The oldest cynodont: new clues on the origin and early diversification of the Cynodontia

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Early mammaliaforms and their extinct relatives, nonmammaliaform cynodonts, have long been the focus of intense research in attempting to unravel how and when major changes toward mammalness occurred. The earliest well-known representatives of cynodonts are latest Late Permian in age. Here, we describe **Charassognathus gracilis gen. et sp. nov.**, from the early Late Permian of South Africa, representing the oldest cynodont yet found. This specimen displays a notch on the dentary in the same location as the base of the masseteric fossa in the basal cynodonts *Procynosuchus* and *Dvinia*, and represents the first indication in theriodonts of an invasion of occlusal musculature onto the dentary. A phylogenetic analysis of seven therocephalians and ten non-mammaliaform cynodonts and equally weighted characters resulted in nine most parsimonious trees, the strict consensus of which shows a basal polytomy in cynodonts, including *Charassognathus*, *Dvinia*, *Procynosuchus* and a clade including the remaining cynodonts. The basal polytomy in the majority rule consensus tree is reduced, as *Procynosuchus* and *Dvinia* form a clade. One most parsimonious tree, from an analysis using implied weights, positions *Charassognathus* as the most basal cynodont. This result implies that the Cynodontia initially diversified in Permian Gondwana, in what is now southern Africa. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **149**, 477–492.

ADDITIONAL KEYWORDS: Karoo Basin – non-mammaliaform cynodont – Permian – South Africa.

INTRODUCTION

The Cynodontia has long been recognized as a crucial therapsid group because it includes mammals as its extant subclade (Rubidge & Sidor, 2001). Extinct members of the group form a paraphyletic assemblage known as non-mammaliaform cynodonts and represent the stage at which many mammalian characteristics first appeared in therapsids. The earliest cynodont records are known from the latest Late Permian and include the genera *Procynosuchus* from South Africa, Tanzania, Germany and Russia (Kemp, 1979; Sues & Boy, 1988; Rubidge, 1995; Tatarinov, 2004), *Cynosaurus* and *Nanictosaurus* from South Africa (Rubidge, 1995; Van Heerden & Rubidge, 1990), and *Dvinia*, *Uralocynodon* and *Nanocynodon* from Russia (Tatarinov, 1968, 1987; Battail & Surkov,

2000). *Procynosuchus* is traditionally recognized as the earliest known cynodont (Rubidge & Sidor, 2001; Sidor & Smith, 2004) ranging from the base to the top of the *Dicynodon* Assemblage Zone [AZ] (Wuchiapingian–Changhsingian) in South Africa (Rubidge, 1995; Sidor & Smith, 2004) and in biostratigraphically equivalent levels in East Africa, western Germany (von Huene, 1950; Kemp, 1979; Sues & Boy, 1988) and Russia (= *Cyrbasiodon*; Tatarinov, 2004). A new cynodont from the older *Tropidostoma* AZ (early Late Permian) described here indicates a South African origin for cynodonts.

MATERIAL AND METHODS

The specimen described herein, SAM-PK-K10369 (in the collections of the Iziko: South African Museum, Cape Town, South Africa), consists of a complete, laterally compressed skull, a partially preserved axis and

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third cervical vertebra, and articulated femur, tibia and fibula. Institutional abbreviations and specimens of the therocephalians and basal cynodonts studied for comparative purposes are presented in Appendices 1 and 2, respectively.

A cladistic analysis using the program TNT (Goloboff, Farris & Nixon, 2003) was performed to determine the phylogenetic position of *Charassognathus*. A data matrix was constructed for 59 cranio-dental characters and 18 theriodont taxa. *Cyonosaurus*, 'one of the rare gorgonopsian skulls to have been thoroughly studied' (Sigogneau-Russell, 1989: 83), was used to root the cladograms. In addition to ten cynodont taxa, seven therocephalian taxa were included in the analysis, as Therocephalia is a sister group of the Cynodontia. A heuristic search was performed with all characters having equal weights. This search consisted of ten random addition sequences (ten Wagner trees randomizing the order of the terminals) and tree-bisection-reconnection swapping, storing ten trees per replication. The run was performed with collapsing rule one (Coddington & Scharff, 1994), which collapses branches with ambiguous support. Increasing the number of replicates did not change the result obtained. A second analysis was performed with similar settings, but using implied weights (Goloboff, 1993). The weighting was made by means of a constant of concavity K. A possible outcome is the decrease in the number of most parsimonious trees by reducing the influence of homoplastic characters. Characters showing many extra steps in the most parsimonious trees are thus down-weighted in relation to the characters that better fit those trees. Analyses were performed with the constant of concavity set at intermediate and low values.

Material examined and literature consulted for each taxon included in the cladistic analysis is presented in Appendix 2, the list of characters and data matrix in Appendix 3, and unambiguous synapomorphies for nodes of the most parsimonious tree obtained with implied weights are presented in Appendix 4.

SYSTEMATIC PALAEONTOLOGY

THERAPSIDA BROOM, 1905
CYNODONTIA OWEN, 1861
***CHARASSOGNATHUS GRACILIS* GEN. ET SP. NOV.**

Diagnosis: This new cynodont is distinguished by the presence of a small notch in the base of the coronoid process, located in a similar position to the base of the masseteric fossa in *Dvinia* and *Procynosuchus*. The angle of the dentary is prominent, appearing more developed than in *Procynosuchus* and *Dvinia*, but less so than in *Nanictosaurus*. The dental formula is ?4·1· 8/3·1·?, and it is distinguished from *Procynosuchus*

and *Dvinia* by the absence of maxillary precanine teeth. The anterior postcanines have a single high cusp in labial view, whereas the posterior postcanines exhibit a main cusp directed slightly backward, and tiny anterior and posterior accessory cusps, with the anterior accessory cusps positioned slightly higher than the posterior accessory cusps.

Comments: The combined presence of the following characters indicates that *C. gracilis* is a cynodont: multicuspidated postcanines; groove in the squamosal for the quadratojugal; two occipital condyles; elongated ascending process of the epipterygoid; frontal excluded from the orbital margin; prominent angle of the dentary; reflected laminar of the angular with small lateral crests and femoral head set off dorsally from the shaft (see Description for more details).

Holotype: SAM-PK-K10369 consists of a complete skull with lower jaw in occlusion, the axis, third cervical vertebra, ?cervical ribs and a few indeterminate bones. Associated material includes a right articulated femur, tibia and fibula.

Etymology: Greek, *charasso*, prefix meaning 'notch' and *gnathus*, 'jaw', referring to the characteristic notch on the dentary. The specific epithet, *gracilis*, Latin, meaning 'slender', refers to the delicate nature of the specimen.

Locality and horizon: The specimen was found in a roadside cutting of highway R353 in Teekloof Pass, between the towns Leeu Gamka and Fraserburg in the Beaufort West District, Western Cape Province, South Africa. The locality lies on the farm Willowdene, a portion of Beato 238 (Fig. 1); exact coordinates are given in the Iziko South African Museum. It is stratigraphically positioned in the upper half of a thick mudrock-dominated succession of fluvio-lacustrine strata, known locally as the Hoedemaker Member of the Teekloof Formation (Rubidge, 1995; Figs 1A, 2A), which is considered to be early Late Permian (Wuchiapingian) in age (Catuneanu *et al*., 2005). The few laterally extensive sandstone bodies in the Hoedemaker Member (Fig. 2B) are interpreted as having been deposited as amalgamated point bars within high-sinuosity Mississippi-sized meandering rivers (Smith, 1987). Most of the vertebrate fossils are found in the thick greenish-grey massively bedded siltstone with minor mudstone intercalations that occur between the main channel sandstones. These sediments occur in 5–10-m-thick coarsening-upward sequences interpreted as prograding crevasse splay sequences. They were laid down by repeated overbank flood events emanating from the channel banks and ponding in the lowland flood basins. The new cynodont specimen was recovered from a 0.25-m-thick lens of fissile, dark purple, mudstone on a parting between two 1-m-thick
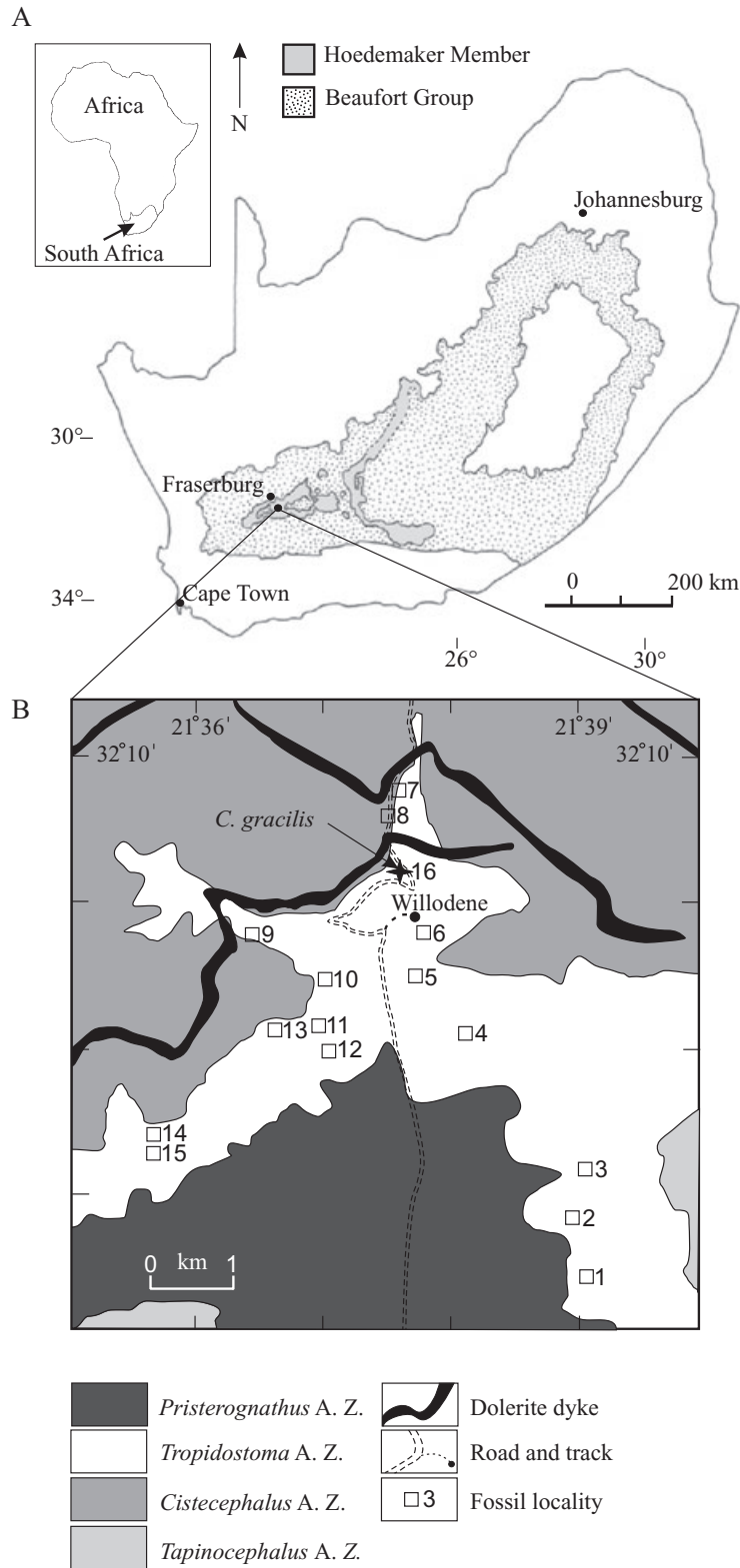
Figure 1. A, map of South Africa showing the extent of the Hoedemaker Member in the Beaufort Group; B, detailed map showing fossiliferous localities of the *Tropidostoma* Assemblage Zone, including the locality where **Charassognathus gracilis gen. et sp. nov.**, SAM-PK-K10369, was found (star, locality 16; for additional information on material found in these localities see Table 1).

A

CHRONO.		BIO.	LITHO.	
Epoch	Stage	AZ	FM.	MEM.
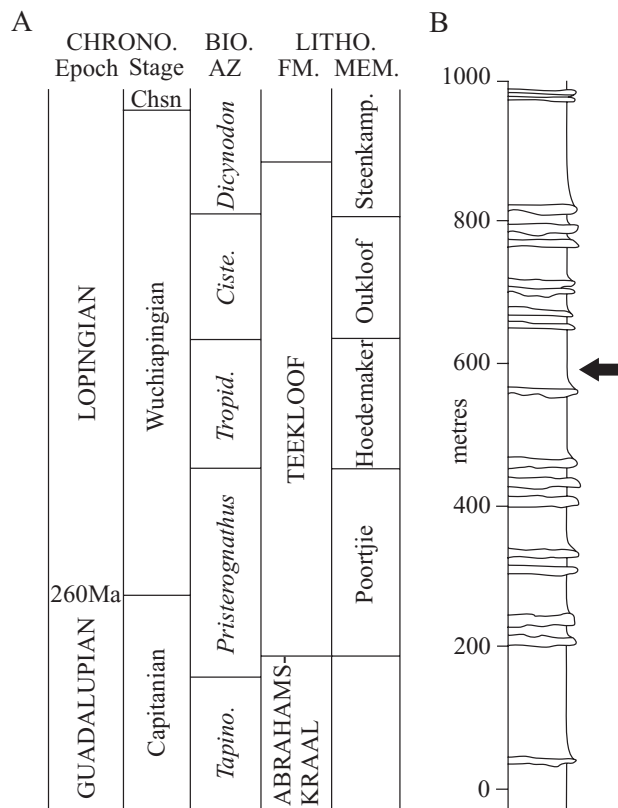
Figure 2. A, chronostratigraphic, lithostratigraphic and biostratigraphic chart of the Permian section of the Beaufort Group; B, sedimentological section of the locality showing the occurrence of ***Charassognathus gracilis* gen. et sp. nov.**, SAM-PK-K10369 (arrow). Abbreviations: AZ, Assemblage Zone; BIO., biostratigraphy; CHRONO., chronostratigraphy; Chsn, Changhsingian; *Ciste.*, *Cistecephalus*; FM., Formation; LITHO., lithostratigraphy; MEM., Member; Steenkamp., Steenkampsberg; *Tapino.*, *Tapinocephalus*; *Tropid.*, *Tropidostoma*.

beds of massive grey siltstone with purple mottles. The massive siltstones contain scattered oblate pedogenic carbonate nodules and are interpreted as proximal floodplain deposits laid down at the base of the meanderbelt slope. The fissile mudstone interlayer in which the study specimen was found is interpreted as a small pond deposit within the splay sequence.

Numerous skulls and skeletons of *Diictodon galeops*, along with other dicynodonts, namely *Oudenodon baini*, *Emydops minor* and *Pristerodon mackayi*, and, most significantly, the biozone indicator fossil *Tropidostoma microtrema* were collected from nearby outcrops (see Fig. 1B and Table 1). The gorgonopsians *Lycaenops ornatus* and *Cyonosaurus longiceps*, the therocephalian *Ictidosuchoides longiceps* and a new burnetiamorph comprise the carnivore fossil fauna collected in the vicinity. The presence of *Tropidostoma*

as well as the abundant *Diictodon galeops*, and the absences of *Pristerognathus*, which characterizes the underlying zone, and *Cistecephalus* and *Aulacephalodon* from the succeeding biozone, biostratigraphically positions this specimen in the upper half of the 180-m-thick *Tropidostoma* Assemblage Zone (Rubidge, 1995).

DESCRIPTION

The skull is complete and well preserved, albeit laterally compressed (Fig. 3A). The snout is slightly shorter (23 mm) than the temporal region (26 mm), which differs from therocephalians and other Late Permian cynodonts (e.g. *Procynosuchus* and *Nanictosaurus*) in which the snout is longer than the temporal region. The latter condition is observed even in juvenile *Procynosuchus* specimens.

The left premaxilla is absent and incompletely preserved on the right side of the snout. The facial process of the septomaxilla is anteroposteriorly wide, a condition that contrasts with that seen in other cynodonts, but is observed in various therocephalians (e.g. *Ictidosuchops*: BP/1/218, *Glanosuchus*: Van den Heever, 1994: fig. 1). Two upper incisors are present on the right side interdigiting with the lower incisors. The preserved incisors are interpreted as the second and fourth uppers and the first and third lowers (Fig. 3B). The portion of premaxilla that is not preserved is assumed to have lodged one more upper tooth. Four upper and three lower incisors is a condition widely distributed in many cynodonts, including most of the South African Late Permian forms. Precanines are absent and instead a diastema between the last incisor and the canine is present and accommodates the lower canine. Absence of precanines is common in most cynodonts apart from *Procynosuchus* and *Dvinia* (Tatarinov, 1968; Kemp, 1979).

The maxilla accommodates a large upper canine and seven postcanines. There is a space between the upper canine and the first postcanine on each side of the jaw, suggesting that another postcanine was lodged here (an alveolus is present on the right side). The canines are proportionately larger than those of *Procynosuchus* specimens of equivalent size. The two anteriormost postcanines are simple and lack accessory cusps, whereas the succeeding postcanines have a high main cusp and tiny anterior and posterior accessory cusps. These accessory cusps are similar in size, although the anterior accessory cusps are located slightly higher on the crown than the posterior accessory cusps. The main cusps of the postcanines decrease in height towards the back of the tooth row. There are two and three lower postcanines preserved on the right and left sides, respectively. The postcanines in *Charassognathus* differ from those of most

Table 1. Localities and taxonomic identification of fossils from the Teekloof Pass between the towns Leeu Gamka and Fraserburg in the Beaufort West District, Western Cape Province. The Hoedemaker Member of the Beaufort Group outcrops in these localities (see Fig. 1)

Locality (see Fig. 1)	Identification
1	*Diictodon galeops* (SAM-PK-K6820)
2	2 *Diictodon galeops* (SAM-PK-K6818, K6819)
3	*Diictodon galeops* (SAM-PK-K6817)
4	4 *Diictodon galeops* (SAM-PK-K6821, K6822, K6827, K6887)
	2 Dicynodontia (SAM-PK-K6823, K6826)
	Emydops minor (SAM-PK-K6824)
	Pristerodon mackayi (SAM-PK-K6825)
5	*Oudenodon baini* (SAM-PK-K6834)
	Lycaenops ornatus (SAM-PK-K6835)
6	4 *Diictodon galeops* (SAM-PK-K6828, K6829, K6831, K6832)
	Dicynodontia (SAM-PK-K6830)
	Emydops minor (SAM-PK-K6833)
7	*Pristerodon mackayi* (SAM-PK-K8301)
	Diictodon galeops (SAM-PK-K8306)
8	15 *Diictodon galeops* (SAM-PK-K6763, K6765-K6778)
	Dicynodontia (SAM-PK-K6764)
9	6 *Diictodon galeops* (SAM-PK-K6754, K6755, K6757, K6759, K6761, K6762)
	Tropidostoma microtrema (SAM-PK-K6756)
	2 Dicynodontia (SAM-PK-K6758, K6760)
10	22 *Diictodon galeops* (SAM-PK-K6782-K6794, K6798, K6799, K6801, K6803-K6807, K6816)
	5 *Tropidostoma microtrema* (SAM-PK-K6795, K6796, K6797, K6808, K6809)
	Oudenodon baini (SAM-PK-K6800)
	Cyonosaurus longiceps (SAM-PK-K6802)
11	*Emydops minor* (SAM-PK-K6779)
	Dicynodontia (SAM-PK-K6780)
	Diictodon galeops (SAM-PK-K6781)
12	15 *Diictodon galeops* (SAM-PK-K6652-K6654, K6656, K6658-K6663, K6665-K6669)
	Burnetiamorpha (SAM-PK-K6655)
	Tropidostoma microtrema (SAM-PK-K6657)
	Dicynodontia (SAM-PK-K6664)
	Ictidosuchoides longiceps (SAM-PK-K6670)
13	*Tropidostoma microtrema* (SAM-PK-K6671)
	7 *Diictodon galeops* (SAM-PK-K6672, K6675-K6680)
	Dicynodontia (SAM-PK-K6673)
	Pristerodon mackayi (SAM-PK-K6674)
14	*Ictidosuchoides longiceps* (SAM-PK-K6681)
	3 *Diictodon galeops* (SAM-PK-K6682-K6684)
15	5 *Diictodon galeops* SAM-PK-K6685, K6687, K6688, K6690, K6691)
	Pristerodon mackayi (SAM-PK-K6686)
	Dicynodontia (SAM-PK-K6689)
	Oudenodon baini (SAM-PK-K6692)
16	**Charassognathus gracilis gen. et sp. nov.** (SAM-PK-K10369)

therocephalians, which usually have a single cusp. However, at least two therocephalians are known to exhibit a more complex crown in the postcanines: the accessory cusps of *Scaloporhinus angulorugatus* (Mendrez, 1967) are virtually indistinguishable from the main cusp in lateral view, whereas the central and accessory cusps of *Ericiolacerta parva* are similarly developed (Crompton, 1962). The therocephalian *Bauria* also shows a more complex postcanine crown pattern, but only one cusp can be seen in labial view (Crompton, 1962; King, 1996). The morphology of the posterior postcanines of *Charassognathus* in labial view is most similar to that of *Nanictosaurus* (Van Heerden, 1976; Van Heerden & Rubidge, 1990), although the latter genus has more prominent accessory cusps that are more strongly differentiated than those on the first postcanine, whereas accessory cusps are absent on the first postcanine of *Charassognathus*.

The nasal extends along the dorsal surface of the snout and contacts the lacrimal, whereas the prefrontal forms the antero-dorsal border of the orbit and contacts the nasal, lacrimal and postorbital. In addition, as is typical in cynodonts, the frontal is excluded from the orbital margin by the prefrontal and postorbital. The parietal appears to be similar to that of other cynodonts, forming a conspicuous sagittal crest, which is broken anteriorly but forms a well-defined sharp crest posteriorly. The parietal foramen is located in the middle of the extension of the sagittal crest (approximately two-thirds along the length of the parietal). The parietal bones are fused behind the parietal foramen as in *Cynosaurus*, *Progalesaurus* and *Galesaurus* (Sidor & Smith, 2004).

The epipterygoid is visible in lateral view and contacts the parietal dorsally and the prootic posteriorly. The dorsal margin shows that the ascending process was anteroposteriorly extended as in all cynodonts and differs from the condition present in most therocephalians (apart from *Theriognathus*).

The jugal contacts the lacrimal and maxilla anteriorly and forms a posterolaterally orientated suture with the maxilla, similar to other basal cynodonts. The squamosal forms the posterior portion of the zygomatic arch, but it is not possible to recognize sutures in the posterior portion of the jugal. On the posterior surface of the temporal fenestra the squamosal deepens posteriorly and contacts the parietal dorsally. In occipital view the squamosal has a deep groove in the shape of an inverted 'V' for the quadratojugal. This groove is deeper and more prominent than that seen in *Procynosuchus*. A well-developed, although deformed, right occipital condyle is observed in the occipital plate, and dorsal to it there is a small protuberance, which is common in cynodonts and is generally interpreted as an articulation for the proatlas (e.g. Romer, 1969). Owing to the lateral compression of the
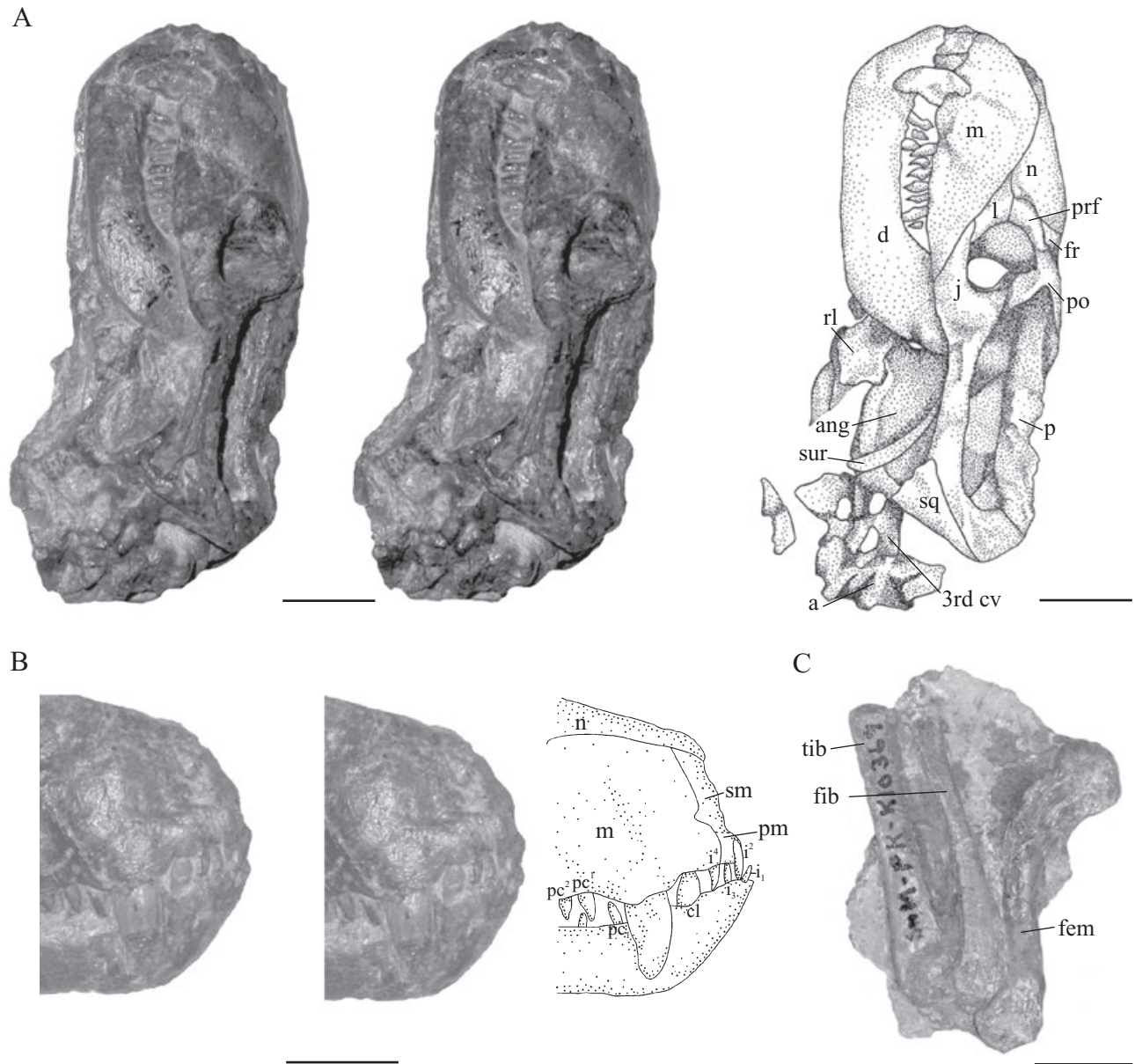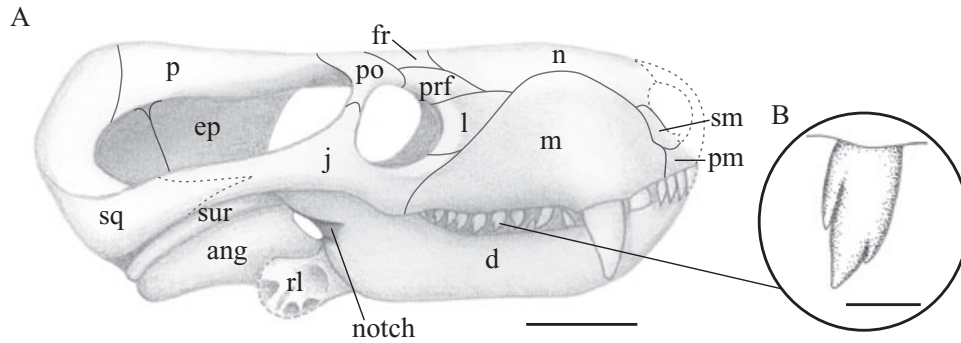
Figure 3. *Charassognathus gracilis* **gen. et sp. nov**. SAM-PK-K10369. A, stereoscopic photograph and interpretative drawing of the left lateral view; B, stereoscopic photograph and interpretative drawing of the right anterior portion of the snout; C, the right articulated femur, tibia and fibula. Abbreviations: 3rd cv, third cervical vertebra; a, axis; ang, angular; cl, lower canine; d, dentary; fem, femur; fib, fibula; fr, frontal; $i_{1,3}$, first and third lower incisors; $i^{2,4}$, second and fourth upper incisors; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; $pc^{1,2}$, first, second upper postcanines; pc_1, first lower postcanine; pm, premaxilla; po, postorbital; prf, prefrontal; rl, reflected lamina; sm, septomaxilla; sq, squamosal; sur, surangular; tib, tibia. Scale bars = 10 mm.

skull, the palatal region could not be observed. The ascending process of the epipterygoid was anteroposteriorly extended, as in all cynodonts.

The lower jaw features of *Charassognathus*, including the deep, robust horizontal rami, the angle of the dentary and the anteroposteriorly extended coronoid process, resemble that of other cynodonts. The man-dibular symphysis, as is typical of basal cynodonts, is unfused. The angle of the dentary in *Charassognathus* is clearly more prominent than in *Dvinia* and *Procynosuchus*. A small notch is present on the dentary (Figs 3A, 4), at the base of the coronoid process, in a similar position to where the base of the masseteric fossa is located in *Dvinia* and *Procynosuchus*. A small

Figure 4. A, reconstruction of the skull of ***Charassognathus gracilis* gen. et sp. nov.**, SAM-PK-K10369, in lateral view; B, high magnification of a postcanine tooth. Abbreviations: ang, angular; d, dentary; ep, epipterygoid; fr, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital; prf, prefrontal; rl, reflected lamina; sm, septomaxilla; sq, squamosal; sur, surangular. Scale bars = 10 mm and 1 mm, respectively.

(approximately 3.6 mm in length), oblong opening is present between the dentary and the angular, posterior to the notch of the dentary. This opening is also known in several therocephalians and in some basal cynodonts (see Brink, 1965c: fig. 49B; Kemp 1979: fig. 6a), although it is usually more developed than what is seen in *Charassognathus*. The angular is widely exposed laterally and, as is usual in basal cynodonts (including *Thrinaxodon*), the surangular forms a narrow strip of bone dorsal to the angular, which overhangs the latter bone in lateral view. The partially preserved reflected lamina of the angular is an osseous plate with some indication of lateral crests and corrugation, but appears less developed than in therocephalians, and is closer to the morphology of *Procynosuchus* and galesaurids.

The axis is articulated with the third cervical vertebra and they are both located on the occipital plate, displaced from their original position. The left side of the fused atlas centrum is visible and shows a large convex area, which is orientated anteriorly. This area is not well preserved, and the articular facets for the atlas arches and intercentrum, as described in *Procynosuchus* and galesaurids (Jenkins, 1971; Kemp, 1980), cannot be recognized. The transverse process of the axis is slightly larger than that of the third cervical vertebra and is more vertically orientated. The latter condition contrasts that reported and illustrated in *Galesaurus* in which the transverse process of the atlas is more horizontally orientated than the processes of the remaining cervical vertebrae (Jenkins, 1971). The postzygapophysis of the axis and the prezygapophysis of the third cervical are subvertically orientated. In contrast to *Thrinaxodon* and *Galesaurus* (Jenkins, 1971), there is no anapophysis in the axis of *Charassognathus*. A flattened bone, approximately rectangular and slightly curved dorsoventrally, is preserved close to the transverse process

of the axis. This bone is tentatively interpreted as a cervical rib.

The femur, tibia and fibula are all approximately equal in length. The femoral diaphysis is short and robust and the head is set off dorsally to the shaft of the bone (Fig. 3C). This last feature is similar to the cynodont condition (Jenkins, 1971) and differs from that in therocephalians (Kemp, 1986) in which the femoral head is directed mostly inward towards the acetabulum.

DISCUSSION

The existence of at least six species of Late Permian cynodonts, together with their widespread distribution in Gondwana (South Africa, Zambia and Tanzania) and Laurasia (Germany and Russia), is a clear indication that cynodonts were already in a first phase of diversification at this stage. *Procynosuchus* is generally regarded as the earliest cynodont, and ranges through the entire *Dicynodon* AZ in South Africa (Sidor & Smith, 2004) and coeval beds in East Africa and Europe. However, the holotype of *Scalopocynodon gracilis* (Brink, 1961), which was synonymized to *Procynosuchus delaharpeae* by Hopson & Kitching (1972), was recovered from the uppermost portion of the *Cistecephalus* Zone of Kitching (1977), which corresponds to the *Cistecephalus* AZ of Rubidge (1995). The presence of *Procynosuchus* in the *Cistecephalus* AZ is confirmed by the recent collection of specimens (SAM-PK-K8511 and PK-K10395, collected by R. Smith) from the uppermost portion of the *Cistecephalus* AZ in the Karoo Basin that are referable to *Procynosuchus*. The discovery of *Charassognathus* in the *Tropidostoma* AZ significantly extends the range of Cynodontia further downwards into the early Late Permian. It also reduces the extensive ghost lineage for the Cynodontia, when considering

that its putative sister group, the Therocephalia, appears in the Middle Permian *Eodicynodon* AZ (Rubidge, 1995).

A cladistic analysis with equally weighted characters resulted in nine most parsimonious trees (MPTs), with the strict consensus tree showing a polytomy of the basal cynodonts: *Charassognathus*, *Procynosuchus*, *Dvinia*, and a clade including the remaining cynodonts. In the majority rule consensus (Fig. 5A), the basal polytomy decreases because *Procynosuchus* and *Dvinia* form a monophyletic clade in five of the nine MPTs. *Cynosaurus* follows the basal polytomy, and the other Late Permian cynodont, *Nanictosaurus*, appears as the sister taxon of the Early Triassic *Thrinaxodon* in the majority rule consensus tree (Fig. 5A). The analyses with implied weights with the different coefficients of concavity resulted in one MPT. The single MPT obtained from the analysis with the coefficient set at six (low value) is similar to one of the nine fundamental trees obtained from the previous analysis (Fig. 5B), whereas the MPT obtained with the coefficient set at three and one (stronger values) shows one difference in that *Bauria* and *Ictidosuchops* have swapped positions. In the trees obtained with implied weights *Charassognathus* is the most basal cynodont, followed by the clade [*Procynosuchus*, *Dvinia*] (Fig. 5B). Hopson & Kitching (2001) also obtained the latter clade as one of their MPTs, but it was not their preferred hypothesis. In agreement with the majority rule consensus with equally weighted characters, *Thrinaxodon* and *Nanictosaurus* are sister taxa in the MPTs in the analysis with implied weights. The latter relationship increases the number of cynodont lineages that crossed the Permo-Triassic boundary in the South African Karoo Basin from two (Sidor & Smith, 2004) to three (Fig. 6), implying that the cynodonts were the most successful therapsid group to survive the end-Permian extinction event.
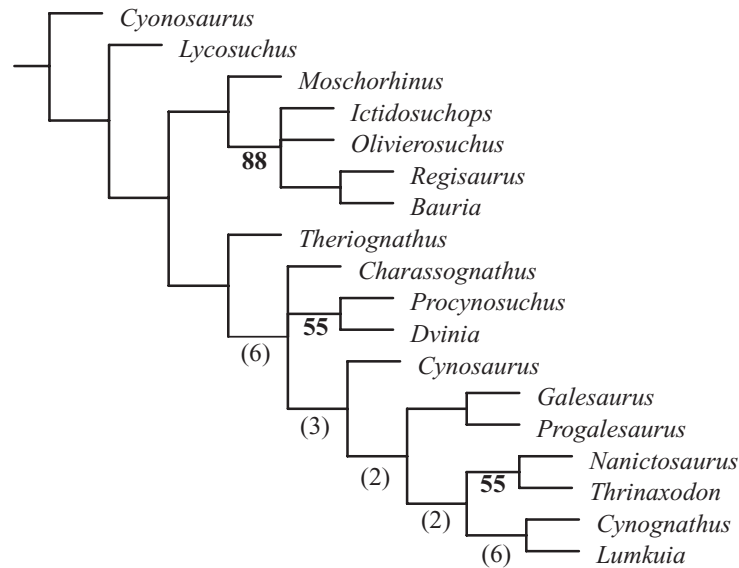
Our results indicate that, contrary to all recent phylogenetic analyses that include several therocephalian taxa (Hopson & Barghusen, 1986; Van den Heever, 1994; Rubidge & Sidor, 2001), Therocephalia is paraphyletic (Fig. 5). *Lycosuchus*, usually considered to be a basal therocephalian (Van den Heever, 1994), is placed outside the majority of 'therocephalians' and the whaitsiid *Theriognathus* is placed as a sister taxon to the cynodonts, a hypothesis previously proposed by Kemp (1972a). Even when the placements of *Lycosuchus*, 'Therocephalia' and *Theriognathus* are poorly supported (Bremer Support = 1), the phylogeny presented here is the best hypothesis provided by our data. It is beyond the scope of the present study to analyse these results in detail. Further studies on the phylogenetic relationships of therocephalians will be addressed elsewhere.

The discovery of *Charassognathus* in the *Tropidostoma* AZ of South Africa and its basal placement in cynodont phylogeny indicates that the origin of this key therapsid group can be traced to the early Late Permian (Lopingian Epoch, Wuchiapingian Stage; Catuneanu *et al.*, 2005) of the Karoo Basin in South Africa (Fig. 6). This finding differs from other recent phylogenies of the group (Hopson & Kitching, 2001; Sidor & Smith, 2004) where the Russian *Dvinia* was considered to be the most basal cynodont. The phylogenetic placement of *Charassognathus* in the MPTs obtained with implied weights (our preferred hypothesis) indicates that, contrary to general opinion (e.g. Hopson & Barghusen, 1986; Hopson & Kitching, 2001), four upper and three lower incisors, a condition that characterizes the majority of non-mammaliaform cynodonts (and also present in three of the four South African Late Permian taxa), was plesiomorphic in this group. Thus, the high number of upper and lower incisors and the presence of precanines (which are generally assumed to be plesiomorphic features in cynodonts) appeared later in cynodont evolution and are synapomorphies for the clade that includes *Dvinia* and *Procynosuchus*.
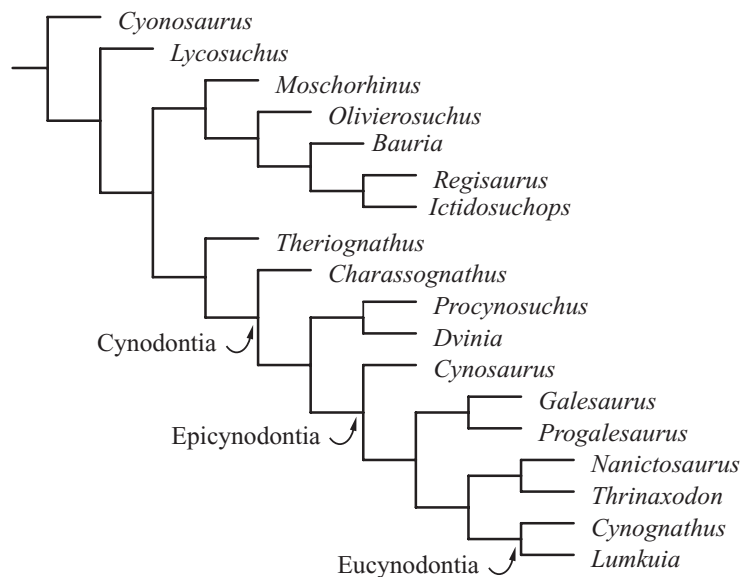
The lateral surface of the ramus mandibulae of the dentary is smooth in 'therocephalians', without any evidence of muscle attachment. The temporal fossa in this group is usually smaller than that in cynodonts (with *Theriognathus* possibly being the only exception) and the ramus mandibulae is placed laterally in the fossa, close to the zygomatic arch of the skull. This kind of arrangement leaves no room for the accommodation of the adductor muscles between the dentary and the zygoma (Barghusen, 1968). The dentary notch of *Charassognathus* is the first evidence of changes occurring on the lateral side of the ramus mandibulae in eutheriodonts. Considering the similar location of the dentary notch of *Charassognathus* and the base of the masseteric fossa in *Procynosuchus* and *Dvinia*, we interpret this notch as related to the invasion of adductor mandibulae externus musculature on the lateral surface of the dentary. A rapid evolution of the masseter insertion area occurred in the latest Late Permian, with two successive stages: (1) the development of a masseteric fossa in *Procynosuchus* and *Dvinia*, with its base having a similar location to the notch in *Charassognathus*, and (2) an extension of the masseteric fossa to the base of the dentary in *Cynosaurus* and *Nanictosaurus*. The location of the masseteric fossa high on the coronoid process in *Procynosuchus* was interpreted as an initial stage in the differentiation of the masseter, which was then followed by the extension of its insertion, reaching the angular region of the dentary (Barghusen, 1968; Bramble, 1978; but see Kemp, 1979, for a different interpretation of masseter evolution).

A

Cyonosaurus
Lycosuchus
Moschorhinus
Ictidosuchops
Olivierosuchus
88
Regisaurus
Bauria
Theriognathus
Charassognathus
55
Procynosuchus
Dvinia
(6)
Cynosaurus
(3)
Galesaurus
Progalesaurus
(2)
Nanictosaurus
Thrinaxodon
55
(2)
Cynognathus
(6)
Lumkuia

B

Cyonosaurus
Lycosuchus
Moschorhinus
Olivierosuchus
Bauria
Regisaurus
Ictidosuchops
Theriognathus
Charassognathus
Cynodontia
Procynosuchus
Dvinia
Cynosaurus
Epicynodontia
Galesaurus
Progalesaurus
Nanictosaurus
Thrinaxodon
Cynognathus
Eucynodontia
Lumkuia

Figure 5. A, majority-rule consensus tree of nine equally parsimonious trees retrieved from an analysis with characters having equal weights. Tree length = 129, consistency index excluding uninformative characters = 0.60, retention index = 0.81. Numbers in bold indicate frequency of clades in the fundamental trees. Nodes without numbers indicate the clades present in the strict consensus. Values of Bremer support above 1 are indicated in parentheses. B, most parsimonious tree obtained from the analysis with implied weights with coefficient of concavity = 6, and one of the nine most parsimonious trees from the analysis with characters having equal weights. Total fit = 62.68, adjusted homoplasy = 6.32.
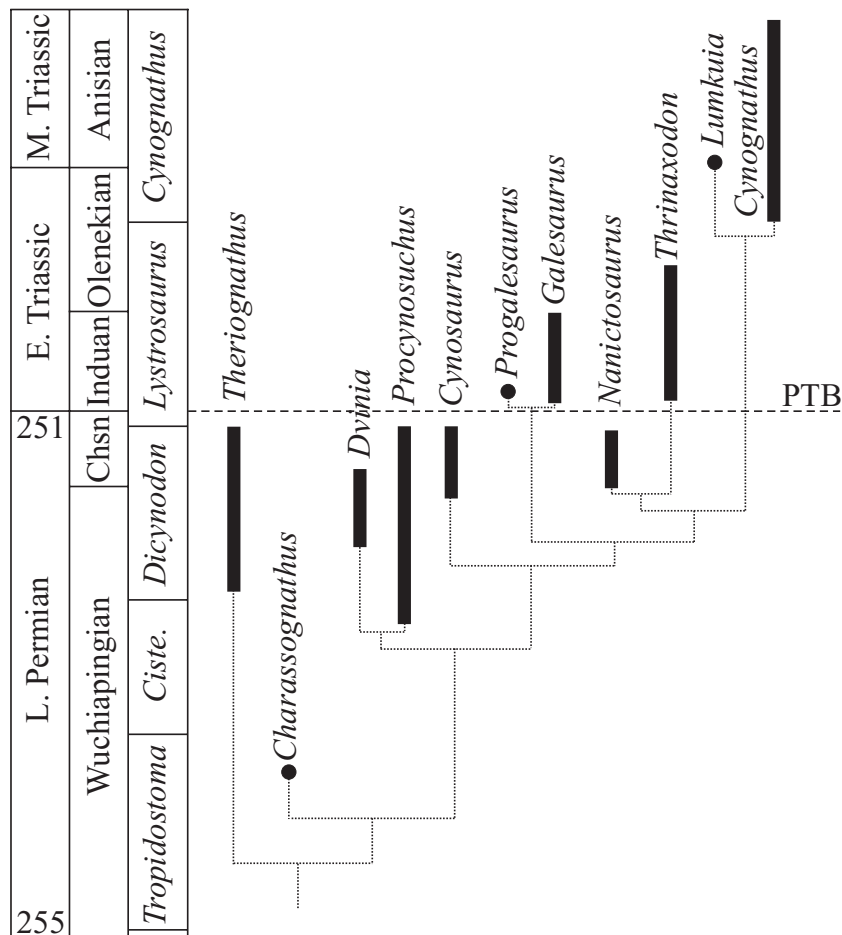
Figure 6. Section of the most parsimonious tree obtained from the cladistic analysis with implied weights (preferred hypothesis) plotted against the South African Permo-Triassic biostratigraphy. Vertical bars and solid circles indicate taxon ranges and single specimen occurrences, respectively. Abbreviations: Chsn, Changhsingian; *Ciste.*, *Cistecephalus* Assemblage Zone; PTB, Permo-Triassic boundary. Numbers indicate million years ago. Stratigraphic chart follows Catuneanu *et al.* (2005).

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APPENDIX 1

INSTITUTIONAL ABBREVIATIONS

AM, Albany Museum, Grahamstown, South Africa; AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; BP/1/, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; BS, Bayerische Staatssammlung

für Paläontologie und historische Geologie, München; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NMQR, National Museum, Bloemfontein, South Africa; OUMNH, Oxford University Museum of Natural History; SAM-PK, Iziko South African Museum, Cape Town, South Africa; UMZC, University Museum of Zoology, Cambridge.

APPENDIX 2

List of material and literature consulted for taxa included in the phylogenetic analysis.

Bauria: BP/1/1180, 1685, 3770, 4655; Boonstra (1938), Brink (1963a, 1965a).

Cynognathus: AM 460, 2190, 3587, 4202, 5800; AMNH 5641; BMNH R2571 R3580; BP/1/1181, 2095, 3755, 4664; BS1934VIII 1, VIII 2, VIII 3, VIII 4, VIII 6; NMQR 1444; PVL 3859; SAM-PK-6224, 6235, 11264, 11484; Seeley (1895), Broili & Schröder (1934, 1935), Brink (1955).

Cynosaurus: AM 4947; BMHN R1718; SAM-PK-4333; BP/1/3926, 4469; Owen (1876), Haughton (1918), Brink (1965b), Van Heerden (1976).

Cyonosaurus: BP/1/137, 735, 2109, 2598; Olson (1937, 1944), Sigogneau (1970), Sigogneau-Russell (1989).

Dvinia: casts of the holotype (UMZC T.1016) represented by a snout and a complete skull originally assigned to *Permocynodon sushkini* (UMZC T.299); Tatarinov (1968).

Galesaurus: AMNH R2223, R2227; BMNH R36220; BP/1/4602, 4637, 5064; NMQR860, 1451, 3340; RC 845; SAM-PK-K-1119, 9956; TM 24, 83; UMCZ T.819, T.823; Watson (1920), Broom (1932), Parrington (1934), Boonstra (1935), Rigney (1938).

Ictidosuchops: BP/1/218, 2125, 3155; Crompton (1955).

Lumkuia: BP/1/2669; Hopson & Kitching (2001).

Lycosuchus: BP/1/276, 499, 1100, 1768; Van den Heever (1987, 1994).

Moschorhinus: BP/1/, 1713, 3983, 4227; Durand (1991).

Nanictosaurus: TM 279; RC 47; Broom (1936), Van Heerden (1976), Van Heerden & Rubidge (1990).

Olivierosuchus: BP/1/3849, NMQR 62; Brink (1965c).

Procynosuchus: BP/1/226, 591, 650, 1545, 1559, 2600, 3758, 5832; OUMNH TSK34; RC 5, 12, 72, 92, 132; SAM-PK-K-338, K8511, K10395; Broom (1937, 1938, 1948), Brink & Kitching (1951), Brink (1963b), Kemp (1979).

Progalesaurus: SAM-PK-K-9954; Sidor & Smith (2004).

Regisaurus: Mendrez (1972).

Theriognathus: BP/1/100, 164, 717, 725, 785, 844, 4008; Brink (1954, 1956); Kemp (1972a,b).

Thrinaxodon: AMNH R9563; BMNH R511, R511a, R845, R1715, R3731, R5480; BP/1/1375, 1376, 2513, 4280, 5208, 5372; BSP 1934VIII 506; MCZ 8892; TM 80, 81, 1486; NMQR24, 811, 812, 1533; SAM-PK-K-378, 380, 381, 1121, 1388, 1461, 1467, 1468, 1483, 1498, 1499, 3592, 10016, 10017; UMCZ T.811, T.813, T.814, T.815, T.816, T.817; Broom (1911), Watson (1920), Parrington (1936, 1946), Estes (1961), Crompton (1963), Van Heerden (1972), Fourie (1974), Gow (1985).

APPENDIX 3

CHARACTER LIST

Abbreviation after the character states indicates authors who previously used the character in data-matrices including non-mammaliaform cynodonts, and the corresponding number of the character. R, Rowe (1988); W, Wible (1991); LL, Lucas & Luo (1993); L, Luo (1994); M, Martinez, May & Forster (1996); HK, Hopson & Kitching (2001); Bonaparte *et al.* (2003); SS, Sidor & Smith (2004). Abbreviations in italics indicate that the character or the character states defined by the author(s) differs from that provided here. + Additive multistate characters.

Multistate characters, in which morphological analysis allowed for the recognition of adjacency of states, were coded as additives [e.g. Zygomatic arch dorsoventral height; slender (0), moderately deep (1), very deep (2)] (Lipscomb, 1992). This was the case for characters 1, 6, 7, 19, 28, 39, 44, 45 and 46. Codification of character 6 reflects differences in the osseous palate condition in *Bauria* and other taxa with partial or complete secondary palates. In this case the plesiomorphic state, i.e. the absence of a secondary palate, is coded as 2; the extension of both maxillary and palatine processes of the palate, without contacting the processes from the opposite side, is coded as 1 and the complete osseous palate formed by the maxilla and palatine is coded as 0. The condition in *Bauria* in which the palatines do not form part of the osseous palate is coded as 3. In making the character additive, the transformation from open palate to a complete palate (formed by the maxilla and palatine) will have an intermediate state in which the palatal processes of both bones are extended to the middle, but do not form a complete palate. In contrast, the osseous palate in *Bauria* in which the palatines do not participate will require one step from the plesiomorphic state.

1. Snout in relation to the temporal region; longer (0), subequal (1), shorter (2). +
2. Septomaxilla facial process; long (0), short (1). SS1
3. Contact between the nasal and lacrimal; absent (0), present (1). HK2, SS2

4. Incisive foramen; absent (0), present (1).

5. Contact between vomer and maxilla in the palate; absent (0), present (1), maxilla covers vomer (2).

6. Osseous secondary palate; complete, with contribution of the palatine (0), maxillo-palatine extensions do not contact medially (1), absent (2), complete, without contribution of the palatine (3). *HK12*, *13*; *SS11*, *12* +

7. Ectopterygoid; contacts maxilla (0), does not contact maxilla (1), absent (2). HK9, SS15 +

8. Palatal teeth; on the pterygoid and palatine (0), on the transverse process of the pterygoid (1), on the pterygoid boss (2), absent (3). *HK16*, *SS14*

9. Interpterygoid vacuity in adults; present (0), absent (1). M27, HK10, B25

10. Boss/crest anterior to interpterygoid vacuity; reduced or absent (0), well developed (1).

11. Suborbital vacuity in palate; absent (0), present (1).

12. Frontal in orbital margin; included (0), excluded (1).

13. Frontal–epipterygoid contact; absent (0), present (1). R39, W48, L61, HK35, SS24

14. Parietal foramen; present (0), absent (1). R8, W12, LL34, L64, M31, HK7, B24

15. Postfrontal; present (0), absent (1). HK4, SS3

16. Postorbital bar; complete narrow (0), incomplete (1), complete wide (2). *R7*, *W2*, *LL33*, *L55*, *M29*, *HK5*, *B40*

17. Parietal region; at the same level as the skull profile (0), high (1). SS7

18. Temporal fossa; widest in the middle (0), widest posteriorly (1). *HK39*

19. Zygomatic arch dorsoventral height; slender (0), moderately deep (1), very deep (2). *R16*, *W40*, *L54*, *M39*, HK18, SS5 +

20. Infraorbital process; absent (0), suborbital angulation between maxilla and jugal present (1), descendant process of the jugal present (2). *M18*, *HK21*, *41*, *B38*

21. Inferior margin of the jugal in the zygoma; poorly developed longitudinally (0), well developed longitudinally almost reaching the posterior end of the zygoma (1).

22. Posterior extension of the squamosal dorsal to the squamosal sulcus; absent (0), incipient (1), well developed (2). *M55*, *HK22*, *B28*, *SS18*

23. Occipital crests; non-confluent proximally (0), confluent (1).

24. Posttemporal fossa large axis in relation to the diameter of the foramen magnum; of the same size or slightly smaller (0), notably smaller (1).

25. Paroccipital process in the base of the posttemporal fossa; present (0), absent (1). *HK24*, *SS16*

26. Tuberculum spheno-occipital; present (0), absent (1).

27. Pterygoid quadrate ramus; present (0), absent (1). *M40*, HK30, B34, SS20

28. Epipterygoid ascending process; rodlike (0), moderately expanded (1), greatly expanded (2). HK32, SS22 +

29. Lateral flange of the prootic; absent (0), present (1). HK34, SS28

30. Pterygo-paraoccipital foramen; absent (0), present (1).

31. Trigeminal exit; between prootic incisure and epipterygoid (0), via foramen between epipterygoid and prootic (1). HK28, SS27

32. Quadrate–paroccipital process contact; present (0), absent (1). R19, W41, *M52*

33. Quadrate notch in the squamosal; absent (0), present (1).

34. Stapes; perforated (0), unperforated (1).

35. Jugular foramen; faces posteriorly (0), ventrally (1). SS30

36. Mastoid and quadrate processes of the paroccipital process; undifferentiated (0), differentiated (1).

37. Occipital condyle; single (0), double (1). HK37, SS31

38. Mandibular symphysis; unfused (0), fused (1). R68, W10, *L19*, M68, HK44, B17, SS34

39. Lateral crest of the dentary; absent (0), incipient (1), well developed (2). +

40. Angular region of the dentary; anterior to the postorbital bar (0), at the same level or posterior (1).

41. Longitudinal depression in the lateral side of the dentary; absent (0), present (1).

42. Location of the coronoid process in the temporal fossa; lateral (0), in the middle (1). SS33

43. Foramen on external surface of the lower jaw between dentary and angular; absent (0), present (1). SS41

44. Reflected lamina of the angular; corrugated plate (0), smooth plate with slight depressions (1), hook-like laminae (2), thin projection (3). *HK52*, *SS44* +

45. Masseteric fossa in the dentary; absent (0), notch at the base of the coronoid process (1), fossa high on coronoid process (2); fossa extends to the angle of dentary (3). *HK45*, *SS36* +

46. Position of the dentary/surangular dorsal contact; closer to postorbital bar (0), midway (1), closer to jaw joint (2). HK48, SS40 +

47. Surangular–squamosal contact; absent (0), present (1). *HK25*, *B30*, *SS19*

48. Upper incisors; more than four (0), four (1). *R81*, *W63*, *?L5*, *M1*, *HK53*, *B3*, *SS45*

49. Lower incisors; four (0), three (1). *M2*, *?L5*, *HK54*, *B4*, *SS46*

50. Incisor cutting margins; serrated (0), smoothly ridged (1). *HK55*, SS47

51. Incisor–canine diastema; present (0), absent (1).

52. Precanine maxillary teeth, absent (0), present (1). SS48

53. Lower canine; large (0), reduced (1). ?*L6*, *HK58*

54. Canine serrations; present (0), absent (1). HK59, SS49

55. Upper postcanine extension; anterior to the orbit (0), below the orbit (1).

56. Upper postcanine morphology; conical simple (0), sectorial (1), transversely wide (2), sectorial with lingual cingulum (3). *L13*, *M5*, *HK60*, *SS51*, *55*

57. Postcanine occlusion; absent (0), present (1). M8

58. Lingual cingulum in lower postcanines; absent (0), present (1). *L12*, *B11*, *12*, *SS56*

59. Posterior postcanines with strongly curved main cusp; absent (0), present (1). *SS52*

DATA MATRIX

Cyonosaurus	0000020000000000A0000000000001000000000000?0000000000000
Lycosuchus	0000020100100000000?0100001000?101000001000001010000000
Ictidosuchops	000012?2011000100100001000010?000101000101000000111110000
Regisaurus	0000120201100110010000100001010000?010???????????0??00??000?0
Theriognathus	00001203000000100100001000020100110100000010000?11001-----
Moschorhinus	0000020301100001000100?01000010100001010000001000000111?100000
Olivierosuchus	00000213011000100100010001010000?0100001010010001010100000
Bauria	0000230301100111010000100000?0?010101000010100101110011021100
Charassognathus	1?1????????1?0100?00?01????2????1???10010?111001110001?1??0
Nanictosaurus	0??20?30001?01000101?1111021?11101010101101??3101110001A1010
Cynosaurus	011001031-0110100010?1?11?102111?1?10101101??3001?100?1010?0
Procynosuchus	001001130001101010000111010211101010100101112000011101030 10
Dvinia	201001030001?0101000111001 0?1111001010010 1?? 2000010101 12110
Galesaurus	011001131-01101000111b11110211111010101101 13101110001a1001
Progalesaurus	011?01?31-011010001111111102111110101010101?? 31?111000101001
Thrinaxodon	011120131-011010001011111102111110101011010231011100010 3010
Cynognathus	011120131-0110120122121001121111101011210103321111000011001
Lumkuia	2111202301 01?11000101111111211111010112101023211 11000111001

A: 0, 1; **B**: 1, 2

APPENDIX 4

Unambiguous synapomorphies for nodes of the most parsimonious tree obtained with implied weights (Fig. 5B).

Number in parentheses following the character indicates the synapomorphic state for the node of a multistate character.

Post *Lycosuchus* 'therocephalians':
15. Postfrontal absent.
30. Pterygoparoccipital foramen present.
50. Incisor margin smoothly ridged.
54. Canine serrations absent.

'Therocephalia' (apart from *Lycosuchus* and *Theriognathus*):
10. Boss/crest anterior to the interpterygoid opening present.
52. Precanine maxillary teeth present.

Olvierosuchus [*Ictidosuchops* [*Regisaurus*, *Bauria*]]
41. Longitudinal depression in the lateral face of the dentary present.

Ictidosuchops [*Regisaurus*, *Bauria*]
5. Contact between vomer and maxilla in the palate present. Parallelism in *Theriognathus*.
53. Lower canine reduced.

[*Bauria*, *Regisaurus*]
14. Parietal foramen absent. Parallelism in *Lumkuia*.
52. Precanine maxillary teeth absent.

Theriognathus + Cynodontia:
28(2). Epipterygoid ascending process greatly expanded.
33. Quadrate notch in the squamosal present.

Cynodontia:
3. Contact between the nasal and lacrimal.

12. Frontal excluded from the orbital margin.
37. Double occipital condyle.
40. Angle of the dentary at the same level or posterior to the postorbital bar.
44(1). Reflected lamina of the angular, smooth plate with slight depressions.
45(1). Notch at the base of the coronoid process.

Post-*Charassognathus* cynodonts:
22. Poorly developed squamosal sulcus depression.
45(2). Masseteric fossa in the base of the coronoid process present.

[*Procynosuchus*, *Dvinia*]:
17. Parietal region of the skull elevated.
52. Precanine maxillary teeth present.
58. Lingual cingulum in lower postcanines present.

Epicynodontia:
2. Facial process of the septomaxilla short.
9. Interpterygoid opening absent.
19(1). Zygomatic arch moderately deep dorsoventrally.
39(1). Lateral crest of the dentary incipient.
45(3). Masseteric fossa in the dentary extends to the angle.

Post-*Cynosaurus* Epicynodontia:
7(1). Ectopterygoid does not contact maxilla.

46(1). Contact between dentary and surangular midway between the postorbital bar and the craniomandibular joint.

[*Galesaurus*, *Progalesaurus*]:
20(1). Suborbital angulation between the jugal and the maxilla.

[[*Nanictosaurus*, *Thrinaxodon*][Eucynodontia]]:
4. Foramen incisivum present.
5(2). Maxilla covers vomer in palatal view.
6(0). Osseous palate complete.
43. Foramen on external surface of the lower jaw between dentary and angular absent.
44(2). Reflected lamina of the angular hook-like.

[*Nanictosaurus*, *Thrinaxodon*]:
27. Contact between pterygoid and quadrate absent.
38. Mandibular symphysis fused.
58. Lingual cingulum in lower postcanines present.

Eucynodontia:
39(2). Lateral crest of the dentary well developed.
46(2). Dentary–surangular dorsal contact closer to the cranio-mandibular joint.
47. Surangular–squamosal articulation with the mandible present.
55. Upper postcanine series extends below the orbit.