THE GIRDLES AND LIMBS OF THE DICYNODONTIA OF THE *TAPINOCEPHALUS* ZONE

By

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(With 6 Text-figures)

CONTENTS

INTRODUCTION

The oldest specimens of the Dicynodontia as yet recovered from the Karroo are from the *Tapinocephalus* Zone of the Lower Beaufort Beds. These are of both the families Endothiodontidae and Dicynodontidae. Hitherto six genera and sixteen species have been described—all based on cranial material alone, viz.

Endothiodontidae

Brachyuraniscus broomi
Brachyuraniscus merwevillensis
Brachyuraniscus reuningi
Broilius antjiesfonteinensis
Koupia koupensis
Pristerodon brachyops
Robertia broomiana

Dicynodontidae

Dicynodon antjiesfonteinensis
Dicynodon gamkaensis

Ann. S. Afr. Mus. **50** (1), 1966: 1–11, 6 figs.

Dicynodon haughtoniscus
Dicynodon huenei
Dicynodon jouberti
Dicynodon megalorhinus
Dicynodon pseudojouberti
Dicynodon schroederi
Dicynodon vanderhorsti.

The Dicynodont fauna at this time consisted of an assemblage of small reptiles, with skull lengths varying from 40 to 130 mm. These small reptiles occur abundantly in the *Tapinocephalus* Zone. The South African Museum Collection alone contains 705 specimens. By far the greater number of specimens have been found as eroded fossils lying loose on the surface. Although a number have been found as isolated specimens—some still *in situ*—they mostly occur concentrated in small patches of loose lying rubble. These have been weathered out of thin layers of about 3–5 inches thickness in the mudstone. In the upper part of the zone these layers tend to be arenaceous. In a number of places in the Koup I have collected over a hundred specimens still *in situ* in such thin layers. These specimens are mostly of skulls and parts of skulls with postcranial parts very rare. This material has obviously been washed into shallow pans or depressions, where they were covered up by the inflowing silt. The paucity of postcranial material is in all probability due to the activities of the contemporary carnivores and carrion eaters.

In one locality only—on the farm Michau's Request—have I found a number of skeletons entombed together in a fairly complete state in a purplish layer of fine mudstone of about 12 inches thickness. This find is of a number of these reptiles which had been overwhelmed by some catastrophe and rapidly imbedded.

These small Dicynodontia must have been present in large numbers (flocks?) and formed the diet of the numerous contemporary Therocephalia.

Although occurring throughout the zone the patches where concentrated assemblages have been encountered are mostly in the upper part of the zone. Often these patches include remains—also mostly skulls—of medium-sized Therocephalia.

Hitherto no part of the postcranial skeleton of any Dicynodont from the *Tapinocephalus* Zone has been described.

Material

In this contribution an account will be given of the girdles and limbs of these specimens from the *Tapinocephalus* Zone in the collection of the South African Museum in which parts of these structures are preserved. From the following table of the available material it is evident that much more collecting will have to be done before a really adequate picture of this early stage in the development of the girdles and limbs of the Dicynodontia can be given.

SAM 11588 Endothiodontid. Skull, partial pectoral girdle and humerus. Cypher, Beaufort West, Low *Tapinocephalus* Zone. Collected Boonstra 1940.

SAM 11760 *Robertia broomiana*. Skull, humerus and epipodial. Klein-Koedoeskop, Beaufort West, Low *Tapinocephalus* Zone. Collected Boonstra 1929.

SAM 11825 ? Partial pelvis. Dubbelefontein, Beaufort West, High *Tapinocephalus* Zone. Collected Boonstra 1947.

SAM 11883 ? Vertebral column and ribs with partial girdles and a femur. Steenboksfontein, Laingsburg, Middle *Tapinocephalus* Zone. Collected Boonstra 1948.

SAM 11885 Endothiodontid. A number of fairly complete skeletons. Michau's Request, Beaufort West. Low *Tapinocephalus* Zone. Collected Boonstra and Jooste 1948.

SAM 12255 ? Part of pectoral girdle, humerus and epipodial. Beukesplaas, Fraserburg. Low? *Tapinocephalus* Zone. Collected Boonstra and Zinn 1959.

SAM K259 ? Partial pectoral girdle. Plaatdorings, Beaufort West. High *Tapinocephalus* Zone. Collected Boonstra and Zinn 1960.

SAM K1134 ? Skull and pectoral girdle. Lammerkraal, Prince Albert. High *Tapinocephalus* Zone. Collected Boonstra and Zinn 1959.

Pectoral Girdle

(Fig. 1)

The following description of the pectoral girdle is based on SAM 11588 consisting of a left scapulo-coracoid and cleithrum, SAM 11885 in which there are a number of girdles partially preserved, SAM 12255, with most of the left half of a girdle, SAM K259, with an incomplete left scapula and an interclavicle and SAM K1134 with a complete girdle preserved.

Of the last specimen I have made a plaster model enlarged three times and checked with the others, and this forms the basis of the accompanying figures (fig. 1).

The coraco-scapula is well developed with the scapular blade lying at right angles to the vertebral axis, with only a slight curving around the thorax; the coracoidal plate is fairly large, moderately long but low, with the greater part of its ventral edge resting on the stem of the interclavicle. There is no supra-glenoid buttress or foramen. The scapular facet of the glenoid faces mostly backwards and the coracoidal facet upwards and outwards. The precoracoid does not enter the glenoid.

The scapular blade is high with its dorsal part expanded and its outer face flattened. Along the inside of its anterior face it receives the splint-like cleithrum. Lower down the anterior edge of the scapula is everted and forms a well-developed and prominent antero-laterally directed acromion process. The Dicynodontia are thus the earliest Therapsids in which the acromion process is developed and when encountered as low down as the *Tapinocephalus* Zone it is already as well developed as in any later Dicynodont. None of the other contemporary Therapsids have even an incipient acromion process. The upper end of the clavicle is applied to the inner face of the acromion process. No scar for the scapular head of the triceps can be seen on the posterior face of the scapula above the glenoid.

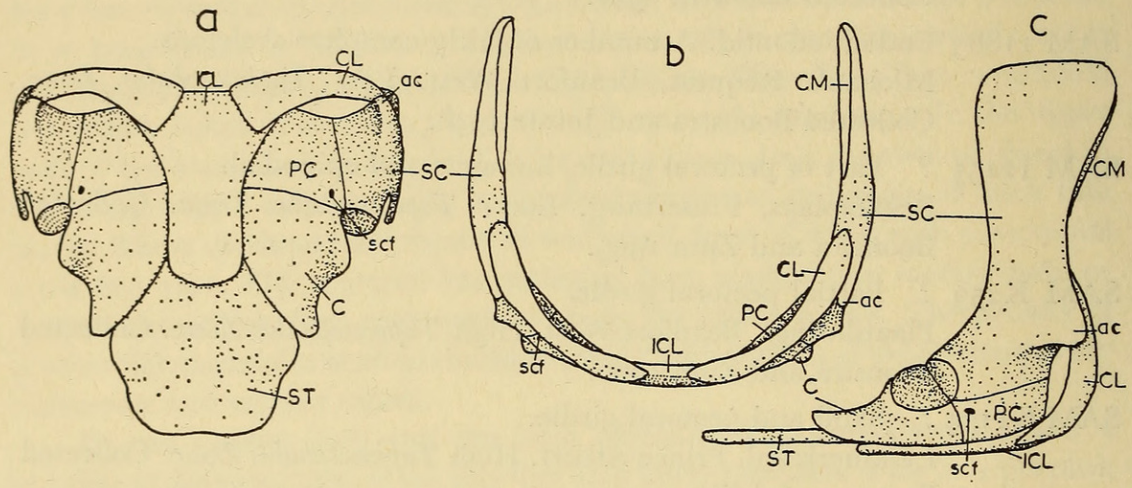

FIG. 1. *Dicynodon jouberti* SAM K1134. Pectoral Girdle × 1.

a. Ventral. b. Anterior. c. Lateral. All figures are orthoprojections.

ac—acromion process
C—coracoid (posterior)
CL—clavicle
CM—cleithrum
ICL—interclavicle
PC—precoracoid (anterior coracoid)
SC—scapula
scf—supracoracoid foramen
ST—sternum

The precoracoid is relatively small; this is mainly due to the lack of development in its anterior part. Its anterior edge does not reach the plane of the clavicle as it does in all the other contemporary Therapsids. The precoracoid is pierced by a moderate foramen supracoracoideum lying in the acute angle formed by the precoracoid anterior to and below the lower edge of the glenoid.

The coracoid is a robust bone with a fairly long upturned posterior process, but there is no special protuberance or scar for the coracoidal head of the triceps.

The dermal clavicular girdle is moderately well developed but the cleithrum is a weak splint-like element lying applied to the inner anterior edge of the scapular blade.

The interclavicle is fairly short; its anterior end, which is expanded, curves slightly upwards and its lateral corners are underlain by the truncated lower ends of the clavicles; the median stem is broad but short without a definite waist or expanded posterior end. The function of an expanded posterior end is apparently exercised by the well-developed ossified sternum.

The clavicle is a well-developed bone, with its expanded ventral end truncated and underlying the antero-lateral corner of the spatulate anterior end of the interclavicle. It ends well away from the median line and does not extend posteriorly under the interclavicle. This relation is thus much as in the contemporary Gorgonopsians and Dinocephalians and quite different from that obtaining in the pristerognathid Therocephalians. From its ventral expanded end the clavicle narrows and curving upwards has its upper end applied to the inner face of the acromion process. The lower part of the scapula and the precoracoid, having little anterior extent, do not lie applied to the inner face of the clavicle, but lie free of it with their anterior edges in a more posterior plane.

The sternum is ossified as a large broad and squarish plate, with its anterior end overlying the posterior end of the stem of the interclavicle, and its antero-lateral edges are underlain by the inner edge of the coracoids. There are no ossified ribs articulating with the sternum.

Pelvic Girdle

(Fig. 2)

Little and poorly preserved pelvic material is available for study. The accompanying figure is a reconstruction based mainly on the specimens SAM 11825 and 11885.

Notwithstanding the inadequate material it is possible to give, in general terms, a statement on the overall nature of the pelvis in these oldest known Dicynodontia, viz. the pelvic girdle is high, short, the pubo-ischium not plate-like, but V-shaped, symphysis absent, pubo-ischiadic fenestra developed; the acetabulum situated above the pubis with its anterior rim on the anterior border of the pelvis. The Dicynodonts of the *Tapinocephalus* Zone are thus the first Therapsids to accomplish the rotation of the pelvis in relation to the acetabulum. This is a *fait accompli* and we know no older forms showing the steps by which this was achieved.

The ilium is high; the iliac blade is large and lies diagonally with the large anterior process directed upwards; the posterior process is weaker, but well developed; the supra-acetabular buttress is strong; about half the acetabulum is formed by the ilium.

The pubis is very short, with its anterior border in a plane posterior to the anterior rim of the acetabulum; its anterior edge carried a well developed tuber which is strongly everted; there is no pubic foramen, but the pubis forms the anterior border of the large pubo-ischiadic fenestra. Ventrally the two pubes

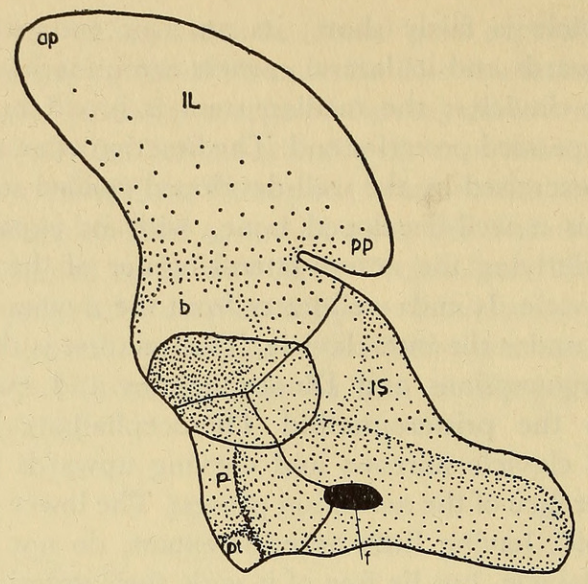

Fig. 2. Dicynodont. Pelvic Girdle × 1. Lateral view.

ap—anterior process of the iliac blade
b—supra-acetabular buttress
f—pubo-ischiadic fenestra
IL—ilium
IS—ischium
P—pubis
pt—everted pubic tuber

meet at an acute angle, but there is no symphysis and no median keel is developed.

The ischium is long; the pair lie at an acute angle, with each other and no median keel is developed. The ischiadic tubera are moderately well-developed. Anteriorly the ischium is pierced by a well-developed pubo-ischiadic fenestra. Here again these early Dicynodonts are the first known Therapsids where the old pubic foramen is superseded by a pubo-ischiadic fenestra.

The Humerus

(Fig. 3)

An indifferently preserved humerus is present in SAM 11760 and in SAM 11885 there are seven humeri and SAM 11588 and 12255 have each a well-preserved humerus.

The humerus is a robust bone with greatly expanded ends, a very strong delto-pectoral crest and a short stout shaft. The rotation of the ends on the shaft varies from 30°–56°.

The proximal surface has the processus medialis and processus lateralis indistinctly demarcated from the caput, which is flattened and narrowly oval in outline.

The delto-pectoral crest is very strongly developed and extends far distally with a thickened bulbous corner for the insertion of the strong m. pectoralis; from here it subsides abruptly into the shaft from where a rounded ridge extends obliquely on to the entepicondyle.

The bicipital fossa is large and fairly deep with a rounded posterior rim, whose posterior face forms a strong and long rectangular area for the origin of the medial head of the m. triceps.

The proximo-dorsal face of the humerus is divided by the anterior dorso-ventral line (ADVL) into two parts. Preaxially to this line lies a triangular area for the insertion of the strong m. deltoideus. Posterior of this line lies the area of insertion for the strong m. latissimus dorsi, whose main insertion is into a hollow extending up to the processus medialis.

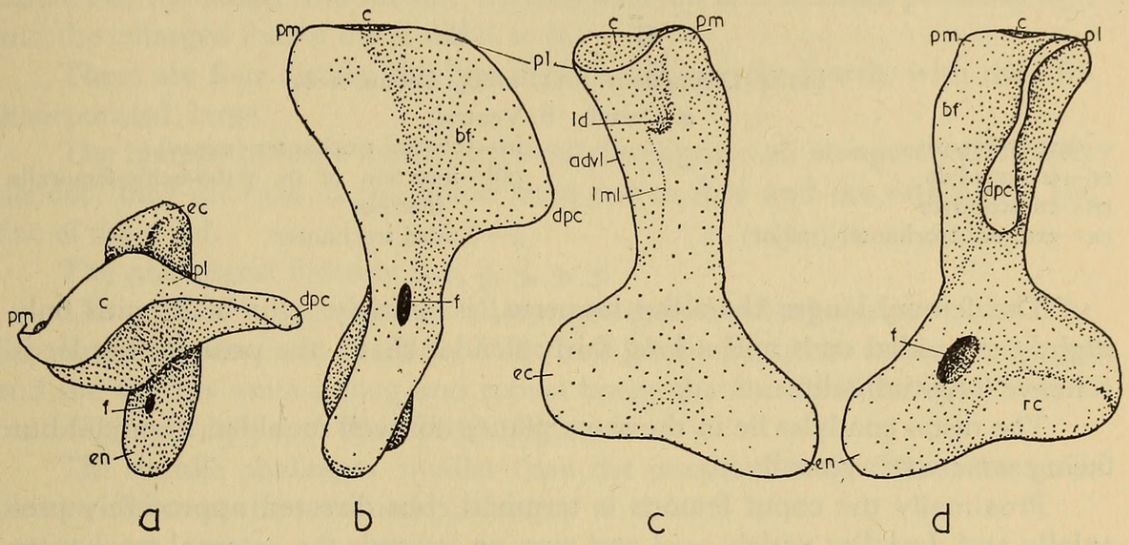

Fig. 3. Dicynodont. SAM 11588. Humerus × ⅔

a. Proximal. b. Posterior. c. Dorsal. d. Ventral.

advl—anterior dorso-ventral line
bf—bicipital fossa
c—caput humeralis
dpc—delto-pectoral crest
ec—ectepicondyle
en—entepicondyle
f—entepicondylar foramen
ld—insertion of m. latissimus dorsi
lml—latero-median line
pl—processus lateralis
pm—processus medialis
rc—radial condyle (capitellum)

Distally the epicondyles are both well developed and robust indicating strong flexors and extensors. The entepicondylar foramen is large and oval in outline. There is no ectepicondylar foramen.

The distal condyles are not strongly developed or well moulded. The radial condyle is directed much ventrally and the epipodial capable of full extension. On the dorso-distal surface the trochlear fossa is very shallow, which feature is related to the absence of an olecranon process to the ulna.

The Femur

(Fig. 4)

In SAM 11855 there are six femora, all small and with the various features not very well shown. The accompanying figure is composite with the features shown only diagrammatically correct.

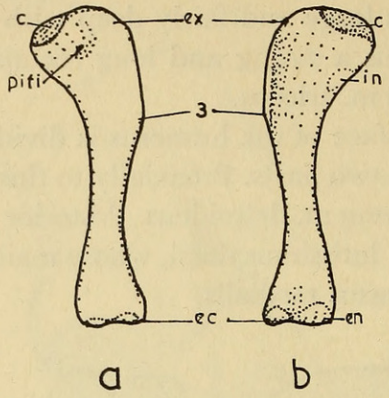

FIG. 4. Dicynodont. SAM 11885. Femur × 1.
a. Dorsal. b. Ventral.

c—caput femoris
ec—ectocondyle
en—entocondyle
ex—external trochanter (major)
in—internal trochanter (minor)
pifi—insertion of m. pubo-ischio-femoralis internus
3—? third trochanter

The femur, longer than the humerus, is a fairly light bone with only slightly expanded ends and a long fairly slender shaft; the preaxial border is concave longitudinally.

The distal condyles lie in the same plane, not well moulded, terminal but facing somewhat ventrally.

Proximally the caput femoris is terminal, but directed appreciably preaxially and dorsally; widely oval and curving towards the external trochanter into which it flows. From the not prominent external trochanter the postaxial edge is thickened rugosely and is turned slightly ventrally; the distal end of this edge forms a slight protuberance and this muscular scar apparently represents a third trochanter.

On the dorso-proximal surface, near the caput femoris, there is an indication of a muscle-scar for the m. pubo-ischio femoralis internus.

On the ventro-proximal surface there is a slight, low mound near the preaxial border of the bone and this represents an internal trochanter for the insertion of the m. pubo-ischio femoralis externus.

The Anterior Epipodial, Carpus and Manus

(Fig. 5)

A good epipodial is preserved in SAM 12255 and in SAM 11760 and in SAM 11885 there are six fairly complete radii and ulnae preserved in natural relation. Under this number there are also eight more or less complete carpi and manus. All are small and not very well preserved so that few details of the structure of the individual bones can be given. The figure given is composite incorporating features from the various specimens.

The olecranon process of the ulna is feebly developed. Proximally the radius abuts against a facet on the ulna and thus forms a continuous articulatory

face sliding round the distal humeral end in extension and flexion. Both the ulna and radius have expanded distal ends.

The proximal row of carpals consists of three elements—a radiale of moderate size, rounded in outline, an ulnare, well developed and elongated, and a laterally compressed intermedium. A disc-like pisiforme lies laterally of the ulna-ulnare articulation.

In the middle row there are two centrals—one, elongated lies between the radiale and the last three distals; the central one, squarish in outline, lies flanked by the ulnare and the first central, with the intermedium proximal to it and the enlarged fourth distal distal to it.

There are four distals; the first three small and the fourth, with the fifth incorporated, large.

The metacarpals are moderately well developed—all elongated and fairly slender; they increase in robustness from one to four and the fifth about the size of the third.

The phalangeal formula is 2, 3, 3, 3, 3.

The proximal phalanges are all elongated, with a long shaft or waist. The first is the smallest and is lightly built and fairly short; the second is longer and the third is quite a long and robust bone; the fourth of the same length but of lighter build and the fifth much shorter.

The middle phalanges, smaller than the proximal ones, follow the same pattern of size as the proximal phalanges.

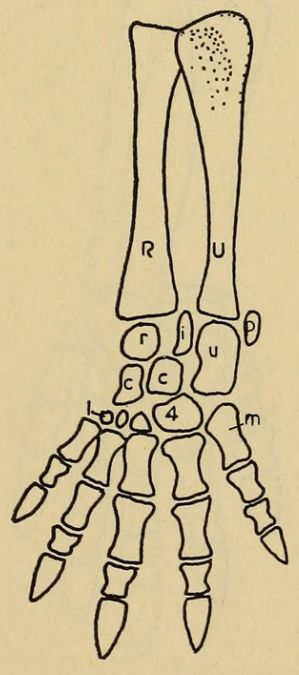

FIG. 5. Dicynodont. SAM 11885. Epipodial and forefoot × $\frac{3}{2}$.

c—centrals
i—intermediam
p—pisiforme
R—radius
r—radiale
U—ulna
u—ulnare
1–4—distal carpals
m—fifth metacarpal

The ungual phalanges are quite broad and apparently carried broad and long nails adapted to digging.

The third digit is the longest and the purchase of the foot mesaxonic.

The Pes

(Fig. 6)

In SAM 11885 I have a nearly complete hindfoot. The preserved mineralized bone has been dissolved with dilute formic acid to leave a good impression of the dorsal surface.

In the proximal row of the tarsus there is a robust astragalus broader than long and a large disc-like calcaneum. The tibia and the fibula articulate with the distal surfaces of the astragalus and calcaneum respectively.

In the middle row there are two centrals. The preaxial one is the larger and lies distally of the astragalus; the smaller central lies lateral of the first and it articulates with the inner edge of the calcaneum.

There are five distal tarsals, all pebble-like except the first, of which the impression in the mould shows only a crescent-shaped ridge. The fifth distal lies far proximally to abut against the outer edge of the calcaneum.

The five metatarsals are of moderate length, but the first is squat.

The phalangeal formula is 2, 3, 3, 3, 3.

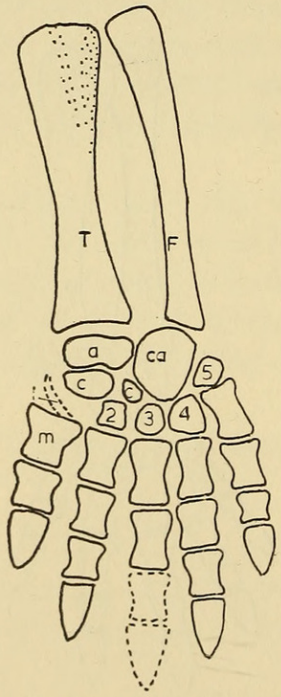

Fig. 6. Dicynodont. SAM 11885. Epipodial and hindfoot × $\frac{3}{2}$.

a—astragalus
ca—calcaneum
c—centrals
F—fibula
T—tibia
1–5—distal tarsals
m—first metatarsal

The phalanges are all fairly long with a good shaft. The proximal one of the third digit is the longest. The ungual phalanges are broad as in the forefoot and probably also carried broad and long nails.

The third digit is the longest and the purchase of the foot was mesaxonic.

Discussion

As I have now completed my study of all the available material of the girdles and limbs of all the Therapsids of the *Tapinocephalus* Zone, I am engaged on a comparative account which will form the concluding paper of this series.

Summary

Descriptions are given of the girdles and limbs of the Dicynodontia of the *Tapinocephalus* Zone in South Africa. Postcranial parts are rarely found and of the 705 specimens in the South African Museum eight have parts of the girdles and limbs present and this account is based on these specimens.

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