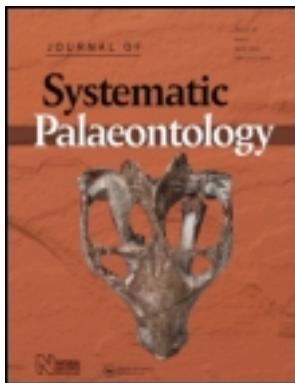


This article was downloaded by: [Smithsonian Institution Libraries]

On: 27 February 2013, At: 08:57

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Systematic Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tjsp20>

Interrelationships of basal synapsids: cranial and postcranial morphological partitions suggest different topologies

Roger B. J. Benson ^a

^a Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, UK

Version of record first published: 27 Mar 2012.

To cite this article: Roger B. J. Benson (2012): Interrelationships of basal synapsids: cranial and postcranial morphological partitions suggest different topologies, *Journal of Systematic Palaeontology*, 10:4, 601-624

To link to this article: <http://dx.doi.org/10.1080/14772019.2011.631042>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Interrelationships of basal synapsids: cranial and postcranial morphological partitions suggest different topologies

Roger B. J. Benson*

Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK

(Received 7 March 2011; accepted 1 June 2011; printed 5 December 2012)

Basal synapsids ('pelycosaurs') form the basalmost portion of the mammalian stem lineage and document the transition from primitive 'reptile-like' basal amniotes to derived, mammal-like therapsids. They dominated terrestrial ecosystems of the latest Carboniferous and Early Permian (~300–271 million years ago), producing large-bodied terrestrial animals (3–6.5 metres long), high-fibre herbivores, and macropredators for the first time in vertebrate history, alongside an array of smaller-bodied forms. Despite numerous recent discoveries and reassessments of fossils collected over the past 250 years, and despite their importance for understanding the early diversification of terrestrial vertebrates, a comprehensive assessment of global relationships among basal synapsids has not been undertaken. A new phylogenetic dataset comprising 45 taxa (plus four outgroups and four therapsids) and 239 characters (147 cranial; 92 postcranial) reveals considerable uncertainty in the relationships of higher clades of basal synapsids. Although cranial data support the current consensus that Caseasauria is the most basal clade, postcranial data and the full dataset suggest that a clade of Ophiacodontidae + Varanopidae occupies this position. Although relationships within higher clades are well supported, relationships among those clades are poorly supported. The likely source of this uncertainty lies in the exceptionally poor early record of the group, which renders determinations of the plesiomorphic condition of higher clades speculative, although cranial data are generally represented by shorter ghost lineages and should perhaps be favoured. The new dataset suggests well-supported phylogenetic placements for several taxa of historically uncertain affinities: *Trichasaurus* is a caseid; *Lupeosaurus* is an edaphosaurid; and *Basicranodon* and *Ruthiromia* are varanopids.

Keywords: Synapsida; 'Pelycosauria'; phylogenetics; character conflict

Introduction

Synapsida comprises Mammalia and all taxa more closely related to mammals than any other group of extant vertebrates (i.e. the mammalian total group). Their earliest fossil appearance is known from Late Carboniferous deposits at Florence, Nova Scotia, dated around 308 million years ago ('Westphalian D' age; Bell 1966; Reisz 1972; Ogg *et al.* 2008). This is slightly younger than, but approximately contemporaneous with, the first appearance of the reptilian stem (Carroll 1964), and predates the first appearance of truly mammal-like taxa in the Late Triassic (e.g. Kemp 2005) by approximately 100 million years. Only a handful of synapomorphies differentiate the most basal synapsids from other primitive amniotes groups (e.g. Romer & Price 1940; Reisz 1986; Kemp 1988), and the 'reptilian' gestalt of many basal synapsids is reflected by the colloquial, but incorrect, term 'mammal-like reptiles'. Thus, a lengthy stem lineage, documented by numerous fossils, provides unique information on the evolutionary assembly of the highly characteristic mammalian body plan (e.g.

Kemp 1982, 1988, 2005; Sidor & Hopson 1998; Rubidge & Sidor 2001; Sidor 2003).

Synapsids were abundant from the latest Carboniferous (*c.*300 Ma) until the Middle Triassic (*c.*230 Ma). The major Carboniferous–Early Permian (308–271 Ma) groups form a paraphyletic grade with respect to the more mammal-like Therapsida. Representatives of this grade were historically referred to 'Pelycosauria' (Cope, 1878), in reference to the tall, rod-like neural spines of a minority of taxa, including *Dimetrodon* and *Edaphosaurus* (e.g. Romer & Price 1940; Reisz 1986). A relationship between therapsids and 'pelycosaurs' was recognized by several early authors (reviewed by Romer & Price 1940) and has long since been widely accepted (Romer & Price 1940; Kemp 1982, 1988, 2005; Reisz 1986). The term 'basal synapsids' will be used in the present work to refer to 'pelycosaurs' (i.e. non-therapsid synapsids).

Basal synapsids dominated terrestrial ecosystems, producing large-bodied terrestrial animals for the first time in vertebrate history, with estimated maximum lengths of approximately 3 metres achieved independently in

*Email: rbb27@cam.ac.uk

most groups (*Dimetrodon gigashomogenes*, *Edaphosaurus cruciger*, *Ophiacodon major*; Romer & Price 1940; Reisz 1986), and 6.5 metres in *Cotylorhynchus hancocki* (Caseidae; Olson 1962, 1968). This occurred contemporaneously with the advent of large size in the stem-amniote diadectomorphs. Basal synapsids also included some of the first high-fibre herbivores from two distinct clades,

Edaphosauridae and Caseidae (Olson 1968; Modesto & Reisz 1992; diadectomorphs and captorhinids contemporaneously gave rise to herbivores), large-bodied, macro-predaceous sphenacodontids such as *Dimetrodon*, superficially monitor lizard-like varanopids (e.g. Langston & Reisz 1981), and the possibly semi-aquatic ophiacodontids (Williston & Case 1913; Romer & Price 1940) (Fig. 1).

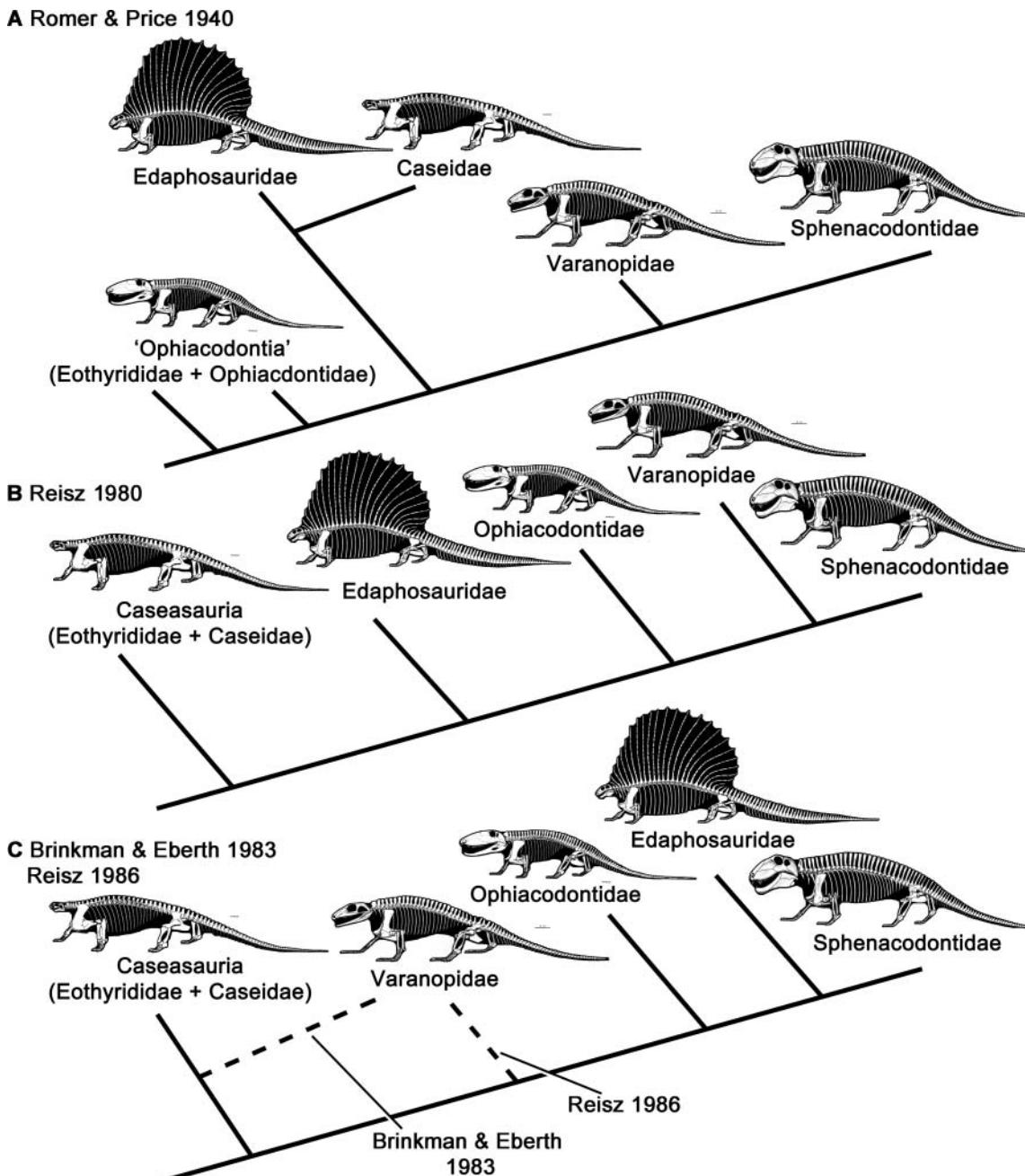


Figure 1. Previous hypotheses of global relationships among basal synapsids. **A**, Romer & Price (1940); **B**, Reisz (1980); **C**, Brinkman & Eberth (1983) and Reisz (1986), dashed lines indicate differences in the placement of Varanopidae between Brinkman & Eberth (1983) and Reisz (1986). Skeletal figures modified from Reisz (1986).

Thus, understanding the evolutionary relationships among ‘pelycosaurs’ is central to understanding the successful colonization of land by vertebrates.

Following their success in the Lower Permian, only two groups survived into Middle Permian, therapsid dominated faunas. The herbivorous caseids, known by *Ennatosaurus* from Russia (Efremov 1956; Maddin *et al.* 2008), and predaceous varanopids, known from the Russian *Mesenosaurus* (Efremov 1938; Reisz & Berman 2001) and specimens representing at least two taxa from South Africa (Broom 1937; Romer & Price 1940; Dilkes & Reisz 1996; Reisz *et al.* 1998; Modesto *et al.* 2001; Anderson & Reisz 2004; Botha-Brink & Modesto 2007, 2009). However, the compelling success of basal synapsids arguably continues to the present day as one group, Sphenacodontia, encompasses all therapsids, including mammals.

The history of basal synapsid discoveries has been comprehensively reviewed twice (Romer & Price 1940; Reisz 1986). Eighty-six nominal species were referred, or tentatively referred to basal synapsids by Reisz (1986), and considerable revision has been undertaken since (see citations throughout this article). The first fossil discovery, a partial skull from Nova Scotia, was made the holotype of *Bathygnathus borealis* by Leidy (1854). However, it was misidentified as an archosaur until much later (Case 1905; von Huene 1905). More recent discoveries yield fascinating palaeoecological inferences such as the earliest evidence of scavenging (Reisz & Tsuji 2006) and parental care (Botha-Brink & Modesto 2007, 2009) among amniotes.

Extremely tall dorsal neural spines appeared independently in edaphosaurids, sphenacodontids and the enigmatic taxon *Echinerpeton* (Reisz 1972). These spines have been a focus of functional studies suggesting that they represent a specialization to improve basking in endothermic basal synapsids (e.g. Romer 1948; Rodbard 1949; Bramwell & Fellgett 1979; Haack 1986; Bennett 1996), or were used primarily as display structures (Bakker 1986; Modesto & Reisz 1990). Some hypotheses suggest that basal synapsids were physiologically restricted to subtropical everwet biomes (Kemp 2006), although this may be a product of the geographically patchy distribution of Late Carboniferous and Early Permian terrestrial faunas (Milner 1993; Berman *et al.* 1997), and certainly Middle Permian varanopids such as *Elliotsmitha* and *Heleosaurus* occurred outside this range (Dilkes & Reisz 1996; Kemp 2006).

The first major revision of basal synapsids was conducted by Romer & Price (1940; earlier reviews were conducted by Case (1907) and Williston (1911, 1912)), drawing on abundant information from all specimens then known. Romer & Price (1940) recognized three major groupings, Ophiacodontia, Sphenacodontia and Edaphosaura (Fig. 1A). Ophiacodontia was explicitly considered as a primitive, ‘stem’ group, including Ophiacodontidae and Eothyrididae (the latter erected as a ‘wastebasket’ for generalized primitive taxa). Sphenacodontia was primarily erected for

the sphenacodontids, derived, predatory taxa, possessing numerous features indicating a relationship with therapsids. Romer & Price (1940, pp. 260–261) observed the predaceous habits of varanopids, and a mosaic of anatomical features shared with sphenacodontids and ophiacodontians. On this basis they proposed that varanopids formed a transitional grade of ‘ancestral’ sphenacodontians. Finally, Edaphosaura, comprised a novel grouping of the two herbivorous clades Edaphosauridae and Caseidae, together with some supposedly unspecialized, basal taxa such as *Mycterosaurus* (now recognized as a varanopid; Reisz & Berman 2001).

Much of the classification of Romer & Price (1940) was founded on observations of the postcranial skeleton. For instance, ‘ophiacodonts’ were proposed as a primitive grade primarily based on the structure of their limbs and limb girdles, which share characteristics with those of other basal and stem-group amniotes (‘advanced cotylosaurs’; Romer & Price 1940, p. 180); the derived features uniting sphenacodontids and varanopids were concentrated in the postcranial skeleton (Romer & Price 1940, p. 268; the varanopid skull was regarded as primitive and ophiacodont-like); and confidence in Edaphosaura was found in the detailed resemblance between edaphosaurid and caseid postcrania, especially of the vertebrae, ribs, pelvis and hind limb, and despite fundamental differences in the braincase and occiput (Romer & Price 1940, pp. 367–369). With a few exceptions, this scheme was followed in subsequent work on basal synapsids (e.g. Fox 1962; Olson 1962; Stovall *et al.* 1966). Watson (1954, 1957) and Langston (1965) however, noted several cranial features shared between *Eothyris*, caseids and *Oedaleops* (Langston 1965), a new eothyridid based on a skull from the Cutler Formation (?latest Carboniferous or Lower Permian) of Camp Quarry, New Mexico. This raised the possibility that eothyridids and caseids formed a group (also proposed by Vaughn 1958a, based on *Colobomycter*, now considered to be a parareptile; Modesto 1999). This grouping conforms to Caseasauria of recent use (Table 1). Later, DeMar (1970) suggested that varanopids may be only distantly related to sphenacodontids, based on the postcranial skeleton of *Milosaurus*, a possible basal varanopid from the Late Carboniferous of Illinois.

Reisz (1980; followed by Kemp 1982) first attempted to frame the anatomical data of Romer & Price (1940) in a phylogenetic context, focusing primarily on the cranial anatomy (20 out of 24 characters considered; Table 2). He concluded that there was strong evidence for a basal grouping of Eothyrididae (*Eothyris* + *Oedaleops*) and Caseidae, forming a monophyletic Caseasauria. Ophiacodontids were displaced further crownward by the recognition of features relating to snout elongation, shared with varanopids and sphenacodontids. Thus, Caseasauria, Edaphosauridae and Ophiacodontidae formed successively more derived branches off the line leading to Varanopidae +

Table 1. Phylogenetic definitions of higher clades within Synapsida.

Clade	Definition
Caseasauria Williston, 1912	<i>Casea broili</i> , and synapsids related more closely to it than to either <i>Varanops brevirostris</i> or <i>Ophiacodon mirus</i> (Reisz <i>et al.</i> 2009, p. 40)
Eothyrididae Romer & Price, 1940	<i>Eothyris parkeyi</i> , and caseasaurians related more closely to it than to <i>Casea broili</i> (Reisz <i>et al.</i> 2009, p. 40).
Caseidae Williston 1912	A stem-based taxon including all taxa more closely related to <i>Casea</i> or <i>Cotylorhynchus</i> than to <i>Eothyris</i> (Reisz 2005, p. 906). Not employed in the present study.
Eupelycosauria Kemp 1982	<i>Varanopidae</i> Romer & Price 1940 (correct spelling of ‘Varanopseidae’ (Langston & Reisz 1981) and ‘Varanopsidae’ (Romer & Price 1940); see Reisz & Dilkes (2003))
Mycterosaurinae Reisz & Berman, 2001	<i>Varanopid</i> synapsids more closely related to <i>Mycterosaurus</i> than to <i>Varanops</i> (Reisz & Berman 2001, p. 114)
Varanodontinae Reisz & Berman, 2001	Varanopid synapsids more closely related to <i>Varanops</i> than to <i>Mycterosaurus</i> (Reisz & Berman 2001, p. 114)
Ophiacodontidae Nopcsa 1923	<i>Ophiacodon mirus</i> and all taxa related more closely to it than to <i>Varanops brevirostris</i> , <i>Eothyris parkeyi</i> , <i>Casea broili</i> , <i>Edaphosaurus cruciger</i> or <i>Sphenacodon ferox</i>
Edaphosauridae Cope 1882	<i>Edaphosaurus cruciger</i> and all taxa related more closely to it than to <i>Ophiacodon mirus</i> , <i>Varanops brevirostris</i> , <i>Eothyris parkeyi</i> , <i>Casea broili</i> , <i>Edaphosaurus cruciger</i> or <i>Sphenacodon ferox</i>
Sphenacodontia Romer & Price 1940	The largest clade that includes <i>Haptodus baylei</i> , <i>Haptodus garnettensis</i> and <i>Sphenacodon ferox</i> , but not <i>Edaphosaurus pogonias</i> (Amson & Laurin 2011)
Sphenacodontidae Marsh 1878	<i>Sphenacodon ferox</i> and all taxa related more closely to it than to <i>Ophiacodon mirus</i> , <i>Varanops brevirostris</i> , <i>Eothyris parkeyi</i> , <i>Casea broili</i> , <i>Edaphosaurus cruciger</i> or <i>Mus musculus</i> ’
Sphenacodontinae (Marsh 1878)	<i>Sphenacodon ferox</i> and sphenacodontids more closely related to it than to <i>Secodontosaurus obtusidens</i>

Sphenacodontidae (Fig. 1B). Brinkman & Eberth (1983) took an alternative approach, studying specimens of well-known representatives of the major clades (*Casea*, *Edaphosaurus*, *Ophiacodon*, *Aerosaurus*, *Varanops*, *Dimetrodon*) in a search for new characters. On the basis of their observations (17 characters, 14 cranial), they suggested a major basal division between a clade of Caseidae + Varanopidae, and a clade comprising Ophiacodontidae as the sister taxon of Edaphosauridae + Sphenacodontidae (Fig. 1C) (Sphenacodontidae therein is equivalent to Sphenacodontia of current usage; Table 1). Reisz (1986, fig. 41) reconciled these different topologies by careful consideration of the supporting homology statements, resulting in a set of 26 characters (22 cranial). These yielded a tree in which Caseasauria was the sister taxon of all other basal synapsids (Eupelycosauria), among which Varanopidae and Ophiacodontidae formed successively more derived branches off the line leading to Edaphosauridae + Sphenacodontia (Fig. 1C). The only difference between this topology and that proposed by Brinkman & Eberth (1983) is the placement of the root between Caseasauria and Varanopidae.

The global framework of basal synapsid relationships proposed by Reisz (1986) was subsequently supported

by larger datasets (Reisz *et al.* 1992a; Modesto 1994; Berman *et al.* 1995; Table 2) and is now accepted as consensus (e.g. Kemp 1988, 2005). Subsequent analyses have focused on the detailed relationships within major clades (Table 2), particularly Sphenacodontia (Reisz *et al.* 1992a; Laurin 1993; Fröbisch *et al.* 2011), Edaphosauridae (Modesto 1994, 1995; Mazierski & Reisz 2010), Varanopidae (Reisz *et al.* 1998; Modesto *et al.* 2001; Reisz & Dilkes 2003; Anderson & Reisz 2004; Reisz & Laurin 2004; Maddin *et al.* 2006; Campione & Reisz 2010), and more recently Caseasauria (Maddin *et al.* 2008; Reisz *et al.* 2009). This has resulted in increasingly larger datasets. However, hypotheses of global relationships are still supported by relatively few characters, and have yet to be tested in the context of recent discoveries and redescriptions of basal taxa (Laurin 1993; Reisz *et al.* 1998, 2009; Anderson & Reisz 2004; Mazierski & Reisz 2010). Furthermore, an uncomfortable disjunction remains between the systematic framework of Romer & Price (1940), which attempted to explain the taxonomic distribution of abundant postcranial data, and the phylogenetic topology of Reisz (1986), which is primarily founded on cranial data. This is illustrative of a wider phylogenetic problem, that different classes of data may support different topologies.

Table 2. Summary information on previous analyses of basal synapsids. Numbers in brackets indicate the number of additional taxa (i.e. outgroups and therapsids) that are not basal synapsids ('Taxa' column), the proportion of cranial or postcranial characters ('Characters' columns), or the proportion of characters shared with the present analysis ('Shared with present analysis' columns).

Analysis	Modified from	Focus	Taxa	Characters			Shared with present analysis		
				Total	Cranial	Postcranial	Total	Cranial	Postcranial
Reisz 1980 Brinkman & Eberth 1983		'Pelycosauria'	6 (+ 3)	24	20 (0.83)	4 (0.17)	20 (0.83)	16 (0.80)	4 (1.00)
		'Pelycosauria'	7	17	14 (0.82)	3 (0.18)	17 (1.00)	14 (1.00)	3 (1.00)
Reisz 1986, fig. 40 Reisz 1986, fig. 41	Reisz 1980	'Pelycosauria'	6 (+ 3)	26	22 (0.85)	4 (0.15)	22 (0.85)	18 (0.82)	4 (1.00)
Reisz <i>et al.</i> 1992a		'Pelycosauria'	6 (+ 1)	22	22 (1.00)	0	21 (0.95)	21 (0.95)	n/a
Laurin 1993		Sphenacodontia	8 (+ 1)	97	66 (0.68)	33 (0.34)	87 (0.90)	62 (0.94)	27 (0.82)
Modesto 1994		Edaphosauridae	9 (+ 2)	121	81 (0.67)	40 (0.33)	91 (0.75)	64 (0.79)	27 (0.68)
Berman <i>et al.</i> 1995		'Pelycosauria'	8	95	72 (0.76)	23 (0.24)	88 (0.93)	66 (0.92)	22 (0.96)
Modesto 1995		Edaphosauridae	8	36	22 (0.61)	14 (0.39)	31 (0.86)	21 (0.95)	10 (0.71)
Reisz <i>et al.</i> 1998		Varanopidae	8 (+ 1)	31	28 (0.90)	3 (0.10)	28 (0.90)	25 (0.89)	3 (1.00)
Sidor & Hopson 1998		'Pelycosauria' + 'Therapsida'	4 (+ 17)	181	122 (0.67)	59 (0.33)	54 (0.30)	36 (0.30)	18 (0.31)
Modesto <i>et al.</i> 2001	Reisz <i>et al.</i> 1998	Varanopidae	8 (+ 1)	31	28 (0.90)	3 (0.10)	28 (0.90)	25 (0.89)	3 (1.00)
Reisz & Dilkes 2003	Reisz <i>et al.</i> 1998	Varanopidae	12 (+ 1)	53	47 (0.89)	6 (0.11)	49 (0.92)	43 (0.91)	6 (1.00)
Sidor 2003		'Pelycosauria' + 'Therapsida'	19 (+ 33)	82	82 (1.00)	0	13 (0.16)	13 (0.16)	n/a
Anderson & Reisz 2004	Reisz <i>et al.</i> 1998	Varanopidae	12 (+ 1)	54	48 (0.89)	6 (0.11)	50 (0.93)	44 (0.92)	6 (1.00)
Reisz & Laurin 2004	Reisz <i>et al.</i> 1998	Varanopidae	13 (+ 1)	58	47 (0.81)	11 (0.19)	53 (0.91)	43 (0.91)	10 (0.91)
Maddin <i>et al.</i> 2006	Reisz <i>et al.</i> 1998	Varanopidae	14 (+ 1)	60	49 (0.82)	11 (0.18)	56 (0.93)	45 (0.92)	11 (1.00)
Maddin <i>et al.</i> 2008		Caseidae	9 (+ 3)	106	73 (0.69)	33 (0.31)	100 (0.94)	71 (0.97)	29 (0.88)
Reisz <i>et al.</i> 2009		Caseasauria	11 (+ 2)	69	59 (0.86)	10 (0.14)	66 (0.96)	56 (0.95)	10 (1.00)
Campione & Reisz 2010	Reisz <i>et al.</i> 1998	Varanopidae	11	58	48 (0.83)	10 (0.17)	54 (0.93)	44 (0.92)	9 (0.90)
Mazierski & Reisz 2010	Modesto 1995	Edaphosauridae	11	39	24 (0.62)	15 (0.38)	33 (0.85)	22 (0.92)	11 (0.73)
Fröbisch <i>et al.</i> 2011		Sphenacodontia	13 (+ 2)	122	79 (0.65)	43 (0.35)	98 (0.80)	64 (0.81)	33 (0.77)
This analysis		'Pelycosauria'	45 (+ 8)	239	147 (0.62)	92 (0.38)	39	6	33
Numbers of new characters									

The primary aim of the present study is to review all previously proposed cladistic characters relevant to basal synapsids and use these, combined with new characters, especially of the postcranial skeleton, to test hypotheses for global relationships among basal synapsids.

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; **BP:** Bernard Price Institute, Johannesburg, South Africa; **BSPHM:** Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CMNH:** Carnegie Museum of Natural History, Pittsburgh, PA, USA; **FMNH:** Field Museum of Natural History, Chicago, IL, USA; **MCZ:** Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; **OMNH:** Sam Noble

Oklahoma Museum of Natural History, Norman, OK, USA; **ROM:** Royal Ontario Museum, Toronto, Canada; **TMM:** Texas Memorial Museum, Austin, TX, USA; **UCMP:** University of California Museum of Paleontology, Berkeley, CA, USA; **USNM:** Smithsonian Institution, Washington, DC, USA.

Methods

Taxon list

The central aim of the present study was to synthesize data relevant to global synapsid relationships and produce a large, taxon-rich topology encompassing most members of all higher clades. Thus, taxon sampling was maximized,

focusing on those taxa of which specimens were directly examined, and those for which detailed descriptions were available. In total, 45 non-therapsid synapsids were included (plus four outgroups and four therapsids; Table 3 and Online Supplementary Material Table 1). One objective of the present analysis was to elucidate the relationships between well-established higher clades of basal synapsids. Because of the importance of taxon sampling for accurate phylogenetic reconstruction (e.g. Graybeal 1998; Poe & Swofford 1999; Rydin & Källersjö 2002; Ketchum & Benson 2010) as many distinct synapsid species as possible have been included. Taxa were only not included if published descriptions were brief or under-informative, and the specimens had not been examined directly. In total, specimens of 35 out of 45 (78%) non-therapsids synapsids included in the analysis were observed directly (68% of all operational taxonomic units, OTUs). Because of the importance of basal taxa, a focused attempt was made to directly examine and include these in particular. Major omissions from the current dataset concern only the most derived representatives of Ophiacodontidae, Sphenacodontidae and Edaphosauridae. These result partly from widely-recognized uncertainty regarding taxa referred to the genera *Ophiacodon* and *Dimetrodon*. The taxonomy of these genera needs updating (Reisz 1986), and reliable descriptions exist only for a minority of specimens. Thus, *Ophiacodon* was represented by a single composite OTU. Although 12 species of *Dimetrodon* are currently recognized (Reisz 1986, 11 North American species; plus the German *Dimetrodon teutonis*, Berman *et al.* 2001) ranging stratigraphically from the ?Artinskian Putnam Formation of the Wichita Group (Romer & Price 1940; Lucas 2006) to the ?Kungurian San Angelo Formation (Olson 1962; Lucas 2006), *Dimetrodon* is also represented only by a single OTU in the present analysis. The character scores for *Dimetrodon* spp. are based primarily on *D. milleri*, the stratigraphically oldest well-known species. A diversity of derived, deep-skulled sphenacodontids such as *Bathygnathus*, *Neosaurus* and *Ctenospondylus* are known from only fragmentary remains (Nopcsa 1923; Leidy 1854; Vaughn 1969; Berman 1978; Eberth 1985), and are also excluded from the present analysis. Finally, although several species of *Edaphosaurus* are well known (e.g. Romer & Price 1940; Reisz 1986; Modesto 1995), only *E. novomexicanus* and *E. boanerges* were included in the present analysis.

Therapsida was represented by two relatively completely known basal taxa, *Biarmosuchus* (Sigogneau & Tchudinov 1972) and *Titanophoneus* (Orlov 1958), and two early taxa from the ?Roadian of China, *Biseridens* (an anomodont; Li & Cheng 1997; Liu *et al.* 2010) and *Raranimus* (Liu *et al.* 2009). *Tetraceratops*, from the Arroyo Formation (Kungurian) of Texas has been proposed as the most basal therapsid (Laurin & Reisz 1990, 1996; Amson & Laurin 2011). However, this assignment is debated and some relevant aspects of the anatomy of *Tetraceratops* are disputed

(Conrad & Sidor 2001; Rubidge & Sidor 2001; Liu *et al.* 2009). The holotype of *Tetraceratops* was not available for study and was not included in the present analysis.

Outgroups preserving most of the skeleton, that have clear taxonomic concepts and adequate published descriptions, are important to establish the primitive state of characters and ensure an accurate phylogenetic reconstruction. Thus, two derived stem-group amniotes were used, the basal diadectomorphs *Limnoscelis paludis* (Williston 1911; Romer 1946; Reisz 2007) and *Tseajaia campi* (Moss 1972), and two basal eureptiles, *Protorothyris archeri* (Clark & Carroll 1973) and *Captorhinus* spp., which has been described in detail many times (Price 1935; Fox & Bowman 1966; de Ricqlès & Bolt 1983; Sumida 1990; Holmes 1977, 2003; Modesto 1998).

Character list

The character list used in the current analysis included 239 characters compiled from a thorough review of all previous analyses including substantial numbers of basal synapsids (Reisz 1980, 1986; Brinkman & Eberth 1983; Reisz *et al.* 1992a, 1998, 2009; Laurin 1993; Modesto 1994, 1995; Berman *et al.* 1995; Sidor & Hopson 1998; Modesto *et al.* 2001; Reisz & Dilkes 2003; Sidor 2003; Anderson & Reisz 2004; Reisz & Laurin 2004; Maddin *et al.* 2006, 2008; Campione & Reisz 2010; Fröbisch *et al.* 2011). All characters were critically assessed for inclusion in the current analysis, and most were accepted. Only 44 characters were excluded. These primarily comprised autapomorphies of single taxa, characters that were deemed redundant with other, included, characters, and therapsid synapomorphies, of which only a limited set were included. Thirty-nine new characters were formulated based on observations made during the present study and previously in the literature (new characters: 7, 28, 79, 87, 99, 145, 148, 149, 152, 155, 159–162, 165–167, 180, 184, 187, 192–196, 199, 201, 203, 210, 212, 214, 220, 222, 226, 230, 232–235). Of these, most concerned the postcranial skeleton (33 characters), which was the focus of this study. The complete character list, with detailed descriptions, discussion, and the rationale behind excluded characters is included in Online Supplementary Material Appendix 1. The proportion of characters shared between the present analysis and previous analyses is given in Table 2.

Data matrix

The data matrix comprised 239 characters and 53 taxa (Online Supplementary Material Appendix 2). In all analyses *Tseajaia campi* and *Limnoscelis paludis* were specified as outgroups, and topology of non-synapsids was constrained so that *Captorhinus* spp. and *Protorothyris archeri* were united in a clade as the sister taxon of Synapsida. This was done to implement the consensus of basal amniote interrelationships (e.g. Laurin & Reisz 1995),

Table 3. List of taxa included in the present analysis with selected provenance information, data sources and the proportion of missing data scored in the matrix. Asterisks indicate taxa scored entirely from published descriptions (i.e. specimens were not examined). Data sources are listed in Online Supplementary Material Table 1.

Taxon	Locality	Horizon	Missing data (%)		
			Total	Cranial	Postcranial
Outgroups					
<i>Tseajaia campi</i> *	San Juan County, Utah	Organ Rock Formation, Cutler Group	17.9	17.0	19.6
<i>Limnocelis paludis</i> *	El Cobre Canyon, New Mexico	Cutler Formation, Cutler Group	15.1	12.9	18.5
<i>Captorhinus</i> spp.	USA	Clear Fork Group and other horizons	8.4	9.5	6.5
<i>Protorothyris archeri</i> *	Archer County, New Mexico	Moran Formation, Wichita Group	31.4	16.3	55.4
Synapsida					
<i>Echinoperon intermedium</i>	Florence, Nova Scotia	Morien Group, above the Lloyd Coal Seam	80.8	86.4	71.7
Caseasauria					
<i>Eothyris parkeyi</i>	Archer County, Texas	Petrolia Formation, Wichita Group	51.5	21.1	100.0
<i>Oedaleops campi</i> *	Rio Arriba County, New Mexico	Cutler Formation, Cutler Group	66.9	46.3	100.0
<i>Oromycter dolesorum</i>	Comanche County, Oklahoma	Fissure fill possibly equivalent to the lowermost Clear Fork Group	82.8	74.1	96.7
<i>Casea broili</i>	Baylor County, Texas	<i>Cacops</i> bonebed, Arroyo/Vale Formation, Clear Fork Group	23.0	27.2	16.3
<i>Trichasaurus texensis</i>	Baylor County, Texas	Arroyo Formation, Clear Fork Group	85.8	100.0	63.0
‘ <i>Casea</i> ’ <i>rutena</i> *	Aveyron, France	Saxonian (Lower Permian)	44.4	21.8	80.4
<i>Ennatosaurus tector</i>	Moroznitsa Locality, near Pinega and Karpoga, Russia	Early Tartarian (late Guadalupian)	26.8	12.2	50.0
<i>Caseopsis agilis</i>	Knox County, Texas	San Angelo Formation, Pease River Group	87.0	95.2	73.9
<i>Angelosaurus dolani</i>	Knox County, Texas	San Angelo Formation, Pease River Group	77.8	100.0	42.4
<i>Angelosaurus romeri</i>	Knox County, Texas	Flowerpot Formation, Pease River Group	56.5	73.5	29.3
<i>Cotylorhynchus romeri</i>	Cleveland and Logan counties, Oklahoma	Hennessey Formation	11.7	16.3	4.3
<i>Cotylorhynchus bransoni</i>	Kingfisher and Blaine counties, Oklahoma	Flowerpot Formation, Pease River Group	63.2	90.5	19.6
<i>Cotylorhynchus hancocki</i>	Hardeman and Knox counties, Texas	San Angelo Formation, Pease River Group	44.8	65.3	11.9
Varanopidae					
<i>Archaeovenator hamiltonensis</i> *	Greenwood County, Kansas	Calhoun Shale Formation, Shawnee Group	28.5	17.0	46.7
<i>Pyozia mesenensis</i> *	Mezen District, Russia	Krasnoschelsk Formation, Lower Tartarian (Late Guadalupian)	78.7	68.0	95.7
<i>Mycterosaurus longiceps</i>	Baylor County, Texas	Clyde Formation, Clear Fork Group	39.3	31.9	51.1
<i>Mesenosaurus romeri</i>	Mezen District, Russia	Lower Tartarian (Late Guadalupian)	28.5	6.1	64.1
<i>Heleosaurus scholtzi</i> *	Cape Province, South Africa	<i>Tapinocephalus</i> Assemblage Zone, Abrahamskraal Formation, Beaufort Group	28.0	18.4	43.5
BP/1/5678 (? <i>Elliotsmithia</i>)	Cape Province, South Africa	<i>Tapinocephalus</i> Assemblage Zone, Abrahamskraal Formation, Beaufort Group	82.0	72.1	97.8
<i>Basicranodon fortillensis</i> *	Comanche County, Oklahoma	Fissure fill possibly equivalent to the lowermost Clear Fork Group	95.4	92.5	100.0
<i>Aerosaurus greenleeorum</i>	El Cobre Canyon, New Mexico	Cutler Formation, Cutler Group	89.1	94.6	80.4
<i>Aerosaurus wellesi</i>	Rio Arriba County, New Mexico	Cutler Formation, Cutler Group	28.0	19.0	42.4
<i>Ruthiromia elcobriensis</i>	El Cobre Canyon, New Mexico	Cutler Formation, Cutler Group	76.6	95.2	46.7

(Continued on next page)

Table 3. List of taxa included in the present analysis with selected provenance information, data sources and the proportion of missing data scored in the matrix. Asterisks indicate taxa scored entirely from published descriptions (i.e. specimens were not examined). Data sources are listed in Online Supplementary Material Table 1. (*Continued*)

Taxon	Locality	Horizon	Missing data (%)		
			Total	Cranial	Postcranial
<i>Varanodon agilis</i>	Blaine County, Oklahoma	Chickasha Formation, El Reno Group	44.8	36.7	57.6
<i>Varanops brevirostris</i>	Baylor County, Texas	<i>Cacops</i> bonebed, Arroyo/Vale Formation, Clear Fork Group	14.6	19.0	7.6
<i>Watongia meieri</i>	Blaine County, Oklahoma	Chickasha Formation, El Reno Group	76.2	88.4	56.5
Ophiacodontidae					
<i>Archaeothyris florensis</i>	Florence, Nova Scotia	Morien Group, above the Lloyd Coal Seam	61.5	64.6	56.5
<i>Varanosaurus acutirostris</i>	Baylor County, Texas; Garvin County, Oklahoma	Arroyo Formation, Clear Fork Group; Wellington Formation	22.6	10.9	41.3
<i>Ophiacodon</i> spp.	Texas and New Mexico	Cutler Formation; Belle Plains, Putnam and Admiral formations, Wichita Group; Clyde Formation, Clear Fork Group; Fort Riley Limestone, Chase Group	6.7	10.9	0.0
<i>Stereophallodon ciscoensis</i>	Clay and Archer counties, Texas	Pueblo Formation, Cisco Group	69.9	68.0	72.8
Edaphosauridae ± Sphenacodontia					
<i>Ianthodon schultzei</i> *	Anderson County, Kansas	Stanton Formation, Lansing Group	69.5	50.3	100.0
Edaphosauridae					
<i>Ianthasaurus hardستiorum</i>	Anderson County, Kansas	Stanton Formation, Lansing Group	43.9	34.7	58.7
<i>Glaucosaurus megalops</i>	Baylor County, Texas	Waggoner Ranch Formation, Wichita Group	82.0	70.7	100.0
<i>Lupeosaurus kayi</i>	Archer County, Texas	Moran Formation, Wichita Group	72.4	100.0	28.3
<i>Edaphosaurus boanerges</i>	Archer County, Texas	Admiral Formation, Wichita Group	10.9	7.5	16.3
<i>Edaphosaurus novomexicanus</i>	Rio Arriba County, New Mexico	Cutler Formation, Cutler Group	52.7	48.3	59.8
Sphenacodontia					
<i>Haptodus garnettensis</i>	Anderson County, Kansas	Stanton Formation, Lansing Group	13.8	7.5	23.9
<i>Pantelosaurus saxonicus</i> *	Saxony, Germany	Döhlen Formation	52.7	38.8	75.0
<i>Cutleria wilmarthi</i>	Near Placerville, Colorado	Cutler Formation, Cutler Group	58.9	44.9	81.5
<i>Secodontosaurus obtusidens</i>	Archer, Wichita and Baylor counties, Texas	Admiral and Petrolia formations, Wichita Group; Arroyo Formation, Clear Fork Group	21.8	8.2	43.5
<i>Cryptovenator hirschbergeri</i> *	Rhineland Palatinate, Germany	Remigius Formation	94.6	91.2	100.0
<i>Ctenorhachis jacksoni</i> *	Archer and Baylor counties, Texas	Admiral and Petrolia formations, Wichita Group	88.7	100.0	70.7
<i>Dimetrodon</i> spp.	Texas, Arizona, New Mexico, Utah, Arizona, Germany	Wichita, Clear Fork and Pease River Groups; Tambach Formation	1.3	2.0	0.0
<i>Sphenacodon</i> spp.	New Mexico	Cutler Formation, Cutler Group	14.6	3.4	32.6
Therapsida					
<i>Biarmosuchus tener</i> *	Ezhovo locality, Russia	Capitanian	33.5	23.1	50.0
<i>Biseridens qilianicus</i> *	Dashankou locality, China	?Roadian	51.9	21.8	100.0
<i>Raranimus dashankouensis</i> *	Dashankou locality, China	?Roadian	85.4	76.9	100.0
<i>Titanophoneus potens</i> *	Near Isheevo	Capitanian	12.1	7.5	19.6

because the data matrix was not designed to test the monophyly of either Reptilia or Synapsida.

Analyses

Full dataset (and analytical protocols)

The full data matrix was analysed in PAUP* 4.0b10 for Macintosh (Swofford 2002) using PAUPRat (Sikes & Lewis 2001) followed by the tree bisection and reconnection (TBR; Swofford & Olsen 1990; Kitching *et al.* 1998) branch swapping algorithm. PAUPRat is an implementation of the Parsimony Ratchet (Nixon 1999), an iterative reweighting scheme that is effective at rapidly discovering islands of minimum-length trees. Results were confirmed using a heuristic search with 500 random addition replicates. These analyses resulted in 15,552 most parsimonious trees (MPTs) of 713 steps; each tree has an ensemble consistency index (CI) of 0.4508, retention index (RI) of 0.7521 and a rescaled consistency index (RC) of 0.3396.

The strict consensus of 15,552 MPTs is generally well resolved (Fig. 2A). The commonly recognized major clades of basal synapsids (e.g. Reisz 1980, 1986) are recovered. However, relationships among these clades differ from recent consensus because Ophiacodontidae and Varanopidae are the most basal synapsid clades, forming a polytomy with *Archaeothyris*, *Echinerpeton*, and a clade comprising Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia. A tree consistent with recent consensus, in which Caseasauria, Varanopidae and Ophiacodontidae form successively more derived branches of a ‘stem’ leading to Edaphosauridae + Sphenacodontia (Reisz 1986; Modesto & Reisz 1992; Reisz *et al.* 1992a; Berman *et al.* 1995) requires a minimum of two additional steps. Analyses enforcing a constraint tree that places Caseasauria as the most basal synapsid clade recover 3888 trees 715 steps long. The strict consensus of these trees is shown in Fig. 3.

Areas of poor resolution within Varanopidae, Caseidae and Sphenacodontidae result from the presence of taxa of uncertain affinities that occupy multiple positions in the set of MPTs (‘wildcard’ taxa). Wildcard taxa are identified by inspecting the Adams consensus, following the approach of Benson (2010) and Ketchum & Benson (2010). For example, *Echinerpeton* (80.8% missing data) occupies three possible positions equally parsimoniously in the set of MPTs, falling either as the most basal synapsid, as the sister taxon of Caseasauria + Edaphosauridae + Sphenacodontia, or as an ophiacodontid more derived than *Archaeothyris* (i.e. the sister taxon of *Varanosaurus* + *Ophiacodon* + *Stereophallodon*). Thus, pruning the MPTs by deletion of *Echinerpeton* results in a reduction from 15,552 to 7776 unique MPTs, and resolution of a basal clade comprising Ophiacodontidae + Varanopidae in the strict consensus of these trees. This prun-

ing approach is an implementation of the Strict Reduced Consensus method (e.g. Wilkinson 2003). Pruning the sphenacodontid *Ctenorhachis jacksoni* (88.7% missing data) results in a reduction to 1728 unique MPTs and full resolution within Sphenacodontidae. Deletion of the caseid *Caseopsis agilis* (87.0% missing data) results in a reduction to 2160 unique MPTs and full resolution of caseid relationships other than within the *Cotylorhynchus* + *Angelosaurus* clade (Fig. 2B). Subsequent deletion of *Angelosaurus dolani* (77.8% missing data) results in a reduction to 432 MPTs and full resolution within Caseidae. Deletion of *Basicranodon fortisillensis* (95.4% missing data) results in a reduction to 7776 MPTs and markedly improved resolution within Varanopidae, although the Middle Permian mycterosaurines *Mesenosaurus*, *Heleosaurus* and BP/1/5678 still form a polytomy. Finally, deletion of all five of these wildcard taxa results in a reduction to 12 MPTs and resolution of all the clades described above (Fig. 2B). Reanalysis of this reduced version of the dataset recovers a smaller set of six MPTs (length = 707 steps; CI = 0.4547; RI = 0.7492; RC = 0.3412) using both the parsimony ratchet and heuristic search algorithms. In the strict consensus of these trees, the position of *Ianthodon* is resolved as the sister taxon of Edaphosauridae + Sphenacodontidae (Fig. 2B). The only remaining polytomies are among Middle Permian mycterosaurines and within Edaphosauridae, comprising *Lupeosaurus*, *Glaucosaurus*, and an *Edaphosaurus* clade. Because *Lupeosaurus* is only known from postcranial material, and *Glaucosaurus* is known only from the skull, this polytomy cannot be resolved (Mazier-ski & Reisz 2010). The full optimization of characters over the strict consensus of the analysis excluding wildcard taxa (Fig. 2B) is given in Online Supplementary Material Table 2.

Bremer support was calculated using commands generated by the ‘Decay Index PAUP File’ function of MacClade 4.01 (Maddison & Maddison 2001). These commands were implemented one by one in PAUP* 4.0b10. Thus each node was tested individually using both PAUPRat (Sikes & Lewis 2001) and a heuristic search (150 random addition replicates with TBR branch swapping, and saving multiple trees) to ensure that the shortest length cladograms were found. The resulting cladograms were inspected to determine the reason for poor support. In most cases, poor support resulted from a single taxon with a high proportion of missing data that could occupy a wide range of different phylogenetic positions in cladograms only slightly longer than the MPTs. For example, given one additional step the sphenacodontid *Cryptovenator hirschbergeri* (94.6% missing data) can be placed within Therapsida or as the sister taxon of the clade comprising *Pantelosaurus saxonicus* and all more derived sphenacodontians; the edaphosaurid *Glaucosaurus megalops* (82.4% missing data) can be placed as the sister taxon

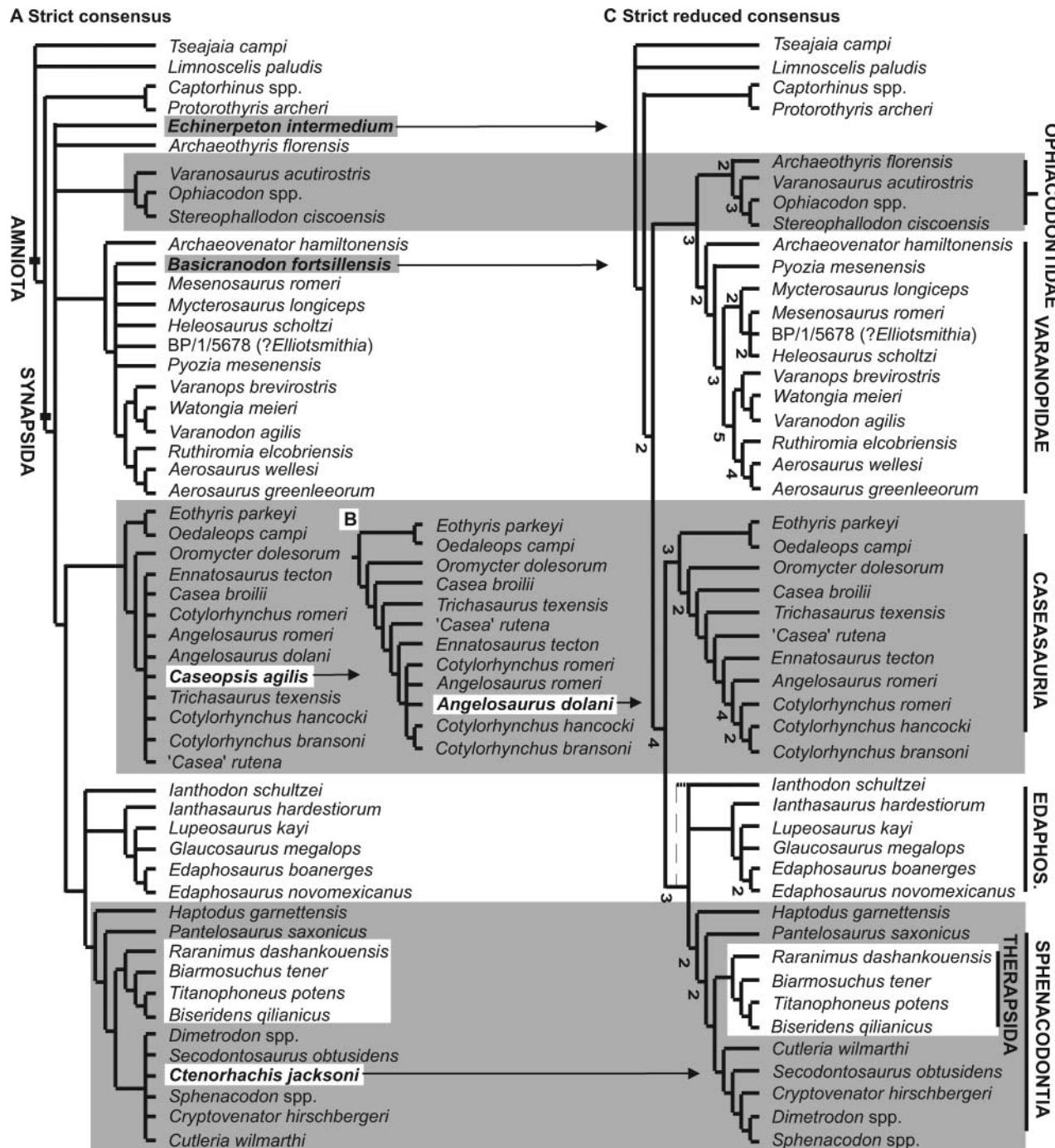


Figure 2. Consensus cladograms of trees derived from analysis of the full dataset. **A**, strict consensus of 15,552 MPTs (length = 713 steps) prior to pruning wildcard taxa (highlighted and in bold type); **B**, local topology within Caseasauria after pruning *Caseopsis agilis*; **C**, strict reduced consensus after pruning wildcard taxa from the full set of MPTs. Numbers below nodes indicate Bremer support values. Dotted lines indicate alternative topologies recovered by reanalysis of the data excluding wildcard taxa. Abbreviation: Edaphos., Edaphosauridae.

of *Edaphosaurus* spp. or as the sister taxon of the clade comprising *Ianthodon* + Edaphosauridae + Sphenacodontia; the caseid *Trichasaurus texensis* (85.8% missing data) can be placed as the sister taxon of the clade comprising *Angelosaurus romeri* and all more derived caseids or as the

most basal caseid; and the varanodontine varanopid *Watongia meieri* (76.2% missing data) can be placed as the most basal varanodontine. Substantially higher branch support was obtained for many clades after deletion of such unstable taxa (see Reduced dataset, below).

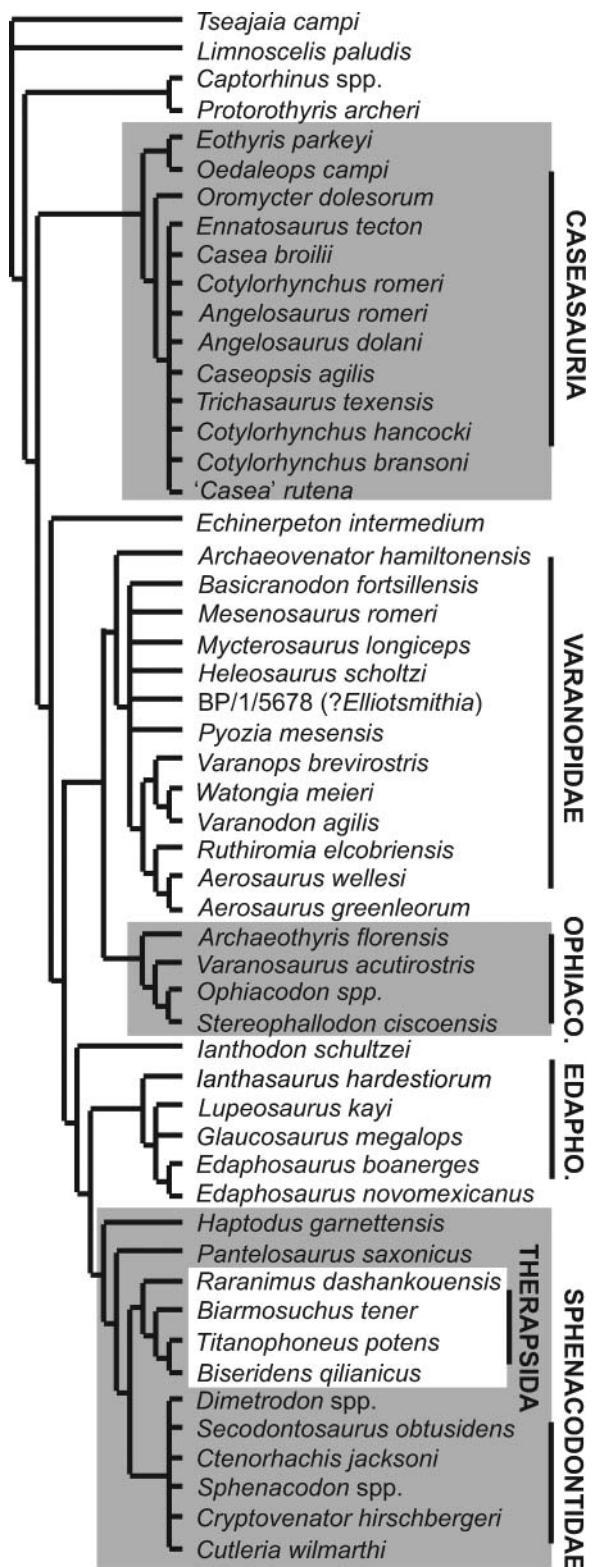


Figure 3. Strict consensus of 3888 suboptimal cladograms (length = 715 steps) derived from analysis of the full dataset constrained so that Caseasauria occupies a basal position within Synapsida. Abbreviations: Edaphos., Edaphosauridae; Ophiacod., Ophiacodontidae.

Cranial dataset

A version of the dataset pruned so that it included only cranial characters, and only those taxa that preserve cranial material, consisted of 49 taxa scored for 147 characters. Thus, taxa known only from postcranial material, *Angelosaurus dolani*, *Ctenorhachis jacksoni*, *Lupeosaurus kayi* and *Trichasaurus texensis*, were not included in the cranial dataset. This matrix was analysed following the procedure outlined above (see Full dataset (and analytical protocols), above), resulting in >100,000 MPTs 459 steps long (CI = 0.4379; RI = 0.7495; RC = 0.3282). The strict consensus of these cladograms was poorly resolved (Fig. 4A). Although Eothyrididae, Caseidae, Varanopidae, Ophiacodontidae (excluding *Archaeothyris*), Edaphosauridae and Sphenacodontia (excluding *Haptodus* and *Ianthodon*) were found as clades, they formed a polytomy with one another, and with *Archaeothyris*, *Echinerpeton*, *Haptodus* and *Ianthodon*. Furthermore, locally unresolved areas existed within Caseidae and Varanopidae, and at the base of Sphenacodontia. Implementation of the Strict Reduced Consensus Method, as conducted above for the full dataset, allowed identification of six wildcard taxa. These included *Echinerpeton*, three varanopids (*Basicranodon fortsillensis*, *Ruthiromia elcobriensis* and *Watongia meieri*), and two caseids (*Caseopsis agilis*, *Cotylorhynchus bransoni*). Pruning *Echinerpeton* improved global resolution, whereas pruning the other taxa had local effects. Pruning all six taxa resulted in a reduction to 66 unique MPTs and substantial improvements in resolution (Fig. 4B); Caseasauria was resolved as the most basal synapsid clade, but among more derived synapsids *Archaeothyris*, Ophiacodontidae (excluding *Archaeothyris*) and Varanopidae formed a polytomy with Edaphosauridae + Sphenacodontia. Reanalysis of this reduced version of the dataset recovered 18 MPTs (length = 458 steps; CI = 0.4389; RI = 0.7453; RC = 0.3271) using both the parsimony ratchet and heuristic search algorithms. The strict consensus of these trees was better resolved than the strict reduced consensus (Fig. 4B); Ophiacodontidae + Varanopidae was found as a clade with identical topology to that recovered from the full dataset, *Haptodus* was resolved as the most basal sphenacodontian, and *Ianthodon* was found as the sister taxon of Edaphosauridae + Sphenacodontia. Polytomies in this tree could not be further resolved.

Relationships within higher clades of basal synapsids derived from the cranial data partition are similar to, though less well resolved than, those derived from the full dataset. However, the relationships among these clades are substantially different as Caseasauria is found as the most basal synapsid clade. This arrangement resembles the recent consensus, in which Caseasauria, Varanopidae and Ophiacodontidae are successively more derived branches off a stem leading to Edaphosauridae + Sphenacodontia (Reisz 1986; Modesto & Reisz 1992; Reisz *et al.* 1992a; Berman *et al.* 1995). However, it differs from this arrangement

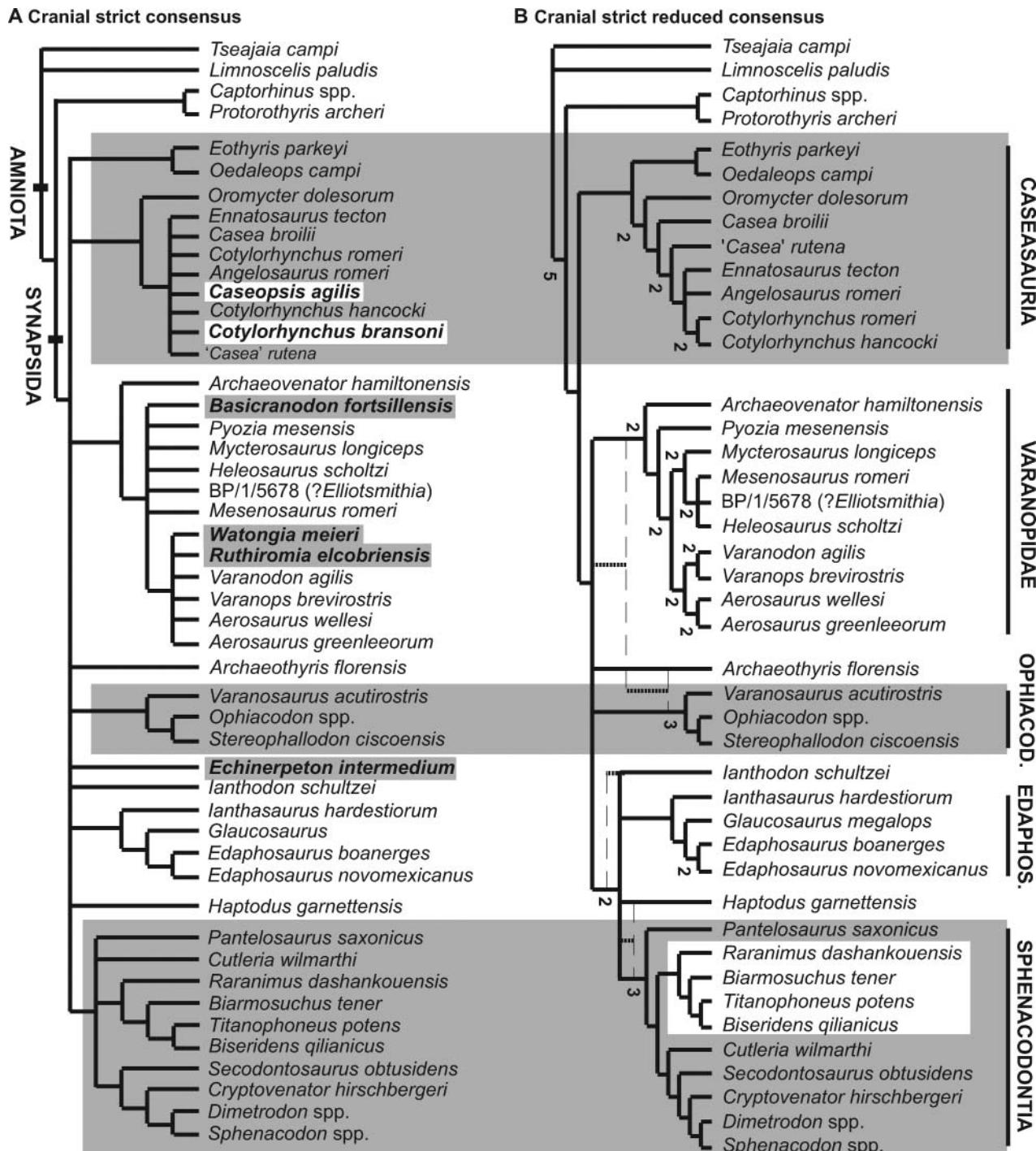


Figure 4. Consensus cladograms of trees derived from analysis of the cranial data partitions. **A**, strict consensus of >100,000 MPTs (length = 459 steps) prior to pruning wildcard taxa (highlighted and in bold type); **B**, strict reduced consensus after pruning wildcard taxa from the full set of MPTs. Numbers below nodes indicate Bremer support values. Dotted lines indicate alternative topologies recovered by reanalysis of the data excluding wildcard taxa. Abbreviations: Edaphos., Edaphosauridae; Ophiacod., Ophiacodontidae.

in that Varanopidae + Ophiacodontidae form a clade (or polytomy; Fig. 4B), rather than being successive branches, on the line leading to *Ianthodon* + Edaphosauridae + Sphenacodontia.

Postcranial dataset

A version of the dataset pruned so that it only included postcranial characters, and only those taxa that preserved postcranial material, consisted of 45 taxa scored for

92 characters. Thus, taxa known only from cranial material, *Basicranodon fortsillensis* (a wildcard in the full dataset), *Cryptovenator hirschbergeri*, *Glaucosaurus megalops*, both eothyridids (*Eothyris parkeyi*, *Oedaleops campi*), and two therapsids (*Biseridens qilanicus*, *Raranimus dashankouensis*), were not included in the postcranial dataset. This matrix was analysed following the procedure outlined above (see Full dataset (and analytical protocols)), resulting in >100,000 MPTs 247 steps long (CI = 0.4878; RI = 0.7697; RC = 0.3770). The strict consensus of these trees was poorly resolved (Fig. 5A). The only clade resolved within Synapsida was Edaphosauridae. Poor

global resolution resulted from placement of the varanopids BP/1/5678 and *Pyozia mesensis* within a range of basal synapsid clades in the set of MPTs. The postcranial skeletons of these taxa are highly incomplete and show few synapomorphies. Pruning these two taxa from the set of MPTs results in the resolution of Varanodontinae and a clade comprising Caseasauria (Caseidae) as the sister taxon of Edaphosauridae + Sphenacodontia. Caseasauria (Caseidae) and Sphenacodontia lack internal resolution. Deletion of the caseids *Caseopsis agilis* and *Oromycter dolesorum*, and the sphenacodontians *Ctenorhachis jacksoni* and *Pantelosaurus saxonicus*, results in a reduction

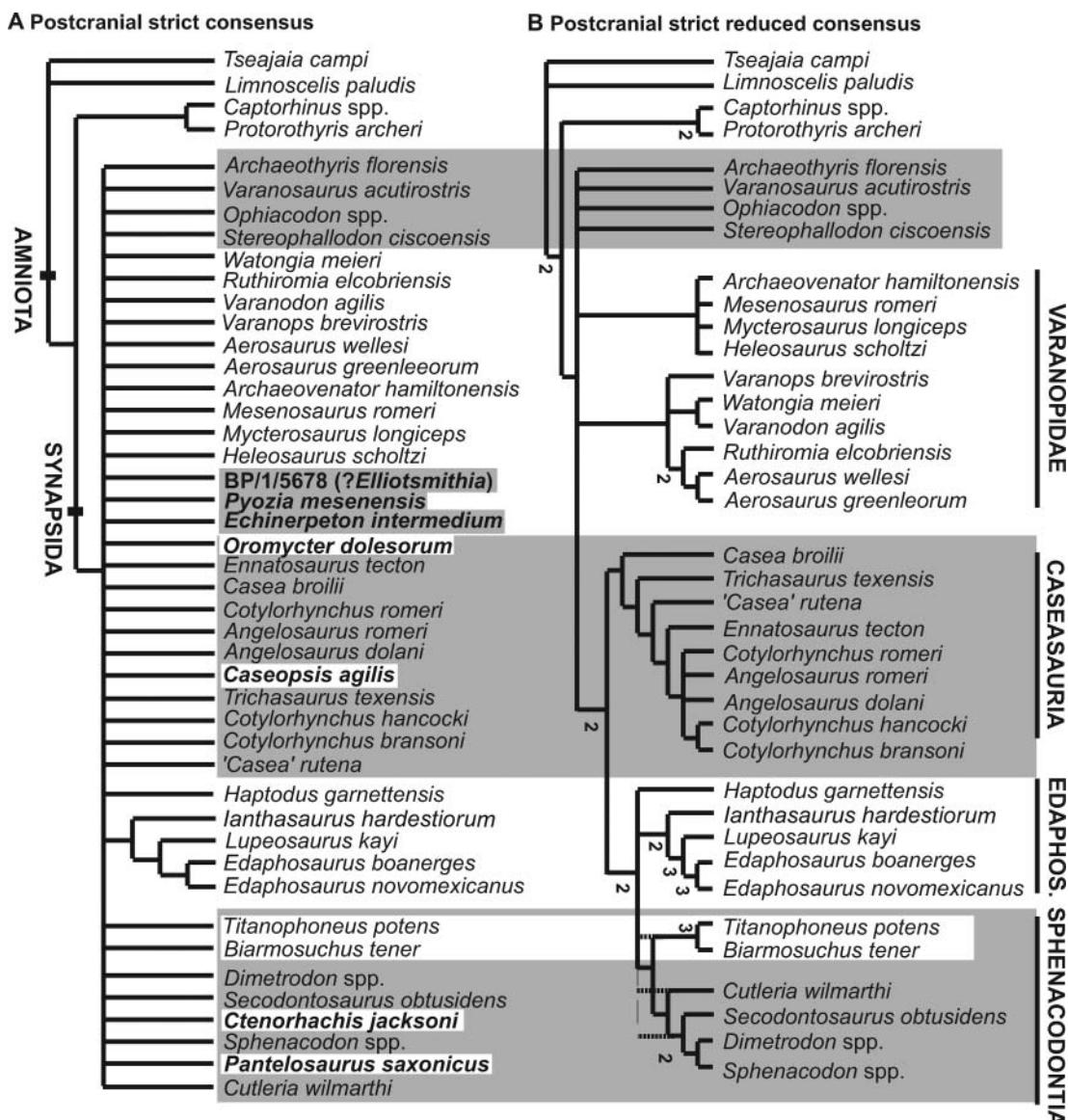


Figure 5. Consensus cladograms of trees derived from analysis of the postcranial data partition. **A**, strict consensus of >100,000 MPTs (length = 247 steps) prior to pruning wildcard taxa (highlighted and in bold type); **B**, strict reduced consensus after pruning wildcard taxa from the full set of MPTs. Numbers below nodes indicate Bremer support values. Dotted lines indicate alternative topologies recovered by reanalysis of the data excluding wildcard taxa. Abbreviation: Edaphos., Edaphosauridae.

in the number of MPTs and increased local resolution (Fig. 5B). Deletion of *Echinerpeton* results in the resolution of Mycterosaurinae, but the ophiacodontid taxa (*Archaeothyris*, *Ophiacodon*, *Stereophallodon*, *Varanosaurus*) form a basal polytomy with Mycterosaurinae and Varanodontinae, and resolution cannot be improved further by taxon deletions. Reanalysis of this reduced version of the dataset recovers 21,600 MPTs (length = 244 steps; CI = 0.4938; RI = 0.7648; RC = 0.3793) using both the parsimony ratchet and heuristic search algorithms. The strict consensus of these trees (Fig. 5B; dotted lines) differs from the strict reduced consensus by the placement of *Cutleria* in a polytomy with Edaphosauridae, *Haptodus*, Sphenacodontidae and Therapsida. Both topologies are identical to the strict consensus of cladograms derived

from analysis of the full dataset, but for the presence of fewer resolved nodes. Polytomies in the strict consensus could not be further resolved.

Reduced dataset

A reduced version of the dataset included only taxa that were not wildcards in any of the preceding analyses, and which preserved both cranial and postcranial data (excluded taxa are listed in Table 4). This resulted in 32 included taxa. Analysis of the reduced dataset (as described above) resulted in a single most parsimonious cladogram 643 steps long (CI = 0.4961; RI = 0.7403; RC = 0.3696). The resulting topology was similar to that of the strict reduced consensus derived from the full dataset, but included fewer taxa.

Table 4. List of taxa excluded from the reduced dataset and the proportion of missing data in those taxa. These taxa behaved as ‘wildcards’ in one or more analysis or entirely lacked either cranial or postcranial data.

Taxon	Wildcard (full dataset)	% missing data	Wildcard (cranial dataset)	% cranial missing data	Wildcard (postcranial dataset)	% postcranial missing data
<i>Synapsida incertae sedis</i>						
<i>Echinerpeton intermedium</i>	Y	80.8	Y	86.4	Y	71.7
<i>Caseasauria</i>						
<i>Eothyris parkeyi</i>		51.5		21.1	N/A	100
<i>Oedaleops campi</i>		66.9		46.3	N/A	100
<i>Caseidae</i>						
<i>Oromycter dolesorum</i>		82.8		74.1	Y	96.7
<i>Trichasaurus texensis</i>		85.8	N/A	100		63.0
<i>Caseopsis agilis</i>	Y	87.0	Y	95.2	Y	73.9
<i>Angelosaurus dolani</i>	Y	77.8	N/A	100		42.4
<i>Cotylorhynchus bransoni</i>		63.2	Y	90.5		19.6
<i>Varanopidae</i>						
<i>Pyozia mesenensis</i>		78.7		68.0	Y	95.7
BP/1/5678		82.0		72.1	Y	97.8
(? <i>Elliotsmithia</i>)						
<i>Basicranodon fortisillensis</i>	Y	95.4	Y	92.5	N/A	100
<i>Ruthiromia elcobriensis</i>		76.6	Y	95.2		46.7
<i>Watongia meieri</i>		76.2	Y	88.4		56.5
<i>Edaphosauridae</i> ± <i>Sphenacodontia</i>						
<i>Ianthodon schultzei</i>		69.5		50.3	N/A	100
<i>Edaphosauridae</i>						
<i>Glaucosaurus megalops</i>		82.0		70.7	N/A	100
<i>Lupeosaurus kayi</i> ,		72.4	N/A	100		28.3
<i>Sphenacodontia</i>						
<i>Pantelosaurus saxonicus</i>		52.7		38.8	Y	75.0
<i>Cryptovenator hirschbergeri</i>		94.6		91.2	N/A	100
<i>Ctenorhachis jacksoni</i>	Y	88.7	N/A	100	Y	70.7
<i>Therapsida</i>						
<i>Biserridens qilanicus</i>		51.9		21.8	N/A	100
<i>Raranimus dashankouensis</i>		85.8		76.9	N/A	100

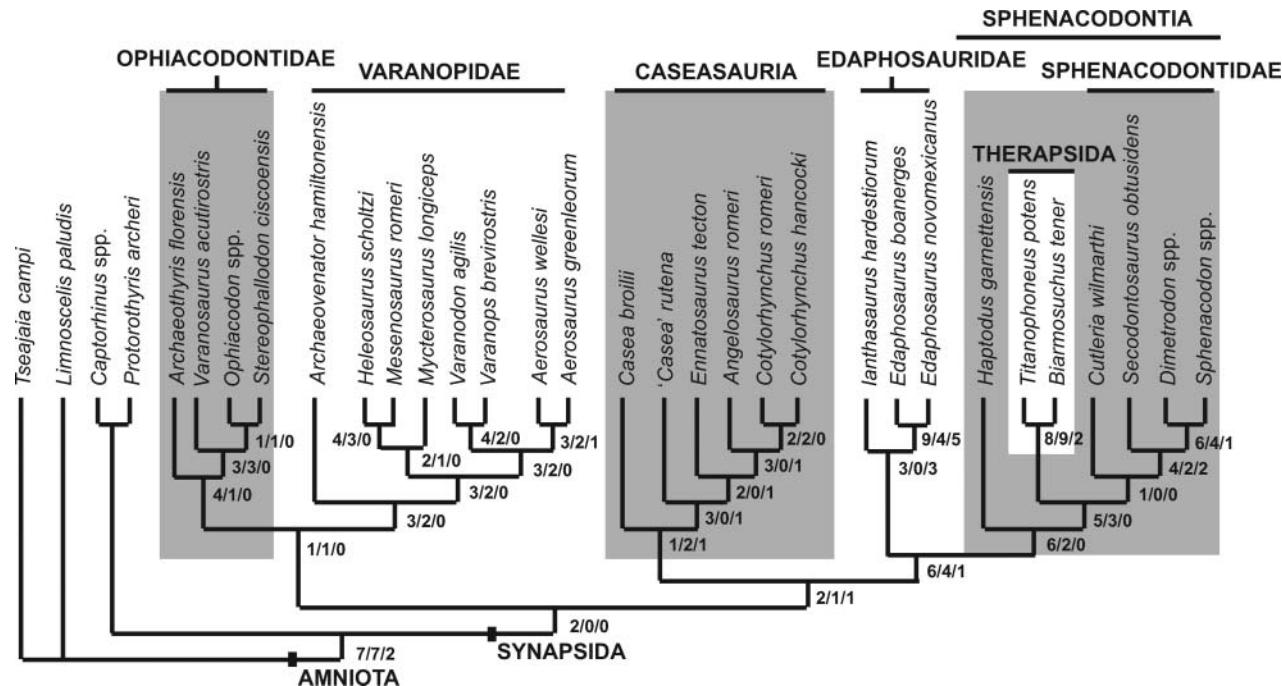


Figure 6. Single most parsimonious cladogram 643 steps long ($CI = 0.4961$; $RI = 0.7403$; $RC = 0.3696$) resulting from analysis of the reduced dataset, excluding taxa listed in Table 4. Numbers below nodes indicate Bremer support recovered using the full dataset, the cranial data partition and the postcranial data partitions (separated by ‘/’s (full dataset/cranial/postcranial)).

This topology was used to calculate Bremer support using the Decay Index PAUP File function of MacClade 4.01 (Maddison & Maddison 2001). The resulting command file was executed to assess the relative support for nodes provided by (1) the full reduced dataset; (2) the cranial partition of the reduced dataset and (3) the postcranial partition of the reduced dataset. The results are given in Fig. 6. Particularly high branch support (six–nine) characterizes Amniota, Therapsida, Sphenacodontinae, Sphenacodontia, *Edaphosaurus* and Edaphosauridae + Sphenacodontia. Intermediate support (three–four) was recovered for Ophiacodontidae, Varanopidae and some nodes within those two clades and within Caseidae. However, nodes uniting higher clades were poorly supported. This result is consistent with the fact that cranial and postcranial data partitions support similar topologies within higher clades, but different topologies between higher clades (Figs 4, 5).

Discussion

Global relationships

The relationships among major clades of basal synapsids recovered here differ from the recent consensus (Reisz 1986; Kemp 1988; Reisz *et al.* 1992a; Berman *et al.* 1995), in which Caseasauria, Varanopidae and Ophiacodontidae form successively more crownward branches on the stem leading to Edaphosauridae + Sphenacodontia. Instead,

when the full dataset is analysed, Caseasauria is recovered as the sister taxon of Edaphosauridae + Sphenacodontia, and a clade of Varanopidae + Ophiacodontidae is the sister taxon of Caseasauria + Edaphosauridae + Sphenacodontia (Fig. 2). Analysis of the postcranial data partition recovers a similar topology (Fig. 5; although ophiacodontid taxa are unresolved and form a basal polytomy with Mycterosaurinae and Varanodontinae in the strict reduced consensus). Only analysis of the cranial partition recovers Caseasauria as the most basal synapsid clade (Fig. 4), and even this data fails to support a derived position of Ophiacodontidae relative to Varanopidae (these families form a clade, or form a polytomy with Edaphosauridae + Sphenacodontia). Other differences between analyses of the cranial and postcranial partitions are minor.

Previous analyses have focused on cranial anatomy, and thus cranial data underlie the consensus topology (Reisz 1986; Kemp 1988; Reisz *et al.* 1992a; Berman *et al.* 1995). An important difference between the current dataset and those used in previous analyses is the inclusion of a substantial number of postcranial characters (91), almost twice as many as the previous analysis including the most postcranial characters (43; Table 2; Fröbisch *et al.* 2011). Although they only comprise 39% of characters, postcranial data are driving the relationships recovered by analysis of the full dataset herein. The highly similar postcranial skeletons of caseids and edaphosaurids previously formed the primary basis of uniting these groups within

'Edaphosaura' (Romer & Price 1940). Although some of these represent putative adaptations to bulk herbivory (e.g. the enlarged, barrel like rib cage, reduced rib tubercula, and robust limbs displaying many common features of the pelvis and femur), others concern the reduction of intercentra (character 157.1), elongated dorsal transverse processes (158.1), an increase in the number of sacral ribs (172.1), reduction of the relative size of the first sacral rib (173.1), remodelling of the iliac blade (215.0, 216.1) and elongation of the calcaneum (239.1) that are also present in Sphenacodontia and are found as unambiguous synapomorphies of Caseasauria + Edaphosauridae + Sphenacodontia in the present analysis. Furthermore, numerous features of the postcranial skeletons of ophiacodontids and varanopids are shared with outgroups and are likely plesiomorphic (Romer & Price 1940; and herein), and these doubtlessly contribute to the basal position of these clades.

Although cranial data support a basal position for Caseasauria, when the basal caseasauers *Eothyris* and *Oedaleops* are deleted from the cranial dataset Caseasauria (represented solely by Caseidae) is no longer supported as

the most basal synapsid clade (Fig. 6; cranial data provide positive branch support for a clade of Caseasauria (Caseidae) + Edaphosauridae + Sphenacodontia). This is not surprising as the skulls of *Eothyris* and *Oedaleops* are highly plesiomorphic and share numerous features with outgroup taxa (Romer 1946; Watson 1954; Langston 1965; Reisz *et al.* 2009), whereas caseid skulls are relatively derived, showing many adaptations for herbivory. However, this result provides a clear illustration of the importance of basal taxa for elucidating relationships among higher clades of basal synapsids. Thus, the absence of preserved postcranial material of *Eothyris* and *Oedaleops* is a cause for concern. Currently, a long ghost lineage precedes the first fossil appearance of the caseasaur postcranial skeleton (in caseids from the Clear Fork Group; Kungurian; Lucas 2006; older caseasauers such as *Eothyris* and *Oedaleops* are known only from skulls) (Fig. 7). This ghost lineage spans more than 30 million years (Ma) from the first representatives of other basal synapsid clades (308 Ma; *Archaeothyris*, *Echinerpeton* and a probable sphenacodontian; Bell 1966; Reisz 1972; Ogg *et al.* 2008). If postcranial character states

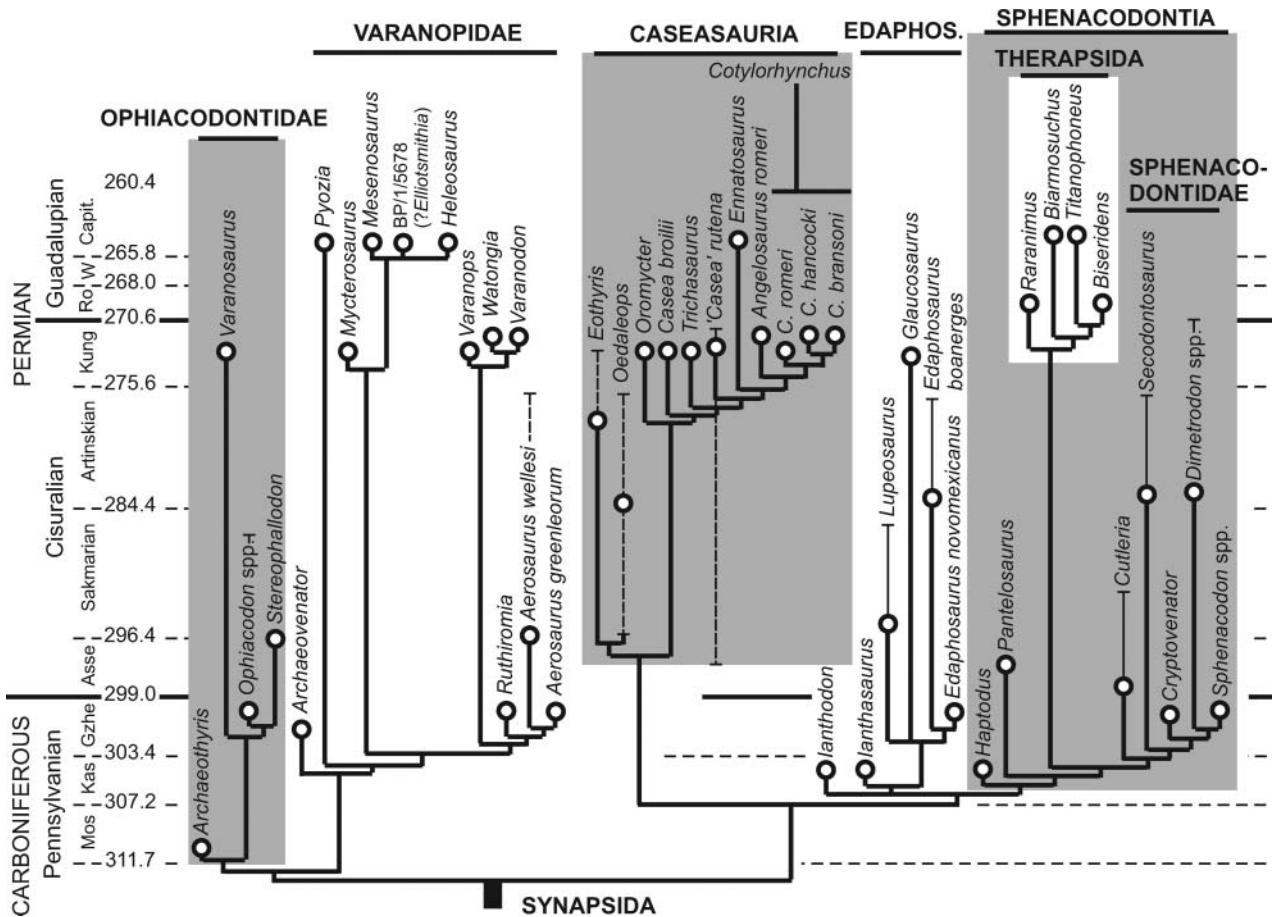


Figure 7. Time calibrated strict reduced consensus cladogram (shown without temporal data in Fig. 2C) arising from analysis of the full dataset. Abbreviation: Edaphos., Edaphosauridae.

shared by caseids and edaphosaurids/sphenacodontians were acquired independently on this ghost lineage, then support for a clade comprising Caseasauria + Edaphosauridae + Sphenacodontia would be eroded. This is plausible, given that some of these features were independently acquired by varanopids (e.g. three sacral ribs, *Aerosaurus*, Langston & Reisz 1981; loss of the lateral shelf of the ilium, *Varanops*, Campione & Reisz 2010; elongation of the calcaneum, *Ruthiromia* + *Aerosaurus* spp.; Eberth & Brinkman 1983), and other basal amniote clades as they became progressively better adapted for terrestrial locomotion. Possible evidence for the independent acquisition of derived postcranial apomorphies in Caseasauria are postcranial materials from Camp Quarry, New Mexico, briefly described and tentatively referred to the basal caseasaur *Oedaleops* by Langston (1965). These include a plesiomorphic ilium similar to those of *Limnoscelis* and *Ophiacodon*, a low, broad scapulocoracoid lacking a supraglenoid foramen (as in some varanopids and caseids), a humerus with a weakly developed fossa between the head and deltopectoral crest (Reisz 1986; a pronounced fossa is present in caseids and varanopids; Brinkman & Eberth 1983), and femora. Although the association of this material with the holotype skull and referred cranial fragments of *Oedaleops* is not reliable (Langston 1965; Reisz 1986; Reisz *et al.* 2009), redescription of this material is in progress and may yield valuable insights (Sumida *et al.* 2009). Similarly, other basal taxa that have been implicated in the origins of major clades such as *Milosaurus* (DeMar 1970; possibly a varanopid, but see Langston & Reisz 1981) and *Nitosaurus* (Romer & Price 1940; as an edaphosaurian although this material may represent multiple individuals from more than one taxon; Reisz 1986), may clarify relationships among higher clades of basal synapsids.

Understanding why cranial data do not unequivocally support a sister taxon relationship between Ophiacodontidae and Edaphosauridae + Sphenacodontia to the exclusion of Varanopidae requires re-examination of synapomorphies proposed to support this topology. Brinkman & Eberth (1983) stated that ophiacodontids shared four synapomorphies with Edaphosauridae + Sphenacodontia: (1) a concave ventral margin of the temporal bar (character 9.1 in the present analysis); (2) posterodorsally inclined anterior surface of the premaxilla (14.0); (3) dorsal process of the stapes articulating in a socket on the paraoccipital process (94.1); and (4) an extended ventral plate of the angular (143.1). Reisz (1986) added to this list that (5) the nasal is longer than the parietal, and Berman *et al.* (1995) recovered five additional synapomorphies of this node: (6) a parietal comprising less than one-fourth of the length of the skull roof; (7) a small pineal foramen (<0.2 times the parietal width; character 84.0); (8) narrow posterior process of the postorbital (69.1); (9) postorbital portion of skull shorter than preorbital portion (2.1); and (10) the jugal makes a wide contribution to the ventral margin of the skull (71.0).

Thus, a total of 10 synapomorphies uniting Ophiacodontidae with Edaphosauridae + Sphenacodontia have been proposed. Eight of these 10 features were included in the present analysis, but do not support the topology proposed by Brinkman & Eberth (1983) or Reisz (1986), either because a different distribution was observed in the present study, or because other character sets present a stronger phylogenetic signal. Thus, some comments are required. Firstly, two characters proposed as synapomorphies of the clade comprising Ophiacodontidae + Sphenacodontia + Edaphosauridae are present in varanopids: the anterior surface of the varanopid premaxilla slopes posterodorsally, unlike the situation in caseasaus (Reisz 1986, p. 91; *contra* Brinkman & Eberth 1983); and it is now known that the jugal makes a broad contribution to the ventral skull margin in basal varanopids (e.g. Reisz & Berman 2001; Reisz & Dilkes 2003), identical to the condition in ophiacodontids, edaphosaurids and sphenacodontids, and unlike the situation in caseasaus (e.g. Reisz *et al.* 2009). Secondly, several of the characters listed above pertain to proportional elongation of the snout and are redundant with one another (nasal longer than parietal; parietal comprises less than one-fourth of the length of the skull; postorbital skull shorter than preorbital skull; equivalent to characters 2, 47 and 56 in the present analysis). Finally, the ventral margin of the temporal bar in ophiacodontids is approximately straight, and not distinctly concave as in edaphosaurids and sphenacodontids. The concave margin reconstructed in *Archaeothyris* by Reisz (1972) cannot be confirmed from preserved material, and *Varanosaurus* has a straight ventral margin (FMNH PR 1760; Berman *et al.* 1995, fig. 11; the left temporal bar is slightly broken ventrally), as do all well-preserved skulls of *Ophiacodon* (Online Supplementary Material Appendix 1 Fig. A1B; USNM 487098, FMNH UC 458; Romer & Price 1940, fig. 3C–D; *contra* Romer & Price 1940, fig. 3B and Reisz 1986, fig. 36, which are based on the highly reconstructed skull of MCZ 1366).

Intraclass relationships

Ophiacodontidae. Ophiacodontidae have received comparatively little recent attention. The analysis of Berman *et al.* (1995), accompanying a redescription of *Varanosaurus*, included the biggest ophiacodontid taxon sample and recovered *Archaeothyris* as the sister taxon of a clade comprising *Ophiacodon* + *Varanosaurus*. Many possible ophiacodontids are only briefly described, and several, including *Baldwinonus* (Brinkman & Eberth 1986) *Clepsydrrops*, *Echinerpeton* (Reisz 1972), *Stereophallodon* (Romer 1937; Brinkman & Eberth 1986) and *Stereorhachis* (Gaudry 1880), have not been included in a phylogenetic analysis. A major impediment to studies of ophiacodontid systematics is the taxonomic complexity of referrals to *Ophiacodon*. Due to the limited scope of observations made during the present study, most of these problems remain. However, *Echinerpeton* and

Stereophallodon were included for the first time in the present analysis. Reisz (1972) suggested that *Echinerpeton*, from the earliest synapsid fauna at Florence, Nova Scotia was an ophiacodontid, based on its possession of webbing of the dorsal transverse processes, slight anteroposterior compression of the dorsal centra, and a similar outline of the astragalus to that of some ophiacodontids. However, he later suggested assignment to ‘Pelycosauria’ *incertae sedis* (Reisz 1986). *Echinerpeton* behaved as a wildcard taxon in the current analysis. It can be placed equally parsimoniously as the most basal synapsid, as the sister taxon of Caseasauria + Edaphosauridae + Sphenacodontia, or as an ophiacodontid more derived than *Archaeothyris*. *Stereophallodon* was redescribed by Brinkman & Eberth (1986), who noted several potential synapomorphies suggesting a sister-taxon relationship with *Ophiacodon*: the transversely broad cultriform process, ventrally directed basipterygoid processes, a ridge extending dorsally from the medial supracanine buttress and a notch on the postero-medial edge of the quadrate. Reisz (1986) concurred with this assessment, and stated that most material referred to *Stereophallodon* was similar to *Ophiacodon*.

The topology recovered within Ophiacodontidae by analysis of the full dataset (Fig. 2) is identical to that recovered by Berman *et al.* (1995), with the addition that *Stereophallodon* is the sister taxon of *Ophiacodon*, as proposed by Brinkman & Eberth (1986). However, analysis of only postcranial data recovers all these taxa in a polytomy at the base of Synapsida (Fig. 5). The strict reduced consensus of the analysis of cranial data resolves *Archaeothyris* in a four-way polytomy with a clade comprising the remaining ophiacodontids, Varanopidae and Edaphosauridae + Sphenacodontia (Fig. 4B). Thus, support for a monophyletic Ophiacodontidae as currently conceived should be considered weak.

Varanopidae. The content and relationships recovered here within Varanopidae (Figs 2–4) are consistent with those of recent studies that posit a clade comprising two subfamilies, Mycterosaurinae and Varanodontinae (Reisz & Berman 2001), to which *Pyozia* and *Archaeovenator* form successively more basal sister taxa (Reisz & Dilkes 2003; Anderson & Reisz 2004; although Maddin *et al.* 2006 suggested that *Pyozia* may not be a varanopid). Despite recent interest in elucidating the anatomy and relationships of Varanopidae, two varanopid taxa included in the present study have not previously been analysed. Both *Basicranodon* and *Ruthiromia* were tentatively assigned to Varanopidae by Reisz (1986), but have been neglected in more recent studies. *Basicranodon*, based on a partial braincase from the ?Kungurian (Lucas 2006; equivalent to uppermost Arroyo Formation; Olson 1968; Sullivan & Reisz 1999; Maddin *et al.* 2006) Richards Spur locality in Oklahoma was reported as a ‘pelycosaur’ with basicranial teeth by Vaughn (1958b). Langston & Reisz (1981) suggested that it

was a varanopid, based on features shared with *Aerosaurus wellesi*: the presence of teeth on the body of the parasphenoid (character 109.1), laterally directed basipterygoid processes (102.0) (both of which are also present in some other basal amniotes), and an abruptly expanded parasphenoid body (105.1). The present analysis confirms varanopid affinities for *Basicranodon*, but the taxon could equally parsimoniously be recovered as the sister taxon of *Pyozia*, or within Mycterosaurinae, and represents a wildcard taxon. Reisz *et al.* (1997) considered *Basicranodon* as a subjective junior synonym of *Mycterosaurus*. Our phylogenetic results are not inconsistent with this assessment. However, there are differences in the distribution of teeth and shape of the dentigerous ventral platform medial to the basipterygoid processes that may indicate taxonomic distinction (Vaughn 1958b; Berman & Reisz 1982). *Ruthiromia*, from the Gzhelian (Fracasso 1980; Berman *et al.* 1997; Lucas 2006) part of the Cutler Formation of El Cobre Canyon, New Mexico was described in detail by Eberth & Brinkman (1983), who suggested varanopid affinities based on the combined presence of excavated presacral neural arches (character 163.2; also present in Sphenacodontidae) and the presence of a fossa on the anteroventral surface of the humerus between the head and the deltopectoral crest (192.0; also present in Caseidae). Observations made during the present study confirm this assignment and provide a high level of support for a clade comprising the Permo-Pennsylvanian varanodontines *Ruthiromia* + *Aerosaurus* spp. (Fig. 2B), united by six unambiguous synapomorphies: the presence of a supraglenoid foramen (character 179.0; primitively absent in Varanopidae), a large triceps process of the coracoid (character 186.1), the anterior surface of the deltopectoral crest is strongly concave, bounded dorsally by a prominent, proximodistally elongate ridge (character 194.1), the latissimus dorsi attachment is located distally on the proximal humerus (character 195.1), and forms a prominent, posteriorly directed tubercle (character 196.1), and the calcaneum is longer proximodistally than wide mediolaterally (character 239.1).

Some disagreement exists over placement of the South African, Middle Permian varanopid *Elliotsmithia* within either Varanodontinae (Reisz *et al.* 1998; Anderson & Reisz 2004; Reisz & Laurin 2004; Maddin *et al.* 2006) or Mycterosaurinae (Modesto *et al.* 2001; Botha-Brink & Modesto 2009) (see Reisz & Modesto 2007). Botha-Brink & Modesto (2009) found that including new data on *Heleosaurus* in the matrix of Maddin *et al.* (2006) resulted in recovery of *Elliotsmithia* within Mycterosaurinae as the sister taxon of *Heleosaurus*. Campione & Reisz (2010) found that the placement of *Elliotsmithia* depended on the relative weighting of stratigraphic data in a stratocladistic analysis. However, a fundamental, unresolved issue is the existence of two alternative anatomical interpretations of the holotype of *Elliotsmithia* (compare Dilkes & Reisz 1996; Reisz *et al.* 1998 with Modesto *et al.* 2001). Because

this specimen has not been examined during the present study, *Elliotsmithia* was not included in the data matrix. However, our analysis confirms that BP/1/5678, which may represent *Elliotsmithia* (Modesto *et al.* 2001) or a distinct taxon (Reisz & Dilkes 2003), falls within Mycterosaurinae.

Botha-Brink & Modesto (2009) recovered low branch support (Bremer support = 1) for most nodes within Varanopidae, and suggested that more anatomical data collection was required. The present analysis recovered higher values for most nodes (Figs 2B, 6), including very strong support for Varanodontinae (5) and a clade comprising *Ruthiromia* + *Aerosaurus* spp. (4). Although cranial data support the same topology within Varanopidae as the full dataset (Fig. 4B), postcranial data recover a less well-resolved topology in which the affinities of *Varanops* lie equally parsimoniously with either *Watongia* + *Varanodon*, or *Ruthiromia* + *Aerosaurus* spp., and *Archaeovenator* forms part of a Mycterosaurine polytomy, instead of being the most basal varanopid (Fig. 5B). This is not surprising given the distinctive, gracile postcranial skeleton of *Archaeovenator* and mycterosaurines. Gracile proportions are likely plesiomorphic for Varanopidae and differ from the more robust proportions of other basal synapsids, including varanodontines.

Caseasauria. A monophyletic Caseasauria, including Caseidae as the sister taxon of Eothyrididae, was recovered by all analyses (Figs 2–6). However, the results from the full dataset and the postcranial data partition are unlike the recent consensus (e.g. Kemp 1988; Reisz 1986; Reisz *et al.* 1992a; Modesto 1994; Berman *et al.* 1995), because Caseasauria is not found as the most basal branch of the synapsid tree (Figs 2, 5). Only analysis of the cranial data partition recovers the consensus, basal position for Caseasauria (Fig. 4).

Only one cladistic study has attempted to elucidate relationships among caseids (Maddin *et al.* 2008). Thus, many likely caseid taxa have not been included in a phylogenetic analysis. This is partly because of justified concerns regarding the taxonomic validity of some North American caseid taxa erected by Olson (1954, 1962; Olson & Beerbower 1953; Olson & Barghusen 1962). Many of these are based on fragmentary material, and most proposed distinctions between nominal species concern skeletal proportions that may vary ontogenetically (Reisz 1986; Maddin *et al.* 2008). These taxa require further attention. However, in the present study an attempt was made to include as many taxa as possible, focusing on those that were examined directly, and consisted of more than just a few bones. Thus, *Trichasaurus* (Williston 1913), *Caseopsis* (Olson 1962), and multiple species of *Angelosaurus* (*A. dolani*, *A. romeri*) and *Cotylorhynchus* (*C. bransoni*, *C. hancocki*, *C. romeri*) (reviewed by Olson 1968; Reisz 1986) were included for the first time in the present analysis.

Although *Angelosaurus dolani* and *A. romeri* have identical scores (apart from the distribution of missing data), the present study provides some data that may support the validity of distinct species within *Cotylorhynchus*. Scores for species of *Cotylorhynchus* were very similar; however, there were some differences. *C. romeri* may possess fewer than 27 presacral vertebrae, whereas *C. hancocki* possesses at least 27 (character 148; Stovall *et al.* 1966; Olson 1968 (although note that Olson 1968 expressed uncertainty over the count in *C. romeri*)); the dorsal prezygapophyses are planar and do not contact on the midline in *C. romeri*, but are transversely concave and contact on the midline in *C. hancocki* and *C. bransoni* (pers. obs.; character 161.1); and a hypophene is uniquely present in the dorsal vertebrae of *C. hancocki* (character 162.1; FMNH UR 703).

The results of the present analysis are consistent with those of Maddin *et al.* (2008). A pectinate grade of basal caseids culminates in a clade comprising *Angelosaurus* + *Cotylorhynchus* spp. (Figs 2, 7). In the strict reduced consensus, all three species of *Cotylorhynchus* form a clade, within which *C. bransoni* and *C. hancocki* are sister taxa (Fig. 2B). *Caseopsis* behaves as a wildcard taxon within the clade of caseids more derived than *Oromycter*, and the fragmentary *Angelosaurus dolani* is equally parsimoniously placed as the sister taxon of either *Angelosaurus romeri* or *Cotylorhynchus romeri*. A non-contradictory topology, although less well resolved, is recovered by analysis of the cranial and postcranial datasets (Figs 4, 5).

The systematic history of *Trichasaurus*, comprising a partial postcranial skeleton from the Arroyo Formation of Texas (Williston 1913) is particularly interesting. Romer & Price (1940, p. 423) suggested that it belonged to an ‘edaphosaurian’, most probably a caseid, whereas Olson (1968) considered edaphosaurid affinities to be more likely and Reisz (1986) referred the taxon to ‘Pelycosauria’ incertae sedis. Discovery of the basal edaphosaurid *Ianthasaurus* (Reisz & Berman 1986; Modesto & Reisz 1990; Mazierski & Reisz 2010) and a focus on characterization of the postcranial skeleton in the present study have resulted in clear indications of caseid affinities of *Trichasaurus*. Direct observation of the holotype (FMNH UC 652) shows that *Trichasaurus* shares two features with caseids that are absent in edaphosaurids: the absence of a ridge on the ventral surface of the proximal femur forming the posterior boundary of the adductor fossa (character 230.0) and dorsal centra that are approximately as long anteroposteriorly as they are high dorsoventrally (155.0). Furthermore, it lacks distinctive postcranial features shared by edaphosaurids and sphenacodontids, such as the presence of tall narrow ungual phalanges (212.1) and a strong posterodorsal expansion of the ischium (222.1).

Edaphosauridae. The edaphosaurid phylogenetic dataset of Modesto (1994, 1995) has undergone iterative modifications, the most recent of which was published by

Mazierski & Reisz (2010). Mazierski & Reisz (2010) included *Ianthasaurus*, *Lupeosaurus*, *Glaucosaurus* and multiple species of *Edaphosaurus*. The taxon set employed in the present study is smaller, including only two species of *Edaphosaurus* (*E. boanerges*, *E. novomexicanus*), but the same topology is recovered (Fig. 2). *Ianthasaurus* is sister taxon of a polytomy comprising *Glaucosaurus* (known only from cranial material), *Lupeosaurus* (known only from postcranial material), and a clade comprising *Edaphosaurus* spp. Branch support for Edaphosauridae and included nodes is low based on the full dataset (Fig. 2B), as in the analysis of Mazierski & Reisz (2010). This is likely due to the irresolvable polytomy comprising *Glaucosaurus*, *Lupeosaurus* and *Edaphosaurus* spp., because branch support is higher in analyses of the postcranial dataset (excluding *Glaucosaurus*), and the reduced dataset (excluding *Glaucosaurus* and *Lupeosaurus*) (Figs 5, 6).

Sphenacodontia. Basal (i.e. non-therapsid) sphenacodontians were the focus of phylogenetic studies by Reisz *et al.* (1992a), Laurin (1993; also modified by Kissel & Reisz 2004) and Fröbisch *et al.* (2011). The basal sphenacodontian *Palaeohatteria* was not included in the present analysis because it is based on very young individuals (Credner 1888; Currie 1979; Laurin 1994). Analysis of the full dataset confirms that *Haptodus garnettensis* is the most basal representative of a well-supported Sphenacodontia comprising *Pantelosaurus* as the sister taxon of a clade comprising Therapsida + Sphenacodontidae. *Cutleria* is the most basal sphenacodontid, contrary to the findings of Laurin (1993) and Fröbisch *et al.* (2011), who recovered *Cutleria* as the sister taxon of Therapsida + Sphenacodontia. *Cutleria* shares a frontal that is more than 2.5 times the length of the parietal (character 56.2; the relatively long anterior process of the frontals was noted by Laurin 1994), a strongly posteroventrally inclined temporal roof (8.1; absent in *Secodontosaurus*; although this was reconstructed in *Haptodus baylei* by Currie 1979, text-fig. 5, the condition is not pronounced in the actual specimens: Currie 1979, text-fig. 3), and a preaxial (lateral) centrale that covers the proximal ends of the first-third distal carpals (202.1; Lewis & Vaughn 1965) with sphenacodontids. However, only one additional step is required to place *Cutleria* outside the therapsid + sphenacodontid clade.

Relationships within Sphenacodontidae have been disputed. Romer & Price (1940) suggested that the deep-skulled sphenacodontids, best represented by *Sphenacodon* and *Dimetrodon*, formed a clade (Sphenacontinae) exclusive of the long-snouted *Secodontosaurus*. This division was provisionally retained by Reisz (1986), but overturned by a later cladistic study (Reisz *et al.* 1992a) in which *Dimetrodon* and *Secodontosaurus* were united as sister taxa by the presence of tall, rod-like dorsal neural spines (character 164.2 in the present analysis) with vertical grooves on the anterior and posterior surfaces, and the presence

of a long nasal-maxilla contact (22.2). The analysis of Fröbisch *et al.* (2011) however, recovered a monophyletic Sphenacontinae (*sensu* Romer & Price 1940), and high branch support for Sphenacontinae after exclusion of the poorly known *Cryptovenator*. A similar result emerges from the present dataset (Figs 2B, 6). Interestingly, both cranial and postcranial datasets recover Sphenacontinae (Figs 4, 5), although the cranial partition contributes most branch support (Fig. 6). It is clear that deep-skulled sphenacodontids share numerous cranial synapomorphies that were not coded by Reisz *et al.* (1992a). Postcranial synapomorphies of Sphenacontinae include the dorsoventrally tall axial neural spine (character 152.2; Reisz *et al.* 1992b) and a new character, the presence of a step-like ridge on the ventral surface of the humerus antero-proximal to the entepicondylar foramen (200.1). The question of whether rod-like neural spines, defining a dorsal sail, are plesiomorphic for Sphenacodontidae, undergoing reversal to a transversely compressed, subrectangular morphology in *Sphenacodon* and *Ctenospondylus*, or whether they were derived independently in *Secodontosaurus* and *Dimetrodon*, is unresolved because the optimization of this character is ambiguous.

Therapsids are characterized by highly distinctive, derived cranial and postcranial anatomy. Most previous authors have posited a monophyletic Therapsida (e.g. Sidor & Hopson 1998; Kemp 2006), although Olson (1962) proposed that taxa currently recognized as therapsids may have arisen from two, or even three, distinct ‘pelycosaurian’ groups, he later suggested that evidence was sparse and this could not be confirmed (Olson 1968). Recent studies have identified as many as 55 therapsid synapomorphies (Kemp 2006; modified from Sidor & Hopson 1998). It is not surprising, therefore, that a monophyletic Therapsida was recovered by the present study. Because of the plastic position of the poorly known *Cryptovenator* (based on a partial mandible which could be placed within Therapsida at the cost of only one additional step), branch support from analysis of the full dataset is low (Fig. 2B). However, analyses of the postcranial and reduced datasets (excluding *Cryptovenator*) yield strong support for a monophyletic Therapsida (Figs 5, 6).

Prospects for basal synapsid phylogeny

The present study reveals considerable uncertainty in relationships among higher clades of basal synapsids. It is possible that these uncertainties can be resolved by continuing character exploration and study of existing specimens. However, one potential cause is the scarcity of fossils prior to the latest Carboniferous (Gzhelian) that may document the differentiation of major synapsid clades. This problem was recognized by Romer & Price (1940, p. 197: “unfortunately, no really primitive pelycosaur is known”) and DeMar (1970). The earliest well-sampled amniote faunas are from the possibly Gzhelian (Fracasso 1980; Berman

et al. 1997) part of the Cutler Formation at El Cobre Canyon, New Mexico. These deposits have yielded derived representatives of most basal synapsid clades, *Edaphosaurus novomexicanus*, *Ophiacodon navajonicus*, *Sphenacodon ferox*, and the varanodontine varanopids *Ruthiromia* and *Aerosaurus greenleeorum* (Case 1907; Romer 1937; Romer & Price 1940; Eberth & Brinkman 1983; Reisz 1986; Modesto & Reisz 1992; Lucas 2006). Such taxa are unlikely to yield transitional character state combinations that can inform our understanding of global relationships. Approximately 10 million years separate this fauna from the earliest records of amniotes, including synapsids (308 Ma; Carroll 1964, 1969; Reisz 1972, 1975). This interval is very poorly sampled, but must represent an important stage of synapsid diversification and the differentiation of major clades. Kasimovian (\sim 304 Ma; Jewett *et al.* 1968) amniotes are known from the productive Garnett Quarry, Kansas (e.g. Lane 1945; Peabody 1952, 1954, 1957; Reisz *et al.* 1982; Kissel & Reisz 2004) and include genuinely plesiomorphic representatives of Sphenacodontia + Edaphosauridae (*Ianthasaurus*; DeMar 1970; Reisz & Berman 1986; Modesto & Reisz 1992; Mazierski & Reisz 2010; *Haptodus*; Currie 1977; Laurin 1993; *Ianthodon*, Kissel & Reisz 2004). The study and description of briefly mentioned forms such as a new ophiacodontid (Peabody 1954, 1957; Reisz & Berman 1986) may contribute greatly to our understanding of basal synapsid interrelationships. The earliest synapsid records are from Florence, Nova Scotia (Reisz 1972; Carroll 1964 described *Protoclepsydrops* from the slightly older fauna at Joggins, but this may not be a synapsid; Reisz 1986) and Nýrany, Czech Republic (Reisz 1975). The material from these localities is fragmentary, but includes transitional taxa such as *Echinerpeton*, which is hard to place with confidence in any of the major clades. These, oldest, localities only hint at an otherwise hidden diversity of small basal amniotes and it is clear that our knowledge of the initial stage of amniote diversification is poor indeed.

Acknowledgements

I thank various curators and researchers for access to specimens, including Mark Norell and Carl Mehling (AMNH), David Berman and Amy Henrici (CMNH); William Simpson and Ken Angielczyk (FMNH); Jessica Cundiff (MCZ); Jennifer Larsen (OMNH) and David Evans (ROM). In particular I thank Robert Reisz for access to specimens in his lab. Brian Davis, Sally Pine, Steve Brusatte provided hospitality during collections visits. Trinity College, Cambridge provided funding for this project. Two anonymous referees and the associate editor, Susan Maidment, provided comments that improved the manuscript.

References

- Amson, E. & Laurin, M. 2011. On the affinities of *Tetraceratops insignis*, an Early Permian synapsid. *Acta Palaeontologica Polonica*, **56**, 301–312.
- Anderson, J. S. & Reisz, R. R. 2004. *Pyozia mesenensis*, a new, small varanopid (Synapsida, Eupelycosauria) from Russia: ‘pelycosaur’ diversity in the Middle Permian. *Journal of Vertebrate Paleontology*, **24**, 173–179.
- Bakker, R. T. 1986. *The dinosaur heresies*. Kensington, New York, 481 pp.
- Bell, W. A. 1966. Carboniferous plants of eastern Canada. *Geological Survey of Canada*, Paper 66–11, 1–76.
- Bennett, S. C. 1996. Aerodynamics and thermoregulatory function of the dorsal sail of *Edaphosaurus*. *Paleobiology*, **22**, 496–506.
- Benson, R. B. J. 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society of London*, **158**, 882–935.
- Berman, D. 1978. *Ctenospondylus ninevehensis*, a new species (Reptilia, Pelycosauria) from the Lower Permian Dunkard Group of Ohio. *Annals of the Carnegie Museum*, **47**, 493–514.
- Berman, D. & Reisz, R. R. 1982. Restudy of *Mycterosaurus longiceps* (Reptilia, Pelycosauria) from the Lower Permian of Texas. *Annals of the Carnegie Museum*, **51**, 423–453.
- Berman, D. S., Reisz, R. R., Bolt, J. R. & Scott, D. 1995. The cranial anatomy and relationships of the synapsid *Varanosaurus* (Eupelycosauria: Ophiacodontidae) from the Early Permian of Texas and Oklahoma. *Annals of the Carnegie Museum*, **64**, 99–133.
- Berman, D. S., Sumida, S. S. & Lombard, R. E. 1997. Biogeography of primitive amniotes. Pp. 85–139 in S. S. Sumida & K. L. M. Martin (eds) *Amniote Origins*. Academic Press, San Diego.
- Berman, D., Reisz, R. R., Martens, T. & Henrici, A. C. 2001. A new species of *Dimetrodon* (Synapsida: Sphenacodontidae) from the Lower Permian of Germany records first occurrence of genus outside North America. *Canadian Journal of Earth Sciences*, **38**, 803–812.
- Botha-Brink, J. & Modesto, S. P. 2007. A mixed-age classed ‘pelycosaur’ aggregation from South Africa: earliest evidence of parental care in amniotes? *Proceedings of the Royal Society of London B*, **274**, 2829–2834.
- Botha-Brink, J. & Modesto, S. P. 2009. Anatomy and relationships of the Middle Permian varanopid *Heleosaurus scholtzi* based on a social aggregation from the Karoo Basin of South Africa. *Journal of Vertebrate Paleontology*, **29**, 389–400.
- Bramwell, C. D. & Fellgett, P. B. 1979. Thermal regulation in sail lizards. *Nature*, **242**, 203–205.
- Brinkman, D. & Eberth, D. A. 1983. The interrelationships of pelycosaurs. *Breviora*, **473**, 1–35.
- Brinkman, D. & Eberth, D. A. 1986. The anatomy and relationships of *Stereophallodon* and *Baldwinonus* (Reptilia, Pelycosauria). *Breviora*, **485**, 1–34.
- Broom, R. 1937. A further contribution to our knowledge of the fossil reptiles of the Karroo. *Proceedings of the Zoological Society*, **B107**, 299–318.
- Campione, N. E. & Reisz, R. R. 2010. *Varanops brevirostris* (Eupelycosauria: Varanopidae) from the Lower Permian of Texas, with discussion of varanopid morphology and interrelationships. *Journal of Vertebrate Paleontology*, **30**, 724–746.
- Carroll, R. L. 1964. The earliest reptiles. *Zoological Journal of the Linnean Society of London*, **45**, 61–83.

- Carroll, R. L.** 1969. A middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *Journal of Paleontology*, **43**, 151–170.
- Case, E. C.** 1905. *Bathygnathus borealis* Leidy, and the Permian of Prince Edward Island. *Science*, new series, **22**, 52–53.
- Case, E. C.** 1907. *Revision of the Pelycosauria of North America*. Carnegie Institute, Washington, 176 pp.
- Clark, J. & Carroll, R. L.** 1973. Romeriid reptiles from the Lower Permian. *Bulletin of the Museum of Comparative Zoology*, **144**, 353–407.
- Conrad, J. & Sidor, C. A.** 2001. Re-evaluation of *Tetraceratops insignis* (Synapsida: Sphenacodontia). *Journal of Vertebrate Paleontology*, **21**, 42A.
- Cope, E. D.** 1878. Descriptions of extinct Batrachia and Reptilia from the Permian formations of Texas. *Proceedings of the American Philosophical Society*, **17**, 505–530.
- Cope, E. D.** 1882. Third contribution to the history of the Vertebrata of the Permian formation of Texas. *Proceedings of the American Philosophical Society*, **20**, 447–461.
- Cope, E. D.** 1895. The reptilian order Cotylosauria. *Proceedings of the American Philosophical Society*, **34**, 436–457.
- Credner, H.** 1888. Die Stegocephalen und Saurier aus dem Rothliegenden des Plauenischen Grundes bei Dresden. VII Theil: *Palaeohatteria longicaudata* Cred. *Zeitschrift der deutschen geologischen Gesellschaft*, **40**, 490–558.
- Currie, P. J.** 1977. A new haptodontine sphenacodont (Reptilia: Pelycosauria) from the Upper Pennsylvanian of North America. *Journal of Paleontology*, **51**, 927–942.
- Currie, P. J.** 1979. The osteology of haptodontine sphenacodonts (Reptilia: Pelycosauria). *Palaeontographica Abteilung A*, **163**, 130–168.
- DeMar, R.** 1970. A primitive pelycosaur from the Pennsylvanian of Illinois. *Journal of Paleontology*, **44**, 154–163.
- Dilkes, D. W. & Reisz, R. R.** 1996. First record of a basal synapsid ('mammal-like reptile') in Gondwana. *Proceedings of the Royal Society of London B*, **263**, 1165–1170.
- Eberth, D. A.** 1985. The skull of *Sphenacodon ferocior*, and comparisons with other sphenacodontines (Reptilia: Pelycosauria). *New Mexico Bureau of Mines & Mineral Resources Circular*, **190**, 1–39.
- Eberth, D. A. & Brinkman, D.** 1983. *Ruthiromia elcobriensis*, a new pelycosaur from El Cobre Canyon, New Mexico. *Breviora*, **474**, 1–26.
- Efremov, J. A.** 1938. Some new Permian reptiles of the USSR. *Academy of Sciences URSS, C.R.*, **19**, 121–126.
- Efremov, J. A.** 1956. American elements in the fauna of Permian reptiles of the USSR. *Doklady Akademii Nauk SSSR*, **111**, 1091–1094.
- Fox, R. C.** 1962. Two new pelycosaurs from the Lower Permian of Oklahoma. *University of Kansas Publications, Museum of Natural History*, **12**, 297–307.
- Fox, R. C. & Bowman, M. C.** 1966. Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). *University of Kansas Paleontological Contributions, Vertebrata*, **11**, 1–79.
- Fracasso, M. A.** 1980. Age of the Permo-Carboniferous Cutler Formation vertebrate fauna from El Cobre Canyon, New Mexico. *Journal of Paleontology*, **54**, 1237–1244.
- Fröbisch, J., Schoch, R. R., Müller, J., Schindler, T. & Schweiss, D.** 2011. A new basal sphenacodontid synapsid from the Late Carboniferous of the Saar-Nahe Basin, Germany. *Acta Palaeontologica Polonica*, **56**, 113–120.
- Gaudry, A.** 1880. Sur un reptile très perfectionné trouvé dans le terrain permien. *Compte rendu hebdomadaire des séances de l'Académie des Sciences Paris*, **91**, 669–671.
- Graybeal, A.** 1998. Is it better to add taxa or characters to a difficult phylogenetic problem? *Systematic Biology*, **47**, 9–17.
- Haack, S.** 1986. A thermal model of the sailback pelycosaur. *Paleobiology*, **12**, 450–458.
- Holmes, R.** 1977. The osteology and musculature of the pectoral limb of small captorhinids. *Journal of Morphology*, **152**, 101–140.
- Holmes, R.** 2003. The hind limb of *Captorhinus aguti* and the step cycle of basal amniotes. *Canadian Journal of Earth Sciences*, **40**, 515–526.
- Huene, F. von.** 1905. Pelycosaurier im deutschen Muschelkalk. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **20**, 321–353.
- Jewett, J. M., Bayne, C. K., Goebel, E. D. O., Connor, H. G., Swineford, A. & Zeller, D.** 1968. The stratigraphic succession in Kansas. *Kansas Geological Survey Bulletin*, **189**, 1–81.
- Kemp, T. S.** 1982. Mammal-like Reptiles and the Origin of Mammals. Academic Press, London, 363 pp.
- Kemp, T. S.** 1988. Interrelationships of the Synapsida. Pp. 23–29 in M. J. Benton (ed.) *The Phylogeny and Classification of the Tetrapods. Volume 2. Systematics Association Special Volume*, **35B**, 23–29.
- Kemp, T. S.** 2005. *The Origin and Evolution of Mammals*. Oxford University Press, Oxford, 342 pp.
- Kemp, T. S.** 2006. The origin and early radiation of the therapsid mammal-like reptiles: a palaeobiological hypothesis. *Journal of Evolutionary Biology*, **19**, 1231–1237.
- Ketchum, H. F. & Benson, R. B. J.** 2010. Global interrelationships of Plesiosaura (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. *Biological Reviews*, **85**, 361–392.
- Kissel, R. A. & Reisz, R. R.** 2004. Synapsid fauna of the Upper Pennsylvanian Rock Lake Shale near Garnett, Kansas and the diversity patterns of early amniotes. Pp. 409–428 in G. Arratia, M. V. H. Wilson & R. Cloutier (eds), *Recent Advances in the Origin and Early Radiation of Vertebrates*. Pfeil Verlag, München.
- Kitching, I. J., Forey, P. L., Humphries, C. J. & Williams, D. M.** 1998. *Cladistics: the theory and practice of parsimony analysis*. 2nd edition. Oxford University Press, Oxford, 248 pp.
- Lane, H. H.** 1945. New mid-Pennsylvanian reptiles from Kansas. *Transactions of the Kansas Academy of Sciences*, **47**, 381–390.
- Langston, W. Jr** 1965. *Oedaleops campi* (Reptilia: Pelycosauria) new genus and species from the Lower Permian of New Mexico, and the Family Eothyrididae. *Bulletin of the Texas Memorial Museum*, **9**, 1–47.
- Langston, W. Jr & Reisz R. R.** 1981. *Aerosaurus wellesi*, new species, a varanopseid mammal-like reptiles (Synapsida: Pelycosauria) from the Lower Permian of New Mexico. *Journal of Vertebrate Paleontology*, **1**, 73–96.
- Laurin, M.** 1993. Anatomy and relationships of *Haptodus garnettensis*, a Pennsylvanian synapsid from Kansas. *Journal of Vertebrate Paleontology*, **13**, 200–229.
- Laurin, M.** 1994. Re-evaluation of *Cutleria wilmarthi*, an Early Permian synapsid from Colorado. *Journal of Vertebrate Paleontology*, **14**, 134–138.
- Laurin, M. & Reisz, R. R.** 1990. *Tetraceratops* is the oldest known therapsid. *Nature*, **345**, 249–250.
- Laurin, M. & Reisz, R. R.** 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society of London*, **113**, 165–223.
- Laurin, M. & Reisz, R. R.** 1996. The osteology and relationships of *Tetraceratops insignis*, the oldest known therapsid. *Journal of Vertebrate Paleontology*, **16**, 95–102.

- Leidy, J.** 1854. On *Bathygnathus borealis* an extinct Saurian of the New Red Sandstone of Prince Edward Island. *Proceedings of the Academy of Natural Sciences of Philadelphia*, second series, **2**, 327–330.
- Lewis, G. E. & Vaughn, P. P.** 1965. Early Permian vertebrates from the Cutler Formation of the Placerville area Colorado. *Geological Survey Professional Paper*, **503-C**, C1–C46.
- Li, J. & Cheng, Z.** 1997. First discovery of eotitanosuchian (Therapsida, Synapsida) of China. *Vertebrata PalAsiatica*, **35**, 268–282.
- Liu, J., Rubidge, B. & Li, J.** 2009. New basal synapsid supports Laurasian origin for therapsids. *Acta Palaeontologica Polonica*, **54**, 393–400.
- Liu, J., Rubidge, B. & Li, J.** 2010. A new specimen of *Biseridens qilianicus* indicates its phylogenetic position as the most basal anomodont. *Proceedings of the Royal Society of London B*, **277**, 285–292.
- Lucas, S. G.** 2006. Global Permian tetrapod biostratigraphy and biochronology. Pp. 65–93 in S. G. Lucas, G. Cassinis & J. W. Schneider (eds) *Non-Marine Permian Biostratigraphy and Biochronology. Special Papers of the Geological Society of London*, **265**, 65–93.
- Maddin, H. C., Evans, D. C. & Reisz, R. R.** 2006. An Early Permian varanodontine varanopid (Synapsida: Eupelycosauria) from the Richards Spur locality, Oklahoma. *Journal of Vertebrate Paleontology*, **26**, 957–966.
- Maddin, H. C., Sidor, C. A. & Reisz, R. R.** 2008. Cranial anatomy of *Ennatosaurus tecton* (Synapsida: Caseidae) from the Middle Permian of Russia and the evolutionary relationships of Caseidae. *Journal of Vertebrate Paleontology*, **28**, 160–180.
- Maddison, D. R. & Maddison, W. P.** 2001. MacClade 4.06 for OSX. Sinauer Associates Inc., Sunderland, Massachusetts.
- Marsh, O. C.** 1878. Notice of new fossil reptiles. *American Journal of Science*, **15**, 409–411.
- Mazierski, D. M. & Reisz, R. R.** 2010. Description of a new specimen of *Ianthasaurus hardestiorum* (Eupelycosauria: Edaphosauridae) and a re-evaluation of edaphosaurid phylogeny. *Canadian Journal of Earth Sciences*, **47**, 901–912.
- Milner, A. R.** 1993. Biogeography of Palaeozoic tetrapods. Pp. 324–353 in J. A. Long (ed.) *Palaeozoic Vertebrate Biostratigraphy and Biogeography*. Belhaven Press, London.
- Modesto, S. P.** 1994. The Lower Permian synapsid *Glaucosaurus* from Texas. *Palaeontology*, **37**, 51–60.
- Modesto, S. P.** 1995. The skull of the herbivorous synapsid *Edaphosaurus boanerges* from the Lower Permian of Texas. *Palaeontology*, **38**, 213–239.
- Modesto, S. P.** 1998. New information on the skull of the Early Permian reptile *Captorhinus aguti*. *PaleoBios*, **18**, 21–35.
- Modesto, S. P.** 1999. *Colobomycter pholeter* from the Lower Permian of Oklahoma: a parareptile, not a protorothyridid. *Journal of Vertebrate Paleontology*, **19**, 466–472.
- Modesto, S. P. & Reisz, R. R.** 1990. A new skeleton of *Ianthasaurus hardestii*, a primitive edaphosaur (Synapsida: Pelycosauria) from the Upper Pennsylvanian of Kansas. *Canadian Journal of Earth Sciences*, **27**, 834–844.
- Modesto, S. P. & Reisz, R. R.** 1992. Restudy of Permo-Carboniferous synapsid *Edaphosaurus novomexicanus* Williston and Case, the oldest known herbivorous amniote. *Canadian Journal of Earth Sciences*, **29**, 2653–2662.
- Modesto, S. P., Sidor, C. A., Rubidge, B. S. & Welman, J.** 2001. A second varanopseid skull from the Upper Permian of South Africa: implications for Late Permian ‘pelycosaur’ evolution. *Lethaia*, **34**, 249–259.
- Moss, J. L.** 1972. The morphology and phylogenetic relationships of the Lower Permian tetrapod *Tseaajaia campi* Vaughn (Amphibia: Seymouriamorpha). *University of California Publications in Geological Sciences*, **98**, 1–72.
- Nixon, K. C.** 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics*, **15**, 407–414.
- Nopcsa, F.** 1923. Die Familien der Reptilien. *Fortschritte der Geologie und Palaeontologie*, **2**, 1–210.
- Ogg, J. G., Ogg, G. & Gradstein, F. M.** 2008. *The Concise Geologic Time Scale*. Cambridge University Press, Cambridge, 177 pp.
- Olson, E. C.** 1954. Fauna of the Vale and Choza: 7. Pelycosaurs: Family Caseidae. *Fieldiana: Geology*, **17**, 193–204.
- Olson, E. C.** 1962. Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R. *Transactions of the American Philosophical Society*, new series, **52**, 1–223.
- Olson, E. C.** 1968. The family Caseidae. *Fieldiana: Geology*, **17**, 221–349.
- Olson, E. C. & Barghusen, H.** 1962. Permian vertebrates from Oklahoma and Texas. *Oklahoma Geological Survey Circular*, **59**, 1–68.
- Olson, E. C. & Beerbower, J. R.** 1953. The San Angelo Formation, Permian of Texas, and its vertebrates. *Journal of Geology*, **61**, 389–423.
- Orlov, Y. A.** 1958. Predatory dinocephalians from the Isheev faunal (titanosuchians). *Trudy Palaeontological Institute of the Academy of Sciences, USSR*, **125**, 1–114 [in Russian].
- Peabody, F. E.** 1952. *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas. *University of Kansas Palaeontological Contribution, Vertebrata*, **1**, 1–41.
- Peabody, F. E.** 1954. Pennsylvanian reptiles of Kansas. *Geological Society of America Bulletin*, **65**, 1293.
- Peabody, F. E.** 1957. Pennsylvanian reptiles of Garnett, Kansas: edaphosaurs. *Journal of Paleontology*, **31**, 947–949.
- Poe, S. & Swofford, D. L.** 1999. Taxon sampling revisited. *Nature*, **389**, 299–300.
- Price, L. I.** 1935. Notes on the brain case of *Captorhinus*. *Proceedings of the Boston Society of Natural History*, **40**, 377–386.
- Reisz, R. R.** 1972. Pelycosaurian reptiles from the Middle Pennsylvanian of North America. *Bulletin of the Museum of Comparative Zoology*, **144**, 27–62.
- Reisz, R. R.** 1975. Pennsylvanian pelycosaurs from Linton, Ohio and Nýrany, Czechoslovakia. *Journal of Paleontology*, **49**, 522–527.
- Reisz, R. R.** 1980. Pelycosauria: a review of phylogenetic relationships. Pp. 553–592 in A. L. Panchen (ed.) *The Terrestrial Environment and the Origin of Land Vertebrates*. Academic Press, London.
- Reisz, R. R.** 1986. Pelycosauria. *Encyclopedia of Paleoherpetology*, **17A**, 1–102.
- Reisz, R. R.** 2005. *Oromycter*, a new caseid from the Lower Permian of Oklahoma. *Journal of Vertebrate Paleontology*, **25**, 905–910.
- Reisz, R. R.** 2007. The cranial anatomy of basal diadectomorphs and the origin of amniotes. Pp. 228–252 in J. S. Anderson & H. -D. Sues (eds) *Major Transitions in Vertebrate Evolution (Life of the Past)*. Indiana University Press, Bloomington.
- Reisz, R. R. & Berman, D. S.** 1986. *Ianthasaurus hardestii* n. sp., a primitive edaphosaur (Reptilia, Pelycosauria) from the Upper Pennsylvanian Rock Lake Shale near Garnett, Kansas. *Canadian Journal of Earth Sciences*, **23**, 77–91.
- Reisz, R. R. & Berman, D. S.** 2001. The skull of *Mesenosaurus romeri*, a small varanopseid (Synapsida: Eupelycosauria) from the Upper Permian of the Mezen River Basin, northern Russia. *Annals of the Carnegie Museum*, **70**, 113–132.

- Reisz, R. R. & Dilkes, D. W.** 2003. *Archaeovenator*, a small varanopseid synapsid from the Upper Pennsylvanian of Kansas. *Canadian Journal of Earth Sciences*, **40**, 527–539.
- Reisz, R. R. & Laurin, M.** 2004. A reevaluation of the enigmatic Permian synapsid *Watongia* and of its stratigraphic significance. *Canadian Journal of Earth Sciences*, **41**, 377–386.
- Reisz, R. R. & Modesto, S. P.** 2007. *Heleosaurus scholtzi* from the Permian of South Africa: a varanopid synapsid, not a diapsid reptile. *Journal of Vertebrate Paleontology*, **27**, 734–739.
- Reisz, R. R. & Tsuji, L. A.** 2006. An articulated skeleton of *Varanops* with bite marks: the oldest known evidence of scavenging among terrestrial vertebrates. *Journal of Vertebrate Paleontology*, **26**, 1012–1023.
- Reisz, R. R., Heaton, M. J. & Pynn, B. R.** 1982. Vertebrate fauna of Late Pennsylvanian Rock Lake Shale near Garnett, Kansas: Pelycosauria. *Journal of Paleontology*, **56**, 741–750.
- Reisz, R. R., Berman, D. S. & Scott, D.** 1992a. The cranial anatomy and relationships of *Secodontosaurus*, an unusual mammal-like reptile (Synapsida: Sphenacodontidae) from the Early Permian of Texas. *Zoological Journal of the Linnean Society of London*, **104**, 127–184.
- Reisz, R. R., Scott, D. & Benedegem, J. van.** 1992b. Atlas-axis complex of *Secodontosaurus*, a sphenacodontid mammal-like reptile (Eupelycosauria: Synapsida) from the Lower Permian of Texas. *Canadian Journal of Earth Sciences*, **29**, 596–600.
- Reisz, R. R., Wilson, H. & Scott, D.** 1997. Varanopseid synapsid skeletal elements from Richards Spur, a Lower Permian fissure fill located near Fort Sill, Oklahoma. *Oklahoma Geology Notes*, **57**, 160–170.
- Reisz, R. R., Dilkes, D. W. & Berman, D. S.** 1998. Anatomy and relationships of *Elliottsmithia longiceps* Broom, a small synapsid (Eupelycosauria: Varanopseidae) from the Late Permian of South Africa. *Journal of Vertebrate Paleontology*, **18**, 602–611.
- Reisz, R. R., Godfrey, S. J. & Scott, D.** 2009. *Eothyris* and *Oedaleops*: do these Early Permian synapsids from Texas and New Mexico form a clade? *Journal of Vertebrate Paleontology*, **29**, 39–47.
- Ricqles, A., de & Bolt, J. R.** 1983. Jaw growth and tooth replacement in *Captorhinus aguti* (Reptilia: Captorhinomorpha): a morphological and histological analysis. *Journal of Vertebrate Paleontology*, **3**, 7–24.
- Rodbard, S.** 1949. On the dorsal sail of *Dimetrodon*. *Copeia*, **1949**, 244.
- Romer, A. S.** 1937. New genera and species of pelycosaurian reptiles. *Proceedings of the New England Zoological Club*, **16**, 89–96.
- Romer, A. S.** 1946. The primitive reptile *Limnoscelis* restudied. *American Journal of Science*, **244**, 150–188.
- Romer, A. S.** 1948. Relative growth in pelycosaurian reptiles. Pp. 45–55 in A. L. Toit (ed.) *Robert Broom Commemorative Volume*. South Africa Royal Society Special Publications, Capetown.
- Romer, A. S. & Price, L. I.** 1940. Review of the Pelycosauria. *Geological Society of America Special Paper*, **28**, 1–538.
- Rubidge, B. S. & Sidor, C. A.** 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Reviews in Ecology and Systematics*, **32**, 449–480.
- Rydin, C. & Källersjö, M.** 2002. Taxon sampling and seed plant phylogeny. *Cladistics*, **18**, 485–513.
- Sidor, C. A.** 2003. Evolutionary trends and the origin of the mammalian lower jaw. *Paleobiology*, **29**, 605–640.
- Sidor, C. A. & Hopson, J. A.** 1998. Ghost lineages and “mammalness”: Assessing the temporal pattern of character acquisition in the Synapsida. *Paleobiology*, **24**, 254–273.
- Sigogneau, D. & Tchudinov, P. K.** 1972. Reflections on some Russian eotheriodonts (Reptilia, Synapsida, Therapsida). *Palaeovertebrata*, **5**, 79–109.
- Sikes, D. S. & Lewis, P. O.** 2001. Beta software, Version 1. PAUPRat: PAUP implementation of the parsimony ratchet. Distributed by the authors. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs.
- Stovall, J. W., Price, L. I. & Romer, A. S.** 1966. The postcranial skeleton of the giant Permian pelycosaur *Cotylorhynchus romeri*. *Bulletin of the Museum of Comparative Zoology*, **135**, 1–30.
- Sullivan, C. & Reisz, R. R.** 1999. First record of *Seymouria* (Vertebrata: Seymouriamorpha) from Early Permian fissure fills at Richards Spur, Oklahoma. *Canadian Journal of Earth Sciences*, **36**, 1257–1266.
- Sumida, S. S.** 1990. Vertebral morphology, alternation of neural spine height, and structure in Permo-Carboniferous tetrapods, and a reappraisal of primitive modes of terrestrial locomotion. *University of California Publications, Zoology*, **122**, 1–129.
- Sumida, S. S., Pelletier, V., Berman, D. & English, L.** 2009. New information on the basal pelycosaurian-grade synapsid *Oedaleops*. *Journal of Vertebrate Paleontology, Program and Abstracts*, 2009, **188A**.
- Swofford, D. L.** 2002. PAUP*: Phylogenetic analysis using parsimony (* and other methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- Swofford, D. L. & Olsen, G. J.** 1990. Phylogeny reconstruction. Pp. 411–501 in D. M. Hillis & C. Moritz (eds) *Molecular Systematics*. Sinauer Associates, Inc., Sunderland.
- Vaughn, P. P.** 1958a. On a new pelycosaur from the Lower Permian of Oklahoma, and on the origin of the Family Caseidae. *Journal of Paleontology*, **32**, 981–991.
- Vaughn, P. P.** 1958b. A pelycosaur with subsphenoidal teeth from the Lower Permian of Oklahoma. *Journal of the Washington Academy of Sciences*, **48**, 44–47.
- Vaughn, P. P.** 1969. Early Permian vertebrates from southern New Mexico and their paleogeographic significance. *Los Angeles County Museum of Natural History Contributions in Science*, **166**, 1–22.
- Watson, D. M. S.** 1954. On *Bolosaurus* and the origin and classification of reptiles. *Bulletin of the Museum of Comparative Zoology*, **111**, 1–449.
- Watson, D. M. S.** 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. *Philosophical Transactions of the Royal Society of London B*, **240**, 325–400.
- Wilkinson, M.** 2003. Missing data and multiple trees: stability and support. *Journal of Vertebrate Paleontology*, **23**, 311–323.
- Williston, S. W.** 1911. *American Permian Vertebrates*. University of Chicago Press, Chicago, 145 pp.
- Williston, S. W.** 1912. Primitive reptiles. A review. *Journal of Morphology*, **23**, 637–666.
- Williston, S. W.** 1913. The skulls of *Araeoscelis* and *Casea*, Permian reptiles. *Journal of Geology*, **21**, 743–747.
- Williston, S. W. & Case, E. C.** 1913. Description of a nearly complete skeleton of *Ophiacodon* Marsh. *Carnegie Institute of Washington Publication*, **181**, 37–59.

Benson — Basal synapsid phylogeny —Appendix Table S1, data sources

Taxon	Authority	Data sources
<u>Outgroups</u>		
<i>Tseajaia campi</i>	Vaughn 1964	Moss 1972
<i>Limnocelis paludis</i>	Williston 1911b	Williston 1911a,b, 1912b; Romer 1946; Reisz 2007
<i>Captorhinus</i> spp.	Cope 1895	MCZ uncatalogued; Price 1935; Fox & Bowman 1966; de Ricqles & Bolt 1983; Sumida 1990; Holmes 1997, 2007; Modesto 1998
<i>Protorothyris archeri</i>	Price 1937	Clark & Carroll 1973
<u>Synapsida</u>		
<i>Echinerpeton intermedium</i>	Reisz 1972	MCZ 4079–4087; Reisz 1972
<u>Caseasauria</u>		
<i>Eothyris parkeyi</i>	Romer 1937	MCZ 1161; Reisz <i>et al.</i> 2009
<i>Oedaleops campi</i>	Langston 1965	Reisz <i>et al.</i> 2009
<i>Oromycter dolesorum</i>	Reisz 2005	FMNH PR 2280–2290; Reisz 2005
<i>Casea broili</i>	Williston 1910 (Williston 1910)	FMNH UC 656, 960; Williston 1911a; Olson 1968
<i>Trichasaurus texensis</i>	Sigogneau-Russell & Russell 1974	FMNH UC 652; Williston 1911a
<i>'Casea' rutena</i>	Efremov 1956	Sigogneau-Russell & Russell 1974
<i>Ennatosaurus tector</i>	Olson 1962	PIN 1580/17; Olson 1968; Maddin <i>et al.</i> 2008
<i>Caseopsis agilis</i>	Olson 1962	FMNH UR 253; Olson 1962, 1968
<i>Angelosaurus dolani</i>	Olson & Beerbower 1953	FMNH UR 149, 401; Olson & Beerbower 1953; Olson 1968
<i>Angelosaurus romeri</i>	Olson & Barghusen 1962	FMNH UR 257–259, 264; Olson & Barghusen 1962; Olson 1968
<i>Cotylorhynchus romeri</i>	Stovall 1937	FMNH PR 272, MCZ 3416, OMNH 00631, 00637, 01704, 04329, 04330; Stovall 1937; Stovall <i>et al.</i> 1966
<i>Cotylorhynchus bransoni</i>	Olson & Barghusen 1962	FMNH specimens listed by Olson & Barghusen 1962
<i>Cotylorhynchus hancocki</i>	Olson & Beerbower 1953	FMNH specimens listed by Olson & Beerbower 1953; Olson 1968
<u>Varanopidae</u>		
<i>Archaeovenator hamiltonensis</i>	Reisz & Dilkes 2003	Reisz & Dilkes 2003
<i>Pyozia mesenensis</i>	Anderson & Reisz 2004	Anderson & Reisz 2004
<i>Mycterosaurus longiceps</i>	Williston 1915	FMNH UC 169, 692; Berman & Reisz 1982
<i>Mesenosaurus romeri</i>	Efremov 1938	PIN uncat.; Reisz & Berman 2001
<i>Heleosaurus scholtzi</i>	Broom 1907	Carroll 1976; Reisz & Modesto 2007; Botha-Brink & Modesto 2007, 2009
BP/1/5678 (<i>Elliottsmithia</i>)	Vaughn 1958b	BP/1/5678; Modesto <i>et al.</i> 2001
<i>Basiscranodon fortisillensis</i>	Romer 1937	Vaughn 1958b
<i>Aerosaurus greenleeorum</i>		MCZ 3427 [casts of FMNH WM 464]; Romer & Price 1940; Langston & Reisz 1981
<i>Aerosaurus wellesi</i>	Langston & Reisz 1981	UCMP 40096–97; Langston & Reisz 1981
<i>Ruthiromia elcobriensis</i>	Eberth & Brinkman 1983	MCZ 3150; Eberth & Brinkman 1983
<i>Varanodon agilis</i>	Olson 1965	FMNH UR 986; Olson 1965
<i>Varanops brevirostris</i>	(Williston 1911a)	FMNH UC 644, UR 2423; MCZ 1926; 73156–73178; TMM 43628-1; Williston 1911a; Maddin <i>et al.</i> 2006; Campione & Reisz 2010
<i>Watongia meieri</i>	Olson 1974	UCMP 143278; Reisz & Laurin 2004
<u>Ophiacodontidae</u>		
<i>Archaeothyris florensis</i>	Reisz 1972	MCZ 4090–4094; Reisz 1972
<i>Varanosaurus acutirostris</i>	Broili 1904	AMNH 4174, BSPHM 1901 XV 20, FMNH PR 1760, UR 34; Broili 1904, 1904–1905; Sumida 1989a; Berman <i>et al.</i> 1995
<i>Ophiacodon</i> spp.	Marsh 1878	Specimens at AMNH, CMNH, FMNH, MCZ, OMNH mostly listed by Romer & Price 1940
<i>Stereophalodon ciscoensis</i>	Romer 1937	MCZ 1535, 1944, 6618 and material at MCZ from Prideaux Pocket; Brinkman & Eberth 1986
<u>Edaphosauridae + Sphenacodontia</u>		
<i>Ianthodon schultzei</i>	Kissel & Reisz 2004	Kissel & Reisz 2004
<u>Edaphosauridae</u>		
<i>Ianthasaurus hardستii</i>	Reisz & Berman 1986	CMNH 34449, 34500, 34576, 34577, 34578, 34579, 34580, 34581, 47700, ROM 29940, 29941, 29942, 37751; Reisz & Berman 1986; Modesto & Reisz 1990; Mazierski & Reisz 2010
<i>Glaucosaurus megaloپس</i>	Williston 1915	FMNH UC 691; Modesto 1994
<i>Lupeosaurus kayi</i>	Romer 1937	MCZ 1455; Romer & Price 1940; Sumida 1989b
<i>Edaphosaurus boanerges</i>	Romer & Price 1940	MCZ specimens; Romer & Price 1940; Modesto 1995
<i>Edaphosaurus novomexicanus</i>	Williston & Case 1913	CMNH 34910, FMNH UC 674; Modesto & Reisz 1992
<u>Sphenacodontia</u>		
<i>Haptodus garnettensis</i>	Currie 1977	ROM 43602, 43604, 43606; Currie 1977; Laurin 1993
<i>Pantelosaurus saxonicus</i>	Von Huene 1925	Von Huene 1925; Laurin 1994
<i>Cutleria wilmarthi</i>	Lewis & Vaughn 1965	USNM 22099; Lewis & Vaughn 1965; Laurin 1994
<i>Secodontosaurus obtusidens</i>	(Cope 1880)	FMNH UC 754; MCZ 1124, 2749, 2944, 5134, 6382–6384, 6998; Reisz <i>et al.</i> 1992a,b
<i>Cryptovenator hirschbergeri</i>	Fröbisch <i>et al.</i> 2011	Fröbisch <i>et al.</i> 2011
<i>Ctenorhachis jacksoni</i>	Hook & Hotton 1991	Hook & Hotton 1991
<i>Dimetrodon</i> spp.	Cope 1878	Numerous specimens at MCZ and AMNH listed by Romer & Price 1940
<i>Sphenacodon</i> spp.	Marsh 1878	FMNH UC 1918; MCZ 1489; Eberth 1985
<u>Therapsida</u>		
<i>Biarmosuchus tener</i>	Tchudinov 1960	Sigogneau & Tchudinov 1972, using data from holotype only
<i>Biseridens gilianicus</i>	Li & Cheng 1997	Li & Cheng 1997, Liu <i>et al.</i> 2010
<i>Raranimus dashankouensis</i>	Liu <i>et al.</i> 2009	Liu <i>et al.</i> 2009
<i>Titanophoneus potens</i>	Efremov 1938	Orlov 1958

Table S1. List of taxa included in the present analysis with taxonomic authority and data sources used during the present analysis.

Additional references

- Broili, F.** 1904. Permische Stegocephalen und Reptilien aus Texas. *Palaeontographica*, **51**, 1–120.
- Broili, F.** 1904–1905. Beiträge zur Naturgeschichte der Vorzeit. 2 Teil. Die Reptilien. *Palaeontographica*, Stuttgart.
- Broom, R.** 1907. On some new fossil reptiles from the Karroo beds of Victoria West, South Africa. *Transactions of the South African Philosophical Society*, **18**, 31–42.
- Carroll, R. L.** 1976. Eosuchians and the origins of archosaurs. Pp. 58–79 in C. S. Churcher (ed.) *Athlon, Essays in Honour of Loris Shano Russell*. Royal Ontario Museum, Toronto.
- Cope, E. D.** 1880. Second contribution to the history of the Vertebrata of the Permian formation of Texas. *Proceedings of the American Philosophical Society*, **18**, 38–58.
- Heaton, M. J.** 1979. Primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian of Oklahoma and Texas. *Oklahoma Geological Survey Bulletin*, **127**, 1–84.
- Hook, R. W. & Hotton, N. III.** 1991. A new sphenacodontid pelycosaur (Synapsida) from the Wichita Group, Lower Permian of north central Texas. *Journal of Vertebrate Paleontology*, **11**, 37–44.
- Huene, F. von** 1925. Ein neuer Pelycosaurier aus der unteren Permformation Sachsens. *Geologische und palaeontologische Abhandlungen*, **14**, 215–264.
- Olson, E. C.** 1965. New Permian vertebrates from the Chickasha Formation in Oklahoma. *Oklahoma Geological Survey Circular*, **70**, 1–70.
- Olson, E. C.** 1974. On the source of therapsids. *Annals of the South African Museum*, **64**, 27–46.
- Sigogneau-Russell, D. & Russell, D. E.** 1974. Étude du premier Caséidé (Reptilia, Pelycosauria) d'Europe occidentale. *Bulletin du Muséum National d'Histoire Naturelle*, **230**, 145–215.
- Stovall, J. W.** 1937. *Cotylorhynchus romeri*, a new genus and species of pelycosaurian reptile from Oklahoma. *American Journal of Science*, **34**, 308–313.
- Sumida, S. S.** 1989a. Reinterpretation of vertebral structure in the Early Permian pelycosaur *Varanosaurus acutirostris* (Amniota, Synapsida). *Journal of Vertebrate Paleontology*, **9**, 451–458.
- Sumida, S. S.** 1989b. New information on the pectoral girdle and vertebral column in *Lupeosaurus* (Reptilia, Pelycosauria). *Canadian Journal of Earth Sciences*, **26**, 1343–1349.
- Tchudinov, P. K.** 1960. [Upper Permian therapsids from the Ezhovo locality]. *Paleontologicheskii Zhurnal*, **4**, 81–94 [in Russian].
- Vaughn, P. P.** 1964. Vertebrates from the Organ Rock Shale of the Cutler Group, Permian of Monument Valley and vicinity, Utah and Arizona. *Journal of Paleontology*, **38**, 567–583.
- Williston, S. W.** 1910. New Permian reptiles: rhachitomous vertebrae. *Journal of Geology*, **18**, 585–600.
- Williston, S. W.** 1911b. A new family of reptiles from the Permian of New Mexico. *American Journal of Science*, **31**, 378–398.
- Williston, S. W.** 1912b. Restoration of *Limnoscelis*, a cotylosaur reptile from New Mexico. *American Journal of Science*, **34**, 457–468.
- Williston, S. W.** 1915. New genera of Permian reptiles. *American Journal of Science*, **39**, 575–579.

Character list

The character list below includes a short character description, citations of previous uses and a longer explanation of the character and its history. Several analyses of varanopids are iterative modifications of the character list of Reisz *et al.* (1998). Only novel characters in these iterations are cited below. The character list of Modesto *et al.* (2001) is a modified version of that of Reisz *et al.* (1998) to which two characters were added (Modesto *et al.* 2001, characters 32 and 33). The character list of Reisz & Dilkes (2003) was modified from that of Modesto *et al.* (2001) by the addition of 20 characters (Reisz & Dilkes 2003, characters 34–53). The character list of Anderson & Reisz (2004) was modified from that of Reisz & Dilkes (2003) by the addition of a single character (Anderson & Reisz 2004, character 54). The character list of Laurin & Reisz (2004) was modified from the analysis of Reisz & Dilkes (2003) by the addition of five characters (Laurin & Reisz 2004, characters 54–58).

Although the data matrix of Maddin *et al.* (2006) is an iterative modification of that of Reisz *et al.* (1998), it is fully cited below to provide an up-to-date representation of the character list. The character list of Campione & Reisz (2010) only differs that of Maddin *et al.* (2006) by the deletion of two characters (Maddin *et al.* 2006, characters 45 and 60) and is not cited below.

The notation ‘+++’ indicates the clade comprising the named taxon and all more derived taxa within its clade. For example, ‘*Varanosaurus* +++’ indicates the clade comprising *Varanosaurus* and all more derived ophiacodontids (i.e. *Varanosaurus* + *Ophiacodon* + *Stereophallodon*). New characters are denoted by a ‘*’. Optimisation corresponds to the tree derived from analysis of the full dataset excluding wildcard taxa (Fig. 2A).

Cranial characters

1. Skull size: large, greater than 30% presacral length (0); small, less than 25% presacral length (1)

Modified from Modesto (1994, character 18; 1995, character 16), Maddin *et al.* (2008, character 51), Mazierski & Reisz (2010, character 17).

Reduction of the proportional size of the skull has long been recognised as a derived feature within the herbivorous clades Edaphosauridae and Caseidae (e.g. Olson 1968; Gould & Littlejohn 1973; Reisz 1986). Romer & Price (1940) proposed that the presence of a small head was diagnostic for ‘Edaphosauria’ (Edaphosauridae + Caseidae). However, Reisz (1980) suggested that it represented parallel adaptation to herbivory.

DELTRAN: *Casea broili* +++ (0->1), *Edaphosaurus* (0->1)

ACCTRAN: Caseasauria (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* (0->1)

2. Snout proportions, antorbital length in relation to temporal length: subequal (0); antorbital 1.1–1.8 times temporal length (1); temporal region longer (2); snout very long, antorbital length at least twice the temporal length (3) (Figures A1, A2).

Modified from Reisz *et al.* (1992, characters 1, 2, 23), Laurin (1993, character 17), Modesto (1994, character 19), Berman *et al.* (1995, characters 2, 25), Modesto (1995, character 17), Sidor & Hopson (1998, character 41), Maddin *et al.* (2008, characters 29, 50), Mazierski & Reisz (2010, character 18), Fröbisch *et al.* (2011, character 95).

Changes in the proportional snout length occurred frequently in basal synapsid evolution and have been central to pelycosaur systematics (e.g. Romer & Price 1940; Langston 1965; Reisz 1980). For instance, Reisz (1986) described the proportionally short snout (state ‘2’) as a plesiomorphic feature retained by Caseasauria. However, data compiled for the present study indicate that the snout is in fact longer than the temporal region in outgroup taxa (state ‘1’; basal diadectomorphs; Williston 1911, pp. 23–47; Romer 1946; Moss 1972; and basal eureptilians e.g. Fox & Bowman 1966; Clark & Carroll 1973) and the most basal representatives of most basal synapsid clades (e.g. Reisz 1972; Currie 1977; Modesto & Reisz 1990; Laurin 1993; Reisz & Dilkes 2003). State ‘1’ is therefore likely plesiomorphic. Additionally, despite their relatively deeper skulls, the proportional snout lengths of *Dimetrodon* (Romer & Price 1940), *Sphenacodon* (Eberth 1985), and basal therapsids (e.g. Orlov 1958) are elongate, similar to that in *Secodontosaurus* (Reisz *et al.* 1992) and *Ophiacodon* (state ‘3’).

Unambiguous: Varanodontinae (1->0), *Varanosaurus* +++ (1->3), ‘Casea’ *rutena* (0->2)

DELTRAN: Eothyrididae (1->2), *Casea broili* +++ (1->0), *Edaphosaurus* (1->2), *Secodontosaurus* + Sphenacodontinae (1->3), *Varanodon agilis* (0->2), *Titanophoneus potens* (1->3), *Biarmosuchus tener* (1->3)

ACCTRAN: *Varanodon* + *Watongia* (0->2), Caseasauria (1->0), Eothyrididae (0->2), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (1->2), Sphenacodontidae + Therapsida (1->3), *Cutleria wilmarthi* (3->1), *Biseridens qilianicus* (3->1)

3. Snout proportions, relative width/depth: broad, wider mediolaterally than tall dorsoventrally and nasal primarily on dorsal surface of skull (0); taller than wide, nasal contributes to lateral surface of snout (1).

Modesto (1994, character 9), Reisz *et al.* (1998, character 12), Reisz & Dilkes (2003, character 53), Maddin *et al.* (2006, character 43), Maddin *et al.* (2008, character 54), Reisz *et al.* (2009, character 27); modified from Sidor & Hopson (1998, character 45)

Reisz (1980; 1986) and Romer & Price (1940; eothyridids) interpreted the broad, low skulls shared by outgroup taxa and caseasaurians as plesiomorphic. Other basal synapsids have proportionally higher skulls.

DELTRAN: Ophiacodontidae + Varanopidae (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: Synapsida (0->1), Caseasauria (1->0)

4. External naris, length: small, <25% preorbital length (0); moderate, 25–50% preorbital length, narrow posterodorsal expansion pinched between nasal and maxilla present (1); long >50% preorbital length (2) (Figure A2).

Reisz & Dilkes (2003, character 43), Maddin *et al.* (2006, character 42), Maddin *et al.* (2008, character 4), Reisz *et al.* (2009, characters 8, 9), modified from Reisz *et al.* (1992, character 29).

In caseids (e.g. Olson 1968; Reisz 1980, 1986 [in caseasaurids]; Maddin *et al.* 2008) and most varanopids (e.g. Reisz & Dilkes 2003; Campione & Reisz 2010) the external naris is anteroposteriorly expanded (state ‘2’) and occupies most of the antorbital length. The mycterosaurines *Heleosaurus* (Botha-Brink & Modesto 2009), *Mesenosaurus* (Reisz & Berman 2001), and *Mycterosaurus* (Berman & Reisz 1986) show a possibly related morphology in which only the posterodorsal portion of the naris is expanded (state ‘1’).

Character 19 includes a state (‘2’) describing the enlarged, sheet-like morphology of the septomaxilla associated with expansion of the naris in some varanopids possessing a fully enlarged external naris (character 4, state ‘2’). The presence of an anteroposteriorly enlarged external naris subdivided by a sheet-like septomaxilla misled Reig (1967, 1970) into positing the presence of an antorbital fenestra (an archosaurian synapomorphy) in the varanopid *Varanodon*. Romer (1971) and Langston & Reisz (1981) suggested instead that this opening resulted from damage to a very thin, fragile lacrimal. The true morphology (effectively, a very large septomaxillary foramen divided from the anterior part of the external naris by a large, sheet-like septomaxilla) was only recognised later (e.g. Reisz & Dilkes 2003).

Unambiguous: Varanopidae (0->2), Mycterosaurinae (2->1), Caseidae (0->2)

5. External naris, height: 30–75% of orbital height (0); >75% orbital height, lacrimal constricted and thus very tall and narrow (1).

Maddin *et al.* (2008, character 5); modified from Maddin *et al.* (2008, character 16).

All caseids possess an anteroposteriorly broad external naris (see character 4, above). In *Ennatosaurus* (Olson 1968; Maddin *et al.* 2008) and *Cotylorhynchus* (Stovall 1937; Olson 1968) the naris is further expanded dorsoventrally. Maddin *et al.* (2008, character 16) coded a second character, describing the dorsoventrally tall, anteroposteriorly narrow morphology of the lacrimal in these genera. However, this is not independent of narial expansion. Although Maddin *et al.* (2008, character 16) scored a tall, narrow lacrimal in ‘*Casea*’ *rutena*, the lacrimals of *Ennatosaurus* and *Cotylorhynchus* are comparatively much more tall and narrow, so ‘*C.*’ *rutena* is excluded from the derived state.

Unambiguous: *Ennatosaurus* +++ (0->1)

6. Temporal fenestra: absent (0); present (1).

Unambiguous: Synapsida (0->1)

Romer & Price (1940) concluded that the lateral temporal fenestra was the only diagnostic feature of Synapsida (‘Pelycosauria’). Reisz (1980), by contrast, considered that it was shared with diapsids. Subsequent studies have demonstrated the existence of stem diapsids (basal eureptilians) such as ‘captorhinomorphs’ that lack

temporal fenestration, so the presence of a fenestra is undoubtedly a synapsid synapomorphy (Reisz 1986).

7. Temporal fenestra morphology: narrow dorsoventrally (<0.5x temporal height) with deep temporal bar [posterior process of the jugal] (0); tall dorsoventrally with narrow temporal bar (1); very large, opens dorsally (2); inapplicable, temporal fenestra absent (?).

Modified from Laurin (1993, characters 22, 33, 36), Modesto (1994, character 16), Berman *et al.* (1995, characters 38, 41), Reisz *et al.* (1998, characters 3, 18), Sidor & Hopson (1998, character 44), Maddin *et al.* (2006, characters 45, 46, 47), Maddin *et al.* (2008, characters 21, 44, 45, 49), Reisz *et al.* (2009, characters 42, 43, 44, 45), Fröbisch *et al.* (2011, character 26).

The states of this character are drawn from various previously used characters describing the thickness of the lower temporal bar (posterior process of the jugal), and the size and orientation of the temporal fenestra. These features do not vary independently and so are here considered as states of a single character. In taxa possessing a large temporal fenestra, the overall shape of the fenestra can be influenced by the slope of the occiput (character 90), so I do not employ a separate character for the shape of the fenestra.

Unambiguous: Ophiacodontidae (1->0), *Secodontosaurus* + Sphenacodontinae (1->0), *Eothyris parkeyi* (1->0)

DELTRAN: *Biarmosuchus* +++ (1->2)

ACCTRAN: Therapsida (1->2)

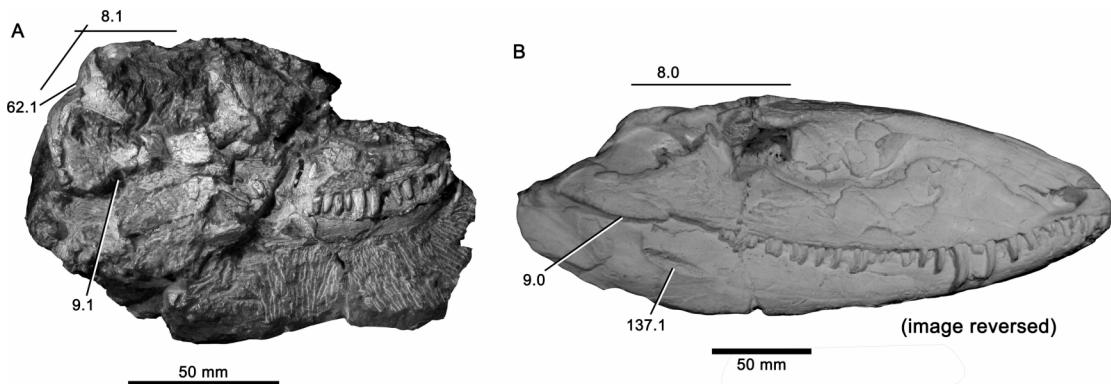


Figure A1. Skulls of **A**, *Cutleria* (USNM 22099) and **B**, *Ophiacodon* (cast of USNM 487098; reversed) in right lateral view indicating states of characters 8, 9, 62 and 137. Lines drawn above the temporal region show the strongly posteroventrally inclined temporal roof of *Cutleria* and the horizontal temporal roof in *Ophiacodon* (character 8). Note that *Ophiacodon* does not possess a concave ventral cheek margin (character 9.1). Scale bars equal 50 mm.

8*. Temporal (postorbital) roof orientation: subhorizontal or weakly inclined posteroventrally (0); strongly inclined posteroventrally, at least 45° (1).

New character (Figure A1).

In *Cutleria* (Lewis & Vaughn 1965; Laurin 1994), *Dimetrodon* (e.g. Romer & Price 1940) and other sphenacodontines (e.g. Eberth 1985) the postorbital portion of the skull is strongly inclined posteroventrally. Although Currie (1979, text-fig. 5) reconstructed the temporal roof of *Haptodus baylei* with a strong slope, this is exaggerated compared to the actual specimens (Currie 1979, text-fig. 3). Similarly, there is little evidence for the strong slope reconstructed in *Ianthodon* by Kissel & Reisz (2004).

DELTRAN: *Dimetrodon* + *Sphenacodon* (0->1), *Cutleria wilmarthi* (0->1), *Biarmosuchus tener* (0->1)

ACCTRAN: Sphenacodontidae + Therapsida (0->1), *Titanophoneus* + *Biseridens* (1->0), *Secodontosaurus obtusidens* (1->0)

9. Skull, ventral outline of temporal bar in lateral view: straight or weakly concave (0); strongly anteroposteriorly concave (1); straight but inflected posteroventrally relative to tooth row (2) (Figure A1).

Modified from Brinkman & Eberth (1983, character 1), Reisz *et al.* (1992, character 35), Modesto (1994, character 17), Berman *et al.* (1995, character 42), Sidor & Hopson (1998, character 43), Reisz & Dilkes (2003, character 52), Maddin *et al.* (2006, character 48).

Romer & Price (1940) considered the depressed position of the jaw joint, significantly ventral to the maxillary tooth row (character 125), as a diagnostic feature of ‘Edaphosauria’ (Edaphosauridae + Caseidae). However, Reisz (1980) suggested that this represented a parallel adaptation to herbivory, and noted that this was achieved in different ways in the two groups. In edaphosaurids the ventral edge of the jugal and quadratojugal is strongly concave and most of the lateral surface of the squamosal extends below the lateral temporal opening (state ‘1’), whereas in caseids the ventral margin of the cheek is inflected posteroventrally (state ‘2’). A separate character codes lowering of the jaw joint relative to the tooth row (character 125).

Previous authors have considered state ‘1’ to be present in ophiacodontids such as *Archaeothyris*, *Ophiacodon* and *Varanosaurus* (Brinkman & Eberth 1983; Reisz 1986; Reisz *et al.* 1992; Berman *et al.* 1995; Maddin *et al.* 2006). This observation originated with Romer & Price (1940, fig. 3B, pl. 1), who figured the highly reconstructed skull of *Ophiacodon uniformis* (MCZ 1366). This figure was reproduced in the influential work of Reisz (1986, fig. 9), and has been central to hypotheses of Ophiacodontidae as the sister taxon of Sphenacodontia + Edaphosauria (e.g. Brinkman & Eberth 1983; Reisz *et al.* 1992). However, ventral margin of the temporal bar is straight in well-preserved specimens of *Ophiacodon* (Fig. A1B; USNM 487098; FMNH UC 458, 671; Romer & Price 1940, fig. 3C–D; *contra* Romer & Price 1940, fig. 3B, pl. 1) and *Varanosaurus* (FMNH PR 1670; Berman *et al.* 1995, fig. 11). It is not preserved in *Archaeothyris*, which was interpreted as concave by Reisz (1972), but is scored as missing data here.

Maddin *et al.* (2008) scored caseids as possessing the concave condition (state ‘1’). This state is reserved for taxa with a strongly concave temporal bar in the present analysis (Edaphosauridae and non-therapsid sphenacodontians). However, a new state (‘2’) describes the condition in caseids, in which the ventral margin of the temporal region is inflected posteroventrally relative to the ventral margin of the maxilla (e.g. Olson 1968; Reisz 1986).

Unambiguous: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

DELTRAN: *Casea broili* +++ (0->2), *Biarmosuchus* +++ (1->0)

ACCTRAN: Caseidae (0->2), Therapsida (1->0)

10. Skull, longitudinal location of posteriormost portion of skull: approximately at the level of the occipital condyle (0); far posterior to occipital condyle (1).

Modified from Laurin (1993, character 46), Maddin *et al.* (2008, character 46), Fröbisch *et al.* (2011, character 34).

The derived state is present in varanodontine varanopids (e.g. Langston & Reisz 1981) and some basal therapsids (Orlov 1958; Li & Cheng 1997). It results in the posterior margin of the skull having an embayed appearance in dorsal view. Reisz (1980) considered the derived state as uniting ophiacodontids, varanopids and sphenacodontians, but it is absent in ophiacodontids and most sphenacodontians.

Unambiguous: Varanodontinae (0->1), *Biseridens qilianicus* (0->1)

DELTRAN: *Ophiacodon* spp. (0->1)

ACCTRAN: *Ophiacodon* + *Stereophalodon* (0->1)

11. Skull table ornamentation: absent or weak (0); unevenly spaced circular pits present (1); evenly and densely distributed, irregular shallow pits (2)

Modified from Maddin *et al.* (2008, character 48), Reisz *et al.* (2009, character 1) by addition of a state ('2') describing the condition in basal eureptilians (e.g. Clark & Carroll 1973).

In many caseids the skull table is ornamented by irregularly distributed circular pits approximately 5 mm in diameter (in *Cotylorhynchus romeri*; OMNH 04329) (Sigogneau-Russell & Russell 1974; Maddin *et al.* 2008).

Unambiguous: Eureptilia (0->2), *Ennatosaurus tector* (1->0)

DELTRAN: *Casea broili* +++ (0->1)

ACCTRAN: Caseidae (0->1)

12. Skull, circumorbital tuberosities ornamenting jugal and likely also the prefrontal: absent (0); present (1).

Reisz *et al.* (1998, character 14), Maddin *et al.* (2006, character 44), Reisz *et al.* (2009, character 30).

The derived state of this character was scored as present in *Elliotsmithia*, *Mycterosaurus* and *Mesenosaurus* by previous authors. However, Reisz & Berman (2001) described the presence of jugal tuberosities in all varanopids, and they are certainly present in *Aerosaurus* and *Varanops* (Campione & Reisz 2010). In both the latter taxa the prefrontal is poorly preserved, so it is difficult to confirm the absence of prefrontal tuberosities and this character is coded primarily based on observation of the jugal in the present analysis.

DELTRAN: Mycterosaurinae + Varanodontinae (0->1), *Varanodon agilis* (1->0)

ACCTRAN: *Pyozia* +++ (0->1), *Watongia* + *Varanodon* (1->0)

13. Premaxilla, ventral margin: approximately horizontal (0); slopes anteroventrally from ventral concavity on maxilla-premaxilla contact (1); slopes anterodorsally (2).

Reisz *et al.* (1992, character 3), Fröbisch *et al.* (2011, character 96); modified from Berman *et al.* (1995, character 3), Sidor & Hopson (1998, character 2).

The ventral margin of the premaxilla slopes anteroventrally in basal diadectomorphs (Romer 1946; Moss 1972), captorhinids (e.g. Fox & Bowman 1966; Clark & Carroll 1973), and many sphenacodontians, including the basal therapsids *Biseridens* and *Raranimus* (Liu *et al.* 2009, 2010). Non-therapsid sphenacodontians with an anterodorsally sloping ventral margin of the premaxilla possess at least a weak precanine step. In some basal therapsids, the ventral margin of the premaxilla instead slopes anterodorsally (e.g. Orlov 1958).

Unambiguous: Sphenacodontia (0->1)

DELTRAN: Synapsida (1->0), *Titanophoneus potens* (1->2), *Protorothyris archeri* (1->0), *Biarmosuchus tener* (1->2)

ACCTRAN: Amniota (1->0), *Biarmosuchus* +++ (1->2), *Captorhinus* (0->1), *Biseridens qilianicus* (2->1)

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

Modified from Brinkman & Eberth (1983, character 5), Reisz & Dilkes (2003, character 51), Maddin *et al.* (2006, character 6), Maddin *et al.* (2008, character 1), Reisz *et al.* (2009, character 2) by addition of state '2' describing the condition in ophiacodontids (Brinkman & Eberth 1986; Berman *et al.* 1995).

Langston (1965) noted the 'obtuse rostrum' (state '1'; 'rostral process' of e.g. Reisz *et al.* 2009) in *Eothyris*, *Oedaleops* and *Casea*. Reisz (1980, 1986) proposed that this was a caseasaurian synapomorphy. Note however, that it is also present in an outgroup taxon, *Limnoscelis* (Romer 1946; Maddin *et al.* 2008) and therefore may be plesiomorphic if caseasaurians occupy a basal position within Synapsida. Brinkman & Eberth (1983) also scored this condition in varanopids. However, the condition in varanopids is more similar to that in non-caseasaurian basal synapsids (Reisz 1986, p. 91). Brinkman & Eberth (1986) described the strong posterodorsal inclination of the premaxilla (state '2') as an ophiacodontid synapomorphy shared by *Ophiacodon* and *Sterophallodon*. It is also present in *Varanosaurus* (Berman *et al.* 1995).

Unambiguous: Caseasauria (0->1), *Titanophoneus potens* (0->2), *Limnoscelis paludis* (0->1)

DELTRAN: *Varanosaurus* +++ (0->2)

ACCTRAN: Ophiacodontidae (0->2)

15. Premaxilla, narial shelf [ventral floor of internal naris formed by the dorsal surface of the premaxillary body] **morphology:** distinct from lateral surface of premaxilla, which is dorsoventrally broad (0); narial shelf extends ventrolaterally to meet the tooth row so there is no lateral surface of the premaxilla ventral to the external naris (1).

Reisz *et al.* (1998, character 2), Maddin *et al.* (2006, character 7), Reisz *et al.* (2009, character 5).

Previous authors have scored the derived state in all varanopids, and proposed that this morphology is unique to varanopids (Reisz *et al.* 1998; Reisz & Berman 2001; Anderson & Reisz 2004). However, the distribution is more complex than this. The primitive state occurs in some derived varanodontines (*Varanodon* and *Varanops*; FMNH UR 986; TMM 43628) and the mycterosaurine *Heleosaurus* (Botha-Brink & Modesto 2009), and the derived state occurs outside of Varanopidae in the ophiacodontid *Varanosaurus* (BSPHM 1901 XV 20; FMNH PR 1760; Berman *et al.* 1995).

Unambiguous: *Varanops* + *Varanodon* + *Watongia* (1->0), *Heleosaurus scholtzi* (1->0)

DELTRAN: Varanopidae (0->1), *Varanosaurus acutirostris* (0->1)

ACCTRAN: Ophiacodontidae + Varanopidae (0->1), *Ophiacodon* + *Stereophallodon* (1->0)

16. Premaxilla subnarial process: short, maxilla forms floor of external naris (0); greatly elongated, maxillary contribution to external naris absent or small (1).

Reisz *et al.* (2009, character 19).

Unambiguous: Amniota (1->0), Eothyrididae (0->1)

17. Premaxilla, marginal tooth count: two–four (0); five–six (1).

Reisz & Dilkes (2003, character 41), modified from Reisz *et al.* (1992, character 63), Laurin (1993, character 68), Berman *et al.* (1995, character 70), Sidor & Hopson (1998, character 102), Maddin *et al.* (2006, character 5), Maddin *et al.* (2008, character 63), Reisz *et al.* (2009, character 4), Fröbisch *et al.* (2011, character 54).

Characters coding the relative length of the premaxillary body are also considered to be redundant with this character (Reisz *et al.*, 1992, character 5; Laurin 1993, character 2; Berman *et al.* 1995, character 6; Fröbisch *et al.* 2011, character 1).

Unambiguous: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->1), *Varanops* + *Varanodon* + *Watongia* (0->1), *Titanophoneus potens* (1->0)

DELTRAN: *Varanosaurus* +++ (0->1), Sphenacodontia (0->1), *Dimetrodon* + *Sphenacodon* (1->0), *Edaphosaurus boanerges* (0->1), *Cutleria wilmarthi* (1->0)

ACCTRAN: Ophiacodontidae (0->1), Edaphosauridae + Sphenacodontia (0->1), Sphenacodontidae (1->0), *Secodontosaurus obtusidens* (0->1), *Glaucosaurus megalops* (1->0)

18. Premaxilla, marginal tooth size: small or subequal to (non-canniniform) maxillary teeth (0); anterior teeth large (1).

Modified from Reisz *et al.* (1992, character 60), Laurin (1993, character 69), Modesto (1994, character 2; 1995, character 3), Sidor & Hopson (1998, character 109), Fröbisch *et al.* 2011, (character 55), and from characters describing the size of the mesialmost tooth relative to other premaxillary teeth: Maddin *et al.* (2008, character 68), Reisz *et al.* (2009, character 3); Mazierski & Reisz (2010, character 3), Fröbisch *et al.* 2011, (character 53).

Basal diadectomorphs (Romer 1946; Moss 1972; Reisz 2007), captorhinids (e.g. Clark & Carroll 1973; de Ricqles & Bolt 1983), many sphenacodontians (e.g. Romer & Price 1940), some caseids (Olson 1968; Reisz 1980, 2005; Maddin *et al.* 2008), and the ophiacodontids *Ophiacodon* (Romer & Price 1940) and *Stereophallodon* (Brinkman & Eberth 1986) possess anterior premaxillary teeth that are significantly larger than their non-canniniform maxillary teeth. Previous datasets coded additional aspects of variation in premaxillary dentition size, such as whether all premaxillary teeth, or just the mesialmost tooth are large. However this level of detail is difficult to code appropriately and was not included in the present study.

Unambiguous: *Ophiacodon* + *Stereophallodon* (0->1), *Titanophoneus potens* (0->1), *Oromycter dolesorum* (0->1), *Ianthodon schultzei* (0->1), *Haptodus garnettensis* (0->1), *Ennatosaurus tector* (0->1)

DELTRAN: Synapsida (1->0), *Secodontosaurus* + Sphenacodontinae (0->1),

Protorothyris archeri (1->0)

ACCTRAN: Amniota (1->0), Sphenacodontidae (0->1), *Captorhinus* (0->1)

19. 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).

Modified from Modesto (1994, character 8), Reisz *et al.* (2009, character 10). State ‘2’ taken from Berman *et al.* (1995, character 7, state 1), Reisz & Dilkes (2003, character 42), Maddin *et al.* (2006, character 8) and Reisz *et al.* (2009, character 11). New states (‘3’ and ‘4’) describe the condition in sphenacodontids and basal therapsids.

Reisz (1980, 1986) described the distinctive morphology of the basal synapsid septomaxilla comprising a broad ventral portion that contacts the premaxilla and maxilla, and a slender, pillar-like dorsal process (state ‘1’; see also Olson 1968, figs 4–5). The dorsal process of the septomaxilla divides the external naris into two subequal openings, the posterior of which is often called the septomaxillary foramen (Romer & Price 1940; Berman *et al.* 1995). In sphenacodontians (Romer & Price 1940, pl. 6; Currie 1979, text-fig. 5; Eberth 1985; Reisz *et al.* 1992), including some basal therapsids (e.g. Orlov 1958) the septomaxillary foramen is reduced (state ‘3’). In other basal therapsids the septomaxillary foramen is absent (state 4; e.g. Liu *et al.* 2009, 2010). Most varanopids possess a large, sheet-like septomaxilla that is broadly exposed in lateral view (e.g. Reisz & Dilkes 2003).

Unambiguous: Synapsida (0->1), Varanopidae (1->2), *Titanophoneus potens* (4->3)

DELTRAN: Therapsida (1->4), *Secodontosaurus* + Sphenacodontinae (1->3)

ACCTRAN: *Pantelosaurus* +++ (1->3), Therapsida (3->4)

20. Septomaxilla, posterodorsal extension on to lateral surface of skull [facial process]: absent (0); present (1).

Reisz *et al.* (1992, character 6), Laurin (1993, character 4), Sidor & Hopson (1998, character 6), Fröbisch *et al.* (2011, character 3).

The derived state is a well-documented synapomorphy of Therapsida (e.g. Sidor & Hopson 1998).

Unambiguous: Therapsida (0->1)

21. Maxilla, lateral surface orientation: vertical or slopes weakly dorsomedially (0); slopes dorsolaterally, overhanging tooth row (1).

Maddin *et al.* (2008, character 2), Reisz *et al.* (2009, character 14).

Langston (1965) and some subsequent authors observed that the lateral surface of the maxilla slopes weakly dorsolaterally in caseids and eothyridids, and that this may represent a synapomorphy of Caseasauria. This morphology is also present in basal diadectomorphs (Romer 1946) and captorhinids (e.g. Fox & Bowman 1966; Modesto 1998) and may be plesiomorphic.

DELTRAN: Ophiacodontidae + Varanopidae (1->0), Edaphosauridae + Sphenacodontia (1->0)

ACCTRAN: Synapsida (1->0), Caseasauria (0->1)

22. Nasal-maxilla contact: absent, lacrimal contributes to posterior margin of external naris (0); present, lacrimal does not contact external naris, but is longer than half the orbito-narial length (1); present, lacrimal does not contact external naris and is shorter than half the orbito-narial length (2).

Modified from Reisz *et al.* (1992, characters 8, 10, 30), Laurin (1993, characters 6, 30, 31), Berman *et al.* (1995, character 11, 13, 35), Sidor & Hopson (1998, character 7), Fröbisch *et al.* (2011, characters 23, 24, 97).

Previous analyses coded three logically dependent aspects of variation as separate characters: (1) contact between the lacrimal and external naris; (2) contact between the maxilla and nasal; (3) the presence of a ‘posteroventral narial process’ of the nasal. These are coded here as a single character because the presence of a posteroventral narial process results in contact between the nasal and maxilla and excludes the lacrimal from the posterior margin of the external naris in some sphenacodontians. Note that although the mycterosaurine varanopids *Mesenosaurus* and *Mycterosaurus* (Berman & Reisz 1982; Reisz & Berman 2001) share state ‘2’ with therapsids and some sphenacodontids (Reisz *et al.* 1992), in mycterosaurines nasal-maxillary contact is achieved by dorsal expansion of the maxilla, whereas in

sphenacodontians it is achieved by posteroventral extension of the anterior portion of the nasal.

Unambiguous: Mycterosaurinae (0->2)

DELTRAN: *Secodontosaurus* + Sphenacodontinae (0->1), Therapsida (0->2)

ACCTRAN: Therapsida (1->2), Sphenacodontoidea (0->1)

23. Maxilla, lateral surface of anterior process bears deep depression dorsally forming narial rim: no (0); yes (1).

Maddin *et al.* (2008, character 17).

In caseids other than *Oromycter*, the anterior process of the maxilla bears part of a distinct circumnarial fossa (Stovall 1937; Olson 1968; Maddin *et al.* 2008).

Unambiguous: *Casea broili* +++ (0->1)

24. Maxilla, subnarial foramina: small or absent (0); present and large (1).

Maddin *et al.* (2008, character 3).

Many amniotes possess small foramina on the lateral surface of the maxilla adjacent to the external naris. These are large in caseids (Stovall 1937; Olson 1968; Maddin *et al.* 2008).

DELTRAN: ‘*Casea' rutena* +++ (0->1)

ACCTRAN: *Casea broili* +++ (0->1)

25. Maxilla, postnarial/preorbital ascending process: absent (0); present, but short and rounded dorsally (1); tall and pointed dorsally, extensively overlapping maxilla and extending to orbital midheight (2); tall, but also anteroposteriorly long, accommodating deeply-implanted tooth roots (3).

Modified from Reisz *et al.* (1992, character 28), Laurin (1993, character 29), Berman *et al.* (1995, character 34), Reisz *et al.* (1998, character 5), Maddin *et al.* (2006, character 9; 2008, characters 8, 9), Reisz *et al.* (2009, character 12), Fröbisch *et al.* (2011, character 22).

A distinct ascending process of the maxilla is absent in outgroup taxa and many basal synapsids, but is present in many caseasaurians, varanopids, *Ophiacodon*, and sphenacodontians. In most of these taxa the process is low, rounded or irregular dorsally, and does not conspicuously overlap the lacrimal (e.g. *Aerosaurus*, Langston & Reisz 1981; *Eothyris*, Reisz *et al.* 2009; *Ennatosaurus*, Maddin *et al.* 2008; *Mycterosaurus*, Berman & Reisz 1981). However, in *Cotylorhynchus* (*C. romeri*, *C. hancocki*; Stovall 1937; Olson 1968), *Varanodon* (Olson 1965) and *Varanops* (Campione & Reisz 2010) the process is tall, narrow, and pointed dorsally, overlapping the lateral surface of the lacrimal. A new state ('3') describes the condition in sphenacodontids (e.g. Romer & Price 1940; Eberth 1985) and therapsids.

Unambiguous: *Varanops* + *Varanodon* + *Watongia* (1->2), Sphenacodontidae +

Therapsida (0->3)

DELTRAN: Mycterosaurinae + Varanodontinae (0->1), Caseidae (0->1),

Cotylorhynchus (1->2), *Ophiacodon* spp. (0->1), *Eothyris parkeyi* (0->1)

ACCTRAN: *Pyozia* +++ (0->1), *Ophiacodon* + *Stereophallodon* (0->1), Caseasauria (0->1), *Angelosaurus* + *Cotylorhynchus* (1->2), *Oedaleops campi* (1->0)

26. Maxilla, ‘lacrimal facet’ at base of dorsal process: absent (0); present, distinct dorsoventral ridge present on ascending process divides anterior and posterior depressions (1).

Modified from Maddin *et al.* (2006, characters 11, 12); state ‘2’ of previous authors was removed as it is an autapomorphy of *Varanodon* (which is scored as ‘1’ herein). Varanodontine varanopids possess a distinct ‘lacrimal facet’ on the maxilla (Maddin *et al.* 2006; Campione & Reisz 2010).

Unambiguous: Varanodontinae (0->1)

27. Maxilla, ventral surface: straight or weakly convex (0); pronounced convexity (1); strongly convex with prominent ‘precanine step’ anteriorly (2).

Reisz *et al.* (1992, character 25), Berman *et al.* (1995, character 31), Fröbisch *et al.* (2011, character 100), modified from Maddin *et al.* (2008, character 12).

It is difficult to objectively divide character states describing convexity of the alveolar margin of the maxilla. Unlike in Maddin *et al.* (2008), the weak convexity of the maxillae of *Cotylorhynchus* (Stovall 1937; Olson 1968) and *Ennatosaurus* (Olson 1968; Maddin *et al.* 2008) is scored as state ‘0’ herein. The ‘strongly convex’ state is scored only in sphenacodontines, most individuals of which possess a pronounced ‘precanine step’ (Romer & Price 1940; Berman 1978; Eberth 1985). Some other sphenacodontians possess a weak precanine step and are scored as state ‘1’. However, the shared presence of the step in these taxa is effectively coded in the present analysis because the precanine step, even when weak, is always seen in the presence of an anteroventrally inclined premaxillary tooth row that is coded by character 13 (above).

Unambiguous: Amniota (1->0), *Varanosaurus* +++ (0->1), Sphenacodontia (0->1)

DELTRAN: *Dimetrodon* + *Sphenacodon* (1->2)

ACCTRAN: Sphenacodontinae (1->2)

28*. Maxilla and dentary, medial surface adjacent to alveoli: smooth (0): rugose, striated bone encloses tooth bases (1).

New character.

In caseids, the medial surfaces of the maxilla and dentary adjacent to the alveoli are rugose and bear dorsoventrally oriented striations (e.g. Reisz 2005, figs 1, 4; Maddin *et al.* 2008, fig. 6). A possible related condition occurs in some sphenacodontids, in which rugose bone appears to have ‘grown’ up the medial surfaces of the tooth bases (Eberth 1985, figs 12, 29). Although many other basal amniotes possess a small

amount of rugose bone around the tooth bases, the conditions in caseids and sphenacodontids coded here are very distinct.

Unambiguous: *Secodontosaurus* + Sphenacodontinae (0->1)

DELTRAN: Caseidae (0->1)

ACCTRAN: Caseasauria (0->1)

29. Maxilla, tooth count: 15–25 (0); <15 (1); >25 (2).

Modified from Laurin (1993, character 73), Berman *et al.* (1995, character 65), Reisz *et al.* (1998, character 28), Sidor & Hopson (1998, character 112), Maddin *et al.* (2006, character 2; 2008, character 64), Reisz *et al.* (2009, character 20); Mazierski & Reisz (2010, character 8); Fröbisch *et al.* (2011, character 59); also modified from characters coding the dentary tooth count (Sidor 2003, character 70).

Reisz (1980) listed a reduced maxillary tooth count as a synapomorphy independently derived by caseids and edaphosaurids. Edaphosaurids in fact possess intermediate numbers of maxillary teeth (Modesto 1995; 18–21 teeth). However, the count is reduced in therapsids, and substantially increased in ophiacodontids and some varanopids.

Unambiguous: Ophiacodontidae + Varanopidae (0->2), Caseidae (0->1), *Cotylorhynchus* (1->0), *Protorothyris archeri* (0->2), *Ianthasaurus hardestiorum* (0->2)

DELTRAN: *Biarmosuchus* +++ (0->1), *Mycterosaurus longiceps* (2->0), *Heleosaurus scholtzi* (2->0)

ACCTRAN: Mycterosaurinae (2->0), Therapsida (0->1), *Mesenosaurus romeri* (0->2)

30. Maxilla, posterior extent of lateral dentition: anterior to posterior orbit margin (0); ventral to postorbital bar (1); posterior to postorbital bar (2); anterior to orbital midlength (3).

Modified from Modesto (1994, character 7), Sidor & Hopson (1998, character 10), Maddin *et al.* (2008, character 11), Reisz *et al.* (2009, character 15) by addition of a new state ‘3’ taken from Berman *et al.* (1995, character 32), Modesto (1995, character 6) and Mazierski & Reisz (2010, character 6); also modified from other non-independent characters that code the posterior extent of the maxilla: Reisz *et al.* (1992, character 26), Maddin *et al.* (2008, character 10).

The posterior extent of the maxilla and maxillary tooth row are variable among basal synapsids. Most sphenacodontians and edaphosaurids possess a short tooth row (state ‘3’; *Glaucosaurus* is an exception; Modesto 1994) that was also reconstructed in *Archaeothyris* by Reisz (1992, fig. 2). In *Mycterosaurus* (Berman & Reisz 1982) and varanodontine varanopids (e.g. Langston & Reisz 1981; Campione & Reisz 2010) the maxillary dentition extends posterior to the postorbital bar (state ‘2’).

Unambiguous: *Protorothyris archeri* (0->1), *Glaucosaurus megalops* (3->1), BP/1/5678 (0->{12}), *Archaeothyris florensis* (0->3)

DELTRAN: Varanodontinae (0->2), Caseasauria (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->3), *Mycterosaurus longiceps* (0->2)

ACCTRAN: *Pyozia* +++ (0->2), *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (2->0), Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (1->3)

31. Maxillary and dentary alveolar ridges: straight (0); twisted (helical), distal teeth inclined laterally (1).

Modesto (1995, character 7), Mazierski & Reisz (2010, character 7).

Unambiguous: *Edaphosaurus* (0->1)

32. Maxilla, precanniniform tooth count: zero–three (0); four–five (1); six or more (2); inapplicable, no canniniform tooth or region (?).

Modified from Reisz *et al.* (1992, character 62), Laurin (1993, character 71), Berman *et al.* (1995, character 69), Sidor & Hopson (1998, character 110), Maddin *et al.* (2008, character 65), Reisz *et al.* (2009, character 16), Fröbisch *et al.* 2011, (character 57).

Unambiguous: Sphenacodontidae + Therapsida (1->0), *Stereophallodon ciscoensis* (2->0), *Secodontosaurus obtusidens* (0->2)

DELTRAN: Varanodontinae (1->2), *Varanosaurus* +++ (1->2), Eothyrididae (1->0), *Mesenosaurus romeri* (1->0), *Ianthasaurus hardestiorum* (1->2), *Archaeothyris florensis* (1->0)

ACCTRAN: Synapsida (1->0), Varanodontinae (0->2), *Varanosaurus* +++ (0->2), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Edaphosauridae (1->2), *Heleosaurus scholtzi* (0->1)

33. Maxilla and dentary, anterior dentary and precanniniform maxillary tooth morphology: similar to lateral teeth (0); distinctive teardrop-shaped morphology (1).

Fröbisch *et al.* (2011, character 49, state 3).

The distinctive morphology of sphenacodontine precanniniform teeth was observed by Evans *et al.* (2009) and Fröbisch *et al.* (2011).

Unambiguous: Sphenacodontinae (0->1)

34. Maxilla, canniniform region/tooth: absent, maxillary teeth approximately subequal in size, diminishing gradually posteriorly (0); canniniform region present (1); large canniniform tooth, or two teeth distinctly larger than other maxillary teeth (2).

Maddin *et al.* (2008, character 69), Reisz *et al.* (2009, character 17), modified from Reisz *et al.* (1992 character 59), Laurin (1993, character 67), Laurin (1993, character 72), Berman *et al.* (1995, character 68), Modesto (1994, characters 3, 4; 1995,

characters 4, 5), Reisz & Dilkes (2003, character 39), Maddin *et al.* (2006, character 4), Mazierski & Reisz (2010, characters 4, 5).

Romer & Price (1940) considered the presence of an isodont dentition (state ‘1’) as diagnostic of ‘Edaphosuria’ (Edaphosauridae + Caseidae). However, Reisz (1980) suggested that the presence of an isodont dentition in both groups represented parallel adaptation to herbivory.

A ‘canniniform region’ is scored in taxa that have enlarged teeth adjacent to their canniniform teeth such as *Limnoscelis* (Romer 1946; Reisz 2007), *Pantelosaurus* (von Huene 1925), and *Varanodon* (Olson 1965). State ‘2’ is scored for taxa in which the canniniform teeth are substantially larger than all other maxillary teeth such as *Sphenacodon* (Eberth 1985) and *Ianthasaurus* (Modesto & Reisz 1992; Mazierski & Reisz 2010), and *Mesenosaurus* (Reisz & Berman 2001). There is great variation in the absolute size of canniniform teeth among basal synapsids (compare *Ianthasaurus* with *Sphenacodon*). This is coded by character 35.

Unambiguous: Varanopidae (2->0), Mycterosaurinae + Varanodontinae (0->1), *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (1->2), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (2->0), *Varanops brevirostris* (1->2), *Pantelosaurus saxonicus* (2->1), *Limnoscelis paludis* (2->1)

DELTRAN: *Casea broili* +++ (2->0), *Oromycter dolesorum* (2->1), *Oedaleops campi* (2->1)

ACCTRAN: Caseasauria (2->1), *Casea broili* +++ (1->0), *Eothyris parkeyi* (1->2)

35. Maxilla, canniniform tooth size: less than twice the height of non-canniniform teeth (0); more than twice the height (1).

Reisz *et al.* (1992, character 59) Berman *et al.* 1995, character 68); modified from Laurin (1993, character 72); Reisz *et al.* (2009, character 17); Fröbisch *et al.* (2011, character 58)

Unambiguous: Therapsida (0->1), *Tseajaia campi* (0->1), *Stereophallodon ciscoensis* (0->1), *Protorothyris archeri* (0->1), *Eothyris parkeyi* (0->1)

DELTRAN: *Dimetrodon* + *Sphenacodon* (0->1)

ACCTRAN: Sphenacodontinae (0->1)

36. Maxilla, lateral buttress: absent (0); dorsally oriented buttress on lateral surface (1) (Figure A2).

Reisz *et al.* (1998, character 10). Reisz *et al.* (2009, character 13).

In some basal synapsids the lateral surface of the maxilla dorsal to the canniniform teeth is expanded laterally forming a vertical buttress. This is distinct from character 37 (below) describing a similar feature on the medial surface of the maxilla.

Unambiguous: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->1), *Varanops* + *Varanodon* + *Watongia* (0->1), *Eothyris parkeyi* (0->1)

DELTRAN: *Varanosaurus acutirostris* (0->1), *Stereophallodon ciscoensis* (0->1)

ACCTRAN: Ophiacodontidae (0->1), *Ophiacodon* spp. (1->0)

37. Maxilla, supracanine buttress on medial surface: absent (0); present, may be expanded into lateral margin of internal naris [choana] (1).

Modified from Reisz *et al.* (1992, character 27), Laurin (1993, characters 28, 70), Berman *et al.* (1995, character 33), Fröbisch *et al.* (2011, characters 21, 56).

It has long been recognised that ophiacodontids and sphenacodontians possess a medial swelling, the ‘supracanine buttress’, of the maxilla that accommodates the caniniform root (Romer & Price 1940; Reisz 1972; Eberth 1985; Brinkman & Eberth 1986).

Unambiguous: Ophiacodontidae (0->1), Sphenacodontia (0->1)

38. 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 (?).

Modified from Reisz *et al.* (1992, character 27, state 2), Laurin (1993, character 28, state 2), Fröbisch *et al.* (2011, character 21).

The supracanine buttress (character 37; above) is braced dorsally by a region of thickened bone in sphenacodontians and basal ophiacodontids (*Archaeothyris*; Reisz 1972). However, in *Ophiacodon* and *Stereophallodon* this is modified to form an anteroposteriorly narrow lamina (Romer & Price 1940; Brinkman & Eberth 1986). This was coded as a distinct state of the character describing the presence or absence of the supracanine buttress in previous analyses, but is better considered as a distinct character to maintain the observation of derived similarity between all taxa possessing a supracanine buttress of any form.

DELTRAN: *Ophiacodon* + *Stereophallodon* (0->1)

ACCTRAN: *Varanosaurus* +++ (0->1)

39. Maxilla, secondary enlargement of teeth posterior to caniniforms: absent (0); present (1).

Maddin *et al.* (2008, character 66), Reisz *et al.* (2009, character 18).

A ‘secondary caniniform region’ located in the central part of the maxillary tooth row, results in two caniniform regions in *Eothyris* and *Oedaleops* (Langston 1965; Reisz *et al.* 2009).

Unambiguous: Eothyrididae (0->1)

40. Lateral dentition, overall tooth morphology: conical may be laterally compressed apically (0); spatulate/slightly bulbous (1); transversely compressed and strongly recurved (2) (Figure A2).

Modified from Laurin (1993, character 63), Berman *et al.* (1995, character 67), Modesto (1994, characters 1, 5; 1995, character 1), Reisz *et al.* (1998, character 1), Reisz & Dilkes (2003, character 34), Maddin *et al.* (2006, character 1), Maddin *et al.* (2008, character 72), Reisz *et al.* (2009, characters 22, 23); Mazierski & Reisz (2010, character 1), Fröbisch *et al.* (2011, character 49).

The morphology of lateral teeth varies among basal synapsids. Three general morphologies are present comprising plesiomorphic conical or peg-like teeth (state '0'; e.g. Berman *et al.* 1995), basally expanded, bulbous, spatulate teeth in herbivorous edaphosaurids and caseids (state '1'; e.g. Olsen 1968; Modesto 1994, 1995; Maddin *et al.* 2008), and the recurved, transversely compressed teeth of most sphenacodontians and varanopids (state '2'; e.g. Evans *et al.* 2009). Reisz (1980) considered this morphology as present in ophiacodontids, suggesting that they formed a clade with Varanopidae and Sphenacodontidae. However, it is actually absent in ophiacodontids (Reisz 1986).

Unambiguous: Mycterosaurinae + Varanodontinae (0->2), Caseidae (0->1), Edaphosauridae (0->1), *Pantelosaurus* +++ (0->2), *Captorhinus* (0->1), *Biseridens qilianicus* (2->1)

41. Maxillary dentition, recurvature: completely absent (0); at least slightly recurved (1), strongly recurved, apex approximately 80-90 degrees from vertical (2).

Maddin *et al.* (2008, character 67).

The degree of recurvature of maxillary teeth varies among basal synapsids and is only partially dependent on the overall tooth morphology (character 40, above). The strongest recurvature is present in some varanopids.

Unambiguous: Synapsida (0->1), Mycterosaurinae + Varanodontinae (1->2), Caseidae (1->0), Edaphosauridae (1->0), *Varanosaurus acutirostris* (1->0), *Biseridens qilianicus* (1->0)

42. Lateral dentition, cutting edges on mesial and distal surfaces: absent or only present distally (0); present (1).

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

Cutting edges are present on the recurved teeth of sphenacodontians, varanopids and in edaphosaurids (Modesto 1995; Mazierski & Reisz 2010).

Unambiguous: Mycterosaurinae + Varanodontinae (0->1), *Biseridens qilianicus* (1->0)

DELTRAN: Edaphosauridae (0->1), *Pantelosaurus* +++ (0->1)

ACCTRAN: Edaphosauridae + Sphenacodontia (0->1), *Haptodus garnettensis* (1->0)

43. Lateral dentition, cutting edge: serrations absent (0); serrations present, density high, 14–24 denticles/mm (1); serration density low, <10 serrations/mm (2); inapplicable, cutting edges absent (?).

Modified from Laurin (1993, character 65), Sidor & Hopson (1998, characters 108, 114), Modesto *et al.* (2001, character ‘32’), Reisz *et al.* (2009, character 21), Fröbisch *et al.* (2011, character 51) by addition of a new state ‘2’ following Evans *et al.* (2009).

The presence and density of serrations is variable among taxa with cutting edges on their lateral teeth. Where present, the serrations of varanopid teeth (state ‘1’) are finer than those of sphenacodontids (state ‘2’) (Evans *et al.* 2009).

Unambiguous: Mycterosaurinae (0->1), Therapsida (0->2), *Dimetrodon* + *Sphenacodon* (0->2), *Biseridens qilianicus* (2->0)

DELTRAN: *Edaphosaurus boanerges* (0->1)

ACCTRAN: Edaphosauridae (0->1)

44. Lateral dentition, number of apical cusps: one (0); three (1); more than three (2).

Maddin *et al.* (2008, character 70), modified from Sidor & Hopson (1998, character 113), Reisz *et al.* (2009, character 21, state 2).

Caseids, other than the basal taxon *Oromycter* (Reisz 2005), possess multicusperate lateral teeth. The number of cusps is especially high in *Angelosaurus* and *Ennatosaurus* (Olsen 1962, 1968; Reisz 1980; Maddin *et al.* 2008).

Unambiguous: *Cotylorhynchus* (2->1)

DELTRAN: ‘Casea’ *rutena* +++ (0->2), *Casea broili* (0->1)

ACCTRAN: *Casea broili* +++ (0->1), *Trichasaurus* +++ (1->2)

45. Lateral dentition, ‘shoulder’ [or ‘heel’] on lingual surface: absent (0); present (1).

Maddin *et al.* (2008, character 73).

The teeth of herbivorous edaphosaurids and caseids possess a low lingual ‘heel’.

Unambiguous: *Biseridens qilianicus* (0->1)

DELTRAN: Caseidae (0->1), *Edaphosaurus boanerges* (0->1)

ACCTRAN: Caseasauria (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1)

46. Lateral dentition, labyrinthine structure: present (0); absent (1).

Labyrinthine infolding of the dentine is plesiomorphically present in tetrapod lateral teeth. This is retained by diadectomorphs (Romer 1937; Moss 1965), but absent in crown-group amniotes.

Unambiguous: Amniota (0->1)

47. Nasal, length: distinctly shorter than the frontal (0); approximately equal to the frontal (1); longer than frontal (2).

Reisz *et al.* (2009, character 7), modified from Reisz *et al.* (1992, character 7), Laurin (1993, character 5), Berman *et al.* (1995, characters 8, 9), Reisz & Dilkes (2003, character 50), Maddin *et al.* (2006, character 14); Fröbisch *et al.* (2011, character 4).

Unambiguous: Eothyrididae (1->0), Edaphosauridae + Sphenacodontia (1->0), *Pantelosaurus* +++ (0->2), Eureptilia (1->0), *Ennatosaurus tector* (1->0), *Biseridens gilianicus* (2->1)

DELTRAN: *Varanosaurus* +++ (1->2)

ACCTRAN: Ophiacodontidae (1->2)

48. Nasal, contribution to external naris: forms posterodorsal margin (0); extends anteroventrally as a blade-like process ('external narial shelf') bearing a lateral fossa (1).

Reisz & Dilkes (2003, character 49), Maddin *et al.* (2006, character 13; 2008, character 6), Reisz *et al.* (2009, character 6).

In caseasaurians, the dorsal margin of the external naris is surrounded by a distinct fossa that occupies an anteriorly expanded portion of the nasal (e.g. Langston 1965; Olson 1968; Reisz 1986; Maddin *et al.* 2008; Reisz *et al.* 2009).

Unambiguous: Caseasauria (0->1)

49. Lacrimal contact with external naris: broad (0); narrow (1); inapplicable, contact absent (?).

Modified from Berman *et al.* (1995, character 36).

This character was originally coded as an autapomorphy of *Varanosaurus* (Berman *et al.* 1995). However, it is also present in *Haptodus* (Laurin 1993). In both taxa the maxilla forms the posteroventral margin of the naris, constricting the lacrimal contact.

Unambiguous: *Varanosaurus acutirostris* (0->1), *Haptodus garnettensis* (0->1)

50. Lacrimal lateral surface of anterior process bears deep depression forming narial rim: no (0); yes (1).

Maddin *et al.* (2008, character 17).

This is independent from character 23, which describes a circumnarial depression on the maxilla. Although these depressions are confluent in many caseids, the maxillary portion of the depression is absent in *Oromycter* (Reisz 2005; Maddin *et al.* 2008).

Unambiguous: Caseidae (0->1)

51. Lacrimal, contribution to orbit margin as seen in lateral view: large (0); small, restricted by a prominent ventral process of the prefrontal (1).

Modified from Laurin (1993, character 32), Maddin *et al.* (2006, character 16), Reisz *et al.* (2009, character 26), Fröbisch *et al.* (2011, character 25).

The prefrontal extends ventrally around the orbital margin, constricting the orbital contact of the lacrimal in some sphenacodontids (e.g. Romer & Price 1940; Eberth 1985; Laurin 1993) and some varanopids (Reisz & Berman 2001; Reisz & Dilkes 2003).

Unambiguous: *Secodontosaurus* + Sphenacodontinae (0->1)

DELTRAN: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->1), *Archaeovenator hamiltonensis* (0->1)

ACCTRAN: Varanopidae (0->1), Varanodontinae (1->0)

52. Lacrimal duct, location of posterior opening: on the posterior surface of the lacrimal (0); on the lateral surface of the lacrimal, near the posterior edge (1); on the lateral surface of the lacrimal more anteriorly, in concave region (2).

Reisz *et al.* (1998, character 19), Maddin *et al.* (2006, character 15), Reisz *et al.* (2009, character 25).

Most basal synapsids exhibit a plesiomorphic condition in which the twin openings of the lacrimal duct are located on the posterior surface of the lacrimal, within the orbital rim (e.g. Reisz 2005, fig. 3). In varanopids the openings are located further anteriorly (Reisz *et al.* 1998; Maddin *et al.* 2006).

DELTRAN: Mycterosaurinae (0->1), Varanodontinae (0->2)

ACCTRAN: *Pyozia* +++ (0->1), Varanodontinae (1->2)

53. Prefrontal-maxilla contact: absent (0); present anterodorsal to lacrimal (1).

Laurin (1993, character 27), Reisz *et al.* (1998, character 6), Sidor & Hopson (1998, character 8), Maddin *et al.* (2006, character 10), Reisz *et al.* (2009, character 24), Fröbisch *et al.* (2011, character 20).

Reisz & Berman (2001) commented that mycterosaurines resembled therapsids in possessing a prefrontal-maxilla contact.

Unambiguous: Mycterosaurinae (0->1)

DELTRAN: *Biarmosuchus* +++ (0->1)

ACCTRAN: Therapsida (0->1)

54. Prefrontal, lateral surface: approximately flat or convex (0); concave, forming antorbital recess [prefrontal pocket] (1).

Reisz *et al.* (1992, character 9), Berman *et al.* (1995, character 12), modified from Laurin (1993, character 11) and Fröbisch *et al.* (2011, character 10).

Laurin (1993) coded an autapomorphic state of the prefrontal pocket, ‘shallow’, in *Haptodus*. In the present study, *Haptodus* was instead scored simply as possessing the antorbital recess (state ‘1’), a condition that has long been recognised in other sphenacodontians (e.g. Romer & Price 1940; Eberth 1985; Reisz *et al.* 1992), and is also present in *Limnoscelis* (Romer 1946), *Ianthasaurus* (Modesto & Reisz 1992) and ophiacodontids (Romer & Price 1940; Brinkman & Eberth 1986; Berman *et al.* 1995).

Unambiguous: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (1->0), *Limnoscelis paludis* (0->1)

DELTRAN: *Varanosaurus* +++ (0->1)

ACCTRAN: Ophiacodontidae (0->1)

55. Prefrontal, ventral process: transversely narrow edge [‘tongue-like’] (0); expanded medially forming antorbital buttress (1).

Modesto (1994, character 10; 1995, character 8), Reisz *et al.* (1998, character 7), Mazierski & Reisz (2010, character 9).

Unambiguous: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1)

56. 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).

Modified from Sidor & Hopson (1998, character 47); modified from Maddin *et al.* (2008, character 25) by addition of a new state ‘2’.

Edaphosaurids, caseasaurians, and basal therapsids have a greatly shortened frontal (state ‘0’) (e.g. Romer & Price 1940; Orlov 1958; Olson 1968; Modesto 1995; Reisz *et al.* 2009). In contrast, the frontal is greatly elongated in sphenacodontids (state ‘2’) relative to the anteroposteriorly shortened parietal (e.g. Romer & Price 1940; Eberth 1985; Reisz *et al.* 1992, character 14).

Unambiguous: Caseasauria (1->0), *Titanophoneus* + *Biseridens* (1->0), Sphenacodontidae (1->2)

DELTRAN: *Edaphosaurus boanerges* (1->0)

ACCTRAN: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (1->0)

57. Frontal width:length ratio: <1, frontal narrow (0); >1.5, frontal transversely broad (1).

Modesto (1995, character 10); Mazierski & Reisz (2010, character 11); modified from Maddin *et al.* (2008, character 52).

The herbivorous edaphosaurids and caseids have a very broad skull table, resulting in a proportionally broad frontal bone (state ‘1’) (e.g. Romer & Price 1940; Olsen 1968; Modesto & Reisz 1992; Modesto 1995; Maddin *et al.* 2008).

DELTRAN: *Ennatosaurus* +++ (0->1), *Edaphosaurus* (0->1)

ACCTRAN: Caseidae (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp.

(0->1)

58. Frontal, anterior process: width equal to that of posterior process (0); narrower than posterior process (1).

Reisz *et al.* (1992, character 12), Laurin (1993, character 7), Berman *et al.* (1995, character 15); Fröbisch *et al.* (2011, character 6).

The preorbital portion of the frontal is transversely narrow relative to the postorbital portion in most sphenacodontids (e.g. Romer & Price 1940; Eberth 1985; Reisz *et al.* 1992).

Unambiguous: *Secodontosaurus* + Sphenacodontinae (0->1)

59. Frontal, anterior process length: short (0); longer than posterior process (1); very long, forming at least 2/3 length of bone (2).

Modified from Reisz *et al.* (1992, character 13), Laurin *et al.* (1993, character 8), Berman *et al.* (1995, character 16); Fröbisch *et al.* (2011, character 7).

Unambiguous: Varanopidae (1->0), Edaphosauridae (1->0), *Secodontosaurus* + Sphenacodontinae (1->2), *Pantelosaurus saxonicus* (1->0), *Captorhinus* (1->0), *Biseridens qilianicus* (1->0)

DELTRAN: *Ennatosaurus* +++ (1->0), *Varanodon agilis* (0->1)

ACCTRAN: *Varanodon* + *Watongia* (0->1), Caseidae (1->0)

60. Frontal, orbital contact (lateral lappet): absent, prefrontal contacts postfrontal, excluding frontal from dorsal orbital rim (0); narrow (1); broad, >1/4 maximum orbital length (2).

Modified from Brinkman & Eberth (1983, character 10); Reisz *et al.* (1992, character 11), Laurin (1993, character 9), Berman *et al.* (1995, character 14), Modesto (1994, character 11; 1995, character 9), Reisz *et al.* (1998, character 13), Maddin *et al.* (2006, character 18; 2008, character 23), Reisz *et al.* (2009, character 29); Mazierski & Reisz (2010, character 10); Fröbisch *et al.* (2011, character 8).

Reisz (1980, 1986) considered a narrow orbital contribution of the frontal (state ‘1’) as a plesiomorphic feature of Caseasauria. However, captorhinomorphs possess a broad lappet so the caseasaurian condition is probably derived. The presence or absence of a distinct lateral lappet (i.e. distinct from the ‘body’ of the frontal; Reisz 1986) was difficult to score as the observed morphologies form a continuum.

Unambiguous: Amniota (0->2), Caseasauria (2->1), *Ennatosaurus tector* (1->2), *Edaphosaurus boanerges* (2->1)

61. Frontal, posterolateral process: short (0); long and narrow, matching length of postfrontal, and substantially separating parietal from postfrontal (1); completely absent (2).

Modified from Reisz *et al.* (1998, character 4), Maddin *et al.* (2006, character 17), Reisz *et al.* (2009, character 28) by addition of a new state ‘2’ taken from Laurin (1993, character 10) and Fröbisch *et al.* (2011, character 9). Characters describing an ‘anterior extension of the parietal’ are redundant with this character (Maddin *et al.* 2006, character 19; Reisz *et al.* 2009, character 34).

Long, distinct posterolateral processes of the frontal (state ‘1’) are present in ophiacodontids and varanopids (e.g. Berman *et al.* 1995; Reisz *et al.* 1998; Botha-Brink & Modesto 2009). They are completely absent (state ‘2’) in outgroup taxa (e.g. Romer 1946; Moss 1972; Clark & Carroll 1973) and most sphenacodontians (e.g. Romer & Price 1940; Orlov 1958; Reisz *et al.* 1992). Most other basal synapsids however, possess short posterolateral processes (e.g. Romer & Price 1940).

Unambiguous: *Pantelosaurus* + + + (0->2)

DELTRAN: Ophiacodontidae + Varanopidae (2->1), Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (2->0)

ACCTRAN: Synapsida (2->0), Ophiacodontidae + Varanopidae (0->1)

62. 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).

Modified from Reisz *et al.* (1992, character 21), Laurin (1993, character 14), Modesto (1994, character 12); Berman *et al.* (1995, character 27) and Fröbisch *et al.* (2011, character 12) by interposition of a new state ‘1’, taken from Berman *et al.* (1995, character 18).

In sphenacodontians the posterior orbital rim and anterodorsal margin of the temporal fenestra are raised laterally so that the central portions of the lateral surface of the postfrontal are recessed medially, giving the bone an anteroposteriorly concave cross-section (state ‘1’; e.g. Eberth 1985; Laurin 1994). A more pronounced, but possibly related, morphology is present in therapsids (state ‘3’; e.g. Orlov 1958; Liu *et al.* 2010). Edaphosaurids and ‘*Casea*’ *rutena* exhibit a different postfrontal morphology, in which the bone is expanded laterally to form a prominent posterior supraorbital shelf (state ‘2’; Olson 1968; Sigogneau-Russell & Russell 1974; Reisz 1980; Berman & Reisz 1986; Modesto 1995).

Unambiguous: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Edaphosauridae (1->2), ‘*Casea*’ *rutena* (0->2)

DELTRAN: *Biarmosuchus* + + + (1->3)

ACCTRAN: Therapsida (1->3)

63. Postorbital-postfrontal contact: overall trend approximately straight (0); incised by postorbital (1).

Reisz *et al.* (1992, character 18), Laurin (1993, character 13), Berman *et al.* (1995 character 23), Fröbisch *et al.* (2011, character 11).

Unambiguous: *Eothyris parkeyi* (0->1)

DELTRAN: Sphenacodontidae (0->1), *Pantelosaurus saxonicus* (0->1)

ACCTRAN: *Pantelosaurus* + + + (0->1), Therapsida (1->0)

64. Postorbital-squamosal contact: present (0); absent, parietal forming lateral margin of skull table in dorsal view, with deeply concave lateral margin (1).

Modified from Modesto (1995, characters 11, 12), Mazierski & Reisz (2010, characters 12, 13).

DELTRAN: *Edaphosaurus* (0->1)

ACCTRAN: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1)

65. Postorbital-squamosal contact: anteroposteriorly short (0); extensive due to long posterior process of the postorbital that obliquely overlaps the squamosal in the posterior half of the temporal region (1).

Modified from Laurin (1993, character 16), Fröbisch *et al.* (2011, character 14).

Laurin (1994) noted that in the holotype and only specimen of *Cutleria* the derived state of this character was present on the right side, but the primitive state was present on the left side. He stated that this seemed to represent genuine asymmetry rather than damage. *Cutleria* is scored herein as possessing the derived state of this character.

DELTRAN: *Dimetrodon* + *Sphenacodon* (0->1), *Heleosaurus scholtzi* (0->1),

Cutleria wilmarti (0->1), BP/1/5678 (0->1)

ACCTRAN: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->1), Sphenacodontidae (0->1), *Secodontosaurus obtusidens* (1->0), *Mesenosaurus romeri* (1->0)

66. Postorbital-supratemporal contact: present (0); absent, (1); inapplicable, supratemporal absent (?).

Laurin (1993, character 25), Berman *et al.* (1995, character 26), Fröbisch *et al.* (2011, character 19); modified from Reisz *et al.* (1992, character 20), Maddin *et al.* (2008, character 27).

DELTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), *Dimetrodon* + *Sphenacodon* (1->0), *Eureptilia* (0->1), *Varanosaurus acutirostris* (0->1), *Varanops brevirostris* (0->1), *Titanophoneus potens* (1->0), *Mesenosaurus romeri* (0->1)

ACCTRAN: Amniota (0->1), *Ophiacodon* + *Stereophallodon* (1->0), Caseasauria (1->0), Therapsida (1->0), Sphenacodontinae (1->0), *Heleosaurus scholtzi* (1->0), *Archaeovenator hamiltonensis* (1->0)

67. Postorbital, lateral process/boss at orbit margin: absent (0); present (1).

Reisz & Dilkes (2003, character 37), Maddin *et al.* (2006, character 23), Reisz *et al.* (2009, character 33).

DELTRAN: Mycterosaurinae (0->1), *Varanodon* + *Watongia* (0->1)

ACCTRAN: *Pyozia* +++, (0->1), *Varanops brevirostris* (1->0)

68. Postorbital, posterior process, length: short (0); long, extending more than half of temporal length (1).

Reversed from Berman *et al.* (1995, character 25), Reisz *et al.* (1998, character 23) and Maddin *et al.* (2006, character 21); modified from Maddin *et al.* (2008, character 15), Reisz *et al.* (2009, character 31).

Langston (1965) described an exceptionally long, tapering posterior process of the postorbital in *Eothyris* and *Oedaleops*. The process is also long in many sphenacodontids and varanopids.

Unambiguous: *Pantelosaurus* +++, (0->1), *Secodontosaurus obtusidens* (1->0)

DELTRAN: Ophiacodontidae + Varanopidae (0->1), *Varanops* + *Varanodon* + *Watongia* (1->0), Caseasauria (0->1)

ACCTRAN: Synapsida (0->1), Varanodontinae (1->0), *Ianthodon* + Edaphosauridae + Sphenacodontia (1->0)

69. Postorbital, posterior process, transverse width: broad (0); narrow (1).

Reisz *et al.* (1992, character 22), Laurin (1993, character 15), Berman *et al.* (1995, character 28), Fröbisch *et al.* (2011, character 13); modified from Maddin *et al.* (2008, character 15), Reisz *et al.* (2009, character 31).

Unambiguous: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (1->0), *Secodontosaurus obtusidens* (1->0)

DELTRAN: Ophiacodontidae + Varanopidae (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: Synapsida (0->1), Caseasauria (1->0)

70. Postorbital and jugal, medial orbital process (deep, dorsoventrally tall medial flange): absent (0); present (1).

Berman *et al.* (1995, character 4).

In *Ophiacodon* and *Varanosaurus* (FMNH PR 1670) a dorsoventrally tall, sheet-like, medial extension of the postorbital bar extends medially, dividing the temporal recess from the orbit. In other basal synapsids the postorbital bar is a transversely narrow strut.

Unambiguous: *Varanosaurus* +++, (0->1)

71. 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).

Reisz *et al.* (2009, character 46), modified from Brinkman & Eberth (1983, character 2), Reisz *et al.* (1992, character 31), Modesto (1994, character 6); Berman *et al.* (1995, character 37), Maddin *et al.* (2008, character 13).

In caseasaurians and some varanopids the jugal is excluded from the ventral margin of the skull by contact between the maxilla and quadratojugal. Brinkman & Eberth (1983) observed the presence of a maxilla-quadratojugal contact in caseasaurians and varanopids, and coded the presence or absence of this contact as a binary character. However, as noted by Langston & Reisz (1981) and Reisz (1986), the morphology of this contact differs between varanopids (state ‘1’) and caseasaurians (state ‘2’). Furthermore, basal varanopids retain the primitive condition of lacking the contact (Reisz & Dilkes 2003; Anderson & Reisz 2004). Reisz *et al.* (1992) and Berman *et al.* (1995) included additional states coding a narrow or wide contribution of the jugal to ventral margin of the skull. These are not employed in the present character, but instead are coded by the relative posterior extent of the maxilla and anterior extent of the quadratojugal (characters 30 and 77).

Unambiguous: Caseasauria (0->2)

DELTRAN: Varanodontinae (0->1), *Mycterosaurus longiceps* (0->1)

ACCTRAN: Mycterosaurinae + Varanodontinae (0->1), *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (1->0)

72. 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 participates in orbit margin (2).

Modified from Reisz *et al.* (1992, character 32), Laurin (1993, character 34), Fröbisch *et al.* (2011, character 27) by addition of state ‘2’, taken from Maddin *et al.* (2008, character 19).

In most sphenacodontians the anterior ramus of the jugal is dorsoventrally deep and anterodorsally expanded (e.g. von Huene 1925; Romer & Price 1940; Orlov 1958; Eberth 1985). In varanopids (e.g. Reisz & Dilkes 2003) and most caseasaurians (e.g. Olsen 1968; *Ennatosaurus* is an exception; Maddin *et al.* 2008) the anterior process of the jugal is short and tapering. In these taxa it does not contact the lacrimal and thus allows the maxilla to participate in the anterodorsal orbital margin (Reisz 1980; 1986).

Unambiguous: Varanopidae (0->2), Caseasauria (0->2), *Pantelosaurus* +++ (0->1), *Ennatosaurus tector* (2->0), *Biseridens qilianicus* (1->0)

73. Jugal, anteroposterior thickness of dorsal ramus (forming postorbital bar): broad, temporal fenestra only weakly emarginates the jugal (0); narrow, jugal strongly emarginated (1); inapplicable, temporal fenestra absent (?).

Modified from Maddin *et al.* (2008, character 20).

This character describes the thickness of the postorbital bar. In all synapsids other than some basal caseasaurians (e.g. Williston 1911; Sigogneau-Russell & Russell 1972; Reisz *et al.* 2009) the temporal fenestra extends close to the orbit anteriorly. Thus the postorbital bar is anteroposteriorly narrow. In basal caseasaurians the postorbital bar is broad because the temporal fenestra only weakly emarginates the jugal, Reisz *et al.* (2009, p. 43) described the resulting appearance as ‘archaic’ in *Eothyris*. However, because all outgroup taxa lack temporal fenestrae, the primitive condition cannot be determined.

DELTRAN: *Eothyris parkeyi* (1->0), ‘*Casea*’ *rutena* (1->0), *Casea broili* (1->0)

ACCTRAN: Caseasauria (1->0), *Ennatosaurus* + + + (0->1), *Oedaleops campi* (0->1)

74. Jugal-squamosal contact on posterior surface of postorbital bar: absent (0); present (1); inapplicable, temporal fenestra absent (?).

Reisz *et al.* (1998, characters 8, 24), Maddin *et al.* (2006, character 24, 26); Reisz *et al.* (2009, characters 38, 41).

Some previous authors employed a character coding the presence of an anterodorsal process of the squamosal that forms the dorsal border of the temporal fenestra in *Elliotsmithia* and varanodontines (Reisz *et al.* 1998, character 8). This contacts the dorsal process of the jugal in varanodontines (but not *Elliotsmithia*) (Modesto *et al.* 2001). Because *Elliotsmithia* is not included in the present analysis, the presence of an anterodorsal process of the quadratojugal is redundant with the present character. Note also that the presence of this process in *Elliotsmithia* is controversial (Modesto *et al.* 2001).

Unambiguous: Varanodontinae (0->1)

75. Jugal, posterior ramus length: short, extending to, or less than, temporal midlength (0); long, extending to posterior end of temporal fenestra (or past temporal midlength in taxa that lack a temporal fenestra) (1).

Reisz *et al.* (2009, character 49); modified from characters describing participation of the quadratojugal in the margin of the temporal fenestra: Maddin *et al.* (2006, character 30), Maddin *et al.* (2008, character 18) [the quadratojugal participates in the margin of the temporal fenestra only in taxa that have a large quadratojugal (character 77), combined with a short posterior process of the jugal (the present character) and short anterior process of the squamosal (character 82)].

Unambiguous: Amniota (1->0), Mycterosaurinae (0->1), *Titanophoneus* + *Biseridens* (0->1), *Pantelosaurus saxonicus* (0->1)

DELTRAN: *Varanosaurus* + + + (0->1), *Dimetrodon* + *Sphenacodon* (0->1), *Eothyris parkeyi* (0->1)

ACCTRAN: Ophiacodontidae (0->1), Eothyrididae (0->1), Sphenacodontinae (0->1)

76. Jugal–squamosal ventral contact, perforated by small, elongate fenestra: absent (0); present, upper margin enclosed by anteroventral extension of the squamosal (1); inapplicable, jugal does not contact squamosal ventrally (?).

Berman *et al.* (1995, character 17).

Romer & Price (1940) observed that in some individuals of *Ophiacodon* the jugal-squamosal contact was perforated by an elongate fenestra. This is also present in *Varanosaurus* (Berman *et al.* 1995).

DELTRAN: *Varanosaurus* +++; (0->1)

ACCTRAN: Ophiacodontidae (0->1)

77. Quadratojugal, size: large and forms much of the ventrolateral portion of the temporal fenestra, extending ventral to postorbital bar (anterior to anteroventral process of the squamosal) (0); large, but only extends anteriorly to approximately temporal midlength (1); small, confined to posteroventral angle of skull and overlapped laterally by the squamosal (2).

Berman *et al.* (1995, character 39); modified from Reisz *et al.* (2009, character 48). States '0' and '1' taken from Reisz *et al.* (1992, character 33), Reisz & Dilkes (2003, character 36) and Maddin *et al.* (2006, character 32). State '2' taken from Brinkman & Eberth (1983, character 11); Laurin (1993, character 38); Modesto (1994, character 15; 1995, character 13); Mazierski & Reisz (2010, character 14), Fröbisch *et al.* (2011, character 30).

The quadratojugal is small in edaphosaurids and sphenacodontians (Reisz 1980 [sphenacodontians only], 1986 [both clades])

Unambiguous: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->2), Eureptilia (0->1), *Limnoscelis paludis* (0->1)

78. Quadratojugal, anterodorsal process exposed on lateral surface of skull: absent or covered by squamosal (0); exposed laterally and contributes to margin of temporal fenestra (1).

Reisz *et al.* (1998, character 11), Reisz & Dilkes (2003, character 35), Maddin *et al.* (2006, character 31), modified from Reisz *et al.* (2009, character 47) by deletion of state '2' (an autapomorphy of *Varanops*, coded as '1' in the present analysis).

Unambiguous: Varanodontinae (0->1)

79*. Squamosal, anteroposterior breadth of posttemporal portion on lateral surface of skull: narrow (0); broad, just over half the breadth of the temporal region, restricting the posterior extent of the temporal fenestra (1); inapplicable, temporal fenestra absent (?)

New character.

The derived state only describes the greatly expanded squamosal of *Ophiacodon* (e.g. Romer & Price 1940) and *Varanosaurus* (Berman *et al.* 1995). Expansion of the squamosal in these taxa limits the posterior extent of the temporal fenestra.

Unambiguous: *Varanosaurus* +++; (0->1)

80. Squamosal, occipital flange covers much of the posterior surface of the quadrate, forming lateral parts of posterior skull surface: present (0); very narrow or absent, posterior surface of quadrate exposed (1).

Berman *et al.* (1995, character 48); modified from Reisz *et al.* (1998, character 15), Maddin *et al.* (2006, character 25), Reisz *et al.* (2009, character 39).

Some previous authors employed a separate state describing a ‘narrow’ flange in ophiacodontids and basal/mycterosaurine varanopids (Maddin *et al.* 2006; Reisz *et al.* 2009). This state was not employed in the present study because ophiacodontids possess a broad flange (e.g. *Varanosaurus*; Berman *et al.* 1995, fig. 9), and in basal varanopids and mycterosaurines the flange is so narrow that it is very similar to the ‘absent’ condition in varanodontines (e.g. *Mesenosaurus*, Reisz & Berman 2001, fig 4B; *Mycterosaurus*, Berman & Reisz 1982, fig. 5B). Thus, all varanopids showing adequate preservation were scored as having a ‘very narrow or absent’ flange (state ‘1’).

Unambiguous: Varanopidae (0->1), *Tseajaia campi* (0->1)

81. Squamosal, small posterior process [posterodorsal process] emerges from posterodorsal part of lateral surface: absent (0); present (1).

Modesto *et al.* (2001, character ‘33’), Maddin *et al.* (2006, character 27), Reisz *et al.* (2009, character 40).

Modesto *et al.* (2001, fig. 5) described this feature as present in *Elliotsmithia*, *Mesenosaurus* and BP/1/5678. It is also present in *Heleosaurus* (Botha-Brink & Modesto 2009). Subsequent works have also scored this process as present in caseasaurians (e.g. Reisz *et al.* 2009). However, in these taxa, the large, sheet-like supratemporal overlaps the posterodorsal angle of the squamosal, so in many cases it is not clear that a posterodorsal process of the squamosal is present, but it is likely that the squamosal is smooth ventral to the supratemporal, and that these taxa lack the posterodorsal process.

DELTRAN: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->1)

ACCTRAN: Mycterosaurinae (0->1)

82. Squamosal, contributes to lower temporal bar [zygomatic arch]: no, distinct anteroventral process absent (0); yes (1); inapplicable, temporal fenestra absent (?).

Reisz *et al.* (1992, character 34), Berman *et al.* (1995, character 40); modified from Reisz *et al.* (2009, character 38).

Reisz (1986) considered the squamosal contribution to the zygomatic arch as a synapomorphy of Ophiacodontidae + Edaphosauridae + Sphenacodontia. However, because outgroup taxa lack a temporal fenestra the polarity of this character cannot be determined.

Unambiguous: Varanodontinae (1->0), Caseasauria (1->0)

83. Parietal, raised rim around pineal foramen: absent (0); surrounded by raised area forming a pineal ‘ridge’ or boss (1).

Reisz *et al.* (1992, character 19), Berman *et al.* (1995, character 24); modified from Laurin (1993, character 21), Sidor & Hopson (1998, character 21), Fröbisch *et al.* (2011, character 18).

A distinction between the ‘ridged’, raised parietal rim of sphenacodontids and the rim that is raised as a boss in therapsids was coded using an additional state by Laurin (1993) and Fröbisch *et al.* (2011). This distinction is real, but was not employed in the present analysis as it would result in loss of primary homology between the sphenacodontid and therapsids conditions.

Unambiguous: Sphenacodontia (0->1)

84. Parietal, pineal foramen, size: small, smaller than foramen magnum and less than 0.2 times parietal width (0); large (1).

Maddin *et al.* (2008, character 24), Reisz *et al.* (2009, character 36); reversed from Reisz *et al.* (1992, character 17), Berman *et al.* (1995, character 22).

Olson (1968) and Langston (1965) noted the large pineal foramen in caseasaurians. This is also present in the Middle Permian mycterosaurine varanopids (Reisz & Berman 2001; Botha-Brink & Modesto 2009) and *Aerosaurus wellesi* (Langston & Reisz 1981).

Unambiguous: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->1), Caseasauria (0->1), *Tseajaia campi* (0->1)

DELTRAN: *Aerosaurus wellesi* (0->1)

ACCTRAN: *Ruthiromia* + *Aerosaurus* spp. (0->1)

85. Parietal, pineal foramen location: anteriorly on parietal midline suture (0); at parietal midlength (1); near posterior end of parietal (2)

Modesto (1994, character 13), Maddin *et al.* (2008, character 26), modified from Laurin (1993, character 20), Reisz *et al.* (1998, character 17), Maddin *et al.* (2006, character 20), Reisz *et al.* (2009, character 35), Fröbisch *et al.* (2011, character 17).

Langston (1965) proposed the presence of a large pineal foramen at parietal midlength as a feature uniting *Eothyris* and *Oedaleops*. Reisz (1980, 1986) listed an anteriorly located pineal foramen as a caseid synapomorphy and a posteriorly located pineal foramen as a synapomorphy of ‘Eupelycosauria’.

Unambiguous: Ophiacodontidae + Varanopidae (1->2), Sphenacodontidae (1->2), *Tseajaia campi* (1->2), *Titanophoneus potens* (1->2), *Captorhinus* (1->0)

DELTRAN: Casea *broili* +++ (1->0), Edaphosauridae (1->2), *Haptodus garnettensis* (1->2)

ACCTRAN: Caseidae (1->0), Edaphosauridae + Sphenacodontia (1->2), *Pantelosaurus* +++ (2->1)

86. Tabular morphology: subrectangular sheet located dorsal to posttemporal fenestra (0); large, sheet-like, L-shaped bone comprising suborthogonal ventral and medial processes that enclose the posttemporal fenestra dorsally and laterally (1); reduced, displaced laterally, now located dorsolateral to posttemporal fenestra, medial portion tapering (2); tabular absent (3).

Modified from Sidor & Hopson (1998, character 54), Reisz & Dilkes (2003, character 46), Maddin *et al.* (2006, character 29), Reisz *et al.* (2009, character 51). State ‘0’ taken from Berman *et al.* (1995, character 55).

Reisz (1986) described the variable morphology of the tabular among basal synapsids. *Casea broili*, ‘*Casea*’ *rutena* and *Cotylorhynchus romeri* exhibit state ‘2’ (Romer & Price 1940, pl. 20; Sigogneau-Russell & Russell 1972; Laurin & Reisz 1995, fig. 5C). Reisz *et al.* (2009) included a ‘narrow, slender’ state, scored in varanopids. This state is not included here as it would mask the overall similarity between varanopids and other taxa possessing state ‘1’. The tabular is absent in *Captorhinus* (state ‘3’; e.g. Fox & Bowman 1969; Modesto 1998)

Unambiguous: *Captorhinus* (1->3)

DELTRAN: *Varanosaurus* +++) (1->0), Eothyrididae (1->0), *Casea broili* +++) (1->2)

ACCTRAN: Ophiacodontidae (1->0), Caseasauria (1->0), Caseidae (0->2)

87*. Tabular, posteromedial process that subdivides posttemporal fenestra and contacts the supratemporal: absent (0); present (1)

New character

The derived morphology was described in *Heleosaurus* and *Mesenosaurus* by Reisz & Berman (2001) and Botha-Brink & Modesto (2009).

Unambiguous: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->1)

88. 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).

Modified from Laurin (1993, character 24), Modesto (1994, character 14), Reisz *et al.* (1998, character 22), Sidor & Hopson (1998, character 22), Maddin *et al.* (2006, character 28; 2008, character 28), Reisz *et al.* (2009, character 37); also modified from characters describing the breadth of the posterolateral process of the parietal, which is dependent on the supratemporal breadth: Reisz *et al.* (1992, character 15), Berman *et al.* (1995, character 20).

Caseasaurians possess a relatively broad supratemporal (e.g. Romer & Price 1940; Olsen 1968; Reisz *et al.* 2009) that has often been assumed to be plesiomorphic (Reisz 1980, 1986). However, Maddin *et al.* (2008) and Reisz *et al.* (2009) coded the caseasaurian condition (state ‘1’) as distinct from that in most outgroup taxa (state ‘0’). Furthermore, some basal stem-group reptiles, such as *Protorothyris* (Clark &

Carroll 1972), exhibit a long, slender supratemporal similar to those of non-caseasaurian basal synapsids (e.g. Romer & Price 1940). Further complexity is added by the presence of a caseasaur-like supratemporal in the basal varanopid *Archaeovenator* (Reisz & Dilkes 2003). Because the supratemporal is a superficial bone of the skull roof in *Captorhinus*, and lacks the long, slender morphology of most basal synapsids, it is scored as ‘0’. This is despite extreme reduction of the supratemporal in *Captorhinus* (Fox & Bowman 1966). The supratemporal is absent in most therapsids (e.g. Sidor & Hopson 1998).

Unambiguous: Caseasauria (2->1), *Archaeovenator hamiltonensis* (2->1)

DELTRAN: Synapsida (0->2), *Protorothyris archeri* (0->2), *Biseridens qilianicus* (2->3), *Biarmosuchus tener* (2->3)

ACCTRAN: Amniota (0->2), Therapsida (2->3), *Titanophoneus potens* (3->2), *Captorhinus* (2->0)

89. Quadrates, condyles: distinct, separate (0); confluent, forming a saddle-shaped articular facet (1).

Modesto (1995, character 14), Mazierski & Reisz (2010, character 15).

Unambiguous: Edaphosauridae (0->1)

90. Occiput, slope: approximately vertical (0); inclined anterodorsally by 10-50 degrees (1); strongly inclined anterodorsally by >60 degrees (2); inclined posterodorsally (3) (Figures A1, A2).

Modified from Modesto (1994, character 20), Reisz *et al.* (1998, character 27), Sidor & Hopson (1998, character 42), Maddin *et al.* (2006, character 34; 2008, character 41), Reisz *et al.* (2009, character 50); also modified from characters describing the shape of the posterior part of the temporal fenestra: Reisz *et al.* (1998, character 9), Reisz *et al.* (2009, character 43).

Reisz (1980, 1986) proposed that anterodorsal inclination of the occiput (state ‘1’) was a synapsid synapomorphy. The angle of inclination is increased in varanodontines (state ‘2’; Olson 1965; Langston & Reisz 1981; Campione *et al.* 2010) but decreased in sphenacodontians and edaphosaurids (e.g. Reisz 1986).

Unambiguous: Varanodontinae (1->2)

DELTRAN: Ophiacodontidae + Varanopidae (0->1), Caseasauria (0->1), *Biarmosuchus* +++ (0->3)

ACCTRAN: Synapsida (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (1->0), Therapsida (0->3)

91. Postparietals: unfused/paired (0); fused to form a midline element (1).

Reisz *et al.* (1992, character 24), Berman *et al.* (1995, character 30), Maddin *et al.* (2008, character 43).

Reisz (1980, 1986) proposed that the presence of a single, median postparietal was a synapomorphy of Synapsida. However, subsequent work has demonstrated that the condition is highly variable among basal synapsids (see optimisation).

Unambiguous: *Ennatosaurus* + + + (1->0), *Eureptilia* (1->0), *Varanosaurus acutirostris* (1->0), *Eothyris parkeyi* (1->0)

DELTRAN: *Mycterosaurinae* (1->0), *Aerosaurus wellesi* (1->0)

ACCTRAN: Varanopidae (1->0), *Varanops* + *Varanodon* + *Watongia* (0->1)

92. Supraoccipital, prominent lateral processes forming dorsal margin of posttemporal fenestra: absent, fenestra bounded dorsally by tabular only (0); present (1)

Brinkman & Eberth (1983, character 15); Laurin (1993, character 47).

Romer & Price (1940) and Reisz (1986) observed prominent lateral processes of the supraoccipital in varanopids and sphenacodontids. They are also present in edaphosaurids (Modesto 1995). *Captorhinus* and *Protorothyris* are scored as lacking the lateral process (state ‘0’) because although the supratemporal contacts the highly enlarged posttemporal fenestra, a distinct lateral process is absent (Fox & Bowman 1966; Clark & Carroll 1973).

Unambiguous: Varanodontinae (0->1), Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

93. Postparietal/s, participation in margin of posttemporal fenestra: absent (0); present, postparietal dorsoventrally slender and transversely broad (1).

Maddin *et al.* (2008, character 14).

Although the postparietal contacts the highly enlarged posttemporal fenestra in *Captorhinus* (Fox & Bowman 1966) and *Protorothyris* (Clark & Carroll 1973), it lacks the distinctive morphology of caseids (e.g. Laurin & Reisz 1995; Sigogneau-Russell & Russell 1972; Maddin *et al.* 2008) and so is scored as state ‘0’.

DELTRAN: ‘*Casea*’ *rutena* + + + (0->1)

ACCTRAN: Caseidae (0->1)

94. Stapes, shaft: rod-like, quadrate process small or indistinct (0); blade-like with prominent quadrate process, substantially longer than dorsal process (1).

Reisz *et al.* (1992, character 39), Berman *et al.* (1995, character 49); modified from Brinkman & Eberth (1983, character 6), Reisz *et al.* (1992, characters 40, 41), Laurin (1993, character 45, 51), Modesto (1994, character 21), Fröbisch *et al.* (2011, character 38).

Reisz (1986) described a dorsal process of the stapes articulating in a socket on the paraoccipital process as a synapomorphy of Ophiacodontidae + Edaphosauridae + Sphenacodontia. Regardless of articulations, the stapes of these clades does have a

distinct, ‘blade-like’ morphology when compared to those of other synapsids. The stapes of *Ophiacodon* (Romer & Price) is mediolaterally long and autapomorphic in some respects but is nonetheless scored as the derived state (‘1’). Brinkman & Eberth (1983), Reisz *et al.* (1992), Laurin (1993, character 45, 51), Berman *et al.* (1995), and Fröbisch *et al.* (2011, character 103) coded more detailed aspects of the stapedial morphology that were not observed during the present study.

Unambiguous: Ophiacodontidae (0->1), *Tseajaia campi* (0->1)

DELTRAN: Edaphosauridae + Sphenacodontia (0->1), *Biarmosuchus* +++ (1->0)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Therapsida (1->0)

95. Exoccipital, lateral wing: tall and narrow (0); broad, extending ventral to paraoccipital process (1).

Reisz *et al.* (2009, character 52).

Reisz *et al.* (2009) described the derived state as a synapomorphy of Caseasauria. However, it is also present in basal diadectomorphs (e.g. Romer 1946; Moss 1972; Reisz 2007) and *Protorothyris* (Clark & Carroll 1972), and may be plesiomorphic.

DELTRAN: Ophiacodontidae + Varanopidae (1->0), Edaphosauridae + Sphenacodontia (1->0)

ACCTRAN: Synapsida (1->0), Caseasauria (0->1)

96. Opisthotic, paraoccipital process: confined between squamosals, not visible in lateral view, height less than supraoccipital (0); posterolateral flange projecting posterior to squamosals, visible in lateral view and blade-like, taller than supraoccipital (1); short and knob-like (2).

Modified from Maddin *et al.* (2008, character 39), by addition of state ‘2’ taken from Berman *et al.* (1995, characters 54, 56), Maddin *et al.* (2006, character 33), Reisz *et al.* (2009, character 53).

Unambiguous: Caseasauria (0->1), *Tseajaia campi* (0->2), *Protorothyris archeri* (0->2)

DELTRAN: *Varanosaurus* +++ (0->2)

ACCTRAN: Ophiacodontidae (0->2)

97. Opisthotic, morphology and orientation of paraoccipital process: robust, horizontal rod (0); slender rod, extends posteroventrolaterally (1); dorsoventrally broad sheet, extends laterally (2).

Modified from Reisz (1986), Reisz *et al.* (1992, characters 46, 47, 48), Laurin (1993, characters 48, 49, 50), Berman *et al.* (1995, character 56), Reisz *et al.* (1998, character 26), Sidor & Hopson (1998, character 65), Fröbisch *et al.* (2011, characters 35, 36, 37). A new state (‘2’) is added to describe the condition in caseids (e.g. Olson 1968; Maddin *et al.* 2008, character 40).

DELTRAN: *Casea broili* +++ (0->2), Sphenacodontidae + Therapsida (0->1)

ACCTRAN: Caseidae (0->2), *Pantelosaurus* +++ (0->1)

98. Basioccipital, occipital condyle orientation: posteriorly directed (0); posteroventrally directed (1).

Maddin *et al.* (2008, character 42).

The occipital condyle is directed posteriorly in most amniotes. However, among basal synapsids it is inclined posteroventrally in caseids (Olsen 1968; Reisz 1986), *Edaphosaurus* (Modesto 1995), and some basal therapsids (with posterodorsally sloping occiputs; character 90).

DELTRAN: *Casea broili* +++ (0->1), *Edaphosaurus* (0->1), *Biarmosuchus* +++ (0->1)

ACCTRAN: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Eothyrididae (1->0), Sphenacodontidae (1->0)

99*. Basioccipital, ventral surface anterior to occipital condyle: smooth (0); prominent anteroposterior ridges (1).

New character

Eberth and Brinkman (1986) described the presence of numerous, parallel, anteroposterior ridges on the ventral surface of the basioccipital in *Ophiacodon* and *Stereophallodon*. These ridges are absent in *Archaeothyris* (Reisz 1972).

DELTRAN: *Ophiacodon* + *Stereophallodon* (0->1)

ACCTRAN: *Varanosaurus* +++ (0->1)

100. Basal articulation [basicranial joint]: present (0); absent (1).

Laurin (1993, character 39); Sidor & Hopson (1998, character 68), Fröbisch *et al.* (2011, character 31).

The basal articulation is absent due to fusion in therapsids (eg. Romer & Price 1940; Sidor & Hopson 1998).

DELTRAN: *Biarmosuchus* +++ (0->1)

ACCTRAN: Therapsida (0->1)

101. Basal articulation, position: approximately level with transverse flange of pterygoid (0); anterior to transverse flange (1); posterior to transverse flange (2).

State ‘1’ taken from Maddin *et al.* (2008, character 34). State ‘2’ taken from Reisz *et al.* (1992, character 42), Berman *et al.* (1995, character 50), Fröbisch *et al.* (2011, character 104). Modified from Sidor & Hopson (1998, character 73). In therapsids, the basal articulation is fused (‘absent’; character 100; above) so the position of the base of the cultriform process is used as a proxy for the location of the articulation.

Although Reisz *et al.* (1992) and Berman *et al.* (1995) scored the basal articulation as posterior to the transverse flange (state ‘2’) in *Haptodus*, it is approximately level with the flange (state ‘0’; Laurin 1993, fig. 3B).

DELTRAN: Synapsida (2->0), *Casea broili* +++ (0->1), *Edaphosaurus* (0->1), Sphenacodontidae + Therapsida (0->2), *Protorothyris archeri* (2->0), *Cotylorhynchus romeri* (1->0)

ACCTRAN: Amniota (2->0), Caseidae (0->1), *Angelosaurus* + *Cotylorhynchus* (1->0), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1), *Pantelosaurus* +++ (0->2), *Captorhinus* (0->2)

102. Basal articulation, orientation of basipterygoid process: laterally directed (0); anterolaterally directed (1); posteroventrally directed (2); inapplicable, basal articulation absent (?).

Modified from Brinkman & Eberth (1983, character 3), Berman *et al.* (1995, character 51).

The long axis of the basipterygoid process is directed almost strictly laterally in varanopids and most caseasaurians (Langston & Reisz 1981; Brinkman & Eberth 1983, fig 7C; Reisz 1986; Maddin *et al.* 2006; Reisz *et al.* 2009). It is directed anterolaterally in *Angelosaurus romeri* (Olsen 1968, fig. 7), edaphosaurids and sphenacodontians (Price 1935; Moss 1972; Clark & Carroll 1973; Brinkman & Eberth 1983; Reisz 1986). The ophiacodontids *Varanosaurus* (Berman *et al.* 1995), *Ophiacodon* and *Sterophallodon* exhibit ventrally directed basipterygoid processes that may also be inclined posteriorly (Eberth & Brinkman 1986). Eberth & Brinkman (1983) considered state ‘1’ as plesiomorphic, based on the morphology in *Archeria* and *Diadectes*. In contrast, Reisz (1986) contended that state ‘0’ was present in *Limnoscelis* and therefore represented the plesiomorphic condition. The condition in *Limnoscelis* was not determined in the present analysis, but state ‘1’ is present in the remaining outgroups: *Captorhinus* (Price 1935), *Protorothyris* (Clark & Carroll 1973) and *Tseajaia* (Moss 1972).

Unambiguous: *Angelosaurus romeri* (0->1)

DELTRAN: Varanopidae (1->0), *Varanosaurus* +++ (1->2), Caseasauria (1->0)

ACCTRAN: Synapsida (1->0), Ophiacodontidae (0->2), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

103. Basal articulation, morphology of articular surface of basipterygoid process: single, rounded articular surface (0); flat anterior facet (1); inapplicable, basal articulation absent (?).

Brinkman & Eberth (1983, character 8).

Edaphosaurids (Modesto 1995) and sphenacodontids (Romer & Price 1940) have a flat anterior facet on the basipterygoid processes (Brinkman & Eberth 1983). This is also present in *Captorhinus* (Price 1935), but not other outgroup taxa.

Unambiguous: *Captorhinus* (0->1)

DELTRAN: Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

104. Parasphenoid, body shape: transversely broad, width greater than length from basipterygoid processes to posterior end (0); transversely narrow, length greater than width (1).

Modified from Reisz *et al.* (1992, character 44), Laurin (1993, character 41), Berman *et al.* (1995, character 52), Maddin *et al.* (2008, character 31).

Unambiguous: *Ophiacodon* spp. (0->1)

DELTRAN: *Secodontosaurus* + Sphenacodontinae (0->1)

ACCTRAN: Sphenacodontidae (0->1)

105. Parasphenoid, expansion of body [ventral plate] posterior to basicranial articulation: gradual (0); abrupt (1).

Maddin *et al.* (2006, character 36).

Unambiguous: *Pyozia mesensis* (0->1), *Mesenosaurus romeri* (0->1)

DELTRAN: *Aerosaurus greeleeorum* + *A. wellesi* (0->1)

ACCTRAN: *Ruthiromia* + *Aerosaurus* spp. (0->1)

106. Parasphenoid, body [ventral plate] median groove: absent, ventral surface flat (0); or shallow concave region between cristae ventrolaterales (1); deep median sulcus present (2).

Modified from Fröbisch *et al.* (2011, character 32); State ‘0’ taken from Maddin *et al.* (2006, character 37). State ‘2’ taken from Reisz *et al.* (1992, character 44), Laurin (1993, character 41), Berman *et al.* (1995, character 52).

DELTRAN: *Aerosaurus greeleeorum* + *A. wellesi* (1->0), *Secodontosaurus* + Sphenacodontinae (1->2)

ACCTRAN: *Ruthiromia* + *Aerosaurus* spp. (1->0), Sphenacodontidae (1->2)

107. Parasphenoid body, posteroventral emargination [basisphenoid shelf]: absent (0); present (1).

Brinkman & Eberth (1983, character 9), Berman *et al.* (1995, character 53).

Brinkman & Eberth (1983) provided a clear description of this character. The shelf/emargination is lost in Edaphosauridae + Sphenacodontia (Reisz 1986).

Unambiguous: *Captorhinus* (1->0)

DELTRAN: Edaphosauridae + Sphenacodontia (1->0)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (1->0)

108. Parasphenoid body, median longitudinal ridge on ventral surface: absent (0); present (1).

Modified from Fröbisch *et al.* (2011, character 32).

A median ridge is present on the parasphenoid body in *Limnoscelis*, *Heleosaurus*, *Mesenosaurus* and *Pyozia* (Moss 1972; Reisz & Berman 2001; Anderson & Reisz 2004; Reisz & Modesto 2007). This is located within the median groove and is thus independent of character 106.

Unambiguous: *Limnoscelis paludis* (0->1)

DELTRAN: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->1), *Pyozia mesensis* (0->1)

ACCTRAN: *Pyozia* +++ (0->1), Varanodontinae (1->0)

109. Parasphenoid, teeth on ventral surface: absent (0); present (1).

Modified from Reisz *et al.* (1992, character 45), Maddin *et al.* (2008, character 32).

Unambiguous: *Pyozia* +++ (0->1), Caseasauria (0->1)

110. Parasphenoid, posterior extent of teeth: anterior to transverse flange of pterygoid (0); posterior to transverse flange of pterygoid (1); inapplicable, parasphenoid edentulous (?).

Modified from Reisz & Dilkes (2003, character 45), Maddin *et al.* (2006, character 38); Maddin *et al.* (2008, character 32), Reisz *et al.* (2009, character 54).

DELTRAN: *Angelosaurus* + *Cotylorhynchus* (1->0)

ACCTRAN: *Ennatosaurus* +++ (1->0)

111. Parasphenoid, teeth on ventral plate: present along edges (0); present across width of plate, forming central denticle field (1); inapplicable, teeth absent from ventral plate (?).

Modified from Reisz & Dilkes (2003, character 45), Maddin *et al.* (2006, characters 37, 38), Reisz *et al.* (2009, character 54).

Unambiguous: Varanodontinae (0->1)

DELTRAN: ‘*Casea*’ *rutena* (0->1)

ACCTRAN: *Trichasaurus* +++ (0->1)

112. Vomer, teeth: present (0); absent (1).

Reisz *et al.* (1992, character 64), Laurin (1993, character 77), Berman *et al.* (1995, character 71), Sidor & Hopson (1998, character 40), Fröbisch *et al.* (2011, character 61).

Unambiguous: Sphenacodontidae + Therapsida (0->1), *Limnoscelis paludis* (0->1), *Captorhinus* (0->1), *Biseridens qilianicus* (1->0)

113. Vomer, internarial shape: widest posteriorly (0); widest near middle (1).

Modified from Sidor & Hopson (1998, character 23).

This is related to the morphology of the choana (internal naris).

Unambiguous: *Biarmosuchus* +++) (0->1)

114. Palatine, teeth: present (0); absent (1).

Laurin (1993, character 78), Sidor & Hopson (1998, character 36)

Unambiguous: Amniota (1->0), *Mesenosaurus romeri* (0->1)

115. Palatine, boss or ridge bears large teeth: absent (although teeth may still be present as a fine shagreen) (0); present (1).

Sidor & Hopson (1998, character 35)

DELTRAN: *Biarmosuchus* +++) (0->1), *Cotylorhynchus romeri* (0->1)

ACCTRAN: *Angelosaurus* + *Cotylorhynchus* (0->1), Therapsida (0->1)

116. Pterygoid, ascending lamina/dorsal flange of the anterior ramus of the pterygoid: low [?poorly ossified] (0); tall (1).

Reisz *et al.* (1992, character 36), Berman *et al.* (1995, character 45), Fröbisch *et al.* (2011, character 101).

DELTRAN: Edaphosauridae + Sphenacodontia (0->1), *Ophiacodon* spp. (0->1)

ACCTRAN: Ophiacodontidae (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

117. Pterygoids, interpterygoid vacuity: anteroposteriorly long (0); short (1).

Laurin (1993, character 42), Fröbisch *et al.* (2011, character 33).

DELTRAN: *Biarmosuchus* +++) (0->1)

ACCTRAN: Therapsida (0->1)

118. Pterygoid, distinct transverse flange: present (0); absent (1).

Modesto (1994, character 22; 1995, character 18), Mazierski & Reisz (2010, character 19).

Unambiguous: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1)

119. Pterygoid, transverse flange, orientation of posterior margin: lateral or posterolateral (0); anterolateral (1).

Maddin *et al.* (2008, character 37).

Unambiguous: *Biseridens qilianicus* (0->1)

DELTRAN: *Ennatosaurus* +++ (0->1)

ACCTRAN: *Trichasaurus* +++ (0->1)

120. Pterygoid, quadrate ramus, medial shelf ('posteromedian flange'; 'tympanic flange'): present (0); absent (1).

Brinkman & Eberth (1983, character 14); Reisz *et al.* (1992, character 37), Fröbisch *et al.* (2011, character 102); modified from Berman *et al.* (1995, character 46).

The medial shelf of the pterygoid is especially prominent in caseosaurs and varanopids, and absent in edaphosaurids and sphenacodontians (Brinkman & Eberth 1983; Reisz 1986). In most ophiacodontids, the flange is present but low (Brinkman & Eberth 1986), and in *Varanosaurus* it is absent (BSPHM 1901 XV 20). Berman *et al.* (1995) included an additional state to code the 'low' condition in some ophiacodontids, but this is not employed here.

Unambiguous: *Varanosaurus acutirostris* (0->1)

DELTRAN: Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

121. Pterygoid, teeth arranged in a transverse row along posterior margin of ventral surface of pterygoid flange: present (0); absent (1).

Modified from Laurin (1993, character 80), Sidor & Hopson (1998, character 38).

Unambiguous: *Titanophoneus* + *Biseridens* (0->1)

122. Pterygoid, teeth in anterolaterally oriented field: present, extends posteromedially to basicranial area (0); does not extend as far as basicranial area (1); pterygoid heavily denticulated, forming 'tooth plates' (2); anterolateral field absent (3) inapplicable, pterygoid edentulous (?).

States '0', '1', and '3' taken from Maddin *et al.* (2008, character 38). States '0' and '1' modified from Reisz *et al.* (1992, character 66), Fröbisch *et al.* (2011, character 107). State '2' taken from Modesto (1995, character 19), Mazierski & Reisz (2010, character 21). State '3' taken from Sidor & Hopson (1998, character 37).

Edaphosaurids possess a massive, crushing palatal dentition (Reisz 1980) that is informally termed 'tooth plates' (e.g. Modesto 1995).

Unambiguous: Amniota (3->0), *Ophiacodon* + *Stereophalodon* (0->1), *Edaphosaurus* (0->2)

DELTRAN: 'Casea' *rutena* +++ (0->1), *Biarmosuchus* +++ (0->1)

ACCTRAN: *Trichasaurus* +++ (0->1), Therapsida (0->1)

123. Pterygoid, teeth on transverse flange: single row along posterior margin of ventral surface (0); additional teeth anterior to single row (1); inapplicable, pterygoid edentulous (?).

Reisz *et al.* (1998, character 30), Maddin *et al.* (2006, character 35), Reisz *et al.* (2009, character 56).

Unambiguous: *Pyozia* + + + (0->1), Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), *Tseajaia campi* (0->1), *Captorhinus* (0->1)

DELTRAN: *Secodontosaurus* + Sphenacodontinae (1->0), *Pantelosaurus saxonicus* (1->0)

ACCTRAN: *Pantelosaurus* + + + (1->0), Therapsida (0->1)

124. Ectopterygoid, teeth: present (0); absent (1); inapplicable, ectopterygoid absent (?).

Reisz *et al.* (1992, character 65), Laurin (1993, character 79), Berman *et al.* (1995, character 72), Sidor & Hopson (1998, character 39), Fröbisch *et al.* (2011, character 62).

Unambiguous: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (1->0)

DELTRAN: *Titanophoneus* + *Biseridens* (0->1)

ACCTRAN: Therapsida (0->1)

125. Jaw suspension: at level of maxillary tooth row (0); quadrate projects far ventral to maxillary tooth row (1).

Modesto (1995, character 15), Sidor (2003, character 52), Mazierski & Reisz (2010, character 16); modified from Laurin (1993, character 54), Fröbisch *et al.* (2011, characters 40, 122).

This character is independent of character 9, describing the concavity of the ventral surface of the temporal bar because (i) *Secodontosaurus* has a concave temporal bar but lacks a ventrally-projecting quadrate (Reisz *et al.* 1992); (ii) basal therapsids possess a convex temporal bar in combination with a ventrally-projecting quadrate (e.g. Orlov 1958). The slight ventral projection of the quadrate in caseids (Reisz 1986) is scored as ‘0’ for the present character but is coded in state ‘2’ of character 9. Ventral projection is absent in ophiacodontids (see character 9; Fig. A1B).

Unambiguous: *Secodontosaurus obtusidens* (1->0)

DELTRAN: Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

126. Mandible, proportions (not including laminar portion of the angular): intermediate proportions, dorsoventral height 0.20–0.26 total length (0); short and robust, dorsoventral height >0.30 total length (1); very long and dorsoventrally slender, maximum height <0.18 total length (2).

Modified from Modesto (1995, character 20), Mazierski & Reisz (2010, character 22) by addition of state ‘2’ modified from Sidor (2003, character 3).

The derived states are independent of overall snout elongation (character 2) because a long slender mandible (state ‘2’) is absent in sphenacodontines, which have

proportionally long preorbital snouts. Romer & Price (1940) considered the short, robust mandible (state '1') as a diagnostic feature of Edaphosauria (Edaphosauridae + Caseidae). Reisz (1980) suggested that it's presence in edaphosaurids and caseids instead reflected parallel adaptation to herbivory.

Unambiguous: Ophiacodontidae + Varanopidae (0->2), *Secodontosaurus obtusidens* (0->2), *Protorothyris archeri* (0->2), *Biseridens qilianicus* (0->1)

DELTRAN: 'Casea' *rutena* +++ (0->1), *Edaphosaurus boanerges* (0->1)

ACCTRAN: *Trichasaurus* +++ (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1)

127. Mandibular symphysis: dorsoventrally low, mandible tapers anteriorly (0); dorsoventrally thick, almost as deep as mandible at midlength of the tooth row (1).

Maddin *et al.* (2008, character 53), Reisz *et al.* (2009, character 57), Fröbisch *et al.* (2011, character 120); modified from Sidor (2003, character 4)

Romer & Price (1940) considered the presence of a deep mandibular symphysis as diagnostic of 'Edaphosauria' (Edaphosauridae + Caseidae). However, Reisz (1980) suggested that this was derived independently in the two groups, noting that it was also present in sphenacodontids.

Unambiguous: *Secodontosaurus obtusidens* (1->0), *Limnoscelis paludis* (0->1)

DELTRAN: Caseidae (0->1), Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Eothyrididae (1->0)

128. Mandible, size of Meckelian foramen: small, <0.10 of jaw length (0); large, >0.25 of jaw length (1).

Maddin *et al.* (2008, character 60).

Unambiguous: Amniota (1->0)

129. 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).

Maddin *et al.* (2008, character 58).

Unambiguous: Caseasauria (0->1), *Captorhinus* (0->1)

DELTRAN: *Edaphosaurus boanerges* (0->1)

ACCTRAN: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1)

130. Mandible, shape of coronoid eminence: slightly convex (0); strongly convex (1); subhorizontal/flat (2).

Modified from Reisz *et al.* (1992, character 51), Laurin (1993, character 53), Berman *et al.* (1995, character 61), Sidor (2003, character 12), Fröbisch *et al.* (2011, character 39) by addition of a new state '2'.

It has long been recognised that edaphosaurids and sphenacodontians possess a tall, highly convex coronoid process (e.g. Reisz 1986; Kemp 2005). The new state ('2') describes the condition in *Varanodon*, *Varanops* and *Watongia*, wherein the coronoid eminence is flat, and thus effectively absent (e.g. Laurin & Reisz 2004; Campione & Reisz 2010).

Unambiguous: *Varanops* + *Varanodon* + *Watongia* (0->2)

DELTRAN: Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

131. Mandible, bone forming dorsal margin of coronoid eminence laterally: coronoid or surangular (0); dentary (1).

Maddin *et al.* (2008, character 71).

Unambiguous: *Cutleria wilmarti* (0->1), *Biseridens qilianicus* (0->1)

DELTRAN: *Casea broili* +++ (0->1), *Haptodus garnettensis* (0->1), *Edaphosaurus boanerges* (0->1)

ACCTRAN: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Eothyrididae (1->0), *Pantelosaurus* +++ (1->0)

132. Mandible, retroarticular process: absent (0); present (1).

Maddin *et al.* (2006, character 41); modified from Laurin (1993, character 61), Berman *et al.* (1995, character 64), Fröbisch *et al.* (2011, character 47).

Reisz (1980) proposed the presence of a well-developed retroarticular process as a possible synapomorphy of Varanopidae + Sphenacodontia. However, this was derived independently in the two clades. It is absent in basal varanopids (Reisz & Dilke 2003), and especially prominent in varanodontines (Reisz & Berman 2001). A clear comparative figure showing the presence and absence of this structure was provided by Brinkman & Eberth (1986, fig. 7).

DELTRAN: Mycterosaurinae + Varanodontinae (0->1), Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Pyozia* +++ (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

133. 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 (?).

Modified from Reisz *et al.* (1992, characters 56, 57), Laurin (1993, characters 60, 61, 62), Berman *et al.* (1995, character 64), Anderson & Reisz (2004, character 54), Maddin *et al.* (2006, character 41), Fröbisch *et al.* (2011, characters 47, 48).

Reisz (1980) noted that the composition of the retroarticular process of varanopids differed from that in sphenacodontids. Reisz (1986) subsequently listed a character coding the downturned retroarticular process of sphenacodontids. Because both these

changes to the retroarticular morphology occur simultaneously, they are combined into a single character here.

DELTRAN: Sphenacodontidae + Therapsida (0->1)

ACCTRAN: *Pantelosaurus* +++ (0->1)

134. Dentary size: comprises >70% the anteroposterior length of the mandible (0); <65% (1).

Modesto (1995, character 21), Mazierski & Reisz (2010, character 23).

DELTRAN: Ophiacodontidae + Varanopidae (1->0), Sphenacodontia (1->0),

Protorothyris archeri (1->0), *Ianthasaurus hardestiorum* (1->0)

ACCTRAN: Amniota (1->0), Caseasauria (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1), *Captorhinus* (0->1)

135. Dentary, enlarged anterior teeth and alveoli: absent, teeth small or only slightly enlarged (0); present (1).

Laurin (1993, character 75); modified from Reisz *et al.* (1992, character 61), Sidor & Hopson (1998, character 107), Fröbisch *et al.* (2011, character 60).

Fröbisch *et al.* (2011) employed a state ‘1’ for basal sphenacodontians such as *Haptodus* (Laurin 1993), specifying that the anterior dentary teeth were only ‘slightly enlarged’. This is effectively coded by character 35 herein (the relative size of the caniniform teeth, which covaries with the relative size of enlarged anterior dentary teeth when they are present) and all sphenacodontians other than *Secodontosaurus* are scored as having enlarged anterior dentary teeth.

Unambiguous: *Oromycter dolesorum* (0->1), *Limnoscelis paludis* (0->1), *Captorhinus* (0->1)

DELTRAN: *Titanophoneus* + *Biseridens* (0->1), Sphenacodontinae (0->1),

Ianthasaurus hardestiorum (0->1), *Haptodus garnettensis* (0->1)

ACCTRAN: *Ianthodon* + *Edaphosauridae* + Sphenacodontia (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (1->0), *Secodontosaurus obtusidens* (1->0), *Biarmosuchus tener* (1->0)

136. Dentary, mesialmost tooth: not enlarged (0); enlarged (1).

Modified from Sidor & Hopson (1998, character 107), Fröbisch *et al.* (2011, character 60).

In some taxa with enlarged anterior dentary teeth, the mesialmost tooth remains small. Thus, enlargement of this tooth is independent of enlargement of the other anterior dentary teeth (character 135).

Unambiguous: *Titanophoneus* + *Biseridens* (0->1), *Oromycter dolesorum* (0->1), *Limnoscelis paludis* (0->1), *Cryptovenator hischbergeri* (0->1)

137. Lateral mandibular fenestra between dentary and angular: absent (0); present (1) (Figure A1).

Reisz *et al.* (1992, character 49), Berman *et al.* (1995, character 57), Sidor (2003, character 64).

DELTRAN: *Varanosaurus* +++ (0->1)

ACCTRAN: Ophiacodontidae (0->1)

138. Splenial, contribution to mandibular symphysis: present, symphysis formed from dentary and splenial (0); absent, symphysis formed solely by dentary (1).

Berman *et al.* (1995, character 58), Sidor (2003, character 25), Maddin *et al.* (2008, character 59), Fröbisch *et al.* (2011, character 121).

Unambiguous: Ophiacodontidae + Varanopidae (0->1), *Secodontosaurus obtusidens* (0->1)

139. Splenial, exposure on lateral surface of mandible: absent (0); narrow, forming one-fifth or less of the lateral surface (1); broad anteriorly, forming one-third or more of the lateral surface (2).

Modified from Berman *et al.* (1995, character 59), Modesto (1995, character 22), Sidor & Hopson (1998, character 90), Sidor (2003, characters 26, 28), Maddin *et al.* (2008, character 55), Mazierski & Reisz (2010, character 24), Fröbisch *et al.* (2011, character 121).

DELTRAN: ‘*Casea*’ *rutena* +++ (0->1), Edaphosauridae + Sphenacodontia (0->1), *Biarmosuchus* +++ (1->0), *Edaphosaurus boanerges* (1->2)

ACCTRAN: *Trichasaurus* +++ (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), *Edaphosaurus* (1->2), Therapsida (1->0)

140. Splenial, contact with posterior coronoid: absent (0); present (1); inapplicable, posterior coronoid absent (?).

Maddin *et al.* (2008, character 57).

DELTRAN: *Varanosaurus* +++ (0->1), *Secodontosaurus obtusidens* (0->1),

Mesenosaurus romeri (0->1), *Ianthasaurus hardestiorum* (0->1)

ACCTRAN: Amniota (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (1->0), Sphenacodontinae (1->0), *Archaeovenator hamiltonensis* (1->0)

141. Coronoids, number in mandible: two, anterior coronoid present (0); one, anterior coronoid absent (1).

Laurin (1993, character 55), Sidor & Hopson (1998, character 89), Sidor (2003, character 58), Maddin *et al.* (2008, character 61), Fröbisch *et al.* (2011, character 41).

DELTRAN: *Captorhinus* (0->1), *Biseridens qilianicus* (0->1)

ACCTRAN: Therapsida (0->1), Eureptilia (0->1)

142. Coronoid [posterior coronoid], **teeth**: absent (0); present (1).

Laurin (1993, character 81), Sidor (2003, character 60), Maddin *et al.* (2008, character 62), Fröbisch *et al.* (2011, character 63).

Unambiguous: Ophiacodontidae + Varanopidae (1->0)

DELTRAN: *Ennatosaurus* +++ (1->0), Sphenacodontidae + Therapsida (1->0)

ACCTRAN: *Trichasaurus* +++ (1->0), *Pantelosaurus* +++ (1->0)

143. Angular, cross-section shape of ventral border of angular: weakly ridged/keeled (0); prominent, sheet-like keel with strongly convex posterior edge (1); reflected lamina separated from mandible by a posterior notch in lateral view (2); ventral surface of angular evenly rounded (3).

State ‘1’ taken from Brinkman & Eberth (1983, character 7), Reisz *et al.* (1992, character 50), Berman *et al.* (1995, character 60, 63), Sidor (2003, character 30). State ‘2’ taken from Reisz *et al.* (1992, characters 54, 55), Laurin *et al.* (1993, characters 56, 57), Modesto (1994, character 24), Sidor & Hopson (1998, character 95), Sidor (2003, character 31), Fröbisch *et al.* (2011, characters 42, 43). State ‘3’ taken from Reisz & Dilkes (2003, character 38), Maddin *et al.* (2006, character 40), Maddin *et al.* (2008, character 56), Reisz *et al.* (2009, character 58).

Many basal synapsids have a ventral ridge on the angular. This is weak in caseasaurians (e.g. *Eothyris*, MCZ 1161). It has long been recognised that ophiacodontids, edaphosaurids and basal sphenacodontians share a morphology of the angular in which the ventral portion is expanded and transversely compressed, forming a keel (Brinkman & Eberth 1983; Reisz 1986). In sphenacodontians other than *Haptodus*, including therapsids, this is modified to form the ‘reflected lamina’ (state ‘2’; e.g. Romer & Price 1940; Reisz 1986; Kemp 2005). Laurin *et al.* (1993) provided states describing the relative size of the reflected lamina, which is largest in therapsids. These states are not employed here. In varanodontine varanopids the ventral surface of the angular is evenly rounded (e.g. Reisz & Dilkes 2003; Reisz & Laurin 2004; Campione & Reisz 2010).

Unambiguous: Varanodontinae (0->3), *Pantelosaurus* +++ (1->2)

DELTRAN: *Varanosaurus* +++ (0->1), Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: Ophiacodontidae (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

144. Angular, reflected lamina, posterior emargination: short (0); long with free posterodorsal margin (1); inapplicable, reflected lamina absent (?).

Modified from Sidor & Hopson (1998, character 96), Sidor (2003, character 33).

DELTRAN: *Biarmosuchus* +++ (0->1)

ACCTRAN: Therapsida (0->1)

145*. Surangular, transverse expansion of dorsal surface: thin, sheet-like surangular, unexpanded (0); transversely expanded dorsally forming broad platform (1).

New character (Figure A2).

Unambiguous: Varanodontinae (0->1)

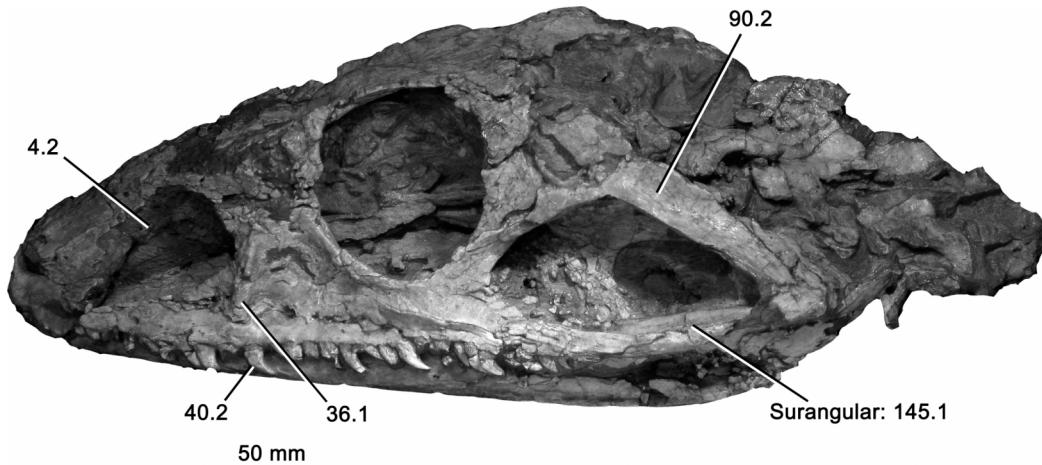


Figure A2. Skull of *Varanodon agilis* (FMNH UR 986) in left lateral view showing states of characters 4, 36, 40, 90 and 145. Scale bar equals 50 mm.

146. Prearticular, medial surface: nearly straight (0); twisted posteriorly (1).

Brinkman & Eberth (1983, character 12), Reisz (1986), Reisz *et al.* (1992, character 52), Modesto (1994, character 23), Berman *et al.* (1995, character 62), Fröbisch *et al.* (2011, character 105).

DELTRAN: Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

147. Prearticular and articular, pterygoideus process: formed by articular and prearticular (0); formed by the articular only and sheathed by the prearticular (1).

Brinkman & Eberth (1983, character 13), Reisz (1986), Reisz *et al.* (1992, character 53), Fröbisch *et al.* (2011, character 106).

DELTRAN: Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

Postcranial characters

148*. Presacral vertebrae, count: 27 or more (0); <27 (1).

New character.

Basal diadectomorphs, *Captorhinus*, *Protorothyris* and some caseids have 26 presacral vertebrae (e.g. Williston 1911; Moss 1972; Sigogneau-Russell & Russell

1972; Clark & Carroll 1973). In contrast, most basal synapsids have 27 presacral vertebrae (e.g. Romer & Price 1940; Reisz 1986). *Cotylorhynchus hancocki* has at least 27 (Olsen 1968). *Ianthisaurus* and *Titanophoneus* have 28 (Orlov 1958; Reisz & Berman 1986).

DELTRAN: Ophiacodontidae + Varanopidae (1->0), Edaphosauridae + Sphenacodontia (1->0), *Cotylorhynchus hancocki* (1->0)

ACCTRAN: Synapsida (1->0), Caseasauria (0->1), *Cotylorhynchus hancocki* + *C. bransoni* (1->0)

149*. Cervical vertebrae, count: 3 or fewer (0); 5 or more (1).

New character.

Basal tetrapods, including the outgroup taxa of this analysis (Moss 1972; Clark & Carroll 1973; Sumida 1990), have short necks comprising three or fewer cervical vertebrae (Janis & Keller 2001). Basal synapsids have longer necks (e.g. Romer & Price 1940; Reisz 1986).

Unambiguous: Synapsida (0->1)

150. 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).

Reisz *et al.* (1992, character 67), Laurin (1993, character 89), Berman *et al.* (1995, character 73).

Reisz (1980) proposed that the derived state of this character was a possible synapomorphy of Varanopidae + Sphenacodontidae.

Unambiguous: Varanopidae (0->1)

DELTRAN: Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

151. Axial neural spine, anteroposterior length of apex: longer than centrum and extends past anterior surface of centrum (0); shorter than centrum (1); short and spine inclined anterodorsally (2).

Modified from Reisz *et al.* (1992, character 68), Berman *et al.* (1995, character 74), Fröbisch *et al.* (2011, character 108) by addition of a new state ‘2’ adapted from Maddin *et al.* (2008, character 80).

Variation in axial neural spine morphology has long been recognised among basal synapsids (Reisz *et al.* 1992b, fig. 1). A new state (‘2’) describes the distinctive morphology of the axial neural spine in edaphosaurids and derived caseids (e.g. Romer & Price 1940, pl. 36A; Sigogneau-Russell & Russell 1974; Reisz *et al.* 1991, fig. 1C).

Unambiguous: Edaphosauridae (0->2), *Secodontosaurus* + Sphenacodontinae (0->1)

DELTRAN: ‘*Casea*’ *rutena* +++ (0->2)

ACCTRAN: *Trichasaurus* +++ (0->2)

152*. Axial neural spine, height: low, subequal to the centrum height (0); tall, at least 1.5 times the height of the centrum (1); very tall, many times the centrum height (2).

New character (Reisz *et al.* 1992b).

Unambiguous: Sphenacodontia (0->1), *Protorothyris archeri* (0->1), *Ianthisaurus hardestiorum* (0->2)

DELTRAN: Mycterosaurinae + Varanodontinae (0->1), *Dimetrodon* + *Sphenacodon* (1->2), *Ophiacodon* spp. (0->1), *Archaeothyris florensis* (0->1)

ACCTRAN: Ophiacodontidae + Varanopidae (0->1), Sphenacodontinae (1->2), *Varanosaurus acutirostris* (1->0), *Archaeovenator hamiltonensis* (1->0)

153. Cervical centra, length: shorter than dorsal centra (0); approximately equal to dorsal centra (1); markedly longer than dorsal centra (2).

Laurin (1993, character 93), Fröbisch *et al.* (2011, character 70); modified from Reisz *et al.* (1992, character 70), Modesto (1994, character 25; 1995, character 23), Mazierski & Reisz (2010, character 25).

Romer & Price (1940) considered the short cervical vertebrae of caseids and edaphosaurids as a diagnostic feature of ‘Edaphosauria’. Reisz (1980) suggested that these were independently derived in the two groups in response to the evolution of a small head adapted for herbivory. This is supported by the presence of long cervical vertebrae in the basal edaphosaurid *Ianthisaurus* (Reisz & Berman 1986).

Unambiguous: Varanodontinae (1->2), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (1->0)

DELTRAN: *Casea broili* +++ (1->0), Sphenacodontidae + Therapsida (1->2)

ACCTRAN: Caseasauria (1->0), *Pantelosaurus* +++ (1->2)

154. Cervicodorsal centra, ventral surface: low, rounded ridge (0); prominent, transversely narrow, sheet-like keel (1).

Reisz *et al.* (1992, character 69); modified from Laurin (1993, character 92), Fröbisch *et al.* (2011, character 69).

Laurin (1993) and Fröbisch *et al.* (2011) included an additional state describing a ‘rounded’ morphology but did not score it as present in any taxon.

DELTRAN: *Secodontosaurus* + Sphenacodontinae (0->1)

ACCTRAN: *Pantelosaurus* +++ (0->1)

155*. Dorsal centra, anteroposterior length: short, subequal to height (0); long, at least 1.5 times as long as high (1).

New character (Romer and Price 1940, p. 95).

Dimetrodon is scored as polymorphic for this character because the proportions of the dorsal centra vary among species (Romer & Price 1940; Berman *et al.* 2001).

Unambiguous: Amniota (0->1), Varanodontinae (1->0), *Varanosaurus* +++ (1->0), *Trichasaurus* +++ (1->0), Sphenacodontia (1->0), *Secodontosaurus obtusidens* (0->1)

156. Dorsal centra (anterior–middle dorsal centra), ventral surface: transversely rounded (0); ventral ridge (1); strongly pinched forming transversely narrow, sheet-like keel (2); ventrally raised platform or keel bearing longitudinal trough (3).

Modified from Berman *et al.* (1995, character 75), Reisz & Dilkes (2003, character 44) and Maddin *et al.* (2006, character 50) by addition of a new state ('3'); also modified from Reisz *et al.* (1992, character 71), Reisz *et al.* (2009, character 62), Fröbisch *et al.* (2011, character 109).

A new state ('3') describes the 'ophiacodont' condition of Romer & Price (1940, p. 214), also described by Lewis and Vaughn (1965, p. C26) and by Brinkman & Eberth (1986) in *Ophiacodon* and *Stereophallodon*. Reisz (1980) considered the ventral keel of the dorsal vertebrae to unite varanopids and sphenacodontids. However, subsequent identifications of basal varanopids and sphenacodontians indicate that it was independently derived in the two groups.

Unambiguous: *Varanodon* + *Watongia* (0->2), *Ophiacodon* + *Stereophallodon* (0->3), *Ianthasaurus hardestiorum* (0->1), *Archaeovenator hamiltonensis* (0->1)

DELTRAN: *Secodontosaurus* + Sphenacodontinae (0->2), *Heleosaurus scholtzi* (0->3)

ACCTRAN: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->3), Sphenacodontidae (0->2)

157. 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).

Modified from Laurin (1993, characters 86, 87), Fröbisch *et al.* (2011, character 68).

Caseids, sphenacodontids and most edaphosaurids possess bevelled pleurocentra, but rarely preserved ossified intercentra, suggesting the presence of cartilaginous elements (state '1'; Stovall *et al.* 1966; Olson 1968).

Unambiguous: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), *Ianthasaurus hardestiorum* (1->0)

DELTRAN: *Biarmosuchus* +++ (1->2)

ACCTRAN: Therapsida (1->2)

158. Dorsal transverse processes: prominent but not elongate, a conspicuous lamina extends anteroventrally along lateral surface of neural arch from base of transverse process (0); extend far laterally, lamina weak or absent (1).

Modesto *et al.* (1994, character 31; 1995, character 29), Mazierski & Reisz (2010, character 32); modified from Brinkman & Eberth (1983, character 17).

Romer and Price (1940, p. 101) observed that in ‘primitive’ taxa the diapophysis does not extend far laterally (‘about 3 ½ units’), whereas in *Dimetrodon* and *Edaphosaurus* it is elongate, extending ‘6 units or more’. Elongate transverse processes are also present in caseids (e.g. Olson 1968).

Unambiguous: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), *Tseajaia campi* (0->1)

159*. Dorsal transverse process, location: approximately at midlength of neural arch, anterior centrodiapophyseal lamina oriented anteroventrally (0); located anteriorly, anterior centrodiapophyseal lamina vertical (1).

New character (Figure A3).

Unambiguous: *Trichasaurus* +++ (0->1), Edaphosauridae (0->1)

160*. Dorsal prezygapophyses: planar, do not contact on midline (0); transversely concave, contact on midline (1); planar and inclined strongly medially, contact on midline (2).

New character (Figures A3, A5).

State ‘2’ describes the condition in *Titanophoneus* (Orlov 1958).

Unambiguous: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1)

DELTRAN: *Angelosaurus* + *Cotylorhynchus* (0->1), *Titanophoneus potens* (0->2)

ACCTRAN: ‘Casea’ *rutena* +++ (0->1), Therapsida (0->2)

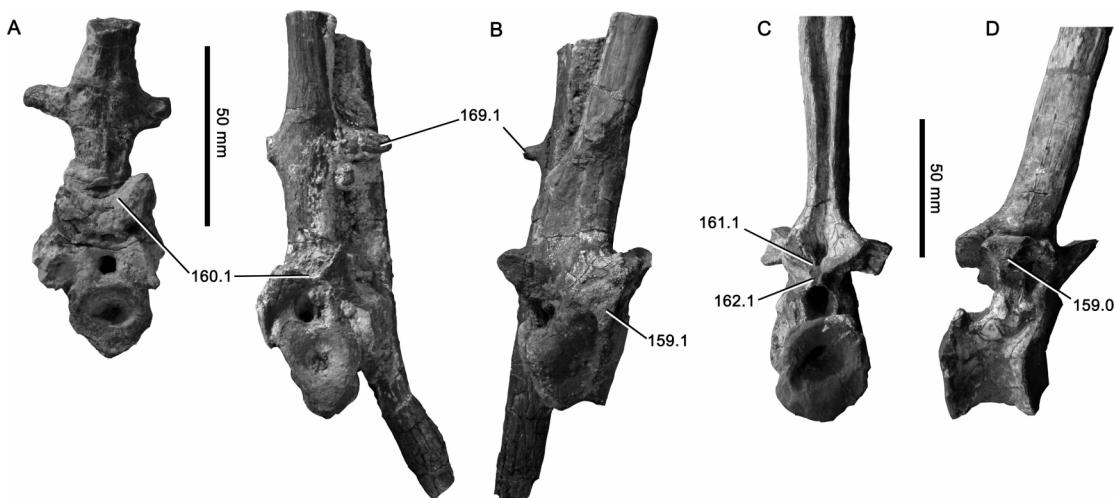


Figure A3. Dorsal vertebrae of A–B, *Edaphosaurus* (MCZ 3417; Moran Formation of Clay County, Texas) and C–D, *Dimetrodon gigashomogenes* (holotype, FMNH UC 112) in anterior (A), right lateral (B, D) and posterior (C) views showing states of characters 159, 160, 161, 162 and 169. Scale bars equal 50 mm.

161*. Dorsal postzygapophyses: widely spaced (0); contact on midline (1).

New character (Figure A3).

Unambiguous: *Cotylorhynchus hancocki* + *C. bransoni* (0->1)

DELTRAN: Edaphosauridae + Sphenacodontia (0->1), *Watonia meieri* (0->1),

Ophiacodon spp. (0->1)

ACCTRAN: *Varanodon* + *Watongia* (0->1), *Ophiacodon* + *Stereophallodon* (0->1),

Ianthodon + Edaphosauridae + Sphenacodontia (0->1)

162*. Dorsal postzygapophyses, hyposhene: absent (0); present and prominent (1).

New character (Figure A3).

The hyposhene is a vertical sheet of bone that extends ventrally from the midline contact of the postzygapophyses.

Unambiguous: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1),

Dimetrodon spp. (0->1), *Cotylorhynchus hancocki* (0->1)

163. Dorsal neural arches, dorsolateral surfaces: flat or weakly concave, not swollen or buttressed (0); swollen and convex (1); excavated by deep depressions (2).

Modified from Brinkman & Eberth (1983, character 16); Modesto (1994, character 30; 1995, character 28) and Reisz *et al.* (2009, character 60) by addition of state ‘2’, taken from Maddin *et al.* (2008, character 74). Modified from Reisz *et al.* (1992, character 79), Laurin (1993, character 84), Berman *et al.* (1995, character 79), Reisz & Dilkes (2003, character 47), Maddin *et al.* (2006, character 51), Mazierski & Reisz (2010, character 31), Fröbisch *et al.* (2011, character 66).

Reisz (1980) noted that amniotes primitively lack swollen dorsal neural arches, although they are present in their outgroups, the diadectomorphs and seymouriamorphs. Swollen neural arches are also present in the ophiacodontid *Varanosaurus* (Sumida 1989a), and captorhinids (Sumida 1990). Romer & Price (1940) and Reisz (1980) proposed that excavated dorsolateral surfaces of the dorsal neural arches may be a synapomorphy of Varanopidae + Sphenacodontia. However, excavations are absent or very shallow in basal varanopids (Reisz & Dilkes 2003; Reisz & Modesto 2007) and were derived independently in the two groups.

Some previous authors (Reisz *et al.* 1992; Laurin 1993; Berman *et al.* 1995; Maddin *et al.* 2006) included separate states for ‘shallow, anteroposteriorly short’ and ‘deep, elongate’ excavations. However, my observations suggest that some taxa scored as having shallow excavations appear similar to taxa that lack the depressions altogether (*Mesenosaurus*; *Mycterosaurus*, FMNH UC 692: see also Berman & Reisz 1982, fig. 8A). Other taxa fall on the continuum represented by taxa with deep depressions, including *Aerosaurus* (UCMP 40096), *Varanodon* (FMNH UR 986), *Ianthasaurus* (ROM 29941) and basal sphenacodontians.

Reisz *et al.* (2007) observed that shallow depressions were present in the cervical vertebrae of *Mesenosaurus* and *Heleosaurus* (but absent in the dorsal

vertebrae, unlike in *Mycterosaurus*). This was not confirmed in the present study, but may form the basis for a character in subsequent analyses.

Unambiguous: Varanodontinae (0->2), *Varanosaurus acutirostris* (0->1)

DELTRAN: Synapsida (1->0), Sphenacodontia (0->2), *Biarmosuchus* +++ (2->0),

Protorothyris archeri (1->0), *Ianthasaurus hardestiorum* (0->2)

ACCTRAN: Amniota (1->0), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->2),

Glaucosaurus + *Lupeosaurus* + *Edaphosaurus* spp. (2->0), Therapsida (2->0),

Captorhinus (0->1)

164. Dorsal neural spines, height: short, approximately 1.5 times centrum height or lower (0); intermediate, 2–3 times centrum height (1); very tall (2).

Modified from Reisz *et al.* (1992, characters 73, 74), Laurin (1993, character 82), Berman *et al.* (1995, character 77), Modesto (1995, character 24), Reisz *et al.* (1998, character 31), Maddin *et al.* (2006, character 52), Reisz *et al.* (2009, character 61), Mazierski & Reisz (2010, characters 26, 27), Fröbisch *et al.* (2011, character 64).

Unambiguous: Edaphosauridae (0->2), *Pantelosaurus* +++ (0->1), *Ophiacodon* spp. (0->1)

DELTRAN: *Varanops* + *Varanodon* + *Watongia* (0->1), *Secodontosaurus* + Sphenacodontinae (1->2), *Ruthiromia elcobriensis* (0->1), *Mycterosaurus longiceps* (0->1)

ACCTRAN: *Pyozia* +++ (0->1), *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (1->0), *Aerosaurus greenleeorum* + *A. wellesi* (1->0), Sphenacodontidae (1->2)

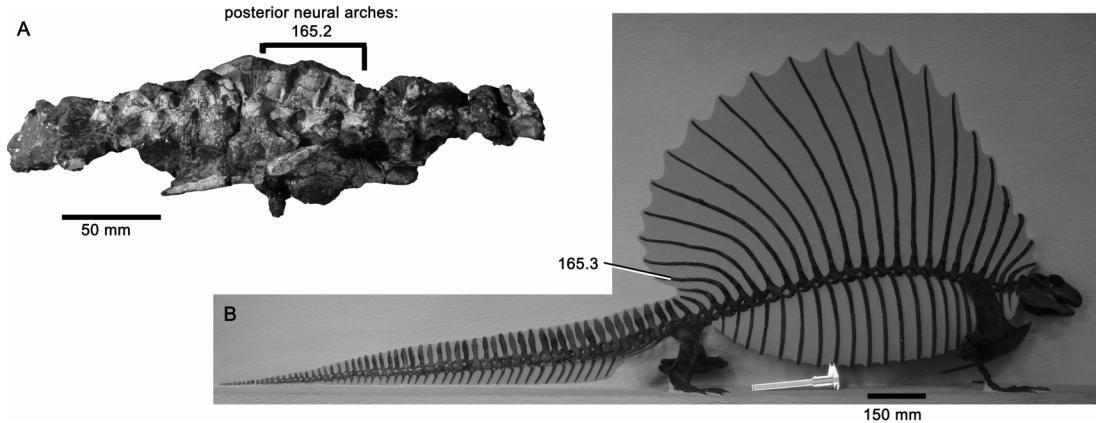


Figure A4. Dorsal and sacral neural spines of **A**, *Ruthiromia elcobriensis* (holotype, MCZ 3150) and **B**, *Edaphosaurus boanerges* (composite mount at MCZ; entire mount shown) in left lateral view showing the orientation of the posterior dorsal neural spines (character 165). Scale bars equal 50 mm (**A**) and 150 mm (**B**).

165*. 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).

New character (Figure A4). State ‘3’ taken from Modesto (1994, character 28).

In *Mycterosaurus* (FMNH UC 692) and *Archaeovenator* (Reisz & Dilkes 2003) only the posteriormost dorsal vertebra has an anterodorsally inclined neural spine. In varanodontines, several of the posterior dorsal neural spines are anterodorsally inclined (e.g. Fig. A4A; Williston 1911a, pl. 2). Edaphosaurids possess posterodorsally inclined posterior dorsal neural spines, resulting in a fan-shaped dorsal sail (Fig. A4B; Romer & Price 1940; Reisz & Berman 1986).

Unambiguous: Varanopidae (0->1), Varanodontinae (1->2), Edaphosauridae (0->3)

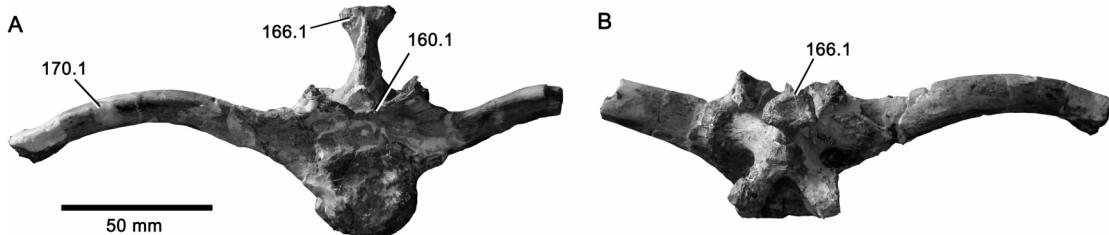


Figure A5. Dorsal vertebra of *Angelosaurus romeri* (FMNH UC 916) in **A**, anterior and **B**, dorsal views showing states of characters 160, 166 and 170. Scale bar equals 50 mm.

166*. Dorsal and sacral neural spines, dorsal end: unexpanded (0); transversely expanded forming spine table (1).

New character (Figure A5).

DELTRAN: *Angelosaurus* + *Cotylorhynchus* (0->1)

ACCTRAN: *Trichasaurus* +++ (0->1)

167*. Dorsal neural spines morphology: consistent along column (0); alternating (1).

New character (Sumida 1989a, 1990).

Unambiguous: Synapsida (1->0), *Varanosaurus acutirostris* (0->1)

168. 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).

Reisz *et al.* (1992, character 75), Berman *et al.* (1995, character 78), Modesto (1994, character 26; 1995, character 25), Mazierski & Reisz (2010, character 28), Fröbisch *et al.* (2011, character 110).

Unambiguous: Edaphosauridae (0->1)

DELTRAN: *Secodontosaurus obtusidens* (0->1), *Dimetrodon* spp. (0->1)

ACCTRAN: Sphenacodontidae (0->1), *Sphenacodon ferox* (1->0)

169. Dorsal neural spines, lateral tubercles: absent (0); present (1) (Figure A3).

Reisz *et al.* (1992, character 77), modified from Modesto (1994, character 29; 1995, character 26), Mazierski & Reisz (2010, character 29).

Lateral tubercles on the dorsal neural spines have long been recognised in many edaphosaurids (e.g. Romer & Price 1940; Reisz 1980). Their presence in *Ianthasaurus* suggests that they are primitive for the clade.

DELTRAN: *Edaphosaurus* (0->1), *Ianthasaurus hardestiorum* (0->1)

ACCTRAN: Edaphosauridae (0->1), *Lupeosaurus kayi* (1->0)

170. Dorsal ribs, curvature: curved proximally, only weakly curved distally (0); strongly arched proximally, curved throughout length enclosing expanded, ‘barrel-shaped’ trunk (1) (Figure A5).

Modesto (1994, character 32; 1995, character 34), Maddin *et al.* (2008, character 79), Mazierski & Reisz (2010, character 37).

Unambiguous: *Edaphosaurus* (0->1)

DELTRAN: *Casea broili* +++ (0->1)

ACCTRAN: Caseasauria (0->1)

171. 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)

Modified from Modesto (1994, character 33; 1995, character 35) and Mazierski & Reisz (2010, character 38) by addition of a new state to describe the condition in *Cotylorhynchus* and *Angelosaurus* (‘2’; e.g. Stovall *et al.* 1966, fig. 5).

The tuberculum is reduced in edaphosaurids and most caseids (Romer and Price 1940, p. 189; Olson 1968).

Unambiguous: *Angelosaurus* + *Cotylorhynchus* (1->2), *Edaphosaurus* (0->1)

DELTRAN: *Casea broili* +++ (0->1)

ACCTRAN: Caseasauria (0->1)

172. Sacral vertebrae, count: two or fewer (0); three or greater (1).

Reisz *et al.* (1992, character 72), Laurin *et al.* (1993, character 94), modified from Sidor & Hopson (1998, character 125), Reisz & Dilkes (2003, character 48), Maddin *et al.* (2006, character 53; 2008, character 75), Reisz *et al.* (2009, character 63).

Reisz (1980) noted an increased number of sacral vertebrae in derived representatives of the major clades of basal synapsids. He suggested that this increase co-occurred with the transition from a long, posteriorly tapering iliac blade to a broad, anteroposteriorly expanded blade (character 213) and from a dorsoventrally thick pubic symphysis to a narrow one (character 217). However, these character vary independently: *Aerosaurus wellesi* has a long posterior process of the ilium and three

sacral ribs (Langston & Reisz 1981); and all varanopids have a narrow pubic symphysis, despite the fact that most of them possess only two sacral ribs.

Unambiguous: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

DELTRAN: *Aerosaurus wellesi* (0->1)

ACCTRAN: *Ruthiromia* + *Aerosaurus* spp. (0->1)

173. 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).

Berman *et al.* (1995, character 76); reversed from Maddin *et al.* (2008, characters 76, 77); modified from Reisz & Dilkes (2003, character 48), Maddin *et al.* (2006, character 53), Reisz *et al.* (2009, character 63).

Unambiguous: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), *Archaeovenator hamiltonensis* (0->1)

174. Sacral and caudal neural spines: smooth (0); rugose with longitudinal ridges on lateral surface and tapering apex ['leaf-shaped'] (1).

Modified from Modesto (1995 characters 30, 31, 32, 33); Mazierski & Reisz (2010, characters 33, 34, 35, 36).

Many authors have recognised the unusual proximal caudal neural spines of *Edaphosaurus* (Romer & Price 1940; Reisz 1980; Modesto and Reisz 1992). Modesto (1995) and Mazierski & Reisz (2010) employed four characters describing this. In the present study, these are represented by a single character.

Unambiguous: *Edaphosaurus* (0->1)

175. Scapulocoracoid, glenoid shape: anteroposteriorly elongate and helical (0); short, faces posterolaterally (1).

Sidor & Hopson (1998, character 131) and characters describing the morphology of the humeral head (Sidor & Hopson 1998, character 144)

DELTRAN: *Biarmosuchus* +++ (0->1)

ACCTRAN: Therapsida (0->1)

176. Scapula, anteroposterior breadth of distal end: broad (0); narrow (1).

Reisz *et al.* (1992, character 80), Berman *et al.* (1995, character 80)

The distal end of the scapula is especially broad in *Cotylorhynchus bransoni* and *Lupeosaurus* (Romer & Price 1940; Olson 1968; Sumida 1988), but other derived caseids, edaphosaurids and the diadectomorph *Limnoscelis* (Williston 1911a,b) also have broad distal scapulae that are also scored as '0' here. Use of the 'broad' state to

describe only those taxa in which the breadth is especially high differs from previous uses of this character.

Unambiguous: *Angelosaurus* + *Cotylorhynchus* (1->0), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (1->0), *Limnoscelis paludis* (1->0)

177. Scapula, anteroposterior breadth of proximal end (base): broad (0); pinched/narrow (1).

Reisz *et al.* (1992, character 81), Laurin (1993, characters 97, 98), Berman *et al.* (1995, character 81), Sidor & Hopson (1998, character 132), Fröbisch *et al.* (characters 73, 74).

Reisz (1980) noted an anteroposteriorly narrow base of the scapular blade in Varanopidae and Sphenacodontidae. In the present study, the ‘narrow’ state (‘1’) was only scored as present in sphenacodontians (excluding *Haptodus*; Currie 1997; Laurin 1993), in which the anterior margin of the scapula blade is located significantly posterior to the anterior margin of the coracoid plate.

Unambiguous: *Pantelosaurus* +++ (0->1)

178. 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) (Figure A6).

Modified from Laurin (1993, character 99) and Fröbisch *et al.* (2011, character 75) by addition of a new state (‘1’) describing the condition in ophiacodontids (Fig. A6).

Unambiguous: *Ruthiromia elcobriensis* (0->1), *Limnoscelis paludis* (0->1)

DELTRAN: *Varanosaurus* +++ (0->1), *Biarmosuchus* +++ (0->2)

ACCTRAN: Ophiacodontidae (0->1), Therapsida (0->2)

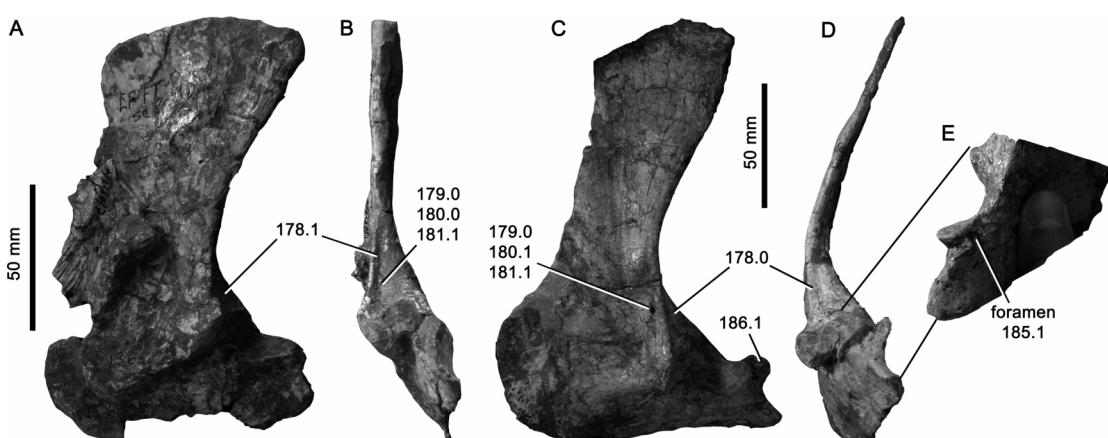


Figure A6. Left scapulocoracoids of **A–B**, *Ophiacodon uniformis* (MCZ 1366) and **C–E**, *Dimetrodon milleri* (MCZ 1365) in lateral (**A**, **C**) and posterior (**B**, **D**) views with a closeup of the glenoid region in posterodorsomedial view (**E**). States of characters 178, 179, 180, 181, 185 and 186 are indicated. Scale bars equal 50 mm.

179. Scapula, supraglenoid foramen: present (0); absent (1) (Figure A6).

Reisz *et al.* (1998, character 29), Laurin & Reisz (2004, character 54), Maddin *et al.* (2006, character 59), Maddin *et al.* (2008, character 84), Reisz *et al.* (2009, character 64); modified from Reisz *et al.* (1992, character 82), Fröbisch *et al.* (2011, character 112).

Reisz (1986) considered the presence of the supraglenoid foramen as a synapomorphy of Varanopidae + Sphenacodontidae. However, the distribution of this feature is more complex. The foramen is absent in most caseids (Olson 1968), but present in *Cotylorhynchus hancocki* (FMNH UR 581). It is absent in most varanopids, but present in *Aerosaurus* (Romer & Price 1940; Langston & Reisz 1981) and *Ruthiromia* (MCZ 3150).

Unambiguous: Varanopidae (0->1), *Ruthiromia* + *Aerosaurus* spp. (1->0), *Cotylorhynchus hancocki* (1->0)

DELTRAN: *Casea broili* +++ (0->1), *Biarmosuchus* +++ (0->1)

ACCTRAN: Caseasauria (0->1), Therapsida (0->1)

180. 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).

Modified from Reisz *et al.* (1992, character 82), Fröbisch *et al.* (2011, character 112) including the addition of a new state ('2').

It has previously been observed that the supraglenoid foramen is located anterior to the supraglenoid buttress in sphenacodontids (e.g. Romer and Price 1940; Lewis and Vaughn 1965, p. C29, C33). The new state ('2') describes the condition in *Cutleria*, *Haptodus*, *Lupeosaurus* and basal eureptilians (Romer & Price 1940; Clark & Carroll 1973; Holmes 1977; Sumida 1988; Laurin 1993; *Cutleria*, USNM 22099), in which the foramen is located on the supraglenoid buttress.

Unambiguous: *Secodontosaurus* + Sphenacodontinae (2->1), Eureptilia (0->2), *Aerosaurus wellesi* (0->1)

DELTRAN: Sphenacodontia (0->2), *Lupeosaurus kayi* (0->2)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->2), *Edaphosaurus* (2->0)

181*. Scapula, location of supraglenoid foramen: immediately dorsal to glenoid (0); 1/3–1/4 blade height dorsal to glenoid (1); inapplicable, supraglenoid foramen absent (?) (Figure A6).

New character.

DELTRAN: Edaphosauridae + Sphenacodontia (0->1), Eureptilia (0->1), *Ophiacodon* spp. (0->1)

ACCTRAN: Amniota (0->1), Varanopidae (1->0), Caseasauria (1->0)

182. Scapula, deep notch in anterior margin around midheight: absent (0); present (1).

Maddin *et al.* (2008, character 86).

Olson (1968, fig. 14) described the derived state in several caseids. A weak notch (Fig. A6C) is present in some other taxa but is scored as the primitive state.

Unambiguous: *Angelosaurus* + *Cotylorhynchus* (0->1)

183. Scapulocoracoid, notch in anterior margin on scapulocoracoid contact (scapulocoracoid notch): absent (0); present (1).

Modified from Laurin (1993, character 100), Fröbisch *et al.* (2011, character 76).

Varanodontines, *Ophiacodon* and *Haptodus* (Langston & Reisz 1981; Romer & Price 1940; Laurin 1993) have a notch in the anterior margin of the scapulocoracoid contact. In *Varanops*, this notch is located entirely within the coracoid (Campione & Reisz 2010). Laurin (1993) and Fröbisch *et al.* (2011) coded four states of the character, some of which represent autapomorphic variation in the morphology of the notch and are not coded here.

Unambiguous: Varanodontinae (0->1), *Haptodus garnettensis* (0->1)

DELTRAN: *Ophiacodon* spp. (0->1)

ACCTRAN: Ophiacodontidae (0->1)

184. Coracoids, number: two (0); one (1).

Maddin *et al.* (2008, character 85).

Unambiguous: Amniota (1->0)

185*. Coracoid, foramen on posterodorsal surface between glenoid and triceps process: absent (0); present (1).

New character (Figure A6E).

DELTRAN: *Secodontosaurus* + Sphenacodontinae (0->1)

ACCTRAN: Sphenacodontia (0->1)

186. Coracoid (posterior coracoid), triceps process: small (0); large (1) (Figure A6).

Reisz *et al.* (1992, character 83), Berman *et al.* (1995, character 82), Fröbisch *et al.* (2011, character 113), modified from Maddin *et al.* (2008, character 83).

Unambiguous: *Ruthiromia* + *Aerosaurus* spp. (0->1), Sphenacodontia (0->1)

187. Clavicle, shape of ventromedial plate: narrow (0); deep (1); intermediate (2); narrow and short, but with additional anterior process (3).

Modified from Berman *et al.* (1995, character 83), Sidor & Hopson (1998, character 139), Laurin & Reisz (2004, character 55), Maddin *et al.* (2006, character 54; 2008, character 82), Reisz *et al.* (2009, character 65).

The variable depth of the ventromedial plate of the clavicle among basal synapsids was noted by Romer & Price (1940) and Reisz (1980), who noted a narrow plate in ophiacodontids and a deep plate in Sphenacodontia [Sphenacodontidae + Varanopidae]. Reisz (1980) considered the narrow plate to be a derived feature of ophiacodontids. However, subsequent discoveries and descriptions add complexity to the distribution of character states.

The ventromedial plate of the clavicle is deep in edaphosaurids and *Dimetrodon* (state '1'; Romer and Price, 1940, p. 115; Sumida, 1989b, p. 1348). Most other basal synapsids have a narrow ventromedial plate (e.g. Romer & Price 1940, fig. 19; Laurin 1993, fig. 18). *Varanops* (MCZ 1026; Carroll 1976) and caseids are intermediate in the degree of expansion (Olsen 1968, fig 15; Sigogneau-Russell & Russell 1974). My observations do not confirm those of Maddin *et al.* (2008), who scored *Cotylorhynchus* and *Angelosaurus* as having narrow ventromedial plates compared to other caseids including '*Casea*' *rutena*. Basal eureptilians possess a distinctive anterior process (state '3'; Clark & Carroll 1973; Holmes 1977).

Unambiguous: *Varanops brevirostris* (0->2)

DELTRAN: Ophiacodontidae + Varanopidae (2->0), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (2->1), Sphenacodontia (2->0), Eureptilia (2->3), *Dimetrodon* spp. (0->1)

ACCTRAN: Amniota (2->0), Caseasauria (0->2), Edaphosauridae (0->1), *Secodontosaurus* + Sphenacodontinae (0->1), Eureptilia (0->3)

188*. Clavicle, orientation of long axis of ventromedial plate relative to shaft: highly obtuse angle (0); almost perpendicular (1).

New character

Unambiguous: Eureptilia (0->1), *Varanops brevirostris* (0->1)

DELTRAN: Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

189. Interclavicle, angle of head: low angle, interclavicle weakly curved in lateral view (0); head sharply upturned (1).

Maddin *et al.* (2008, character 81).

DELTRAN: *Angelosaurus* + *Cotylorhynchus* (0->1)

ACCTRAN: Caseasauria (0->1)

190. Interclavicle, shape of anterior end: triangular, pointed anteriorly with 'diamond-shaped' appearance (0); truncated anteriorly (1); trapezoidal with narrow, straight anterior margin (2).

Modified from Berman *et al.* (1995, character 84).

State ‘1’ describes the condition in caseids (Olson 1968). State ‘2’ in varanopids (e.g. Reisz & Dilkes 2003). See Romer & Price (1940, fig. 21) for comparative images.

Unambiguous: Varanopidae (0->2)

DELTRAN: ‘*Casea' rutena* +++ (0->1)

ACCTRAN: Caseasauria (0->1)

191. Interclavicle, shape of posterior margin of head: distinctly offset from shaft by posterolateral emargination (0); grades gradually into shaft (1).

Modified from Berman *et al.* (1995, character 84).

DELTRAN: ‘*Casea' rutena* +++ (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1), *Dimetrodon* spp. (0->1)

ACCTRAN: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Sphenacodontia (1->0), Sphenacodontidae (0->1)

192. Humerus, ridge connecting deltopectoral crest to head: double, paired ridge enclosing proximolateral fossa, deltopectoral crest anteroposteriorly expanded and ‘tuberous’ (0); single, fossa absent (1) (Figure A7).

Brinkman & Eberth (1983, character 1), Reisz *et al.* (1992, character 85), Berman *et al.* (1995, character 88).

Brinkman & Eberth (1983) suggested that the presence of two ridges between the head and deltopectoral crest, defining an anteroventral fossa, united caseids and varanopids in a clade. However, this is likely plesiomorphic as it is present in outgroups. Reisz (1986) described an intermediate condition in which a ridge was present but was low, and did not define a fossa in captorhinids, *Oedaleops*, *Varanosaurus* and *Varanops*. My observations suggest that captorhinids possess the derived state. Also, most basal synapsids do have a very weak ridge in this region, this ridge is more prominent in outgroups, caseids and varanopids, resulting in the derived state. Thus, the ‘intermediate’ condition of Reisz (1986) probably corresponds to state ‘0’ employed herein, which is widely distributed among basal synapsids. The state ‘1’ is only scored as present where the ridge is conspicuous and the fossa pronounced.

Unambiguous: Ophiacodontidae (0->1)

DELTRAN: Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

193*. Humerus, ventral surface of proximal end: extends proximally forming a low, anteroposteriorly oriented crest posteroventral to head (0); extends far proximally, forming a prominent crest (1).

New character (Figure A7).

This character was scored as ‘?’ in cases of extreme crushing, which is common among caseids and obscures the original morphology.

Unambiguous: Ophiacodontidae + Varanopidae (1->0), *Aerosaurus greenleeorum* + *A. wellesi* (0->1), *Casea broili* (1->0)

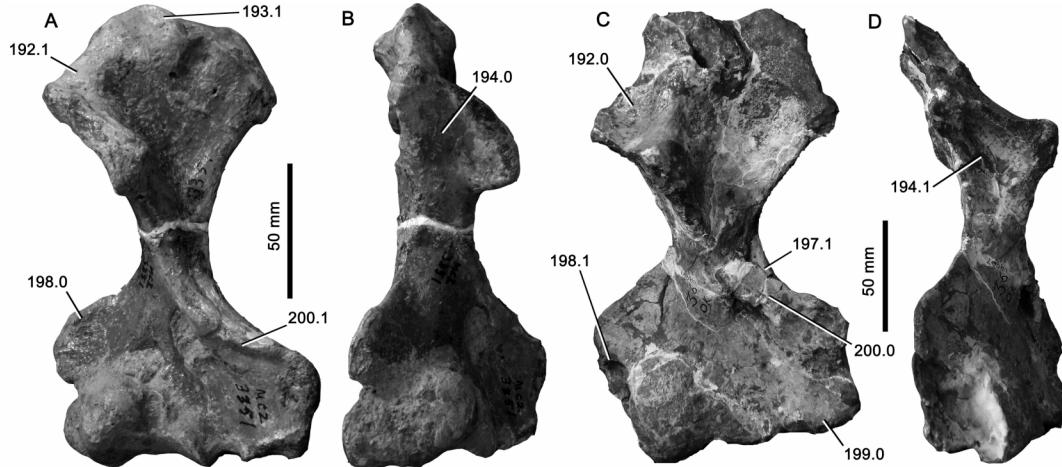


Figure A7. Right humeri of **A–B**, *Dimetrodon* cf. *grandis* (MCZ 1969) and **C–D**, *Angelosaurus romeri* (FMNH UR 907) in ventral (**A, C**) and anterior (**B, D**) views showing states of characters 192, 193, 194, 197, 198, 199 and 200. Scale bars equal 50 mm.

194*. Humerus, anterior surface of deltopectoral crest: weakly concave (0); strongly concave, bounded dorsally by a prominent, proximodistally elongate ridge (1).

New character (Figure A7).

Unambiguous: *Ruthiromia* + *Aerosaurus* spp. (0->1)

DELTRAN: *Angelosaurus* + *Cotylorhynchus* (0->1)

ACCTRAN: ‘*Casea*’ *rutena* +++ (0->1)

195*. Humerus, position of latissimus dorsi attachment (Romer and Price 1940, fig. 29): proximal, adjacent to internal epicondyle (0); distal (1).

New character.

Unambiguous: *Ruthiromia* + *Aerosaurus* spp. (0->1)

DELTRAN: *Angelosaurus* + *Cotylorhynchus* (0->1)

ACCTRAN: ‘*Casea*’ *rutena* +++ (0->1)

196*. Humerus, morphology of latissimus dorsi attachment: step-like transverse ridge or mound (0); prominent, posteriorly-directed tubercle (1).

New character.

Unambiguous: *Ruthiromia* + *Aerosaurus* spp. (0->1)

DELTRAN: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1)

ACCTRAN: Edaphosauridae (0->1)

197*. 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).

New character (Figure A7)

Unambiguous: Synapsida (1->0), *Archaeothyris florensis* (0->1)

DELTRAN: *Ennatosaurus* +++ (0->1)

ACCTRAN: *Trichasaurus* +++ (0->1)

198. Humerus, ectepicondylar (radial epicondylar) **foramen**: absent, ectepicondylar groove not enclosed and supinator process proximodistally short (0); present (1); long supinator process, but epicondylar foramen not enclosed (2); supinator process very low or absent (3) (Figure A7).

Modified from Laurin (1993, character 103), Berman *et al.* (1995, character 87), Sidor & Hopson (1998, characters 142, 143), Maddin *et al.* (2008, character 87), Fröbisch *et al.* (2011, character 79) by addition of state ‘2’ describing the condition in basal caseids (Olsen 1968) and state ‘3’ describing the condition in captorhinomorphs (Clark & Carroll 1973; Holmes 1977).

An ectepicondylar foramen (state ‘1’) is present in most edaphosaurids (Romer & Price 1940; Reisz 1980), the varanopid *Heleosaurus* (Botha-Brink & Modesto 2009), and some caseids (Olson 1968; Reisz 1980). Stovall *et al.* (1966) suggested that the formation of the ectepicondylar foramen proceeded from state ‘2’ to state ‘1’ through ontogeny, but this was based on comparison between small basal caseids (possessing state ‘2’) and larger, derived caseids (with state ‘1’) rather than an ontogenetic series of a single taxon. Thus, the distinction between these states may reflect phylogeny rather than ontogeny.

Unambiguous: *Angelosaurus* + *Cotylorhynchus* (2->1), *Eureptilia* (0->3)

DELTRAN: *Casea broili* +++ (0->2), *Titanophoneus potens* (0->1), *Heleosaurus scholtzi* (0->1), *Edaphosaurus boanerges* (0->1), *Biarmosuchus tener* (0->3)

ACCTRAN: *Mesenosaurus* + *Heleosaurus* + BP/1/5678 (0->1), *Caseasauria* (0->2), *Edaphosaurus* (0->1), *Therapsida* (0->1), *Biarmosuchus tener* (1->3)

199. Humerus, entepicondyle (ulnar epicondyle), **transverse width**: moderate makes up just less than half of transverse width of distal expansion (0); reduced (1); enlarged, makes up more than 2/3 of the distal transverse width (2) (Figure A7).

Berman *et al.* (1995, character 86).

Unambiguous: Mycterosaurinae (0->1)

DELTRAN: *Ophiacodon* spp. (0->2)

ACCTRAN: *Varanosaurus* +++ (0->2)

200*. Humerus, ventral surface (faces anteroventrally) **of entepicondyle**: flat or weakly convex (0); low, anteroproximally directed ridge on posterior margin (1).

New character (Figure A7).

DELTRAN: *Dimetrodon* + *Sphenacodon* (0->1)

ACCTRAN: Sphenacodontinae (0->1)

201. Manus, width:length ratio of radiale: subequal or < 1.0 (0); > 1.0 (1).

Laurin & Reisz (2004, character 56), Maddin *et al.* (2006, character 55), Reisz *et al.* (2009, character 67).

Unambiguous: ‘*Casea*’ *rutena* (0->1)

DELTRAN: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (1->0),

Ophiacodon spp. (1->0)

ACCTRAN: Synapsida (1->0), Varanopidae (0->1)

202*. Manus, preaxial (lateral) centrale overlaps proximal surface of third distal carpal: no (0); yes (1).

New character.

Lewis and Vaughn (1965, p. C33) observed that the preaxial centrale is medially expanded and articulates with the base of the third distal carpal in *Cutleria* and sphenacodontids (see comparative figure in Romer & Price 1940, fig. 40).

Unambiguous: Sphenacodontidae (0->1)

203. Manus, intermedium size: larger than medial centrale (0); smaller than medial centrale (1).

Laurin (1993, character 104), Sidor & Hopson (1998, character 150), Fröbisch *et al.* (2011, character 80).

Unambiguous: *Tseajaia campi* (0->1), *Heleosaurus scholtzi* (0->1)

DELTRAN: *Biarmosuchus* +++ (0->1)

ACCTRAN: Therapsida (0->1)

204*. Manus, ulnare proportions: long (0); short, width >0.6–0.7 times length (1).

New character

Stovall *et al.* (1966, p. 22) observed that the ulnare is relatively narrow in caseids. This is also the case in outgroups and varanopids.

DELTRAN: Sphenacodontia (1->0), *Ophiacodon* spp. (1->0)

ACCTRAN: Ophiacodontidae (1->0), *Ianthodon* + Edaphosauridae + Sphenacodontia (1->0)

205. Manus length, fourth metacarpal:radius length ratio: <0.25 (0); 0.30–0.45 (1); >0.50 (2).

Maddin *et al.* (2008, character 93), modified from Maddin *et al.* (2006, character 57).

DELTRAN: Varanodontinae (1->2), ‘*Casea’ rutena* +++ (1->0), *Titanophoneus potens* (1->0), *Mesenosaurus romeri* (1->2)

ACCTRAN: Varanopidae (1->2), *Trichasaurus* +++ (1->0), Therapsida (1->0), *Heleosaurus scholtzi* (2->1)

206. Manus, metapodial shape: long and slender, two–three times longer than maximal width (0); short and fat with small diaphysis (1).

Maddin *et al.* (2008, character 94).

Olson (1968), Reisz (1980) observed the short, fat epipodials of caseids.

Unambiguous: Amniota (1->0), ‘*Casea’ rutena* +++ (0->1)

207. Manus, McV:McIV length ratio: >0.65 (0); <0.65 (1).

Laurin & Reisz (2004, character 57), Maddin *et al.* (2006, character 56), Reisz *et al.* (2009, character 68).

Unambiguous: Ophiacodontidae + Varanopidae (0->1), ‘*Casea’ rutena* (0->1)

208. Manus, digital formula: X3YZ3 (0); X2YZ2 (1).

Modified from Maddin *et al.* (2008, characters 89, 92).

Olson (1968), Stovall *et al.* (1966, pp. 23–24), and Reisz (1980) noted reduction of phalangeal counts in caseids. This character codes reduction of the digits II and V, which occurs simultaneously, early in caseid evolution. Maddin *et al.* (2008) coded separate characters for these two digits. In the present analysis, characters 208, 209 and 210 were sometimes scored by inference based on the pes when the manus was not preserved. Thus, they are modified from Laurin (1993, character 121), Maddin *et al.* (2008, characters 103, 104, 105, 106) and Fröbisch *et al.* (2011, character 94).

Unambiguous: *Ennatosaurus* +++ (0->1)

209. Manus, phalanges in digit III: four (0); three (1).

Maddin *et al.* (2008, character 90).

Reduction of digit III occurs in caseids (Olson 1968; Stovall *et al.* 1966; Reisz 1980) and therapsids (Hopson 1995).

Unambiguous: *Ennatosaurus* +++ (0->1)

DELTRAN: *Titanophoneus potens* (0->1)

ACCTRAN: *Titanophoneus* + *Biseridens* (0->1)

210. Manus, phalanges in digit IV: five (0); four or fewer (1).

Maddin *et al.* (2008, character 91); modified from Sidor & Hopson (1998, character 153).

Reduction of digit IV occurs in caseids (Olson 1968; Stovall *et al.* 1966; Reisz 1980) and therapsids (Hopson 1995).

DELTRAN: ‘*Casea*’ *rutena* +++ (0->1), *Titanophoneus potens* (0->1)

ACCTRAN: Caseasauria (0->1), Therapsida (0->1)

211*. Manus, phalanges, distal articular surface orientation: distal (0); ventrodistal (1).

New character (Reisz 2005)

DELTRAN: Caseidae (0->1)

ACCTRAN: Caseasauria (0->1)

212. Manus, ungual phalanges, height:width ratio: low, ratio <1.1 and blood vessel grooves may be visible on the dorsolateral surfaces of the phalanx (0); high, ratio >1.5, strongly recurved and blood vessel grooves are located on the lateral surfaces of the phalanx (1).

Modified from Maddin *et al.* (2006, character 58), Maddin *et al.* (2008, character 95), Reisz *et al.* (2009, character 69).

State ‘1’ corresponds to the broad, flat morphology described in detail by Maddin and Reisz (2007).

DELTRAN: Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

213*. Manus, ungual phalanges, flexor tubercle: single bulbous eminence (0); paired, medial and lateral eminences (1); absent (2).

New character (Figure A8; Maddin & Reisz 2007)

DELTRAN: Synapsida (2->0), *Cotylorhynchus* (0->1)

ACCTRAN: Amniota (2->0), *Trichasaurus* +++ (0->1)

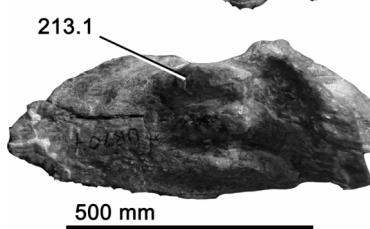


Figure A8. Manual ungual phalanx of *Cotylorhynchus hancocki* (FMNH UR 704) in lateral (top) and ventral (bottom) views showing state 1 of character 213. Scale bar equals 500 mm.

214. Pelvic girdle, acetabulum, outline: suboval and shallow, lacking supracetabular buttress (0); subcircular and deep, supracetabular buttress present (1).

Modified from Laurin (1993, characters 108, 109, 110), Sidor & Hopson (1998, characters 159, 160), Fröbisch *et al.* (2011, characters 83, 84, 85).

DELTRAN: *Biarmosuchus* + + + (0->1)

ACCTRAN: Therapsida (0->1)

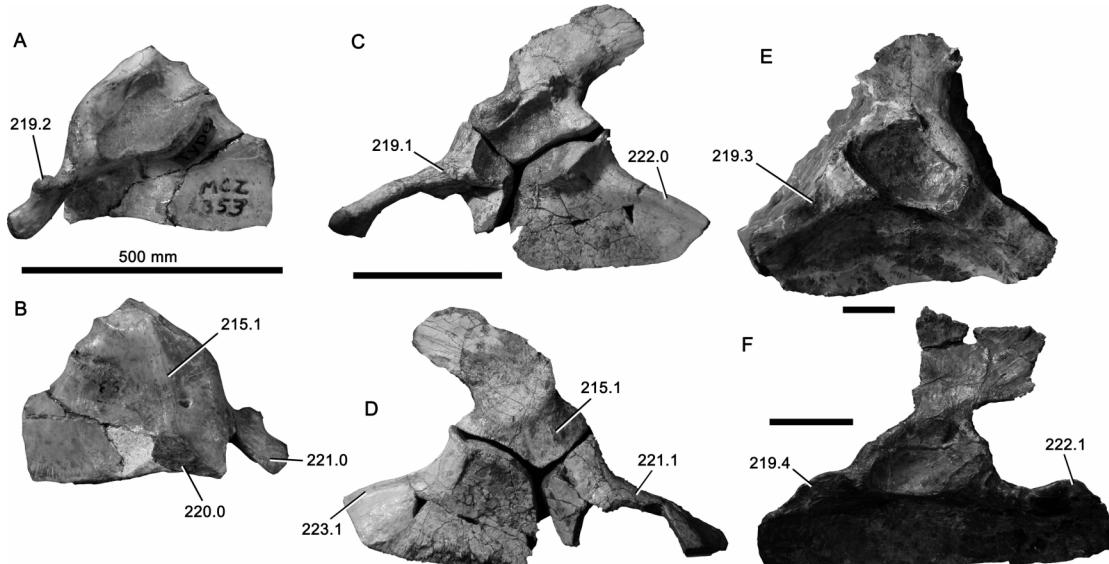


Figure A9. Left ilia of A–B, *Varanosaurus milleri* (holotype MCZ 1353), C–D, *Varanops brevirostris* (TMM 43628-1), E, *Angelosaurus romeri* (FMNH UR 980), F, *Edaphosaurus boanerges* (FMNH UR 733) in lateral (A, C, E–F) and medial (B, D) views. States of characters 215, 219, 200, 221, 222 and 223 are indicated. Scale bars equal 500 mm.

215*. Ilium, medial surface: weakly concave or flat (0); anteroventrally oriented ridge contacts pubic articulation (1).

New character (Figure A9).

The ridge is very prominent in ophicaodontids and outgroups, a weaker ridge is present in varanopids.

Unambiguous: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (1->0)

216. 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).

Modified from Reisz *et al.* (1992, characters 88, 89), Laurin (1993, character 107), Modesto (1994, character 34), Berman *et al.* (1995, character 90), Maddin *et al.* (2008, character 97), Fröbisch *et al.* (2011, character 82).

Caseasaurians, edaphosaurids and sphenacodontians have a tall, anterodorsally expanded, plate-like iliac blade (Romer and Price 1940; Stovall *et al.* 1966, p. 15). Ophiacodontids and varanopids have a plesiomorphic, long, low posterior process of the ilium (e.g. Reisz 1980; Campione & Reisz 2010). More detailed complexities of the morphology of the iliac blade in caseids (Olson 1968; Reisz 1980; Maddin *et al.* 2008) were not coded in the present analysis because many caseid ilia are poorly preserved.

Unambiguous: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

217. Ilium, fossa on dorsal surface [dorsal groove], or external shelf: dorsal groove present (0); external shelf present (1); both absent, ilium plate-like (2).

Modified from Reisz *et al.* (1992, character 87), Laurin (1993, character 106), Berman *et al.* (1995, character 89), Maddin *et al.* (2008, character 98), Fröbisch *et al.* (2011, character 81).

The primitive state ('0') is coded for taxa with a deep, cup-like 'dorsal groove' such as diadectomorphs and ophiacodontids (Williston 1911a; Romer & Price 1940). State '1' is scored for taxa with a weaker groove facing dorsolaterally, such as *Captorhinus* and most varanopids (Langston & Reisz 1981; Holmes 2003).

DELTRAN: Mycterosaurinae + Varanodontinae (0->1), Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->2), *Varanops brevirostris* (1->2), *Captorhinus* (0->1)

ACCTRAN: Amniota (0->1), *Varanops* + *Varanodon* + *Watongia* (1->2), Ophiacodontidae (1->0), Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (1->2)

218. Pubis, length relative to acetabulum: >1.5 times (0); 1.0–1.5 times (1).

Modified from Sidor & Hopson (1998, character 161)

DELTRAN: Synapsida (1->0), *Biarmosuchus* +++ (0->1), *Protorothyris archeri* (1->0)

ACCTRAN: Amniota (1->0), Therapsida (0->1), *Captorhinus* (0->1)

219. Pubis, pubic tubercle anteroventral to acetabulum: absent (0); present, projects laterally (1); present, projects dorsally (2); broad, concave region on lateral surface (3; new state; derived caseids); highly striated region bounded by a longitudinal crest dorsally (4) (Figure A9).

Modified from Reisz *et al.* (1992, character 90), Berman *et al.* (1995, character 91), Maddin *et al.* (2008, character 100). New states describe the condition in some ophiacodontids and varanopids such as *Varanosaurus* (Broili 1904-1905) and *Mycterosaurus* (FMNH UC 169) (state '2'); and the condition in some caseids (state '3') and edaphosaurids (state '4').

Reisz (1980) considered the pubic tubercle as primitively present in synapsids but absent in edaphosaurids and sphenacodontids. The present study revealed a more complex pattern.

Unambiguous: Ophiacodontidae (1->2)

DELTRAN: *Angelosaurus* + *Cotylorhynchus* (1->3), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (1->4), *Ophiacodon* spp. (2->0), *Mycterosaurus longiceps* (1->2), *Casea broili* (1->2), *Captorhinus* (1->0)

ACCTRAN: Mycterosaurinae (1->2), *Ophiacodon* + *Stereophallodon* (2->0), Caseasauria (1->2), *Trichasaurus* +++ (2->3), Edaphosauridae (1->4), Eureptilia (1->0)

220. Pubis, midline symphysial contact: enlarged, dorsoventrally broad (0); subequal to height of ischial midline symphysis, restricted to peripheral margin of medial surface (1) (Figure A9).

Reversed from Maddin *et al.* (2008, character 99).

Reisz (1980) noted the thickened pubic symphysis shared by ophiacodontids and other basal amniotes.

DELTRAN: Mycterosaurinae + Varanodontinae (0->1), Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

ACCTRAN: Synapsida (0->1), Ophiacodontidae (1->0)

221*. Pubis, ventral surface of pubic apron: flat or convex, pubes extend ventromedially (0); strongly concave, pubes extend approximately medially (1).

New character (Figure A9).

In varanopids (e.g. Campione & Reisz 2010, fig. 13) and sphenacodontians (e.g. Romer & Price 1940; Hook & Hotton 1991), including therapsids (Orlov 1958, fig. 50) the pubic apron is almost horizontal. Botha-Brink & Modesto (2009) stated that the pubic apron of one specimen of *Heleosaurus* had been rotated so that it was horizontal. However, this may be the original orientation based on the presence of the same orientation in other varanopids.

Unambiguous: Varanopidae (0->1)

DELTRAN: *Pantelosaurus* +++ (0->1)

ACCTRAN: Sphenacodontia (0->1)

222. Ischium: slender, tapering posteriorly (0); expanded posterodorsally (1) (Figure A9).

Reisz *et al.* (1992, character 91), Fröbisch *et al.* (2011, character 116).

DELTRAN: Edaphosauridae + Sphenacodontia (0->1), *Biarmosuchus* +++ (1->0)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Therapsida (1->0)

223*. Ischium, dorsal margin of medial surface: smooth (0); longitudinal crest (1).

New character (Figure A9).

See Figure A9 and Campione & Reisz (2010, fig. 13B)

DELTRAN: Varanodontinae (0->1)

ACCTRAN: Varanopidae (0->1)

224. Femur, proportions: short and broad, maximum length less than three times distal width (0); long and slender, maximum length more than three times distal width (1).

Reisz *et al.* (1998, character 21), Maddin *et al.* (2006, character 60), Reisz *et al.* (2009, character 66); modified from characters describing the proportional limb length (Reisz *et al.* 1992, character 84).

Several previous authors have noted the long, slender limbs of sphenacodontids and varanopids (e.g. Reisz 1980). Campione & Reisz (2010) removed this character in their modified version of the matrix of Maddin *et al.* (2006), stating that the femoral width and length were strongly correlated, and that any differences were likely due to allometry. This is unlikely however, both small- and large-bodied taxa show the primitive (e.g. *Casea*, *Cotylorhynchus*, *Edaphosaurus*) and derived (e.g. *Mycterosaurus*, *Dimetrodon*) states of this character.

DELTRAN: Mycterosaurinae (0->1), Sphenacodontidae + Therapsida (0->1),

Archaeovenator hamiltonensis (0->1)

ACCTRAN: Varanopidae (0->1), Varanodontinae (1->0), *Pantelosaurus* +++ (0->1)

225. Femur, orientation of head: terminal and anteroposteriorly elongate (0); inflected medially and subshpherical (1).

Modified from Laurin (1993, characters 112, 114), Sidor & Hopson (1998, characters 167, 168), Fröbisch *et al.* (2011, characters 87, 89).

DELTRAN: *Biarmosuchus* +++ (0->1)

ACCTRAN: Therapsida (0->1)

226. Femur, greater trochanter: absent (0); present (1).

Sidor & Hopson (1998, character 170)

DELTRAN: *Biarmosuchus* +++ (0->1)

ACCTRAN: Therapsida (0->1)

227*. Femur, mound-like eminence on dorsal surface of proximal end: extensive, prominent and longitudinally elongate (0); small (1).

New character.

Unambiguous: Varanodontinae (0->1), Sphenacodontia (0->1)

DELTRAN: *Varanosaurus* + + + (0->1), *Captorhinus* (0->1)

ACCTRAN: Ophiacodontidae (0->1), Eureptilia (0->1)

228. Femur, ventral ridge system (internal and fourth trochanters): prominent (0); low and feebly developed (1).

Reisz *et al.* (1992, character 93), Laurin (1993, character 116), Berman *et al.* (1995, character 93), Fröbisch *et al.* (2011, character 91).

Reisz (1980) noted that the internal and fourth trochanters ('adductor crest') of the femur were low and rugose, rather than forming a prominent crest in some varanopids and sphenacodontians.

DELTRAN: Sphenacodontidae + Therapsida (0->1), *Varanops brevirostris* (0->1)

ACCTRAN: Varanops + *Varanodon* + *Watongia* (0->1), Sphenacodontia (0->1)

229. Femur, intertrochanteric fossa: prominent (0); reduced or absent (1).

Modified from Reisz *et al.* (1992, character 92), Laurin (1993, character 111), Sidor & Hopson (1998, character 166), Fröbisch *et al.* (2011, character 86).

DELTRAN: *Biarmosuchus* + + + (0->1)

ACCTRAN: Therapsida (0->1)

230. Femur, posterior longitudinal ridge located proximally on ventral surface: absent, internal fossa not enclosed posteriorly (0); present, enclosing posterior margin of internal fossa (1).

Maddin *et al.* (2008, character 102).

Unambiguous: *Dimetrodon* spp. (1->0)

DELTRAN: *Casea broili* + + + (1->0), *Titanophoneus potens* (1->0)

ACCTRAN: Caseasauria (1->0), Therapsida (1->0)

231*. Femur, prominent longitudinal ridge extending posterodistally from distal end of internal fossa: absent or low (0); present as a prominent rugose crest (1); present as a prominent angular ridge forming the posteroventral surface of femoral shaft (2); present but low and does not extend far distally, instead forming a distinct fourth trochanter (3).

New character (Figure A10).

Unambiguous: *Ophiacodon* spp. (0->2)

DELTRAN: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1),

Sphenacodontidae + Therapsida (0->3), *Varanops brevirostris* (0->3), *Ruthiromia elcobriensis* (0->1), *Captorhinus* (0->3)

ACCTRAN: Varanodontinae (0->1), *Varanops* + *Varanodon* + *Watongia* (1->3), Edaphosauridae (0->1), *Pantelosaurus* + + + (0->3), Eureptilia (0->3)

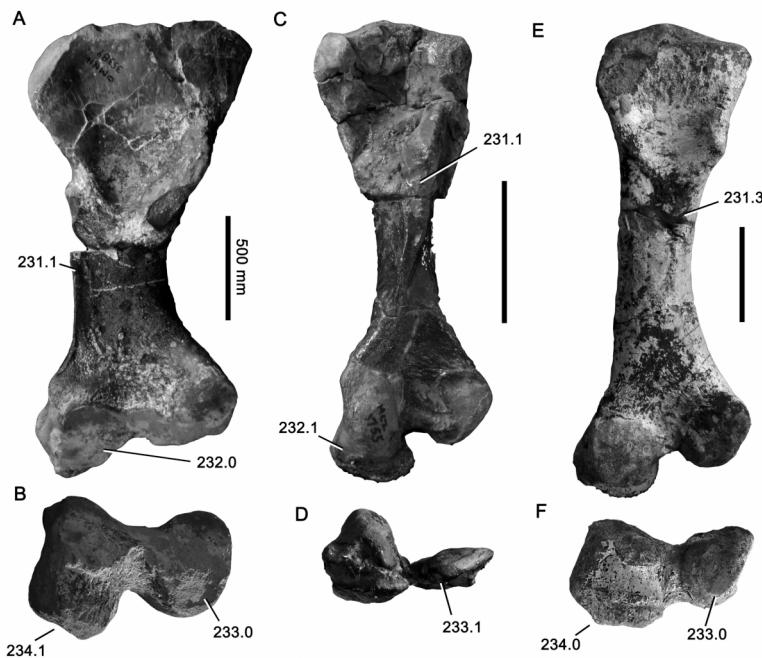


Figure A10. Femora of **A–B**, *Ophiacodon* ?sp. (OMNH 35389; left femur), **C–D**, *Edaphosaurus boanerges* (MCZ 1755), **E–F**, *Dimetrodon* cf. *grandis* (MCZ 1969; right femur, reversed) in ventral (**A**, **C**, **E**) and distal (**B**, **D**, **F**) views. States of characters 231, 232, 233 [although the anterior condyle is crushed in **D** it is representative of an originally dorsoventrally low morphology] and 234 are indicated. Scale bars equal 500 mm.

232. Femur, condyles: prominent and well-separated, posterior condyle extends slightly further distally than anterior condyle (0); posterior condyle projects far distally (1); condyles both low and indistinctly separated (2) (Figure A10).

Modified from Laurin (1993, characters 113, 115), Sidor & Hopson (1998, character 169), Fröbisch *et al.* (2011, characters 88, 90) by addition of state ‘1’ to describe the condition in edaphosaurids (Fig. A10C).

Unambiguous: *Cotylorhynchus romeri* (0->1)

DELTRAN: *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1),

Biarmosuchus +++ (0->2)

ACCTRAN: Edaphosauridae (0->1), Therapsida (0->2)

233*. Femur, anterior condyle: dorsoventrally thick (0); dorsoventrally compressed (1).

New character (Figure A10).

DELTRAN: *Casea broili* +++ (0->1), *Glaucosaurus* + *Lupeosaurus* + *Edaphosaurus* spp. (0->1)

ACCTRAN: Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Sphenacodontia (1->0)

234*. Femur, posterior condyle, dorsal surface: convex (0); transversely concave, bearing longitudinal trough (1).

New character (Figure A10).

DELTRAN: *Varanosaurus acutirostris* (0->1), *Ophiacodon* spp. (0->1), *Mycterosaurus longiceps* (0->1)

ACCTRAN: Ophiacodontidae + Varanopidae (0->1), Varanodontinae (1->0),

Stereophallodon ciscoensis (1->0)

235*. Tibia, cnemial crest: low (0); prominent and distinct (1).

New character.

DELTRAN: Edaphosauridae + Sphenacodontia (0->1), *Captorhinus* (0->1)

ACCTRAN: *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Eurestilia (0->1)

236. Astragalus: absent (0); present (1).

The astragalus is an amniote synapomorphy (e.g. O'Keefe 2006).

Unambiguous: Amniota (0->1)

237. Astragalus, orientation of tibial articular surface: mediadistal (0); anterodorsal (1).

Laurin (1993, character 117), Fröbisch *et al.* (2011, character 92).

DELTRAN: *Titanophoneus potens* (0->1)

ACCTRAN: Therapsida (0->1)

238. Astragalus, proximal neck region: short (0); long (1).

Reisz *et al.* (1992, character 95), Fröbisch *et al.* (2011, character 118).

Unambiguous: *Stereophallodon ciscoensis* (0->1), *Ruthiromia elcobriensis* (0->1), *Archaeovenator hamiltonensis* (0->1)

DELTRAN: *Cotylorhynchus* (0->1), Edaphosauridae + Sphenacodontia (0->1), *Titanophoneus potens* (1->0)

ACCTRAN: *Angelosaurus* + *Cotylorhynchus* (0->1), *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1), Therapsida (1->0)

239. Calcaneum (fibulare), proportions: length approximately equal to width (0); length conspicuously greater than width (1).

Reisz *et al.* (1992, character 96), Berman *et al.* (1995, character 94), Fröbisch *et al.* (2011, character 119).

Unambiguous: *Ruthiromia* + *Aerosaurus* spp. (0->1), Caseasauria + *Ianthodon* + Edaphosauridae + Sphenacodontia (0->1)

DELTRAN: *Titanophoneus potens* (1->0)

ACCTRAN: Therapsida (1->0)

Excluded characters

X1. Skull, contour of temporal region: smooth curve between skull table and lateral surface of skull (0); sharp angle between skull table and lateral surface (1).

Maddin *et al.* (2006, character 22; 2008, character 22), Reisz *et al.* (2009, character 32)

During the present study it was difficult to find an unambiguous criterion for assessing the distinction between states of this character.

X2. Premaxilla, length: short (0); intermediate [robust] (1); long and slender (2).

Reisz *et al.* (1992, character 5), Laurin (1993, character 2), Berman *et al.* (1995, character 6)

The first two states of this character are not independent of the premaxillary tooth count (character 17) or character 16, describing the long subnarial process of the premaxilla of eothyridids. The ‘robust’ state (‘2’) probably codes the possible presence of deep tooth roots in the sphenacodontian premaxilla (Laurin 199, character 66; Fröbisch *et al.* 2011, character 52). However, the distinction between the condition of the premaxilla in sphenacodontians and other basal synapsids was not confirmed in the present study.

X3. Premaxilla, terminus of ascending (supranarial) process: single, tapering prong (0); bifurcates, resulting in paired prongs (1).

Berman *et al.* (1995, character 5)

The derived state is an autapomorphy of *Varanosaurus* and is thus parsimony uninformative.

X4. Premaxilla, palatal (vomerine) process; absent (0); present (1).

Reisz *et al.* (1992, character 4), Laurin (1993, character 3), Sidor & Hopson (1998, character 3), Fröbisch *et al.* (2011, character 2)

Previous authors scored the palatal process as absent in some or all sphenacodontids. However, the condition is difficult to assess in many taxa and this distribution was not confirmed during the present study. Although *Haptodus* possesses an especially long palatal/vomerine ramus of the premaxilla that distinguishes it from sphenacodontids (Laurin 1993). Other basal synapsids, including therapsids, show a continuum of variation (e.g. Eberth 1985; Modesto 1995; Reisz & Berman 2001).

X5. Premaxillary tooth size: decreasing posteriorly (0); subequal size (1).

Laurin (1993, character 67), Fröbisch *et al.* (2011, character 53)

This character is difficult to score as some basal synapsids have very few premaxillary teeth, and observed morphologies form a continuum.

X6. Maxilla, ascending process, morphology: smoothly curving posterior margin (0); angular emargination in posterior margin so apex of process is located anteriorly (1).

Maddin *et al.* (2008, character 9)

This character was difficult to score because of the irregular form of the ascending processes in most of the taxa scored for the derived state by Maddin *et al.* (2008).

X7. Nasal, premaxillary process: broad (0); narrow (1).

Berman *et al.* (1995, character 10)

This character is not independent of the proportional snout width (character 3) and length (character 2)

X8. Jugal-squamosal suture orientation: posteroventral (0); indented (1); anteroventral (2); jugal indented (3).

Laurin (1993, character 35); Fröbisch *et al.* (2011, character 28)

There is a clear distinction between the inclined jugal-squamosal suture of basal synapsids, and the indented condition in therapsids. *Cutleria* posseses an apomorphic state ('3'; Laurin 1994). This character could be included in future analyses, but was excluded from the present one, which included only a subset of characters for resolving therapsid monophyly.

X9. Squamosal, posterodorsal process: absent (0); present (1).

Maddin *et al.* (2006, character 27), Reisz *et al.* (2009, character 40)

Previous analyses scored the absence of the process in ophiacodontids and varanopids. However, the description is unclear and I was not able to identify the distinction between character states.

X10. Squamosal external acoustic meatus: absent (0); present (1).

Laurin (1993, character 35), Fröbisch *et al.* (2011, character 29).

This character could be included in future analyses but was excluded from the present one, which included only a subset of characters for resolving therapsid monophyly.

X11. Parietal: width/length ratio lower than 0.8 (0); width/length ratio higher than 0.8 (1).

Laurin (1993, character 19); Fröbisch *et al.* (2011, character 16)

This character is not independent of character 56, which describes the length of the frontal relative to that of the parietal.

X12. Parietal, lateral edge: concave or straight (0); convex (1)

Reisz (1992, character 16).

The derived state of this character results from (and is thus not independent of) extreme lateral expansion and anteroposterior shortening of the parietal in sphenacodontids (see character 56).

X13. Parietal, anterior extension between orbits: absent (0); present (1).

Reisz *et al.* (1998, character 16), Maddin *et al.* (2006, character 19), Reisz *et al.* (2009, character 34)

The derived state results from (and is thus not independent of) the combination of an inclined occiput (character 90) and prominent posterolateral processes of the frontals (character 61) in some varanopids.

X14. Parietal, supratemporal notch: shallow (0); deep (1).

Laurin (1993, character 18), Fröbisch *et al.* (2011, character 15)

This possible sphenacodontian synapomorphy was difficult to score based on data collected during the present study.

X15. Palatine, width: broad (0); narrow (1; ophiacodontids).

Berman *et al.* (1995, character 44)

This character is probably not independent of rostrum length (character 2).

X16. Pterygoid, 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).

Mazierski & Reisz (2010, character 20)

This character is not independent of the skull proportions (character 2)

X17. Basisphenoid, basal tubera: short, broad, with short articular facets facing anterolaterally (0); long and wing-like, with long articular facets facing anteriorly (1; varanopids); small [=short and broad], with short articular facets facing anteriorly (ophiacodontids).

Reisz *et al.* (1992, character 43), Reisz *et al.* (1998, character 20); modified from Reisz *et al.* (2009, character 55).

These morphologies were difficult to observe.

X18. Basipterygoid processes: short, broad, with short articulating facets facing anterolaterally (0); wing-like, with articulating facets facing anterolaterally (1).

Maddin *et al.* (2006, character 39), Maddin *et al.* (2008, character 35)

The wing-like condition is an autapomorphy of *Varanops* and is thus parsimony uninformative.

X19. Vomer, width of ventral surface: broad (0); narrow (1).

Berman *et al.* (1995, character 43)

The proportions of the vomer are related to skull elongation (character 2), and are often difficult to determine.

X20. Palatine, two anterior dental fields: separate (0); confluent (1).

Maddin *et al.* (2008, character 36).

The range of variation in palatal tooth distribution was difficult to characterise across all basal synapsids.

X21. Pterygoid, distinct process projects medially from transverse flange: absent (0); present (1).

Berman (1995, character 51), as an ophiacodontid synapomorphy.

Posteromedian flange of the pterygoid: absent (0); present (1).

Laurin (1993, character 40), as a therapsid synapomorphy.

This process is present in some basal synapsids but its distribution is not fully understood, and in some taxa a small process is present that confuses the situation. This character may be included in future analyses.

X22. Pterygoid, quadrate ramus: short (0); long, forming most of the medial margin of the subtemporal fenestra (1).

Reisz *et al.* (1992, character 38), Berman *et al.* (1995, character 47)

It is difficult to score this character based on available data.

X23. Hyoid: short, directed to quadrate region (0); long, directed posteriorly beyond skull (1).

Maddin *et al.* (2006, character 49), Reisz *et al.* (2009, character 59)

This character can only be scored for four taxa that preserve hyoids. The hyoid is short in *Ennatosaurus* (Olson 1968) and ‘*Casea*’ *rutena* (Sigogneau-Russell & Russell 1972). It is long in *Pyozia* and *Heleosaurus* (Anderson & Reisz 2004; Reisz & Modesto 2007).

X24. Angular, reflected lamina: shallow (0); deep (1); not applicable, reflected lamina absent (?).

Laurin (1993, character 57)

Because *Palaeohatteria* was not included in the present study this character was parsimony-uninformative (only ‘shallow’ in *Pantelosaurus* and *Palaeohatteria*).

X25. Surangular contribution to notch of reflected lamina: absent (0); small (1); large (2).

Laurin (1993, character 58); Fröbisch *et al.* (2011, character 44).

The derived states of this character are autapomorphic.

X26. Splenial overlaps angular: along complex suture (0); ventrally (1); dorsally (2); ventrally and dorsally (3).

Laurin (1993, character 59); Fröbisch *et al.* (2011, character 45).

The apparent distribution of this character may primarily be influenced by damage and incomplete preservation.

X27. Posterior end of surangular: straight (0); strongly curved ventrally (1).

Laurin (1993, character 60); Fröbisch *et al.* (2011, character 46).

It is difficult to score this character using data collected during the present study.

X28. Vertebral centra, notochordal canal: present in adults (0); absent in adults (1).

Laurin (1993, character 85), Sidor & Hopson (1998, character 123), Fröbisch *et al.* (2011, character 67).

Previous authors scored therapsids as lacking a notochordal canal. However, the basal therapsids employed in the present study have notochordal centra. Thus, this character is parsimony uninformative.

X29. Cervical ribs, anterior process: present (0); absent (1).

Laurin (1993, character 95), Fröbisch *et al.* (2011, character 71).

Previous authors found the absence of the anterior process as a synapomorphy of *Palaeohatteria* and all more derived sphenacodontians. However, it was difficult to score this character for most taxa and it was not included in the present study.

X30. Presarcal neural spines: anterior spines extend dorsally (0) or lean anteriorly (1).

Modesto (1994, character 27).

This character is not independent of the inclination of the posterior dorsal neural spines (character 165), which lean posterodorsally in some edaphosaurids, forming a ‘fan’-shape in concert with the anterodorsally inclined anterior dorsal neural spines.

X31. Dorsal neural spines, longitudinal grooves on anterior and posterior surfaces: absent (0); present (1).

Reisz *et al.* (1992, character 78), Fröbisch *et al.* (2011, character 111).

Pronounced grooves, resulting in a ‘figure-of-eight’ cross section to the dorsal neural spines, are only present in some species of *Dimetrodon* (*Dimetrodon milleri*, included in the present study lacks the grooves; Berman *et al.* 2001). Shallow grooves are present in all taxa with tall, rod-like neural spines (character 168) that lack lateral tubercles (character 169), including the edaphosaurid *Lupeosaurus*, so a character coding shallow grooves would be redundant with other characters in the dataset.

X32. Dorsal neural spines, anterior spines: slender, not expanded dorsally (0); expanded dorsally giving club-shaped appearance (1).

Modesto (1995, character 27), Mazierski & Reisz (2010, character 30).

This character is present in *Edaphosaurus cruciger* and *Edaphosaurus pogonias*, but was not coded in the present analysis, which included neither taxon.

X33. Dorsal neural spines, when elongate: without ‘shoulders’ (0); with ‘shoulders’ (1).

Reisz *et al.* (1992, character 76), Laurin (1993, character 83), Fröbisch *et al.* (2011, character 65).

‘Shoulders’ are present in all taxa with rod-like neural spines, so this character is redundant with character 164 (above). In these taxa the base of the neural spine, presumably the portion that was embedded in the body, is transversely compressed and sheet-like. It is differentiated from the rod-like portion of the spine by ‘shoulders’.

X34. Appendicular skeleton, limb proportions: short and stout (0); long and slender (1).

Reisz *et al.* (1992, character 84), Berman *et al.* (1995, character 85), Fröbisch *et al.* (2011, character 114).

This character is vague. Although, it codes the valid distinction between long and short-limbed basal synapsids, this is also coded by character 224, which quantifies the femoral proportions.

X35. 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).

Modified from Laurin (1993, character 101) and Fröbisch *et al.* (2011, character 77) by addition of a state ('0') describing the condition in *Tseajaia* (e.g. Moss 1972).

This is a valid character. However, the therapsids included in the present analysis do not preserve cleithra so the character is parsimony-uninformative.

X36. Humerus, ‘distinct shaft’: absent (0); present (1).

Maddin *et al.* (2008, character 88)

This character is vaguely defined.

X37. Ulna, broad olecranon (0); narrow, elongate olecranon (1); small (2).

Reisz *et al.* (1992, character 86); Fröbisch *et al.* (2011, character 115).

This character may be valid. However, I was not confident scoring it because in many taxa the olecranon is slow to ossify.

X38. Ilium, height of dorsal process.

Modesto (1995, character 36), Maddin *et al.* (2008, character 96), Mazierski & Reisz (2010, character 39).

Various characters describing the height of the dorsal process of the ilium above the acetabulum were used by previous authors. Taxa with high dorsal processes also have anteriorly expanded dorsal processes, so this character is redundant with character 216.

X39. Pubis, pectineal ridge: absent (0), present (1).

Maddin *et al.* (2008, character 101)

The meaning of this character was not understood during the present study.

X40. Femur, proximal articular surface [head] proportions: narrow dorsoventrally (0); broad dorsoventrally (1).

Berman *et al.* (1995, character 92)

Data collected during the present study suggest that the proportions of the femoral head vary continuously and this character was thus difficult to quantify.

X41. Fibula, distal head/shaft diameter: less than 3:1 (0); more than 3:1 (1).

Reisz *et al.* (1992, character 94), Fröbisch *et al.* (2011, character 117)

The distal end of the fibular was approximately three times the minimum width of the shaft in all taxa examined in the present study.

X42. Lateral centrale: present (0); absent (1).

Reisz *et al.* (1992, character 97)

All basal synapsids (e.g. Romer & Prices 1940, fig. 40), including basal therapsids (e.g. Orlov 1958) possess a lateral centrale so this character is parsimony uninformative.

X43. Pes, lateral centrale: no larger than second or third distal tarsals (0); large than second or third distal tarsals (1); absent (2).

Modified from Reisz *et al.* (1992, character 97), Laurin (1993, characters 118, 119), Berman *et al.* (1995, character 95)

Only a limited set of characters designed to support therapsids monophyly were included in the present study, so this character was not included.

X.44. Pes, distal tarsal V: present (0); absent (1).

Laurin (1993, character 120)

Only a limited set of characters designed to support therapsids monophyly were included in the present study, so this character was not included.

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	1	2	3	4	5	6	7	8	9	10	11	12
Taxon												
<i>Tseajaia campi</i>	0	1	0	0	0	0	?	0	0	0	0	0
<i>Limnoscelis paludis</i>	0	1	0	0	0	0	?	0	0	0	0	0
<i>Captorhinus</i> spp.	0	1	0	0	0	0	?	0	0	0	2	0
<i>Protorothyris archeri</i>	0	1	0	0	0	0	?	0	0	0	2	0
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	?	2	0	0	0	1	0	0	0	0	0	?
<i>Oedaleops campi</i>	?	2	0	0	0	1	1	0	0	0	0	0
<i>Oromycter dolesorum</i>	?	?	?	2	?	?	?	?	?	?	?	?
<i>Casea broili</i>	1	0	0	2	0	1	1	0	2	0	1	0
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	?	2	0	2	0	1	1	0	2	0	1	0
<i>Ennatosaurus tecton</i>	1	0	0	2	1	1	1	0	2	0	0	0
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	1	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus romeri</i>	1	0	0	2	1	1	1	0	2	0	1	0
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus hancocki</i>	1	0	?	2	1	1	1	0	?	?	?	?
<i>Archaeovenator hamiltonensis</i>	0	1	1	2	0	1	1	0	0	0	0	0
<i>Pyozia mesensis</i>	?	1	?	?	?	?	?	?	?	0	?	?
<i>Mycterosaurus longiceps</i>	0	1	1	1	0	1	1	0	0	0	0	1
<i>Mesenosaurus romeri</i>	0	1	1	1	0	1	1	0	0	0	0	1
<i>Heleosaurus scholtzi</i>	0	1	1	1	0	1	1	0	0	0	0	1
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	1	1	0	0	0	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	0	0	1	2	0	1	1	0	0	1	0	1
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	0	2	1	2	0	1	1	0	0	1	0	0
<i>Varanops brevirostris</i>	0	0	1	2	0	1	1	0	0	1	0	1
<i>Watonia meieri</i>	?	?	?	?	?	1	1	?	0	?	?	?
<i>Archaeothyris florensis</i>	0	1	?	?	?	1	0	0	?	?	0	0
<i>Varanosaurus acutirostris</i>	0	3	1	0	0	1	0	0	0	0	0	0
<i>Ophiacodon</i> spp.	0	3	1	0	0	1	0	0	0	1	0	0
<i>Stereophallodon ciscoensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthodon schultzei</i>	?	1	1	0	0	1	1	0	1	?	0	0
<i>Ianthasaurus hardestii</i>	0	1	1	0	0	1	1	0	1	0	0	0
<i>Glaucosaurus megalops</i>	?	?	1	0	0	1	1	?	1	?	?	0
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	1	2	1	0	0	1	1	0	1	0	0	0
<i>Edaphosaurus novomexicanus</i>	1	2	?	?	?	1	1	0	?	0	0	0
<i>Haptodus garnettensis</i>	0	1	1	0	0	1	1	0	1	0	0	0
<i>Pantelosaurus saxonicus</i>	0	1	1	0	0	1	1	0	1	0	0	0
<i>Cutleria wilmarthi</i>	?	1	1	?	?	1	1	1	1	0	0	0
<i>Secodontosaurus obtusidens</i>	0	3	1	0	0	1	0	0	1	0	0	0
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	0	3	1	0	0	1	0	1	1	0	0	0
<i>Sphenacodon</i> spp.	0	3	1	0	0	1	0	1	1	0	0	0
<i>Biarmosuchus tener</i>	0	3	1	0	0	1	2	1	0	0	0	0
<i>Biseridens qilianicus</i>	?	1	1	0	0	1	2	0	0	1	0	0
<i>Raranimus dashankouensis</i>	?	?	1	0	0	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	0	3	1	0	0	1	2	0	0	0	0	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	13	14	15	16	17	18	19	20	21	22	23	24
Taxon												
<i>Tseajaia campi</i>	1	?	0	1	0	1	?	0	1	0	0	0
<i>Limnoscelis paludis</i>	1	1	0	1	0	1	0	0	1	0	0	0
<i>Captorhinus</i> spp.	1	0	0	0	0	1	0	0	1	0	0	0
<i>Protorothyris archeri</i>	0	0	?	0	0	0	0	0	?	0	0	0
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	0	?	?
<i>Eothyris parkeyi</i>	0	1	0	1	0	0	?	?	1	0	0	0
<i>Oedaleops campi</i>	0	1	0	1	0	0	?	?	1	0	0	0
<i>Oromycter dolesorum</i>	0	1	0	0	0	1	?	?	?	0	0	0
<i>Casea broili</i>	0	1	0	0	0	0	1	0	1	0	1	?
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	0	1	0	0	0	0	1	0	1	0	1	1
<i>Ennatosaurus tecton</i>	0	1	0	0	0	1	1	0	1	0	1	1
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	0	1	0	?	0	0	?	?	?	?	?	?
<i>Cotylorhynchus romeri</i>	0	1	0	0	0	0	?	?	1	0	1	1
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus hancocki</i>	?	?	0	0	?	?	?	?	?	?	1	1
<i>Archaeovenator hamiltonensis</i>	0	0	1	0	0	0	2	0	0	0	0	0
<i>Pyozia mesensis</i>	?	?	1	?	0	0	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	0	0	1	0	0	0	?	?	0	2	0	0
<i>Mesenosaurus romeri</i>	0	0	1	0	1	0	?	?	0	2	0	0
<i>Heleosaurus scholtzi</i>	0	0	0	0	1	0	?	0	0	2	0	0
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	0	0	1	0	0	0	2	0	0	0	0	0
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	0	0	0	0	1	0	2	0	0	0	0	0
<i>Varanops brevirostris</i>	0	0	0	0	1	0	2	0	0	0	0	0
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	?	?	?	?	?	?	?	?	?	0	0	?
<i>Varanosaurus acutirostris</i>	0	2	1	0	1	0	1	0	0	0	0	0
<i>Ophiacodon</i> spp.	0	2	0	0	1	1	1	0	0	0	0	0
<i>Stereophallodon ciscoensis</i>	0	2	0	0	1	1	?	?	?	?	?	0
<i>Ianthodon schultzei</i>	0	0	?	0	0	1	?	?	?	0	0	0
<i>Ianthasaurus hardestii</i>	?	?	?	?	?	?	?	?	0	0	0	0
<i>Glaucosaurus megalops</i>	0	?	0	0	0	0	?	0	0	0	0	0
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	0	0	0	1	0	?	?	0	0	0	0
<i>Edaphosaurus novomexicanus</i>	?	?	?	?	?	?	?	?	0	?	?	?
<i>Haptodus garnettensis</i>	1	0	0	0	1	1	1	0	0	0	0	0
<i>Pantelosaurus saxonicus</i>	1	0	0	?	1	0	?	?	0	0	?	0
<i>Cutleria wilmarti</i>	1	?	?	?	0	?	?	?	0	?	0	0
<i>Secodontosaurus obtusidens</i>	1	0	0	0	1	1	3	0	0	2	0	0
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	1	0	0	0	0	1	3	0	0	2	0	0
<i>Sphenacodon</i> spp.	1	0	0	0	0	1	3	0	0	1	0	0
<i>Biarmosuchus tener</i>	2	0	0	0	1	0	4	1	0	2	0	0
<i>Biseridens qilianicus</i>	1	0	0	0	1	0	4	1	0	2	0	0
<i>Raranimus dashankouensis</i>	1	0	0	0	1	0	4	1	0	2	0	0
<i>Titanophoneus potens</i>	2	2	0	0	0	1	3	1	0	2	0	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	25	26	27	28	29	30	31	32	33	34	35	36
Taxon												
<i>Tseajaia campi</i>	0	0	1	0	0	0	0	1	0	2	1	0
<i>Limnoscelis paludis</i>	0	0	1	0	0	0	0	1	0	1	0	0
<i>Captorhinus</i> spp.	0	0	0	0	0	0	0	1	0	2	0	0
<i>Protorothyris archeri</i>	0	0	0	?	2	1	0	1	0	2	1	0
<i>Echinerpeton intermedium</i>	0	?	0	0	0	?	0	1	0	2	0	?
<i>Eothyris parkeyi</i>	1	0	0	?	0	1	0	0	0	2	1	1
<i>Oedaleops campi</i>	0	0	0	?	0	1	0	0	0	1	0	0
<i>Oromycter dolesorum</i>	1	0	0	1	1	?	0	?	0	1	0	0
<i>Casea broili</i>	1	0	0	?	1	1	0	?	0	0	0	0
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	1	0	0	?	1	1	0	?	0	0	0	0
<i>Ennatosaurus tecton</i>	1	0	0	1	1	1	0	?	0	0	0	0
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	0	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	?	?	?	?	1	?	0	?	0	?	?	?
<i>Cotylorhynchus romeri</i>	2	0	0	1	0	1	0	?	0	0	0	0
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	0	?	?	?
<i>Cotylorhynchus hancocki</i>	2	0	0	1	0	?	0	?	0	0	0	0
<i>Archaeovenator hamiltonensis</i>	0	0	0	0	2	0	0	?	0	0	0	0
<i>Pyozia mesensis</i>	?	?	?	?	2	?	0	?	0	0	0	0
<i>Mycterosaurus longiceps</i>	1	0	0	?	0	2	0	?	0	1	0	0
<i>Mesenosaurus romeri</i>	1	0	0	0	2	0	0	0	0	2	0	1
<i>Heleosaurus scholtzi</i>	1	0	0	?	0	0	0	1	0	2	0	1
BP/1/5678 (? <i>Elliotsmithia</i>)	1	?	0	?	?	{12}	0	?	0	2	0	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	1	1	0	?	2	2	0	2	0	1	0	0
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	2	1	0	?	2	2	0	?	0	1	0	1
<i>Varanops brevirostris</i>	2	1	0	0	2	2	0	2	0	2	0	1
<i>Watonia meieri</i>	?	?	?	0	?	?	0	?	0	?	?	?
<i>Archaeothyris florensis</i>	0	0	0	0	2	3	0	0	0	2	0	?
<i>Varanosaurus acutirostris</i>	0	0	1	?	2	0	0	2	0	2	0	1
<i>Ophiacodon</i> spp.	1	0	1	?	2	0	0	2	0	2	0	0
<i>Stereophallodon ciscoensis</i>	?	0	1	0	?	?	?	0	0	2	1	1
<i>Ianthodon schultzei</i>	0	0	0	0	0	3	0	1	0	2	0	0
<i>Ianthasaurus hardestii</i>	0	0	0	?	2	3	0	2	0	2	0	0
<i>Glaucosaurus megalops</i>	0	0	0	?	0	1	0	?	?	0	0	0
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	0	0	0	0	3	1	?	0	0	0	0
<i>Edaphosaurus novomexicanus</i>	?	?	0	?	0	3	1	?	0	0	0	0
<i>Haptodus garnettensis</i>	0	0	1	0	0	3	0	1	0	2	0	0
<i>Pantelosaurus saxonicus</i>	0	0	1	?	0	3	0	1	0	1	0	0
<i>Cutleria wilmarti</i>	?	0	1	0	0	3	0	0	0	2	0	0
<i>Secodontosaurus obtusidens</i>	3	0	1	1	0	3	0	2	0	2	0	0
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	0	?	1	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	3	0	2	1	0	3	0	0	1	2	1	0
<i>Sphenacodon</i> spp.	3	0	2	1	0	3	0	0	1	2	1	0
<i>Biarmosuchus tener</i>	3	0	1	?	1	3	0	0	0	2	1	0
<i>Biseridens qilianicus</i>	3	0	1	?	1	3	0	0	0	2	1	0
<i>Raranimus dashankouensis</i>	3	0	1	?	?	?	0	?	0	2	1	0
<i>Titanophoneus potens</i>	3	0	1	0	1	3	0	0	0	2	1	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	37	38	39	40	41	42	43	44	45	46	47	48
Taxon												
<i>Tseajaia campi</i>	?	?	0	0	0	0	?	0	0	0	1	?
<i>Limnoscelis paludis</i>	?	?	0	0	0	0	?	0	0	0	1	0
<i>Captorhinus</i> spp.	0	?	0	1	0	0	?	0	0	1	0	0
<i>Protorothyris archeri</i>	?	?	?	0	0	0	?	0	?	?	0	0
<i>Echinerpeton intermedium</i>	1	0	0	0	0	0	?	0	?	1	?	?
<i>Eothyris parkeyi</i>	?	?	1	0	1	0	?	0	?	?	0	1
<i>Oedaleops campi</i>	?	?	1	0	1	0	?	0	?	?	0	1
<i>Oromycter dolesorum</i>	0	?	0	1	0	0	?	0	1	1	?	?
<i>Casea broili</i>	0	?	0	1	0	0	?	1	1	1	1	1
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	?	?	0	1	0	0	?	2	1	1	?	1
<i>Ennatosaurus tecton</i>	0	?	0	1	0	0	?	2	1	1	0	1
<i>Caseopsis agilis</i>	?	?	?	1	0	0	?	1	1	1	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	?	?	?	1	0	0	?	2	1	1	?	?
<i>Cotylorhynchus romeri</i>	0	?	0	1	0	0	?	1	1	1	1	1
<i>Cotylorhynchus bransoni</i>	?	?	?	1	0	0	?	1	1	1	?	?
<i>Cotylorhynchus hancocki</i>	0	?	0	1	0	0	?	1	1	1	?	?
<i>Archaeovenator hamiltonensis</i>	0	?	0	0	1	0	?	0	0	1	1	0
<i>Pyozia mesensis</i>	?	?	0	0	1	0	?	0	?	?	?	?
<i>Mycterosaurus longiceps</i>	?	?	0	2	2	1	1	0	?	?	1	0
<i>Mesenosaurus romeri</i>	?	?	0	2	2	1	1	0	0	1	1	0
<i>Heleosaurus scholtzi</i>	?	?	0	2	2	1	1	0	?	1	1	0
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	0	2	2	1	?	0	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	0	?	0	2	2	1	0	0	0	1	?	0
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	?	?	0	2	2	1	?	0	?	?	1	0
<i>Varanops brevirostris</i>	0	?	0	2	2	1	0	0	0	1	1	0
<i>Watonia meieri</i>	?	?	?	2	2	1	0	0	0	1	?	?
<i>Archaeothyris florensis</i>	1	0	0	0	1	?	?	0	0	1	?	?
<i>Varanosaurus acutirostris</i>	?	?	0	0	0	0	?	0	0	1	2	0
<i>Ophiacodon</i> spp.	1	1	0	0	1	0	?	0	0	1	2	0
<i>Stereophallodon ciscoensis</i>	1	1	?	0	?	?	?	?	?	?	?	?
<i>Ianthodon schultzei</i>	0	?	0	0	1	0	?	0	0	?	1	0
<i>Ianthasaurus hardestii</i>	?	?	0	1	0	1	?	0	0	1	?	0
<i>Glaucosaurus megalops</i>	?	?	0	?	?	?	?	0	?	?	?	?
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	?	0	1	0	1	1	0	1	1	0	0
<i>Edaphosaurus novomexicanus</i>	?	?	0	1	0	?	?	0	?	?	0	0
<i>Haptodus garnettensis</i>	1	0	0	0	1	0	?	0	0	1	0	0
<i>Pantelosaurus saxonicus</i>	?	?	0	2	1	1	?	0	?	?	2	?
<i>Cutleria wilmarti</i>	?	?	0	2	1	1	0	0	0	1	2	0
<i>Secodontosaurus obtusidens</i>	1	0	0	2	1	1	0	0	0	1	2	0
<i>Cryptovenator hirschbergeri</i>	?	?	?	2	1	1	0	0	0	1	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	1	0	0	2	1	1	2	0	0	1	2	0
<i>Sphenacodon</i> spp.	1	0	0	2	1	1	2	0	0	1	2	0
<i>Biarmosuchus tener</i>	?	?	0	2	1	1	2	0	?	1	2	0
<i>Biseridens qilianicus</i>	1	?	0	1	0	0	0	0	1	1	1	0
<i>Raranimus dashankouensis</i>	1	?	?	2	1	1	{12}	0	0	1	?	0
<i>Titanophoneus potens</i>	1	0	0	2	1	1	2	0	0	1	2	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	49	50	51	52	53	54	55	56	57	58	59	60
Taxon												
<i>Tseajaia campi</i>	0	0	0	?	0	0	?	1	0	0	1	0
<i>Limnoscelis paludis</i>	0	0	0	?	0	1	?	1	0	0	1	0
<i>Captorhinus</i> spp.	0	0	0	0	0	0	0	1	0	0	0	2
<i>Protorothyris archeri</i>	0	0	0	0	0	0	0	1	0	0	1	2
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	0	0	0	0	0	0	0	0	0	0	1	1
<i>Oedaleops campi</i>	0	0	0	0	0	0	0	0	0	0	1	1
<i>Oromycter dolesorum</i>	0	1	0	0	0	?	?	?	?	?	?	?
<i>Casea broili</i>	0	1	0	?	?	0	0	?	?	?	?	?
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	0	1	0	0	0	0	0	?	?	0	?	1
<i>Ennatosaurus tecton</i>	0	1	0	?	0	0	0	0	1	0	0	2
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus romeri</i>	0	1	0	0	0	0	0	0	1	0	0	1
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus hancocki</i>	?	1	?	?	?	?	?	?	?	?	?	?
<i>Archaeovenator hamiltonensis</i>	0	0	1	0	0	0	0	1	0	0	0	2
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	?	0	?	1	1	0	?	?	0	0	?	2
<i>Mesenosaurus romeri</i>	?	0	1	1	1	?	0	1	0	0	0	2
<i>Heleosaurus scholtzi</i>	?	?	1	?	1	0	?	1	0	0	0	2
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	1	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	0	0	0	2	0	?	0	?	0	0	?	2
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	0	0	0	2	0	0	0	1	0	0	1	2
<i>Varanops brevirostris</i>	0	0	0	2	0	0	0	1	0	0	0	2
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	?	?	?	?	?	?	?	1	0	0	1	?
<i>Varanosaurus acutirostris</i>	1	0	0	?	0	1	0	1	0	0	1	2
<i>Ophiacodon</i> spp.	0	0	?	?	?	1	0	1	0	0	1	2
<i>Stereophalodon ciscoensis</i>	?	?	?	?	?	1	?	?	?	?	?	?
<i>Ianthodon schultzei</i>	0	0	0	?	0	1	?	1	0	0	1	2
<i>Ianthasaurus hardestii</i>	0	0	0	0	0	1	0	1	0	0	0	2
<i>Glaucosaurus megalops</i>	0	0	0	?	0	0	1	?	?	?	?	?
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	0	0	?	0	0	1	0	1	0	0	1
<i>Edaphosaurus novomexicanus</i>	?	?	0	?	?	0	1	?	1	0	?	2
<i>Haptodus garnettensis</i>	1	0	0	0	0	1	0	1	0	0	1	2
<i>Pantelosaurus saxonicus</i>	?	?	0	?	0	1	?	1	0	0	0	2
<i>Cutleria wilmarti</i>	?	0	0	?	?	?	?	0	2	0	0	1
<i>Secodontosaurus obtusidens</i>	?	0	1	0	0	1	0	2	0	1	2	2
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	?	0	1	0	0	1	0	2	0	1	2	2
<i>Sphenacodon</i> spp.	?	0	1	0	0	1	0	2	0	1	2	2
<i>Biarmosuchus tener</i>	?	0	0	?	1	1	?	1	0	0	1	2
<i>Biseridens qilianicus</i>	0	0	0	?	1	1	?	0	0	0	0	?
<i>Raranimus dashankouensis</i>	0	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	?	0	0	0	1	1	0	0	0	0	1	2

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	61	62	63	64	65	66	67	68	69	70	71	72
Taxon												
<i>Tseajaia campi</i>	2	0	0	0	0	0	0	0	0	?	0	0
<i>Limnoscelis paludis</i>	2	0	0	0	0	0	0	0	0	?	0	0
<i>Captorhinus</i> spp.	2	0	0	0	0	1	0	0	0	0	0	0
<i>Protorothyris archeri</i>	2	0	0	0	0	1	0	0	0	0	0	0
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	0	0	1	0	0	0	?	1	0	0	2	2
<i>Oedaleops campi</i>	0	0	0	0	0	0	0	1	0	?	?	2
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	?	?	?	?	?	?	0	?	?	0	?	2
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	0	2	0	?	?	0	0	1	0	0	2	2
<i>Ennatosaurus tecton</i>	0	0	0	0	0	0	0	1	0	0	2	0
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus romeri</i>	0	0	?	0	0	?	0	1	0	0	2	2
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus hancocki</i>	?	?	?	?	?	?	?	?	?	?	?	2
<i>Archaeovenator hamiltonensis</i>	1	0	0	0	0	0	0	1	1	0	0	2
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	0	?
<i>Mycterosaurus longiceps</i>	1	0	0	0	0	?	1	1	1	?	1	2
<i>Mesenosaurus romeri</i>	1	0	0	0	0	1	1	1	0	0	0	2
<i>Heleosaurus scholtzi</i>	1	0	0	0	1	0	1	1	0	?	0	2
BP/1/5678 (? <i>Elliotsmithia</i>)	?	0	?	0	1	?	?	1	0	?	?	2
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	1	0	0	0	?	?	?	?	?	0	1	2
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	1	0	0	0	0	?	1	0	1	0	1	2
<i>Varanops brevirostris</i>	?	?	0	0	0	1	0	0	1	0	1	2
<i>Watonia meieri</i>	1	?	?	?	?	?	1	?	?	?	?	?
<i>Archaeothyris florensis</i>	1	?	0	?	?	?	?	?	?	0	0	0
<i>Varanosaurus acutirostris</i>	1	0	0	0	0	1	0	1	1	1	0	0
<i>Ophiacodon</i> spp.	1	0	0	0	0	0	0	1	1	1	0	?
<i>Stereophalodon ciscoensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthodon schultzei</i>	0	1	0	0	0	1	0	0	1	0	0	?
<i>Ianthasaurus hardestii</i>	0	2	0	0	0	1	0	0	1	0	0	0
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	0	0
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	2	0	1	?	1	0	0	1	0	0	0
<i>Edaphosaurus novomexicanus</i>	?	2	0	1	?	1	0	0	1	0	0	?
<i>Haptodus garnettensis</i>	0	1	0	0	0	1	0	0	1	0	0	0
<i>Pantelosaurus saxonicus</i>	2	1	1	0	0	1	0	1	1	?	0	1
<i>Cutleria wilmarti</i>	2	1	1	0	1	1	0	1	1	?	0	?
<i>Secodontosaurus obtusidens</i>	2	1	1	0	0	1	0	0	0	0	0	1
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	2	1	1	0	1	0	0	1	1	0	0	1
<i>Sphenacodon</i> spp.	2	1	1	0	1	0	0	1	1	0	0	1
<i>Biarmosuchus tener</i>	2	3	0	?	?	?	0	1	?	?	0	1
<i>Biseridens qilianicus</i>	2	3	0	0	0	?	0	1	1	?	0	0
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	2	3	0	0	0	0	0	1	1	0	0	1

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	73	74	75	76	77	78	79	80	81	82	83	84
Taxon												
<i>Tseajaia campi</i>	?	?	1	0	0	0	?	1	0	?	0	1
<i>Limnoscelis paludis</i>	?	?	1	0	1	0	?	0	0	?	0	0
<i>Captorhinus</i> spp.	?	?	0	0	1	0	?	0	0	?	0	0
<i>Protorothyris archeri</i>	?	?	0	0	1	0	?	0	0	?	0	0
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	0	0	1	0	0	0	0	0	?	0	0	1
<i>Oedaleops campi</i>	1	0	?	0	?	0	0	0	0	?	0	1
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	0	0	?	0	?	?	0	0	0	?	?	1
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	0	?	0	0	0	?	0	0	0	?	0	1
<i>Ennatosaurus tecton</i>	1	0	0	0	0	0	0	0	?	0	0	1
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus romeri</i>	1	0	0	?	0	0	0	0	?	0	0	1
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus hancocki</i>	1	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeovenator hamiltonensis</i>	1	0	0	?	0	0	0	1	?	1	0	0
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	1	0	1	0	0	0	0	1	?	1	0	0
<i>Mesenosaurus romeri</i>	1	0	1	0	0	0	0	1	1	1	0	1
<i>Heleosaurus scholtzi</i>	1	0	1	0	0	0	0	1	1	1	0	1
BP/1/5678 (? <i>Elliotsmithia</i>)	1	0	?	0	0	0	0	1	1	1	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	1	1	0	0	0	1	0	1	0	0	0	1
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	1	1	0	0	0	1	0	1	0	0	0	0
<i>Varanops brevirostris</i>	1	1	?	?	?	1	0	1	0	?	?	0
<i>Watonia meieri</i>	?	?	?	?	0	1	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	?	0	?	?	0	?	0	?	?	?	0	0
<i>Varanosaurus acutirostris</i>	1	0	1	1	0	0	1	0	0	1	0	0
<i>Ophiacodon</i> spp.	1	0	1	1	?	0	1	0	0	?	0	0
<i>Stereophallodon ciscoensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthodon schultzei</i>	1	0	0	0	2	0	0	?	0	1	?	0
<i>Ianthasaurus hardestii</i>	1	0	0	0	2	0	0	?	?	1	0	0
<i>Glaucosaurus megalops</i>	1	0	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	1	0	0	0	2	0	0	0	0	1	0	0
<i>Edaphosaurus novomexicanus</i>	?	0	?	?	2	0	0	0	0	1	0	0
<i>Haptodus garnettensis</i>	1	0	0	0	2	0	0	?	0	1	1	0
<i>Pantelosaurus saxonicus</i>	1	0	1	0	2	0	0	0	0	1	?	0
<i>Cutleria wilmarti</i>	1	0	0	0	2	0	0	?	0	1	?	0
<i>Secodontosaurus obtusidens</i>	1	0	0	0	2	0	0	0	0	1	1	0
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	1	0	1	0	2	0	0	0	0	1	1	0
<i>Sphenacodon</i> spp.	1	0	1	0	2	0	0	0	0	1	1	0
<i>Biarmosuchus tener</i>	1	0	0	0	2	0	0	0	0	1	1	0
<i>Biseridens qilianicus</i>	1	0	1	0	2	0	0	0	0	1	1	0
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	1	0	1	0	2	0	0	0	0	1	1	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	85	86	87	88	89	90	91	92	93	94	95	96
Taxon												
<i>Tseajaia campi</i>	2	1	0	0	0	?	1	?	0	1	1	2
<i>Limnoscelis paludis</i>	1	1	0	0	0	0	1	0	0	?	1	0
<i>Captorhinus</i> spp.	0	3	0	0	0	0	0	0	0	0	?	0
<i>Protorothyris archeri</i>	1	1	0	2	0	0	0	0	0	0	1	2
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	1	0	0	1	0	1	0	1	0	?	1	1
<i>Oedaleops campi</i>	1	0	0	1	?	1	1	1	0	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	0	2	0	1	?	1	?	?	?	0	1	1
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	0	2	0	1	?	1	1	1	1	0	1	1
<i>Ennatosaurus tecton</i>	0	?	?	1	0	?	0	?	1	?	?	1
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	?	?	?	?	?	1	?	?	?	?	1	1
<i>Cotylorhynchus romeri</i>	0	2	0	?	?	1	0	1	1	?	1	1
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus hancocki</i>	?	?	?	?	?	1	?	?	?	?	1	1
<i>Archaeovenator hamiltonensis</i>	2	?	?	1	?	1	?	?	0	?	?	?
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	2	1	0	2	?	1	0	0	0	0	0	0
<i>Mesenosaurus romeri</i>	2	1	1	2	0	1	0	0	0	0	0	0
<i>Heleosaurus scholtzi</i>	2	1	1	2	?	1	0	0	0	?	?	0
BP/1/5678 (? <i>Elliotsmithia</i>)	2	?	?	?	?	1	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	2	1	0	?	?	2	0	1	0	?	0	0
<i>Ruthiromia elcobriensis</i>	?	?	?	?	0	?	?	?	?	?	?	0
<i>Varanodon agilis</i>	2	?	?	?	?	2	?	?	?	?	?	0
<i>Varanops brevirostris</i>	2	1	0	2	?	2	1	1	0	0	?	?
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	2	?	?	?	?	?	1	0	?	1	0	?
<i>Varanosaurus acutirostris</i>	2	0	0	2	0	1	0	0	0	1	0	2
<i>Ophiacodon</i> spp.	2	0	0	2	0	1	1	0	0	1	0	2
<i>Stereophallodon ciscoensis</i>	?	?	?	?	0	?	?	?	?	?	?	?
<i>Ianthodon schultzei</i>	1	?	?	2	?	?	1	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	2	?	?	2	1	?	?	?	?	?	?	?
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	2	1	0	2	1	0	1	1	0	1	0	0
<i>Edaphosaurus novomexicanus</i>	?	?	?	2	1	0	1	?	0	1	0	0
<i>Haptodus garnettensis</i>	2	1	0	2	0	0	?	1	?	1	0	0
<i>Pantelosaurus saxonicus</i>	1	?	?	2	?	0	?	?	?	?	?	?
<i>Cutleria wilmarti</i>	2	1	0	2	?	0	1	1	?	?	?	?
<i>Secodontosaurus obtusidens</i>	2	1	0	2	0	0	1	1	0	1	0	0
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	2	1	0	2	0	0	1	1	0	1	0	0
<i>Sphenacodon</i> spp.	2	1	0	2	0	0	?	1	0	1	0	0
<i>Biarmosuchus tener</i>	1	1	0	3	?	3	1	1	0	0	0	0
<i>Biseridens qilianicus</i>	1	1	0	3	?	3	1	1	0	?	?	0
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	2	1	0	2	0	3	1	1	0	0	0	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	97	98	99	100	101	102	103	104	105	106	107	108
Taxon												
<i>Tseajaia campi</i>	0	0	0	0	2	1	0	0	0	1	1	?
<i>Limnoscelis paludis</i>	0	0	0	0	2	?	0	0	0	1	1	1
<i>Captorhinus</i> spp.	0	0	0	0	2	1	1	0	0	1	0	0
<i>Protorothyris archeri</i>	0	0	0	0	0	1	0	0	0	1	1	?
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	0	0	0	0	0	0	0	0	0	1	?	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	2	1	?	0	1	0	0	0	0	1	1	?
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	2	1	0	0	1	0	0	0	0	1	1	0
<i>Ennatosaurus tecton</i>	2	1	0	0	1	?	?	0	0	1	1	0
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	2	1	0	0	?	1	0	0	0	1	1	0
<i>Cotylorhynchus romeri</i>	2	1	0	0	0	0	0	0	0	1	1	0
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus hancocki</i>	?	1	0	0	?	0	0	0	0	1	1	0
<i>Archaeovenator hamiltonensis</i>	?	0	0	0	0	0	0	0	0	1	1	0
<i>Pyozia mesensis</i>	?	?	?	0	0	0	0	0	1	?	?	1
<i>Mycterosaurus longiceps</i>	0	0	?	0	0	0	0	0	0	1	?	?
<i>Mesenosaurus romeri</i>	0	0	0	0	0	0	0	0	0	1	1	1
<i>Heleosaurus scholtzi</i>	0	?	?	0	0	0	0	0	0	1	1	1
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	0	?	0	0	0	1	1	1	1
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	0	1	0	1	0
<i>Aerosaurus wellesi</i>	0	0	0	0	0	0	0	0	1	0	1	0
<i>Ruthiromia elcobriensis</i>	0	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	0	?	?	?	?	?	?	?	?	?	?	?
<i>Varanops brevirostris</i>	?	0	0	0	0	0	0	0	0	1	1	?
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	?	?	0	?	?	?	?	?	?	?	?	?
<i>Varanosaurus acutirostris</i>	0	0	?	0	0	2	0	0	0	1	1	0
<i>Ophiacodon</i> spp.	0	0	1	0	0	2	0	1	0	1	1	0
<i>Stereophallodon ciscoensis</i>	?	0	1	0	?	2	0	0	0	1	1	0
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	?	?	?	0	0	?	?	?	?	?	?	?
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	1	0	0	1	1	1	0	0	1	0	0
<i>Edaphosaurus novomexicanus</i>	0	1	0	0	1	1	1	0	0	1	0	0
<i>Haptodus garnettensis</i>	0	?	0	0	0	1	1	0	0	1	0	0
<i>Pantelosaurus saxonicus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cutleria wilmarthi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Secodontosaurus obtusidens</i>	1	0	0	0	2	?	?	1	0	2	0	0
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	1	0	0	0	2	1	1	1	0	2	0	0
<i>Sphenacodon</i> spp.	1	0	0	0	2	1	1	1	0	2	0	0
<i>Biarmosuchus tener</i>	1	1	0	1	2	?	?	?	0	?	?	?
<i>Biseridens qilianicus</i>	1	1	?	?	2	?	?	?	?	?	?	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	1	1	0	1	2	?	?	0	0	1	0	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	109	110	111	112	113	114	115	116	117	118	119	120
Taxon												
<i>Tseajaia campi</i>	0	?	?	0	?	1	0	?	0	0	0	?
<i>Limnoscelis paludis</i>	0	?	?	1	0	1	0	?	0	0	0	0
<i>Captorhinus</i> spp.	0	?	?	1	0	0	0	0	0	0	0	0
<i>Protorothyris archeri</i>	0	?	?	0	0	0	0	?	0	0	0	0
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	1	1	?	?	?	?	?	?	0	0	0	0
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	1	1	0	0	0	0	0	?	0	0	0	0
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	1	1	1	?	?	0	0	?	0	?	0	0
<i>Ennatosaurus tecton</i>	1	?	?	0	0	0	0	0	0	0	1	0
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	1	0	?	?	?	?	?	?	0	0	1	0
<i>Cotylorhynchus romeri</i>	1	0	?	?	?	0	1	?	0	0	1	0
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	0	0	1	0
<i>Cotylorhynchus hancocki</i>	1	0	?	?	?	?	?	?	?	?	?	?
<i>Archaeovenator hamiltonensis</i>	0	?	?	?	?	?	?	0	0	0	0	?
<i>Pyozia mesensis</i>	1	1	0	0	0	?	?	?	0	0	0	0
<i>Mycterosaurus longiceps</i>	1	1	0	?	?	?	?	?	?	?	?	0
<i>Mesenosaurus romeri</i>	1	1	0	0	0	1	0	0	0	0	0	0
<i>Heleosaurus scholtzi</i>	1	1	0	0	0	0	0	0	0	0	0	0
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	1	1	0	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	1	1	1	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	1	1	1	?	?	?	?	?	?	0	0	0
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanops brevirostris</i>	1	1	1	?	?	?	?	?	?	?	?	?
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanosaurus acutirostris</i>	0	?	?	0	0	0	0	?	0	0	0	1
<i>Ophiacodon</i> spp.	0	?	?	?	0	?	?	1	0	0	0	0
<i>Stereophallodon ciscoensis</i>	0	?	?	?	?	?	?	?	0	0	0	0
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	?	?	?	?	?	?	?	1	?	0	0	?
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	1	?	?
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	?	?	0	0	0	0	1	0	1	?	?
<i>Edaphosaurus novomexicanus</i>	?	?	?	?	?	0	0	?	0	1	?	1
<i>Haptodus garnettensis</i>	0	?	?	0	0	0	0	1	0	0	0	1
<i>Pantelosaurus saxonicus</i>	?	?	?	0	0	0	0	?	0	0	0	?
<i>Cutleria wilmarthi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Secodontosaurus obtusidens</i>	?	?	?	?	?	?	?	1	?	0	0	1
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	0	?	?	1	0	0	0	1	0	0	0	1
<i>Sphenacodon</i> spp.	0	?	?	1	0	0	0	1	0	0	0	1
<i>Biarmosuchus tener</i>	0	?	?	1	1	0	1	?	1	0	0	?
<i>Biseridens qilianicus</i>	?	?	?	0	1	0	1	?	1	0	1	?
<i>Raranimus dashankouensis</i>	?	?	?	1	0	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	0	?	?	1	1	0	1	?	1	0	0	1

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	121	122	123	124	125	126	127	128	129	130	131	132
Taxon												
<i>Tseajaia campi</i>	0	3	1	?	0	0	0	1	0	0	0	0
<i>Limnoscelis paludis</i>	0	3	0	?	0	0	1	1	0	0	0	0
<i>Captorhinus</i> spp.	0	0	1	?	0	0	0	0	1	0	0	0
<i>Protorothyris archeri</i>	0	0	0	1	0	2	0	0	0	0	0	0
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	0	0	1	?	0	0	0	?	1	0	0	0
<i>Oedaleops campi</i>	?	?	?	?	0	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	1	0	?	?	?	?
<i>Casea broili</i>	0	0	1	?	0	0	1	?	1	0	1	0
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	0	1	1	?	0	1	1	?	?	0	?	0
<i>Ennatosaurus tecton</i>	0	1	1	0	0	1	1	0	1	0	1	0
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	0	1	1	?	?	?	1	?	?	?	?	?
<i>Cotylorhynchus romeri</i>	0	1	1	?	0	1	1	0	1	0	1	0
<i>Cotylorhynchus bransoni</i>	0	1	1	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus hancocki</i>	?	?	?	?	?	?	1	?	?	?	1	?
<i>Archaeovenator hamiltonensis</i>	0	0	0	1	0	2	0	0	0	0	0	0
<i>Pyozia mesensis</i>	0	0	1	?	0	2	0	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	?	?	1	?	0	2	?	?	0	0	?	?
<i>Mesenosaurus romeri</i>	0	0	1	1	0	2	0	0	0	0	0	1
<i>Heleosaurus scholtzi</i>	0	0	?	?	0	2	0	?	0	?	?	1
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	0	2	0	0	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	0	?	?	?	0	2	0	0	0	0	?	1
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanodon agilis</i>	?	?	1	?	0	2	0	?	0	2	?	1
<i>Varanops brevirostris</i>	?	?	1	?	0	2	0	?	0	2	0	1
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	?	?	?	?	?	2	0	?	?	?	?	?
<i>Varanosaurus acutirostris</i>	0	0	0	?	0	2	0	?	0	0	0	0
<i>Ophiacodon</i> spp.	0	1	0	?	0	2	0	0	0	0	0	0
<i>Stereophalodon ciscoensis</i>	0	1	0	?	?	?	0	?	?	?	?	0
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	0	0	1	?	1	0	1	?	0	1	?	?
<i>Glaucosaurus megalops</i>	? 013}	?	?	?	?	?	1	?	?	1	?	?
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	2	1	0	1	1	1	0	1	1	1	1
<i>Edaphosaurus novomexicanus</i>	0	2	1	?	1	?	?	?	?	?	?	?
<i>Haptodus garnettensis</i>	0	0	1	?	1	0	1	?	0	1	1	1
<i>Pantelosaurus saxonicus</i>	0	?	0	?	1	0	1	?	0	1	0	1
<i>Cutleria wilmarti</i>	?	?	?	?	1	0	1	?	0	1	1	?
<i>Secodontosaurus obtusidens</i>	0	0	0	?	0	2	0	0	0	1	0	1
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	1	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	0	0	0	0	1	0	1	0	0	1	0	1
<i>Sphenacodon</i> spp.	0	0	0	?	1	0	1	0	0	1	0	1
<i>Biarmosuchus tener</i>	0	1	1	?	1	0	1	?	0	1	?	?
<i>Biseridens qilianicus</i>	1	1	?	1	1	1	1	0	0	1	1	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	1	?	?	1	1	0	1	0	0	1	0	1

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	133	134	135	136	137	138	139	140	141	142	143	144
Taxon												
<i>Tseajaia campi</i>	?	1	0	0	0	0	0	0	0	1	0	?
<i>Limnoscelis paludis</i>	?	1	1	1	0	0	0	0	0	1	0	?
<i>Captorhinus</i> spp.	0	1	1	0	0	0	0	?	1	?	0	?
<i>Protorothyris archeri</i>	?	0	0	0	0	?	0	?	?	?	0	?
<i>Echinerpeton intermedium</i>	?	?	0	0	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	?	1	0	0	0	?	0	?	?	?	0	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	1	1	?	?	0	?	?	?	?	?
<i>Casea broili</i>	?	1	0	0	0	0	0	?	0	1	0	?
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	?	1	?	?	0	0	1	?	?	?	0	?
<i>Ennatosaurus tecton</i>	?	1	0	0	0	0	1	?	0	0	0	?
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus romeri</i>	?	?	0	0	0	0	1	?	?	0	0	?
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cotylorhynchus hancocki</i>	?	?	0	0	?	?	?	?	?	?	?	?
<i>Archaeovenator hamiltonensis</i>	?	0	0	0	0	1	0	0	?	0	0	?
<i>Pyozia mesensis</i>	?	0	0	0	0	1	0	?	?	0	?	?
<i>Mycterosaurus longiceps</i>	?	0	?	?	0	?	?	?	?	?	?	?
<i>Mesenosaurus romeri</i>	0	0	0	0	0	1	0	1	?	0	0	?
<i>Heleosaurus scholtzi</i>	0	0	0	0	0	?	0	?	?	?	0	?
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	0	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	0	0	0	0	0	1	0	?	?	?	3	?
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	?	3	?
<i>Varanodon agilis</i>	0	?	0	0	0	?	?	?	?	?	3	?
<i>Varanops brevirostris</i>	0	0	0	0	0	1	0	?	0	0	3	?
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	?	?	0	0	?	?	?	?	?	?	?	?
<i>Varanosaurus acutirostris</i>	?	0	0	0	1	1	0	1	?	0	1	?
<i>Ophiacodon</i> spp.	?	0	0	0	1	1	0	1	0	0	1	?
<i>Stereophallodon ciscoensis</i>	?	?	0	0	?	1	0	?	?	?	1	?
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	?	0	1	0	0	0	?	1	?	1	1	?
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	1	?	?	?	?	?
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	1	0	0	0	0	2	0	0	1	1	?
<i>Edaphosaurus novomexicanus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Haptodus garnettensis</i>	0	0	1	0	0	0	1	?	0	1	1	?
<i>Pantelosaurus saxonicus</i>	?	0	?	?	0	?	?	?	?	?	2	0
<i>Cutleria wilmarthi</i>	?	0	?	?	0	?	?	?	?	?	2	0
<i>Secodontosaurus obtusidens</i>	1	0	0	0	0	1	1	1	0	0	2	0
<i>Cryptovenator hirschbergeri</i>	?	?	1	1	?	?	1	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	1	0	1	0	0	0	1	0	0	0	2	0
<i>Sphenacodon</i> spp.	1	0	1	0	0	0	1	0	0	0	2	0
<i>Biarmosuchus tener</i>	?	0	0	0	0	?	0	?	?	?	2	1
<i>Biseridens qilianicus</i>	?	0	1	1	0	0	0	?	1	0	2	1
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	1	0	1	1	0	0	0	?	?	?	2	1

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	145	146	147	148	149	150	151	152	153	154	155	156
Taxon												
<i>Tseajaia campi</i>	0	0	0	1	0	0	0	0	?	0	0	0
<i>Limnoscelis paludis</i>	0	0	0	1	0	0	0	0	?	0	0	0
<i>Captorhinus</i> spp.	0	0	0	1	0	?	0	0	1	0	1	0
<i>Protorothyris archeri</i>	0	0	0	?	0	?	0	1	1	?	1	?
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	0	?	?	0	0	0
<i>Eothyris parkeyi</i>	0	?	?	?	?	?	?	?	?	?	?	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	0	?	?	1	1	0	0	0	0	0	1	0
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	0	0
' <i>Casea</i> ' <i>rutena</i>	0	0	0	?	?	?	2	0	?	0	?	?
<i>Ennatosaurus tecton</i>	0	0	0	?	?	?	2	0	0	0	0	0
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	0	0
<i>Angelosaurus romeri</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Cotylorhynchus romeri</i>	0	?	?	1	1	0	2	0	0	0	0	0
<i>Cotylorhynchus bransoni</i>	?	?	?	?	?	?	?	?	0	0	0	0
<i>Cotylorhynchus hancocki</i>	?	?	?	0	1	?	?	?	0	0	0	0
<i>Archaeovenator hamiltonensis</i>	0	0	?	0	1	1	0	0	1	0	1	1
<i>Pyozia mesensis</i>	0	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	0	?	?	?	?	?	?	?	1	0	1	0
<i>Mesenosaurus romeri</i>	0	0	?	0	1	?	?	?	?	?	?	?
<i>Heleosaurus scholtzi</i>	0	?	?	?	1	?	0	1	1	0	1	3
BP/1/5678 (? <i>Elliotsmithia</i>)	0	?	?	?	?	?	0	1	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	2	0	0	0
<i>Aerosaurus wellesi</i>	1	0	0	0	1	?	0	1	2	0	0	0
<i>Ruthiromia elcobriensis</i>	1	0	0	?	?	?	?	?	?	0	0	0
<i>Varanodon agilis</i>	1	?	?	0	1	1	0	1	2	?	?	2
<i>Varanops brevirostris</i>	1	0	0	0	1	?	0	1	2	0	0	0
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	2	?	0	2
<i>Archaeothyris florensis</i>	?	?	?	?	?	?	0	1	1	?	1	0
<i>Varanosaurus acutirostris</i>	0	?	?	0	1	0	0	0	1	0	0	0
<i>Ophiacodon</i> spp.	0	0	0	0	1	0	0	1	1	0	0	3
<i>Stereophalodon ciscoensis</i>	0	0	0	?	?	0	?	?	1	0	0	3
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	0	1	1	0	1	?	2	2	1	?	1	1
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	?	?	?	?	?	?	?	?	0	0	1	0
<i>Edaphosaurus boanerges</i>	0	1	1	?	?	?	2	0	0	0	1	0
<i>Edaphosaurus novomexicanus</i>	?	?	?	?	1	?	2	0	0	0	1	0
<i>Haptodus garnettensis</i>	0	1	1	0	1	1	0	1	1	0	0	0
<i>Pantelosaurus saxonicus</i>	?	?	?	0	1	?	?	?	?	?	?	?
<i>Cutleria wilmarti</i>	0	?	?	?	?	1	0	1	?	?	?	?
<i>Secodontosaurus obtusidens</i>	0	1	1	?	?	1	1	1	2	1	1	2
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	1	?	?	?	1	1	0	2
<i>Dimetrodon</i> spp.	0	1	1	0	1	1	1	2 {12}	1 {01}	2		
<i>Sphenacodon</i> spp.	0	1	1	?	?	1	1	2	2	1	0	2
<i>Biarmosuchus tener</i>	0	?	?	?	1	?	?	?	2	?	0	?
<i>Biseridens qilianicus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	0	1	1	0	1	?	0	1	2	?	0	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

<u>Character:</u>	157	158	159	160	161	162	163	164	165	166	167	168
Taxon												
<i>Tseajaia campi</i>	0	1	0	0	0	0	1	0	?	0	1	0
<i>Limnoscelis paludis</i>	0	0	0	0	0	0	1	0	0	0	?	0
<i>Captorhinus</i> spp.	0	0	0	0	0	0	1	0	0	0	1	0
<i>Protorothyris archeri</i>	0	0	?	?	?	?	0	0	?	?	?	0
<i>Echinerpeton intermedium</i>	?	0	0	0	?	?	0	2	0	0	0	0
<i>Eothyris parkeyi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	1	1	0	0	0	0	0	0	0	0	0	0
<i>Trichasaurus texensis</i>	1	1	1	0	0	?	0	?	?	?	?	0
' <i>Casea</i> ' <i>rutena</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ennatosaurus tecton</i>	?	1	?	?	0	?	?	0	?	?	?	0
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	1	1	1	1	0	0	0	0	?	1	?	0
<i>Angelosaurus romeri</i>	1	1	1	1	0	0	0	0	0	1	0	0
<i>Cotylorhynchus romeri</i>	1	1	1	1	0	0	0	0	0	1	0	0
<i>Cotylorhynchus bransoni</i>	1	1	1	1	1	0	0	0	0	1	0	0
<i>Cotylorhynchus hancocki</i>	1	1	1	1	1	1	0	0	0	1	0	0
<i>Archaeovenator hamiltonensis</i>	0	0	0	?	?	?	0	0	1	0	0	0
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	0	0	0	?	?	?	0	1	1	0	0	0
<i>Mesenosaurus romeri</i>	?	?	?	?	?	?	0	0	?	0	0	0
<i>Heleosaurus scholtzi</i>	0	0	0	?	?	?	0	0	?	0	0	0
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	?	?	?	?	?	?	2	0	?	0	0	0
<i>Ruthiromia elcobriensis</i>	0	0	0	?	?	?	2	1	2	0	0	0
<i>Varanodon agilis</i>	?	0	?	?	?	?	2	1	2	0	0	0
<i>Varanops brevirostris</i>	0	0	0	0	0	0	2	1	2	0	0	0
<i>Watonia meieri</i>	0	0	?	0	1	0	2	1	?	0	0	0
<i>Archaeothyris florensis</i>	0	0	0	0	?	?	0	0	0	0	0	0
<i>Varanosaurus acutirostris</i>	0	0	0	0	0	0	1	0	0	0	1	0
<i>Ophiacodon</i> spp.	0	0	0	0	1	0	0	1	0	0	0	0
<i>Stereophallodon ciscoensis</i>	0	0	0	0	?	?	0	0	?	0	?	0
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	0	1	1	0	1	0	2	2	3	0	0	1
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	?	1	1	1	1	1	0	2	3	0	0	1
<i>Edaphosaurus boanerges</i>	1	1	1	1	1	1	0	2	3	0	0	1
<i>Edaphosaurus novomexicanus</i>	?	1	1	1	1	1	0	2	?	0	0	1
<i>Haptodus garnettensis</i>	{12}	1	0	?	?	?	2	0	0	0	0	0
<i>Pantelosaurus saxonicus</i>	?	?	?	?	?	?	2	1	0	0	0	0
<i>Cutleria wilmarti</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Secodontosaurus obtusidens</i>	1	?	0	0	1	0	2	2	0	0	0	1
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	1	1	0	?	?	?	2	2	0	0	0	0
<i>Dimetrodon</i> spp.	1	1	0	0	1	1	2	2	0	0	0	1
<i>Sphenacodon</i> spp.	1	1	0	0	1	0	2	2	0	0	0	0
<i>Biarmosuchus tener</i>	2	?	0	?	?	?	0	1	0	0	0	0
<i>Biseridens qilianicus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	2	1	0	2	?	0	0	1	0	0	0	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	169	170	171	172	173	174	175	176	177	178	179	180
Taxon												
<i>Tseajaia campi</i>	0	0	0	0	0	0	0	1	0	?	0	0
<i>Limnoscelis paludis</i>	0	0	?	0	?	0	0	0	0	1	0	0
<i>Captorhinus</i> spp.	0	0	0	0	0	0	0	1	0	0	0	2
<i>Protorothyris archeri</i>	0	0	0	0	0	0	0	1	0	0	0	2
<i>Echinerpeton intermedium</i>	0	0	0	0	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	0	1	1	1	1	0	0	1	?	0	1	?
<i>Trichasaurus texensis</i>	?	?	?	1	1	0	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ennatosaurus tecton</i>	0	1	1	1	1	0	0	1	0	0	1	?
<i>Caseopsis agilis</i>	?	1	2	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	0	?	?	1	1	0	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	0	1	2	1	1	0	0	0	0	0	1	?
<i>Cotylorhynchus romeri</i>	0	1	2	1	1	0	0	0	0	0	1	?
<i>Cotylorhynchus bransoni</i>	0	1	?	1	1	0	0	0	0	0	1	?
<i>Cotylorhynchus hancocki</i>	0	1	?	1	1	0	0	0	0	0	0	0
<i>Archaeovenator hamiltonensis</i>	0	0	?	0	1	0	?	1	0	?	1	?
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	0	?	0	?	?	?	0	?	0	0	1	?
<i>Mesenosaurus romeri</i>	0	0	?	0	?	?	?	1	?	0	?	?
<i>Heleosaurus scholtzi</i>	0	0	0	?	?	?	0	1	0	0	1	?
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	0	0
<i>Aerosaurus wellesi</i>	0	0	0	1	0	0	0	1	0	0	0	1
<i>Ruthiromia elcobriensis</i>	0	?	?	?	?	?	?	?	?	1	0	0
<i>Varanodon agilis</i>	0	0	0	0	0	0	?	1	0	?	?	?
<i>Varanops brevirostris</i>	0	0	0	0	0	0	0	1	0	0	1	?
<i>Watonia meieri</i>	0	?	?	?	?	?	0	1	0	0	1	?
<i>Archaeothyris florensis</i>	0	0	0	?	0	0	?	?	?	?	?	?
<i>Varanosaurus acutirostris</i>	0	?	?	0	0	0	?	?	0	1	?	?
<i>Ophiacodon</i> spp.	0	0	0	0	0	0	0	1	0	1	0	0
<i>Stereophallodon ciscoensis</i>	0	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	1	0	0	?	?	?	0	1	0	?	?	?
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	0	0	0	1	1	0	0	0	?	0	0	2
<i>Edaphosaurus boanerges</i>	1	1	1	1	1	0	0	0	0	0	0	0
<i>Edaphosaurus novomexicanus</i>	1	1	1	?	?	1	0	0	?	0	0	0
<i>Haptodus garnettensis</i>	0	0	0	?	?	?	0	1	0	0	0	2
<i>Pantelosaurus saxonicus</i>	0	0	?	1	?	?	0	1	1	?	?	?
<i>Cutleria wilmarti</i>	?	?	?	?	?	?	0	1	1	0	0	2
<i>Secodontosaurus obtusidens</i>	0	?	?	?	1	0	0	?	1	0	0	1
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	0	0	0	1	1	0	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	0	0	0	1	1	0	0	1	1	0	0	1
<i>Sphenacodon</i> spp.	0	0	?	?	?	?	0	1	1	0	0	1
<i>Biarmosuchus tener</i>	0	?	?	?	?	?	1	1	1	2	1	?
<i>Biseridens qilianicus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	0	0	0	1	1	0	1	1	1	2	1	?

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	181	182	183	184	185	186	187	188	189	190	191	192
Taxon												
<i>Tseajaia campi</i>	0	0	0	1	0	0	2	0	0	?	0	0
<i>Limnoscelis paludis</i>	0	0	0	1	0	0	2	0	?	0	0	?
<i>Captorhinus</i> spp.	1	?	0	0	0	0	3	1	0	?	0	0
<i>Protorothyris archeri</i>	1	0	0	?	?	0	3	1	0	0	0	?
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	0	0	0	?
<i>Eothyris parkeyi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	?	?	0	?	0	0	?	?	?	?	?	0
<i>Trichasaurus texensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	?	?	?	?	?	?	2	0	?	1	1	?
<i>Ennatosaurus tecton</i>	?	0	?	?	0	0	?	?	?	1	1	0
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus romeri</i>	?	1	0	0	0	0	?	?	1	1	1	0
<i>Cotylorhynchus romeri</i>	?	1	0	0	0	0	2	0	1	1	1	0
<i>Cotylorhynchus bransoni</i>	?	1	0	0	0	0	2	0	1	1	1	0
<i>Cotylorhynchus hancocki</i>	0	1	0	0	0	0	2	0	1	1	1	0
<i>Archaeovenator hamiltonensis</i>	?	0	0	?	?	0	0	0	?	2	0	?
<i>Pyozia mesensis</i>	?	?	?	?	?	?	0	0	0	?	0	?
<i>Mycterosaurus longiceps</i>	?	0	?	?	?	?	?	?	?	?	?	?
<i>Mesenosaurus romeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Heleosaurus scholtzi</i>	?	0	0	?	?	0	0	?	?	?	?	?
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	0	?	?	0	0	1	?	?	?	?	?	0
<i>Aerosaurus wellesi</i>	0	0	1	?	?	?	?	?	?	?	?	0
<i>Ruthiromia elcobriensis</i>	0	?	?	?	0	1	?	?	?	?	?	0
<i>Varanodon agilis</i>	?	?	?	?	?	?	0	0	?	?	?	?
<i>Varanops brevirostris</i>	?	0	1	0	0	0	2	1	0	2	0	0
<i>Watonia meieri</i>	?	0	?	?	?	?	0	0	0	?	?	0
<i>Archaeothyris florensis</i>	?	?	?	?	?	?	?	?	?	?	?	1
<i>Varanosaurus acutirostris</i>	?	?	?	?	?	0	?	?	?	?	?	1
<i>Ophiacodon</i> spp.	1	0	1	0	0	0	0	0	0	0	0	1
<i>Stereophallodon ciscoensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	?	0	0	0	?	?	?	?	?	?	?	1
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	1	?	?	?	0	0	1	1	0	0	1	1
<i>Edaphosaurus boanerges</i>	1	0	0	0	0	0	1	1	0	0	1	1
<i>Edaphosaurus novomexicanus</i>	1	?	?	?	0	0	1	1	0	0	1	?
<i>Haptodus garnettensis</i>	1	0	1	?	?	1	0	1	0	0	0	1
<i>Pantelosaurus saxonicus</i>	?	?	0	?	?	?	?	?	?	?	?	?
<i>Cutleria wilmarti</i>	1	0	0	0	?	?	0	1	?	?	?	?
<i>Secodontosaurus obtusidens</i>	1	0	?	0	1	1	?	?	?	?	?	1
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	1	0	0	0	1	1	1	1	0	0	1	1
<i>Sphenacodon</i> spp.	1	0	0	0	1	1	?	?	?	?	?	1
<i>Biarmosuchus tener</i>	?	0	0	0	?	?	?	?	?	?	0	?
<i>Biseridens qilianicus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	?	0	?	?	?	?	?	?	?	?	?	1

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	193	194	195	196	197	198	199	200	201	202	203	204
Taxon												
<i>Tseajaia campi</i>	1	?	?	?	1	0	0	0	1	?	1	1
<i>Limnoscelis paludis</i>	?	?	?	?	1	0	0	0	1	?	?	1
<i>Captorhinus</i> spp.	?	0	0	0	1	3	0	0	1	0	0	1
<i>Protorothyris archeri</i>	?	?	0	?	1	3	0	0	?	?	?	?
<i>Echinerpeton intermedium</i>	?	?	?	?	0	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	0	0	0	0	0	2	0	0	0	?	0	1
<i>Trichasaurus texensis</i>	?	0	0	0	?	?	?	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	?	?	?	?	?	?	?	?	1	0	0	1
<i>Ennatosaurus tecton</i>	?	?	?	?	1	2	0	?	?	?	?	1
<i>Caseopsis agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Angelosaurus dolani</i>	1	1	1	0	1	1	0	0	?	?	?	?
<i>Angelosaurus romeri</i>	1	1	1	0	1	1	0	0	?	?	?	?
<i>Cotylorhynchus romeri</i>	?	1	1	0	1	1	0	0	0	0	0	1
<i>Cotylorhynchus bransoni</i>	?	1	1	0	1	1	0	0	?	?	?	?
<i>Cotylorhynchus hancocki</i>	1	1	1	0	1	1	0	0	?	?	?	?
<i>Archaeovenator hamiltonensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	?	0	?	?	?	0	1	?	?	?	?	?
<i>Mesenosaurus romeri</i>	?	?	?	?	?	?	1	?	1	0	0	1
<i>Heleosaurus scholtzi</i>	?	?	?	?	?	1	1	?	1	0	1	1
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	1	1	1	1	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	1	1	?	?	?	0	?	0	1	0	0	1
<i>Ruthiromia elcobriensis</i>	0	1	1	1	?	0	0	?	?	?	?	?
<i>Varanodon agilis</i>	?	0	0	0	?	?	?	?	1	0	0	1
<i>Varanops brevirostris</i>	0	0	0	0	0	0	0	0	1	0	0	1
<i>Watonia meieri</i>	?	0	0	?	?	0	0	?	1	0	0	1
<i>Archaeothyris florensis</i>	0	0	0	0	1	0	0	0	?	?	?	?
<i>Varanosaurus acutirostris</i>	0	0	?	?	?	?	?	?	?	?	?	?
<i>Ophiacodon</i> spp.	0	0	0	0	0	0	2	0	0	0	0	0
<i>Stereophallodon ciscoensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	1	?	?	?	?	0	0	0	?	?	?	?
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	1	0	0	1	0	0	0	0	?	?	?	?
<i>Edaphosaurus boanerges</i>	1	0	0	1	0	1	0	0	?	?	?	?
<i>Edaphosaurus novomexicanus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Haptodus garnettensis</i>	?	0	0	0	?	0	0	?	?	?	?	0
<i>Pantelosaurus saxonicus</i>	?	?	?	?	0	0	0	?	?	?	?	?
<i>Cutleria wilmarti</i>	?	?	?	?	?	?	?	?	?	1	?	0
<i>Secodontosaurus obtusidens</i>	1	0	0	0	0	0	0	0	?	?	?	?
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	1	0	0	0	0	0	0	1	0	1	0	0
<i>Sphenacodon</i> spp.	1	0	0	0	0	0	0	1	?	?	?	?
<i>Biarmosuchus tener</i>	?	?	?	?	0	3	0	?	0	0	1	0
<i>Biseridens qilianicus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	?	0	?	?	0	1	0	0	0	0	1	0

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	205	206	207	208	209	210	211	212	213	214	215	216
Taxon												
<i>Tseajaia campi</i>	1	1	0	0	0	0	0	0	2	0	?	0
<i>Limnoscelis paludis</i>	1	1	0	0	0	0	0	0	2	0	1	0
<i>Captorhinus</i> spp.	1	0	0	0	0	0	0	?	?	0	1	0
<i>Protorothyris archeri</i>	?	?	?	?	?	?	?	?	?	0	?	?
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Eothyris parkeyi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	1	0	0	?	?	?
<i>Casea broili</i>	1	0	0	?	?	?	1	0	0	0	?	1
<i>Trichasaurus texensis</i>	?	0	?	?	?	?	?	0	?	0	0	1
' <i>Casea</i> ' <i>rutena</i>	0	1	1	0	0	1	1	?	?	?	?	?
<i>Ennatosaurus tecton</i>	?	1	0	1	1	?	?	0	?	0	?	1
<i>Caseopsis agilis</i>	?	?	?	?	?	?	1	?	?	0	0	1
<i>Angelosaurus dolani</i>	?	1	?	1	1	1	?	?	?	0	0	1
<i>Angelosaurus romeri</i>	?	?	?	?	?	?	1	?	?	0	0	1
<i>Cotylorhynchus romeri</i>	0	1	0	1	1	1	1	0	1	0	0	1
<i>Cotylorhynchus bransoni</i>	?	1	?	1	1	1	?	?	?	0	0	1
<i>Cotylorhynchus hancocki</i>	?	1	?	1	1	1	?	0	1	0	0	1
<i>Archaeovenator hamiltonensis</i>	?	?	?	?	?	?	?	?	?	0	?	0
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	?	?	?	?	?	?	?	?	?	0	?	0
<i>Mesenosaurus romeri</i>	2	0	1	0	0	0	0	0	?	0	?	0
<i>Heleosaurus scholtzi</i>	1	0	1	?	?	?	0	?	?	0	?	0
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	2	0	1	0	0	0	0	0	?	0	?	0
<i>Ruthiromia elcobriensis</i>	?	?	?	?	?	?	?	?	?	0	1	0
<i>Varanodon agilis</i>	2	0	1	0	0	0	0	0	?	?	?	?
<i>Varanops brevirostris</i>	2	0	?	?	?	?	0	0	0	0	1	0
<i>Watonia meieri</i>	2	0	1	0	0	0	0	0	?	?	?	?
<i>Archaeothyris florensis</i>	?	?	?	?	?	?	?	?	?	0	?	?
<i>Varanosaurus acutirostris</i>	?	?	?	?	?	?	?	?	?	0	1	0
<i>Ophiacodon</i> spp.	1	0	1	0	0	0	0	0	0	0	1	0
<i>Stereophallodon ciscoensis</i>	?	?	?	?	?	?	?	?	?	?	?	0
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	?	0	?	?	?	?	?	?	?	0	?	1
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	?	0	?	?	?	?	0	?	?	0	0	1
<i>Edaphosaurus boanerges</i>	?	?	?	?	?	?	?	1	0	0	0	1
<i>Edaphosaurus novomexicanus</i>	?	0	?	?	?	?	0	?	?	?	?	?
<i>Haptodus garnettensis</i>	?	0	0	0	0	0	0	1	?	0	0	1
<i>Pantelosaurus saxonicus</i>	?	?	?	?	?	?	?	?	?	?	?	1
<i>Cutleria wilmarti</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Secodontosaurus obtusidens</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	0	?	1
<i>Dimetrodon</i> spp.	1	0	0	0	0	0	0	1	0	0	0	1
<i>Sphenacodon</i> spp.	?	?	?	?	?	?	?	?	?	?	0	1
<i>Biarmosuchus tener</i>	?	0	0	0	0	?	0	1	?	1	?	1
<i>Biseridens qilianicus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	0	0	0	0	1	1	0	1	0	1	0	1

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

Character:	217	218	219	220	221	222	223	224	225	226	227	228
Taxon												
<i>Tseajaia campi</i>	0	1	?	?	0	0	?	0	0	0	?	0
<i>Limnoscelis paludis</i>	0	1	1	0	0	0	0	0	0	0	?	0
<i>Captorhinus</i> spp.	1	1	0	0	0	0	0	0	0	0	1	0
<i>Protorothyris archeri</i>	?	0	?	?	0	?	?	?	0	0	?	?
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Eothyris parkeyi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	2	0	2	1	0	0	0	0	0	0	0	0
<i>Trichasaurus texensis</i>	2	0	?	1	0	?	?	0	0	0	?	0
' <i>Casea</i> ' <i>rutena</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ennatosaurus tecton</i>	2	?	?	?	?	0	?	0	0	?	?	?
<i>Caseopsis agilis</i>	2	0	3	1	0	0	0	0	0	0	0	0
<i>Angelosaurus dolani</i>	2	0	3	1	0	0	0	0	0	0	0	0
<i>Angelosaurus romeri</i>	2	0	3	1	0	0	0	0	0	0	0	0
<i>Cotylorhynchus romeri</i>	2	0	3	1	0	0	0	0	0	0	0	0
<i>Cotylorhynchus bransoni</i>	2	0	3	1	0	0	0	0	0	0	0	0
<i>Cotylorhynchus hancocki</i>	2	0	3	1	0	0	0	0	0	0	0	0
<i>Archaeovenator hamiltonensis</i>	?	0	1	?	1	0	?	1	0	0	0	0
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	1	0	2	?	1	0	?	1	0	0	0	0
<i>Mesenosaurus romeri</i>	1	?	?	?	?	?	?	1	0	0	?	0
<i>Heleosaurus scholtzi</i>	?	0	{12}	1	1	0	?	1	0	0	0	0
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus wellesi</i>	1	?	?	?	?	0	?	?	?	?	?	?
<i>Ruthiromia elcobriensis</i>	1	0	1	?	1	0	1	0	0	0	1	0
<i>Varanodon agilis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Varanops brevirostris</i>	2	0	1	1	1	0	1	0	0	0	1	1
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	?	0	2	?	0	0	?	0	0	0	?	0
<i>Varanosaurus acutirostris</i>	0	0	2	0	0	?	?	0	0	0	1	0
<i>Ophiacodon</i> spp.	0	0	0	0	0	0	0	0	0	0	1	0
<i>Stereophallodon ciscoensis</i>	0	?	?	?	?	?	?	0	?	?	?	?
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	2	?	?	?	?	1	?	?	?	?	?	?
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	2	0	4	1	0	1	0	0	0	0	0	0
<i>Edaphosaurus boanerges</i>	2	0	4	1	0	1	0	0	0	0	0	0
<i>Edaphosaurus novomexicanus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Haptodus garnettensis</i>	2	0	?	1	?	1	0	0	0	0	1	?
<i>Pantelosaurus saxonicus</i>	2	0	?	?	1	1	?	?	?	?	?	?
<i>Cutleria wilmarti</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Secodontosaurus obtusidens</i>	?	?	?	?	?	?	?	1	0	0	1	1
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	2	0	1	?	1	1	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	2	0	1	1	1	1	0	1	0	0	1	1
<i>Sphenacodon</i> spp.	2	0	1	1	1	1	0	1	0	0	1	1
<i>Biarmosuchus tener</i>	2	1	?	?	?	0	?	1	1	1	1	1
<i>Biseridens qilianicus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	2	1	1	1	1	0	0	1	1	1	1	1

Benson, RBJ — Basal synapsid phylogeny — Appendix S2, data matrix

<u>Character:</u>	229	230	231	232	233	234	235	236	237	238	239
Taxon											
<i>Tseajaia campi</i>	0	1	0	0	?	?	?	0	?	?	0
<i>Limnoscelis paludis</i>	0	1	0	0	?	?	0	0	?	?	0
<i>Captorhinus</i> spp.	0	1	3	0	0	0	1	1	0	0	0
<i>Protorothyris archeri</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Echinerpeton intermedium</i>	?	?	?	?	?	?	?	?	?	0	0
<i>Eothyris parkeyi</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Oedaleops campi</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Oromycter dolesorum</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Casea broili</i>	0	0	0	0	1	0	0	1	0	0	1
<i>Trichasaurus texensis</i>	0	0	0	0	1	0	?	?	?	?	?
' <i>Casea</i> ' <i>rutena</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Ennatosaurus tecton</i>	?	?	?	?	?	?	?	1	0	0	1
<i>Caseopsis agilis</i>	0	0	0	0	0	0	?	?	?	?	?
<i>Angelosaurus dolani</i>	0	0	0	0	1	0	0	1	0	1	?
<i>Angelosaurus romeri</i>	0	0	0	0	1	0	?	?	?	?	?
<i>Cotylorhynchus romeri</i>	0	0	0	1	1	0	0	1	0	1	?
<i>Cotylorhynchus bransoni</i>	0	0	0	0	1	0	0	1	0	1	1
<i>Cotylorhynchus hancocki</i>	0	0	0	0	1	0	0	1	0	1	1
<i>Archaeovenator hamiltonensis</i>	0	?	?	?	?	?	?	1	0	1	0
<i>Pyozia mesensis</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Mycterosaurus longiceps</i>	0	1	0	0	0	1	?	1	0	0	0
<i>Mesenosaurus romeri</i>	?	?	?	0	?	?	?	?	?	?	?
<i>Heleosaurus scholtzi</i>	?	?	?	?	?	?	?	1	0	0	?
BP/1/5678 (? <i>Elliotsmithia</i>)	?	?	?	?	?	?	?	?	?	?	?
<i>Basicranodon fortsillensis</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Aerosaurus greenleeorum</i>	?	?	?	?	?	?	?	1	0	0	?
<i>Aerosaurus wellesi</i>	?	?	?	?	?	?	?	1	0	0	1
<i>Ruthiromia elcobriensis</i>	0	1	1	0	0	?	0	1	0	1	1
<i>Varanodon agilis</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Varanops brevirostris</i>	0	1	3	0	0	0	0	1	0	0	0
<i>Watonia meieri</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeothyris florensis</i>	0	1	?	?	?	?	?	?	?	?	?
<i>Varanosaurus acutirostris</i>	0	1	0	0	0	1	0	1	0	0	?
<i>Ophiacodon</i> spp.	0	1	2	0	0	1	0	1	0	0	0
<i>Stereophallodon ciscoensis</i>	?	?	0	0	0	0	0	1	0	1	?
<i>Ianthodon schultzei</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus hardestii</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Glaucosaurus megalops</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Lupeosaurus kayi</i>	0	1	1	1	1	0	?	?	?	?	?
<i>Edaphosaurus boanerges</i>	0	1	1	1	1	0	1	1	0	1	?
<i>Edaphosaurus novomexicanus</i>	?	?	?	?	?	?	1	?	?	?	?
<i>Haptodus garnettensis</i>	0	1	0	0	?	?	?	1	0	1	1
<i>Pantelosaurus saxonicus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Cutleria wilmarti</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Secodontosaurus obtusidens</i>	0	1	3	0	0	0	1	?	?	?	?
<i>Cryptovenator hirschbergeri</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Ctenorhachis jacksoni</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Dimetrodon</i> spp.	0	0	3	0	0	0	1	1	0	1	1
<i>Sphenacodon</i> spp.	0	1	3	0	0	0	?	?	?	?	?
<i>Biarmosuchus tener</i>	1	?	?	2	?	?	?	?	?	?	?
<i>Biseridens qilianicus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Raranimus dashankouensis</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Titanophoneus potens</i>	1	0	3	2	?	0	1	1	1	0	0

Benson — Basal synapsid phylogeny—Appendix Table S2, optimisation by clade

AMNIOTA

Unambiguous: 16(1->0), 27(1->0), 46(0->1), 60(0->2), 75(1->0), 114(1->0), 122(3->0), 128(1->0), 155(0->1), 184(1->0), 206(1->0), 236(0->1); ACCTRAN: 13(1->0), 18(1->0), 66(0->1), 88(0->2), 101(2->0), 134(1->0), 140(0->1), 163(1->0), 181(0->1), 187(2->0), 213(2->0), 217(0->1), 218(1->0)

EUREPTILIA

Unambiguous: 11(0->2), 47(1->0), 77(0->1), 91(1->0), 180(0->2), 188(0->1), 198(0->3); DELTRAN: 66(0->1), 181(0->1), 187(2->3); ACCTRAN: 141(0->1), 187(0->3), 219(1->0), 227(0->1), 231(0->3), 235(0->1)

SYNAPSIDA

Unambiguous: 6(0->1), 19(0->1), 41(0->1), 149(0->1), 167(1->0), 197(1->0); DELTRAN: 13(1->0), 18(1->0), 88(0->2), 101(2->0), 163(1->0), 213(2->0), 218(1->0); ACCTRAN: 3(0->1), 21(1->0), 32(1->0), 61(2->0), 68(0->1), 69(0->1), 90(0->1), 95(1->0), 102(1->0), 148(1->0), 201(1->0), 220(0->1)

Ophiacodontidae + Varanopidae

Unambiguous: 29(0->2), 85(1->2), 126(0->2), 138(0->1), 142(1->0), 193(1->0), 207(0->1); DELTRAN: 3(0->1), 21(1->0), 61(2->1), 68(0->1), 69(0->1), 90(0->1), 95(1->0), 134(1->0), 148(1->0), 187(2->0); ACCTRAN: 15(0->1), 61(0->1), 152(0->1), 234(0->1)

Varanopidae

Unambiguous: 4(0->2), 19(1->2), 34(2->0), 59(1->0), 72(0->2), 80(0->1), 150(0->1), 165(0->1), 179(0->1), 190(0->2), 221(0->1); DELTRAN: 15(0->1), 102(1->0); ACCTRAN: 51(0->1), 91(1->0), 181(1->0), 201(0->1), 205(1->2), 223(0->1), 224(0->1)

Pyozia + Mycterosaurinae + Varanodontinae

Unambiguous: 109(0->1), 123(0->1); ACCTRAN: 12(0->1), 25(0->1), 30(0->2), 52(0->1), 67(0->1), 108(0->1), 132(0->1), 164(0->1)

Mycterosaurinae + Varanodontinae

Unambiguous: 34(0->1), 40(0->2), 41(1->2), 42(0->1); DELTRAN: 12(0->1), 25(0->1), 132(0->1), 152(0->1), 217(0->1), 220(0->1); ACCTRAN: 71(0->2)

Mycterosaurinae

Unambiguous: 4(2->1), 22(0->2), 43(0->1), 53(0->1), 75(0->1), 199(0->1); DELTRAN: 52(0->1), 67(0->1), 91(1->0), 224(0->1); ACCTRAN: 29(2->0), 81(0->1), 219(1->2)

Mesenosaurus + Heleosaurus + BP/1/5678

Unambiguous: 17(0->1), 34(1->2), 36(0->1), 69(1->0), 84(0->1), 87(0->1); DELTRAN: 51(0->1), 81(0->1), 108(0->1); ACCTRAN: 30(2->0), 65(0->1), 71(1->0), 156(0->3), 164(1->0), 198(0->1)

Varanodontinae

Unambiguous: 2(1->0), 10(0->1), 26(0->1), 74(0->1), 78(0->1), 82(1->0), 90(1->2), 92(0->1), 111(0->1), 143(0->3), 145(0->1), 153(1->2), 155(1->0), 163(0->2), 165(1->2), 183(0->1), 227(0->1); DELTRAN: 30(0->2), 32(1->2), 52(0->2), 71(0->1), 205(1->2), 223(0->1); ACCTRAN: 32(0->2), 51(1->0), 52(1->2), 68(1->0), 108(1->0), 224(1->0), 231(0->1), 234(1->0)

Varanops + Varanodon + Watongia

Unambiguous: 15(1->0), 17(0->1), 25(1->2), 36(0->1), 130(0->2); DELTRAN: 68(1->0), 164(0->1); ACCTRAN: 91(0->1), 217(1->2), 228(0->1), 231(1->3)

Varanodon + Watongia

Unambiguous: 156(0->2); DELTRAN: 67(0->1); ACCTRAN: 2(0->2), 12(1->0), 59(0->1), 161(0->1)

Ruthiromia + Aerosaurus wellesi + A. greenleorum

Unambiguous: 179(1->0), 186(0->1), 194(0->1), 195(0->1), 196(0->1), 239(0->1); ACCTRAN: 84(0->1), 105(0->1), 106(1->0), 172(0->1)

Aerosaurus wellesi + A. greenleorum

Unambiguous: 193(0->1); DELTRAN: 105(0->1), 106(1->0); ACCTRAN: 164(1->0)

Ophiacodontidae

Unambiguous: 7(1->0), 37(0->1), 94(0->1), 192(0->1), 219(1->2); ACCTRAN: 14(0->2), 17(0->1), 36(0->1), 47(1->2), 54(0->1), 75(0->1), 76(0->1), 86(1->0), 96(0->2), 102(0->2), 116(0->1), 137(0->1), 143(0->1), 178(0->1), 183(0->1), 204(1->0), 217(1->0), 220(1->0), 227(0->1)

Varanosaurus + Ophiacodon spp. + Stereophallodon

Unambiguous: 2(1->3), 27(0->1), 70(0->1), 79(0->1), 155(1->0); DELTRAN: 14(0->2), 17(0->1), 32(1->2), 47(1->2), 54(0->1), 75(0->1), 76(0->1), 86(1->0), 96(0->2), 102(1->2), 137(0->1), 140(0->1), 143(0->1), 178(0->1), 227(0->1); ACCTRAN: 32(0->2), 38(0->1), 99(0->1), 199(0->2)

Ophiacodon + Stereophallodon

Unambiguous: 18(0->1), 122(0->1), 156(0->3); DELTRAN: 38(0->1), 99(0->1); ACCTRAN: 10(0->1), 15(1->0), 25(0->1), 66(1->0), 161(0->1), 219(2->0)

CASEASAURIA + Ianthodon + Edpahpsauridae + Sphenacodontia

Unambiguous: 92(0->1), 123(0->1), 124(1->0), 157(0->1), 158(0->1), 172(0->1), 173(0->1), 215(1->0), 216(0->1), 239(0->1); DELTRAN: 61(2->0), 201(1->0), 217(0->2), 220(0->1); ACCTRAN: 30(0->1), 98(0->1), 127(0->1), 131(0->1), 191(0->1), 217(1->2), 233(0->1)

Table S2. Optimisation of characters by node in the cladogram. The notation ‘+++’ indicates the clade comprising the named taxon and all more derived taxa within its clade. For example, ‘*Varanosaurus* +++’ indicates the clade comprising *Varanosaurus* and all more derived ophiacodontids (i.e. *Varanosaurus* + *Ophiacodon* + *Stereophallodon*).

Benson — Basal synapsid phylogeny—Appendix Table S2, optimisation by clade

CASEASURIA

Unambiguous: 14(0->1), 48(0->1), 56(1->0), 60(2->1), 71(0->2), 72(0->2), 82(1->0), 84(0->1), 88(2->1), 96(0->1), 109(0->1), 129(0->1); DELTRAN: 30(0->1), 68(0->1), 90(0->1), 102(1->0); ACCTRAN: 1(0->1), 2(1->0), 3(1->0), 21(0->1), 25(0->1), 28(0->1), 34(2->1), 45(0->1), 66(1->0), 69(1->0), 73(1->0), 86(1->0), 95(0->1), 134(0->1), 148(0->1), 153(1->0), 170(0->1), 171(0->1), 179(0->1), 181(1->0), 187(0->2), 189(0->1), 190(0->1), 198(0->2), 210(0->1), 211(0->1), 219(1->2), 230(1->0)

Eothyrididae

Unambiguous: 16(0->1), 39(0->1), 47(1->0); DELTRAN: 2(1->2), 32(1->0), 86(1->0); ACCTRAN: 2(0->2), 75(0->1), 98(1->0), 127(1->0), 131(1->0)

Caseidae

Unambiguous: 4(0->2), 29(0->1), 40(0->1), 41(1->0), 50(0->1); DELTRAN: 25(0->1), 28(0->1), 45(0->1), 127(0->1), 211(0->1); ACCTRAN: 9(0->2), 11(0->1), 57(0->1), 59(1->0), 85(1->0), 86(0->2), 93(0->1), 97(0->2), 101(0->1)

Casea broili +++

Unambiguous: 23(0->1); DELTRAN: 1(0->1), 2(1->0), 9(0->2), 11(0->1), 34(2->0), 85(1->0), 86(1->2), 97(0->2), 98(0->1), 101(0->1), 131(0->1), 153(1->0), 170(0->1), 171(0->1), 179(0->1), 198(0->2), 230(1->0), 233(0->1); ACCTRAN: 24(0->1), 34(1->0), 44(0->1)

Trichasaurus +++

Unambiguous: 155(1->0), 159(0->1); ACCTRAN: 44(1->2), 111(0->1), 119(0->1), 122(0->1), 126(0->1), 139(0->1), 142(1->0), 151(0->2), 166(0->1), 197(0->1), 205(1->0), 213(0->1), 219(2->3)

'Casea' rutena +++

Unambiguous: Unambiguous: 206(0->1); DELTRAN: 24(0->1), 44(0->2), 93(0->1), 122(0->1), 126(0->1), 139(0->1), 151(0->2), 190(0->1), 191(0->1), 205(1->0), 210(0->1); ACCTRAN: 160(0->1), 194(0->1), 195(0->1)

Ennatosaurus +++

Unambiguous: 5(0->1), 91(1->0), 208(0->1), 209(0->1); DELTRAN: 57(0->1), 59(1->0), 119(0->1), 142(1->0), 197(0->1); ACCTRAN: 73(0->1), 110(1->0)

Angelosaurus + Cotylorhynchus romeri + C. bransoni + C. hancocki

Unambiguous: 171(1->2), 176(1->0), 182(0->1), 198(2->1); DELTRAN: 110(1->0), 160(0->1), 166(0->1), 189(0->1), 194(0->1), 195(0->1), 219(1->3); ACCTRAN: 25(1->2), 101(1->0), 115(0->1), 238(0->1)

Cotylorhynchus romeri + C. bransoni + C. hancocki

Unambiguous: 29(1->0), 44(2->1); DELTRAN: 25(1->2), 213(0->1), 238(0->1)

Cotylorhynchus bransoni + C. hancocki

Unambiguous: 161(0->1); ACCTRAN: 148(1->0)

Ianthodon + Edaphosauridae + Sphenacodontia

Unambiguous: 9(0->1), 54(0->1), 62(0->1), 77(0->2); DELTRAN: 3(0->1), 30(0->3), 66(0->1), 69(0->1); ACCTRAN: 30(1->3), 32(0->1), 68(1->0), 90(1->0), 94(0->1), 102(0->1), 103(0->1), 107(1->0), 116(0->1), 120(0->1), 125(0->1), 130(0->1), 132(0->1), 135(0->1), 139(0->1), 143(0->1), 146(0->1), 147(0->1), 150(0->1), 161(0->1), 163(0->2), 180(0->2), 188(0->1), 192(0->1), 204(1->0), 212(0->1), 222(0->1), 235(0->1), 238(0->1)

Edaphosauridae + Sphenacodontia

Unambiguous: 47(1->0); DELTRAN: 21(1->0), 94(0->1), 95(1->0), 103(0->1), 107(1->0), 116(0->1), 120(0->1), 125(0->1), 127(0->1), 130(0->1), 132(0->1), 139(0->1), 143(0->1), 146(0->1), 147(0->1), 148(1->0), 161(0->1), 181(0->1), 188(0->1), 192(0->1), 212(0->1), 222(0->1), 235(0->1), 238(0->1); ACCTRAN: 17(0->1), 42(0->1), 85(1->2)

Edaphosauridae

Unambiguous: 40(0->1), 41(1->0), 59(1->0), 62(1->2), 89(0->1), 151(0->2), 159(0->1), 164(0->2), 165(0->3), 168(0->1); DELTRAN: 42(0->1), 85(1->2); ACCTRAN: 32(1->2), 43(0->1), 169(0->1), 187(0->1), 196(0->1), 219(1->4), 231(0->1), 232(0->1)

Lupeosaurus + Glaucosaurus + Edaphosaurus novomexicanus + E. boanerges

Unambiguous: 34(2->0), 54(1->0), 55(0->1), 118(0->1), 153(1->0), 160(0->1), 162(0->1), 176(1->0); DELTRAN: 187(2->1), 191(0->1), 196(0->1), 219(1->4), 231(0->1), 232(0->1), 233(0->1); ACCTRAN: 1(0->1), 2(1->2), 45(0->1), 56(1->0), 57(0->1), 64(0->1), 101(0->1), 126(0->1), 129(0->1), 134(0->1), 135(1->0), 140(1->0), 163(2->0)

Edaphosaurus novomexicanus + E. boanerges

Unambiguous: 31(0->1), 122(0->2), 170(0->1), 171(0->1), 174(0->1); DELTRAN: 1(0->1), 2(1->2), 57(0->1), 64(0->1), 98(0->1), 101(0->1), 169(0->1); ACCTRAN: 139(1->2), 180(2->0), 198(0->1)

SPHENACODONTIA

Unambiguous: 13(0->1), 27(0->1), 37(0->1), 83(0->1), 152(0->1), 155(1->0), 186(0->1), 227(0->1); DELTRAN: 17(0->1), 134(1->0), 150(0->1), 163(0->2), 180(0->2), 187(2->0), 204(1->0); ACCTRAN: 185(0->1), 191(1->0), 221(0->1), 228(0->1), 233(1->0)

Table S2. Optimisation of characters by node in the cladogram. The notation ‘+++’ indicates the clade comprising the named taxon and all more derived taxa within its clade. For example, ‘Varanosaurus +++’ indicates the clade comprising *Varanosaurus* and all more derived ophiacodontids (i.e. *Varanosaurus* + *Ophiacodon* + *Stereophallodon*).

Benson — Basal synapsid phylogeny—Appendix Table S2, optimisation by clade

Pantelosaurus +++

Unambiguous: 40(0->2), 47(0->2), 61(0->2), 68(0->1), 72(0->1), 143(1->2), 164(0->1), 177(0->1);
DELTRAN: 42(0->1), 221(0->1); ACCTRAN: 19(1->3), 63(0->1), 85(2->1), 97(0->1), 101(0->2), 123(1->0), 131(1->0), 133(0->1), 142(1->0), 153(1->2), 154(0->1), 224(0->1), 231(0->3)

Sphenacodontoidae

Unambiguous: 22(0->2), 25(0->3), 32(1->0), 112(0->1); DELTRAN: 97(0->1), 101(0->2), 133(0->1), 142(1->0), 153(1->2), 224(0->1), 228(0->1), 231(0->3); ACCTRAN: 2(1->3), 8(0->1)

Sphenacodontidae

Unambiguous: 56(1->2), 85(1->2), 202(0->1); DELTRAN: 63(0->1); ACCTRAN: 17(1->0), 18(0->1), 65(0->1), 98(1->0), 104(0->1), 106(1->2), 156(0->2), 164(1->2), 168(0->1), 191(0->1)

Secodontosaurus + *Sphenacodontinae*

Unambiguous: 7(1->0), 28(0->1), 51(0->1), 58(0->1), 59(1->2), 151(0->1), 180(2->1); DELTRAN: 2(1->3), 18(0->1), 19(1->3), 104(0->1), 106(1->2), 123(1->0), 154(0->1), 156(0->2), 164(1->2), 185(0->1); ACCTRAN: 187(0->1)

Sphenacodontinae

Unambiguous: 33(0->1); DELTRAN: 135(0->1); ACCTRAN: 27(1->2), 35(0->1), 66(1->0), 75(0->1), 140(1->0), 152(1->2), 200(0->1)

Dimetrodon + *Sphenacodon*

Unambiguous: Unambiguous: 43(0->2); DELTRAN: 8(0->1), 17(1->0), 27(1->2), 35(0->1), 65(0->1), 66(1->0), 75(0->1), 152(1->2), 200(0->1)

THERAPSIDA

Unambiguous: 20(0->1), 35(0->1), 43(0->2); DELTRAN: 19(1->4); ACCTRAN: 7(1->2), 9(1->0), 19(3->4), 29(0->1), 53(0->1), 62(1->3), 63(1->0), 66(1->0), 88(2->3), 90(0->3), 94(1->0), 100(0->1), 115(0->1), 117(0->1), 122(0->1), 123(0->1), 124(0->1), 139(1->0), 141(0->1), 144(0->1), 157(1->2), 160(0->2), 163(2->0), 175(0->1), 178(0->2), 179(0->1), 198(0->1), 203(0->1), 205(1->0), 210(0->1), 214(0->1), 218(0->1), 222(1->0), 225(0->1), 226(0->1), 229(0->1), 230(1->0), 232(0->2), 237(0->1), 238(1->0), 239(1->0)

Biarmosuchus +++

Unambiguous: 113(0->1); DELTRAN: 7(1->2), 9(1->0), 29(0->1), 53(0->1), 62(1->3), 90(0->3), 94(1->0), 98(0->1), 100(0->1), 115(0->1), 117(0->1), 122(0->1), 139(1->0), 144(0->1), 157(1->2), 163(2->0), 175(0->1), 178(0->2), 179(0->1), 203(0->1), 214(0->1), 218(0->1), 222(1->0), 225(0->1), 226(0->1), 229(0->1), 232(0->2); ACCTRAN: 13(1->2)

Titanophoneus + *Biseridens*

Unambiguous: 56(1->0), 75(0->1), 121(0->1), 136(0->1); DELTRAN: 124(0->1), 135(0->1); ACCTRAN: 8(1->0), 209(0->1)

Table S2. Optimisation of characters by node in the cladogram. The notation ‘+++’ indicates the clade comprising the named taxon and all more derived taxa within its clade. For example, ‘*Varanosaurus* +++’ indicates the clade comprising *Varanosaurus* and all more derived ophiacodontids (i.e. *Varanosaurus* + *Ophiacodon* + *Stereophallodon*).