nasal and lacrimal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Lacrimal and naris</td>
<td>0.20%</td>
</tr>
<tr>
<td>Frontal and parietal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Frontal and postfrontal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Parietal and nasal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Prefrontal and jugal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Postfrontal and postorbital</td>
<td>0.40%</td>
</tr>
<tr>
<td>Squamosal and postorbital</td>
<td>0.20%</td>
</tr>
<tr>
<td>Squamosal and opisthotic</td>
<td>0.20%</td>
</tr>
<tr>
<td>Bone Combination</td>
<td>Percentage</td>
</tr>
<tr>
<td>----------------------------------------</td>
<td>------------</td>
</tr>
<tr>
<td>Squamosal and pro-otic</td>
<td>0.20%</td>
</tr>
<tr>
<td>Postorbital and supratemporal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Postorbital and temporal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Postorbital and Jugal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Jugal, maxilla and quadratojugal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Jugal, maxilla and lacrimal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Jugal and squamosal</td>
<td>0.60%</td>
</tr>
<tr>
<td>Quadratojugal, maxilla and squamosal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Vomer and palatine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Pterygoid and basipterygoid process</td>
<td>0.80%</td>
</tr>
<tr>
<td>Epipterygoid and parietal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Epipterygoid and pro-otic</td>
<td>0.40%</td>
</tr>
<tr>
<td>Epipterygoid and frontal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Tabular and opisthotic</td>
<td>0.20%</td>
</tr>
<tr>
<td>Quadrate, occipital and squamosal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Quadrate and quadratojugal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Opisthotic, squamosal and suporoccipital</td>
<td>0.20%</td>
</tr>
<tr>
<td>Prearticular and articular</td>
<td>0.20%</td>
</tr>
<tr>
<td>Dentary and angular</td>
<td>0.40%</td>
</tr>
<tr>
<td>Any tooth</td>
<td>0.40%</td>
</tr>
<tr>
<td>Any lateral tooth</td>
<td>1.39%</td>
</tr>
<tr>
<td>Premaxillaiy teeth</td>
<td>0.99%</td>
</tr>
<tr>
<td>Premaxillaiy or maxillaiy teeth</td>
<td>1.59%</td>
</tr>
<tr>
<td>Maxillaiy teeth</td>
<td>1.79%</td>
</tr>
<tr>
<td>Maxillaiy or dentary teeth</td>
<td>0.80%</td>
</tr>
<tr>
<td>Dentary teeth</td>
<td>0.99%</td>
</tr>
<tr>
<td>Coronoid teeth</td>
<td>0.20%</td>
</tr>
<tr>
<td>Caniniform teeth</td>
<td>0.99%</td>
</tr>
<tr>
<td>Pterygoid teeth</td>
<td>0.80%</td>
</tr>
<tr>
<td>Ectopterygoid teeth</td>
<td>0.20%</td>
</tr>
<tr>
<td>Vomerine teeth</td>
<td>0.20%</td>
</tr>
<tr>
<td>Palatine teeth</td>
<td>0.60%</td>
</tr>
<tr>
<td>Parasphenoid teeth</td>
<td>0.60%</td>
</tr>
<tr>
<td>Tooth plates</td>
<td>0.20%</td>
</tr>
<tr>
<td>-----------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>Antorbital region of skull</td>
<td>3.78%</td>
</tr>
<tr>
<td>Orbital region of skull</td>
<td>2.39%</td>
</tr>
<tr>
<td>Postorbital region of skull</td>
<td>6.36%</td>
</tr>
<tr>
<td>Whole skull</td>
<td>1.39%</td>
</tr>
<tr>
<td>Occiput</td>
<td>1.39%</td>
</tr>
<tr>
<td>Whole skull and Mandible</td>
<td>0.20%</td>
</tr>
<tr>
<td>Proximal mandible</td>
<td>1.79%</td>
</tr>
<tr>
<td>Distal mandible</td>
<td>0.80%</td>
</tr>
<tr>
<td>Complete mandible</td>
<td>0.99%</td>
</tr>
</tbody>
</table>

**Axial skeleton - 9.58%**

<table>
<thead>
<tr>
<th>Any vertebral centrum</th>
<th>0.40%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Any presacral vertebral centrum</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any anterior cervical vertebral centrum</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any cervical vertebral centrum</td>
<td>0.40%</td>
</tr>
<tr>
<td>Any dorsal vertebral centrum</td>
<td>1.59%</td>
</tr>
<tr>
<td>All Presacral vertebrae</td>
<td>0.20%</td>
</tr>
<tr>
<td>All Presacral and sacral vertebrae</td>
<td>0.20%</td>
</tr>
<tr>
<td>All cervical vertebrae</td>
<td>0.20%</td>
</tr>
<tr>
<td>All sacral vertebrae</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any neural spine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any presacral neural spine</td>
<td>0.80%</td>
</tr>
<tr>
<td>Any cervical neural spine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any anterior cervical neural spine</td>
<td>0.40%</td>
</tr>
<tr>
<td>Any posterior cervical or anterior dorsal neural spine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any anterior dorsal neural spine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any mid-dorsal neural spine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any posterior dorsal neural spine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any dorsal neural spine</td>
<td>0.99%</td>
</tr>
<tr>
<td>Bone Type</td>
<td>Percentage</td>
</tr>
<tr>
<td>----------------------------------------------</td>
<td>------------</td>
</tr>
<tr>
<td>Any dorsal or sacral neural spine</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any sacral or caudal neural spine</td>
<td>0.40%</td>
</tr>
<tr>
<td>Any caudal neural spine</td>
<td>0.40%</td>
</tr>
<tr>
<td>Cervical rib</td>
<td>0.40%</td>
</tr>
<tr>
<td>Thoracic rib</td>
<td>0.60%</td>
</tr>
<tr>
<td>Sacral rib</td>
<td>0.40%</td>
</tr>
<tr>
<td>Any cervical vertebra and any posterior dorsal vertebra</td>
<td>0.20%</td>
</tr>
</tbody>
</table>

**Pectoral girdle - 4.37%**

<table>
<thead>
<tr>
<th>Bone Type</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proximal interclavicle</td>
<td>0.80%</td>
</tr>
<tr>
<td>Interclavicle shaft</td>
<td>0.20%</td>
</tr>
<tr>
<td>Proximal scapula</td>
<td>1.19%</td>
</tr>
<tr>
<td>Scapula shaft</td>
<td>0.20%</td>
</tr>
<tr>
<td>Distal scapula</td>
<td>0.20%</td>
</tr>
<tr>
<td>Corocoid</td>
<td>0.20%</td>
</tr>
<tr>
<td>Proximal coracoid</td>
<td>0.40%</td>
</tr>
<tr>
<td>Sternum</td>
<td>0.20%</td>
</tr>
<tr>
<td>Clavicle</td>
<td>0.40%</td>
</tr>
<tr>
<td>Cleithrum</td>
<td>0.20%</td>
</tr>
<tr>
<td>Cleithrum and scapula</td>
<td>0.20%</td>
</tr>
<tr>
<td>Scapula and corocoid</td>
<td>0.20%</td>
</tr>
</tbody>
</table>

**Forelimb - 6.19%**

<table>
<thead>
<tr>
<th>Bone Type</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proximal humerus</td>
<td>0.80%</td>
</tr>
<tr>
<td>Humerus shaft</td>
<td>0.40%</td>
</tr>
<tr>
<td>Humerus disal end and shaft</td>
<td>0.20%</td>
</tr>
<tr>
<td>Distal humerus</td>
<td>0.99%</td>
</tr>
<tr>
<td>Part</td>
<td>Percentage</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>------------</td>
</tr>
<tr>
<td>Medial carpi</td>
<td>0.40%</td>
</tr>
<tr>
<td>Lateral carpi</td>
<td>0.40%</td>
</tr>
<tr>
<td>Ulnare</td>
<td>0.20%</td>
</tr>
<tr>
<td>Radiale</td>
<td>0.20%</td>
</tr>
<tr>
<td>Fourth and fifth metacarpus</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any metacarpus</td>
<td>0.20%</td>
</tr>
<tr>
<td>Manual phalanges from digits 2 or 5</td>
<td>0.20%</td>
</tr>
<tr>
<td>Manual phalanges from digit 3</td>
<td>0.20%</td>
</tr>
<tr>
<td>Manual phalanges from digit 4</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any ungual</td>
<td>0.40%</td>
</tr>
<tr>
<td>Any maul phalanx</td>
<td>0.20%</td>
</tr>
<tr>
<td>Radius</td>
<td>0.20%</td>
</tr>
<tr>
<td>Proximal ulna</td>
<td>0.40%</td>
</tr>
<tr>
<td>Fourth metacarpus and radius</td>
<td>0.20%</td>
</tr>
<tr>
<td>Humerus and radius</td>
<td>0.20%</td>
</tr>
</tbody>
</table>

**Pelvic girdle - 3.2%**

<table>
<thead>
<tr>
<th>Part</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proximal pubis</td>
<td>0.20%</td>
</tr>
<tr>
<td>Pubis shaft and distal end</td>
<td>0.40%</td>
</tr>
<tr>
<td>Distal pubis</td>
<td>0.40%</td>
</tr>
<tr>
<td>Ischium shaft</td>
<td>0.20%</td>
</tr>
<tr>
<td>Distal ischium</td>
<td>0.20%</td>
</tr>
<tr>
<td>Dorsal Ilium</td>
<td>0.40%</td>
</tr>
<tr>
<td>Complete Ilium</td>
<td>0.40%</td>
</tr>
<tr>
<td>Complete pelvic girdle</td>
<td>0.20%</td>
</tr>
<tr>
<td>Acetabulum</td>
<td>0.20%</td>
</tr>
<tr>
<td>Acetabulum and pubis</td>
<td>0.20%</td>
</tr>
<tr>
<td>Pubis and ischium</td>
<td>0.40%</td>
</tr>
</tbody>
</table>
### Hindlimb - 5.37%

<table>
<thead>
<tr>
<th>Bone/Structure</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proximal femur</td>
<td>1.59%</td>
</tr>
<tr>
<td>Femoral shaft</td>
<td>0.20%</td>
</tr>
<tr>
<td>Distal femur</td>
<td>0.60%</td>
</tr>
<tr>
<td>Whole femur</td>
<td>0.20%</td>
</tr>
<tr>
<td>Lateral tarsals and distal tarsals</td>
<td>0.20%</td>
</tr>
<tr>
<td>Distal tarsals</td>
<td>0.20%</td>
</tr>
<tr>
<td>Distal fibula and shaft</td>
<td>0.20%</td>
</tr>
<tr>
<td>Proximal tibia</td>
<td>0.20%</td>
</tr>
<tr>
<td>Astragulus</td>
<td>0.60%</td>
</tr>
<tr>
<td>Calcaneum</td>
<td>0.40%</td>
</tr>
<tr>
<td>Fifth metatarsal</td>
<td>0.20%</td>
</tr>
<tr>
<td>Tibia, astragulus, fourth metatarsal and digit</td>
<td>0.20%</td>
</tr>
<tr>
<td>Astragulus and calcaneum</td>
<td>0.40%</td>
</tr>
<tr>
<td>Fourth metatarsal and pedal digit 4</td>
<td>0.20%</td>
</tr>
</tbody>
</table>

### Multiple elements from different regions

<table>
<thead>
<tr>
<th>Bone/Structure</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole skull and single dorsal vertebra</td>
<td>0.20%</td>
</tr>
<tr>
<td>Whole skull and complete presacral series</td>
<td>0.20%</td>
</tr>
<tr>
<td>Hindlimb and complete dorsal series</td>
<td>0.20%</td>
</tr>
<tr>
<td>Femoral shaft and humerus shaft</td>
<td>0.20%</td>
</tr>
<tr>
<td>Femur and humerus</td>
<td>0.20%</td>
</tr>
<tr>
<td>Two metapodials from the same limb</td>
<td>0.20%</td>
</tr>
<tr>
<td>Any complete limb</td>
<td>0.20%</td>
</tr>
</tbody>
</table>
Appendix H

The percentage volume of different regions measured from different skeletons (calculated by treating each region as a geometric shape), and the mean percentages calculated for each region used in calculating the Skeletal Completeness Metric (SCM)

<table>
<thead>
<tr>
<th></th>
<th>Varanops brevirostris</th>
<th>Cotylorhynchus romeri</th>
<th>Ophiacodon uniformis</th>
<th>Dimetrodon milleri</th>
<th>SCM percentages</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FMNH 644</td>
<td>AMNH 7517</td>
<td>MCZ 1366</td>
<td>MCZ 1365</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Volume (mm$^3$)</td>
<td>Volume (mm$^3$)</td>
<td>Volume (mm$^3$)</td>
<td>Volume (mm$^3$)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Percentage</td>
<td>Percentage</td>
<td>Percentage</td>
<td>Percentage</td>
<td></td>
</tr>
<tr>
<td>Skull (Cone)</td>
<td>81712.56</td>
<td>882771.26</td>
<td>117672.87</td>
<td>38155.24</td>
<td>18.13%</td>
</tr>
<tr>
<td></td>
<td>20.28%</td>
<td>4.01%</td>
<td>27.53%</td>
<td>20.72%</td>
<td></td>
</tr>
<tr>
<td>Pectoral girdle (Triangular prism)</td>
<td>85045.22</td>
<td>677980.80</td>
<td>8948.78</td>
<td>4560.96</td>
<td>7.19%</td>
</tr>
<tr>
<td></td>
<td>21.11%</td>
<td>3.08%</td>
<td>2.09%</td>
<td>2.48%</td>
<td></td>
</tr>
<tr>
<td>Humerus (Cylinder)</td>
<td>8825.06</td>
<td>2150899.26</td>
<td>20401.21</td>
<td>5250.53</td>
<td>4.89%</td>
</tr>
<tr>
<td></td>
<td>2.19%</td>
<td>9.76%</td>
<td>4.77%</td>
<td>2.85%</td>
<td></td>
</tr>
<tr>
<td>Ulna (Cylinder)</td>
<td>5576.35</td>
<td>1059676.41</td>
<td>12568.60</td>
<td>3769.66</td>
<td>2.79%</td>
</tr>
<tr>
<td></td>
<td>1.38%</td>
<td>4.81%</td>
<td>2.94%</td>
<td>2.05%</td>
<td></td>
</tr>
<tr>
<td>Radius (Cylinder)</td>
<td>5429.76</td>
<td>371315.22</td>
<td>2712.99</td>
<td>1047.04</td>
<td>1.06%</td>
</tr>
<tr>
<td></td>
<td>1.35%</td>
<td>1.68%</td>
<td>0.63%</td>
<td>0.57%</td>
<td></td>
</tr>
<tr>
<td>Manual Digit 1 (Cylinder)</td>
<td>1998.55</td>
<td>149280.93</td>
<td>539.94</td>
<td>298.65</td>
<td>0.37%</td>
</tr>
<tr>
<td></td>
<td>0.50%</td>
<td>0.68%</td>
<td>0.13%</td>
<td>0.16%</td>
<td></td>
</tr>
<tr>
<td>Digit 2 (Cylinder)</td>
<td>873.80</td>
<td>167111.57</td>
<td>650.53</td>
<td>286.06</td>
<td>0.32%</td>
</tr>
<tr>
<td></td>
<td>0.22%</td>
<td>0.76%</td>
<td>0.15%</td>
<td>0.16%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------------</td>
<td>----------------</td>
<td>----------------</td>
<td>----------------</td>
<td>----------------</td>
<td>----------------</td>
</tr>
<tr>
<td><strong>Digit 3</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1981.32</td>
<td>0.49%</td>
<td>198164.28</td>
<td>0.90%</td>
<td>1105.85</td>
</tr>
<tr>
<td><strong>Digit 4</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3896.82</td>
<td>0.97%</td>
<td>132706.67</td>
<td>0.60%</td>
<td>1923.70</td>
</tr>
<tr>
<td><strong>Digit 5</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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Appendix J

List of source trees used in the formation of the expanded supertree. For references in which more than one dataset was analysed, the tree used in the study is identified by the figure in which the results were presented.

Archosauromorpha

Bennett CS (2012) The phylogenetic position of the Pterosauria within the Archosauromorpha re-examined. *Historical Biol.* 25: 1-19

Figure 2 and 3


Figures 14 and 15


**Ichthyopterygia**


Thorne PM, Ruta M, Benton MJ (2011) Resetting the evolution of marine reptiles at the
Mini-supertree 3 is formed from Motani (1999) and Thorne et al. (2011)

**Lepidosauriformes**
Apesteguia S, Novas FE (2003) Large Cretaceous sphenodontian from Patagonia provides
insight into lepidosaur evolution in Gondwana. *Nature* 425: 609-612
Apesteguia S, Gomez RO, Rougier GW (2012) A basal sphenodontian (Lepidosauria) from
the Jurassic of Patagonia: new insights on the phylogeny and biogeography of
Evans SE, Borsuk-Bialyncka M (2009) A small lepidosauromorph reptile from the Early
*Phylogenetic Relationships of the Lizard Families*, eds Estes, RJ, Pregill, GK
(Stanford University Press: Stanford, California), pp. 16-98.
from the Late Jurassic of Germany with a dentition that is unique amongst tetrapods.
*PlosOne* 7: e46739
Reynoso VH (2000) An unusual aquatic sphenodontian (Reptilia: Diapsida) from the Tlayua
Formation (Albian), Central Mexico. *J. Paleontol.* 74: 133-148
Sues, H-D, Shubin, NH & Olsen, PE (1994) A new sphenodontian (Lepidosauria:
Rhynchocephalia) from the McCoy Brook formation (Lower Jurassic) of Nova Scotia,

**Parareptilia**
A procolophonoid reptile with temporal fenestration from the Middle Triassic of
Brazil. *P. Roy Soc. B.* 271: 1541-1546
Bassin d'Argana, Maroc. *Geodiversitas* 27: 35-132

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Figures 7 A,B, 8


*Mini-supertree 4 is formed from Jalil & Janvier 2005 and Tsuji & Müller 2008*

*Mini-supertree 5 is formed from Lyson et al 2010, MacDougal & Reisz 2012 and Modesto & Reisz 2009*

**Sauropterygia**


*Figure 7*


Synapsida


Angielczyk KD, Rubidge BS (2012) Skeletal morphology, phylogenetic relationships and stratigraphic range of Eosimops newtoni Broom, 1921, a ptyalcephalid dicynodont (Therapsida, Anomodontia) from the Middle Permian of South Africa. *J. Syst. Palaeontol.* 11: 191-231


Mini-supertree 7 is formed from Botha Brink & Modesto 2009, Campione & Reisz 2010 and Maddin et al 2006

Mini-supertree 8 is formed from Cisneros et al. 2012 and Kammerer 2011

Mini-supertree 9 is formed from Sidor & Smith 2007 and Smith et al. 2006

Chelonia


*Mini-supertree 10 is formed from Li et al. 2008 and Sterli 2010*

Basal


Hill RV (2005) Integration of morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. *Syst. Biol.* 54: 530-547


*Mini-supertree 1 formed from Bickelmann et al. 2009, Evans 2009 and Reisz et al. 2011*  
*Mini-supertree 2 formed from Hill 2005 and Li et al. 2009*
Appendix K

List of taxa removed from the expanded supertree due to the inability to resolve their phylogenetic position

“Basal” taxa

_Anthracodromeus longiceps_
_Protorothyris archeri_
_Cephalerpeton ventriarmatum_
_Hylonomus lyelli_
_Hovasaurus boulei_
_Thadeosaurus colcanapi_
_Galesphyrus capensis_
_Kenyasaurus mariakaniensis_

_Synapsida_
_Traversodon stahlekeri_
_Propelanomodon devilliersi_
_Dicynodon trigonocephalus_
_Uralokannemeyeria vjuschkovi_
_Xiyukannemeyeria brevirostris_
_Zambiasaurus submersus_
_Prorubidgea spp._
_Lystrosaurus youngi_
_Cteniosaurus platyceps_
_Mirotenthes digitipes_
_Ictidostoma hemburyi_
_Hofmeyria atavus_
_Euchambersia mirabilis_

_PARAREPTILIA_
_Bunostegos akolanensis_
_Koiloskiosaurus cogburgensis_
_Nanoparia luckhoffi_
Sauropterygia

ELASMOSAURIDAE

Neusticosaurus peyeri
Neusticosaurus.toeplitzchi
Neusticosaurus edwardsi
Microcleidus homalospondylus
Saurosphargis volzi
Hanosaurus hupehensis
Wumengosaurus delicatomandibularis
Qianxisaurus chajiangsensis
Dianopachysaurus dingi
Diandongosaurus acutidentatus
Chicenia sungi
Kwangsisaurus orientalis
Sanchiaosaurus dengi
Sinosaurosphargis yunguiensis
Nothosaurus haasi
Nothosaurus giganteus
Nothosaurus jagisteus
Nothosaurus edingerae
Nothosaurus marchicus
Nothosaurus winterswijkensis
Nothosaurus youngi
Nothosaurus juvenilis
Nothosaurus tchernovi
Nothosaurus winkelhorsti
Nothosaurus yangjuanensis
Ceresiosaurus spp.

Lepidosauromorpha

Polysphenodon muelleri
Clevosaurus wangi
Archosauroomorpha
Nicrosaurus kapffi
Nicrosaurus meyeri
Eocursor parvus
Mystriosuchus planirostris
Ebrachosuchus neukami
Boreopricea funerea
Jesairosaurus lehmani
Malerisaurus robinsonae
Pseudohesperosuchus jachaleri
Turfanosuchus dabensis
Yonghesuchus sangbiensis
Procompsognathus triassicus
Gojirasaurus quayi
Segisaurus halli
Saltoposuchus connectens
Preondactylus buffarinii
Chilenosuchus forttae
Jingshanosaurus xinwaensis
Yunnanosaurus spp.

Ichthyopterygia
Thaisaurus chonglakmanii
Guizhouichthyosaurus tangae
Appendix L

The expanded supertree, containing 686 amniotes from the late Carboniferous until the end of the Triassic. Nodes with negative support according the V support metric (Wilkinson et al. 2005)

Figure L1: Portion of the time calibrated expanded supertree showing the relationships of diadectomorphs and basal eureptiles
Figure L.2: Portion of the time calibrated expanded supertree showing the relationships of pelycosaurian-grade synapsids
Figure L3: Portion of the time calibrated expanded supertree showing the relationships of basal therapsids, including biarmosuchians and dinocephalians.
Figure L4: Portion of the time calibrated expanded supertree showing the relationships of anomodont therapsids. Black arrows indicate nodes with negative support.
Figure L5: Portion of the time calibrated expanded supertree showing the relationships of eutheriodont therapsids
Figure L.6: Portion of the time calibrated expanded supertree showing the relationships of parareptiles
Figure L7: Portion of the time calibrated expanded supertree showing the relationships of lepidosauriform saurians

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Figure L.7: Portion of the time calibrated expanded supertree showing the relationships of basal archosauriformes.
Figure L9: Portion of the time calibrated expanded supertree showing the relationships of crurotarsan archosaurs. Black arrows indicate nodes with negative support.
Figure L.10: Portion of the time calibrated expanded supertree showing the relationships of ornithodiran archosaurs. Black arrow indicates a node with negative support.
## Appendix M

All species included in the expanded supertree, and their age ranges.

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<th>Species</th>
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<th>Age range (localities of uncertain age restricted to two or less time bins)</th>
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## Synapsida

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**Basal Eureptiles**

| **Acrosodontosaurus** | *piveteau* | Wuchapingian-Changsingian | Wuchapingian |
| **Agkistrognathus** | *campbelli* | Late Olenekian-Early Ladinian | Late Anisian-Early Ladinian |
| **Anshunsaurus** | *wushaensis* | Ladinian | Ladinian |
| **Anshunsaurus** | *huangguosuensis* | Early Carnian | Early Carnian |
| **Araeoscelis** | *spp* | Artinskian-Kungurian | Artinskian-Kungurian |
| **Askeptosaurus** | *italicus* | Late Anisian | Late Anisian |
| **Brouffia** | *orientalia* | Late Moscovian | Late Moscovian |

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**Chelonia**

| **Odontocheles** | semitestacea | Early Carnian | Early Carnian |
| **Palaeochersis** | talampayensis | Rhaetian | Rhaetian |
| **Proganochelys** | quenstedtii | Late Norian-Early Rhaetian | Late Norian-Early Rhaetian |
| **Proterochersis** | intermedia | Late Norian | Late Norian |

**Archosauromorphia**

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| <strong>Aetosauroidea</strong> | scagliai | Carnian | Carnian |
| <strong>Aetosaurus</strong> | spp | Late Carnian-Early Rhaetian | Late Carnian-Early Rhaetian |
| <strong>Agnosphitys</strong> | cromhallensis | Late Norian-Rhaetian | Rhaetian |
| <strong>Ammorhynchus</strong> | navajoi | Early Anisian | Early Anisian |
| <strong>Angistorhinus</strong> | spp | Carnian-Norian | Carnian-Norian |
| <strong>Antetonitrus</strong> | ingeniceps | Norian | Norian |
| <strong>Archeopelta</strong> | arborensis | Ladinian-Early | Ladinian |</p>
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Appendix N

The clades in the expanded supertree which are found to have experienced substantial (p<0.1) and significant (p<0.05) diversification rate shifts relative to their sister. Method of time slicing, ages used in dating the tree, and the treatment of poorly supported nodes indicated at the top of the tables.

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Ruta method of time slicing; ages of taxa taking uncertainty of dating into account; poorly supported nodes retained.
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Ruta method of time slicing; ages of uncertainly dated formations are restricted to at most two substages; poorly supported nodes retained.

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