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1975
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Palaeont. afr., **18**, 137—142 (1975)

THE SKELETON OF THE TRIASSIC ANOMODONT *KANNEMEYERIA WILSONI* BROOM

by

A. R. I. Cruickshank

ABSTRACT

The general structure of the post-cranial skeleton of many Triassic anomodonts is now well known, but in Africa that of the stratigraphically important Lower Triassic (? Scythian) genus *Kannemeyeria* is known only from dissociated elements. A brief description is given for the first time of an almost complete skeleton ascribed to this genus. The environment of deposition is described briefly. The locality of the type species of the genus is also noted.

INTRODUCTION

In December 1934 Mr. R. McEwan the (then) owner of the farm Ravenskloof, Tarkastad District (Long. 31° 50′, Lat. 26° 20′), situated 24 km (15 miles) north-east of Tarkastad, brought into the East London Museum some bone fragments he found 100 m (300 yards) north-east of the old homestead. The farm Ravenskloof is composed of portions of the farms Van Wyk's Kraal, Hartebeeste Fontein and Honde Nek where they meet. The name Ravenskloof does not appear on the 1 : 250 000 Topocadastral series of the Republic of South Africa.

The Curator of the museum, Miss (now Dr.) M. Courtenay-Latimer, mounted an expedition in January of the following year which recovered most of the specimen as it now exists, and a further trip was made in 1936 to try to recover the missing portions (Table 1) (Broom, 1937; Courtenay-Latimer, 1948).

The purpose of this short paper is to place on record the salient features of this specimen in recognition of the extremely careful way that it was excavated. It is unfortunate that with the passage of the years other as complete specimens of Triassic anomodonts have been described, which has robbed this individual of the impact it might have had on their study.

I am grateful to Dr. Courtenay-Latimer for allowing me access to her personal and correspondence files covering this period, from which the following extracts are taken.

The locality is described as follows:
"Sandstones, mudstones and shales were the prevailing rocks; the banks of the intermediate sandstone could be seen thickening and thinning out within varying distances . . . the site was found to be . . . at the top of an erosion ravine and immediately below a horizontal outcrop of sandstone" (letter M. C-L to National Monuments Commission dated 12th November, 1941).

The skeleton was excavated from four levels and some additional remains were recovered from the surface.

On the surface lay (i) portion of a femur, (ii) portion of a tibia, (iii) 6 vertebrae, (iv) portion of left shoulder girdle, (v) 4 ribs.

Under this was Layer A. "Fine red gravel shale, 9″ thick" from which was recovered (i) lower jaw, (ii) right hand ramus of lower jaw (two feet away), (iii) humerus, (iv) portion of radius, (v) ulna, (vi) collar bone [*sic*], (vii) three vertebrae. Layer B was a "coarse compact red shale 15″ thick" and held (i) eighteen ribs (numbered 1—18), (ii) sixteen vertebrae (numbered 19—34) with twelve of them (21—32) in a natural articulation, (iii) complete shoulder girdle, (iv) humerus. Layer C, a solid red shale, was 12″ thick. It yielded (i) the ?RH pelvis, (ii) the ?RH shoulder girdle, (iii) five ribs, (iv) radius, (v) ulna, (vi) tibia, (vii) fibula, (viii) clavicle. The final productive layer, D, comprised a loose coarse red shale and was 12″ thick. It yielded (i) the skull, partly embedded in the underlying gray shale, (ii) one quadrate, (iii) sternum, (iv) the ?LH pelvis, (v) two feet, (vi) the other quadrate (M. C-L Field notes January, 1935).

The subsequent expedition in 1936 recovered, by sieving, isolated fragments of bone from the spoil heap and most of the missing femur.

Miss Courtenay-Latimer communicated news of her find to Dr. Robert Broom at the Transvaal Museum, having started to make a mounted reconstruction of the skeleton following Pearson's (1924b) reconstruction of the dissociated material in the British Museum and with the aid of her father.

Broom replied on the 26th July, 1935 (TM 33/33) "Your beast is grand. You have I think, the leg bones wrongly arranged, and also the pelvis. Your supposed tibia is clearly the ulna."

There follows a suggestion that he should be sent one each of all the limb-bones, which would be marked as to place and orientation on a diagram.

"All this would cost you nothing as the specimens can come O.H.M.S. and be returned similarly and it ought not to take more than a couple of weeks."

Nonetheless, the overall impression gained from the skeleton as reconstructed is of an animal which had suddenly come to a halt after running headlong, and as will be discussed below, several errors in identification of the bones have resulted in only a generally accurate reconstruction of the skeleton.

The taxonomy of the genus *Kannemeyeria* has been discussed recently (Cruickshank, 1970, 1972) and it was concluded that the genus contains only four species, viz. the large commonly found South African species *K. simocephalus* (Weit.), the equally large but rarer form *K. wilsoni* Broom (the subject of this description), *K. argentinensis* Bonaparte, a small form from S. America, otherwise similar to *K. simocephalus,* and *K. latirostris* Crozier, a medium-sized species which may be based on a juvenile specimen and which may warrant a new taxonomic placing. All are known from the Lower Trias (Scythian, (Anderson and Anderson, 1970)) except *K. latirostris* which is from the Zambian Middle Triassic (? Anisian) N'tawere Formation. *K. simocephalus* is also known from an Anisian (?) horizon in the East African Manda Formation (see Cruickshank, 1965, 1970, 1972 for details) and from S.W.A. (Keyser, 1973), in the Omingonde Formation which is very close to the *Cynognathus* zone in age.

It is possible that the relatively minor differences between *K. simocephalus* and *K. wilsoni* could be ascribed to sexual dimorphism, but the evidence is inconclusive at present and the two species are here recognised as separate (Cruickshank, 1970, 1972).

The importance of *Kannemeyeria* in South Africa is that it is of very common occurrence in the Upper Beaufort and in many ways a better zone fossil than *Cynognathus*, at the time of writing, being present on eighteen of the 33 *Cynognathus* zone localities recorded by Kitching (1972) whereas *Cynognathus* is known from only seventeen. Until recently the locality of the holotype of *K. simocephalus* was not even vaguely known (Cruickshank, 1970), but it seems to be from the fram Dwaarsvley (Alt. Q. 1—11) in the Aliwal North District (letter from R. L. Dorrington, Elandshoek, Aliwal North dated 24th October, 1970 refers. See also Cruickshank (1970, Table 1)). The information in the catalogue of the Natural History Museum, Vienna reads:

Type *Dicynodon simocephalus* Weit. 1888.

Museum No. 8178. Acquisition 1886 xv. 4.

Altersstufe — Karroo

Fundort — Südafrika

Coll — Adler. (the then German Consul in Port Elizabeth. [Ed.])

Dorrington (litt. cit.) says "He (Alfred Brown) strongly maintained . . . that the blocks of stone containing the fossil (were) to be shipped to British Museum but . . . ended up in Vienna and that (he) was always annoyed that he never received money or recognition for his efforts." At this distance in time the truth may never be discovered, and this is probably the best approximation likely as to the original site of this specimen.

MATERIAL

It was very difficult to examine this specimen properly as it was mounted in a close fitting glass case with the vertebrae strung on an iron rod and the limbs and skull supported by an iron pipe-and-strip framework. However, by kind permission of Dr. Courtenay-Latimer I was able to dismount some of the bones.

The majority of the photographs taken for record purposes were made using a "Polaroid" Model 180 camera with type 107 black and white film rated at 3 000 ASA and with a flash gun. A "Stereo-tach" stereo attachment proved invaluable and was used wherever possible. Colour and black and white photographs were taken with a conventional 35 mm camera as a backup service. The Polaroid films were frequently overdrawn with details taken from the specimen at hand.

This specimen is numbered E.L.M. 1.

DESCRIPTION

Skull

Further detailed description of the skull of *Kannemeyeria* is unnecessary since several adequate accounts have already been given in the past (Pearson, 1924a; Camp, 1956; Bonaparte, 1966; Cruickshank, 1965, 1970). Let it suffice to say that the skull of *K. wilsoni* differs from that of *K. simocephalus* only in the flatter snout region which is also less ridged and in the maxillary flanges which are smaller. These differences may be due to sexual dimorphism (Cruickshank, 1970, p. 50).

This skull was found in 53 pieces and the tusks are reconstructed in wood. Although their tips point downwards on leaving the maxilla, the roots run in line with the jugal arches (Cruickshank, 1970, p. 50).

The palate is not visible as the skull is mounted, and no description can therefore be given of it.

The lower jaw is typical of the anomodont's except that the tip appears to be horizontal rather than turned up as is the more usual case (Cruickshank, 1970).

Axial skeleton

As the vertebrae are rigidly mounted, it was not possible to examine each one individually, and the numbers recorded by Courtenay-Latimer at the time of collection could not be seen. Therefore, the sequence of articulated vertebrae she excavated from "Layer B" could not be identified.

The axial skeleton as preserved comprises forty-six vertebrae. It is difficult to distinguish between those that are cervical and thoracicolumbar, but it seems clear that there are at least 15 caudals present.

Nine of the remainder have been restored to a greater or lesser extent. The atlas/axis has not been completely prepared, but seems little different from those already described.

If there were six sacral vertebrae (Cruickshank, 1967, p. 194), then the presacral count amounts to 25. Therefore this specimen seems to possess an almost complete vertebral column, a fact almost unique among the recorded Triassic anomodonts. Likewise, the skeletal proportions of the specimen can be regarded as being realistic, if not exactly correct.

There was nothing to indicate that these vertebrae would differ from those described by Pearson (1924b).

Ribs

Twenty-four ribs are mounted on the skeleton, all on the left-hand side. It would appear likely that no cervical ribs are preserved (but see below) and no record was found of the remaining three ribs not incorporated into the mounted skeleton.

There are a number of errors of positioning of the ribs, viz. those that are mounted ahead of the scapula being in fact posterior thoracic or lumbar ribs, having the small triangular single head as described for *Tetragonias* (Cruickshank, 1967, Figure 7). Six ribs with swollen ends, and thus likely to be originally in contact with the sternum and hence anterior thoracic ribs, have been mounted in the mid-region of the rib cage. Several ribs from the right-hand side were included in this sequence on the left.

In more detail, it would appear that the first rib as mounted is the only one which might be a cervical, as it seems to have the remnant of a divided head, but in all probability it is a posterior lumbar rib as are numbers two to four. Numbers five to ten inclusive are from the thoracic-lumbar region anterior to the foregoing. Number eleven is a true first thoracic rib as it has both the divided head and a swollen end for contact with the sternum (Cruickshank, 1967). Rib number twelve as mounted is probably an anterior thoracic rib, as are ribs numbers thirteen and fourteen. Rib number fifteen is in all probability the matching first thoracic for number eleven, but its identity is in doubt because of damage to the head region. Rib number sixteen is clearly an anterior thoracic and the remaining smaller ribs are clearly from the posterior thorax-lumbar region.

In summary there is little in the rib-cage of this species to indicate any special adaptations or to distinguish it in detail from *Tetragonias*. The reconstruction should show therefore that the rib-cage was deep anteriorly becoming gradually shallower towards the pelvis (e.g. Cox, 1965, p. 478, Figure 11).

Pectoral girdle

Both pectoral girdles are more or less completely preserved and in addition there was the remnant of a sternum. It is regrettable that nothing resembling an interclavicle was recovered from the excavation (Cruickshank, 1967, p. 208). Bonaparte (1966) illustrates one from *K. argentinensis*.

The left scapula has a broken acromion process, but the right is complete in this respect.

The prespinous fossae are much smaller than in the scapula figured by Pearson (1924b), but nonetheless are still relatively much bigger than in *Tetragonias* (Cruickshank, 1967, Figure 8). In this respect the scapula is much more advanced than those normally associated with the Triassic anomodonts. The scapulae are tall narrow bones in the typically anomodont pattern. The glenoid is large and faces almost entirely backwards with only a small proportion of the articulating surface facing outwards. The articulating surfaces are equally divided between the scapula and the coracoid. It is therefore likely that the elbow was drawn into the side of the animal and that protraction was limited during each stride. The humerus must have been held horizontally, because the lower lip to the glenoid, formed by the coracoid, would have prevented much adduction. Also, the remains of the substantial sternum seem to indicate large ventral pectoral muscles and hence a clumsy posture and slow gait.

The coracoid and precoracoid are subequal and the precoracoid seems to be excluded from the glenoid. The coracoid foramen is entirely on the precoracoid, equally spaced from the posterior and dorsal margins.

Clavicle

The clavicles in *K. wilsoni* are relatively long, flat bones. The one from the right-hand side of the mounted skeleton is the more complete of the pair, although only the left-hand one shows a knob or boss towards its distal end as mounted, which may have served to locate it against the interclavicle.

Humerus

Both humeri are present and almost complete, although crushed. The condyles were apparently poorly ossified and the proportion seems different from the humerus figured by Pearson (1924b), but this feature is at most certainly due to the crushing they have suffered.

Sternum

The sternum is a poorly preserved irregularly-shaped flat plate of bone, which has been wrongly mounted at an angle, in contact with the clavicles.

Radius and ulna

Only the left ulna is preserved, although both radii were present. The radius and ulna are subequal, and there is no evidence of there having been a separately ossified olecranon process as described in some other Triassic anomodonts (Cox, 1965) and it is possible that this feature is not as universally

present as Cox believed. The ulna is flattened antero-posteriorly. The radii have moderately expanded ends and are rounded in section. The ulna seems broadly similar to that figured by Pearson (1924b).

Fore-foot

In describing the feet of this specimen, reference is made to the field notes kept by Dr. Courtenay-Latimer in which she states that two feet were recovered from layer "D" (see p. 137 above). However, as reconstructed, 29 elements have been incorporated into the fore-foot and 33 into the hind. Therefore, at least two extra bones have been used in the reconstruction of the fore-foot (27 bones used by Camp, 1956, Figure 58a; 25 bones used by Cruickshank, 1967, Figure 17) and eight extra in the hind foot (25 bones used by Camp, 1956, Figure 58b; 23 bones used by Cruickshank, 1967, Figure 22). Therefore, although only 10 terminal phalanges have been incorporated into the two reconstructed feet, at least 10 supernumerary foot bones are also present and quite clearly the remains of more than two feet must have been present in this specimen.

Owing to the fact that it was almost impossible to remove the fore-limb from the mounted skeleton, no attempt has been made to describe the foot bones in detail. Likewise, at this interval of time it is almost impossible to make an accurate reconstruction from the remembered field association, if any, of the foot bones.

The impression gained from an examination of the preserved material is that the fore-feet of *K. wilsoni* were shorter and broader than in *Tetragonias*, and certainly the terminal phalanges were considerably different in proportion. The fore-feet of *Tetragonias* have long sub-rectangular claws, whereas these are broad and triangular. Camp's *Kannemeyeria* material had no complete terminal phalanges (1956, Figure 58) and Cox's descriptions and figures of *Dinodontosaurus turpior* are also different (1965, Figure 18).

Pelvis

Both halves of the pelvis are preserved, though the left pubo-ischiadic plate has been reversed on mounting and is thus viewed from the inside. The ilium is remarkable for its distinct "hook" on the long anterior blade, which is partly matched in *Ischigualastia* (Cox, 1965, Figure 9), but apparently not in the material described by Pearson (1924b, Figure 29). This character has also been noted by Cruickshank (1970) as being of taxonomic importance in association with the similarly contrasting scapula characters, and serves at present to help distinguish *K. simocephalus* and *K. wilsoni*.

The dorsal rim of the ilium is a regular curve and the external surface is smooth. On the internal face there seem to be six facets for the sacral vertebrae, though this is not clear on the left ilium. On the right ilium, immediately behind the front edge of the pillar-like ventral part of this bone, there is a buttress, behind which, at its dorsal extremity, is a small depression. Following posteriorly from this there are a further five clear sets of sacral-vertebrae attachments, and thus it would seem that the sacral count in this species is six, confirming Pearson's (1924b) estimate.

The ischium and pubis are very similar to those described by Pearson. The former has the same inturned posterior portion and the latter a pubic process similar to the one figured by Pearson. There is a large obturator foramen placed high up under the cup-shaped acetabulum.

Femur

The femora are substantial bones, not nearly as flattened as in the specimen figured by Pearson and possessing inturned and rounded heads. The proportions of the femora of this specimen are very similar to the femur of *Tetragonias* (Cruickshank, 1967, Figure 19).

The head of the femur is not separated from the body of the bone by any constriction and there does not seem to be any indication of a trochanter minor. A small step on the proximal end of the femur similar to that in *Tetragonias* might likewise indicate the limit of the trochanter major. The distal condyles are somewhat ventrally placed, showing that the femur was probably held horizontally out from the body, with the lower limbs in a splayed position. However, there is not the prominent adductor femoris tubercle as is seen in *Tetragonias*.

Tibia and fibula

Only the left tibia is preserved. It is a massive bone, and had been subjected to considerable crushing during fossilisation. As a result of this, the cnemial crest had been flattened into the main body of the bone and the ends are now in fact much thinner than the columnar shaft of the bone. The fibula is in comparison an almost insignificant bone, with the proximal end tapering to fit against the lateral condyle of the femur. It is slightly shorter than the tibia and distinctly rounded in section.

Hind feet

As with the fore-foot, no genuine reconstruction of the hind foot can be attempted, at this late stage in time. However, a selection of foot bones corresponding to those illustrated by Camp (1956, Figure 58) can be arranged to make up a hind foot. Only one fibulare (calcaneum) is present. As in the fore-foot the terminal phalanges are short triangular bones, and they do not seem to have been offset as in the *Tetragonias* specimen described by Cruickshank (1967, Figure 22).

DISCUSSION

Affinities

The affinities of this specimen are clearly with the genus *Kannemeyeria* as redefined (Cruickshank,

1970), and the possibility is that it is either a female of *K. simocephalus* or a different species as is assumed here. As the whole question of the interrelationship of the Triassic anomodonts is under review at the present time, any further discussion under this heading is unwarranted.

Depositional environment

The descriptions given above by Dr. Courtenay-Latimer can quite clearly be interpreted in terms of the similar Molteno sequence described by Turner (1969, 1972a). The main differences between the Molteno and the Upper Beaufort are the coarser sandstones of the former and the persistent red colour of the latter. Turner (1972a, p. 313) concludes that the Molteno sediments were laid down on a river flood plain crossed by braided river channels with the sandstones representing point-bar complexes fining upwards into coals and carbonaceous shales, which in turn represent back swamp areas. However, in the Upper Beaufort no coals are found and of course the Molteno is almost totally devoid of known vertebrate fossils (Turner, 1972b; Jubb, 1973). The fauna of the Upper Beaufort on the other hand contains lungfish (cf. *Neoceratodus*), palaeoniscids (Hutchinson, 1972), labyrinthodont amphibians and a rich reptilian fauna.

Therefore in summary it seems that the Upper Beaufort environment comprised a slow-flowing seasonal river system with adjacent swamps. The large anomodont *Kannemeyeria* would have fed on the vegetation growing along the riverbanks, and the specimen recorded here was probably mired in a somewhat deeper mud pool than it might have expected. The carcase was clearly not disturbed by either scavengers or secondary reworking by river currents and on the body disintegrating the heavy head sank to the bottom, the remainder floating for a while to give the depth distribution recorded by Dr. Courtenay-Latimer when she excavated the specimen.

ACKNOWLEDGEMENTS

This paper was made possible through the kindness of Dr. Courtenay-Latimer allowing me access to the specimen and sending me at various times colour and black-and-white photographs of it. Financial support has been given by the University of the Witwatersrand and the C.S.I.R.

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TABLE 1
Principal measurements of *Kannemeyeria wilsoni* Broom E.L.M. 1

CLAVICLES	LEFT	29 cm long
	RIGHT	30 cm long; 9,5 cm wide proximally; 6,5 cm wide distally
SCAPULAE	LEFT	46 cm overall height; 15 cm wide at top
	RIGHT	44 cm overall height; 19 cm wide at top
CORACOID PLATES	LEFT	24 cm along dorsal edge; 12 cm high
	RIGHT	22 cm along dorsal edge; 12 cm high
HUMERI	LEFT	35 cm overall length; 24 cm wide proximally; 21 cm across distal condyles
	RIGHT	36 cm overall length; 23 cm wide proximally; 21 cm across distal condyles
LEFT ULNA		29 cm overall length; 11 cm wide at sigmoid notch; 8 cm wide distally
RADII	LEFT	23 cm overall length; 9 cm wide proximally; 8 cm wide distally
	RIGHT	23 cm overall length; 8,5 cm wide proximally; 6 cm wide distally
LEFT ILIUM		33 cm maximum length of blade; 28 cm depth of ilium (acetabulum to dorsal rim); 10 cm width of acetabular pillar; 8,5 cm diameter of acetabulum
FEMORA	LEFT	34,5 cm overall length; 16,5 cm wide proximally; 14,5 cm wide over distal condyles
	RIGHT	33 cm overall length; 14,5 cm wide proximally; 15,5 cm wide over distal condyles
LEFT TIBIA		26,5 cm overall length; 11 cm wide proximally; 8,5 cm wide distally
FIBULAE	LEFT	23 cm overall length; 6 cm wide proximally; 5 cm wide distally; shaft 2,4 cm diameter
	RIGHT	22 cm overall length; 7 cm wide proximally; 6 cm wide distally
OVERALL LENGTH MOUNTED SKELETON		1,93 metres
GLENOID-ACETABULUM DISTANCE		80 cm approximately