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Dicynodont postcrania from the Triassic of Namibia and their implication for the systematics of Kannemeyeriiforme dicynodonts

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Recent years have seen a renewed interest in the postcranial anatomy of Triassic dicynodonts from Africa. This study investigates the previously undescribed dicynodont postcrania from the Omingonde Formation of Namibia. Two valid dicynodont species, based upon crania, are known from this formation: *Dolichuranus primaevus* and *Kannemeyeria lophorhinus. Dolichuranus* displays a primitive generalized cranial anatomy that has made it difficult to place in Triassic dicynodont phylogeny. Some of the postcranial specimens can be positively identified as *D. primaevus* on the basis that they were associated with skulls of this species. Two scapula morphologies can be distinguished among the postcranial specimens that are not positively associated with diagnostic cranial remains. One of these shares similarities with the scapula of *Kannemeyeria simocephalus* from South Africa and is provisionally referred to *K. lophorhinus.* The other displays unusual characters such as the absence of an acromion and a tubercle on the lateral surface of the scapula at the level where the acromion would be expected. Inclusion of the new postcranial data in a cladistic analysis of Triassic dicynodonts resolves the position of *D. primaevus* as a member of Sinokannemeyeriidae. It also causes an enigmatic unnamed postcranial taxon from equivalently aged beds in South Africa to fall within the Sinokannemeyeriidae. These results highlight the importance of including postcranial data in analyses of Triassic dicynodont relationships.

Keywords: *Dolichuranus;* dicynodont, Triassic, Namibia.

INTRODUCTION

The Triassic strata of Namibia, collectively known as the Etjo Sandstones, are found in the northern part of the country and date to the late Early to early Middle Triassic (Keyser 1973). The Triassic beds were once considered to be non-fossiliferous (Keyser 1973; Keyser 1974), but at least 25 vertebrate fossils were collected by Keyser (Keyser 1973). Among these fossils were two new medium to large dicynodont taxa, *Dolichuranus primaevus* Keyser, 1973 and *Rhopalorhinus etioensis* Keyser, 1973, along with a specimen referred to the otherwise South African species *Kannemeyeria simocephalus* (Weithofer, 1888). Keyser (1973) concluded that *Dolichuranus* was morphologically intermediate between the Late Permian taxon *Daptocephalus* and the Late Triassic taxon *Dinodontosaurus.* He found that the general shape of the skull of *Dolichuranus primaevus* was similar to that of *Kannemeyeria latirostris* Crozier, 1970, which showed a number of differences that distinguished it from other *Kannemeyeria* species (Crozier 1970). Keyser (1973) referred *K. latirostris* to *Dolichuranus* as *D. latirostris* (Crozier, 1970). Keyser & Cruickshank (1979) upheld Keyser's (1973) inclusion of *K. latirostris* in the genus *Dolichuranus.* A re-examination of *Dolichuranus primaevus* Keyser, 1973 and *Rhopalorhinus etionensis* Keyser, 1973 showed that these taxa represented two extremes of a morphological series (Keyser & Cruickshank 1979). They therefore placed *Rhopalorhinus* into synonymy with *Dolichuranus,* but still recognized two species (Keyser & Cruickshank 1979). Cooper (1980) took this one step further and suggested that if these two taxa represent extremes of a morphological series then only one species should be recognized, namely *Dolichuranus primaevus.*

Maisch (2001) suggested that *Dolichuranus* could not be assigned to a specific family because it lacked synapomorphies that characterized the four families he recognized (*viz.* Shansiodontidae, Kannemeyeriidae, Stahleckeriidae, Dinodontosauridae). He considered it an undifferentiated Triassic dicynodont taxon (Maisch 2001). He also concluded that because the postcranial skeleton is not known and the cranial osteology is incompletely known *Dolichuranus primaevus* should be considered Kannemeyeriiformes *incertae sedis* (Maisch 2001). A recent detailed study of the cranial anatomy of *Dolichuranus primaevus* also undertook a phylogenetic analysis of Triassic dicynodonts (Damiani *et al.* 2007). They suggested that *Dolichuranus* meets the requirements put down by Keyser (1973), Surkov (2000) and Maisch (2001) to be a basal member or close outgroup of the Stahleckeriidae (Damiani *et al.* 2007). The relationships of this taxon within Kannemeyeriiformes are unresolved and new data may help to resolve this problem. Since it is a rather primitive, undifferentiated taxon it is likely to have key combinations of character states that will affect our interpretation of Triassic dicynodont phylogeny.

MATERIAL

BP/1/4578 consists of partial cranial material, a complete hindlimb and some pelvic bones. The femora of this specimen were already prepared. The cranial material has been referred to *Dolichuranus* by Damiani *et al.* (2007). Locality: Mount Etjo (outcrop above Bobbejaankloof), Otjiwarongo, Omingonde Formation.

R 334: postcrania belonging to holotype of *Dolichuranus*

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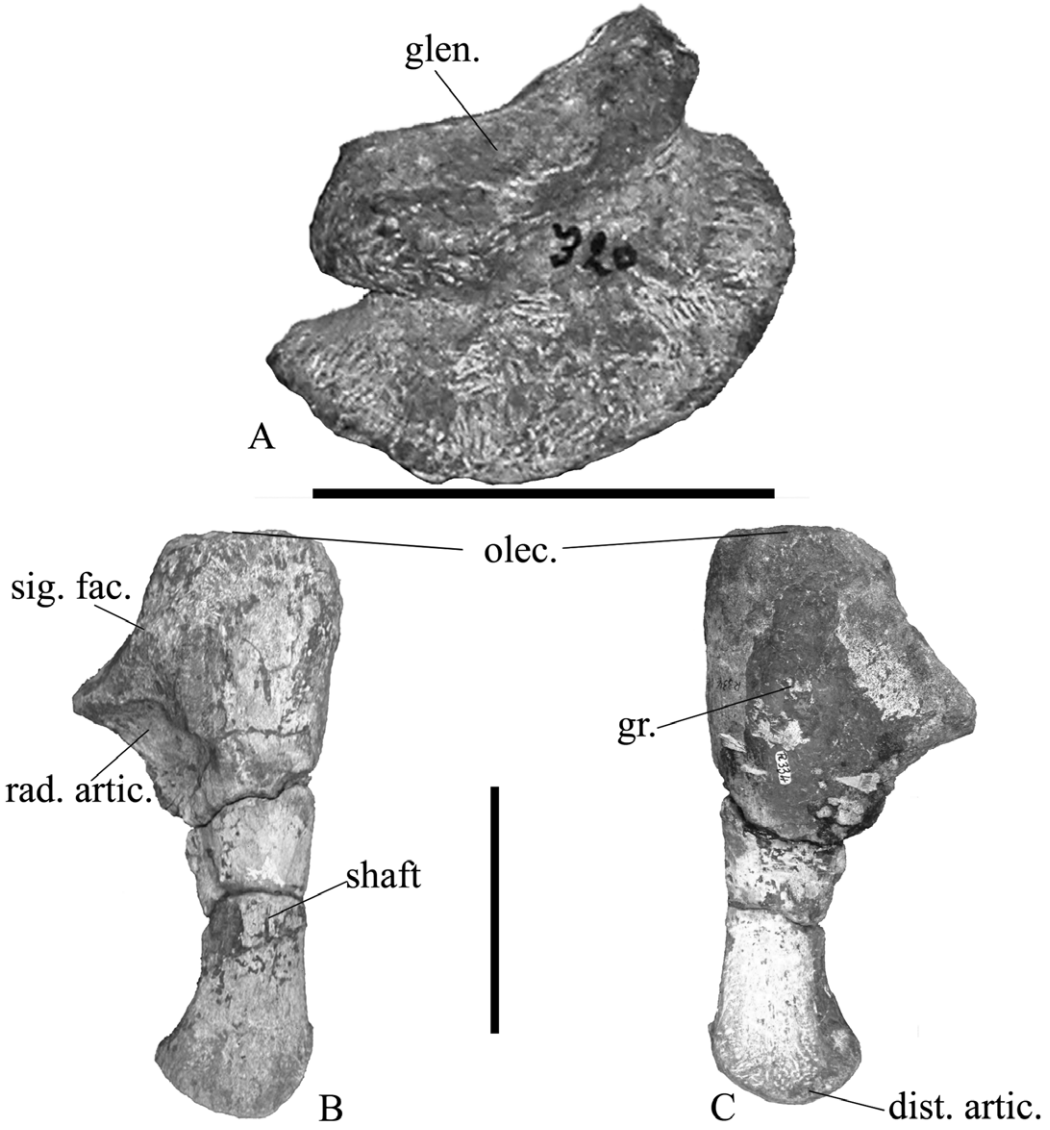

Figure 1. **A**, Lateral view of the coracoid (CGP/1/191B) of *Dolichuranus*. **B**, Lateral and **C**, medial view of the ulna (R334) of *Dolichuranus*. Scale = 10 cm

*primaevu*s. It consists of an ulna, radius and partial femur. The skull is now housed in the Council for Geosciences (CGP/1/711).

R320 consists of a tibia, fibula, coracoid and various bones of the foot. The skull (identified as *Dolichuranus primaevus*) associated with this material is catalogued as CPG/1/712.

R316 consists of incomplete material belonging to scapulae, humeri, an ilium that is fairly complete and a complete fibula. This specimen is provisionally identified as *Kannemeyeria lophorhinus.*

CGP/1/191A is a humerus belonging to a small individual. It is well preserved and has only been damaged along the dorsal border. It is tentatively identified as *Dolichuranus primaevus.*

CGP/1/191B is a small scapula. At least the proximal third of the scapula blade and the anterior border have been broken off. The bone is also broken along the plane where the distal end begins. It is tentatively identified as *Dolichuranus primaevus.*

CGP/1/412 is a second large humerus and was also used in these descriptions. It is tentatively identified as *Kannemeyeria lophorhinus.* Locality: Etjo South (Namibia).

DESCRIPTION OF THE POSTCRANIAL SPECIMENS

Dolichuranus primaevus

Pectoral girdle

Coracoid. The coracoid (R320) is small which would suggest that it belonged to a small individual (Fig. 1A). It is a complete, well-preserved bone. The glenoid articulation is a narrow, elongated oval that is wide posteriorly. Its articulating surface is concave in the middle and becomes convex posteriorly where it ends as a ridge. Below the glenoid there is a narrow groove (Fig. 1A). Distally the border of the coracoid is curved with a concave articulating surface that is divided in two: anterior one narrow and elongated and posteriorly a smaller rectangular, concave articulating surface. The medial surface is deeply concave.

Forelimb

Ulna. The complete left ulna of *Dolichuranus* is preserved in R334 (Fig. 1B,C). It is robust bone with a curved shaft. On the proximo-posterior border of the bone the surface forms a low wide flat surface. The surface is flat to slightly concave which would suggest that the olecranon was

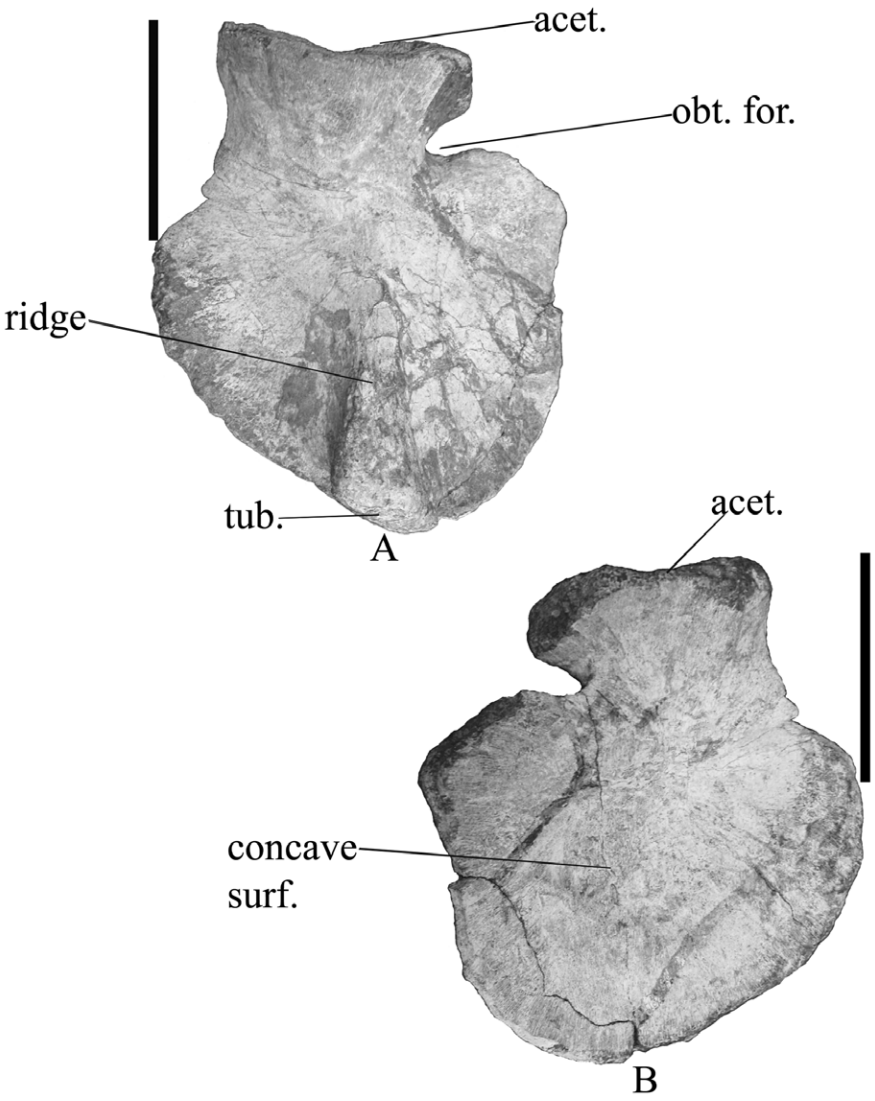

Figure 2. **A**, Lateral view and **B**, medial view of the ischium (BP/1/4578) of *Dolichuranus*. Scale = 10 cm.

most likely separately ossified. Anterior to the olecranon is the sigmoidal facet (Fig. 1B). It is directed anteriorly with an elongated, concave posterior face that is limited anteriorly by a thin ridge. The lateral face of the facet is convex and shorter than the posterior facet. It is directed laterally and its limit is demarcated by a thin ridge.

Posterior to this ridge there is a longitudinal groove that extends to the proximal end of the shaft. In front of the ridge there is an irregular oval radial facet with a deeply concave surface (Fig. 1B). The shaft is narrow with a concave anterior margin and an almost straight posterior border. Below the olecranon on the anterior surface there is a broad, concave groove that extends down the entire length of the bone to end just above the distal articulation. The distal articulation is a narrow oval with a convex surface.

Pelvic girdle

Ischium. The right ischium (BP/1/4578) is a teardrop-shaped bone that is almost completely preserved (Fig. 2). The acetabular facet forms an elongated oval that is fairly wide and more concave in the middle with raised and flat anteriorly and posteriorly. It is demarcated by a thin ridge. There is a short, fairly wide neck just below the acetabulum facet. In front of this neck there is an elongated, narrow groove that represents the posterior part of the obturator foramen. This would suggest that the obturator foramen is an elongated oval (Fig. 2A). A ridge that runs along the distal half of the bone has resulted in the anterior end of the bone being positioned at an angle to the posterior end. Laterally the surface of the bone is concavo-convex. The anterior two-thirds of the bone is flat to convex while the posterior third is narrow and concave (Fig. 2).

The ridge that is present on the distal half of the bone terminates at the distal end as a tubercle. This tubercle forms an elongated oval and is angled towards the posterior border of the bone. It is raised above the surface of the bone and narrows in the lateral direction. This surface becomes narrow laterally to form a ridge that projects up the bone to end halfway. It is on either side of this tubercle that the anterior and posterior ends of the bone are angled towards each other. Posteriorly the bone is less flared than the anterior and rises upward to form a thickened posterior end. Along the distal border of the ischium the surface is very rugose.

Medially the surface of the ischium is more deeply concave in the middle of the bone. The anterior and posterior parts of the bone become flattened (Fig. 2B).

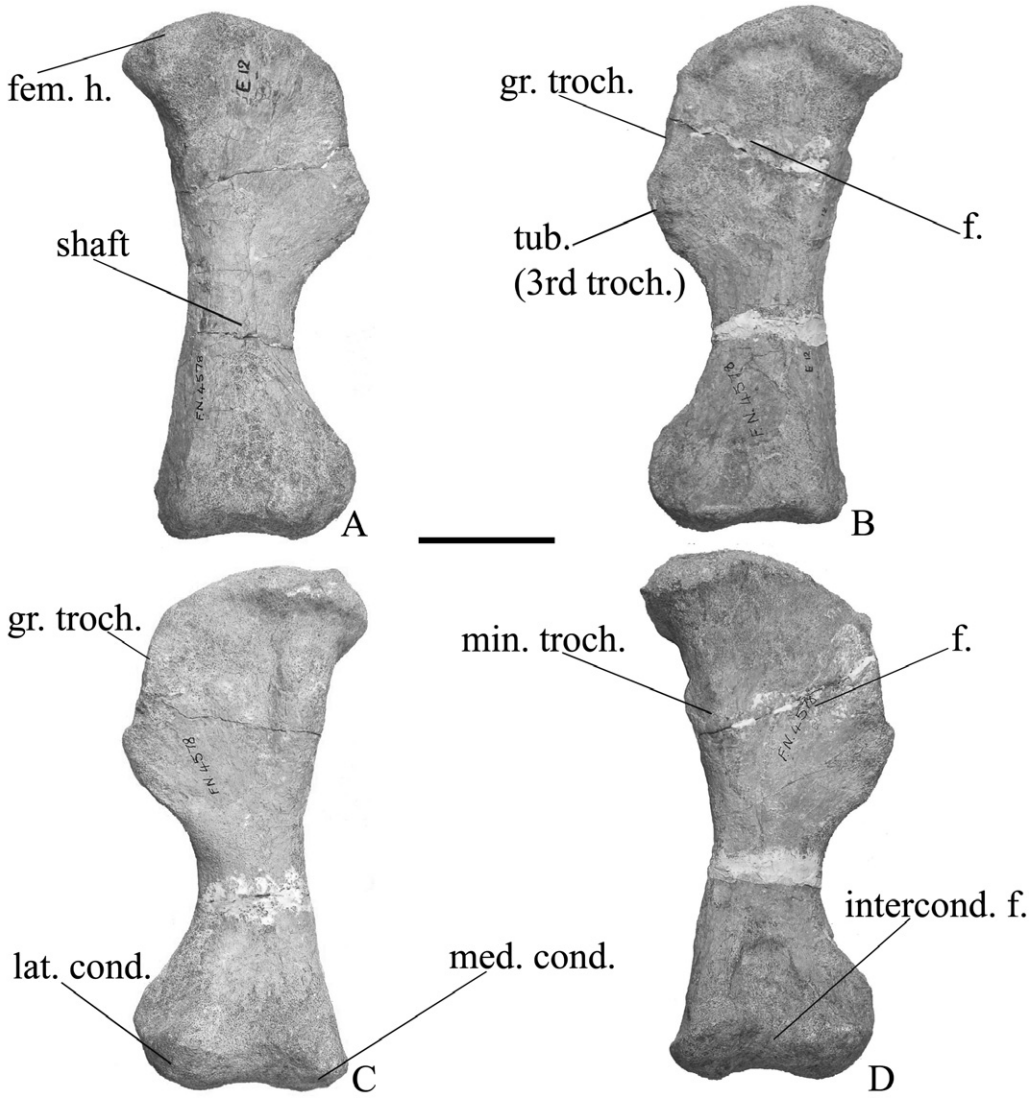

Figure 3. Left and right femora (BP/1/4578) of *Dolichuranus.* **A & B**, Dorsal view; **C & D**, ventral view. Scale = 10 cm.

Hindlimb

Femur. Both the left and right femora are preserved in BP/1/4578 and both are used to describe the femur (Fig. 3). The femur is dorso-ventrally flat, short and robust. It has a broad proximal expansion and a narrow distal expansion that is antero-posteriorly thicker than the proximal end. The medial border of the femur is thick and almost straight while the lateral border is concave.

The head of the femur overhangs the ventral surface slightly (Fig. 3C,D). When viewed from dorsally the head is triangular with the narrowest part facing laterally and it is not separated from the greater trochanter (Fig. 3A,B). Although the head of the femur is inflected medially, its articulating surface is directed dorsally. In front of the head is a very shallow, broad elliptical fossa that extends to below the greater trochanter (and the tubercle below it) to merge with the proximal end of the shaft.

Ventrally, below the head along the medial border, is an elongated tubercle which represents the minor trochanter (Fig. 3C,D). On the right femur the tubercle is divided in two with the posterior part higher than the anterior part. The posterior part of the tubercle is elongated and is separated from the anterior part by a very shallow groove. The anterior part of the tubercle is also elongated and narrow but it projects onto the anterior border. This tubercle is separated from the head by wide, shallow groove on the right femur. On the left femur the tubercle is not divided into two facets but there is a groove in the middle of the tubercle. The tubercle projects onto the medial border as a sharp ridge.

Anterior to the minor trochanter is a shallow fossa (Fig. 3C,D) that is broad and elliptical and is concave in the medial direction. Its lateral border is formed by the greater trochanter. The greater trochanter is short and dorso-ventrally broad, and its surface is reflected onto the dorsal and ventral surfaces of the right femur while on the left femur it is reflected onto the ventral surface and is twisted onto the border of the fossa on the dorsal surface. Below the great trochanter is another tubercle which represents the third trochanter that is separated from the greater trochanter by a thick ridge.

The distal end is medio-laterally narrow. A broad, concave groove passes from the distal end of the shaft in the lateral direction in front of the lateral condyle to end at the ventral border of the condyle. The lateral condyle is thicker than the medial condyle and the articulating surfaces of the condyles are directed ventrally and project only slightly onto the ventral surface (Fig. 3). Although the

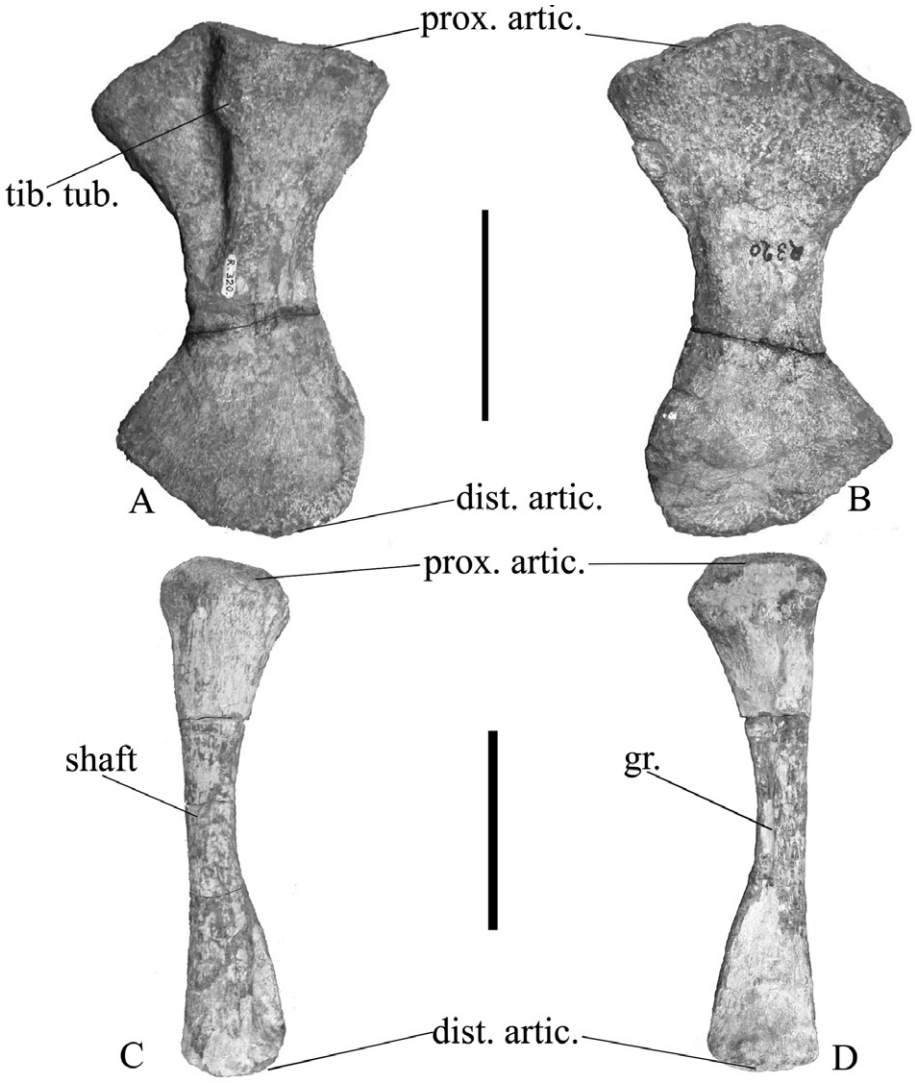

Figure 4. **A**, Anterior view and **B**, posterior view of the tibia (R320); **C**, anterior and **D**, posterior view of the fibula (BP/1/4578) of *Dolichuranus*. Scale = 10 cm.

lateral condyle's articulating surface is bigger than that of the medial condyle it ends at the same level as the medial condyle in the ventral direction. Along the ventral border the condyles are separated by a broad, shallow groove and on the ventral surface by the intercondylar fossa. On the left femur the almost circular intercondylar fossa is much shallower than the right fossa. The medial condyle is skewed in the proximo-anterior direction with a flat surface. The posterior condyle reaches the proximal end of the articulating facet, which is situated slightly below a ridge. On the left femur it is almost rectangular and is convex with the middle of the surface being concave. The articulating facet is narrow and slightly below the ridge (ridge of the condyles starts at its distal end) on the right femur and is not very convex.

Distally there is a very shallow triangular fossa (popliteal fossa) between the condyles on the dorsal surface (Fig. 3A, B). On the posterior border of the lateral condyle there is another very shallow, narrow fossa that has a concave surface that extends onto the surface of the lateral condyle. The articulating surface of the condyles does not extend onto the dorsal surface.

There is a fossa on the medial margin of the medial condyle. The fossa extends from the edge of the articulating surface onto the medial border of the right femur and has an irregular edge marked by a low sharp ridge. It has a concave surface with the deepest part closer to the articulating surface separated from the rest of the fossa by a ridge. On the left the fossa's distal end is located at the proximal edge of the medial condyle. The fossa is oblong with the deepest part distally and is located on the dorsal margin of the femur.

Tibia. The tibia (R320) is short and robust, and has suffered some damage (Fig. 4A,B). Distally the bone is distorted in the antero-posterior direction giving it a flattened appearance. Proximally the tibia appears to have a natural triangular shape which most likely has been exaggerated by flattening in an antero-posterior direction (Fig. 4A). When viewed anteriorly the middle of the proximal expansion projects above the rest of the bone. The tibial tubercle is prominent with an oval shape. Lateral to the tubercle is a broad concave groove that narrows to end on the shaft. It is limited by a narrow ridge medially. The shaft is narrow and short with slightly concave lateral and medial borders.

Distally the appearance of the tibia is possibly as a result of distortion which has resulted in it being widely expanded (Fig. 4A,B). Posteriorly the surface of the bone is almost

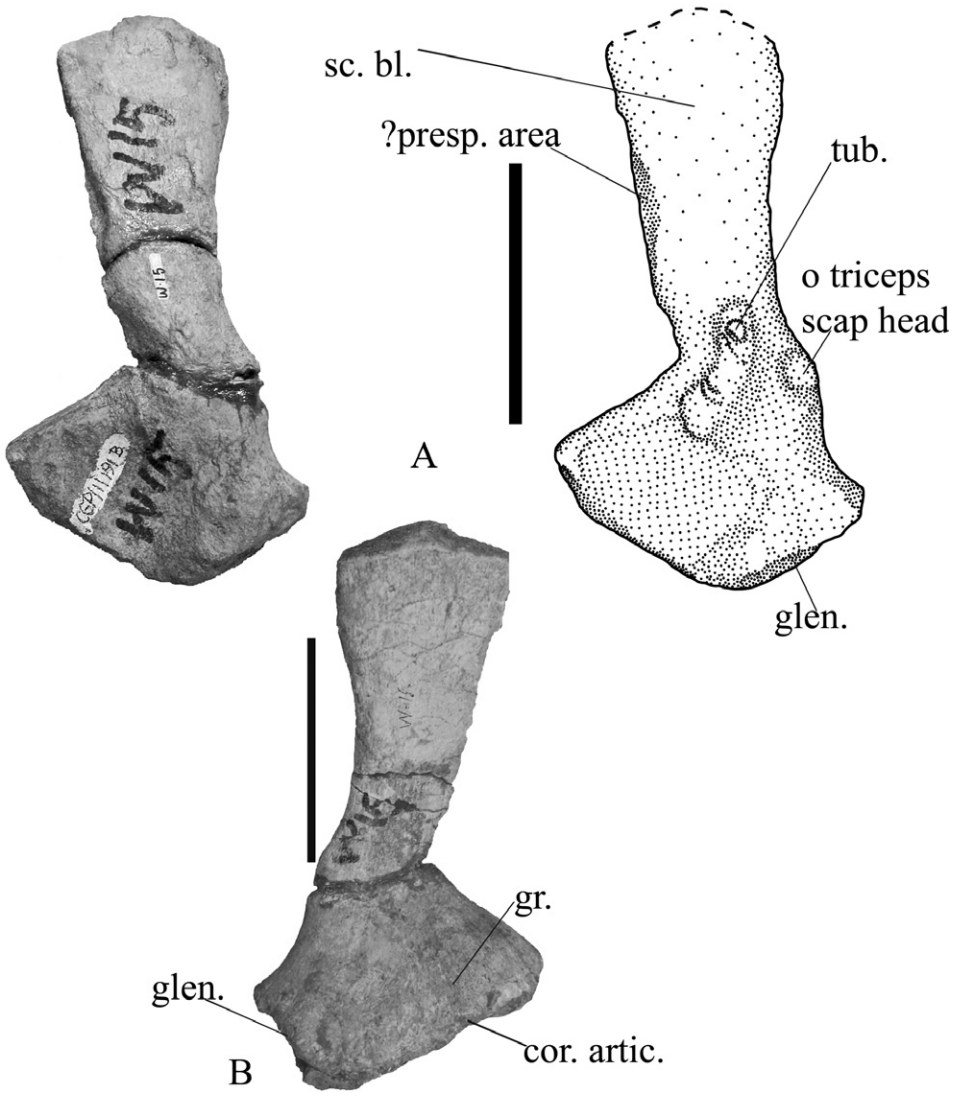

Figure 5. **A**, Lateral view and **B**, medial view of the scapula (CGP/1/191B) *cf. Dolichuranus.* Scale = 10 cm.

featureless except for a broad concave groove that extends down the entire length of the bone from just below the proximal articulation.

The proximal articulation is made up of two facets: a triangular medial facet and a narrow elongated oval lateral one. Both have concave surfaces that slope anteriorly.

Fibula. The fibula (BP/1/4578) of *Dolichuranus* is a slightly curved, gracile bone with slightly expanded ends. In anterior view the proximal expansion is slightly larger than the distal one (Fig. 4C,D). The proximal expansion is antero-posteriorly flattened while the distal expansion is antero-posteriorly thicker.

Proximally the articulating surface is oblong and convex (BP/1/4578) and slopes posteriorly becoming concave. It is demarcated by a broad rugose ridge. Just below this ridge the surface of the bone is rugose (Fig. 4C,D). Along the medial border there is a shallow elongated fossa. Below this fossa the bone surface is raised. From the proximal end the bone narrows to form the shaft. It is long and slender with a straight lateral and concave medial one (Fig. 4C,D). Distally the articulating surface is slightly convex and almost circular. This surface is demarcated by a thin ridge. Above the distal articulating surface there is a fossa along the medial border. This fossa is also surrounded by rugose bone surface.

In posterior view the surface of the proximal expansion is concave and extends to the proximal end of the shaft (R320; BP/1/4578) (Fig. 4D). A fairly deep groove passes down the bone along the medial border. Posteriorly it is demarcated by a narrow, flat ridge that is positioned towards the lateral border. This groove appears to be restricted to the shaft of the fibula.

cf. Dolichuranus primaevus

This material cannot be referred to *Dolichuranus primaevus* with certainty since the remains were not associated with any other diagnostic material. However, they differ significantly from the equivalent bones referred to *Kannemeyeria lophorhinus* and there is no evidence for a third dicynodont species in the Omingonde Formation.

Pectoral girdle

Scapula. The scapula blade (CGP/1/191B; Fig. 5) is convex laterally, antero-posteriorly narrow and the dorsal portion is angled anteriorly. Along the anterior margin of the scapula the bone is damaged proximally and appears to be incomplete (Fig. 5A). Although the anterior margin

has been damaged there is a concave area that could represent a prespinous region. Preservation suggests that the anterior margin of the scapula is complete at the level of the acromion and that there is no acromion process present on this specimen; however, at the level where one would expect to find the acromion a tubercle is present on the lateral surface. The tubercle is directed diagonally towards the posterior border and is distinctly separated from the anterior margin (Fig. 5A). The tubercle is narrow proximally and becomes wide ventrally (Fig. 5A). Near the ventral end of the tubercle is a round prominent projection. In front of the tubercle the surface is curved and slightly concave with a slightly rugose surface. The posterior border is concave and becomes convex proximally.

Approximately one-third of the way from the dorsal border is a narrow, convex tubercle. Towards the lateral surface of the posterior border is an elongated oval tubercle that has been damaged distally and which represents the origin of the scapula head of triceps. Behind this tubercle the posterior border becomes flat and it becomes narrow towards the glenoid facet. A thick, broad ridge marks the dorsal border of the glenoid facet on the lateral surface.

Ventrally the scapula is broad and is medio-laterally flattened (Fig. 5B). The ventral end thins in the anterior direction and the lateral surface is concave below the tubercle on the lateral surface at the level of the acromion. Posteriorly, on the ventral end, is the glenoid facet. The glenoid is almost round and flattened along the medial border and faces postero-ventrally (Fig. 5). The bone is medio-laterally flattened so that the coracoid articulation is wide, concave and oblong and makes up most of the ventral articulating surface than the glenoid facet. The shape of the damaged surface at the anterior tip of the distal end suggests the possible presence of a triangular tubercle.

The medial surface of the scapula blade is concave in an anterior direction and is narrowest just above the beginning of the distal end. Just above the distal end of the scapula is an elongated, concave area. On the distal end a shallow, broad groove is positioned on the medial surface of the anterior coracoid facet (Fig. 5B). The groove is more or less in the middle of the articulation and extends along the entire distal expansion. Both the coracoid and the glenoid articulations are directed ventrally.

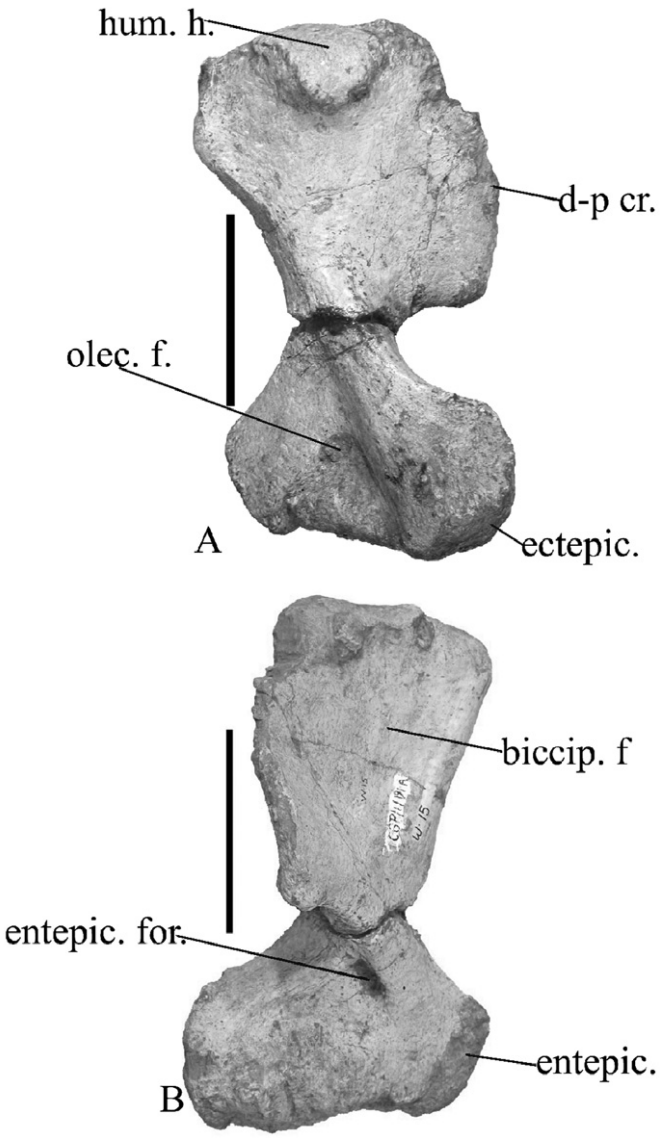

Figure 6. Dorsal view **A**, CGP/1/412; **B**, CGP/1/191A and ventral view **C**, CGP/1/412 and **D**, CGP/1/191A of the humerus *cf. Dolichuranus*. Scale = 10 cm.

Forelimb

Humerus. The proximal expansion of the humerus is narrower than the distal expansion in CGP/1/191A (Fig. 6). Proximally the expansion is antero-posteriorly is flatter and much thinner in CGP/1/191A (Fig. 6B). The proximal expansion is rounded and oblong and narrows marginally towards the shaft. In CGP/1/191A the head is positioned closer to the middle of the dorsal border. The almost triangular head of CGP/1/191A overhangs the dorsal surface to a greater degree than the ventral surface (Fig. 6A,B). Its articulating surface is directed dorsally in CGP/1/191A but also extends onto the dorsal surface of the humerus. The surface along the entire dorsal border including the head is rugose and pitted, which suggests that the surface was covered by cartilage in life (Fig. 6A,B). Posteriorly, below the dorsal border is an elongated tubercle that is visible from the dorsal and posterior views. Anteriorly and posteriorly the head is bordered by a groove with the posterior one much deeper.

Anteriorly the proximal expansion grades into the delto-pectoral crest. The delto-pectoral crest is directed anteriorly with the distal end directed medially. It is plate-like in CGP/1/191A (Fig. 6B,D) with the proximal and distal parts of the anterior border thickened. The delto-pectoral crest is directed anteriorly (Fig. 6A, B).

The anterior border of the delto-pectoral crest is thin along its entire length (CGP/1/191A ; Fig. 6B,D). Distally the delto-pectoral crest is twisted towards the biccipital fossa. The anterior surface delto-pectoral crest extends onto the dorsal surface but is limited by a ridge on the ventral surface. Below the distal end of the delto-pectoral crest on the anterior border is a narrow, elongated oval tubercle. Along the anterior surface is the entepicondylar ridge. Posterior to this ridge is the opening of the entepicondylar foramen, which has an oval opening in the large

individual and an elongated almost oblong opening in the smaller specimen.

The shaft in both individuals is short and thick. There is a distinct difference in the degree of the offset between the proximal and distal ends of the humerus. In CGP/1/191A this offset results in the ectepicondyle being directed antero-dorsally.

The distal end when viewed anteriorly is triangular, broad and thin antero-posteriorly (Fig. 6). In front of the entepicondyle ridge the surface slopes towards the ventral surface and is concave towards the ventral border. The articulation for the radius and ulna is narrow and is closer to the ectepicondyle. A triangular facet is present for articulation with the ulna. Its surface is convex proximally and becomes concave towards the ventral border. The radial facet is much smaller and is closer to the ventral border with a slightly concave surface.

In ventral view the head projects only slightly above the proximal surface. Proximally the postero-ventral 'corner' of the bone forms a thick, round border. In front of this border is an elongated tubercle that is broad proximally and narrows distally. Below the tubercle is a wide ridge that narrows where it merges with the shaft. The biccipital fossa is directed towards the delto-pectoral crest and is concave in that direction (Fig. 6). A groove starts below the biccipital fossa and ends above the entepicondylar foramen. The ventral opening of the entepicondylar foramen is oval.

The distal expansion is flared. A shallow, triangular olecranon fossa is present with thick ridges on the entepicondyle and ectepicondyle (Fig. 6C,D). The posterior border is concave below the dorsal border, while the dorsal border is dorso-ventrally thick and rounded, and it projects beyond the posterior surface. Below this the border thins towards the entepicondyle where it is very thin. In front of the dorsal projection the surface is deeply concave.

The ectepicondyle is round with a convex surface that projects dorsally. It is thicker than the entepicondyle but is proximo-distally narrower than the entepicondyle in anterior view. The ectepicondyle is lower than the entepicondyle and in CGP/1/191A it is evident that the direction of growth is antero-ventrally. The entepicondyle is proximo-distally broad and antero-ventrally thin in anterior view (Fig. 6A,B). In ventral view the articulating surface of the entepicondyle is elongated and convex, and is raised slightly above the rest of the entepicondyle in the small individual. The surface is the same in the larger individual except that it is broader proximally.

cf. Kannemeyeria lophorhinus

R316 is provisionally referred to *Kannemeyeria lophorhinus* on the basis that it shares characters with *Kannemeyeria simocephalus,* such as the presence of an acromion process and a relatively broad, straight-sided scapula blade that are not present in *cf. Dolichuranus primaevus.*

Pectoral girdle

Scapula. There are three scapulae present in R316. The left scapula is complete whereas the right one consists of two pieces (Fig. 7) while a third consist only of the proximal end of the scapula. There are also a number of fragments which represent various parts of the scapula. On the lateral surface the left scapula has been flattened so that it has a fan-shaped appearance dorsally; however, the right one has not been distorted, showing that the dorsal border is only slightly expanded and that its surface is more convex in the middle. In all the scapulae (R316) the anterior margin of the dorsal border is rounded. Just below the dorsal border the lateral surface is slightly concave. The scapula blade is fairly wide along its entire length as seen in the left scapula (Fig. 7).

About a third of the way down the anterior margin marks the beginning of the scapula spine. It is does not project far anteriorly and is not very prominent. Although the anterior border is damaged it is most likely that the spine ends at the proximal end of the acromion process (Fig. 7A,C). In all examples the acromion is broken off at the base which indicates that it is possible that the acromion was directed antero-laterally when present.

Below the acromion the bone narrows to form the distal end. Anteriorly the articulation for the coracoid is directed antero-ventrally in both the left and right scapula (Fig. 7A, C). The glenoid is directed slightly postero-ventrally with the medial wall slightly lower than the lateral which gives the oval articulating surface the appearance of facing laterally. Along the anterior margin of the glenoid there is a very small round projection.

Proximo-medially the surface is concave (Fig. 7B,D). Along the anterior border there is evidence of a very narrow concave prespinous region that possibly widens as it reaches the acromion. There is no evidence that either a tubercle or a fossa is present at the proximo-posterior border of the acromion's medial surface; however, from the posterior border of the acromion there is a groove that extend along the medial surface of the coracoid articulation to its ventral extent (Fig. 7B,D).

Forelimb

Humerus. The right humerus (R316) consists of proximal and distal ends which do not necessarily belong to the same individual while the left humerus (R316) consists of a complete bone from below the delto-pectoral crest (Fig. 8). It is possible that part of the right humerus actually represents a smaller individual (Fig. 8A,C). The delto-pectoral crest has not been preserved in proximal expansion of the right humerus. The distal end is almost completely preserved and fairly widely expanded.

On the left humerus (R316) the proximal expansion has been almost completely damaged with only the distal end of the delto-pectoral crest preserved (Fig. 8B,D). From this fragment we can deduce that the delto-pectoral crest was broad (Fig. 8D). In dorsal view it can be seen that at least the distal end of the delto-pectoral crest is twisted so that it faces antero-medially.

Although the dorsal margin of the right humerus (R316) has not been completely prepared it is evident that the head of the bone forms an inverted triangle and is located close to the posterior border of the delto-pectoral crest with a more dorsally directed articulating surface

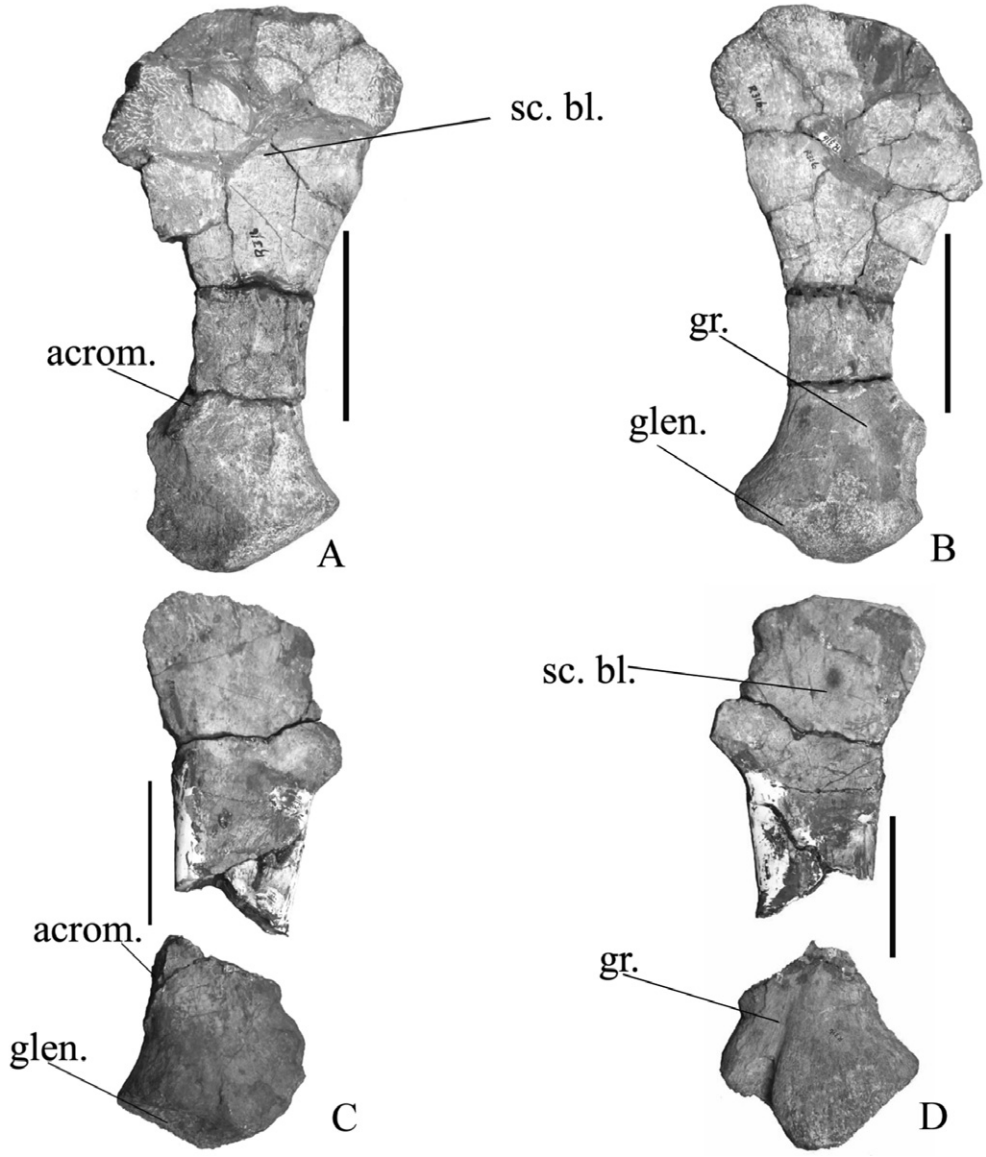

Figure 7. **A**, Lateral and **B**, medial view of the left; **C**, lateral and **D**, medial of right scapula (R316) *cf. Kannemeyeria lophorhinus.* Scale = 10 cm.

(Fig. 8A). Proximally along the posterior border of the narrow proximal expansion is a low elongated tubercle.

The head of the right humerus (R316) has not been prepared but it can be seen that the head of the bone is close to the posterior border of the delto-pectoral crest. It forms an inverted triangle but the articulating surface is directed more dorsally. The delto-pectoral crest is not preserved in this specimen but its dorsal and ventral extents are clearly visible.

Distally the humerus is widely expanded in both the left and right humeri (R316) with a wide triangular shallow olecranon fossa. The rounded ectepicondyle is larger than the entepicondyle and is raised above the dorsal surface (Fig. 8).

The biccipital fossa is incomplete on the left humerus while the right humerus (R316) it forms a narrow triangle with a concave surface (Fig. 8C,D). It narrows distally as it merges with the shaft. Distally the entepicondylar foramen forms a narrow oval slit that runs diagonally across the bone. The articulation for the ulna and the radius forms a concavo-convex surface with the radius articulation being more convex than the ulna articulation.

Pelvic girdle

Ilium. The ilia are represented by a number fragments and a single incomplete right ilium (R316; Fig. 9A). It has an incomplete anterior process while the posterior process and most of the posterior part of the iliac blade are missing. The incomplete anterior end is fairly wide and higher than the posterior process and is directed slightly laterally (Fig. 9A). Distally the blade narrows to form a short neck that grades to a short, wide acetabular (superior) ridge.

A circular acetabulum is present with incisures present along the anterior and posterior (supra-acetabular notch) margins of the lateral border. The articulating surface faces more ventrally and very slightly laterally. In front of the acetabulum the articulation for the pubis is higher and medio-laterally wider than that for the ischium (Fig. 9A).

Hindlimb

Fibula. There is a well-preserved right fibula that forms part of R316 (Fig. 9B,C). Proximally and distally the expansions are not widely expanded and are joined by a narrow shaft which is fairly straight but is curved along its medial

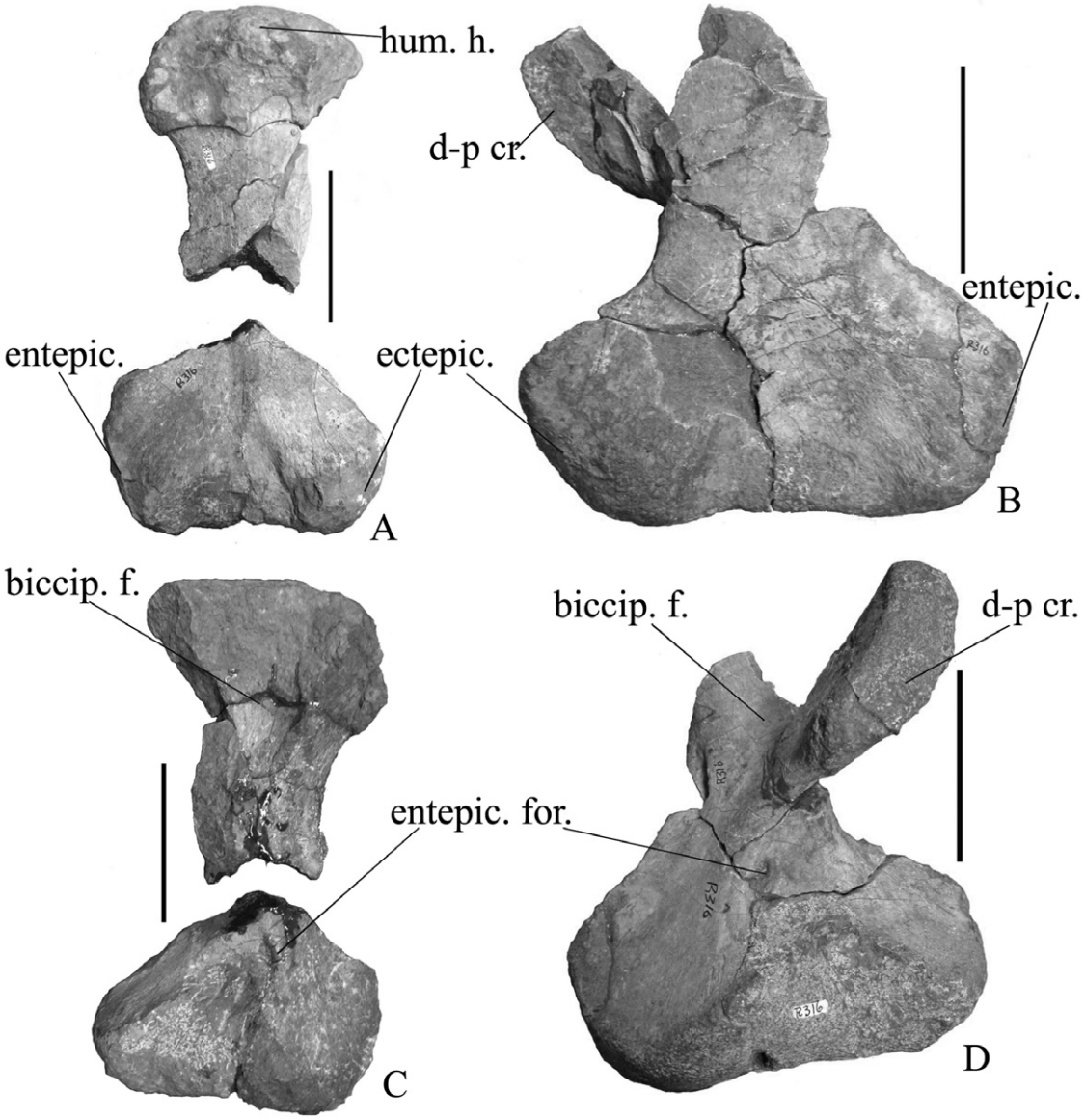

Figure 8. Dorsal view **A**, right and **B**, left and ventral view of **C**, right and **D**, left humerus (R316) *cf. Kannemeyeria lophorhinus*. Scale = 10 cm.

border. A ridge runs along the medial border on the anterior surface and becomes less distinct distally. On the posterior surface the proximal expansion is concave (Fig. 9C). A groove runs down the shaft along the medial border and it becomes wide distally. The proximal articulation is oval with a convex articulating surface that slopes medially while the distal articulation is a narrow, elongated oval with a flat to slightly convex surface.

Dicynodontia *incertae sedis*

Humerus. There is a complete humerus associated with CGP CGP/1/191A. A comparison shows that these two bones are different. It does, however, seem to share some similarities with the partial humeri currently identified as *Kannemeyeria lophorhinus.*

The proximal expansion of the humerus is narrower than the distal expansion in CGP/1/412 (Fig. 6A). Proximally the expansion is antero-posteriorly narrow in CGP/1/412 (Fig. 6A). The proximal expansion is rounded and oblong and narrows marginally towards the shaft. In CGP/1/412 the head is hemispherical and its articulating surface is directed more dorsally. The surface along the entire dorsal border including the head is rugose and pitted, which suggests that the surface was covered by cartilage in life (Fig. 6A). Posteriorly, below the dorsal border is an elongated tubercle that is visible from the dorsal and posterior views. Anteriorly and posteriorly the head is bordered by a groove with the posterior one much deeper.

Anteriorly the proximal expansion grades into the delto-pectoral crest. The delto-pectoral crest is directed anteriorly with the distal end directed medially. It is plate-like to crescent-shaped in CGP/1/412 (Fig. 6A).

The anterior border of the delto-pectoral crest is thick distally with the thickest part in the middle in CGP/1/412 (Fig. 6A). In CGP/1/412 only proximo-posterior part of the biccipital fossa is visible when viewed anteriorly. Distally the delto-pectoral crest is twisted towards the biccipital fossa. The anterior surface delto-pectoral crest extends onto the dorsal surface but is limited by a ridge on the ventral surface. Below the distal end of the delto-pectoral crest on the anterior border is a narrow, elongated oval tubercle. Along the anterior surface is the entepicondylar ridge. Posterior to this ridge is the opening of the

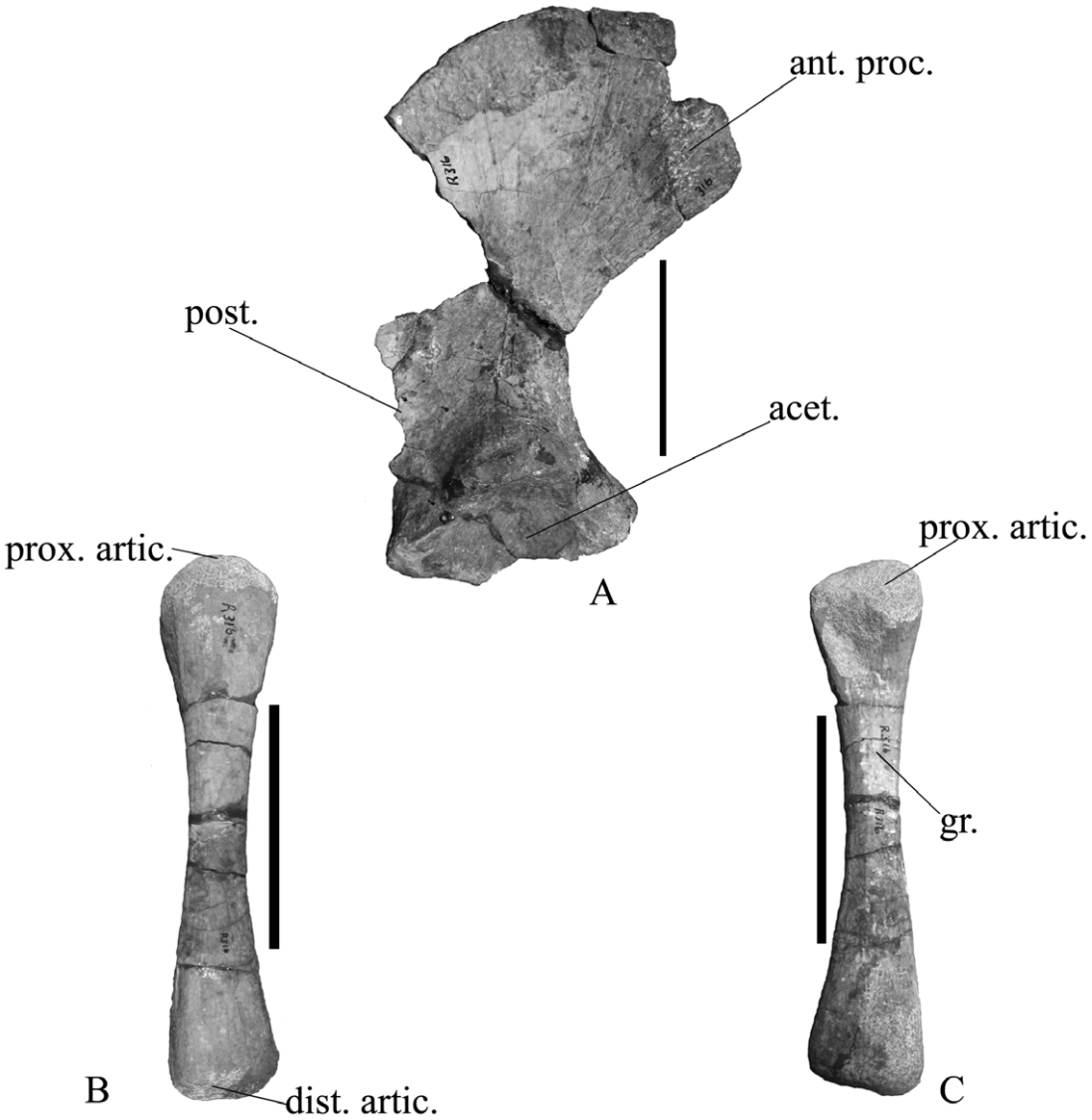

Figure 9. **A**, Lateral view of the right ilium (R316); **B**, anterior view and **C**, posterior view of the fibula (R316) *cf. Kannemeyeria lophorhinus*. Scale = 10 cm.

entepicondylar foramen, which has an oval opening in the large individual and an elongated almost oblong opening in the smaller specimen.

The shaft is short and thick. There is a distinct degree of the offset between the proximal and distal ends of the humerus which results in the ectepicondyle being directed dorsally.

The distal end when viewed anteriorly is triangular, broad and thin antero-posteriorly (Fig. 6A). In front of the entepicondyle ridge the surface slopes towards the ventral surface and is concave towards the ventral border. The articulation for the radius and ulna is narrow and is closer to the ectepicondyle. A triangular facet is present for articulation with the ulna. Its surface is convex proximally and becomes concave towards the ventral border. The radial facet is much smaller and is closer to the ventral border with a slightly concave surface.

In ventral view the head projects only slightly above the proximal surface. Proximally the postero-ventral 'corner' of the bone forms a thick, round border. In front of this border is an elongated tubercle that is broad proximally and narrows distally. Below the tubercle is a wide ridge that narrows where it merges with the shaft. The biccipital fossa is antero-posteriorly narrow, which has resulted in the fossa being deep in CGP/1/412 (Fig. 6A). A groove starts below the biccipital fossa and ends above the entepicondylar foramen. The ventral opening of the entepicondylar foramen is oval.

In CGP/1/412 the distal end faces slightly more posteriorly and the distal expansion is flared. A shallow, triangular olecranon fossa is present with thick ridges on the entepicondyle and ectepicondyle (Fig. 6A). The posterior border is concave below the dorsal border, while the dorsal border is dorso-ventrally thick and rounded, and it projects beyond the posterior surface. Below this the border thins towards the entepicondyle where it is very thin. In front of the dorsal projection the surface is deeply concave.

The ectepicondyle is round with a convex surface that projects dorsally. It is thicker than the entepicondyle but is proximo-distally narrower than the entepicondyle in anterior view. The entepicondyle is proximo-distally broad and antero-ventrally thin in anterior view (Fig. 6A, B). In ventral view the articulating surface of the entepicondyle is elongated and convex, and is raised slightly above the rest of the entepicondyle in the small individual.

The surface is the same in the larger individual except that it is broader proximally.

PHYLOGENETIC ANALYSIS

We examined the phylogenetic position of *Dolichuranus* by including the new postcranial data for *Dolichuranus* in a cladistic analysis. Only postcranial characters that could be positively ascribed to *Dolichuranus* were scored, characters of the scapula and humerus were not scored. A broad range of Triassic dicynodonts were included in this analysis (*Lystrosaurus, Shansiodon, Tetragonias, Kannemeyeria, Wadiasaurus, Rechnisaurus, Dolichuranus, Sinokannemeyeria, Parakannemeyeria, Dinodontosaurus, Placerias, Ischigualastia, Jachaleria, Angonisaurus, Stahleckeria* and '*Kannemeyeria*' *argentinensis*). An unnamed enigmatic form known only from postcranial remains from the late Early Triassic of South Africa ('morphotype B') was also included. The Triassic emydopoids *Myosaurus* and *Kombuisia* were excluded because their relationships are distant from these taxa (Angielcyzk & Kurkin 2003). The Permian *Vivaxosaurus* was included because it has been shown that it is more closely related to *Kannemeyeria* than *Lystrosaurus* (Angielczyk & Kurkin 2003). *Aulacephalodon* and *Dicynodon* (based on *D. trigonocephalus*) were employed as outgroups bringing the total number of taxa in the data matrix to 20. Characters were obtained (with some modifications) from the following sources: Damiani *et al.* (2007), Surkov *et al.* (2005), Vega Dias *et al.* (2004), Surkov & Benton (2004), Angielczyk & Kurkin (2003), Maisch (2000, 2002). All informative characters from these references were included as well as seven new characters of the postcrania, bringing the total number of characters to 85 (Appendix 1). Four of the multistate characters (10, 15, 16 and 54) represent sequential transformation series and are treated as ordered (additive). All characters were equally weighted. The authors have not had an opportunity to examine many of the relevant specimens and so have relied heavily upon the literature for character scores and for this reason the analysis should be viewed as preliminary.

The data matrix (Appendix 2) was analysed using T.N.T 1.1 (Goloboff *et al.* 2003) with the following search parameters: a traditional search using Wagner trees as the starting trees, with 100 addition sequence replicates, tree bisection reconnection was used as the swapping algorithm, saving 10 trees per replication.

The search found a single most parsimonious tree with a length of 269 steps (Fig. 10A). The tree does not represent a robust hypothesis as can be seen by the very low Bremer support values for all of the internal nodes, except *Shansiodon* + *Tetragonius* (Fig. 10B). Bootstrap values are similarly low with only two clades having a frequency of more than 50%. These are *Shansiodon* + *Tetragonius* (83%) and *Parakannemeyeria* + *Sinokannemeyeria* (52%), which is a clade that is not present in the MPT. These results indicate that a more thorough investigation of kannemeyeriiform relationships is required. Nevertheless the data are sufficient to highlight the influence that postcranial characters have for analyses of Triassic dicynodont relationships. If the postcranial data for *Dolichuranus* are excluded from the analysis a single most parsimonious tree of 267 steps results. In this tree *Dolichuranus* no longer attracts morphotype B to the Sinokannemeyeriidae which instead forms a sistergroup relationship with *Placerias,* inside the Stahleckeriidae (Fig. 11). *Dolichuranus* still nests within the Sinokannemeyeriidae, but the ancestral state reconstructions are sufficiently changed to cause the Permian *Vivaxosaurus* to nest above the Shansiodontidae as the sister-group of a clade containing *Kannemeyeria, Wadiasaurus,* Sinokannemeyeriidae and Stahleckeriidae.

DISCUSSION

In the Triassic sediments of Namibia there are two medium to large dicynodonts, namely *Dolichuranus primaevus* and *Kannemeyeria lophorhinus.* The cranial material that belongs to these taxa have been described and studied in detail (e.g. Renaut 2000; Diamiani *et al.* 2007). This study examined the postcranial material from the same unit. Unfortunately some of the postcranial material was not associated with cranial material and therefore it is not possible to definitively identify this material.

Nevertheless two scapula morphologies can be recognized and these are tentatively identified as the belonging to the two species based on cranial material. The scapula blade morph ascribed to *Dolichuranus primaevus* (exemplified by CGP/1/191B) is distinctly narrower and has a more strongly curved anterior border than that ascribed to *Kannemeyeria lophorhinus* (exemplified by R316). CGP/1/191B is also unusual in that the acromion is absent: a derived condition shared with some stahleckeriids (e.g. *Ischigualastia*; Cox 1965). In contrast R316 has an acromion and a relatively broader prespinous region to support it. CGP/1/191B shares a narrow prespinous region and a scapula spine that does not project anteriorly with the enigmatic 'morphotype B' from the *Cynognathus* subzone B of the main Karoo Basin. Morphotype B co-occurs with *Kannemeyeria simocephalus* but is known only from postcranial remains at the present time (Govender 2006; Govender & Yates, submitted). However, morphotype B retains an acromion that is not present in CGP/1/191B. Like advanced sinokannemeyeriids and morphotype B the length of the scapula of CGP/1/191B is greater than three times the width of scapula at the acromion. Similarly the humerus provisionally referred to *Dolichuranus* (CG/1/191A) shares a delto-pectoral crest set at an angle to the humeral shaft with *Sinokannemeyeria* and *Parakannemeyeria* (Sun *et al.* 1963).

The larger of the two humeri (CGP/1/412) tentatively referred to *Kannemeyeria lophorhinus* has an arc-shaped deltopectoral crest which is a derived condition shared with *Zambiasaurus* (Cox 1969; R9068; R9069), *Angonisaurus* (Cox & Li 1983; U12/1) and morphotype B. In contrast the smaller humerus (CG/1/191A) is more rectangular similar to the general kannemeyeriiforme condition (e.g. *Kannemeyeria simocephalus*; Govender 2006; Govender *et al.* 2008). The humeral head also differs between these two specimens with CG/1/412 having an antero-posteriorly expanded, hemispherical head, whereas it is less expanded and sub-triangular in CG/1/191A. These differences may be ontogenetic, but further specimens

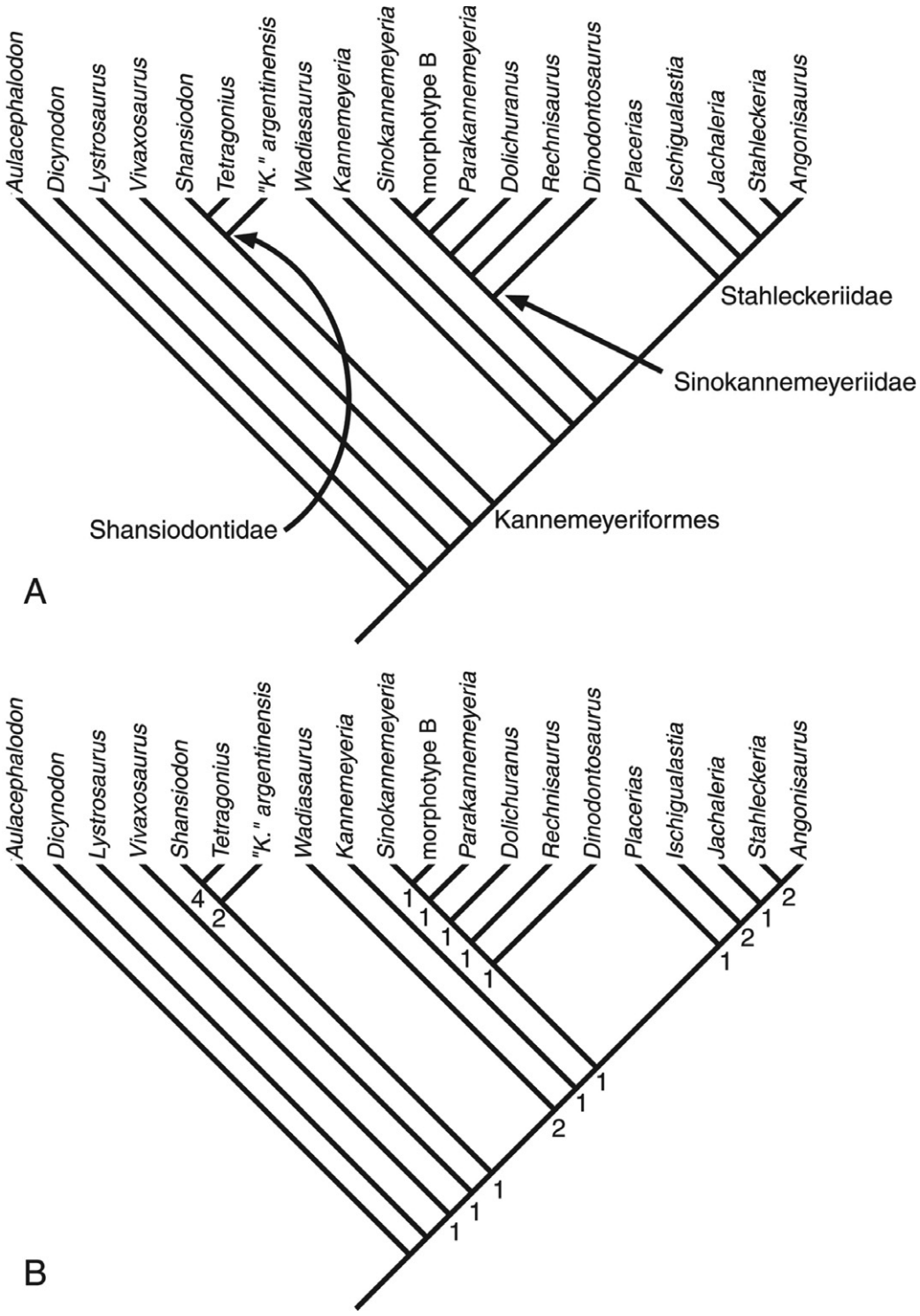

Figure 10. Single most parsimonious tree found resulting from an analysis of kannemeyeriiforme dicynodont relationships (20 terminal taxa; 85 characters). Tree has a length of 269 steps. **A**, Tree labelled with named clades; **B**, tree labelled with Bremer support values.

associated with diagnostic material are required to rule out individual variation or taxonomic mixing.

The olecranon of the ulna of *Dolichuranus* (R334) is similarly low and broad like that of *Zambiasaurus* (R9098), *Parakannemeyeria* (Sun, 1963) and morphotype B, further reinforcing a relationship with sinokannemeyeriids.

The proximal and distal expansions of the femur of *Dolichuranus* (BP/1/4578; R320) are not widely expanded as seen in *Kannemeyeria* (Govender *et al.* 2008), *Zambiasaurus* (R9118), *Ischigualastia* (Cox, 1965) and *Placerias* (Camp & Welles, 1956). Like most Triassic dicynodonts the femoral head is directed dorsally but is not offset from the rest of the bone as seen stahleckeriids (Camp & Welles 1956; Cox 1965), derived sinokannemeyeriids (Sun 1960, 1963; Young 1937) and morphotype B. The fibula (R316) does not conform to *K. simocephalus* but rather resembles that of morphotype B in that it is has slightly expanded ends with an almost straight shaft.

The specimen R316 does not resemble the other specimens from the Omingonde but tends to resemble that of *K. simocephalus,* supporting its referral to *K. lophorhinus.* The scapula blade is fairly straight, slightly wide and the

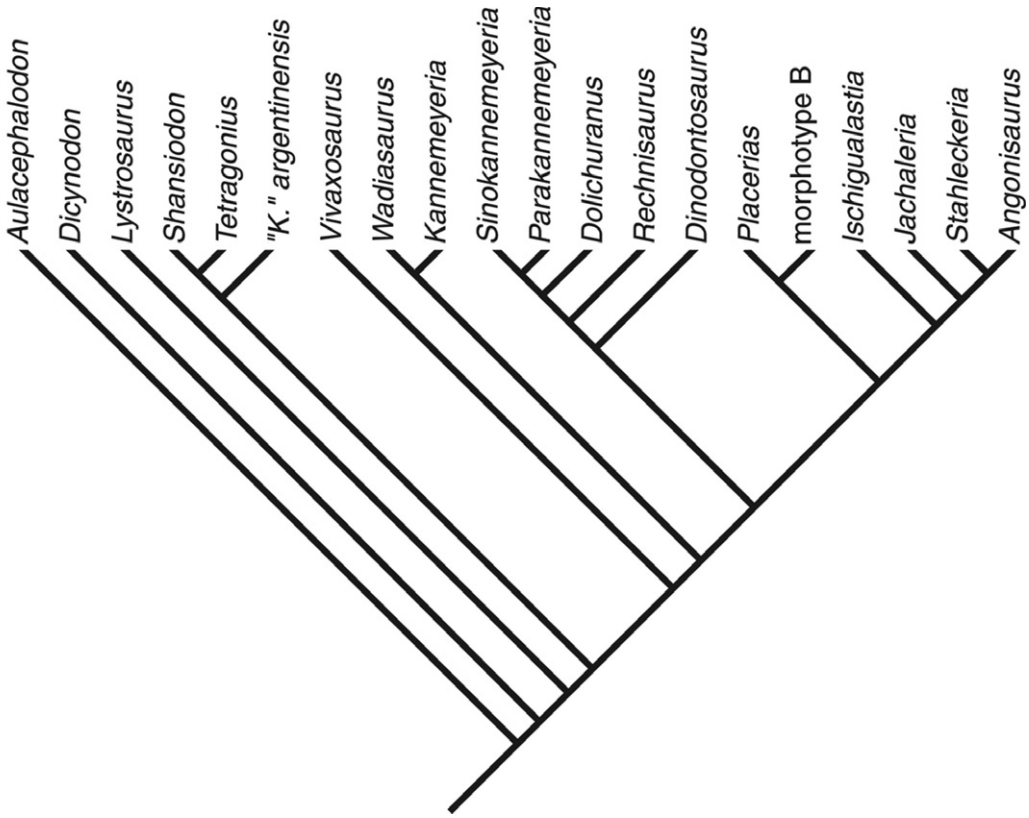

Figure 11. Single most parsimonious tree resulting from an analysis that excludes all postcranial character state data from Dolichuranus. Tree has a length of 267 steps.

acromion would have been directed antero-laterally. The proximal expansion of the right humerus is rectangular as seen in the smaller *K. simocephalus* specimen (BP/1/6160). Although incomplete posteriorly the ilium that forms part of the specimen (R316), the form of the ilium does resemble that of *K. simocephalus.* The anterior process is short antero-posteriorly but wide dorso-ventrally and it is situated higher than the posterior process. Also the acetabulum faces laterally and the superior acetabular ridge is antero-posteriorly short and wide. The only element that does not closely resemble *K. simocephalus* is a fibula which resembles that of morphotype B. Based on the above comparison we suggest that R316 represents *K. lophorhinus.*

Preliminary cladistic analysis suggests that *Dolichuranus* is a sinokannemeyeriid. Most of the character data supporting this position reside in the skull; however, the postcranial data do exert an influence on the analysis. In particular *Dolichuranus* attracts the poorly known morphotype B to the Sinokannemeyeriidae. In the absence of postcranial data from *Dolichuranus* morphotype B clusters in the Stahleckeriidae which is an unusual result, for morphotype B would then be the only stahleckeriid known from outside the Americas. A close relationship between *Dolichuranus* and morphotype B is supported by their shared presence of a third trochanter on the femur. Further derived characters supporting this relationship may be found in the scapula (a scapula blade that is three times longer than the width at the acromion) and the humerus (a deltopectoral crest that is set at an angle relative to the humeral shaft); however, these bones can only be tentatively referred to *Dolichuranus.*

CONCLUSION

The postcranial skeletons of both dicynodont species in the Omingonde can be recognized although only some material is positively associated with *Dolichuranus primaevus.* Preliminary cladistic analysis resolves *Dolichuranus* as a sinokannemeyeriid although the postcrania displays similarities to both sinokannemeyeriids and stahleckeriids. Including the postcranial characters for *Dolichuranus* in the analysis, causes the poorly known South Africa taxon, morphotype B, to group with the Sinokannemeyeriidae as well.

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INSTITUTIONAL ABBREVIATIONS

BPI	Bernard Price Institute for Palaeontological Research, Johannesburg.
CGP	Council for Geosciences, Pretoria.
R	Geological Survey of Namibia, Windhoek.

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APPENDIX 1

Character list

1. Shape of the distal margin of the caniniform process: rounded (0) or pointed (1) (modified from Vega-Dias 2004).
2. Tusks: present (0) or absent (1) (Vega-Dias 2004).
3. Position of the caniniform process: anterior to the orbit (0), underneath orbit (1) (Vega-Dias 2004).
4. Depth of the caniniform process: much shallower than the basal length (0) approximately as deep, or deeper than, the basal length (1).
5. Posterior margin of the caniniform process: not furrowed (0) with a postero-ventral furrow (1) (modified from Damiani *et al.* 2007).
6. Length of nasal symphysis: greater than 50% of the length of the nasals (0) or less than 50% of the length of the nasals (1) (Vega-Dias 2004).
7. Anterior tip of the nasal: anterior to the premaxilla-maxilla suture (0) or level with to posterior to the premaxilla-maxilla suture (1) (modified from Vega-Dias 2004).
8. Shape of the premaxillary beak in dorsal view: bluntly rounded to squared (0) or sharply pointed (1).
9. Median premaxillary ridge: short (0), elongate extending onto frontals (1) or absent (2) (Vega-Dias 2004).
10. Shape of fronto-nasal suture: irregular to straight (0) or strongly convex anteriorly (1) (Vega-Dias 2004).
11. Nasal bosses: paired, separate (0), single median boss (1), paired, meeting posteriorly (2), or absent (3) (modified from Angielczyk and Kurkin 2003).
12. Postnasal fossa behind the external naris: absent (0) or present (1) (Vega-Dias 2004).
13. Maxilla: excluded from pterygoid girder (0) or extending onto lateral surface of pterygoid girder (1) (Damiani *et al.* 2007).
14. Nasal-lacrimal contact: absent (0) or present (1) (Damiani *et al.,* in press).
15. Lacrimal-septomaxilla contact: absent (0) or present (1) (Vega-Dias 2004).
16. Shape of the prefrontal: longer than wide (0), equant (1) or wider than long (2) (Vega-Dias 2004).
17. Antorbital sulcus: present (0) or absent (1) (Damiani *et al.* 2007).
18. Adult orbit size: diameter less than 20% of the skull length (0) or greater than 20% (1).
19. Maxilla-squamosal contact: simple butt or scarf joint (0), interdigitating suture (1) (Vega-Dias 2004).
20. Posterior tips of the frontals: lateral to the parietal foramen (0), no further posterior than the anterior margin of the parietal foramen (1) or posterior to parietal foramen (2) (Damiani *et al.,* in press).
21. Posterolateral margin of the skull in lateral view: sloping anteroventrally (0) vertical (1) (Vega-Dias 2004).
22. Postorbital-squamosal contact: present (0) or absent (1) (Vega-Dias 2004).
23. Preparietal: present (0) or absent (1) (Vega-Dias 2004).
24. Intertemporal region: broad, flattened dorsal surface (0), transversely compressed intertemporal crest (1) (modified from Maisch 2001).
25. Parietal exposure on the dorsal skull roof: broad flat exposure (0), exposed only in a narrow trough (1) (Angielczyk and Kurkin 2003).
26. Ventral extent of parietal: not contacting the periotic (0) or contacting the periotic (1) (Surkov and Benton 2004).
27. Interparietal contribution to the dorsal skull roof: absent (0) narrow contribution on the rim of the skull roof (1) anteriorly extensive contribution (1) (Vega-Dias 2004).
28. Orientation of posterior process of the postorbital: facing dorsolaterally (0) vertical (1) (Angielczyk and Kurkin 2003).
29. Height of intertemporal region above orbit: less than the diameter of the orbit (0) or greater than the diameter of the orbit (1) (modified from Vega-Dias 2004).
30. Postfrontal: present (0) or absent (1) (Maisch 2001).
31. Dorsal margin of the squamosal in posterior view: notched (0) or entire (1) (modified from Angielczyk and Kurkin 2003).
32. Length of the temporal fenestra: greater than 33% of the length of the skull (0), less than 33% of the length of the skull.
33. Squamosal width: forming less than 50% of the width of the occiput (0) or forming at least 50% of the width of the occiput (1) (Vega-Dias 2004).
34. Disposition of the orbits: narrow interorbit with dorsolaterally facing orbits (0) broad interorbital region with laterally facing orbits (1) (Vega-Dias 2004).
35. Length of the prepineal region of the skull: less than the postpineal (0) or greater than the postpineal region of the skull (1) (modified from Vega-Dias 2004).
36. Skull shape in dorsal view: longer than wide (0) or as wide as long (1) (Vega-Dias 2004).
37. Height of the suspensorium: less than 60% of the skull length (0) greater than 60% of the skull length (1) (Vega-Dias 2004).

38. Skull length: well over 300 mm (0) or no more than 300mm (1) (Vega-Dias 2004).
39. Pilla antotica and trigeminal opening: pilla is present forming a notched opening for the trigemijnal nerve (0), pilla is absent so that the trigeminal opening is a horizontal hollow (1) (Surkov and Benton 2004).
40. Dorsum sella: distinct hollow (0), indistinct (1) (Surkov and Benton 2004).
41. Height of dorsum sella: under pilla antotica or less than 33% of interior endocranial cavity (0) or reaching level of pilla antotica or greater than 33% of the interior endocranial cavity (if pilla antotica is absent) (1) (Surkov and Benton 2004).
42. Carotid foramina on sella turcica: single median (0) or paired (1) (Surkov and Benton 2004).
43. Intertuberal ridge on basisphenoid: present (0) or absent (1) (Maisch 2001).
44. Basitrabecular process: terminating posterior to interpterygoid vacuity (0) or contributing to the margin of the interpterygoid vacuity (1).
45. Cultriform process: compressed and blade-like (0) or broad, nearly filling the interpterygoid vacuity (1) (Surkov and Benton 2004).
46. Shape of the interpterygoid vacuity: elongate oval (0) or broad oval to rhomboidal opening that is almost as wide as it is long (1) (Surkov and Benton 2004).
47. Mid ventral plate of the vomers: broad flat ventral surface (0) or blade like ventral surface (1).
48. Width of the pterygoid girder: longer than wide (0), as wide as long (1) wider than long and occupying half the distance between the quadrate condyles (2) (modified from Vega-Dias 2004) ordered.
49. Position of the ectopterygoid: on ventral surface of palate (0), dorsally displaced (1) or absent (2) (Damiani *et al.* 2007).
50. Symphyseal margin of the dentaries: raised with a scooped-out posterior surface (0) or level, wedge-shaped with a narrow median groove on the posterior surface (1) (modified from Angielczyk and Kurkin 2003).
51. Shape of the dentary table: lateral and medial ridges of equal height (0) or medial ridge much taller than lateral ridge and blade-like (1) (modified from Angielczyk and Kurkin 2003).
52. Size of the reflected lamina of the angular: small with a large gap between the posterior margin and the articular (0) or expanded with posterior margin closely following, if not contacting, the articular (1) (Vega-Dias 2004).
53. Coronoid emeinence: present (0) or absent (1).
54. Shape of the axis: much longer than high (0), or massive with a height:length ration of approximately 0.9 (1) (Surkov *et al.* 2005).
55. Triceps projection on the scapula: present (0) or absent (1) (Vega-Dias 2004).
56. Acromion: large projection (0) or a small knob (1) (Vega-Dias 2004).
57. Scapula blade: narrow (0) or broad (1).
58. Anteriorly projecting scapula spine attached to the acromion: absent (0) or present (1) (Vega-Dias 2004).
59. Position of the coracoid foramen: on the precoracoid (0) or on the precoracoid-scapula suture (1) (Vega-Dias 2004).
60. Precoracoid contribution to the glenoid; present (0) or absent (1).
61. Dorsal expansion of the scapula: less than 1.5 times the width of the scapula at the acromion (0) or greater than 1.5 times the width of the scapula at the acromion (2) (Vega-Dias 2004).
62. Constriction of the sternum in dorsal view posterior to the sternal bosses: absent (0) or present (1) (Vega-Dias 2004).
63. Number of sternal bosses: two (0) or four (1) (Vega-Dias 2004).
64. Twist between the transverse axes of the proximal and distal ends of the humerus: less than 60° (0) or more than 60° (1) (Vega-Dias 2004).
65. Size of the deltopectoral crest: occupying approximately 50% of the length of the humerus (0), much larger than 50% (1) or much smaller than 50% (2) (Vega-Dias 2004).
66. Length of humerus relative to the femur: less than the femur (0) or at least as long as the femur (1).
67. Proportion of the ulna that is distal to the sigmoid notch: longer than the portion proximal to the sigmoid notch (0), shorter than the proximal portion (1) or equal to the proximal portion (2) (Vega-Dias 2004).
68. Shape of the radius: elongate and slender (0), short and robust (1) (Vega-Dias 2004).
69. Anteroventral corner of the preacetabular lobe of the ilium: dorsal to the level of the acetabulum (0) extending ventral to the level of the dorsal rim of the acetabulum (1) (Vega-Dias 2004).
70. Shape of the acetabulum: dorsally notched (0) subcircular without a dorsal notch (1) (Vega-Dias 2004).
71. Dorsal projection of the ischium: not reaching the level of the ventral rim of the acetabulum (0) projecting dorsal to the level of the ventral rim of the acetabulum (1) (Vega-Dias 2004).
72. Anterior extension of the pubic tubercle: not extending as far as the level of the anterior rim of the acetabulum (0) extending anterior to the anterior rim of the acetabulum (1) (Vega-Dias 2004).
73. Shape of the femoral head in lateral view: anterior and posterior expansions of the head are equal (0) anterior expansion of the head greater than posterior expansion (1) (Vega-Dias 2004).
74. Shape of the greater trochanter of the femur: a straight ridge parallel to the shaft of the femur (0) a straight ridge set obliquely to the long axis of the femoral shaft (1) or sigmoidally curved (2) (Vega-Dias 2004).
75. Size of the greater trochanter: lateral edge no more than 33% of the length of the femur (0) lateral edge over 33% of the length of the femur (1) (Vega-Dias 2004).
76. Orientation of the coracoid facet of the scapula: facing antero-ventrally (0) or facing ventrally (1).
77. Orientation of the scapular glenoid: faces laterally (0), faces postero-ventrally (1), faces ventrally (2).
78. Profile of the deltopectoral crest: subrectangular with a straight anterior margin (0) rounded with a curved, convex anterior margin (1).
79. Olecranon ossification: part of the ulna, even in juveniles (0) develops from a separate centre of ossification (1) (Maisch 2001).
80. Shape of the olecranon process: tall, narrow and wedge-shaped (0) low, broad and rounded (1).
81. Orientation of the deltopectoral crest: anterior margin parallel with the humeral shaft (0) or set at an angle to the shaft (1).
82. Shape of the scapula blade: no more than three times longer than the width at the acromion (0) much longer than three times the width at the acromion (1) (modified from Maisch 2001).
83. Shape of the ilium: with moderate, subequal pre- and postacetabular lobes (0), preacetabular lobe markedly enlarged (1) or preacetabular lobe very enlarged while postacetabular lobe is very reduced (2) (Maisch 2001).
84. Relationship of femoral head with greater trochanter: confluent (0) or disjunct (1).
85. Third femoral trochanter: absent (0) or present (1).

APPENDIX 2

Character-taxon matrix. P = Polymorphic character (0,1), X = polymorphic character (1,2).

Aulacephalodon	00000	00000	00001	00000	00000	00100	00??0	00000	00P00	00000	000?0	0010?	10100	10?00	??000	01001	01010
Dicynodon	00000	00000	10000	01000	00011	00000	00000	0000P	00000	01000	00000	01000	0??00	00000	00001	00?00	00000
Vivaxosaurus	00000	?0000	20000	00002	00000	?2110	00001	000??	??1?0	1102?	????0	1000?	1??01	????1	?????	020??	00???
Lystrosaurus	00100	01000	P0111	20001	10000	00000	00001	10000	10000	11021	001P0	01010	10002	00000	00000	0210?	1?000
Shansiodon	00100	??01?	30100	?01?1	01?11	10?01	00?00	001?1	01???	?002?	100?1	0?00?	0??10	0000?	??000	12100	1?01?
Tetragonias	00100	00000	00111	101?1	01011	10001	00000	00101	0??11	00021	100?1	01101	00010	10000	01000	12101	10101
Kannemeyeria argentinensis	00000	11000	20101	00101	00011	?2101	00010	001??	??1??	1102?	100?1	01001	10?00	10000	01?10	01001	?0000
Wadiasaurus	0P00?	?100?	?0?00	?10??	0?011	?X12?	00000	000??	??1??	??1?1	00110	00111	??110	?201?	00011	01010	00100
Kannemeyeria	000?1	?1010	20110	01012	00011	12121	00000	00010	00110	11121	00110	00101	11?00	00000	01101	01000	00100
Dolichuranus	?0001	1?021	21000	10012	?0011	?1111	01011	000??	??1?0	01111	111??	???0?	?????	?????	??010	????1	???01
Dolichuranus (cranial only)	?0001	1?021	21000	10012	?0011	?1111	01011	000??	??1?0	01111	111??	?????	????	?????	?????	?????	?????
Morphotype B	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	????0	1?10?	1????	?????	??111	01101	11?01
Parakannemeyeria	0001?	00001	21??0	1?00?	001?1	?001?	01011	000??	?????	??1?1	?0??1	0010?	0??10	0210?	00001	01001	0101?
Sinokannemeyeria	0001?	0000?	?1??0	1?00?	001?1	?0011	01011	000??	?????	??2??	?0?11	0010?	00010	?210?	??101	01100	1111?
Dinodontosaurus	00000	01000	?0000	01011	01010	?1?01	01001	000??	??1?1	11111	011?1	01101	00000	10101	11?21	01011	00100
Placerias	10010	0?101	?0001	0101P	01000	12?11	10000	01010	11111	10??1	01110	00101	?0012	?11??	01011	01111	10?1?
Angonisaurus	11100	??00?	20???	?10??	10111	1110?	00110	11001	01111	1?2?1	1?100	01101	?????	????1	10???	11?00	?02??
Stahleckeria	01000	10001	20?00	21010	10100	01001	10101	11010	11110	?0121	01110	0?101	00112	11111	11111	???0?	?????
Ischigualastia	11000	11111	30000	01012	01000	12111	10010	010??	??1??	1?221	011?1	21011	1?1?1	?11??	??110	00010	00210
Jachaleria	11100	10021	00001	20012	11011	?2111	10010	010??	?????	11221	????0	2101?	111??	??100	11???	01???	??1??
Rechnisaurus	0001?	01000	00?00	1?0?1	01011	??1?1	01?11	?0010	10110	??1??	???1?	?0??1	?????	?????	?????	?????	?????