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Gow, C. E.; Grine, F. E.

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AN ARTICULATED SKELETON OF A SMALL INDIVIDUAL OF *DIADEMODON* (THERAPSIDA; CYNODONTIA)

by

C. E. Gow* and F. E. Grine†

**Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg 2001.*
†Department of Anatomy, University of the Witwatersrand Medical School.
Present address: South African Museum, P.O. Box 61, Cape Town 8000.

ABSTRACT

This paper records a nearly complete, articulated skeleton of *Diademodon* in undoubted association with a skull of that animal. Previously, only portions of postcranial skeleton have been found in association with cranial remains of this genus. The skeleton is that of a relatively small (ontogenetically young) individual. Skeletal proportions are tabulated, rib and vertebral differentiation is described and discussed. *Diademodon* is shown to have had a long tail.

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INTRODUCTION

The skeleton of *Diademodon* is poorly known. In fact, it is not possible at this time to assign with any certainty isolated postcranial remains of the vast majority of *Cynognathus* zone cynodonts even to their appropriate genus.

Seeley (1895a and b) described an associated skull and skeleton of *Cynognathus* and a supposedly associated mandible and skeleton of *Microgomphodon eumerus*. Although Brink (1955) considered the mandibular fragment to be that of a juvenile *Diademodon*, one of us (F.E.G.) has examined the specimen (BMNH R. 3581)*, which consists of a small, broken fragment of right dentary with the remains of some eight lower and six upper postcanine teeth in tight occlusion, and concurs with Hopson and Kitching (1972) that the taxonomic designation of this fragment must remain in doubt. It may represent a bauriamorph as easily as a diademodontid, but the postcranial skeleton which Seeley (1895a) associated with this dentary fragment is that of a cynodont. A skeletal reconstruction of *Diademodon*, modelled on a nearly complete axial skeleton without a skull (NM 531), was drawn by Brink (1955). This specimen lacks a skull and cannot, therefore, be identified positively. Furthermore, as pointed out by Jenkins (1971), Brink's illustration of the actual fossil does not represent adequately the original specimen, in that the drawing does not portray the fact that many of the features either have been reconstructed in plaster or are otherwise missing or damaged. Until now, only a single reasonably complete postcranial skeleton in undoubted association with a skull of *Diademodon* (USNM 23352, collected in 1961 from the farm "Winnaarsbaken", Cape Province) has been procured. As Jenkins (1971) noted, however, this fossil provides a very limited amount of information. More recently, Keyser (pers. comm.) has recovered a beautiful skull and associated postcranial skeleton of what appears to be a distinctive diademodontid (*Diademodon crassus* (Keyser)) from the Omingonde Mudstone Formation (Lower Etjo Beds) of S.W.A./Namibia.

The specimen described here consists of a very nearly complete, articulated skeleton, in undoubted association with a skull, of a relatively small individual of *Diademodon*. It is from the *Cynognathus* zone sediments of the Cape Province, South Africa. The specimen provides information on skeletal proportions and rib differentiation; also, it possesses a rather longer tail than has been considered previously to have been the case.

* Institutional abbreviations used in this paper:
BMNH — British Museum (Natural History) London
BPI — Bernard Price Institute for Palaeontological Research, Johannesburg
NM — National Museum, Bloemfontein
SAM — South African Museum, Cape Town
USNM — United States National Museum, Washington, D.C.

MATERIAL AND METHODS

The specimen (SAM K5266) was recovered from *Cynognathus* zone sediments on the farm "The Pines", in the Hofmeyr district of the northern Cape Province, South Africa. It was contained in an extremely hard, fine-grained siltstone nodule which was some 50 cm in maximum diameter and which had a mass of some 112 kg. The nodule had split through the plane of the skeleton. The bone of the skull is in good condition, with very little having been lost in the break or by subsequent weathering. Unfortunately, the cranium is not so well exposed as to permit its designation to either the Type One, Two or Intermediate cranial morphotypes expressed in *Diademodon* (Grine, 1978a and b; Grine, Hahn and Gow, 1978). Apart from exposing sufficient of the skull to obtain a measurement of the basal skull length, as defined by Grine and Hahn (1978), cranial morphology has been ignored in this study.

Much of the postcranial skeleton is preserved as a mould, where the bone has been removed by humic acids in the weathering process. These acids have also softened the matrix to depths varying from a few millimetres to more than a centimetre in places. The half of the nodule which contains the impression of the dorsal portion of the skeleton had been covered by lichen, which has damaged surface detail somewhat. The other half of the nodule is in better condition.

Acid preparation to remove remaining bone was not possible generally, not only as it worsened the effects of the natural weathering, but also because resistant areas of some of the bones are composed almost entirely of matrix of the same composition as the surrounding rock, due to the highly vascular nature of the bone.

Surplus nodular rock was removed with a diamond saw after fibreglass copies of the entire matching surface of each half of the nodule had been made. Peels of the two slabs were made with black latex reinforced with cotton fibre. Drawings of the specimen were made from photographs (102 × 127 mm negatives) of the latex positives. Measurements were taken on the original specimen. Three-dimensional silicone rubber casts of the skeleton were made from keyed plaster moulds, and several individual bones were cut from these casts.

SKELETAL PROPORTIONS

The basal skull length of the specimen (SAM K5266) is 74 mm (table 1). We consider this specimen as a "small" individual of *Diademodon*. The term "small" is used here in preference to words such as "young" or "juvenile" because the latter may be construed as signifying sexual immaturity. We refer only to the developmental size attained by an individual specimen at the time of its death. Basal length of *Diademodon* skulls ranges from approximately 40 mm to about 300 mm.

The dimensions of those skeletal parts which were amenable to measurement are recorded in Table 1. The proportional indices of these parameters as compared with basal skull length are presented in Table 2.

The length of the vertebral column, from the atlas to a plane transecting the acetabula, is just over 160 per cent longer than the cranial length (table 2). This proportional relationship appears to be rather similar to that shown by Jenkins (1971, frontispiece figure) for the galesaurid *Thrinaxodon*, and quite unlike Brink's (1955, fig. 7) reconstruction of a megacephalic *Diademodon*. The tail of the specimen, although incomplete, is nearly 42 per cent longer than the skull (table 2), and it appears to be at least 53 per cent of the length of the rest of the vertebral column, as defined above. The evidence provided by this specimen indicates that *Diademodon* possessed a longer tail than has been considered previously to have been possessed either by this genus (Brink, 1955) or by African cynodonts in general (Jenkins, 1971).

TABLE 1
Skeletal Measurements (mm)

Measurement	*SAM K5266*
1. Basal skull length	113
2. Humerus length	57
3. Ulna length	54
4. Femur length	65
5. Tibia length	56
6. Vertebral column (atlas to acetabulum) length	300
7. Vertebral column (tail) length	160+
8. Pelvis width (at acetabulum)	42

TABLE 2
Skeletal Proportion Indices

Index	*SAM K5266*
1. Humeral (2/1 × 100)*	50,4
2. Ulnar (3/1 × 100)	47,8
3. Femoral (5/1 × 100)	57,5
4. Tibial (6/1 × 100)	49,6
5. "Vertebral" (7/1 × 100)	265,5
6. Tail (8/1 × 100)	141,6+
7. Pelvic (9/1 × 100)	37,2

* Numbers refer to the measurements enumerated in Table 1.

AXIAL SKELETON

In the present specimen most of the vertebrae have been broken so that only the neural arch remains, except in the cervical and caudal regions, where portions of the centra are visible. Jenkins (1971) determined that both *Thrinaxodon* and *Cynognathus* possessed seven cervical vertebrae; unfortunately, however, it is not possible to determine the number of cervical vertebral elements in the present specimen.

Only four sacral vertebrae can be distinguished with any certainty in this fossil, although a fifth may have been present (Jenkins, 1971, has recorded that both *Thrinaxodon* and *Cynognathus* possessed five sacral vertebrae). The sacral elements present are interpreted here as representing the first four vertebrae, by comparison of their positions relative to the iliac

blade with Jenkins' (1971) illustration of the same region in *Thrinaxodon*. The sacral ribs are poorly-preserved in the present specimen.

Traces of the tail, which curves round to (almost) touch the snout, can be followed. The tail, in so far as it is preserved, comprises some 15 caudal elements, and it is evident that the tail originally contained at least 18 (to perhaps 20) caudal vertebrae. Jenkins (1971) recorded that *Thrinaxodon* possessed from ten to perhaps 15 caudal vertebrae, and that the tail of *Cynognathus* contained only four to possibly six elements. It is evident, from the present specimen, that *Diademodon* possessed a longer tail, composed of a larger number of vertebrae, than either this genus (Brink, 1955) or other African cynodonts have been credited with hitherto (Jenkins, 1971; Parrington, 1978). The tail of *Diademodon* is, however, comparable both in length and vertebral composition to that described by Jenkins (1970) for the traversodontid *Massetognathus*. The caudal vertebrae of the present specimen decrease gradually in size distally and the last few centra are very small; it is not possible to distinguish any caudal ribs.

Thoracic–lumbar transition

Jenkins (1971) based his separation of the thoracic and lumbar regions of the axial skeleton of cynodonts upon a complete and well-preserved skeleton of *Thrinaxodon*. He noted that the thoracolumbar transition is not marked, but is defined rather by slight morphological differences, and that the thoracic and lumbar ribs are morphologically intergra-

tal tubercles. The immediately preceding pair of ribs are characteristically unexpanded thoracic costae.

If Jenkins' (1971) definition of the lumbar vertebrae of *Cynognathus* (or *Diademodon*) is accepted then the present specimen would appear to possess eight lumbar vertebrae — again, one more than Jenkins determined.

We propose that the lumbar vertebrae be defined, at least for *Diademodon*, as: those vertebrae whose associated ribs possess costal plates that have costal tubercles. Accordingly, the present specimen of *Diademodon* is judged to possess eight lumbar vertebrae, despite the fact that the first pair of lumbar costae have short shafts.

From the foregoing, then, a continuous series of only the last ten thoracic vertebrae can be discerned from associated rib morphology, in the present specimen. The original number of thoracic vertebrae cannot be determined accurately. Jenkins (1971) has determined that whilst *Thrinaxodon* possessed 13 thoracic vertebrae, *Cynognathus* showed 15 elements. The thoracic costae are elongate and slender but are expanded somewhat at their proximal ends. The capitular and tubercular heads, which are visible on the last three pairs of this group, are set at an angle of approximately 110° to each other. The last thoracic rib possesses a moderately long shaft, and it evinces the first indication of the ridge which, in the succeeding lumbar ribs, becomes a costal plate.

APPENDICULAR SKELETON

have been affected. Several disarticulated phalanges from the left manus can be distinguished.

Pelvic girdle and hind-limb

On the left side there is an impression of the entire dorsal surface and most of the ventral surface, save the acetabular facet, of the ischium. Damaged portions of the iliac acetabular facet are present also on this side.

The right side of the pelvis is present, but the region posterior to the acetabulum has not been preserved. A vertically orientated bony element which contacts the sacrum is part of the iliac blade. The dorsal border of this element, as represented in

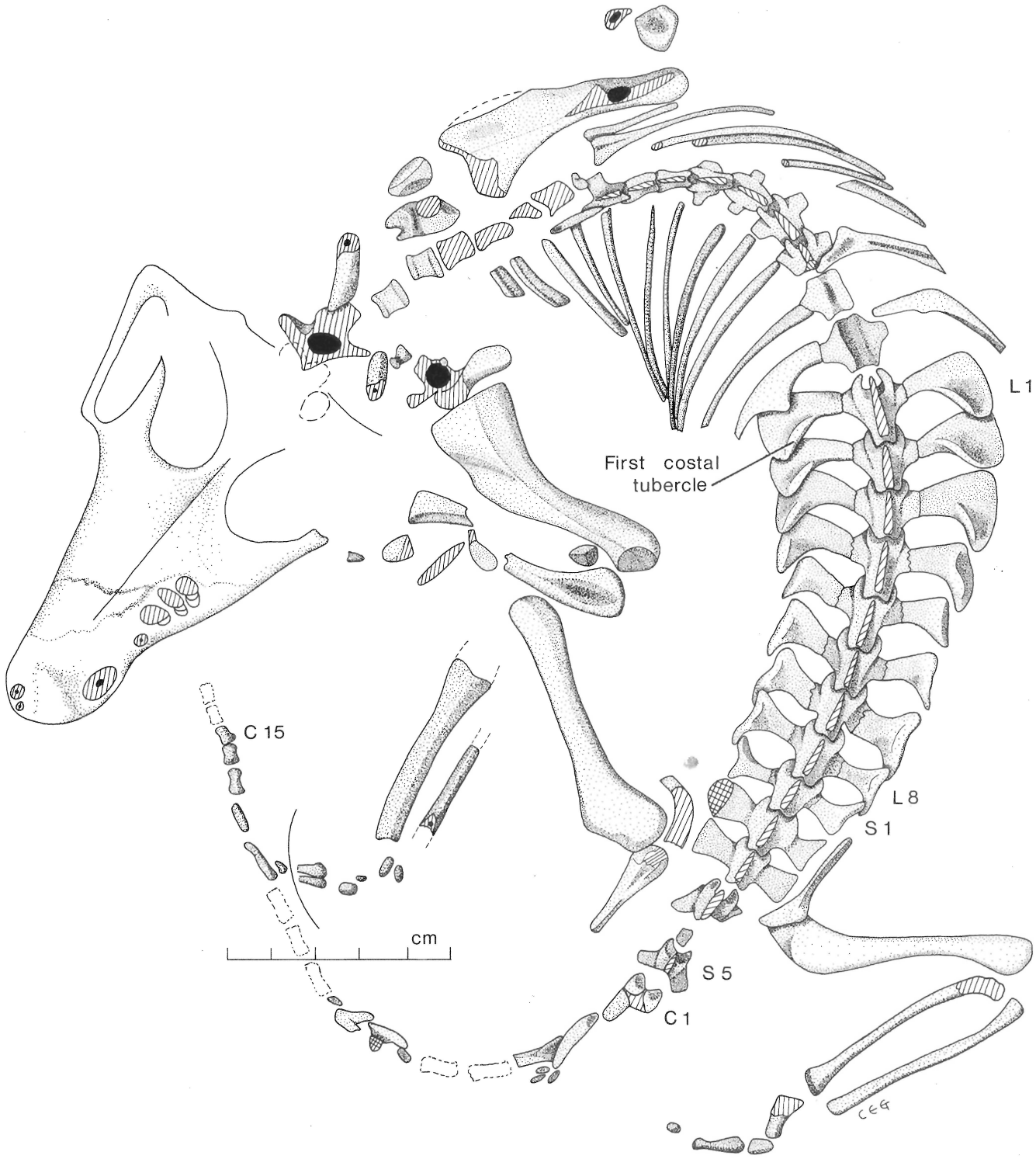
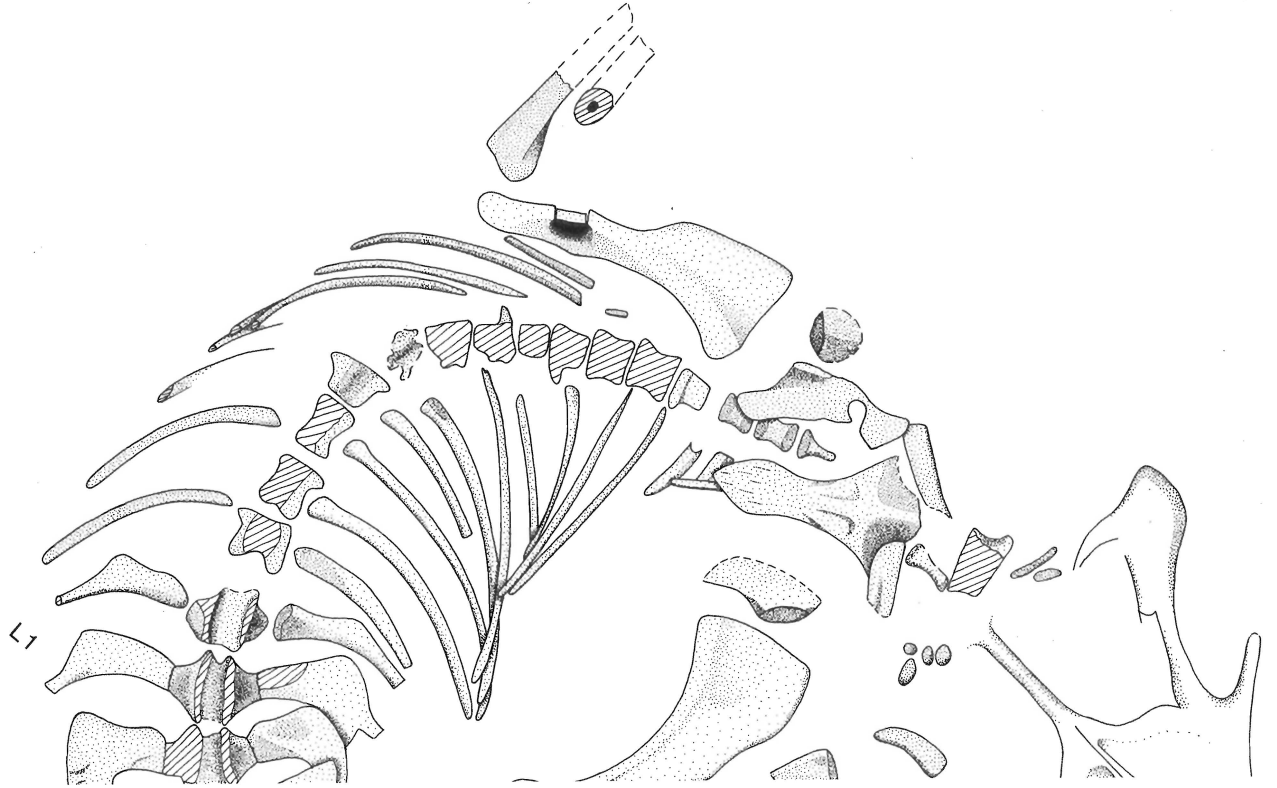


Figure 1. *Diademodon* SAM K5266. Dorsal surface of the skeleton as preserved.

the cast, is incomplete; some of the bone remains embedded in the matrix. On the left side the ventral border of the iliac blade, as well as the whole of the iliac acetabular facet, is perfectly preserved. There appears to be less of a "neck" between the blade and the acetabular region in this specimen than is the case either in large *Cynognathus* ilia (Jenkins, 1971) or in isolated pelves which have been assigned to *Diademodon*. It is possible that the morphology of the region between the acetabulum and the iliac blade could have been affected by growth, but it is feasible also that the shape of this area in the present speci-



men is an artefact of the diagenetic pressure to which this particular skeleton was subjected.

Both femora are preserved and are in articulated positions. The right tibia, but not the fibula from this side was amenable to measurement (table 1). Several tarsal bones and bits of phalanges from each pes can be discerned.

SUMMARY AND CONCLUSIONS

A nearly complete, articulated skeleton in undoubted association with a skull of *Diademodon* has been described briefly. The fossil is that of a relatively small (ontogenetically young) individual. Skeletal proportions of this specimen indicate that the skull of *Diademodon* was not as large, relative to body size, as was suggested by Brink (1955). Also, it is evident that *Diademodon* possessed a longer tail than either this genus (Brink, 1955) or other African cynodonts (Jenkins, 1971) have been credited with. The tail of *Diademodon* is comparable in length to that described for the traversodontid, *Massetognathus*, by Jenkins (1970).

The axial skeleton reveals that, on the basis of rib morphology, two vertebrae (the last thoracic and the first lumbar) constitute a morphologically intermediate grade between preceding thoracic and succeeding lumbar elements. There appears to be no morpholgical gradient along the series of thoracic ribs. The first pair of lumbar ribs exhibit traces of rib shafts which are lacking entirely in the rest of the lumbar series. This specimen of *Diademodon* possesses eight lumbar vertebrae, as defined here.

No evidence of bony epiphyses was found in any of the skeletal elements.

The ilium of this specimen appears to possess less of a "neck" between the blade and the acetabular facet than is present in either large *Cynognathus* pelves (Jenkins, 1971) or in a number of isolated innominates which have been assigned to *Diademodon*. This finding may be an artefact of diagenetic distortion, or the area in question may be subject to rather radical growth changes. Alternatively, it may indicate that those isolated ilia which have been assigned to *Diademodon* belong, in fact, to *Cynognathus*.

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