

## CYNODONTS FROM THE UPPERMOST BURGERSDORP FORMATION, SOUTH AFRICA, AND THEIR BEARING ON THE BIOSTRATIGRAPHY AND CORRELATION OF THE TRIASSIC *CYNOGNATHUS* ASSEMBLAGE ZONE

FERNANDO ABDALA<sup>1</sup>, P. JOHN HANCOX<sup>2</sup>, and JOHANN NEVELING<sup>3</sup>

<sup>1</sup>Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa, abdalaf@geosciences.wits.ac.za;

<sup>2</sup>School of Geosciences, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa; hancoxp@geosciences.wits.ac.za

<sup>3</sup>Council for Geoscience, Private Bag X112, Pretoria 0001, South Africa, jneveling@geoscience.org.za

**ABSTRACT**—The Burgersdorp Formation in the Beaufort Group of the South African Karoo Basin records a diverse and rich vertebrate fauna that is referred biostratigraphically to the *Cynognathus* Assemblage Zone. Recent collecting efforts, and taxonomic and biostratigraphic studies on this formation, resulted in a proposed subdivision of the *Cynognathus* Assemblage Zone into three subzones informally known as A, B, and C. Cynodont fossils constitute an important component of the fauna of the uppermost subzone C of the *Cynognathus* Assemblage Zone. As in the middle subzone B, cynognathids, diademodontids, and trirachodontids are represented in subzone C, although the latter group—instead of *Diademodon*—is the dominant taxon. The presence of *Cynognathus* in the faunas of the three subzones confirms that this genus is the correct choice as the index taxon of the assemblage zone. The large size attained by trirachodontid specimens from subzone C represents an unusual characteristic. One complete skull measured 160 mm in length, although fragmentary remains of other specimens indicate even larger sizes. These skull lengths are well above the 100 mm that characterize trirachodontids recovered from the older subzones A and B. The large size, and particularly the ovoid overall pattern of the upper gomphodont postcanines allows the assignment of the trirachodontid specimens from subzone C to *Cricodon metabolus*, previously known from the Manda Formation in Tanzania. The *Cynognathus* Assemblage Zone of South Africa is shown to be the most temporally complete Early-Middle Triassic nonmarine sequence in southern Gondwana, and is the template against which other sequences of similar age may be compared.

### INTRODUCTION

Non-mammalian cynodonts are a clade of therapsids that form an important component of many Late Permian to Middle Jurassic terrestrial faunas. This group has been intensely studied taxonomically and phylogenetically due to their close relationship with early mammals (basal Mammaliaformes sensu Rowe, 1988). Cynodonts are also an important source of evidence of the origin of mammalian traits, including aspects of the feeding (Crompton and Hylander, 1986; Crompton, 1995), auditory (Allin, 1975; Allin and Hopson, 1992) and locomotor systems (Jenkins, 1971), among others.

Cynodont early evolution is particularly well documented in the rocks of the Beaufort Group (Karoo Supergroup) of South Africa, where they first appear in the uppermost Permian Balfour Formation (*Dicynodon* Assemblage Zone [AZ]; Kitching, 1995a). They survive the Permian-Triassic extinction event, and are fairly abundant in the Lower and Middle Triassic Katberg and Burgersdorp formations (*Lystrosaurus* and *Cynognathus* AZs respectively). Representatives in the *Lystrosaurus* AZ include *Thrinaxodon*, *Progalesaurus*, *Galesaurus*, and *Platycranielus* (Groenewald and Kitching, 1995; Sidor and Smith, 2004), while five genera of cynodonts (the maximum for any assemblage zone of the Beaufort Group) are recorded in the *Cynognathus* AZ. Three of these genera, *Cynognathus*, *Diademodon*, and *Trirachodon* are relatively common, while *Lumkuia* and *Bolotridon* are rare records (Seeley, 1895; Haughton and Brink, 1954; Kitching, 1995b; Hopson and Kitching, 2001).

The *Cynognathus* AZ has recently been the focus of much new research, which has allowed for a threefold faunal subdivision to be proposed (Hancox et al., 1995; Shishkin et al., 1995) based primarily on the spatial and temporal ranges of a number of key temnospondyl index taxa, and supported to a lesser degree by

their associated faunas. However, research has been concentrated on the fauna of the lower and middle subzones (Welman et al., 1991; Hancox et al., 1995; King, 1996; Damiani, 1999; Gow, 1999; Neveling et al., 1999, 2000, 2001; Damiani et al., 2000; Renaut, 2000; Groenewald et al., 2001; Hopson and Kitching, 2001; Neveling, 2002; Bender and Hancox, 2004), with little attention paid to the fauna of the upper subzone.

During fieldwork over the past decade, a new tetrapod faunal assemblage, including cynodonts, dicynodonts, and amphibians, has been discovered in the rocks of the uppermost 150 m of the southernmost exposures of the Burgersdorp Formation in the Bamboeshoek Valley of the Eastern Cape Province (Fig. 1). Although cynodonts are the dominant component of this faunal association, studies on them have been neglected, and only components of the dicynodont (Hancox and Rubidge, 1994, 1996; Hancox, 1998) and amphibian fauna (Hancox et al., 2000; Damiani and Hancox, 2003) have been described.

The aim of this paper is to present the first account of the cynodont fauna of the uppermost levels of the Burgersdorp Formation (*Cynognathus* AZ, Subzone C; Hancox et al., 1995). In particular we provide a succinct description of new fossils of Trirachodontidae focusing on their tooth morphology and compare them with other members of the family from the Burgersdorp and Manda formations of South Africa and Tanzania respectively. We furthermore utilize the cynodont fauna of the *Cynognathus* AZ to refine the biostratigraphy of the zone, in the correlation of the continental Triassic, as well as discussing their potential for global biochronological studies.

**Institutional Abbreviations**—**AM**, Albany Museum, Grahamstown; **BP**, Bernard Price Institute for Palaeontological Research, Johannesburg; **NMQR**, National Museum, Bloemfontein; **SAM**, South African Museum, Cape Town; **UMZC**, University Museum of Zoology, Cambridge.

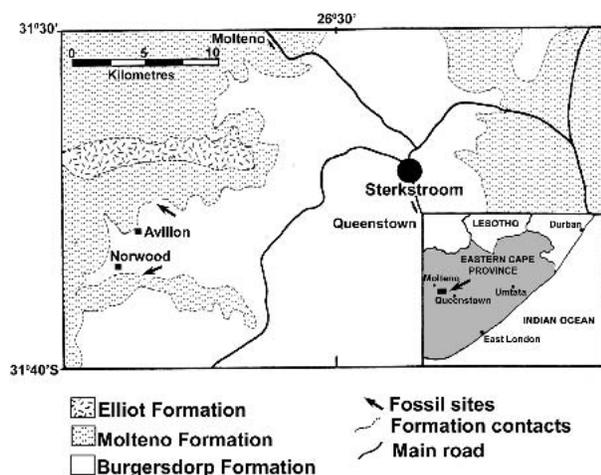


FIGURE 1. Locality map.

### AGE OF THE *CYNOGNATHUS* ASSEMBLAGE ZONE

Although the *Cynognathus* AZ has been intensely researched over the years, the age of the biozone has been the subject of much debate until fairly recently. This is for the most part because of the misdiagnosis and uncertain taxonomic assessment of a number of amphibian genera, which have in turn led to incorrect correlations. The biozone has variously been regarded as Late Permian (Cooper, 1982; Johnson, 1994), Early Triassic (Cosgriff, 1965; Anderson and Anderson, 1970; Chernin, 1978), late Early Triassic (Anderson and Cruickshank, 1978; Cosgriff, 1984; Battail, 1988, 1993; Lucas, 1998), Middle Triassic (Huene, 1940; Cruickshank, 1986; Ochev and Shishkin, 1989) or Late Triassic (Broom, 1904) in age.

Crucial steps toward the resolution of this conundrum have recently been made, and careful stratigraphic assessment coupled with new discoveries has shown that the *Cynognathus* AZ actually encompasses the boundary between the Early and Middle Triassic (Hancox et al., 1995; Shishkin et al., 1995; Hancox and Rubidge, 1996; Hancox, 1998, 2000; Damiani and Hancox, 2003). Presently, the lowermost subzone A is regarded as late Olenekian (Hancox et al., 1995; Damiani, 1999; Hancox, 2000), the middle subzone B as early Anisian (Ochev and Shishkin, 1989; Hancox, 1998, 2000) and the uppermost subzone C as latest Anisian (Hancox and Rubidge, 1996; Hancox, 1998, 2000; Hancox et al., 2000; Damiani and Hancox, 2003).

### MATERIALS

Cynodont materials from the uppermost 150 m of the Burgersdorp Formation (*Cynognathus* AZ, subzone C) are listed in Table 1. BP/1/5538, 5540, 5542, 5543, 5833, 5835, and 6159 come from the farm Avillion, while BP/1/5541 and 6102 were collected

from the farm Norwood (Fig. 1). Both farms occur in the Bamboeshoek Valley, Sterkstroom District, Eastern Cape Province.

### DESCRIPTION

Cynodont material collected from the uppermost Burgersdorp Formation includes three taxa, *Cynognathus*, *Diademodon*, and a trirachodontid. *Cynognathus* is represented by an anterior portion of a lower jaw (BP/1/5543; Fig. 2A, B). This specimen has a canine that protrudes outward, and the first five alveoli of the postcanines evidence sectorial-shaped teeth. *Diademodon* is represented by a partial anterior lower jaw (BP/1/5542) that does not have the canines directed outward and that features two very small circular postcanine roots (Fig. 2C). Considering that these two tiny anterior roots are very close to the canine, it is probable that they represent the remnant of lost anterior conical simple teeth (Seeley, 1908; Fourie, 1963). In addition, there is a complete lower jaw (BP/1/5541) that may be assigned to *Diademodon* (Fig. 2D). The incisors do not show serrations, while there is evidence of serrations on the posterior edge of the right large canine. A diastema is absent between the incisors and canine, while a short one is present between the canine and first postcanine. Ten or eleven postcanines constitute the tooth row, all of them with their crowns poorly preserved or missing. Most of the teeth display a circular outline, except for the last two that seem to be sectorial teeth. The approximate length of the lower jaw indicates a medium-sized representative of the genus.

### Specimens of Trirachodontidae

The most significant feature of the trirachodontid material from the Sterkstroom District is the large size attained by three of the specimens (Table 2; Fig. 3) compared with that recorded from the other subzones of the *Cynognathus* AZ (Table 3). BP/1/5540, the only complete skull, measures approximately 160 mm in basal length (Fig. 3A); BP/1/6102 (a complete snout; Fig. 3B) probably presents the same skull length, whereas BP/1/5835 (the anterior portion of the snout and fragments of upper and lower jaws in occlusion; Fig. 3D) and the snout fragment of BP/1/6159 (Fig. 3C) demonstrate larger individuals. The last specimen indicates that this taxon may have reached more than 200 mm in skull length, an increase of approximately 50% compared to trirachodontids from subzones A and B.

The incisors featured in BP/1/5540 and BP/1/6102 have high crowns with a posterior serrated edge, while the canine has serrations on both anterior and posterior edges (Fig. 4B). BP/1/5540 shows a hypertrophied upper canine, almost reaching the ventral border of the lower jaw (Fig. 3A). There is a well-developed diastema between the last upper incisor and the canine. The crowns of the incisors in BP/1/6102 are very high compared with those of the postcanines (Fig. 4B). Thus, comparison of the heights between the fourth incisor and the highest postcanine resulted in a ratio of 0.42.

BP/1/6102 has nine upper postcanines, with the last two being sectorials (Fig. 4A, B), while the larger BP/1/6159 shows incom-

TABLE 1. Cynodont material from the uppermost Burgersdorp Formation

Specimen	Taxa	Description
BP/1/5538	<i>Cricodon</i>	Posterior portion of snout and orbits, with posterior postcanines well preserved (Fig. 5)
BP/1/5540	<i>Cricodon</i>	Complete skull poorly preserved (Fig. 3A)
BP/1/5541	<i>Diademodon</i>	Almost complete lower jaw (Fig. 2D)
BP/1/5542	<i>Diademodon</i>	Anterior portion of lower jaw (Fig. 2C)
BP/1/5543	<i>Cynognathus</i>	Anterior portion of lower jaw (Fig. 2A, B)
BP/1/5833	<i>Cynodontia</i>	Fragment of maxilla with canine
BP/1/5835	<i>Cricodon</i>	Anterior portion of snout and attached lower jaw, and three fragments of skull and lower jaw in occlusion (Fig. 3D)
BP/1/6102	<i>Cricodon</i>	Snout with postcanine tooth row (Figs. 3B, 4)
BP/1/6159	<i>Cricodon</i>	Portion of snout and anterior lower jaw (Fig. 3C), associated with many fragments numbered BP/1/5548

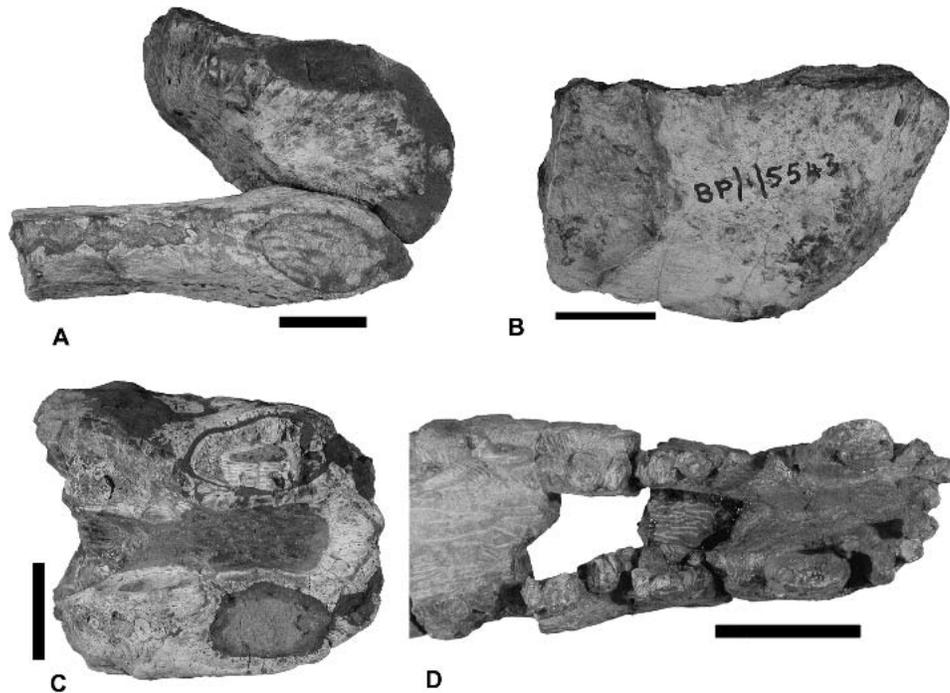


FIGURE 2. *Cynognathus* and *Diademodon* specimens from subzone C of the *Cynognathus* Assemblage Zone. **A**, BP/1/5543, dorsal, and **B**, lateral view of the anterior portion of the lower jaw of *Cynognathus*. **C**, BP/1/5542, anterior portion of the lower jaw in dorsal view of *Diademodon*; **D**, BP/1/5541, lower jaw in dorsal view of *Diademodon*. Scale equals 3 cm.

pletely preserved postcanine rows, with nine teeth, all of which are gomphodont. BP/1/5538, a small-sized individual when compared with the specimens mentioned above, has the last four postcanines preserved, only the last one being sectorial (Figs. 5, 6).

The upper postcanine pattern is best observed in BP/1/6102 and especially 5538. There is a broad contact between the anterior and posterior borders of adjacent postcanines. The crown is ovoid, featuring three cusps united by a transverse crest along the midline (Figs. 5B, 6A); the labial cusp is higher and more developed than the central and lingual cusps, the last two being very close to each other (Figs. 5B, 6A). The best-preserved gomphodont tooth of BP/1/5538 features, besides the main labial cusp, small anterior and posterior cingular cusps on the labial edge (Fig. 6A). In BP/1/6102 there is some indication of the presence of the accessory labial cusp, but its presence cannot be confirmed unquestionably. Small cuspsles making up the crenulated posterior border are preserved in BP/1/6102, while in BP/1/5538 there is evidence of a crenulated posterior border, but the cuspsles are worn away. The anterior portions of the preserved postcanines in the two specimens are worn or poorly preserved, and it is not possible to observe evidence of cuspsles. The last sectorial tooth in BP/1/5538 is well developed with a main anterior cusp backwardly recurved, and three smaller posterior accessory cusps that decrease in size posteriorly, extending to

nearly the middle of the crown length (Figs. 5A, 6B). This tooth is broken close to its base, and this results in an artifact simulating an external cingulum extending from the middle of the main cusp to the middle of the first accessory cusp (Fig. 6B).

## DISCUSSION

The new cynodont fauna from the uppermost levels of the Burgersdorp Formation adds a number of parameters to our understanding of the *Cynognathus* AZ. First, it has shown that *Cynognathus* and *Diademodon*, typical representatives from the classical *Cynognathus* AZ (i.e., subzone B), also reach the younger subzone C. Second, the records of trirachodontids in the latter subzone are remarkable because they are of a substantially larger size than those recovered from the older subzones (Tables 2, 3).

There is some discrepancy about the validity of the *Trirachodon* species acknowledged from subzone B of the *Cynognathus* AZ. Hopson and Kitching (1972) synonymised three genera and five species and placed them in *Trirachodon berryi*. Afterward, Kitching (1977) reinstated *T. kannemeyeri* as a valid species, while Neveling (2002) agreed with Hopson and Kitching's (1972) proposition recognizing only one species for subzone B. Recent work (Neveling et al., 2000; Neveling, 2002) has shown that a distinct species of *Trirachodon*, hitherto undescribed, exist in subzone A. This species is differentiated from *T. berryi* based on its postcanine tooth morphology (Neveling, 2002). In this contribution we recognize one valid species of *Trirachodon* (*T. berryi*) for the subzone B and an unnamed second species for the subzone A. A more extensive treatment of the taxonomy of the Trirachodontidae will be addressed in a forthcoming contribution. In addition to the Karoo species, *Cricodon metabolus* (UMCZ T 905) from the Manda Formation in Tanzania (Crompton, 1955), *Sinognathus gracilis* from the Chinese Upper Ermaying Formation (Sun, 1988), and the recently described *Neotrirachodon expectatus* from the Donguz Formation in Russia (Ta-

TABLE 2. Measurements of *Cricodon* specimens from Subzone C of the *Cynognathus* AZ (in mm); \* incomplete row

	Skull length	Incisors+canine length	4th incisor height	Canine height	Postcanine row length
BP/1/5540	160	42	16	31	
BP/1/5835		52	15	37	
BP/1/6102		44	13		36
BP/1/6159					46*

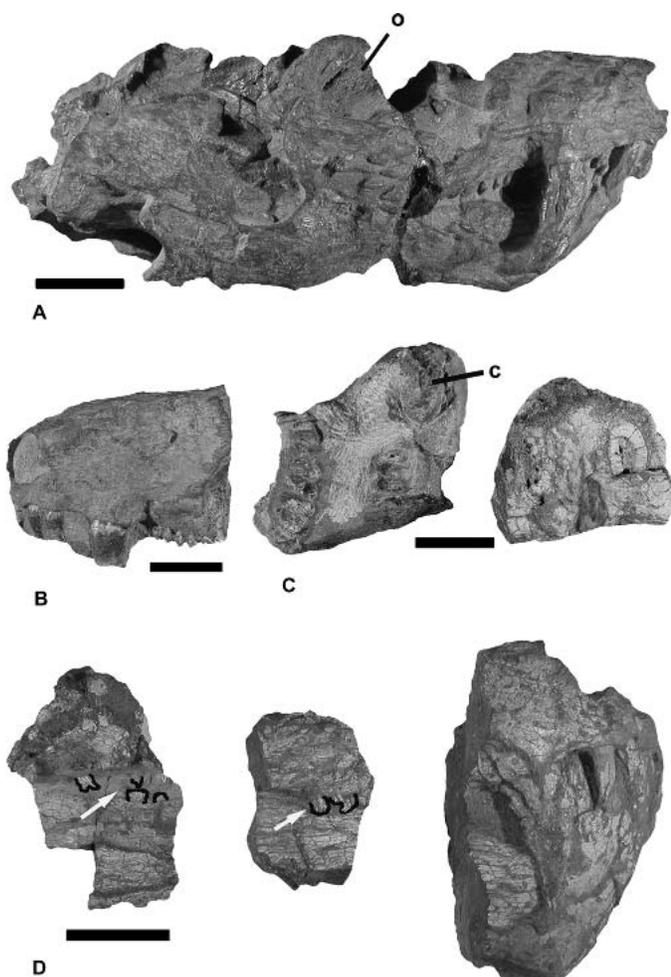


FIGURE 3. Large-sized trirachodontid specimens from subzone C of the *Cynognathus* Assemblage Zone. **A**, right lateral view of BP/1/5540; **B**, left lateral view of BP/1/6102 (see also Fig. 4); **C**, palatal view of the skull and dorsal view of the mandibular fragment of BP/1/6159; **D**, anterior portion of the snout (right), lateral view of upper and lower jaw in occlusion (center), and medial view of upper and lower jaw in occlusion (left) of BP/1/5835. Arrows indicate occluding postcanine teeth. Silhouettes of the postcanines are shown. The fragment in the center represents the two last postcanines of the row, with the sectorial pattern in the penultimate tooth clearly visible. **Abbreviations:** c, canine; o, orbit. Scale equals 3 cm.

tarinov, 2002), are the other nominated species included in the Trirachodontidae. To these should be added isolated teeth coming from the Yerrapali Formation of India (Bandyopadhyay and Sengupta, 1999), a series of skulls from the Omingonde Formation of Namibia (Smith and Swart, 2002) and a taxonomically dubious record from the Redonda Formation in the United States (Lucas et al., 1999).

Three cusps forming a transverse crest in the middle of the tooth and a series of circular cusps located in the anterior and posterior margin of the tooth characterize the gomphodont postcanines of trirachodontids. This pattern is quite similar in upper and lower teeth, but the latter differ in having a more ovoid (i.e., less expanded bucco-lingually) postcanine shape. Variations in the upper gomphodont crown morphology can be observed between different trirachodontids. *Trirachodon berryi* features a crown that is ellipsoid (i.e., more expanded bucco-lingually; Fig. 7B), with bucco-lingual (b-l)/antero-posterior (a-p) ratio in the

TABLE 3. Skull length of the largest *Trirachodon* specimens from subzones A and B of the *Cynognathus* AZ and *Sinognathus* from the upper Ermaying Formation, China (in mm).

	Skull Length	References
BP/1/4661	*87	
BP/1/4658	99	
AM 461	*100	Seeley (1895)
NMQR 3255	100	
NMQR 1349	*102	
BP/1/5362	113	
<i>Sinognathus</i>	121	Sun (1988)

\*Estimated.

widest postcanines ranging between 0.40 and 0.50. A similar ellipsoid condition seems to be present in the poorly preserved postcanines of *Sinognathus* (Sun, 1988; fig. 4). On the other hand, the undescribed species from subzone A of the *Cynognathus* AZ shows an almost circular outline of the gomphodont upper postcanines (Fig. 7A). In the holotype and single specimen of *Cricodon metabolus* (UMCZ T 905) they are less expanded bucco-lingually than in *T. berryi* resulting in an ovoid tooth (Crompton, 1955; Fig. 7C). In *C. metabolus*, one postcanine has a b-l/a-p ratio equal to 0.46, while in the remaining upper teeth the ratio ranges between 0.52 and 0.55.

The ovoid condition of the upper postcanines in BP/1/6102 (b-l/a-p ratio between 0.52 to 0.53 in the posterior postcanines) and BP/1/5538 (b-l/a-p ratio 0.63) closely resemble the pattern that characterizes *Cricodon metabolus* (see Figs. 6 and 7). In both *T. berryi* and *C. metabolus* the central and lingual cusps of the transverse crest are close to each other, being slightly closer in *C. metabolus* and in BP/1/5538 (Figs. 6, 7B, C). The proximity of the central and lingual cusps is particularly interesting because the same pattern is recorded in all the traversodontid cynodonts featuring three cusps in the transverse crest (Abdala and Ribeiro, 2003). Another interesting feature in trirachodontids is the development of the anterior dentition with incisors showing crowns notably higher than those of the postcanines. The ratio (0.42) between the height of the fourth incisor and the highest postcanine of the row in BP/1/6102 shows the postcanine crown height to be lower than the middle of the incisor height. The same ratio in smaller specimens of trirachodontids from subzone B, such as NMQR 3280, was 0.61.

The skull of *C. metabolus* is fragmentary, but the preserved mandibles suggest that this species may have reached 150–160 mm in length, thus approaching the size of the smaller trirachodontid specimens from the subzone C. The extensive record of *Trirachodon* in the older subzones A and B show only smaller sizes (ca. 100 mm). *Trirachodon berryi* from subzone B is known from a minimum of five sites (Kitching, 1977), some of them, e.g., Winaarsbaken, presenting hundreds of individuals.

Given the above-mentioned similarities in their overall postcanine shape, we consequently assign the subzone C trirachodontid specimens to *C. metabolus*. In addition, the larger size of the trirachodontids from the subzone C is compatible with the 150 or 160 mm of skull length estimated for the Tanzanian species.

#### CORRELATION OF THE FAUNA

Although the fauna of the uppermost Burgersdorp Formation (*Cynognathus* AZ, subzone C) is the least well documented of the three subzones, it is now known to comprise the cynodonts *Cynognathus*, *Diademodon*, and *Cricodon*, the dicynodonts *Angonisauros* (Hancox and Rubidge, 1994, 1996), an undescribed shansiodont (Hancox, 1998), and the mastodontosaurid amphibian *Paracyclotosaurus* (Hancox et al., 2000; Damiani and Hancox, 2003).

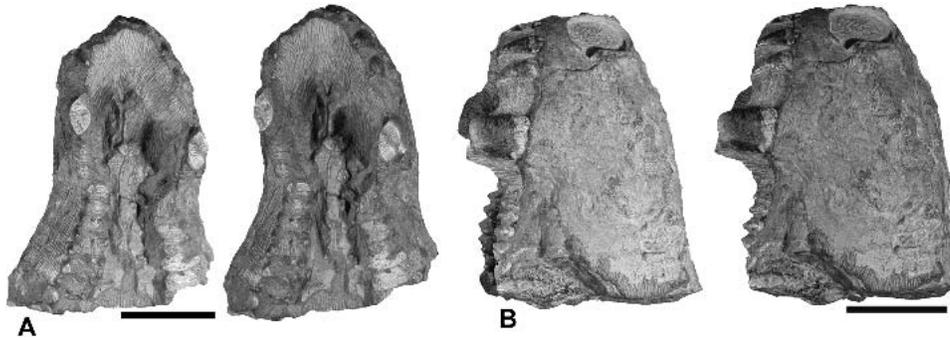


FIGURE 4. Trirachodontid specimen BP/1/6102. **A**, stereopair of the palatal view; **B**, stereopair of left lateral view. Scale equals 3 cm.

Based on the co-occurrence of the dicynodont *Angonisaurus* (Cox and Li, 1983) and the gomphodont cynodonts *Diademodon* and *Cricodon* (Crompton, 1955), subzone C may be directly correlated with the fauna from the Manda Formation of Tanzania, East Africa (Fig. 8). The Manda Formation fauna is variously considered as Anisian (Cox, 1991; King, 1993), uppermost Anisian (Cox and Li, 1983), and ?upper Anisian (Cruikshank, 1986). In addition, there are suggestions that the fauna from the Manda Formation could be represented by more than one age (Boonstra 1953; Charig, 1963; Gay and Cruikshank, 1999). This idea is also strongly supported by the notable differentiation of the traversodontid cynodont from that formation (Crompton, 1955, 1972; Hopson, 1984; Abdala and Ribeiro, 2003). These putative Manda faunas may contain not only components of subzone C fauna, but also a slightly younger fauna as well (Fig. 8).

The presence of *Paracyclotossaurus* within the subzone C assemblage allows for it to be directly correlated with the Denwa Formation of the Satpura Basin, India, and the Ashfield Shale of the Wianamatta Group of the Sydney Basin, Australia (Fig. 8; Damiani and Hancox, 2003). The upper fauna of the Denwa Formation from India is considered as lowermost Anisian, based on the presence, in its upper part, of a brachyopid amphibian most similar to *Hadrokkosaurus* (= *Vigilius*; Warren and Marsicano, 2000), which is known from the Holbrook Member of the Moenkopi Formation of U.S.A. (Bandyopadhyay and Sengupta, 1999). The presence of the mastodontosaurid *Cherninia denwai* (= *Parotosuchus denwai* of Bandyopadhyay and Sengupta, 1999; Damiani, 2001a) and in particular, *Paracyclotossaurus crookshanki* (= *Parotosuchus crookshanki* of Bandyopadhyay and Sengupta, 1999; Damiani, 2001b; Damiani and Hancox, 2003) in the Denwa Formation indicate that a younger age (i.e., latest Anisian) is also possible for this unit (Damiani, pers. comm.). The Wianamatta Group is dated as Anisian-Ladinian on the basis of palynomorphs and plant macrofossils (Warren and Marsicano, 1998). The Ashfield Shale occurs at the base of the Wianamatta Group and is probably late Anisian in age (Damiani and Hancox, 2003).

Although it shares a number of taxa with the *Cynognathus* Subzone C, correlation with the fauna of Omingonde Formation of Namibia is less clear-cut. The Namibian sequence contains the dicynodonts *Kannemeyeria cristarhynchus* and *Dolichuranus*, as well as numerous cynodont taxa including *Cynognathus*, *Diademodon*, *Titanogomphodon*, and *Trirachodon* (Keyser, 1973; Smith and Swart, 2002), with the last genus being particularly abundant in the fauna of the upper part of the Upper Omingonde Formation (Smith and Swart, 2002). It is significant that the *Trirachodon* specimens from Namibia, like *Cricodon* from subzone C and the Manda Formation, attain a larger size than specimens from the older *Cynognathus* subzone faunas. The Up-

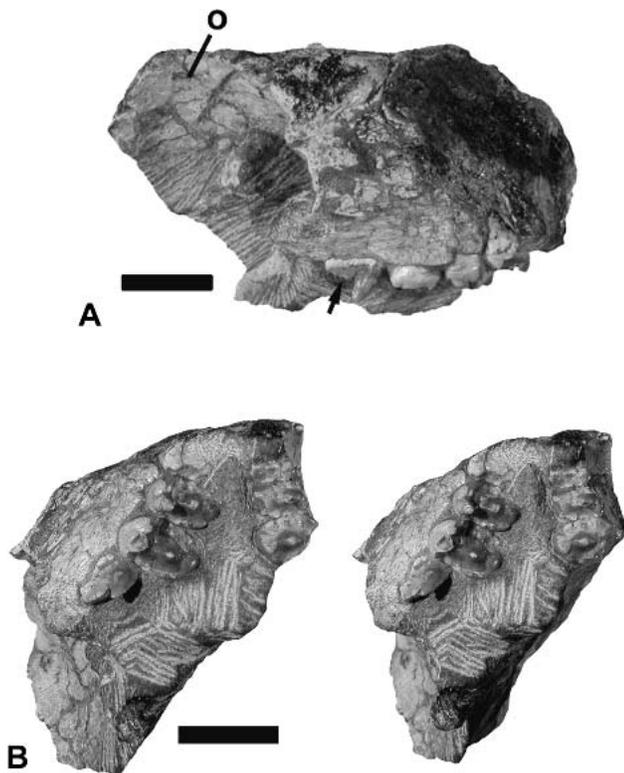


FIGURE 5. Trirachodontid specimen BP/1/5538. **A**, lateral view of the snout fragment; Arrow indicates sectorial postcanine. **B**, stereopair showing the postcanine pattern. **Abbreviation:** o, orbit. Scale equals 1 cm.

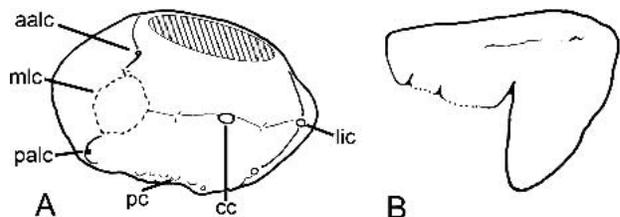


FIGURE 6. Trirachodontid specimen BP/1/5538. **A**, occlusal view of the last right gomphodont postcanine; posterior cingulum is from BP/1/6102; labial, left; anterior, top. **B**, lateral view of the right sectorial postcanine; anterior, right. **Abbreviations:** aalc, anterior accessory labial cusp; cc, central cusp; lic, lingual cusp; mlc, main labial cusp; palc, posterior accessory labial cusp; pc, posterior cingulum. Hatched pattern indicates wear.



uncertainty exists regarding 'index fossil,' as it is not consistently applied throughout Lucas's (1998) proposition (i.e., the cynodont genus *Exaeretodon*, an index fossil for the Berdyankian LVF, is also cited for faunas of the Otischalkian and Adamanian LVF's). In addition, the status of *Trirachodon* as an index fossil for the Nonensian remains doubtful until more detailed taxonomic studies on the Namibian trirachodontids are made.

In conclusion, interbasinal correlations suggest an Anisian age for the fauna of the *Cynognathus* Subzone C, with some evidence implying a late Anisian age. The *Cynognathus* Assemblage Zone as a whole would therefore range from the late Olenekian to the late Anisian. Taking into account the non-marine faunachrons proposed by Lucas (1998), the subzones A and B of the *Cynognathus* AZ are considered as part of the Nonensian LVF, while the younger subzone C is included in the Perovkan LVF.

#### ACKNOWLEDGMENTS

For access to various collections, gratitude is extended to B. de Klerk (Albany Museum, Grahamstown), M. A. Raath (Bernard Price Institute for Palaeontological research, University of the Witwatersrand), J. Welman (National Museum Bloemfontein), S. Kaal and R. Smith (South African Museum, Cape Town) and J. Clack (University Museum of Zoology, Cambridge). PJH is grateful to the farmers in the Bamboeshoek Valley of the Eastern Cape for permission to work on their farms, their interest in this research, and their generous hospitality. FA is particularly grateful to J. Clack and M. Allinson from Cambridge for their support and help while he was in the U. K. We thank R. Damiani for discussions about Triassic amphibian faunas. Comments by G. King, M. C. Langer, S. G. Lucas, and C. A. Sidor have been especially appreciated. Financial support was provided by the University of the Witwatersrand Research Council through a Postdoctoral Research Fellowship to FA. The Royal Society and PAST (Palaeo-Anthropological Scientific Trust, Johannesburg) provided FA grants that made possible a research visit to the U.K. paleontological collections.

#### LITERATURE CITED

- Abdala, F., and N. P. Giannini. 2000. Gomphodont cynodonts of the Chañares Formation: the analysis of an ontogenetic sequence. *Journal of Vertebrate Paleontology* 20:501–506.
- Abdala, F., and A. M. Ribeiro. 2003. A new traversodontid cynodont from the Santa Maria Formation (Ladinian-Carnian) of southern Brazil, with a phylogenetic analysis of Gondwanan traversodontids. *Zoological Journal of the Linnean Society* 139:529–545.
- Allin, E. F. 1975. Evolution of the mammalian middle ear. *Journal of Morphology* 147:403–438.
- Allin, E. F., and J. A. Hopson. 1992. Evolution of the auditory system in Synapsida ("Mammal-like Reptiles" and primitive Mammals) as seen in the fossil record; pp. 587–614 in D. B. Wester, R. R. Fay, and A. N. Popper (eds.), *The Evolutionary Biology of Hearing*. Springer Verlag, New York.
- Anderson, J. M., and H. M. Anderson. 1970. A preliminary review of the biostratigraphy of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland. *Palaeontologia africana* 13:1–23.
- Anderson, J. M., and A. R. I. Cruickshank. 1978. The biostratigraphy of the Permian and Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontologia africana* 21:15–44.
- Bandyopadhyay, S., and D. P. Sengupta. 1999. Middle Triassic vertebrates of India. *Journal of African Earth Sciences* 29:233–241.
- Battail, B. 1988. Biostratigraphie des formations Permo-Triasiques continentales à Vertébrés tétrapodes et biogéographie du Gondwana. *Annales de la Société Géologique du Nord* 107:37–44.
- Battail, B. 1993. On the biostratigraphy of the Triassic therapsid bearing formations; pp. 31–35 in S. G. Lucas and M. Morales (eds.), *The Nonmarine Triassic*. New Mexico Museum of Natural History and Science Bulletin 3.
- Bender, P., and P. J. Hancox. 2004. Newly discovered fish faunas from the Early Triassic, Karoo Basin, South Africa, and their correlative implications. *Gondwanan Research* 7:185–192.
- Boonstra, L. D. 1953. A report on a collection of fossil reptilian bones from Tanganyika Territory. *Annals of the South African Museum* 42:5–18.
- Broom, R. 1904. On a new South African labyrinthodont (*Cyclotosaurus albertyni*). *Records of the Albany Museum* 1:178–180.
- Charig, A. J. 1963. Stratigraphical nomenclature in the Songea Series of Tanganyika. *Records of the Geological Survey of Tanganyika* 10:47–53.
- Chernin, S. 1978. Three capitosaurids from the Triassic of South Africa: *Parotosuchus africanus* (Broom 1909), *Kestrosaurus dreyeri* (Haughton 1925) and *Parotosuchus dirus* sp. nov. *Palaeontologia africana* 21:79–100.
- Cooper, M. R. 1982. A mid-Permian to earliest Jurassic tetrapod biostratigraphy and its significance. *Arnoldia* 9:77–104.
- Cosgriff, J. W. 1965. A new genus of Temnospondyl from the Triassic of Western Australia. *Journal of the Royal Society of Western Australia* 48:65–90.
- Cosgriff, J. W. 1984. The temnospondyl labyrinthodonts of the earliest Triassic. *Journal of Vertebrate Paleontology* 4:30–46.
- Cox, C. B. 1991. The Pangaea dicynodont *Rechnisaurus* and the comparative biostratigraphy of Triassic dicynodont faunas. *Palaeontology* 34:767–784.
- Cox, C. B., and Li, J.-L. 1983. A new genus of Triassic dicynodont from East Africa and its classification. *Palaeontology* 26:389–406.
- Crompton, A. W. 1955. On some Triassic cynodonts from Tanganyika. *Proceedings of the Zoological Society of London* 125:617–669.
- Crompton, A. W. 1972. Postcanine occlusion in cynodonts and tritylodontids. *Bulletin of the British Museum of Natural History, Geology*, London 21:27–71.
- Crompton, A. W. 1995. Masticatory function in nonmammalian cynodonts and early mammals; pp. 55–75 in J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, New York.
- Crompton, A. W., and W. L. Hylander. 1986. Changes in mandibular function following the acquisition of a dentary-squamosal jaw articulation; pp. 263–282 in N. Hotton III, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), *The Ecology and Biology of Mammal-like Reptiles*. Smithsonian Institution Press, Washington D. C.
- Cruickshank, A. R. I. 1986. Biostratigraphy and classification of a new Triassic dicynodont from East Africa. *Modern Geology* 10:121–131.
- Damiani, R. 1999. *Parotosuchus* (Amphibia, Temnospondyli) in Gondwana: biostratigraphic and palaeobiogeographic implications. *South African Journal of Science* 95:458–460.
- Damiani, R. 2001a. Cranial anatomy of the giant Middle Triassic temnospondyl *Cherninia megarhina* and a review of feeding in mastodontosaurids. *Palaeontologia Africana* 37:41–52.
- Damiani, R. 2001b. A systematic revision and phylogenetic analysis of Triassic mastodontosaurids (Temnospondyli: Stereospondyli). *Zoological Journal of the Linnean Society* 133:379–482.
- Damiani, R., and P. J. Hancox. 2003. New mastodontosaurid temnospondyls from the *Cynognathus* Assemblage Zone (Upper Beaufort Group; Karoo Basin) of South Africa. *Journal of Vertebrate Paleontology* 23:54–66.
- Damiani, R., J. Neveling, J. Hancox, and B. Rubidge. 2000. First trematosaurid temnospondyl from the *Lystrosaurus* Assemblage Zone of South Africa and its biostratigraphic implications. *Geological Magazine* 137:659–665.
- Farabee, M. J., E. L. Taylor, and N. T. Taylor. 1990. Correlation of Permian and Triassic palynomorph assemblages from the central Transantarctic Mountains, Antarctica. *Review of Palaeobotany and Palynology* 65:257–265.
- Fourie, S. 1963. Tooth replacement in the gomphodont cynodont *Dia-demodon*. *South African Journal of Science* 59:211–213.
- Gay, S. A., and A. R. I. Cruickshank. 1999. Biostratigraphy of the Permian tetrapod faunas from the Ruhuhu Valley, Tanzania. *Journal of African Earth Sciences* 29:195–210.
- Gow, C. 1999. The Triassic reptile *Palacrodon browni* Broom, synonymy and a new specimen. *Palaeontologia Africana* 35:21–23.
- Groenewald, G. H., and J. W. Kitching. 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone; pp. 35–39 in B. S. Rubidge (ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series 1.
- Groenewald, G. H., J. Welman, and J. A. MacEachern. 2001. Vertebrate burrow complexes from the Early Triassic *Cynognathus* Zone

- (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaios*:148–160.
- Hammer, W. R. 1988. The *Cynognathus* Zone (late Early Triassic) vertebrate fauna from Antarctica. *Antarctic Journal of the United States* 23:1–10.
- Hammer, W. R. 1990. Triassic terrestrial vertebrate faunas of Antarctica; pp. 42–50 in T. N. Taylor and E. L. Taylor (eds.), *Antarctic Paleobiology: its role in the reconstruction of Gondwanaland*. Springer-Verlag, New York.
- Hammer, W. R. 1995. New therapsids from the Upper Fremouw Formation (Triassic) of Antarctica. *Journal of Vertebrate Paleontology* 15:105–112.
- Hancox, P. J. 1998. A Stratigraphic, Sedimentological and Palaeoenvironmental synthesis of the Beaufort-Molteno contact in the Karoo Basin. Ph.D. Thesis, University of the Witwatersrand, Johannesburg, 404 pp.
- Hancox, P. J. 2000. The Continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie, Teil I, Heft 11–12*, 1998: 1285–1324.
- Hancox, P. J., and B. S. Rubidge. 1994. A new dicynodont therapsid from South Africa: implications for the biostratigraphy of the Upper Beaufort (*Cynognathus* Assemblage Zone). *South African Journal of Science* 90:98–99.
- Hancox, P. J., and B. S. Rubidge. 1996. The first specimen of the Mid-Triassic dicynodont *Angonisaurus* from the Karoo of South Africa: implications for the dating and biostratigraphy of the Upper Beaufort Group. *South African Journal of Science* 92:391–392.
- Hancox, P. J., and B. S. Rubidge. 2001. Breakthroughs in the biodiversity, biogeography, biostratigraphy and basin analysis of the Beaufort Group. *Journal of African Earth Sciences* 33:563–577.
- Hancox, P. J., R. J. Damiani, and B. S. Rubidge. 2000. First occurrence of *Paracyclotossaurus* (Temnospondyli, Capitosauridae) in the Karoo Basin of South Africa and its biostratigraphic significance. *South African Journal of Science* 96:135–137.
- Hancox, P. J., M. A. Shishkin, B. S. Rubidge, and J. W. Kitching. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographic implications. *South African Journal of Science* 91:143–144.
- Haughton, S., and A. S. Brink. 1954. A bibliographic list of Reptilia from the Karoo Beds of Africa. *Palaeontologia Africana* 25:1–187.
- Hopson, J. A. 1984. Late Triassic traversodont cynodonts from Nova Scotia and southern Africa. *Palaeontologia Africana* 25:181–201.
- Hopson, J. A., and J. W. Kitching. 1972. A revised classification of cynodonts (Reptilia; Therapsida). *Palaeontologia Africana* 14:71–85.
- Hopson, J. A., and J. W. Kitching. 2001. A probainognathian cynodont from South Africa and the phylogeny of the nonmammalian cynodonts. *Bulletin of the Museum of Comparative Zoology* 156:5–35.
- Huene, F. von. 1940. Die Saurier der Karoo-, Gondwana- und verwandten Ablagerungen in faunistischer, biologischer und phylogenetischer Hinsicht. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Abt. B* 149:1–65.
- Jenkins, F. A., Jr. 1971. The postcranial skeleton of African cynodonts. *Peabody Museum of Natural History, Bulletin* 36:1–216.
- Johnson, M.A. 1994. *Lexicon of South African Stratigraphy*. Council for Geosciences, Pretoria, 56 pp.
- Keyser, A. W. 1973. A new vertebrate fauna from South West Africa. *Palaeontologia Africana* 16:1–15.
- Keyser, A. W., and A. R. I. Cruickshank. 1979. The origins and classification of Triassic dicynodonts. *Transactions of the Geological Society of South Africa* 82:81–108.
- King, G. M. 1993. Ecology and biogeography of Triassic non-mammalian therapsids. *Palaeontologia Lombarda della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, Nuova Serie* 2:73–82.
- King, G. M., 1996. A description of the skeleton of a bauriid therapsid from the Early Triassic of South Africa. *Annals of the South African Museum* 104:379–393.
- Kitching, J. W. 1977. The distribution of the Karoo vertebrate fauna. *Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Memoir* 1:1–131.
- Kitching, J. W. 1995a. Biostratigraphy of the *Dicynodon* Assemblage Zone; pp. 29–34 in B. S. Rubidge (ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series 1.
- Kitching, J. W. 1995b. Biostratigraphy of the *Cynognathus* Assemblage Zone; pp. 40–45 in B. S. Rubidge (ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series 1.
- Lucas, S. G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 143:347–384.
- Lucas, S. G. 1999a. A tetrapod-based Triassic timescale. *Albertiana* 22: 31–40.
- Lucas, S. G. 1999b. The epicontinental Triassic, an overview. *Zentralblatt für Geologie und Paläontologie, Teil I, Heft 7–8*, 1998:475–496.
- Lucas, S. G., J. W. Estep, A. B. Heckert, and A. P. Hunt. 1999. Cynodont teeth from the Upper Triassic of New Mexico, USA. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1999:331–344.
- Neveling, J. 2002. Biostratigraphic and sedimentological investigation of the contact between the *Lystrosaurus* and *Cynognathus* Assemblage Zones (Beaufort Group: Karoo Supergroup). Ph.D. Thesis, University of the Witwatersrand, Johannesburg, 232 pp.
- Neveling, J., B. S. Rubidge, and P. J. Hancox. 1999. A lower *Cynognathus* Assemblage Zone fossil from the Katberg Formation (Beaufort Group, South Africa). *South African Journal of Science* 95:555–556.
- Neveling, J., J. Welman, and B. Battail. 2001. A new species of *Trirachodon* (Cynodontia): consequences for cynodont evolution. *Paleobios* 21 (Supplement 2):91.
- Neveling, J., P. J. Hancox, R. Damiani, and B. S. Rubidge. 2000. Early Triassic faunas from the *Lystrosaurus* and *Cynognathus* Assemblage Zones, South Africa. *Journal of Vertebrate Paleontology* 20:60A.
- Ochev, V. G., and M. A. Shishkin. 1989. On the principles of global correlation of the continental Triassic on the tetrapods. *Acta Palaeontologica Polonica* 34:149–173.
- Renaut, A. J. 2000. A re-evaluation of the cranial morphology and taxonomy of the Triassic dicynodont genus *Kannemeyeria*. Ph.D. Thesis, University of the Witwatersrand, Johannesburg, 294 pp.
- Ross, C. A., A. Baud, and M. Menning. 1994. Project Pangea Time Scale. p. 10 in G. D. Klein (ed.), *Pangea: Paleoclimate, Tectonics and Sedimentation During Accretion, Zenith, and Breakup of a Supercontinent*. Geological Society of America, Special Paper 288.
- Rowe, T. 1988. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology* 8:241–264.
- Seeley, H. G. 1895. Researches on the structure, organization and classification of the fossil Reptilia. Part IX. Section 4. On the Gomphodontia. *Philosophical Transactions of the Royal Society of London* 186:1–57.
- Seeley, H. G. 1908. On the dentition of the diastema in some fossil reptiles referred to Gomphodontia, from the Upper Karoo rocks of the Cape Colony. *Annals and Magazine of Natural History* 8:376–382.
- Shishkin, M. A., B. S. Rubidge, and P. J. Hancox. 1995. Vertebrate biozonation of the Upper Beaufort Series of South Africa – a new look on correlation of the Triassic biotic events in Euramerica and southern Gondwana; pp. 39–41 in A. Sun and Y. Wang (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. China Ocean Press, Beijing.
- Sidor, C. A., and R. M. H. Smith. 2004. A new galesaurid (Therapsida: Cynodontia) from the Lower Triassic of South Africa. *Palaeontology* 47:535–556.
- Smith, R. M. H., and R. Swart. 2002. Changing fluvial environments and vertebrate taphonomy in response to climatic drying in a Mid-Triassic rift valley fill: the Omingonde Formation (Karoo Supergroup) of central Namibia. *Palaios* 17:249–267.
- Sun, A. 1988. Additional study on *Sinognathus gracilis* (Cynodontia; Reptilia). *Vertebrata Palasiatica* 26:173–180.
- Tatarinov, L. P. 2002. Gomphodont cynodonts (Reptilia, Theriodontia) from the Middle Triassic of the Orenburg Region. *Paleontological Journal* 36:176–179.
- Warren, A., and C. Marsicano. 1998. Revision of the Brachyopidae (Temnospondyli) from the Triassic of the Sydney, Carnarvon and Tasmanian Basins, Australia. *Alcheringia* 22:329–342.
- Warren, A., and C. Marsicano. 2000. A phylogeny of the brachyopoidea (Temnospondyli, Stereospondyli). *Journal of Vertebrate Paleontology* 20:462–483.
- Welman, J., G. H. Groenewald, and J. W. Kitching. 1991. Confirmation of the occurrence of *Cynognathus* Zone (*Kannemeyeria-Diademodon* Assemblage-zone) deposits (uppermost Beaufort Group) in the northeastern Orange Free State, South Africa. *South African Journal of Geology* 94:245–248.