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An investigation into the cladistic relationships and monophyly of therocephalian therapsids (Amniota: Synapsida)

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A comprehensive phylogenetic investigation was performed to elucidate the cladistic relationships and possible monophyly of therocephalian therapsids (Amniota: Synapsida). The phylogenetic positions of 30 therapsid taxa were examined under maximum parsimony, including 23 therocephalian genera. The analysis incorporated 110 cranial and postcranial characters in order to assess the interrelationships of basal therocephalians and eutherocephalians and their relationships to Cynodontia, representing the most complete review of therocephalian phylogeny to date. The analysis supports the hypothesis that Therocephalia represents the monophyletic sister taxon to Cynodontia, with as many as 15 morphological synapomorphies, in contrast with other recent analyses of lesser taxon sampling. The results also support the hypothesis that Scylacosauridae is more closely related to Eutherocephalia than to the basal therocephalian family Lycosuchidae, supporting a 'Scylacosauria' clade. The taxa suggested here to be neotenic forms (e.g. *Ictidosuchoides* and *Ictidosuchops*) are positioned near the base of a monophyletic Baurioidea. Neotenic development of the therocephalian feeding apparatus and evolutionary parallelism with cynodonts are suggested to have been important trends in the early evolution of baurioid therocephalians into the Late Permian and Early Triassic.

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ADDITIONAL KEYWORDS: Eutheriodontia – homoplasy – ontogeny – phylogeny – Scaloposauridae.

INTRODUCTION

Among Permo-Triassic therapsids, ontogeny and phylogeny have been most extensively studied in non-mammalian cynodonts because of their close proximity to the origin of mammals (Hopson & Kitching, 1972; Rowe, 1986, 1988; Hopson, 1991; Sidor & Hopson, 1998; Abdala & Giannini, 2000, 2002; Rubidge & Sidor, 2001). Consequently, few studies have focused on the need to resolve systematic problems within the nearest sister taxon of the cynodonts, 'Therocephalia' (Fig. 1). Therocephalians are a diverse group of 'mammal-like' therapsids whose evolutionary radiation appears to have paralleled that of the cynodonts in many respects (Hopson, 1991; Hotton, 1991; Rubidge & Sidor, 2001). Together, cynodonts and therocephalians have been demonstrated with robust character support to form a monophyletic clade, 'Eutheriodontia' ('Therosauria' of Kemp, 1982; Hopson & Barghusen, 1986; Hopson, 1991; Sidor & Hopson, 1998).

The suborder Therocephalia was established by Broom (1903), who recognized the basal carnivorous family Scylacosauridae, the highly derived and diminutive Ictidosuchidae and other therapsids that are no longer regarded as therocephalians (i.e. the gorgonopsians *Aelurosaurus* and *Gorgonops*, and the dinocephalians *Deuterosaurus*, *Rhopalodon* and *Titanosuchus*). Watson (1931) and Broom (1932) described other taxa with apparent therocephalian affinities, but distinguished them from therocephalians in a separate suborder termed 'Bauriamorpha'. Soon after, Boonstra (1934) provided a major contribution to the study of therocephalians and recognized seven families, including Alopecopsidae, Ictidosuchidae, Pristerognathidae (formerly Scylacosauridae), Scaloposauridae (including some 'bauriamorphs'), Whaitsidae (sic), Euchambersidae (sic) and Lycideopsidae. Later, Boonstra (1953) divided Therocephalia

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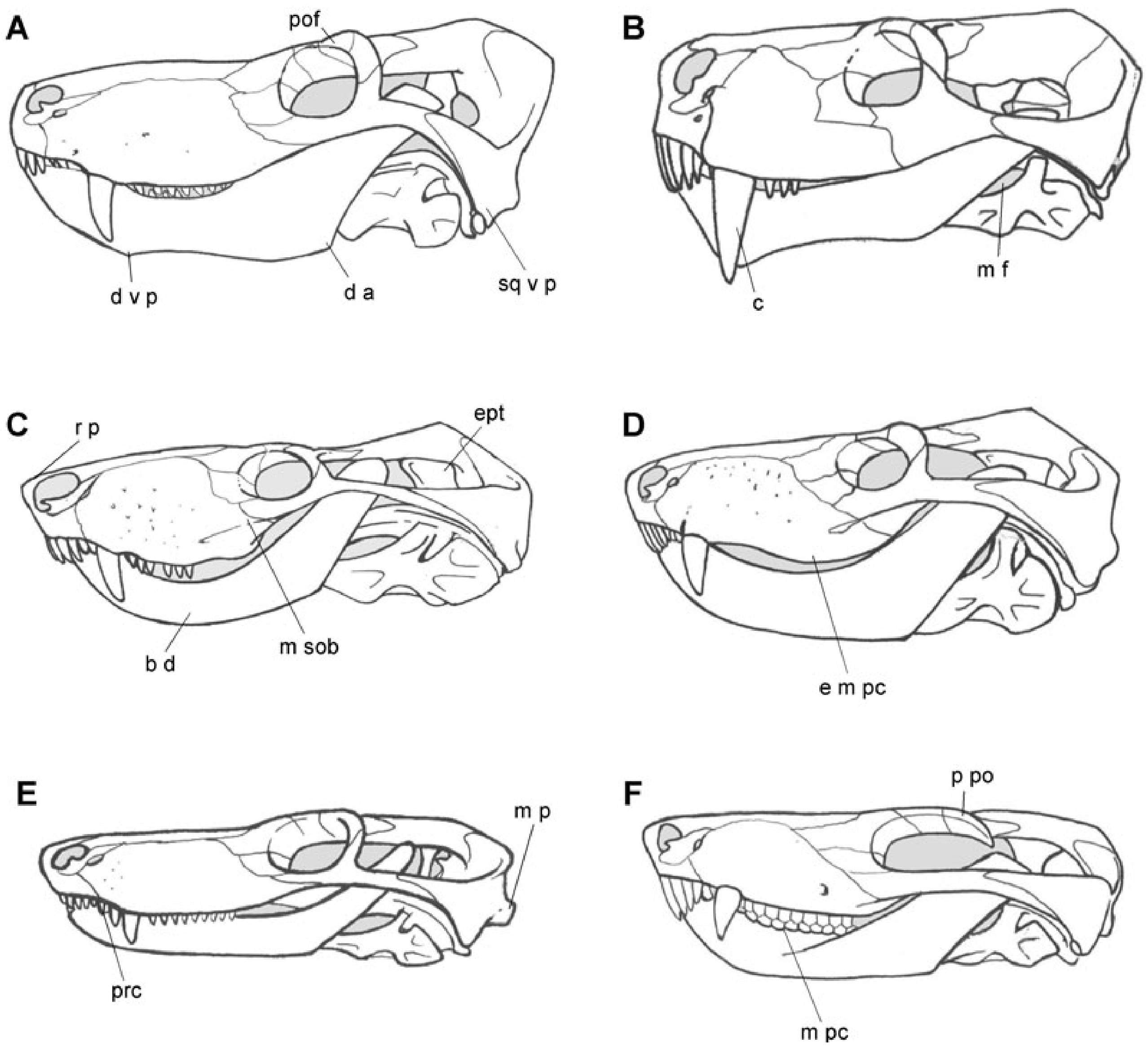

Figure 1. Skulls of selected therocephalians in left lateral view (not to scale): A, the scylacosaurid *Glanosuchus* (based on van den Heever, 1994); B, the akidnognathid eutherocephalian *Moschorhinus* (redrawn from Durand, 1991); C, the eutherocephalian *Mirotenthes* (based on UCMP 40467); D, the whaitsiid eutherocephalian *Theriognathus* (based on UCM 23381 and Brink, 1980); E, the basal baurioid *Ictidosuchoides* (modified from Brink, 1960b, 1988); F, the derived baurioid *Bauria* (redrawn from Brink, 1963). Abbreviations: b d, bowed dentary; c, dominant caniniform; d v p, dentary ventral process; e m pc, edentulous maxillary postcanine plate; ept, epipterygoid; m p, mastoid process; m pc, multicusped postcanines; m sob, maxillary extension of the suborbital bar; p po, postorbital process; pof, postfrontal; prc, precanine; r p, premaxilla rostral process; sq v p, squamosal ventral process.

into two major groups: Pristerosauria and Scaloposauria. The Scaloposauria included a single family, Scaloposauridae, which, according to Boonstra (1953: 605), 'flow[ed] directly into the Bauriamorpha'. Boonstra thus recognized a relationship between the diminutive scaloposaurids and the 'bauriamorphs.'

By the middle part of the 20th century, Brink (1960a) suggested that the scaloposaurid therocephalians were highly derived and gave rise to cynodonts via a silphedestid–scaloposaurid stock. This hypothesis required that at least some therocephalians constitute a paraphyletic assemblage or 'grade' with respect to the origins of Cynodontia. By contrast, Colbert & Kitching (1981: 2) stated: 'The Scaloposauria constitute a group of small, Middle Permian to Lower Triassic theriodonts, probably derived independently from an early Permian sphenacodont pelycosaur stock, but separated from their sphenacodont precursors by a substantial time gap'. These scenarios have since fallen out of favour, as Kemp (1982) suggested that Scaloposauridae may be a 'waste basket' group of juvenile ictidosuchids, another family of small, relatively gracile therocephalians acknowledged by Broom (1903) and Boonstra (1934). The name 'Scaloposauridae' was abandoned by Hopson & Barghusen (1986) and Kemp (1986) on the basis that the family is diagnosed only by juvenile characteristics and by an absence of shared derived characters present in adults of other taxa. Thus, the mosaic of derived and 'primitive' characteristics observed by some authors (e.g. Brink, 1960a; Colbert & Kitching, 1981) may have an ontogenetic explanation rather than a phylogenetic one, as most of the specimens attributed to Scaloposauridae are based on immature individuals. Hopson (1991) discussed similar issues in the cynodont family 'Silphedestidae,' declaring it to be an artificial taxon based on juvenile specimens.

The systematic studies of Kemp (1986), Hopson & Barghusen (1986) and, more recently, van den Heever (1994) have presented many complex issues involved in resolving therocephalian interrelationships (see Fig. 2), among them high levels of homoplasy and the recognition of problematic artificial groups (e.g. Scaloposauridae). Hopson & Barghusen (1986) were the first to examine the phylogenetic relationships of the major families of Therocephalia in detail, based on studies by Mendrez (1975) and C. H. Mendrez (unpubl. data), alluding to convergence and evolutionary parallelism in cynodonts and various therocephalian groups. These authors were the first to convincingly demonstrate the possible monophyly of Therocephalia, with a list of proposed synapomorphies, and also distinguished between basal therocephalians and the newly recognized 'Eutherocephalia' (Fig. 2A). van den Heever (1994) emphasized the diversity of basal therocephalians, re-establishing and revising the families Lycosuchidae and Scylacosauridae, and uniting scylacosaurids with the more derived eutherocephalians in a taxon called 'Scylacosauria' (although this was not the only hypothesis presented in that study; see Fig. 2B). Although van den Heever's work has greatly advanced what is known about the cranial morphology of early therocephalians, little is known about the patterns or mechanisms that have characterized and shaped early eutheriodont evolution. This lack of progress is largely a result of limited taxon and character sampling (particularly among therocephalians) and, by extension, an incomplete understanding of eutheriodont phylogeny.

Only very recently have progressive joint efforts been attempted to elucidate the cladistic relationships of therocephalian therapsids and to better resolve eutheriodont systematics and evolutionary patterns (Abdala, 2007; Botha, Abdala & Smith, 2007; Huttenlocker & Marcot, 2007; Huttenlocker, Marcot & Fox, 2007). In particular, the recent discovery of a basal cynodont, *Charassognathus gracilis*, from the *Tropidostoma* Assemblage Zone prompted a re-examination of the early eutheriodont radiation recorded in the Beaufort Group of southern Africa, and necessitated a phylogenetic analysis incorporating both therocephalian and basal cynodont taxa (Botha *et al.*, 2007). The results of the study resurrected the notion that 'therocephalians' may constitute a paraphyletic assemblage of basal eutheriodonts, nesting Cynodontia amongst 'therocephalians' as the sister taxon to the whaitsiid *Theriognathus* (an hypothesis previously suggested by Kemp, 1972a). It should be noted, however, that the primary objective of the above analysis was to assess the relative position of *Charassognathus* amongst basal cynodonts and to reveal the order of the acquisition of 'cynodont' characters during the course of eutheriodont evolution. As such, only a limited sample of therocephalian taxa ($N = 7$) was incorporated into the analysis. More recent efforts have similarly been aimed at the evolution of the cynodont condition, and have thus necessarily abandoned the broader diversity and intrarelationships of early therocephalian therapsids (Abdala, 2007).

By contrast, the aim of this paper was to expose the areas of consensus in therocephalian research, based on the foundations of Hopson & Barghusen (1986) and van den Heever (1994), and with new insights from Botha *et al.* (2007) and Abdala (2007). The present goal was to assess the monophyly and offer a detailed hypothesis of the cladistic relationships of therocephalian therapsids and, ultimately, to establish a consensus framework upon which future studies of therocephalian and eutheriodont systematics may be built.

Institutional abbreviations are as follows: AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, UK; BPI, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; GS, Geological Survey of South Africa, Pretoria, South Africa; UCM, University of Colorado Museum of Natural History, Boulder, CO, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA.

PHYLOGENETIC ANALYSIS

Early cladistic analyses of therocephalian therapsids have helped to both revise and support the validity of previously known families (Hopson & Barghusen, 1986). However, the higher level relationships of

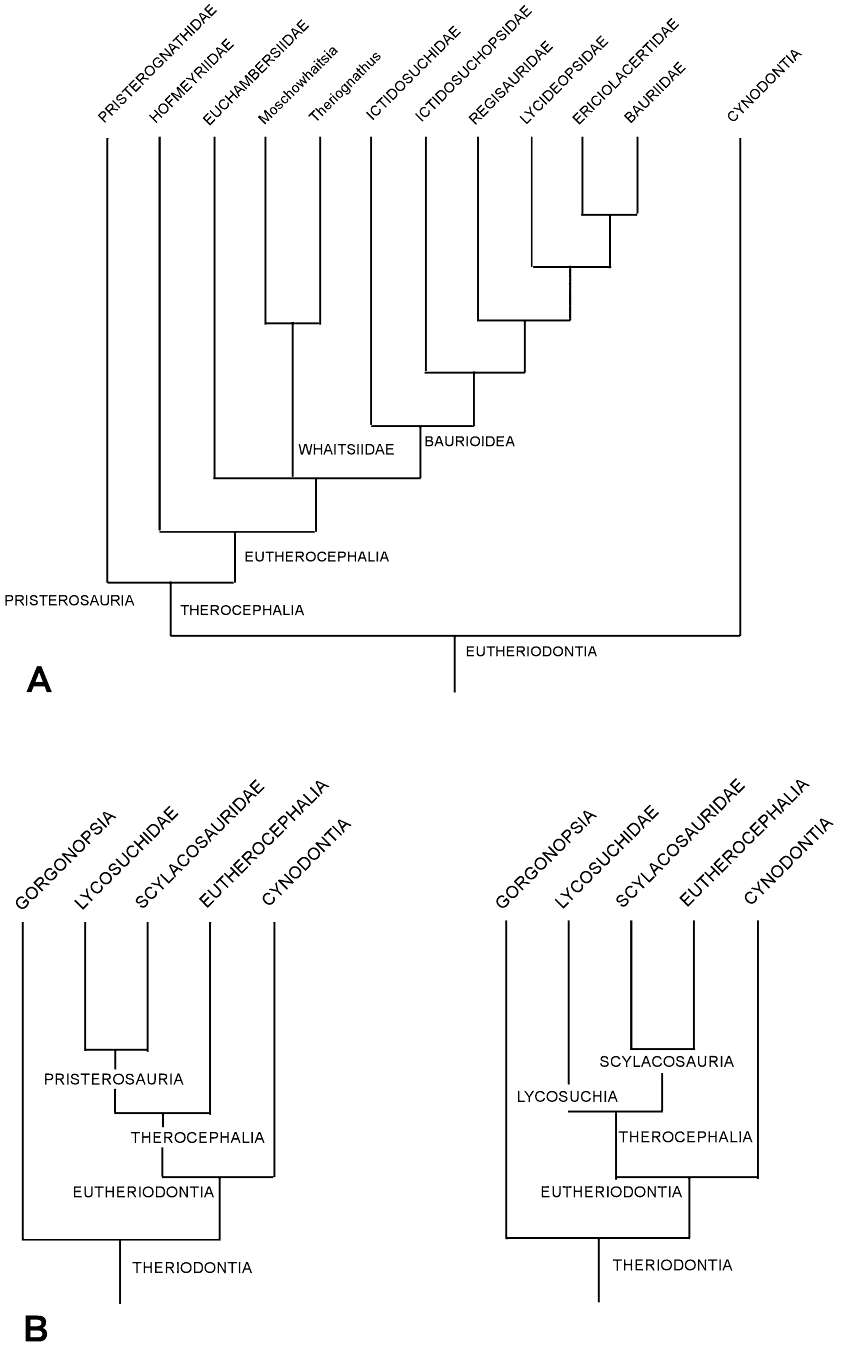

Figure 2. Hypotheses of therocephalian relationships: A, Hopson & Barghusen (1986); (B) van den Heever (1994). Two hypotheses of basal therocephalian relationships are demonstrated in (B): the ‘Pristerosauria’ hypothesis (left) and the ‘Scylacosauria’ hypothesis (right).

therocephalians have proven difficult to refine and have remained open to interpretation (Hopson, 1991). Hopson & Barghusen (1986) discussed therocephalian relationships at the familial level (Fig. 2A), but noted errors in their observations of specimens representing the basal eutherocephalian clade ‘Hofmeyriidae’ (p. 83). This resulted in a polytomy among Hofmeyriidae, Euchambersiidae (= Akidnognathidae), Whaitsiidae and Baurioidea (collectively termed ‘Eutherocephalia’). van den Heever (1994) advocated the existence of two basal therocephalian families, Lycosuchidae and Scylacosauridae, and argued for a sister group relationship between Scylacosauridae and Hopson & Barghusen’s (1986) Eutherocephalia (see Fig. 2B). van den Heever named this inclusive clade ‘Scylacosauria.’ Subsequent discussions and analyses utilizing therocephalian relationships (Sidor, 2001, 2003) relied solely on these sources (Hopson & Barghusen, 1986; van den Heever, 1994). However, more recent studies focusing on the early diversification of cynodont therapsids have also explored the cladistic relationships of at least a few therocephalian taxa (Abdala, 2007; Botha *et al.*, 2007). The analyses of Botha *et al.* (2007) also supported a relationship between the ‘higher’ eutherocephalians to the exclusion of the more basal lycosuchids (represented by *Lycosuchus*). However, the authors suggested a sister taxon relationship between the whaitsiid therocephalian *Theriognathus* and Cynodontia based on two critical synapomorphies (following Kemp, 1972a): (1) an expanded epipterygoid ascending process; and (2) a quadrate notch present in the squamosal. This was the first computer-assisted cladistic analysis to support the possible paraphyly of Therocephalia. Subsequent analyses (Abdala, 2007) have continued to emphasize the evolution of the cynodont condition and, in doing so, have not sampled a significantly broader diversity of therocephalian taxa or characters.

SELECTION OF TAXA AND CHARACTERS

The phylogenetic relationships of 30 therapsid taxa, including 23 therocephalian genera, were evaluated by performing a comprehensive cladistic analysis of therocephalian therapsids at the genus level (Appendices 2, 3). Seven non-therocephalian taxa were selected in order to assess the higher level relationships of the major therapsid clades (including Eutheriodontia). *Biarmosuchus* and *Titanophoneus* served as outgroups. Gorgonopsia and Anomodontia were employed to test the strength of a Theriodontia clade (see Fig. 2), and thus the higher level relationships of Therocephalia to other therapsids. For this reason, representatives of Cynodontia were also incorporated in the analysis (including *Charassognathus*, *Dvinia* and *Procynosuchus*). The 23 therocephalian genera employed in the ingroup included: *Lycosuchus*, *Glanosuchus*, *Ictidosaurus*, *Pristerognathus*, *Moschorhinus*, *Euchambersia*, *Olivierosuchus*, *Promoschorhynchus*, *Ictidostoma*, *Hofmeyria*, *Mirotenthes*, *Viatkosuchus*, *Moschowhaitsia*, *Theriognathus*, *Ictidosuchus*, *Ictidosuchops*, *Ictidosuchoides*, *Regisaurus*, *Scaloposaurus*, *Lycideops*, *Tetracynodon*, *Ericiolacerta* and *Bauria*. A complete record of the therocephalian and non-therocephalian specimens and literature investigated for this study is listed in Appendix 1. Appendix 2 lists and discusses the 110 craniodental and postcranial characters examined in the analysis, and Appendix 3 presents the character matrix. Most of the characters utilized here were adapted from the literature (Hopson & Barghusen, 1986; van den Heever, 1994; Sidor & Hopson, 1998; Modesto, Rubidge & Welman, 1999; Sidor, 2001, 2003; see Appendix 2 for additional references), but a few characters are new.

METHODS OF ANALYSIS

The analysis was performed using the branch-swapping algorithm tree bisection–reconnection (TBR) on PAUP 4.0 beta 10 (Swofford, 1999). The optimality criterion was set to ‘parsimony.’ A heuristic search was performed using a random addition sequence with 100 replicates. All characters had equal weight and were unordered. In an alternative analysis, palatal characters (37 and 105) were ordered (with regard to the stepwise evolution of the secondary palate; Maier, 1999), but the topology did not differ from the most-parsimonious trees (MPTs) in the unordered run (discussed below). The four resulting MPTs were combined into a 50% majority-rule consensus and bootstrap resampling was performed for additional support. The dataset was subsequently trimmed to the taxon sampling of Botha *et al.* (2007), and a Kishino–Hasegawa (K–H) test (Kishino & Hasegawa, 1989) was performed to compare the resulting consensus topology with that hypothesized by Botha *et al.* (2007). The following taxa were included in this analysis: Gorgonopsia, Anomodontia, *Charassognathus*, *Dvinia*, *Procynosuchus*, *Lycosuchus*, *Olivierosuchus*, *Moschorhinus*, *Theriognathus*, *Regisaurus*, *Ictidosuchops* and *Bauria*. The K–H test allows statistical comparisons of the ability of disparate phylogenetic hypotheses to explain patterns within the sampled character data. As such, the K–H test can determine whether a suboptimal hypothesis is statistically different in its ability to explain the sampled data. The results and detailed discussions of significant clades and their character support are reported below.

RESULTS AND DISCUSSION

The heuristic search recovered four MPTs of equal length [260 steps; consistency index (CI), 0.5346; retention index (RI), 0.7763; rescaled CI, 0.4150) and differing only in their reconstructions of the intrarelationships within Akidnognathidae (discussed below). A 50% majority-rule consensus, with consensus indices and bootstrap values, is illustrated in Figure 3 (and Fig. 4 in stratigraphic context), demonstrating a monophyletic Therocephalia as the sister taxon to Cynodontia (Eutheriodontia *sensu* Hopson & Barghusen, 1986). The K–H test (restricted to the taxon sampling of Botha *et al.*, 2007) revealed that ten additional steps than the MPT (168 steps with

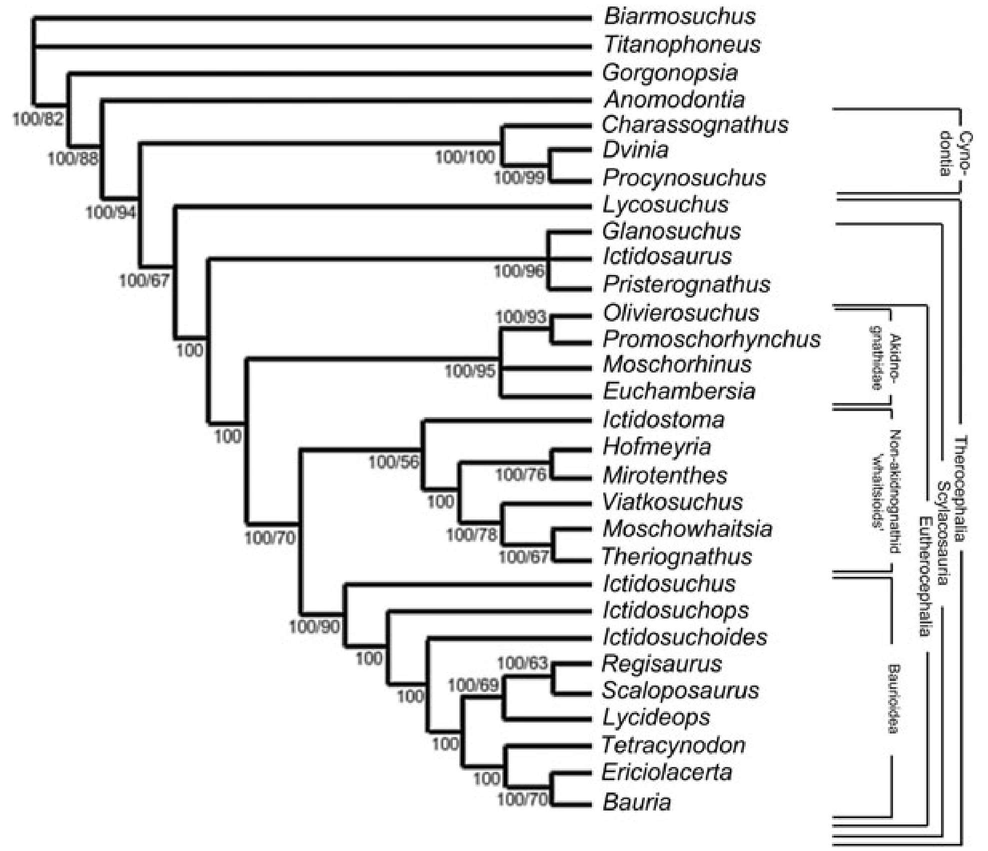

Figure 3. An hypothesis of the cladistic relationships of therocephalian therapsids, based on a 50% majority-rule consensus of four most-parsimonious trees (MPTs). Tree length, 260; consistency index (CI), 0.5346; retention index (RI), 0.7763; rescaled CI, 0.4150. Numbers at the nodes indicate consensus indices/bootstrap values. Note that *Ictidostoma*, *Mirotenthes*, *Hofmeyria*, *Viatkosuchus*, *Moschowhaitsia* and *Theriognathus* form a monophyletic clade, and relationships within Baurioidea are illustrated by a pectinate tree topology with *Ericiolacerta* + *Bauria* located in a crownward position.

restricted taxon sampling) were required to produce the topology of Botha *et al.* (2007) (178 steps), with Cynodontia positioned as the sister taxon to *Theriognathus*. A *P* value of 0.0677 suggests that the trees are not statistically different in their ability to explain the observed distribution of character changes. However, the lack of a statistically significant signal may be a result of the very small sample size (i.e. seven therocephalian taxa). The difference in the ability of these trees to explain the observed data may be better assessed with increased taxon sampling for the data of Botha *et al.* (2007).

HIGHER LEVEL RELATIONSHIPS OF THEROCEPHALIA

Given the current dataset, the results of the present analysis provide strong support for an Anomodontia + Eutheriodontia clade (as hypothesized by Kemp, 1982; Rowe, 1986, 1988; Modesto *et al.*, 1999; Rybczynski, 2000; Angielczyk, 2004), as opposed to a Gorgonopsia + Eutheriodontia clade ('Theriodontia'). Bootstrap resampling recovered an Anomodontia + Eutheriodontia clade in 88% of the trees. Cynodontia appears as the sister group to Therocephalia, forming a monophyletic Eutheriodontia, as demonstrated by Hopson & Barghusen (1986). However, although this node is well supported, with a bootstrap value of 94%, a monophyletic Therocephalia only occurred in 67% of the trees. Low support from bootstrap sampling may be a result of the apparent aberrant nature of the basal therocephalian *Lycosuchus*.

Monophyly of Therocephalia

Botha *et al.* (2007), Abdala (2007) and, most recently, Abdala, Rubidge & van den Heever (2008) have advocated the paraphyly of Therocephalia, supporting Kemp's (1972a) view that the whaitsiid genus *Theriognathus* represents the sister taxon to Cynodontia. The present analysis, however, supports the previous consensus of a monophyletic Therocephalia (Hopson

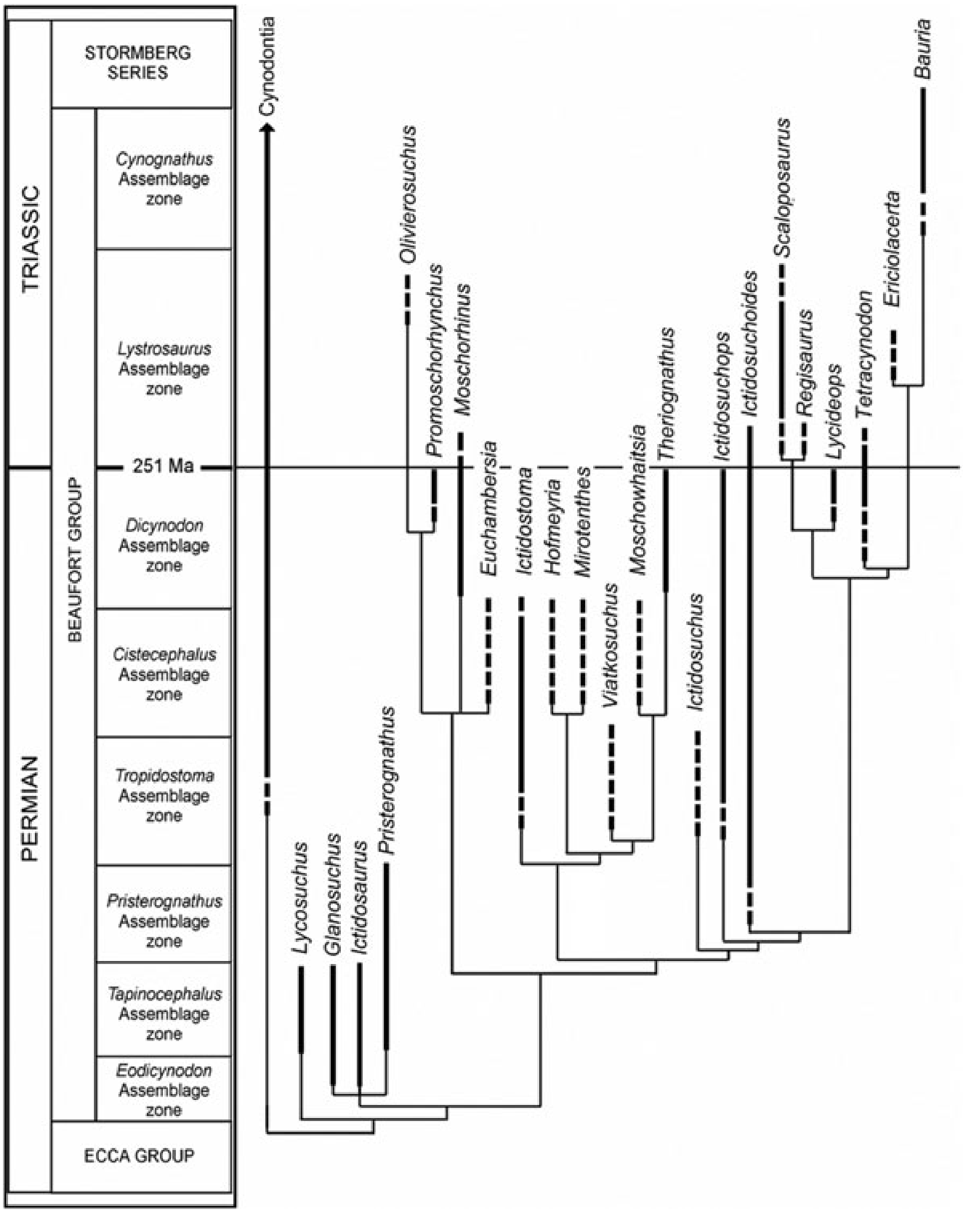

Figure 4. Temporal distribution and diversification of therocephalian therapsids during the Late Permian and Early Triassic (standardized to the stratigraphy of the Beaufort Group, Karoo Supergroup, southern Africa). Taxon sampling and tree topology are from the consensus tree illustrated in Figure 3. Broken lines indicate uncertain ranges. Temporal distributions are largely reconstructed from Rubidge (1995), Ward *et al.* (2005) and Abdala *et al.* (2008).

& Barghusen, 1986; Hopson, 1991; van den Heever, 1994; Sidor & Hopson, 1998; Rubidge & Sidor, 2001).

Among therocephalians, *Lycosuchus* appears as the basal outgroup to all others sampled in the analysis. *Lycosuchus* shares several unambiguous cranial synapomorphies with other therocephalians (Fig. 5), including: (1) palatal fenestra for the lower canine that is confluent with the internal naris (except in some akidnognathids and *Bauria*, as a result of their derived nature; convergent in Gorgonopsia); (2) moderately expanded vomer that broadens anteriorly; (3) ventromedian process on the pterygoid plate (present in the form of a small tubercle in lycosuchids; van den Heever, 1994); (4) large suborbital vacuities that do not close through ontogeny (with possible exceptions in *Euchambersia* and *Theriognathus*; see Hopson & Barghusen, 1986); (5) moderately expanded pterygoid transverse processes with a sharp posterior extension (except in *Euchambersia*); (6) reduced or absent dorsal process of stapes (except in *Viatkosuchus* and,

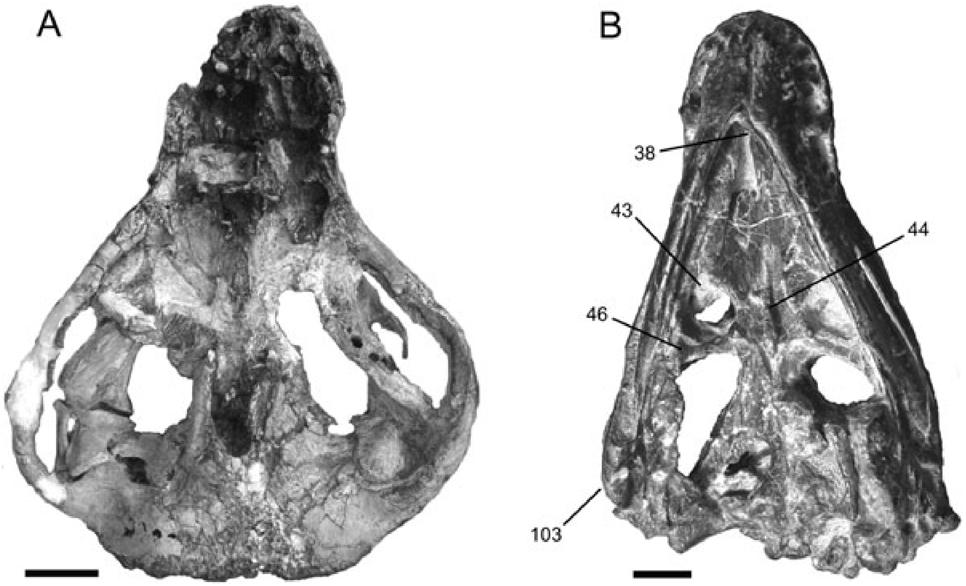

Figure 5. Comparison of the ventral skull of the cynodont *Procynosuchus delaharpeae* (AMNH FR 8220) (A) and a subadult specimen of the akidnognathid therocephalian *Olivierosuchus parringtoni* (BPI 3849) (B). Numbers 38, 43, 44, 46 and 103 refer to selected therocephalian synapomorphies listed in Appendix 4. Scale bars equal 10 mm.

possibly, some specimens of *Glanosuchus*); (7) stapedial foramen absent (except in *Viatkosuchus*; convergent in Anomodontia); and (8) temporal fenestra widest posteriorly (convergent in cynognathian cynodonts). Based on the evidence presented here, the seemingly primitive characteristics of *Lycosuchus* either represent evolutionary reversals, or the shared characteristics between Cynodontia and more advanced therocephalians are best regarded as convergences. *Lycosuchus* and other taxa attributed to the Lycosuchidae (van den Heever, 1994) occupy the most basal position of a monophyletic Therocephalia. A complete list of characters supporting the monophyly of Therocephalia (as many as 15 proposed cranial and postcranial synapomorphies) is listed in Appendix 4. A few selected characters of the ventral skull are illustrated in Figure 5.

Scylacosauria

The MPTs placed a monophyletic Scylacosauridae as the sister taxon to Eutherocephalia, supporting van den Heever's (1994) 'Scylacosauria' hypothesis. However, bootstrap analysis showed a Scylacosauria clade occurring in less than 50% of the trees (although the clade is present in all of the MPTs: consensus index, 100). These post-*Lycosuchus* therocephalians share the following synapomorphies: (1) well-developed medial process of the squamosal contributing to the pterygo-paroccipital foramen; (2) marked development of the crista choanalis; (3) a narrow ventromedian crest on the posterior portion of the vomer (possibly convergent in Cynodontia); (4) a ventromedian pterygoid crest (as opposed to a tubercle); (5) absence of pterygoid transverse flange teeth (also in Cynodontia and Anomodontia); and (6) a splenial that is completely obscured by the dentary in lateral view (also obscured in some basal cynodonts, but exposed in *Procynosuchus*; see character 71 in Appendices 2, 3).

The family Scylacosauridae is a diverse group of carnivorous basal therocephalians, but is only represented here by *Glanosuchus*, *Ictidosaurus* and *Pristerognathus*. These taxa clustered together in 96% of trees in the bootstrap analysis, providing strong support for the monophyly of this family (although the intrarelationships of these three genera relative to other scylacosaurids have yet to be examined in detail). A detailed discussion of basal therocephalians and the characteristics of Scylacosauridae is provided by van den Heever (1994) and Abdala *et al.* (2008).

Eutherocephalia

The sister group to Scylacosauridae is Eutherocephalia, which is shown here to be composed of three major clades (Akidnognathidae, non-akidnognathid 'whaitsioids' and Baurioidea) of which the akidnognathids form the monophyletic sister group to the other two. A monophyletic Eutherocephalia occurred in less than 50% of the trees in the bootstrap analysis, but is supported by the following suite of synapomorphies: (1) anterodorsal-most tip of premaxilla forms a rostral process, overhanging incisors; (2) orbit positioned relatively low in the skull (except in baurioid eutherocephalians; convergent in cynodonts); (3) postfrontal absent (polymorphic in the holotype of *Hofmeyria*: F. Abdala, University of Witwatersrand, Johannesburg, pers. comm., 2006; convergent in cynodonts); (4) vomers are unpaired and have either fused anteriorly or completely fused (convergently fused in cynodonts); (5) dorsal surface of the paroccipital process is deeply hollowed in the floor of the post-temporal fenestra; (6) tabular is withdrawn from contact with the opisthotic (but contacts opisthotic in non-akidnognathid 'whaitsioids', *Ictidosuchus* and *Bauria*); (7) tabular just barely contacts the post-temporal fenestra (extends below in non-akidnognathid 'whaitsioids'); (8) mandibular fenestra present, penetrating the mandible and visible laterally; (9) incisor cutting margins smoothly ridged (convergent in cynodonts); (10) lower incisors number four; and (11) parasagittal ridges present, running from medial posterior flare of transverse flanges to basioccipital (convergent in *Lycosuchus*).

INTRARELATIONSHIPS WITHIN EUTHEROCEPHALIA

Akidnognathidae

Haughton & Brink (1954) erected the family Akidnognathidae ['Akidognathinae' (sic) Nopsca, 1928] to include a mixture of currently valid akidnognathid taxa (e.g. *Akidnognathus parvus*) and some scylacosaurid taxa, probably as a result of plesiomorphic similarities. Soon after, Watson & Romer (1956) classified many of the akidnognathid taxa within the family Whaitsiidae, but Mendrez (1974a, b) and, more recently, Durand (1991) have contested this relationship. A more general interpretation might be that the akidnognathid forms are morphologically intermediate between basal therocephalians (e.g. scylacosaurids) and whaitsiid-like forms, a view that compromises the hypotheses of the above authors. Likewise, Tatarinov (1995a) placed representatives of the Akidnognathidae and Whaitsiidae within the superfamily 'Whaitsioidea,' although this group is regarded as paraphyletic here (see Figs. 3, 4). Mendrez (1974a) was the first to recognize the major akidnognathid taxa in their modern sense as subfamilies within her monophyletic 'Moschorhinidae', although she later used the name 'Annatherapsididae' (Mendrez, 1975). She divided the group into three subfamilies: Annatherapsidinae, Moschorhininae and Euchambersiinae.

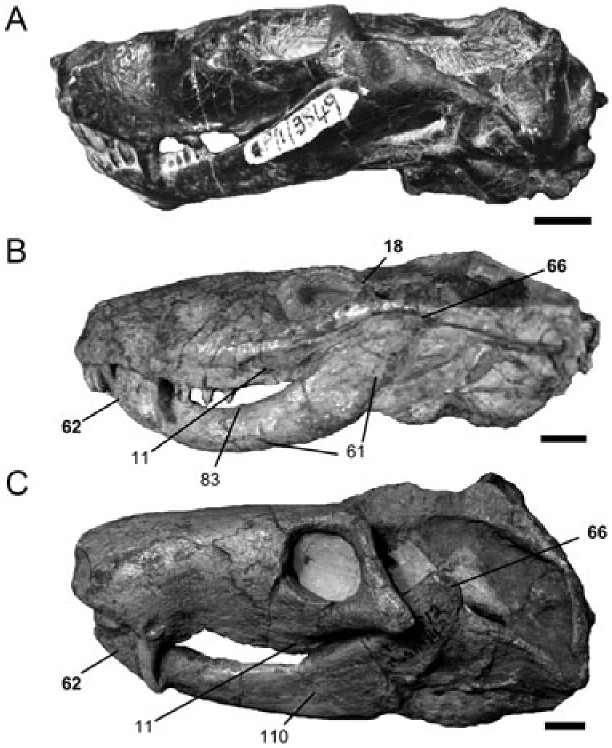

Figure 6. Comparison of the left lateral skull roof and lower jaws of the akidnognathid *Olivierosuchus parringtoni* (BPI 3849) (A), the 'hofmeyriid' eutherocephalian *Mirotenthes digitipes* (UCMP 40467) (B) and the derived whaitsiid *Theriognathus* (BPI 512) (C). Numbers 11, 61, 83 and 110 refer to selected synapomorphies for the clade of 'hofmeyriids' plus whaitsiids (see Appendix 4). Bold numbers (18, 62, 66) refer to selected synapomorphies for the clade comprising all non-akidnognathid eutherocephalians ('hofmeyriids,' whaitsiids and baurioids). Scale bars equal 10 mm.

The first family name used to describe any of these taxa was 'Euchambersidae' (sic), erected by Boonstra (1934) for the genus *Euchambersia*. The spelling of the name was later corrected and designated 'Euchambersiidae' by von Huene (1940), and was the preferred name of Hopson & Barghusen (1986) for Mendrez's (1974a) 'Moschorhinidae.' However, although the principle of priority [Article 23 in International Commission on Zoological Nomenclature (ICZN)] indicates that Euchambersiidae Boonstra (1934) should be the preferred name, the principle of coordination (Article 36 in ICZN) presents limitations, stating that the proper name for a family-level group should be established on the oldest genus name within that family (i.e. *Akidnognathus* Haughton 1918). Thus, the name Akidnognathidae, as used by Haughton & Brink (1954), has precedence over any of the other names suggested for this family, and is accordingly becoming more widely used in the literature (Rubidge & Sidor, 2001; Sigurdsen, 2006).

The family Akidnognathidae is represented here by *Olivierosuchus* (Figs. 5, 6), *Promoschorhynchus*, *Moschorhinus* and *Euchambersia*, which form a monophyletic clade at the base of Eutherocephalia (Fig. 3). Mendrez (1974a) suggested that taxa previously assigned to Annatherapsididae, Moschorhinidae and Euchambersiidae are closely related (discussed above), and Hopson & Barghusen (1986) agreed that these taxa form a monophyletic clade. A monophyletic Akidnognathidae occurred in 95% of the trees in the bootstrap analysis, and a sister group relationship between *Promoschorhynchus* and *Olivierosuchus* is supported with a bootstrap value of 93%.

Synapomorphies uniting the akidnognathids include: (1) a septomaxilla that is well exposed outside of the external naris, broadly overlapping the premaxilla anteriorly; (2) enlarged, anteriorly facing external nares; (3) a vomer that is expanded beyond the primitive therocephalian condition, broadly overlapping the vomerial process of the premaxilla; and (4) contribution of the premaxilla and maxilla to a fossa for the lower canine on the palatal surface. Akidnognathids also lack certain features of more derived eutherocephalians, such as a more gracile dentary that tapers rather than thickens anteriorly, a more rounded coronoid process and a reflected lamina of the angular that is more elongate and spade-shaped (lacking the rounded, ventrally extending margin of more basal therocephalians and other therapsids).

Non-akidnognathid 'whaitsioids'

Many of the akidnognathid forms mentioned above have at one time been placed within the Whaitsiidae (von Huene, 1940; Watson & Romer, 1956; Romer, 1966). Tatarinov (1995a) included the families Annatherapsididae, Moschorhinidae, Euchambersiidae, Moschowhaitsiidae and Whaitsiidae within the more inclusive 'Whaitsioidea.' However, the results of Hopson & Barghusen (1986) and this analysis indicate that representatives of the Annatherapsididae, Moschorhinidae and Euchambersiidae constitute a monophyletic family, Akidnognathidae, which is removed from the Whaitsiidae and Baurioidea (see above). Mendrez (1974a) also separated akidnognathids from Whaitsiidae and removed other forms which she did not see fit in either of the two groups, such as *Hofmeyria*, *Mirotenthes* and *Proalopecopsis*. Attridge (1956) regarded *Mirotenthes* as a possible whaitsiid based on the classification schemes of previous authors, and Brink (1956) included *Hofmeyria* within the Whaitsiidae. Two major clades of post-akidnognathid eutherocephalians are acknowledged here: non-akidnognathid 'whaitsioids' and Baurioidea. Bootstrap resampling supported the monophyly of this clade in 70% of the trees (Fig. 3).

Representatives of non-akidnognathid 'whaitsioids' utilized in this analysis include *Ictidostoma*, *Hofmeyria*, *Mirotenthes* (Figs 1C, 6B), *Viatkosuchus*, *Moschowhaitsia* and *Theriognathus* (Figs 1D, 6C). A monophyletic grouping of these taxa occurred in 56% of the trees in the bootstrap analysis. Relationships have been suggested between *Hofmeyria* and *Ictidostoma* (Hopson & Barghusen, 1986) and *Theriognathus* and *Moschowhaitsia* (Kemp, 1972a; Mendrez, 1974a; Hopson & Barghusen, 1986; Tatarinov, 1995a). Except for the upper dentition, the skull roof and lower jaws of the 'hofmeyriid' *Mirotenthes* are strikingly similar to those of *Theriognathus* (Fig. 6). These similarities include the short, stout rostrum with a shallow but broad constriction behind the canine and laterally expanded suborbital and zygomatic arches. This lateral expansion has led to a sharp and high maxillary facial branch of the suborbital bar (very well developed in *Ictidostoma*; see Brink, 1960b), under which the posterior portion of the maxillary facial plate is folded onto the palatal surface (Fig. 1C, D). This configuration allows a significant portion of the lateral surface of the maxilla to be seen in a ventral view of the skull. Such an arrangement of the suborbital region is absent in basal therocephalians, akidnognathids and basal baurioids (e.g. *Ictidosuchops*, *Karenites*, *Ictidosuchoides*, *Tetracynodon* and *Regisaurus*), with the possible exception of *Ictidosuchus*. The expansion has also produced highly frontated and converged orbital rotation and a temporal fenestra that is more expanded than in all other therocephalians (approximating the cynodont condition).

Additional synapomorphies proposed here in support of a monophyletic grouping of all non-akidnognathid 'whaitsioids' include: (1) a very short parietal crest (except in *Theriognathus*); (2) small suborbital vacuities in derived forms (i.e. *Viatkosuchus* and *Moschowhaitsia*; vacuities close completely in adult *Theriognathus*); (3) a broad epipterygoid as well as a trigeminal notch in whaitsiids; (4) tabular contacting the opisthotic (convergent in Bauria); (5) a bowed dentary (except in *Viatkosuchus* and some specimens of *Theriognathus*); and (6) an absence of lower postcanines in some forms (i.e. *Mirotenthes*, *Theriognathus* and, possibly, *Hofmeyria*; uncertain in *Viatkosuchus* and *Moschowhaitsia*). Postcanine dentary teeth are present in the genus *Ictidostoma*, but they are extremely reduced in size, number and spacing (A. Huttenlocker, pers. observ.; J. Hopson, University of Chicago, IL, pers. comm., 2005).

Baurioidea

The consensus tree presented in Figures 3 and 4 illustrates Baurioidea as the monophyletic sister taxon to the non-akidnognathid 'whaitsioids.' Bootstrap resampling recovered a monophyletic Baurioidea in 90% of the trees (Fig. 3). Hopson & Barghusen (1986) suggested a monophyletic grouping of Baurioidea based on extensive palatal exposure of the maxilla. Additional synapomorphies presented here include: (1) a long, low maxillary facial plate (except in *Bauria*); (2) low rostrum depressed just anterior to the orbits, which are positioned relatively high in the skull; (3) sharp mastoid process with a large contribution from the squamosal (Crompton, 1955; Mendrez, 1972); (4) a long, slender dentary; (5) tall coronoid process; and (6) six upper incisors (except in *Bauria*, where the upper incisors are reduced to four). Also, compared with more basal therocephalians, the baurioids show a general trend towards smaller sizes and more gracile skulls and postcrania.

One of the most obvious features of baurioid evolution is the nature of the development of the secondary palate (Mendrez, 1975; Hopson & Barghusen, 1986; Maier, 1999). The presence of a complete, ossified secondary palate in advanced baurioids may have contributed to earlier classifications placing some cynodonts amongst therocephalians (Brink, 1960a; Romer, 1966). However, most authors agree that the secondary palate evolved multiple times in therapsids, an indication of the prevalence of parallel evolution in the group. The independent acquisition of a complete secondary palate in baurioid therocephalians and cynodonts may imply similar developmental factors, but the most parsimonious representations of therapsid phylogeny and subtle morphological differences (e.g. absence of an incisive foramen in baurioid therocephalians) do not permit a common evolutionary origin for these structures in the two groups (see Appendix 2, character 37 and Maier, 1999 for further discussion).

Traditional classifications have placed basal baurioid taxa amongst 'scaloposaurids' in the scaloposaurian taxon 'Ictidosuchoidea' ('Ictidosuchia' of Boonstra, 1972; see Mendrez, 1972: 209; Brink, 1986, 1988). *Olivierosuchus*, based on subadult specimens, was originally placed in Ictidosuchidae (Brink, 1965; Findlay, 1968), another family of 'ictidosuchoids.' However, the small baurioid taxa utilized in this analysis (*Ictidosuchops*, *Ictidosuchoides*, etc.) are clearly established on adult specimens based on evidence for well-developed temporal musculature and a fused braincase, whereas *Olivierosuchus* is shown to be an akidnognathid as suggested by Colbert & Kitching (1981: 2) based on characteristics of the palate, dentition and lower jaw (Fig. 3).

Curiously, basal baurioids show certain characteristics that may be attributed to juvenile therocephalians. For example, *Ictidosuchus*, *Ictidosuchoides*, *Ictidosuchops* and *Regisaurus* display enlarged orbits which are placed high in the skull roof. Baurioids also retain a long, slender jaw into maturity with little development of the dominant caniniforms, retain numerous precanine teeth (Parrington, 1936; absent in some advanced baurioids) and display a relatively wide, heart-shaped interpterygoid vacuity. If these taxa are not exclusively based on juveniles and the specimens examined represent mature individuals (as indicated above), the characteristics described here may suggest that neotenic processes were involved in the early evolution of Baurioidea. Other processes, such as the continued development of the secondary palate and the appearance of multicusped postcanines (which may also be neotenic; Sidor & Welman, 2003), were important as well, leading to apparent parallel evolution in baurioids and cynodonts.

CONCLUSIONS

Over the past 20 years, little effort has been made to resolve the systematic problems of therocephalians, except for the significant contributions of Hopson & Barghusen (1986) and van den Heever (1994). Since this work, the recent efforts of Botha *et al.* (2007) (and, most recently Abdala, 2007) have sparked new interest in therocephalian systematics, but have failed to recover robust hypotheses of monophyly at either familial or suprafamilial levels. Here, the analyses attempted by previous authors have been expanded, based on increased taxon and character sampling, and it has been demonstrated that Therocephalia represents a unique and diverse group of 'mammal-like' therapsids. The incorporation of numerous eutherocephalian and basal therocephalian taxa in a computer-assisted cladistic analysis now provides a useful framework for examining patterns in origins and evolution of the major therocephalian groups.

Further work is required to resolve the relationships within scylacosaurids and lycosuchids. Although their higher level relationships are relatively well understood, little remains known about the interrelationships of the various lycosuchid and scylacosaurid genera (e.g. *Lycosuchus*, *Glanosuchus*). More detailed analyses of basal therocephalian taxa will shed light on the diversity of these early therocephalian predators (van den Heever, 1994; Abdala *et al.*, 2008).

Likewise, additional work focusing on akidnognathid systematics is beginning to resolve some of the problems in this group (Sigurdsen, 2006). Akidnognathid systematics would benefit from an analysis of additional genera, including eastern European representatives. Likewise, the monophyly of non-akidnognathid 'whaitsioids' should be further tested with a closer analysis of the proposed representatives, such as the 'hofmeyriids' *Hofmeyria* and *Ictidostoma*, and, in particular, the eastern European forms (i.e. *Viatkosuchus* and *Moschowhaitsia*).

More work is required on baurioids to elucidate the problems surrounding their evolutionary radiation. As a result of a lack of resolution of basal baurioid relationships in the bootstrap analysis, more focus should be given to these early forms. In addition, no-one has yet linked the juvenile 'scaloposaurids' with their respective adult forms. Baurioid systematics would benefit from more developmental studies, in order to resolve the confusion surrounding certain forms that are based solely on juveniles (e.g. *Tetracynodon*, *Scaloposaurus*). More detailed systematic studies will expose the diversity and relationships of baurioids and other enigmatic therocephalians.

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APPENDIX 1

List of therapsid taxa, specimens examined and literature cited for this study

Taxon	Source
Akidnognathus parvus	BPI 641 (cast); Brink (1960b)
Anomodontia	AMNH 5536 (*Galeops whaitsi*); AMNH 5541 (*Galepus jouberti*); Brinkman (1981); Rubidge & Hopson (1990, 1996); Modesto *et al.* (1999); Rybczynski (2000)
Anteosaurus minor	AMNH 2224; King (1988)
Bauria cynops	UCM 39522 (cast); UCMP 42804; Brink (1963)
Biarmosuchus tener	Sigogneau & Tchudinov (1972); Sigogneau-Russell (1989); Sidor & Welman (2003)
'Cynariognathus' platyrhinus	AMNH 5502; UCMP 42667; Broom (1932); Boonstra (1954); Cys (1967); Brink (1986)
Dvinia prima	UCMP 177307 (cast); Hopson & Barghusen (1986); Sidor & Hopson (1998)
Ericiolacerta parva	AMNH 9542; AMNH 9550; Watson (1931); Colbert & Kitching (1981); Hopson & Barghusen (1986)
Euchambersia mirabilis	BPI 4009; Boonstra (1934); Hopson & Barghusen (1986); Brink (1988)
Glanosuchus macrops	Boonstra (1954); van den Heever (1994); Abdala *et al.*, 2008
Gorgonopsia	AMNH 5515 & UCM 23384 (*Gorgonops torvus*); AMNH 5537 (*Lycaenops angusticeps*); Kemp (1969); Laurin (1998)
Hofmeyria atavus	BPI 4401; BPI 4404; Broom (1932); Hopson & Barghusen (1986); Brink (1988); Sidor (2001, 2003)
Ictidosaurus angusticeps	Abdala *et al.* (2008)
Ictidostoma hemburyi	AMNH 5520; AMNH 5521; AMNH 21451; BPI 3052; Broom (1932); Boonstra (1935); Brink (1960b); Hillenius (2000)
Ictidosuchoides longiceps	UCMP 42702; Boonstra, 1934; Brink (1960b, 1988); Mendrez (1975); Sidor (2003)
Ictidosuchops baurioides	Brink (1960b, 1988)
Ictidosuchops intermedius	BPI 218; BPI 223; Crompton (1955); Brink (1960b)
Ictidosuchus primaevus	AMNH 5529; Broom (1932); Boonstra (1935); Hopson & Barghusen (1986); Brink (1988)
Karenites ornamentatus	Tatarinov (1995b)
Lycideops longiceps	BMNH R5695; Boonstra (1934); Mendrez (1975); Brink (1988); Hopson & Barghusen, 1986
Lycosuchidae indet.	UCMP 42395 (unidentified lycosuchid); van den Heever (1994), figs. 4, 5, & 7 (GS C60, Lycosuchidae indet.)
Lycosuchus vanderrieti	van den Heever (1980, 1994); Brink (1988)
Mirotenthes digitipes	UCMP 40467; Attridge (1956); Cys (1971)
Moschorhinus kitchingi	BPI 4227; BPI 4636; Mendrez (1974a); Hopson & Barghusen (1986); Durand (1991); Sidor (2003)
Moschowhaitsia vjuschkovi	Kemp (1972a); Brink (1986); Hopson & Barghusen (1986)
Olivierosuchus parringtoni	BPI 3849; Brink (1965); Findlay (1968); Sidor (2001, 2003)
Pristerognathus polyodon	Mendrez (1975) (BMNH R2581); Boonstra (1954) (= *Ptomalestes avidus*); van den Heever (1994) (= *Ptomalestes avidus*)
Procynosuchus delaharpeae	AMNH 8220; Kemp (1979)
Promoschorhynchus platyrhinus	BPI 484; Mendrez (1974b)
Regisaurus jacobi	Mendrez (1972)
Scaloposaurus constrictus	BMNH R1723; Mendrez-Carroll (1979)
Tetracynodon spp.	BPI 2710 (*T. darti* holotype); UCMP 42869 & UCMP 78394 (cf. *T. darti*); Sigogneau (1963); Brink (1988)
Theriognathus spp.	BPI 182 ('*Aneugomphius*' type); BPI 512; BPI 785; BPI 844; BPI 4008; UCM 23381; UCM 39524 (cast); UCMP 42675; UCMP 42676; Kemp (1972a, b); Brink (1956, 1957, 1980)
Thrinaxodon liorhinus	AMNH 5630 (cast); UCMP 42866; UCMP 42865; UCMP 42877; UCMP 42878; Estes (1961)
Titanophoneus potens	King (1988)
Unidentified juvenile therocephalians	UCMP 40499 ('scaloposaurid'); UCMP 42782 ('scaloposaurid')
Unidentified scylacosaurid	UCMP 42669 (cf. *Glanosuchus macrops*)
Viatkosuchus sumini	Tatarinov (1995a); Sidor (2001, 2003)

APPENDIX 2

List and discussion of 110 craniodental and postcranial characters examined for phylogenetic analysis of 30 therapsid taxa. Characters are borrowed primarily from Hopson & Barghusen (1986), van den Heever (1994), Sidor & Hopson (1998), Botha *et al.* (2007), or are newly adapted for the present analysis (see below for detailed discussions of individual characters and states).

1. Premaxilla does not overhang the incisor region (0) or anterodorsal-most tip of premaxilla forms a rostral process, overhanging the incisors (1). (New.)
2. Septomaxilla is a long, narrow element that is moderately well exposed on the facial region (0) or is enlarged and well exposed outside of the external naris, broadly overlapping the premaxilla anteriorly (1). (From Botha *et al.*, 2007.)
3. External nares are moderately large and face anterolaterally (0) or are extremely enlarged, close-set and face more anteriorly (1). (New.)
4. Rostrum is moderately long and narrow (0), short and broad (1), or moderately long and about as high as broad (2). (From van den Heever, 1994.)
5. Dorsal profile of the preorbital region convex (0) or relatively straight (1). (From Sidor & Hopson, 1998.)
6. Constriction of the snout directly behind the caniniform(s) absent (0) or present (1). (From van den Heever, 1994.)

Euchambersia is coded '?' for this character, because the region behind its single canine tooth bears a highly specialized pit.

7. Preorbital depression anterior to a thickened ridge on the anterior margin of the orbit is absent (0) or present, extending anteroventrally from the lacrimal to the canine buttress of the maxilla (1). (New.)
8. Maxillary facial plate high (0) or low with a height less than 40% its length (1). (New.)
9. Concave ventral step in maxillary facial plate between caniniform(s) (or anterior-most maxillary teeth) and incisors present (0) or absent (1). (New.)
10. Broad excavation or pit in the maxilla immediately posterior to the dominant canine absent (0) or present (1). (New.)
11. Posterior region of the maxillary facial plate is folded inward onto the palatal region, so that the maxilla is well exposed ventrally just anterior to the orbit: absent (0) or present (1). (New.)
12. Suborbital bar shallow (0) or deep (1). (From van den Heever, 1994.)
13. Suborbital bar is not laterally expanded (0) or is slightly expanded and extends from the jugal onto the posterior part of the maxillary facial plate, contributing to a pronounced degree of orbital convergence (i.e. orbits facing forward and appearing more triangular than oval in dorsal view) (1). (New.)
14. Long, low rostrum just anterior to orbital region absent (0) or present (1). (New.)
15. Orbit positioned relatively high, elevated to or above the dorsal temporal margin (0), or low in the skull (1). (New.)
16. Anterior border of orbit located on posterior half of the skull (0), anterior half of skull (1) or transverse midline (2). (Modified from van den Heever, 1994.)
17. Postorbital process of jugal is present (0) or absent (1). (New.)
18. Postorbital bar moderately well-built (0), extremely slender (1) or absent/unossified (2). (New.)
19. Posteroventral extension of the zygomatic arch just below the orbit slightly present (0), absent, the zygomatic arch is relatively straight (1), steep immediately behind the orbit (2), or curved, having a distinctly concave ventral margin throughout its length (3). (Modified from Rubidge & van den Heever, 1997; Rybczynski, 2000.)
20. V-shaped, posterior border of nasals pointing towards the occiput absent (0) or present (1). (Modified from van den Heever, 1994.)
21. Median fronto-nasal crest absent (0) or present (1). (New.)
22. Postfrontal present (0) or absent (1). (From Hopson & Barghusen, 1986; Sidor, 2001; Botha *et al.*, 2007.)

Hofmeyria is coded '0' and '1' for this character. Hopson & Barghusen (1986) discussed the presence of a postfrontal in 'hofmeyriids,' but then noted their observation as an error in the addendum (p. 83). van den Heever (1994) discussed the possibility of a postfrontal in *Hofmeyria*, but Sidor (2001) dismissed the presence of such a bone in his study on synapsid cranial simplification. Examination of the holotype confirms the presence of this bone on only one side of the skull, indicating that the state is polymorphic (F. Abdala, University of Witwatersrand, Johannesburg, pers. comm., 2006).

23. Parietal (= pineal) opening in adults present (0) or absent/extremely reduced (1). (Modified from Rubidge & van den Heever, 1997; Botha *et al.*, 2007.)
24. Temporal fenestra in adults subequal in size (0) or larger (1) than the orbit. (Modified from Rubidge & Kitching, 2003.)

25. Zygomatic arch moderately deep (0), very slender (1) or extremely deepened (2). (From Hopson & Kitching, 2001.)
26. Participation of the parietal in the temporal fenestra dorsal border absent (0) or present (1). (From Hopson & Barghusen, 1986.)
27. Parietal expanded posteriorly on the midline behind the region of the parietal foramen absent (0) or present (1). (From Hopson & Barghusen, 1986.)
28. Parietal crest long, just over half the temporal fenestra length (0), short, less than half the temporal fenestra length (1), or very long, approximating the temporal fenestra length (2). (New.)

Biarmosuchus, *Titanophoneus*, *Gorgonopsia* and *Anomodontia* have been coded '?' as these taxa lack a parietal crest.

29. Posterodorsal inclination of the temporal region, reaching its maximum height where the parietal crest meets the lambdoidal (= occipital) crest present (0) or absent (1). (New)

Biarmosuchus, *Titanophoneus*, *Gorgonopsia* and *Anomodontia* have been coded '?' as these taxa lack a parietal crest.

30. Intertemporal region in adults wide (0), slightly reduced (1) or narrow with vertical lateral faces (2). (Modified from Kemp, 1972a; Hopson & Barghusen, 1986.)
31. Anteroposterior enlargement of the temporal fenestra absent (0) or present (1). (From Sidor & Hopson, 1998.).
32. Posteroventral process of the squamosal absent (0) or present (1). (From Rybczynski, 2000.)
33. Medially directed process of the squamosal contacting the pro-otic absent (0) or present, enclosing the pterygoparoccipital foramen (1). (From Kemp, 1972a, 1982.)

A pro-otic process of the squamosal is apparently not well developed in cynodonts and is completely absent in the therocephalian *Lycosuchus*. Although Hopson & Barghusen (1986) regarded this process as a eutherocephalian feature, van den Heever (1994) noted its presence in scylacosaurids as well. All therocephalian taxa where this region is preserved have been coded '1,' except for *Lycosuchus*. *Ictidosaurus*, *Lycideops* and *Ericiolacerta* are coded '?' as a result of poor preservation of this region of the skull.

34. Quadrate and quadratojugal relatively large (0) or reduced in height (1). (From Hopson & Barghusen, 1986.)
35. Quadrate and quadratojugal situated in a depression on the anterior face of the squamosal (quadrate recess) absent (0) or present (1). (From Hopson & Barghusen, 1986; Sidor & Hopson, 1998.)
36. Palatal fenestra for lower caniniform absent (0), present and confluent with internal naris (1), a separate palatal housing for the lower canine is created by an extension of the premaxilla and maxilla (2), or a fossa for the lower canine is present where the maxilla and premaxilla meet on the ventral surface of the secondary palate (3). (Modified from Hopson & Barghusen, 1986; van den Heever, 1994.)

Hopson & Barghusen (1986) noted a separate palatal housing for the lower canine as being a diagnostic feature for Akidnognathidae. A similar structure is present in cynodonts and *Bauria*, but differs from that of akidnognathids in that it is created by extensions of the secondary palate. Thus, *Moschorhinus* and *Euchambersia* have been coded '2' for this character, whereas the cynodont taxa (*Charassognathus*, *Dvinia* and *Procynosuchus*) and *Bauria* have been coded '3.'

37. Palatal processes of the maxillae are absent (0), form a well-developed crista choanalis with a ridge extending posteriorly onto the palatine (1), contact or nearly contact the ventrally extending vomer with no sutural connection (2); bear a moderately long sutural connection with the lateral margins of the vomer (3), or meet at the midline, sharing a sutural connection and obscuring most of the vomer on the palatal surface (4). (Modified from Hopson & Barghusen, 1986; van den Heever, 1994; Botha *et al.*, 2007.)

In the cynodont *Procynosuchus*, the incipient secondary palate shows a superficial resemblance to that of *Ictidosuchoides* and *Ictidosuchops*. However, it differs in the well-developed ventromedial processes of the palatines which nearly contact each other, and extends far below the vomer. On the other hand, the most basal cynodont *Dvinia* shows a completely closed secondary palate, more similar to that of *Ericiolacerta* and *Bauria*. It has also been suggested that the cynodont secondary palate closed in a posteroanterior direction, as opposed to the anteroposterior closure hypothesized for therocephalians (Maier, 1999; see character 105).

38. Portion of vomer separating the choanae is slightly bulbous, narrowing towards its contact with the premaxilla (0), expands anteriorly and is widest at its contact with the premaxilla (1), or bears specialized transverse processes just behind the contact with the premaxilla overlapping vomerial processes of the crista choanalis

(2). (From Hopson & Barghusen, 1986; van den Heever, 1994.)

Viatkosuchus, *Moschowhaitsia* and *Theriognathus* display a vomer that is expanded more posteriorly, as is the primitive condition for therapsids. However, this is a result of the derived nature of the lateral processes of the vomer in these taxa. Because of the nature of the lateral processes of the vomer, these taxa are coded '2' for this character.

39. Anterior-most portion of the vomer briefly contacts the vomerial process of the premaxilla (0) or broadly overlaps the ventral surface of the premaxilla (1). (From Hopson & Barghusen, 1986.)

Biarmosuchus and *Lycosuchus* are both coded '?' for this character, because they lack a well-defined vomerial process of the premaxilla.

40. Vomers paired (0), fused anteriorly (1) or completely fused (2). (From Rubidge & Kitching, 2003.)
41. Ventromedian crest between palatines on posterior portion of vomer absent (0) or present (1). (Modified from Kemp, 1972a; van den Heever, 1994.)
42. Palatine teeth present (0) or absent (1). (Modified from Sidor & Hopson, 1998; Rubidge & Kitching, 2003.)
43. Large suborbital vacuities bound by the palatine, pterygoid and ectopterygoid are absent in adults (0) or present throughout ontogeny (1). (Modified from Hopson & Barghusen, 1986.)
44. Pterygoid bears no median tubercle/crest (0) or a ventromedian tubercle/crest is present anterior to the interpterygoid vacuity (1). (Modified from van den Heever, 1994; Botha *et al.*, 2007.)

Contrary to Hopson & Barghusen (1986), a ventromedian process on the pterygoids is not restricted to eutherocephalian taxa, as it exists in lycosuchids and scylacosaurids as well (A. Huttenlocker, pers. observ.). Such a structure has been reported in the form of a tubercle in lycosuchids or as a crest in scylacosaurids (van den Heever, 1994). Like scylacosaurids, all eutherocephalians display this structure in the form of a crest.

45. Teeth on transverse processes of pterygoids present (0) or absent (1). (From van den Heever, 1994.)
46. Pterygoid flange expansion moderate (0), reduced (1) or sharp, posteriorly projecting wings with slight posterolateral expansion (2). (New.)

Except for *Euchambersia*, all of the therocephalians examined clearly show expanded pterygoid transverse flanges, nearly contacting the medial margins of the maxilla and jugal. *Euchambersia* is coded '1' for this character.

47. Pterygoid transverse flanges are positioned more anterior to the centre of the orbit (0) or more posterior to the centre of the orbit (1). (New.)
48. Ventral rim of pterygoid transverse flanges sweeps posteriorly at the midline vacuity (0) or does not sweep posteriorly at the vacuity (1). (Modified from van den Heever, 1994.)
49. Interpterygoid vacuity of adults present (0), absent/extremely reduced (1), enlarged and somewhat heart-shaped, with the anterior end positioned between the transverse flanges of the pterygoids (2). (Based on Kemp, 1972a.)
50. Epipterygoid separate from parietal (0) or contacts parietal (1). (From Modesto *et al.*, 1999.)
51. Epipterygoid ascending process appears as a thin rod (0), is slightly expanded anteroposteriorly (1) or is extremely expanded (2). (Modified from Kemp, 1972a; Hopson & Barghusen, 1986; Botha *et al.*, 2007.)

An expanded epipterygoid has been thoroughly discussed in cynodonts and whaitsiids (Kemp, 1972a; Hopson & Barghusen, 1986). However, Attridge (1956) noted an expanded epipterygoid as a diagnostic feature for *Mirotenthes*. The epipterygoid is also expanded in the 'hofmeyriid' *Hofmeyria* (which was placed in Whaitsiidae by Brink, 1956; Watson & Romer, 1956), but neither are as expanded as in the whaitsiid *Theriognathus*. Cynodontia and *Theriognathus* are coded '2' for this character.

52. Posterior apophysis of the epipterygoid contacting or nearly contacting the pro-otic absent (0) or present, enclosing an aperture presumably for the trigeminal nerve (1). (From Kemp, 1972a; Hopson & Barghusen, 1986.)
53. Laterally directed processes of the pro-otic participating in the pterygoparoccipital foramen absent (0) or present (1). (From Hopson & Barghusen, 1986.)
54. Basal tuber small (0) or large, approximately one-third the occipital breadth (1). (From van den Heever, 1994.)
55. Dorsal surface of the paroccipital process is relatively smooth or straight (0). or deeply hollowed (1) in the floor of the post-temporal fenestra. (From Hopson & Barghusen, 1986.)
56. Paroccipital process of the opisthotic orientation strongly posteroventral (0), moderately posteroventral (1). or transverse (2) relative to horizontal. (From Rubidge & Kitching, 2003.)
57. 'Mastoid process' absent or poorly developed (0) or squamosal and paroccipital processes of the

opisthotic form a distinct, posteriorly projecting 'mastoid process' (1). (Based on Crompton, 1955.)

58. Tabular contacts the opisthotic (0) or is withdrawn from contact with the opisthotic (1). (From Modesto *et al.*, 1999.)
59. Tabular extends below (0) or just barely contacts (1) the post-temporal fenestra. (Modified from Sidor & Hopson, 1998.)
60. Dorsal process of stapes present (0) or reduced/absent (1). (New.)

Viatkosuchus is coded '0' for this character, as reported by Tatarinov (1995a).

61. Overall dentary shape is best described as deep/robust (0), short and banana-shaped (1), or long, slender, and relatively straight with a smooth ventral edge (2). (Modified from Hopson & Barghusen, 1986; Sidor, 2003.)
62. Dentary deepens anteriorly (0) or continuously tapers to a narrow anterior edge (1). (Modified from Sidor, 2003.)
63. Symphyseal region of the dentary is only moderately expanded mediolaterally with a low mentum angulation in ventral view (0) or is anteroposteriorly thickened (1). (Based on Mendrez, 1974b.)
64. Lateral surface of the dentary is relatively smooth (0) or bears a marked constriction behind the canine (1) in dorsal and ventral views. (Based on Mendrez, 1974b.)
65. Dentary angle, lateral to the reflected lamina, is absent/rounded (0), moderate/sharp (1) or pronounced, protruding with an angle of < 120° (2). (New.)

Theriognathus has been coded both '0' and '1' for this character. From a large sample, most of the skulls examined showed a bowed dentary with a smooth ventral edge having no distinct angle. A few, relatively robust specimens displayed a dentary with a well-developed angle. This variation may be within the genus or even within a single species (i.e. sexual dimorphism; see Brink, 1980).

66. The posterodorsal terminal margin of the coronoid process is straight (0), more rounded (1) or comes to a sharp point (2). (Modified from Sidor, 2003.)
67. Coronoid process dorsal extent in adults terminates below middle of orbit (0) or in upper half of orbit (1). (From Sidor, 2003.)
68. Dentary height increased posteriorly and postdentary bones reduced to form a free standing coronoid process absent (0) or present (1). (Modified from Sidor & Hopson, 1998; Rubidge & Kitching, 2003.)
69. Postdentary bones' height relative to total dentary height equal (0), between one-half and equal (1) or much less than one-half (2). (Modified from Sidor & Hopson, 1998.).
70. Ventral margins of angular and dentary confluent (0) or angular (= tympanic) positioned dorsal to ventral margin of dentary (1). (From Hopson & Barghusen, 1986; Sidor & Hopson, 1998; Sidor, 2003.).
71. Splenial exposed laterally near symphysis (0) or obscured by dentary (1). (From Sidor & Hopson, 1998; Sidor, 2003.)

Although Sidor & Hopson (1998) coded all cynodont taxa as '1' in their data matrix, Sidor (2003) noted that the splenial is in fact laterally exposed in the basal cynodont *Procynosuchus*. *Procynosuchus* has been coded '0' for this character.

72. Mandibular fenestra absent (0), penetrating the mandible and visible laterally (1), or surangular above and prearticular below a small fenestra on the medial surface of the mandible (2). (Modified from Kemp, 1972a; Gauthier, Kluge & Rowe, 1988; Sidor & Hopson, 1998.)
73. Reflected lamina shape and ventral extent: rounded, projecting below the ventral margin of the dentary at about the level of the second groove (0), slightly anteroposteriorly elongate (spade-shaped) and does not appear to extend below the dentary (1), or is extremely reduced and spoon-shaped (2). (New.)
74. Interlocking incisors present (0) or absent (1). (Modified from Rubidge & Kitching, 2003; Sidor & Welman, 2003.)

Biarmosuchus and *Titanophoneus* have been coded '0' for this character, as their upper and lower incisors have been shown to interlock (King, 1988; Sigogneau-Russell, 1989; Rubidge & Kitching, 2003). Anomodontia has been coded '?', because of the highly specialized nature of the anomodont dentition. Although Kemp (1969) demonstrated that the upper and lower incisors of gorgonopsids would interlock if the lower jaw moved far forward, Laurin (1998) has shown that the well-braced quadrate–quadratojugal complex and lack of a streptostylic jaw joint prevented such movement. For this reason, Gorgonopsia has also been coded '?' for this character. Rubidge & Kitching (2003) suggested that the upper and lower incisors of scylacosaurids interlock. However, none of the scylacosaurids examined here show evidence of interdigitating incisors. van den Heever (1994) showed that the lower incisors fit comfortably behind the uppers and do not interlock when the jaw is closed. All of the therocephalian taxa (where the front of the snout and lower jaws are known) have been coded '1' for this character.

75. Upper incisors few, up to five (0), or numerous, more than five (1). (New.)
76. Upper incisors lack (0) or bear (1) longitudinal grooves. (From Hopson & Barghusen, 1986.)
77. Incisors relatively straight and conical (0) or spatulate, concave lingually with mesiolingual and distolingual crests (1). (From Hopson & Barghusen, 1986.)
78. Functional upper precanines in adults absent (0) or present (1). (Modified from Hopson & Barghusen, 1986; van den Heever, 1994; Botha *et al.*, 2007.)

Moschorhinus and *Euchambersia* are coded '0' for this character. Hopson & Barghusen (1986) observed a reduction from two precanines to one in akidnognathids. This observation, however, may be ontogenetic. Mendrez (1974a) described a subadult *Moschorhinus kitchingi* with a small precanine tooth. Durand (1991) published a revised description based on two new mature *M. kitchingi* specimens, showing no evidence of precanine teeth. Adult specimens of *Euchambersia* also show no precanine teeth (Boonstra, 1934; Brink, 1986). *Mirotenthes* and *Viatkosuchus* are coded '?' and this reasoning is described in the discussion (they may undergo a caniniform tooth replacement process similar to *Thrinaxodon* and *Theriognathus*, and thus may have fully developed adults lacking precanine teeth; see above). *Ictidosuchus* is coded '?' because the region of the maxilla just anterior to the dominant caniniform is unknown (Broom, 1932; Boonstra, 1935; Brink, 1986). *Ericiolacerta* is coded '?' because no distinct canine is present in the maxilla (Watson, 1931), possibly as a result of its immature or neotenic nature.

79. Upper dominant canine in adults large relative to maxillary height (0), medium (1) or extremely reduced (2). (From Rubidge & van den Heever, 1997.)
80. Deep pit or groove running vertically along the anterior surface of the dominant canine absent (0) or present (1). (New.)
81. Upper postcanines in adults numerous, more than five (0), few, five or less (1), or absent (2). (Modified from Kemp, 1972b; van den Heever, 1994.)

Lycosuchus and the sampled akidnognathids (*Olivierosuchus*, *Promoschorhynchus*, *Moschorhinus* and *Euchambersia*) demonstrate upper postcanine dentitions that are reduced from the plesiomorphic eutheriodont condition, and are coded '1.' Previous descriptions of *Mirotenthes* have shown the presence of only five postcanines (Attridge, 1956; Cys, 1971). Personal observation of the type specimen (UCMP 40467) has revealed evidence of a sixth alveolus, just behind the caniniform. Most of the crown is missing. Thus, *Mirotenthes* has been coded '0' as in other 'hofmeyriids.'

82. Lower canine in adults large (0), medium (1) or reduced (2). (Modified from Botha *et al.*, 2007.)
83. Postcanine teeth in lower jaw present (0) or absent (1). (New.)

Anomodontia has been coded '?' for this character because of the derived nature of the anomodontian dentition, which lacks lower caniniforms even in the known basal forms. Without the presence of a dominant lower caniniform tooth, the postcanine field could not be properly identified. *Theriognathus* and *Mirotenthes* are coded '1' for this character. The well-sampled genus *Theriognathus* lacks postcanine teeth in both the upper and lower jaws. The lower dentition of *Mirotenthes digitipes* has not been discussed in detail, but personal observation of the holotype (UCMP 40467) has revealed a complete absence of lower postcanines. *Hofmeyria* and *Viatkosuchus* have been coded '?' for this character as a result of dorsal compression of the lower jaw into the palate in the referred specimens (see Appendix 1). Tatarinov (1995a) did not describe the lower postcanine dentition of *Viatkosuchus*. Similarly, *Ictidosuchops* is coded as '?' for this character. Most of the data from the lower jaws of *Euchambersia* and *Regisaurus* could not be obtained in this analysis. Thus, these taxa have been coded '?' as well.

84. Sharp anterior process of the dorsal iliac plate (ischial tuber) absent (0) or present above a ventral concavity (1). (Based on Kemp, 2005.)
85. Pubis and ischium orientation relatively vertical (0) or more horizontal, forming a broad puboischiatic plate (1). (Based on Kemp, 2005.)
86. Obturator foramen size is small (0), moderately enlarged (1) or extremely enlarged (2). (From Sidor & Hopson, 1998.)
87. Distinct trochanter minor of the femur absent (0) or present (1). (Based on Kemp, 2005.)
88. Parietal crest located posteriorly (0) or extends forwards in adults to include the parietal foramen (1). (From Hopson & Kitching, 2001.)

Biarmosuchus, *Titanophoneus*, Gorgonopsidae and Anomodontia are coded '?' as they lack a sagittal crest altogether. *Viatkosuchus*, *Theriognathus*, *Regisaurus*, *Ericiolacerta* and *Bauria* are coded '?' as the parietal foramen appears to be absent either throughout ontogeny, or in adults of these taxa.

89. Nasal–lacrimal contact absent (0) or present (1). (From Hopson & Kitching, 2001; Botha *et al.*, 2007.)
90. Prefrontal–postorbital contact in adults absent (0) or present, excluding the frontal from the

dorsal margin of the orbit (1). (From Hopson & Kitching, 2001; Botha *et al.*, 2007.)

91. Palatal exposure of maxilla behind 'canine' less than (0) or greater than (1) 20% distance from 'canine' to posterior end of palatine. (From Hopson & Kitching, 2001.)

Anomodontia and *Ericiolacerta* are coded '?' for this character as homology of the caniniform is unclear in these taxa (especially in basal anomodonts).

92. Trigeminal nerve exit exists between pro-otic incisure and epipterygoid (0), via a foramen between the pro-otic and epipterygoid (1), or via multiple foramina (2). (From Hopson & Kitching, 2001.)

Viatkosuchus and *Theriognathus* are coded '1' for this character because of the presence of the single foramen. Cynodonts also show an enclosed foramen in this region ('trigeminal foramen'). According to Hopson & Barghusen (1986), however, the cynodont condition differs from *Theriognathus* in which the foramen is separately formed by the epipterygoid (not including the pro-otic), although this foramen has a whaitsiid-like structure in some cynognathian cynodonts (formed solely by the epipterygoid).

93. Posteroventral process on quadrate in posterior notch of squamosal absent (0) or present (1). (From Hopson & Kitching, 2001; Botha *et al.*, 2007.)

Hopson & Kitching (2001) used the derived character state as a synapomorphy for cynodonts based on its absence in *Lycosuchus* (their only representative taxon for Therocephalia). However, this feature is apparently present in the eutherocephalian genus *Theriognathus* (Botha *et al.*, 2007), which is coded '1' in the present analysis.

94. Epipterygoid (= alisphenoid)–pro-otic overlap absent (0) or present (1). (From Hopson & Kitching, 2001.)
95. Lateral flange of pro-otic absent (0) or present (1). (From Hopson & Kitching, 2001.)

There is a process in scylacosaurian therocephalians similar to the lateral pro-otic flange of cynodonts (Hopson & Kitching, 2001), but differing from that of cynodonts in that it is located more posteriorly where it articulates directly with an anteromedial process of the squamosal, enclosing the pterygoparoccipital foramen. All scylacosaurian taxa have been coded '?', as the homology of these structures is questionable. *Lycosuchus* is coded '?' because this region of the skull is poorly preserved in that taxon.

96. Epipterygoid–frontal contact absent (0) or present (1). (From Hopson & Kitching, 2001.)
97. Occipital condyle single (0) or double (1). (From Hopson & Kitching, 2001; Botha *et al.*, 2007.)
98. Stapedial foramen oriented posteroventrally (0), dorsoventrally (1) or reduced/absent (2). (Modified from Hopson & Kitching, 2001.)
99. Dentary masseteric fossa in adults absent (0), present high on coronoid process (1) or enlarged, extending to the ventral border of the dentary (2). (From Hopson & Kitching, 2001; Botha *et al.*, 2007.)
100. Reflected lamina of angular (= tympanic) size: large (0) or reduced (1). (Modified from Hopson & Kitching, 2001.)
101. Incisor cutting margins serrated (0), smoothly ridged (1) or denticulated (2). (From Hopson & Kitching, 2001.)
102. Postcanines lacking cusps (0) or having two or more cusps in line (1). (From Hopson & Kitching, 2001.)
103. Greatest width of zygomatic arches towards middle (0) or at the back (1) of the arch. (From Hopson & Kitching, 2001.)
104. Lower incisors number four (0) or less (1). (New.)
105. Formation of secondary palate occurs such that the posterior portion of the maxillae and palatines approach at the midline, but are slightly open anteriorly, thus creating an incipient incisive fissure or foramen (0), or the anterior portion is more closed than the posterior, leaving no indication of an incisive foramen (1). (Based on Maier, 1999.)

Biarmosuchus, *Titanophoneus*, Gorgonopsidae, Anomodontia and *Lycosuchus* are coded '?' for this character because basal representatives lack any indication of a secondary palate or crista choanalis.

106. Parasagittal ridges running from medial posterior flare of transverse flanges to basioccipital absent (0) or present (1). (Modified from van den Heever, 1994; Rubidge & Kitching, 2003.)

This character was adapted from Rubidge & Kitching (2003) in which the derived state was originally applied to burnetiid biarmosuchians. A similar morphology of the pterygoids is convergently present in all non-scylacosaurid therocephalians, including lycosuchids and eutherocephalians. Thus, these taxa are coded '1' for this character.

107. Upturning of alveolar margin of premaxilla moderate (0), absent/horizontal (1), exaggerated (2). (Adapted from Rubidge & van den Heever, 1997.)
108. Vomer anterior vault present (0) or absent (1). (Modified from Sidor & Hopson, 1998.)

The anterior vault is plesiomorphic for eutheriodonts, as it is present in other basal therapsid clades.

Sidor & Hopson (1998) coded its presence in Therocephalia (as it is present in the basal *Lycosuchus*) and the basal cynodonts *Dvinia*, *Procynosuchus* and Galesauridae. However, the authors noted its loss in post-galesaurid epicynodonts (e.g. *Thrinaxodon*). A similar loss is noted here within Scylacosauria (coded '1'), corroborated by van den Heever (1994), and supporting the observation that it was convergently lost in scylacosaurians and epicynodonts.

109. Area between left and right dentaries widens greatly posteriorly (0) or remains relatively long and narrow (almost slit-like) just posterior to symphyseal region (1). (New.)
110. Lateral sulcus along the ramus and coronoid process of the dentary, absent (0) or present (1). ('Longitudinal depression' of Botha *et al.*, 2007.)

APPENDIX 3

Character matrix of 110 craniodental and postcranial characters examined for phylogenetic analysis of 30 therapsid taxa, including 23 therocephalians (corresponding to characters in Appendix 2). Standard character states are '0–4', missing or inapplicable data are coded '?'

Biarmosuchus 00000000000000000000000000??000000000??0000000010?00000000000000??0000000000000000000?0000000000000000?00000

Titanophoneus 000000000001000000 2?0001000??10000000000000000000000000000000000??0000000000000000010?0000000000000000?02000

Gorgonopsia 00021000000000000000001000??11001110002000000000100000100000010020110000?000000000000?0000000000000000?00100

Anomodontia 00010?00000000100300000100??111001?0000010001100?0000010110001?0??000020?100?????0010?00?000000200?00??00000

Charassognathus ?0?111000001011001001011110?211011??????????????120????????01001001111101001000000???0?11?111?01?11101??0??0

Dvinia 00011100100010110010011111002110113?0021100111?01201?0200000100100111?2211010000000020111111111111110?001?00

Procynosuchus 00011100100010110010010111002110113?0021100111?01201?0200000100100111022110100000000201111111111111100001000

Lycosuchus 00011100000100110031000101100211011101?0011102110110?1?????100002001111201000000100????000000?002000011?10001

Glanosuchus 000211100000002003000010110021111111100111112111110100201110000100111120110000000011 1?000000?002000011100101

Ictidosaurus 00021110000000 20?3??0?11????21????11???????????????????????00002001111201100100000?????00???????000011?01?01

Pristerognathus 00021110000000200300001111002111111110011111211111010020 11?000010011112011000000001 11?000000?002000011100101

Olivierosuchus 11121100100001200301101111002111112111111111210011110121 00?00001001111101001100100????100000?00?001010110101

Promoschorhynchus 111211001000??2??3?1??11????211111211111111121001111012111?000010011111010?1100100????100000?00200?010110101

Moschorhinus 01111000000001100301111111002111112111111111210011110120 11?00111001??1101001000100????100000?00200?010110101

Euchambersia 01111??01100001100300111111002111112111?11011110011?10120???????????????????0010012??????100000?00200?01011010?

Mirotenthes 10011000001010110130010111110211111111?11111210011?101200011100011111111000?000111?1000?00??002001010?10110

Hofmeyria 10011000001010110130 0(01)0111110211111111011111121001 1?1012000111000 1
111111110100000?????000000??00200?010110110

Ictidostoma 10011000101010 1?01?0010111110211???1110111111 2100???????????11000101?
?1??1000000000????0000?????0?0??0?0110110

Viatkosuchus 100110001011101100300111111102111111120211111210011010120??001001?011
11111010?000???????00010??00200101?11010?

Moschowhaitsia 1001110010111??10030?11111???21????1120211111 2101????????????????????
?????0??0??0??????0000?????0?????1?1?01??

Theriognathus 1001110010111011003011111110021111111 20(12)1101121011211012000111 00
(01)1011111110100002011111?001111?002001?10110110

Ictidosuchus ?0011101000001 0?013001011110021111111 21??111?1210?1101012101?210001111
1111111010000?????0001?????0?0???1?11?1?1

Ictidosuchops 10011101100001020?3001011111?2111111210111111210211010 12111?210001111
11111100100000????100100??00?001010110101

Ictidosuchoides 1000110110000102013001011110021111112101111112102110101 21??1210001111
11111100110010????100100??002001010110101

Regisaurus 10001101000001020130011011101211111131011111121021111012111?2???01?1?
1????1?00?00??1111?0010?1?00???1?10110101

Lycideops ?0001101000001?2?1?001?1??1????????1310?111112?0?????????????210001?11
111111?0?10010?????001?0???0?011???1?0101

Tetracynodon 100010011000010212100 11?111?1?11111121011111121021101012011121000 1011
11111100?10020?????101000?002001010110101

Scaloposaurus 1000110100000102???001?0111?1?1111113101111112102110101 2111?210001011
11111?00?10010?????001001?00?001111110101

Ericiolacerta ?0011?011010100212 10011?111?1?11?11?4102111?12102????0?21???210000011
11?111?0?2??20111??00??????0?01?11?110?01

Bauria 10011100101010011230011111121211111341021111121 0211?1012101?210010111
11211000010 0?0?????001001?00?001110110?01

APPENDIX 4

List of character states supporting the monophyly of Therocephalia and the intrarelationship of major therocephalian subclades (from Appendices 2, 3)

THEROCEPHALIA (15 characters)

19. Posteroventral extension of the zygomatic arch just below the orbit slightly curved, having a distinctly concave ventral margin throughout its length (3).
36. Palatal fenestra for lower caniniform present and confluent with internal naris (1).
38. Portion of vomer separating the choanae expands anteriorly and is widest at its contact with the premaxilla (1). (From Hopson & Barghusen, 1986; van den Heever, 1994; specialized transverse bars contacting the maxilla are present in Whaitsiidae).
43. Large suborbital vacuities bound by the palatine, pterygoid and ectopterygoid are present throughout ontogeny (1). (Absent in adults of *Theriognathus* and *Euchambersia*.)
44. Pterygoid bears a ventromedian tubercle/crest anterior to the interpterygoid vacuity (1).
46. Pterygoid flange expansion produces sharp, posteriorly projecting wings with slight posterolateral expansion, nearly contacting the zygomatic arch (2). (Reduced in *Euchambersia*, as it is in cynodonts.)
51. Epipterygoid ascending process is slightly expanded anteroposteriorly (1). (Modified from Kemp, 1972a; Hopson & Barghusen, 1986; extremely expanded in *Theriognathus* and Cynodontia, which were coded '2'.)
60. Dorsal process of stapes reduced/absent (1). (Apparently present in *Viatkosuchus*, as reported by Tatarinov, 1995a.)

71. Splenial laterally obscured by dentary (1). (From Sidor & Hopson, 1998; Sidor, 2003; either conv. in non-*Procynosuchus* cynodonts or plesiomorphic for Eutheriodontia with a primitive reversal in *Procynosuchus*, which displays a laterally exposed splenial and is coded '0'.)
84. Sharp anterior process of the dorsal iliac plate (ischial tuber) present above a ventral concavity (1).
85. Pubis and ischium orientation slightly horizontal, forming a broad puboischiatic plate (1).
87. Distinct trochanter minor of the femur present (1).
98. Stapedial foramen reduced/absent (2). (Modified from Hopson & Kitching, 2001; conv. in Anomodontia; *Viatkosuchus* is coded '0' for this character, as reported by Tatarinov, 1995a.)
103. Greatest width of zygomatic arch is at the back of the arch (1). (From Hopson & Kitching, 2001; conv. in cynognathian cynodonts.)
110. Lateral dentary sulcus extending from the coronoid process to the ramus present (1). (Shallow, but present in lycosuchids and scylacosaurids, as observed by van den Heever, 1994; completely absent in some non-akidnognathid 'whaitsioids' and coded '0' for those taxa.)

SCYLACOSAURIA (six characters)

33. Medially directed process of the squamosal contacting the pro-otic present, enclosing the pterygoparoccipital foramen (1).
37. Palatal processes of the maxillae are present, forming a well-developed crista choanalis with a ridge extending posteriorly onto the palatine (1).
41. Ventromedian crest between palatines on posterior portion of vomer present (1). (Modified from Kemp, 1972a; van den Heever, 1994; conv. in cynodonts.)
45. Teeth absent from transverse processes of pterygoids (1). (From van den Heever, 1994; conv. in cynodonts.)
105. Anterior portion of the crista choanalis/bony secondary palate is more closed than the posterior portion, leaving no indication of an incisive foramen or fissure (1). (Lycosuchids lack a distinct crista choanalis, and the secondary palate of cynodonts closes posteroventrally, leaving an anterior incisive foramen or fissure. Thus, only scylacosaurian therocephalians demonstrate the phenomenon as described above; discussed in more detail by Maier, 1999.)
108. Vomer anterior vault absent (1).

Scylacosauridae (six characters)

4. Rostrum is moderately long and about as high as it is broad (2).
7. A shallow preorbital depression anterior to a thickened ridge on the anterior margin of the orbit is present, extending anteroventrally from the lacrimal to the canine buttress of the maxilla (1).
15. Orbit positioned relatively high, elevated to or above the dorsal temporal margin (0). (Reversal to the primitive therapsid condition; conv. in baurioids.)
16. Anterior border of orbit located on transverse midline of skull (2). (Modified from van den Heever, 1994; conv. in *Olivierosuchus*, *Promoschorhynchus* and baurioids.)
49. Interpterygoid vacuity of adults extremely reduced (1). (From Kemp, 1972a; conv. in *Theriognathus*.)
75. Upper incisors numerous, more than five (1). (Conv. in Anomodontia, non-*Charassognathus* cynodonts and all baurioids except *Bauria*.)

EUTHEROCEPHALIA (11 characters)

1. Anterodorsal-most tip of premaxilla forms a rostral process, overhanging incisors (1). (Absent in *Euchambersia* and adult specimens of *Moschorhinus*.)
15. Orbit positioned relatively low in the skull (1). (Positioned high in baurioid eutherocephalians; conv. in cynodonts.)
22. Postfrontal absent (1). (From Hopson & Barghusen, 1986; Sidor, 2001; polymorphic in the holotype of *Hofmeyria* being present on only one side, F. Abdala, University of Witwatersrand, Johannesburg, pers. comm., 2006; conv. in cynodonts.)
40. Vomers are unpaired and have either fused anteriorly (1) or completely fused (2). (From Hopson & Barghusen, 1986; Rubidge & Kitching, 2003; convergently fused in cynodonts.)
55. Dorsal surface of the paroccipital process is deeply hollowed (1) in the floor of the post-temporal fenestra.
58. Tabular is withdrawn from contact with the opisthotic (1). (Contacts opisthotic in non-akidnognathid 'whaitsioids', *Ictidosuchus* and *Bauria*.)
59. Tabular just barely contacts the post-temporal fenestra (1). (Extends below in non-akidnognathid 'whaitsioids'.)
72. Mandibular fenestra present, penetrating the mandible and visible laterally (1).
101. Incisor cutting margins smoothly ridged (1). (From Hopson & Kitching, 2001; conv. in cynodonts.)
104. Lower incisors number four (0). [The typical condition for early Late Permian eutheriodonts (including *Charassognathus*, lycosuchids and scylacosaurids) is less than four lower incisors, a

possible synapomorphy for the clade Eutheriodontia. Thus, the addition of an extra lower incisor is interpreted as a primitive reversal for eutherocephalians to the primitive therapsid condition. It is important to note, however, that there are fewer than four incisors in the Triassic *Scaloposaurus* (coded '1') and that many non-*Charassognathus* cynodonts share the condition of four lower incisors (coded '0') with eutherocephalians. Thus, the present utility of this character as a synapomorphy for Eutherocephalia may be equivocal.]

106. Parasagittal ridges running from medial posterior flare of transverse flanges to basioccipital present (1). (From van den Heever, 1994; Rubidge & Kitching, 2003; conv. in *Lycosuchus*.)

Akidnognathidae (eight characters)

2. Septomaxilla is enlarged and well exposed outside of the external naris, broadly overlapping the premaxilla anteriorly (1).
3. External nares are enlarged, close-set and face anteriorly (1).
21. Median fronto-nasal crest present (1). (Absent in *Euchambersia*; conv. in *Theriognathus*.)
36. A separate palatal housing for the lower canine is created by an extension of the premaxilla and maxilla (2).
39. Anterior-most portion of the vomer broadly overlaps the ventral surface of the premaxilla (1).
77. Incisors relatively spatulate, concave lingually with mesiolingual and distolingual crests (1). (From Hopson & Barghusen, 1986; conv. in cynodonts.)
81. Upper postcanines in adults few, five or less (1) or completely absent (2). (Modified from Kemp, 1972b; van den Heever, 1994; conv. in lycosuchids and *Theriognathus*, which also appear to have reduced the postcanine dentition.)
88. Parietal crest extends forward in adults to include the parietal foramen (1). (From Hopson & Kitching, 2001; conv in cynodonts, *Ictidosuchops* and *Ictidosuchoides*.)

Olivierosuchus + *Promoschorhynchus* (two characters)

57. Squamosal and paroccipital processes of the opisthotic form a distinct, posteriorly projecting 'mastoid process' (1). (Modified from Crompton, 1955; conv. in baurioids.)
78. Functional upper precanines in adults present (1). (Modified from Hopson & Barghusen, 1986; van den Heever, 1994.)

NON-AKIDNOGNATHID 'WHAITSIOIDS' + BAURIOIDEA (four characters)

18. Postorbital bar extremely slender (1) or absent (2). (Except in the derived whaitsiids where it is moderately robust.)
62. Dentary continuously tapers to a narrow anterior edge (1). (Modified from Sidor, 2003; conv. in some cynodonts.)
66. The posterodorsal terminal margin of the coronoid process is rounded (1). (Modified from Sidor, 2003; straight in *Ericiolacerta* and *Bauria*.)
73. Reflected lamina shape and ventral extent: slightly anteroposteriorly elongate (spade-shaped) and does not extend ventrally below the dentary (1).

Non-akidnognathid 'whaitsioids' (seven characters)

11. Posterior region of the maxillary facial plate is folded inward onto the palatal region, so that the maxilla is well exposed ventrally just anterior to the orbit (1). (Conv. in *Ericiolacerta* and *Bauria*.)
13. Suborbital bar is laterally expanded, contributing to a pronounced degree of orbital convergence (i.e. orbits facing forward and appearing more triangular than oval in dorsal view) (1). (Conv. in cynodonts; *Ericiolacerta* and *Bauria* have also been coded '1' because of the apparent expansion of the suborbital bar, but differ from 'whaitsioids' in that the orbits are placed high within the skull as in other baurioids and do not appear triangular in dorsal view.)
28. Parietal crest short, less than half the temporal fenestra length (1). (Conv. in *Ictidosuchops*; long in the whaitsiid *Theriognathus*.)
58. Tabular contacts the opisthotic (0). (Interpreted as a reversal to the primitive therocephalian condition; conv. in *Ictidosuchus* and *Bauria*.)
59. Tabular extends below the post-temporal fenestra (0). (Interpreted as a reversal to the primitive therocephalian condition.)
61. Overall dentary shape is short and banana-shaped (1). (Banana-shaped in small specimens of *Theriognathus*, but more robust with a steep angle in larger specimens.)
110. Lateral dentary sulcus extending from the coronoid process to the ramus absent (0). (Interpreted as primitive reversal.)

Hofmeyria/*Mirotenthes* + Whaitsiidae (one character)

83. Postcanine teeth in lower jaw absent (1). (Absent in *Mirotenthes*, *Theriognathus* and, possibly, *Hofmeyria*, although the condition is uncertain in *Viatkosuchus* and *Moschowhaitsia*.)

Whaitsiidae, including *Viatkosuchus* (nine characters)

12. Suborbital bar deep (1). (Conv. in *Lycosuchus*.)
18. Postorbital bar moderately well-built (0). (Interpreted as a reversal to the primitive therocephalian condition.)
23. Parietal (= pineal) opening in adults absent/extremely reduced (1). (Conv. in *Dvinia*, *Euchambersia* and derived baurioids.)
38. Portion of vomer separating the choanae bears specialized transverse processes just behind the contact with the premaxilla overlapping vomerial processes of the crista choanalis (2).
40. Vomers completely fused (2). (From Rubidge & Kitching, 2003.; conv. in cynodonts, *Ericiolacerta* and *Bauria*; polymorphic in *Theriognathus*, with some specimens only partially fused.)
65. Dentary angle, lateral to the reflected lamina. is moderate/sharp (1). [Interpreted as a reversal to the primitive eutheriodont condition (shared with cynodonts, lycosuchids, scylacosaurids and akidnognathids, but not 'hofmeyriids' or most baurioids); conv. in *Bauria*; *Theriognathus* has been coded both '0' and '1' for this character. This variation may be within the genus or even within a single species (i.e. sexual dimorphism; see Brink, 1980).]
67. Coronoid process dorsal extent in adults terminates below middle of orbit (0). (From Sidor, 2003; interpreted as primitive reversal; conv. in *Ictidostoma* and derived baurioids.)
76. Upper incisors bear longitudinal grooves (1). (From Hopson & Barghusen, 1986; conv. in *Mirotenthes* and *Ictidosuchus*; however, this character may be more widespread within Eutherocephalia as suggested by Hopson & Barghusen, 1986.)
92. Trigeminal nerve exits via a foramen between the pro-otic and epipterygoid (1).

Moschowhaitsia + *Theriognathus* (one character)

49. Interpterygoid vacuity of adults absent/extremely reduced (1). (From Kemp, 1972a; conv. in scylacosaurids.)

BAURIOIDEA (ten characters)

8. Maxillary facial plate low with a height less than 40% its length (1).
14. Long, low rostrum just anterior to orbital region present (1). (Absent in *Ericiolacerta* and *Bauria*, as a result of their relatively abbreviated rostrum.)
15. Orbit positioned relatively high, elevated to or above the dorsal temporal margin (0). (Interpreted as a reversal to the primitive therapsid condition.)
16. Anterior border of orbit located on transverse midline (2). (Modified from van den Heever, 1994; conv. in scylacosaurids and some akidnognathids; located in anterior half of skull in *Bauria*.)
37. Palatal processes of the maxillae contact or nearly contact the ventrally extending vomer (2); bear a moderately long sutural connection with the lateral margins of the vomer (3), or meet at the midline, sharing a sutural connection and obscuring most of the vomer on the palatal surface (4). (Modified from Hopson & Barghusen, 1986; van den Heever, 1994.)
49. Interpterygoid vacuity of adults enlarged and somewhat heart-shaped, with the anterior end positioned between the transverse flanges of the pterygoids (2). (Based on Kemp, 1972a; Colbert & Kitching, 1981.)
57. Squamosal and paroccipital processes of the opisthotic form a distinct, posteriorly projecting 'mastoid process' (1). (Modified from Crompton, 1955; conv. in *Olivierosuchus* and *Promoschorhynchus*.)
61. Overall dentary shape is long, slender and relatively straight with a smooth ventral edge (2).
75. Upper incisors numerous, more than five (1). [There are typically six upper incisors in baurioids (conv. in some scylacosaurids), except in *Bauria*, where the incisors are reduced to four; all other eutherocephalians have five upper incisors.]
91. Palatal exposure of maxilla behind canine greater than 20% distance from canine to posterior end of palatine (1). (From Hopson & Kitching, 2001; conv. in *Theriognathus* and cynodonts.)

(*Lycideops* + (*Regisaurus* + *Scaloposaurus*)) + (*Tetracynodon* + (*Ericiolacerta* + *Bauria*)) (four characters)

23. Parietal (= pineal) opening absent/extremely reduced (1). (Modified from Rubidge & van den Heever, 1997.)

29. Posterodorsal inclination of the temporal region absent (1).
37. Palatal processes of the maxillae are extremely well developed, contacting and sharing a connection with the vomer (3) or contacting each other at the midline (4). (Modified from Hopson & Barghusen, 1986; sutural connection absent in *Tetracynodon*.)
79. Upper caniniform reduced in size (1). (Extremely reduced in *Ericiolacerta*; also in *Ictidosuchoides*.)

***Lycideops* + (*Regisaurus* + *Scaloposaurus*) (two characters)**

9. Concave ventral step in maxillary facial plate between caniniform(s) (or anterior-most maxillary teeth) and incisors present (0). (Interpreted as a primitive reversal; conv. in *Ictidosuchus* among baurioids.)
37. Palatal processes of maxillae share a sutural connection with the lateral margin of the vomer (3).

***Regisaurus* + *Scaloposaurus* (one character)**

24. Temporal fenestra subequal to orbit in size (0). (Modified from Rubidge & Kitching, 2003.)

***Tetracynodon* + (*Ericiolacerta* + *Bauria*) (four characters)**

17. Postorbital process of jugal absent (1).
18. Postorbital bar absent or unossified (2).
19. Posteroventral extension of the zygomatic arch just below the orbit is absent, the zygomatic arch is relatively straight (1). (Modified from Rubidge & van den Heever, 1997; Rybczynski, 2000; present and concave posteriorly in *Bauria* as in other therocephalians.)
82. Lower canine reduced in size (1).

***Ericiolacerta* + *Bauria* (six characters)**

4. Rostrum short and broad (1). (Rostrum is typically elongate in other baurioids, so this is interpreted as a reversal to the primitive eutherocephalian condition.)
11. Posterior region of the maxillary facial plate is folded inward onto the palatal region, so that the maxilla is well exposed ventrally just anterior to the orbit (1). (Conv. in non-akidnognathid ‘whaitsioids’.)
13. Suborbital bar is laterally expanded, contributing to a pronounced degree of orbital convergence (1). (Conv. in cynodonts and non-akidnognathid ‘whaitsioids’.)
14. Dorsal margin of rostrum is high and straight anterior to the orbit, rather than long and low-lying (0). (The rostrum is long and low in all other baurioids, so the condition in *Ericiolacerta* and *Bauria* is interpreted as a primitive reversal.)
37. Palatal processes of maxillae meet at midline, obscuring part of the vomer (4).
102. Postcanines having two or more cusps in line (1). (Conv. in cynodonts and *Scaloposaurus*.)