

# Re-evaluation of the postcranial skeleton of the Triassic dicynodont *Kannemeyeria simocephalus* from the *Cynognathus* Assemblage Zone (Subzone B) of South Africa

Romala Govender<sup>1\*</sup>, Phillip John Hancox<sup>2</sup> & Adam M. Yates<sup>1</sup>

<sup>1</sup>Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa

<sup>2</sup>CCIC South Africa, Postnet Suite 81, Private Bag X9, Melville, 2109 South Africa

Received 18 October 2007. Accepted 29 January 2008

*Kannemeyeria simocephalus* is probably the best known Middle Triassic dicynodont from South Africa and has been the standard against which other Triassic dicynodonts are compared. In the past studies have concentrated on the cranial morphology of *K. simocephalus* and its implications for Triassic dicynodont taxonomy and phylogeny. There has been little work on the postcranial anatomy of *K. simocephalus*, which remains poorly understood. An analysis of the postcranial skeleton of *K. simocephalus* has identified characters that diagnose the postcranial skeleton. These include a tubercle on the proximo-posterior corner of the medial surface of the acromion; almost straight lateral border of the femur. Material previously described as *K. simocephalus* by Pearson (1924) and Cruickshank (1975) was also included in this study. Some of the material was found to be significantly different from what is understood to be *K. simocephalus* and as a result has been included a separate study. It was therefore concluded that the referred specimen BP/1/5624 is currently the most complete and positively identified as *K. simocephalus*.

**Keywords:** Triassic, Dicynodont, *Kannemeyeria*, South Africa, *Cynognathus* Assemblage Zone.

## INTRODUCTION

*Kannemeyeria simocephalus* is a medium to large dicynodont from the *Cynognathus* Assemblage Zone of the South Africa. Hancox *et al.* (1995) noted that it is limited to the middle part of the zone, which they labelled as Subzone B (also see Shishkin *et al.* 1995). A recent study of the cranial anatomy of South African *Kannemeyeria* (Renaut 2000) concluded that all known material can be referred to a single species, *K. simocephalus*, and this finding has renewed interest in the postcranial morphology of this species. To date there have only been two studies that have focused on the postcranial skeleton of *Kannemeyeria*, Pearson (1924) and Cruickshank (1975), both of which are incomplete for various reasons. The most serious problem faced by Pearson (1924) was that the elements she studied had suffered considerable damage due to crushing, whereas Cruickshank (1975) provided only a brief description of what was considered a fairly complete specimen.

Although poor preservation has been an issue in previous studies of postcranial material, recent collecting efforts have provided more complete and better preserved specimens. Furthermore, a large proportion of the older material is made up of isolated elements that have been collected over many years, and all of which have been assumed to be *Kannemeyeria*. This assumption is typically based on the premise that *Kannemeyeria* was the only dicynodont present in the *Cynognathus* Assemblage Zone B. An important part of the present study was to identify postcranial autapomorphies of *Kannemeyeria simocephalus* that could be used to refer isolated postcranial material to this species with confidence. Therefore, elements were not used in order to minimize the chance of inadvertently including material that did not belong to *K. simocephalus*.

## MATERIALS AND METHODS

The holotype of *Kannemeyeria simocephalus* (HMV 8173) has no known associated postcrania. Therefore the descriptions of the postcranial morphology are based on the following referred specimens of Renaut (2000).

The specimen BP/1/5624 was recovered at the Bethel/Slootkraal locality, Rouxville District, South Africa, *Cynognathus* Assemblage Zone, Subzone B. The skeletal elements are well preserved, but all the bones have experienced some breakage and distortion. Renaut (2000) described the left and right sides of the skeleton of BP/1/5624 as having suffered two different types of distortion. The right femur has been dorso-ventrally flattened so that the natural shape is exaggerated, while the left femur has been rolled and possibly compressed along the anterior and posterior margins. This compression has resulted in the shaft of the femur having a circular shape in transverse section. The scapulae from BP/1/5624 and BP/1/6104 also show different types of distortion; with the scapula of BP/1/5624 twisted so that the anterior dorsal end of the bone approached the distal end. The skeletal material consists of eight vertebrae, a number of rib fragments, all the elements of the forelimb, the scapula, the pelvic girdle and two elements of the hindlimb (left and right femur and right tibia). The postcranial skeleton was found articulated and associated with a complete skull.

Most of the skeleton of BP/1/6160 caudal to the pectoral girdle was lost during the roadworks that exposed the specimen. Only the pectoral girdle, some cervical vertebrae, the forelimbs, and the skull and lower jaw could be collected, but this material was articulated and orientated north-northeast to west-southwest. Locality: Bethel/Slootkraal, Rouxville District, South Africa. *Cynognathus*

\*Author for correspondence. E-mail: romala@discoverymail.co.za

Assemblage Zone (subzone B). The specimen was found in green channel sandstone with abundant rip up clasts.

SAM-PK-3017 consists mainly of a skull and a series of vertebrae. Locality: Winnaarsbaken, Burgersdorp District, South Africa. *Cynognathus* Assemblage Zone (Subzone B). The material is well preserved but was not found in articulation; however, it must be noted that although the vertebrae might form a sequence there is no point of reference as to its position in the vertebral column. Although the vertebrae might form a sequence there is no point of reference as to its position in the vertebral column.

ELM 1 consists of a skull and a number of postcranial elements, including vertebrae, ribs, scapulae, coracoids, clavicles, sternum, humeri, radii, ulnae, pelvic girdle (left and right), femora, tibia and fibulae. The mounted material belongs to a single specimen (Courtney-Latimer, 1948), but there are other elements not included in the mount that bear the same catalogue number, indicating that more than one individual is present. Locality: Losberg Mountain on the farm 'Ravenskloof', Tarkastad. *Cynognathus* Assemblage Zone (Subzone B). According to Courtney-Latimer (1948) material that makes up the mounted skeleton was collected in two separate expeditions to the same locality.

Material described by Pearson (1924) housed in the British Museum of Natural History was also re-examined. The following material was included in this study BMNH R3761 the pelvic girdle and R3760 – atlas-axis complex. R3740 consisting of both scapulae and femora. All these specimens came from the Seeley collection of 1910. These specimens were collected in the Burgersdorp district of South Africa.

## AXIAL SKELETON

The axial skeleton of *K. simocephalus* is described from both isolated and associated vertebrae. Only vertebrae are described here because the ribs are fragmentary and no complete rib could be reconstructed, despite the fact that the fragments are from a single specimen. BP/1/5624 has eight vertebrae preserved but all have been damaged to some degree. The atlas is the best preserved, whereas the remaining vertebrae are all damaged dorsally. The neural spines, transverse processes, prezygapophyses and postzygapophyses are no longer present. SAM-PK-3017 has at least fifteen vertebrae preserved. The axis is complete and well preserved while the remaining vertebrae are mostly complete with a few that have suffered some damage. Structurally the remaining vertebrae are very similar which suggests that they may belong to the same section of the vertebral column. However, the lack of other associated vertebral columns makes it difficult to determine exactly where these vertebrae fit in.

## Cervical region

*Atlas*. In BP/1/5624 both sides of the atlas are preserved, but it has suffered some damage dorsally and posteriorly. The left and right neurapophyses do not meet in the midline when viewed dorsally (R3760, Fig. 1A). Anteriorly on the medial side of the neurapophysis are two concave

facets that lie next to each other producing a 'butterfly' shape, but are separated by a flat, raised ridge. The postero-dorsal border of the posterior facet is higher than the antero-dorsal border, while the antero-ventral border is lower than the postero-ventral border and it most likely that these facets represent the articulation with the occipital condyle (Fig. 1B). The anterior facet is deeply concave in the cranial direction and is C-shape (Fig. 1B). It becomes raised in the medial direction towards the middle of the bone. The ventral end of the ridge separating the two facets is very broad (Fig. 1B).

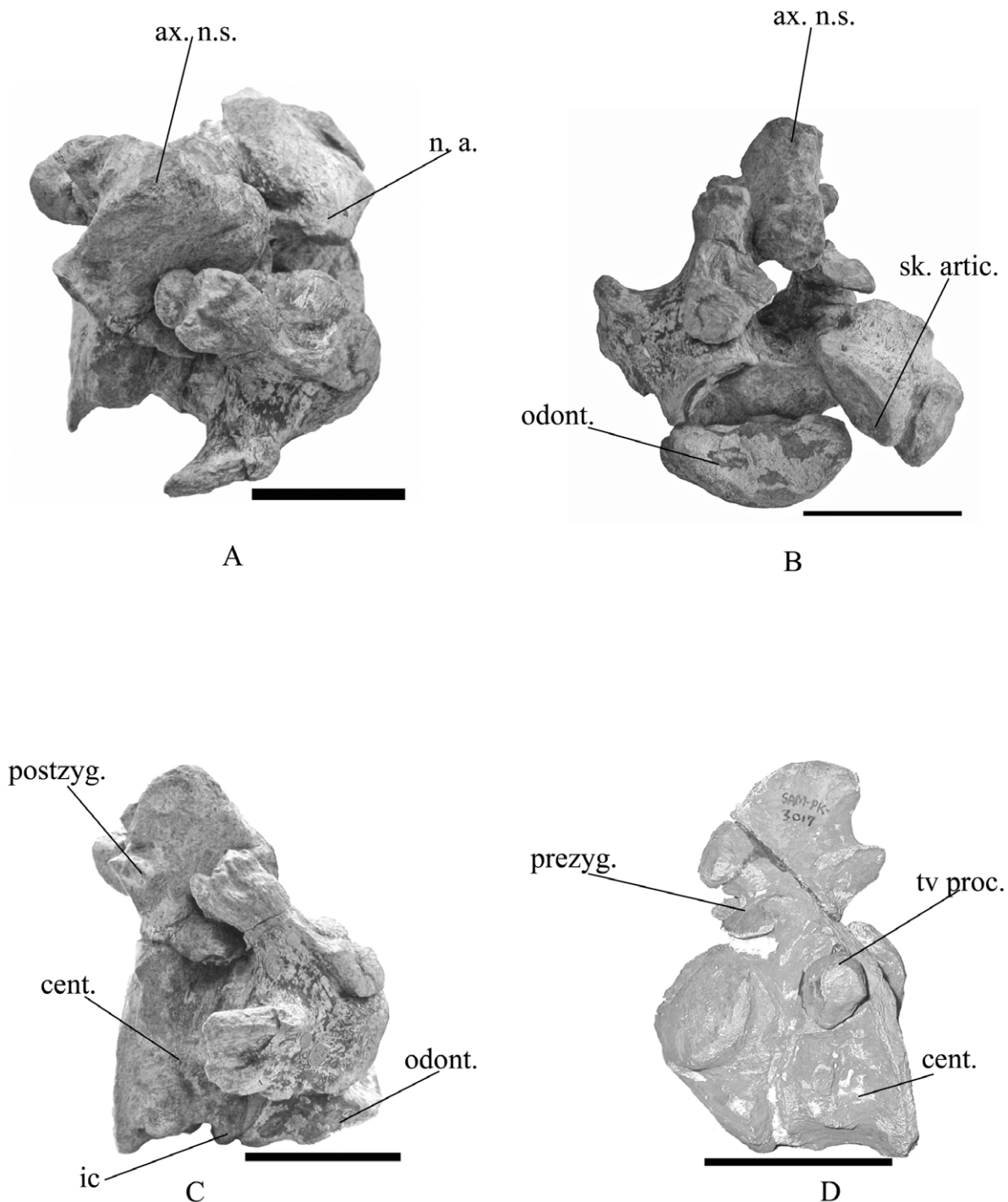
*Axis*. The axis of *K. simocephalus* in SAM-PK-3017 and R3760 is a well preserved, robust and relatively large bone (Fig. 1C,D). The neural spine is short, antero-posteriorly elongated, and thicker anteriorly. When compared with the remaining vertebrae, the axis appears to be more robust. In dorsal view the surface of the neural spine is rugose and transversely flared at its anterior and posterior ends.

In SAM-PK-3017 the prezygapophyses are small, flared and project slightly beyond the anterior end of the neural spine (Fig. 1D). They have smooth, slightly convex articulating surfaces that are directed antero-dorsally. Posteriorly, the postzygapophyses are wide, and are aligned with the posterior end of the neural spine (Fig. 1C,D). Their wide, smooth and convex articulating surfaces are directed ventro-laterally. On the axis the postzygapophyses are positioned closer together than the prezygapophyses. Close to the prezygapophyses, and below them, lie the transverse processes. They are short and become wider towards their free ends (Fig. 1C,D). The transverse processes are narrow and triangular, with a rounded lateral tip.

In lateral view the centrum is antero-posteriorly elongated with the posterior end larger and extending lower than the anterior end. Laterally, the surface of the centrum is concave and extends to the proximal end of the ventral keel (Fig. 1C,D).

The centrum of the atlas of *K. simocephalus* is not fused to the rest of the atlantal components. Instead it is fused to the axis forming the odontoid process (Romer 1956). In anterior view it is crescent shaped (Fig. 1D) with an incomplete dorsal border and three possible articulating sites. Laterally on the odontoid process there are two oval, flat to convex articulating facets, while the third articulating facet is situated ventrally and is oval laterally, with a concave articulating surface. In anterior view the intercentrum of the axis is visible ventrally and is oval. When viewed laterally it is difficult to distinguish between the axis intercentrum and the odontoid process. Ventrally, the intercentrum is triangular when seen in lateral view (Fig. 1C).

*Post axial cervical vertebra*. BP/1/5624 has two vertebrae in articulation and from the form of the damaged neural spine one is the axis. It is preserved in articulation with another vertebra, which can be assumed to be the first cervical vertebra. Owing to the extent of the damage there are no details of the dorsal part of the vertebrae preserved. The centrum is antero-posteriorly elongated and narrow with no ventral keel.



**Figure 1.** Atlas–axis complex of *Kannemeyeria simocephalus*. **A, B**, right and left lateral views of the atlas, BP/1/5624; **C**, lateral view of the axis, BP/1/3017; **D**, anterior view of the axis, BP/1/3017. Scale bars = 5 cm.

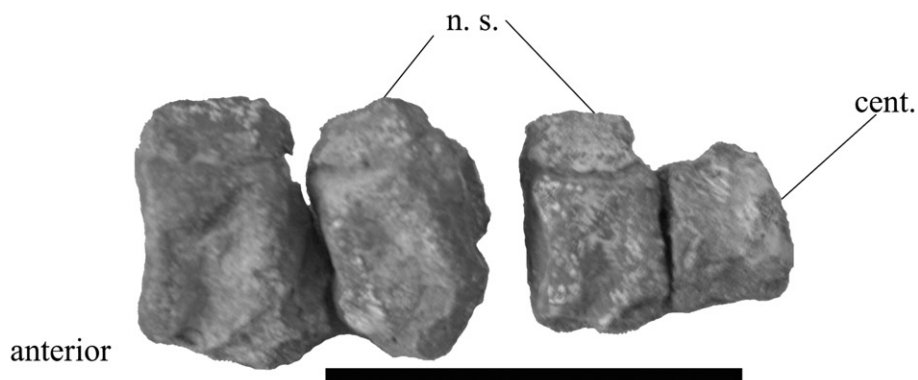
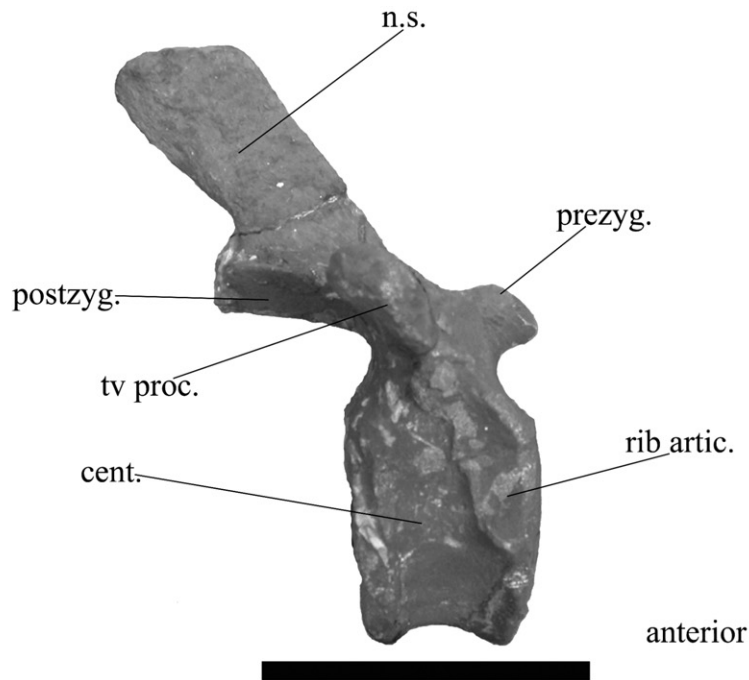
*Dorsal vertebrae.* The dorsal vertebrae of SAM-PK-3017 have a similar morphology and are therefore considered to belong to the same section of the vertebral column. The neural spine is antero-posteriorly narrow, long and inclined posteriorly (Fig. 2A). It projects well beyond the posterior extent of the centrum. In dorsal view the surface of the neural spine is rugose and broad.

Anteriorly, the prezygapophyses are located well in front of the neural spine. The flat articulating surfaces face dorso-medially, and the distal ends of the prezygapophyses almost meet in the midline. This makes the articulating surface appear continuous and that it forms a cup or cradle for the postzygapophyses. The postzygapophyses

are very short and do not extend beyond the neural spine in lateral view (Fig. 2A). The articulating surface is flat and directed ventrally, and almost meets in the midline.

The transverse processes are wing-like. They are short and are directed dorsally (Fig. 2A). The lateral ends of the transverse processes are thickened and have rugose surfaces. In dorsal view the surface of the transverse process is concave towards the body of the vertebra.

The centrum is antero-posteriorly short with deeply concave sides (Fig. 2A). Along the anterior margin of the centrum there is an elongated, concave facet that extends almost to the ventral end of the centrum. This facet most likely represents the articulation for the rib.



**Figure 2.** Lateral view of (A) dorsal vertebra (BP/1/5624) and (B) caudal vertebrae (BP/1/5624). Scale bars = 5 cm.

*Caudal vertebrae.* There are four poorly preserved caudal vertebrae associated with BP/1/5624 (Fig. 2B). The distal ends of the neural spines are missing. Although damaged, the presence of articulating facets on the anterior and posterior ends of the ventral surface of the centrum suggest the presence of a haemal arch. The centra are very short and round with no evidence for the presence of transverse processes (Fig. 2B). Laterally each centrum is concave. The neural spine of the smallest caudal vertebra is not completely fused to the rest of the vertebra.

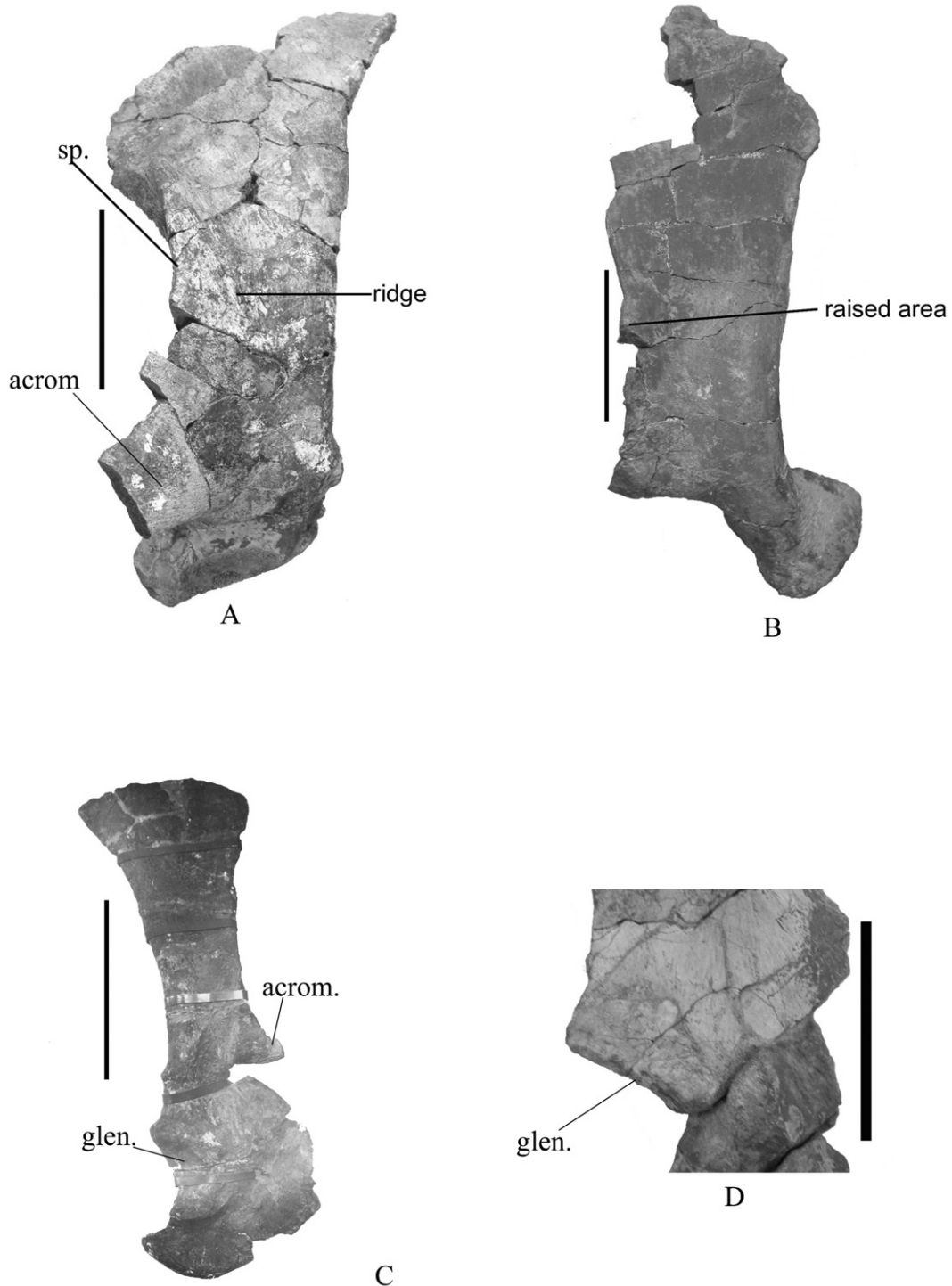
### Pectoral girdle

*Scapula.* The scapula blade of *K. simocephalus* is a long and gracile bone that is straight in lateral view but laterally bowed in anterior view (Fig. 3A). It widens distally to form the coracoid plate and glenoid articulations. Approximately a third of the way below the broad dorsal border is the scapula spine which extends to the proximal end of the acromion process. The spine projects beyond the

anterior margin and is more prominent in the larger individual (BP/1/5624; ELM 1) (Fig. 3 A,C). The base of the spine is marked by a ridge in ELM 1 and BP/1/5624. On the anterior surface of the scapula is a narrow, concave prespinous region.

The acromion forms a narrow elongated triangle that is directed antero-laterally with a slightly flattened anterior end (Fig. 3C). Below the acromion the lateral surface of the glenoid is concave. The posterior border of scapula is narrow at the level of the acromion and becomes slightly flattened above the glenoid. Distally on the posterior border towards the lateral surface is a small oval to sub-circular tubercle for the origin of the scapula head of the triceps.

Distally the bone flares out to form the glenoid and coracoid articulation. The coracoid articulation is set at an angle to the glenoid. The glenoid and coracoid articulation are separated by a round, thick convex tubercle limited to the lateral side of the glenoid (Fig. 3C,D). The circular



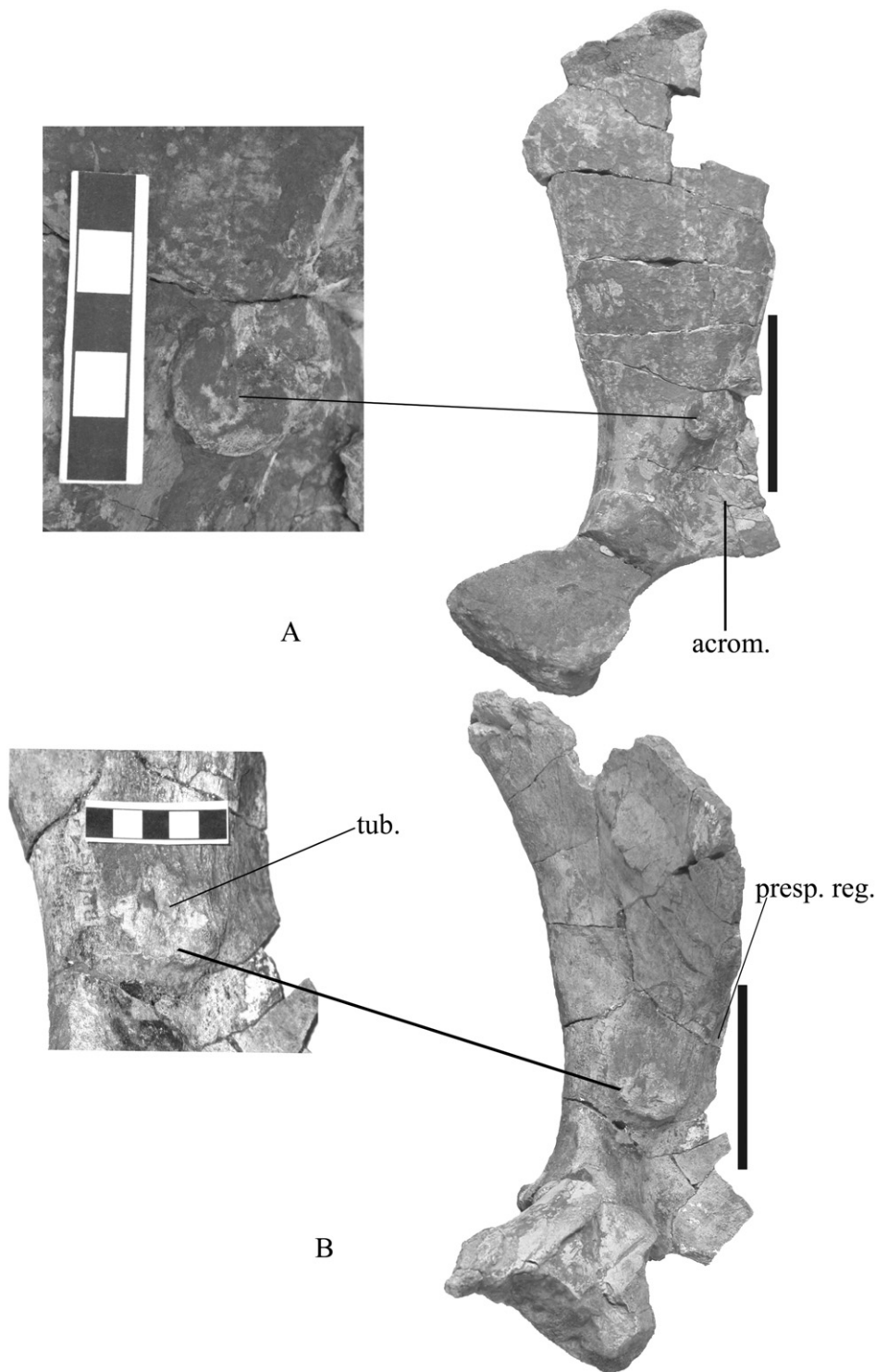
**Figure 3.** Lateral view of the scapula of *Kannemeyeria simocephalus*. **A**, BP/1/5624; **B**, BP/1/6160; **C**, ELM 1; **D**, BP/1/6104 shows the glenoid. Scale bars = 10 cm.

glenoid is directed postero-ventrally with a wide concave surface (Fig. 3C).

Medially, the scapula is shallowly concave to flat (Fig. 4). The medial surface of the acromion process is longitudinally concave. On the postero-dorsal corner of the acromion there is a triangular to U-shaped tubercle (Fig. 4A,B). The surface of the tubercle is low and rugose. A broad, shallow groove runs between the glenoid and the coracoid articulation on their medial surface. This groove probably represents the path where blood vessels and nerves of the shoulder joint pass.

*Precoracoid.* Based on ELM 1 *K. simocephalus* has a semi-

circular precoracoid (Fig. 5A). In this specimen the bone is broken anteriorly and ventrally, perhaps due to its thinness; however, it is unlikely that this has caused the bone's shape to change significantly. Along the posterior border the precoracoid is fused with the coracoid. Although the contact is not very distinct the surface is slightly raised and thickened. Dorsally, the precoracoid forms a distinct sutural contact with the scapula. The coracoid foramen is located in the proximo-posterior 'corner' close to the coracoid and the glenoid, but enclosed entirely by the precoracoid. It is elliptical in the proximo-posterior to antero-ventral direction. The lateral



**Figure 4.** Medial view of the scapula of *Kannemeyeria simocephalus* showing a tubercle on the postero-dorsal corner of the acromion. **A**, BP/1/6160; **B**, BP/1/5624. Scale bars = 10 cm.

surface of the precoracoid is concave in an anterior and ventral direction, resulting in the formation of two possible attachment sites for possibly part of the supracoracoideus and for the coraco-brachialis muscles. On the medial surface there is a groove at the proximal end of the coracoid foramen.

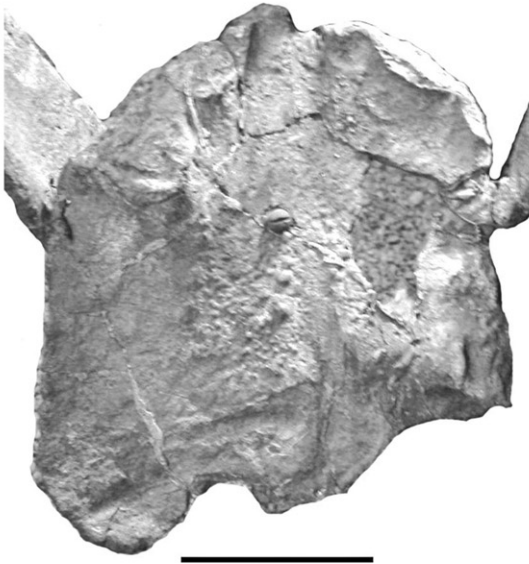
*Coracoid.* The coracoid (ELM 1) (Fig. 5A) is almost sickle shaped and is thicker than the precoracoid. Most of the dorsal part of the coracoid is made up of the glenoid facet. The facet is triangular and faces laterally and very slightly posteriorly. Its surface is undulating and concave proxi-

mally. The distal end of the glenoid facet is bordered by a thin ridge that forms the dorsal margin of a concave area ventral to the glenoid. Posteriorly, the coracoid tapers to a narrow rounded end that is thicker than the anterior end of the bone. It projects beyond the glenoid facet of the scapula. The ventral margin of the coracoid is thickened posteriorly and progressively thins towards the anterior end.

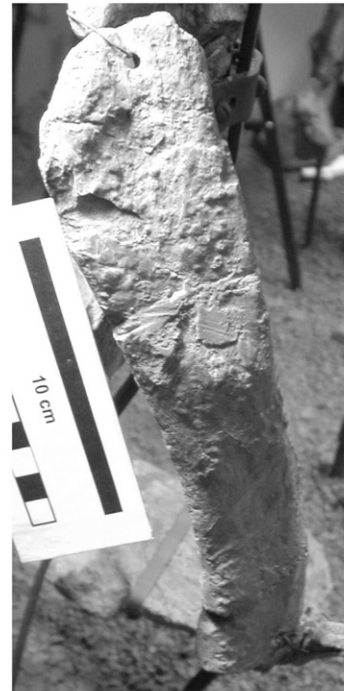
*Clavicle.* A clavicle is present in ELM 1 (Fig. 5C). It is a thin bone that is expanded proximally and distally. Proximally, the head of the bone is thickened in the dorsal direction



A



B



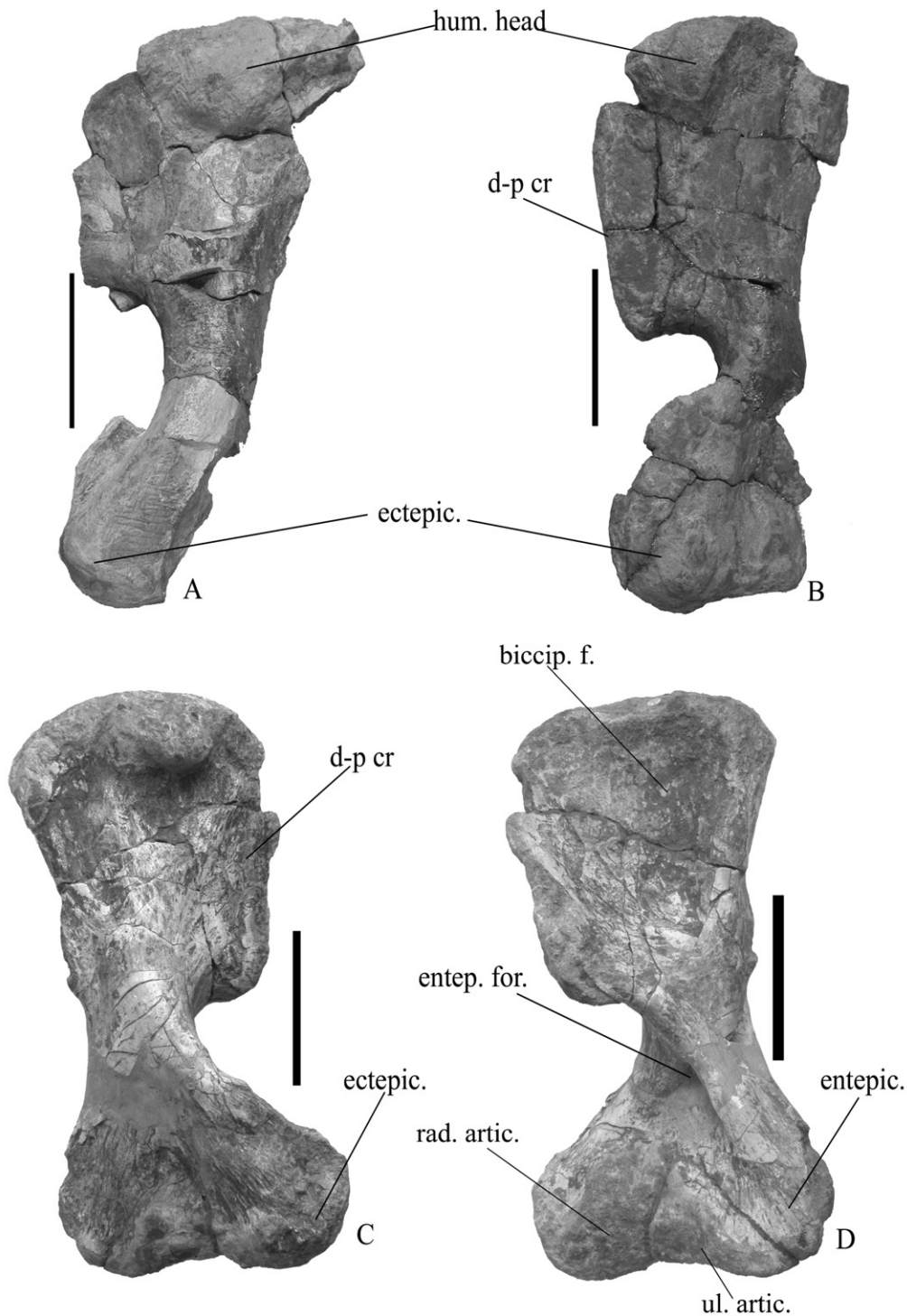
C

**Figure 5.** A, lateral view of the glenoid, ELM 1; B, dorsal view of the sternum ELM 1; C, ventral view of the clavicle, ELM 1, of *Kannemeyeria simocephalus*. Scale bars = 10 cm.

with a rugose surface. The antero-proximal corner is rounded with a broad, shallow groove on the proximal end. Anteriorly, the surface of the shaft is slightly rugose and thickened. Along the distal end of the clavicle is a broad, shallow groove. Along the posterior surface of the clavicle the lateral border is thickened. In front of this is a groove. The posterior surface of the clavicle shaft is broad and concave. On the proximo-anterior corner of the lateral there is an oval tubercle that projects above the surface of the bone. The dorsal surface of the clavicle is convex, and the posterior border is concave. Distally, the

bone is broken but remnants indicate that the bone was flat, broad and thin.

*Sternum.* The sternum (ELM 1; Fig. 5B) of *K. simocephalus* is a thin, proximo-distally oblong with a thickened anterior end. The anterior end bears a rugose dorsal and ventral surface that bears two oval tubercles on each side of the midline. Each ventral tubercle is flanked by a broad concave area. On the dorsal surface there are two laterally placed, dorsal tubercles and two grooves. The grooves are broad, shallow and lie medial to the tubercles. Posteriorly, the sternum is rounded.



**Figure 6.** Humerus of *Kannemeyeria simocephalus*, dorsal view: **A**, BP/1/5624; **B**, BP/1/6160; **C**, BMNH R3740; ventral view: **D**, BMNH R3761. Scale bars = 10 cm.

### Forelimb

**Humerus.** The humerus of *K. simocephalus* is a fairly robust bone (Fig. 6). In all the specimens (BP/1/6160; ELM 1; R3740; BP/1/5624) the proximal expansion is rectangular and is wider than the distal expansion. An inverted triangular head of the humerus is located anteriorly along the dorsal border (BP/1/6160; ELM 1; R3740; BP/1/5624) and it is raised above the dorsal surface of the proximal expansion (Fig. 6A,B,C). The dorsal border of the humerus is very rugose and thickened which would suggest that it, including the head, was covered by cartilage (Fig. 6C). Below the head there is a broad, low ridge, which is more

prominent in the large individual (BP/1/5624; R3740). There are concave surfaces anterior and posterior to the ridge, with the posterior narrower than the anterior. In the small individual (BP/1/6160) the surface posterior to and below the head is a shallow, concave fossa. This posterior fossa represents the origin of the lateral humeral head of the triceps (King 1981) while the anterior one represents the origin of the scapulo-humeralis anterior (King 1981).

Anteriorly the proximal expansion terminates in the delto-pectoral crest which is rectangular and is 90° to the long axis of the bone (Fig. A–C). The delto-pectoral crest is

dorso-ventrally wide along its entire length and the dorsal surface of the delto-pectoral crest is concave. On the dorsal surface of the delto-pectoral crest is the insertion of the robust deltoideus muscle while on the ventral surface is an area for the insertion of the pectoralis muscle (King 1981) (Fig. 6D). At the proximo-posterior corner of the bone there is a narrow, oval tubercle that thins distally to form the posterior border. A third of the way below the dorsal border in BP/1/5624 there is a small triangular tubercle while in ELM 1 it forms an elongated oval.

The shaft of the humerus is not broad and is twisted so that the ectepicondyle is directed anteriorly (ELM 1; BP/1/6160; R3740) while in BP/1/5624 it is directed more dorsally. This feature of the humerus is possibly as a result of varying ages of the various specimens (Fig. A–C).

Almost the entire distal end of the humerus is made up by the olecranon fossa which forms a rather large shallow triangle that is directed posteriorly (Fig. 6A–C). The olecranon fossa is much shallower in BP/1/6160 which again might well be an indication of a variation in the ages of various specimens. Its distal end is marked by the articulating surface of the radius and ulna facets which are reflected onto the distal end of the posterior surface. It is bordered anteriorly and posteriorly by the ectepicondyle and entepicondyle, respectively. The ectepicondyle is not as well developed in BP/1/6160 as it is R3740, ELM 1 and although damaged BP/1/5624 (Fig. 6A–D).

The ectepicondyle is larger and wider than the entepicondyle; however, in BP/1/6160 the condyles are not as well defined as in the other specimens (e.g. R3740; ELM 1; BP/1/5624). Ventrally the ectepicondyle and entepicondyle surfaces are convex.

In ventral view it can be seen that almost the entire proximal expansion is made of the bicapital fossa which forms a rectangle that is fairly deep (R3740; Fig. 6D). It is bordered anteriorly and posteriorly by the delto-pectoral crest and by a broad low ridge, respectively. A ridge runs diagonally across the bone from the delto-pectoral crest to the entepicondyle. This ridge forms the dorsal border of the elongated oval entepicondylar foramen. Below the foramen the surface is slightly concave and extends down posterior to the articulation for the radius and ulna. A shallow groove surrounds the continuous articulating surface for the radius and ulna. The radial articulation (capitulum) is wide, almost rectangular, and appears to extend slightly higher than the smaller triangular ulna articulation (trochlea) (Fig. 6D).

*Radius.* Although ELM 1 consists of a complete forelimb the radius and ulna are considered to be different from those of BP/1/5624 and BP/1/6160 and have therefore been excluded from the description. The proximal expansion of the radius is slightly smaller than the distal expansion. The distal expansion is slightly more expanded than the proximal one.

In both BP/1/5624 and BP/1/6160 the proximal and distal articulating surfaces are medio-laterally narrow and concave. The proximal articulation forms a continuous articulating surface with the sigmoidal facet of the ulna for the distal end of the humerus (Fig. 7). Anteriorly, the proximal end has a straight margin which becomes

concave along the shaft. Along the proximo-posterior border of the radius there is an oblong tubercle with a convex surface for articulation with the ulna. Below this articulation the posterior border of the radius is concave. In the large and small specimens the posterior border is more concave than the anterior. Along the anterior border of the proximal expansion is another not as well developed tubercle that probably represents the insertion site for muscles that act on the radioulna joint.

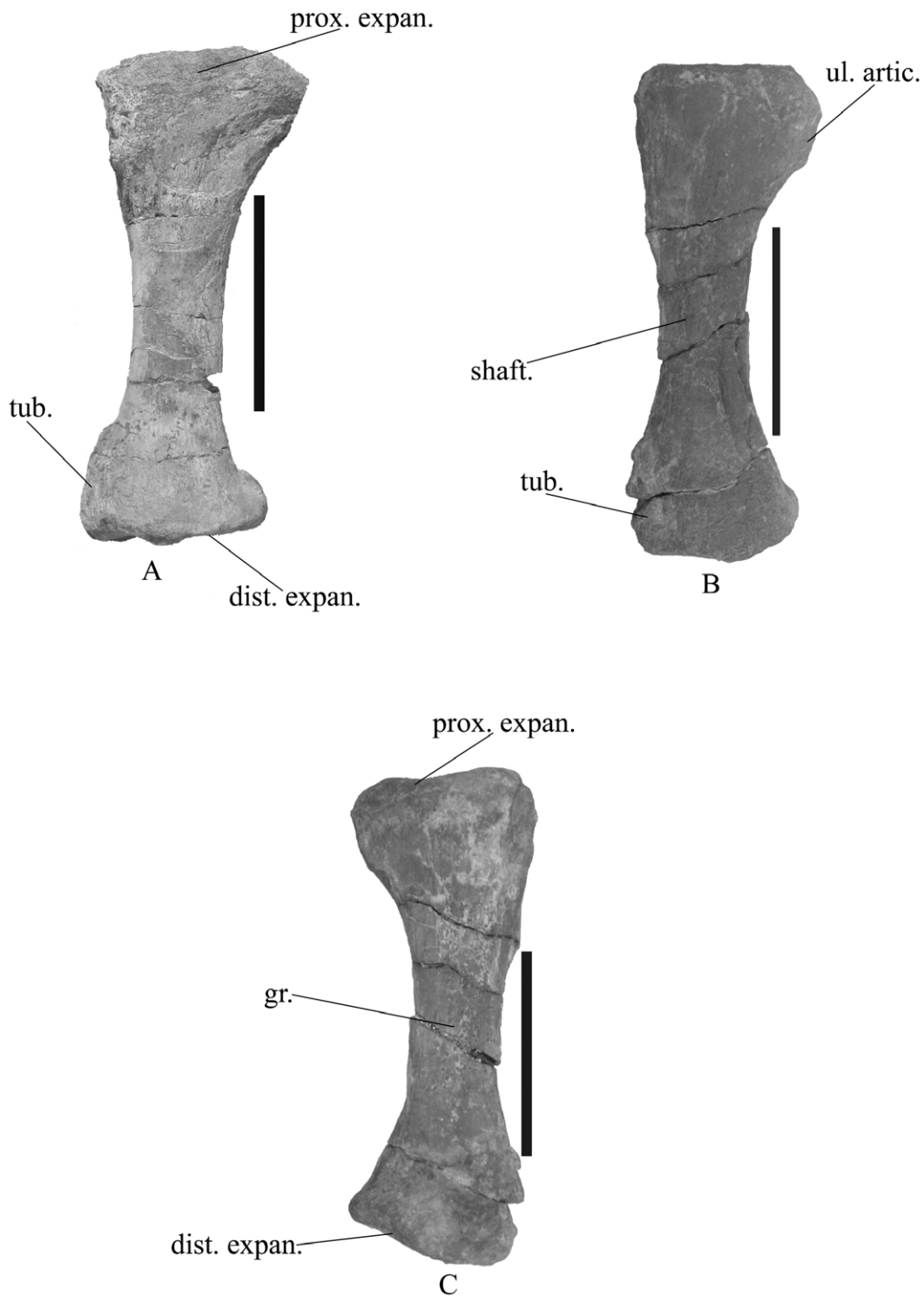
The distal end of the radius is marked by an undulating rim that projects more ventrally closer to the posterior border (Fig. 7). Along the distal third of the anterior border there is a rectangular, medio-laterally and antero-posteriorly narrow tubercle. In BP/1/6160 this tubercle is very narrow when compared with the larger BP/1/5624. There is also a very low, round tubercle along the rim of the distal end of the radius. It is located more towards the middle of the rim in the large individual and closer to the posterior border in the smaller individual.

In medial view there is a groove close to the anterior border (Fig. 7C). This groove extends from below the proximal rim to a third of the bone length above the distal end. The groove is shallow and wide proximally, and narrows towards the distal end. Medially, the distal end is thickened towards the anterior border to form a wide, flattened surface. Although this surface narrows towards the posterior border it is still broad; however, in BP/1/6160 this part of the distal end is very narrow. This part of the rim in the small individual is also directed more proximally, which has made the distal articulating surface visible in medial view. The space between radius and ulna shafts would have been filled with the blood vessels and nerves that innervated the lower forelimb and foot.

*Ulna.* The ulna is broad proximally and narrows to form the shaft, which has the same width as the distal end (Fig. 8). The proximal part of the ulna is triangular, and narrows proximally to form the olecranon. The low olecranon is narrow and triangular with a round dorsal border in BP/1/5624 and BP/1/6160. There is no evidence of a sutural contact between the olecranon and the rest of the ulna in either specimen. In lateral view, the ulna of BP/1/5624 is more expanded than BP/1/6160.

The sigmoidal facet is wide and has a slightly concave surface in BP/1/5624 and BP/1/6160 (Fig. 8A,B). In the middle of the sigmoidal facet the surface faces antero-laterally. Part of the articulating surface is directed ventrally and forward toward the anterior border. The sigmoidal facet projects laterally thus forming a thin ridge in BP/1/5624 and BP/1/6160. The surface of the sigmoidal facet in BP/1/6160 and BP/1/5624 is triangular and laterally broad. This lateral projection of the sigmoidal facet merges with the shaft below the distal end of the radial facet.

The radial facet is located below the anterior border of the sigmoidal facet of the ulna, and forms an inverted triangle. Its base is formed by the anterior border of the sigmoidal facet and it narrows distally, ending at the same level as the ridge on the lateral surface. The surface of the radial facet is concave along its entire length and rugose proximally. Distally the surface is not deeply concave and



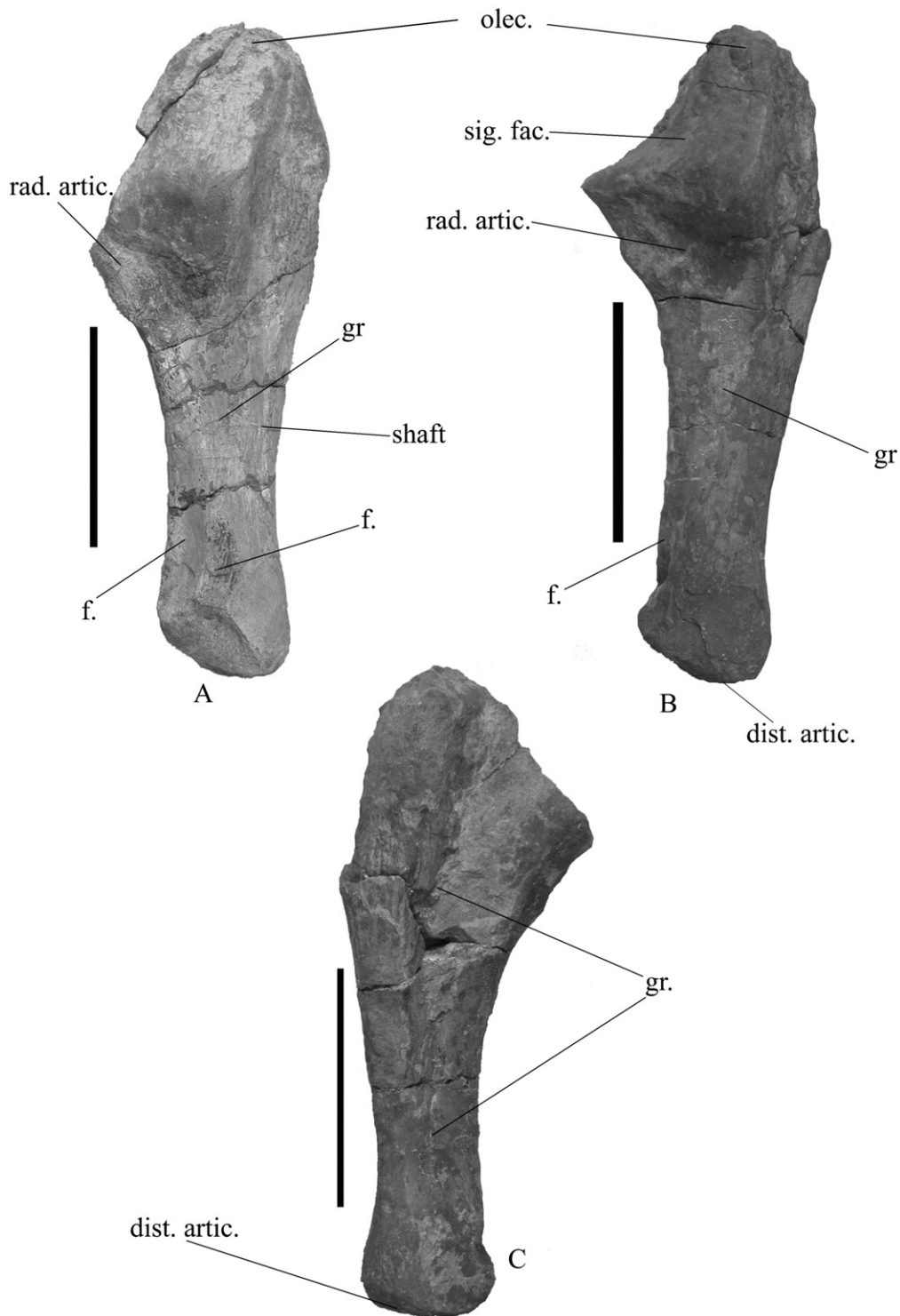
**Figure 7.** Radius of *Kannemeyeria simocephalus*, lateral view: **A**, BP/1/5624; **B**, BP/1/6160; medial view: **C**, BP/1/6160. Scale bars = 10 cm.

is smooth. The anterior and posterior borders of the radial facet are sharply demarcated.

Distally, along the anterior border of the ulna of *K. simocephalus* is a shallow fossa that starts approximately at the midlength of the bone. It is elongated, and is narrowest proximally and widest distally. The entire surface of the fossa is concave, but it is more deeply excavated distally. Its distal border is a round thin ridge. In BP/1/6160 the distal fossa extends onto the medial surface while in BP/1/5624 it is limited to the anterior margin (Fig. 8). On the lateral border of this fossa there is an elongated tubercle with a rugose surface. The position of this tubercle

suggests that it may have been the attachment site for the interosseus ligament or possibly interosseus membrane. Posterior to the sigmoidal facet is a narrow, deep groove. In the middle of the shaft is a shallow fossa that extends to the postero-distal end and was separated from the anterior fossa by a narrow ridge.

The medial surface of the olecranon (Fig. 8C) is flattened postero-proximally with a raised rugose surface that extends from the olecranon, and is bound posteriorly by a ridge. A fossa occurs in front of the ridge, which is broad proximally, narrowing distally. A groove begins near the distal end of the fossa and extends to the distal end of the



**Figure 8.** Ulna of *Kannemeyeria simocephalus*, lateral view: **A**, BP/1/5624; **B**, BP/1/6160; medial view: **C**, BP/1/6160. Scale bars = 10 cm.

bone, where it ends as a deep depression. This groove most probably accommodated the tendons of muscles of the forelimb.

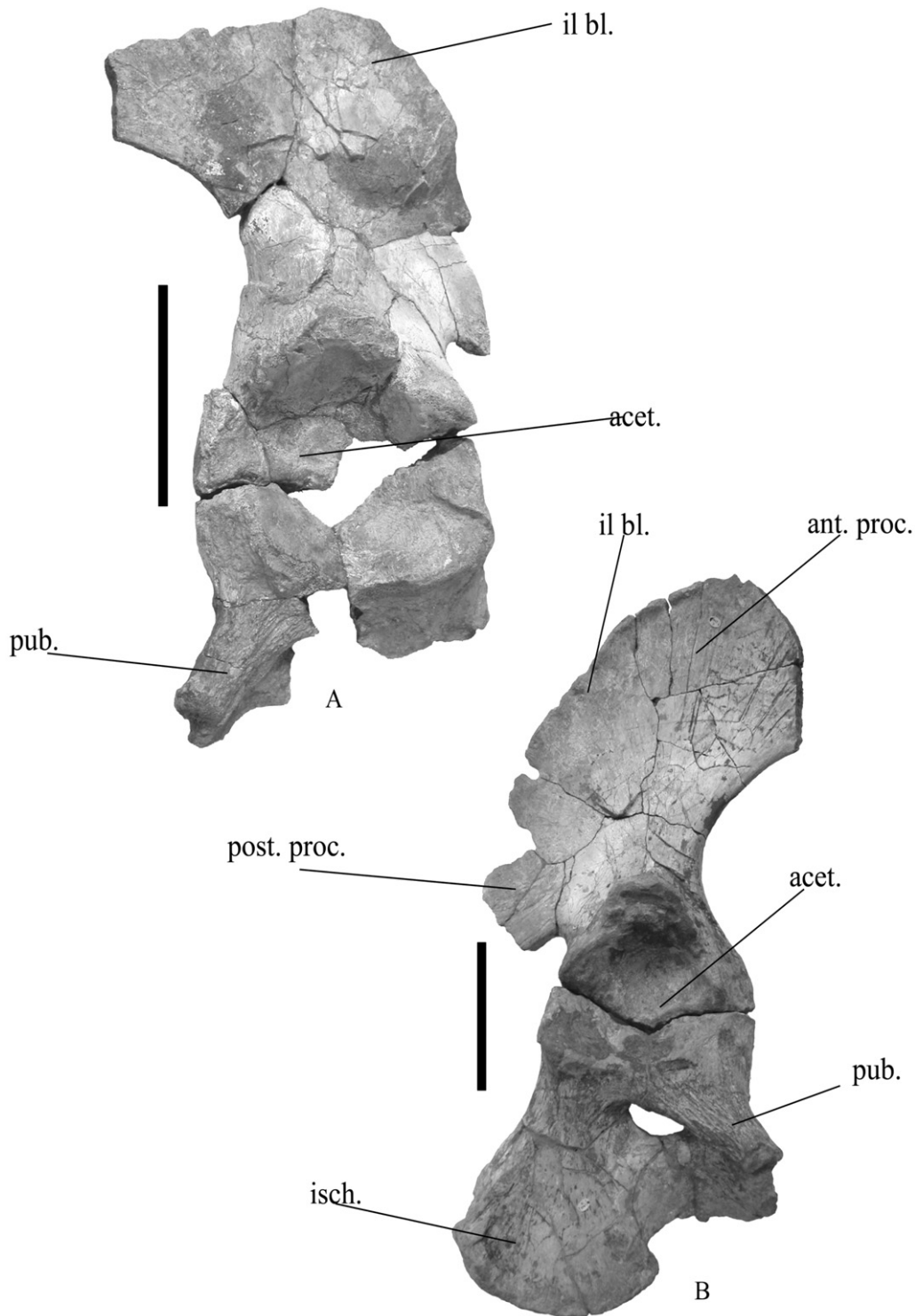
The distal articulation is directed ventrally and forms an elongated oval (Fig. 8c). Its surface is concave and broad posteriorly, while it is narrow anteriorly. The articulating surface slopes medially and extends onto the distal medial surface.

#### **Pelvic girdle**

The description of the pelvic girdle is based on BP/1/5624 and BMNH R3761 because the pelvic girdle that is part of

ELM 1 shows a morphology that is significantly different from the other two specimens.

*Ilium.* In BP/1/5624 the dorsal border of the ilium is not preserved but this area is preserved in BMNH R3761 (Fig. 9). The dorsal border of that specimen is convex and is slightly lower towards the posterior border (Fig. 9). Laterally, the surface of the blade is concave and the anterior process is directed laterally in BP/1/5624 than in BMNH R3761. The anterior process is antero-posteriorly short and wide when compared with the posterior process and is situated higher than the posterior one. It projects far in front of the pubis. The posterior process is located



**Figure 9.** Lateral view of the pelvic girdle of *Kannemeyeria simocephalus*. **A**, BP/1/5624; **B**, BMNH R3761. Scale bars = 10 cm.

close to the acetabulum and the ventral border is concave. It is dorso-ventrally wide and short antero-posteriorly.

Below the anterior process the anterior border of the ilium narrows gradually to form an almost straight border, whereas the posterior border narrows rapidly resulting in a concave border. Anteriorly, the pillar like neck narrows more than it does posteriorly.

The acetabulum is circular, broad, deep and faces laterally (Fig. 9B). Dorsally, the lateral surface of the acetabulum is bordered by supra-acetabular ridge. It is wide and does not project far laterally. The anterior two-thirds of the acetabular facet is separated from the posterior part by the

supra-acetabular notch; however, the articulating surface remains continuous. The posterior part of the rim is narrow and sharply demarcated.

Dorsally, the acetabulum facet is bound by the supra-acetabular buttress. This buttress is narrow anteriorly and posteriorly, and broad in the middle. Two-thirds of the way up the posterior border of the supra-acetabular buttress is the supra-acetabular notch, which is narrow and deep in BP/1/5624. The anterior border of the ilium, above the acetabular facet and the dorsal part of the anterior border of the pubis is flattened with a roughened surface.

On the anterior border of the acetabulum, in front of the acetabular facet, is a facet for the pubis. This elongated and concave facet is located on the medial border. Behind the acetabular facet is a concave, almost square facet for the ischium, which is situated higher than the pubic facet. Medially the bone surface of the iliac blade is convex dorsally and becomes concave above the acetabulum. Although the bone has been damaged, five sacral rib facets are visible.

*Pubis.* The pubis and ischium are fused into a pubo-ischiadic plate in *K. simocephalus* (Fig. 9B). The left pubis of BP/1/5624 is broad proximally and narrows distally. Dorsally, the anterior part of the bone is higher and is directed more medially than posteriorly. The ventral part of the pubis is narrow, and the anterior part of the bone is directed more antero-ventrally. Anteriorly the pubis narrows to form a round tubercle that is directed anteriorly and ventrally. The lateral surface of the tubercle is very rugose in both BP/1/5624 and BMNH R3761. Behind the tubercle the bone extends posteriorly towards the ischium. This part of the bone is thin and the surface is concave.

A small, oval acetabular facet is present on the dorsal surface (Fig. 9B). The surface of this facet is smooth and only slightly concave, and is continuous with the ischial facet.

Laterally, the border of the facet is distinctly lower and the facet faces laterally. The medial wall of the pubic facet extends dorsally to meet the medial wall of the iliac acetabular facet. In front of the acetabular facet is the rectangular, convex facet for articulation with the ilium, which has a rugose surface that projects dorsally creating forming small pillars. This surface matches the surface of the facet anterior to the iliac acetabular facet. It would suggest that these bones interdigitate in order to form a firmly immobile suture. Laterally, the surface below the articulation is rough and is covered by thin ridges. It narrows in the anterior direction to end in a round, concave facet that also has a rugose surface. Along the posterior border of the pubis there is a C-shaped groove that extends across the surface of the bone. It forms the sub-circular anterior border of the obturator foramen.

*Ischium.* The ischium is triangular and is expanded ventrally (Fig. 9B). Dorsally, the ischial acetabular facet is elongated and has a slightly concave surface. It is separated from the rest of the bone by a ridge. The lateral wall of the facet is lower than the medial one, which rises to form a rugose dorsal border. Posterior to the acetabular facet is the facet that articulates with the ilium. It is a narrow, elongate triangle that has a convex surface. In BP/1/5624 it appears that the ischium is directed medially; however, this may be as a result of the bone being broken and the distal end has been lost. In BMNH R3761 the distal part of the ischium is fairly widely expanded. Along the posterior edge of the distal expanse is a narrow, convex tubercle. Distally the ischium is slightly lower than the pubis.

Anteriorly, the ischium meets the pubis below the acetabular facet to form the concave dorsal border of the obturator foramen. The short, concave, almost circular

posterior border of the obturator foramen is formed by the ischium. In *K. simocephalus* the obturator foramen forms a narrow, elongated oval that is slightly wider towards the ischium (Fig. 9B).

### Hindlimb

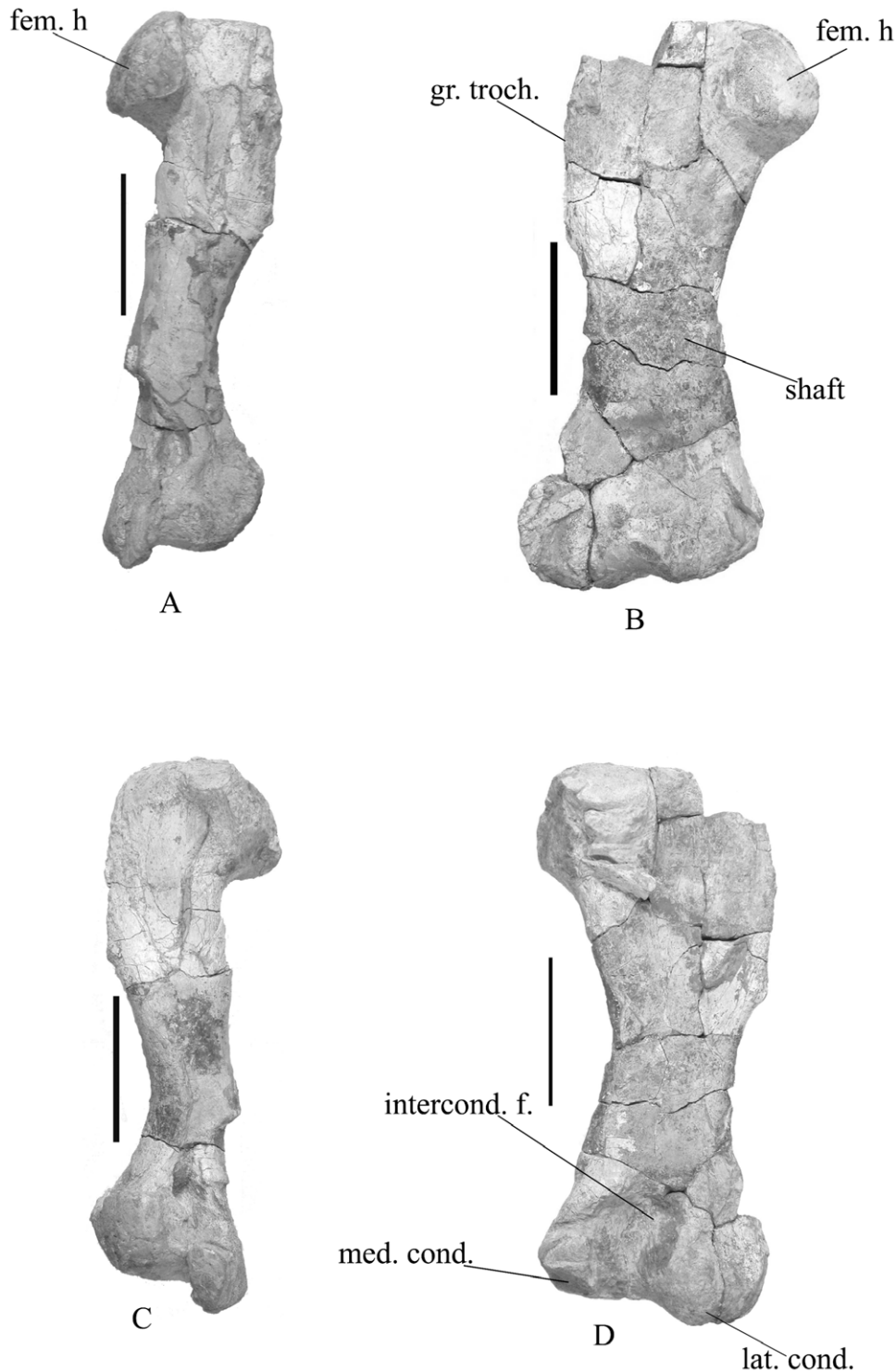
*Femur.* The femur of *K. simocephalus* is a long, dorso-ventrally flattened (Fig. 10B,D) bone with a straight shaft that has concave anterior and posterior borders. The proximal and distal expansions are of equal width. The right femur of BP/1/5624 has been compressed antero-posteriorly, resulting in a dramatically different shape of the bone in comparison to the left femur of the same individual. Owing to its marked deformation the right femur has been omitted from this description (Fig. 10A,C).

The femoral head is round and medially inflected (Fig. 10B). In ventral view the head of the left femur of BP/1/5624 is surrounded by a shallow groove that is steep towards the head. This groove makes the head more prominent in ventral view. In front of the head is a shallow fossa that is broad proximally and narrows distally where it merges with the shaft. The posterior boundary is marked by the presence of the greater trochanter. Below the head of the bone is a low, flat ridge that extends to the posterior border. No internal trochanter is present.

The greater trochanter is elongated and extends along the proximal third of the posterior border of the femur and is almost straight (parallel to the long axis of the bone) (Fig. 10D). It is antero-posteriorly narrow with a rugose surface and is clearly demarcated from the rest of the bone. Dorsally, the greater trochanter is rounded and thick and is not separated from head of the femur and forms a continuous surface along its entire length.

Distally, the articular condyles are separated by a circular intercondylar fossa (Fig. 10D). It is deep and is situated slightly above and between the proximal borders of the condyles. The lateral condyle projects farther onto the dorsal surface than does the medial condyle. It is also directed more ventrally and is slightly lower than the medial condyle in dorsal view. Postero-dorsally to the medial condyle is a broad, shallow groove that terminates at the proximal end of the ventral border. The lateral condyle is smaller than the posterior condyle and its dorsal surface is skewed in the proximal direction. It also is rugose pitted. Distally, the condyles are separated by a broad, deep groove which is steeper towards the posterior condyle.

The ventral articulating surface is present on the distal end of the condyles (Fig. 10B). The articulating condyles are separated on the ventral surface by a broad, antero-posteriorly oblong fossa. This fossa has a shallow, concave surface that is bordered anteriorly and posteriorly by prominent ridges. It extends above the condyles to merge with the shaft above. Distally, the articulating surface of the condyles is directed ventrally and is convex. The articulating surface of the posterior condyle projects more ventrally than that of the anterior condyle. The material studied from the British Museum of Natural History and ELM 1 was found to be significantly different from BP/1/5624 and BMNH R3761.

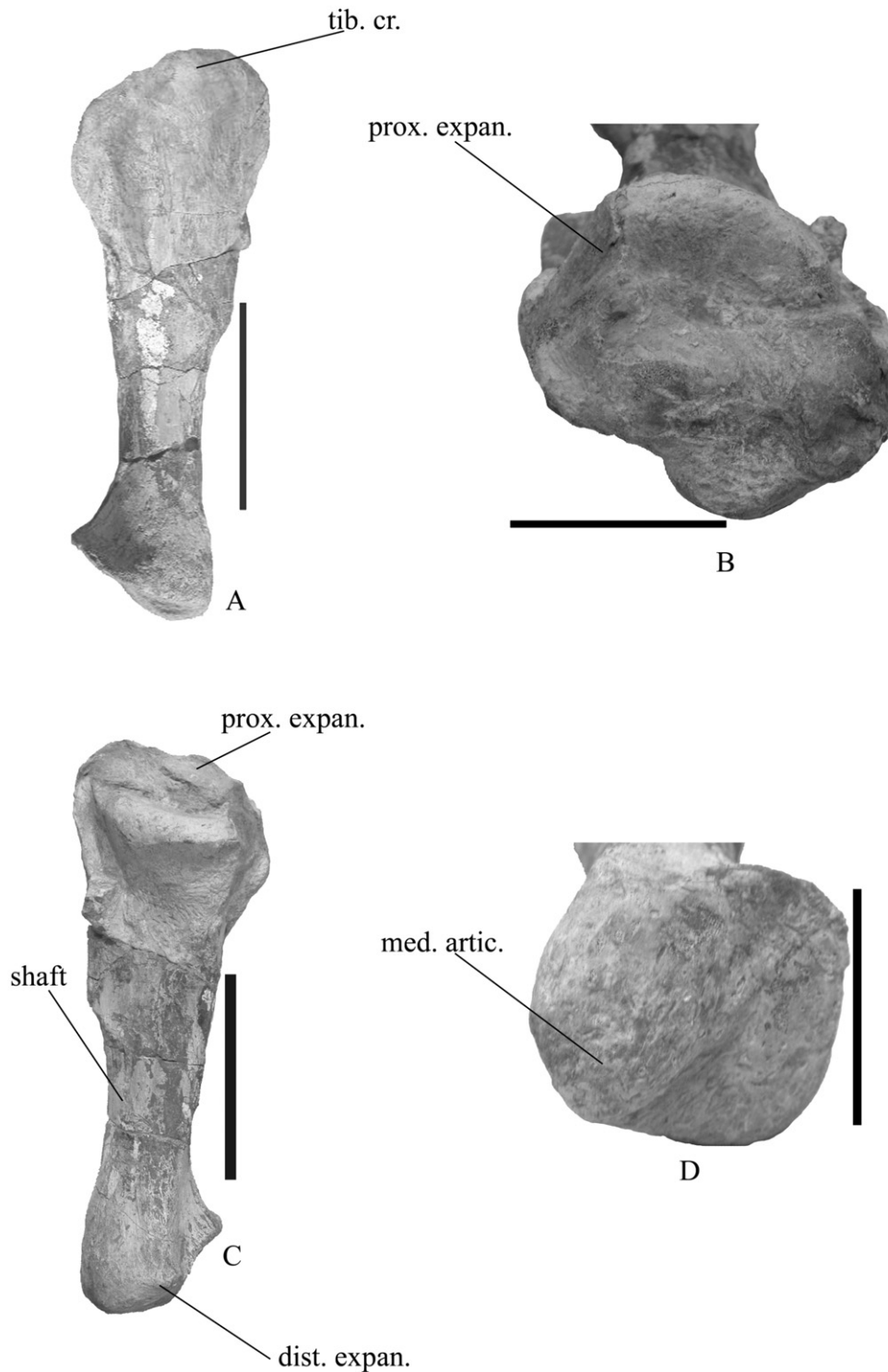


**Figure 10.** Femur of *Kannemeyeria simocephalus*, dorsal view: **A, B**, BP/1/5624; ventral view: **C, D**, BP/1/5624. Scale bars = 10 cm.

*Tibia.* Only the right tibia of BP/1/5624 has been preserved (Fig. 11). It has an almost cylindrical appearance and is flattened antero-posteriorly. Both the proximal and the distal ends are expanded with the proximal being larger than the distal.

Proximally, the tibial tuber faces antero-laterally (Fig. 11A). A round tubercle projects laterally from this surface and is bounded ventrally by a narrow ridge. The surface of the tuberculum is rugose and extends slightly medially. This surface is raised above the rest of the bone and grades down into the anterior margin. Anteriorly, the surface of the margin is broad and roughened.

Lateral to the tibial tuberosity is a shallow groove that extends halfway down the bone (Fig. 11A). It is narrow proximally where the tibial tuberosity projects over this groove and is bound by a lateral ridge. The lateral border of the tibia flares out and a shallow fossa is present below the proximal ridge, which represents the articulation for the fibula. Below this the bone has been damaged. Approximately halfway down the shaft there is a shallow fossa. Distally the bone curves laterally forming a ridge that gives the bone a squared off appearance. Anteriorly the shaft has lost all definitive features due to cracking and damage. Medially the bone was damaged resulting in



**Figure 11.** Tibia of *Kannemeyeria simocephalus*, anterior view: **A**, BP/1/5624, **B**, proximal articulation BP/1/5624; posterior view: **C**, BP/1/5624; **D**, distal articulation BP/1/5624. Scale bars = 10 cm.

the middle of the shaft being compressed.

The proximal end of the bone (Fig. 11B) is round and higher anteriorly than posteriorly. It has a single slightly concave articulating surface. Posteriorly, the head is bound by a thick, flat ridge. This structure extends onto the posterior surface and has a roughened appearance. It merges with the surface, which grades into the shaft. Below this the bone is damaged.

Posteriorly, in the middle of the shaft, is a shallow fossa and distally, the concave surface of the shaft ends as a broad ridge above the articulating surface. This distal

articular surface is divided into two facets. The medial facet is located more ventrally and has a round, convex surface that is directed ventrally, whereas the lateral facet is a square and directed ventrally with a flat to slightly concave surface (Fig. 11D).

*Fibula.* The fibula of *K. simocephalus* is along, thin bone and is represented here by BMNH R3761 (Fig. 12). Laterally, the border is concave while the medial border is straight. Proximally, the bone is expanded and a small, hemispherical tubercle rises above the surface. Along the lateral border of the distal expansion is a groove that

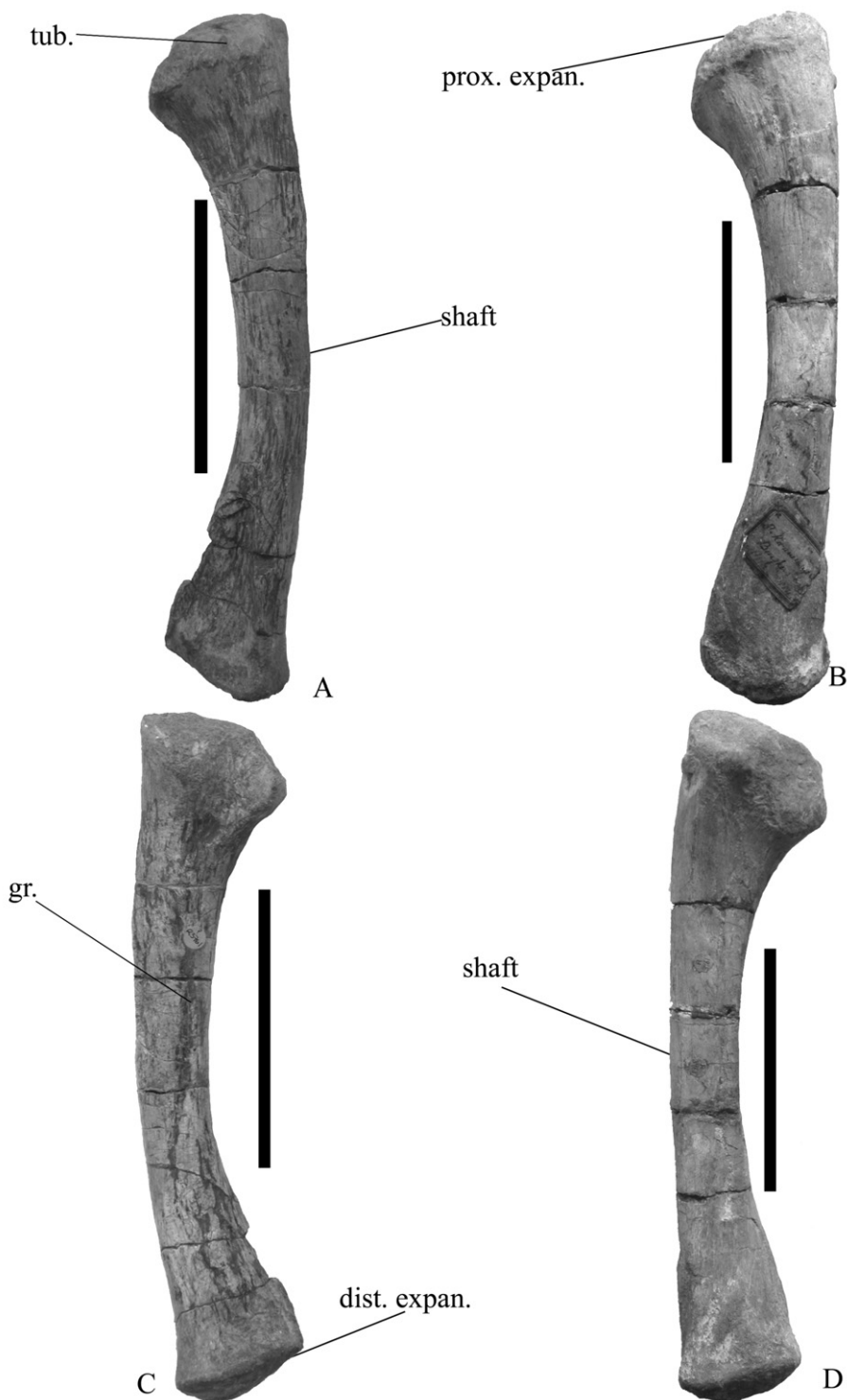


Figure 12. Fibula of the *Kannemeyeria simocephalus*, anterior view: A, B, BMNH R3761; posterior view: C, D, BMNH R3761. Scale bars = 10 cm.

extends to the distal end. Both the proximal and distal ends have convex surfaces.

#### DISCUSSION

A detailed analysis of the cranial morphology of *Kannemeyeria* resulted in the identification of a generalist cranial morphology (Renaut 2000) which led to a question as to what kind of postcranial morphology would be seen in *K. simocephalus*. A comparison with other Triassic dicynodonts would also give us an idea as to how *K. simocephalus* fitted into the greater picture that is the relationships of Triassic dicynodonts. The comparison with other Triassic

dicynodonts is based largely on the literature available and wherever possible on comparison with actual specimens.

When compared with *Lystrosaurus* the dorsal border of the scapula *K. simocephalus* is not as widely expanded but is rather moderately expanded as seen in other Triassic dicynodonts (e.g. Cox 1965; Bandyopadhyay 1988). The almost straight anterior and posterior borders of the scapula blade of *K. simocephalus* are similar to that of *Lystrosaurus* but more closely resembles that of *Sinokannemeyeria* (Sun 1960; 1963) which also has a tall, moderately wide scapula. It differs from *Wadiasaurus* (Bandyo-

padhyay 1988; Ray 2006) and *Parakannemeyeria* (Sun 1960; 1963) in that the anterior border of these two taxa is slightly concave while other Triassic dicynodonts such as *Tetragonias* (Cruickshank 1967; mounted specimen Tübingen), *Dinodontosaurus* (Cox 1965), *Ischigualastia* (Cox 1965) and *Jachalera* (Vega-Dias & Schultz 2004) the scapula blades are short, broad with concave anterior and posterior margins.

*Kannemeyeria* shares an elongated scapula spine on the lateral surface of the scapula with *Placerias* (Camp & Welles 1956) and *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006). Other Triassic dicynodonts have lower scapula spines that are not as prominent and do not project far anteriorly (e.g. *Parakannemeyeria* (Sun 1960; 1963), *Ischigualastia* (Cox 1965), *Tetragonias* (Cruickshank 1967), *Zambiasaurus* (Cox 1969; R9140) and *Rhinodicynodon* (Surkov 1998)) or are absent altogether (e.g. *Dinodontosaurus* (Cox 1965)) and has not been described in *Jachalera* (Vega-Dias & Schultz 2004).

The shape of the acromion process varies among the Triassic dicynodonts. It is short and directed anteriorly in *Placerias*, while a rectangular acromion process that is directed antero-laterally occurs in *Angoniasaurus* (Cox & Li 1983; U12/1), *Sinokannemeyeria* (Sun 1960; 1963) and *Dinodontosaurus* (Cox 1965). An antero-laterally directed triangular acromion process occurs in *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006), *Kannemeyeria*, *Parakannemeyeria* (Sun 1960; 1963), *Rhinodicynodon* (Surkov 1998), *Tetragonias* (Cruickshank 1967) and probably also in *Zambiasaurus* (Cox 1969; R9140); however, the acromion process is either absent or vestigial in *Ischigualastia* (Cox 1965) and *Jachalera* (Vega-Dias & Schultz 2004).

Medially the acromion process is longitudinally in all Triassic dicynodonts (Sun 1960, 1963; Cox 1965, 1969; R9140; Cruickshank 1967; Cox & Li 1983; U12/1; Bandyopadhyay 1988; Ray 2006). In *Kannemeyeria* there is a tubercle on the proximo-posterior corner of the medial surface of the acromion. It varies from triangular in the large specimen (BP/1/5624) to round and oval in the small specimen. A review of the literature found that no similar structure has been described in Triassic dicynodonts; however, an examination of the mounted specimen of *Tetragonias* (at Tübingen) shows the presence of the tubercle on the proximo-posterior corner of the acromion's medial surface.

In the forelimb the humerus of the Triassic dicynodonts remains fairly conservative in design and does not change much amongst the taxa. *Kannemeyeria* has a low narrow olecranon that is part of the ulna and does not show any signs of sutural contact with the rest of the ulna, even in the juvenile specimen (BP/1/6160). Thus we infer that the ulna, including the olecranon grew from a single ossification centre in *Kannemeyeria* as it did in earlier dicynodonts. However, in most Triassic dicynodonts (e.g. *Sinokannemeyeria*, *Parakannemeyeria*, *Wadiasaurus*, *Dinodontosaurus*, *Ischigualastia*, *Jachalera* and *Placerias*) the olecranon forms from a separate centre of ossification which may fuse to the rest of the ulna in aged individuals (Camp 1956; Sun 1963; Cox 1969; Bandyopadhyay 1988; Vega-Dias & Schultz 2004; Camp & Welles 1956). The

olecranon is either poorly developed or absent in *Lystrosaurus* (Young 1935; Ray 2006), while in *Kannemeyeria*, *Sinokannemeyeria* (Sun 1960, 1963), *Parakannemeyeria* (Sun 1960, 1963), *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006), *Dinodontosaurus* (Cox 1965), *Ischigualastia* (Cox 1965), *Placerias* (Camp & Welles 1956) and probably *Jachalera* (Vega-Dias & Schultz 2004) the olecranon is triangular but showing varying states of development.

In *Kannemeyeria* the femoral head is continuous with the major trochanter, as it is in *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006) and many Permian taxa (e.g. *Diictodon*, *Kingoria*, '*D.* *trigonocephalus*'), whereas it separated from it by a weak groove in *Sinokannemeyeria* (Sun 1960, 1963), *Ischigualastia* (Cox 1965) and *Placerias* (Camp & Welles 1956). The femoral head of *Kannemeyeria* is round and inflected medially as in *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006) and *Dinodontosaurus* (Cox 1965) as compared with the new world stahleckeriids (Cox 1965; Camp & Welles 1956) and sinokannemeyeriids (Sun 1960, 1963) where there is either a distinctly developed neck or the presence of an incipient neck.

Surkov (1998) considered that large Triassic dicynodonts (*Dinodontosaurus* and *Placerias*) had massive limbs and hemispherical humeral heads and that the ectepicondyle extended far distally. *K. simocephalus*, although large, has an inverted triangular head like that seen in *Parakannemeyeria* and *Sinokannemeyeria* and the ectepicondyle does not extend far distally. It points to a possible move to more upright forelimbs which would result in the trunk being raised above the ground. This above observation would suggest that these larger animals were probably predisposed to having more effective and efficient locomotor systems.

Some of the material previously described as *Kannemeyeria* has not been included in these descriptions. It was noted during this study that some of the material previously assigned to *Kannemeyeria* showed significant variation from what is currently known as *Kannemeyeria*. This material includes specimens previously described by Pearson (1924) and Cruickshank (1975). These include many of the elements of the pectoral girdle and forelimb as well as the pelvic girdle and hindlimb.

It has been noted that there are a number of differences between the ulnae of BP/1/5624 and BP/1/6160, and ELM 1. The radial facet of ELM 1 is narrower than that of BP/1/5624 and BP/1/6160 and the laterally projecting ridge on the lateral surface of the ulna is also located further anteriorly in ELM 1 than in BP/1/5624 and BP/1/6160. Also the shape of the olecranon of ELM 1 is round and wide, whereas the olecranon of BP/1/5624 and BP/1/6160 are triangular or wedge shaped. Both BP/1/5624 and BP/1/6160 are associated with skulls that have been identified as *K. simocephalus*. The ulna of ELM 1 is distinctly different from that of BP/1/5624 and BP/1/6160 and suggests that it does not belong to this taxon.

There are also differences between the radii BP/1/6160 and ELM 1. The radius of BP/1/5624 was not considered for all comparisons as it has suffered some damage. The ends of the radius (BP/1/6160) of *K. simocephalus* are expanded, forming narrow articulating surfaces both

proximally and distally. This is different from that of ELM 1, which does not have greatly expanded ends, and which has the proximal and distal articulating surfaces that are wide and nearly circular. On the proximal expansion of the radius facing more posteriorly is the ulna articulation. In ELM 1 the ulna articulation is proximo-distally narrow and triangular, while in both BP/1/5624 and BP/1/6160 the ulna articulation forms a narrow rectangle, with both having a convex surface. Thus we consider the affinities of the radius incorporated into the ELM 1 mount to be uncertain. Although the skull of ELM 1 and most of the postcranial elements have been found to belong to *Kannemeyeria* the above mentioned elements show definite difference from other specimens of *Kannemeyeria*. From notes on the collection of the original (Courtney-Latimer 1948) it would seem that material was collected was incomplete and fragmentary so the mounted specimen was completed with material that had been previously collected (Courtney-Latimer 1948). It is therefore possible that some elements that form part of this specimen may show an anatomy that is different from what is known as *Kannemeyeria simocephalus*.

Scapulae (R3740) described by Pearson (1924) after been examined was found to be significantly different from that described as a part of *K. simocephalus* (BP/1/5624; BP/1/6160) in particular they have a narrower blade, the anterior margin is slightly concave and the prespinous region is much narrower to mention a few of the differences. The femora (R3740) described by Pearson (1924) have wider shafts and the femoral articulating surface is directed more dorsally. The pelvic girdle of ELM 1 shows a morphology that is different from that of BP/1/5624 and R3761 in that the ilium's anterior process is much longer and has a curved appearance. These are just some of the notable differences; however, this material forms the focus of a separate, more detailed analysis.

#### Diagnosis of *Kannemeyeria simocephalus*

We consider the following characters of the postcranial skeleton to be diagnostic for *K. simocephalus*, and they be added to the current specific cranial diagnosis (Renaut 2000, pp. 114–115, ). However, it must be noted that at this time *K. lophorhinus*, the other valid species of *Kannemeyeria*, is poorly represented. Therefore, it is not possible to determine whether the characters listed below are diagnostic of the species *K. simocephalus* or the genus *Kannemeyeria* as a whole. The polarity of the characters was determined by comparison with '*D.*' *trigonocephalus* (based on King 1981 including using figures).

*Kannemeyeria simocephalus* is a kannemeyeriiforme dicynodont with the following autapomorphies: a U-shaped tubercle at the proximo-posterior corner of the medial surface of the acromion (a similar feature (round) is also present in *Tetragonias* but is not as well developed as seen in *K. simocephalus*); the ventral articulating surface of the lateral condyle of the femur is lower than the medial; lateral border of the femur is almost straight.

*Kannemeyeria simocephalus* can be further distinguished from all non-kannemeyeriiforme dicynodonts by the presence of the following kannemeyeriiforme synapo-

morphies: antero-posteriorly expanded dorsal scapula border; scapula spine present; triangular acromion; distal end of scapula flared; distal scapula projects in front of scapula spine; proximal and distal expansions of the humerus are more or less of equal length; anterior process of ilium is wide and posterior process is narrow; anterior process well in front of acetabulum; supra-acetabular notch present; femur has concave posterior border; femoral head is medially inflected; narrow greater trochanter.

It differs from other kannemeyeriiformes by retaining the following pleisomorphic characters: scapula has straight anterior and posterior border; glenoid lower than coracoid articulation; round glenoid articulation; olecranon fused to shaft; triangular olecranon. Supra-acetabular notch present on ilium. Pubis and ischium are fused; oblong obturator foramen; femoral head continuous with greater trochanter; the greater trochanter is parallel to the long axis of the femur; third trochanter absent.

#### CONCLUSION

An examination of the postcranial skeleton of *K. simocephalus* led to a revision of the postcranial characters that diagnose it. The presence of a U-shaped tubercle on the medial surface of the scapula at the proximo-posterior corner of the acromion and the articulating surface of the posterior condyle is lower than that of the anterior one are found to be unique to *K. simocephalus*. Although there is no mention of a similar feature in the literature describing Triassic dicynodonts, an examination of the mounted specimen of *Tetragonias* showed a round tubercle in a similar position.

Material previously described by Pearson (1924) was also re-examined and some of the material was found to be significantly different from BP/1/5624 in particular the scapulae and femora. The mounted specimen ELM 1 was also studied it was found to contain elements that could be identified as *K. simocephalus* while some long bone elements were found to be significantly different. Courtney-Latimer (1948) also stated although a substantial amount of this skeleton comes from a specimen collected in 1948, a fair amount was incomplete and was actually replaced by material that had been collected and housed at the museum. This therefore suggests that ELM 1 is a chimera. The material that was excluded from *K. simocephalus* has been included in a separate study.

It therefore makes BP/1/5624 the most complete positively associated *K. simocephalus* specimen currently known, and thus makes it a suitable standard for the referral of postcranial material to *K. simocephalus*.

We wish to extend our thanks to the National Research Foundation for funding the PhD and Post Doctoral Fellowship that resulted in this work. Many thanks to Alain Renaut for his initial work on the cranial morphology of *Kannemeyeria simocephalus* which spurred the interest in the postcranial skeleton of the species, and for his involvement and assistance at the outset of this project. My thanks to Sandra Chapman at the Natural History Museum, London for allowing me access to the *Kannemeyeria* material housed there. Thanks to Dr Michael Maisch for his hospitality and access to the Triassic material housed at the University of Tübingen, Stuttgart. Thank you to Mr Kevin Cole of the East London Museum, South Africa for allowing us access to the mounted specimen as well as for extra photographs of ELM 1. My thanks to Ms Sheena Kaal of the South African Museum, Cape Town for all her help during my visit to examine Triassic dicynodont material housed there. We express our gratitude to Dr Ken Angielczyk and an anonymous reviewer for their helpful comments.

## ABBREVIATIONS

### Institutional

BP	Bernard Price Institute for Palaeontological Research, Johannesburg
SAM-PK	South African Museum, Cape Town
BMNH	British Museum of Natural History, London
ELM	East London Museum, East London, South Africa

### Anatomical

acet.	acetabulum
acrom.	acromion
ant. proc.	anterior process
atl	atlas
ax.	axis
biccip. f.	bicipital fossa
cent.	centrum
d-p cr.	delto-pectoral crest
ectepic.	ectepicondyle
entepic.	entepicondyle
entepic. for.	entepicondylar foramen
fem. h.	femoral head
glen. f.	glenoid facet
gr. troch.	greater trochanter
hum. h.	humeral head
ic.	intercentrum
il. bl.	ilium blade
intercond. f.	intercondylar fossa
isch.	ischium
lat. cond.	lateral condyle
med. cond.	medial condyle
n. s.	neural spine
n.a	neurapophysis
obt. for.	obturator foramen
odont.	odontoid Process
olec.	olecranon
olec. f.	olecranon Fossa
post. proc.	posterior process
postzyg.	postzygapophysis
prezyg.	prezygapophysis
prox. exp.	proximal expansion
pub. tub.	pubic tubercle
rad. artic.	radial articulation
sig. fac.	sigmoidal facet
sk. artic	skull articulation
sp.	scapula spine
tub.	tubercle
ul. artic.	ulna articulation

## REFERENCES

- BANDYOPADHYAY, S. 1988. A kannemeyeriid dicynodont from the Middle Triassic Yerrapalli Formation. *Philosophical Transactions of the Royal Society, London, Series B* **320**, 185–233.
- CAMP, C.L. & WELLES, S.P. 1956. Triassic Dicynodont Reptiles. Part 1. The North American genus *Placerias*. *Memoirs of the University of California* **13**(4), 255–304.
- CAMP, C.L. 1956. Triassic Dicynodont Reptiles. Part 2. Triassic Dicynodonts compared. *Memoirs of the University of California* **13**(4), 305–348.
- COURTENAY-LATIMER, M. 1948. *Kannemeyeria wilsoni* Broom; how it came to the East London Museum. In: du Toit, A.L. (ed.), *Special Publications of the Royal Society of South Africa. The Robert Broom Commemorative Volume*, 107–109. Cape Town, Royal Society of South Africa
- COX, C.B. 1965. New Triassic dicynodonts from South America, their origins and relationships. *Philosophical Transactions of the Royal Society, London, Series B* **248**(753), 457–516.
- COX, C.B. 1969. Two new dicynodonts from the Triassic N'tawere Formation, Zambia. *Bulletin of the British Museum (Natural Museum) Geology* **17**(6), 255–294.
- COX, C.B. & LI, J.-L. 1983. A new genus of Triassic dicynodont from East Africa and its classification. *Palaeontology* **26**(2): 389–406.
- CRUICKSHANK, A.R.I. 1967. A new dicynodont genus from the Manda Formation of Tanzania (Tanganyika). *Journal of Zoology, London* **153**, 163–208.
- CRUICKSHANK, A.R.I. 1975. The skeleton of the Triassic anomodont *Kannemeyeria wilsoni* Broom. *Palaeontologia africana* **18**, 137–142.
- HANCOX, P.J., SHISHKIN, M.A., RUBIDGE, B.S. & KITCHING, J.W. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographical implications. *South African Journal of Science* **91**, 143–144.
- MAISCH, M.A. 2001. Observations on Karoo and Gondwana vertebrates. Part 2: A new skull-reconstruction of *Stahleckeria potens* von Huene, 1935 (Dicynodontia, Middle Triassic) and a reconsideration of kannemeyeriiform phylogeny. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **2000**, 15–28.
- RENAUT, A.J. 2000. *A re-evaluation of the cranial morphology and taxonomy of Triassic dicynodont genus Kannemeyeria*. Unpublished Ph.D. thesis, University of the Witwatersrand
- ROMER, A.S. 1956. *Osteology of Reptiles*. University of Chicago Press, Chicago.
- SUN, A.-L. 1960. On a new genus of kannemeyeriids from Ningwu, Shansi. *Vertebrata Palasiatica* **4**(2), 67–81.
- SUN, A.-L. 1963. The Chinese kannemeyeriids. *Palaeontologica Sinica* **17**, 73–109.
- SURKOV, M.V. 1998. The postcranial skeleton of *Rhinodicynodon gracile* Kalandadze, 1970 (Dicynodontia). *Paleontological Journal* **32**(4), 402–409.
- VEGA-DIAS, C. & SCHULTZ, C.L. 2004. Postcranial material of *Jachaleria candelariensis* Araújo and Gonzaga 1980 (Therapsida, Dicynodontia), Upper Triassic of Rio Grande do Sul, Brazil. *Paleobios* **24**(1), 7–31.