

THE POSTCRANIAL SKELETON OF THE EARLIEST DICYNODONT SYNAPSID *EODICYNODON* FROM THE UPPER PERMIAN OF SOUTH AFRICA

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ABSTRACT. Comparison of postcranial skeletal elements of the Upper Permian *Eodicynodon oosthuizeni* (the earliest member of the Dicynodontia) and other dicynodonts, shows distinctive features of the *Eodicynodon* humerus, scapula, femur and ilium which are diagnostic at the generic level, and which may therefore aid stratigraphical studies.

Both the fore- and hind limbs and girdles show a less derived condition than in other dicynodonts. The forelimb adopted a sprawling position and was supported by extensive postural musculature as evidenced by the broad blade of the scapula where the serratus anterior and levator scapulae attached, and by the large ventral girdle for attachment of the pectoralis and coraco-brachialis. The more distal insertions of the deltoideus and pectoralis muscles on the delto-pectoral crest suggest that the characteristic slow and powerful forelimb action of later dicynodonts was not yet in evidence in *Eodicynodon*. It appears that the hind limb adopted a sprawling or semi-sprawling position. The femur lacks a developed trochanter major, and the ilium is without marked anterior and posterior processes. The ilio-femoralis was predominantly an elevator, retraction of the femur having been carried out by the caudi-femoralis and ventral musculature attached to the extensive pubo-ischiadic plate.

EODICYNODON Barry, 1974, is the earliest and most primitive member of the Dicynodontia (*sensu* Rubidge and Hopson 1990; = 'higher dicynodonts' of King 1988), which were herbivorous mammal-like reptiles abundant during the Permian and Triassic. *Eodicynodon* is a medium-sized dicynodont with a total body length of about 450 mm, and it stood about 150 mm high at the shoulder. The genus contains two species, *E. oosthuizeni* (Barry, 1964) and *E. oelofseni* (Rubidge, 1990c), and is known from the Late Permian *Eodicynodon-Tapinocaninus* Assemblage Zone (Rubidge 1990a), the lowermost biozone of the Abrahamskraal Formation of the Beaufort Group in South Africa. Although the cranial morphology has been described in considerable detail (Barry 1974; Cluver and King 1983; Rubidge 1984; 1990b) and analysed in functional terms (King *et al.* 1989) the postcranial skeleton has so far received no treatment. Well-preserved and -prepared material of *Eodicynodon oosthuizeni* is now available, so this gap can be filled.

A detailed knowledge of the skeleton of *Eodicynodon* is important for two reasons. First, since *Eodicynodon* is the least derived dicynodont known, an understanding of its postcranial skeleton is necessary before a review of dicynodont postcranial function can be undertaken. Secondly, it is important as part of a complete revision of the postcranial skeleton of the principal anomodont genera, the aim of which is to recognize generic characteristics in postcranial elements. These elements can then be used for biostratigraphical purposes.

In this paper the distinguishing features of the postcranial skeleton of *Eodicynodon oosthuizeni* are described and compared with other described dicynodont postcrania (*Robertia broomiana* (King 1981b), *Dicynodon trigonocephalus* (King 1981a), *Cistecephalus* (Cluver 1978), *Kingoria nowacki* (Cox 1959; King 1985)), and an undescribed specimen of *Diictodon galeops* (SAM K1633). Apart from *Robertia*, these forms occur in later assemblage zones than does *Eodicynodon*. *Robertia* overlaps with *Eodicynodon* in the *Eodicynodon-Tapinocaninus* assemblage zone, but is not found as low in that zone as *Eodicynodon* (see below).

The study is based on several well-preserved specimens because no one specimen is complete. Most specimens consist of the major parts of articulated skeletons found in association with cranial material and we can therefore be confident of the generic identification of the individual skeletal elements.

There is a small size range in the specimens. The femur of the largest specimen (NMQR 3153) is *c.* 20 per cent longer than that of the smallest (NMQR 3155). Although there are indications of some allometric changes (e.g. shaft diameter of the femur becomes proportionally greater with increasing femur length) these do not appear to be very great.

MATERIAL STUDIED

Specimens of *Eodicynodon* used in this study from the South African Museum, Cape Town (SAM) and the National Museum Bloemfontein (NMQR) are:

NMQR 2991; coracoid plate, humeri, femora, tibia, fibula, atlas and other vertebrae, ribs (Text-fig. 1A); from Modderdrift, Prince Albert, Cape Province, South Africa.

NMQR 2992; skull, lower jaw, scapulocoracoid, clavicles, interclavicle, radius, atlas-axis complex, vertebrae and ribs; from Tuinkraal, Prince Albert, Cape Province, South Africa.

NMQR 3153; scapula, part of coracoid, humerus, radius, part of manus, femur, tibiae, fibulae, vertebrae and ribs (Text-figs 2A–B); from Modderdrift, Prince Albert, Cape Province, South Africa.

NMQR 3154; occiput, left ramus of lower jaw, scapulae, clavicles, humeri, radii, ulnae, manus, vertebrae and ribs (Text-figs 1B, 2C, 3, 4B); from Botterkraal, Prince Albert, Cape Province, South Africa.

NMQR 3155; ilia, pubo-ischiadic plates, femur, tibiae, fibulae, pes, vertebrae and ribs (Text-fig. 5A–B); from Combrinckskraal, Prince Albert, Cape Province, South Africa.

NMQR 3156; most of the left manus; from Botterkraal, Prince Albert, Cape Province, South Africa.

NMQR 3158; Posterior half of skull, scapula, humerus, radius, ulna, manus (Text-fig. 4A); from Swartgrond, Rietbron, Cape Province, South Africa.

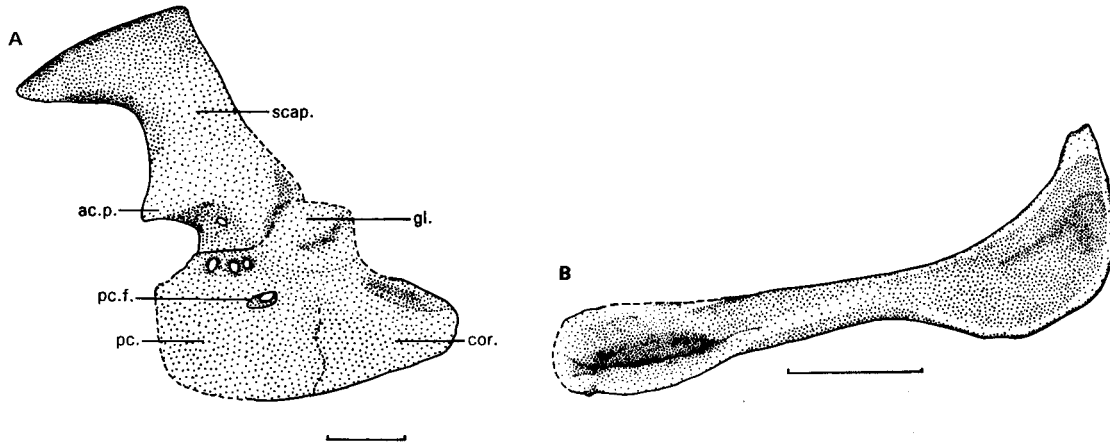
POSTCRANIAL SKELETON

Scapula

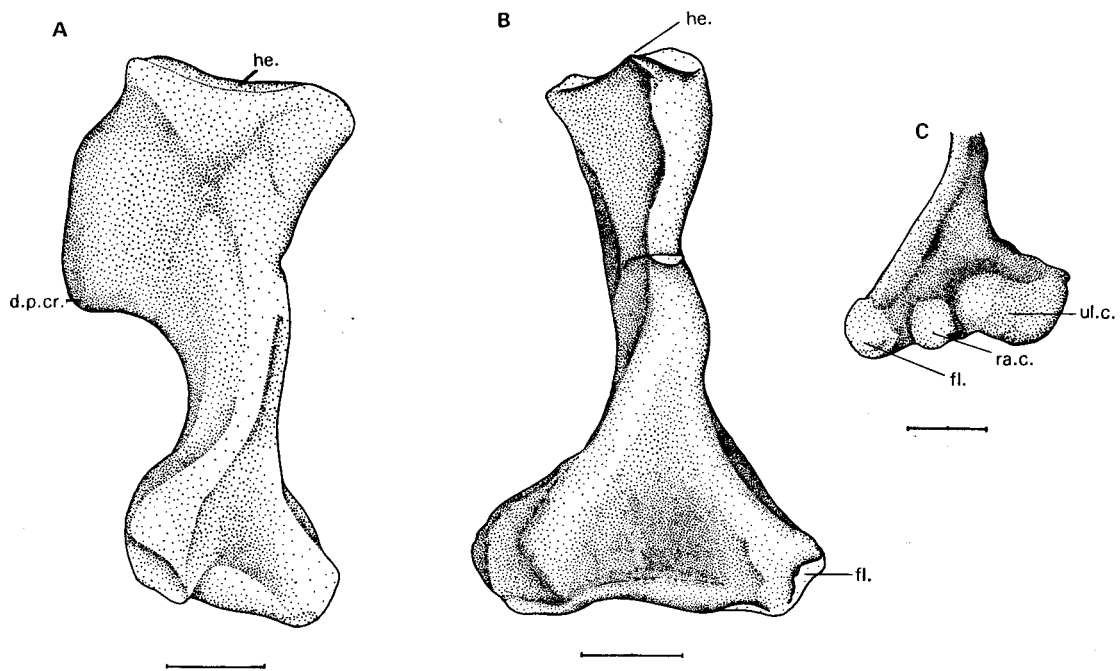
The scapula (Text-fig. 1A) has a well-marked acromion process clearly demarcated from the rest of the bone. The blade is broad and not as constricted above the acromion process as in other dicynodonts. Dorsally the blade fans out to form a dorsal edge which is considerably broader than in *Dicynodon trigonocephalus*, *Kingoria*, *Robertia* and *Cistecephalus* (Cluver 1978).

Coracoid and procoracoid

These two bones together form a large plate (Text-fig. 1A). The procoracoid is roughly square and contains a procoracoid foramen (Text-fig. 1A; pc.f). Smaller foramina near the border with the scapula are probably due to damage to the bone. The coracoid is a smaller bone which tapers posteriorly (Text-fig. 1A; cor). The glenoid facet of the coracoid is well-developed, rounded and faces postero-medially. The coracoid plate is much larger, compared with the size of the scapula, than that of *Robertia* and *D. trigonocephalus*, but is comparable with that of *Diictodon* (SAM K1633).



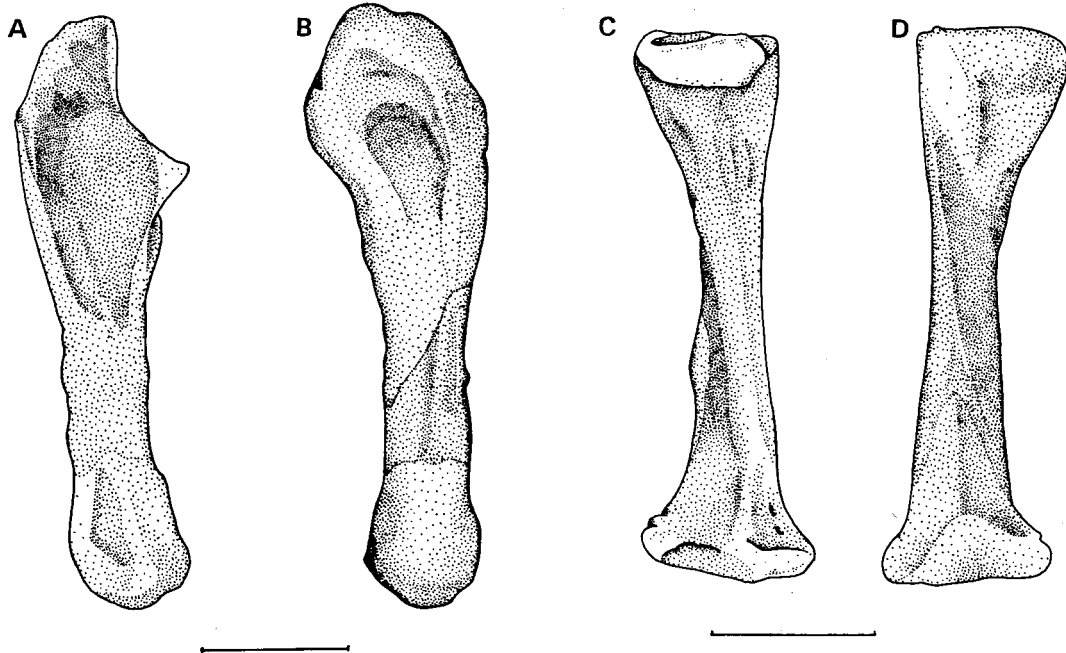
TEXT-FIG. 1. Scapula and clavicle of *Eodicynodon*. A, scapula of NMQR 2991. B, clavicle of NMQR 3154 with proximal end in dorsal view. Part of distal end reconstructed from NMQR 2991. Scale represents 10 mm.



TEXT-FIG. 2. Humerus of *Eodicynodon*. A, NMQR 3153 in anterior view. B, NMQR 3153 in dorsal view. C, distal end of NMQR 3154 in ventral view. Scale represents 10 mm.

Clavicle

The clavicle (Text-fig. 1B) is of typical dicynodont shape, being a slender rod of bone with both proximal and distal ends expanded and oriented at right angles to one another. The expanded ends are markedly bigger than in *Dicynodon trigonocephalus* and are comparable with those of *Robertia*.



TEXT-FIG. 3. Radius and ulna of *Eodicynodon*. NMQR 3154. A, left ulna lateral view. B, left ulna in medial view. C, left radius in lateral view. D, left radius in medial view. Scale represents 10 mm.

Interclavicle

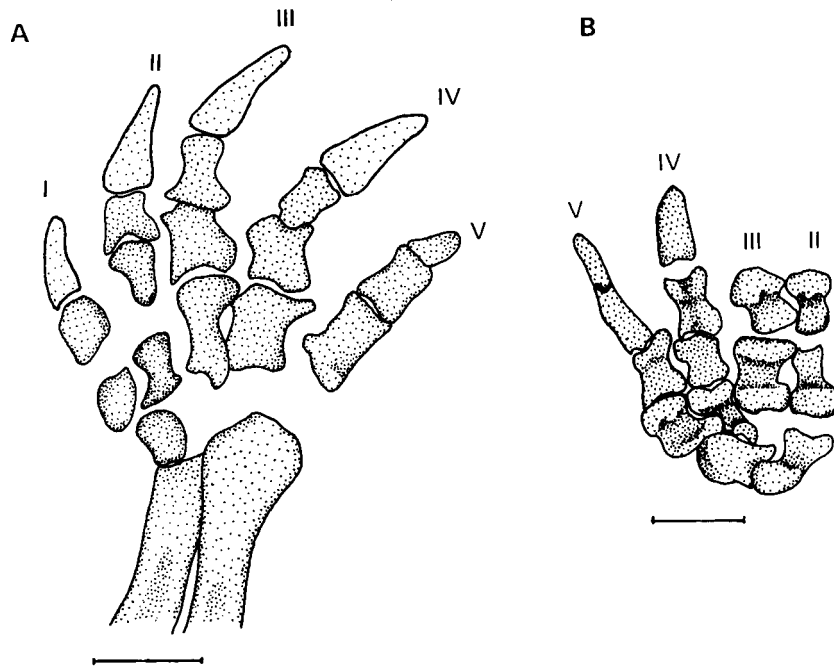
The interclavicle is not exposed fully in the specimens available but is overlain by the clavicles. It has a long posterior projection and would presumably be T-shaped if fully exposed. This would approximate to the condition in *Robertia* and contrast with the smaller, squarish interclavicle of *D. trigonocephalus*. No sternum is present in the specimens available for study.

Humerus

The humerus (Text-fig. 2) is a robust bone. The proximal and distal ends are set at an angle of *c.* 80–90° to one another, which is considerably greater than in the other dicynodonts used here for comparison. There is not trace of an ectepicondylar foramen. This is in contrast to the condition in the slightly later form, *Robertia*, where a notch can be seen in the position of the ectepicondylar foramen (King 1981*b*, fig. 4*c*). Both the proximal and distal ends are wide compared with the shaft of the bone. The distal end has prominent rounded condyles for articulation with the ulna and radius (Text-fig. 2*c*). The posterior edge of the entepicondyle bears a rounded well-marked attachment area for the lower limb flexor muscles (Text-fig. 2*B–C*; fl.). The deltopectoral crest is large and distinctive (Text-fig. 2*A*; d.p.cr.). It takes the form of a triangular plate extending from the proximal surface of the bone to *c.* 40 per cent the length of the bone. The proximo-ventral edge is very thin. The distal end of the crest grades smoothly into the body of the bone. The form of the crest contrasts with that of later forms such as *Dicynodon*. Here the crest is an oval plate of bone which extends much farther down the shaft, occupying *c.* 60 per cent of the length of the bone (King 1981*a*, fig. 19*c*). The head of the humerus (Text-fig. 2*A–B*; he.) is indistinct, in contrast to the ulnar and radial condyles (Text-fig. 2*c*; ul.c., ra.c.) which are well-developed.

Radius and ulna

The radius and ulna (Text-fig. 3) are both slender bones compared with those of *Diictodon* and *Dicynodon trigonocephalus*, and more similar to those of *Robertia*. The ulna is larger than the radius and has a well-marked olecranon process. The bone is medio-laterally compressed. There are well-marked hollows on its anterior and



TEXT-FIG. 4. Manus of *Eodicynodon*. A, right manus of NMQR 3158 in dorsal view. B, right manus of NMQR 3154 in ventral view. Scale represents 10 mm.

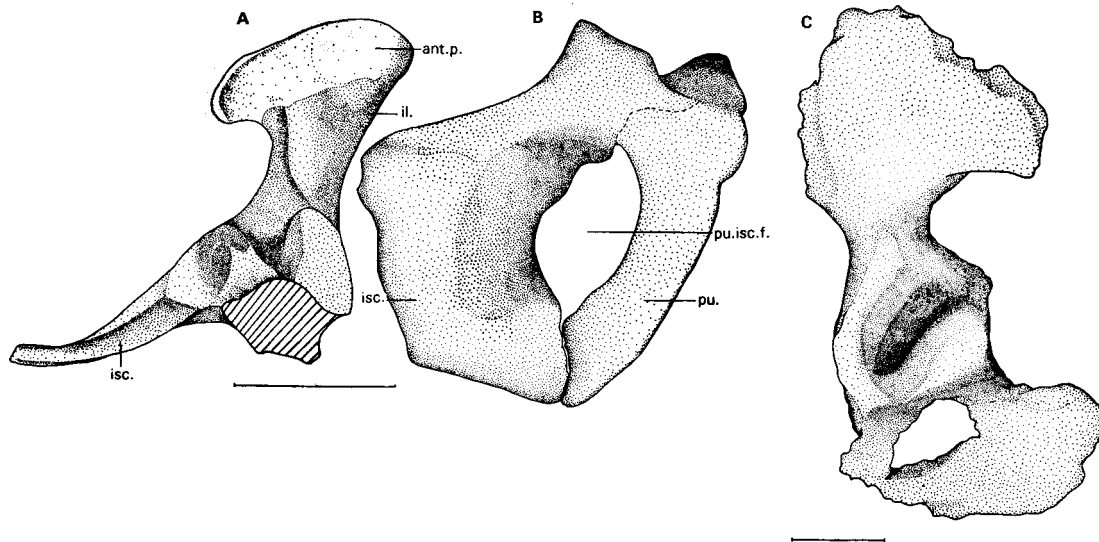
posterior surfaces, presumably for muscle attachment. The ends of the radius are noticeably expanded. Rugose ridges along the length of the bone mark the division between extensor and flexor muscle groups.

Manus

The manus (Text-fig. 4) is broad with long slender ungual phalanges. Other phalanges are slightly longer than broad. Metacarpals are not markedly longer than phalanges. The most complete manus (NMQR 3156), which contains three virtually complete digits, indicates that the phalangeal formula was probably 2, 3, 3, 3, 3, as in all Anomodontia (includes the families Galechiridae and Dicyodontidae *sensu* Rubidge and Hopson 1990) including *Patranomodon* (Rubidge and Hopson 1990), which is the least derived anomodont known. The terminal phalanges are long and claw-like. It is not possible to ascertain the number of carpals. As in other dicyodonts, the manus is short and wide. This contrasts with the more slender foot found in *Patranomodon* (Rubidge and Hopson, work in progress), and *Galechirus* (Brinkman 1981) where the metacarpals are approximately twice as long as the phalanges. In *Eodicynodon* the lengths of the metacarpals and phalanges are subequal.

Ilium

The ilium (Text-fig. 5) is small compared with the pubo-ischiadic plate, unlike the condition in *Robertia*, *Dicynodon trigonocephalus* or *Kingoria* where the two elements are subequal. The blade of the ilium has small anterior and posterior processes. The anterior process (Text-fig. 5A; ant.p.) is not sharply demarcated from the rest of the bone, but grades smoothly into the anterior edge as in *Robertia*. The ilia of *Robertia* and *Eodicynodon* are very similar except that the ilium of *Eodicynodon* is taller owing to a longer neck between the



TEXT-FIG. 5. Pelvic girdle of *Eodicynodon*. A, right side of pelvis of NMQR 3155 in lateral view. B, right ischium of NMQR 3155 in ventro-lateral view. C, left side of pelvis of NMQR 2902 in lateral view. Hatching indicates a break through the bone. Scale represents 10 mm.

acetabulum and dorsal blade. This gives the bone a tall, thin, somewhat delicate appearance. At least two and possibly three ribs make contact with the ilium, compared with five in *D. trigonocephalus*, four in *Kingoria* and three in *Patranomodon* and *Cistecephalus*. The most posterior of these ribs would have attached ventro-posteriorly on the neck of the ilium. The anterior and posterior corners of the acetabulum are rounded and built up where the ischium and pubis articulate. The acetabulum (Text-fig. 5C) is roughly hemispherical.

Pubo-ischiadic plate

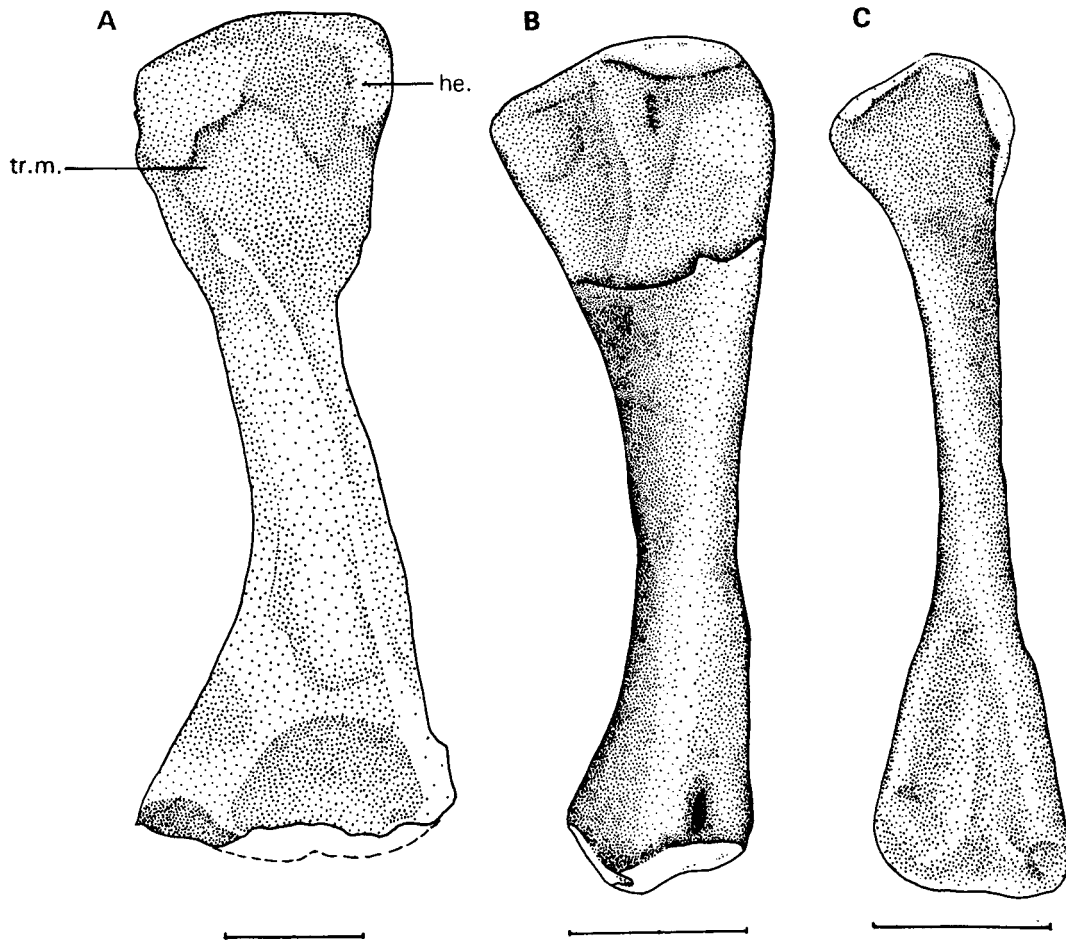
The pubis (Text-fig. 5B; pu.) is a thin L-shaped bone, the short limb of the L making contact with the antero-ventral corner of the acetabulum, and the long limb being directed postero-ventrally to meet the ischium. There is a large pubo-ischiadic fenestra (Text-fig. 5B; pu.isc.f.) between the two bones. The ischium is basically a square bone from which a large notch has been cut antero-ventrally to form one half of the pubo-ischiadic fenestra. Both bones are thin plates except where they are built up proximally to form their contributions to the acetabulum.

Femur

The femur (Text-fig. 6A) is a fairly slender bone, c. 10 per cent longer than the humerus. The head (Text-fig. 6A; he.) has a reasonably distinct condyle which is offset from the proximo-anterior corner of the bone, giving the femur a very slight S-curvature. The distal condyles are not well marked, in contrast to those of the humerus. The trochanter major (Text-fig. 6A; tr.m.) is not large, and is not set off from the shaft of the bone as in *D. trigonocephalus*, but grades into the shaft as in *Robertia*. However, the femur of *Eodicynodon* appears to be more slender than that of *Robertia*, partly due to less expansion of the proximal and distal ends (especially the proximal) and partly because the shaft portion of the bone is proportionally longer.

Tibia and fibula

These are both slender bones (Text-fig. 6B-C), c. 80 per cent the length of the femur. There is a well-marked cnemial crest on the tibia, but little to distinguish them from these same elements in other genera.



TEXT-FIG. 6. Femur, tibia and fibula of *Eodicynodon* NMQR 3153. A, right femur in anterior view. B, left tibia in anterior view. C, left fibula in anterior view. Scale represents 10 mm.

Pes

Little information is available concerning the structure of the pes. Ungual phalanges are slender and approximately the same length as other phalanges. The calcaneum is a flat ovoid plate of bone. The astragalus is more spherical and a deep notch can be seen in the surface that is visible. These elements appear to be very similar to those described in *Kingoria*. Few other tarsi are available for comparison.

Vertebrae and ribs

The axial skeleton (including the atlas-axis complex) does not appear to have any features which would distinguish *Eodicynodon* from other dicynodont genera. No specimen is sufficiently complete to permit an estimate of the number of presacral vertebrae. There are probably three sacral vertebrae. At least six caudal vertebrae are present.

DISTINCTIVE FEATURES OF *EODICYNODON* POSTCRANIAL ELEMENTS

This description permits several features of *Eodicynodon* to be recognized which distinguish this genus from all other dicynodont genera: (i) the scapula has a broad dorsal edge and is not so constricted above the acromion process as in other genera; (ii) the coracoid plate is large in

comparison with the scapula; (iii) the humerus has a large plate-like triangular delto-pectoral crest, well-developed distal condyles, and proximal and distal ends at a large angle to one another; (iv) the clavicles have very large expanded ends; (v) the radius and ulna are slender bones. In the pelvic girdle: (vi) the pubo-ischiadic plate is very large; (vii) the ilium is tall and thin with a small anterior process; (viii) the femur is a slender bone with a long shaft and comparatively little expansion of the proximal end.

Owing to the shape of the delto-pectoral crest, the humerus is the most distinctive bone of the postcranium and would serve alone to distinguish *Eodicynodon* from other genera. The proportions of the ilium are also different from those of other dicynodont ilia.

Recently it has become apparent that for stratigraphical purposes an important distinction is to be able to differentiate *Eodicynodon* from *Robertia*. Currently the stratigraphical range of *Robertia* is uncertain, largely because of the lack of an adequate generic diagnosis of this form. The type of *Robertia* has been more fully prepared and described (King and Rubidge 1993) and it is now evident that there are many more specimens of *Robertia* in collections than were previously recognized. Systematic fossil collecting in the lowermost rocks of the Beaufort Group has revealed that *Eodicynodon* and *Robertia* occur together in the upper parts of the *Eodicynodon-Tapinocanius* assemblage zone (Rubidge 1990a).

The humerus most easily distinguishes *Eodicynodon* from *Robertia*. The distinction is not based on bone element proportions, and therefore comparative material (either from the rest of the skeleton, or from other genera) is not necessary. However, the ilium, femur, scapula, and coracoid plate all show differences in proportions from *Robertia* as indicated above, and comparative material would distinguish between the two genera.

FUNCTIONAL MORPHOLOGY

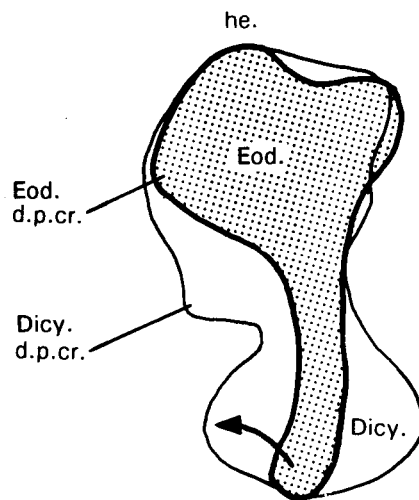
Eodicynodon has a distinctive postcranial morphology. In some respects this morphology appears to comprise less derived character states than other dicynodonts: the large ventral parts of the limb girdles, the robust humerus with its expanded ends, the very small iliac blade with small anterior process, the small number of sacral ribs. However, in other respects *Eodicynodon* is as derived as later dicynodonts: the well-developed and everted acromion process, and the absence of any remnant of the ectepicondylar foramen in the humerus.

It is clear, that as is usual for most dicynodonts, there is a large difference in morphology between the fore- and hindlimbs. Although the hindlimb is the longer, it is much more gracile. However, the discrepancy in *Eodicynodon* is more marked than in other less derived dicynodonts such as *Dicynodon trigonocephalus*: the ends of the humerus are more expanded, and the distal condyles are very prominent. These features, together with the robust ventral shoulder girdle, slightly expanded dorsal margin of the scapula, large olecranon process of the ulna, and broad manus with long sharp claws are reminiscent of those found in digging forms such as *Cistecephalus* (Cluver 1978) and *Kawingasaurus* (Cox 1972) which used forearm flexion to dig, although the features are much less marked in *Eodicynodon*. However, it is much more likely that these features reflect the primitive condition of the forelimb and girdle in dicynodonts.

In the pelycosaur *Dimetrodon* the scapula also flares dorsally (Romer 1922). The posterior, anterior and dorsal margins of the scapula blade, which are emphasized by this flaring, are where postural muscles such as the levator scapulae and serratus anterior inserted. It is possible that narrowing of the blade in later dicynodonts and therapsids in general is correlated with a reduction in this part of the postural musculature as a more 'mammalian' stance was adopted. However, the reduction of postural musculature does not seem to be a simple process in dicynodonts. Although it seems that the superficial postural muscles were reduced, other muscles involved in support of the anterior part of the body (the deltoids, pectoralis and biceps) were emphasized. This emphasis is reflected in the form of the delto-pectoral crest.

The distinctive appearance of the delto-pectoral crest of *Eodicynodon* compared with that of other dicynodonts is due to a lack of development of the distal part of the crest (Text-fig. 7). Muscles

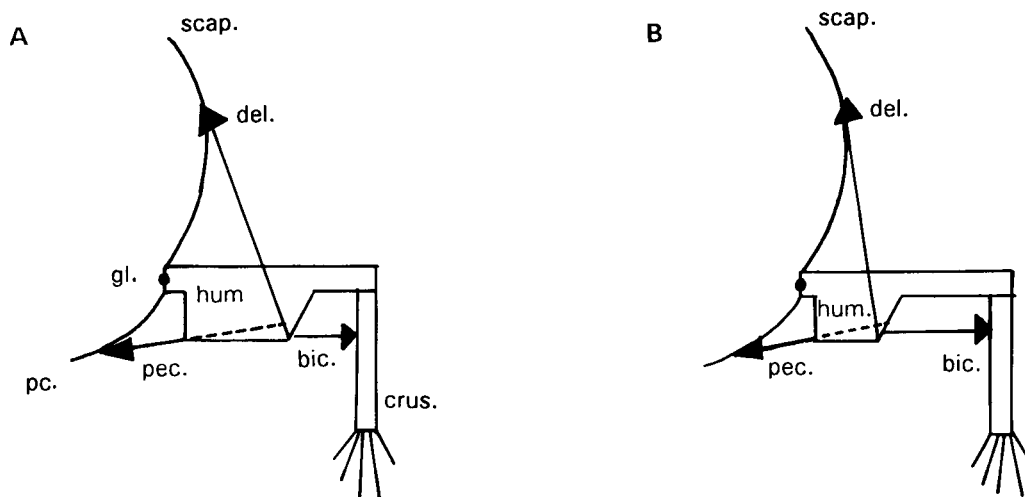
TEXT-FIG. 7. Humerus of *Eodicynodon* superimposed on that of *Dicynodon* showing the rotation of the distal end relative to the proximal (arrow), and the larger development of the distal part of the delto-pectoral crest. The proximal end is in dorsal view.



which would have attached to this area of the crest in dicynodonts were part of the deltoideus, part of the pectoralis, and the biceps and brachialis (King 1981*a*). Developing the delto-pectoral crest distally, as happened in more derived dicynodonts, allowed the deltoideus and pectoralis to insert more distally. Being farther from the articulation of the humerus, these muscles would have acted more powerfully (but also more slowly) on the humerus. Elevation and protraction (deltoideus) and depression and protraction (pectoralis) would have become powerful actions. Being farther from the articulation also made the muscles more effective in a postural role (Text-fig. 8).

The drawback of this arrangement is that the biceps muscle would have become rather short and its role in limb flexion and support was presumably diminished.

The emphasis on the activity of the deltoideus and pectoralis muscles in dicynodonts more derived than *Eodicynodon* may be reflecting in these forms an emphasis on powerful, if slow,



TEXT-FIG. 8. Schematic representation of the deltoid and pectoral musculature of A, *Dicynodon* and B, *Eodicynodon*. The diagrams show a cross-section through the body, head towards the observer. Scale = 10 mm.

movement and possibly larger body size. This corroborates the usual interpretation of most dicynodonts as slow but powerful animals. Powerful anterior postural musculature may have been important to dicynodonts in supporting a large abdomen in which plant matter was slowly digested, and in supporting the robust head equipped with powerful jaw adductor muscles.

The new insertional position of the deltoideus and pectoralis may be one of the reasons that the coracoid-procoracoid plate, so extensive in *Eodicynodon*, has been reduced in later forms. The more advantageously placed pectoralis muscle might thus have required a less extensive area of origin.

The greater angulation of the proximal and distal ends of the humerus reflects a condition where the humerus projects laterally from the glenoid. If the humerus is positioned so that the distal end of the bone is horizontal, the delto-pectoral crest hangs down as a near-vertical plate. So positioned, there is no restriction on the large size of the plate which can accommodate large postural, as well as limb-protracting, muscles. The vertical alignment of the delto-pectoral crest also allows muscles to pass under the smooth antero-ventral edge of the shaft of the bone to attach to the ventral ectepicondylar surface.

The origins of the supracoracoideus and scapulo-humeralis in *Eodicynodon* show an intermediate condition between those of pelycosaur and those of later dicynodonts. The coracoid plate is extremely large and no doubt accommodated a large part of the origin. However, a strongly everted acromion process is also present. The lower edge of this is sharp and does not provide a route for the supracoracoideus to reach the medial side of the scapula. There is, however, a smooth hollow ventral to the acromion process where part of the supracoracoideus might have originated. This would confirm the suggestion (King 1981*b*) that the everted acromion process had initially very little to do with muscle attachment.

The primitive nature of the forelimb and pectoral girdle is reinforced by the pelvic girdle and limb where the small anterior process of the ilium and the lack of development of the trochanter major would also be primitive features, reflecting the lack of a forwardly-pulling part of the ilio-femoralis, the precursor of the mammalian gluteals. The height of the ilium would also enhance the levator action of the ilio-femoralis. Presumably at the *Eodicynodon* stage the femur was protracted mainly by the pubo-ischio-femoralis internus. Retraction would have been accomplished by part of the ilio-femoralis on the posterior iliac process, the ischio-trochantericus and the caudi-femoralis. The large ischiadic plate would have accommodated adequate ischio-trochantericus muscles. As far as the caudi-femoralis is concerned, in *Eodicynodon* there are at least four post-sacral vertebrae which have long, flat, robust ribs attached to them which would have afforded an origin for the caudi-femoralis. However there is no obvious insertion for the muscle on the femur.

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ABBREVIATIONS

ac.p.	acromion process	Eod.	<i>Eodicynodon</i>	pec.	pectoralis muscle
ant.p.	anterior process	Eod.d.p.cr.	<i>Eodicynodon</i> delto- pectoral crest	pu.	pubis
bic.	biceps muscle	fl.	attachment area for flexor muscles	pu.isc.f.	pubo-ischiadic fenestra
cor.	coracoid	gl.	glenoid	ra.c.	radial condyle
d.p.cr.	delto-pectoral crest	he.	head	scap.	scapula
del.	deltoideus muscle	hum.	humerus	tr.m.	trochanter major
Dicy.	<i>Dicynodon</i>	il.	ilium	ul.c.	ulnar condyle
Dicy.d.p.cr.	<i>Dicynodon</i> delto- pectoral crest	isc.	ischium	I-V	digits I to V
		pc.	procoracoid		
		pc.f.	procoracoid foramen		