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The postcranial skeleton of the basal therocephalian *Glanosuchus macrops* (Scylacosauridae) and comparison of morphological and phylogenetic trends amongst the Theriodontia

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The postcranial morphology of the early scylacosaurid therocephalian *Glanosuchus macrops* from the *Pristerognathus* Assemblage Zone of the Beaufort Group is described and compared with that of later therocephalians. This database is used as a basis to identify postcranial differences between therocephalians, gorgonopsians and cynodonts in an attempt to increase understanding of the postcranial anatomy of theriodont therapsids. It is demonstrated that some postcranial elements can be used to identify particular theriodont groups. The T-shaped interclavicle, absence of ossified sternum, humerus without shaft area, and large pubic foramen are characteristics of therocephalians from the *Tapinocephalus* Assemblage Zone of the Beaufort Group of South Africa.

Keywords: Therocephalia, *Glanosuchus,* therapsid postcranium, Theriodontia.

INTRODUCTION

The rocks of the Karoo Supergoup are internationally acclaimed for their richness and diversity of fossil therapsids of Mid Permian to Early Jurassic age. Despite being one of the six important therapsid clades, the Therocephalia has received relatively little recent research attention, apart from the basal forms (Abdala *et al.* 2008; van den Heever 1994). Therocephalians have a wide geographic distribution, being known from southern and eastern Africa (Keyser & Brink 1979; Boonstra 1935; Drysdall & Kitching 1963; Boonstra 1969; Kitching 1977), China (Li & Cheng 1995), Russia (Tatarinov 1974), eastern Europe (Golubev 2000), and Antarctica (Colbert & Kitching 1981) and together with dicynodonts, have the longest stratigraphic range of any therapsid clade.

As relatively little work has been done on the postcranial anatomy of basal therocephalians this description of a recently discovered skeleton of a scylacosaurid is of importance in our understanding of the development and functioning of early therapsid postcranial morphology. Broom (1936) superficially described the incomplete skeleton of *Pristerognathus baini* (now *Glanosuchus*) (van den Heever 1994) and Boonstra (1964) described the girdles and limbs of the Lycosauria and the Scylacosauria. Cys (1967) described the postcranium of *Cynariognathus platyrhinus.* Ray *et al.* (2004), as part of a groundbreaking comparative study of bone microstucture of selected therocephalian, gorgonopsian and cynodont genera, described the bone histology of *Pristerognathus.* Our study is the first description of both the axial and appendicular skeleton of a scylacosaurid therocephalian and provides a comparison with postcranial elements of other theriodont nonmammalian therapsids.

MATERIAL

The specimen of *Glanosuchus macrops* (SAM-PK K 7809) which forms the basis of this study was found in 1989 by Roger Smith on the farm La de Da, Beaufort West, which is situated in the *Pristerognathus* Assemblage Zone (Lower Teekloof Formation) of the Beaufort Group. Mechanical preparation, carried out by Annelise Crean at the Iziko South African Museum, exposed the dorsal side of the curled-up skeleton (Fig. 1). In comparison with other therocephalian postcrania from the lower Beaufort, which are generally poorly and incompletely preserved (van den Heever 1994), this articulated specimen is uniquely well preserved and fairly complete.

Basal Therocephalia comprises two clades, Scylacosauridae and Lycosuchidae, which are both characterized by the presence of serrated teeth, three lower incisors, large canines, narrow unfused vomer and a well-developed postfrontal. *Glanosuchus* is identified on cranial features as a large scylacosaurid with dental formula I5+1, C1, Pc5; first five incisors large but sixth inconstant and when present very small; canine large and strong; postcanines moderately to weakly developed; skull large (maximum length 315–321); preorbital hollow fairly shallow, not sharply demarcated and really not more than a groove stretching from the orbit in the direction of the canine; septomaxilla and septomaxillary foramen well developed; snout broader than high, slightly narrowed between orbit and canines; orbits well in posterior half of skull; mandibular symphyses formed solely by dentaries with weak, unankylosed sloping mentum; epipterygoid only slightly widened; sagittal crest of parietals only moderately high but fairly sharp (van den Heever 1994).

POSTCRANIAL DESCRIPTION

Only the left side of the skull of SAM-PK K 7809 is exposed and the left forelimb, including the articulated manus, is well preserved close to the cranium (Fig. 1). The right forelimb is beneath the body and has not been prepared. Most of the dorsal view of the pectoral girdle is obscured by thoracic vertebrae and ribs, allowing description of only parts of the clavicles. Well-preserved and

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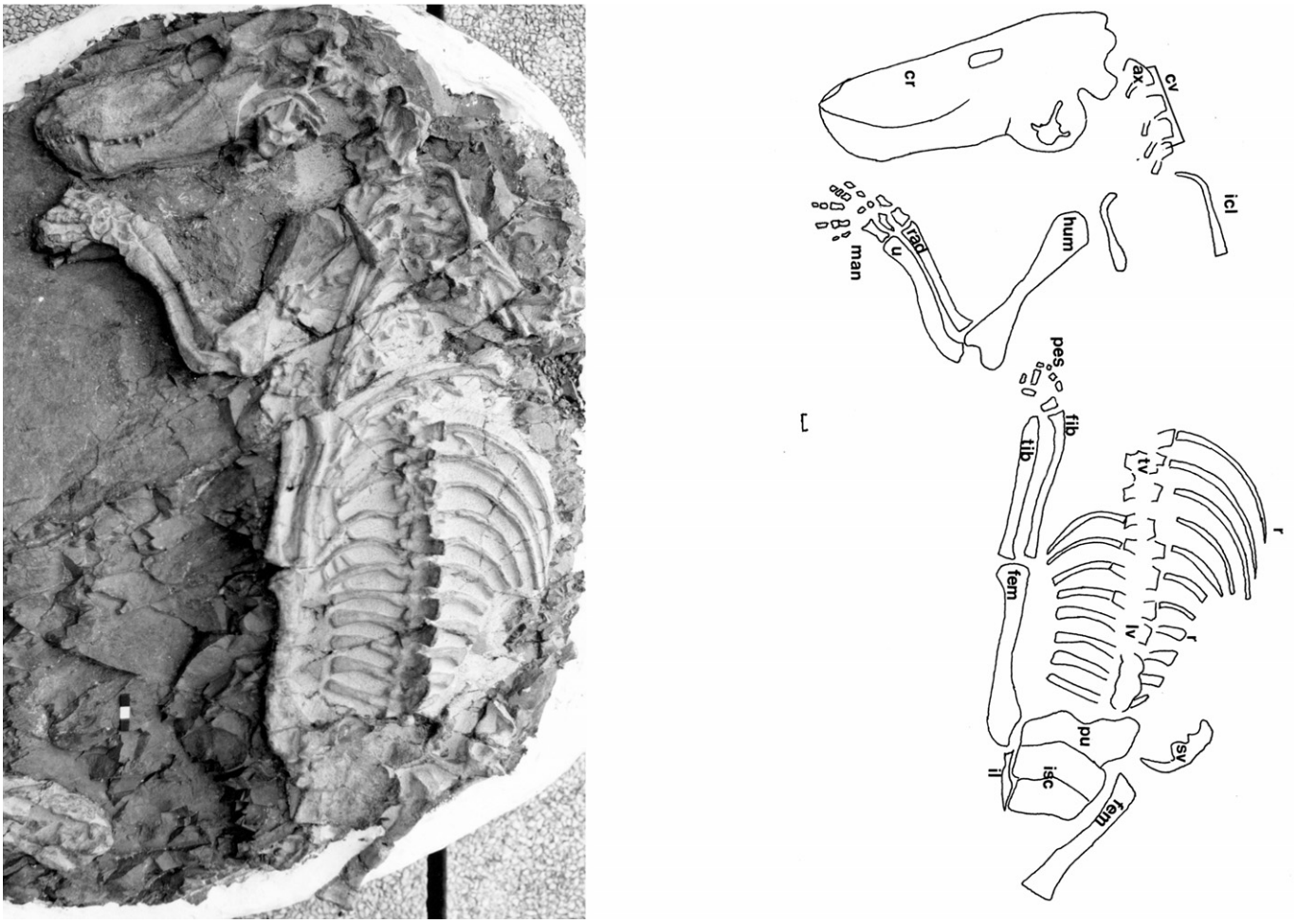


Figure 1. Dorsal view of *Glanosuchus macrops* (SAM-PK K 7809) to illustrate the position in which the postcranial elements are preserved (scale 10 mm) and photograph of dorsal view of *Glanosuchus macrops* (SAM-PK K 7809) to show morphological detail (scale 10 mm).

fully articulated dorsal vertebrae are present behind the clavicles, making it possible to differentiate between thoracic and lumbar vertebrae and their respective ribs. In the sacral region only one sacral vertebra and one pair of ribs are visible. Of the pelvic girdle, both the pubes and ischia, and only the left ilium are preserved. The right hind limb lacks the tibia, fibula and pes, while the left hind limb is well preserved with the exception of the pes which is crushed. Only a few of the caudal vertebrae are preserved.

Vertebrae

The vertebral column, which is almost completely articulated, allows a vertebral count of at least forty-one vertebrae (Fig. 2). This figure includes 28 presacrals, one sacral, four caudals and eight unidentifiable vertebrae. Presacrals are divided into cervical, thoracic and lumbar vertebrae and are easy to distinguish on morphological grounds (Fourie 2001). Of these, six cervicals are preserved; the first five vertebrae (including the atlas and axis) are in articulation and the posterior cervical was disarticulated and displaced prior to fossilization. At least 22 dorsal vertebrae (sixteen thoracic, six lumbar) are preserved with attached ribs.

Very little of the proatlas can be described as only a very small portion of the right neural arch of this vertebra is visible in dorsal view as a rectangular piece of bone. The atlas neural arch is wider laterally than medially with a convex dorsal surface. The axis is preserved in articulation with the remaining three or four cervicals and has the same morphology as described for *Cynariognathus* (Cys 1967), a baurioid (Kemp 1986), and *Regisaurus* (Fourie & Rubidge 2007). The longitudinally expanded axial neural spine, when viewed from above, is thin dorsally, almost sharp and slopes gently anteroventrally making it higher posteriorly than anteriorly (Fig. 2A). Of all the cervical vertebrae, the neural spine of the axis has the greatest anteroposterior expansion and is widest at its most dorsal extremity. The postzygapophysis, which protrudes posteriorly beyond the centrum, is disc-like with slightly rounded dorsal, posterior and posterolateral areas. Anteroventral to the postzygapophysis the long, rectangular transverse process slopes slightly ventrally. The prezygapophysis is positioned anterior to the transverse process and extends anteriorly beyond the centrum. In lateral view the centrum is hourglass-shaped and in anterior view it is amphicoelus.

Apart from the atlas and axis there are 3–4 additional cervical vertebrae which have narrower rectangular neural spines and a triangular dorsal surface with the apex pointing anteriorly. The morphology of the rest of the vertebra is similar to that of the axis. As in other therocephalians (Fourie & Rubidge 2007), cervical vertebrae are easily distinguished from those of the thoracic-lumbar

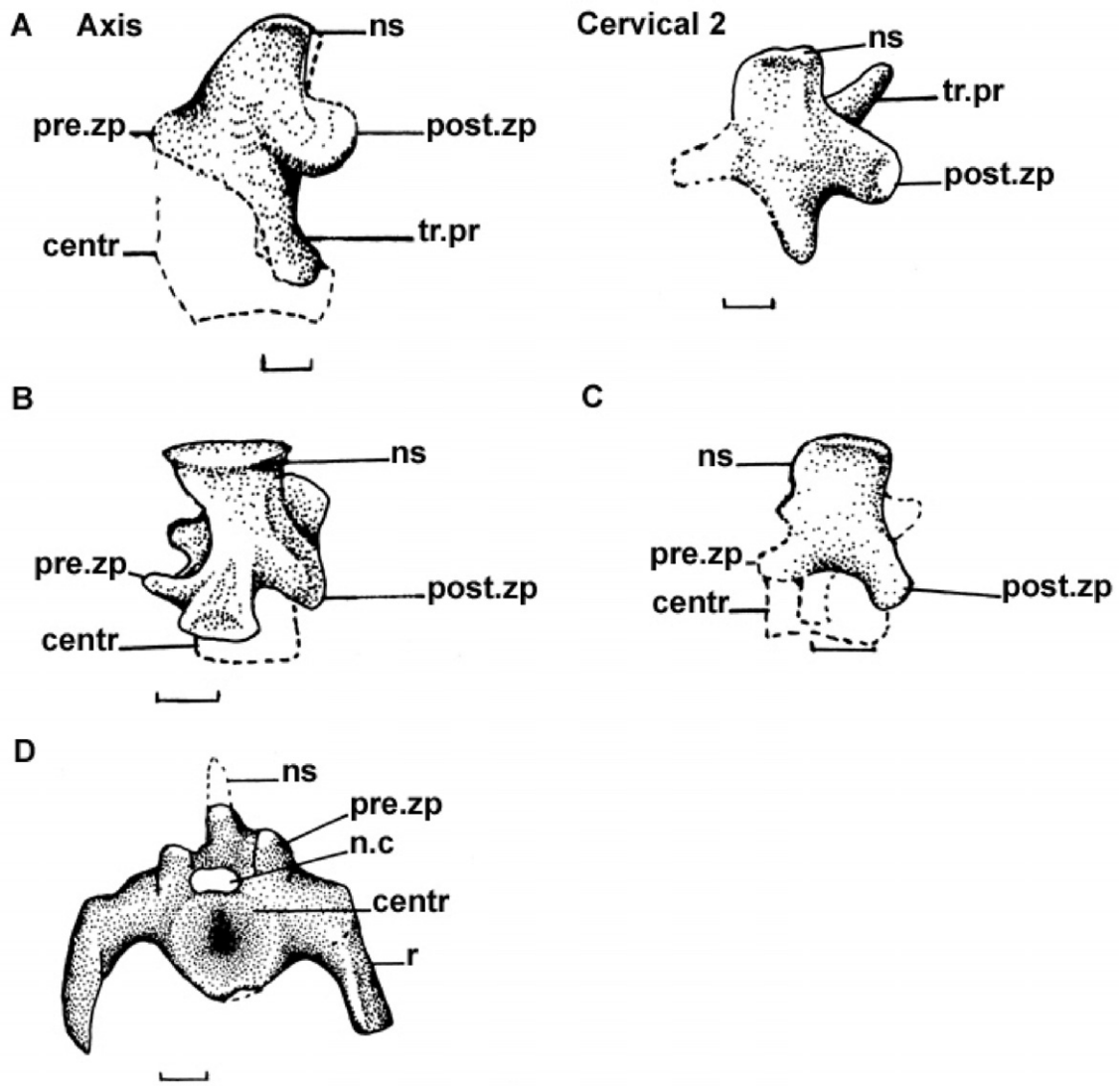


Figure 2. Vertebrae of *Glanosuchus macrops* (SAM/K 7809); **A**, axis and cervical C2 (lateral view); **B**, thoracic T13 (lateral view); **C**, lumbar L2 (lateral view); **D**, sacral (anterior view) (scale 10 mm).

region in that the cervicals are more massive.

Sixteen thoracic vertebrae are present in SAM-PK K 7809 and each has the same general morphology as the cervical and lumbar vertebrae (Fig. 2B) described for *Glanosuchus* and *Cynariognathus* (Cys 1967). In comparison with the thoracic vertebrae, in lateral view the lumbar neural spines (Fig. 2C) are shorter and broader, with that of the first lumbar being the broadest. In addition, lumbar vertebrae are easily recognized by their short and broad posteroventrally sloping transverse processes and shorter ribs which are fused to the transverse process and have no connection with the sternum.

Only one sacral vertebra is preserved and is exposed in anterior view (Fig. 2D). The amphicoelus centrum is large, concave towards the centre and round with a circular neural canal. A slight longitudinal elongated depression is present between the centrum and the base of the neural canal. The terminally rounded prezygapophysis, situated dorsolateral of the neural canal, slopes posteroventrally towards the transverse process. The transverse process is large and rounded dorsally.

The caudal series is incomplete, but the presence of four vertebrae indicates that the number in life was in excess of this. The first caudal vertebra is large, has prominent transverse processes, and appears to have the same morphology as that of other therocephalian genera (Fourie & Rubidge 2007). The short neural spine slopes down towards the almost square transverse process which is short, thick and rounded dorsally.

Ribs

Most of the ribs of SAM-PK K 7809 are preserved semi-articulated with their corresponding vertebrae (Fig. 3). The only preserved cervical rib was displaced prior to fossilization and is visible only in posterior view. This rib is short, slender and slightly curved with a double head. The tuberculum is thicker than the capitulum which is longer and thinner and has a short groove extending midway down the posterior side of the shaft as far as the distal end. The shaft portion of the rib is anteroposteriorly flattened with both dorsal and ventral edges rounded.

The anteriormost thoracic ribs are disarticulated and are preserved in the pectoral region, while five posterior thoracic ribs are preserved in articulation and are not fused to their corresponding vertebrae. Ribs in the thoracic region are long with double-heads, the capitulum

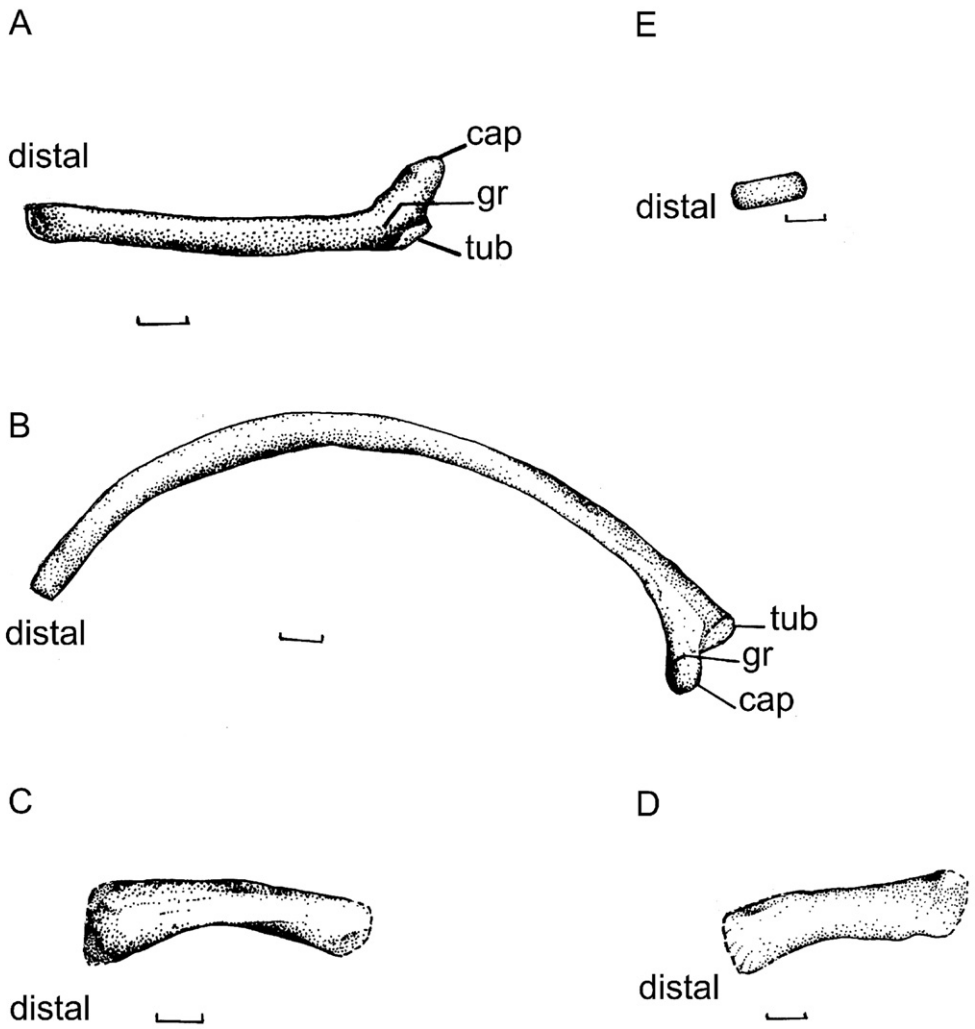


Figure 3. Ribs of *Glanosuchus macrops* (SAM-PK K7809); **A**, cervical (posterior view); **B**, thoracic (posterior view); **C**, lumbar (posterior view); **D**, sacral (anterior view); **E**, caudal (posterior view) (scale 10 mm).

being longer than the small rounded tuberculum. The middle thoracic rib (±14) is the longest, posteriorly they become progressively shorter towards the lumbar region (Fig. 1). Thoracic ribs (Fig. 3B) are similar in morphology to cervical ribs, but the shaft region curves ventrally for only one-third of its length, and the rest of the shaft is almost straight.

Six single-headed, short flat and straight lumbar ribs (Fig. 2B) are fused to the transverse processes of their respective vertebrae. These ribs become progressively shorter and straighter posteriorly and have rounded dorsal and concave ventral surfaces.

Only one pair of laterally expanded and single-headed sacral ribs is preserved (Fig. 3D). These are fused to the sacral vertebrae and have both proximal and distal ends enlarged to give the ribs a dorsoventrally flattened hourglass shape. In other Therocephalia there are normally three to four pairs of sacral ribs (Fourie & Rubidge 2007) and we presume the same would be true for *Glanosuchus.*

Four caudal vertebrae are present, each having a short rib which is fused to the transverse process. The ribs are single-headed, rectangular, short, and have rounded dorsal and ventral surfaces (Fig. 3E). The anteriormost caudal rib is the longest, and the remaining ribs become progressively shorter posteriorly.

Pectoral girdle

The scapula of scylacosaurids is a broadly fan-shaped bone which is slightly medially curved to follow the shape of the thorax. A prominent glenoid cavity has a dorsal scapular facet which faces dorso-laterally and slightly posteriorly, while the coracoid forms the ventral margin (Boonstra 1964).

The clavicle of *Glanosuchus* (Fig. 4A) has the same morphology as that described for *Lycosuchus (Zinnosaurus)* (Boonstra 1964) and is a long, thin and curved bone with expanded ends. Proximolaterally the bone surface is convex and narrows towards the middle of the almost circular shaft. It points upward past the anterior end of the procoracoid and lower part of the scapula to meet the anterior edge of the scapular blade. Only fragmentary sections of the procoracoid and interclavicle are preserved, and are positioned between displaced thoracic vertebrae. For all scylacosaurids the coracoidal plate rests on the upper face of the interclavicle and comprises a large procoracoid and a smaller posterior coracoid which curve gently inwards towards the mid-line. The procoracoid takes no part in the formation of the glenoid cavity. The foramen procoracoideus is present in the procoracoid only. Ventrally the spatulate end of each clavicle curves below around the anterior end of the interclavicle to fit into an

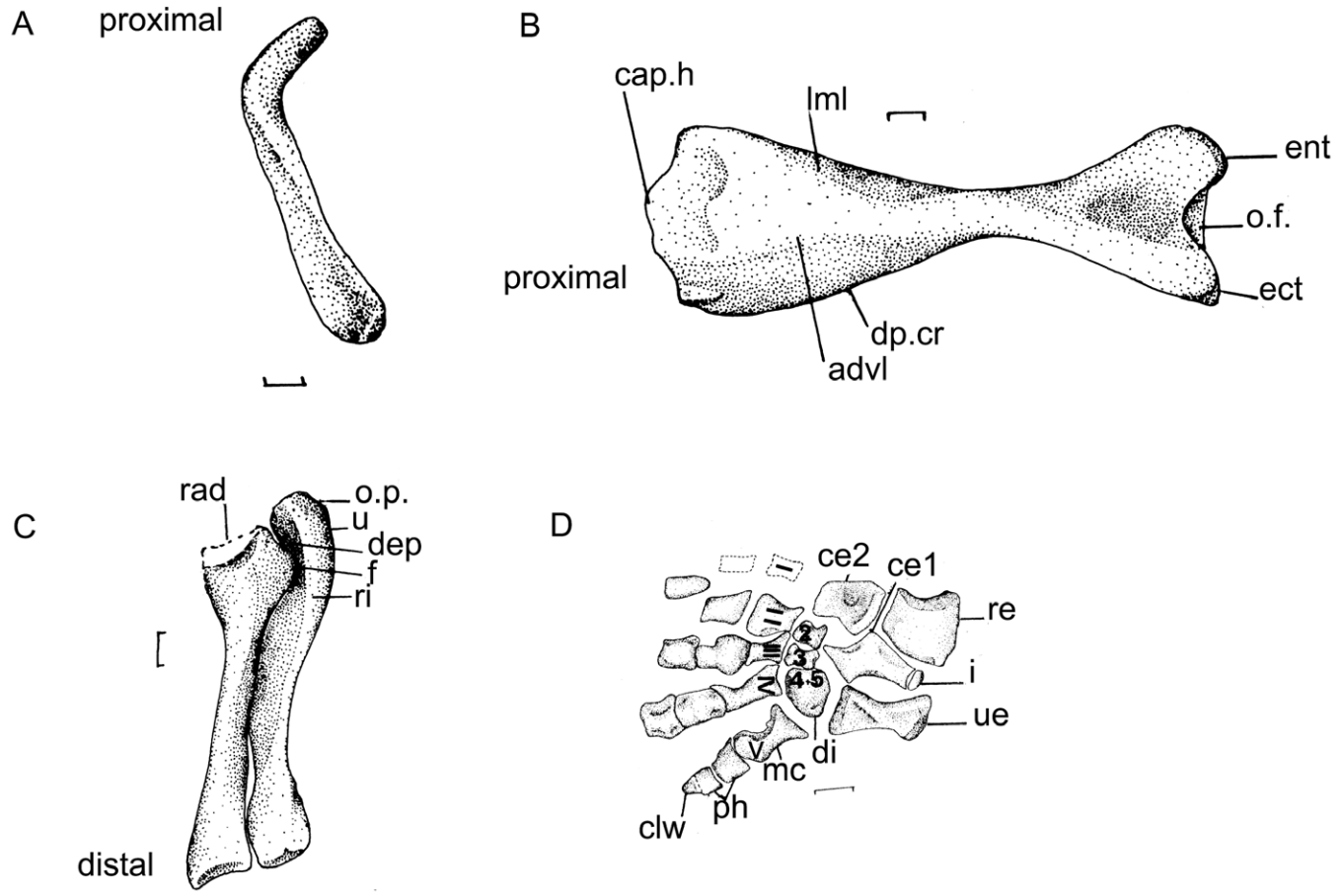


Figure 4. Left clavicle and forelimb of *Glanosuchus macrops* (SAM-PK K 7809); **A**, clavicle (anterior view); **B**, humerus (anterior view); **C**, radius and ulna (anterior view); **D**, manus (dorsal view) (scale 10 mm).

oval hollow on the under face of this bone. The interclavicle is a long bone with the anterior end rounded, and curving slightly upwards. The sternum is not preserved and is considered to have been cartilaginous (Boonstra 1964). It presumably lay above the posterior end of the interclavicle and extended to the coracoids.

Postcranial morphological trends through time in the pectoral girdle of Therocephalia have been discussed by Fourie & Rubidge (2007). It is recognized that suites of postcranial characters can be used to identify specific genera. For example, *Regisaurus* is identified by a slender scapula with a low ridge and shallow depression; procoracoid foramen in procoracoid; interclavicle short and broad; and ossified sternum. *Lycosuchus* has a broad scapula with a low ridge lacking a depression next to it; procoracoid foramen in procoracoid; interclavicle T-shaped; and lack of an ossified sternum (Table 1). An obvious morphological trend through time in the therocephalian pectoral girdle is the position of the procoracoid foramen. This is entirely enclosed within the procoracoid in *Lycosuchus* (Boonstra 1964), *Cynariognathus* (Cys 1967), *Mirotenthes* (Attridge 1956), *Ictidosuchus* (Broom 1901), *Regisaurus* (Kemp 1978); is present on the procoracoid-coracoid suture in *Ericiolacerta* (Watson 1931), *Tetracynodon* (Sigogneau 1963), baurioid (Kemp 1986), *Macroscelesaurus* (Haughton 1918); and on the procoracoid-scapula suture in *Bauria* (Watson 1931). The sternum is unknown in the basal scylacosaurid and lycosuchid therocephalians and has been considered to have been cartilaginous (Boonstra 1964), but more derived therocephalians such as *Regisaurus* and *Olivierisuchus* (Fourie 2001) have an ossified sternum.

Forelimb

The left humerus (Fig. 4B) is preserved in articulation with the ulna and radius and is fifteen centimetres long. It is robust, lacking a well-defined shaft. A dorsoventrally expanded deltopectoral crest is positioned proximally, followed more distally by a short shaft area and the double condyle at the distal end. The articulation surface of the caput humerus (Fig. 4B, cap.h) with the scapulocoracoid is thin and curved. The anterior surface of the deltopectoral crest is characterized by three regions or processes edged by the lateromedial line (Fig. 4B, lml) and the anterior dorsoventral line (Fig. 4B, advl) (*sensu* Boonstra 1964) which are slightly raised linear surfaces of bone. As is the case in all scylacosaurids the bicipital fossa is deep (Boonstra 1964) and well-developed capitellum and radial condyles are present. The morphology of the *Glanosuchus* bicipital fossa differs from that of *Lycosuchus* (SAM-PK K 12185) where the proximal extremity of the fossa has a gentle curve in *Glanosuchus,* but in *Lycosuchus* it slopes steeply towards the ventral side of the shaft. Small rounded entepicondylar and ectepicondylar foramina are present as in all scylacosaurids (Boonstra 1964). On the dorso-distal surface, the trochlear fossa is shallow with a small distal lip which prevented the olecranon from dislocating.

Table 1. Comparison of postcranial characters in different therocephalian genera.

Genus	***Glanosuchus***	***Lycosuchus***	***Mirotenthes***	***Theriognathus***	***Regisaurus***	***Bauria***
Biozone	*Tapinocephalus*	*Tapinocephalus*	*Cistecephalus*	*Dicynodon*	*Lystrosaurus*	*Cynognathus*
Vertebra						
Cervical	5–6		7	>5	6	?
Thoracic	>16		?	14–16	17	>2
Lumbar	6		?	6–7	5	>2
Sacral	>1		3–4	4	3–4	?
Caudal	>4		14	>3	>4	?
Presacral	27–28		>7	>25	28	27
Scapula	?	Broad	Slender	Slender	Broad	Broad
Ridge	?	Low	Low	?	Low	Prominent
Depression	?	Absent	Absent	?	Shallow	Deep
Pc/Cc foramen	?	Absent	Absent	?	Absent	?
Pc/Sc foramen	?	Absent	Absent	?	Absent	?
Pc foramen	?	Present	Present	?	Present	?
Interclavicle	T-shaped	T-shaped	?	Short/broad	Short/broad	?
Sternum (ossified)	Absent	Absent	?	?	Present	?
Humerus						
Entepicondylar foramen	?	Present	Absent	?	Present	Present
Ectepicondylar Foramen	?	Present	?	?	Absent	Present
Humerus shaft	Short	Short	Long	Long	Long	Long
Manus						
Mc IV longest	Yes	No	Yes	?	Yes	Yes
Pelvis						
Obturator foramen	Absent	?	?	Large	Large	Large
Pubic foramen	Large	?	?	Absent	Absent	Absent
Pes						
Os calcis	?	?	Absent	?	Present	Present

The sigmoid curved ulna is long and thin (Fig. 4C). Proximally it is greatly expanded and extends dorsally into a short thickened olecranon with a rugose surface. The sigmoid face of the articulatory area for the reception of the humerus is shallow with a well-developed medial coronoid process. On its dorsal side, the ulna is concave to receive the head of the radius in a marked depression. The ulna has an anterior ridge which extends from the proximal extremity down the middle of the anterior surface to the lateral surface of the shaft and fades away about three quarters of the distance down the shaft. On the medial side of this ridge is a slight depression (Fig. 4C, dep). The distal articulation facet with the ulnare is slightly ovoid.

The radius is an elongate, straight and lateromedially flattened bone which is situated medial to the ulna. The proximal extremity is expanded and concave medially to provide an articulation facet for the humerus while the distal end receives the radiale in a shallow oval depression.

Manus

Only the dorsal side of the manus (Fig. 4D) has been prepared. All the elements of the wrist are preserved, except for the pisiforme. The ulnare (Fig. 4D, ue) is longer and more slender than the radiale (Fig. 4D, re) and is hour-glass-shaped. Proximally the ulnare contacts the ulna along most of the length of the distal end of the ulna in a slightly convex contact area of the ulna such that the proximal head of the ulnare is smaller than the ulnar condyle.

Proximally the dorsal surface of the ulnare is flat and has a slight ridge on the medial side which extends only half way down the length of the bone. At the distal extremity the ulnare is slightly concave with a flat dorsal surface. Both proximal and distal articulating facets are ridged towards the dorsal side. The ulnare contacts the intermedium proximomedially, centrale 1 (medially) in a concave facet of the ulnare, and the fused distals four and five distally.

The radiale, which is the largest element in the wrist of *Glanosuchus,* is roughly quadrangular. It is twice as wide as long and has a convex dorsal surface for the proximal articulation with the radius. It is in contact with the intermedium posteromedially, centrale 1 anteromedially and centrale 2 distally and is dorsally rounded and not depressed as is the situation in *Regisaurus* (Fourie & Rubidge 2007). Centrale 1 has a medial concave facet to accommodate the rounded contact surface of the radiale.

The intermedium, which also has a rounded dorsal surface, is a small oval elongate bone situated between the ulnare, radiale, and centrale 1 which in turn has a concave articulation facet for the intermedium.

Centrale 1 is a broadly L-shaped bone situated between the ulnare laterally, intermedium proximally, radiale proximomedially, distals 3, 4 and 5 distolaterally, and distal 2 and centrale 2 distomedially. Proximally it is thin and long to fit between the ulnare and radiale. Centrale 1 widens distolaterally so that it is widest in the middle of the bone which is in contact with centrale 2. The dorsal surface of centrale 1 is rounded with slight depressions on either side. Centrale 2, one of the larger wrist bones, is roughly rectangular with rounded sides. It has contact with the radiale proximally, centrale 1 medially and distal 2 distomedially. The dorsal surface is slightly depressed.

Distals 2 and 3 which have rounded dorsal surfaces, are

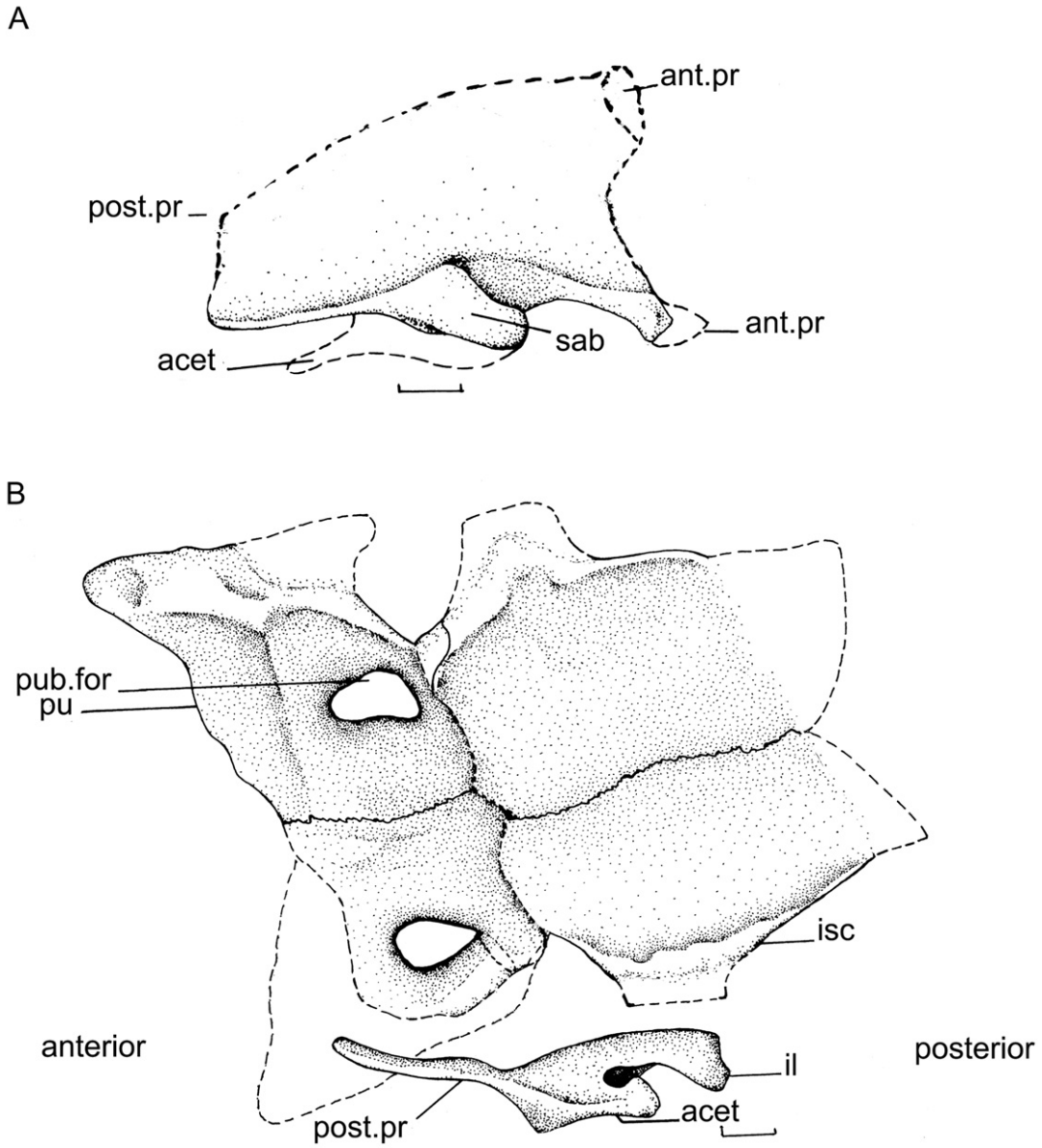


Figure 5. Pelvis of *Glanosuchus macrops* (SAM-PK K 7809); **A**, ilium (lateral view); **B**, pubis, ischium and ilium (dorsal view) (scale 10 mm).

almost square in outline, are slightly constricted towards the middle and have rounded ends. Distal 2 contacts centrale 2 proximally and metacarpal II on the distal side. Distal 3 contacts centrale 1 proximally, distal 2 medially, fused distals 4 and 5 laterally, and metacarpal III on the distal side. Distal bones 4 and 5 are fused to a single bean-shaped element which is situated lateral to distal 3 and the ulnare proximally, and metacarpal IV and V, distally.

Metacarpal I is not preserved and metacarpals II, III, IV and V, which are hourglass-shaped, are preserved in contact with their corresponding phalanges. Metacarpals II and III are short and wide, wider distally than proximally. Metacarpal IV is the longest in *Glanosuchus,* but not in *Lycosuchus* (Boonstra 1964). Metacarpal V is the second longest and the thinnest of all the metacarpals.

Phalanges are almost square with slightly narrower mid-sections and double condyles at each end. The terminal phalanges are missing except for digit 5 which has a triangular claw which is rounded at the apex and blunt on the opposite side.

Pelvic girdle

The pelvic girdle of SAM-PK K 7809 has been dorsoventrally compressed and is badly distorted so that the original shape and orientation cannot easily be determined. The left ilium is exposed in lateral view. The iliac blade is large, flat in lateral view, and has two anterior processes and one large posterior process as in all other Therocephalia (Fig. 5A; Fourie 2001). The ilium narrows towards the ventrolaterally situated acetabulum which is large, shallow, almost circular in outline and faces laterally. Mediolaterally the ilium has attachment sites for the sacral ribs. The lateral surface of the blade is flat, slopes ventrally, but increases in width towards the region of the strong supra-acetabular buttress. Above the buttress, to the back of the ilium blade, is the posterior process which is bigger and more robust than the slimmer anterior processes. One anterior process is situated high up on the blade and the other is lower down. A supra-acetabular notch is situated behind the supra-acetabular buttress.

In anterior view the roughly rectangular pubis is concave and slopes medially to meet its counterpart in a straight

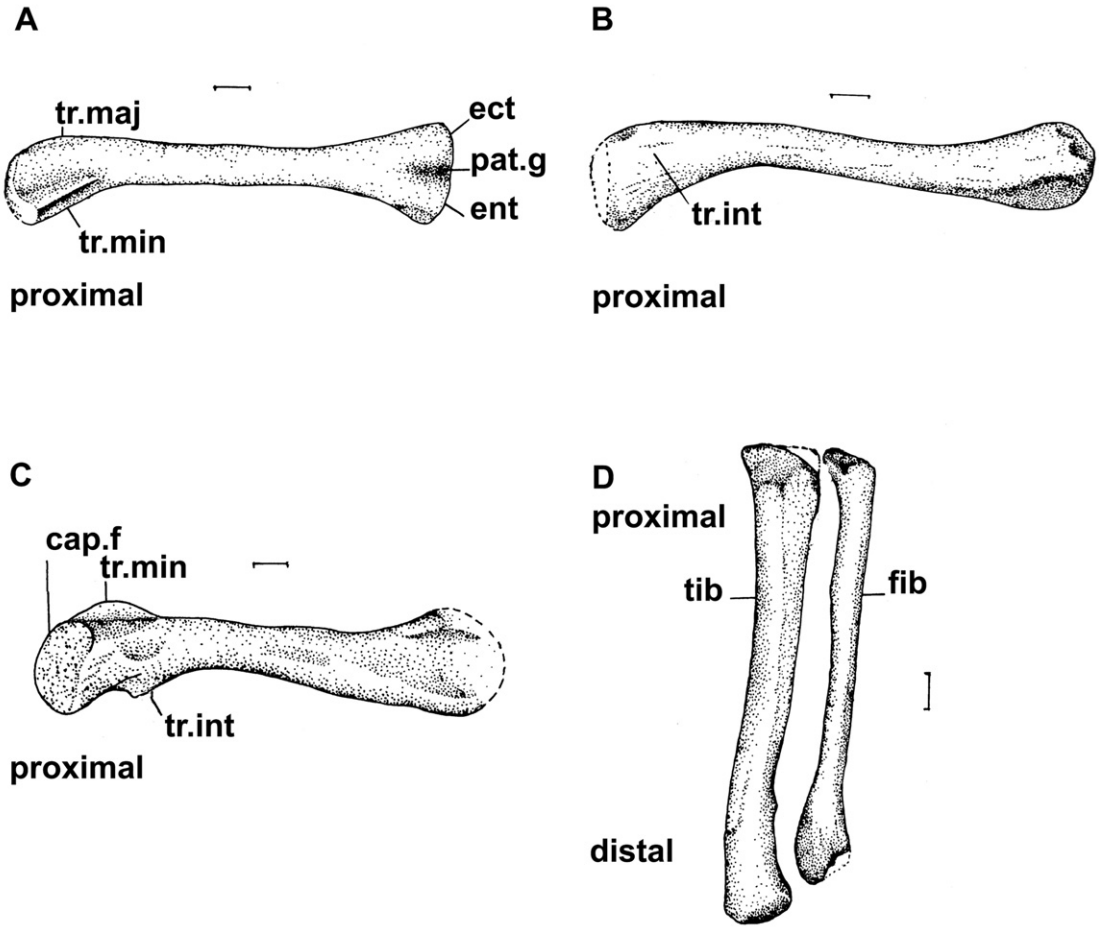


Figure 6. Hindlimb of *Glanosuchus macrops* (SAM-PK K 7809); **A**, left femur (dorsal view); **B**, right femur (ventral view); **C**, right femur (posterior view); **D**, left tibia and fibula (anterior view) (scale 10 mm).

midline symphysis. At its posterior end the pubis curves medially and forms a deep, rounded area for a short contact with the ischium. Laterally the pubis is concave with a rounded anterior edge and a posterior acetabular portion. The contribution of the pubis to the acetabulum is oval and small. The large pubic foramen described for scylacosaurids (Boonstra 1964), and present in *Glanosuchus,* is not present in any other Therocephalia.

Only the anterior portion of the blade-like ischium is preserved with the left side of the girdle being displaced over the more ventrally situated right side (Fig. 5B).

Hind limb

Both femora are preserved (Fig. 6A–C), with the left one complete and the right femur lacking a small part of the shaft. The femur is long and more massive than that of other therocephalians, with a gentle sigmoid curve. It has a flattened proximal end which is expanded anteroposteriorly, and a slightly expanded double condyle at the distal end. A large trochanter minor (anterodorsal), small trochanter major (posterodorsal), and trochanter internus (ventral) are all present on the proximal head. At the proximal extremity the caput femoris (Fig. 6, cap.f) curves medially. Rounded ente- and ectepicondyles, with a shallow ventral triangular patella groove between them (Fig. 6, pat.gr), are present on the distal end of the bone.

The left tibia and fibula (Fig. 6D) are preserved in articulation with the femur as long, straight bones. The tibia, the major weight-supporting element of the lower leg, is more robust and longer than the fibula. Its proximal end is flattened anteroposteriorly and expanded lateromedially, while the slightly expanded distal facet for the articulation of the astragalus is concave and oval. The fibula is a straight, slender bone with slightly expanded proximal and distal ends. On the medial surface is a small proximal tuberosity, and a proximal facet for the tibia and a terminal oval facet for the femur. The shaft, which has a medial groove, thins towards its mid-section and broadens distally to form an elongated oval articulation facet with the proximal end of the calcaneum.

The left pes is not well preserved and only the astragalus, calcaneum, one centrale, distal 1 and fused distal 4 and 5 are recognizable. The almost rectangular calcaneum is larger than the astragalus with two distinct ridges, one near the distal end of the fibula and the other on the outside edge, with a deep depression between them. It abuts against the astragalus medially and fused distal 4 and 5 posteriorly. A tuber calcis is lacking on the calcaneum of *Glanosuchus,* lycosuchids and other scylacosaurids (Boonstra 1964).

The astragalus articulates with the tibia (dorsally) and centrale (posteriorly). This bone is robust and roughly ovoid, it has a slightly indented area for the articulation with the tibia. A shallow median depression and calcano-astragular foramen are present. The centrale, which has

been displaced, is a prominent square bone. Rounded distal 1 is displaced and fused distals 4 and 5 is rectangular. Distals 2 and 3 are not preserved.

Only metatarsals IV and V and three phalanges are present but are poorly preserved. Triangular unguals are present.

DISCUSSION

Therocephalians and dicynodonts bear the unique distinction in that they are the only therapsid clades to be represented in all the biozones of the Beaufort Group (Rubidge 1995). They survived the Permo-Triassic extinction event, and were represented for a period of at least 65 million years (Rubidge 2005; Sidor 2000). Research on the postcrania of a number of therocephalian genera from different biozones eg. *Bauria* (King 1996; Fourie 2001), baurioid (Kemp 1986), *Regisaurus* (Fourie & Rubidge 2007; Kemp 1978), *Aneugomphius* (Brink 1958), *Ictidosuchoides* (Broom 1938), *Mirotenthes* (Attridge 1956), *Tetracynodon* (Sigogneau 1963), *Silpholestes* (Broom 1948), *Cynariognathus* (Cys 1967), *Lycosuchus* (Boonstra 1964) and *Glanosuchus* (this study) offers the opportunity to compare the postcranium of different therocephalian genera, determine postcranial morphological differences between the genera, and assess postcranial evolutionary trends over the extended time that therocephalians were present. In addition, because the postcrania of therapsids are relatively poorly known, our study has enabled comparison of various postcranial elements of different theriodont taxa and provided information to taxonomically identify isolated theriodont postcranial elements. This has biostratigraphic application in areas where fossils are not plentiful.

The general postcranial morphology of therocephalians is consistent amongst the different genera, but there are important generic differences which are highlighted here. Enhanced understanding of postcranial morphological variation amongst different therocephalian genera has further enabled broad scale comparison between postcranial elements of therocephalians, cynodonts and gorgonopsians as far as they are currently known.

Vertebrae

The axis in all therocephalians has a robust construction and the laterally wide neural spine is a distinctive feature, as in gorgonopsians (Sigogneau 1970; van Rooyen 1990) but not in cynodonts where axial morphology is similar to that of the remaining cervical series (Jenkins 1971). In all therocephalians a slight increase in width of the neural spine of the last cervical vertebra marks the end of that series, whereas in gorgonopsians it is the upward shifting of the parapophyseal facet, and the change of the zygapophyseal articulation from a horizontal plane to one of 45° (Boonstra 1934). In cynodonts it is the abrupt change in zygapophyseal orientation from 45° to 55° and the tallest neural spine (Jenkins 1971) which are the only definite markers separating cervical (seventh) from thoracic (eighth) vertebrae.

Intercentra are present between the first seven vertebrae in the therocephalian genus *Ordosia* (Lianhai 1979), but they are absent in all other therocephalian genera. They are absent in all postcervical vertebrae of cynodonts and therocephalians (Jenkins 1971), but are present between the cervical and anteriormost thoracic vertebrae in the gorgonopsian *Lycaenops* (Colbert 1948).

Thoracic vertebrae of all therocephalians have their transverse processes positioned further ventrally and posterolaterally than those of the preceding cervical vertebrae. In gorgonopsians the width across the zygapophyses in the dorsal vertebrae abruptly decreases at the transition from the cervical to the dorsal vertebrae; the diapophysial processes increase in length and are more horizontally directed, so that the facet is at a higher level than in the cervicals; the parapophysial facets shift higher up on to the centrum (Boonstra 1934). Cynodont thoracic vertebrae differ from the cervical vertebrae in being longer and wider, the presence of broader posteriorly situated transverse processes, and abrupt change in zygapophyseal orientation (Jenkins 1971).

Therocephalian lumbar vertebrae have anteroposteriorly wider neural spines than those of the thoracic region, and the transverse processes are shorter and more robust. Colbert (1948) and Sigogneau (1970) did not distinguish between thoracic and lumbar vertebrae in the Gorgonopsia, but described them together as dorsals. In cynodonts, Jenkins (1971) distinguished lumbar from thoracic vertebrae by a slight increase in centrum width, development of robust transverse processes, and by the presence of synapophyses.

In all three infraorders the sacral series commences with the first vertebra having a fused rib which touches the medial surface of the iliac blade. Sacral vertebrae have lower neural spines when compared to the lumbar series and have fused holocephalous ribs which are grooved on the posterior side. In Therocephalia (Fourie 2001) and Cynodontia (Jenkins 1971) sacral zygapophyseal facets articulate at high angles, and the zygapophyses are much smaller than lumbar zygapophyses, while the situation in gorgonopsians is unknown.

Up to 14 caudal vertebrae have been reported in some therocephalian genera (Attridge 1956; Brink 1958). Isolated therocephalian and cynodont caudal vertebrae are distinguished by their small, short and robust transverse processes and only small neural spines which decrease in height posteriorly so that they are absent in the more posterior caudals. Gorgonopsian caudals have low neural spines, and the transverse processes are strong and extend as far laterally as the external iliac surface (Boonstra 1934) Amongst theriodonts, gorgonopsians have the longest tails, up to 26 vertebrae (Boonstra 1934), as compared to the 10–14 of therocephalians (Fourie & Rubidge 2007), and 16 of cynodonts (Jenkins 1971).

Ribs

Cervical ribs of therocephalians (Fourie & Rubidge 2007) and gorgonopsians (Boonstra 1934; von Huene 1950) are short with a double head whereas Jenkins (1971) described cynodont cervical ribs as short having a triangular head without distinct processes.

In therocephalians, gorgonopsians and cynodonts

thoracic ribs are dichocephalous, long and slender. Thoracic ribs of therocephalians and cynodonts differ from those of gorgonopsians (Colbert 1948; von Huene 1950) by not having the tubercle positioned on a long pedicle and by having an interconnecting sheet of bone between the two heads of the rib (Cys 1967; Jenkins 1971). Sternal segments are described for thoracic ribs of therocephalians (Fourie 2001) and gorgonopsians (Boonstra 1934) but not for cynodonts. Posterior grooves on rib shafts are present in therocephalians and cynodonts, but they are absent in gorgonopsians. Very distinct costal plates are present in the thoracic vertebrae of cynodonts (Jenkins 1971), but are lacking in gorgonopsians and therocephalians.

Therocephalian lumbar ribs have the distal end slightly expanded, while in most of the advanced cynodonts the distal end is not expanded and the proximal half of the short rib bears a broad, flange-like posterior process (costal) that overlaps and interlocks with the next posterior rib (Cys 1967; Jenkins 1971). Lumbar ribs of therocephalians are shortened relative to those of the thoracic vertebrae and have blunt ends. This reduction, which is less than that of cynodonts, is suggestive of the presence of a diaphragm (Brink 1958). Colbert (1948) noted that gorgonopsians have double-headed dorsolumbar ribs, but then added that the last four were single-headed and there are no ribs immediately anterior to the sacrum in *Lycaenops*. Boonstra (1934) also described the single-headed nature and the lack of ribs immediately anterior to the sacrum in the Gorgonopsia.

All three theriodont groups have single-headed sacral ribs but therocephalians and gorgonopsians lack the costal plates which are present in cynodonts. In gorgonopsians the first sacral rib extends far ventrally to abut below the upper half of the acetabulum, the posterior two abut higher up on the ilium (Boonstra 1934).

Caudal ribs are single-headed, very short and often fused to the vertebrae. Each rib is hourglass-shaped and dorsoventrally flattened.

Pectoral girdle

Theriodont scapulae are curved around the ribcage and bear a high, narrow blade with an expanded end. The slightly curved scapula of therocephalians is distinctive whereas a broader, straighter scapular blade with its outer surface distinctly concave is characteristic of cynodonts (Brink 1955) and gorgonopsians (Colbert 1948; Sigogneau 1970). The gorgonopsian scapula is a tall and slender bone with the dorsal part of its blade considerably expanded (Boonstra 1934), and a low ridge is present on the posterolateral side (Sigogneau 1970). An acromion process is absent in therocephalians (Fourie 2001), gorgonopsians (Boonstra 1934) and most cynodonts (Colbert 1948) but has been described for *Diademodon* (Brink 1955) and *Cynognathus* (Watson 1917). Therocephalians have a prominent ridged fossa on the lateral side of the scapular blade which appears to be absent in cynodonts (Jenkins 1971).

The medial surface of the scapular blade of both therocephalians and gorgonopsians is concave with the gorgonopsian concavity being less accentuated. In cynodonts this surface is convex (Jenkins 1971). In therocephalians the glenoid facet comprises the coracoid and scapula while in gorgonopsians (Sigogneau 1970; van Rooyen 1990) and cynodonts (Jenkins 1971) the procoracoid, scapula and coracoid together make up the glenoid cavity. An exception is the gorgonopsian, *Lycaenops*, which has a reduced coracoid region with the procoracoid not present in the glenoid facet (Cys 1967).

The position of the procoracoid foramen is variable in therocephalians (see above). Gorgonopsians (Boonstra 1934; Colbert 1948; Sigogneau 1970; Watson 1917) and cynodonts (Broom 1906; Jenkins 1971; Watson 1917) have the procoracoid foramen entirely enclosed by the procoracoid.

There are varying reports on the presence of a cleithrum in theriodonts; cynodonts do not have a cleithrum (Jenkins 1971), it is present in the gorgonopsians *Aelurognathus* and *Scylacops* (Boonstra 1934), and amongst therocephalians is reported as present in *Ericiolacerta* (Watson 1931), but in all the therocephalian specimens studied for this research we found no evidence of a cleithrum.

Some therocephalians as well as gorgonopsians (Boonstra 1934; Colbert 1948; Sigogneau 1970) do have an ossified sternum, but an ossified sternum has not yet been described for cynodonts (Jenkins 1971).

Claviculae and interclaviculae are difficult to recognize in theriodonts as there are few specimens where they are well preserved. In addition there appear to be few morphological differences amongst different genera of the same clade. Persistent minor variations are mostly due to differences in ossification. Cynodont interclaviculae are cruciate in *Thrinaxodon* (Jenkins 1971) and T-shaped in *Cynognathus* (Watson 1917) with the anterior half bearing a median tuberosity from which four ridges radiate. Therocephalia show the same feature trend where it is T-shaped in the basal genera such as *Lycosuchus* (Boonstra 1964), while in more derived genera the interclavicle is short and broad as in *Regisaurus* (Fourie & Rubidge 2007). This is also true for the Gorgonopsia (Boonstra 1934; Watson 1917).

Forelimb

The humerus of all therocephalians has a large deltopectoral crest with a deep bicipital fossa. A similar condition is found in the great majority of gorgonopsians and cynodonts. The therocephalian humeral distal end is not as wide as that of gorgonopsians or cynodonts. Of the therocephalian specimens studied, only *Bauria* has a triangular fossa for the ectepicondylar foramen as in gorgonopsians (Sigogneau 1970) and cynodonts (Jenkins 1971). The cynodont humerus shows three prominent ventral depressions; one depression is for the ectepicondylar foramen, the other for the entepicondylar foramen and the third one for radial articulation (Jenkins 1971). The olecranon fossae on the humerus in therocephalians, gorgonopsians and cynodonts are not very deep and a lip is present mediodistally.

The ulna also manifests differences. In both thero-

cephalians and gorgonopsians (Sigogneau 1970) the ulna exhibits a deep posterior depression, lateral ridge and radial depression, in cynodonts the depression is medial (Jenkins 1971). At the distal end of the ulna, the olecranon process of therocephalians (Kemp 1986) and cynodonts (Jenkins 1971) is described as weak in contrast to the robust process of gorgonopsians (Watson 1917).

Another important character on the forelimb of theriodonts is the oval and convex articulation facet of the radiale with the radius. In gorgonopsians this facet (Boonstra 1934) is smaller than that of therocephalians (Fourie & Rubidge 2007), while in cynodonts it is more rounded (Jenkins 1971).

In the manus the radiale of therocephalians is rectangular or round (Fourie & Rubidge 2007), rounded in gorgonopsians (Colbert 1948), and oval in cynodonts (Jenkins 1971). Therocephalian, gorgonopsian and cynodont ulnares are rectangular, but in cynodonts this bone has rounded corners and a slight concave dorsal surface. The intermedia of therocephalians, gorgonopsians and cynodonts all have different shapes; in Therocephalia they are oval and long (Fourie & Rubidge 2007), in Gorgonopsia they are elongated (Colbert 1948), and in cynodonts they are rectangular (Jenkins 1971).

For each of the theriodont families metacarpal IV (Hopson 1995) is the longest and I is the shortest such that IV > III > V > II > I. In therocephalians the terminal phalanges are shorter than those of gorgonopsians and cynodonts which have long slender, tapering cones. The phalangeal formula for Therocephalia is 2.3.3.3.3; Gorgonopsia is variable 2.3.4.5.3 (*Lycaenops*) (Colbert 1948), 2.3.4.4.3 (*Aelurognathus*) (Sigogneau-Russel 1989) and 2.3.4.5.3 (*Dinogorgon*) (Boonstra 1934); for cynodonts 2.3.4.4.3 *(Thrinaxodon)* (Jenkins 1971) (Parrington 1939) (*Procynosuchus*) (Hopson 1995) and later forms 2.3.3.3.3 (*Cynognathus*) (Watson 1917).

Pelvic girdle

The ilium of all theriodonts comprises a thin, moderately to greatly expanded iliac blade separated from a base (acetabulum) by a constricted neck. In therocephalians, gorgonopsians and cynodonts the ilium has a large, wide and prominent posterior process which extends back beyond the last sacral vertebra. Two anterior processes are uniquely present on all therocephalian ilia (Kemp 1978), while cynodonts (Jenkins 1971) and gorgonopsians (Boonstra 1934) only have one anterior process. The dorsal border of the ilium in all therocephalians is straight and not convex as in gorgonopsians (Boonstra 1934) and cynodonts (Jenkins 1971). This bone forms more than half of the acetabulum in the Gorgonopsia (Boonstra 1934) and only half in Therocephalia (Fourie 2001) and Cynodontia (Jenkins 1971).

In therocephalians and cynodonts the pubis and ischium have contact on both inside and outside the acetabulum, but in all the gorgonopsians (Colbert 1948) the ischium and pubis contact only within the acetabulum.

The pubis and ischium of the therocephalian genera studied lie horizontal, whereas in both cynodonts and gorgonopsians, the ischium had a vertical orientation (Colbert 1948; Cys 1967; Jenkins 1971). The ischium, like the pubis, comprises a head and a ventromedially directed rectangular plate and an oval concave acetabular facet is present for all theriodonts. Therocephalian genera may either have a pubic foramen (e.g. *Glanosuchus*) or obturator foramen (e.g. *Regisaurus*), cynodonts have only a small obturator foramen (Jenkins 1971), while in gorgonopsians the obturator foramen may be absent (Boonstra 1934), or present in the pubis as the pubic foramen (von Huene 1950).

Hind limb

The femur of therocephalians and cynodonts has the same degree of curvature in the shaft while in gorgonopsians the curvature is more pronounced. The intertrochanteric fossa of the femur is shallow in therocephalians (Fourie 2001), deep in cynodonts (Jenkins 1971) and absent in gorgonopsians (Boonstra 1934). In therocephalians the internal trochanter is situated close to the caput femoris and extends a short distance along the shaft, in gorgonopsians it is situated further from the caput femoris and extends along the entire shaft. In cynodonts the trochanter is as in therocephalians, but extends onto the shaft for only a very short distance. Both the trochanter minor and major of the therocephalians and cynodonts are low ridges wheras in the gorgonopsians they are very prominent.

The distal end of the theriodont femur bears a robust lateral condyle and a narrower medial one. The medial (anterior) condyle projects further ventrally than does the lateral condyle in both Therocephalia and Cynodontia (Jenkins 1971) and in gorgonopsians the condyles are confluent with the medial condyle (Colbert 1948). A deep patellar groove is present in therocephalians, while in cynodonts (Jenkins 1971) and gorgonopsians (Boonstra 1934) it is shallow.

The tibia has a similar morphology in all the theriodont families, but that of the Therocephalia is more slender (Cys 1967). Therocephalian and cynodont tibia are fairly straight and therefore have a small interosseal space with the fibulae, in gorgonopsians this space is large as the tibia and fibula are bowed (Colbert 1948). The oval proximal end expands laterally and somewhat anteriorly to support a large articular surface. Distally it expands in a similar fashion but less extensively. The shaft is flattened anteroposteriorly and the therocephalian and cynodont (Jenkins 1971) tibia have a shallow longitudinal groove present on the proximoposterior side of the shaft with a slight median ridge close to it.

The fibula is slender and curved laterally in all theriodonts. While the shaft of the fibula of all theriodonts has the same basic structure, the ends do differ. Therocephalian fibulae have greatly expanded proximal ends, with little expansion distally, gorgonopsians (Boonstra 1934) and cynodonts (Jenkins 1971) have both ends greatly expanded.

The shape of the calcaneum varies from square in therocephalians, disc shaped in gorgonopsians and oval in cynodonts. Two medial articulating facets for the

astragalus are present in both therocephalians (Kemp 1978) and cynodonts (Jenkins 1971). A tuber calcis is present on the calcaneum of some Therocephalia (*Regisaurus*) (Kemp 1978), Gorgonopsia and Cynodontia, but lacking in *Thrinaxodon* (Jenkins 1971).

The foot of Therocephalia has only one centrale, Gorgonopsia have two (Hopson 1995), and an irregular oval centrale is present in Cynodontia (Jenkins 1971). Of the five metatarsals, number IV is the longest in therocephalians, V the longest in cynodonts, and unknown for gorgonopsians. The pedal phalangeal formula of therocephalians (Fourie 2001) and cynodonts is 2.3.3.3.3 (Jenkins 1971), while in gorgonopsians it is variable 2.3.4.5.3 (Boonstra 1934) or 2.3.3.4.3 (Colbert 1948).

CONCLUSIONS

Boonstra (1964) described the girdles and limbs of the basal Therocephalia, but our research is the first to describe the complete dorsal view of a scylacosaurid. *Glanosuchus* can be identified by the following suite of postcranial characters: humerus lacking a distinct thinner shaft section; pelvis with large pubic foramen and lacking an obturator foramen; robust but long femur.

This description and that of Fourie & Rubidge (2007) have highlighted the similarities in postcranial morphology in different therocephalian genera and also manifested certain phylogenetic trends such as scapula morphology, position of procoracoid foramen, presence or absence of an ossified sternum, presence or absence of a pubic foramen which are set out in Table 1.

Comparison of postcranial elements in the Therocephalia, Gorgonopsia and Cynodontia has shown that diagnostic differences are present in the vertebral column, pectoral girdle and forelimb, and pelvic girdle and hind limb. There are a few single element postcranial characters which define a therocephalian, cynodont or a gorgonopsian, but a suite of characters can be used to reliably identify these taxa. These postcranial differences will be useful for broad scale identification in biostratigraphic studies when there is no associated cranial material, and also for phylogenetic studies which up till now have relied largely on cranial characters.

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ABBREVIATIONS

Figures

acet	acetabulum
a.dv.l	anterior dorsoventral line
ant.pr	anterior process
ax	axis
cap	capitulum
cap.h	caput humerus
cap.f	caput femoris
ce1	centrale 1
ce2	centrale 2
centr	centrum
clw	claw
cr	cranium
cv	cervical vertebra
dep	depression
di	distal
dp.cr	deltopectoral crest
ect	ectepicondyle
ent	entepicondyle
f	facet
fem	femur
fib	fibula
gr	groove
hum	humerus
i	intermedium
icl	interclavicle
il	ilium
isc	ischium
lm.l	lanteromedial line
lv	lumbar vertebra
man	manus
mc	metacarpal
n.a	neural arch
n.c	neural canal
n.p	neural process
n.s	neural spine
o.f	olecranon fossa
o.p.	olecranon process
pat.gr	patella groove
pes	pes
ph	phalange
post.pr	posterior process
postzp	postzygapophysis
prezp	prezygapophysis
pu	pubis
pub.for	pubic foramen
r	rib
rad	radius
re	radiale
ri	ridge
sa.b	supra-acetabular buttress
sa.n	supra-acetabular notch
sv	sacral vertebra
tib	tibia
tr.int	internal trochanter
tr.pr	transverse process
tr.maj	major trochanter
tr.min	minor trochanter
tub	tuberculum
tv	thoracic vertebra
u	ulna
ue	ulnare

Tables

Cc	coracoid
mc	metacarpal
Pc	procoracoid
Sc	scapula
?	not preserved / described

Institutions

SAM-PK K	Iziko South African Museum, Cape Town, South Africa
TM	Transvaal Museum, Pretoria, South Africa
UCMP	University of California Museum, Berkeley, U.S.A

REFERENCES

ABDALA, F., RUBIDGE, B.S. & VAN DEN HEEVER, J. A. 2008. The oldest therocephalians (Therapsida, Eutheriodontia) and the early diversification of Therapsida. *Palaeontology* **51**, 1011–1024.

ATTRIDGE, J. 1956. The morphology and relationships of a complete therocephalian skeleton from the *Cistecephalus* Zone of South Africa. *Proceedings of the Royal Society, Edinburgh* B **IV**, 59–93.

BOONSTRA, L.D. 1934. A contribution to the morphology of the Gorgonopsia. *Annals of the South African Museum* **31**, 137–174.

BOONSTRA, L.D. 1935. On some South African Reptiles of the suborder Therocephalia preserved in the American Museum of Natural History. *American Museum Novitates* **771**, 1–12.

BOONSTRA, L.D. 1964. The girdles and limbs of the Pristerognathid Therocephalia. *Annals of the South African Museum* **48**(5), 121–165.
BOONSTRA, L.D. 1969. The fauna of the *Tapinocephalus* Zone (Beaufort beds of the Karoo). *Annals of the South African Museum* **56**, 1–73.
BRINK, A.S. 1955. A study of the skeleton of *Diademodon. Palaeontologia africana* **3**, 3–40.
BRINK, A.S. 1958. On the skeleton of *Aneugomphius ictidoceps* Broom and Robinson. *Palaeontologia africana* **5**, 29–37.
BROOM, R. 1901. On *Ictidosuchops primaevus. Transactions of the South African Philosophical Society* **11**, 177–184.
BROOM, R. 1906. On a new cynodont reptile (*Aelurosuchus browni*). *Transactions of the South African Philosophical Society* **16**, 376–378
BROOM, R.1936. On some new genera and species of Karoo fossil reptiles, with notes on some others. *Annals of the Transvaal Museum* **18**(4), 349–386.
BROOM, R. 1938. On a nearly complete therocephalian skeleton. *Annals of the Transvaal Museum* **19**(2), 257–261.
BROOM, R. 1948. The skeleton of a very small therocephalian. *Annals of the Transvaal Museum* **21**(1), 39–41.
COLBERT, E.H. 1948. The mammal-like reptile *Lycaenops. Bulletin of the American Museum of Natural History* **89**(6), 353–404.
COLBERT, E.H. & KITCHING, J.W. 1981. Scaloposaurian reptiles from the Triassic of Antartica. *American Museum Novitates* **2709**, 8–16.
CYS, J.M. 1967. Osteology of the Pristerognathid *Cynariognathus platyrhinus* (Reptilia: Theriodontia). *Journal of Paleontology* **41**(3), 776–790.
DRYSDALL, A.R. & KITCHING, J.W. 1963. A re-examination of the Karoo succession and fossil localities of part of the Upper Luangwa Valley. Northern Rhodesia Ministry of Labour and Mines, *Memoirs of the Geological Survey* **1**, 1–62.
FOURIE, H. 2001. *Morphology and function of the postcrania of selected genera of Therocephalia (Amniota: Therapsida).* Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.
FOURIE, H. & RUBIDGE, B.S. 2007. The postcranial skeletal anatomy of the therocephalian *Regisaurus* (Therapsida: Regisauridae) and its utilisation for biostratigraphic correlation. *Palaeontologia africana* **42**, 1–16.
GOLUBEV, V.K. 2000. The faunal assemblage of Permian terrestrial vertebrates from eastern Europe. *Palaeontological Journal* **34**(2), 211–224.
HAUGHTON, S.H. 1918. Investigations in South African fossil reptiles and amphibians. Some new carnivorous Therapsida with notes upon the brain case in certain species. *Annals of the South African Museum* **12**(11), 175–180.
HOPSON, J.A. 1995. Patterns of evolution in the manus and pes of non-mammalian therapsids. *Journal of Vertebrate Paleontology* **15**(3), 615–639.
JENKINS, F.A. Jr. 1971. The postcranial skeleton of African cynodonts. *Peabody Museum of Natural History Bulletin* **36**, 1–215.
KEMP, T.S. 1978. Stance and gait in the hindlimb of a therocephalian mammal-like reptile. *Journal of the Zoological Society, London* **186**, 143–161.
KEMP, T. 1986. The skeleton of a baurioid therocephalian from the lower Triassic (*Lystrosaurus* Zone) of South Africa. *Journal of Vertebrate Paleontology* **6**(3), 215–232.
KEYSER, A.W. & BRINK, A.S. 1979. A new bauriamorph (*Herpetogale marsupialis*) from the Omigonde Formation (Middle Triassic) of South West Africa. *Annals of the Geological Survey of South Africa* **12**, 91–105.
KING, G.M. 1996. A description of the skeleton of a bauriid therocephalian from the early Triassic of South Africa. *Annals of the South African Museum* **104**(11), 379–393.
KITCHING, J.W. 1977. The distribution of the Karoo vertebrate fauna. *Memoir of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand* **1**, 1–131.
LI, J. & CHENG, Z. 1995. A new Late Permian vertebrate fauna from Dashanku, Gansu with comments on Permian and Triassic vertebrate Assemblage Zones of China. **In**: Sun, A.L. & Wang, Y.Q. (eds), *Short Papers of the Sixth Symposium on Mesozoic Terrestrial Ecosysytems and Biota,* 33–37. Beijing, China Ocean Press.
LIANHAI, H. 1979. On a new theriodont from Inner Mongolia. *Vertebrata PalAsiatica* **17**(2), 1–30.
PARRINGTON, F.R. 1939. On the digital formulae of the theriodont reptiles. *Annals and Magazine of Natural History* (11)**3**: 209–214.
RAY,S., BOTHA, J. & CHINSAMY, A. 2004. Bone histology and growth patterns of some nonmammalian therapsids. *Journal of Vertebrate Paleontology* **24**, 634–648.
RUBIDGE, B.S. (ed.) 1995. *Biostratigraphy of the Beaufort Group.* South African Committee for Stratigraphy, Biostratigraphic Series No. 1. Council for Geoscience, Pretoria.
RUBIDGE, B.S. 2005. Re-uniting lost continents – Fossil reptiles from the ancient Karoo and their wanderlust. *South African Journal of Geology* **108**, 135–172.
SCHAEFFER, B.1941. The pes of *Bauria cynops* Broom. *American Museum Novitates* **1103**, 1–7.
SIDOR, C.A. 2000. *Evolutionary trends and relationships within the Synapsida.* Unpublished Ph.D. thesis, University of Chicago, Chicago, Illinois.
SIGOGNEAU, D. 1963. Note sur une nouvelle espèce de scaloposauridae. *Palaeontologia africana* **8**, 13–37.
SIGOGNEAU, D. 1970. Revision systematique des Gorgonopsiens Sudafricains. *Cahiers de Paléontologie.* Pars: Éditions du Centre National de la Recherche Scientifique.
SIGOGNEAU-RUSSEL, D. 1989. Theriodontia I. **In**: Wellnhofer P. (ed.), *Encyclopedia of Paleoherpetology,* Part 17 B/I, 1–127. Gustav Fischer Verlag, Stuttgart.
TATARINOV, L.P. 1974. Theriodonts of the USSR (in Russian). *Transactions of the Palaeontology Institute* **143**, 1–250.
VAN DEN HEEVER, J.A. 1994. The cranial anatomy of the early Therocephalia (Amniota: Therapsida). *Universiteit van Stellenbosch Annale* **1994/1**, pp. 1–59.
VAN ROOYEN, J.M.1990. *The osteology and functional anatomy of the postcranial skeleton of* Gorgonops torvus *Owen (Gorgonopsia: Therapsida).* Unpublished M.Sc. thesis, University of the Orange Free State, Bloemfontein.
VON HUENE, F. 1950. Die Theriodontier des ostafrikanischen Ruhu-Gebietes in der Tübinger Sammlung. *Neues Jahrbuch für Mineralogie, Geologie und Paläeontologie, Berlagabände* **78**, 47–235.
WATSON, D.M.S. 1917. The evolution of the tetrapod shoulder girdle and forelimb. *Journal of Anatomy* **52**(1), 1–63.
WATSON, D.M.S. 1931 On the skeleton of a bauriamorph reptile. *Proceedings of the Zoological Society* **3**, 1173–1202.