PRELIMINARY PHYLOGENETIC ANALYSIS AND STRATIGRAPHIC CONGRUENCE OF THE DICYNODONT ANOMODONTS (SYNAPSIDA: THERAPSIDA)

by

Kenneth D. Angielczyk

*Department of Integrative Biology and Museum of Paleontology,
1101 Valley Life Sciences Building, University of California, Berkeley, CA 94720-4780 USA
e-mail: etranger@socrates.berkeley.edu*

ABSTRACT

A preliminary phylogenetic analysis of 20 well-known dicynodont taxa was conducted using modern cladistic methods. Many past phylogenetic hypotheses were corroborated, but others conflict with the results of this analysis. Most notably, *Diictodon, Robertia,* and *Pristerodon* are reconstructed in more basal positions than previously suggested, whereas *Endothiodon* and *Chelydontops* occupy a more crownward position. These findings are consistent with novel evolutionary scenarios for characters such as the presence of postcanine teeth and anterior palatal ridges.

The Relative Completeness Index and Gap Excess Ratio were used to examine the degree of fit between the most parsimonious cladograms of this study and the stratigraphic record of the dicynodonts. Although the results of this analysis suggest that the preferred cladogram is relatively consistent with stratigraphy, the presence of some ghost ranges and ghost lineages imply that the fossil record of dicynodonts is not as complete as is sometimes stated. These findings are important because there is a long tradition of intensive collecting in regions where dicynodont fossils are common; sections of several dicynodont lineages may not be preserved in these areas.

KEYWORDS: Dicynodontia, Phylogeny, Stratigraphy, Anomodontia, Synapsida, Karoo Basin

INTRODUCTION

The dicynodont therapsids (*sensu* Hopson & Barghusen 1986; Modesto *et al.* 1999; Rybczynski 2000) represent a diverse radiation of specialized herbivorous non-mammalian synapsids that range in age from the Late Permian to Late Triassic and are known from every continent. The dicynodont fossil record from the Beaufort Group of South Africa is especially rich and well documented since the first description of therapsid fossils by Owen (1845). Together with a handful of more basal forms (e.g., *Patranomodon, Venyukovia, Otsheria, Ulemica, Suminia*), dicynodonts form the Anomodontia (*sensu* Hopson & Barghusen 1986; Modesto *et al.* 1999; Rybczynski 2000), a clade of basal eutherapsids (Sidor & Hopson 1998). The exact placement of Anomodontia within Therapsida is still unclear (compare e.g., Gauthier *et al.* 1988; Hopson & Barghusen 1986; Sidor & Hopson 1998), but this issue is not the focus of this paper.

Despite the large number of specimens and the long history of work surrounding the group, the phylogenetic relationships of dicynodonts are still problematic. Many early workers, such as Robert Broom, concentrated on simply collecting and describing isolated, often poorly preserved or prepared skulls, and paid less attention to issues such as functional morphology, systematics, or even descriptions of postcranial skeletal elements. As a result, the group was extremely over-split (see Haughton & Brink's 1954 bibliographic database for the results of

this tendency). Recent workers (e.g., Cluver & Hotton 1981; Cluver & King 1983; Keyser 1975, 1993; Keyser & Cruickshank 1979; King 1988, 1993; King & Rubidge 1993) have reduced the number of recognized taxa to a more manageable number, but the lineage status of most of these taxa has not been rigorously tested. Cluver & King (1983), King (1988; 1990), Cox (1998), and Surkov (2000) published cladistic analyses of the group, but the absence of a list of characters examined or character codings for the taxa included in these works makes it difficult to independently test their hypotheses. The analyses of Modesto *et al.* (1999), Modesto & Rybczynski (2000), and Rybczynski (2000) are methodologically stronger, but the focus of these works has been on the relationships of non-dicynodont anomodonts and they include relatively few dicynodont taxa. Nevertheless, all of these analyses represent important first steps toward an understanding of dicynodont phylogeny.

In the following study, I present a new, preliminary phylogenetic analysis of the dicynodonts. My primary goal is to examine the interrelationships of the better known Permian dicynodont taxa using up-to-date methods and technologies, such as the computer parsimony algorithm PAUP. Because considerable work remains to be conducted on most dicynodont taxa, the present analysis is not intended to be an exhaustive treatment of dicynodont phylogeny. Instead, it represents a rigorous test of the hypotheses of relationship and homology made by previous authors. Furthermore, I examine the results of this phylogenetic

analysis in the context of stratigraphy to determine how well the morphologically parsimonious cladograms fit the known fossil record.

INSTITUTIONAL ABBREVIATIONS

AM: Albany Museum, Grahamstown, South Africa
AMNH: American Museum of Natural History, New York, USA
BMNH: Natural History Museum, London, England
BP: Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa
GSP: Geological Survey of South Africa, Pretoria, South Africa
NM: National Museum, Bloemfontein, South Africa
PIN: Paleontological Institute, Moscow, Russian Federation
ROZ: Roy Oosthuizen Collection, South African Museum, Cape Town, South Africa
SAM: South African Museum, Cape Town, South Africa
TM: Transvaal Museum, Pretoria, South Africa
UCMP: University of California Museum of Paleontology, Berkeley, USA

METHODS
Phylogenetic Analysis

A matrix consisting of 20 anomodont taxa and 40 morphological characters was constructed and subjected to a maximum parsimony analysis using PAUP 4.0b4a (Swofford 2000). The characters used are listed and discussed in detail in Appendix 1, the matrix is shown in Appendix 2, and the sources of character codings are given in Appendix 3. Multistate characters were treated as unordered and all characters were equally weighted. Unknown and inapplicable characters were coded "?" (Strong & Lipscomb 2000). The heuristic search algorithm was used and 1000 random addition sequence replicates were run to prevent the searches from becoming trapped in a local tree-length minimum (Maddison 1991). Support for the recovered clades was measured by decay analysis (Bremer 1988).

Many of the characters in this analysis are based on proposed synapomorphies that have been used by King (1988, 1990), Cox (1998), and Surkov (1998, 2000) to diagnose dicynodont clades or grades of organization they have proposed or characters used in Modesto et al. (1999) and Rybczynski (2000). As noted above, although all of these authors used cladistic principles to construct their phylogenetic hypotheses, only the analyses of Modesto et al. (1999) and Rybczynski (2000) were based on discrete-state characters and constructed using a computer parsimony algorithm (e.g., PAUP). Accordingly, I have reinterpreted many of the characters so that they have discrete states that can be coded in a matrix. The character states and codings that I have used are based mainly on my observations of dicynodont specimens in various institutions in the United States, South Africa, and Russia. A detailed discussion of the character states and my reasons for coding different taxa as I have are provided in Appendix 1. Because this analysis includes many characters from past phylogenetic analyses of dicynodonts and newer methods than most, it represents a rigorous test of previous phylogenetic hypotheses.

The skull has long been the primary focus of studies of dicynodonts, and this bias is reflected in collections of dicynodont material as well as studies of their morphology and systematics. Early dicynodont taxonomists placed much emphasis on skull proportions, patterns of facial and skull roof sutures, and the presence or absence of bones such as the postfrontal or septomaxilla (e.g., Broom 1932). I have avoided many of these characters because more recent authors (e.g., Cluver & Hotton, 1981; Cluver & King, 1983; Keyser 1975; King 1993; Rubidge 1984; Toerien 1953; Tollman et al. 1980) have shown that they are highly variable within dicynodont genera, species, and presumed age classes. They are also susceptible to alteration by taphonomic processes such as weathering or plastic deformation. Since the seminal work of Toerien (1953), much greater attention has been paid to the structure and functional relationships of the palate and mandible of dicynodonts because these regions are rich sources of potentially informative characters that show less individual variation. Other potentially informative regions of the skull, such as the braincase, have not been thoroughly examined to determine if they preserve a useful phylogenetic signal. The majority of the cranial characters I have used in this analysis are features of the palate and mandible, although some deal with other regions of the skull.

So much attention has been paid to the dicynodont skull, including the recent focus on the feeding system, that other sources of phylogenetic characters have remained almost completely unexplored in the dicynodont literature. Despite well over a century of collection and description, the postcranial skeleton of dicynodonts remains poorly known; only scattered descriptions of its osteology or functional morphology are available (e.g., Boonstra 1966; Broom 1905; Camp & Welles 1956; Cluver 1978; Cox 1959, 1972; DeFauw 1986; King 1981a, 1981b, 1985; Olson & Byrne 1938; Pearson 1924; Rubidge et al. 1994; Walter 1986; Watson 1960). This lack of published information is unfortunate because these works and others that have attempted to include postcranial characters in systematic studies (Camp 1956; King 1988; Surkov 1998) strongly suggest that dicynodont postcrania preserve a valuable and informative phylogenetic signal. The consideration of postcranial characters has enabled more parsimonious explanations of patterns of evolution to be discovered in broader studies of synapsids (Hopson 1995; Rowe & van den Heever 1986). The five postcranial characters that I have included appear to be phylogenetically informative and are easily coded even for poorly preserved or prepared specimens.

Eighteen dicynodont genera form the ingroup and two non-dicynodont anomodonts (*Patranomodon* and *Otsheria*) are used as outgroups. Because the monophyly of the Anomodontia is accepted (Hopson, 1991; Hopson & Barghusen 1986; Modesto et al. 1999; Rybczynski

2000; Sidor & Hopson 1998) and I am concerned only with relationships among dicynodonts, I did not include any non-anomodont outgroups in this analysis. *Patranomodon* is a useful outgroup because it is a basal anomodont (Modesto *et al.* 1999; Rubidge & Hopson 1990, 1996; Rybczynski 2000) represented by a very well-preserved skull and associated postcranial elements that retain many primitive anomodont characters. *Otsheria* is a venyukovioid anomodont (*sensu* Modesto *et al.* 1999; Rybczynski 2000), and represents a slightly more advanced grade of anomodont evolution. *Anomocephalus*, the most basal known anomodont (Modesto & Rubidge 2000; Modesto *et al.* 1999), was not used as an outgroup because the only known specimen (BP/1/5582) does not preserve many of the characters I have used.

The ingroup taxa in this analysis are known primarily from the Late Permian of Africa, with the exceptions of *Lystrosaurus*, *Myosaurus*, and *Kannemeyeria*, which appear in the Triassic. The focus of this analysis is the pattern of relationships among the Permian dicynodont taxa, and I have tried to include as many of the well-known genera as possible. The Triassic genera are mainly intended to serve as place-holders, and the results of this and other studies (Cluver & King 1983; Cox 1965, 1998; Cox & Li 1983; Keyser & Cruickshank 1979; King 1988, 1990) suggest that most Triassic dicynodonts are members of the monophyletic clade including *Dicynodon*, *Lystrosaurus*, and *Kanne–meyeria*. Future analyses that include additional Triassic taxa can be used to test this assumption. All included genera have been recently described, redescribed, or revised in the literature, and I have had the opportunity to personally examine specimens that can be referred confidently to these taxa (Appendix 3). Although the taxonomy of the included genera is not the focus of this paper, my treatment of *Eodicynodon*, *Chelydontops*, and *Tropidostoma* necessitates some explanation.

Two described species currently are assigned to the genus *Eodicynodon*, *Eodicynodon oosthuizeni* (Barry 1974a) and *Eodicynodon oelofseni* (Rubidge 1990b). Although the taxa share several diagnostic features, a number of notable differences also exist, including the presence or absence of a canine tusk, the size and arrangement of the postcanine teeth, and the morphology of the lower jaw (Rubidge 1990b). Also, many more specimens of *E. oosthuizeni* have been collected (over 20 well-preserved skulls versus the holotype and a second specimen (NM QR3003) that is probably referable to *E. oelofseni*, both of which are poorly preserved; Rubidge, 1990a; personal observation) and its cranial and postcranial osteology have been much more thoroughly described (Barry 1974b; Cluver & King 1983; Rubidge 1984, 1985, 1990a; Rubidge *et al.* 1994). Because of these discrepancies, I have considered only *E. oosthuizeni*, and my character state codings for *Eodicynodon* should be considered valid only for this species.

Cluver (1975) described the taxon *Chelydontops altidentalis* based on two specimens (SAM 11558 and SAM 12259) discovered in the *Tapinocephalus* Assemblage Zone. Recently, Cox (1998) has proposed synomymizing *C. altidentalis* with the genus *Prodicynodon*, creating the new combination *Prodicynodon altidentalis*. Although the holotype (SAM 11558) and referred (SAM 12259) specimens of *Chelydontops* are not completely preserved, they do show a distinct, diagnostic suite of features, including a relatively wide intertemporal bar, a dome-like pineal boss, a shelf-like area lateral to the upper postcanine teeth, a large, leaf-shaped palatal exposure of the palatine, a distinctly developed coronoid eminence, and a median palatal ridge that has a flattened, expanded, diamond-shaped area anteriorly. The holotypes of both *Prodicynodon pearstonensis* (AM 2551) and *P. beaufortensis* (AMNH 5509) are very fragmentary and preserve only the snout and anterior portion of the lower jaw. The palate is not fully exposed in either specimen, and the details of the intertemporal region are also unknown. Because both specimens preserve almost no information regarding their possible affinities with *Chelydontops altidentalis*, I believe it is premature to refer this taxon to the genus *Prodicynodon*. I agree with Keyser (1993) that both *P. pearstonensis* and *P. beaufortensis* should be regarded as *nomina dubia* until more informative material is discovered. The codings for *Chelydontops* in this analysis are based on my observations of the two SAM specimens.

The genus *Tropidostoma* is problematic because although there is considerable variation in the width of the intertemporal region in the taxon, most of the specimens referred to it are otherwise very similar. Keyser (1973) largely ignored this variation in his revision of *Tropidostoma*, but Cluver & King (1983) favored placing specimens with narrow intertemporal regions in *Tropidostoma* while retaining the genus *Cteniosaurus* for specimens with wider intertemporal regions. The holotype specimen for *Tropidostoma* (BMNH R868) has a relatively narrow intertemporal region, with the parietals exposed in a median depression between the postorbitals, which partially overlap them. In my observations, I have found that this pattern is relatively constant, although the depth of the depression, degree of overlap, and overall width of the intertemporal bar can be quite variable. These features also are highly susceptible to alteration by plastic deformation (for example, the holotype of *T. dunni* (BMNH R866) has a narrower intertemporal region than the holotype of *T. microtrema* (BMNH R868), but the former specimen has clearly been laterally compressed). For these reasons, as well as the fact that there is almost no other morphological difference between *Cteniosaurus* and *Tropidostoma*, I have followed Keyser (1973) and treat them as synonyms.

Stratigraphic Analysis

The biostratigraphic relationships of dicynodonts, especially those of the Karoo Basin of South Africa, have a long history of study (e.g., Broom 1906; Keyser

& Smith 1977-1978; Kitching 1977; Lucas 1996, 1998; Rubidge 1995a; Seeley 1892; Watson 1914) and frequently have been used to add a temporal dimension to phylogenetic and adaptational hypotheses about the group. Because of this tradition, and the fact that the Beaufort Group and its eight assemblage zones have been the subject of recent scrutiny (Rubidge 1995a), dicynodonts are an ideal group with which to examine the fit between stratigraphy and phylogeny.

A number of methods have been proposed recently to measure the fit between stratigraphic data and cladograms (e.g., Benton & Storr, 1994; Gauthier *et al.* 1988; Huelsenbeck 1994; Norell & Novacek 1992a, 1992b; Wills, 1999). There has also been debate over whether and how one should include stratigraphic data in phylogenetic analyses (e.g., Clyde & Fisher 1997; Fisher 1992, 1994, 1997; Fox *et al.* 1997, 1999; Norell & Novacek 1997; Rieppel 1997; Smith 2000; Thewissen 1992). In this analysis the Relative Completeness Index (RCI) metric of Benton & Storrs (1994) and the Gap Excess Ratio (GER, Wills, 1999) were used to examine the nature of the gaps in the fossil record required by the morphologically parsimonious cladograms. A cladogram that implies fewer or shorter gaps in the fossil record is a more highly corroborated hypothesis than an equally parsimonious cladogram that requires longer or more numerous gaps.

I calculated the RCI and GER for all of the most parsimonious cladograms of this analysis. In addition, these metrics were calculated for cladograms up to four steps longer and a cladogram based on the topology of King (1988, 1990), but only including the taxa I examined (Figure 1c), to determine if any of these hypotheses fit the known fossil record better than the morphologically most parsimonious cladograms. The Basic program "Ghosts" (version 2.4, 1000 random replicates, polytomies resolved as the worst case; Wills 1999) also was used to determine whether the most parsimonious cladograms of this analysis and the cladogram of King (1988, 1990) fit the fossil record significantly better than random. Stratigraphic data were taken from Rubidge (1995a) and King (1988). Because all taxa in the analysis except *Otsheria* are known from southern Africa, potential biases caused by different preservation rates or biostratigraphic correlation difficulties should be minimal. Taxa known to occur in only part of an assemblage zone were not treated differently than taxa found throughout an assemblage zone. This assumption simplifies data analysis, but reduces resolution.

To calculate the RCI (Benton & Storrs 1994; see also Benton & Hitchin 1996; Benton & Simms 1995; Benton & Storrs 1996; Hitchin & Benton 1997a) Minimum Implied Gaps (MIGs; see Benton 1994; Norell 1993; Norell & Novacek 1992a, 1992b; Smith & Littlewood 1994; Storrs 1993; Weishampel & Heinrich 1992) were assessed for the most parsimonious cladograms as well as the cladogram based on King's (1988, 1990) topology. This is easily done by coding a stratigraphic character (Appendices 1, 2) in MacClade 3.08 (Maddison &

Maddison 1999; see also Fisher 1992) and noting the number of steps added. The Simple Range Length (SRL; Storrs, 1993) for each taxon was measured by counting the number of assemblage zones in which that taxon appears. These values were then substituted into the equation given in Benton & Storrs (1996) and the equation was solved for RCI. Because the RCI takes into account time duration and missing time, not just the relative ranks of clades, it has been suggested as an estimate of the completeness of the fossil record of the group in question implied by a phylogenetic hypothesis (Hitchin & Benton 1997a; although see Wagner 2000).

The RCI is known to be sensitive to the choice of taxa and magnitude of time examined (Benton & Storrs 1994; Hitchin & Benton 1997a). It may also be affected by number of taxa and clade asymmetry (Siddall 1996; 1997; but see Benton *et al.* 1999; Hitchin & Benton 1997a, 1997b). However, these biases should not be a problem in this analysis because the identities and number of included taxa, as well as the magnitude of time in consideration, are the same for all of the cladograms in question. Although there are slight differences in asymmetry among the cladograms, they are unlikely to be large enough to affect the results seriously. The randomization procedure implemented in "Ghosts" also helps to control for cladogram size and balance biases when estimating the significance of the RCI (Wills 1999).

The Gap Excess Ratio (GER) has been proposed by Wills (1999) as a means to examine the fit of a cladogram to stratigraphy by examining the amount of ghost ranges required. The GER represents the excess ghost range above and beyond the minimum possible value for a set of stratigraphic data, expressed as a fraction of the total range of ghost values possible for that data (Wills 1999). To calculate the GER, the minimum and maximum number of implied gaps possible for the stratigraphic data set used here were calculated. These values were then substituted into equation 3 of Wills (1999) with the MIG (see above) for each of the most parsimonious cladograms of this analysis, the cladograms several steps longer, and the cladogram of King (1988, 1990). The GER appears not to be biased by the number of taxa included in the cladograms being compared (Benton *et al.* 1999; Wills 1999), but this potential source of error is not a concern because all of the cladograms included in this analysis have the same number of taxa. It can be affected by symmetry differences among examined cladograms (Benton *et al.* 1999), but variation in symmetry among the cladograms in this analysis is minimal and should not cause undue bias. As with the RCI, the randomization procedure of "Ghosts" helps to control for cladogram size and shape biases when calculating the significance of the GER (Wills 1999).

RESULTS
Phylogenetic analysis

The parsimony analysis recovered a single most parsimonious cladogram with a length of 125 steps, a consistency index of 0.57, and a retention index of 0.67

(Figure 1a). The topological results of the analysis are presented in Figure 1. For comparison, a cladogram based on the topology of King (1988, 1990), but including only the taxa and characters examined here (Figure 1c), has a length of 136 steps, a consistency index of 0.53, and a retention index of 0.59.

Tree decay analysis shows that most of the hypothesized clades in this phylogeny are relatively weakly supported. At 126 to 127 steps, the major clades of dicynodonts are resolved, but most resolution within these clades is lost (Figure 1b). The observed loss of resolution is likely due to the generally short branch lengths within the major clades. At 128 steps, the ingroup is resolved from the outgroup, but no branches within the ingroup are resolved. All resolution is lost at 133 steps. A large number of character state changes take place on the branch separating the ingroup from the outgroup, resulting in the strong decay support for that node.

The topological results of this analysis are generally compatible with those of King (1988, 1990), although some differences do exist. Most notably, *Robertia* and *Diictodon*, and *Pristerodon* are reconstructed in a more basal position, whereas *Endothiodon* and *Chelydontops* appear in a more crownward position. Although clades including the same taxa as the Cryptodontinae and Emydopidae of King (1988, 1990) are present in the most parsimonious cladogram of this analysis, the relationships within these clades are slightly different (Figure 1a, Nodes I, L; Figure 1c, Nodes C, E). The results are also compatible with those of Modesto *et al.* (1999), Modesto & Rybczynski (2000), Rybczynski (2000) and Surkov (2000), although there are notable differences in taxon sampling.

Character state transformations were optimized on the most parsimonious cladogram using the Delayed Transformation (DELTRAN) algorithm of MacClade 3.08a (Maddison & Maddison, 1999) to arrive at the following diagnoses of the recovered clades.

The clade including *Eodicynodon, Kannemeyeria*, and all descendants of their most recent common ancestor (= Dicynodontia *sensu* Modesto *et al.* 1999; Rybczynski 2000; Figure 1a, Node A) is diagnosed by the absence of premaxillary teeth (Character 2, State 1), the presence of a caniniform process (6, 1), a posterior median ridge with an expanded, flattened anterior area on the palatal surface of the premaxilla (8, 1), a lateral squamosal fossa for the origination of the lateral branch of the M. Adductor Mandibulae Externus (21, 1), a rounded, bulbous surface of the palatal exposure of the palatine suggesting a keratinized covering (22, 1), a single, median nasal boss (23, 1), a dorsolateral notch in the squamosal (32, 1), a relatively long interpterygoid vacuity that does not reach the level of the palatal exposure of the palatines (33, 1), and a lateral palatal fenestra located at the level of the anterior portion of the palatal exposure of the palatines (35, 1). It is important to note that some of these characters (e.g., 21,1) would likely diagnose more inclusive clades if more non-dicynodont anomodonts were included in the analysis.

The clade including *Robertia, Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node B) is diagnosed by the presence of fused premaxillae (3,1), upper postcanine teeth located medially, with the more posterior teeth approaching the lateral margin of the maxillae (4, 1), lower postcanine teeth located on a medial shelf or swelling (10, 1), and a reduced transverse flange of the pterygoid (37, 1). In addition, this clade is ambiguously diagnosed by the presence of a symphyseal region of the lower jaw with an upturned margin and a scooped-out depression on its posterior surface (18,1).

The clade including *Diictodon, Robertia*, and all descendants of their most recent common ancestor (= Robertiidae *sensu* King 1988, 1990; Figure 1a, Node C; Figure 1c, Node A) is diagnosed by the presence of a caniniform process with a notch anterior to it (6, 2), paired anterior ridges that converge posteriorly on the palatal surface of the premaxilla (7, 1), contact between the anterior portion of the squamosal and the maxilla (34, 1), the presence of an ectepicondylar foramen (38, 1), and the presence of a cleithrum (39, 1). In addition, this clade is ambiguously diagnosed by the presence of an elongate dentary table bounded medially by a tall, thin, dorsally-convex blade (15, 2), and a relatively small lateral dentary shelf (17,1). The presence of paired, anterior palatal ridges that converge posteriorly may diagnose a more inclusive clade, but the testing of this hypothesis must wait until future analyses that include currently undescribed specimens collected in the lower *Tapinocephalus* Assemblage Zone of South Africa (Rubidge, personal communication, 2000; also see Appendix 1).

The clade including *Endothiodon, Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node D) is diagnosed by the presence of a relatively flat surface of the premaxillary secondary palate lateral to the posterior median palatal ridge (9,2), the presence of a posterior dentary sulcus (16, 1), and a relatively smooth palatal surface of the palatine with fine pitting suggestive of a keratinized covering (22, 2).

The clade including *Endothiodon, Chelydontops*, and all descendants of their most recent common ancestor (= Endothiodontoidea *sensu* King 1988, 1990; Figure 1a, Node E; Figure 1c, Node B) is diagnosed by the presence of a shelf-like area lateral to the upper post-canine teeth (5, 1), paired nasal bosses located near the dorsal margin of the external nares (23, 2), and a strongly developed bony boss around the pineal foramen (26, 1).

The clade including *Pristerodon, Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node F) is diagnosed by contact between the palatine and premaxilla (27, 1), and contact between the anterior portion of the squamosal and the maxilla (34,1).

The clade including *Kingoria, Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node G) is diagnosed by the absence of upper postcanine teeth (4, 3), a posterior median palatal

ridge that lacks an expanded, flattened anterior area (8, 2), the absence of lower postcanine teeth (10, 2), a mid-ventral vomerine plate that is of constant width (12, 1), and an expanded femoral head that encroaches on the anterior surface of the bone (31, 1).

The clade including *Kingoria, Myosaurus*, and all descendants of their most recent common ancestor (Figure 1a, Node H) is diagnosed by the presence of a postcaniniform keel (1,1), an embayment of the palatal rim anterior to the caniniform process (14, 1), the absence of a dentary table (15, 0), and a shovel-shaped symphyseal region of the lower jaw (18, 3). This clade is also ambiguously diagnosed by the presence of a well-developed lateral dentary shelf (17,3), although this feature may characterize a more inclusive clade.

The clade including *Emydops, Myosaurus*, and all

descendants of their most recent common ancestor (= Emydopidae *sensu* King, 1988, 1990, although see above; Figure 1a, Node I; Figure 1c, Node C) is diagnosed by the presence of groove-like depressions lateral to the posterior median palatal ridge (9, 1), a narrow, blade-like mid-ventral vomerine plate (13, 1), a squamosal with a relatively straight contour in occipital view (32, 0), and the presence of an ectepicondylar foramen on the humerus (38, 1).

The clade including *Myosaurus, Cistecephalus*, and all descendants of their most recent common ancestor (Figure 1a, Node J; also see Cluver, 1974b) is diagnosed by the presence of a foramen on the palatal surface of the palatine (24, 1) and a partial closing-off of the snout by the anterior margins of the orbits (25, 1).

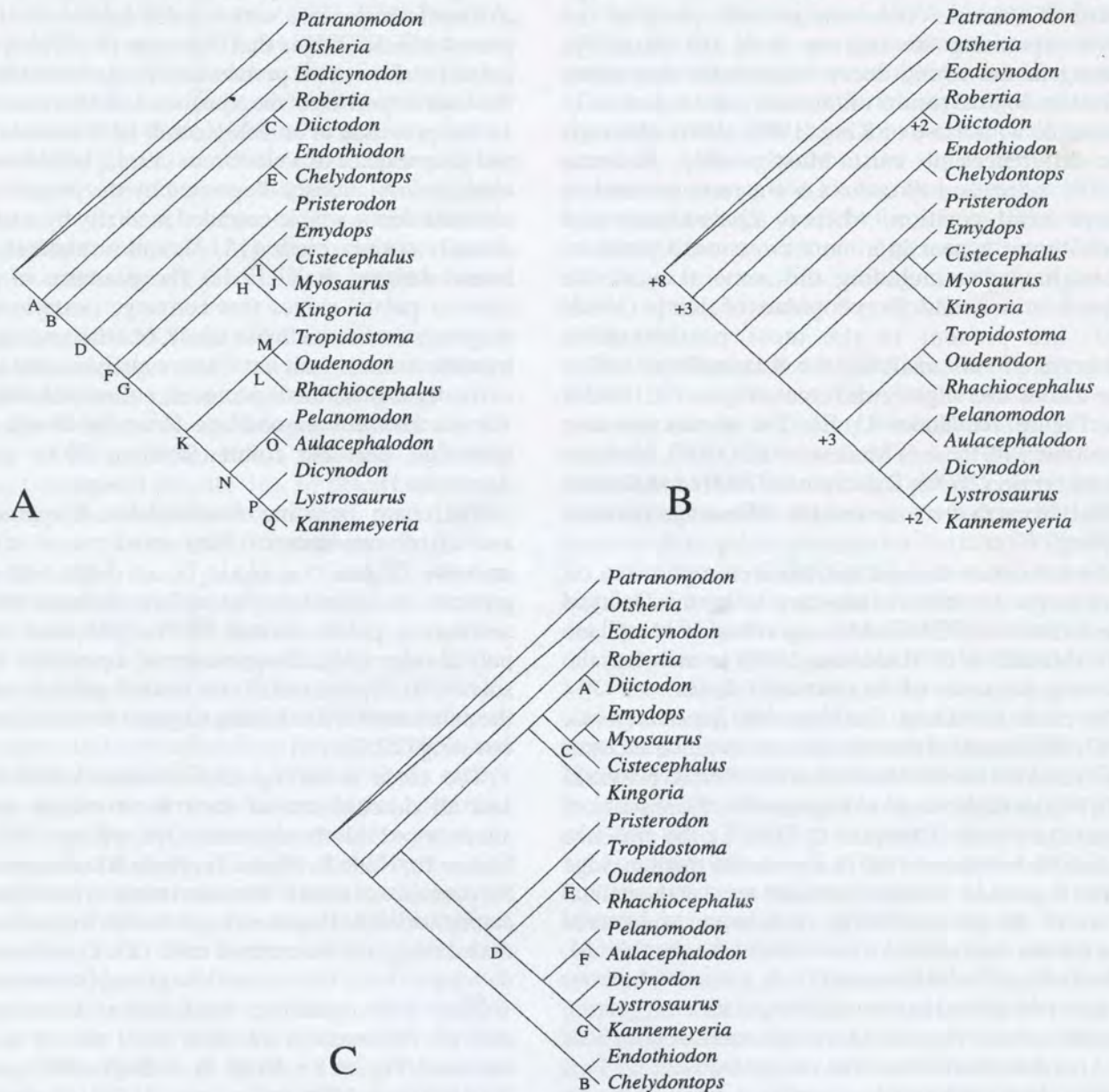The clade including *Tropidostoma, Kannemeyeria*,

Figure 1:   A: Single most parsimonious cladogram of this analysis (length 125 steps, CI = 0.57, RI = 0.67). The lettered nodes are discussed in the text. B: Cladogram showing the results of the decay analysis. Numbers indicate the number of steps beyond the most parsimonious cladogram required for a given node to collapse. Unnumbered nodes collapse at one step beyond the most parsimonious cladogram. C: Cladogram based on the topology of King (1988, 1990), but including only the taxa examined in this analysis. Lettered nodes are higher taxa given in King (A = Robertiidae, B = Endothiodontoidea, C = Emydopidae, D = Dicynodontidae, E = Cryptodontinae, F = Aulacephalodontinae, G = Kannemeyeriinae).

TABLE 1

Results of the stratigraphic analysis. SMIG is the sum of Minimum Implied Gaps for each cladogram examined (= the number of steps added by the stratigraphic character in MacClade). RCI is the Relative Completeness Index for each cladogram examined. GER is the Gap Excess Ratio for each cladogram examined. The cladograms from the decay analysis have been broken down by their length, given in parentheses. Because more than one cladogram exists at each of the lengths in the decay analysis, the range of SMIG, RCI, and GER values is given.

Cladogram	SMIG	RCI	GER
Preferred Cladogram	14	0.632	0.863
King (1988, 1990)	18	0.526	0.784
Decay Results (126)	13 - 18	0.658 - 0.526	0.882 - 0.784
Decay Results (127)	12 - 28	0.684 - 0.263	0.902 - 0.588
Decay Results (128)	11 - 30	0.711 - 0.211	0.922 - 0.549
Decay Results (129)	11 - 31	0.711 - 0.184	0.922 - 0.529

and all descendants of their most recent common ancestor (= Dicynodontidae *sensu* King, 1988, 1990; Figure 1a, Node K; Figure 1c, Node D) is diagnosed by the presence of paired anterior ridges that do not converge posteriorly (7, 2), a narrow, blade-like mid-ventral vomerine plate (13, 1), a palatal surface of the palatine that is highly rugose and pitted, suggesting a keratinized covering (22, 3), paired nasal bosses near the dorsal or posterodorsal margin of the external nares (23, 2), an expanded humeral head that encroaches on the dorsal surface of the bone (30, 1), and the presence of five sacral vertebrae (36, 2). In addition, this clade is ambiguously diagnosed by an elongate dentary table that is bounded by low ridges (15, 3) and a relatively small lateral dentary shelf (17, 1), although both of these features may characterize a more inclusive clade.

The clade including *Tropidostoma*, *Rhachiocephalus*, and all descendants of their most recent common ancestor (= Cryptodontinae *sensu* King, 1988, 1990, although see above; Figure 1a, Node L; Figure 1c, Node E) is diagnosed by the presence of a postcaniniform crest (28, 1).

The clade including *Tropidostoma*, *Oudenodon*, and all descendants of their most recent common ancestor (Figure 1a, Node M) is diagnosed by parietals that are exposed in a groove or depression between the postorbitals, which partially overlap them (20, 1) and a relatively long interpterygoid vacuity that reaches the level of the palatal exposure of the palatines (33, 2).

The clade including *Pelanomodon*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node N) is diagnosed by the presence of a labial fossa (19, 1).

The clade including *Pelanomodon*, *Aulacephalodon*, and all descendants of their most recent common ancestor (= Aulacephalodontinae *sensu* King, 1988, 1990; Figure 1a, Node O; Figure 1c, Node F) is diagnosed by a relatively wide intertemporal region in which the postorbitals are steeply placed on the lateral sides of the skull and concave laterally (20, 2) and the presence of a transverse ridge across the snout at the level of the prefrontals (40, 1).

The clade including *Dicynodon*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node P) is diagnosed by a moderately rugose

and pitted palatal surface of the palatine that is suggestive of the presence of a keratinized covering (22, 4) and a relatively short interpterygoid vacuity that does not reach the level of the palatal surface of the palatines (33, 0).

The clade including *Lystrosaurus*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Kannemeyeriinae *sensu* King, 1988, 1990; Figure 1a, Node Q; Figure 1c, Node G) is diagnosed by a wedge-shaped symphyseal region of the lower jaw (18, 4) and six sacral vertebrae (36, 3).

Stratigraphic Analysis

The results of the stratigraphic analysis are summarized in Table 1. The most parsimonious cladogram has a MIG value of 14, an RCI value of 0.632 and a GER value of 0.863. The RCI value is above the mean value of 0.498 found by Hitchin & Benton (1997) for continental tetrapods, and comparable to the mean of 0.601 reported by Benton *et al.* (1999) for five non-mammalian synapsid cladograms. The GER values are notably higher than the average of 0.654 for the same five non-mammalian synapsid cladograms and the average of 0.765 for continental tetrapods (Benton *et al.* 1999). The cladogram of King (1988, 1990) has a MIG value of 18, an RCI value of 0.526, and GER value of 0.784. Both the most parsimonious cladogram of this analysis and the cladogram of King were found to fit the fossil record significantly better than random (p < 0.001).

As noted above, MIG, RCI, and GER values were also calculated for cladograms up to four steps longer than the most parsimonious cladogram (i.e., up to 129 steps) to determine if any of these topologies fit the fossil record better than the most parsimonious cladogram. MIG values for these cladograms range from 11 to 31, RCI values range from 0.711 to 0.184, and GER values range from 0.922 to 0.529. Thus, although some of these topologies fit the known stratigraphic record of dicynodonts better than the morphologically most parsimonious cladogram, most require more and/or longer gaps. Also, the cladograms that are closest in length to the most parsimonious cladogram have metric scores that are less variable and closer to those of the most parsimonious cladogram than those that are longer (i.e., the 126 step cladograms have MIG values of 13-18, while the 129 step cladograms have MIG values of

11-31). The cladograms that do have a closer fit to the fossil record have topologies that are generally congruent with that of the most parsimonious cladogram. Many of the major clades of dicynodonts are resolved in these cladograms (e.g., Figure 1a, nodes C, H, K, P, and Q), but the relationships among the taxa in these clades varies. Also, the positions of *Endothiodon*, *Chelydontops* and *Pristerodon* tend to be variable in these cladograms.

DISCUSSION

The topologies of the cladograms recovered in this analysis differ in some respects from those published by past authors, but are similar in others. Because this analysis represents a test of these previous hypotheses of homology and relationship, cases of congruence can be interpreted as corroboration, whereas cases of incongruence represent falsification. However, similarities between the results presented here and those of past workers also may reflect the fact that many of the characters examined are based on features that they used to construct their trees. In addition, the large number of palatal and jaw characters included could be misleading if these areas are prone to homoplasy related to feeding methods and dietary preferences. Future analyses that include a greater diversity of characters should be able to test this phylogenetic signal. In the following discussion, I have limited my comparisons mainly to the cladogram of King (1988, 1990) because only that cladogram and the cladogram of Cluver & King (1983), which has a nearly identical topology, include taxon sampling comparable to that undertaken in this analysis. Although the topological differences are discussed in some detail, it is important to note that the results of this analysis are largely compatible with those of Cluver & King (1983) and King (1988, 1990), corroborating many of their results.

The preferred cladogram of this analysis reconstructs the clade including *Robertia*, *Diictodon*, and their most recent common ancestor (= Robertiidae of King 1988, 1990) in a relatively basal position, just one node above *Eodicynodon* (Figure 1a, Node B). King (1988, 1990) favored a more crownward position for this clade, nesting it within the clade including *Kingoria*, *Myosaurus*, and all descendants of their most recent common ancestor (Figure 1c). Much of the available evidence is equivocal when comparing these two alternatives. For example, the postcranial skeleton of *Robertia* and *Diictodon* retain several plesiomorphic character states, such as relatively weakly developed humeral and femoral heads (DeFauw 1986; King 1981; Surkov 1998). The postcrania that have been described for *Kingoria* and *Cistecephalus* (Cluver 1978, DeFauw 1986, King 1985) suggest that at least some members of that clade possess more derived postcranial skeletons (although my observations of two undescribed *Emydops* humeri, SAM K5974, SAM K10009, suggest that taxon retained a more primitive humeral morphology). However, members of both clades possess an ectepicondylar foramen and an ossified cleithrum, features that are otherwise rare in dicynodonts and suggestive of close relationship.

Differing interpretations of morphological features are also an issue. King (1988, 1990) considered the notch anterior to the caniniform process of *Diictodon* and *Robertia* to be homologous with the embayment of the palatal rim found in taxa such as *Emydops* and *Myosaurus*. I have treated these features as separate characters; a notched caniniform process is considered to be a type of caniniform process (Character 6, State 2), whereas the embayment is an unrelated feature (Character 14). My justification for this decision is based on the fact that in my observations of specimens of *Diictodon* and *Robertia*, I found little evidence of the pronounced lateral bowing of the palatal rim that forms the embayment in taxa such as *Emydops* or *Myosaurus*. Also, there is not a depression on the medial surface of the palatal rim near the caniniform process as in *Kingoria*. Instead, the notch seems to be formed by a modification of the anterior edge of the caniniform process, such that the edge originates medial to the palatal rim, as opposed to being contiguous with it. Thus the notch likely represents a transformation of the caniniform process, and therefore a notched caniniform process must be considered a type of (i.e., homologous with) caniniform process. This interpretation of these characters is more consistent with the hypothesis that *Diictodon* and *Robertia* are not closely related to taxa such as *Kingoria* or *Emydops*. The more basal placement of *Diictodon* and *Robertia* also better fits the known fossil record of dicynodonts (Figure 2) and more parsimoniously explains the evolution of characters such as the posterior dentary sulcus, postcaniniform keel, and the morphology of the dentary symphysis.

King (1988, 1990) also favored a more basal position for *Endothiodon* and *Chelydontops* than I have presented here (Figure 1a, Node D; Figure 1c, Node B). In some ways (e.g., presence of premaxillary teeth, relatively short premaxillary secondary palate, long, narrow maxillae that lack a caniniform process, midventral plate of vomers with an expanded area posterior to the junction with the premaxilla) the cranial morphology of *Endothiodon* is highly suggestive of this taxon being part of a very basal dicynodont lineage, perhaps even more basal than *Eodicynodon*. However, several other features (e.g., relatively narrow intertemporal region, jugal modified for the possible origination of a masseter-like muscle; Cox 1964; Ray 2000), reduced transverse flange of the anterior pterygoid process, quadrate that allows propalinal sliding of the jaw, presence of a posterior dentary sulcus) as well as its stratigraphic occurrence in the *Pristerognathus* to *Cistecephalus* Assemblage Zones of South Africa (Rubidge 1995a) suggest that *Endothiodon* is actually a more advanced, highly autapomorphic dicynodont. If the hypothesis that *Chelydontops* is the sister taxon of *Endothiodon* is correct (supported in this analysis by two synapomorphies; see Results and below), then the more crownward position of these taxa becomes more logical.

Chelydontops is known from the *Tapinocephalus* Assemblage Zone of South Africa and possesses two synapomorphies (a shelf lateral to the maxillary teeth and a dome-like pineal boss) that unite it with *Endothiodon* in this analysis (I do not consider *Chelydontops* to possess premaxillary teeth; see Appendix 1, Character 2). In most other respects, *Chelydontops* is much more similar to "typical" dicynodonts than to *Endothiodon*. In particular, the relatively wide intertemporal region, possible evidence for the secondary loss of the anterior palatal ridges (Appendix 1, Character 7), and the morphology of the palatines, posterior median palatal ridge, and lower jaw give the two known specimens of *Chelydontops* a very *Pristerodon*-like appearance. This superficial similarity may indicate that the lineages including *Endothiodon* and *Chelydontops* (Figure 1a, Node E) and *Pristerodon* and *Kannemeyeria* (Figure 1a, Node F) evolved from a *Pristerodon*-like common ancestor, supporting the more crownward placement of *Endothiodon* and *Chelydontops* proposed here. In addition, this hypothesis suggests that some apparently plesiomorphic features of *Endothiodon*, such as premaxillary teeth and the unusual morphology of the premaxilla and maxilla, are actually reversals, and that *Chelydontops* may be a useful model for many features of a hypothetical ancestor of *Endothiodon* (also see Cox 1998).

The more basal position of *Pristerodon* suggested in this analysis (Figure 1a, node F) is supported by the retention of several plesiomorphic character states in that taxon, including weakly developed anterior palatal ridges that converge with an expanded area of the posterior median ridge, a relatively wide intertemporal region, a relatively small dentary table, a relatively large lateral dentary shelf, the presence of maxillary and dentary teeth, and the relatively smooth but finely pitted palatal surface of the palatines. King (1988, 1990) favored a more crownward placement (Figure 1c) based on the modification of the posterior dentary sulcus into a "deep, thin-walled sulcus" (King 1988, p. 71). Although I have included only the presence or absence of a dentary sulcus in the data matrix presented here, in my personal observations I have found the dentary sulcus of *Pristerodon* to more closely resemble that of *Chelydontops* or *Endothiodon* than that of taxa such as *Tropidostoma*. I consider these observations to be consistent with the more basal position suggested by the preferred cladogram, and future analyses that take into account the detailed morphology of the dentary sulcus (not just its presence or absence) can further test this hypothesis.

The placement of *Pristerodon* suggested by this analysis also has important implications for one other character, the presence of paired anterior ridges that converge posteriorly. When this character is optimized on the preferred cladogram of this analysis, it appears to have evolved independently in *Pristerodon* and the common ancestor of *Robertia* and *Diictodon*. However, this reconstruction is likely to be an artifact of the taxa included in the analysis. In addition to *Diictodon*,

Robertia, and *Pristerodon*, several specimens collected in the lower *Tapinocephalus* Assemblage Zone (e.g., BP/1/5580, BP/1/5589, NM QR3145, NM QR3505; Rubidge, personal communication, 2000) also possess this arrangement of the palatal ridges. In all cases the ridges converge with an expanded, flattened area of the posterior median ridge. In some specimens (e.g., NM QR3145, NM QR 3505) the expanded area of the posterior median ridge is Y-shaped, while in others (e.g., BP/1/5589, *Diictodon, Pristerodon*) the expanded area is narrower and V-shaped. Although not included in this analysis, the morphology and stratigraphic occurrence of these specimens suggest that they likely would fall on the branch between *Eodicynodon* and the clade including *Robertia* and *Diictodon* in the cladogram presented here (Modesto & Rubidge pers. comm.). If this hypothesis is correct, then it is possible that convergent anterior ridges evolved only once, and were later lost in the clades including *Chelydontops* and *Endothiodon* (Figure 1a, Node E) and *Kingoria* and *Myosaurus* (Figure 1a, Node H). These hypothesized losses are corroborated by the fact that both *Chelydontops* and *Emydops* possess posterior palatal ridges with an expanded anterior area and an anterior palatal morphology suggestive of being derived from an ancestor that possessed ridges (Appendix 1, Character 7). The parallel anterior ridges in taxa such as *Tropidostoma* or *Dicynodon* likely represent a modification of the convergent ridge morphology.

The taxa *Emydops, Myosaurus,* and *Cistecephalus* are reconstructed as forming a clade (Figure 1a, Node I) that has the same membership as the Emydopidae of King (1988, 1990; Figure 1c, Node C). However, the relationships among the taxa in the clade presented here are different than those of King; instead of *Emydops*, *Cistecephalus* is reconstructed as the sister taxon of *Myosaurus*. This pattern of relationship is supported by two synapomorphies in this analysis (the presence of a foramen on the palatal surface of the palatine, and posteromedially extended anterior orbital margins that partially close off the back of the snout). Both of the proposed synapomorphies are quite distinctive, and I have only observed these features in *Cistecephalus, Myosaurus,* and *Cistecephaloides* (which Cluver (1974a) proposed was closely related to *Cistecephalus*; a palatal foramen has also been reported in *Kawingasaurus*, another potential relative of *Cistecephalus* (Cox, 1972); also see Appendix 1, Characters 24, 25). In addition, the synapomorphies King (1988, 1990) proposed to support a close relationship between *Myosaurus* and *Emydops* to the exclusion of *Cistecephalus* (reduced upper teeth, long, straight anterior pterygoid rami, and a shortened basicranial region) also can be found in *Cistecephalus*, and are thus diagnostic of a more inclusive clade. Cluver (1974b) also noted the possibility of a close relationship between *Cistecephalus* and *Myosaurus*, and suggested that both taxa could be derived from a *Myosauroides*-like ancestor.

Tropidostoma, Oudenodon, and *Rhachiocephalus* form a clade (Figure 1a, Node L) that has the same membership as the Cryptodontinae of King (1988, 1990; Figure 1a, Node E), but here again the relationships of the taxa within the clade are different. In this case, *Oudenodon* and *Tropidostoma* are reconstructed as being more closely related to each other than either is to *Rhachiocephalus,* whereas King favored a sister group relationship between *Oudenodon* and *Rhachiocephalus.* King (1988, 1990), used the loss of teeth as a synapomorphy to unite *Rhachiocephalus* and *Oudenodon* and exclude *Tropidostoma.* Although *Tropidostoma* does possess upper and lower postcanine teeth (some specimens also possess tusks), there are several other features that strongly suggest a close relationship between *Tropidostoma* and *Oudenodon.*

In this analysis, two synapomorphies unite *Oudenodon* and *Tropidostoma,* the presence of a relatively long interpterygoid vacuity that reaches the level of the anterior portion of the palatines and a temporal region in which the postorbitals partially overlap the parietals, with the parietals exposed in a median groove or depression. King (1988, 1990) used the latter feature to diagnose her Tropidostomini, but in my observations this character state also characterizes nearly all *Oudenodon* specimens, suggesting it is diagnostic for a more inclusive clade. The intertemporal region of *Rhachiocephalus* is distinctly different because it is narrower and the postorbitals nearly completely overlap the parietals. In addition, the detailed morphology of the nasal bosses also supports the topology presented here. All three taxa possess paired nasal bosses, but the bosses of *Tropidostoma* and *Oudenodon* are less elongate and usually centered approximately over the center of the external narial openings. The bosses of *Rhachiocephalus* tend to be more elongate and ridge-like, and usually are located posterodorsal to the narial opening. *Rhachiocephalus* also tends to be larger than either *Oudenodon* or *Tropidostoma,* and it possesses a distinct pineal boss, which the other taxa lack. However, it is important to note that the results of the decay analysis show that only one additional morphological step is required to make *Rhachiocephalus* the sister taxon of *Oudenodon.*

The evolutionary history of the dentition of dicynodonts implied by the preferred cladogram of this analysis also deserves mention because it requires gains and losses of teeth that initially seem somewhat counter-intuitive. Basal anomodonts possess laterally placed teeth on the premaxilla, maxilla, and dentary, whereas many advanced dicynodonts have completely replaced their teeth with a keratinized beak. Several other dicynodonts possess a keratinized beak but also retain some teeth. Some of these taxa (e.g., *Robertia, Emydops, Pristerodon, Tropidostoma*) have been considered basal members of toothless clades that document the process of tooth loss (Cox 1998; Watson 1948). However, the preferred cladogram of this analysis implies that the presence of teeth in some of these taxa represent reversals to a toothed state from a toothless ancestor.

The cladogram presented here suggests that premaxillary teeth were lost in the common ancestor of *Eodicynodon* and *Kannemeyeria* (Figure 1a, Node A), but a reversal later occurred in *Endothiodon.* This reversal may characterize the lineage including both *Endothiodon* and *Chelydontops* (Figure 1a, Node D), depending on how the palate of *Chelydontops* is interpreted (Appendix 1, Character 2). I do not consider *Chelydontops* to possess premaxillary teeth, but the presence of teeth very close to the maxilla/premaxilla suture in that taxon supports the hypothesis that a secondary anterior lengthening of the upper tooth row occurred in this clade.

Maxillary teeth were independently lost in *Diictodon* and the common ancestor of *Kingoria* and *Kannemeyeria* (Figure 1a, Node G). The loss in *Diictodon* is corroborated by an undescribed, toothed *Diictodon*-like specimen from the lower *Tapinocephalus* Assemblage Zone (Rubidge pers. comm., 2000). The loss in the ancestor of *Kannemeyeria* and *Kingoria* is more interesting because it implies reversals to a toothed state in *Emydops* and *Tropidostoma.* However, these reversals are also required in some optimizations of this character on the cladogram of King (1988, 1990), as is an additional reversal to a toothed state in *Robertia.* The implied reversal in *Robertia* is not well supported because the undescribed, toothed *Diictodon*-like specimen strongly suggests that the common ancestor of *Diictodon* and *Robertia* was also toothed.

A similar pattern is observed for the dentary teeth. The presence of dentary teeth is the basal character state for Anomodontia, and medially-placed dentary teeth characterize the clade including *Robertia, Kannemeyeria,* and all descendants of their most recent common ancestor (Figure 1a, Node B). The complete loss of teeth took place independently in *Diictodon* and the common ancestor of *Kingoria* and *Kannemeyeria* (Figure 1a, Node G), and reversals to a toothed state occurred in *Emydops* and *Tropidostoma.* Some optimizations of this character on the cladogram of King (1988, 1990) also require a similar pattern of loss and reversal, as well as an additional reversal to a toothed state in *Robertia.* However, this reversal appears less likely because the undescribed, toothed *Diictodon*-like specimen strongly suggests that the common ancestor of *Diictodon* and *Robertia* possessed a toothed dentary.

The patterns of tooth loss and gain in the skull and jaw implied by the preferred cladogram of this analysis suggest that some degree of plasticity existed in the developmental processes responsible for the formation of the dentition in dicynodonts. This perhaps is not surprising given that much of tooth development is the result of epithelium-mesenchyme interactions that can be altered easily by slight modifications in developmental sequences or the behavior of cell populations. In addition, it has been shown that chick epithelium retains the ability to participate in tooth formation (Kollar 1972; Kollar & Fisher 1980), despite coming from a lineage that has been toothless since at least the Early Tertiary. The
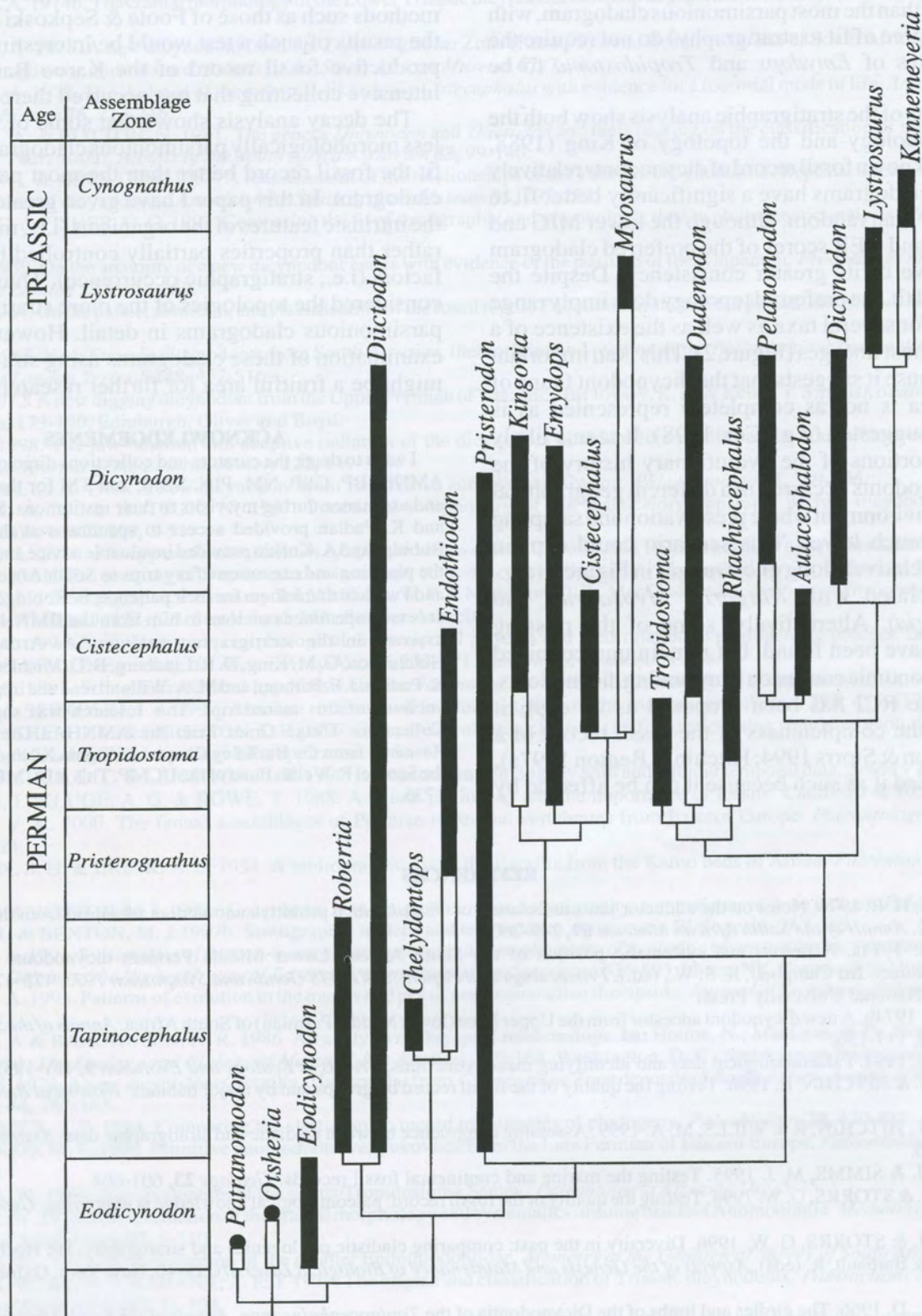
Age	Assemblage Zone
TRIASSIC	*Cynognathus*
	Lystrosaurus
PERMIAN	*Dicynodon*
	Cistecephalus
	Tropidostoma
	Pristerognathus
	Tapinocephalus
	Eodicynodon

Taxa (left to right across cladogram): *Patranomodon*, *Otsheria*, *Eodicynodon*, *Robertia*, *Chelydontops*, *Endothiodon*, *Diictodon*, *Pristerodon*, *Kingoria*, *Emydops*, *Cistecephalus*, *Tropidostoma*, *Myosaurus*, *Oudenodon*, *Rhachiocephalus*, *Pelanomodon*, *Aulacephalodon*, *Dicynodon*, *Lystrosaurus*, *Kannemeyeria*

Figure 2: Cladogram based on that of Figure 1a showing the stratigraphic ranges of the included taxa. Solid bars indicate known ranges and open bars indicate ghost ranges implied by the cladogram. Thin lines indicate ghost lineages implied by the cladogram. Stratigraphic ranges and assemblage zones are based on Rubidge (1995a). Because *Patranomodon* and *Otsheria* are each known from a single specimen their stratigraphic ranges are approximate. The stratigraphic range of *Chelydontops* also is not well constrained and therefore approximate. The range of *Kingoria* is an approximation based on data presented in King (1988).

losses and reversals required by this cladogram likely occurred over a much shorter period of time, possibly ten million years or less. It is important to note that slightly less parsimonious cladograms (two morphological steps longer than the most parsimonious cladogram, with the same degree of fit to stratigraphy) do not require the toothed states of *Emydops* and *Tropidostoma* to be reversals.

The results of the stratigraphic analysis show both the preferred topology and the topology of King (1988, 1990) fit the known fossil record of dicynodonts relatively well. Both cladograms have a significantly better fit to stratigraphy than random, although the lower MIG and higher RCI and GER scores of the preferred cladogram are indicative of its greater consistency. Despite the good general fit, the preferred topology does imply range extensions for several taxa as well as the existence of a number of ghost lineages (Figure 2). This is an important finding because it suggests that the dicynodont fauna of South Africa is not as completely represented as is sometimes suggested (e.g., Cox 1998). It seems likely that some portions of the evolutionary history of the Karoo dicynodonts occurred in a different geographical location or environment where preservation and sampling rates were much lower. This scenario could explain some of the relatively long ghost ranges in Figure 2 (e.g., those associated with *Kingoria*, *Myosaurus*, and *Kannemeyeria*). Alternatively, some of the missing taxa could have been found, but remain unrecognized due to the taxonomic confusion surrounding dicynodonts. Although the RCI has been proposed as an explicit measure of the completeness of the fossil record of a group (Benton & Storrs 1994; Hitchin & Benton 1997a), I have not used it as such because it can be affected by factors such as the accuracy of the cladogram examined, sampling rates, and extinction (Paul 1998; Wagner 1998, 2000). The gaps implied by the preferred cladogram can be tested independently through the use of statistical methods such as those of Foote & Sepkoski (1996), and the results of such a test would be interesting given the productive fossil record of the Karoo Basin and the intensive collecting that has occurred there.

The decay analysis shows that some of the slightly less morphologically parsimonious cladograms actually fit the fossil record better than the most parsimonious cladogram. In this paper I have given greater weight to the intrinsic features of the organisms (i.e., morphology) rather than properties partially controlled by extrinsic factors (i.e., stratigraphic occurrence). Thus I have not considered the topologies of the more stratigraphically parsimonious cladograms in detail. However, further examination of these cladograms using stratocladistics might be a fruitful area for further research.

ACKNOWLEDGEMENTS

REFERENCES

BARGHUSEN, H. R. 1976. Notes on the adductor jaw musculature of *Venjukovia*, a primitive anomodont therapsid from the Permian of the U.S.S.R. *Annals of the South African Museum* **69,** 249-260.

BARRY, T. H. 1974a. Affinities and systematic position of the South African Lower Middle Permian dicynodonts (Therapsida: Dicynodontidae). In: Campbell, K. S. W., (ed.), *Proceedings and Papers. 3rd IUGS Gondwana Symposium 1973,* 475-479. Canberra, Australian National University Press.

BARRY, T. H. . 1974b. A new dicynodont ancestor from the Upper Ecca (lower Middle Permian) of South Africa. *Annals of the South African Museum* **64,** 117-136.

BENTON, M. J. 1994. Palaeontological data and identifying mass extinctions. *Trends in Ecology and Evolution* **9,** 181-185.

BENTON, M. J. & HITCHIN, R. 1996. Testing the quality of the fossil record by groups and by major habitats. *Historical Biology* **12,** 111-157.

BENTON, M. J., HITCHIN, R & WILLS, M. A. 1999. Assessing congruence between cladistic and stratigraphic data. *Systematic Biology* **48,** 581-596.

BENTON, M. J. & SIMMS, M. J. 1995. Testing the marine and continental fossil records. *Geology* **23,** 601-604.

BENTON, M. J. & STORRS, G. W. 1994. Testing the quality of the fossil record: paleontological knowledge is improving. *Geology* **22,** 111-114.

BENTON, M. J. & STORRS, G. W. 1996. Diversity in the past: comparing cladistic phylogenies and stratigraphy. In: Hochberg, M. E., Colbert, J. & Barbault, R, (eds), *Aspects of the Genesis and Maintenance of Biological Diversity,* 19-40. New York, Oxford University Press.

BOONSTRA, L. D. 1966. The girdles and limbs of the Dicynodontia of the *Tapinocephalus* zone. *Annals of the South African Museum* **50,** 1-11.

BRINKMAN, D. 1981. The structure and relationships of the dromasaurs (Reptilia: Therapsida). *Breviora* **465,** 1-34.

BREMER, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42,** 795-803.

BROOM, R. 1905. On the structure and affinities of the endothiodont reptiles. *Transactions of the South African Philosophical Society* **15,** 259-282.

BROOM, R. 1906. On the Permian and Triassic faunas of South Africa. *Geological Magazine* **5,** 29-30.

BROOM, R. 1932. *The Mammal-like Reptiles of South Africa and the Origin of Mammals.* London, H. F. and G. Witherby.

CAMP, C. L. 1956. Triassic dicynodont reptiles: part II. Triassic dicynodonts compared. *Memoirs of the University of California* **13,** 305-341.

CAMP, C. L. & WELLES, S. P. 1956. Triassic dicynodont reptiles: part I. The North American genus *Placerias. Memoirs of the Univeristy of California* **13,** 255-304.

CLUVER, M. A. 1971. The cranial morphology of the dicynodont genus *Lystrosaurus. Annals of the South African Museum* **56,** 155-274.

CLUVER, M. A. 1974a. The skull and mandible of a new cistecephalid dicynodont. *Annals of the South African Museum* **64,** 137-155.

CLUVER, M. A. 1974b. The cranial morphology of the Lower Triassic dicynodont *Myosaurus gracillis. Annals of the South African Museum* **66,** 35-54.

CLUVER, M. A. 1975. A new dicynodont from the *Tapinocephalus* Zone (Karoo System, Beaufort Series) of South Africa, with evidence of the jaw adductor musculature. *Annals of the South African Museum* **67,** 7-23.

CLUVER, M. A. 1978. The skeleton of the mammal-like reptile *Cistecephalus* with evidence for a fossorial mode of life. *Annals of the South African Museum* **76,** 213-246.

CLUVER, M. A. & HOTTON, N. 1981. The genera *Dicynodon* and *Diictodon* and their bearing on the classification of the Dicynodontia (Reptilia, Therapsida). *Annals of the South African Museum* **83,** 99-146.

CLUVER, M. A. & KING, G. M. 1983. A reassessment of the relationships of the Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. *Annals of the South African Museum* **91,** 195-273.

CLYDE, W. C. & FISHER, D. C. 1997. Comparing the fit of stratigraphic and morphologic data in phylogenetic analysis. *Paleobiology* **23,** 1-19.

COX, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proceedings of the Zoological Society of London* **132,** 321-367.

COX, C. B. 1964. On the palate, dentition, and classification of the fossil reptile Endothiodon and related genera. *American Museum Novitates* **2171,** 1-25.

COX, C. B. 1965. New Triassic dicynodonts from South America, their origins and relationships. *Philosophical Transactions of the Royal Society of London Series B* **248,** 457-516.

COX, C. B. 1972. A new digging dicynodont from the Upper Permian of Tanzania. **In:** Joysey, K. A. & Kemp, T. S., (eds), *Studies in Vertebrate Evolution,* 173-190. Edinburgh, Oliver and Boyd.

COX, C. B. 1998. The jaw function and adaptive radiation of the dicynodont mammal-like reptiles of the Karoo basin of South Africa. *Zoological Journal of the Linnean Society* **122,** 349-384.

COX, C. B. & LI, J.-l. 1983. A new dicynodont from East Africa and its classification. *Palaeontology* **26,** 389-406.

CROMPTON, A. W. & HOTTON, N. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). *Postilla* **109,** 1-51.

DEFAUW, S. L. 1986. *The appendicular skeleton of African dicynodonts.* Unpublished Ph.D. Thesis, Wayne State University, Detroit.

EWER, R. F. 1961. The anatomy of Daptocephalus leoniceps (Owen). *Proceedings of the Zoological Society of London* **136,** 375-402.

FISHER, D. C. 1992. Stratigraphic Parsimony. **In:** Maddison, W. P. & Maddison, D. R., MacClade (eds), *Analysis of Phylogeny and Character Evolution,* Version 3, 124-129. Sunderland, MA, Sinauer Associates.

FISHER, D. C. 1994. Stratocladistics: morphological and temporal patterns and their relation to phylogenetic process. **In:** Grande, L. & Reippel, O. (eds), *Interpreting the Hierarchy of Nature,* 133-171. San Diego, Academic Press.

FISHER, D. C. 1997. Stratocladistics and hypothesis choice. *Journal of Vertebrate Paleontology* **17** (supplement to 3), 46A.

FOOTE, M. & SEPKOSKI, J. J. 1999. Absolute measures of the completeness of the fossil record. *Nature* **398,** 415-417.

FOX, D. L., FISHER, D. C. & LEIGHTON, L. R. 1997. Comparison of stratocladistics and cladistics using simulated evolutionary histories. *Journal of Vertebrate Paleontology* **17** (supplement to 3), 47A.

FOX, D. L., FISHER, D. C. & LEIGHTON, L. R. 1999. Reconstructing phylogeny with and without temporal data. *Science* **284,** 1816-1819.

GAUTHIER, J., KLUGE, A. G. & ROWE, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* **4,** 105-210.

GOLUBEV, V. K. 2000. The faunal assemblages of Permian terrestrial vertebrates from Eastern Europe. *Paleontological Journal* **34,** S211-S224.

HAUGHTON, S. H. & BRINK, A. S. 1954. A bibliographic list of the Reptilia from the Karoo beds of Africa. *Paleontologia Africana* **2,** 1-187.

HITCHIN, R. & BENTON, M. J. 1997a. Congruence between parsimony and stratigraphy: comparisons of three indices. *Paleobiology* 20-32.

HITCHIN, R. & BENTON, M. J.1997b. Stratigraphic indices and tree balance. Systematic Biology 46, 563-569.

HOPSON, J. A. 1991. Systematics of the non-mammalian Synapsida and implications of evolution in synapsids. **In:** Schultze, H.-P. & Trueb, L., (eds), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus,* 635-693. Ithaca, NY, Comstock Publishing Associates.

HOPSON, J. A. 1995. Patterns of evolution in the manus and pes of non-mammalian therapsids. *Journal of Vertebrate Paleontology* **15,** 615-639.

HOPSON, J. A.& BARGHUSEN, H. R. 1986. An analysis of therapsid relationships. **In:** Hotton, N., MacLean, P. D., Roth, J. J., & Roth, E. C., (eds), *The Ecology and Biology of Mammal-like Reptiles,* 159-168. Washington, D. C , Smithsonian Institution Press.

HOTTON, N. 1974. A new dicynodont (Reptilia, Therapsida) from *Cynognathus* Zone deposits of South Africa. *Annals of the South African Museum* **64,** 157-165.

HUELSENBECK, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology* **20,** 470-483.

IVAKHNENKO, M. F. 1996. Primitive anomodonts, venyukoviids from the Late Permian of Eastern Europe. *Paleontological Journal* **30,** 575-582

KEYSER, A. W. 1973. A re-evaluation of the genus Tropidostoma Seeley. *Paleontologia Africana* **16,** 25-35.

KEYSER, A. W. 1975. A re-evaluation of the cranial morphology and systematics of some tuskless Anomodontia. *Memoirs of the Geological Survey of South Africa* **67,** 1-110.

KEYSER, A. W. 1993. A re-evaluation of the smaller Endothiodontidae. *Memoirs of the Geological Survey of South Africa* **82,** 1-53.

KEYSER, A. W. & CRUICKSHANK, A. R. I. 1979. The origins and classification of Triassic dicynodonts. *Transactions of the Geological Society of South Africa* **82,** 81-108.

KEYSER, A. W & SMITH, R. M. H. 1977-1978. Vertebrate biozonation of the Beaufort Group with special reference to the Western Karoo Basin. *Annals of the Geological Survey of South Africa* **12,** 1-35.

KING, G. M. 1981a. The functional anatomy of a Permian dicynodont. *Philosophical Transactions of the Royal Society of London Series B* **291,** 243-322.

KING, G. M. 1981b. The postcranial skeleton of *Robertia broomiana,* an early dicynodont (Reptilia, Therapsida) from the South African Karoo. *Annals of the South African Museum* **84,** 203-231.

KING, G. M. 1985. The postcranial skeleton of *Kingoria nowacki* (von Huene) (Therapsida: Dicynodontia). *Zoological Journal of the Linnean Society* **84,** 263-289.

KING, G. M. 1988. *Anomodontia*. Handbuch der Paläoherpetologie, 17C. Stuttgart , Gustav-Fischer Verlag.

KING, G. M. 1990. *The Dicynodonts: A Study in Palaeobiology*. New York, Chapman and Hall.

KING, G. M. 1993. How many species of *Diictodon* were there? *Annals of the South African Museum* **102,** 303-325.

KING, G. M. 1994. The early anomodont *Venjukovia* and the evolution of the anomodont skull. *Journal of Zoology, London* **232,** 651-673.

KING, G. M., RUBIDGE, B. S. & OELOFSEN, B. W. 1989. The evolution of the dicynodont feeding system. *Zoological Journal of the Linnean Society* **96,** 185-211.

KING, G. M. & RUBIDGE, B. S. 1993. A taxonomic revision of small dicynodonts with postcanine teeth. *Zoological Journal of the Linnean Society* **107,** 131-154.

KITCHING, J. W. 1977. The distribution of the Karoo vertebrate fauna. *Memoirs of the Bernard Price Institute for Palaeontological Research* **1,** 1-131.

KOLLAR, E. J. 1972. The development of the integument: spatial, temporal, and phylogenetic factors. *American Zoologist* **12,** 125-135.

KOLLAR, E. J. & FISHER, C. 1980. Tooth induction in chick epithelium: expression of quiescent genes for enamel synthesis. *Science* **207,** 993-994.

LATIMER, E. M., GOW, C. E & RUBIDGE, B. S. 1995. Dentition and feeding niche of *Endothiodon* (Synapsida; Anomodontia). *Palaeontologia Africana* **32,** 75-82.

LUCAS, S. G. 1996. Vertebrate biochronology of the Mesozoic of China. *Memoirs of the Beijing Natural History Museum* **55,** 110-149.

LUCAS, S. G. 1998. *Placerias* (Reptilia, Dicynodontia) from the Upper Triassic of the Newark Supergroup, North Carolina, USA, and its biochronological significance. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **1998,** 432-448.

MADDISON, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Systematic Zoology 40, 315-328.

MADDISON, W. P. & MADDISON D. R. 1999. *MacClade: Analysis of Phylogeny and Character Evolution*, Version 3.08a. Sunderland, MA, Sinauer Associates.

MODESTO, S. & RUBIDGE, B. S. 2000. A basal anomodont therapsid from the lower Beaufort Group, Upper Permian of South Africa. *Journal of Vertebrate Paleontology* **20,** 515-521.

MODESTO, S. & RUBIDGE, B. S. & WELMAN, J. 1999. The most basal anomodont therapsid and the primacy of Gondwana in the evolution of the anomodonts. *Proceedings of the Royal Society of London Series B.* **266,** 331-337.

MODESTO, S. & RYBCZYNSKI, N. 2000. The amniote faunas of the Russian Permian: implications for Late Permian terrestrial vertebrate biogeography. In: Benton, M. J., Kurochkin, E. N., Shishkin, M. A., & Unwin, D. M., (eds), *The Age of Dinosaurs in Russia and Mongolia,* 17-34. Cambridge: Cambridge University Press.

NORELL, M. A. 1993. Tree-based approaches to understanding history: comments on ranks, rules, and the quality of the fossil record. *American Journal of Science* **293A,** 407-417.

NORELL, M. A. & NOVACEK, M. J. 1992a. The fossil record and evolution. Comparing cladistic and paleontologic evidence for vertebrate history. *Science* **255,** 1690-1693.

NORELL, M. A. & NOVACEK, M. J. 1992b. Congruence between superpositional and phylogenetic patterns: comparing cladistic patterns with fossil records. *Cladistics* **8,** 319-337.

NORELL, M. A. & NOVACEK, M. J. 1997. The ghost dance: a cladistic critique of stratigraphic approaches to paleobiology and phylogeny. *Journal of Vertebrate Paleontology* **17** (supplement to 3), 67A.

OLSON, E. C. and BYRNE, F. 1938. Osteology of *Aulacocephalodon peavoti*. *Journal of Geology* **46,** 177-190.

OWEN, R. 1845. Description of certain fossil crania discovered by A. G. Bain, Esq., in the sandstone rocks at the southeastern extremity of Africa, referable to different species of an extinct genus of Reptilia (*Dicynodon*), and indicative of a new tribe or suborder of Sauria. *Transactions of the Geological Society of London* **7,** 59-84.

PAUL, C. R. C. 1998. Adequacy, completeness and the fossil record. **In:** Donovan, S. K. & Paul, C. R. C., (eds), *The Adequacy of the Fossil Record,* 1-22. New York, John Weily and Sons.

PEARSON, H. S. 1924. A dicynodont reptile reconstructed. *Proceedings of the Zoological Society of London* **1924,** 827-854.

RAY, S. 2000. Endothiodont dicynodonts from the Late Permian Kundaram Formation, India. *Palaeontology* **43,** 375-404.

REIPPEL, O. 1997. Falsificationist versus verificationist approaches to history. *Journal of Vertebrate Paleontology* **17** (supplement to 3) 71A.

ROWE, T. & VAN DEN HEEVER, J. A. 1986. The hand of *Anteosaurus magnificus* (Dinocephalia: Therapsida) and it bearing on the origin of the mammalian manual phalangeal formula. *South African Journal of Science* **82,** 641-645.

RUBIDGE, B. S. 1984. The cranial morphology and palaeoenvironment of *Eodicynodon* Barry (Therapsida: Anomodontia). *Navorsinge van die Nasionale Museum Bloemfontein* **4,** 325-404.

RUBIDGE, B. S. 1985. The first record of a complete snout of the primitive dicynodont *Eodicynodon oosthuizeni*, Barry 1974 (Therapsida, Dicynodontia. *Navorsinge van die Nasionale Museum Bloemfontein* **4,** 501-512.

RUBIDGE, B. S. 1990a. Redescription of the cranial morphology of *Eodicynodon oosthuizeni* (Therapsida, Dicynodontia). *Navorsinge van die Nasionale Museum Bloemfontein* **7,** 1-25.

RUBIDGE, B. S. 1990b. The cranial morphology of a new species of *Eodicynodon* (Therapsida, Dicynodontia). *Navorsinge van die Nasionale Museum Bloemfontein* **7,** 29-42. 6

RUBIDGE, B. S. (Ed.). 1995a. Biostratigraphy of the Beaufort Group (Karoo Supergroup). South African Committee for Stratigraphy Biostratigraphic Series 1: 1-46.

RUBIDGE, B. S. 1995b. Biostratigraphy of the *Eodicynodon* Assemblage Zone. **In:** Rubidge, B. S., (ed), *Biostratigraphy of the Beaufort Group (Karoo Supergroup),* 3-7. South African Committee for Stratigraphy Biostratigraphic Series 1.

RUBIDGE, B. S. & HOPSON, J. A. 1990. A new anomodont therapsid from South Africa and its bearing on the ancestry of Dicynodontia. *South African Journal of Science* **86,** 43-45.

RUBIDGE, B. S. & HOPSON, J. A. 1996. A primitive anomodont therapsid from the base of the Beaufort Group (Upper Permian) of South Africa. *Zoological Journal of the Linnean Society* **117,** 115-139.

RUBIDGE, B. S., JOHNSON, M. R., KITCHING, J. W., SMITH, R. M. H., KEYSER, A. W., & GROENEWALD, G. H. 1995. An introduction to the biozonation of the Beaufort Group. **In:** Rubidge, B. S., (ed), *Biostratigraphy of the Beaufort Group (Karoo Supergroup),* 1-2. South African Committee for Stratigraphy Biostratigraphic Series 1.

RUBIDGE, B. S., KING, G. M. & HANCOX, P. J. 1994. The postcranial skeleton of the earliest dicynodont synapsid *Eodicynodon* from the Upper Permian of South Africa. *Palaeontology* **37,** 397-408.

RYBCZYNSKI, N. 2000. Cranial anatomy and phylogenetic position of Suminia getmanovi, a basal anomodont (Amniota: Therapsida) from the Late Permian of Eastern Europe. *Zoological Journal of the Linnean Society* **130,** 329-373.

SEELEY, H. G. 1892. Researches on the structure, organization, and classification of the fossil Reptilia. Further observations on *Pareiasaurus*. *Philosophical Transactions of the Royal Society of London Series B* **183,** 311-370.

SIDDALL, M. E. 1996. Stratigraphic consistency and the shape of things. *Systematic Biology* **45,** 111-115.

SIDDALL, M. E.. 1997. Stratigraphic indices and tree balance: a reply to Hitchin and Benton. *Systematic Biology* **46,** 569-573.

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.

SMITH, A. 2000. Stratigraphy in phylogeny reconstruction. *Journal of Paleontology* **74,** 763-766.

SMITH, A. & LITTLEWOOD, D. T. 1994. Paleontological data and molecular phylogenetic analysis. *Paleobiology* **20,** 259-273.

SMITH, R. M. H. & KEYSER, A. W. 1995. Biostratigraphy of the *Tapinocephalus* Assemblage Zone. **In:** Rubidge, B. S., (ed), B*iostratigraphy of the Beaufort Group (Karoo Supergroup)*, 8-12. South African Committee for Stratigraphy Biostratigraphic Series 1.

STORRS, G. W. 1993. The quality of the Triassic sauropterygian fossil record. *Revue de Paléobiologie* **7,** 217-228.

STRONG, E. E. & LIPSCOMB, D. 2000. Character coding and inapplicable data. *Cladistics* **15,** 363-371.

SURKOV, M. V. 1998. Morphological features of the postcranial skeleton in anomodonts reflecting the evolutionary development of the group. *Paleontological Journal 32,* 620-623.

SURKOV, M. V. 2000. On the historical biogeography of Middle Triassic Anomodonts. *Paleontological Journal* **34,** 84-88.

SWOFFORD, D. L. 2000. PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4.0b4a. Sunderland, Massachusetts, Sinauer Associates.

THEWISSEN, J. G. M. 1992. Temporal data in phylogenetic systematics: an example from the mammalian fossil record. *Journal of Paleontology* **66,** 1-8.

TOERIEN, M. J, 1953. Evolution of the palate in some anomodonts and its classificatory significance. *Palaeontologia Africana* **1,** 49-117.

TOLLMAN, S. M., GRINE, F. E. & HAHN, B. D. 1980. Ontogeny and sexual dimorphism in *Aulacephalodon* (Reptilia, Anomodontia). *Annals of the South African Museum* **81,** 159-186.

WAGNER, P. J. 1998. Phylogenetic analyses and the adequacy of the fossil record. **In:** Donovan, S. K. & Paul, C. R. C., (eds), *The Adequacy of the Fossil Record*, 165-188. New York, John Weily and Sons.

WAGNER, P. J. 2000. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Systematic Biology* **49,** 65-86.

WALTER, L. R. 1986. The limb posture of kannemeyeriid dicynodonts: functional and ecological considerations. **In:** Padian, K. (ed), *The Beginning of the Age of Dinosaurs*, 89-98. New York, Cambridge University Press.

WATSON, D. M. S. 1914. On the nomenclature of the South African pareiasaurians. *Annals and Magazine of Natural History* **14,** 98-102.

WATSON, D. M. S.. 1948. *Dicynodon* and its allies. *Proceedings of the Zoological Society of London* **188,** 823-877.

WATSON, D. M. S. 1960. The anomodont skeleton. *Transactions of the Zoological Society of London* **29,** 131-208.

WEISHAMPEL, D. B. & HEINRICH, R. E. 1992. Systematics of Hypsolophodontidae and basal Iguanodontia (Dinosauria: Ornithopoda). *Historical Biology* **6,** 159-184.

WILLS, M. A. 1999. Congruence between phylogeny and stratigraphy: randomization tests and the gap excess ratio. *Systematic Biology* **48,** 559-580.

APPENDIX 1

Description and discussion of characters used in phylogenetic analysis

Morphologic Characters

1) Keel-like extension of the palatal rim posterior to the caniniform process present (1) or absent (0).

A postcaniniform keel is found in *Emydops, Kingoria, Cistecephalus,* and *Myosaurus.* The holotypes of *Kombuisia* (BP/1/5344) and *Cistecephaloides* (SAM 6243) also possess this feature, although these taxa have not been included in this analysis. The keel has a rounded ventral edge, a steep-sided, wall-like lateral side, bears teeth in some *Emydops* specimens, and is formed by a continuation of the lateral palatal rim posterior to the caniniform process. Its height is variable; *Kingoria* and *Emydops* tend to have taller keels whereas *Cistecephalus* and *Myosaurus* have lower, less distinct keels. The postcaniniform keel is distinct from the postcaniniform crest (Character 28) because the crest has a sharp ventral edge, a smoothly sloping lateral side, and, in well-preserved specimens (e.g., SAM K5227, *Oudenodon*), can be seen to arise from the posteromedial side of the caniniform process. The character has been coded as "?" for taxa that lack caniniform processes because it is not directly applicable to them.

2) Premaxillary teeth present and located laterally (0), medially (1), or absent (2).

Most non-dicynodont anomodonts (*sensu* Modesto *et al.,* 1999; Rybczynski 2000) resemble the majority of synapsids by possessing premaxillary teeth that are located near the anterior or lateral margins of the palatal surface of the bone. *Galeops* may be an exception to this trend (Brinkman 1981), although undescribed specimens tentatively identified as *Galeops* in the collections of the South African Museum (SAM 4005, SAM 12261) have clear evidence of premaxillary teeth located near the margins of the palate. *Endothiodon* possesses 2 premaxillary teeth, but these are located posteromedially on the premaxillary secondary palate, well away from the margins of the premaxilla. *Chelydontops* also has been reported as having at least one tooth very near the premaxilla/maxilla suture (Cluver 1975), but my examination of the holotype (SAM 11558) and referred specimen (SAM 12259) has shown the suture to be poorly preserved in both cases. The most anterior tooth may touch the premaxilla/maxilla suture in the holotype, but it is not completely or nearly completely surrounded by the premaxilla as the premaxillary teeth are in *Endothiodon,* and as a result I have coded *Chelydontops* as lacking premaxillary teeth. All other dicynodont taxa included in this analysis clearly lack premaxillary teeth.

3) Premaxillae fused (1) or unfused (0).

The premaxillae are unfused and sutured together in the majority of synapsid taxa. A suture between the premaxillae is also visible in non-dicynodont anomodonts and in well- preserved specimens of *Eodicynodon* (e.g., ROZ 1, NM QR 2905, NM QR2989, NM QR2990). The premaxillae are indistinguishably fused in all other described dicynodont taxa.

4) Upper postcanine teeth located near lateral margins of maxilla (0), located more medially, but with more posterior teeth often approaching the lateral margin of maxilla (1), located medially and with teeth a constant distance from the margin of the maxilla (2), or absent (3).

The upper postcanine teeth are located near the lateral margin of the maxillae in non-dicynodont anomodonts, an arrangement similar to that of the majority of synapsid taxa. *Eodicynodon* is unique among dicynodonts in having postcanine teeth placed far laterally. In *E. oosthuizeni* the teeth are in line with the midline of the canine tusk on the posterior surface of the caniniform process, while in *E. oelofsoni* a tusk is absent and a row of teeth is present near the lateral margin of the palate (Rubidge, 1990b). A few specimens of *E. oosthuizeni* also have one or two medially placed postcanine teeth (e.g., ROZ 9, ROZ 11, NM QR2905, NM QR2989), but the nature of this variation has not yet been examined in detail. Because of the relative rarity of these specimens and the distinct lateral placement of at least some of the postcanine teeth visible in most *E. oosthuizeni* and *E. oelofsoni* specimens, I have chosen to code *Eodicynodon* as having laterally placed teeth.

In *Pristerodon, Robertia,* and *Chelydontops* the postcanine teeth are found in rows that are located on the medial part of the maxilla anteriorly, but approach the lateral margin of the palate more posteriorly. There are minor variations in this pattern (e.g., the "rows" are sometimes poorly formed in *Robertia,* the exact placement of the teeth is variable in *Pristerodon*; Keyser, 1993), but this variation does not appear to be of phylogenetic importance. I have given this coding to *Emydops* and *Tropidostoma* as well, although these taxa tend not to show the pattern as clearly. Their tooth rows are usually short (i.e., have few teeth) and located towards the posterior and lateral portion of the maxilla, although not as far laterally as in *Eodicynodon.* They often show a weak medial to lateral trend, and these teeth may be homologous with the more posterior teeth in the other taxa. If this hypothesis is accurate, then the coding used here should not be misleading.

The postcanine teeth of *Endothiodon* are located in medially placed, laterally concave rows. Although curved, these tooth rows remain a constant distance from the lateral margins of the palate because they also are laterally concave. This morphology is unlike the condition in e.g. *Pristerodon* because there the tooth rows approach the lateral margin of the palate posteriorly. All other taxa included in this analysis lack postcanine teeth.

5) Shelf-like area lateral to the upper postcanine teeth present (1) or absent (0).

Endothiodon and *Chelydontops* possess a flattened or slightly concave, shelf-like area lateral to the upper postcanine teeth (Cluver 1975; Cox 1964). When well preserved, these areas have a somewhat rugose texture suggesting a keratinous covering (e.g., BP/1/1659, *Endothiodon,* SAM 12259, *Chelydontops*). In *Chelydontops* the shelf is raised slightly above the level of the more anterior portion of the secondary palate, whereas in *Endothiodon* it is closer to the level of the anterior portion of the palate. The shelf is relatively longer in *Endothiodon,* but this may be related to the relatively longer tooth rows present

in that taxon. The non-dicynodont anomodonts and other toothed dicynodonts included in this analysis do not possess a shelf lateral to the upper tooth rows. The toothless dicynodonts have been coded as "?" because the character is not directly applicable to them.

6) Caniniform process absent (0), present (1), present with notch anterior to it (2).
In non-dicynodont anomodonts and *Endothiodon* the maxillary rim of the palate is not extended ventrally into a caniniform process. In his description of *Chelydontops*, Cluver (1975) reported that a caniniform process was absent. However, a caniniform process is present in SAM 12259, albeit weakly developed. The majority of dicynodonts (including *Chelydontops*) possess a caniniform process that is a smooth continuation of the palatal rim. The detailed morphology of the process in varies among taxa (compare e.g., *Placerias, Kannemeyeria, Emydops, Oudenodon,* and *Cistecephalus*). This variation is likely related to factors such as function and presence or absence of a canine tusk, and I have not distinguished the variants in my codings. In *Diictodon* and *Robertia* a distinctive notch in the palatal rim is present so that the anterior edge of the caniniform process is set off from the palatal rim and meets the palatal surface of the maxilla medial to the rim. Well-preserved specimens of *Eodicynodon* posses a notch in the palatal rim anterior to the canine tusk, but this is not homologous with the condition in *Diictodon* or *Robertia* because the notch is within the caniniform process and the anterior edge of the process is not set off from the palatal rim.

7) Paired anterior ridges on premaxilla absent (0), present but converge posteriorly (1), or present and do not converge (2).
Non-dicynodont anomodonts and *Eodicynodon* do not possess paired anterior ridges on the palatal surface of the premaxilla. Several undescribed dicynodont specimens collected in the lower *Tapinocephalus* Assemblage Zone (e.g., NM QR3145, NM QR3505; Rubidge, personal communication, 2000) possess weakly-developed, paired anterior ridges that converge with a Y-shaped, expanded, flattened anterior portion of the median palatal ridge. A similar condition is found in *Robertia, Diictodon,* and *Pristerodon,* except that the ridges are more weakly convergent and the expanded, flattened portion of the posterior median ridge is narrower and V-shaped. I did not distinguish between these morphologies in my coding of this character because the undescribed specimens were not included in this analysis.
Tropidostoma, Oudenodon, Rhachiocephalus, Aulacephalodon, Dicynodon, Lystrosaurus, and *Kannemeyeria* all possess well-developed anterior ridges that are roughly parallel, although some individual specimens of these taxa (e.g., SAM K1496, *Lystrosaurus*) show slight convergence of the ridges. A variably developed depression is often present between the ridges in these taxa.
Chelydontops, Endothiodon, Emydops, Kingoria, Cistecephalus, Myosaurus, and *Pelanomodon* lack distinct anterior palatal ridges. Some specimens of these taxa (e.g., BP/1/3858 and BP/1/1562, *Kingoria*; SAM 11060 and SAM K6623, *Emydops*; SAM 11558, *Chelydontops*) bear a depression at the front of the mouth that has slightly raised lateral edges that are suggestive of highly reduced ridges, indicating that the ridgeless condition in these and closely related taxa may represent a secondary loss. *Pelanomodon* also lacks anterior ridges (Cluver and King, 1983) and the anterior area of the premaxillary secondary palate of specimen GSP AF9183 is smooth and flat. Anterior palatal ridges are absent in *Endothiodon,* and the premaxillary secondary palate is unique in being highly vaulted (Cox, 1964; Latimer *et al.,* 1995; Ray, 2000).

8) Posterior median ridge on premaxilla absent (0), present with a flattened, expanded anterior area (1), or present without a flattened, expanded anterior area (2).
Non-dicynodont anomodonts do not possess a posterior median ridge on the palatal surface of the premaxilla. A wide, thick median ridge that flattens and fans out anteriorly is present in *Eodicynodon.* The ridge is thinner and more blade-like in most other dicynodont taxa. *Robertia, Diictodon, Pristerodon, Emydops,* and several undescribed specimens collected in the lower *Tapinocephalus* Assemblage Zone (e.g., NM QR3145, NM QR3505; Rubidge, personal communication, 2000) possess a thinner median ridge that flattens and expands into a slightly raised, Y-shaped or V-shaped area that converges with the anterior ridges in some cases (see Character 7). The median ridge of *Chelydontops* also flattens and expands anteriorly, but the expanded area is diamond-shaped. Most of the other taxa included in this analysis possess a thin median ridge that becomes lower anteriorly but lacks a distinct expanded area. The median ridge is relatively weakly developed in *Kingoria,* and unusually modified so that it is T-shaped in cross-section in *Myosaurus* (Cluver, 1974b). For simplicity, I have distinguished only between taxa that possess an expanded anterior portion of the median ridge and those that do not when the ridge is present. This distinction should be appropriate for the level of taxon sampling attempted in this analysis, although further subdivision of this character may be desirable in future analyses that include a greater number of taxa.

9) Palatal surface of premaxilla with well-defined depressions with curved sides lateral to median ridge (0), with groove-like depressions that have straight sides and a rounded anterior end (1), or relatively flat with poorly defined or no depressions present (2).
Non-dicynodont anomodonts do not possess a median palatal ridge, and those included in this analysis (*Patranomodon* and *Otsheria*) have been coded as "?" because this character is not directly applicable to them. *Eodicynodon* possesses a distinct depression in the premaxillary secondary palate on each side of the posterior median ridge. The depressions are roughly oval-shaped with the long axis of the oval trending antero-posteriorly. The sides of the depressions are curved and the anterior and posterior ends are slightly pointed. Similar depressions are found in *Diictodon* and *Robertia,* although the depressions are slightly shallower in *Robertia* than in the other two taxa.
Emydops, Cistecephalus, and *Myosaurus* possess more groove-like depressions lateral to the median ridge that have straight

edges, a rounded anterior end, and an open posterior end. *Myosaurus* is unique in having thin, channel-like depressions that are partially enclosed by the crossbar of the T-shaped median ridge located between the median ridge and the depressions in the palatal surface. Cluver (1974b) compared these channels to features found on the dorsal surface of the premaxilla in *Lystrosaurus* that may have been associated with a vomeronasal organ. I have given *Myosaurus* the same coding as *Emydops* and *Cistecephalus* because all three taxa possess groove-like palatal depressions, and the channels medial to them in *Myosaurus* seem to be unrelated, autapomorphic features.

The rest of the taxa in this analysis have do not possess depressions set off from the rest of the palatal surface by distinct margins. Instead, the palatal surface lateral to the median ridge is flat or slightly concave and smoothly merges with the palatal rim. The exact morphology of the area seems to be variable both among and within these taxa and is susceptible to alteration by plastic deformation of the skull. I have included this series of morphologies under a single character state because they all can be distinguished easily from the other two states and the variability among them appears to be random.

10) Lower teeth present on dorsal surface of dentaries (0), present on a medial swelling or shelf (1), or absent (2).
   The lower teeth of all non-dicynodont anomodonts for which jaws are known are located on the dorsal surface of the dentaries. In *Patranomodon* and *Suminia* the teeth are located slightly medially on the dorsal surface, and the dentary forms a narrow rim just lateral to base of the tooth crowns. The dorsal surface of the jaw has been expanded laterally to form a wide, flat surface in *Ulemica*, especially in large specimens (Ivakhnenko, 1996). The teeth are located on the medial side of this surface, but still clearly on the dorsal surface of the jaw. I have not distinguished between these variants in coding this character because only *Patranomodon* is included in this analysis. A lower jaw is not known for *Otsheria*, although Ivakhnenko (1996) noted that it may have been very similar to the jaw specimens assigned to *Venyukovia*. *Eodicynodon* also has teeth located towards the medial side of the dorsal dentary surface (Rubidge, 1984, 1990a, 1990b).
   The other toothed dicynodonts included in this analysis all have dentary teeth located on some type of medial shelf or swelling. *Robertia* and an undescribed, toothed, *Diictodon*-like specimen collected in the lower *Tapinocephalus* Assemblage Zone (BP/1/5589; Rubidge, personal communication, 2000) possess a row of teeth on the blade-like ridge that forms the medial boundary of dentary table. *Endothiodon* and *Chelydontops* have teeth located on a swelling of the dentary ramus that is medial and slightly below the level of the posterior dentary sulcus, although the condition is more strongly developed in *Endothiodon*. *Emydops* and *Pristerodon* possess teeth on a raised swelling or shelf that is medial to the posterior dentary sulcus. In *Tropidostoma* the dentary teeth are located on a raised swelling that is medial to the junction of the dentary table and posterior dentary sulcus. I have not distinguished between these variations in coding this character because the differences between the variants are relatively minor. All other taxa in this analysis lack dentary teeth. I have coded *Pelanomodon* as "?" because no jaw that is definitely referable to this taxon is currently known (Cluver and King, 1983).

11) Vomers fused (1) or unfused (0).
   Most non-dicynodont anomodonts and *Eodicynodon* resemble many other basal synapsids in possessing a clear midline suture between the vomers. Although the mid-ventral plate of the vomers is poorly preserved in the only known specimen of *Otsheria* (PIN 1758/5), careful scrutiny has uncovered no indication of a midline suture. The vomers may also be fused for at least part of their length in *Suminia* (Rybczynski 2000). All other dicynodont taxa included in this analysis possess vomers that are indistinguishably fused.

12) Mid-ventral plate of vomers with an expanded area posterior to junction with premaxilla (0) or with out a notably expanded area posterior to junction with premaxilla (1).
   The palatal exposure of the mid-ventral plate of the vomers of *Patranomodon*, *Eodicynodon*, *Robertia*, an undescribed *Diictodon*-like specimen collected in the lower *Tapinocephalus* Assemblage Zone (BP/1/5589, Rubidge, personal communication, 2000), and well-preserved specimens of *Endothiodon* (e.g., BP/1/1659) possess a small, oval-shaped expansion just posterior to the premaxilla/vomer suture. The expanded area is slightly larger in *Patranomodon* than in the other taxa. All of the other dicynodont taxa included in this analysis and *Otsheria* possess mid-ventral vomerine plates that are of constant width in palatal view.

13) Mid-ventral plate of vomers relatively wide in ventral view (0) or more narrow and blade-like in ventral view (1).
   The mid-ventral vomerine plates of most non-dicynodont anomodonts, *Eodicynodon*, *Robertia*, *Pristerodon*, *Tropidostoma*, *Endothiodon*, *Chelydontops*, *Kingoria*, and *Aulacephalodon* all have relatively wide ventral surfaces. In some of these taxa (e.g., *Tropidostoma*, *Pristerodon*) the lateral edges of the plate have the form of slightly raised ridges in palatal view, giving the ventral surface of the plate a trough-like appearance. In coding this character I have not distinguished between taxa that have vomerine troughs and those that do not because distortion or damage can easily remove the thin edges of the trough. Although not preserved well in the only known specimen, the mid-ventral plate of the vomers of *Otsheria* appears to have had a relatively narrow palatal surface, a condition unique among non-dicynodont anomodonts (although the plate may have widened dorsally). The rest of the taxa included in this analysis have vomerine plates that are quite thin and blade-like in palatal view.

14) Embayment of palatal rim anterior to caniniform process or tusk absent (0) or present (1).
   The palatal rims of *Emydops*, *Cistecephalus*, and *Myosaurus* all bow laterally anterior to the level of the caniniform process, forming an embayment on the surface of the secondary palate. The palatal rim of *Kingoria* does not have a strong embayment,

although a small, shallow depression on the medial surface of the rim just anterior to the caniniform process is present. I have coded this feature as an embayment because its morphology and position strongly suggest that is likely to be either a reduced or incipiently-developed embayment. Nearly all other taxa included in this analysis possess palatal rims that do not bow laterally to form an embayment. I have coded *Patranomodon*, *Otsheria*, and *Endothiodon* as "?" because they lack a distinct caniniform process, and thus this character is not directly applicable to them.

15) Dentary table absent (0), present as a small, rounded expansion of the dorsal surface of the dentary located near the symphysis (1), present as an elongate grooved surface on the dorsal surface of the dentary bounded laterally by a low ridge and medially by a tall, thin, dorsally convex blade (2), or present as an elongate grooved surface on the dorsal surface of the dentary bounded by low ridges (3).

The anterior dorsal surface of the dentary rami of non-dicynodont anomodonts are not expanded laterally to form a distinct dentary table. Although not included in this analysis, I do not consider the expanded dorsal surface of the dentary found in some large specimens of *Ulemica* (e.g., PIN 157/5, PIN 157/1113) to be homologous with the dentary table because it is located relatively posteriorly on the jaw ramus and is not dorsally-concave.

Eodicynodon possess a dentary table that has the form of a small, dorsally-concave, oval-shaped expansion of the dorsal surface of the dentary ramus just posterior to the dentary symphysis. A similar condition is also found in *Chelydontops* (SAM 12259) and *Pristerodon* (e.g., SAM K1658, SAM 10161, although this feature is more weakly developed in some *Pristerodon* specimens).

In *Robertia* and *Diictodon* the dentary table is more elongate and has a groove-like morphology. The lateral margin of the groove is formed by a low ridge and the medial margin is formed by a tall, thin, dorsally-convex blade. The blade bears teeth in *Robertia* and an undescribed *Diictodon*-like specimen collected in the lower *Tapinocephalus* Assemblage Zone (BP/1/5589, Rubidge, personal communication, 2000), but is toothless in *Diictodon*. *Tropidostoma*, *Oudenodon*, *Rhachiocephalus*, *Aulacephalodon*, *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria* also possess elongate, groove-like dentary tables, but in these taxa both the lateral and medial margins are formed by low ridges.

Kingoria, *Emydops*, *Myosaurus*, *Cistecephalus*, and *Endothiodon* all lack a distinct dentary table. However, some *Kingoria* specimens (e.g., SAM K8069, SAM K1260a) posses a small dentary table-like expansion of the dorsal dentary surface that is reminiscent of the condition in *Eodicynodon*, suggesting that the absence of a table in this taxon may be a secondary loss. I have coded *Pelanomodon* and *Otsheria* as "?" because no jaw material that is definitely referable to these taxa is currently known (Cluver and King 1983; Ivakhnenko 1996).

16) Posterior dentary sulcus present (1) or absent (0).

Many dicynodont taxa possess a longitudinal sulcus on the dorsal surface of the dentary rami posterior to the jaw symphysis. The sulcus is usually relatively deep, has a concave floor, and is located posterior to the dentary tables and lateral to the dentary teeth when they are present. However, the exact morphology of the sulcus varies among the taxa included in this analysis. In *Oudenodon*, *Tropidostoma*, *Rhachiocephalus*, *Aulacephalodon*, *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria* the sulcus is relatively narrow with tall, thin walls, and it merges with the dentary tables anteriorly. The sulcus is wider with lower walls in *Chelydontops*, *Endothiodon*, and *Pristerodon*, and it also extends farther forward in these taxa than in taxa such as *Oudenodon*. In *Emydops* the sulcus is relatively shallow and not as distinctly developed as in some taxa, but is still relatively long. Some specimens of *Cistecephalus* (e.g., SAM 10665) possess a small, shallow groove, bounded laterally by a raised ridge and a groove-like depression, in the same position as the sulcus in other taxa. For simplicity, I have chosen not to code these variants with different states in this analysis because they all share some morphological features and a similar position. However, subdivision of this state into one or more additional states may be desirable for more detailed future analyses that include additional taxa.

A dentary sulcus is absent in non-dicynodont anomodonts, *Eodicynodon*, *Diictodon*, *Robertia*, *Kingoria*, and *Myosaurus*. I do not consider the expanded dorsal surface of the dentary found in large specimens of *Ulemica* to be homologous with the dentary sulcus because the surface is not concave and lacks distinct lateral and medial walls. Although the occlusal pits developed on this surface are suggestive of being an incipient sulcus, the phylogenies of Modesto *et al.* (1999) and Rybczynski (2000) strongly suggest they are an autapomorphy of *Ulemica*. I have coded *Pelanomodon* and *Otsheria* as "?" because no jaw material that is definitely referable to these taxa is currently known (Cluver and King 1983; Ivakhnenko 1996).

17) Lateral dentary shelf present but relatively small (1), present as a boss-like swelling that is located near ventral margin of jaw ramus (2), present and well-developed (3), or absent (0).

The lateral dentary shelf of dicynodonts represents the insertion point for the lateral branch of the M. Adductor Mandibulae Externus (Barghusen 1976; Cluver 1971, 1975; Crompton and Hotton 1967; King 1981a, 1994; King *et al.*, 1989). This feature is absent in *Patranomodon* and not strongly developed in *Galeops* (Brinkman 1981; King 1994). A depression on the coronoid eminence with a relatively short shelf leading anteriorly from it likely represents the insertion in *Ulemica* and *Suminia* (Barghusen 1976; King 1994, King *et al.*, 1989; Rybczynski 2000). The shelf tends to have a wider, more rounded lateral surface in *Ulemica*, while in *Suminia* the lateral surface is thinner and narrower.

In *Eodicynodon*, *Emydops*, *Cistecephalus*, *Myosaurus*, and *Pristerodon* the shelf is relatively large and tends to project prominently from the lateral surface of the jaw, although there is minor variation in its exact morphology and position. Almost all of the other dicynodont taxa included in this analysis possess much more weakly developed lateral shelves. Although there is also some variation among these taxa, the shelves generally tend to have a low, rounded, somewhat rugose, lump-

like or ridge-like morphology anteriorly that grades into a thinner, more shelf-like area posteriorly. In *Endothiodon* the insertion of the lateral external adductor is uniquely modified into a prominent, bulbous, oval-shaped swelling on the lateral surface of the jaw, just anterior to the mandibular fenestra and extending to the ventral margin of the ramus (Ray 2000). I have coded *Pelanomodon* and *Otsheria* as "?" because no jaw material that is definitely referable to these taxa is currently known (Cluver and King 1983; Ivakhnenko 1996).

18) Symphyseal region of lower jaw with an upturned margin that is raised above the level of the dorsal surface of the jaw rami and has a scooped-out depression on its posterior surface (1), drawn into a sharp, spiky beak (2), shovel-shaped with a rounded or squared-off edge and a weak depression on its posterior surface (3), with a wedge-shaped margin that does not extend much above the dorsal surface of the jaw rami and has a groove-like depression on its posterior surface (4), or smoothly rounded and bearing teeth (0).

The jaw symphysis of non-dicynodont anomodonts resembles that found in most synapsid taxa. The anterior surface of the symphysis is smoothly rounded and the dorsal surface bears teeth. In *Eodicynodon*, the symphysis is shovel-shaped, toothless, projects anterodorsally, and bears a weak depression on its posterior surface. A similar condition is found in *Kingoria, Emydops, Cistecephalus*, and *Myosaurus*. The detailed morphology of the region varies slightly among these taxa (i.e., the symphysis is relatively wider in *Cistecephalus* than in *Kingoria* or *Emydops* and the dorsal edge is rounded in *Kingoria* and *Emydops* and squared-off in *Myosaurus* and *Cistecephalus*), but the overall appearance is similar enough in all of these taxa to be accurately represented by a single character state.

Most of the other taxa included in this analysis possess a curved, upturned, toothless jaw symphysis that projects nearly vertically above the level of the dorsal surface of the dentary rami. A depressed area is present on the posterior surface of the symphysis, but it is deeper and more elongate than in taxa such as *Kingoria*, giving it a more groove-like appearance. The jaw symphyses of *Lystrosaurus* and *Kannemeyeria* are relatively straight and wedge-shaped, and the anterodorsal end does not project far above the dorsal surface of the dentary rami. The depressed area on the posterior surface is deeper and more elongate and distinctly groove-like in these taxa than in others included in this analysis. *Endothiodon* is unique among the taxa examined here in possessing a jaw symphysis that is drawn into a conical spike that projects nearly vertically above the dentary rami. I have coded *Pelanomodon* and *Otsheria* as "?" because no jaw material that is definitely referable to these taxa is currently known (Cluver and King 1983; Ivakhnenko 1996).

19) Labial fossa present (1) or absent (0).

The labial fossa is a distinctive foramen bounded by the palatine, jugal, and maxilla located on the posterior surface of the caniniform process, and likely served as a passage for a blood vessel (Cluver 1971; King 1981a). *Pelanomodon, Aulacephalodon, Dicynodon, Lystrosaurus*, and *Kannemeyeria* all possess labial fossae, while all other taxa in the analysis do not.

The holotype of *Patranomodon* (NM QR3000) is interesting because it possesses a single foramen on the right side and two foramina that are divided by a thin bar on the left side that are bounded by the jugal, palatine, and maxilla. Although these features are potential positional homologues of the labial fossa, I have not coded them as such for two reasons. First, despite the similarity in position, the overall morphology of the foramina as well as the area surrounding them are very different than what is typical of the labial fossa. Second, because the holotype is the only known specimen of *Patranomodon*, it is difficult to be certain that the foramina are real features, and not the result of postmortem damage, pathology, or individual variation. If additional specimens of *Patranomodon* that also possess these foramina are discovered, a reassessment of the homologies of the labial fossa may be necessary.

20) Parietals widely exposed on the skull roof (0), postorbitals partially overlap parietals on skull roof, but parietals are exposed in a central groove or depression (1), parietals exposed on skull roof and postorbitals steeply placed on the lateral sides of the skull and concave laterally (2), postorbitals overlap parietals nearly completely but intertemporal region not crest-like (3), or postorbitals form a narrow, crest-like intertemporal region with minor exposure of parietals along the dorsal surface (4).

In non-dicynodont anomodonts and *Eodicynodon* the intertemporal skull roof is relatively wide and the parietals have a broad exposure between the postorbitals. A similar condition is found in *Emydops, Chelydontops* (although both the holotype and referred specimen of this taxon have been laterally compressed, making the intertemporal region appear narrower), *Robertia, Pristerodon*, and *Myosaurus*. However, in these taxa the intertemporal region is slightly longer relative to the total length of the skull than in *Eodicynodon* or the non-dicynodont anomodonts. *Cistecephalus* also possesses a wide intertemporal region, but in that taxon (as well as *Cistecephaloides* and *Kawingasaurus*; Cluver 1974a; Cox 1972) it has been modified so that it is rounded, dorsally convex, and partially roofs over the temporal openings. I have also coded *Lystrosaurus* with this state, although in that genus the postorbitals slope slightly more ventrolaterally than in the other taxa. Even though the intertemporal regions of *Aulacephalodon* and *Pelanomodon* are also wide, they have been given a separate character state because the postorbitals are nearly perpendicular to the parietal portion of the intertemporal skull roof and are concave laterally (the postorbitals of all other examined taxa are flat to slightly convex).

Diictodon, Tropidostoma, Oudenodon, and *Kingoria* all possess narrower intertemporal regions in which the postorbitals overlap the parietals fairly extensively, but some exposure of the parietals on the skull roof is still present. In *Oudenodon* and *Tropidostoma* (also see Methods) the parietals are exposed between the postorbitals in a groove-like depression, whereas in *Diictodon* and *Kingoria* the parietal exposure is flatter and less groove-like. The postorbitals make contact along the midline of the skull in some specimens of *Kingoria* and *Diictodon*, although this morphology can be exaggerated by

postmortem lateral compression of the skull (Keyser 1975). Although there are slight differences between the morphologies seen in *Diictodon* and *Kingoria* versus those of *Oudenodon* and *Tropidostoma*, I have coded all four taxa with the same state for simplicity. Subdividing this state into two separate states does not alter the topological results of this analysis. *Dicynodon* and *Rhachiocephalus* possess relatively narrow intertemporal regions characterized by complete or nearly complete overlap of the postorbitals over the parietals for most of the intertemporal length of the skull. The postorbitals in these taxa slope ventrolaterally at a sub-vertical angle. *Kannemeyeria* and *Endothiodon* are also characterized by narrow intertemporal regions, but in these taxa the postorbitals are nearly vertical, giving the region a more distinctly crest-like appearance. There is minor exposure of the parietals in the dorsal surface of the crest in both taxa, although the exposure is somewhat wider and more groove-like in *Endothiodon*.

21) Squamosal with lateral fossa for the origin of the lateral branch of the M. Adductor Mandibulae Externus (1) or without lateral fossa (0).
All of the dicynodonts included in this analysis possess an expanded, shallow fossa on the posterolateral surface of the squamosal from which the lateral branch of the external adductor muscle arose (Barghusen 1976; Crompton and Hotton 1967; King 1994; King et al., 1989). A similar, although somewhat more weakly developed condition is found in *Ulemica* and *Suminia*, indicating that some non-dicynodont anomodonts possessed a musculature arrangement similar to dicynodonts (Barghusen 1976; King 1994; King et al., 1989; Rybczynski 2000). However, the posterolateral surface of the squamosal in *Patranomodon* is relatively narrow and thin, and lacks a distinct fossa; which King (1994) interpreted as evidence for the absence of an external lateral adductor in this taxon. Although the squamosals of the only known specimen of *Otsheria* (PIN 1758/5) are not fully prepared, in my examination of the specimen I found the exposed area resembles the squamosals of *Patranomodon* much more closely than those of *Suminia* or *Ulemica*. I have interpreted this as indicative of the absence of lateral fossa , and thus the absence of an external lateral adductor. Further preparation of the holotype and/or discovery of additional specimens of *Otsheria* will be necessary to test this hypothesis.

22) Palatal surface of the palatine without evidence of a keratinized covering (0), with a rounded, bulbous surface texture that may have had a keratinized covering (1), relatively smooth, but with fine pitting and texturing suggestive of a keratinized covering (2), highly rugose and textured with pitting suggestive of a keratinized covering (3), moderately rugose with pitting suggestive of a keratinized covering (4).
The palatines of *Patranomodon* posses an anterior process that extends for a short distance along the medial surface of the maxilla. This palatal exposure of the palatines is relatively smooth and does not show evidence of the many small nutritive foramina necessary for a keratinized covering. There is some evidence that small palatal teeth or denticles were present on the posterior portion of the palatines near their junction with the pterygoids in *Patranomodon* (Rubidge and Hopson 1996). The palatines of *Otsheria* also possess a short anterior process that meets the maxilla, and the palatal surface of the bone is very smooth along its entire length, showing no signs of the presence of denticles or a keratinized covering.
Recently, Rybczynski (2000) hypothesized that the rugose surface texture of the palatines of *Suminia* was indicative of the presence of palatine denticles in that taxon as well. She also coded the dicynodonts included in her data matrix (*Dicynodon*, *Pristerodon*, and *Eodicynodon*) as possessing an "area of the palatines [that is] rugose and pitted as if to hold denticles" (Rybczynski 2000, p.356). In my examination of *Suminia* specimens that have the palatines exposed (PIN 2212/33, PIN 2212/62), I found that the more anterior portion of the palatal exposure of the palatines possessed many small pits that intersect with the surface of the bone at a low angle, whereas the more posterior portion included a few large pits that were nearly perpendicular with the surface of the bone. Although the larger, posterior pits may indeed be alveoli for denticles, the morphology of the smaller, anterior pits strongly resembles the nutritive foramina found on horn-covered areas of the secondary palate of dicynodonts and turtles. I interpret these observations as indicating that at least the anterior portion of the palatal exposure of the palatine possessed a keratinized covering, although denticles were likely present more posteriorly. The pits on the palatal exposure of the palatines of well-preserved dicynodont specimens also tend to be very small and meet the surface of the bone at a low angle, which is more consistent with nutritive foramina for a keratinized covering than alveoli for teeth or denticles.
Each of the palatines of *Eodicynodon* possess a raised, oval-shaped area that meets the maxillary contribution of the secondary palate. This area has a rounded, bulbous surface and it has been suggested that it played a role in mastication (Cox 1998, King 1990). The fine details of the surface texture of the bone are not well preserved in most specimens, but three acid prepared specimens in the Roy Oosthuizen Collection (ROZ 1, ROZ 9, and ROZ 11) possess a slightly rugose, pitted texture that is suggestive of the presence of a keratinized covering in life.
Diictodon, Robertia, Pristerodon, Chelydontops, Emydops and *Cistecephalus* possess palatines that have a medially expanded anterior area at the level of the secondary palate. The shape of this expanded area varies from roughly square in *Emydops* and *Robertia* to leaf-shaped in *Pristerodon* and *Chelydontops*. The bone surface of the palatal exposure of the palatines in these taxa is relatively smooth but contains numerous small nutritive foramina that provide strong evidence for the presence of a keratinized covering. The surface of palatal exposure of the palatines in *Endothiodon* has a different shape and a slightly rougher texture, but is otherwise very similar to the condition in these taxa.
The palatal exposure of the palatines of *Oudenodon, Tropidostoma, Aulacephalodon,* and *Rhachiocephalus* all possess a highly rugose posterior area that is raised slightly above the level of the secondary palate and a less rugose anterior area that is flush with the secondary palate. Both areas are covered with numerous small nutritive foramina that indicate the presence of a keratinized covering. *Dicynodon, Lystrosaurus,* and *Kannemeyeria* also possess rugose palatines with nutritive foramina, although they differ from the those of taxa such as *Oudenodon* in two important respects. First, the

rugosity is not as distinctly developed as in the posterior area of *Oudenodon*. Second, the surface rugosity is evenly developed over the entire palatal surface, instead of being more rugose posteriorly and less so anteriorly.

The palatines of most specimens of *Myosaurus* lack nutritive foramina, and Cluver (1974b) interpreted this as evidence for the absence of a keratinized covering. One of the co-types of this taxon (SAM 3526a) bears a few small pits on the surface of the palatine. However, I do not think these pits provide sufficient evidence to overturn Cluver's hypothesis because this specimen was acid prepared and the pits could easily be artifacts of preparation. The palatines of *Kingoria* are notably reduced compared to those of most other dicynodont taxa and have a relatively smooth surface. I have coded *Kingoria* as "?" in this data set because none of the specimens I have examined have had the palatines sufficiently well-prepared to say decisively whether nutritive foramina were present or absent.

23) Nasal bosses absent (0), present as a single median swelling (1), present as paired swellings near the dorsal or posterodorsal margin of external nares (2), present as paired swellings that meet in the midline to form a swollen anterodorsal surface on the snout (3).

The nasals of *Patranomodon* and *Otsheria* are relatively smooth and do not show evidence of a boss. The surface of the nasals is not well preserved in either of the co-types of *Myosaurus* (SAM 3526, SAM 3526a), making it difficult to definitely determine whether nasal bosses were present in either specimen. However, this area is well preserved in another specimen (BP/1/2690), and a nasal boss is clearly absent.

Diictodon, Robertia, Eodicynodon, Emydops, Kingoria, and *Pristerodon* all possess a single, median, oval-shaped swelling on the nasals that is covered with numerous small, nutritive foramina, likely indicating the presence of a keratinized covering in life. A similar boss is also present in *Cistecephalus*, although it tends to be smaller and more weakly developed than in the other taxa.

Chelydontops, Oudenodon, Tropidostoma, Aulacephalodon, Pelanomodon, Rhachiocephalus, and *Dicynodon* possess paired nasal bosses that that tend to be located over the dorsal or posterodorsal margin of the external nares and do not meet along the mid-line of the skull. The exact morphology of the bosses varies among the included taxa (compare e.g. *Oudenodon, Aulacephalodon, Rhachiocephalus*, and *Dicynodon*), as well as within them in some cases (e.g., Tollman *et al.*, 1980 described sexually dimorphic and ontogenetic variation in the size and shape of the bosses of *Aulacephalodon*). *Endothiodon* also possesses paired nasal bosses, although these tend to be more elongate and ridge-like than in the other taxa, and a median ridge is often present between them. Paired nasal bosses occur in at least some species of *Lystrosaurus* (Cluver 1971), although the unusual downturning of the snout in that genus makes them appear less obvious. In all of these taxa the bosses bear numerous nutritive foramina, likely indicating the presence of a keratinized covering in life. I have coded all of these taxa with a single character state because they all share paired bosses that do not meet along the mid-line of the skull. Further subdivision of this character, while theoretically possible, would be difficult because of the minor variations in boss morphology that occur among individual specimens.

The nasal bosses of *Kannemeyeria* are unique among the taxa included in this analysis. Although it has paired bosses, these are anteroposteriorly elongated, rugose, and meet along the midline of the skull, giving the entire dorsal surface of the snout a raised, swollen appearance. Nutritive foramina also are present, indicating that this entire surface likely possessed a keratinized covering in life.

24) Foramen present on the palatal surface of the palatine (1) or absent (0).

The majority of anomodont taxa do not possess a palatal foramen. The palatal foramen is present in *Myosaurus* and *Cistecephalus*. It is most distinct in *Myosaurus*, where it is relatively large, round, and passes entirely through palatal surface of the palatine. It is clearly distinct from the nutritive foramina found on palatines of many dicynodonts because the nutritive foramina tend to be much smaller and do not pass completely through the surface of the bone. The foramen is relatively smaller in *Cistecephalus*. Although not included in this analysis, at least two other dicynodonts appear to possess this feature. The holotype of *Cistecephaloides* (SAM 6243) may possess a palatal foramen, although the palatal surface of the palatines in that specimen is not well preserved, making it difficult to determine if the apparent foramen is a real feature or postmortem damage. Cox (1972) also figures what may be a palatal foramen in *Kawingasaurus*, although in that genus it is near the anterior end of the palatine and bounded anteriorly by the maxilla.

25) Anterior margin of orbit extended posteromedially to partly close off the snout from the rest of the skull (1) or snout open to back of the skull (0).

In the majority of dicynodonts and non-dicynodont anomodonts a wide orbitonasal opening leading into the back of the snout is present. However, in *Myosaurus* the frontal, prefrontal, and lacrimal extend medially and posteriorly so that the front of the orbits nearly completely closes off the snout from the rest of the skull (Cluver 1974b). A similar, though less extreme condition is present in *Cistecephalus* and *Cistecephaloides* (although the latter genus is not included in this analysis). In these taxa the front of the orbits also extend posteriorly and medially, but a relatively wide orbitonasal opening remains between them.

26) Pineal foramen flush or nearly flush with dorsal surface of skull (0), surrounded by a strong, rugose boss (1), or surrounded by a thin, smooth, chimney-like boss. (2).

Nearly all dicynodonts and non-dicynodont anomodonts possess a pineal foramen on the dorsal surface of the skull (*Kawingasaurus* and *Kombuisia* are exceptions and lack a pineal foramen; Cox 1972; Hotton 1974). In the majority of the taxa included in this analysis the pineal foramen is flush with the dorsal surface of the skull or surrounded by a thin, slightly

raised rim. I have not distinguished between these morphologies in my coding of this character because they are very similar and the rim can be lost easily if the skull roof is weathered or damaged.

Endothiodon, Chelydontops, Aulacephalodon, and *Rhachiocephalus* all possess a prominent, rugose, bony boss around the pineal foramen. The bosses of *Chelydontops* and *Endothiodon* have a dome-shaped morphology, while that of *Rhachiocephalus* is more cylindrical. The pineal boss of *Aulacephalodon* appears to be an ontogenetically variable character, with large specimens tending to have much more pronounced bosses. The morphology of the boss in *Aulacephalodon* is generally intermediate between the more dome-shaped and cylindrical forms. A pineal boss is also present in the non-dicynodont anomodonts *Otsheria, Ulemica* and *Suminia*. However, in these taxa the boss has a slightly tapered, chimney-like morphology, with thin, smooth walls. I consider this morphology to be sufficiently distinct from the morphology of taxa such as *Rhachiocephalus* to warrant a separate character state. Although a pineal foramen is absent in *Kawingasaurus* and *Kombuisia*, I have omitted an "absent" character state because neither of these taxa were included in this analysis.

27) Anterior portion of palatine contacts the premaxilla (1) or does not contact the premaxilla (0).

All of the taxa included in this analysis possess an anterior portion of the palatine that contacts the maxilla on the ventral surface of the skull. In *Otsheria, Chelydontops, Pristerodon, Emydops, Cistecephalus, Myosaurus, Tropidostoma, Oudenodon, Aulacephalodon, Pelanomodon, Rhachiocephalus, Kannemeyeria*, and *Dicynodon* the palatine also contacts the posterior edge of the premaxilla. Although there is minor variation in the exact morphology and extent of the contact between the palatine and premaxilla, I have chosen not to subdivide the states of this character further because factors such as weathering or damage from preparation can easily alter the details of the contact (Keyser 1993).

28) Postcaniniform crest present (1) or absent (0).

Tropidostoma, Rhachiocephalus, Oudenodon, and *Pelanomodon* possess a postcaniniform crest. The crest has a sharp ventral edge, a smoothly-sloping lateral surface, bears teeth in *Tropidostoma*, and arises from the posteromedial side of the caniniform process. The degree of development of the crest varies slightly among taxa and among specimens within a given taxon, but this variation is not great enough to warrant different character states. The postcaniniform crest can be distinguished from the postcaniniform keel (Character 1) because the keel has a rounded ventral edge, a steep, wall-like lateral surface, and is formed from a continuation of the lateral palatal rim posterior to the caniniform process. I have coded taxa that lack a distinct caniniform process as "?" because this character is not directly applicable to them.

29) Stapedial foramen absent (1) or present (0).

The presence of a stapedial foramen characterizes several synapsid clades. *Patranomodon*, the most basal anomodont for which a stapes is known, lacks a stapedial foramen, although a dorsal process that contacts the paroccipital process is present (Rubidge & Hopson 1996). A stapes in not known in *Otsheria*, but the stapes of *Suminia* also lacks a foramen. Some specimens of *Eodicynodon* (e.g., NM QR2989, ROZ 9) possess a stapedial foramen that is completely or nearly completely enclosed, whereas other specimens (e.g., NM QR2912) lack a distinct stapedial foramen. Although the significance of this variation is not well understood, I have chosen to code *Eodicynodon* as possessing a stapedial foramen in this analysis (= the globally basal condition for Synapsida). A fully enclosed stapedial foramen is consistently present in *Cistecephalus* and *Kawingasaurus* (Cox 1972), although the latter taxon is not included in this analysis. All other taxa examined here lack a stapedial foramen.

30) Proximal articular surface of humerus a slightly convex area on proximal surface of bone without much expansion onto the dorsal surface (0), somewhat expanded with some encroachment onto the dorsal surface (1), or strongly developed and set off from rest of humerus by a weak neck (2).

A humerus is not preserved for *Patranomodon* or *Otsheria*. However, other non-dicynodont anomodonts (e.g., *Galepus, Suminia*)possess humeral heads that are a slightly raised, rounded swellings with the articular surface limited to the proximal end of the bone, establishing polarity for this character. *Eodicynodon, Robertia, Diictodon*, and *Pristerodon* also possess humeral heads of this morphology. The humeral heads of most of the other included taxa are present as sub-hemispherical swellings in which the articular surface has some encroachment on the dorsal surface of the humerus. The degree to which the head is developed is somewhat variable among these taxa (e.g., it is limited in *Oudenodon* but more distinct in *Kingoria*), but I have not divided this state up further because it also appears to be susceptible to alteration by postmortem weathering or damage as well as ontogenetic factors. *Cistecephalus* and *Kawingasaurus* possess strongly developed humeral heads that are set off from the shaft of the bone by a weak but distinct neck.

I coded *Chelydontops* and *Pelanomodon* as "?" because humeri that definitely can be attributed to these taxa are not known. At least one specimen of *Myosaurus* (BP/1/4269) includes partial humeri, but I also coded this taxon as "?" because the articular surfaces are currently imbedded in matrix and could not be examined.

31) Proximal articular surface of femur present as a weak swelling that is mostly limited to the proximal surface of the bone (0), present as a more rounded, hemispherical swelling that has some encroachment on the anterior surface of the femur (1), or present as a rounded, hemispherical to subspherical swelling that is set off from the proximal surface by a neck (2).

In non-dicynodont anomodonts, *Eodicynodon, Robertia, Diictodon, Pristerodon*, and *Endothiodon* the femoral head is present as a weak, rounded swelling of the anterior corner of the proximal surface of the bone (assuming that the femur is positioned in a "sprawling" orientation). The articular surface does not extend onto the anterior surface of bone, and it is not separated from the rest of the proximal surface by a distinct neck. The majority of the other taxa included in this analysis possess femoral heads that are rounded to subspherical, with articular surfaces that encroach upon the anterior surface of

the bone (again assuming a "sprawling" posture). The degree of development of the femoral head is variable in these taxa (e.g., the head in *Kingoria* is more spherical than in most other taxa), but none possess a distinct neck that separates the head from the dorsal surface of the femur. *Cistecephalus* is unique among the included taxa because a well-developed neck separates the head from the rest of the femur. The head is also highly spherical in this taxon. Although not included in this analysis, a femoral neck also has been reported in some Triassic dicynodonts (e.g., *Placerias*, Camp and Welles, 1956). Well-preserved femora that can definitely be assigned to the taxa coded "?" are not known.

32) Squamosal with a distinct dorsolateral notch in posterior view (1) or with a relatively straight contour (0).

The zygomatic and occipital portions of the squamosal of *Emydops*, *Cistecephalus*, *Myosaurus*, *Otsheria*, and *Patranomodon* meet at roughly a right angle, giving the lateral margins of the skull a relatively straight contour in posterior view. In the other taxa included in this analysis, the lateral edge of the occipital portion of the squamosal ventral to the zygomatic portion bows laterally before curving medially to meet the zygomatic portion. This lateral convexity gives the lateral margin of the skull a distinctly notched appearance just below the zygomatic branch of the squamosal in posterior view. Although these character states are unmistakable in well-preserved specimens, they are easily altered if a specimen has undergone plastic deformation. Dorsoventral crushing tends to make unnotched taxa appear as if a notch was present, whereas lateral compression can make notched specimens appear to have a much straighter contour.

33) Interpterygoid vacuity relatively short and does not reach the level of the palatal exposure of the palatines (0), relatively long but does not reach the level of the palatal exposure of the palatines (1), long and reaches the level of the palatal exposure of the palatines (2), or absent (3).

In non-dicynodont anomodonts, the interpterygoid vacuity is relatively short compared to the length of the skull, completely enclosed by the pterygoids, and does not extend forward to the level of the portions of the palatines that contact the maxillae. The interpterygoid vacuities of *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria* also are relatively short and do not reach the level of the portions of the palatines that meet the maxillae (and premaxillae in some taxa). However, in these taxa the anterior margin of the vacuity is formed by the vomers. I have not distinguished between these morphologies in coding this character because I am only concerned with the relative length of the vacuity, not the bones that contribute to its formation.

In *Eodicynodon*, *Robertia*, *Diictodon*, *Chelydontops*, *Pristerodon*, *Emydops*, *Kingoria*, *Rhachiocephalus*, and *Aulacephalodon* the interpterygoid vacuity is relatively long compared to the length of the skull but does not reach the level of the anterior portions of the palatines that contact the maxillae and premaxillae. *Tropidostoma*, *Oudenodon*, and *Pelanomodon* also possess relatively long interpterygoid vacuities, but in these taxa the vacuity does reach the level of the anterior portions of the palatines that contact the maxillae and premaxillae. In both groups of taxa the vomers form the anterior margin of the vacuity. *Cistecephalus* is unique among the included taxa in lacking an interpterygoid vacuity.

The majority of the specimens referable to *Endothiodon* that I have had the opportunity to examine do not preserve this area well. Of these specimens, BP/1/1659 possess the best interpterygoid vacuity, which appears likely to have been relatively short and not to have reached the level of the anterior portion of the palatines. However, because of the poor preservation of the feature in this specimen and my inability to confirm or disconfirm the observation in other specimens, I have chosen to code *Endothiodon* as "?". I coded *Myosaurus* as "?" because the co-type specimens (SAM 3525 and SAM 3526a) conflict in regard to this character. In SAM 3526a, which is slightly better preserved, the vacuity is long, but does not reach the anterior portion of the palatines. In SAM 3526 the vacuity is long and does appear to reach the anterior portion of the palatines. The other specimens of *Myosaurus* that I have had the opportunity to examine do not preserve the feature well enough to allow confident resolution of the conflict.

34) Anterior portion of squamosal contacts maxilla (1) or does not contact maxilla (0).

In *Patranomodon*, *Otsheria*, *Eodicynodon*, *Endothiodon*, *Kingoria*, and *Myosaurus* the zygomatic branch of the squamosal is separated from the maxilla by the jugal. In all other taxa included in this analysis, the anterior end of the zygomatic branch of the squamosal contacts the maxilla. I have coded *Chelydontops* as "?" because neither the holotype (SAM 11558) or referred specimen (SAM 12259) preserve the zygomatic branch of the squamosal.

35) Lateral palatal foramen present at level of the anterior, expanded palatal exposure of the palatines (1), present posterior and dorsal to the level of the anterior, expanded palatal exposure of the palatines (2),or absent (0).

Most of the taxa included in this analysis possess a small foramen located between the palatine and the anterior pterygoid ramus. The exact size and shape of this foramen varies, but in most cases it is at the same level as the expanded, anterior portion of the palatine that meets the maxilla (and premaxilla in some taxa). Many specimens of *Emydops* do not show good evidence of this foramen, but it is present in some specimens (e.g., SAM K1671, SAM K6623). The foramen tends to be very small in these individuals, suggesting that it would easily be lost if even minor lateral compression of the skull occurred.

A lateral palatal foramen, bounded by the palatine and the anterior pterygoid ramus, is also present in *Pristerodon* and *Endothiodon*, although its location is notably different. In these taxa, the foramen is located posterior and somewhat dorsal to the expanded, anterior portion of the palatine so that the it is more a part of the dorsolateral wall of the choana than the palatal surface of the skull.

The non-dicynodont anomodonts *Ulemica* and *Otsheria* do not possess a lateral palatal foramen, but the foramen is present in *Suminia* (Rybczynski 2000). A small foramen bounded by the pterygoid and palatine is present on the right side of the skull in the holotype of *Patranomodon* (NM QR3000). Although this foramen is a potential positional homologue of the lateral palatal fenestra, I have not coded it as such because a corresponding foramen is not present on the left side of the skull.

Because the holotype is the only known specimen of *Patranomodon*, it is difficult to determine whether the foramen is a real feature or the result of postmortem damage, individual variation, or pathology. If additional specimens of *Patranomodon* that also possess this foramen are discovered, a reassessment of the homologies of the lateral palatal foramen may be necessary.

36) Three (0), four (1), five (2) or six (3) sacral vertebrae present.

The number of sacral vertebrae is most accurately counted in specimens in which the sacrum and pelvis are articulated. However, counts can also be made in disarticulated specimens by observing the number of vertebrae that possess expanded sacral ribs or the number of facets for sacral vertebrae on the medial side of the ilium. The latter methods can be less accurate because the last sacral vertebra sometimes has relatively small ribs, and the facets often have a complex morphology that makes them difficult to count (DeFauw 1986).

Three sacral vertebrae are present in *Patranomodon*, *Eodicynodon*, *Robertia*, and *Cistecephalus*. Four are present in *Diictodon*, *Endothiodon*, and *Kingoria*. Most of the other taxa included in this analysis possess five sacral vertebrae, but six are present in *Lystrosaurus* and *Kannemeyeria*. I have coded *Otsheria*, *Chelydontops*, *Emydops*, *Tropidostoma*, *Myosaurus*, and *Pelanomodon* as "?" because sacra that can definitely be referred to these taxa are not known.

37) Transverse flange of the anterior pterygoid process well-developed (0) or reduced (1).

The transverse flange of the anterior pterygoid process is large and laterally directed in non-dicynodont anomodonts, although it is unusual among therapsids in not descending below the level of the palate (Rubidge and Hopson 1996). A well-developed transverse flange of the pterygoid is also present in *Eodicynodon* as well as several undescribed specimens collected in the lower *Tapinocephalus* Assemblage Zone (Rubidge, personal communication, 2000). However, in these forms the flange is ventrally directed. I have not distinguished between these morphologies in coding this character because I am concerned only with the relative size of the flange. Modesto *et al.* (1999) and Rybczynski (2000) subdivided this state, but their analyses included additional non-dicynodont anomodonts as well as several non-anomodont outgroups. Similar subdivision of this state also may be desirable in future analyses that include a greater number of lower *Tapinocephalus* Assemblage Zone dicynodonts.

The transverse flange of the pterygoid is ventrally directed and highly reduced in all other taxa included in this analysis. Some taxa possess small, plate-like extensions (e.g., *Kingoria*) or keels (e.g., *Diictodon*) on the ventral surface of the anterior pterygoid ramus, but these features are of notably different morphologies and never as large as the flange in *Eodicynodon*.

38) Ectepicondylar foramen on humerus present (1) or absent (0).

The presence of an ectepicondylar foramen characterizes several clades of synapsids, and the reconstruction of the ancestral character states for Anomodontia on many recent cladograms (e.g., Sidor and Hopson 1998) suggests that the foramen was present in the common ancestor of all anomodonts. Humeri are not known for *Anomocephalus*, *Patranomodon*, *Otsheria*, or *Ulemica*, but an ectepicondylar foramen has been reported in *Galepus* and *Galechirus* (Brinkman 1981). The foramen is absent in *Galeops* and *Suminia* (Brinkman 1981; personal observation). If *Galepus* and *Galechirus* represent a grade of anomodont evolution more basal than either *Galeops* or the venyukovioids (*sensu* Modesto *et al.*, 1999; Rybczynski 2000), then it is likely the phylogenetic inference is correct and the presence of an ectepicondylar foramen is the basal state for anomodonts. However, because *Galepus* and *Galechirus* have not been included in any of the recent cladistic analyses of anomodonts, this hypothesis has yet to be rigorously tested. The discovery of humeri referable to a greater number of basal anomodonts also will help to resolve this issue.

King (1981b) noted the presence of a probable ectepicondylar foramen in *Robertia*, and DeFauw (1986) hypothesized that the foramen was likely present in *Kingoria* based on her examination of a damaged specimen. I have been able to confirm King's (1981b) observation regarding the foramen in *Robertia* (e.g., SAM 11885). In addition, I also have observed an ectepicondylar foramen in *Diictodon* (e.g., SAM K1633, UCMP V3691/42053), *Emydops* (e.g., SAM K10009), and *Cistecephalus* (e.g., BP/1/696, BP/1/2915), indicating that this feature is more widely distributed among dicynodonts than previously recognized. All other taxa included in this analysis lack an ectepicondylar foramen. Well-preserved humeri that can definitely be attributed to the taxa coded "?" are not known. I have included *Kingoria* in this group because the only report of an ectepicondylar foramen in that taxon is based on a specimen that is damaged in the region of the foramen (DeFauw 1986).

39) Cleithrum present (1) or absent (0).

The pectoral girdles of most non-dicynodont anomodonts are very poorly known, making the polarity of this character difficult to establish for Anomodontia. Cleithra appear to be absent in *Galeops* and *Suminia* (Brinkman 1981; personal observation), but the pectoral girdles of other basal anomodonts are either unknown or too poorly preserved to be informative. Reconstruction of the ancestral state for this character based on recent cladograms of Synapsida suggests a cleithrum was present in the common ancestor of all anomodonts.

Cleithra have been reported in several dicynodont taxa, including *Oudenodon*, *Kannemeyeria*, and *Rhachiocephalus*, but most of these accounts are incorrect (DeFauw 1986; personal observation). Cluver (1978) and DeFauw (1986) noted that a cleithrum was present in *Cistecephalus* and *Diictodon* respectively, and I have been able to confirm these observations. There is also strong evidence of a cleithrum in *Robertia* (SAM 11885, cast 3 of King 1981b). A cleithrum is likely present in *Kawingasaurus* (Cox, 1972), although this taxon is not included in this analysis. All other taxa examined here for which pectoral girdles are known do not possess a cleithrum. Well preserved pectoral girdles that can definitely be attributed to taxa coded "?" are not known.

40) Transverse ridge across snout at level of prefrontals present (1) or absent (0).
Several dicynodont taxa (e.g., *Rhachiocephalus, Oudenodon, Aulacephalodon*) possess prefrontal bosses of some type. In the majority of these taxa, the dorsal surface of the snout between these bosses is relatively smooth and flat. *Aulacephalodon* and *Pelanomodon* possess a low, rounded, transverse ridge that connects the prefrontal bosses on the dorsal surface of the snout. Some species of *Lystrosaurus* (e.g., *L. declivis, L. murrayi*) also possess a transverse ridge in a similar position on the skull (the frontonasal ridge of Cluver 1971), but the pronounced downturning of the snout in that taxon gives it a slightly different appearance. I have given *Lystrosaurus* the same coding as *Aulacephalodon* and *Pelanomodon* because the ridge is present in nearly the same location (i.e., between the prefrontals, near the nasal-frontal suture), making a strong positional argument for homology. In all other taxa included in this analysis the surface of the snout lacks a distinct transverse ridge between the prefrontals.

Stratigraphic character

41) First occurrence in *Eodicynodon* Assemblage Zone (0), *Tapinocephalus* Assemblage Zone (1), *Pristerognathus* Assemblage Zone (2), *Tropidostoma* Assemblage Zone (3), *Cistecephalus* Assemblage Zone (4), *Dicynodon* Assemblage Zone (5), *Lystrosaurus* Assemblage Zone (6), or *Cynognathus* Assemblage Zone (7).
The stratigraphic data used to code this character are based on those presented in King (1988) and Rubidge (1995a). Most of the data were taken directly from these sources, but my treatment of three taxa that are known from very limited material necessitates some explanation.
Otsheria is represented by a single specimen from the Ocher Subassemblage of the Dinocephalian Fauna of Golubev (2000). This fauna is likely of Late Kazanian to Early Tartarian age (Golubev 2000). Rubidge (1995b) suggests a Kazanian age for the *Eodicynodon* Assemblage Zone of South Africa, and Smith and Keyser (1995) propose an early Tartarian age for the *Tapinocephalus* Assemblage Zone. The Upper Permian strata of Russia are not well correlated with those of South Africa, and I have chosen to include *Otsheria* as a point occurrence in the upper *Eodicynodon* Assemblage Zone. However, this should be regarded as an approximation, and including *Otsheria* in the *Tapinocephalus* Assemblage Zone does not significantly alter the results of the stratigraphic analysis.
Patranomodon is also represented by a single specimen, but this was collected in the *Eodicynodon* Assemblage Zone of South Africa, eliminating correlation problems. Because only one specimen exists, the range of *Patranomodon* is not well constrained at this time and I have chosen to represent it as a point occurrence in Figure 2.
Chelydontops is known from two specimens. The holotype was collected on the farm Die Cypher, near Beaufort West South Africa (Cluver 1975). Kitching (1977) places this locality in the lower *Tapinocephalus* Assemblage Zone. The second specimen was discovered on the farm Beukesplaas, near Fraserburg, which is close to the *Tapinocephalus/Pristerognathus* Assemblage Zone boundary in Figure 1 of Rubidge *et al.* (1995). *Chelydontops* is not included among the taxa for which ranges are given in Smith and Keyser (1995), and the lack of material suggests its range may not be well constrained. I have chosen to represent it as having a short range in the middle of the *Tapinocephalus* Zone, but it may be possible to extend its range to encompass most of the zone. Such a range extension does not have a significant effect on the stratigraphic analysis other than necessitating a shorter ghost range for *Endothiodon*.

APPENDIX 2
Data matrix showing codings for characters and taxa used in this analysis.

Patranomodon and *Otsheria* are outgroups.

Patranomodon	?0000000?0	000?000000	0000000?1?	0000000??0	0
Otsheria	?0000000??	11??????00	0000?21???	?0000?0??0	0
Eodicynodon	0200010100	0000103300	1110000000	0110100000	0
Robertia	0211021101	1000201100	1110000010	0111101110	1
Diictodon	0213?21102	1110201101	1110000010	0111111110	1
Endothiodon	?112100221	100?012204	1220010?10	01?0211000	2
Chelydontops	0211110121	1100111100	122001001?	?11?1?1??0	1
Pristerodon	0211011121	1000113100	1210001010	0111221000	1
Emydops	1211010111	1111013300	1210001010	?0111?11?0	3
Kingoria	1213?102?2	1101003301	1?10000011	1110111?00	4
Cistecephalus	1213?10212	1111013300	1211101002	2031101110	3
Myosaurus	1213?10212	1111003300	100110101?	?0?01?1??0	6
Tropidostoma	0211012221	1100311101	1320001111	11211?1000	3
Oudenodon	0213?12222	1110311101	1320001111	1121121000	4
Rhachiocephalus	0213?12222	1110311103	1320011111	1111121000	3
Pelanomodon	0213?1022?	1110????12	1320011??	?1211?1??1	5
Aulacephalodon	0213?12222	1100311112	1320011011	1111121001	4
Dicynodon	0213?12222	1110311113	1420001011	1101121000	4
Lystrosaurus	0213?12222	1110311410	1420000011	1101131001	6
Kannemeyeria	0213?12222	1110311414	1430001011	1101131000	7

APPENDIX 3
Reference Specimens

Patranomodon: NM QR3000

Otsheria: PIN 1758/5

Eodicynodon: NM QR2902, NM QR2904, NM QR2905, NM QR2906, NM QR2909, NM QR2911, NM QR2912, NM QR2978, NM QR2989, NM QR2990, NM QR2991, NM QR 3002, NM QR3007, NM QR3014, NM QR3153, NM QR3154, NM QR3155, NM QR3157, NM QR3158, ROZ 1, ROZ 9, ROZ 11, SAM 11879

Robertia: SAM 11461, SAM 11761, SAM 11885, SAM K7807

Diictodon: AMNH 5532, AMNH 5533, AMNH 5609, GSP STH36, GSP T72, SAM 1242, SAM 10086, SAM K1633, SAM K5105, SAM K7725, TM 253, UCMP V3504/32131, UCMP V3504/32125, UCMP V3504/42837, UCMP V3691/41791, UCMP V3691/42053, V3691/42057, UCMP V3694/42396

Endothiodon: AMNH 5562, AMNH 5565, AMNH 5570, AMNH, 5572, AMNH 5573, AMNH 5574, AMNH 5603, BP/1/1659, BP/1/5743, BP/1/5744, BP/1/5747, BP/1/5748, BP/1/5751, BP/1/5754, BP/1/5756, SAM 629, SAM 2676, SAM K7252

Chelydontops: SAM 11558, SAM 12259

Pristerodon: AM 2825, AMNH 5507, BP/1/241, BP/1/2642, GSP FL102, GSP M336, GSP WB106, SAM 10141, SAM 10161, SAM K1658, TM 313, UCMP V3694/42396

Emydops: AMNH 8209, BP/1/262, BP/1/2366, GSP M1000, SAM 3721, SAM 10153, SAM 10172, SAM 10009, SAM 11060, SAM K1671, SAM K5974, SAM K6623, SAM K10009, TM 242

Kingoria: BP/1/1562, BP/1/3858, NM QR479, SAM 3723, SAM 6043, SAM 10666, SAM K1260a, SAM K8620, SAM K8069

Cistecephalus: BP/1/696, BP/1/2915, BP/1/31, BP/1/506, BP/1/1696, BP/1/2450, BP/1/2915, BP/1/4086, GSP RMS410, SAM 10664, SAM 10665, SAM K6814

Myosaurus: BP/1/2690, BP/1/2701b, BP/1/4269, SAM 3526, SAM 3526a

Tropidostoma: BMNH R860, BMNH R866, BMNH R868, GSP RMS183, GSP RMS631, GSP RS327, SAM K8633, SAM K9960, TM 249, TM 250, TM 383, TM 384, TM 385

Oudenodon: AM 4545, AMNH 5300, AMNH 5313, AMNH 5635, BP/1/749, BP/1/788, GSP M208, GSP M845, GSP MIF133, SAM 6045, SAM 10066, SAM 11114, SAM K5227, SAM K7688

Rhachiocephalus: BP/1/1512, BP/1/2548a, BP/1/2889, GSP C82, GSP RS240, SAM K1393

Pelanomodon: GSP AF9183

Aulacephalodon: AMNH 5562, BP/1/304, BP/1/634, BP/1/766, BP/1/2460, GSP CBT53, GSP MJF129, NM QR1478, SAM 8789, SAM K6404, SAM K7158

Dicynodon: BP/1/2188, BP/1/2784, BP/1/5287, GSP AF9683, SAM K1191, SAM K7011, SAM K7591, SAM K7806, UCMP V36102/33431

Lystrosaurus: AM 404, AM 2731, AM 4040, AM 5009, NM C150, NM C 299, NM C6547, SAM K1469, TM 37, TM 4050, SAM 4523, UCMP V65341/31363, UCMP V76019/42870

Kannemeyeria: AM 5008, BP/1/1168, BP/1/2902, BP/1/3638, BP/1/4523, BP/1/4524, BP/1/5624, BP/1/4550, NM QR1127, SAM 10555, UCMP V36113/38373, UCMP V47047/42916