

https://dspace.org/

The postcranial skeletal anatomy of the therocephalian Regisaurus (Therapsida: Regisauridae) and its utilization for biostratigraphic correlation

Fourie, Heidi; Rubidge, Bruce S.

2007

BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH

http://hdl.handle.net/10539/16101

Downloaded from a DSpace repository. https://dspace.org/

The postcranial skeletal anatomy of the therocephalian *Regisaurus* (Therapsida: Regisauridae) and its utilization for biostratigraphic correlation

Heidi Fourie* & Bruce S. Rubidge

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, Private Bag 3, WITS, 2050 South Africa

Received 25 August 2006. Accepted 18 April 2007

The postcranial morphology of the therocephalian genus *Regisaurus* from the *Lystrosaurus* Assemblage Zone of South Africa is described. The remarkably complete state of preservation of the vertebral column has, for the first time, provided a full vertebral count for a therocephalian and demonstrates that it is possible to differentiate between cervical, thoracic, lumbar, sacral and caudal vertebrae. It is demonstrated that some postcranial elements can be used to identify particular therocephalian groups and will be of use in biostratigraphic studies in areas where cranial remains have not been found. A slender scapula, low scapular ridge, shallow scapular depression, short and broad interclavicle, oval sternum, and a small obturator foramen are characteristics of therocephalians known from the *Cistecephalus, Dicynodon* and *Lystrosaurus* assemblage zones of the Beaufort Group of South Africa.

Keywords: Therapsida, Therocephalia, *Regisaurus,* postcranium.

INTRODUCTION

Therocephalians form a significant component of the therapsid faunas from the Karoo of South Africa, and together with dicynodonts are the therapsid clade that have the longest stratigraphic range in the rocks of the Karoo Supergroup. They also have a wide geographic range being known from Permian and Triassic rocks of southern and eastern Africa (Boonstra 1935, 1969; Drysdall & Kitching 1963; Kitching 1977; Keyser & Brink 1979), China (Li & Cheng 1995), Russia (Tatarinov 1974), and Antarctica (Colbert & Kitching1981). Many therocephalian taxa from South Africa have been described, and although several relatively recent descriptions on the cranial morphology are known (e.g. van den Heever 1987; 1994; Durand 1991; Hillenius 1992, 1994), studies on the postcranium of this important group have lagged behind. This paper describes a unique and almost completely preserved therocephalian skeleton (BP/1/3973). The presence of a long and high lacrimal; jugal meets the postorbital posteriorly and makes up the ventral portion of the postorbital bar; parietal present on dorsal part of occipital surface; upper dental formula of I6 C1 PC10; absence of precanines; palatal teeth on pterygoid boss; and apparent absence of a pineal foramen enables us to identify the specimen as *Regisaurus* (Mendrez 1975). Mendrez (1972) described the holotype of *Regisaurus* (BP/1/5394) on cranial morphology alone even though isolated elements of the hind limb, pelvic and pectoral girdles, and vertebral fragments are preserved. Kemp (1978) described the ilium and hind limb of the same specimen and made conclusions on the stance and gait of the genus.

MATERIAL

BP/1/3973 was collected by J.W. Kitching in 1964 from the *Lystrosaurus* Assemblage Zone on the farm Nooitgedacht, Bethulie, South Africa. *Proterosuchus* and *Lystrosaurus* are co-occurring genera from the same horizon at this locality, whereas *Dicynodon* (=*Daptocephalus*) and *Moschorhinus* are recorded from stratigraphically lower levels (Kitching 1977).

The specimen was preserved in a single calcareous nodule and was exposed by mechanical preparation using compressed air-driven engravers fitted with tungsten carbide tips. Because of the uniquely complete nature of the specimen great care was taken to preserve the original bone surface. For comparative purposes several therocephalian specimens that have postcranial elements preserved were studied in various museum collections (Table 1).

POSTCRANIAL DESCRIPTION

The skeleton of BP/1/3973 is almost complete, lacking only the right manus, left pes, left femur, left ilium and portion of the left tibia and right tibia and fibula. Parts of the pelvic girdle were disarticulated prior to fossilization and are preserved on the left side of the body close to the distal tibia and fibula (Figs 1B, 2B). As the holotype preserves only parts of the ilium and hind limb and elements of the shoulder girdle, specimen BP/1/3973 has much to contribute to our understanding of therocephalian postcranial anatomy. In the following description the 'in life' dorsal, ventral, lateral, and medial orientation of the different bones is assumed.

Vertebrae (Fig. 3)

A remarkable feature of BP/1/3973 is that, apart from the most distal caudals, the entire vertebral column is preserved in articulation. It is thus possible, for the first time, to accurately document the vertebral count of 32, excluding the caudals, for *Regisaurus.* A list of vertebral counts for a variety of therocephalian genera is provided (Table 2).

*Author for correspondence. Present address: Transvaal Museum, P.O. Box 413, Pretoria, 0001 South Africa. E-mail: hfourie@nfi.co.za

Table 1. List of therocephalian specimens used for comparative purposes.

Specimen No.	Genus	Assemblage Zone	Description
UCMP V 42667	*Cynariognathus platyrhinus*	*Tapinocephalus*	Cys (1967)
SAM 4321	*Blattoidealestes gracilis*	*Tapinocephalus*	Boonstra (1954)
SAM 12185	*Zinnosaurus (Lycosuchus)*	*Tapinocephalus*	Boonstra (1964)
SAM/K 7809	*Glanosuchus macrops*	*Tapinocephalus*	Fourie (2001)
SAM 4004	*Macroscelesaurus janseni*	(Gemsbokfontein)	Haughton (1918)
?	*Pristerognathus baini*	*Tapinocephalus*	Broom (1936)
SAM 6004	*Macroscelesaurus*	*Pristerognathus*	Haughton, 1918
TM 1608	*Silpholestes jackae*	*Tropidostoma*	Broom (1948)
RC 104	*Ictidosuchoides intermedius*	*Cistecephalus*	Broom (1938)
UCMP V 40467	*Mirotenthes*	*Cistecephalus*	Attridge (1956)
AMNH 5529	*Ictidosuchus primaevus*	(near Pearston)	Broom (1901)
BP/1/182	*Aneugomphius*	*Dicynodon*	Brink (1958)
BMNH R5694/5755	*Whaitsia*	*Dicynodon*	Boonstra (1934)
BP/1/2294	*Ictidosuchops intermedius*	*Dicynodon*	Not described
BP/1/3155	*Ictidosuchops intermedius*	*Tropidostoma*	Not described
BP/1/1341	*Scaloposaurus constrictus*	*Lystrosaurus*	Not described
BP/1/2710	*Tetracynodon darti*	*Lystrosaurus*	Sigogneau (1963)
BP/1/3849	*Olivieria parringtoni*	*Lystrosaurus*	Brink (1965)
BP/1/3973	*Regisaurus*	*Lystrosaurus*	Fourie (2001)
BP/1/5394	*Regisaurus jacobi*	*Lystrosaurus*	Kemp (1978)
SAM K 1392	*Zorillodontops gracilis*	*Lystrosaurus*	Cluver (1969)
AMNH 9550	*Ericiolacerta parva*	Fremouw Formation, Antarctica	Colbert & Kitching (1981)
DMSW R377/ MZC 7369	*Ericiolacerta parva*	*Lystrosaurus*	Watson (1931)
UMZC T 837	Baurioid	*Lystrosaurus*	Kemp (1986)
BP/1/1180	*Bauria cynops*	*Cynognathus*	Not described
AMNH 5622	*Bauria cynops*	*Cynognathus*	Broom (1937), Boonstra (1938), Schaeffer (1941)
V 4786	*Ordosia*	Er-Ma-Ying Formation	Lianhai (1979)
BMNH 4095	*Bauria cynops*	*Cynognathus*	Watson (1931)
NMQR 3189	*Bauria cynops*	*Cynognathus*	King (1996), Fourie (2001)
?	Bauriamorph	*Cynognathus*	Watson (1931)

Specimen BP/1/3973 preserves six articulated cervical vertebrae (including the atlas). A proatlas is not preserved and of the atlas, only the left transverse process is preserved. The axis is the largest of the cervical vertebrae and is easily distinguishable from the rest as it has the widest neural process which, in dorsal view, is triangular with rounded sides. The area below the neural spine (neural arch) is broadly rectangular in outline when viewed dorsally, with the enlarged prezygapophyses comprising the anterior rounded corners and the smaller postzygapophyses situated posterolaterally. The dorsal surface between the left and right prezygapophyses and left and right postzygapophyses is concave. Dorsally, the prezygapophysis is oval with a convex articulation surface, whereas the postzygapophysis has the same shape, but a concave articulation facet. Ventrally the prezygapophysis is concave and dips laterally towards the transverse process. The rectangular transverse process is placed closer to the prezygapophysis than to the postzygapophyses and at a lower level (Fig. 3A). In lateral view the anteroposteriorly expanded neural spine rises vertically, slightly overhanging the neural arch. It is broadly rectangular with concave anterior and posterior sides and slopes ventrolaterally towards the transverse process. An oval

Table 2. Table of vertebral counts of different therocephalian genera from both the literature and personal observation. The final row provides a summary of the range of recorded vertebral counts for well-preserved therocephalian specimens.

Specimen	Total (excl. caudal)	Presacral	Cervical	Thoracic	Lumbar	Sacral	Caudal
Glanosuchus, SAM/K7809	>28–29	27–28	5–6	>16	6	>1	>4
Macroscelesaurus, SAM4004	>30	27	7	>15	>5	3	
Cynariognathus, UCMPV42667	>30	27	7	>15	5	3	14
Mirotenthes, UCMPV3695	>10–11	>7	7			3–4	14
Aneugomphius, BP/1/182	>29	>25	>5	14–16	6–7	4	>3
Zorillodontops, SAMK1392	>15	>15–17	6–7	>5–6	>4		
Regisaurus, BP/1/3973	>32	28	6	17	5	4	>4
Scaloposaurus, BP/1/1341	>26	>24–25	6	>13	5–6	3–4	>2
Ericiolacerta, MZC7369	>19	>17–18	6–7	8	>3	3	>2
Baurioid, UMZCT837	>28	>19–21	14–15	5–6	3	>9–10	
All Therocephalia	28–32	27–28	6–7	15–17	5–6	3–4	>9

>= counts may be larger as the table is based on preserved material only.

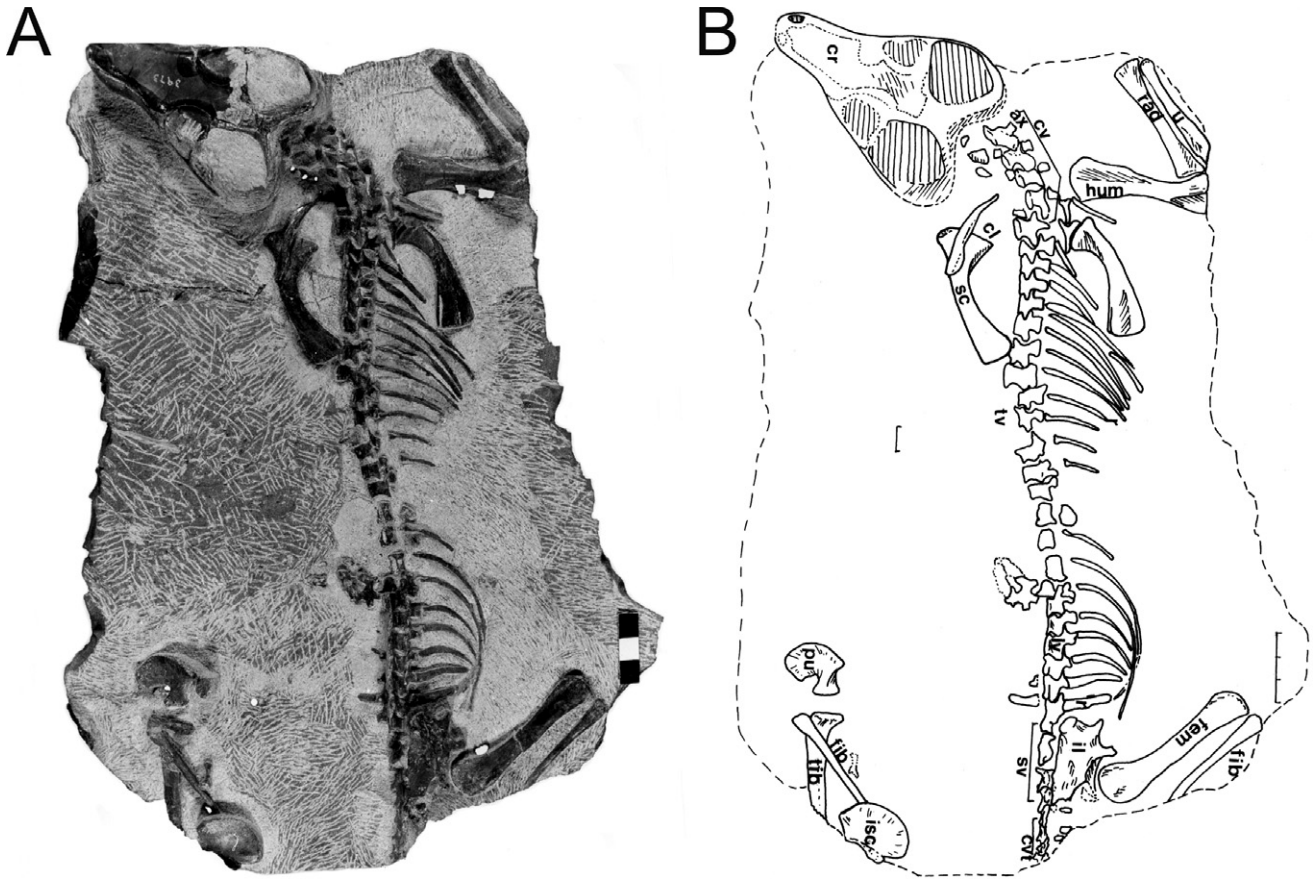

Figure 1. Dorsal view of *Regisaurus* sp. (BP/1/3973). Scale bar = 10 mm.

facet, which is thickened for the articulation with the tuberculum of the rib, is situated on the lateral extremity of the transverse process. The spindle-shaped amphicoelous centrum thins toward the middle.

The remaining four cervical vertebrae (Fig. 3B) have the same general shape as the axis, except that the neural spine is not anteroposteriorly expanded. The sixth cervical has a slightly wider neural spine than those of the preceding four vertebrae, but is not as wide as that of the axis.

As in all therocephalian genera the 17 thoracic vertebrae

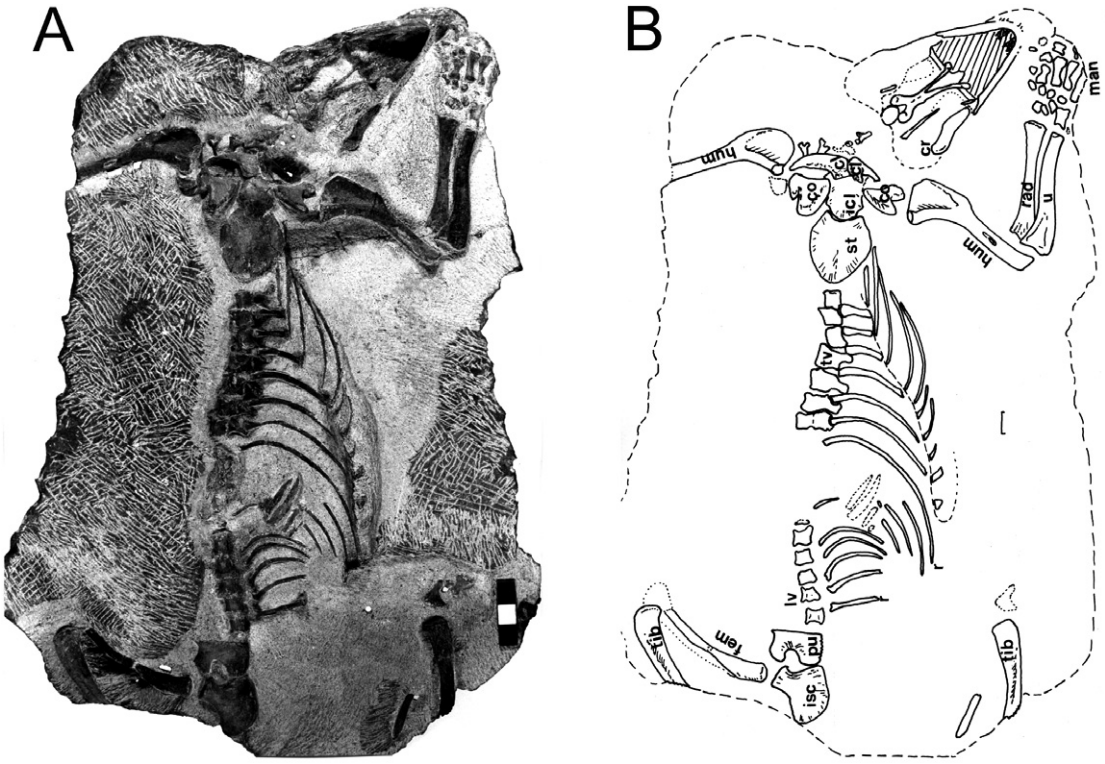

Figure 2. Ventral view of *Regisaurus* sp. (BP/1/3973). Scale bar = 10 mm.

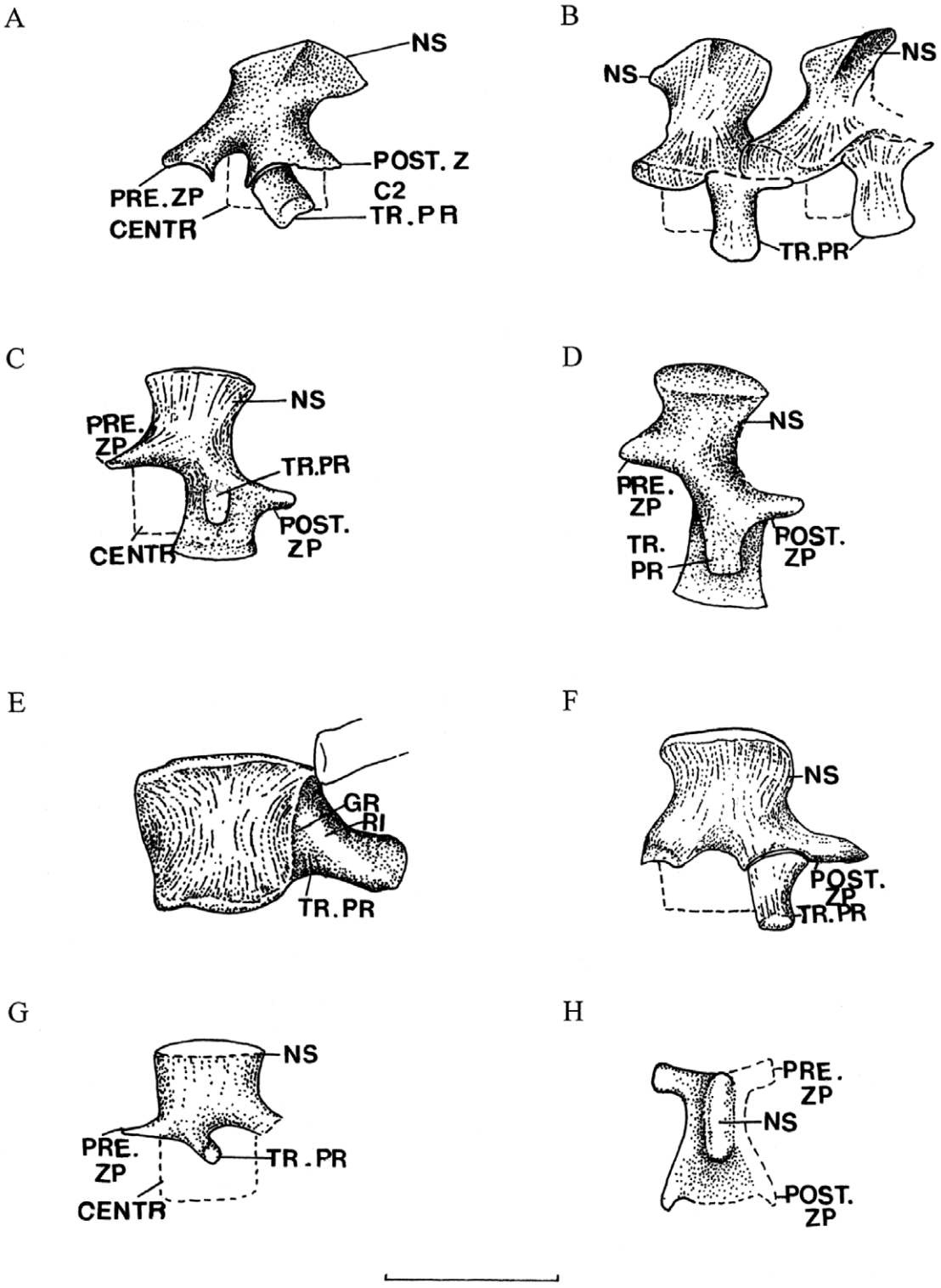

Figure 3. Vertebrae of *Regisaurus* sp. (BP/1/3973): **A**, axis (lateral view); **B**, cervical C3, C4 (lateral view); **C**, thoracic T1 (lateral view); **D**, thoracic T10 (lateral view); **E**, thoracic T 10 centrum showing groove (ventral view); **F**, lumbar L4 (lateral view); **G**, sacral S3 (lateral view); **H**, sacral S3 (dorsal view). Scale bar = 10 mm.

of BP/1/3973 (Fig. 3C,D) are similar in shape to the cervical vertebrae, but differ in that they are more lightly built. In ventral view the transverse process of each of the 17 thoracic vertebrae is broadly triangular with the apex extending posterolaterally and ventrally to contact its corresponding rib. The anterior border of the process is straight while the posterior one is slightly concave. A ridge is present on the anteroventral edge of the transverse process and has an elongated groove extending parallel to it (Fig. 3E). The transverse process was not ossified to the centrum, as can be seen clearly in T11 and T12 (Fig. 3B), suggesting this was a young individual.

The five lumbar vertebrae have the same general shape as those of the cervical and thoracic regions. In lateral view, the neural spines of the lumbar vertebrae are longer than those of the thoracic vertebrae whereas the transverse processes are shorter, more robust and wider (Fig. 3F). In these vertebrae the transverse processes point laterally

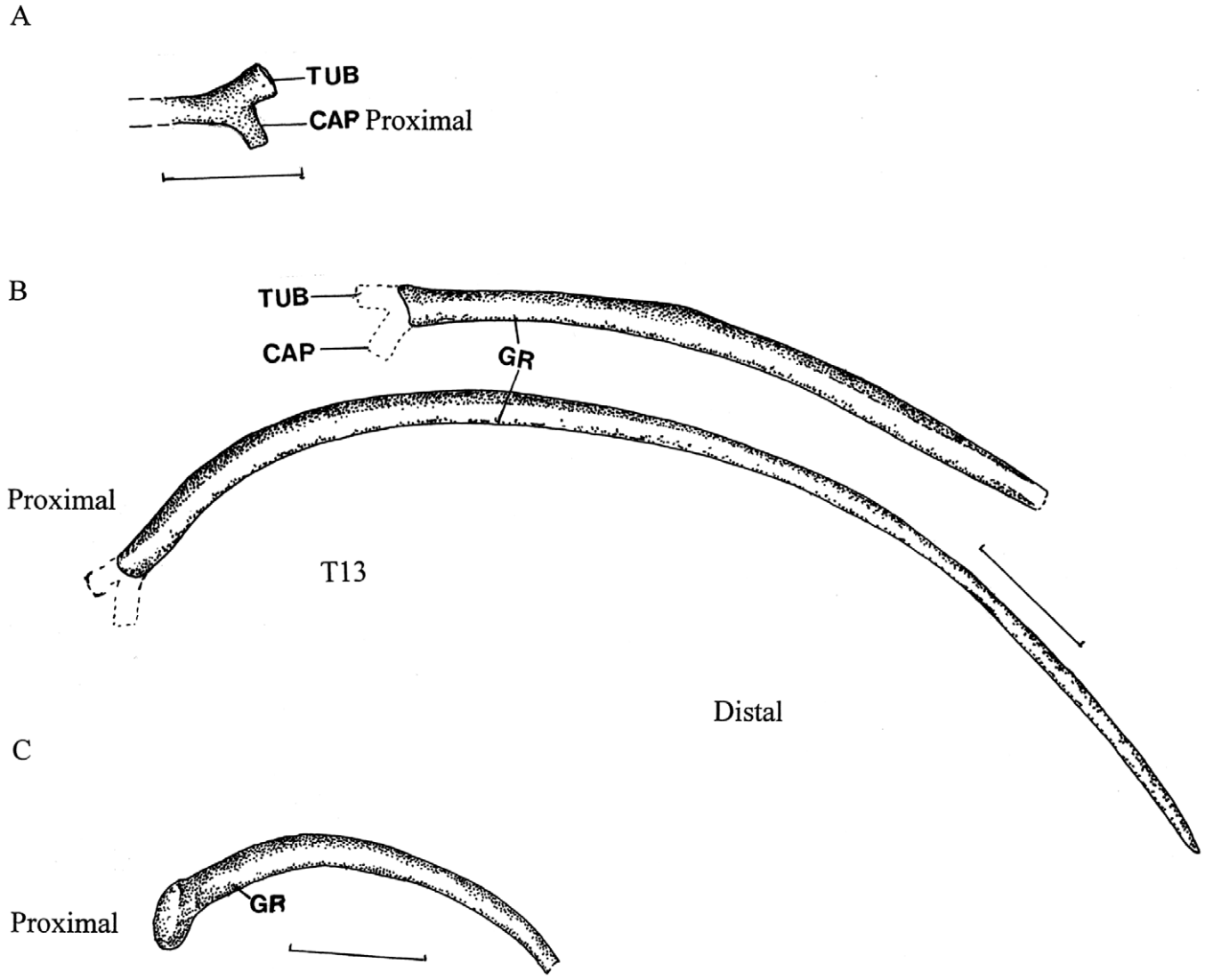

Figure 4. Ribs of *Regisaurus* sp. (BP/1/3973): **A**, cervical, proximal end; **B**, thoracic T5 and T13 (posterior view); **C**, Lumbar L3 (posterior view). Scale bars =10 mm.

rather than posterolaterally as in the cervical and thoracic vertebrae.

In general shape the four sacrals are similar to the other vertebrae, but each has a shorter and thinner neural spine, and a shorter transverse process (Fig. 3G,H). In dorsal view the transverse process is rectangular with a rounded upper surface and is fused to its corresponding sacral rib.

Only the anteriormost four caudal vertebrae are preserved. Although they are similar in shape, they are much smaller than the other vertebrae and decrease in size posteriorly. The transverse processes slope ventrally and are short, thick and rounded dorsally with a concave contact area for the ribs at their distal extremity. These vertebrae have low neural spines which decrease in size posteriorly. As the last caudal vertebrae of all therocephalians, where they are preserved, comprise only centra, it is expected that in BP/1/3973 caudal neural spines, transverse processes and ribs disappear posteriorly.

Ribs (Fig. 4)

Although the rib cage of specimen BP/1/3973 was flattened in the fossilization process many of the ribs are preserved (Fig. 1). In the cervical region most of the ribs are broken, but two well-preserved ribs demonstrate that the cervical ribs have a short, thin, and slightly curved shaft with a dichocephalous head. The tuberculum is wider and more stocky than the capitulum (Fig. 4A), which in turn is longer and thinner. The articulation facet of the tuberculum for the transverse process (diapophysis) is slightly flattened compared to that of the capitulum for the centrum (parapophysis) which is rounded. A groove which lines up with the groove on the transverse process extends from the tuberculum to the distal end of the rib. These ribs, which are very short, did not contact the sternum.

The dichocephalous thoracic ribs of BP/1/3973, which are attached to the sternum, are longer and more slender than the cervical ribs and a broad sheet of bone joins the tuberculum and capitulum. The proximal part of the rib is wider than the distal end and flattened anteroposteriorly. As in the cervical ribs, a groove (Fig. 4B, GR) extends on the posterior side of the rib from the tuberculum to the distal end. The flattened rib shaft curves away ventrally from the vertebral column for a short distance and straightens towards the distal end to meet the sternal segment. In BP/1/3973 12 sternal segments are visible in

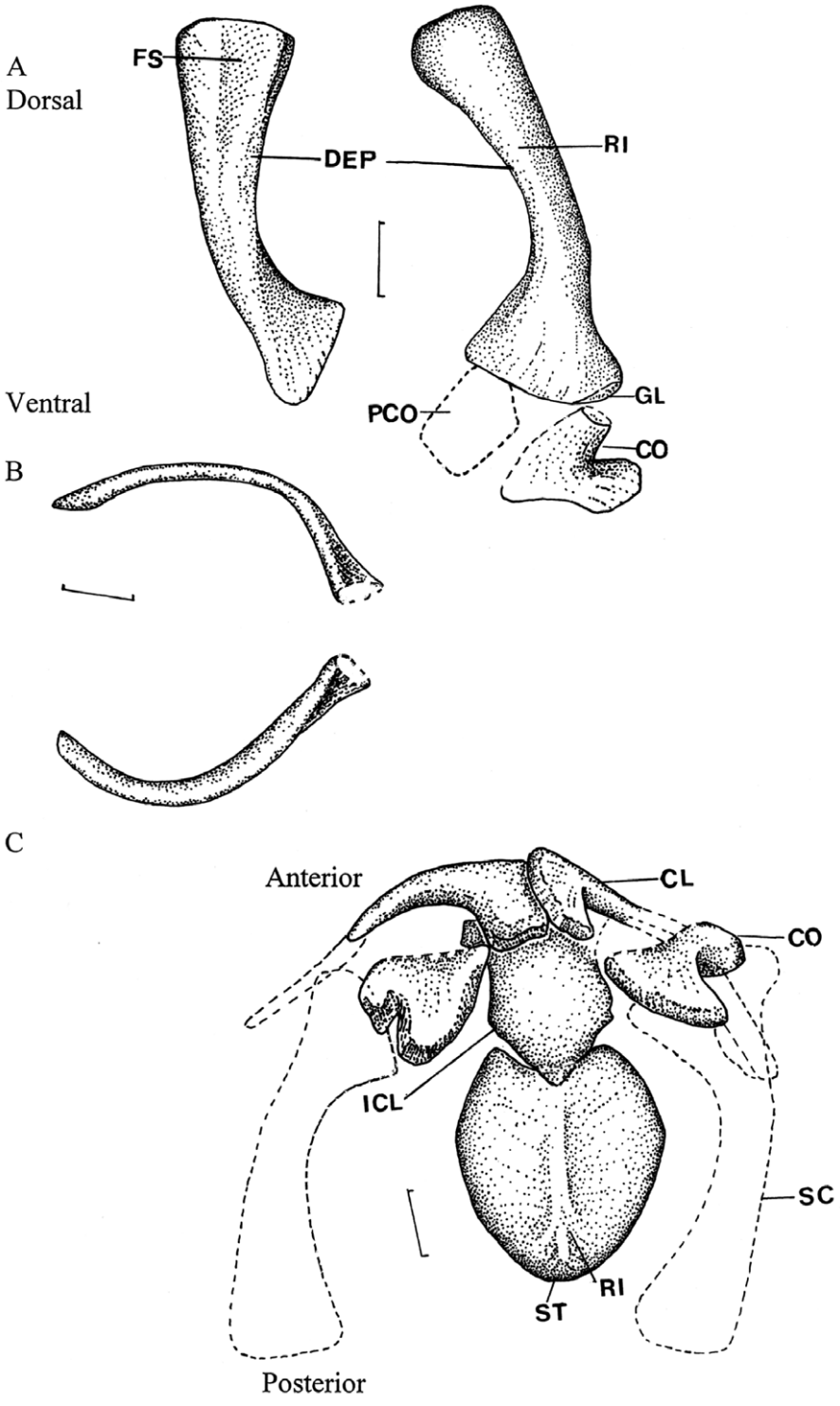

Figure 5. Pectoral girdle of *Regisaurus* sp. (BP/1/3973): **A**, scapula and coracoid (lateral view); **B**, claviculae (dorsal view); **C**, ventral view showing coracoids, interclavicle and sternum. Scale bars = 10 mm.

ventral view. These are attached to the sternum and decrease in length posteriorly. Rib 14 is the longest, and from this point the ribs become progressively shorter both anteriorly and posteriorly.

Lumbar ribs, which are much shorter and broader than the thoracic ribs, are fused to the vertebrae and decrease in size posteriorly. These dorsally rounded ribs are all single-headed (Fig. 4C) and are expanded both dorso-ventrally and anteroposteriorly with the proximal end being the widest. The first three lumbar ribs curve ventrally (the third less than the first) and the last two are straight. Distally the shafts of all the lumbar ribs have a rounded end.

In dorsal view the caudal ribs are rectangular and much shorter than those of the lumbar region. These single headed ribs are fused to the vertebrae and curve ventrally. The distal end is blunt.

Pectoral girdle (Fig. 5)

The interclavicle of BP/1/3973 (Fig. 5C), visible in ventral view, is situated between the coracoids, clavicles and sternum and is a broad flat circular bone. A posteromedial

ridge is present as seen in *Ericiolacerta* (Watson 1931). Both clavicles, which are 55 mm long, are preserved but the right one lacks the distal end. In ventral view the rectangular proximal end of the left clavicle is displaced over the right, and they both overlie the interclavicle. Dorsally the oval end fits loosely against the bottom third of the scapula. Both procoracoids and coracoids are preserved, but they are displaced in such a way that the procoracoids are tilted and not much of them are visible. The large oval sternum is ossified with a longitudinal median ridge extending down the ventral side of the thin plate. Both humeri, which are robust bones, are preserved in a sprawling position and are articulated distally with the lower leg.

The scapula of only the holotype (BP/1/5394) has the ventral portion preserved and so the complete scapula of BP/1/3973 affords the best description. This bone, which is approximately 80 mm in length, is the largest element of the pectoral girdle (Fig. 5B). Both scapulae of BP/1/3973 are tilted so that the lateral surface is exposed on the dorsal side of the specimen. It is a curved bone which is flattened lateromedially and has slightly expanded proximal and distal ends. In lateral view the dorsal end is expanded anteroposteriorly. The entire flattened lateral surface has striations extending from the proximal to the distal end of the shaft. From the dorsal end, the scapula narrows towards the middle of the bone where the shaft is semi-circular in cross-section. The lateral surface has a median ridge that extends dorsoventrally (Fig. 5B, RI) on the shaft to terminate on the glenoid facet. Ventrolaterally the bone surface is flat and only slightly rounded in the glenoid area. The glenoid facet is concave and oval. The ventral end of the scapula is much more expanded anteroposteriorly than on the dorsal end and it flares further posteriorly towards the glenoid facet than towards the anterior side. The extreme ventral surface of the bone is curved downwards. An area above the glenoid facet is striated towards the shaft in a dorsal direction. Striations are present on the medial depressed surface in a dorsal direction, both striated areas terminating on the shaft. These striations extend in an anteromedial and posteromedial direction. The medial surface of the scapula curves posteroventrally to overlie the thoracic ribs. As in all therocephalians in which the scapula is known, this bone lacks an acromion process.

The presence of an ossified cleithrum in therocephalians is uncertain, and has been described in only a few genera (Boonstra 1964; Watson 1931) as a very small splint of bone attached to the anterior edge and outer surface of the upper end of the scapula as seen in *Scymnosaurus* and *Pristerognathus,* The lack of a cleithrum in BP/1/3973 and the absence of facets on the anterior edge of the scapula of suggests that an ossified cleithrum may not have been present.

The coracoid (Fig. 5C) is blade-like and the surface is almost flat. It has a smooth contact with the sternum and a sutural contact with the procoracoid. The dorsal edge is unattached forming the concave glenoid facet. The blade surface is slightly convex with striations that extend from the glenoid towards the medial edge.

In ventral view the thin sternum is oval with an indentation at the anterior end to accommodate the overlapping interclavicle (Fig. 5C). A prominent midline ridge which increases posteriorly in height extends from the centre of the bone towards the posteriormost edge to end pointed. On either side of this ridge is a slightly depressed area. Striations extend in a flaring pattern from the centre of the sternum outwards towards the edge.

Forelimb (Figs 6 & 7)

The humerus of BP/1/3973 is a robust and relatively long bone (Fig. 6) with the deltopectoral crest situated proximally and the double condyle at the opposite end. The bone is twisted such that the deltopectoral crest was oriented vertically in life, while the distal end of the humerus had a horizontal orientation. A marked triangular recess between the ente- and ectepicondyles on the dorsal side of the humerus served as the fossa for the olecranon, while a small lip at the distal end of the fossa prevented the olecranon from dislocating.

The deltopectoral crest is expanded dorsoventrally, but narrows towards the circular short shaft. The proximal extremity of the caput humerus curves outwards towards the glenoid. Long proximodistally oriented striations on the anterior side of the deltopectoral crest are interpreted as muscle scars.

In ventral view (Fig. 6D) the proximal end of the deltopectoral crest curves posteriorly and has a thin rounded edge. A small oval elongated entepicondylar foramen is present close to the distal end where the ente- and ectepicondyles have a concave triangular recess in which the entepicondylar foramen is situated. No ectepicondylar foramen is present as is the situation in *Mirotenthes* (Attridge 1956), *Cynariognathus* (Cys 1967), Regisauridae (Kemp 1986), Scylacosauridae (Boonstra 1964), *Silpholestes* (Broom 1948) and *Whaitsia* (Boonstra 1934). The presence of this foramen in *Bauria* (NMQR 3189) indicates that this feature is variable in therocephalians or only present in the more derived forms.

The sigmoid curved ulna of BP/1/3973 is long and thin with an expanded olecranon process at the proximal end (Fig. 7A,B). It is blunt distally where it has an ovoid articulation facet for the ulnare. In anterior view the proximal end is lateromedially expanded with a longitudinal groove (Fig. 7A) which extends half-way down the bone. The shaft is thin and flattened. The ulna exhibits a weak olecranon process (Fig. 7B). Posteroventral to the olecranon process is a triangular depression area with the apex pointing distally (Fig. 7B, DEP). The ulna and radius cross to some degree with the proximal ulna positioned medial to the radius.

The radius (Fig. 7) is an elongated bone with a relatively thin shaft and lateromedially expanded ends, with the proximal end much broader than the distal. The proximal articulating facet is slightly concave on the anterior side where it articulates with the entepicondyle of the humerus. Both the proximal and distal extremities are oval and concave. An incipient ridge (Fig. 8B, RI) extends on the posterior side of the bone from a position two-thirds down the length of the radius to the distal end. In *Bauria*

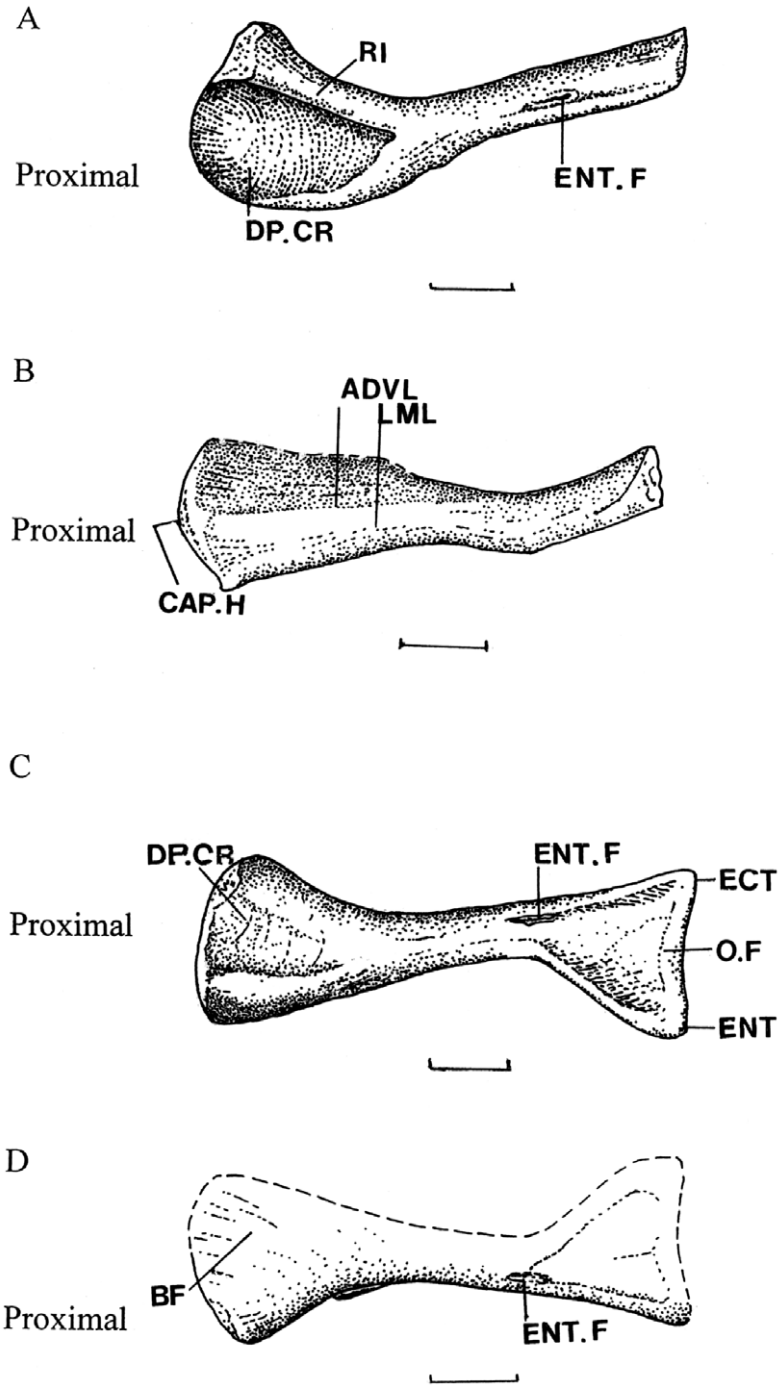

Figure 6. Left humerus of *Regisaurus* sp. (BP/1/3973): **A**, posterior view; **B**, anterior view; **C**, dorsal view; **D**, ventral view. Scale bars = 10 mm.

(NMQR 3189) there is a ridge on the anterior surface.

The carpals are remarkably well preserved with the ulnare, radiale, pisiforme, intermedium, one centrale and three distals being preserved in articulation (Fig. 7C). These bones are present in two rows with the radiale, ulnare, intermedium, pisiforme and the centrale at the proximal end of the wrist, and the distals in the second row. The ulnare is the largest of the carpal bones and is dorsoventrally flattened and rectangular. It has a round proximal facet for articulation with the distal end of the ulna. As in all therocephalians the ulnare is hour-glass shaped in dorsal view with expanded ends. A distinct groove is present between the ulnare and centrale 1 on the dorsal side while the ventral surface of the ulnare has a longitudinal groove. The flattened proximal end has its lateral edge truncated into an articular facet for the pisiforme. Centrale 1 articulates with the medial surface of the ulnare while the fused distals 4 and 5 articulate with the distal side of the ulnare.

The radiale is the second largest wrist bone and articulates with the radius. This quadrangular bone is positioned at the distal end of the radius. Both medial and lateral sides are straight with the anterior and posterior ends rounded and a central concavity is present on the dorsal surface. The posteriorly situated radial articular surface is broad and slightly convex, while anteriorly, centrale 1 articulates with the radiale in a concave facet as in all therocephalians where this bone is preserved.

Both the pisiforme and intermedium are small bones, the rounded pisiforme being present on the lateral side of

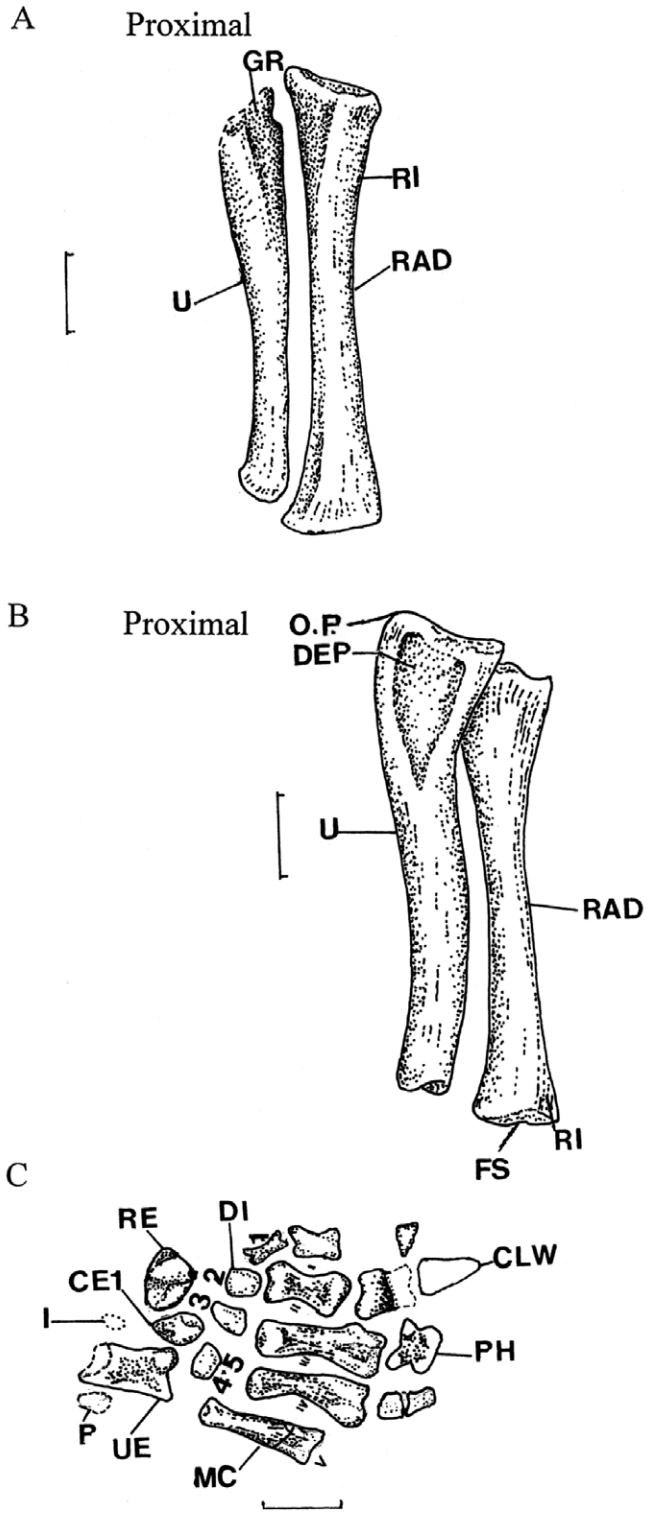

Figure 7. Distal forelimb of *Regisaurus* sp. (BP/1/3973): **A**, radius and ulna (anterior view); **B**, radius and ulna (posterior view); **C**, manus (ventral view). Scale bars = 10 mm.

the wrist next to the ulnare, and the oval intermedium between the ulnare and radiale. Only one centrale is preserved in this specimen and is situated between the ulnare and the radiale. Three distal carpals are preserved, as distals 4 and 5 are fused and distal 1 is absent. These are relatively small quadrangular bones and are positioned at the proximal end of their corresponding metacarpal and the displaced fused distal 4 and 5 is situated above metacarpals 4 and 5.

A single, almost circular centrale is rounded posteriorly with a depression present close to the ulnare and a ridge on the opposite side. There is a slight concavity close to where distal 1 is supposed to be preserved between the radiale and distal 2. Distal 2 is squarish with rounded corners and is situated close to metacarpal II. The dorsal surface is convex. Distal 3 is round with a convex dorsal surface and articulates with metacarpal III. Fused distal 4 and 5 is a small bean-shaped bone situated on the proximal ends of metacarpals IV and V and has a round posterior edge.

All five metacarpals are preserved and are the longest bones of the hand (Fig. 7C). They are elongated with a long, thin, rounded shaft, and expanded ends. Metacarpal I, the smallest, has been slightly displaced towards the radiale. It is relatively short with a rounded dorsal surface and constricted towards the middle to have an hour-glass shape. The proximal articulating surface is concave while the distal surface is rounded to form double condyles. The more laterally positioned metacarpals are larger with Metacarpal IV being the longest and Metacarpal III longer than V. Distally all the metacarpals are more expanded laterally than medially.

Only four phalanges are preserved of which two are terminal. The proximal phalanges are almost square in outline with a slight narrowing in the middle, and double condyles at the ends. Unguals are triangular, ventrally curved, forming blunt pointed claws.

Pelvic girdle (Fig. 8)

All components of the right pelvis of BP/1/3973 are preserved almost in articulation. As is evident from both this specimen and the holotype, the ilium (Fig. 8A) is a large antero-posteriorly elongated bone with a slightly expanded blade. It has an almost vertical orientation in the body parallel to the sacral vertebrae. One posterior and two anterior processes are present on the blade, and the acetabulum is situated ventrolaterally. The blade is relatively large with striations on the lateral surface extending from the dorsal edge towards the acetabulum. Dorsally the blade is flat and thin and slopes postero-ventrally as well as anteroposteriorly. The acetabulum is a concave facet forming a lunate surface with a large prominent capping supra-acetabular buttress (Fig. 8A, SAB) with rounded, ridged edges as described in the holotype (Kemp 1978). Anterior to the acetabulum the blade curves anteriorly to form the thin and pointed ventral anterior process. The dorsal anterior process is larger and rounded. A slight triangular depression (Fig. 8A, DEP) is present between the two anterior processes on the medial surface. As in the holotype (Kemp 1978) two distinctive larger depressions are visible on the lateral surface of the blade, one between the anterior processes and one just below the ventral anterior process. At the posterodorsal side of the acetabulum, just posterior to the buttress, is the supra-acetabular notch.

In ventral view the pubis is roughly rectangular with a prominent posterior indentation which forms the anterior margin of the obturator foramen which is situated between the pubis and the ischium. A slightly concave

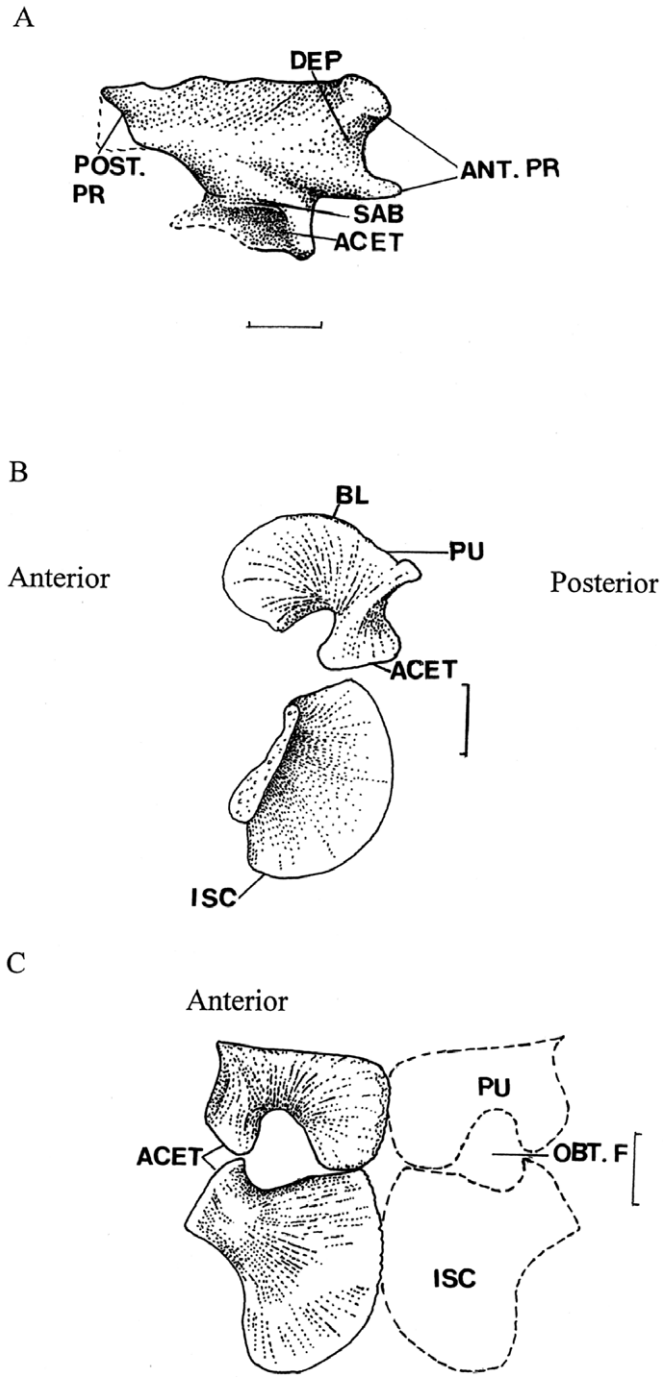

Figure 8. Pelvic girdle of *Regisaurus* sp. (BP/1/3973): **A**, right ilium (lateral view); **B**, left pubis and ischium (dorsal view); **C**, pubis and ischium (ventral view). Scale bars = 10 mm.

acetabular portion of the pubis is less developed than that of the ischium. The dorsal surface of the pubis is convex while the ventral side is concave.

The ischium has a mushroom-shaped outline (Fig. 8B,C) when viewed from the ventral side. It has a relatively large, thin blade with marked striations fanning out from the centre. The flared blade surface is convex ventrally and concave dorsally, and meets its counterpart medially in a slightly convex symphysis. The acetabular facet is slightly concave.

Hind limb (Figs 9 & 10)

The left hind limb of BP/1/3973 is not well preserved but the right limb is reasonably complete and articulated with the pelvis. The distal end of the leg, including the ankle and pes, is missing. Unidentifiable elements of the left pes are scattered in the matrix.

As the left hind limb of the holtype is particularly well preserved (Kemp 1978) this description will refer to the holotype in areas where BP/1/3973 is not well preserved.

The femur is an elongated bone with a slight sigmoid curvature in dorsal view and both proximal and distal ends are expanded (Fig. 9). In dorsal view the rounded caput femoris is anteroposteriorly expanded. Elongated striations extend from the proximal end down the shaft which is dorsoventrally flattened with the posterior side thinner than the anterior side. A prominent posteriorly positioned trochanter major (external trochanter) is present immediately behind the head. The trochanter minor (internal trochanter) is situated anteriorly opposite the trochanter major and is positioned further from the proximal edge of the bone than the trochanter major as in the holotype (BP/1/5394).

As in the holotype, distal to the major and minor trochanters the shaft is circular in cross-section and ends distally in a double condyle. On the dorsal surface there is a triangular depression, the patella groove, between the condyles (Fig. 9D, PAT.GR). The internal trochanter is visible on the ventral side of the proximal end of the femur just below the caput femoris and slopes towards the shaft. It is smaller than the trochanter major and the same size as the trochanter minor. An oval fossa is situated anterior to the internal trochanter, whereas a slight depression is placed posteriorly (Fig. 9C, DEP). Proximally to the internal trochanter is a deep fossa that can also be seen in posterior view.

Only the proximal portions of the left and right tibiae are preserved in BP/1/3973. The tibia is an elongated lateromedially flattened bone with striations extending down the shaft as in the holotype (BP/1/5394). In lateral view the proximal end is rounded and expanded further posteriorly than anteriorly. As has been reported for *Bauria* (King 1996) a shallow longitudinal groove is present on the posterior side of the proximal end of the shaft (Fig. 10B, GR). Medially the shaft is rounded and has an elongated short ridge (Fig. 10A, RI). No cnemial crest is present on the shaft (Kemp 1978). Stretching from the proximal end, the lateral face has a broad, flat fossa which terminates about two centimetres from the ventral end of the bone as a distinct groove (Kemp 1978). Distally the tibia is only slightly expanded, with its astragalar face slightly concave as seen in *Bauria* (Schaeffer, 1941). Kemp (1978) described the tibia of the holotype as flattened lateromedially with the articulation surface for the astragalus as flat, apart from the notch for the fibula, which is circular in outline.

The fibula is a long, straight and slender bone which is slightly expanded proximally (Fig. 10C,D). It is slightly bowed such that it is gently concave towards the tibia. The shaft is ovoid in cross-section, being slightly flattened on the anterior and posterior sides as in the holotype (Kemp 1978). Kemp described the distal end as even more flattened and terminating in an oval-shaped, distally-facing facet for the articulation with the calcaneum.

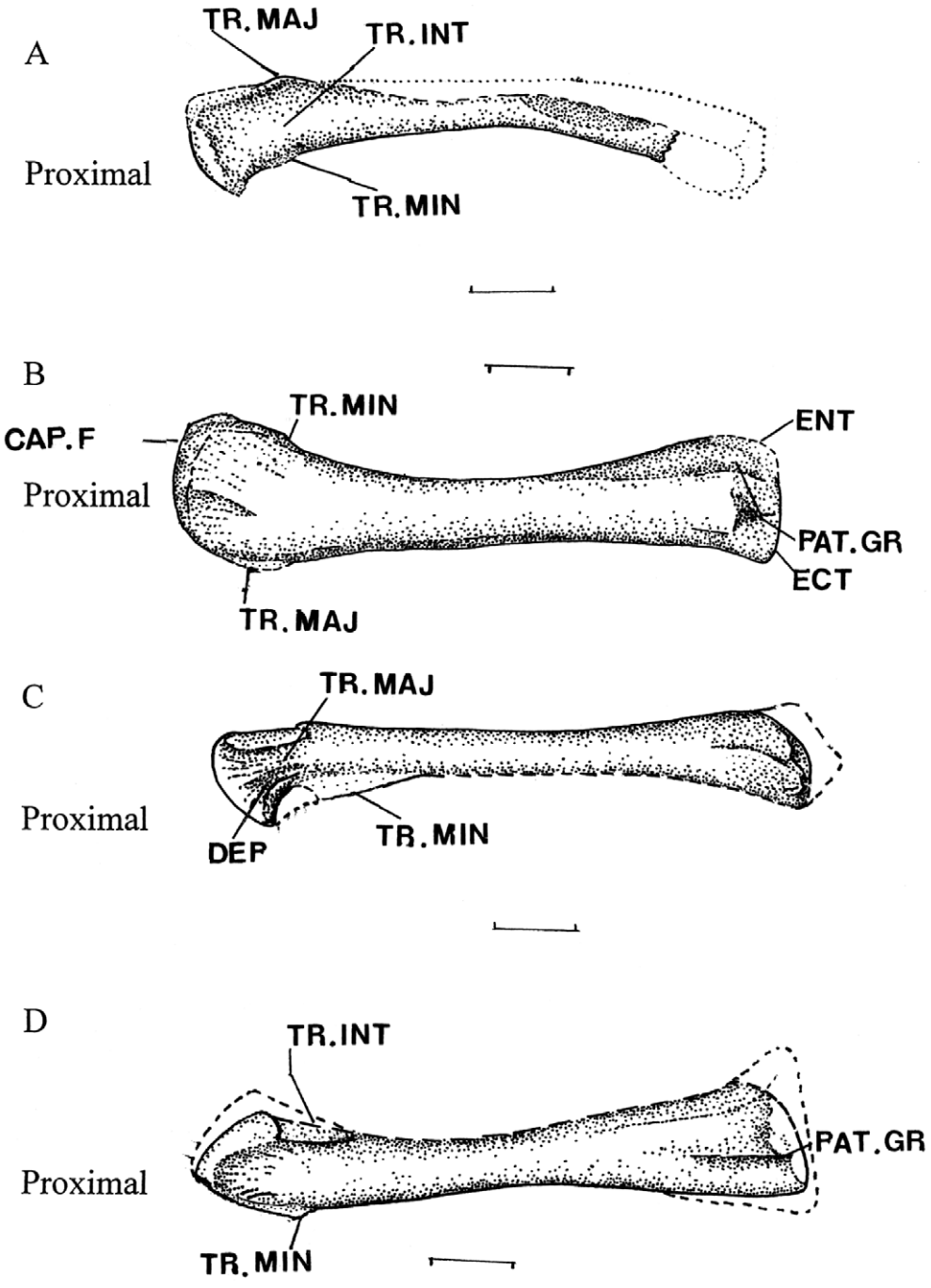

Figure 9. Right femur of *Regisaurus* sp. (BP/1/3973): **A**, ventral view, **B**, dorsal view, **C**, posterior view, **D**, anterior view. Scale bars = 10 mm.

DISCUSSION

The remarkably complete state of preservation of *Regisaurus* (BP/1/3973) has enabled, for the first time, the description of the postcranial anatomy of an almost complete skeleton of a therocephalian. Because this specimen preserves a complete vertebral column, except for some distal caudals, it has been possible to compare the vertebral morphology of *Regisaurus* with that of other therocephalian genera based on both personal observation and literature studies. This description has determined that *Regisaurus* has six cervical, 17 thoracic, five lumbar, and four sacral vertebrae. This figure differs from previous descriptions for a variety of therocephalian genera (Table 2), but most of these are based on incomplete specimens.

In the literature vertebrae have been described for the following therocephalian genera; *Cynariognathus* (Cys 1967), *Pristerognathus* (Broom 1936), *Macroscelesaurus* (Haughton 1918), *Ictidosuchoides* (Broom 1938), *Mirotenthes* (Attridge 1956), *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Zorillodontops* (Cluver 1969), *Tetracynodon* (Sigogneau 1963), *Aneugomphius* (Brink 1958), *Ictidosuchus* (Broom 1901), *Ericiolacerta* (Watson 1931; Colbert & Kitching 1981), *Olivieria* (Brink 1965), *Regisaurus* (Kemp 1978), a baurioid (Kemp 1986), *Ordosia* (Lianhai 1979), a bauriamorph (Watson 1931) and *Bauria* (King 1996; Fourie 2001).

Cervical vertebrae of all therocephalians, as in other therapsids, can be morphologically separated into the pro-atlas, atlas, axis and remaining cervical vertebrae. The difference in the morphology of different cervical vertebrae in *Regisaurus* is characterized by the morphology of the

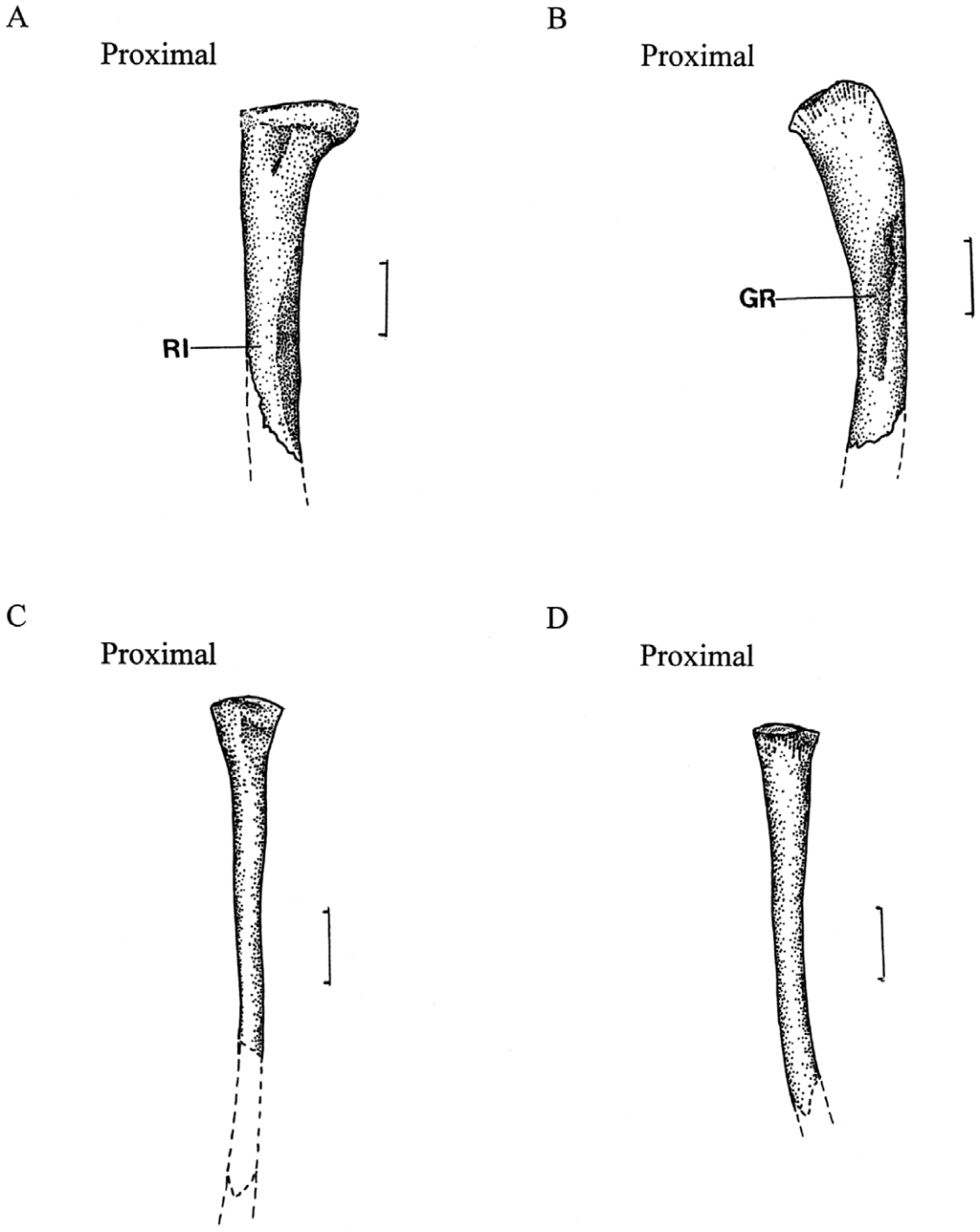

Figure 10. Proximal tibia and fibula of *Regisaurus* sp. (BP/1/3973): **A**, left tibia (anterior view); **B**, left tibia (posterior view); **C**, left fibula (lateral view); **D**, right fibula (medial view). Scale bars = 10 mm.

neural spine as the last cervical has a more anteroposteriorly expanded neural spine than the rest of the cervicals, but even this is not as expanded as the neural spine of the axis. No intercentra are present in the cervical region of *Regisaurus* as in *Cynariognathus* (Cys 1967), *Macroscelesaurus* (Haughton 1918) and *Aneugomphius* (Brink 1958). They have however been recorded between the cervical vertebrae in the Chinese genus *Ordosia* (Hou Lianhai 1979). Kemp (1986) reported poor ossification of the ends of the centra of an unidentified baurioid and considered this as an indication of the presence of unossified intercentra between the atlas and axis.

Thoracic vertebrae of *Regisaurus* have the same anatomy as the preceding cervical vertebrae, but are more lightly built with longer, thinner transverse processes that extend posterolaterally rather than laterally. The lumbar vertebrae are characterized by wider neural spines and short, wide transverse processes. Sacral and caudal vertebrae have thin neural spines with short ribs. The sacral vertebrae have higher neural spines when compared to the caudal vertebrae, but vertebrae from both these regions are characterized by having fused holocephalous ribs which are grooved on the posterior side.

None of the specimens studied have a fully preserved caudal series but it is evident that *Regisaurus,* as in all therocephalians, must have had a short stocky tail with many small and short vertebrae as has been reported for *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Mirotenthes* (Attridge 1956), *Cynariognathus* (Cys 1967) and *Aneugomphius* (Brink 1958), *Ictidosuchoides* (Broom 1938),

Ericiolacerta (Watson 1931; Colbert & Kitching 1981) and an unidentified bauroid (Kemp 1986). King (1996) described remnants of haemal arches on the caudal vertebrae of *Bauria* (NMQR 3189), but these have more recently been interpreted as remnants of the neural spines of the dorsal vertebrae (Fourie 2001).

Ribs in most therocephalian specimens are not well preserved and have been described for *Cynariognathus* (Cys 1967), *Macroscelesaurus* (Haughton 1918), *Zorillodontops* (Cluver 1969), *Mirotenthes* (Attridge 1956), *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Tetracynodon* (Sigogneau 1963), *Aneugomphius* (Brink 1958), *Olivieria* (Brink 1965), *Ericiolacerta* Watson 1931; Colbert & Kitching 1981), *Bauria* (King 1996; Fourie 2001) and a baurioid (Kemp 1986). In *Regisaurus* the ribs from the different regions of the body all have differing morphologies. By far the longest ribs are those of the thoracic region which also have their sternal segments preserved. The only other therocephalian which has sternal segments preserved is *Olivieria* (BP/1/3849), while they were considered to have been cartilaginous in *Mirotenthes* (Attridge 1956). The cervical and thoracic ribs are of *Regisaurus* as in other therocephalians where they are described (see above) are dichocephalous whereas the lumbar, sacral and caudal ribs are holocephalous.

The pectoral girdle has been preserved in skeletons of the following therocephalian genera: *Cynariognathus* (Cys 1967), *Pristerognathus* (Broom 1936), *Macroscelesaurus* (Haughton 1918), *Silpholestes* (Broom 1948), *Zinnosaurus* (Boonstra 1964), *Glanosuchus* (Fourie 2001), *Zorillodontops* (Cluver 1969), *Ictidosuchus* (Broom 1901), *Ictidosuchoides* (Broom 1938), *Aneugomphius* (Brink 1958), *Regisaurus* (Kemp 1978), *Ordosia* (Lianhai 1979), *Tetracynodon* (Sigogneau 1963), *Mirotenthes* (Attridge 1956), *Ericiolacerta* (Watson 1931), *Olivieria* (Brink 1965), *Bauria* (King 1996; Fourie 2001) and a baurioid (Kemp 1986). All of these descriptions are based on incomplete material, while BP/1/3973 affords the opportunity to describe a completely articulated pectoral girdle and forelimb for the first time. There are significant differences in the pectoral girdle of different therocephalian genera and it is apparent that three definite scapular shapes are present. Scylacosaurids and lycosuchids have a short and broad scapula, while *Ictidosuchops, Mirotenthes, Aneugomphius, Ictidosuchus, Tetracynodon, Zorillodontops, Olivieria* and *Regisaurus* have a less broad scapula, while that of *Bauria* and *Ordosia* is delicate and narrow. The scapula of *Bauria* is diagnostic in that a prominent lateral ridge is present on the blade surface with a deep depression positioned next to it (King 1996, fig. 5). The ridge on the scapular blade is present although remarkably reduced in the *Tapinocephalus* Assemblage Zone therocephalians (Boonstra 1964) while an acromion process of the scapula is not present in any therocephalian genus.

The cleithrum of therocephalians is splint-like and has been described in *Pristerognathus* (Broom 1936), *Bauria* (Watson 1931) and *Ericiolacerta* (Watson 1931), but appears to have been absent in *Cynariognathus* (Cys 1967), *Mirotenthes* (Attridge 1956), *Regisaurus* (BP/1/3973), a baurioid (Kemp 1986) and *Bauria* (King 1996). The scapular facet of the glenoid in all therocephalians is oval, facing posteriorly and laterally, with the procoracoid either forming a part of the glenoid as in *Cynariognathus* (Cys 1967) or taking no part in the formation of the glenoid as in *Zinnosaurus* (Boonstra 1964), *Macroscelesaurus* (Haughton 1918), *Ericiolacerta* (Watson 1931), *Mirotenthes* (Attridge 1956), *Ictidosuchus* (Broom 1901), *Regisaurus* (Kemp 1978) and a baurioid (Kemp 1986). The procarocoid of *Regisaurus* is an irregular quadrangular bone and has a long, broad articulation with the scapula. The presence of a procoracoid foramen has variously been reported on the procoracoid–coracoid suture in *Ericiolacerta* (Watson 1931), *Tetracynodon* (Sigogneau 1963), and a baurioid (Kemp 1986), *Macroscelesaurus* (Haughton 1918); on the procoracoid–scapula suture in *Bauria* (Watson 1931); and in the procoracoid in *Zinnosaurus* (Boonstra 1964), *Cynariognathus* (Cys 1967), *Mirotenthes* (Attridge 1956), *Ictidosuchus* (Broom 1901) and *Regisaurus.*

An ossified sternum has been reported only in more derived therocephalians such as *Regisaurus* (BP/1/3973), *Ictidosuchoides* (Broom 1938), *Tetracynodon* (Sigogneau 1963), *Olivieria* (Brink 1965), *Ericiolacerta* (Watson 1931), and in a baurioid (Kemp 1986; Watson 1931). As a sternum is not preserved in any of the early therocephalians, Boonstra (1964) concluded that scylacosaurids did not have an ossified sternum. In the South African Karoo record the earliest therocephalian to have a sternum is a specimen of *Ictidosuchoides* from the *Cistecephalus* Assemblage Zone (Broom 1938).

Another variable feature in different therocephalian genera is the morphology of the interclavicle. Taxa from the lowermost biozones of the Beaufort Group (scylacosaurids) have a long thin interclavicle (*Zinnosaurus, Cynariognathus*) (Boonstra 1964; Cys 1967), while *Regisaurus* (BP/1/3973), *Ictidosuchoides* (Broom 1938), *Aneugomphius* (Brink 1958) and *Olivieria* (Brink 1965), which occur in the younger biozones, have a clavicle which is short and broad. Some of the most derived forms from the *Lystrosaurus* Assemblage Zone (e.g. *Ericiolacerta*) have a cruciform interclavicle (Watson 1931).

The forelimbs of the following therocephalian genera have been described to varying degrees in the literature; *Cynariognathus* (Cys 1967), *Macroscelesaurus* (Haughton 1918), *Pristerognathus* (Broom 1936), *Zinnosaurus* (Boonstra 1964), *Ictidosuchoides* (Broom 1938), *Zorillodontops* (Cluver 1969), *Mirotenthes* (Attridge 1956), *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Tetracynodon* (Sigogneau 1963), *Ictidosuchus* (Broom 1901), *Whaitsia* (Boonstra 1934), *Aneugomphius* (Brink 1958), *Ericiolacerta* (Watson 1931), *Olivieria* (Brink 1965), *Ordosia* (Lianhai 1979), a bauriamorph (Watson 1931), *Bauria* (King 1996; Fourie 2001) and a baurioid (Kemp 1986). Forelimbs of different therocephalian genera are all very similar in morphology, but they do vary in degree of robustness. A short and robust humerus with a very short shaft is present in the scylacosaurids (Boonstra 1964) and *Macroscelesaurus* (Haughton 1918). In contrast the humerus of *Regisaurus* is long and slender, as is that of *Whaitsia* (Boonstra 1934), *Aneugomphius* (Brink 1958), *Tetracynodon* (Sigogneau 1963), *Zorrilodontops* (Cluver 1969) and

Olivieria Brink 1965), while a very slender humerus is present in *Ericiolacerta* (Watson 1931), *Bauria* (King 1996) and the baurioids (Kemp 1986). Most therocephalian genera lack an ectepicondylar foramen, with *Bauria* being the only exception (King 1996). The ulna of all therocephalians is characterized by the presence of an anterior groove extending down the proximal end towards the shaft. In posterior view the ulna has a proximal triangular depression below the olecranon process. This process is weakly developed and in life probably extended further as a cartilaginous structure (Kemp 1986). The radius is characterized, in posterior view, by a short distal ridge in all therocephalian genera and an anterior depression is present at the proximal end, which, in *Bauria* is particularly deep (Fourie 2001).

In the manus of all therocephalians, the radiale is rectangular or oval and the ulnare is hour-glass shaped. Both the intermedium and pisiforme are very small and because of their small size are preserved in very few specimens. Centrale 1 is larger than centrale 2 and the former is distinguished by its L-shape in comparison with the rectangular centrale 2. Distals 4 and 5 are fused in all therocephalian specimens where they are preserved. The metacarpals are wide proximally while the distal end is expanded more distolaterally and Metacarpal IV is always the longest.

Therocephalian genera for which the pelvic girdles have been described are *Cynariognathus* (Cys 1967), *Zinnosaurus* (Boonstra 1964), *Pristerognathus* (Broom 1936), *Macroscelesaurus* (Haughton 1918), *Glanosuchus* (Fourie 2001), *Zorillodontops* (Cluver 1969), *Silpholestes* (Broom 1948), *Mirotenthes* (Attridge 1956), *Aneugomphius* (Brink 1958), *Regisaurus* (Kemp 1978), *Ericiolacerta* (Watson 1931; Colbert & Kitching 1981), *Ordosia* (Lianhai 1979), *Bauria* (King 1996; Fourie 2001), and an unidentified baurioid (Kemp 1986). The iliac blade of all therocephalians is a thin flat bone which is expanded anteroposteriorly with a straight dorsal border and two anterior processes, a character found only in the Therocephalia, but is not very prominent in scylacosaurids (Boonstra 1964). Two distinctive large depressions are present on the lateral surface of the iliac blade above and below the ventral anterior process (Kemp 1978). A supra-acetabular buttress is present on the ilium above the acetabulum in all therocephalians and has a medial supra-acetabular notch. Depressions for attachment of the sacral ribs are present medially on the surface of the blade. The contribution of the ischium to the acetabulum is larger than that of the pubis and is slightly concave. An apparent phylogenetic trend is found with the pubic foramen present in the pubis (*Glanosuchus, Zinnosaurus*) or between the counterparts of the pubis (*Regisaurus*) (BP/1/3973) with a small obturator foramen (e.g. in *Zorillodontops, Regisaurus, Aneugomphius*), and a large obturator foramen (e.g. in *Ericiolacerta, Bauria,* baurioid).

Hind limb morphology has been described for *Cynariognathus* (Cys 1967), *Blattoidealestes* (Boonstra 1954), *Macroscelesaurus* (Haughton 1918), *Zinnosaurus* (Boonstra 1964), *Pristerognathus* (Broom 1936), *Glanosuchus* (Fourie 2001), *Silpholestes* (Broom 1948), *Ictidosuchus* (Broom 1901), *Ictidosuchoides* (Broom 1938), *Tetracynodon* (Sigogneau 1963), *Mirotenthes* (Attridge 1956), *Aneugomphius* (Brink 1958), *Regisaurus* (Kemp 1978), *Ericiolacerta* (Watson 1931; Colbert & Kitching 1981), *Bauria* (Boonstra 1938; Schaeffer 1941; King 1996; Fourie 2001) and a baurioid (Kemp 1986).

The morphology of the femur, which is a long and massive bone with a gentle sigmoid shape, is very similar in all therocephalians. Three trochanters are present, but in derived forms such as *Bauria,* the trochanters are not distinct as the bone is straighter with a less prominent proximal end. The tibia is long, slightly curved with a flattened shaft and an expanded proximal end. Medially it has a distinct groove with a prominent ridge next to it. The slender, gently curved fibula is probably the thinnest long bone in the body with the least distinguishable characters, except for slightly expanded proximal and distal ends and a medial groove on the shaft.

CONCLUSIONS

This description is the first on the complete postcranial anatomy of the therocephalian *Regisaurus.* Because the described specimen is so well preserved it has demonstrated the possibility of identifying therocephalian groups from certain isolated postcranial elements. This could have useful application for biostratigraphic work in areas where no diagnostic skulls have been discovered.

The following suite of postcranial characters are diagnostic of *Regisaurus* when taken together: procoracoid foramen which is positioned in procoracoid only; slender scapula with a low ridge and shallow depression alongside the ridge; ossified sternum; interclavicle which is short, broad and almost square; very small obturator foramen which is less than half the length of the contact between the pubis and ischium; slender humerus and femur with clearly defined shaft and proximal and distal ends.

In the pelvic girdle of all therocephalians the ilium, ischium and pubis all meet in the acetabulum. The life-orientation of the ilium was vertical while the pubis and ischium were medially inclined. The latter two bones are firmly attached at the midline symphysis and form a pubo-ischiadic plate. In comparison with other therapsids the ilium of all therocephalians is unique in having two anterior processes.

In the hind limb of all therocephalians three trochanters are present on the proximal femur. The proximal ends of both the tibia and fibula have large areas of articulation with the femur, but do not appear to have contact with each other medially. The heel process on the calcaneum of the pes is present only in the more derived forms such as *Bauria* (King 1996).

Comparison of different therocephalian genera reveals a decrease in body size with younger stratigraphic age, and with this decrease in size the long bones become slender and acquire a well-defined shaft.

Specimen BP/1/3973 is unique as it has an almost complete (save for a few distal caudals) articulated vertebral column and has enabled the determination of accurate vertebral counts for the first time in a therocephalian genus. Furthermore, the articulated preservation of the limbs and their associated girdles has enabled a full

description of these elements and facilitated deductions as to the stance and gait of the genus which is the subject of a future paper.

The authors are indebted to the University of the Witwatersrand, Transvaal Museum, National Research Foundation of South Africa and the Palaeontological Scientific Trust (PAST) for financial assistance, and Saskia Waters for preparing the figures. We are grateful to Anita Dreyer for reading several drafts of this manuscript and her valuable comments. We acknowledge the great assistance of Fernando Abdala in discussion and for his useful comments on an earlier draft of the manuscript.

ABBREVIATIONS

Anatomical

ACET	Acetabulum
ADVL	Anterior dorsoventral line
ANT.PR	Anterior process
AS	Astragalus
AX	Axis
BL	Blade
CA	Calcaneum
CAP	Capitulum
CAP.H	Caput humerus
CAP.F	Caput femorus
CC	Cnemial crest
CE1	Centrale 1
CE2	Centrale 2
CENTR	Centrum
CL	Clavicle
CO	Coracoid
CR	Cranium
CV	Cervical vertebra
CVT	Caudal vertebra
DEP	Depression
DI	Distal
DP.CR	Deltopectoral crest
ECT	Ectepicondyle
ECT.F	Ectepicondylar foramen
ENT	Entepicondyle
ENT.F	Entepicondylar foramen
F	Facet
FEM	Femur
FIB	Fibula
GL	Glenoid
GR	Groove
HUM	Humerus
I	Intermedium
ICL	Interclavicle
IL	Ilium
ISC	Ischium
LML	Lateromedial line
LV	Lumbar vertebrae
MAN	Manus
MC	Metacarpal
N.C	Neural canal
N.P	Neural process
N.S	Neural spine
OBT.F	Obturator foramen
O.F	Olecranon fossa
O.P	Olecranon process
P	Pisiforme
PAT.GR	Patella groove
PES	Pes
PH	Phalange
POST.PR	Posterior process
POST.ZP	Postzygapophysis
PRE.ZP	Prezygapophysis
PU	Pubis
R	Rib
RAD	Radius
RE	Radiale
SAB	Supra-acetabular buttress
SAN	Supra-acetabular notch
SC	Scapula
ST	Sternum
SV	Sacral vertebra
TIB	Tibia
TR.INT	Trochanter internal
TR.PR	Transverse process
TR.MAJ	Trochanter major
TR.MIN	Trochanter minor
TUB	Tuberculum
TV	Thoracic vertebra
U	Ulna
UE	Ulnare

Institutional

AMNH	American Museum of Natural History, New York, U.S.A.
BMNH	Natural History Museum, London, United Kingdom.
BP	Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg, South Africa.
CUMZ	University Museum of Zoology, Cambridge, United Kingdom.
DMSW R/ MZCD	M.S. Watson Collections, Cambridge, United Kingdom.
IVPP V	Institute for Vertebrate Palaeontology, Peking, China.
NMQR	National Museum, Bloemfontein, South Africa.
RC	Rubidge Collection, Wellwood, Graaff-Reinet, South Africa.
SAM	Iziko Museums, Cape Town, South Africa.
TM	Northern Flagship Institution, Pretoria, South Africa.
UCMP	University of California Museum, California, U.S.A.

REFERENCES

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 mammal-like reptiles of the suborder Therocephalia. *Annals of the South African Museum* **31**, 252–260.

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. 1938. On a South African mammal-like reptile, *Bauria cynops. Palaeobiologica* **6**, 165–183.

BOONSTRA, L.D. 1954. Scaloposaurid from the *Tapinocephalus* Zone. *Annals and Magazine of Natural History* (12)**7**, 154–165.

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. 1958. On the skeleton of *Aneugomphius ictidoceps* Broom and Robinson. *Palaeontologia africana* **5**, 29–37.

BRINK, A.S. 1965. A new ictidosuchid (Scaloposauria) from the *Lystrosaurus* Zone. *Palaeontologia africana* **9**, 129–138.

BROOM, R. 1901. On *Ictidosuchops primaevus. Transactions of the South African Philosophical Society* **11**, 177–184.

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 Museu*m **19**(2), 257–261.

BROOM, R. 1948. The skeleton of a very small therocephalian. *Annals of the Transvaal Museum* **21**(1), 39–41.

CLUVER, M.A. 1969. *Zorillodontops*, a new scalopsaurid from the Karoo. *Annals of the South African Museum* **52**(8), 183–188.

COLBERT, E.H. & KITCHING, J.W. 1981. Scaloposaurian reptiles from the Triassic of Antarctica. *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.

DURAND, J.F. 1991. A revised description of the skull of *Moschorhinus* (Therapsida, Therocephalia). *Annals of the South African Museum* **99**(11), 381–413.

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.
HILLENIUS, W.J. 1992. The evolution of nasal turbinates and mammalian endothermy. *Paleobiology* **18**(1), 17–29.
HILLENIUS, W.J. 1994. Turbinates in therapsids: evidence for Late Permian origins of mammalian endothermy. *Evolution* **48**(2), 207–229.
KEMP, T.S. 1978. Stance and gait in the hindlimb of a therocephalian mammal-like reptile. *Journal of the Zoological Society of London* **186**, 143–161.
KEMP, T.S. 1986. The skeleton of a baurioid therocephalian therapsid from the lower Triassic (*Lystrosaurus* Zone) of South Africa. *Journal of Vertebrate Paeontology* **6**(3), 215–232.
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 Karroo vertebrate fauna. *Memoir of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand* **1**, 1–131.
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.
LIANHAI, H. 1979. On a new theriodont from Inner Mongolia. *Vertebrata PalAsiatica* **17**(2), 1–130.
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 Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota,* 33–37. Beijing, China, China Ocean Press.
MENDREZ, C.H. 1975. Principales variations du palais chez les Thérocéphales Sud-Africains (Pristerosauria et Scaloposauria) au cours du permian supérieur et du trias inférieur. *Colloque international C.N.R.S.* **218**, 379–408.
SCHAEFFER, B. 1941. The pes of *Bauria cynops* Broom. *American Museum Novitates* **1103**, 1–7.
SIGOGNEAU, D. 1963. Note sur une nouvelle espèce de scaloposauridae. *Palaeontologia africana* **8**, 13–37.
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), 1–59.
WATSON, D.M.S. 1917. The evolution of the terapod shoulder girdle and forelimb. *Journal of Anatomy* **52**(1), 22.
WATSON, D.M.S. 1931. On the skeleton of a bauriamorph reptile. *Proceedings of the Zoological Society* **3**, 1173–1202.