NEW TRIASSIC ARCHOSAURS FROM TANGANYIKA

including

Mandasuchus and Teleocrater

being a dissertation submitted for the degree of Doctor of Philosophy in the University of Cambridge

by

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PREFACE

DECLARATION OF ORIGINALITY OF DISSERTATION

I hereby declare that the work embodied in this dissertation is entirely original, except where specific references to the publications of other authors have been made in the text.

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1. INTRODUCTION

a) GENERAL INTRODUCTION

Mr. F.R. Parrington, present Director of the University Museum of Zoology in Cambridge, made a large collection of fossils during 1933 in the Ruhuhu district of Tanganyika. This dissertation consists mainly of a description of the archosaur reptiles (including two new genera) which occur in the Parrington collection, and of a discussion of matters of taxonomy and stratigraphy arising out of that description.

Mr. Parrington kindly accepted responsibility from the Board of Research Studies for the direct supervision of the research. The author wishes to express his thanks to Mr. Parrington for his unfailing advice and encouragement as well as for the loan of his material. Thanks are also due to the Department of Scientific and Industrial Research, whose award made this work possible; to Professor Sir James Gray, F.R.S., the Supervisor appointed by D.S.I.R.; to Professor Baron von Huene of Tübingen, for his advice, for the loan of all the original Spondylosoma material and for permission to photograph the latter;

to Dr. E.H. Colbert of New York, for copies of unpublished drawings of *Coelophysis*; to Mr. A.D. Walker of Newcastle-upon-Tyne, for unpublished information on *Stagonolepis* and "*Aëtosaurus*"; to my wife; and to many others.

b) HISTORICAL SURVEY OF THE STRATIGRAPHY OF THE RUHUHU VALLEY

The Ruhuhu coalfields lie in Tanganyika Territory, to the east of Lake Nyasa. The appearance of the Karroo Formation in this part of Africa was first postulated by STROMER von REICHENBACH (1896), who based his conjectures on the scanty reports of travellers. Limited geological investigations of the district were made in 1895-1897 by the German geologist BORNHARDT (1900), and later by DANTZ (1903) and GILLMAN (1927). None of these workers records the collection of any fossil vertebrates; the strata were identified on plant remains.

In 1930, however, STOCKLEY of the Tanganyika Geological Survey spent five months in the field investigating the stratigraphy of the district, and while so doing collected a quantity of fossil material. A detailed account of the stratigraphy of the region was published (1931, 1932).

NOWACK's expedition of 1934-1936 was mainly palaeontological in purpose, but supplementary stratigraphical observations were made. They are included in his description of the expedition (1937).

A short synopsis of the knowledge of the stratigraphy of the Ruhuhu district is given by Teale and Stockley (HAUGHTON 1936).

c) HISTORICAL SURVEY OF THE PALAEONTOLOGY OF THE RUHUHU VALLEY

The palaeontology of the Ruhuhu coalfields remained entirely unknown until 1932. In 1930, however, the first collections were made by Stockley during his work in the area. His expedition was not primarily palaeontological in purpose, and the material consisted largely of weathered surface fragments from four distinct fossiliferous beds. These were the Ruhuhu Beds (Stockley's K.5), the so-called "Lower Bone Bed" (K.6), the Kingori Sandstones (K.7), and the "Upper Bone Bed" occurring within the Manda Beds (K.8). (In a discussion of Stockley's paper Watson pointed out that the term "bone bed" is properly applied to a single horizon on which bones are exceedingly abundant, and not to a bed, such as those found in the Ruhuhu district, in which bones merely happen to occur sporadically).

The fossils found included plants, lamellibranchs and vertebrates; whereas the plants are described by Walton in an appendix to STOCKLEY's own paper (1932), the lamellibranchs are described by COX in a separate paper (1932) and the vertebrates by HAUGHTON (1932).

The Ruhuhu Beds yielded no vertebrates whatsoever, the only fossils determined being five species of the lamellibranch Palaeomutela and assorted plant material. The "Lower Bone Bed" yielded several dicynodonts and a small quantity of labyrinthodont, pareiasaur and gorgonopsid bones, in addition to the gymnosperm Dadoxylon. As Haughton pointed out, "the fossils from the Lower Bone Bed have a strong facial resemblance to those from the Lower Beaufort Beds of the Union" (of South Africa), and there seems to be little reason to doubt the Permian age of the Ruhuhu Beds and "Lower Bone Bed". The Kingori Sandstones yielded two nearly complete neural arches compared by Haughton to those of Titanosuchus, although he himself remarked that the fossil occupies an anomalous position if this is correct; von HUENE (1950) refers to this specimen as a large dicynodont. The only other material found in these Sandstones consisted of the quadrate and squamosal of an indeterminate dicynodont and various fragments of limb-bones and girdles. No subsequent worker has shown the presence of diapsids in any of the three strata mentioned above.

The yield of the "Upper Bone Bed" resembled that of the "Lower" in that it contained dicynodonts, although the only genus common to both beds was Dicynodon itself, and no common species of that genus was recognised in both. The "Upper Bone Bed" also included a quantity of diapsid material and, in addition, two pieces of a large labyrinthodont skull, the lamellibranch Unio, and the wood of Rhexoxylon. Haughton noted that in South Africa dicynodonts do not occur above the Upper Beaufort Beds (Cynognathus zone), while diapsids of the type found in Tanganyika do not occur below the Red Beds. The Molteno Beds, which lie between the Beaufort and the Red Beds and in which a mingling of their two faunas might be expected, have unfortunately proved to be virtually barren except of plants. Haughton accordingly suggested that the "Upper Bone Bed" was probably homotaxial with these Molteno Beds.

Haughton determined the following diapsids from the "Upper Bone Bed" of the Ruhuhu:

1. Stenaulorhynchus stockleyi gen. et sp. nov.

The type of this species is the proximal half of a right humerus. Paratypes included other fragments of humeri and femora belonging to animals of different sizes; three dorsal vertebrae attached to one of the femoral fragments and a similar vertebra found in isolation; and a skull portion consisting of parts of the maxillae. Haughton remarked upon the resemblance of the limb-bones to those of the Brazilian rhynchosaurs Cephalonia and Scaphonyx described by von HUENE (1926b, 1935-1942); but noted also the differences between the vertebrae of Stenaulorhynchus and those of the Brazilian animals, commenting that "the Tanganyika bones - if the association of limb-bones and vertebrae is justified - must belong to the Archosauria, in which the dorsal ribs are attached exclusively to the arch (at least in the anterior part of the column) by two articulations." The nature of the narrow snout portion with its large teeth seems further justification for Haughton's assignment of this genus to the Thecodontia.

2. Stenaulorhynchus major sp. nov.

This type is founded upon the distal half of a left humerus, larger than that of S. stockleyi but otherwise similar. The almost exactly similar distal half of a right humerus was also found.

3. Thecodontosaurus(?) alophos sp. nov.

Four incomplete vertebrae - two anterior cervicals and two dorsals - were assigned by Haughton to the Theropoda, and placed temporarily in the genus Thecodontosaurus.

4. Theropod gen. et sp. indet.

An isolated incomplete dorsal vertebra was also assigned to the Theropoda.

Parrington's expedition to the Ruhuhu district in 1933 was the first conducted in the area for expressly palaeontological purposes. A large collection was obtained, consisting mainly of reptile material. It had not proved possible to undertake a serious examination of the diapsid content of this collection until the present writer began work on it in 1951, except in that four specimens were sent for description to Professor von Huene in Tübingen. One, already prepared by Parrington, consisted of a right maxilla, eight dorsal and three caudal vertebrae (some incomplete), an incomplete left scapula, the proximal half of a left ischium, dermal scutes, and an unrecognisable fragment. Von HUENE (1939b) made it into the type-specimen of the new genus and species Parringtonia gracilis, a small pseudosuchian. The second specimen was identified as two adjacent fragments of the left maxilla of a saurischian of indeterminate genus, and was described in the same paper. The other two specimens proved to be respectively portions of the left and right maxillae of Stenaulorhynchus (see below); they are described and figured in von Huene's paper on that animal.

From this collection PARRINGTON described a new

Permian cynodont (Parathrinaxodon proops, 1936a); he also mentioned other portions of theriodont skulls and jaws, too fragmentary to be named, in a subsequent paper on tooth-replacement (1936b). A new species of a Triassic cynodont, Trirachodon angustifrons, was later described from the "Upper Bone Bed" (1946).

A further collection from the Ruhuhu valley was made by Nowack in the period 1934-1936, his material being distributed between von Huene in Tübingen, Broili and Schröder in Munich, and Parrington in Cambridge. From such material two new gorgonopsids - Tetraodon nowaki and another unnamed, - were described by BROILI & SCHRÖDER (1936). Both animals are represented only by preorbital skull fragments from the "Lower Bone Bed". In the same paper Broili and Schröder also described five isolated cynodont teeth from the "Upper Bone Bed".

Von HUENE described two diapsids from his part of Nowack's collection. One was a large rhynchosaur of which several individual skeletons are available, some - including the skull - in a remarkably complete state of preservation; detailed description of the entire beast was possible (1938b). It was at once apparent that the limb-bones of Haughton's Stenaulorhynchus stockleyi belonged to the same species. The vertebrae and skull fragments described by Haughton as _Stenaulorhynchus stockleyi_ were, however, quite different from those of von Huene's animal, being (as Haughton himself had pointed out) markedly archosaur in character. It was therefore evident that Haughton's doubts in associating these bones with the limb-bones were well justified, even though three of the vertebrae were found adhering to a fragment of femur (itself indisputably _Stenaulorhynchus_); and that his tentative identification of the type-specimen as thecodont was incorrect.

The other diapsid described by von HUENE (1938a) from Nowack's collection was another pseudosuchian, a large stagonolepid to which he gave the name _Stagonosuchus nyassicus_. Two specimens were available. The post-cranial skeleton was fairly well represented, but of the skull only one postfrontal was found.

A list of the diapsids known from the "Upper Bone Bed" of Tanganyika is included in von HUENE's faunal lists (1940a). He gives _Stenaulorhynchus stockleyi_ as the only rhynchosaur, making no mention of Haughton's _S. major_, which latter he had referred in an earlier paper (1939b) to _Stagonosuchus_. As pseudosuchians he gives _Parringtonia gracilis_, _Stagonosuchus nyassicus_, and the vertebrae and skull fragments described by Haughton as _Stenaulorhynchus_. As saurischians he lists the maxilla of indeterminate genus collected by Parrington; Haughton's "Thecodontosaurus" vertebrae, possibly belonging to the same genus as the maxilla but not to the genus Thecodontosaurus; and Haughton's isolated anterior dorsal vertebra, again possibly belonging to the same genus, but, if so, to an earlier growth stage.

Subsequent publications by von HUENE have described the dicynodonts (1942b), pareiasaurs (1944) and theriodonts (1950) from the Tübingen portion of Nowack's collection. Other publications of von HUENE refer more generally to the Ruhuhu fauna and its relationships (1938c, 1939a,c,d).

A more recent faunal list for the Ruhuhu area - that of 1940 together with the dicynodonts, pareiasaurs and theriodonts described later - is given on pp. 130-131 of von HUENE's paper on the theriodonts of the district (1950). (This paper, presumably in error, omits all reference to Parringtonia gracilis; while Parathrinaxodon proops from the "Lower Bone Bed" is incorrectly described as occurring in the Manda Beds).

BOONSTRA (1953) described a quantity of Ruhuhu material collected by Stockley. From the "Lower Bone Bed" he described various dicynodonts, two pareiasaur vertebrae, the new gorgonopsid Tangagorgon tenuirostris and therocephalian snout fragments. (The pareiasaur Anthodon minusculus HAUGHTON is mentioned as occurring in the "Upper Bone Bed", but it seems more likely that this specimen was actually found in the "Lower Bone Bed" and that there was an error in labelling). From the "Upper Bone Bed" Boonstra reported the dicynodonts Lystrosaurus, Kannemeyeria and ?Aulacephalodon, the cynodont Trirachodon, the rhynchosaur Stenaulorhynchus stockleyi, a new species of Stagonosuchus (S. tanganyikaensis) based on a single humerus, and a single anterior caudal vertebra which he compared to that of Thecodontosaurus.

CROMPTON (1955, in press) has described new cynodonts from the Parrington collection. These include the new genus Scalenodon, based on the former Trirachodon angustifrons PARRINGTON; Cricodon metabolus; Aleodon brachyrhamphus; and an animal compared to Gomphodontosuchus brasiliensis von HUENE.

2. FOSSIL MATERIAL

a) DESCRIPTION OF MATERIAL AND ITS CONDITION OF PRESERVATION

The localities from which Parrington collected his specimens were those discovered by Stockley and were numbered, as in Stockley's paper, B1-B35; some were divided into sections, e.g. B9/1, B9/2. One new locality, B36, was found near Mkongoleko.

Most of the specimens were collected on or near the surface and were contained within a matrix of marl or reddish-brown felspathic sandstone. STOCKLEY (1932) describes the lithology of the Manda Beds as "variegated marls and pink and purple felspathic sandstones . . . (in which) . . . a reptilian bone bed was found, usually associated with a concretionary ferruginous limestone." The layer of matrix surrounding the fossils was not usually thick enough (less than 3mm.) to disguise the form of the more characteristic bones, especially when the latter were unbroken. The hardness of the matrix varied considerably from specimen to specimen; in some cases (e.g. specimen no. 2) the rock was soft and much of it could be removed quite easily with a hand-needle, whilst in others (e.g. specimen no. 13) much was extraordinarily hard and could be chipped off effectively only by repeated full-strength blows of the automatic mallet. An interesting feature, useful in preparation, was the frequent appearance of a thin reddish layer of matrix immediately next to the bone surface. Calcite crystals had also been deposited around some of the bones, particularly in concavities, and filled the hollow shafts of the major limb-bones.

Many of the bones had been broken into several pieces and had sometimes been found scattered over a wide area, but their restoration was facilitated by Mr. Parrington's careful method of collection. The bones themselves, however, were in general remarkably well preserved and showed little sign of crushing or distortion, although such phenomena were not entirely absent. Their colour varied from shades of white, tinged with purple, blue, green or yellow, to a light reddish-brown.

It was evident that many of the field-collections, to which Parrington had assigned consecutive numbers, contained more than one individual. The method of differentiating these individuals (by alphabetical suffixes) is given in Appendix I.

b) LABORATORY METHOD

The entire collection was examined for the remains of diapsid reptiles; which, thanks to the nature of their preservation, were usually recognisable in the matrix before they were prepared. The results of this examination are summarised in Appendix II. Apart from the archosaur material described in Chapters 3 and 5 below, there was only abundant material of Stenaulorhynchus, one very small badly weathered skull (specimen no. 119a), and perhaps two small mandible fragments (specimen no. 120c).

The fossils selected for development were first soaked in water and gently scrubbed to remove the mud and loose matrix adhering to them. Broken surfaces were matched and glued together, restoring the broken bones in some degree. Friable bones were painted with a solution of "Durofix" in amyl acetate diluted with acetone in order to harden them. The matrix was then removed mechanically, most of the work being done with the automatic mallet (using a tempered gramophone- or darning-needle as the actual striking point), and the rest with dental burrs and hand-needles. Chemical preparation with 15% acetic acid (TOOMBS, 1948, and RIXON, 1949) was tested but was generally found to be less reliable; the acid damaged the surface of the bone, even when the latter was protected by a film of polystyrene dissolved in ethyl acetate, and attacked the matrix filling in the cracks. This method nevertheless proved useful in certain instances, notably with some of the more incomplete specimens. The process of matching broken surfaces and glueing them together was continued after the removal of the matrix until no further restoration appeared possible. Cracks and joints in the bones were filled with a mixture of modelling clay and gum acacia, and the heavier limb-bones were reinforced internally by metal pins; the specimens were thus rendered easier to handle.

In the case of specimen no. 13 one fragment of matrix bore a small number of dermal scutes, the inner surfaces of which were exposed; the matrix was exceptionally hard and up to 20mm. thick, while the scutes were very soft and often less than 1mm. thick. Mechanical preparation being therefore impracticable, the scutes were developed by a combination of treatment with acetic acid and the "Transfer Method" of TOOMBS & RIXON (1950), by which latter process both sides of delicate specimens may be rendered visible. The material was embedded in a block of synthetic resin; before the resin had set completely, it was cut away to expose the upper surface of the fragment (i.e., the surface <u>not</u> bearing the scutes). When the resin was quite hard the other faces of the block were ground smooth and polished. The exposed rock surface was then treated with 15% acetic acid, and the matrix gradually disintegrated; the outer surfaces of the scutes eventually appeared. When all the matrix had been removed and the scutes well washed and dried, the cavity in the block was filled with more resin; and, when this had hardened, the upper surface of the block was also ground smooth and polished. The scutes, being now embedded in a transparent rectangular block of resin, are clearly visible on all sides and may be handled with perfect safety.

3. DESCRIPTION OF NEW TYPES

Each of four specimens in the collection (nos. 11b, 13, 48b and 63) appears to represent a considerable part of the post-cranial skeleton of a hitherto undescribed archosaur. In addition, jaw fragments are present in specimens nos. 11b and 63.

Three of these specimens (nos. 11b, 13 and 63) may be referred to the same new genus (*Mandasuchus*); and, at least provisionally, to the same species (*M. longicervix*). The fourth specimen (no. 48b) is quite distinct from the others, and is described as the type-species of a second new genus (*Teleocrater tanyura*). A fragmentary specimen (no. 53a) is also referred to *Teleocrater tanyura*.

The order of the Archosauria into which these new reptiles should be placed is not entirely self-apparent, and a brief discussion at this point may clarify the matter. Von HUENE (1921) listed characters by which the Pseudosuchia (order Thecodontia) might be distinguished from the Coelurosauria (order Saurischia). The Saurischia indeed "represent an orthogenetic continuation of certain Pseudosuchia without break, systematic separation is artificial, but preferable for practical reasons" (von HUENE, 1948). The new genera described below, especially _Teleocrater_, are probably closer to the line of this systematic separation than any animals described previously, and show certain characters which, considered alone, would justify the inclusion of the genera in either order. In the past it has appeared desirable to select one simple character, differing in the two groups, which might be regarded as absolutely diagnostic of the groups. The character usually chosen has been the nature of the acetabulum: closed in the Pseudosuchia, open in the Saurischia. The acetabulum is closed in both the new genera; under the existing scheme of classification they must therefore be regarded as Pseudosuchia. Comments on this scheme of classification appear in Chapter 4 below.

Most of the fragments of each specimen have been illustrated in several aspects.

a) MANDASUCHUS LONGICERVIX gen. et sp. nov.

The generic name Mandasuchus refers to the Manda Beds in which the genus occurs, and the trivial name longicervix to the elongation of the neck, a feature formerly thought to be unusual in pseudosuchians.

Specimen no. 11b, the most complete of the three skeletons concerned, was chosen as the type of the new genus and species. The other two specimens differ markedly in size from the type-specimen, one (no. 13) being much smaller and the other (no. 63) much larger. An indication of the order of difference is given by the following measurements, which represent the ventral length of the centrum in the seventh or supposed seventh cervical vertebra of each animal:

no. 13	26mm.
no. 11b (type-specimen)	35mm.
no. 63	45mm.

Such differences as exist between the type-specimen on one hand and specimens nos. 13 and 63 on the other are indicated in detail in the descriptions of the latter two skeletons. These differences, other than those attributable to post-mortem distortion, appear to consist only of differences in proportion (which could be due to variations in rates of growth in different parts of the body); there are no significant differences in form. On the contrary, corresponding bones bear a detailed resemblance to each other which is often striking. Specimens nos. 13 and 63 are therefore referred to the genus Mandasuchus. Whether or not they are truly co-specific with the type-specimen is a question which is discussed more fully below (Sub-section vi); to designate them as separate species appears undesirable at the present time.

Under these circumstances it is felt that the following helpful procedures are both legitimate:

i) The diagnosis of the type-species, while based very largely on the type-specimen, has been amplified to a small extent by the inclusion of certain facts obtained from a study of the other two specimens. These facts refer to the presence and general form of a few bones lacking in the type-specimen, and not to their relative proportions; and it may be inferred with confidence that such information would be equally true of the type-specimen.

ii) The probable positions of the preserved vertebrae in the incomplete vertebral column of the type-specimen, which would otherwise have been difficult or impossible to determine, have been deduced as far as possible by correlation of this vertebral column with those of the other two specimens. These also lack many vertebrae, but a fairly complete idea of the vertebral succession in the genus may be obtained from a comparative study of all three skeletons. The method by which this correlation has been done is given below (Sub-section ii) and summarised in the accompanying Table. In the following descriptions of the three specimens most of the vertebrae whose positions cannot be determined with certainty are accordingly referred to as the "supposed fourth cervical", "supposed first dorsal" and so on; and, where the position of the vertebra cannot be deduced with a fair degree of probability (as in the tail), a phrase such as "possible sixth caudal" is used instead. The characters of the vertebral column as given in the diagnosis are also based to some extent upon this method of correlation.

It should nevertheless be emphasised that the <u>detailed description of the type-specimen</u> of <u>Mandasuchus longicervix</u> is based entirely on specimen no. 11b and no other. The other specimens are described separately, and only in so far as they supplement the description of the type-specimen, confirm characters shown but poorly by the type-specimen, or differ from the latter; it may otherwise be assumed that they resemble it in detail.

i) Diagnosis

Mandasuchus gen. nov.: as for *M. longicervix* below.

Mandasuchus longicervix gen. et sp. nov.:

Pseudosuchian tending towards large size.

Skull unknown, except for fragments of maxilla and dentary, former showing presence of large antorbital vacuity; jaws long. Dentition thecodont; teeth recurved, laterally somewhat compressed, with anterior and posterior borders crenulated.

Vertebrae with length of centrum never much less than its diameter and usually greater; centra lightly amphicoelous; floor of neural canal deeply concave within each centrum, except in posterior caudal region; zygapophyses moderately oblique; tops of neural spines, especially in anterior part of column, flattened and expanded to bear dorsal scutes. Axial and caudal intercentra only. At least twenty-five pre-sacral vertebrae represented, actual count may be slightly higher. Eight cervical vertebrae (by arbitrary definition) including atlas; axis slightly elongated, other cervical vertebrae much elongated (up to 50% over typical dorsals), elongation being greatest in fifth; axis and third cervical with prominent keel, faint ventromedial ridge in others; neural spines low; axial and cervical ribs present, latter crocodiloid. At least seventeen dorsal vertebrae; centra mostly rounded beneath, some slightly flattened; typical archosaurian shift in position of rib-articulation, parapophysis being borne entirely on centrum in second dorsal, on both centrum and neural arch in third and fourth, and on neural arch alone in fifth; diapophysis supported by oblique radiating buttresses in anterior dorsals; parapophysis and diapophysis tend to form "spectacles"-shaped rib-articulation and then to fuse in posterior dorsals; most, if not all dorsal vertebrae with hyposphene. Sacral vertebrae two in number. Caudal vertebrae, except most anterior members, flattened ventrally and with haemapophyses (absent in first three); distal caudals with small median pre-neural spine between prezygapophyses, anterior to neural spine proper; rami of proximal end of each haemapophysis joined by bridge, at least in distal part of tail.

Major limb-bones moderately long and slender, with hollow shafts; propodials longer than epipodials; bones of fore-limb about two-thirds as long as corresponding bones of hind-limb. Scapula broad both dorsally and ventrally, only moderately inflected; coracoid with small foramen; dermal elements of pectoral girdle not known. Humerus with high delto-pectoral crest, well marked supinator process and ectepicondylar groove, no entepicondylar foramen or groove; ulna without olecranon; manus unknown. Acetabulum closed; ilium with short anterior spine, long posterior spine, well developed supra-acetabular crest, forms most of acetabulum; pubis long, with small obturator foramen, twisted proximally in typical pseudosuchian manner, distally plate-like and directed steeply downwards, thickening of lateral corner of distal end; ischium also elongate, peduncle flattened laterally and with sharp anteroventral edge, possibly not meeting its fellow in mid-line but diverging from it distally, distal end lightly thickened. Femur slightly sigmoidal, with prominent fourth trochanter high on shaft; fibula with anterior muscle-process; fibulare crocodiloid, pes otherwise unknown.

Paramedian dorsal scutes, not corresponding in number with vertebrae but more numerous, keeled externally, each notched posteriorly and overlapping anterior spine of scute behind it, without ornament.

ii) Correlation of the three incomplete vertebral columns

(specimens nos. 11b, 13 and 63)

General method.

The individual vertebrae in each column were placed in an antero-posterior series. In certain cases some of the vertebrae had been found either cohering in the matrix or else lying adjacent to each other in the field and apparently *in situ*; and in other cases the disordered fragments presented broken surfaces which, fitted together in the laboratory, provided further evidence of succession. In particular, zygapophyses were often broken off and attached to the neighbouring vertebrae. This evidence was supplemented by observation of the general characters of the vertebrae and of trends in changes of dimensions and form. Correlation between the columns was then effected on the form of the vertebrae; the scheme is set out below and is summarised in the following Table. (See pp. 46-48).

Distinction between cervical and dorsal regions.

The distinction between the cervical and dorsal regions of the vertebral column is usually based upon the fact that the cervical ribs, unlike the dorsal ribs, are not attached to the sternum. Alternatively, the cervical region may be defined as that part of the column lying in front of the pectoral girdle. These criteria cannot be applied in the case of a fossil such as Mandasuchus, where, in all specimens discovered, most of the ribs and sternum are not preserved, and where the relative positions of the bones are still unknown. It therefore becomes necessary to make an arbitrary division between neck and trunk upon the characters of the vertebrae themselves; and even these change gradually along the length of the column, without abrupt discontinuity at the hinder end of the neck. The following three characters have been selected as the best upon which to base this distinction:

Cervical region

1. Centra elongated.
2. Diapophysial buttresses absent.
3. Diapophysis low on neural arch.

Dorsal region

1. Centra not elongated.
2. Diapophysial buttresses present.
3. Diapophysis high on neural arch.

Nomenclature.

The typical archosaur vertebra is remarkable in that the diapophysis is often supported by four radiating diagonal buttresses; these are especially well developed in the anterior dorsal region. It is thought that the description of a large number of these vertebrae will be facilitated by the introduction of a standard nomenclature for these buttresses and for certain other unnamed features to which frequent reference must be made.

It is proposed that the buttresses be known as the diapophysial buttresses. The anterodorsal buttress originates in the region of the diapophysis and runs upwards and forwards towards the prezygapophysis, sometimes becoming confluent with the outer edge of the latter. The anteroventral buttress runs downwards and forwards and may connect with the parapophysis. The posterodorsal buttress runs upwards and backwards towards the postzygapophysis, sometimes becoming confluent with its outer edge. The posteroventral buttress runs downwards and backwards. The anterior buttresses may be called the anterodorsal lamella and the anteroventral lamella when they assume the form of thin plates; the posterior buttresses likewise.

It is further proposed that the deep hollows which lie between these buttresses be known as the pleural concavities. The anterior pleural concavity lies in front of the diapophysis, between the antero-dorsal and the anteroventral buttresses (or lamellae).

The posterior pleural concavity lies behind the diapophysis, between the posterodorsal and posteroventral buttresses. The superior pleural concavity lies above the diapophysis, at the base of the neural spine. The inferior pleural concavity lies below the diapophysis, between the anteroventral and posteroventral buttresses.

Finally, it is suggested that the two great ridges which diverge downwards and forwards from the anterior border of the neural spine and which normally terminate in the prezygapophyses should be known as the anterior spinal buttresses, and the hollow between them as the anterior spinal concavity. It is correspondingly proposed that the ridges which diverge downwards and backwards from the posterior border of the neural spine and which terminate in the postzygapophyses should be called the posterior spinal buttresses, and the hollow between them the posterior spinal concavity.

Abbreviations.

The cervical vertebrae are indicated by the abbreviations Ce1, Ce2 etc.; the dorsal vertebrae by D1, D2 etc.; the sacral vertebrae by S1 and S2; the caudal vertebrae by Ca1, Ca2 etc.; and a series of posterior caudal vertebrae by PC1, PC2 etc. Specimen no. 11b is indicated by the use of these abbreviations alone; specimen no. 13 by the use of a single apostrophe (Ce1', Ce2' etc.); and specimen no. 63 by the use of a double apostrophe (Ce1", Ce2" etc.).

Scheme of correlation.

Vertebrae Ce1" to Ce8" form an unbroken series beginning with the odontoid (part of Ce1") and axis (Ce2") and continuing through five complete centra with portions of neural arches and ribs attached to Ce8", represented only by the anterior part of the centrum. The exact identity of these vertebrae is therefore not open to doubt. A large fragment is very probably the neural spine of the axis (Ce2"), but there is no direct evidence for this.

In specimen no. 11b one centrum is present which is not much elongated and which bears a ventromedial keel; in these characters it resembles Ce2" and is plainly that of the axis (Ce2). The characteristic neural spine with postzygapophysis is also present, and is almost certainly that of the axis, although again there is no direct evidence for the association. Three cohering cervical vertebrae follow Ce2; the first of these is very incomplete, but resembles Ce3", and only Ce3", in the extreme shallowness of the depression on either side of the base of the neural spine. It is therefore presumed to be Ce3; the two vertebrae which follow it are Ce4 and Ce5.

In specimen no. 13 a centrum is present which again is obviously that of the axis (Ce2'); confirmation of this is provided by the form of the anterior face, which is shaped to receive the odontoid and the axial intercentrum. Another centrum, slightly more elongated and with a ventromedial ridge far better developed than in the following vertebrae, resembles Ce3" and is taken to be Ce3'. Ce3' is followed by two coherent cervical vertebrae and then by an unbroken run of another six and a half. Considerations of vertebral length and of general form lead to the belief that no vertebrae are missing after Ce3'; if the next pair be Ce4' and Ce5', then all three columns agree very well in that the length of the centrum increases from the axis backwards to reach a maximum in Ce5, Ce5' and Ce5", and then decreases again towards the posterior end of the neck. (The centra of Ce3, Ce4 and Ce5 are preserved only in part; but Ce3 is clearly shorter than the other two, and the relative lengths of the centra of Ce4 and Ce5 may be estimated from a comparison of their respective measurements from the front of the root of the prezygapophysis to the back of the root of the postzygapophysis).

Let it be supposed that no vertebrae are missing between Ce5' and the most anterior of the next coherent series, the members of which will therefore be numbered Ce6'-Ce8' and Dl'-D4' (D4' being represented by its anterior half only). Ce6', Ce7' and Ce8' are then moderately elongated, while Dl' and the succeeding vertebrae are very much shorter. Comparing the necks of specimens nos. 13 and 63 in ventral view, with particular reference to the gradually increasing distance between the parapophyses of either side, Ce8' is most nearly comparable to Ce6"; since it is absolutely certain that the latter vertebra is indeed the sixth cervical, there appears to be no reason to suppose the existence of additional vertebrae between Ce5' and Ce6'. In specimen no. 11b three other elongated vertebrae are present, and these have been numbered Ce6, Ce7 and Ce8; the longest has been assigned the number Ce6 and, since the other two are of approximately equal length, one has been numbered Ce7 by comparison with the very similar vertebra Ce7'. These, unlike Ce8', have no anterior pleural concavity (similarly absent in Ce7" and present in Ce8").

Specimen no. 11b includes some rather poorly preserved anterior dorsal vertebrae. One of these bears a parapophysis in a low position, comparable to that seen in Dl', and is probably Dl. Another possesses the characteristic diapophysial buttresses of the anterior dorsals; it has a large parapophysis, most of which is borne on the neural arch and the upper end of which is approximately level with the middle of the neural canal. In these features it most nearly approaches D4', and has therefore been numbered D4.

The posterior half of the centrum of an anterior dorsal vertebra of specimen no. 13 and the greater part of the succeeding vertebra are present; the latter resembles the anterior half of D4'. It is therefore probable that these two vertebrae are the posterior half of D4' (with the anterior half of which it makes an approximate fit) and the major portion of D5'.

Three anterior dorsals of specimen no. 63 are also present. The most anterior of these is represented only by a fragment of the centrum bearing a low parapophysis. As in D1', but in contrast to the condition in D2', the anteroventral lamella does not approach this parapophysis closely; this vertebra could therefore be D1". The other two are consecutive, better preserved, and, in the more elevated position of the parapophysis and in the arrangement of the buttresses, approach most closely to D4' and D5' respectively. They have therefore been numbered D4" and D5". In D4", as in D4 and D4', the neural arch appears to bear most of the parapophysis; in D5' and D5" the neural arch bears the whole of the parapophysis. In these latter two vertebrae the whole height of the parapophysis is just about level with the whole height of the neural canal.

In specimen no. 11b the remaining vertebrae of the pre-sacral series are probably all present. What appears to be the most anterior of these bears a parapophysis in a fairly high position, its base lying above the base of the neural canal; it cannot therefore correspond to D5' and must be at least D6. One centrum, so broken and weathered that no traces of neural arch or parapophysis remain, must on general form belong to this region and is probably D5. As the parapophysis rises posteriorly in the series, so the anterior pleural concavity becomes narrower and finally disappears; a run of five well preserved vertebrae (found in their natural relative positions) has been numbered D8-D12, for an exceptionally well preserved vertebra found on its own appears intermediate between D6 and D8 in this respect and has been numbered D7. The positions _inter se_ of the last five pre-sacral vertebrae preserved are more open to doubt than those of most of the other vertebrae. One of these, which has been numbered D13, has a neural spine closely resembling that of D12 and differing from those of the others. Of the remaining four, numbered D14-D17, D16 is represented by a centrum only and is attached to the posterior face of D15. That D14 lies in front of both D15 (and hence D16) and D17 is shown by the fact that in D14, as in D12 and the preceding vertebrae, the parapophysis and the diapophysis are not fused together; in D15 and D17 they are so fused. A difficulty arises here because of the fact that certain characters of D13, such as the fusion of the parapophysis and the diapophysis, and the downwardly directed nature of the latter, tend to indicate that this vertebra should lie behind D14 and in front of D15. The succession would then be D12, "D14", "D13", D15. However, this cannot be correct. D14 cannot follow D12, for, if the two centra are aligned, the postzygapophyses of D12 are too high to articulate with the prezygapophyses of D14. The reverse holds true when the posterior face of D14 is applied to the anterior face of D13. Moreover, one of the postzygapophyses of D14 has what may be part of the following prezygapophysis attached to it, admittedly rather displaced; this could not belong to D13, which is complete in this respect, but could well belong to D15. On the other hand, the posterior face of D13 fits the anterior face of D14 very well, the zygapophyses fitting neatly together and the hyposphene of D13 sliding into the gap between the prezygapophyses of D14. The succession indicated has therefore been chosen as the most probably correct. As far as the last four pre-sacral vertebrae are concerned, D14 and D17 possess similar neural spines, both being remarkable for considerable antero-posterior elongation above; at first sight it might be thought that this would justify their being placed together, that is (since D14 has already been shown to be the most anterior of these four vertebrae) that D17 should lie in front of D15 and D16. However, if similarity should imply juxtaposition, consideration of the badly weathered condition of the neural spine of D15 and of the complete lack of the neural spine of D16 shows that D14 and D17 need not be placed together, for D15 and D16 may also have had similar neural spines. Further reflection shows that similarity <u>cannot</u> imply juxtaposition in this case, for a vertebra such as D14, with a neural spine elongated in a backward direction, cannot have lain immediately anterior to a similar vertebra; if D17 be placed immediately behind D14 with the two centra in natural orientation (allowing a small gap for an intervertebral disc), then the back of the neural spine of D14 will overlap the front of the neural spine of D17 to the extent of some 6mm. It would be absurd to suppose that the neural spines did not all lie in the same plane. D17 has therefore been placed behind the D15-D16 block. In this difficulty, as in the other mentioned above, a possible solution would be to postulate the existence of other vertebrae not preserved; it should be pointed out that this would increase the pre-sacral count beyond the number characteristic of the Thecodontia (see below).

In specimen no. 13 two centra are preserved from the middle or posterior dorsal region of the column. These resemble D5-D10 in that they are somewhat flattened beneath; but, in the absence of special distinguishing features, it would be difficult to assign them to any more exact position.

In specimen no. 63 a run of four vertebrae appears to correspond best to D6-D9, the most anterior not differing greatly from D5" and having an anterior pleural concavity relatively much wider than that of D7; these vertebrae have therefore been numbered D6"-D9". D9" still has a well developed posteroventral buttress, which in specimen no. 11b is well developed only as far back as D10; in D11 it is weakly developed and virtually absent thereafter. A small section of the anterior part of the centrum of the succeeding vertebra, attached to the posterior face of D9", has been numbered D10".

The total pre-sacral count of twenty-five which is obtained by this correlation is characteristic of the Thecodontia; von HUENE (1936a,b) gives this same figure in his definitions of the Phytosauria, Stagonolepidae, and "Other Pseudosuchia".

Only one sacral vertebra is preserved in specimen no. 11b, out of the two which are indicated by the size of the articulating surface on the ilium. The ventral part of the sacral rib is directed obliquely forwards and the dorsal part obliquely backwards; in this respect it resembles the second and supposed third sacrals of Spondylosoma (especially the latter) and not the first, in which the reverse holds true. It is therefore presumed that S1 is absent and that this must be S2. The likelihood that this vertebra is the last sacral, i.e. in this case S2, is increased by the fact that the posterior face of its centrum (which would then articulate with the first caudal vertebra) seems to have been much smaller than the anterior face (which would then articulate with the other sacral).

No sacral vertebrae are preserved in specimens nos. 13 and 63.

Specimen no. 11b has three further vertebrae which bear no facets on the centrum for the articulation of haemapophyses, and only one of these is flattened beneath in the manner characteristic of caudal vertebrae. The two vertebrae which are rounded beneath could be assigned to a position immediately in front of the sacrum; but since they are both markedly shorter than the other pre-sacral vertebrae, such as D16 and D17, and since this would mean an increase in the usual pre-sacral count of twenty-five, these vertebrae are probably pygals, i.e. anterior caudals without haemapophysial articulations. There being no evidence to the contrary, they are presumed to be immediately post-sacral in position, and have been numbered, in order of diminishing length, Ca1, Ca2 and Ca3. The pygal with the ventral flattening is thus numbered Ca3, which is more likely to resemble the vertebrae which succeed it in this respect than are Ca1 or Ca2.

Two centra of specimen no. 63 have been correlated with Ca1 and Ca2, and have been numbered Ca1" and Ca2".

Typical anterior caudal vertebrae with haemapophysial facets then follow in specimens nos. 11b and 63; some of the vertebrae from one animal may be approximately correlated with some from the other. The diameter of the centrum tends to decrease posteriorly and the relative length tends to increase. There is no evidence to show that the series did not include a few other vertebrae (one at least was present); but in the absence of such evidence the vertebrae preserved have been numbered Ca5-Ca8, Ca10, Ca11 in one specimen, and Ca4"-Ca7" in the other. (There is no Ca4 corresponding to Ca4"; and, because of the disparate sizes of the articular surfaces of their centra, a gap must exist between Ca8 and Ca10).

One badly preserved centrum of specimen no. 13, on considerations of size, is probably from a region of the tail not far behind the eleventh caudal.

Six relatively much smaller caudal vertebrae are present in specimen no. 63. Four of these were preserved together in a run; the other two, one of which is represented only by the anterior half of the centrum, were found alone. This half-centrum has the greatest diameter and has been numbered PC1"; the run of four has been numbered PC2"-PC5"; and the other isolated centrum, which is the smallest, has been designated PC6". Again, it is quite possible that there may have been other vertebrae present between PC1" and PC2" and between PC5" and PC6".

CORRELATION TABLE

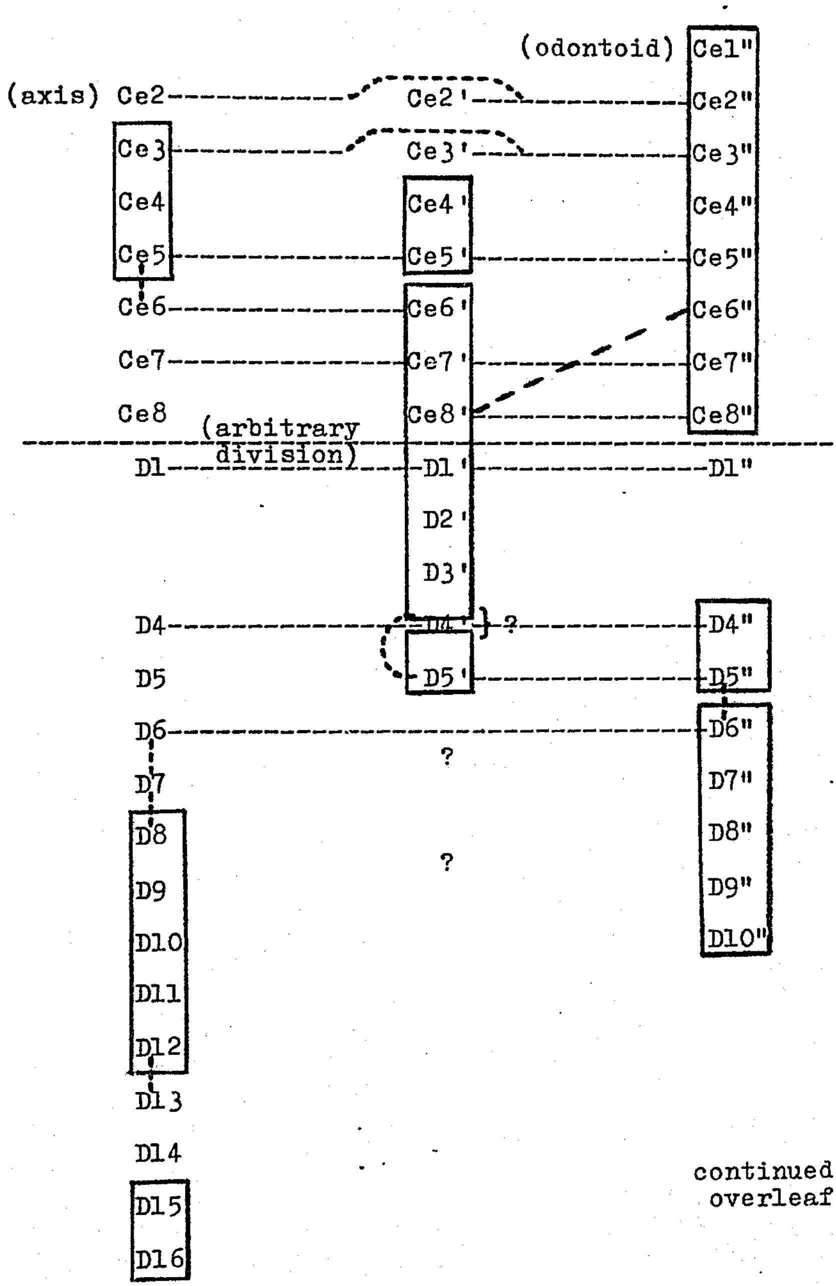
See overleaf.

A series of vertebrae is enclosed in a "box" where there is direct and indisputable evidence for the succession.

Correlation on form is shown by red lines connecting the vertebrae in question.

CORRELATION TABLE

specimen no. 11b   specimen no. 13   specimen no. 63



continued overleaf

specimen no. 11b	specimen no. 13	specimen no. 63
D17		
- (1st sacral)		
S2		
Ca1		Ca1"
Ca2		Ca2"
Ca3		
		Ca4"
Ca5		Ca5"
Ca6		Ca6"
Ca7		Ca7"
Ca8		
-		
Ca10		
Ca11		
	?	
		PC1"
		PC2"
		PC3"
		PC4"
		PC5"
		PC6"

iii) Description of the type-specimen (no. 11b)

Field notes.

Field collection no. 11 was found in locality B5 at Irundi. It includes, in addition to the bones listed below, several indeterminate weathered fragments whose general texture and order of size indicates that they probably belong to the type-specimen itself; about nine bones of a smaller pseudo-suchian (specimen no. 11a); several unrecognisable fragments of a larger animal (specimen no. 11c); and one small dicynodont centrum. The specimen is of a whitish colour, generally well preserved and not much weathered, and was contained in a brown matrix rather softer than that surrounding the other major specimens.

Material available.

Maxilla: fragments of both left and right, containing teeth.

Dentary: fragment of right.

Vertebrae: parts of at least 32, including axis, probably all remaining cervicals (6), most of dorsals (15), 1 sacral and 9 caudals; together with neural arches and spines and other fragments which cannot be identified as belonging to any particular vertebra.

Dorsal rib: fragment of shaft.

Scapula: both left and right.

Coracoid: articular part of left.

Humerus: right, lacking proximal part of shaft.

Radius and ulna: probable end-pieces.

Pelvis: almost complete on both sides, lacking only both pubo-ischiadic junctions and central part of left ischium.

Femur: both left and right.

Tibia: both left and right.

Fibula: proximal part of right.

Metatarsal: possible proximal part.

Dermal scutes: several fragments, including three *in situ* on neural spine of supposed sixth cervical vertebra.

As in all these specimens, there is a complete lack of material from the skull (except for the jaw fragments), from the manus and from the pes (except for the supposed metatarsal in this specimen and the left fibulare in specimen no. 63).

Maxilla. (Plate 1).

The left maxilla is the better preserved. The fragment consists of a dentigerous bar 92mm. long, extending backwards from just in front of the ascending process and broken off at either end through an alveolus. Twelve alveoli are represented, including these two, and at least five of these contain the remains of teeth.

The form of the fragment is shown in the illustrations. The bar is curved outwards both before and behind, while its centre is swung inwards; this curvature may be due to post-mortem distortion, for the corresponding part of the right maxilla is curved in the same and not in the opposite direction (that is, its outer surface is convex instead of concave). Anteriorly, below the ascending process, the bar is 22mm. high; shortly behind the ascending process it reaches a maximal height of 26mm., and then tapers off below the antorbital vacuity to a height of 14mm. at the hinder end of the fragment. The bar is approximately 10mm. thick, being rather thicker than this in front and thinner behind. A comparison of this fragment with the post-cranial skeleton shows that the animal possessed jaws which were relatively long.

The ascending process lies above the second and third of the preserved alveoli; only the basal 4mm. remains. Its stump runs across the dorsal surface of the bar from posteromedial to anterolateral, being slightly convex on the medial side and slightly concave on the lateral; the broken surface is 12mm.

long and 4mm. broad. The dorsal surface of the extreme hind end of the fragment bears a shallow groove along its length; this is bordered laterally by a thin vertical wall which forms a dorsal extension of the lateral surface of the maxilla and which is broken off above, the basal remnant being nowhere more than 2mm. high. Presumably this groove received the jugal.

The lateral surface of the bone shows a series of small foramina 4-6mm. above its lower edge; their apertures are directed somewhat ventrally. In the hinder part of the fragment they seem to alternate with the alveoli.

The medial surface of the bone bears a downwardly directed ledge. This runs some 7-8mm. above the lower border in the anterior region of the fragment but approaches it more closely behind.

The alveoli themselves have been badly damaged, especially their medial walls and the walls between adjacent alveoli. They are very deep, extending upwards as much as 13mm. to within 3-4mm. of the dorsal surface of the bone. Some idea of the shape of the alveoli may be obtained from the illustration of the maxilla in crown view.

The 2nd, 3rd, 4th, 6th, and 10th of the preserved alveoli contain the remains of teeth; the 8th and 11th may also contain such remains, though these latter are too badly shattered to be identified with certainty. The tooth in the 6th preserved alveolus is the only one to show much structure; it had not yet erupted but is fairly large, 8mm. of the crown being visible through the broken lateral wall. The tooth is recurved, its apex being directed posteriorly and a little laterally; it appears to have been roughly triangular in transverse section, with anterior, posterior and medial edges. The anterior and posterior surfaces each bear a row of fine perpendicular crenulations. The 3rd and 4th of the preserved alveoli contain the stumps of large erupted teeth; these are roughly oval in section, being elongated from front to back, and show neither anterior nor posterior cutting edges. That in the 4th preserved alveolus is 9mm. long, 5mm. broad and has walls about 1mm. thick where broken off flush with the surface of the maxilla. There is no evidence for alternate replacement.

Two fragments of the right maxilla are also preserved. The more anterior of these is 29mm. long and corresponds to the front end of the fragment of the left maxilla, the anterior break being through the corresponding alveolus and about 4mm. further forward. The ascending process is broken off about 2mm. higher, and the posterior break is through the "4th" alveolus. The "1st" and "3rd" alveoli contain the remains of teeth. The posterior fragment of the right maxilla is 34mm. long; the break at its front end is also through the alveolus which corresponds to the 4th preserved alveolus of the left maxilla. (The posterior fragment probably lies immediately behind the anterior fragment, although their broken ends are too badly weathered to afford evidence of this connexion). The position of the hinder end of the posterior fragment corresponds to the wall between the 7th and 8th preserved alveoli of the left maxilla. The "6th" alveolus contains a prominent tooth stump. These fragments of the right maxilla seem to differ from their fellow only in the convexity, rather than the concavity, of the lateral wall (as mentioned above); and in that the posterior fragment appears to be a little deeper dorsoventrally, the dorsal surface of the left maxilla being badly shattered in this region.

Dentary. (Plate 1).

A fragment of a dentary is preserved. The fact that the alveoli are weakly inclined in a direction which is presumed to be backwards rather than forwards is the only evidence for its being part of the right dentary rather than of the left. It consists of a fairly straight bar 43mm. long and broken off at either end through an alveolus. Seven alveoli are represented, including these two, and all appear to be empty.

The bar is 17mm. high at its front end, 15mm. high in the middle, and 16mm. high behind; its maximal thickness is 9mm. In transverse section it is roughly oval. The lateral surface bears a series of upwardly directed foramina some 4mm. below its dorsal edge; these alternate with the alveoli. On the medial surface a well defined groove runs the length of the fragment 4-5mm. above its ventral edge. (A similar groove on the lateral surface of the posterior half of the fragment may well be artificial). The medial surface also bears an upwardly directed ledge running about 4-5mm. below its dorsal border. The alveoli, the medial walls of which are in some cases broken away, extend downwards to within 2mm. of the groove on the medial surface; that is, they are typically about 9mm. deep. As mentioned above, they are inclined slightly backwards and presumably contained teeth which were recurved like those in the upper jaw.

Vertebral column.

Cervical region.

Table of principal measurements. See overleaf. The "elongation ratio" of a centrum is the ratio of its length to its mean diameter.

Axis. (Plates 2, 5 and 7). The centrum and the neural spine are preserved as two separate fragments; the lower part of the anterior face of the centrum, the sides of the neural arch, the prezygapophyses (if present) and the left postzygapophysis are missing. The body of the centrum is concave below in lateral view and is excavated on its dorsal side to form a deepening in the floor of the neural canal. The middle of the centrum is also constricted laterally so that the base of the neural arch appears to project sideways; the presence of a marked ventromedial keel is indicated. The posterior articulating surface is moderately hollow. The diapophysis is represented by a small downwardly directed boss near the antero-dorsal corner of the centrum; from its vicinity the neurocentral suture passes backwards, ascending slightly to a peak in the middle of the vertebra, and no. 11b - TABLE OF PRINCIPAL MEASUREMENTS OF THE CERVICAL VERTEBRAE (millimetres)

Centrum:	Ce2 (axis)	Ce3	Ce4	Ce5	Ce6	Ce7	Ce8
length below	-	-	-	-	40	35	35
length above	27	-	40	-	-	-	-
anterior height	-	16	-	-	22	22	23
anterior width	-	19	-	-	23	25	23
posterior height	18	-	-	-	22	23	24
posterior width	19	-	-	-	24	23	25
mean diameter	18½	17½	-	-	23	23	24
elongation ratio	-	-	-	-	1.74	1.52	1.46
minimal transverse thickness	7	-	-	-	13	11	12
Neural spine:							
height (measured from top of centrum)	37	-	33	32	32	33	-
axial length above	42	-	31	32	32	26	-
maximal transverse width above	7	-	10	11	16	15	-

then descends gently towards the posterior margin. The neural spine is much longer than the centrum, and, in what seems to be a reasonable reconstruction of the whole vertebra, projects before and behind the centrum to a considerable extent. It is shaped like a hatchet, being blade-like in front and becoming higher and thicker posteriorly. The dorsal surface is not expanded, however, and reaches a maximum width of 7mm. behind. The large and powerful postzygapophysis is set rather obliquely, and a deep posterior spinal concavity lies medial to it.

Supposed third, fourth and fifth cervicals. (Plates 2 and 7). These three vertebrae are in natural connexion, but all are incomplete. The supposed third cervical is represented only by the anterior part of the centrum and by the neural arch, without either prezygapophyses or neural spine; the supposed fourth lacks the whole of the ventral part of the centrum; and the centrum of the supposed fifth is almost entirely missing. It appears that there is a progressive increase in the length of the centrum in successive vertebrae; the centrum of the supposed third cervical could not have been longer than 35mm., and a comparison of other dimensions leads to the conclusion that the centrum of the supposed fifth cervical was at least as long as that of the supposed fourth (40mm.), if not slightly longer. The anterior face of the centrum of the supposed third cervical is moderately concave. A trace of a badly preserved parapophysis is visible low down on the anterior margin of the centrum of the supposed third cervical, and in all three of these vertebrae traces of a diapophysis may be seen in the anterodorsal region of the centrum. A peculiarity of these cervical vertebrae is that the anterior outline of the neural canal is markedly elliptical, being much wider than high. The zygapophyses are large and powerful, the anterior in particular projecting well beyond the centrum; a shallow basin lies between the prezygapophyses, and a deep spinal concavity, separated from the neural canal by a thin bony floor, lies between the postzygapophyses. On either side of the neural arch an ascending ridge runs backwards to become the outer border of the postzygapophysis; and a depression is present on either side of the base of the neural spine, medial and dorsal to this ridge. This depression is less well developed in the supposed third cervical than in its successors. The neural spines of the supposed fourth and fifth cervical vertebrae are rather low; their sharp anterior margins slope upwards and forwards, while their posterior margins slope upwards and backwards. (This posterior margin is much shorter and is sometimes produced into a narrow vertical median lamella which runs down for a short way between the posterior spinal buttresses). Thus, although the bases of the neural spines are slender and short from front to back, their dorsal surfaces are broader and longer; these are almost flat, a little broader in front than behind and somewhat expanded both axially and transversely so that their edges protrude horizontally all round. It is presumed that they served for the support of dermal scutes.

Supposed sixth cervical. (Plates 2, 5 and 7). This vertebra is nearly complete, and in its general characters (including the length of the centrum) resembles those which precede it. The ventral margin of the centrum appears concave when seen from the side; the centrum is laterally constricted in the middle and is smooth beneath. The articulating surfaces are only very slightly concave. The parapophysis is a large facet at the anteroventral margin of the centrum. The diapophysis is situated further back, seemingly on the neurocentral suture; it projects but slightly from the side of the vertebra, is directed obliquely downwards, and a considerable hollow lies beneath it. The anterior end of the neural canal is 6mm. high and 13mm.

wide. The neural spine is of about the same height and same axial length as those of the preceding vertebrae, but its dorsal surface is expanded transversely to a much greater extent, the maximal width being near the anterior end. Parts of three dermal scutes are present _in situ_ upon this expanded surface (see below for details of their structure).

Supposed seventh cervical. (Plates 2, 5, 7 and 8). This vertebra is fairly complete, lacking only the prezygapophyses; it resembles its immediate predecessor, but is markedly shorter. Other points in which this vertebra differs from the supposed sixth cervical are the definite presence of a faint ventromedial ridge; the greater distance apart of the parapophyses (seen from below); the greater projection of the diapophysis, and the greater development of the hollow beneath; the greater depth of the depression on either side of the base of the neural spine, behind the anterior spinal buttress; the absence of a median ridge between the posterior spinal buttresses; the slightly greater height of the neural spine; and the comparative shortness of the latter from front to back.

Supposed eighth (last) cervical. (Plates 2 and 5). This consists only of a badly preserved centrum of the same length as the one before it. The deepening of the floor of the neural canal within the centrum, typical of all these vertebrae, is clearly shown. The ventral surface is not well enough preserved to give any indication of a ventromedial ridge. The parapophysis is fairly well preserved on one side; there is a faint trace of what may be an anterior pleural concavity on one side, but the neural arch and diapophysis are broken off too short to allow this to be stated with certainty.

Dorsal region.

Table of principal measurements. See overleaf.

Supposed first dorsal vertebra. (Plates 2 and 5). This consists of a badly preserved and somewhat distorted centrum, much shorter than the supposed last cervical and broader anteriorly. Traces of the parapophyses remain; these are situated further apart, and therefore more laterally and less ventrally, than in the posterior cervical vertebrae. The condition of preservation does not allow of further description.

Supposed fourth dorsal vertebra. (Plates 2 and 5). This consists of a centrum together with the anterior part of the neural arch on one side, including parts of the diapophysis and prezygapophysis. It is of the same length as the supposed first dorsal. Its middle no. 11b - TABLE OF PRINCIPAL MEASUREMENTS OF THE DORSAL VERTEBRAE (millimetres)

	D1	D4	D5	D6	D7	D8	D9	D10	D11	D12	D13	D14	D15	D16	D17
Centrum:															
length below	29	29	30	29	28	29	30	28	30	31	29	30	27?	31	31
anterior height	23	22	24	20	23	23	23	23	25	26	24	24	-	25	26
anterior width	28	25	23	22	23	25	24	25	26	25	24	24	-	28	27
posterior height	22	22	22	20	21	24	23	25	26	26	25	24	24	27	26
posterior width	24	21	24	22	23	24	23	25	26	27	27	26	28	29	29
mean diameter	24	22½	23	21	22½	24	23	24½	26	26	25	24½	26	27	27
elongation ratio	121	129	130	138	124	121	130	114	115	115	116	122	-	115	115
minimal transverse thickness	-	12	12	11	11	12	11	12	13	14	14	12	17	18	15
Neural spine:															
height (measured from top of centrum)	-	-	-	-	35	36	38	38	40	42	42	41	43	-	44
axial length above	-	-	-	-	24	25	25	25	28	25	21	34	-	-	32
maximal transverse width above	-	-	-	-	13	14	15	10	11	8	7	8	-	-	8

is more or less equally constricted below and at the sides, the ventral surface being smoothly rounded; and the articulating surfaces are very nearly amphiplatyan. The parapophysis is present on one side and lies much higher than in the cervical vertebrae, its upper end being approximately level with the middle of the neural canal; and, if (as seems possible) the fracture in the specimen does indeed indicate the level of the neurocentral suture, then most of the parapophysis is borne on the neural arch and only a small part on the centrum. It is situated a short way behind the anterior margin of the vertebra, projecting laterally a few millimetres; the facet is rather weathered, but the outline seems to have been roughly elliptical, with the longer axis nearly vertical. The diapophysis is represented by a stump lying obliquely above and behind the parapophysis, and connected to it by an anteroventral lamella; most of the diapophysis, however, has been broken off with the rest of the neural arch. Traces of a posteroventral buttress remain, running backwards and downwards, and a sharp anterodorsal buttress connects the diapophysis with the prezygapophysis. These buttresses also lie obliquely, each forming a very approximate right angle with the anteroventral buttress. The anterior and inferior pleural concavities which lie between these buttresses are broad and deep. The prezygapophysis is short, scarcely projecting beyond the anterior margin of the centrum.

Supposed fifth and sixth dorsal vertebrae. (Plates 2 and 5). These two vertebrae, although not in natural connexion, resemble each other closely. The supposed fifth consists of a centrum only; the supposed sixth of a centrum together with the anterior part of the neural arch on one side, including the parapophysis, part of the diapophysis and the prezygapophysis. The centra resemble that of the supposed fourth dorsal except in that they show a slight flattening of the ventral surface and a more pronounced longitudinal groove on each lateral surface, below the attachment of the neural arch. The parapophysis of the supposed sixth dorsal vertebra is borne entirely on the neural arch, at about the height of the neural canal; it consists of a projection about 5mm. long, directed very slightly downwards and bearing a more or less circular facet of some 5mm. diameter, to which part of the capitulum of the dorsal rib is still attached. The diapophysis, of which only a fragment remains, lies behind and not much above the parapophysis, to which it is connected by a nearly horizontal antero-ventral lamella. As in the supposed fourth dorsal vertebra, traces of the posteroventral buttress can be seen, and a deep inferior pleural concavity lies beneath the diapophysis. An anterodorsal buttress runs from the diapophysis towards the prezygapophysis; since this, like the anteroventral lamella, is nearly horizontal, the anterior pleural concavity between the two is very narrow. The prezygapophysis projects beyond the front of the centrum.

Supposed seventh dorsal vertebra. (Plates 3, 5, 7 and 8). This vertebra is exceptionally well preserved and lacks only the postzygapophyses. The length of the centrum conforms to the uniform 28-31mm. found in all the dorsal vertebrae. The middle is constricted both ventrally and laterally. The ventral surface shows a slight but definite flattening of 5mm. width; the centrum is weakly amphicoelous; and there is a considerable longitudinal depression on either side below the neural arch. The parapophysis is a horizontal peg-like projection 4mm. long situated on the side of the root of the prezygapophysis and at the height of the upper half of the neural canal; it bears a slightly elliptical facet. The diapophysis lies above and behind the parapophysis, to which it is connected by a delicate anteroventral lamella; measured from the superior pleural concavity outwards it is 11mm. long (if the end-surface on the left-hand side is indeed true surface), it is directed backwards and slightly upwards, and its presumed terminal facet is twice as long as high. It is supported by a short, fairly stout posteroventral buttress; a horizontal anterodorsal lamella runs towards the prezygapophysis; and a short, stout posterodorsal buttress is also present. All four pleural concavities are developed; the anterior is very narrow, while the superior consists of a shallow pit in the middle of the base of the upper surface of the diapophysis, just below the neural spine. The anterior end of the neural canal is 9mm. high and 9mm. wide, and is bordered on either side by a sharp ridge running up towards the prezygapophysis. The latter is much weaker than in the cervical vertebrae and its articulating facet lies less obliquely; it projects a short way in front of the centrum. A deep concavity lies between the anterior spinal buttresses. The neural spine lies well back and is higher than in the cervical vertebrae; the flattened front edge is more or less vertical, while the even broader hind edge runs upwards and backwards so that the upper surface of the spine is longer than its base, projecting behind the centrum. This upper surface is flattened and expanded and of a characteristic form (see figure), with a slight median longitudinal depression.

<u>Supposed eighth to fourteenth dorsal vertebrae.</u> (Plates 3, 5, 7 and 8). These seven vertebrae, of which the first five (D8-D12) were found in their natural relative positions, are all fairly well preserved and show a general resemblance to the supposed seventh dorsal vertebra described above. The supposed thirteenth and fourteenth are beautifully preserved, especially the former, but in the others some of the processes for the rib-articulations are broken off and some of the zygapophyses are missing. The centra are fairly constant in length, and are constricted like that of the supposed seventh dorsal vertebra. The flattening of the ventral surface persists only up to the supposed tenth dorsal vertebra, and is less well marked than in the supposed seventh; the more posterior vertebrae are rounded below. Most of the centra are weakly amphicoelous, with the anterior face more strongly concave than the posterior face; the latter is quite flat in certain vertebrae, such as the supposed eighth dorsal. The lateral longitudinal depression persists throughout the series. The length and form of the parapophysis are more or less constant; its height is approximately that of the neural canal; and the direction in which it projects

seems to vary in an irregular manner between horizontal and slightly downwards. The length of the diapophysis is difficult to determine, for in many cases it is hard to decide whether the process is broken off or not; measurements obtained for the supposed eleventh and thirteenth dorsal vertebrae are 13mm. and 15mm. respectively. The diapophysis shows a gradual change in the direction in which it projects from backwards and slightly upwards (as in the supposed seventh dorsal) to lateral and horizontal (as in the supposed eleventh) and then to slightly forwards and downwards (as in the supposed thirteenth). Thus the terminal facet of the diapophysis comes to lie closer to that of the parapophysis; the anteroventral lamella connecting the two becomes shorter, forming a "spectacles"-shaped rib-articulation, and in the supposed thirteenth dorsal vertebra the two facets are fused into one, as in all vertebrae posterior to the supposed fourteenth. (In the supposed fourteenth the facets are not quite fused. It might therefore be thought that the supposed order of the vertebrae is incorrect, and that the supposed fourteenth vertebra should precede the supposed thirteenth; but, as is shown in the preceding Sub-section, the very tentative succession adopted is based on other considerations).

The posteroventral buttress is well developed as far back as the supposed tenth dorsal vertebra; it is weakly developed in the supposed eleventh and virtually absent thereafter. The anterodorsal lamella is present in the supposed eighth and ninth dorsal vertebrae only, and the posterodorsal buttress dies out altogether after the supposed eleventh. Of the pleural concavities, the anterior is present as a mere slit in the supposed eighth and ninth dorsal vertebrae only; the posterior is well developed in the supposed eighth, ninth and tenth, weakly developed in the supposed eleventh, barely discernible in the supposed twelfth, and absent after that; and the inferior and superior pleural concavities are developed throughout the series in much the same form as in the supposed seventh dorsal vertebra. The neural canal shows an increase in size towards the end of the series, its anterior opening being 10mm. high and 12mm. wide in the supposed thirteenth dorsal vertebra; this vertebra, like its successor, still shows the sharp ridges bounding the opening on either side. The zygapophyses are constant in form, being fairly well developed, moderately oblique, and projecting a short way before and rather further behind the centrum respectively. The exit for the spinal nerve is beneath the postzygapophysis and produces a concavity in the posterior outline of the vertebra when seen from the side. The spinal buttresses and concavities are moderately developed and show little variation in form. A hyposphene is developed in the last three of these vertebrae, that is, in the supposed twelfth to fourteenth; this part is not well preserved in the more anterior vertebrae. The hyposphene is best preserved in the supposed thirteenth dorsal vertebra, where it consists of a longitudinal ridge projecting downwards beneath the postzygapophyses; it is about 6mm. long and 2mm. deep, and fits neatly into the gap between the prezygapophyses of the following vertebra. The form of the neural spine is fairly constant in all these vertebrae as far back as and including the supposed thirteenth dorsal, the spines becoming progressively higher. The degree of expansion of the flattened tops of the neural spines decreases from front to back, those of the supposed twelfth dorsal vertebra and its successors being merely flattened and not expanded to any great extent; the greatest width is near the hinder end. As will be seen from the measurements, the neural spine of the supposed fourteenth dorsal vertebra is very much longer from front to back than those of its predecessors; the elongation appears to be mainly in a backward direction, the hinder end of the dorsal surface of the spine projecting posteriorly beyond the postzygapophyses.

Supposed fifteenth, sixteenth and seventeenth (last) dorsal vertebrae. (Plates 3, 5, 6 and 7). The remains of the supposed fifteenth dorsal vertebra consist of a centrum, badly weathered at the anterior end; together with part of the neural arch, one transverse process, postzygapophyses and neural spine, all badly weathered. The remains of the supposed sixteenth dorsal vertebra consist only of a centrum attached to the posterior face of its predecessor. The supposed seventeenth vertebra is better preserved and lacks only the zygapophyses. In most respects these vertebrae resemble those which lie immediately in front. The posterior faces of the centra of the supposed sixteenth and seventeenth dorsal vertebrae are almost flat. The parapophysis and diapophysis are fused into a single transverse process, of which, however, the component parts are clearly distinguishable. The neural canal is still bordered anteriorly by a sharp ridge on either side in the supposed seventeenth dorsal vertebra. The neural spine of this vertebra is rather similar to that of the supposed fourteenth, but it does not project backwards so noticeably and there is no appreciable dorsal expansion. It does not seem that the badly weathered neural spine of the supposed fifteenth dorsal vertebra and the missing neural spine of the supposed sixteenth can have been as long as those of the supposed fourteenth and seventeenth; for, assuming that all the neural spines lay in the same plane, their elongated upper ends, being longer than their centra, would interfere with each other spatially.

Sacrum.

Supposed second sacral vertebra. (Plates 3, 6, 7 and 8). This consists of the centrum, the neural arch and the sacral ribs, one of the latter being broken off near its base; the prezygapophyses are badly preserved, and the postzygapophyses and neural spine are missing. The whole vertebra is distorted obliquely in the transverse plane. The centrum is 31mm. long below, and 29mm. high and 32mm. wide in front; the hinder face is partly broken away, but seems to have been much smaller. The body of the centrum is constricted below and at the sides, its minimal transverse thickness being 16mm., and it is rounded beneath. The ends are virtually amphiplatyan. The sacral rib is ankylosed to a prominence on the side of the upper part of the centrum and the neural arch; it occupies the greater part of the length of the vertebra, being situated nearer to the front than to the hinder end. The rib is bordered ventrally by a slightly swollen suture; it projects more or less horizontally and is divisible into two parts. The ventral ("parapophysial") portion is fairly stout and is directed obliquely forwards; its outer end, facing obliquely forwards, may conceivably be a true surface serving for articulation with the ilium. (It is 20mm. long from front to back and 14mm. high). The dorsal ("diapophysial") part of the rib, laminar in nature and directed obliquely backwards, lies directly upon the upper surface of the ventral part; its distal end is broken off. The sharp anterior border of this dorsal part of the rib curves round anteriorly above a slight excavation at the side of the neural canal to terminate on the outer side of the root of the prezygapophysis; this ridge is the equivalent of the anterodorsal buttress. Little can be said of the prezygapophyses save that they are small, very wide apart (width across both 27mm.), and project a short way in front of the centrum. The anterior spinal concavity is wide and shallow.

Caudal region.

Table of principal measurements. See overleaf.

no. 11b - TABLE OF PRINCIPAL MEASUREMENTS OF THE CAUDAL VERTEBRAE (millimetres)

	Ca1	Ca2	Ca3	Ca5	Ca6	Ca7	Ca8	Ca10	Ca11
Centrum:									
length below	27	27	26	24	30	27	28	25	25
anterior height	26	26	27	24	24	24	24	18	19
anterior width	28	27	26	25	24	22	21	14	18
posterior height	26	27	26	24	24	22	19	20	16
posterior width	27	25	25	24	21	19	19	16	14
mean diameter	27	26	26	24	23	22	21	17	17
elongation ratio	100	104	100	100	130	123	133	147	147
minimal transverse thickness	15	15	14	15	14	11	12	9	10
Neural spine:									
height (measured from top of centrum)	46	-	-	49	-	-	-	-	-
axial length above	20	-	-	20	-	-	-	-	-
maximal transverse width above	7	-	-	7	-	-	-	-	-

Supposed first caudal vertebra. (Plates 4, 6, 7 and 9). This vertebra is fairly well preserved, but the ends of the transverse processes and of the zygapophyses are broken off. The centrum is not very different from those immediately in front of the sacrum, except in that it is shorter. It is rounded beneath, without haemapophysial facets, and is very weakly amphicoelous. The longitudinal depression between centrum and neural arch is well developed. The transverse process is not divisible into parapophysial and diapophysial parts; it is situated on the side of the neural arch, fairly well back, is directed horizontally outwards, and slopes gently downwards from front to rear. The anterior edge is sharp and curves round towards the prezygapophysis, with a depression lying beneath it. The posterior edge is thicker and rounded, and is level with the top of the posterior face of the centrum. The broken end of the transverse process is 14mm. long and 5mm. deep. The neural spine is slender and directed a little obliquely backwards; its anterior and posterior margins are more or less parallel, the former being rather sharp and the latter thicker and more rounded. Its dorsal surface is flattened but not expanded at all.

Supposed second caudal vertebra. (Plates 4 and 6). This consists only of a well preserved centrum together with the sides of the neural arch and the bases of the transverse processes. Haemapophysial facets are absent and the centrum is rounded beneath. A saddle-shaped articulation between the centra makes its first appearance here; the dorsal margin of the anterior face of the centrum bears a slight forward projection on either side, just below the neural arch and roughly triangular in form. These articulate with two scarcely discernible facets in a corresponding position on the posterior face of the preceding (supposed first caudal) vertebra. The facets on the hinder face of the centrum of this supposed second caudal vertebra are better developed. Other differences between this vertebra and the supposed first caudal are the weaker development of the longitudinal depression between the centrum and the neural arch, and the more horizontal nature of the base of the transverse process.

Supposed third caudal vertebra. (Plates 4 and 6). This also consists only of a centrum with the sides of the neural arch and the bases of the transverse processes. It differs from its predecessor in being flattened beneath, the flattening being 10mm. wide;

there are still no haemapophysial facets. It differs also in the greater development of the forward projections on the anterior face of the centrum, and in the absence of a lateral longitudinal depression. The transverse process is directed somewhat posteriorly.

<u>Possible fifth caudal vertebra</u>. (Plates 4, 6, 7 and 9). This vertebra lacks only the zygapophyses; the transverse process is nearly complete on one side. The centrum is much shorter than any which precede it, and is shorter too than those which follow. Its narrowest part is no longer in the middle but nearer to the hinder end. The most striking feature is the development of a pair of large facets for the haemapophysis on the lower margin of the posterior face, triangular in form and facing obliquely downwards. A ridge runs forward from each facet along the ventral surface of the centrum, and a well marked groove some 7mm. wide lies between these ridges. The anterior face of the centrum is markedly concave, while the posterior face is saddle-shaped; the centrum thus tends towards procoely. There is no longitudinal depression on the side of the vertebra. The transverse process is less well developed than in the more anterior vertebrae; the neural canal is much

narrower than in the supposed first caudal; and the neural spine resembles that of the supposed first caudal except in that it is longer.

Possible sixth, seventh and eighth caudal vertebrae. (Plates 4 and 6). The first of these consists of a centrum with the base of the neural arch on both sides and the base of the transverse process on one side; the next consists of a centrum only; and the last of a centrum with the base of the neural arch and of the transverse process on one side only. The three centra vary considerably in their proportions but all are much longer than the possible fifth caudal, which they resemble in general form. The possible sixth is the stoutest of the three. The form of the articulating surfaces seems to be another variable feature; thus, while the centrum of the possible sixth caudal vertebra has a concave anterior face and a convex, saddle-shaped posterior face, both faces of the possible seventh caudal are markedly concave (although it is not inconceivable that the posterior concavity is an artifact). The faces of the centrum of the possible eighth caudal are more like those of the sixth. The base of the transverse process of the possible sixth caudal resembles that of the possible fifth, while that of the possible eighth is a more delicate structure, being only 2mm. thick where broken off.

Possible tenth and eleventh caudal vertebrae. (Plates 4, 6, 7 and 9). The first of these consists only of a badly weathered centrum; the second, also very badly preserved, includes the centrum, neural arch, transverse process, zygapophyses, and the lower part of the neural spine. Both are much smaller than any of the other vertebrae, but they seem to have a general resemblance to those described immediately above. Features still present in the possible eleventh include a deepening of the neural canal within the centrum, haemapophysial facets, a grooved ventral surface, and the small transverse process. The poor condition of preservation does not allow of a more detailed description.

Fragmentary vertebral material.

The only fragments which are of interest are some unattached neural spines.

It seems probable that three of these, bearing parts of their zygapophyses, are the neural spines of some of the first six dorsal vertebrae; or perhaps of the last cervical. They are short and stout and are rather weathered. Their dorsal surfaces are broadly expanded, being very short axially (dimensions 21mm.

long by 14mm. wide, 20mm. by 13mm., and 19mm. by 12mm.); the greatest width tends to be nearer the front. All three show traces of the depression found on either side of the base of the neural spine in the posterior cervical vertebrae, especially in the supposed seventh cervical.

Another neural spine, with a good part of the neural arch and zygapophyses attached, is badly weathered. It seems likely, however, that it comes from the anterior part of the tail. It is of the same general form as that of the possible fifth caudal vertebra (the most posterior neural spine preserved in attachment to its vertebra, and also the longest), but seems to have been a few millimetres longer still.

The tops of other neural spines from the tail are preserved. One of these closely resembles that of the possible fifth caudal; three others differ only in being transversely thinner. The dimensions of their dorsal surfaces are:

length 20mm.	maximal width 7mm.
21mm.	5mm.
21mm.	4mm.
20mm.	3mm.

Dorsal rib. (Plate 9).

Only a fragment of one shaft, 84mm. long, remains. The transverse diameter decreases from 12mm. at one end (presumably dorsal) to 10mm. at the other, while the maximum axial diameter decreases from 8mm. to 7mm. The shaft is slightly curved and is compressed antero-posteriorly; both anterior and posterior faces are grooved throughout their length.

Pectoral girdle.

Scapula. (Plate 10).

Both scapulae are preserved, the left still connected to part of the coracoid. In neither case is the bone complete, for the fragile anterior margins have been broken away almost everywhere.

The scapula consists essentially of a curved blade which is presumed to have lain more or less upright; the inner and outer surfaces are respectively concave and convex in a dorsoventral direction. The bone is about 155mm. long, measured externally along the curve. In lateral view it is seen to be expanded above and below, the middle part of the blade being much narrower. Thus the dorsal breadth is estimated to have been approximately 60mm. (both anterodorsal corners are broken off); the actual width in the narrowest part is 27mm. in one scapula and 30mm. in the other; and the ventral breadth, even though incomplete anteriorly, must have been at least as great as the dorsal breadth. The upper margin of the bone is slightly convex in profile; the end-surface is flattened in one scapula and gives indications of incomplete ossification in the other, and it tapers from a maximal width of 6mm. near its hinder end to a sharp point in front. The anterior edge of the whole bone seems to have been correspondingly knife-like; the thin anterior part of the blade is broken away almost everywhere, but a short length of true edge is preserved in the centre of the bone. The profile of the anterior edge seems to have been fairly straight above, and to have curved forward below to form a prominent deltoid flange. This latter is preserved in part in the right scapula only, and is directed forwards, inwards and a little upwards. The posterior edge of the scapula is thick and rounded; it becomes gradually thicker ventrally to terminate in the broad semicircular facet (12mm. high and 23mm. wide) of the scapular portion of the glenoid fossa, which is directed obliquely backwards and downwards. The profile of the posterior edge is markedly concave, its curvature being greatest in the ventral region just above the glenoid. In posterior view it is apparent that the curvature of the scapula in the transverse plane is not regular, but that there is a marked inflexion at a distance from the glenoid of about one-quarter of the length of the whole bone. The lateral margin of the posterior edge bears the remains of a large muscle-process which presumably served for the origin of the anconaeus scapularis lateralis externus muscle; this begins some 7mm. from the upper border of the glenoid facet and is roughly oval in shape, extending another 12mm. dorsally and being 5mm. wide. The ventral surface of the scapula, which articulates with the coracoid, is triangular in form and is bounded posteriorly by the base of the scapular portion of the glenoid facet. The straight lateral margin and slightly convex inner margin approach each other rapidly anteriorly, and the apex of this triangle is produced into the ventral surface of the deltoid flange; this is of fairly constant thickness (3-4mm.). Since the flange is in line with the lateral margin of the triangle, the inner margin of the ventral surface appears strongly concave when considered as a whole.

Coracoid. (Plate 10).

Only the articular part of the left coracoid remains, still connected to the scapula and extending ventrally at least 40mm. beyond it. Like the scapula, it is massive behind and thinner in front. Except in the region of the glenoid fossa, the margins of the fragment are everywhere incomplete. The coracoid portion of the glenoid articulating surface is much larger than the scapular portion and forms a prominent lip, protruding backwards and facing upwards. The whole of the glenoid fossa is directed somewhat laterally. The remains of the coracoid foramen lie on the broken front edge of the bone, some 15mm. anterior to the glenoid and 7mm. below the scapula; this foramen seems to have been of about 7mm. diameter and to have been directed obliquely inwards, upwards and forwards.

Fore-limb.

Humerus. (Plates 11 and 12).

Both ends of the right humerus are fairly well preserved, but the proximal part of the shaft is missing. In a reconstruction of the entire bone the length of the missing part has been taken as 22mm.; this would give the humerus a total overall length of 152mm. The presumed relative orientation of the two ends of the bone about its longitudinal axis has been based upon the alignment of what are taken to be corresponding ridges and surfaces on the two broken ends of the shaft, and upon a comparison of the bone with the more complete humeri of another specimen of Mandasuchus (no. 13) and of related animals.

The proximal end is expanded, presumably antero-posteriorly, to a maximal width of 50mm.; it is convex above and concave below. The pre-axial side of the head is produced obliquely downwards and forwards into a prominent deltopectoral crest; while the post-axial side is produced obliquely downwards and backwards into a processus latissimi dorsi, the apex of which (caput humeri) is broken off. The projection of the latter behind the shaft is nevertheless greater than the projection of the former in front. The profile of the head of the bone is very strongly convex in ventral or dorsal view, and the articulating surface extends right around it from the apex of the deltopectoral crest to the apex of the processus latissimi dorsi. The latter apex must have lain a little higher than the former; an imaginary line connecting the two would cross the longitudinal axis of the bone at an angle of about 80 degrees and at a distance of some 22mm. from the extreme proximal end. The dorsal surface is demarcated from the forwardly directed upper surface of the deltopectoral crest by a square-cut edge which terminates proximally in a muscle-scar beginning at the level of the apex of the crest. Much of the proximal articulating surface has been corroded, and only the central portion and a small portion next to the apex of the deltopectoral crest are preserved complete; it is very narrow above the apex of the deltopectoral crest and becomes gradually thicker, reaching a maximum of 18mm. at its highest point (where there is a definite tuberosity on the dorsal edge) and then decreasing a little to end bluntly above the apex of the processus latissimi dorsi. The anterior margin of the deltopectoral crest, running down towards the shaft, is correspondingly quite sharp, while the posterior margin of the processus latissimi dorsi is broad and rounded. The shaft is 15mm. broad and 10mm. deep at the break; it is hollow with thin walls, and seems to have been nearly straight.

If it be assumed that the proximal expansion lies antero-posteriorly, then the degree of torsion between the two ends of the bone would appear to be such (about 60 degrees) that the distal expansion would lie in an oblique plane running from anterodorsal to posteroventral. Consequently, one of the two sides of the expansion would face forwards and slightly downwards, the other backwards and slightly upwards. In actual fact, most of the expansion is in a posteroventral direction, for the post-axial profile of the bone is markedly concave while the pre-axial is only very slightly so. The expansion reaches a maximal width of 39mm. and is hollowed out on both sides between the ridges which run down to the radial and ulnar condyles; the hollow on the posterodorsal side extends some 35mm. from the distal articulating surface towards the shaft, while that on the anteroventral side is bounded distally by a transverse ridge and does not extend so far proximally, being almost semicircular in form. The distal articulating surface is partly divided by a central constriction into radial and ulnar condyles of approximately equal size, and is continued for a short way along the pre-axial surface of the distal end of the bone (ectepicondyle). This latter surface bears an ectepicondylar groove some 20mm. long which curves slightly forwards as it approaches the distal end of the radial condyle and which is bordered anteriorly by a supinator process about 2mm. high. The shaft, which is roughly isodiametric (13mm.) at the broken end, has a pronounced square-cut edge on its anterior side; this was probably continuous with the similar edge on the proximal end.

Radius. (Plate 12).

Two fragments may be the proximal parts of the radii; their size agrees with this presumption, which, however, must be regarded as very tentative. One is not well preserved, but probably includes the greater part (78mm.) of the length of the bone; the shaft seems to narrow considerably and then begins to thicken again before reaching the point of fracture. The remaining part of its fellow (right?) is only 39mm. long, but this fragment is well preserved. The end-surface has an egg-shaped outline with a slight but definite indentation on one side and measures 16mm. by 11mm. From its narrow end a ridge runs down most of the preserved length of the shaft; the latter is otherwise featureless. Its broken end measures 9mm. by 9mm. and shows that the bone was hollow.

Ulna. (Plate 12).

It seems probable that another pair of fragments are the proximal ends of the ulnae. They agree well with the rest of the skeleton both in manner of preservation and, assuming that they are indeed parts of the fore-limb epipodials, in size; at the same time, they seem to be too large and too highly differentiated to be either the proximal ends of the radii (possibly represented by the fragments described immediately above) or the distal ends of any of the fore-limb epipodials. Further, their form agrees fairly well with that of the proximal end of the ulna of a modern crocodile. On the other hand, it must be pointed out that these supposed Mandasuchus ulnae might also be the proximal ends of the tibiae of the much smaller pseudosuchian specimen no. 11a, whose very incomplete remains were found intermingled with those of the Mandasuchus type-specimen; they are of about the same size as the distal end of the femur of specimen no. 11a, as they would be if such an association were correct.

The two fragments are approximately mirror-images of each other. The supposed right ulna is slightly smaller, however, and much the better preserved; the fracture is 24mm. below the head. The end-surface is in the rough form of a broad-based triangle with rounded corners and with the blunt apex directed forwards; each of the shorter sides is slightly concave, especially the inner, while the base is almost straight. This surface bears no olecranon process; it measures 24mm. from side to side and 17mm. from front to back. The bone narrows rapidly towards the broken end of the shaft, which is hollow with walls 1-2mm. thick; it measures 13mm. from side to side and 8mm. from front to back. Seen from behind, the head appears to be inclined medially, for the lateral edge of the bone is convex and the medial more strongly concave. The posterior surface is almost plane, but a very slight depression runs down its centre. If the bone be viewed from the side, it is apparent that the proximal surface is tilted a little forwards, especially the anterior apex, which protrudes forwards and downwards to form a well-marked lip; beneath this the anterior profile of the head is also strongly concave.

Pelvic girdle.

Ilium. (Plates 13, 14, 15 and 16).

Both ilia are preserved. The left lacks much of the posterior spine and the extreme ventral part of the acetabular portion; the right lacks only the tip of the posterior spine but rather more of the acetabular portion, including the whole of the articulating surface for the pubis. The dimensions given below are taken, as far as possible, from the right ilium.

The bone may be described as consisting of a lower acetabular portion and a more dorsal region produced into anterior and posterior spines. The ilium appears to have constituted the greater part of the acetabulum, which is a large well-formed elliptical socket some 55mm. long and 45mm. wide and of which the longer axis ran obliquely downwards and forwards. There seems to be little doubt that this acetabulum was imperforate. The ventral margin of the iliac portion is V-shaped, the tip of the V being broken off in both ilia; the two limbs of the V, which are virtually straight and together form an angle of about 100 degrees, are the contact-surfaces for the pubis (in front) and the ischium (behind). Each surface is stout and rounded in outline towards its upper end and tapers off towards the ventral corner of the ilium, the medial edges being weakly convex when seen from below and the lateral (acetabular) edges more strongly concave. The surface for the pubis has a maximal breadth of 18mm. and is only 4mm. wide where broken off; its total length is estimated at 40mm. The surface for the ischium is a little longer but rather less powerful; it has a maximal breadth of 15mm., is 5mm. wide where broken off, and its total length is estimated at 46mm. The total distance across the acetabulum from the anterodorsal end of the pubic articulation to the posterodorsal end of the ischiadic articulation is 58mm., and the vertical height of the iliac portion of the acetabulum is estimated at 48mm. from the missing ventral corner to the supra-acetabular crest. This latter, which runs back from just behind the anterodorsal end of the pubic articulation to form the anterodorsal and dorsal margins of the acetabulum, projects 24mm. laterally above the bottom of the socket; it terminates posteriorly 22mm. above the hinder end of the ischiadic articulation. The posterior border of the acetabulum is thick and rounded, but is not raised into a crest. The anterodorsal face of the acetabular portion of the ilium is broad and rounded above the supra-acetabular crest, passing over into the medial surface. This latter surface is slightly convex; its upper part served for connexion with the sacral ribs.

The dorsal, non-acetabular portion of the ilium extends another 27mm. above the hinder part of the supra-acetabular crest, at the level of which its transverse thickness is 23mm. The thickness decreases rapidly towards the upper margin, which is horizontal, more or less straight and fairly sharp. It is produced into an anterior spine which is prominent but rather short (11mm.) and which does not extend as far forwards as the anterior corner of the acetabular portion; its anterior profile is bluntly rounded. The posterior spine, on the other hand, is very long and strong and, even without its broken-off tip, stretches 61mm. behind the posterior border of the acetabular portion and 112mm. behind the tip of the anterior spine. Its lower border, seen in lateral view, curves upwards and then backwards from behind the acetabulum, gradually approaching the upper border towards the distal end of the spine; the main body of the spine is 39mm. high at its base, and is 14mm. high and 13mm. thick below at the distal fracture, tapering upwards to the sharp dorsal edge. The medial surface of this part of the bone is vertical and fairly flat, except in that a strong axially directed ledge, the medial crest, projects internally at a level a little below that of the external projection of the supra-acetabular crest. This begins above the middle of the acetabular portion and runs horizontally backwards, separating the medial surface of the dorsal portion of the bone from the medial surface of the acetabular portion (which latter forms a slight concavity beneath the crest); it meets the lower border of the posterior spine and continues as a ventromedially directed flange from the ventromedial margin of the spine, becoming even higher distally.

Pubis. (Plates 13, 14, 15 and 16).

Both pubes are preserved; both lack that posteroventral portion of the acetabular region which presumably lay next to the ischium, and both have the thin medial border of the pubic plate broken away almost everywhere. Further, the left pubis is broken across near its narrowest point (that is, at the point of torsion), and the broken ends are much weathered; while the proximal end-surface of the right is badly corroded. The dimensions given below are taken, as far as possible, from the right pubis.

The pubis is a narrow bone 131mm. long directed obliquely forwards and downwards in a curve of gradually increasing steepness; that is, the upper surface is slightly convex when seen from the side, the lower slightly concave. In the acetabular region it seems to have been expanded ventrally so that it appears very massive in lateral or medial view; and then, at a distance from the end-surface of about one-quarter the length of the entire bone (30-35mm.), the plane of its greatest extension is suddenly twisted inwards and upwards so that it is directed medially towards its fellow. That part of the bone proximal to the twist terminates in a facet for articulation with the ilium, its shape corresponding to that of the previously described facet on the latter element; this part of the bone appears accordingly thick and rounded when viewed from above, its width tapering from 19mm. at the end-surface to some 12mm. at the point of torsion. A small part of the acetabular surface, facing outwards and backwards, lies ventral to the main part of the facet for the ilium and lateral to the narrow ventral prolongation of that facet; it seems probable that the iliac facet, the pubic part of the acetabular surface and the thin ventral expansion of the bone were all continued posteroventrally to meet the ischium. The ventral margin of this part of the bone is in fact broken away entirely; the broken profile is interrupted by the remains of the obturator foramen, which is 9mm. wide, is separated from the acetabular surface by a bar of bone 10mm. wide and 5mm. thick, and lacks its lower border. Beyond the obturator foramen the ventral extension of the bone is wafer-thin and is shortly twisted inwards and upwards. The medial surface is more or less flat, but the lateral surface bulges below; a ridge, originating some 15mm. from the proximal end, runs below and almost parallel to the dorsal profile of the bone, and becomes its lateral border beyond the twist. Viewed from above or below, the outer border of the pubis appears concave; it lies furthest from the mid-line proximally and converges towards it to run parallel to it in its distal part.

That part of the bone distal to the twist consists of a flat plate with its transverse axis running horizontally towards its fellow. The lateral edge is thick (about 7-9mm.) and the plate becomes thinner towards its wafer-thin medial edge, its lower surface showing a slight transverse concavity. The medial edge is broken away everywhere except for a short length of the symphysial surface (4mm. thick) at the distal end of the bone, where the plate is 31mm. across. The symphysis did not extend to the extreme end of the bone, for the medial edge begins to diverge from the mid-line a few millimetres proximal to it. The end of the plate is slightly thickened, especially on the ventral side of the lateral corner. The distal end-surface is roughly triangular with the base above and the apex below, and with a thin medial prolongation; it has a maximal thickness of 12mm., and is incompletely ossified in the centre.

Ischium. (Plates 13, 14, 15 and 16).

The right ischium is much better preserved than the left, lacking only the anteroventral corner which lay adjacent to the pubis. The left is a little more complete in this region, but the whole base of the peduncle and part of the distal end are missing, and the general state of preservation is poor. The dimensions given below refer to the right ischium.

The ischium is 132mm. long as preserved and is directed posteroventrally, the peduncle less steeply than the proximal (acetabular) part. The latter is fairly massive and is expanded in the parasagittal plane, being thick above and becoming thinner below towards a broken edge. It narrows posteriorly and passes into the laterally flattened peduncle. This is a fairly straight and slender blade some 90mm. long; it has a broad posterodorsal margin and a knife-like anteroventral margin, and its distal end is lightly thickened. The proximal end bears a facet whose general shape resembles that of the facet on the ilium with which it articulates; laterally lies a small part of the acetabulum (rather larger than the part borne by the pubis), in this case directed outwards and forwards and with a sharp outer edge. The arrangement of iliac facet, acetabular surface and thin ventral expansion of the bone closely resembles the arrangement found in the pubis (except in that it is reversed in the antero-posterior direction), and it seems likely that each surface was continued antero-ventrally to meet the corresponding surface on the pubis. The dorsal thickness of the ischium decreases from 24mm. at the proximal end to 9mm. at the base of the peduncle.

The posterodorsal margin of the peduncle, seen from the side, is virtually straight; and, while it is broad and flattened for most of its length, its distal third is rather sharp and rises a little some 14mm. before the end. The anteroventral margin forms a narrow keel for the whole of its length and is slightly concave; thus the width of the peduncle is 21mm. at the base, 16mm. in the middle, and 24mm. at the distal end. The lateral surface is concave proximally and slightly convex distally, while the medial surface is slightly convex proximally and more strongly convex distally. The distal end-surface is roughly almond-shaped, the maximal width being 12mm., and its profile lies more or less at right angles to the longitudinal axis of the peduncle. The plane of expansion of the distal part of the peduncle is inclined at a small angle to the parasagittal plane, so that its upper border is directed a little laterally and its lower border a little medially.

Whether or not there was an ischiadic symphysis is a question of some difficulty. Judging entirely from the right ischium (for the left is too badly preserved to afford any information on this point), it seems that the distal end of the peduncle is curved away from the mid-line; that is, the bone appears convex medially and concave laterally when viewed from above. Further, when the elements of both halves of the pelvis were restored as far as possible from their fellows of the opposite side, and when the two halves were re-assembled, it proved impossible to orientate them in such a way that the distal ends of the two ischia were in contact with each other while, at the same time, the symphysis between the pubes was not disturbed. (It will be noted that the only other Mandasuchus ischium known, the left of specimen no. 63, shows a similar outward curvature to an even more marked extent). On the other hand, this outward curvature may be due to post-mortem distortion; and it is certainly true that the ventral half of the medial surface of the distal part of the peduncle gives the impression of having served as a contact-surface for the other ischium (or as an area of muscle origin).

Hind-limb.

Femur. (Plates 17 and 18).

Both femora are preserved virtually complete. The shaft of the left was broken into numerous small fragments, which, nevertheless, were fitted together successfully. Measurements given below refer to the right femur, except where stated otherwise.

The bone is 218mm. long (left 224mm.) and appears sigmoidally curved when viewed from above, the anterior border being concave proximally and convex distally. The distal part is also turned a little medially. Both ends are expanded and somewhat flattened, but their respective planes of expansion are inclined at a considerable angle (about 70 degrees) one to the other; thus, if the outer flattened surface of the proximal end be supposed to face upwards and a little forwards (so that the direction of elongation of the proximal end-surface corresponds to the direction of elongation of the acetabular socket), then the outer flattened surface of the distal end will face directly forwards.

The proximal end or head has a fairly strong anterior projection, the presence of which further increases the concavity of the anterior profile mentioned above. The end-surface is not arched but is more or less flat and measures 49mm. by 22mm. The outer (dorsal) surface is also flat except in that it is bounded by a low ridge anteriorly. The inner (ventral) surface of the bone bears a powerful hump-shaped elevation, the fourth trochanter, at a distance from the acetabular articulating surface of about one-quarter the length of the whole bone (some 55-60mm.); this bears a large muscle-scar on its anterior side. Just below the proximal end-surface and above the fourth trochanter there is a short longitudinal ridge, behind which there lies a broad but shallow longitudinal deepening running down towards the fourth trochanter. This groove contains a conspicuous foramen nutritivum 38mm. below the end-surface.

The shaft of the femur is not divided sharply from the head. It is flattened to some extent (the inner surface being flatter than the outer) and appears ovoid in cross-section, its pre-axial border being a well-rounded ridge while the post-axial forms a much sharper ridge. The dimensions vary little along the length of the shaft; in the centre the antero-posterior diameter is 23mm., the dorsoventral diameter 15mm. The shattered shaft of the left femur shows very plainly that it was hollow, the walls of the shaft being about 4mm. thick.

The distal end of the femur is club-like in shape. The end-surface seems to have been incompletely ossified, for it is deeply excavated in the centre of both left and right; its greatest diameter is 45mm., and its breadth is 25mm. between the condyles. Its front surface is flat or very slightly concave, while the hinder surface has a broad groove lying between two ridges which run down to the (corroded or incompletely ossified) tibial and fibular condyles.

The form of the femur seems to indicate that it projected horizontally and laterally rather than downwards, and formed a marked angle with the epipodials. This is confirmed by the nature of the acetabulum with its projecting ventral lip.

<u>Tibia</u>. (Plates 19 and 20).

The left tibia is complete and is much better preserved than the right, except in that part of the proximal end is slightly displaced relative to the rest of the bone. The right tibia is broken into three pieces of approximately equal length, but all the broken surfaces (and much of the true outer surface) are badly weathered. Measurements are taken from the left tibia as far as possible.

The tibia is 175mm. long and is quite straight. Both ends are expanded, especially the proximal; the expansions are mainly posteromedial in direction and to a lesser extent lateral. The anterior border of the bone is formed proximally by the cnemial crest, rounded and not particularly prominent, and distally by a sharper ridge, situated a little more medially and not continuous with the cnemial crest, and which tends to fade out as a distinct ridge towards the distal end of the bone. The whole anterior profile is quite straight. Another ridge, moderately well developed throughout its length, runs the entire length of the bone on its posteromedial side; this is markedly concave in profile. There is also a slight lateral ridge on the proximal part of the tibia and a very well-marked anterolateral ridge on the extreme distal part (which is thus triangular in section, with faces directed anteriorly, medially and postero-laterally). The medial surface of the bone is more or less plane; its width is 44mm. at the proximal end, 17mm. in the middle of the shaft and 29mm. distally. The central part of the shaft bears no ridges on its lateral side, which is strongly convex between the cnemial crest and the posteromedial ridge.

The outline of the proximal end is very roughly pear-shaped, with its greatest diameter of 46mm. running from anterolateral to posteromedial; the end-surface has a maximal width of 32mm. in a direction perpendicular to this diameter. Its central region is hollowed out to some extent. The outline of the distal end corresponds to the form of the section of the distal end already described; it resembles a broad-based triangle with rounded corners, the base (directed backwards and outwards) being 31mm. long and the height of the triangle 20mm. The two shorter sides face forwards and inwards respectively. The distal end-surface is flat except in that there is a slight anterolateral excavation which presumably received the astragalus. The only other feature visible on the shaft is a small cavity, probably a foramen nutritivum, lying on the medial surface some 40mm. below the proximal end and 19mm. behind the cnemial crest; its opening faces backwards. (This is present on the right tibia but does not seem to be developed on the left). The shaft of the bone is hollow.

<u>Fibula</u>. (Plates 19 and 20).

Only the proximal part of the right fibula is preserved (78mm. long); the left is missing entirely. Its correct orientation is a matter of some difficulty;

it has been decided to follow von HUENE (1935-1942) and to orientate the fragment in the same way as the fibula of the <u>Prestosuchus</u> <u>chiniquensis</u> type-specimen, in which the whole shank and foot are preserved in their natural spatial relationship.

The fibula is flattened from front to back. The flat proximal end-surface, which has a straight anterior margin and a strongly convex posterior margin, measures 24mm. transversely and 13mm. parasagittally. The lateral border forms a well defined ridge and is slightly concave in profile. The medial edge is rounded and much thicker and is fairly straight for a distance of some 55mm. from the proximal end, after which it inclines towards the lateral edge so that the shaft of the bone becomes suddenly narrower just above the break. The anterior surface is virtually plane in its proximal part; a powerful muscle-process extending 12mm. down the shaft projects 4mm. anteriorly from its medial border at a mean distance of 55mm. from the proximal end-surface. A low but distinct ridge begins at this process and runs down the shaft, passing a little obliquely towards the lateral side. The posterior surface has a low backwardly directed ridge running down its medial margin, beginning about 30mm. from the proximal end;

a slight concavity lying between this and the lateral margin extends upwards to the proximal lateral corner.

Possible metatarsal. (Plate 20).

A small piece of bone 26mm. long may be the proximal end of a metatarsal. The end-surface is slightly arched and measures 17mm. by 7mm. One side of the bone is lightly concave and has a V-shaped fossa just below the articulating surface; its transverse width decreases from 17mm. at the articulating surface to 8mm. at the broken end, and both its margins are concave in profile. The opposite side is badly preserved, but seems to have been convex with at least one longitudinal ridge.

Dermal scutes. (Plates 2 and 21).

The remains of three consecutive paramedian dorsal scutes of the right side are preserved *in situ* upon the neural spine of the supposed sixth cervical vertebra. Several other very fragmentary pieces of scute material were found unattached, but only those four which are figured merit consideration; each of these includes the remains of two or three consecutive scutes. These fragments are manifestly so incomplete and poorly preserved that individual descriptions would be of little value. Yet although no scute is preserved complete, all the fragments found seem to conform to the general pattern of the three scutes found *in situ*, and there is no reason to suppose that they were not also members of a double row lying along the middle of the animal's back. The structure of the typical scute as described below and as illustrated in Plate 21 may be inferred without difficulty from that of the scutes *in situ* and that of the several fragments (referred to in the description, quite arbitrarily, as "P", "Q", "R" and "S"); but it must be remembered that details of proportion will vary in scutes from different regions of the body.

Each scute overlaps the scute behind it as do tiles on a roof, and consequently each must dip a little towards its front end. Each bears a prominent longitudinal keel on the outer surface which projects up to 3mm. dorsally and which divides the plate into a medial portion and a lateral portion; these two surfaces are inclined to one another at an angle which, while not susceptible of exact measurement, does not differ much from 110 degrees in any of the fragments. Thus (as is well shown by the scutes *in situ*) the medial portion lay more or less horizontally upon the top of a neural spine, its inner border contiguous with that of its fellow, while the lateral portion sloped steeply down the animal's side at an angle of about 70 degrees to the horizontal.

The scutes are more numerous than the vertebrae, at least in the cervical region; for, of the three found apparently undisturbed upon the neural spine of the supposed sixth cervical vertebra (the centrum of which is 40mm. long), the posterior border of the second scute lies only 15mm. behind the posterior border of the first. Similar measurements of the distances between corresponding points on consecutive scutes (that is, of the length of scute exposed) have been made on some of the other fragments. These are tabulated overleaf, together with measurements of the length of each scute overlain by its predecessor, the total length of one scute estimated by addition of the two preceding measurements, and measurements of the widths of the medial and lateral portions in the exposed parts of the scutes.

The following tentative general conclusions may be drawn from these measurements of the small quantity of material available. Each scute is about 29mm. long, of which the anterior 13mm. is overlain by the preceding scute and the posterior 16mm. is exposed.

no. 11b - TABLE OF MEASUREMENTS OF THE DERMAL SCUTES (millimetres)

fragment	in situ on Ce6	"P"	"Q"	"R"	"S"
(side of body	right	right	right	left	left)
length exposed	15	17	?	18	14, 17
length overlain	?	13	13	?	14
total length	?	30	?	?	28
width of medial part	7	7	11	14 plus	15
width of lateral part	16	13 plus	17	17	17

These measurements do not seem to vary much. Thus the dermal armour is two layers thick over a great part of the area which it covers, but is nowhere more than two layers thick. The width of the lateral portion of the exposed outer surface is fairly constant, usually about 17mm.; but the width of the medial portion is highly variable, ranging from 7mm. to at least 15mm. (Paradoxically enough, the scutes with the narrowest medial portion are resting upon the vertebra with the broadest neural spine). Thus the plates are, on an average, about as wide as long. The distance between consecutive scutes is in every case much less than the length of any known centrum. No centrum of the neck or trunk is shorter than 28mm., and none in the tail is shorter than 24mm.; the actual distances between corresponding points on successive vertebrae must have been even greater than these measurements if it be presumed that intervertebral discs were present.

The exposed portion of each scute is roughly rectangular in outline. Both medial and lateral borders are fairly straight and parallel to one another. The posterior border, lying more or less at right angles to these, bulges slightly behind the medial portion of the plate and again behind the lateral portion; a small notch or bight between these two convexities and behind the longitudinal keel fits over the keel of the following scute. The posterior corners are not square but are a little rounded. When the scutes are viewed from the inner side, it is seen that each has a bluntly rounded anterior outline continuous with the lateral and medial margins; and, from the front of this, a narrow spine projects forwards some 7mm., apparently continuous with the keel on the outer surface. While the lateral portion of the outer surface of the scute is quite plane up to the top of the keel, the medial portion lies below the level of the top of the keel and thus appears concave. The inner side of the scute shows no trace of the outer division into medial and lateral portions, but is weakly concave as a whole; and it bears a deep forwardly projecting depression in the centre of its hinder end, just anterior to the bight in the hinder margin, into which the anterior spine of the following scute fitted exactly.

The plates are 2-3mm. thick, being thicker than this beneath the keel and thinner towards the edges. They are smooth and quite devoid of ornament, there being neither pits nor sculpture of any sort.

The flattening and expansion of the tops of the neural spines of the vertebrae should give some indication of the distribution of the dorsal scutes. As already described, such expansions are well developed in the anterior part of the column, including the neck; but they decrease in size after the middle of the back, so that the tops of the spines of the posterior dorsals and anterior caudals, though flattened, are hardly expanded at all.

iv) Description of specimen no. 13

Field notes.

Field-collection no. 13, like no. 11, was found in locality B5 at Irundi. All the bones appear to belong to a single individual, and vary in colour from grey or yellow to a purplish brown. Most of the specimen is extremely well preserved; nevertheless, since the specimen itself is rather soft and since the surrounding matrix was generally much harder, the removal of the latter proved difficult in places. (One piece of rock, bearing a small number of dermal scutes, was prepared by a combination of treatment with acetic acid and the "Transfer Method" - see

Chapter 2, Section (b) above - by which the scutes were eventually embedded in a transparent block of resin).

Material available.

Maxilla: fragment of right, containing tooth.

Vertebrae: parts of at least 15, including axis, all remaining cervicals, first 5 dorsals, 2 possible middle dorsals and 1 possible caudal; together with neural arches and spines and other fragments which cannot be identified as belonging to any particular vertebra.

Ribs: both axial; fragment of shaft of dorsal.

Scapula: both left and right.

Coracoid: articular part of right.

Humerus: both left and right, left lacking distal end and right lacking part of proximal end, but together rendering complete restoration possible.

Radius: probable end-pieces of both left and right.

Ulna: left, lacking distal end.

Dermal scutes: five in approximately natural connexion, together with several fragments.

Maxilla. (Plate 22).

Part of the right maxilla is preserved in the form of a straight bar 30mm. long and broken off at each end. There are three alveoli, the middle one containing a tooth.

The height of the bar decreases from 12mm. at its anterior end to some 9mm. behind; the maximal thickness of the bar decreases likewise from 7mm. to 6mm. The lateral wall is extended upwards as a thin lamella, inclined slightly inwards and increasing in height backwards from 1mm. to 4mm. as the height of the bar itself becomes less; thus in lateral view the whole fragment appears to be of constant height (13-14mm.) along its length. A shallow groove lies between the concave medial surface of this lamella and the dorsal surface of the bar. The lateral wall bears at least two minute downwardly directed foramina about 2mm. above its lower border.

The form of the alveoli is shown in the illustration of the fragment in crown view; they are 5-7mm. long and 3-4mm. wide. The middle alveolus contains an erupting tooth which is preserved almost complete. The crown, of which some 6mm. is visible, is strongly compressed laterally and is inclined backwards at an angle of about 70 degrees to the perpendicular, the apex of the tooth being recurved; the anterior cutting edge is therefore directed downwards, while the posterior cutting edge (if present) cannot be seen. The anterior cutting edge is fairly sharp and finely crenulated, there being 6-7 crenulations to the millimetre.

The absence of any trace of the ascending process and the relatively great development of the dorsal extension of the lateral wall would appear to indicate that this fragment comes from the hinder part of the maxilla, beneath the antorbital vacuity.

A fragment of unidentified plate-like bone adheres closely to the lateral surface of the maxillary fragment.

Vertebral column.

Table of principal measurements of the vertebrae. See overleaf.

Cervical region.

Axis. (Plates 22 and 23). The centrum is preserved together with the bases of the sides of the neural arch, but the lower part of the posterior face is missing. Fragments of the axial ribs adhere to the sides. The anterior articulating surface is complete and of a characteristic shape; a concavity for the odontoid occupies the upper half, and ventral and no. 13 - TABLE OF PRINCIPAL MEASUREMENTS OF THE VERTEBRAE (millimetres)

Centrum:	Ce2 (axis)	Ce3	Ce4	Ce5	Ce6	Ce7	Ce8	D1	D2	D3	D4	D5	"X"	"Y"	"Z"
length below	17	25	28	29	28	26	24	20	19	19	19e	-	23	22	21
length above	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-
anterior height	14	14	14	14	15	16	17	16	16	15	15	15	20	-	14
anterior width	12	15	16	16	17	17	19	20	21	20	19	18	18	17	13e
posterior height	-	15	14	15	16	16	17	16	17	16	15	-	17	20	-
posterior width	13	14	15	16	16	17	19	19	19	18	17	-	17	17	12e
mean diameter	13	14½	15	15	16	16½	18	18	18	17	16½	16½	18	18	13
elongation ratio	131	172	187	193	175	158	133	111	106	112	115	-	128	122	162
minimal transverse thickness	4	6	7	8	7	8	8	8	9	8	-	8	8	9	5
Neural spine:															
height (measured from top of centrum)	-	-	27	-	-	27	26	-	26	26	-	27	-	-	-
axial length above	-	-	18e	-	-	20	15	-	15	15	-	18	-	-	-
maximal transverse width above	-	-	5	-	-	6	7	-	6	6	-	5	-	-	-

(e - estimated)

lateral to this lies a crescentic facet for the axial intercentrum, tapering below to a point. The parapophysis is an indistinct facet lying half-way up the lateral margin of the anterior face. The neurocentral suture is very distinct.

Supposed third to eighth (last) cervicals. (Plates 22 and 23). These vertebrae are, on the whole, better preserved than those of the type-specimen. The supposed third consists of a centrum together with the bases of the sides of the neural arch. The supposed fourth and fifth are in natural connexion; the former is almost complete, lacking only the ends of the prezygapophyses and the upper corners of the neural spine, while the latter has the postzygapophyses and the whole of the neural spine broken off. The supposed sixth, seventh and eighth are in natural connexion with the first four dorsal vertebrae; the supposed sixth lacks prezygapophyses and neural spine, the supposed seventh is virtually complete, and the last lacks only the ends of the diapophyses.

The lengths of the centra show, as in the type-specimen, a degree of elongation which reaches its maximum in the supposed fifth cervical. The supposed third is much longer than the axis; the supposed fourth, fifth and sixth are the longest of the whole column, with the fifth perhaps a very little longer than the fourth and sixth; the supposed seventh is shorter than the supposed sixth, and the supposed eighth shorter still (though much longer than the dorsal vertebrae). A peculiarity of these vertebrae which is not apparent in the poorly preserved cervical centra of the type-specimen is that, if a vertebra be placed with its articulating faces vertical, then the anterior face lies higher than the posterior; or, alternatively, the anterior face is inclined a little downwards as well as forwards relative to the longitudinal axis of the centrum, the posterior a little upwards as well as backwards. This feature is especially well marked in the supposed fourth cervical and is developed to a lesser extent at the hinder end of the neck; it indicates that the animal carried its head above the level of its back. The upward curvature of the neck is also shown by the connected vertebrae when considered as a whole. The centrum of the supposed third cervical has no median keel beneath but a narrow, clearly developed ridge resembling a strip of beading; the others are all rounded below, except for a faint ridge in the posterior half of the centrum of the supposed seventh. The anterior faces of the centra are moderately concave; the posterior face is almost plane in the supposed third, fourth and fifth cervicals, lightly concave in the supposed sixth and seventh, and moderately concave in the supposed eighth. The diameter of the faces increases gradually from 14-15mm. in the supposed third cervical to 17-19mm. in the supposed eighth. The form of the parapophysis is fairly constant; it is a small facet lying low down on the anterior margin of the centrum, but it may be seen in ventral view that the distance between left and right parapophyses increases down the series:

Ce3	5mm.
Ce4	5mm.
Ce5	7mm.
Ce6	9mm.
Ce7	10mm.
Ce8	11mm.

The diapophysis is a somewhat similar facet in the supposed third, fourth and fifth cervicals, lying directly above the parapophysis in the anterodorsal corner of the centrum and apparently upon the neurocentral suture. In the supposed sixth cervical, however, it extends a little further back and projects a little laterally. In the supposed seventh it is borne entirely on the neural arch and lies some 3mm. behind the anterior border of the centrum, to which it is connected by a short sharp ridge; it projects further laterally, its terminal facet facing obliquely downwards. In the supposed eighth cervical the broken-off stump of the diapophysis is set back almost half the length of the centrum, from which it seems to have projected a considerable distance; it differs from the other cervical diapophyses in that short but well developed anteroventral, posteroventral, and anterodorsal buttresses are present, together with fairly deep anterior and inferior pleural concavities; the anteroventral buttress does not reach the parapophysis. The neurocentral suture is clearly defined in all these vertebrae. It begins on either side of the upper margin of the anterior face of the centrum at the base of the neural canal, running obliquely downwards and outwards across the face towards the front edge of the diapophysis; it then passes along the side of the vertebra through or below the diapophysis, ascends to a peak near the middle of the vertebra, descends gently towards the posterior margin, and finally ascends sharply again towards the gap for the exit of the spinal nerve. The neural arch thus contributes to the formation of the anterior face of the "centrum", but forms no part of the posterior face. In the supposed eighth cervical the centrum and neural arch have become partially separated on one side so that a great hollow lies beneath the diapophysis. This indicates post-mortem displacement of the two incompletely ankylosed vertebral elements of what is presumed to have been a young animal. The ascending ridge which runs back on either side of the neural arch to form the outer border of the postzygapophysis is present in these vertebrae as in those of the type-specimen; in the supposed eighth cervical, although this does not extend downwards as far as the diapophysis, a clearly defined posterior pleural concavity is present beneath it. The neural spines appear to be relatively a little higher than in the type-specimen; and their tops, while flattened and fairly broad, are not expanded at all. Thus, whereas in the type-specimen the maximum width of the upper surface of the neural spine of the supposed fourth cervical vertebra is 25% of the length of the centrum, the corresponding figure in this specimen is only 11%. Similar ratios for the supposed seventh cervical vertebra are 43% in the type-specimen and 23% in this specimen.

Dorsal region.

First to supposed fifth dorsal vertebrae. (Plates 22 and 23). These are also better preserved than the corresponding vertebrae of the type-specimen. The first three and the anterior half of the fourth are in natural connexion with the last three cervicals; the supposed posterior half of the fourth, with the anterior half of which it makes an approximate fit, was joined by matrix to the supposed fifth. The first lacks the diapophysis on one side and the posterior half of the neural arch, including both postzygapophyses and the neural spine; the second and third lack only the ends of the diapophyses (and one prezygapophysis of the second); the fourth lacks diapophyses and the posterior half of the neural arch, including postzygapophyses and the neural spine; and the supposed fifth lacks the whole hinder part of the centrum and the postzygapophyses, together with the ends of the diapophyses and the prezygapophyses.

The centra of these vertebrae are all of about the same length but considerably shorter than the cervical centra. The broken end of the supposed fifth dorsal centrum shows that, because of the ventral concavity and the dorsal excavation in the floor of the neural canal, the vertical thickness of the centrum is only 7mm. in the middle. The centra are rounded beneath; their articulating surfaces are very lightly concave or nearly flat, and their width reaches a maximum in the second dorsal, after which it begins to decrease again a little. The parapophysial facet is extremely large in the first three dorsals, especially the second and third; it is borne entirely on the centrum in the first two, lying ventrally in the first but a little higher up in the second. In the third dorsal, however, the upper third of the parapophysis is borne on the neural arch; this is clearly shown on the right side of the vertebra, where the centrum and the neural arch have been separated after death. In the fourth dorsal the parapophysial facet is badly weathered but it can yet be seen that it lies with its upper end at about the level of the middle of the neural canal; its greater part is borne on the neural arch but its lower third is still on the centrum. In the supposed fifth dorsal the badly preserved and much smaller parapophysial facet is borne entirely on the neural arch and projects laterally on a short peduncle at the level of the neural canal. The diapophysis is unusually well preserved on one side of the first dorsal, where it projects obliquely outwards and downwards from the middle of the vertebra as a stout process about 16mm. long terminating in a roughly circular facet of some 7mm. diameter; in the other vertebrae it is broken off short, but, from the nature of its stump in the supposed fifth dorsal, it seems that it was weaker in that vertebra and did not project downwards. All four diapophysial buttresses appear to be present in all the vertebrae, as far as the latter are preserved. The anteroventral buttress of the first dorsal is lamelliform and short, reaching neither the parapophysis nor the anterior margin of the vertebra; it is a little longer in the second and longer still in the third, connecting with the parapophysis. As the anteroventral buttress moves its anterior end dorsally with the parapophysis towards a more horizontal position, so the anterodorsal buttress converges towards it; and thus the anterior pleural concavity between them, wide and deep in the first dorsal, becomes reduced to a comparatively narrow opening in the supposed fifth. The posterior and inferior pleural concavities are also well developed in all these vertebrae where preserved. The neurocentral suture is of much the same form as that found in the cervical region, rising to a peak in the middle of the vertebra. The zygapophyses are rather smaller than those in the cervical region and do not extend so far laterally, but resemble them otherwise. The neural spines of the second and third dorsal vertebrae are of almost exactly the same height, axial length and transverse width as that of the last cervical; the neural spine of the supposed fifth dorsal is of about the same height but is rather longer axially and perhaps a little narrower.

Possible middle dorsal vertebrae. (Plates 22 and 23). Two similar centra, referred to as "X" and "Y" in the Table of Measurements, are appreciably longer than those of the anterior dorsals described above; their almost flat end-faces (the lower part of one of which is broken off in "Y") are a little higher and narrower than those of the anterior dorsals. Front and back cannot be distinguished with certainty. The vertebrae are slightly flattened beneath, and there are no facets for ribs or haemapophyses. The neural arches may have broken away cleanly along the line of the neurocentral suture, for a small triangular projection lies in the centre of three of the four broken surfaces above.

These vertebrae might come from the middle dorsal region of the column, for the supposed fifth to tenth dorsals of the type-specimen show a similar ventral flattening. The greater length of these centra, however, is a little puzzling; in the type-specimen the lengths of the dorsal centra are all much the same, while the caudal centra (except two) are shorter.

Caudal region.

Possible caudal vertebra. (Plates 22 and 23). This badly preserved little centrum, referred to as "Z" in the Table of Measurements, is slightly longer than those of the anterior dorsals but shorter than the two possible middle dorsal centra described immediately above. It seems to be very strongly compressed in a lateral direction, and, once again, front cannot be distinguished from back. One end is broken away below and at one side; it may be that this end was the posterior and bore haemapophysial facets. The end-surfaces are weakly concave and seem to have been smaller than those of any other vertebra (except the axis). Considerations of size alone indicate that this vertebra may be from the tail.

Fragmentary vertebral material.

An unattached neural arch and five unattached neural spines, some with zygapophyses, are also preserved. None merits spécial attention. The dimensions of the dorsal surfaces of the neural spines are:

length 14mm.	maximal width 6mm.
17mm.	4mm.
18mm.	7mm.
20mm.	5mm.
21mm.	5mm.

Ribs.

Axial ribs.

Fragments of the ribs adhere to the sides of the axis; but they are so small, fragile and badly preserved that no details of their structure are visible.

Dorsal rib.

A small piece of a shaft, sub-cylindrical in form and slightly flattened on one side, is 14mm. long and of some 4mm. diameter.

Pectoral girdle.

Scapula. (Plate 24).

Both scapulae are preserved. The left lacks the posterodorsal corner and most of the fragile anterior and dorsal margins; the right lacks the whole of the upper end and of the anterior margin. The preserved lengths, measured externally along the curve, are 85mm. and 71mm. respectively.

The left scapula may be complete below, where its breadth is 37mm.; the deltoid flange, forming the anterior expansion, is extraordinarily thin and its preparation was very difficult. The scapular portion of the glenoid fossa forms a facet 8mm. high and 17mm. wide. The muscle-process on the posterolateral margin of the bone begins some 7mm. from the upper border of this facet.

Coracoid. (Plate 24).

Only the articular part of the right coracoid is preserved; relatively less remains than of the coracoid of the type-specimen. Traces of the coracoid foramen are visible on the broken anterior edge 10mm. in front of the glenoid and 6mm. below the surface for the scapula.

Fore-limb.

Humerus. (Plates 24 and 25).

Neither humerus is complete, but the left lacks only the distal end and the right the proximal end (the caput of the right is preserved as a separate fragment). The bone may therefore be restored completely.

The reconstructed humerus appears to have been about 105mm. long. The proximal expansion is 36mm. wide; the profile of the head of the bone appears much less convex in ventral or dorsal view than in the type-specimen, but this is because the apex of the processus latissimi dorsi is broken off in the latter. The proximal articulating surface is virtually complete and reaches its greatest thickness of 11mm. at the dorsal tuberosity. The straight shaft is 9-10mm. broad and 7-8mm. deep at its narrowest point in the centre of the bone.

The degree of torsion between the two ends of the bone appears to be less (about 40 degrees) than in the type-specimen; but a considerable error may be involved in this comparison, for all the bones concerned have been partly reconstructed. The maximal width of the distal expansion is 27mm.; the hollow on the posterodorsal side extends 31mm. proximally from the distal articulating surface and is therefore relatively longer than in the type-specimen. The ectepicondylar groove and supinator process are exactly as in the type-specimen.

<u>Radius</u>. (Plate 25).

Two pieces of bone may represent the proximal parts of the radii. The longer of these, 27mm. long, measures 13mm. by 9mm. at the end-surface and 9mm. by 6mm. where the hollow shaft is broken across. In the form of the end-surface and in the presence of a ridge running down the shaft the fragment agrees with the proportionately larger supposed proximal end of the left radius of the type-specimen. A somewhat shorter fragment, to the side of which adheres a piece of an unidentified plate-like bone, appears to be the fellow of this.

Another rather similar end-piece may be the distal end of one of the radii. It is 24mm. long and measures 11mm. by 9mm. at the end-surface and 7mm. by 5mm. at the break. One side of the shaft is slightly flattened.

<u>Ulna</u>. (Plate 25).

A large well preserved fragment is taken to be the left ulna; this presumption is based on considerations of size, form, and the fact that most of the remains of this animal come from the anterior end of the trunk and from the fore-limb. It nevertheless differs to some extent from the supposed proximal end of the ulna of the type-specimen.

The bone is 75mm. long as preserved and is incomplete at the distal end, but only a few millimetres can be missing. The form of the end-surface is very roughly similar to that found in the type-specimen - a broad-based triangle with the blunt apex directed forwards, - but the medial corner is produced into a short blunt process with concavities on either side, and the outer edge is slightly convex. The end-surface measures 21mm. from side to side and 16mm. from front to back; its outer part is not flat but is raised into a low hummock, presumably a very weakly developed olecranon process. The head tapers rapidly into the shaft, the proximal part of which is exactly as described in the type-specimen; it has a convex lateral edge, a more strongly concave medial edge, and a plane posterior surface with a light central groove. The anterior surface, rounded in its proximal part, becomes flatter below and develops a central groove; so that, at a distance of some 30-35mm. from the end-surface, both front and back of the shaft are flattened and grooved. The shaft has a minimal breadth of 10mm. and a minimal thickness of

5mm. in its middle region. Distally it becomes broader and thicker (the expansion being mainly medial and anterior, as at the proximal end), and the grooves die out; the hollow shaft measures 14mm. by 7mm. at the broken surface.

Dermal scutes. (Plates 25 and 26).

Several pieces of rock contain the delicate dermal scutes, usually visible in transverse section. The best piece, however, showed the inner surfaces of five scutes which seemed to be in their more or less natural positions relative to each other; these were prepared and embedded in a transparent block of synthetic resin. Their form confirms the general picture obtained from a study of the incomplete fragments of the type-specimen. The actual shape of each scute is not shown particularly well, for, even with the greatest care, it was impossible to avoid breaking the fragile edges of the scutes in places; but the presence of a double row of plates and their method of overlap are clearly seen. These scutes also show that the longitudinal keel on the outer surface becomes more prominent anteriorly and forms the anterior spine. In some, but not all, the lateral portion of the outer surface seems to slope down less steeply relative to the medial portion than in the type-specimen; the two portions are of approximately equal width. Each scute appears to have been about 15mm. long.

v) Description of specimen no. 63

Field notes.

Field-collection no. 63 was found in locality B15/2 at Mkongoleko/Njalila. All the bones appear to belong to a single individual; they are of a whitish hue, mottled with brown and purple. The containing matrix was of a variable nature, consisting in places of densely packed calcite crystals which were very resistant to mechanical preparation.

Material available.

Vertebrae: parts of at least 28, including odontoid, axial intercentrum and axis, all remaining cervicals, 8 dorsals and 12 caudals (6 of them distal caudals); together with neural arches and spines and other fragments which cannot be identified as belonging to any particular vertebra.

Ribs: 3 cervicals of left side; proximal part of dorsal of right side; numerous fragments.

Haemapophysis: proximal end.

Pelvis: left side, lacking only central part of pubis and pubo-ischiadic junction.

Femur: fragments of shaft of right.

Tibia: left.

Fibula: proximal part of right.

Fibulare: left.

Dermal scutes.

Vertebral column.

The neural spines of the preserved vertebrae of this specimen are all broken off and weathered so that, of the many found, none may be related to its proper vertebra.

Cervical region.

Table of principal measurements. See overleaf.

Odontoid, axial intercentrum and axis. (Plate 27). These three elements are fixed together quite firmly in the fossil specimen; yet it seems unlikely that the ankylosed condition obtained in the living animal, for the odontoid is situated not quite centrally with respect to the axis, appearing to have been displaced a little to the left.

The odontoid and axial intercentrum are preserved no. 63 - TABLE OF PRINCIPAL MEASUREMENTS OF THE CERVICAL VERTEBRAE (millimetres)

Centrum:	Ce1 (odontoid)	Ce2 (axis)	Ce3	Ce4	Ce5	Ce6	Ce7	Ce8
length below	-	31	43	49	50	49	45	-
length above	14	37	-	-	-	-	-	-
anterior height	9	29	29	30	30	33	35	37
anterior width	24	25	28	29	32	-	38	40
posterior height	20	31	32	33	35	37	36	-
posterior width	24	27	31	33	36	39	41	-
mean diameter	-	28	30	31	33	$35\frac{1}{2}$	$37\frac{1}{2}$	$38\frac{1}{2}$
elongation ratio	-	1.11	1.43	1.58	1.52	1.38	1.20	-
minimal transverse thickness	-	10	13	15	16	16	15	17

complete; the axis is represented only by the centrum together with a small piece of the neural arch and by the isolated neural spine.

The odontoid is attached to the upper half of the anterior face of the axial centrum and projects 14mm. forwards. Its upper surface is more or less flat with a large but shallow central depression. Its anterior face, 9mm. high and 24mm. wide, is slightly crescentic in outline with the concave margin above; it is weakly convex and faces directly forwards. Its posterior surface, 20mm. high and 24mm. wide, is applied to the anterior face of the axis; these two faces diverge below and the axial intercentrum fits into the gap thus formed. The sides of the odontoid, though very short antero-posteriorly, are laterally constricted so that the upper surface, 24mm. wide both in front and behind, is narrower (16mm.) in the centre. Since the hind face is so much deeper than the front, it follows that the so-called "ventral" surface ascends steeply from its posterior border; it then becomes almost horizontal 3mm. behind its anterior border. This surface is not clearly demarcated from the lateral surfaces of the odontoid.

The axial intercentrum is shaped like the segment of an orange with the outer surface facing downwards. This outer surface is 11mm. broad sagittally and tapers to a point on either side, the transverse distance between the points being 23mm. The anterior border is smoothly convex between these two points; the posterior border runs parallel to this and is much shorter, forming a small concavity 11mm. wide. A straight margin some 14mm. long and directed posterolaterally connects the ends of the anterior and posterior borders on each side. A light transverse groove runs across the middle of the outer surface so that the latter appears concave in lateral view. The crescentic posterior face of the intercentrum faces a little upwards and is applied to the lower half of the anterior face of the axis; while the anterior face of the intercentrum, also crescentic and facing a little upwards, is freely exposed except for a small part above which is hidden by the base of the odontoid. In lateral view the axial intercentrum is 15mm. high both anteriorly and posteriorly.

The ventromedial keel of the axis is very prominent. The parapophysis is an indistinct, slightly recessed facet situated on the junction of the posterior face of the axial intercentrum and the anterior face of the axis, just below the lateral horn of the former; a small part of the head of the axial rib appears to be attached to it on one side. The diapophysis is clearly visible on the same side. The separately preserved neural spine is broken off above its junction with the neural arch and lacks its hindermost tip; its dorsal surface, which is neither flattened nor expanded, is 48mm. long as preserved, 4mm. wide in front and 8mm. wide at the posterior break. Traces of the posterior spinal buttresses and of the groove which lies between them are the only features shown.

Third to eighth (supposed last) cervicals. (Plate 27). Five more or less complete centra and the anterior half of a sixth follow the axis; the order of succession is indisputably correct, for adjacent vertebrae were connected in every case either by their centra or by their zygapophyses. All except the last retain some part of the neural arch and zygapophyses; and, while in some instances the ends of the capitulum and tuberculum of the cervical rib are still attached to the parapophysis and diapophysis respectively, in others the latter two processes are broken off.

Since this series of centra is larger and more complete than that of either of the other two specimens, the typical trends in the dimensions are more apparent. The length of the centrum varies as in specimen no. 13, reaching a maximum in the fifth cervical. At the same time it must be noted that the cervical vertebrae of specimen no. 63, as indeed those from other regions of the column, are considerably stouter relative to their own length than are the corresponding vertebrae of either of the other specimens; this is clearly shown by the lower values obtained for their elongation ratios. The mean diameter of the centrum increases steadily up to the seventh vertebra, at which point it has reached the approximate value characteristic of the dorsals. The minimal transverse thickness also increases up to the fifth vertebra, after which it fluctuates a little about the value found there.

One feature shown by the cervical vertebrae of specimen no. 13, namely the slightly oblique disposition of their end-faces relative to the longitudinal axis of each centrum, is scarcely discernible here; nevertheless the whole neck has been preserved with a marked upward curvature. The third vertebra has a well developed ventromedial keel, but the subsequent cervicals bear only a light ridge below. The concavity of the articulating faces of the centra is more pronounced in this specimen than in the others; only the posterior face of the seventh cervical is almost plane. The transverse distance below between left and right parapophyses increases down the series in the following manner:

Ce3	10mm.
Ce4	11mm.
Ce5	16mm.
Ce6	19mm.
Ce7	33mm.

The diapophysis is better preserved here than in the other specimens; even in the third cervical it already lies 4mm. behind the anterior margin of the centrum and projects 1mm. laterally to terminate in a circular facet of some 8mm. diameter. Posteriorly it tends to move a little further back from the anterior margin, to project further laterally and to increase in size. Too little is preserved of the eighth vertebra to show more than that the diapophysis was set far back, that an anteroventral lamella which did not reach the parapophysis was present, and that an anterior pleural concavity is first represented here. The neural canal is much broader than high in front, as in the cervicals of the type-specimen; it measures 16mm. by 7mm. in the sixth cervical. The prezygapophyses project far beyond the centrum, the postzygapophyses hardly at all. The right postzygapophysis of the third cervical is well enough preserved to show a feature shown by no other known vertebra of this genus - a small ridge at the base of the posterior spinal buttress, directed inwards and backwards, which presumably served for muscle attachment. A hyposphene is definitely absent in these vertebrae.

Dorsal region.

Table of principal measurements. See overleaf.

Supposed first dorsal vertebra. (Plate 28). This is represented by a fragment of the anterior part of the centrum. The only recognisable features are the depression in the floor of the neural canal, part of the anterior face, a parapophysis in a low position and an anteroventral lamella which does not reach the parapophysis.

Supposed fourth to tenth dorsal vertebrae. (Plates 28 and 29). There is no direct evidence for the succession of the supposed fifth dorsal by the supposed sixth, but the sequence is otherwise placed beyond dispute by the connexion of the vertebrae. All no. 63 - TABLE OF PRINCIPAL MEASUREMENTS OF THE DORSAL VERTEBRAE (millimetres)

Centrum:	D1	D4	D5	D6	D7	D8	D9	D10
length below	-	37	36	-	38	38	38	-
anterior height	-	37	37	37	36	36	36	38
anterior width	-	39	38	37	37	37	37	38
posterior height	-	35	37	-	35	37	36	-
posterior width	-	37	37	-	38	37	38	-
mean diameter	-	37	37	37	36½	37	37	38
elongation ratio	-	1.00	0.97	-	1.04	1.03	1.03	-
minimal transverse thickness	-	17	16	15	16	15	15	-

except the supposed tenth are fairly complete, lacking only various rib-facets and zygapophyses in addition to the neural spines; the ends of the diapophyses are broken off everywhere. The supposed sixth dorsal also lacks much of the hinder face of the centrum and one side of the neural arch. The supposed tenth is represented by a mere slice of the centrum attached to the posterior face of the supposed ninth.

The only important differences discernible between these vertebrae and the corresponding vertebrae of the type-specimen lie in the relative stoutness of their centra (length and mean diameter being approximately equal) and in the absence of any flattening below, such as may be seen on all the corresponding vertebrae of the type-specimen except the supposed fourth. (A very slight flattening may be present beneath the supposed seventh of this specimen). The depressions on the sides of the vertebrae are well developed. The parapophysis projects 6mm. laterally in the supposed seventh vertebra and its facet is 11mm. high and 7mm. broad; in the supposed fourth and fifth, and to a less obvious extent in the supposed sixth, it is connected by a short stout ridge to the prezygapophysis. The anterodorsal buttress is almost horizontal in the supposed fourth dorsal, is very weakly developed in the supposed seventh, and is virtually absent thereafter; the anterior pleural concavity disappears with it. The neural canal is 11mm. high and 13mm. wide at its anterior end in the supposed seventh dorsal vertebra. The supposed fourth, seventh, eighth and ninth all possess a powerful hyposphene, a feature not preserved in the anterior dorsals of the type-specimen.

Caudal region.

Table of principal measurements. See overleaf.

Supposed first and second caudal vertebrae. These two are represented by their centra together with the sides of the neural arches and the bases of the transverse processes. Both are rounded beneath and appear to resemble their presumed counterparts in the type-specimen in every respect except in that they are not shorter than the dorsals but are of about the same length; and whereas in the type-specimen the mean diameter of the centrum is roughly equal to its length, in this animal it is appreciably greater, being greater than in any other vertebrae.

no. 63 - TABLE OF PRINCIPAL MEASUREMENTS OF THE CAUDAL VERTEBRAE (millimetres)

Centrum:	Ca1	Ca2	Ca4	Ca5	Ca6	Ca7	PC1	PC2	PC3	PC4	PC5	PC6
length below	38	36	36	33	35	33	-	27	27	26	28	26
anterior height	43	41	40	40	39	-	18	17	17	16	16	15
anterior width	43	-	39	-	-	29	17	16	16	15	15	14
posterior height	41	42	39	36	36	31	-	17	16	16	16	15
posterior width	-	40	35	-	32	28	-	16	15	15	14	14
mean diameter	42	41	38	38	36½	29	17½	16½	16	15½	15	14½
elongation ratio	0.90	0.88	0.95	0.87	0.96	1.14	-	1.64	1.69	1.68	1.87	1.79
minimal transverse thickness	22	20	18	19	18	16	9	8	8	7	7	7

Possible fourth to seventh caudal vertebrae. (Plates 28 and 29). These four vertebrae consist only of the centra with, in the possible fourth and fifth, the sides of the neural arches and the bases of the transverse processes, and, in the possible sixth, one side of the neural arch. The anterior face of the centrum of the possible seventh caudal is broken away below. The tentative positions assigned to these vertebrae have been given on considerations of size and proportions and from a comparison with the possible fifth, sixth and seventh caudals of the type-specimen (which, however, are relatively more slender). All four bear facets for haemapophyses, all are flattened beneath, and all except the possible fourth have a longitudinal groove in the middle of the flattening. The possible fourth otherwise resembles the possible fifth of the type-specimen and is presumed to be the first vertebra with haemapophysial facets. These centra also show a slight bending back of the ventral margin of the anterior face for the accommodation of the haemapophysis. The possible fifth caudal of this specimen shows the saddle-shaped type of articulation between the centra especially clearly.

Distal caudal vertebrae. (Plates 28 and 29). Five small centra and the anterior half of a sixth must come from the distal part of the tail. Four of the whole centra were preserved together in a run. The half-centrum has a mean diameter slightly greater than that of the most anterior of this series and presumably lay a short distance before it, if not immediately in front; the other whole centrum has a mean diameter slightly less than that of the last of the series and probably lay directly or not far behind it. The third of the whole series (i.e., "PC3") retains the prezygapophysis on one side; the fourth retains the whole of one side and the roof of the neural arch, including the base of the prezygapophysis, the postzygapophysis with the tip of the following prezygapophysis attached, and the base of the neural spine; and the fifth retains a small part of the side of the neural arch. The proximal end of a haemapophysis remains between the second and third centra; it is described below.

These centra are all of about the same length; their mean diameter diminishes a little down the series. The ratio of length to mean diameter is greater than in any other vertebrae of this specimen, being approximately equal to that found in the longest cervicals of the other two specimens of <u>Mandasuchus</u>. The ventral margin of each centrum appears concave when seen from the side. In contrast to the condition observed in all the other known vertebrae of this genus, the floor of the neural canal is not deepened at all within each vertebra but is perfectly flat throughout its length. The middle of each centrum is constricted laterally in the usual manner. Facets for haemapophyses are developed at both ends of the centrum, those behind having the characteristic double appearance while those in front are simply crescentic. The ventral surface is lightly flattened but not grooved at all. The ends of the centrum are moderately concave above the haemapophysial facets. There is no transverse process; but the neural arch is broader than the upper part of the centrum and consequently forms a narrow downwardly facing ledge which runs the whole length of the vertebra. The zygapophyses project laterally just beyond the centrum; the prezygapophysis also projects several millimetres forwards, while the end of the postzygapophysis is level with the back of the centrum. The neural spine is set far back; in the fourth vertebra of the series, where the centrum is 27mm. long above, the broken-off base of the neural spine is only 9mm. long and yet its hinder margin lies only just in front of the hinder margin of the centrum. Its anterior margin does not diverge into two anterior spinal buttresses but is produced forwards into a light median ridge running along the top of the neural arch and rising again into a median prominence between and just behind the prezygapophyses. A similar feature has been described in other animals (see Chapter 4 below); it is suggested that it be called the pre-neural spine. In this specimen it seems to project forwards, but its anterior tip is broken off; nevertheless, as preserved, its highest point lies 3mm. above the saddle separating the neural and pre-neural spines. Immediately below and in front of the pre-neural spine lies the concavity between the prezygapophyses.

Fragmentary vertebral material.

An isolated fragment of a neural arch seems to come from a region of the tail not much anterior to that of the distal caudal vertebrae described immediately above, for it is but little larger in its proportions. It comprises the posterior part of the arch together with the postzygapophyses (to one of which is attached the end of the following prezygapophysis) and the lower part of the neural spine. A deep posterior spinal concavity lies between the postzygapophyses. The neural spine, which measures 10mm. by 3mm. where broken off some 7mm. above its base, shows a strong backward inclination; its anterior edge makes an angle of about 25 degrees with the vertical.

Thirteen pieces are recognisable as the upper ends of neural spines. Some are well preserved, others are badly weathered; but, as mentioned previously, none may be related to any particular vertebra. In their varied forms they correspond to the various neural spines of the type-specimen. Many of the spines have the poorly preserved remains of dermal scutes attached to their dorsal surfaces. The dimensions of the dorsal surfaces are:

length 41mm.	maximal width 12mm.	probable cervicals
42mm.	14mm.	
37mm.	15mm.	
35mm.	21mm.	probable dorsals
34mm.	22mm.	
31mm.	20mm.	
29mm.	22mm.	
27mm.	24mm.	

length 27mm.	maximal width 13mm.	probable
28mm.	11mm.	posterior
28mm.	9mm.	dorsals or
27mm.	9mm.	anterior
26mm.	8mm.	caudals

These proportions are similar to those of the type-specimen except in that the supposed dorsals are relatively much broader.

Ribs.

Cervical ribs. (Plate 30).

The fragment illustrated includes a fairly complete cervical rib of the left side, to which are attached large parts of the preceding and following ribs; this rib, however, lacks the capitulum and tuberculum. Although several broken-off rib-heads are attached to the appropriate facets of the cervical vertebrae, only one of these is on the left side (of the fifth vertebra). It appears probable, but not certain, that this rib-head belongs to one of the ribs preserved, probably to the middle rib of the three; the distance between the posterior end of the first rib of the three and the posterior end of the second (61mm.) and the distance between the anterior end of the second and the anterior end of the third (55mm.)

indicate that the vertebrae which bore these ribs were themselves long. (Lengths of fourth, fifth and sixth cervical centra of this specimen - 49mm., 50mm. and 49mm. respectively). A convincing restoration of a whole rib has accordingly been made from this middle rib and the rib-head on the fifth cervical vertebra, using very little plaster.

The axial breadth of the capitular facet is 18mm. and that of the tubercular facet 20mm. The two articulating processes unite a short distance from the centrum and project ventrolaterally to form what may be called the vertebral process of the rib; it is in this region that the rib is fractured and a few millimetres appear to be missing. Beyond the missing part the rib expands into an anterior process and a posterior process, the whole forming a boat-shaped element lying more or less parallel with the vertebral column and with its rounded ventral keel, weakly convex in lateral view, directed downwards and outwards. This is 89mm. long; the distance from the anterior tip to the middle of the vertebral process is 33mm., and from the latter point to the posterior tip (from which a little has been broken off) 56mm. The external breadth of the anterior process is 16mm. just in front of the vertebral process, that of the posterior process 15mm. just behind the vertebral process. The axial breadth of the base of the vertebral process is some 20mm. Both anterior and posterior processes taper distally. The anterior process curves a little inwards; the posterior process is expanded horizontally so that it has a broad concave upper surface upon which rests the anterior process of the next rib. The amount of overlap is 32mm. between the first and second ribs, 34mm. between the second and third. The inner and outer margins of this concave surface curve forwards, upwards and inwards to become the hinder edges of the capitulum and tuberculum respectively; the anterior edges of the capitulum and tuberculum are formed by the bifurcation of the single upper margin of the anterior process.

The posterior process of the preceding rib and the anterior process of the following rib are both preserved complete, each including the base of the vertebral process.

The broken-off rib-heads attached to the other cervical vertebrae afford very little additional information. That on the third cervical is much smaller than that described above. The vertebrarterial canal must have been very small in this animal, if indeed present at all.

Dorsal ribs. (Plate 30).

The specimen includes the well preserved proximal part of a dorsal rib of the right side; the fragment is 39mm. long. The shaft (as far as preserved) is fairly straight and terminates in the tuberculum. The capitulum extends 16mm. beyond the tuberculum, curving forwards and inwards; this indicates that the vertebra to which the rib was attached bore a diapophysis much longer than the parapophysis and was therefore anterior in position. The capitular facet is a little longer than high, measuring 11mm. by 9mm.; the tubercular facet is 10mm. long and 6mm. high. A sharp ridge runs along the posterodorsal side of the capitulum, connecting its facet with the anterior end of the tubercular facet; and another ridge runs from the tubercular facet down the posterodorsal side of the shaft. The latter is roughly triangular in section, with sides directed backwards, downwards and anterodorsally; the widths of these three sides at the broken surface are 9mm., 7mm. and 10mm. respectively. The anterior margin is smoothly rounded.

Other short fragments of rib-shaft of similar form and dimensions are also preserved.

Haemapophysis. (Plates 28 and 29).

The proximal end of a haemapophysis lies between the ventral margins of the apposed ends of two distal caudal centra. Viewed from below, it is seen that there is a flat central portion linking the bases of the centra, 7mm. long in the axial direction and about 4mm. broad. This is bordered on either side by one of the two rami of the shaft, broken off short; so that on one side a parapet of bone 1.5mm. thick projects 2-3mm. downwards, while on the other almost nothing remains. It is nevertheless possible to see that the shaft was directed strongly backwards as well as downwards. The outer surface of each ramus is produced anterodorsally to form a roughly triangular face filling in the gap between the centra. The inner (dorsal) surface of the haemapophysis is concave; thus the central portion, which forms a bridge connecting the two rami, is only 1.5mm. thick in the middle. The transverse width of the whole proximal end is 12mm.

Pelvic girdle.

Ilium. (Plate 31).

The left ilium is preserved virtually intact; a small piece is broken away from the posterior border of the acetabulum.

The ventral apex of the bone is complete and shows that the acetabulum of this animal must be imperforate. In almost every detail of form this ilium resembles the ilium of the type-specimen, except in the very slight upward and outward curvature of the posterior spine and the more rounded dorsal edge of the latter. Its proportions, however, show considerable variation when analysed. The dimensions are given below:

Whole acetabulum: maximal length	95mm.
width	62mm.
Angle between pubic and ischiadic contact-surfaces	ca. 105 degrees
Pubic contact-surface: length	67mm.
maximal width	30mm.
Ischiadic contact-surface: length	69mm.
maximal width	21mm.
Anterodorsal end of pubic contact-surface to posterodorsal end of ischiadic contact-surface	101mm.
Vertical height of iliac portion of acetabulum (ventral apex to supra-acetabular crest)	75mm.

Lateral projection of supra-acetabular crest above bottom of acetabulum	35mm.
Supra-acetabular crest to dorsal margin of ilium	37mm.
Transverse thickness in region of supra-acetabular crest	31mm.
Length of anterior spine	17mm.
Length of posterior spine (behind posterior border of acetabulum)	94mm.
Anterior end of anterior spine to posterior end of posterior spine	175mm.
Vertical height of posterior spine at base	50mm.

Pubis. (Plate 31).

Two separate fragments of the left pubis are preserved. One of these, 64mm. long, is the proximal (articular) portion, up to and including the twist; it lacks the thin posteroventral extension which lay adjacent to the ischium, and shows but little trace of the obturator foramen. The other fragment is a considerable length (101mm.) of the distal end of the plate, with the thin medial border broken away.

The twist is situated about 45mm. from the iliac articulation, which latter has a maximal width of 31mm.

The lateral edge of the pubic plate is 11mm. thick at the proximal break, and the maximal width of the plate as preserved is 45mm. The distal end is much thickened below, relatively enormously more than in the type-specimen; its greatest thickness is 31mm., and it is not hollowed out as in the type-specimen but is slightly convex.

Ischium. (Plate 31).

The left ischium lacks the anteroventral region which approached the pubis and the ventral margin of the proximal part of the peduncle; the iliac articulating surface and the ischiadic portion of the acetabulum are corroded in places.

A particularly striking feature is that the whole peduncle is not only bent outwards as in the type-specimen but is also curved very strongly upwards; in the type-specimen the posterodorsal margin of the peduncle is comparatively straight. That the outward flexure at least could be due to post-fossilisation shearing forces is shown by the fact that the terminal portion of the peduncle, about 22mm. long, is actually displaced laterally through some 3-4mm. Further, such an extraordinary curvature would give the complete pelvis a grotesque appearance with widely diverging ischia, an appearance which it is difficult to imagine as natural. But, on the other hand, the presence of this outward flexure in the ischia of both the type-specimen and specimen no. 63, the many other bones of both of which show little or no distortion, can hardly be coincidental.

In other respects the ischium resembles that of the type-specimen, except in its altogether stouter build; its length as preserved is 181mm. Seen from above, the bone is 43mm. thick at the proximal end and 17mm. thick at the base of the peduncle. The maximal width of the distal end-surface is 21mm.

Hind-limb.

Femur.

Two large fragments are recognisable as parts of the right femur. The more massive is 63mm. long and includes the fourth trochanter; the other is 60mm. long and must come from a region not far below the middle of the shaft. These fragments show the same features as the femur of the type-specimen, being nearly one and a half times as large in their linear dimensions.

Tibia.

The almost complete left tibia is 223mm. long. It differs very little from that of the type-specimen in form; but careful measurements show that its proportions vary considerably, and it seems to be relatively stouter. All the ridges are less prominent except the anterolateral ridge on the distal part of the shaft, which is lightly but very distinctly developed for about three-quarters of the way towards the proximal end. The width of the medial surface, which is moderately convex just below the proximal end, is 59mm. proximally, 25mm. in the middle of the shaft and 35mm. distally. The proximal end-surface is not hollowed out, but is slightly convex and measures 63mm. by 51mm.; the distal end-surface measures 43mm. by 32mm. The supposed foramen nutritivum is very well developed; it lies some 65mm. below the proximal end and 16mm. behind the cnemial crest.

Fibula.

The proximal 61mm. of the right fibula is preserved. The end-surface, measuring 33mm. transversely and 20mm. parasagittally, is not flat as in the type-specimen but is higher laterally than medially, dipping also towards the rear. A low ridge begins near the proximal lateral corner of the posterior surface and runs obliquely distally and medially, approaching the medial side some 30mm. below the end-surface. The shaft is hollow.

Fibulare. (Plate 32).

The left fibulare (calcaneum) is well preserved; the only part missing is the dorsomedial corner of the posterior end of the tuber. Its greatest length is 48mm. and its greatest width 41mm. The form is not easy to describe and is best seen from the illustrations. The anterior surface and the anterior part of the dorsal surface form a smoothly rounded, cushion-like condyle 24mm. thick; behind this the rather broader tuber projects backwards, becoming thicker at its hinder end. The lateral, ventral, and (as far as can be seen) posterior surfaces are all more or less perpendicular to each other; they are not flat but are pitted and ridged in an irregular manner. In particular, a deep narrow pit (presumably a vessel-duct) enters the bone in the middle of the lateral surface, and a great broad pit is present on the underside of the tuber. A vertically placed lip-like process 20mm. long and 20mm. wide projects from the middle of the medial surface; its convex side faces backwards, its concave side forwards. In front of this is a large hollow; the hollow and the lip together form a socket which probably served for articulation with the tibiale.

Dermal scutes. (Plate 32).

Some of the fragments of scute material are in isolation and others are attached to the ends of neural spines; all are badly preserved. Such details of the form of the scutes as can be discerned conform to the pattern observed in the other two specimens. These scutes, however, seem to be relatively more massive and in some instances are 6mm. thick. The angle between the medial and lateral portions of each scute is approximately 120 degrees. The anterior ends of the scutes are inclined downwards at an angle of about 30 degrees to the dorsal surfaces of the neural spines, and the distance between corresponding points on consecutive scutes varies from 12mm. to 17mm.

vi) On the specific identity of the three specimens

The similarities and differences between the type-specimen of Mandasuchus longicervix (no. 11b) on one hand and specimens nos. 13 and 63 on the other have been indicated above. The natural differences may now be analysed. There can be very little doubt that all three specimens should be referred to the same genus; and their slight variations in form, together with their greater variations in proportions, might conceivably be attributed to the considerable difference in absolute size between three specimens which represent the same species at different periods in its life-history. On the contrary, they could indicate that the specimens represent separate species of the genus.

The Table overleaf lists a few selected relative dimensions of the two referred specimens, the corresponding dimensions of the type-specimen being taken as 100 in every case.

The most conspicuous differences between the three specimens are those concerning the proportions of the vertebral centra. Analysis of the dimensions of the centra is no easy task; accurate measurements

TABLE OF COMPARATIVE MEASUREMENTS OF THE THREE SPECIMENS OF MANDASUCHUS

(measurements of type-specimen, no. 11b, taken as 100)

	specimen no. 13	specimen no. 63
Seventh or supposed seventh cervical vertebra:		
length of centrum below	74	129
mean diameter of centrum	72	163
Supposed fourth dorsal vertebra:		
length of centrum below	66?	128
mean diameter of centrum	73	164
Supposed ninth dorsal vertebra:		
length of centrum below	-	127
mean diameter of centrum	-	161
Supposed first caudal vertebra:		
length of centrum below	-	141
mean diameter of centrum	-	156
Supposed fourth cervical vertebra:		
height of neural spine (measured from top of centrum)	82	-
axial length of neural spine above	58?	-
maximal transverse width of dorsal surface of neural spine	30	-
Supposed seventh cervical vertebra:		
height of neural spine (measured from top of centrum)	82	-
axial length of neural spine above	77	-
maximal transverse width of dorsal surface of neural spine	40	-

	specimen no. 13	specimen no. 63
Scapula:		
length	55?	-
height of scapular portion of glenoid facet	67	-
width of scapular portion of glenoid facet	74	-
Humerus:		
width of proximal expansion	72	-
width of distal expansion	69	-
Radius:		
greatest diameter of proximal end-surface	81	-
Acetabulum:		
maximal length	-	173
width	-	138
Ilium:		
greatest width of pubic contact-surface	-	167
greatest width of ischiadic contact-surface	-	140
anterodorsal end of pubic contact-surface to posterodorsal end of ischiadic contact-surface	-	174
supra-acetabular crest to dorsal margin of ilium	-	137
length of anterior spine	-	155
Pubis:		
greatest width of iliac contact-surface	-	163
maximal thickness of distal end	-	258

	specimen no. 13	specimen no. 63
Ischium:		
length	-	137
maximal width of distal end-surface	-	175
Tibia:		
length	-	127
width of medial surface:		
proximally	-	134
in middle of shaft	-	147
distally	-	121
greatest diameter of proximal end-surface	-	137
greatest diameter of distal end-surface	-	139
Fibula:		
parasagittal diameter of proximal end-surface	-	154
transverse diameter of proximal end-surface	-	138

cannot be obtained from specimens which are even slightly imperfect, be it through incompleteness, weathering or post-mortem distortion. Further, the positions of the vertebrae cannot usually be determined with certainty. It is nevertheless apparent that the centra are shorter (relative to their own mean diameter) in the larger specimen no. 63 than in the type-specimen. An inspection of the "elongation ratios" of the various centra shows this very clearly; the figures in parentheses denote the relation of the elongation ratio of each centrum to that of the supposedly corresponding centrum of the type-specimen, and would be 100 in every case if the centra were of exactly the same proportions:

	specimen no. 13	specimen no. 11b	specimen no. 63
Ce2	1.31	-	1.11
Ce3	1.72	-	1.43
Ce4	1.87	-	1.58
Ce5	1.93	-	1.52
Ce6	1.75 (101)	1.74 (100)	1.38 (79)
Ce7	1.58 (104)	1.52 (100)	1.20 (79)
Ce8	1.33 (91)	1.46 (100)	-
D1	1.11 (92)	1.21 (100)	-
D4	1.15 (89)	1.29 (100)	1.00 (78)
D5	-	1.30 (100)	0.97 (75)
D7	-	1.24 (100)	1.04 (84)
D8	-	1.21 (100)	1.03 (85)
D9	-	1.30 (100)	1.03 (79)

	specimen no. 13	specimen no. 11b	specimen no. 63
Ca1	-	1.00 (100)	0.90 (90)
Ca2	-	1.04 (100)	0.88 (85)
Ca5	-	1.00 (100)	0.87 (87)
Ca6	-	1.30 (100)	0.96 (74)
Ca7	-	1.23 (100)	1.14 (93)

However, it seems reasonable to expect more massive centra in a larger animal; if the size of the beast were to increase absolutely proportionately throughout, its weight would increase as the cube of the increase in linear dimensions, but the area of transverse section of the vertebral column (and hence its ability to support weight) only as the square thereof. Thus, since the distribution of such elongation as occurs is more or less the same in the vertebral column of specimens nos. 11b and 63 - that is, with the greatest elongation in the neck, especially in the fourth, fifth and sixth cervicals, - there seems to be no reason why such differences in the degree of elongation should be thought to indicate separate species. Admittedly the elongation ratios of the centra of specimen no. 63 vary from 74% to 90% of the elongation ratios of the supposedly corresponding centra of the type-specimen; but such variations may not be entirely natural but may be partly due to inaccuracies in determination of the positions of the vertebrae in the column and in measurement. Other differences in the proportions of the vertebrae are not brought out by this method of comparison of elongation ratios. For example, the supposed first two caudals of specimen no. 63 are, even relatively, altogether larger; they are not shorter than the dorsals (as are the presumed corresponding vertebrae of the type-specimen) but are of about the same length and relatively <u>much</u> stouter.

If the centra of the larger specimen no. 63 are relatively shorter and stouter than those of the type-specimen, it should follow that in the smaller specimen no. 13 the centra would be longer (relative to their own mean diameter). This does not appear to be the case. There are very few centra preserved where a direct comparison is possible; but the centrum of the supposed sixth cervical of specimen no. 13 is of virtually the same proportions as that of the type-specimen, that of the supposed seventh is relatively a little longer, and those of the supposed eighth cervical, first dorsal and fourth dorsal are (relatively) markedly shorter. In other words, the disparity between the lengths of the posterior cervical and anterior dorsal centra is much greater in specimen no. 13; if the length of a typical anterior dorsal centrum be taken as unity, then the cervical centra will appear to be relatively longer:

	specimen no. 11b	specimen no. 13
Ce6	1.38	1.47
Ce7	1.21	1.37
Ce8	1.21	1.26

Another anomalous feature of specimen no. 13 is the presence of the two centra "X" and "Y" described as "possible middle dorsals"; these are appreciably longer than the anterior dorsal centra preserved. In the type-specimen, where nearly all the dorsal vertebrae seem to be preserved, all their centra are of about the same length.

The vertebrae of the three specimens differ also in certain minor details of form. The supposed third cervical vertebra of specimen no. 13 bears a narrow ventromedial ridge which resembles a strip of beading, while the third cervical of specimen no. 63 has a well developed longitudinal keel beneath. (The type-specimen is incomplete in this respect). Similarly, the cervicals behind the supposed third are rounded below in specimen no. 13 (the posterior half of the supposed seventh showing a faint ridge), while all are lightly ridged in specimen no. 63; no information is available on the condition in the type-specimen, except that the supposed sixth cervical centrum is rounded below and the supposed seventh faintly ridged. The articulating surfaces of the cervicals of specimen no. 63 are more concave than those of the other two animals, and the supposed fifth to ninth dorsals of that specimen are not flattened below as in the type-specimen.

The neural spines of specimen no. 13 are relatively a little higher than in the type-specimen; and a more important difference is that their dorsal surfaces, while flattened and fairly broad, are not expanded at all. The supposed dorsal neural spines of specimen no. 63 are relatively much broader than in the type-specimen; this might be correlated with the relatively more massive nature of the dermal scutes in the former animal.

The angle between the planes of expansion of the proximal and distal ends of the humerus seems to be less in specimen no. 13 than in the type-specimen; but it should be pointed out that all the bones concerned have been partly reconstructed. The ridges on the shaft of the humerus are less well developed in the smaller animal, and the shallow excavation on the posterodorsal side of the distal end is relatively longer. Greater significance might be attached to the substantial difference in form between the supposed proximal ends of the ulnae in the two specimens, that of the type-specimen lacking the very weak olecranon found in no. 13.

The pelvic girdles of the type-specimen and specimen no. 63 differ in certain respects. The ilia are of rather different proportions, and the posterior spine shows a very slight upward and outward curvature and has a more rounded dorsal edge in the larger beast. The distal end of the pubis is thickened below to a very much greater extent in specimen no. 63, and its end-surface is weakly convex rather than concave as in the type-specimen. The ischium of specimen no. 63 is relatively stouter; as has been indicated in the description above, the strong upward curvature of its peduncle is probably artificial.

The tibia of specimen no. 63 is relatively stouter than that of the type-specimen; that is, its shaft is less constricted in the middle of the bone. The proximal end-surface is slightly convex instead of being hollowed out, and the ridges on the shaft are less prominent. The proximal end-surface of the fibula of specimen no. 63 is not flat as in the type-specimen.

The smallest specimen, no. 13, shows incomplete ankylosis of centrum and neural arch in two of its vertebrae; and the neurocentral sutures are more clearly visible than in the two larger animals. This may indicate that specimen no. 13 represents the skeleton of a juvenile. The type-specimen shows incomplete ossification of the ends of certain bones of the appendicular skeleton.

The significance of these differences is hard to assess. There appear to be no important differences in form between specimen no. 63 and the type-specimen; there are greater differences in form between specimen no. 13 and the other two skeletons. In particular, the proximal end of the ulna of specimen no. 13 differs from that of the type-specimen; but no definite conclusions can be based on this difference, for it is not absolutely certain that the "proximal ends of the ulnae" of the type-specimen should be described as such.

The differences in the proportions of the three skeletons are quite considerable; and it was thought that an examination of the post-cranial skeletons of various crocodilians, the nearest living relatives of the Pseudosuchia, might give some indication of the value of such differences. It had been hoped at first that an examination could be made of a whole growth-series of skeletons of each species, the specimens having been identified by competent authorities and, as far as possible, coming from the same area so that regional variations within the species might be excluded. Unfortunately this proved impossible. Among the material available in the British Museum (Natural History) and in the University Museum of Zoology in Cambridge only three very incomplete series could be found: three specimens of *Crocodilus niloticus*, three of *C. porosus*, and four of *Tomistoma schlegelii*. Several of the specimens were themselves incomplete, and, in the case of the smaller animals, some of the figures had to be regarded with suspicion because of the difficulty of making measurements on skeletons which could not be disarticulated and which were inadequately prepared. Certain proportions were measured, such as the "elongation ratios" of some of the vertebrae and the ratios of the lengths of the pubis and the femur to the length of a typical dorsal vertebra. Two definite conclusions were drawn from the results. First, the proportions vary within each species to a considerable extent; though whether this variation is of a magnitude equal to that observed in <u>Mandasuchus</u> seems open to doubt. Secondly, the dorsal and sacral vertebrae of the crocodilians appear to become relatively shorter and stouter as the animals increase in size; there are certain anomalies in some of the series, probably due to inaccuracies in the measurements, but the general picture is clear. Beyond this, little can be deduced from so few measurements made on such poor material.

It now remains to decide, on the evidence available, whether the differences observed between the three specimens of <u>Mandasuchus</u> are specific differences or merely individual variations. While it seems probable that specimen no. 63 should be referred to the species <u>M.</u> <u>longicervix</u>, the evidence in the case of specimen no. 13 is more controversial and does not point definitely in either direction. It has been decided, however, that it is better <u>not</u> to found a new species without definite evidence; and, accordingly, specimen no. 13 has also been referred to <u>M.</u> <u>longicervix</u> for the present. It must be remembered that this specimen was found in the same locality as the type-specimen and gives indications of being a young animal.

b) TELEOCRATER TANYURA gen. et sp. nov.

The generic name *Teleocrater* refers to the completeness of the acetabular cup; this character was quite unexpected, preliminary examination of the vertebral column having led to the belief that the animal was a coelurosaur. The trivial name *tanyura* refers to the fact that the tail is presumed to have been long.

Specimen no. 48b is the type of the new genus and species. The other specimen, no. 53a, consists only of two incomplete vertebrae, the distal part of the left humerus and the end of an unidentified limb-bone; it appears to be of about the same size.

The following diagnosis of the type-species is based entirely on the type-specimen and, since the type-specimen includes no humerus, on the humerus of specimen no. 53a.

i) Diagnosis

Teleocrater gen. nov.: as for *T. tanyura* below.

Teleocrater tanyura gen. et sp. nov.:

Pseudosuchian of moderate size, lightly

constructed.

Skull unknown.

Vertebrae with length of centrum always greater than its diameter, sometimes several times as great; centra constricted below and at sides; floor of neural canal not noticeably deepened within each vertebra, except in neck; ends of centra lightly concave except in neck and most anterior part of back, where anterior face tends to be flat and posterior moderately concave; zygapophyses oblique; form of neural spines unknown. Intercentra unknown. Vertebral formula unknown. Anterior cervical(s) greatly elongated, with long diapophysial flange and long ridges running to zygapophyses; posterior cervicals comparatively short, with parapophysis in low position. Anterior dorsals even shorter, though still elongated, with typical archosaurian shift in position of rib-articulation, position of parapophysis becoming higher down the series, long diapophysis supported by oblique radiating buttresses; posterior dorsals short and stout, parapophysis and diapophysis tend to form "spectacles"-shaped rib-articulation and then to fuse, buttresses absent. Sacral vertebrae unknown. Caudal vertebrae with centra becoming relatively more elongated down the series, haemapophysial facets present except in most distal members.

Major limb-bones long and slender, with hollow shafts; propodials longer than epipodials; bones of fore-limb about five-eighths as long as corresponding bones of hind-limb. Pectoral girdle unknown. Humerus with well marked supinator process and ectepicondylar groove, no entepicondylar foramen or groove; ulna without proper olecranon; manus unknown. Pelvis unknown except for ilium; acetabular portion of ilium with V-shaped ventral margin, showing absence of acetabular fenestration in this bone and probable presence of complete acetabulum; ilium with very short anterior spine, posterior spine, well developed supra-acetabular crest. Femur slightly sigmoidal, without fourth trochanter but with low muscle-ridge in its place; fibula with lateral trochanter; pes unknown.

Dermal armour unknown.

ii) <u>Description of the type-specimen (no. 48b)</u>

<u>Field notes.</u>

Field-collection no. 48 was found in locality

B9/1 between Kihoho and Mkongoleko. It includes, in addition to the bones listed below, a considerable part of a large labyrinthodont (specimen no. 48a, not yet described); the proximal part of a rib, probably of a dicynodont (specimen no. 48c); part of an unidentified sacrum, and a pair of problematical bones belonging to some large animal. The specimen is of a mottled brown colour and is generally well preserved.

Material available.

Vertebrae: parts of 28, including 2 cervicals, 8 dorsals, 3 posterior dorsals or pygals and 15 caudals.

Dorsal rib: proximal end.

Radius: distal part of left, all of right.

Ulna: right.

Ilium: left, lacking posterior spine.

Femur: both left and right.

Tibia: both left and right.

Fibula: left.

Vertebral column.

The vertebrae were found scattered in the field, and in no case was a portion of one vertebra attached to that of another. Consequently there is no direct evidence whatsoever for the succession of the vertebrae, and no vertebra can be assigned to a definite position in the series. For easy reference, particularly to the illustrations, the vertebrae of neck, trunk and tail have been lettered alphabetically in what appears to be the most likely order as indicated by trends in changes of dimensions and form; missing vertebrae are not considered. Thus "CeA" is probably the first preserved cervical, "DC" the third preserved dorsal, and "CaN" the fourteenth preserved caudal vertebra.

All or most of the neural spine is broken off in all the vertebrae, with the possible exception of one caudal. (The three smallest caudal vertebrae do not have neural spines).

Table of principal measurements of the pre-sacral vertebrae. See overleaf.

Cervical region.

Supposed anterior cervical vertebra. (Plates 33, 34, 35 and 36). This vertebra ("CeA") is extraordinarily long, the length of its centrum being nearly four times the mean diameter of its posterior face; and its form is so unlike that of the other vertebrae that, at first sight, it might be thought no. 48b - TABLE OF PRINCIPAL MEASUREMENTS OF THE PRE-SACRAL VERTEBRAE (millimetres)

Centrum:	CeA	CeB	DA	DB	DC	DD	DE	DF	DG	DH	DI	DJ	DK
length below	53	32	26	25	24	25	28	30	26	21	22	21	21
anterior height	-	14	14	14	14	13	14	13	14	14	17	16	16
anterior width	-	15	15	15	17	15	16	17	16	17	20	-	17
posterior height	14	14	15	15	13	13	13	14	15	14	15	17	16
posterior width	15	15	15	16	17	15	16	18	18	17	18	18	17
mean diameter	13½	14½	15	15	15	14	15	15½	16	15½	17½	17	16½
elongation ratio	393	221	173	167	160	179	187	194	162	135	126	124	127
minimal transverse thickness	8	7	7	7	8	7	7	6	8	9	10	9	10

to belong to a different animal altogether. This seems unlikely, however, for it agrees with the other vertebrae in the size of its articulating surface, in its general texture and appearance, and in its undoubted archosaur origin.

The vertebra lacks the anterior end of the centrum, including the parapophyses; parts of the diapophysial ridges; both prezygapophyses and the left postzygapophysis; and the whole of the neural spine.

In lateral view the centrum shows a marked concavity below; it seems to be of negligible vertical thickness at a point about two-fifths of its length back from the anterior end, for at that point the ventral margin reaches nearly as far dorsally as the upper edge of the posterior articulating surface. From here the ventral margin descends obliquely backwards in a fairly steep straight line towards the posteroventral corner and obliquely forwards towards the missing anteroventral corner. The anterior face is broken away, but it must have lain higher than the posterior face relative to the longitudinal axis of the centrum. The centrum also shows a moderate degree of lateral constriction in its middle. The front part of its ventral surface is strongly concave between a pair of ridges projecting downwards and a little outwards (each of which probably originated in the parapophysis of its side); the middle part is flat, with a light but distinct medial ridge; the hinder part is rounded and bears no ridge. The posterior articulating surface is more or less circular and moderately concave.

The parapophyses are broken away but seem to have lain anteriorly and ventrally. Each diapophysis, from either of which the articulating facet is also missing, was borne on a strong flange projecting downwards and outwards; this began about half-way up the anterior border of the centrum, runs backwards and a little upwards to a point just in front of the middle of the centrum, and then descends towards the middle of the posterior border, dying out about 13mm. before it reaches it. Thus it lies roughly parallel to the lower border of the centrum throughout its length. Its lateral projection reaches up to 4mm. No neurocentral suture is visible. The aperture of the neural canal is flattened at the anterior end, where it is 6mm. high and 12mm. wide, and is smaller and more nearly circular at the posterior end, where its diameters are 5mm. and 8mm. respectively. The prezygapophyses are broken off short but were obviously wide apart; a high ridge some 20mm. long begins on the side of the neural arch and runs forwards, a little upwards and a little outwards to become the outer border of each. A shallow basin with a flat floor lies between these two ridges, and near their posterior ends a small anterior spinal buttress arises from the inside of each and unites with its fellow to form the base of the neural spine. The postzygapophysis faces obliquely downwards and outwards; it projects beyond the centrum laterally and also a very little behind it. Another ridge begins on the side of the neural arch, lateral to the beginning of the ridge running to the prezygapophysis, and runs backwards to become the outer border of the postzygapophysis. A sharp posterior spinal buttress runs steeply upwards from the hinder corner of the postzygapophysis and unites with its fellow, being separated from it lower down by the deep cleft of the posterior spinal concavity. The broken-off base of the neural spine lies well back and is 30mm. long; it is 2mm. broad in front and 4mm. broad behind.

The fact that this vertebra seems to have possessed strong prezygapophyses indicates the improbability of its being the axis.

<u>Supposed posterior cervical vertebra</u>. (Plates 33, 34, 35 and 36). This vertebra ("CeB"), while lacking everything above the level of the base of the neural arch, is quite complete below. The centrum is much shorter than that of the anterior cervical just described, but its length is still more than twice as great as its mean diameter. The ventral border is concave in lateral view and the anterior face lies a little higher than the posterior; the neural canal is deepened a little in the middle of the vertebra; and the middle of the centrum is constricted laterally. The ventral surface is concave in front between the parapophyses, flat in the middle without any trace of a medial ridge, and rounded behind. The anterior articulating surface is flat, the posterior moderately concave; both faces are of the same height as the posterior face of "CeA" and a little broader.

The parapophysis is a large, roughly triangular facet lying ventrally just behind the anterior margin and projecting a little laterally. A strong horizontal ridge (the lateral border of the flattened ventral surface) runs backwards from it on the left side, and above this is a deep hollow in the side of the centrum; but, since both ridge and hollow are absent on the other side, this appearance is probably artificial. The lower ends of both anteroventral and posteroventral buttresses remain, the former directed towards but barely reaching the parapophysis; their presence indicates that this vertebra lay right at the back of the neck, and may indeed have been an anterior dorsal. It is, however, longer than the other dorsals, and the parapophysis lies more ventrally. The buttresses also show that the diapophysis lay in the middle of the vertebra.

Dorsal region.

Supposed anterior dorsal vertebrae. (Plates 33, 34, 35 and 36). Six vertebrae have been assigned to this category and have been lettered "DA" to "DF" in such a way that the parapophysis lies a little higher in each vertebra than in that supposed to precede it. All the centra are complete. Nothing else remains of "DF"; "DA" has a very little of the bases of the sides of the neural arch, "DC" a little more. The other three vertebrae, on the contrary, are nearly complete. "DB" lacks only the ends of the diapophyses and most of the neural spine; "DD" lacks these and the end of the right prezygapophysis; while "DE" lacks the right diapophysis and the end of the left, the whole of the postzygapophyses and all trace of the neural spine.

"DD" and "DE" resemble each other greatly and are probably consecutive.

The length of each centrum is rather less than twice its mean diameter; all are shorter than the supposed posterior cervical vertebra described above. The first four are of more or less equal length; "DE" is a little longer and "DF" longer still. The centra are concave below in lateral view; this is less marked in "DE" and "DF" than in the others. The neural canal is hardly deepened at all within the centrum, but the middle of each centrum shows a strong lateral constriction. "DA" is noticeably flattened below, being concave in front between the ventrally situated parapophyses; "DB" is slightly flattened, with a very faint medial ridge; and the other centra are rounded beneath, all except the last with the faintest trace of a median ridge. The articular faces are a little broader than high; "DA" is opisthocoelous, the anterior face being flat and the posterior moderately concave, while the other centra are lightly amphicoelous.

The parapophysis of "DA" is situated ventrally but is not quite so low as in "CeB". Its anterior margin lies 1.5mm. behind the anterior face of the centrum; it projects laterally 4-5mm. from the side of the centrum; its facet is directed outwards and a little downwards and is 8mm. high by 4mm. broad, the longer axis being inclined but very slightly backwards at its upper end. The parapophysis of "DB" is of similar shape and size but lies a little higher, its middle being about half-way up the centrum. That of "DC" is level with the upper part of the centrum and its facet is only 5mm. high. The parapophysis of "DD" is level with the lower part of the neural canal; it forms a peg-like process projecting some 3mm. outwards and a little downwards, and bears a small elliptical facet of 3-4mm. maximal diameter, this longest axis being inclined obliquely upwards and backwards. The parapophysis of "DE" is very similar but lies a little higher, being situated at the junction of the anteroventral lamella with a ridge which runs towards the lower border of the prezygapophysis. No parapophysis is preserved in "DF".

The diapophyses of "DB", "DD" and "DE" all originate in the middle of the vertebra, high on the side of the neural arch and at the level of the top of the neural canal. In no case is the end preserved with its facet. It is nevertheless apparent that the process was much longer than that of the parapophysis, projecting horizontally outwards and a little backwards; that of "DB" is very powerfully built, while those of "DD" and "DE" are much weaker and flattened dorsoventrally. All four diapophysial buttresses are present as strongly built lamellae. In "DA" the anteroventral lamella ascends almost vertically from the upper corner of the parapophysial facet towards the broken edge, and a trace of the posteroventral is also visible. "DB" shows these diapophysial buttresses best of all; they are developed very roughly at right angles to each other. The anteroventral lamella runs forwards and downwards to the parapophysis; the posteroventral runs to a point 5mm. in front of the posterodorsal corner of the centrum; the anterodorsal runs to the outer margin of the prezygapophysis; and the posterodorsal to the outer margin of the postzygapophysis. Anterior, posterior and inferior pleural concavities are also well developed, the inferior extending well into the side of the middle of the centrum; dorsally a shallow depression lies above the diapophysis at the side of the base of the neural spine. Traces of the ventral lamellae remain in "DC". In "DD" and "DE" the lamellae are more horizontal in position, especially the dorsals; the upper surfaces of the anterodorsal lamella, the diapophysis itself and the posterodorsal lamella together form one plane surface, and the anterior and posterior pleural concavities are correspondingly narrower. The inferior pleural concavity is also much less well developed than in "DB", being confined to the side of the neural arch, and the superior is virtually absent. In "DE" alone the anteroventral lamella extends beyond the parapophysis, and a low ridge connects the latter with the lower edge of the prezygapophysis. Thus a shallow concavity, facing forwards and slightly outwards, is found just in front of the parapophysis. The prezygapophyses where preserved project in front of the centrum and are placed obliquely; in "DB" a fairly sharp ridge, which forms the anterior margin of the neural arch on either side of the neural canal, runs up to each from below. The prezygapophyses also extend further laterally in "DB" than in "DD" or "DE"; they are separated by a shallow basin, behind which a pair of small anterior spinal buttresses supports the base of the neural spine. The postzygapophyses do not project behind the back of the centrum but are more or less level with it; they too are wider apart in "DB" than in "DD". The strong posterior spinal buttresses rise steeply from them and are separated by a deep posterior spinal concavity. The base of the neural spine of "DB" is 17mm. long and is 1.5mm. wide in front and 4mm. wide behind; that of "DD", broken off at about the same height, is 18mm. long and is more slender (less than 1mm. wide in front and 2mm. wide behind).

Supposed posterior dorsal vertebrae. (Plates 33, 34, 35 and 36). The two vertebrae described under this head, "DG" and "DH", resemble each other in that the base of the transverse process, though not supported by buttresses, is arched upwards in lateral view and is not straight as in the caudals; and in "DH" it is still divided into parapophysial and diapophysial portions. "DG" lacks the tips of the prezygapophyses, the whole of the postzygapophyses and the neural spine; "DH" lacks all zygapophyses and the neural spine.

The vertebrae differ markedly in length, however, "DG" being of approximately the same length as the anterior dorsals and "DH" only four-fifths as long, as short as any vertebra in the series. The characters of the centra otherwise resemble those of the hinder anterior dorsals; they are smoothly rounded beneath, and their articular faces, which are broader than high, are lightly concave. The transverse process of "DG", as far as it is preserved, appears to consist of a thin curved lamina extending laterally from the side of the neural arch; it runs back from just behind the anterodorsal corner of the centrum, first obliquely upwards, then horizontally and finally a little downwards to terminate some way in front of the posterodorsal corner of the centrum. Any facets for a rib which it may have borne are not preserved; a hollow lies beneath it. In "DH" the transverse process is situated almost entirely in the front half of the vertebra; it is much shorter from front to back and much stouter, and bears a "spectacles"-shaped terminal facet with the diapophysial portion behind the upper end of the parapophysial. It is also quite short laterally (12mm. outwards from the base of the neural spine) and is directed a little forwards and downwards. The excavation beneath it is extremely deep. The prezygapophyses of "DG" seem to resemble those of the anterior dorsals, projecting beyond the centrum; there are no anterior spinal buttresses.

Possible posterior dorsal or pygal vertebrae. (Plates 33, 34, 35 and 36). These three vertebrae, "DI", "DJ" and "DK", probably come from somewhere near the sacrum, for they are shorter and stouter than any of the other vertebrae preserved (except "DH"). They bear no facets for haemapophyses, as do the typical caudals; but, on the other hand, the transverse process (or as much of it as remains) shows no trace of the division into parapophysial and diapophysial parts usual in the dorsal vertebrae. There is no evidence for their occurrence in any particular order, the lettering being quite arbitrary. "DI" and "DJ" each consist only of a centrum, partly broken away on one side and with the base of the side of the neural arch and the base of the transverse process present on the other; "DK" is more complete, lacking only the tips of the prezygapophyses, the whole of the postzygapophyses and the neural spine.

The centra have a general resemblance to that of "DH". All are constricted below and at the sides, but whereas "DI" and "DJ" are rounded beneath ("DI" perhaps even a little flattened), "DK" has a faint but distinct ventromedial ridge. The end-surfaces are a little broader than high and weakly concave. The form of the transverse process, however, is a variable feature. In "DI" it is rather similar to that found in "DH", for it lies in the front half of the vertebra, is short from front to rear and fairly stout, and is directed a little forwards and downwards; but its broken-off end, measuring only 6mm. by 2mm., is not divided into parapophysial and diapophysial portions. It is supported by a strong ridge running obliquely downwards towards the front edge of the centrum, and is underlain by a very deep hollow. The transverse process of "DJ" is very badly preserved, but stretches further back and seems to have been more horizontal in position; it is arched from front to back, rather like that of "DG", and the line of the neurocentral suture shows clearly beneath it. The transverse process of "DK" bears a greater resemblance to the type of transverse process found in the caudals; a horizontal ridge-like base extends almost the entire length of the vertebra along the upper margin of the centrum and is produced laterally into the fairly stout, axially long transverse process, nearer to the hinder margin of the vertebra than to the front and directed slightly backwards. The distal end is broken off on both sides, and the broken surface is not quite straight but has a slightly wavy outline. Another sharp longitudinal ridge runs along the side of the neural arch in "DK", some 4mm. above the transverse process and just below the level of the top of the neural canal; it separates the steeply sloping side of the neural arch from its almost horizontal roof. All that can be ascertained of the zygapophyses and the neural spine from the little that remains is that the base of the neural spine is very thin; it is supported by anterior spinal buttresses.

Caudal region.

Table of principal measurements. See overleaf.

Caudal vertebrae. (Plates 33, 34, 35 and 36). Those fifteen vertebrae preserved which are certainly caudals have been lettered "CaA" to "CaO"; the order is based partly on diminishing size and partly on the gradual disappearance of the transverse processes and neural spine. The centra are all complete, but the ends of the transverse processes (where of appreciable size) and of the zygapophyses are usually broken off; likewise the neural spine, where present, is broken off at or near the base except in "CaB".

The length of the centrum is remarkably constant throughout the series, varying irregularly between 22mm. and 25mm. The mean diameter, on the other hand, decreases steadily from 13½mm. in "CaA" to 6½mm. in "CaO". Thus it will be noted that the distal vertebrae have a much higher elongation ratio than the proximals; it is between 2.00 and 3.00 in all the caudal vertebrae except the two largest, "CaA" and no. 48b - TABLE OF PRINCIPAL MEASUREMENTS OF THE CAUDAL VERTEBRAE (millimetres)

Centrum:	CaA	CaB	CaC	CaD	CaE	CaF	CaG	CaH	CaI	CaJ	CaK	CaL	CaM	CaN	CaO
length below	24	23	23	23	23	23	24	25	23	22	22	25	24	25	22
anterior height	14	13	12	11	11	10	9	10	10	10	9	10	9	10	7
anterior width	13	12	12	11	11	10	9	9	10	10	9	10	9	10	6
posterior height	14	12	11	10	11	11	10	12	10	10	9	10	9	8	6
posterior width	13	12	11	11	11	10	9	9	10	10	9	10	9	9	7
mean diameter	13½	12	11½	11	11	10	9	10	10	10	9	10	9	9	6½
elongation ratio	178	192	200	209	209	230	267	250	230	220	244	250	267	278	338
minimal transverse thickness	7	7	6	6	5	5	5	3	5	6	5	6	5	5	3

"CaB" (where it is less than 2.00) and the smallest, "CaO" (where it is 3.38). The form of the centra generally resembles that found in the pre-sacral vertebrae, constricted below and at the sides and with weakly concave ends. The main difference lies in the presence of a facet for a haemapophysis on the hinder face of each vertebra back to and including "CaK"; the characteristic double form appears in the better-preserved vertebrae. A ridge runs forwards from each side of the facet towards the middle of the underside of the centrum, and there is a groove between the ridges; from "CaE" to "CaK" light continuations of these ridges extend almost to the anterior edge of the centrum, and a narrow flattened area lies between them. The smaller distal caudals without haemapophysial facets are rounded beneath.

The transverse process, where present, consists of or arises from a straight horizontal ridge running along the side of the vertebra at the junction of the centrum and the neural arch, at the level of the base of the neural canal. In "CaA" the posterior two-thirds of this ridge was extended laterally into a large but thin transverse process directed slightly upwards; it is broken off near the base. The succeeding vertebrae may have possessed similar but smaller transverse processes, but in each case little remains beyond the basal ridge along the side of the vertebra. In "CaH", however, a very thin process projects 4-5mm. laterally from one side of the vertebra. In "CaI" and "CaJ" the ridge is still well developed, but it appears doubtful whether it bore any lateral extension; in "CaK" a weak ridge is confined to the posterior two-thirds of the vertebra; and in "CaL" to "CaO" there is no trace of a transverse process. The zygapophyses are nowhere well preserved; it may be said, however, that, in general, the prezygapophyses are wide apart and project in front of the centrum, while the postzygapophyses are close together and their hinder margins are level with the back of the centrum. No spinal buttresses are developed. All these caudal vertebrae except the last three possessed a neural spine; in "CaB", where its whole height may be preserved, it is situated in the posterior half of the vertebra and rises 21mm. above the top of the centrum, at first vertically and then curving a little backwards. In the hinder members ("CaH", "CaI", "CaK") the spine is axially narrower, being restricted to the posterior third of the vertebra; in "CaL" it consists only of a small thorn-shaped process rising 12mm. above the top of the hinder end of the centrum.

"CaO", the smallest vertebra preserved, consists mainly of a slender, elongated, lightly amphicoelous centrum, constricted a little below and at the sides; a neural arch with a uniformly curved outer surface encloses a narrow neural canal and probably bore small zygapophyses. No other structures are represented.

Dorsal rib. (Plate 37).

This fragment, 20mm. long, seems to be part of the proximal end of a dorsal rib; it does not merit detailed description, for nearly all the edges are broken away. Two flattened shafts, joined along their inner edges and with their flattened surfaces diverging at an angle of about 110 degrees, are obviously the capitulum and the tuberculum; but it is difficult to decide which is which and whether the rib comes from the left side or the right. One process is broken off short, but the other is complete and terminates in a roughly oval facet measuring 8mm. by 5mm.; a thin web of bone joined the two processes together. A high flange arises from the back of the rib, giving the broken-off distal end an almost symmetrically triradiate appearance. The outer borders of the capitulum, tuberculum and flange all diverge from the central axis of the rib as they approach its proximal end. The process with the facet bears a well defined ridge running 9mm. down its back.

Fore-limb.

Radius. (Plate 37).

The right radius is preserved virtually complete, but the medial side of the distal third is somewhat crushed. The distal part of the left radius, however, is also preserved and is not crushed; restoration of the entire bone is thus rendered possible. The tentative orientation of this bone, like that of the ulna, has been assigned to it after a careful comparison with the corresponding bone of the crocodile.

The radius is 88mm. long and the central part of the shaft shows a strong inward curvature; thus the medial edge, when seen from front or rear, shows a strong convexity in the middle, while the lateral edge is concave. In a similar manner the anterior margin appears concave when viewed from the side and the posterior weakly convex. The proximal end is expanded, mainly antero-posteriorly; it has a flattened lateral surface and a convex medial surface. The end-surface measures 16mm. from front to rear and 9mm. across; it lies approximately at right angles to the axis of the bone and is almost flat, having a slight depression in the middle of the lateral side. A light ridge runs down the medial surface, dying out towards the middle of the shaft. The latter measures 7mm. by 6mm. at its narrowest point and is hollow, the walls being just over 1mm. thick. The middle of the shaft bears a light ridge on its hinder side. The distal end of the radius is also expanded, rather more uniformly; again the lateral surface is flattened and the medial surface convexly rounded. The end-surface measures 12mm. from front to rear and 10mm. across; it stands perpendicular to the bone axis and is very lightly concave. The anterior edge of the lateral surface forms a fairly sharp ridge, running up the radius towards its middle and then curving a little backwards across the lateral side.

Ulna. (Plate 37).

The right ulna is preserved entire; it is 92mm. long and is virtually straight. The proximal end-surface is very roughly in the form of a right-angled triangle, with a long side facing forwards, a short convexly curved side facing outwards, and the hypotenuse facing posteromedially; the greatest diameter of this surface is 20mm., and the width perpendicular to the greatest diameter is 13mm. The whole surface is inclined to the axis of the bone so that the anteromedial end is much lower than the posterolateral, which latter thus forms a kind of simple olecranon. Beneath the long posteromedial edge a rather flat surface extends the whole length of the bone to the distal end; its anteromedial profile is slightly concave, the posterolateral almost straight. Each margin forms a fairly sharp ridge except in the immediate vicinity of the end-surfaces. This posteromedial surface is 19mm. wide above, 8mm. wide at its narrowest point in the middle of the shaft, and 12mm. wide below. The whole shaft is rather flattened, its anterior and lateral sides being formed by a single rounded surface whose greatest convexity is lateral above and anterior below. The minimal diameter of the shaft is only 5mm. in the middle. The distal end-surface is flat and perpendicular to the axis of the bone; it measures 13mm. by 8mm.

Pelvic girdle.

Ilium. (Plate 38).

The left ilium is preserved but lacks the whole of the posterior spine; it includes the greater part of the acetabulum. The lower margin is V-shaped, the angle at the apex being a little more than a right angle. The anterior limb of the V is 27mm. long and the whole of it forms a contact-surface for the pubis; the upper half is thick and rounded in outline, its greatest thickness being 12mm., while the lower half, next to the apex, is slender and tapering. The posterior limb of the V is much longer (37mm.); the edge is not quite straight, but consists of two slight bulges of roughly equal size. The upper bulge forms a facet for the ischium (19mm. by 8mm.), rounded at its upper end and tapering below, while the lower bulge is almost uniformly thin (2mm.) and may have been either a prolongation of the contact-surface for the ischium or else a free edge. Thus, if the acetabulum was open at all, it would appear that such fenestration was restricted to the small part formed by the ischium; the ilium ossified completely and did not leave a gap in the middle of the acetabulum between a pre-acetabular process and a post-acetabular process. The total distance across the acetabulum from the anterior corner to the posterodorsal end of the ischiadic articulation is 47mm., and the vertical height from the ventral apex to the supra-acetabular crest is 35mm. The latter is high and sharp, beginning at the pubic contact-surface and curving smoothly, first upwards and backwards and then backwards; it projects 15mm. laterally above the bottom of the acetabular cup and dies out posteriorly above the middle of the ischiadic articulation. The posterior border of the acetabulum is rounded; the anterodorsal face of the acetabular portion of the bone, above the supra-acetabular crest, is broad (11mm.) and flat, and passes over into the weakly convex medial surface.

The dorsal, non-acetabular portion of the ilium is preserved only at its anterior end, where a stout pillar-like thickening extends 17mm. above the supra-acetabular crest. In front of this is the very short anterior spine (6mm.), curving medially towards its end; behind it, and above the supra-acetabular crest, the surface of the bone is moderately concave. Only some 20mm. of the dorsal border is preserved, but this upper edge is fairly thick and shows numerous transverse serrations. The upper part of the medial surface of the ilium is excavated for articulation with the sacral ribs, and shows the beginning of a strong medial crest running backwards and a little upwards in the direction of the missing posterior spine.

Hind-limb.

Femur. (Plates 38 and 39).

Both femora are preserved complete; each is 174mm. long and is sigmoidally curved in dorsal view, bending a little towards the front proximally and towards the rear distally. Both ends are flattened and expanded, the angle between the respective planes of expansion being about 60 degrees; the outer surface of the proximal end may be supposed to face upwards and a little forwards, that of the distal end directly forwards.

The proximal end bears an anterior projection; the end-surface is flat, with a well marked central groove running from front to back, and measures 33mm. by 17mm. The flat outer (dorsal) surface is bordered anteriorly by a low rounded ridge; the inner (ventral) surface is also flat. The pre-axial border is broad and rounded, the post-axial rather narrow and sharp. The head passes imperceptibly into the hollow shaft, flattened in the same plane (diameters 20mm. and 12mm. in the middle) and likewise with a rounded pre-axial margin and a sharp post-axial margin. The lower side of the pre-axial edge, however, bears a fairly sharp ridge in its more distal portion. The proximal part of the shaft shows a low but well defined ridge running across its inner surface, beginning anteriorly and passing obliquely distad towards the rear to approach the post-axial border of the shaft near its middle. This is the equivalent of the ridge which bears the fourth trochanter in other animals, but here there is no definitive fourth trochanter; on the anterior side of the proximal part of the ridge there is a large concave muscle-scar. A small foramen enters the outer surface of the shaft just behind its pre-axial border, 69mm. from the proximal end.

The distal end of the femur is club-shaped; the flat end-surface is bounded by a low ridge in front and is divided by a concavity in its posterior border into a large fibular condyle above and a somewhat smaller tibial condyle below. Its length is 36mm. and the breadth across the fibular condyle is 26mm. The front surface of the distal end is almost flat; the hinder surface bears a deep groove between the two ridges which run down to the tibial and fibular condyles. The upper ridge, running to the fibular condyle, is much the better developed and is continuous with the sharp post-axial border of the shaft. Another fairly sharp edge separates the anterior and ventral surfaces of the distal end.

This type of femur is usually associated with a horizontal posture of the thigh and a considerable angle at the knee-joint.

Tibia. (Plates 39 and 40).

Both tibiae are preserved complete; each is a straight bone, the left being appreciably longer than the right (149mm. and 145mm. respectively). The proximal end is considerably expanded, mainly in a posteromedial direction; the distal end is expanded only a little. The cnemial crest, which forms the anterior margin of the bone, is not especially prominent and fades out distally; at a distance of some 40mm. from the proximal end it bears a slight medial swelling, on the inner side of which is a shallow depression. The only other distinct ridges on the surface of the bone lie laterally near the proximal end and anterolaterally in the distal third.

The proximal end-surface is not flat but very slightly rounded; it has a short, straight antero-lateral border, from which the surface extends 29mm. in a posteromedial direction, gradually narrowing from its maximal thickness of 25mm. (in the left tibia) and tapering to a rounded posteromedial profile. The shaft measures 14mm. by 10mm. at its narrowest point. The distal end is much smaller than the proximal; the flat end-surface, of which the direction of expansion is mainly lateral, measures 22mm. by 18mm.

Fibula. (Plates 39 and 40).

Only the left fibula is preserved and is quite complete. Its correct orientation is uncertain and that adopted below, which is different from that adopted for *Mandasuchus*, must be regarded as tentative.

The bone is straight and is markedly shorter than the tibia (143mm.). The upper third shows a longitudinal flattening so pronounced that the proximal end-surface, which is flat and stands at right angles to the bone axis, measures 21mm. from front to rear and only 8mm. from side to side. It is apparent that this proximal end is expanded backwards, for its hinder border converges obliquely downwards towards the straight anterior border; at a distance of 38mm. from the end-surface it lies only 11mm. behind the anterior border, and it runs parallel to it thereafter. The median surface of this part of the bone is almost flat; its anterior margin forms a well defined ridge, behind which there lies a shallow depression some 20mm. below the end. The lateral surface is weakly convex and is not sharply demarcated from the narrow anterior and posterior edges.

A well developed muscle-ridge begins on the lateral surface, 38mm. below the proximal end and just behind the anterior border. It runs obliquely downwards and backwards towards the posterior border and then bends to continue less prominently down the posterolateral edge of the bone almost to its distal end. In the middle third of the bone the anterior border forms a very sharp edge, and a weak posteromedial ridge is also present; the shaft is thus roughly triangular in section, with a narrow face (7mm. wide) directed backwards and broader faces (each 9mm. wide) directed to either side and converging towards the sharp anterior edge. Distally the bone tends to expand again, especially anteromedially, and all the ridges tend to fade out; the anterior ridge becomes much weaker but persists almost to the end. The distal end-surface is oval, measuring 18mm. by 12mm.; it is not flat, but is inclined upwards in front and projects downwards towards the back of the medial edge.

iii) Description of specimen no. 53a

Field notes.

Field-collection no. 53 was found in locality B9/2; that is, in the same locality as that in which the type-specimen of Teleocrater tanyura was found (B9, between Kihoho and Mkongoleko), but in a different section. It includes, in addition to the bones listed below, a single caudal vertebra (specimen no. 53b) which is far too large to belong to this animal (see Chapter 5).

Material available.

Vertebrae: 1 anterior dorsal, 1 posterior dorsal or pygal.

Humerus: distal part of left.

End of unidentified limb-bone.

Supposed anterior dorsal vertebra. (Plate 41).

This vertebra lacks the left parapophysis, the ends of the diapophyses and prezygapophyses, the whole of the left postzygapophysis, and all trace of the neural spine.

The centrum is 25mm. long, 14mm. high and 15mm. wide in front, and 15mm. high and 16mm. wide behind; its minimal transverse thickness is 6mm. Despite its incompleteness, the vertebra bears a striking resemblance in both size and form to the vertebra "DD" of the <u>Teleocrater tanyura</u> type-specimen; it is entirely upon this similarity that specimen no. 53a has been referred to that species. Differences to be noted in this vertebra consist only of the presence of a more clearly defined ventromedial ridge; the slightly lower position of the parapophysis; and the fact that the anterior margin of the neural arch rises up directly from the anterodorsal corner of the centrum, and not a short way behind it as in the type-specimen.

<u>Possible posterior dorsal or pygal vertebra</u>. (Plate 41).

This consists only of a short stout centrum bearing the weathered bases of the sides of the neural arch; it is 20mm. long, 16mm. high and 17mm. wide anteriorly, 16mm. high and 17mm. wide posteriorly, and has a minimal transverse thickness of 11mm. It is smoothly rounded beneath, without haemapophysial facets; the anterior face is very lightly concave, the posterior more deeply so. The transverse process is broken away completely, but from the nature of its base it appears that it was centrally situated, axially short and rather stout, and inclined a little upwards in front. The vertebra does not exactly resemble any of the "possible posterior dorsal or pygal" vertebrae of the type-specimen.

Humerus. (Plate 41).

The lightly built distal part of the left humerus is preserved in good condition. The fragment is 49mm. long, and the greatest width of its distal expansion is 33mm. Most of this expansion lies post-axially; for, while the pre-axial margin curves only very slightly forwards, the post-axial curves strongly backwards. A rounded ridge runs along the pre-axial border of the posterodorsal surface to terminate in the radial condyle, and behind this lies a shallow triangular depression. The anteroventral surface, on the other hand, is almost plane; a small pit lies a few millimetres proximal to the distal end-surface, between the radial and ulnar condyles. The end-surface itself is divided by a constriction into the radial condyle and the rather longer ulnar condyle. The pre-axial side of the distal end bears a shallow but well defined ectepicondylar groove some 17mm. long, bordered anteriorly by a strong supinator process; both groove and process curve forwards a little as they approach the end of the bone. The post-axial side of the distal end is rather narrow and sharp. The broken surface of the hollow shaft measures 9mm.

by 10mm.

Unidentified limb-bone.

This fragment bears a slight similarity to the proximal end of the left fibula of the type-specimen; but it is very much smaller, whereas the anterior dorsal vertebrae of the two specimens are of exactly the same size. It does not resemble either end of any of the other major limb-bones of the type-specimen. The piece is 23mm. long; from the end-surface, measuring 16mm. by 7mm., the bone tapers regularly towards the broken-off end of the hollow shaft, which measures 8mm. by 5mm. One side is flat with a slight longitudinal concavity in the centre, while the other is more rounded; both edges are more or less straight.

4. COMPARISONS AND TAXONOMY

a) MANDASUCHUS

i) General discussion

It has been shown already (Chapter 3 above) that Mandasuchus must be regarded as a pseudosuchian if the distinction between the Pseudosuchia and the Saurischia is to be based upon the nature of the acetabulum. Other characters of this genus should now be considered in relation to those of other pseudosuchians and saurischians in order to ascertain of which group they are supposedly typical; this may provide further clarification of the animal's systematic position. It should nevertheless be remembered that the characters regarded as "pseudosuchian" (von HUENE, 1921 , 1932) are not infallibly diagnostic of the sub-order. For example, a short neck is considered to be a pseudosuchian character, but Chasmatosaurus and Hesperosuchus have elongated cervical vertebrae; pseudosuchians usually have but two sacral vertebrae, yet Ornithosuchus has three; and Erythrosuchus, unlike most members of its sub-order, is not definitely known to have any dermal armour. No great reliance should be placed on any single character;

the real value of such an assessment lies in its totality.

"Pseudosuchian" characters of Mandasuchus, differing from those usually found in saurischians, include the following in addition to the closed acetabulum. There are only eight cervical vertebrae (though the posterior limit of the neck has been decided arbitrarily); their neural spines are well developed, though fairly low, and, like those of most of the dorsal vertebrae, have flat expanded tops. This is correlated with the presence of a dermal armour, absent in saurischians. There are only two vertebrae in the sacrum. The scapula is broad and only moderately inflected; it is fairly long, however, and von Huene remarks that the very similar scapula of Spondylosoma is typically saurischian in form. The propodials are longer than the epipodials; this character is found in some groups of saurischians (carnosaurs, Plateosaurus but not all prosauropods, sauropods) as well as in pseudosuchians. The humerus has a deltopectoral crest whose apex lies very near the proximal end of the bone, and the distal end bears an ectepicondylar groove. The head of the femur does not form a marked angle with the shaft.

On the contrary, the presence of cervical vertebrae which are considerably longer than the other vertebrae shows a similarity to the Saurischia, if not an affinity with them. The form of the sacral ribs is again very similar to that found in Spondylosoma, which, according to von Huene, is like that of primitive saurischians and differs fundamentally from that of Thecodonts. The lack of any trace of the secondary shoulder girdle is a saurischian character; no weight should be attached to this, however, for both clavicle and interclavicle are present in the closely related Prestosuchus and their absence in all three specimens of Mandasuchus may well be fortuitous. More important is the absence of any definite olecranon process on the ulna. LYDEKKER (1885) refers to the presence of a bridge connecting the two rami of the proximal end of each haemapophysis as a "Dinosaurian" character; but it is doubtful whether this character has much validity, for the bridge is certainly absent in some saurischians, such as Saltopus, and is present in some other pseudosuchians, such as Rauisuchus. Finally, Mandasuchus shows a general saurischian trend in its tendencies towards large size and comparatively long and slender limb-bones.

On balance, it seems reasonable to consider Mandasuchus as an advanced pseudosuchian whose form shows certain saurischian trends.

ii) Comparison with Prestosuchus

Mandasuchus seems to resemble Prestosuchus more closely than it does any other known animal; the two genera have therefore been compared in great detail.

Prestosuchus is a large pseudosuchian from the upper Rio do Rasto Beds of Brazil and was described by von HUENE (1935-1942), who distinguished two species of the genus.

Prestosuchus chiniquensis, the type-species, is known from three specimens, one of them very poor and only doubtfully assigned to the species. The best (type-)specimen consists of tooth-bearing fragments of both jaws; some vertebrae, with ribs and haem-apophyses; most of the girdle- and limb-bones; and abdominal ribs. The second specimen consists of the sacrum and adjacent vertebrae, part of an ilium, and a connected row of dermal scutes on the neural spines of the vertebrae. The third (doubtful) specimen consists only of a few miserable surface-fragments of two phalanges, a claw and an abdominal rib, and does not merit further consideration.

Prestosuchus loricatus is known from two specimens. The type-specimen consists of a tooth-apex; fragmentary cervical and dorsal vertebrae with ribs, and caudal vertebrae; parts of a scapula and an ischium, a fibulare, and parts of two metatarsals; and paramedian dermal scutes. The second (doubtful) specimen consists only of the neural arch of an anterior dorsal vertebra, a dorsal centrum and a fibulare.

The distinction between the two species of *Prestosuchus* is ignored in the following comparison.

Size.

The *Prestosuchus chiniquensis* type-specimen is approximately two and a half times as large as that of *Mandasuchus longicervix* (no. 11b) in its linear dimensions.

Maxilla.

The small fragment of the upper jaw of *Prestosuchus chiniquensis* consists largely of premaxilla, together with very small pieces of the palatine wing of the maxilla and of the prevomer.

This part of the maxilla is not preserved in Mandasuchus and hence no comparison is possible.

Dentary.

The small piece of dentary preserved in Mandasuchus is too short and featureless to allow of any comparison with the corresponding bone of Prestosuchus.

Teeth.

There is a great resemblance between the teeth of the two genera. In both cases they are bilaterally compressed; the lightly recurved crown tapers to a point, and its sharp anterior and posterior cutting edges bear very fine perpendicular crenulations. The Prestosuchus loricatus tooth has anterior crenulations along its entire length, as far as preserved; the teeth of P. chiniquensis, however, are broadly rounded anteriorly in their basal halves, perhaps because of wear.

Vertebral column.

Cervical region.

Prestosuchus is represented in this region by two poorly preserved fragments of the type-specimen of P. chiniquensis, and by a well preserved neural spine with zygapophyses of the type-specimen of P. loricatus. These are sufficient to allow the following comparison with Mandasuchus. The centra of Mandasuchus are longer in the cervical than in the dorsal region; in Prestosuchus they are not, for a centrum from the hinder part of the neck is of about the same length as an anterior dorsal centrum, and the supposed last cervical is indeed shorter. Both these centra were probably less than three-quarters as long as high. The two genera resemble each other in that the centra are lightly amphicoelous, with the floor of the neural canal greatly deepened within each; but the posterior cervical centra of Mandasuchus are rounded beneath, or with but a very faint median ridge, while the preserved posterior cervical centrum of Prestosuchus has a very high and narrow ventromedial keel. Moreover, this Prestosuchus centrum bears a peculiar shelf running horizontally along its flank, backwards from the parapophysis; and above this shelf there is a deep hollow, extending beneath the diapophysis. As in Mandasuchus, the diapophysial buttresses are barely indicated except in the last cervical, where, together with the inferior pleural concavity lying between them, they are well developed. In both animals this last cervical has also a well developed anterior pleural concavity between the diapophysis and the neural canal and underlying the prezygapophysis, but this does not extend so far dorsally in _Mandasuchus_ as it does in _Prestosuchus_. In contrast to these differences, there is a most striking resemblance between the neural spine and zygapophyses of a mid-cervical (fourth, or perhaps fifth) of the type-specimen (no. 11b) of _Mandasuchus_ and the fragment of _P. loricatus_. Both neural spines are rather low, axially broad, with the front edge sloping upwards and forwards and the hinder edge sloping upwards and backwards, so that the spine is much wider above than at its base; the upper surface is broader in front than behind, axially and transversely slightly expanded so that the edges project horizontally all round, and almost flat with corrugations near the edges. The form of the zygapophyses and spinal buttresses is much the same in the two animals, except that in _Mandasuchus_ the zygapophysial facets are situated more ventrally than in _Prestosuchus_, i.e., in the latter animal the prezygapophyses (seen in lateral view) ascend a little anteriorly, and likewise the postzygapophyses descend less steeply posteriorly. The medially directed projection just above the postzygapophysis (on which, according to von Huene, a ligament of the articulating capsule probably originated) has been observed in both animals; the type-specimen of _Mandasuchus_ does not show it because of poor preservation, but the third cervical of specimen no. 63 shows it well. The sixth, and, to a lesser extent, the fourth cervical vertebrae of the type-specimen of Mandasuchus show the remains of a narrow vertical median lamella between the diverging posterior spinal buttresses, as is recorded of Prestosuchus. The only apparent difference between the two specimens lies in the presence, in Prestosuchus, of a deep narrow niche beneath the prezygapophysis, corresponding to an anterior pleural concavity; in Mandasuchus this does not appear until the last (eighth) cervical. A sharply projecting descending ridge borders this niche posteriorly.

Dorsal region.

The dorsal vertebrae of Prestosuchus are not well known, being represented only by poor fragments of two connected anterior dorsals (second and third, or perhaps first and second) of the type-specimen of P. chiniquensis, a fragment of the last dorsal of the second specimen of P. chiniquensis, a neural spine with postzygapophysis of the type-specimen of P. loricatus, and an anterior dorsal centrum and an anterior dorsal neural arch of the second specimen of P. loricatus. In the anterior part of the trunk these vertebrae appear to be much like those of Mandasuchus except in that their centra are higher than long and in that their neural spines are relatively much more elevated. As in Mandasuchus, the centra are no longer keeled but are rounded beneath (the isolated anterior dorsal centrum of P. loricatus has a ventromedial keel, as do the posterior cervicals of P. chiniquensis), they are strongly constricted and the posterior face is deepened but little. The parapophysis is in the upper half of the centrum at the anterior edge, projecting peg-like downwards and sideways, and is longer than in Mandasuchus. As in the latter animal, the diapophysis must have been long. The ventral buttresses are high, thin lamellae, running together dorsally at an acute angle; the anterodorsal buttress is a horizontal plate connecting the diapophysis with the prezygapophysis; and the posterodorsal buttress passes into the lateral edge of the postzygapophysis with a deep posterior pleural concavity beneath it. Two buttresses beneath the prezygapophysis - one is the border of the neural canal, the other runs almost parallel to the first and originates halfway up the anteroventral buttress - are not clearly defined in Mandasuchus, where these vertebrae are not well preserved. The postzygapophysis of Prestosuchus is completely separated from its partner of the opposite side, as is also the case in the cervicals, and von Huene notes that this appears to be characteristic of the species or genus; the same is not true of the dorsals of _Mandasuchus_, where a hyposphene is present. The neural spine appears to have been axially narrow, transversely thick and perpendicular as in _Mandasuchus_. Its dorsal end-surface is flatly arched and very broad, being sometimes broader than long (e.g., 25mm. long, 35mm. broad); no _Mandasuchus_ neural spine has its upper surface broader than long, although some in the anterior part of the trunk are indeed very wide. The posterior edge of the _Prestosuchus_ neural spine bears a raised longitudinal ridge in the mid-line, as do some of the cervical neural spines of _Mandasuchus_. There is a deep anterior spinal concavity, with a horizontal floor at the height of the prezygapophysis.

The last dorsal of the second specimen of _P. chiniquensis_ has a thick centrum, broadly rounded below, which contrasts with the supposed last dorsal centrum of _Mandasuchus_ in that it seems to be substantially shorter than the sacral centra. This last dorsal also has both ventral buttresses supporting the transverse process, the anteroventral being high and strong; _Mandasuchus_ has no buttresses in this part of the column.

Sacrum.

The sacrum of Prestosuchus, probably like that of Mandasuchus, is composed of two vertebrae. In the type-specimen of P. chiniquensis the centrum and a rib of the second vertebra are preserved; in the second specimen of the same species both sacral vertebrae are preserved in good condition. As in the East African animal, the centrum is constricted in the middle, but it is not so long relative to its own mean diameter; the rib-base takes in most of the length of the centrum and is surrounded by a swelling; the rib broadens distally and is clearly divisible into a ventral parapophysial part and a dorsal diapophysial part. In the second sacral of Prestosuchus, as in the supposed second sacral of Mandasuchus, the ventral part is the stronger and is directed forwards, while the dorsal part is directed backwards. Von Huene notes that, on the underside of the second sacral rib of Prestosuchus, a thickening runs from the front end of the centrum, perpendicular to the vertebral axis, towards the ilium; this thickening cannot be discerned in Mandasuchus. The upper surface of the sacral rib, however, slopes evenly and obliquely towards the ilium. Other features of the Prestosuchus sacrals which may be of interest are: the facets of the zygapophyses converge obliquely downwards; the anterior and posterior edge-ridges of the sacral ribs are continuous with the outer edges of the zygapophyses; the neural spines are high, axially broad and thin, and inclined weakly backwards; and the upper ends of the neural spines are lightly thickened.

Caudal region.

The first six caudal vertebrae of the *Prestosuchus chiniquensis* type-specimen are preserved in natural connexion. After the second there is a weakly ossified intercentrum, after the third and subsequent vertebrae there are proper haemapophyses; in *Mandasuchus* the absence of facets on the supposed first three vertebrae would appear to indicate that the most anterior caudal to bear a haemapophysis was the supposed fourth. As in *Mandasuchus*, the posterior haemapophysial facets of *Prestosuchus* are well developed, while the anterior facets are hardly visible. The centra of these vertebrae are higher than long, as in the largest specimem of *Mamdasuchus*, no. 63 (although in the type-specimen, no. 11b, the length and height are approximately equal); and, as in the East African animal, length, height and width of the centrum all decrease distally, except that in

Mandasuchus the possible sixth caudal shows a sudden and substantial increase in length, and this phenomenon has not been recorded of Prestosuchus. In Prestosuchus the ventral surface of the first caudal centrum shows slight indications of a longitudinal ridge, that of the second bears a well formed medial keel, and subsequent centra have a broad longitudinal furrow below. (Von Huene remarks that there is obviously a correlation between the presence of a longitudinal ventral furrow and the presence of a haemapophysis, for in Prestosuchus they appear simultaneously on the third caudal). In Mandasuchus, on the other hand, the centra of the supposed first two caudals are rounded below, those of the supposed third and fourth are flattened (the latter with the barest indication of a furrow), and the possible fifth and subsequent centra bear a longitudinal furrow posteriorly. The first four Prestosuchus caudals have an axial, channel-shaped depression in the upper half of the centrum, a little below the transverse process; in Mandasuchus this is present in the first two only. The transverse processes of the Prestosuchus vertebrae resemble those of Mandasuchus in being broad and flat, directed a little obliquely backwards, and in having a thick base, although it can hardly be said of the supposed first caudal of Mandasuchus - as von Huene says of its Prestosuchus counterpart - that the base of its transverse process is almost as strong as that of a sacral rib. In both animals the anterior edge of the transverse process of the first caudal is continuous with the lateral border of the prezygapophysis; and in both animals the massiveness of the base of the transverse process decreases backwards along the series. A feature peculiar to the first two caudals of Prestosuchus is the presence of a broadening beneath the transverse process resembling an independent element upon the centrum, sharp below and (this is also true of the third caudal) defined from the flat dorsal part of the transverse process on every side. There appears to have been a distal cartilaginous continuation of this, lying ventral to the broad, flat transverse process proper; that is, these transverse processes resemble sacral ribs in that they seem to have been composed of separate "parapophysial" and "diapophysial" parts. In both Prestosuchus and Mandasuchus the prezygapophyses project anteriorly beyond the centrum. The neural spines of the anterior caudals of Prestosuchus had a very short base and were therefore axially narrow and probably high; in Mandasuchus the bases of these neural spines are not so short, especially in the supposed first caudal, but the spines are indeed high, and their tops, though flattened, are not expanded. The tops of the neural spines are not preserved in _Prestosuchus_.

The only other available anterior caudal material of _Prestosuchus_ is a fragment of the first caudal of the second specimen of _P_. _chiniquensis_.

The _P_. _chiniquensis_ type-specimen includes the damaged centra of more distal caudals; these are about as long as high. The _P_. _loricatus_ type-specimen includes better material, two middle caudals and four distals. As in _Mandasuchus_, the centra are moderately constricted in the middle and become elongated in increasing measure down the length of the tail (length relative to mean diameter, not absolute length, becoming greater). The middle caudals have their articulating faces deepened but little; the flattened transverse process is attached to the side of the vertebra at the height of the neural canal and is directed obliquely backwards; there are anterior spinal buttresses, and a basin-shaped anterior spinal concavity; and the neural spine has a narrow base which is thin and becomes thinner anteriorly, and is inclined slightly backwards. Direct comparison of these vertebrae with the corresponding vertebrae of Mandasuchus is difficult because the latter are not particularly well preserved, but they seem to be of the same general type. The distal caudals show a strong resemblance to the distal caudals of Mandasuchus (specimen no. 63). In both genera the centrum has no ventral longitudinal furrow; there is no transverse process, but in its place there is a shelf-like, projecting longitudinal thickening, lying approximately on the neurocentral suture; the neural spine is inclined weakly backwards; and there is a small median pre-neural spine, connected by a low saddle with the base of the neural spine proper. The Prestosuchus material includes one vertebra more distal in position than any of the Mandasuchus vertebrae; it has strongly divergent prezygapophyses, a very obliquely backwardly directed rudimentary neural spine, and no pre-neural spine.

Dorsal ribs.

Both Prestosuchus type-specimens include a small quantity of dorsal rib material. The head of a mid-dorsal rib of P. chiniquensis compares with the solitary preserved dorsal rib-head of Mandasuchus, but its tuberculum is missing; it was connected by a thin web-like lamella to the anteriorly directed capitular branch. In the middle, below the tuberculum, there is a sharp longitudinal edge on the anterior side; this is absent in _Mandasuchus_. The distal part of the mid-dorsal rib is oval, with a flat longitudinal channel, bordered by sharp edges, on its posterior surface; this is narrow at first and becomes broader distally. Von Huene suggests that it may be a contact-surface for the abdominal ribs, which are indeed present in _Prestosuchus_. Such a groove is present on both sides of the rib-shaft in _Mandasuchus_.

Two good ribs and an isolated capitulum of _P. loricatus_ are preserved. These are of the same general type as that of _Mandasuchus_, having a long capitular branch and a high, thin lamella connecting capitulum and tuberculum. Here again, however, there is a sharply projecting anterior longitudinal ridge, absent in _Mandasuchus_, and a deep longitudinal groove lies beneath it.

Haemapophyses.

The haemapophyses of _Prestosuchus_ are known only from those which follow the third, fourth, fifth and sixth caudals of the _P. chiniquensis_ type-specimen. There are no bony bridges connecting the two rami of each proximal end; but von Huene remarks that the last of these inclines towards bridge formation, and that the more distal haemapophyses would certainly have bridges like those of Rauisuchus. Only distal haemapophyses are known in Mandasuchus, and these have bridges.

Pectoral girdle.

The pectoral girdle of the Prestosuchus chiniquensis type-specimen is preserved virtually complete and naturally articulated. It includes small, short clavicles and a long dagger-shaped interclavicle; these bones are not known in Mandasuchus.

Scapula.

This bone is described as being short and broad in Prestosuchus; but, according to the dimensions quoted, is not much more so than is the Mandasuchus scapula. The constriction in the centre, however, is less strongly marked. As in the East African animal, the inflexion is moderately strong in the lower third; the anterior longitudinal edge is thin and sharp; the posterior edge is thick, relatively much more so than in Mandasuchus. In Prestosuchus the scapular blade seems to curve anterodorsally, its posterior border being more or less straight; in Mandasuchus the blade seems to curve posterodorsally, the posterior border being markedly concave. In both animals the glenoid articulating surface is formed mainly by the coracoid and to a much lesser extent by the scapula. The outer surface just above the articulation is almost plane except for a shallow depression for the insertion of the trapezius muscle; the medial surface just above the articulation is strongly concave; and on the thickened posterior edge, again not far from the border of the glenoid, there is an oval, strongly projecting process for the origin of the anconaeus scapularis lateralis externus muscle. Von Huene notes that in Prestosuchus there is a groove on the inner surface of the basal part of the scapula, just where the thickened articular portion passes forwards into the thin (deltoid) flange, and that this groove runs into the coracoid foramen; such a groove has not been observed in Mandasuchus.

The articulating end of the scapula of the P. loricatus type-specimen is also preserved, and differs only in detail from that of P. chiniquensis.

Coracoid.

The coracoids of Prestosuchus and of Mandasuchus appear to be very similar, as far as can be told from the articular fragments which are all that remain of this bone in the latter animal. The foramen is in a similar position in both genera and runs obliquely through the bone towards the scapula.

Fore-limb.

Humerus.

The only remains of this bone in *Prestosuchus* are three badly preserved fragments of the *P. chiniquensis* type-specimen - both proximal ends and part of a distal end without the articulating surface. A detailed comparison is impossible, but, as far as can be seen, the bone had proportions similar to those of the *Mandasuchus* humerus. In both animals the shaft is hollow and must have been almost straight; the breadth of the distal end increases strongly on the post-axial side and much less on the pre-axial; and there is a light depression on the anteroventral side of the distal end.

Radius.

Only a small fragment of this bone is preserved in the type-specimen of *Prestosuchus chiniquensis* and none at all in the other specimens of the genus; no comparison with *Mandasuchus* is possible.

Pelvic girdle.

Ilium.

In the type-specimen of *P. chiniquensis* the ilium, lacking its anterior part, is preserved in natural connexion with the sacral ribs, pubis and ischium; in the second specimen of the same species the upper half of the ilium is preserved in connexion with the sacral ribs. The proportions of the bone appear to be very similar to those of the *Mandasuchus* ilium. The acetabulum is closed and very large; the lower border is formed by two straight surfaces which meet at an angle below and to which are applied the pubis and the ischium; the upper edge is straight; the anterior spine is incomplete, but was probably not curved downwards; the posterior spine is broad and a high, sharp crest for articulation with the second sacral rib runs axially along its medial surface. The bone is thickened over the furthest projecting point of the supra-acetabular crest, which descends forwards and downwards in a flat arch and almost reaches the pubic contact-surface.

Pubis.

In the *P. chiniquensis* type-specimen both pubes are preserved virtually complete except for a break above the middle. The proportions are very much like those of the *Mandasuchus* pubis. As in the latter animal the pubis is a narrow plate, directed steeply downwards at an angle of about 55 degrees to the axis of the sacral vertebrae (45 degrees in *Mandasuchus*), with a proximal twist and with an obturator foramen of similar relative size in a similar position; the lateral longitudinal edge is thick and each plate becomes thinner medially towards the symphysis with its fellow; the plate is plane above, but distally there is a lump-shaped thickening below towards the lateral edge. This thickening forms a rough triangle in transverse section, with the base above and the apex below; it is more marked in *Prestosuchus* than in the *Mandasuchus* type-specimen (no. 11b), but it is also very well marked in the largest specimen of *Mandasuchus* (no. 63). The symphysis does not extend to the extreme distal end of the bone; the same holds true in *Mandasuchus*, although in the latter animal it reaches relatively nearer to it.

Ischium.

Both ischia are well preserved in the *P. chiniquensis* type-specimen and retain their natural connexions. The form of the bone is remarkably similar to that of the *Mandasuchus* ischium; at the same time von Huene notes (op. cit., p. 175) that "Das Ischium ist abgesehen von der Art des Iliumkontakts nicht von dem eines Saurischiers zu unterscheiden" and (p. 176) "... die ganze Gestalt ist völlig gleich wie bei den triassischen Prosauropoden und Carnosauriern." In both Prestosuchus and Mandasuchus the lower acetabular edge is very sharp; the anterior part of the proximal expansion is thin; there is a long straight peduncle, directed downwards from the axis of the sacral vertebrae at an angle of about 25 degrees, thick on its posterodorsal side (relatively thicker in Prestosuchus) and thinning to a keel anteroventrally; and the distal end of the peduncle is lightly thickened. In Prestosuchus there is a symphysis between the ischia of the two sides; the medial contact-surface is broader in Prestosuchus than in Mandasuchus, if indeed it exists at all in the latter animal. On the posterodorsal side of the peduncle of the P. chiniquensis ischium a longitudinal channel runs from the anterior expansion up to the middle of the bone near its medial edge and fades out gradually at both ends, exactly as in Triassic pachypodosaurs; in Mandasuchus such a channel cannot be seen unless it be for faint traces.

In the type-specimen of P. loricatus the peduncles of both ischia are preserved together and seem to be co-ossified. As in Mandasuchus, the longitudinal channel referred to above is absent.

Hind-limb.

Femur.

The complete hind-limb of the P. chiniquensis type-specimen is preserved in natural connexion with the pelvis. The femur is powerful, being of the same relative thickness but relatively shorter than that of Mandasuchus; the proximal half is more or less straight, while near the distal end the shaft is bent strongly downwards and is somewhat twisted. Its form shows that its natural position was approximately horizontal. The anterior projection of the head extends relatively further than it does in Mandasuchus. The outer (dorsal) surface of the proximal end is not arched but is flat as in Mandasuchus and has a depression in the middle. The fourth trochanter is a hump-shaped elevation, again as in Mandasuchus, and lies in a similar position; three rounded-off edges run from its highest point, two proximally and one distally, but these have not been observed in the East African animal. Both animals possess the short, strongly thickened longitudinal ridge just below the proximal end-surface and the broad longitudinal deepening behind it running down towards the fourth trochanter. (In Mandasuchus this groove contains a foramen nutritivum). The distal end of the femur is relatively broader in Prestosuchus than in Mandasuchus. Both ends of the bone are without arched epiphyses and are flat or even lightly deepened in the middle; in Mandasuchus the proximal end is more or less flat, while the distal end appears to be incompletely ossified and is deeply excavated in the femora of both sides.

Tibia.

This bone is relatively longer and more slender in Mandasuchus than in Prestosuchus (P. chiniquensis type-specimen). In both genera the longer axis of the transverse section runs obliquely from anterolateral to posteromedial, and in neither is there any real tuberosity. In Prestosuchus the lateral surface of the shaft is fairly flat but is deeply furrowed at the distal end; in Mandasuchus the distal end is barely perceptibly furrowed in the same position. In both animals a weakly developed ridge on the medial surface extends proximally from just above the middle of the distal end and runs obliquely towards the front, dying out in the middle of the shaft. About one-third of the way down the shaft of the *Prestosuchus* tibia there lies, posteromedially, a deep downwardly directed depression, which is probably a foramen nutritivum; this is very well marked in specimen no. 63 of *Mandasuchus*, although perhaps not quite so far down the bone, and may be present in one tibia of the type-specimen (no. 11b).

Fibula.

This is preserved entire in the *P. chiniquensis* type-specimen, but only the proximal part is known in *Mandasuchus*. In both genera the proximal end-surface is flat; distally the shaft diminishes suddenly where the medial edge approaches the lateral; one-third of the way down from the proximal end there is a high muscle-ridge on the medial border of the anterior surface (less prominent in the type-specimen of *Mandasuchus* than in the larger *Prestosuchus*); and the posterior surface is somewhat concave.

Fibulare.

Fibularia are preserved in the *P. chiniquensis* type-specimen and in both specimens of *P. loricatus*. In the former the bone is *in situ* and, according to von Huene, "Eigenartig ist das Fibulare gebaut." It nevertheless resembles that of _Mandasuchus_ in high degree; the latter seems to have a relatively greater sagittal length. A large backwardly directed tuber is present in both genera. In both animals a rounded cushion-like region lies anteriorly and anterodorsally, extending up to the lateral edge; in _Prestosuchus_ the medial part articulates with the tibiale, fitting exactly upon a corresponding concave surface, and upon the upper part rests the lateral portion of the distal end of the fibula. In both animals the lateral surface is smooth and vertically placed, and a vessel-duct penetrates into the bone in its anterior half; the ventral surface is smooth in front, while further back lies a great broad pit; and the posterior surface of the tuber (partly broken off in _Mandasuchus_) is smooth and vertical. The _Prestosuchus_ fibulare has a posteromedial concavity for the tibiale.

The fibulare of _P. loricatus_ is narrower and relatively longer than that of _P. chiniquensis_.

Von Huene says of the _P. chiniquensis_ fibulare, "Dieses Fibulare ist grundsätzlich gleich wie das von _Episcoposaurus horridus_, das ich 1915 beschrieben und abgebildet habe. Nur in Kleinigkeiten unterscheiden sich beide." His orientation of the two fibularia nevertheless seems to differ:

Prestosuchus	Episcoposaurus
Dorsal	Posterior
Anterior	Dorsal
Ventral	Anterior
Posterior	Ventral

Dermal scutes.

The scutes of Mandasuchus resemble those of Prestosuchus very closely, far more closely than they do those of any other known animal. Von Huene considers that all the known scutes of Prestosuchus (except one, concerning which see below) are paramedian dorsals. They include seven from the second specimen of P. chiniquensis (of which six are in situ on the tops of the neural spines of the last dorsal and the two sacral vertebrae) and seven from the type-specimen of P. loricatus (presumed, for some unspecified reason, to be mostly derived from the tail region).

All the paramedian scutes of Prestosuchus are of the same general type. They are more numerous than the vertebrae, perhaps 2-3 per vertebral segment, and each overlaps the plate behind it as do tiles on a roof. (In _P. chiniquensis_ the length of a scute up to the overlap of the next is 3.4cm., and the sacral centra are each 8cm. long). The scutes are about as long as wide (5-6cm. in _P. chiniquensis_). Each is divided longitudinally by a keel, weak in _P. chiniquensis_ and better developed in _P. loricatus_, which becomes more prominent anteriorly. Some of the scutes are almost symmetrical, but the figures of _P. loricatus_ show that at least some of the scutes are divided unequally, with the portion lateral to the keel considerably wider than the medial portion; the same variety is found in _Mandasuchus_. The two parts of each scute are inclined to one another at an angle. The scute increases in width backwards and has a rounded-off posterolateral corner. The internal surface is concave. The plate becomes rapidly narrower anteriorly and is produced into a narrow forwardly projecting spine continuous with the longitudinal keel. The posterior margin has a slight bay in the middle, and on the inner surface there is a deep depression in the centre of the hinder end to receive the anterior spine of the following vertebra. There is no pitting or sculpture, but very distinct fibres radiate from the elevated centre of the outer surface of each plate. The edges are irregularly notched.

The _P. chiniquensis_ material also includes one small, narrow, elongated scute; this has a longitudinal elevation in the middle, an anteriorly directed point, and a blunt posterior end. The two parts of the outer surface are inclined to each other at a more acute angle than in the other plates. Von Huene considers this to be a lateral scute from the proximity of the dorsal double row of plates and compares it with those of _Rauisuchus_. There seems to be no good reason why this should not be a paramedian scute from the more distal part of the tail. On the other hand, it may well be a lateral scute in very fact, indicating that the armour of _Prestosuchus_ is not restricted to two paramedian dorsal rows of plates. In the latter event, it nevertheless remains true that in both _Prestosuchus_ and _Mandasuchus_ the nature of the finds appears to show that the armour (other than abdominal ribs) consisted very largely of plates of remarkably similar form arranged along the back of the animal in two paramedian rows.

The close resemblance between the genera extends also to the location of the flattened expansions of the tops of the neural spines, serving for the support of the overlying scutes. Von Huene remarks of the fragmentary dorsal vertebra of the type-specimen of

P. loricatus "Es ist sehr wichtig, dass man aus diesem Wirbel erkennen kann, dass die Unterlage der Rückenpanzerplatten von vorn nach hinten sehr schnell an Stärke und Breite abnimmt. Die Dornfortsätze der Schwanzwirbel sind oben gar nicht, die der Rückenwirbel mässig, die der Halswirbel ungeheuer verdickt," and this description applies equally well to *Mandasuchus*.

Summary.

Prestosuchus and *Mandasuchus* are remarkably alike in their osteology. The most striking similarity is in the form and distribution of the dermal scutes. The girdle- and limb-bones are also very similar, especially the rather peculiar fibularia. The vertebrae of the two animals, particularly their neural spines, bear a general resemblance to each other; the resemblance extends to such small details as the presence of a muscle-ridge just above the cervical postzygapophysis and of a pre-neural spine in the distal caudals. The teeth of the two genera are also of the same type.

The essential difference between *Prestosuchus* and *Mandasuchus* lies, not in the fact that the cervical centra of the former are higher than long (such a

difference might be expected in a much larger beast; see Chapter 3 above), but in the fact that they are no longer than the anterior dorsals and bear a very high and narrow ventromedial keel. It must be admitted that the few <u>Prestosuchus</u> cervicals known are poorly preserved and from the posterior part of the neck, and longer vertebrae may have been present further forward. Another difference, if natural, is the absence of a hyposphene in <u>Prestosuchus</u> and the presence of a gap between the postzygapophyses instead. The hind-limb of <u>Prestosuchus</u> (the fore-limb is not properly known) is relatively more massive than in <u>Mandasuchus</u>, but again this would be expected in a larger animal. The absence of clavicles and interclavicle in <u>Mandasuchus</u> may well be artificial; and the fact that the most anterior haemapophysis follows the possible fourth caudal vertebra instead of the third is probably of no great importance.

iii) <u>Comparison with the Stagonolepidae</u>

<u>Prestosuchus</u>, which appears to be closely allied to <u>Mandasuchus</u>, was originally placed by von HUENE (1935-1942, 1936a,b) in the family Stagonolepidae. He

included it with his other new genus <u>Rauisuchus</u> from the same beds, designating the two as a new sub-family (Rauisuchinae). It is clear, however, that von HUENE no longer considers <u>Rauisuchus</u> and <u>Prestosuchus</u> to form part of the Stagonolepidae, for in a later publication (1948) he introduces a new family (Rauisuchidae). This family is characterised by "paramedian pairs of dorsal scutes, rounded at their lateral end", while the Stagonolepidae have "rectangular dorsal scutes in (a) transverse direction"; the two families are placed alone together in the "Family circle Chirotherioidea", which are "precursors of Ornithischia".

On such a definition, and because of its similarity to <u>Prestosuchus</u>, <u>Mandasuchus</u> would certainly be a member of the Rauisuchidae. A comparison of the new genus (in many respects better known than either <u>Rauisuchus</u> or <u>Prestosuchus</u>) with the true Stagonolepidae may help to clarify the distinction between the two families.

The family name "Stagonolepidae" has been employed rather loosely in the past, and for the purposes of this comparison membership of the family must be more rigidly defined. The type-genus, Stagonolepis AGASSIZ, was originally described from the Elgin Sandstones, which are supposedly of Lettenkohle or Lower Keuper age. The remains, first thought by Agassiz to be those of a fish, were recognised as reptilian by HUXLEY (1859, 1875, 1877), who considered the animal to be a primitive crocodile. Subsequent publications by von HUENE (1902, 1911b, 1935-1942, 1936a,b) placed the animal first in the Parasuchia and then in the Pseudosuchia, simultaneously increasing our knowledge of its osteology.

Other remains, discovered by RILEY & STUTCHBURY (1840) in the Magnesian Conglomerate near Bristol, were described by von HUENE (1902, 1908, 1911b) as a genus of phytosaur, Rileya. There is only a tooth, two caudal vertebrae, a haemapophysis and bones of the fore-limb. Later, however (1935-1942), von HUENE realised that at least part of the Rileya material was identical with Stagonolepis.

A "Parasuchier-Humerus" was described by von HUENE (1920b) from the Upper Muschelkalk of Bayreuth. He later (1935-1942) expressed the opinion that it was closely related to the genus Stagonolepis, if not in fact belonging to it.

It has been shown by WALKER (paper read at the

Symposium on Vertebrate Palaeontology and Comparative Anatomy held in the Department of Zoology at University College, London, on 22nd September, 1954) that *Stagonolepis* is generically (though not specifically) identical with the German *Aëtosaurus* O. FRAAS (1877; E. FRAAS, 1907; von HUENE, 1920a, 1921), the former name having priority. The Scottish species (*S. robertsoni*) has a maximum of eight ventral plates per transverse row on the belly, while the German species (*S. ferratus*, *S. crassicauda*) have up to twelve ventral plates per transverse row and rather fewer teeth. The genus is probably herbivorous. No Stagonolepids other than *Stagonolepis* itself have yet been found in Europe; the poorly known *Dyoplax* O. FRAAS (1867) from Germany, hitherto sometimes classified with "*Aëtosaurus*" in the family "Aëto-sauridae", is really quite different and seems to be much more nearly related to *Erpetosuchus*, especially in the form of its skull and dermal armour.

Several Stagonolepids have been described from the west of North America, but their inter-relation-ships and possible synonymies were much confused until recently. These animals possess a superficial resemblance to the phytosaurs and have sometimes been classified with them. The three chief genera were

Typothorax COPE (1875, 1877, 1887b, 1893; von HUENE, 1915; CAMP, 1930; SAWIN, 1947; GREGORY, 1953a), Episcoposaurus COPE (1887b, 1892; von HUENE, 1915; CAMP, 1930, 1933; WILSON, 1950) and Desmatosuchus CASE (1920, 1921, 1922, 1929; CAMP, 1930); while a fragmentary specimen was described by MEHL as Acompsosaurus (1915; MEHL, TOEPELMAN & SCHWARTZ, 1916). GREGORY has now shown (1953b) that the type-species of Episcoposaurus, E. horridus, is synonymous with the type-species of Typothorax, T. coccinarum; and that the other species of "Episcoposaurus", E. haplocerus, is synonymous with the type-species of Desmatosuchus, D. spurensis. (The latter thus becomes Desmatosuchus haplocerus (COPE)). Acompsosaurus may also be synonymous with Typothorax. The best description of Typothorax is that of a new species, T. meadei, by SAWIN (1947). Stegomus MARSH (1896; JEPSEN, 1948) is another probable Stagonolepid from eastern North America, but its osteology is not well known; WALKER (private communication) would place it "provisionally" within the family.

The supposed Stagonolepids of South America, if Rauisuchus and Prestosuchus be removed from the family, include only the very poorly known Hoplitosuchus, Procerosuchus and Rhadinosuchus from the same beds.

These too were described by von HUENE (1935-1942).

Stagonosuchus von HUENE (1938a) from the "Upper Bone Bed" of Tanganyika has also been described as a Stagonolepid. It will be considered more fully in Sub-section vi) below.

ROMER's lists (1945) place Rauisuchus and Prestosuchus among the Stagonolepidae and include, in addition, Stegomosuchus von HUENE from North America and Platyognathus YOUNG (1944, 1951) from China. Little is known of these genera.

Von HUENE's classification of 1935-1942 divided the Stagonolepidae into sub-families; these are, in addition to the Rauisuchinae already mentioned, the Stagonolepinae (Stagonolepis), the Desmatosuchinae (Desmatosuchus, Acompsosaurus and ?Hoplitosuchus), the Episcoposaurinae (Episcoposaurus and ?Stegomus) and, in an unnamed and doubtful sub-family, Procerosuchus.

A comparison of Mandasuchus with particular genera of the Stagonolepidae would be rendered difficult by the inadequacy of our knowledge of many of the latter, and would also be hindered by cases of uncertain reference or of possible synonymy. Among the better known Stagonolepids, however, many common characteristics may be recognised, and a more general consideration of the family should suffice. Thus the following comparison of Mandasuchus is with the Stagonolepids of Europe (based on material described as Stagonolepis and "Aëtosaurus") and those of western North America (based on material described as Typothorax, "Episcoposaurus", Desmatosuchus and Acompsosaurus). Walker agrees that Stagonolepis (including "Aëtosaurus") is very closely related to Typothorax and Desmatosuchus, these genera at least forming a very well defined compact family with characteristic specialisations. The South American genera (Hoplitosuchus, Procerosuchus and Rhadinosuchus) are rather different and must be considered separately.

Dermal armour.

The most striking differences between Mandasuchus and the Stagonolepids lie in the nature of the dermal armour. In Mandasuchus the only armour known consists of the two paramedian rows of dorsal scutes on the neck and trunk and perhaps on the tail. As already described, these are more numerous than the vertebrae, rest upon the flattened and expanded tops of the neural spines, and are usually about as broad as long; each bears a longitudinal keel externally and is thus divided into medial and lateral portions which are inclined to one another at a considerable angle; the keel is produced forwards into a tapering spine which fits beneath a notch in the hinder border of the next anterior plate; and the outer surface is devoid of ornament. In the Stagonolepids, on the other hand, the dermal armour is more extensive; it either sheathes the body entirely (Stagonolepis, "Aëtosaurus", Typothorax) or consists of at least two rows of plates on either side of the dorsal mid-line (as in Desmatosuchus, where one small plate found may have been a ventral and where the presence of a complete ventral armour, though not known, is certainly suspected). The Stagonolepid scutes usually correspond to the vertebrae in number and position except in the neck region of certain genera, where the plates may be even longer and fewer than the vertebrae (Typothorax and Desmatosuchus); from the shoulder backwards the armour is in overlapping transverse rows, metamerically arranged and forming complete rings. (The ventral rows of the belly region may be slightly more numerous than the vertebrae in Stagonolepis). The scutes of the trunk are supported by the expanded, blade-like dorsal ribs in Typothorax and Acompsosaurus; this is not known to be the case in any other Thecodont. It is suspected, however, that the transverse processes of the caudal vertebrae performed a similar function in *Stagonolepis*, "*Aëtosaurus*" and *Desmatosuchus*. The paramedian scutes of the neck and trunk (but not necessarily those of the tail, nor, in *Typothorax*, those at the front of the neck) are transversely elongate rectangles, being up to three times as wide as long ("*Aëtosaurus*"). The presence of a longitudinal keel on these scutes is not usual, although it has been recorded of some of the material described as "*Stagonolepis*"; in *Typothorax* there may be a low conical or pyramidal eminence near the centre of the posterior edge, while in *Desmatosuchus* there is a low blunt spine or knob. The anterior margin bears no spine (although its lateral corner may be extended into a thorn-like projection in "*Aëtosaurus*") but is often bevelled or grooved for articulation with the overlapping scute in front; the posterior edge is not notched but is usually more or less straight; the lateral margin may be oblique (*Stagonolepis*, "*Aëtosaurus*"). Further, while the inner surfaces of the plates are quite smooth, their outer surfaces are usually sculptured. Those of *Stagonolepis* and "*Aëtosaurus*" are ornamented with irregular drop-shaped pits and grooves radiating from a more or less smooth area situated a little behind the centre, and behind this area, in the pelvic region, there is a boss or longitudinal ridge; the scutes of Typothorax have shallow round pits of uniform size; and those of Desmatosuchus bear a similar but coarser and less regular pitting and ridging.

The lateral dorsal scutes are present as a longitudinal row on either side of the paramedians; and in Typothorax and Desmatosuchus each bears a projecting spine. In the shoulder region of Desmatosuchus one pair of these spines (the fifth) is prolonged into a pair of enormous horns which curve horizontally forwards.

Teeth.

The maxillary teeth of the Stagonolepids seem to be fewer than those of Mandasuchus; unlike the latter, they are not usually recurved, and their edges are not serrated. The preserved fragment of the maxilla of the Mandasuchus longicervix type-specimen must have contained at least twelve teeth; and the isolated maxilla of specimen no. 77a, referred to the same genus, is more complete at its anterior end, where it contains two more alveoli. A total of at least fourteen maxillary teeth may therefore be supposed for the genus if it be assumed that there were no intra-generic differences in the tooth count. In the Stagonolepids, on the other hand, Desmatosuchus has but twelve or thirteen maxillary teeth, Stagonolepis ten or eleven, Typothorax nine or ten, and "Aëtosaurus" only nine. Those of Stagonolepis are described as sub-cylindrical in form, having a pear-shaped crown which tapers towards an obtuse point, has neither anterior nor posterior ridges, and is separated from the cylindrical root by a constriction. In "Aëtosaurus" their form is similar, but the crown is somewhat compressed laterally, with sharp edges before and behind, and in this case the tips are lightly recurved. The maxillary teeth of Typothorax are bluntly conical and are also constricted between root and crown. In Desmatosuchus the form of the teeth is unknown, but the shape of the alveoli does not suggest any antero-posterior elongation.

Vertebral column.

The number of pre-sacral vertebrae in the Stagonolepids, where known, is, as in Mandasuchus, approximately twenty-five. In "Aëtosaurus" there are seven cervicals and eighteen dorsals; in Typothorax, on the other hand, there are ten cervicals and presumably correspondingly fewer dorsals. The sacral vertebrae, where known (Stagonolepis, "Aëtosaurus", Acompsosaurus), are two in number and not ankylosed.

There are between forty and fifty caudal vertebrae in "Aëtosaurus". The vertebrae of Stagonolepis decrease in size rapidly before and behind the pelvis; their centra are constricted in the middle and weakly amphicoelous, their zygapophyses are narrow and steeply inclined.

Cervical region.

The cervical vertebrae of these animals, in contrast to those of Mandasuchus, are shorter than the dorsals; their centra are keeled beneath in Stagonolepis and "Aëtosaurus" but not in Desmatosuchus. In Typothorax and Desmatosuchus the posterior cervicals already possess long diapophyses; in the latter animal the posteroventral buttress first appears in the sixth vertebra and a low sharp anteroventral buttress is present in the ninth. The neural spines are described as high, narrow and apically expanded in Stagonolepis, moderately high and strongly transversely thickened above in "Aëtosaurus"; in Desmatosuchus they seem to have been low, axially long and thin in the middle of the neck, but further back they become higher and bear an apical knob or expansion. Desmatosuchus shows an interesting similarity to Mandasuchus in that each of its anterior cervical vertebrae (including the axis) bears a strong spinous process just above the facet of the postzygapophysis; unlike the inwardly directed prominence of Mandasuchus, however, this process extends outwards and backwards in the North American beast.

Dorsal region.

The dorsal vertebrae of the Stagonolepids may be twice as long as the cervicals (Stagonolepis); they tend to become longer and heavier posteriorly (Typothorax, Desmatosuchus). In Stagonolepis their faces are higher than wide. The most anterior vertebra of Desmatosuchus in which the parapophysis is borne entirely on the neural arch is the thirteenth, just as in Mandasuchus; in the phytosaur Machaeroprosopus, on the other hand, it is the twelfth, although such a character could well be subject to individual variation. The diapophysis is very long and is well supported by buttresses in Stagonolepis and Desmatosuchus, though not in Typothorax; in the anterior dorsals of Stagonolepis it is directed obliquely upwards at a considerable angle. In Desmatosuchus, passing backwards down the column, the parapophysial facet gradually comes to lie on the anterior side of the transverse process and it then approaches the diapophysial facet, the supporting ridges dying out. Spinal buttresses and concavities are present in that genus as in *Mandasuchus*. The neural spines, tall again in *Stagonolepis*, possess expanded tops; but these differ from those of *Mandasuchus* in that they tend to become heavier posteriorly.

Sacrum.

In *Stagonolepis* and "*Aëtosaurus*" the second sacral vertebra seems to have provided the major support for the ilium; in the former animal its rib is more expanded distally than is the first sacral rib. The single poorly preserved sacral of *Desmatosuchus* has a very heavy neural spine.

Caudal region.

The caudal vertebrae of the Stagonolepids are generally very similar to those of *Mandasuchus*, although certain differences must be noted. There is only one pygal vertebra in "*Aëtosaurus*" and probably two or three in *Desmatosuchus*; *Mandasuchus* has three. The faces of the centra are higher than wide in the Stagonolepids. The proximal caudals of "*Aëtosaurus*" have long, very strong expanded transverse processes which probably helped to support the dermal armour; those of *Stagonolepis* and *Desmatosuchus* also possess very long transverse processes, curving downwards distally, which may well have served a similar purpose. The neural spines of the proximal caudals may be like those of the East African reptile in being very high ("Aëtosaurus"); in Typothorax, on the other hand, they are shorter than those of the dorsal vertebrae, and in Desmatosuchus they are described as heavy with thickened apices. Finally, no pre-neural spine has been observed or figured in the mid- or distal caudals of any Stagonolepid.

Ribs.

The cervical ribs of the Stagonolepids generally resemble those of Mandasuchus; those of Stagonolepis, however, are very long and thin, while those of "Aëtosaurus" are described as powerful. The dorsal ribs, where known, are of the typical dicephalous form. In Typothorax and Acompsosaurus, as already mentioned, they are expanded proximally into blades which support the dermal armour, and in the former reptile there is a prominent spine on the anteromedial surface at the base of the tuberculum extending for one-third of the length of the rib; these features are not known in Mandasuchus.

Haemapophyses.

Haemapophyses are known in some Stagonolepids. The two rami of the proximal end are not united by a bridge in Stagonolepis ("Rileya") or in Desmatosuchus;

in *Typothorax*, on the other hand, a bridge is present.

Pectoral girdle.

The pectoral girdle of the Stagonolepids bears a general resemblance to that of *Mandasuchus*; but clavicles and interclavicle, not yet found in the latter genus, are known in *Stagonolepis* and "*Aëtosaurus*". The scapula is usually massive below and blade-like above, becoming thinner anteriorly and dorsally; in *Stagonolepis* it is strongly bent dorsoventrally and widely expanded above, terminating acutely postero-dorsally; in "*Aëtosaurus*" it is exceptionally narrow in the middle. The coracoid, ankylosed to the scapula where preserved, is oval in form (*Stagonolepis*), not elongated (*Typothorax*), and is perforated by a foramen passing upwards and inwards (*Desmatosuchus*). In *Stagonolepis* and "*Aëtosaurus*" the glenoid cavity is very deep and is supported by a strong ledge of the coracoid.

Fore-limb.

The fore-limbs of the Stagonolepids, as is usual in archosaurs, are shorter and more lightly constructed than the hind-limbs. The humerus is longer than the epipodials ("*Aëtosaurus*"). As in *Mandasuchus*, the proximal expansion of the humerus is greater than the distal, the angle between the two being about 45 degrees (*Typothorax*); in *Stagonolepis* the amount of torsion is much less than this. The shaft is slender (*Typothorax*) and shows a weak sigmoidal curvature ("*Aëtosaurus*"). The deltopectoral crest is placed high in both these genera. An ectepicondylar groove and supinator process seem to be present in every case except in *Typothorax*, which has an ectepicondylar foramen instead of a groove; radial and ulnar condyles are well developed, but in *Stagonolepis* there is no hollowing on either side of the distal end such as is found in the East African animal. Little can be said about the radius, which is well known only in *Typothorax*. The ulna is massive proximally and differs from that of *Mandasuchus* in that it bears a large olecranon (*Stagonolepis*, *Typothorax*) and a deep concavity on the medial side of the proximal end (*Stagonolepis*, "*Aëtosaurus*").

Pelvic girdle.

The elements of the pelvic girdle, while varying within the *Stagonolepidae* to some extent, are clearly distinguishable from those of *Mandasuchus*.

Ilium.

As in *Mandasuchus*, the ilium of the Stagonolepids forms the greater part of the surface of the large acetabulum; the latter is completely closed and is bordered dorsally by a sharp and prominent supra-acetabular crest. The anterior spine of the ilium is short; it is hooked and slightly recurved in *Stagonolepis* and "*Aëtosaurus*". The posterior spine is well developed in those two genera; it is broad and moderately long, though not so long as in *Mandasuchus*. In *Typothorax* the posterior spine is broad, bluntly tapered, and weakly concave in transverse section; the inner surface of the acetabular region of the ilium is convex and is bordered above by a well developed medial crest. (The correct association of the *Typothorax meadei* ilium is uncertain).

Pubis.

The pubis of the Stagonolepids resembles that of *Mandasuchus* in that it forms only a small part of the acetabulum and is united with its fellow in a long symphysis, the two together forming a broad, transversely disposed sheet which lies almost vertically. It is, however, comparatively short and broad, that of "*Aëtosaurus*" being a little shorter and broader than that of *Stagonolepis*, while the *Typothorax* pubis is very short. The part which articulates with the ilium is very thick, but where it approaches the ischium the bone is extremely thin. There are two pubic foramina (a point on which the Mandasuchus pubes are too incomplete to provide information); and in the Stagonolepis pubis there is a deep excavation beneath the point of torsion.

Ischium.

The Stagonolepid ischium seems to be either moderately elongate (Acompsosaurus) or short (Stagonolepis); in any event it is shorter than that of Mandasuchus. It forms the posteroventral part of the acetabulum, being thickened in the region of the iliac articulation and being much thinner towards the pubic articulation (which latter was probably cartilaginous in "Aëtosaurus"). Information on the presence and form of the peduncle varies surprisingly; that of Stagonolepis is described at one time as absent, at another as phytosaurian rather than pseudosuchian in form, while that of the co-generic "Aëtosaurus" has been described as very short and spiky. The narrow Typothorax ischium has a peduncle which (together with its fellow) is dorsally concave and of which the distal end has bluntly rounded borders. In all three of these animals, however, there is a long and powerful median symphysis between the ischia.

Hind-limb.

Femur.

The Stagonolepid femur is not unlike that of *Mandasuchus*. The shaft, variously described as stout (*Stagonolepis*), long (*Typothorax*), thick and strong ("*Episcoposaurus*"), is sigmoidally curved to some extent except in the last-named, where it appears to be straight throughout most of its length, only the distal end being bent. This appearance, however, may be due to the angle at which it is figured. The proximal end is not much expanded, less so than the distal (as in *Mandasuchus*), nor is it much differentiated; the prominent fourth trochanter is always present and is situated high on the shaft; there is a projection of the lateral margin of the bone opposite the fourth trochanter; and the distal end is thick and club-shaped, as in *Mandasuchus* and other pseudosuchians.

Tibia.

The tibia of *Stagonolepis* is straight and stout. The whole tibia of *Typothorax* appears to differ greatly from that of *Mandasuchus*; it is relatively very short and stout, and the shaft, triangular in section, bears an oval rugosity on the anterior angular border of its lateral face less than a third of the way down the bone. The proximal end is thick and expanded in every case, while the distal end of the "_Episcoposaurus_" tibia is described as being divided into two processes and therefore strikingly saurischian-like. No such processes are present in _Mandasuchus_.

Fibula.

The fibulae of the Stagonolepids are much alike and show a strong sigmoidal or double curvature in lateral view (_Stagonolepis_, "_Aëtosaurus_"); that of _Typothorax_ is short and stout and hence very different to the _Mandasuchus_ fibula, resembling it only in that it has a flattened and expanded head. Near or just above the middle of the shaft there is a large lateral trochanter in all three of the above-mentioned Stagonolepids; in _Stagonolepis_ and "_Aëtosaurus_" this sometimes forms a high narrow ridge passing obliquely downwards and backwards to merge with the posterior margin, and in _Typothorax_ it is double. (The great muscle-ridge of the _Mandasuchus_ fibula has been described as projecting forwards, but the bone may be wrongly orientated).

Fibulare.

The Stagonolepids possess fibularia (not known in _Stagonolepis_ itself) which, in general, are not greatly different from that of Mandasuchus (and Prestosuchus); there is a very well developed tuber extending upwards and posteromedially in "Aëtosaurus" and Typothorax. The nature of the connexion with the astragalus seems to vary within the family if the descriptions be indeed correct; "Episcoposaurus" is described as having no such connexion, in "Aëtosaurus" fibulare and astragalus are reported to be joined by simple synostosis, and Typothorax in particular seems to resemble Mandasuchus in that the fibulare possesses "anteromesially a semicircular concavity (which) provides an articular surface for the ventral hooked process of the tibiale" (SAWIN, 1947).

Summary.

A broad general resemblance exists between the skeleton of Mandasuchus and that typical of the Stagonolepids. This is shown in particular by the similarity in form of the dorsal vertebrae; in the anterior part of the back the diapophysis is long and is supported by buttresses, further back it is shorter and, together with the adjacent parapophysis, forms a "spectacles"-shaped rib-articulation. There is also a strong general similarity in the form of the girdles and the limbs. On the other hand, the differences between Mandasuchus and the Stagonolepidae are many;

they are summarised in the following Table:

	Mandasuchus	Stagonolepidae
Dermal armour		
	2 paramedian rows of dorsal scutes only	Complete dermal armour
Dorsal scutes		
	More numerous than the vertebrae	Correspond to vertebrae in number or fewer
	Rest upon tops of neural spines only	Also supported by dorsal ribs and/or transverse processes of caudal vertebrae
	Usually approximately isodiametric	Usually transversely elongate
	Longitudinal keel	No true keel
	Anterior spine	No anterior spine
	No ornament	Outer surface usually sculptured
Maxillary teeth		
	Probably 14 or more	9 - 13
	Recurved	Not usually recurved
	Laterally compressed	Not usually compressed
	Edges serrated	Edges, where present, not serrated
	Not constricted between root and crown	Constricted between root and crown
Vertebrae		
	Cervicals elongated	Cervicals shorter than dorsals

Mandasuchus	Stagonolepidae
Apical expansions of neural spines decrease in size after middle of back	Apical expansions of neural spines increase in size posteriorly
No such expansions	Proximal caudals with long, strong, expanded transverse processes
Distal caudals with pre-neural spine	Pre-neural spine not known

<u>Ribs</u>

Blade-like expansions not known	Proximal blade-like expansions of dorsal ribs

<u>Pectoral girdle</u>

Clavicles and inter-clavicle not known	Clavicles and inter-clavicle present

<u>Fore-limb</u>

No olecranon	Ulna with large olecranon
No such concavity	Ulna with deep concavity on medial side of proximal end

<u>Pelvic girdle</u>

Pubis comparatively long	Pubis comparatively short and broad
?	2 pubic foramina
Ischiadic peduncle long	Ischiadic peduncle shorter or absent
?	Ischia united in symphysis

Mandasuchus	Stagonolepidae
Hind-limb	
No such projection	Lateral margin of femur projects opposite fourth trochanter

The skull and pes of Mandasuchus are virtually unknown; but it may be relevant to note that, according to von Huene, Prestosuchus differs from the Stagonolepinae in its relatively larger skull and in its relatively shorter metatarsus.

Anticipating conclusions reached later and on entirely independent grounds, it might also be pointed out that both Mandasuchus and the closely related Prestosuchus occur in the Middle Triassic of Gondwanaland. On the other hand, all those genera which may be included with certainty in the family Stagonolepidae (that is, those employed for the purposes of the above comparison) have been found only in the Upper Triassic of Laurasia.

The South American "Stagonolepids".

The three "Stagonolepids" found in the upper Rio do Rasto Beds of Brazil with Rauisuchus and Prestosuchus are so poorly known that little can be said of their affinities.

The name _Hoplitosuchus_ does indeed refer in the first instance to a pair of massive dermal scutes which are strongly reminiscent of certain plates of _Desmatosuchus_ but which are completely different from those of _Prestosuchus_ and _Mandasuchus_. With these scutes may be associated (the probability of the correctness of the association varying in each case) fragments of a vertebra, ilium and ischium, the femur and the tibia, and two fibularia. The massive femur is of the general pseudosuchian type, with a very powerful fourth trochanter in a high position; the tibia resembles that of _Prestosuchus_; and the fibulare is also described as resembling that of _Prestosuchus_ but it is relatively longer.

Procerosuchus, which includes parts of the skull but unfortunately neither vertebrae nor dermal scutes, is a very slender animal in which the pectoral girdle and major limb-bones are known and seem to differ from those of _Prestosuchus_ and _Mandasuchus_ in no important respect. Clavicles and interclavicle are present. The humerus is but little longer than the epipodials; the planes of expansion of its ends lie at 45 degrees to one another, and the apex of the deltopectoral crest is in a very high position. The distal end of the tibia is triangular in section, and there is a foramen (nutritivum?) about one-quarter of the length of the bone down the medial surface. The fibula is sigmoidally curved; a high and very powerful muscle-process lies on the anterior edge of its lateral side, beginning at a distance of just over one-quarter the length of the bone from the proximal end, and a ridge runs obliquely from this process over the lateral surface.

Rhadinosuchus is a very small animal known only from parts of the skull, two cervical vertebrae, a cervical rib, a metatarsal and abdominal ribs. The teeth are pointed, recurved, moderately compressed from side to side, and their sharp longitudinal edges are finely crenulated; the cervical vertebrae are fairly long (elongation ratio 1.50) and have a ventro-medial keel; the cervical rib is straight and very thin.

All that might be inferred from these remains is that _Hoplitosuchus_ might conceivably be an ally of _Desmatosuchus_ and hence a member of the Stagonolepidae, the apparent nature of its dermal armour seeming to preclude the possibility of close relationship to _Prestosuchus_ (and _Mandasuchus_); _Procerosuchus_, on the other hand, could well be related to the latter two genera, despite the fact that its dermal armour (if it possessed any) remains unknown. Rhadinosuchus was classified by von HUENE (1939c) as a Rauisuchid; no reason is given for this, but it may have been suggested by the form of the teeth.

iv) Comparison with Rauisuchus

It has been shown that there is a clear distinction (based primarily upon the nature of the dermal armour) between Prestosuchus and Mandasuchus on one hand and the Stagonolepidae of Europe and North America on the other. Prestosuchus has always been classified with Rauisuchus until now; a comparison of Mandasuchus with Rauisuchus may help to indicate whether or not it is correct to refer the latter genus to the same family (Rauisuchidae) as the other two genera.

Like Prestosuchus, Rauisuchus is a large pseudosuchian from the upper Rio do Rasto Beds of Brazil and was described by von HUENE (1935-1942) from five specimens of a single species, R. tiradentes. The type-specimen consists of several fragments of skull and lower jaw, together with isolated teeth; several vertebrae with ribs and haemapophyses (sacrum unknown);

some of the girdle- and limb-bones; and dermal scutes of several different types. Other finds consisted of a fragmentary maxilla with no teeth; a posterior cervical vertebra, a rib-fragment, two haemapophyses and an ilium; and two separate tooth-fragments.

Maxilla.

The second specimen of Rauisuchus consists of most of the posterior half of a maxilla, the outer surface of which is distinguished by an anteriorly ascending longitudinal ledge. This ledge is absent in the type-specimen of Mandasuchus longicervix (no. 11b), but there is a ledge which may correspond to this in the isolated maxilla referred to the same genus (specimen no. 77a; see Chapter 6 below).

Teeth.

In the teeth of both genera the lightly recurved crown tapers to a point; it is laterally compressed, and its sharp anterior and posterior cutting edges bear very fine perpendicular crenulations. However, while the teeth of Mandasuchus are inclined (if not bent) in a labial direction, those of Rauisuchus are described as being inclined a very little towards the lingual side.

Vertebral column.

Cervical region.

The cervical material of Rauisuchus consists of all the vertebrae of the type-specimen, not in natural connexion and in varying conditions of preservation. There is also one poorly preserved centrum from the third specimen.

Odontoid. There is a general similarity between the odontoids of the two animals; in Rauisuchus small parapophysial facets are visible in the lateral corners.

Axial intercentrum. This is present in both genera, fitting into a concavity in the lower part of the anterior face of the axis.

Axis. In Rauisuchus there are two parallel longitudinal ridges on the underside of the centrum instead of the single prominent ventromedial keel of Mandasuchus. The position and form of the diapophysis are much the same in the two genera; but whereas in Mandasuchus the postzygapophysis projects behind the centrum, in Rauisuchus it does not do so. The neural spine, which projects forwards beyond the centrum in both genera, is much lower in Mandasuchus than in

Rauisuchus, where the anterior edge ascends more steeply and where the complete spine must have been of a considerable height.

Third to eighth cervical vertebrae. These are markedly different in the two genera. In contrast to those of Mandasuchus, all the cervical centra of Rauisuchus are shorter than the dorsals and are rather higher than long; they are strongly constricted in the middle and all bear a ventromedial keel (except the eighth, where the keel has degenerated into a ridge). In most of their other features the cervical vertebrae of Rauisuchus (including the eighth, transitional in form to the dorsals) resemble the corresponding vertebrae of Mandasuchus; the only other important differences lie in the form of the neural spines. In Rauisuchus these are long, thin, axially narrow at the base and even narrower dorsally, and without expanded apices (the apex may be slightly thickened in the third cervical); they stand more or less vertical with sharp anterior edges and thick posterior edges. Von Huene observes that the cervical vertebrae of Rauisuchus are very similar to those of Stagonolepis and Desmatosuchus.

Dorsal region.

The type-specimen of Rauisuchus includes seven dorsal vertebrae, some not well preserved; a point of interest is that two of the more anterior centra seem to be co-ossified. The resemblance between the genera is otherwise much greater here than in the neck. Von Huene remarks that Rauisuchus differs from Prestosuchus (and the Stagonolepinae) in that its diapophyses are shorter and possess less well developed buttresses; it differs from Mandasuchus likewise. In almost every other detail of their structure and in the gradual changes which occur along the length of the column the dorsal vertebrae of the two reptiles are alike. It should be noted that the dorsal neural spines of Rauisuchus, unlike the cervical neural spines, possess flattened and expanded tops.

Caudal region.

Seventeen vertebrae, some in good condition, are preserved from various parts of the tail of the Rauisuchus type-specimen; they include no pygals. No important differences can be observed between these and the caudals of Mandasuchus; in particular, it is not recorded of any of them that the top of the neural spine is flattened or expanded. In the last preserved vertebra of Rauisuchus, which is too small to bear haemapophysial facets, the neural spine is represented only by a very small backwardly directed thorn on the concrescent postzygapophyses; the neural arch is rounded above in the middle of the vertebra.

A noteworthy similarity lies in the presence in the distal caudals of both animals (and perhaps in the middle caudals too) of the small median pre-neural spine, situated in front of the base of the neural spine proper and between the roots of the prezygapophyses. Unfortunately the middle caudals of _Mandasuchus_ are nowhere well enough preserved to show whether this was present or not; in a middle caudal of _Rauisuchus_ (op. cit., Plate 26, Fig. 14) the spine appears as a pointed horn, curving upwards in an arc, and connected with the base of the neural spine by a saddle. Indisputable evidence of the existence of this spine is afforded by a distal caudal vertebra of _Mandasuchus_ (specimen no. 63), and similarly in the distal caudals of _Rauisuchus_ it is represented by a small elevated thorn lying on the median ridge which runs forwards from the base of the neural spine. Even in the very last preserved vertebra of _Rauisuchus_, where the neural spine itself is virtually absent, there is a tiny thorn between the roots of the prezygapophyses.

Ribs.

The only preserved dorsal rib-head of Mandasuchus compares most nearly with the Rauisuchus rib described by von Huene as being approximately fifth dorsal in position. In the latter the tubercular facet does not stand upon a free branch; the capitulum forms a short process passing obliquely from the corner of the tubercular facet. In Mandasuchus there are no traces of what, in Rauisuchus, von Huene calls the "Flügellamelle" beneath the middle of the tuberculum.

Haemapophyses.

The haemapophyses of Rauisuchus, at least those belonging to the larger caudal vertebrae, possess a bony bridge joining the proximal ends of the two rami. In this respect they resemble the single preserved haemapophysis of Mandasuchus (from a distal caudal vertebra of specimen no. 63).

Pectoral girdle.

Scapula.

As far as can be judged from von Huene's description and photograph, the scapulae of the two animals are of similar proportions. Von Huene comments, "Die Scapula ist für einen Pseudosuchier äusserst schlank." In both animals there is the muscle-process on the posterior edge above the articulation; in *Rauisuchus*, but not in *Mandasuchus*, the depression marking the field of insertion of the trapezius muscle is recognisable externally above the articulation.

Coracoid.

In neither animal is more than the glenoid region of the coracoid preserved; these fragments seem to be similar.

Pelvic girdle.

Ilium.

The general proportions of the two ilia are remarkably alike. In both there is a very short anterior spine and a long posterior spine, the latter with a high medial crest running along the lower edge of its inner face. In *Rauisuchus*, but not in *Mandasuchus*, a thickening runs dorsally from the anterior end of the supra-acetabular crest to the upper edge of the ilium; behind this thickening the lateral surface of the upper part of the bone is slightly concave. In *Rauisuchus*, and again not in *Mandasuchus*, the acetabulum is bordered ventrally by a high sharp ridge; and the anteroventral corner forms a more acute angle in the Brazilian reptile.

Pubis.

In almost every respect the pubes are alike. The proximal twist is strong in both animals, but in *Rauisuchus* it occurs relatively further from the iliac articulation.

Hind-limb.

Tibia and fibula.

Comparison is difficult because some sort of pathological condition appears to be present in *Rauisuchus*; fibrous exostoses are present on the bones, especially on the fibula, and there are irregular pits and depressions on their surfaces as though from caries. The proximal ends of the two bones, which seem to be co-ossified, may be deformed not only pathologically but also otherwise.

The length of the tibia is about the same as that of the tibia of specimen no. 63 of *Mandasuchus* (the dorsal vertebrae of the two animals being of comparable size), but the bone is much thicker in *Rauisuchus*; while the tibial head has much the same transverse diameter in *Mandasuchus* as in *Rauisuchus*, and indeed a greater sagittal diameter, the shaft and the distal end are much more slender in the East African beast. The *Rauisuchus* tibia has a longitudinal ridge anterolaterally in its proximal and central parts; this is not well marked in Mandasuchus. The distal articulating surfaces of both tibiae are excavated laterally to receive the astragalus.

The fibular head is enormously larger in Rauisuchus, having an area about three times as great as that of the head of the fibula of specimen no. 63.

Dermal scutes.

All the dermal scutes of Mandasuchus which have so far been discovered conform to the one general pattern already described. The scutes of Rauisuchus, on the other hand, are of several different types; none was found *in situ* on the neural spines of the vertebrae, and hence their arrangement in the living animal must remain a matter for conjecture. It should be noted, however, that the flattening and expansion of the tops of the neural spines should give some indication of the distribution of the plates. Rauisuchus differs from Mandasuchus in that there is no expansion of the tops of the neural spines in the neck region, and in the trunk they are thickened and expanded to an only moderate extent. Neural spines of the sacral vertebrae are preserved in neither animal, and in neither are those of the caudals expanded.

Some at least of the Rauisuchus plates appear to have been paramedian in position, for in one case fragments fit together to form a symmetrical complex which must almost certainly have lain in the mid-line, and in another case two plates which are mirror-images of each other are suturally united. Von Huene suggests that the latter are from the neck and the former from the tail. Another scute is supposed to be a paramedian dorsal from the trunk; this has a straight edge which is perpendicular to the outer surface, vertically grooved and much thickened below in the middle, and which is presumed to have lain in the mid-line. Whether or not these paramedian scutes agreed in number with the vertebrae is a question which cannot be resolved at present. The overall length of each scute always exceeds the length of a vertebral centrum of the region from which it is supposed to have been derived, the "caudal" scute being especially long; but von Huene assumes that each plate of Rauisuchus overlapped that which lay behind it. Thus the scutes may have equalled or even exceeded the vertebrae in number. In Mandasuchus, on the other hand, the scutes are sometimes shorter than the vertebrae, and they certainly overlapped each other considerably; they must therefore have been more numerous.

All these three types of plate described by von Huene - "cervical", "dorsal" and "caudal" - are longer than broad. In the "cervical" there is a light longitudinal ridge on the outer surface, in the "dorsal" there is no ridge, and in the "caudal" there is a high oblique elevation with its summit lying close behind the anterolateral corner; in the "cervical" and the "caudal" that portion of the plate which lies medial to the ridge or elevation is wider than that which lies lateral to it. In the "cervical" the whole outer surface is lightly arched in a transverse direction, sloping down laterally from the ridge; in the "dorsal" it is similarly arched downwards at the side. The "cervical" is wider behind than in front and has a rounded-off posterolateral corner; the "dorsal" plate is very slightly wider behind and has a broad and obliquely rounded-off posterolateral corner; the "caudal" is of more or less uniform width, with the posterolateral corner extended backwards to form a rounded acute angle and with the posterior border forming a "swallow-tail" with its fellow of the opposite side. The internal surface of the "dorsal" scute is described as being deeply concave in a longitudinal direction. The "cervical" and the "caudal" bear an anteriorly directed spine - in the "cervical" this seems to be a forward prolongation of the longitudinal ridge - which is perhaps more lateral in position than is the corresponding spine in Mandasuchus, for its lateral edge is continuous with the lateral edge of the main part of the scute; in the "dorsal" an anteriorly directed spine seems to have been broken off from near the anterolateral corner. No notch or excavation for the reception of the anteriorly directed spine of the next posterior plate is described in either the "cervical" or the "caudal"; on the inner side of the "dorsal" plate, however, a slight longitudinal deepening is present in the lateral part of the scute near its posterior edge and is deepest near that edge. The "cervical" is described as being without sculpture, showing only radiating fibres towards its edges. The twin "caudal" plates rest upon (and are grown together with) median rectangular plates which lie ventrally and show transverse fibrosity; von Huene suggests that this represents the transition from a double row of scutes on the trunk and proximal half of the tail to a single median row on the distal half of the latter, as in Saltoposuchus.

Other plates described are narrower and smaller than those mentioned above; they are from two to two and a half times as long as broad. One end is long and tapering, the other blunt. The outer side bears a keel-shaped elevation in the middle, often with a summit-point, and has radiating fibres towards its edges; the inner side is more or less flat or lightly arched and is free of ornament. Some of the plates are symmetrical; these have a median concavity at the blunt end which presumably overlapped the pointed end of the scute which followed. Von Huene suggests that these may be paramedian scutes from the anterior caudal region, despite the fact that they are much smaller than the plates from his supposed "transition region" (see preceding paragraph). The other scutes are slightly asymmetrical, and von Huene supposes that they may be derived from the animal's flanks - from the sides of the body or the sides of the tail, according to their size.

There is also a pair of very small, almost smooth, roughly oval scutes; these could be part of the armour of the limbs.

Our knowledge of the dermal armour of Rauisuchus is obviously very inadequate. The following paragraph nevertheless attempts to summarise such tentative conclusions as the comparison with Mandasuchus will at present allow.

The scutes of Mandasuchus and Rauisuchus resemble each other in that they are not transversely elongated; in that an external longitudinal keel is present (not always in Rauisuchus); in that there is usually an anteriorly directed spine; in that there is, on the underside of at least some of the plates, a depression for the reception of the anterior spine of the following scute; and in that the plates are devoid of any form of pitting or sculpture. On the other hand, only one general type of scute (paramedian dorsal) is known in Mandasuchus, while in Rauisuchus several different types are known, including some which were probably not paramedian in position; the lateral portion of the scute may be wider than the medial in Mandasuchus, in the ridged scutes of Rauisuchus the reverse holds true; the anterior spine is placed more laterally in Rauisuchus; and, while the tops of the neural spines in the neck region of Mandasuchus are much flattened and expanded for the support of the dermal scutes, in the neck of Rauisuchus there is no such flattening or expansion.

Summary.

Both the resemblances and the differences between the dermal armour of Mandasuchus and that of Rauisuchus have been summarised immediately above.

Other important similarities lie in the form of the teeth and of the dorsal vertebrae. The presence of a pre-neural spine in the distal caudals of both may not be particularly significant, for a similar structure has been reported in many reptiles, both archosaurs and others (as, for example, the protorosaurs Araeoscelis and Microcnemus, the pseudosuchians Prestosuchus, Stagonosuchus and Saltoposuchus, the marine crocodilian Geosaurus and the modern gavials). The bridge uniting the proximal ends of the two rami of each haemapophysis is likewise a fairly common structure. The girdle-bones of Mandasuchus and Rauisuchus are generally similar but nevertheless quite distinct; the limb-bones of the latter genus are so poorly known that valid comparisons cannot be made. On the other hand, there are certain striking differences in addition to those of the dermal armour. These concern the length of the cervical vertebrae (long in Mandasuchus, short in Rauisuchus), the absence (in Mandasuchus) and presence (in Rauisuchus) of a keel beneath those vertebrae, the form of the cervical neural spines, and the length and buttressing of the diapophysis in the anterior dorsals.

In those characters in which it differs from Mandasuchus (excepting the shortness of its neck and the presence of a keel beneath its cervical centra) Rauisuchus differs also from Prestosuchus. In addition, von Huene notes that reconstructions of the skulls of the two Brazilian reptiles appear to differ to a considerable extent, Prestosuchus being relatively irregular in its few positively known skull characters, and that the scapula is much stouter and relatively shorter in Prestosuchus. Thus it will be seen that the differences between Prestosuchus and Mandasuchus on one hand and Rauisuchus on the other are far greater than those between Prestosuchus and Mandasuchus. It would therefore seem that Rauisuchus, although more closely related to the other two genera than to the Stagonolepidae, should not be considered a member of the same narrowly defined family as Prestosuchus and Mandasuchus. Its systematic position must remain in doubt until better material of the genus is discovered; information concerning the arrangement of its several different types of dermal scute is particularly desirable.

A necessary consequence of the exclusion of Rauisuchus from the family which includes Prestosuchus and Mandasuchus is that the family cannot retain the name Rauisuchidae. It is proposed that the new family, defined below, be called the Prestosuchidae.

v) The new family Prestosuchidae

Definition.

Very large pseudosuchians in which the main part, if not all, of the dermal armour (other than abdominal ribs) consists of two paramedian dorsal rows of overlapping scutes resting upon the flattened and expanded tops of the neural spines; these latter are especially well developed in the neck and the anterior part of the trunk. The scutes are more numerous than the vertebrae. Each scute is approximately as broad as long and is divided externally by a longitudinal keel into a medial horizontal portion and a lateral portion which is inclined to the former at a considerable angle. The keel is produced forwards into a spine which lies beneath the next anterior scute, fitting into a depression in the inner surface of the hinder end of the latter. The weakly concave inner surface is smooth; the outer surface may be decorated with radiating fibres, but is otherwise free of pitting or sculpture.

Includes:
- Prestosuchus from the upper Rio do Rasto Beds of Brazil;
- Mandasuchus from the "Upper Bone Bed" of Tanganyika.

Other probable characters of the family include the following:

Dentition thecodont; teeth recurved, laterally compressed, anterior and posterior borders crenulated.

Vertebral centra generally lightly amphicoelous; floor of neural canal deeply concave within each centrum, except in posterior caudal region; tops of neural spines, especially in anterior part of column, flattened and expanded to bear dorsal scutes. About twenty-five pre-sacral vertebrae. Cervical vertebrae sometimes longer than dorsals. Dorsal vertebrae with typical archosaurian shift in position of rib-articulation; diapophysis supported by oblique radiating buttresses in anterior dorsals; parapophysis and diapophysis tend to form "spectacles"-shaped rib-articulation and then to fuse in posterior dorsals. Caudal vertebrae, except most anterior members, flattened or furrowed beneath and with haemapophyses; mid- and/or distal caudals with pre-neural spine.

Major limb-bones with hollow shafts; propodials longer than epipodials. Scapula broad both dorsally and ventrally, only moderately inflected; coracoid with small foramen. Humerus with high deltopectoral crest, supinator process and ectepicondylar groove. Acetabulum closed; ilium with short anterior spine and long posterior spine; pubis long, with small obturator foramen, twisted proximally in typical pseudosuchian manner, distally plate-like and directed steeply downwards, thickening of lateral corner of distal end; ischium also elongate, peduncle flattened laterally and with sharp anteroventral edge, distal end lightly thickened. Femur slightly sigmoidal, with prominent fourth trochanter high on shaft; fibula with anterior muscle-process; fibulare crocodiloid.

Although the definition of the family is based primarily upon the nature of the dermal armour, it must be extended to include certain archosaurs in which the dermal armour appears to have been lost but in which the anatomy of the internal skeleton seems to indicate a close relationship to Prestosuchus and to Mandasuchus.

Other material referred to the Prestosuchidae consists of two previously described genera, one probably with and one probably without dermal armour (see Sub-sections vi) and vii) below), together with certain unnamed specimens, some of which are new (see Chapters 5 and 6 below). All this material was also found either in the upper Rio do Rasto Beds of Brazil or in the "Upper Bone Bed" of Tanganyika. Both these strata are usually considered to be of Middle Triassic age, for which opinion further evidence will be adduced below (Chapter 8). The Prestosuchidae may therefore be described as characteristic of the Middle Triassic of Gondwanaland.

vi) Comparison with Stagonosuchus

Nowack's Ruhuhu collection of 1934-1936 included two specimens of a very large pseudosuchian from the "Upper Bone Bed". These remains, consisting of the post-frontal bone and much of the post-cranial skeleton, were described by von HUENE (1938a) as Stagonosuchus nyassicus. To the same species he also referred (1939b) the distal ends of two humeri, described by HAUGHTON (1932) as "Stenaulorhynchus major".

BOONSTRA (1953) claims that a single humerus collected in the Ruhuhu by Stockley represents a new species of this genus, S. tanganyikaensis. This bone is much smaller than the humerus described by von Huene and differs slightly in details of form and proportion.

Von HUENE (1939b) has also suggested that the pseudosuchian skull fragment erroneously described by

HAUGHTON (1932) as "*Stenaulorhynchus stockleyi*" may also have belonged to *Stagonosuchus*. Presumably this suggestion is based only on the great size of the fragment.

Stagonosuchus is one of the only two genera of pseudosuchian already described from the "Upper Bone Bed"; indeed, it is the only genus which is fairly well known. Because of this, and because of certain apparent similarities to *Mandasuchus*, it has been compared with the latter in detail.

Vertebral column.

Like *Mandasuchus*, *Stagonosuchus* has lightly amphicoelous centra with the floor of the neural canal greatly deepened within each. The most striking differences between the vertebrae of the two genera are those which could perhaps be attributed to their disparity in size. In the much larger *Stagonosuchus* the centra are comparatively stouter, most of them being higher than long, and the neural canal is relatively smaller; they also possess larger facets for the articulation of the ribs, especially in the anterior dorsal region, where these facets are enormous.

Cervical region.

The cervical vertebrae are much longer than the dorsals in both animals; this elongation is not immediately apparent in the case of Stagonosuchus because of the altogether stouter and higher build of all the vertebrae. In Mandasuchus the longest vertebra is the fifth cervical, in Stagonosuchus the supposed fourth.

In Mandasuchus the axis is a little shorter than the anterior dorsals, in Stagonosuchus it is not so; but in both reptiles it has a high ventromedial keel. The axis of Mandasuchus lacks the deep lateral hollows possessed by that of Stagonosuchus, and the respective neural spines appear to be rather different.

In both genera the only other cervical vertebra to bear a ventromedial keel is the third; and in both genera this vertebra has the additional peculiarity of a muscle-process projecting backwards over each postzygapophysial facet. The more posterior cervicals resemble each other in having strongly constricted centra which are either rounded beneath or with but the faintest indication of a median ridge. One difference, however, lies in the fact that Mandasuchus has no intercentra after that of the axis, while in Stagonosuchus the third, probable fourth and probable fifth cervical centra (but not subsequent pre-sacrals) appear to have facets for intercentra below their posterior faces.

Dorsal region.

Von Huene's "posterior cervical" of Stagonosuchus compares most closely with the first dorsal of Mandasuchus. Both vertebrae are considerably shorter than the corresponding mid-cervicals. The parapophysis is situated low down on the anterior edge of the centrum, although no longer quite ventrally, and the diapophysis is directed a little downwards. The diapophysial buttresses are well developed; the anterodorsal buttress continues to the end of the prezygapophysis as a projecting ridge; and there are deep anterior and inferior pleural concavities.

Subsequent dorsals differ in Stagonosuchus, as mentioned above, in their enormous para- and diapophysial facets. The parapophysis is situated halfway up the side of the centrum, while the diapophysis stands high above the latter. In both animals the buttresses and pleural concavities are well developed; the anterodorsal buttress continues to the end of the prezygapophysis, and the anterior pleural concavity is broad.

In a yet more posterior vertebra of Stagonosuchus the parapophysis is still at the front edge of the centrum but is dorsal in position; the rib-facets are no longer so large, and the diapophysial facet is inclined less steeply than in the more anterior part of the column. In what seems to be a corresponding vertebra of <u>Mandasuchus</u> the buttresses are still quite powerfully developed; in this vertebra they are not.

Vertebrae from the middle of the back resemble each other closely in the two reptiles, except in those general features mentioned above. The parapophysis lies almost as high as the diapophysis and the prezygapophysis, being connected to the former by a short and thin anteroventral lamella. The upper ends of the neural spines are thickened in <u>Stagonosuchus</u> and each bears a longitudinal groove above; this probably indicates that dermal scutes were present along the middle of the animal's back. The hollowings in the sides of the more posterior vertebrae of this region are situated higher in <u>Mandasuchus</u> than in <u>Stagonosuchus</u>.

In the hinder part of the trunk the neural spines of <u>Stagonosuchus</u> differ from those of <u>Mandasuchus</u> in being much thickened above. Their dorsal surfaces are concave.

<u>Sacrum</u>.

The only preserved sacral vertebra of <u>Mandasuchus</u>, the supposed second, is best compared with the second sacral of Stagonosuchus. Both centra are almost amphiplatyan. The base of the sacral rib, around which there is a swelling, begins half-way up the side of the centrum; the rib incorporates almost the whole length of the centrum and is tilted forwards and downwards. The upper surface of the rib is almost horizontal at the height of the neural canal and is directed backwards (less strongly so in Mandasuchus than in Stagonosuchus). The neural spine seems to have been relatively thinner in Mandasuchus.

Caudal region.

The caudal vertebrae of the two animals are generally similar, except in that their centra appear to be relatively shorter in Stagonosuchus. In Mandasuchus the centra of the supposed first two caudals are rounded below, those of the supposed third and fourth are flattened (the latter with the barest indication of a furrow), and the fifth and subsequent centra bear a longitudinal furrow posteriorly; in Stagonosuchus the first two centra are similarly rounded, the third is flattened with a very light furrow, and the fourth and following centra bear a broad furrow. Facets for the haemapophyses probably begin with the fourth caudal in Mandasuchus, with the third in Stagonosuchus (where there may even be slight indications of these facets on the second). The transverse processes turn obliquely backwards in both animals, being broadest in the first caudal; in Mandasuchus there are very faint indications of the ventral buttresses on the supposed first caudal only, in Stagonosuchus these indications are present on the second caudal also and, to a smaller extent, on the third. There is a hollow beneath the transverse process of the supposed first caudal in Mandasuchus, and a trace of the same in the second; in Stagonosuchus the hollowing is deep, of a rather different shape, and is present in the first caudal only. The neural spines are inclined slightly backwards in both animals.

One preserved distal caudal of Mandasuchus (specimen no. 63) bears a pre-neural spine; this vertebra has no transverse process. The isolated neural arch of a middle caudal of Stagonosuchus, still bearing a small transverse process, has a similar but more powerful pre-neural spine.

Pectoral girdle.

The scapula and coracoid of Stagonosuchus are so badly preserved that they are useless for comparative purposes.

Fore-limb.

Humerus.

There is a great resemblance between the genera. The humerus of Mandasuchus, however, is relatively longer and more slender than that of Stagonosuchus, and the degree of torsion between the ends may be a little less. Features common to both humeri include: a deltopectoral crest with its apex lying nearly as high as the caput; a supinator process and an ectepicondylar groove of remarkably similar form; a continuation of the distal articulating surface on to the pre-axial surface of the ectepicondyle; a semicircular deepening in the middle of the anteroventral side of the distal end; and a similar deepening on the posterodorsal side, less sharply defined and reaching further proximally.

Radius.

A small fragment of Stagonosuchus is described as being either the distal end of the right radius or the proximal end of the left. In fact it is like neither of the supposed ends of the radius of Mandasuchus, for its end-surface stands obliquely inclined to its longitudinal axis and is irregularly crescentic in form. Further, the shaft bears two longitudinal hollows near its end, one deep and the other shallower;

neither of these is present in _Mandasuchus_.

Pelvic girdle.

Ilium.

Here there is a great similarity. The long and powerful posterior spine, bearing the medial crest on its inner surface, is relatively a little longer in _Mandasuchus_.

Pubis.

There is again a strong resemblance extending to almost every detail. The _Stagonosuchus_ pubis is long, narrow and plate-like, forming but a small part of the acetabular surface; a small oval obturator foramen lies near the proximal end; the thick lateral edge becomes thicker distally and terminates in a club-shaped swelling beneath the plate; the thin medial edge bears a somewhat thicker contact-surface for the other pubis just before the distal end; and the distal end-surface is convexly rounded. The only apparent differences between the two animals lie in the curvature of the bone. The torsion at the neck of the pubis seems to be greater in _Mandasuchus_. Viewed from the side, the pubis of _Mandasuchus_ is seen to be curved in a regular manner, the plate becoming directed gradually more and more ventrally towards its distal end; that of Stagonosuchus is curved irregularly, for it is bent downwards fairly strongly near its proximal end, is then straight for some distance, and finally bends a little upwards. Viewed from above or below, the outer border of the pubis appears concave in Mandasuchus, being furthest from the mid-line proximally and then converging towards it to run parallel to it in its distal part; in Stagonosuchus, on the other hand, the outer margin is more or less straight.

Ischium.

The general likeness is somewhat obscured by the fact that the outline of the bone is a little more rounded in Mandasuchus and more angular in Stagonosuchus. For example, the acetabular border forms a smooth curve in Mandasuchus, while in Stagonosuchus it contains a fairly sharp angle of about 105 degrees. In almost every other respect the two ischia are alike; each bears a more substantial part of the acetabular surface than does the pubis; and each has a long peduncle, which is thick posterodorsally, narrows to a sharp keel anteroventrally, and is thickened at its distal end. However, Mandasuchus shows no trace of the deep groove which in Stagonosuchus runs along the posterodorsal edge of the peduncle, in the possession of which it resembles Prestosuchus and the Triassic pachypodosaurs; nor is there any trace of the small muscle-scar which in Stagonosuchus lies anteriorly on the lateral face of the peduncle, just behind and below the proximal expansion. (It must be admitted that no ischium of Mandasuchus is well preserved in this region). The existence of a median symphysis between the two ischia is not in doubt in Stagonosuchus, for in one specimen the two bones are preserved in their natural juxtaposition.

Hind-limb.

Tibia.

The proximal end of the tibia of Stagonosuchus, all that is preserved of this bone, is completely different from that of any other known Thecodont (including Mandasuchus); and, according to von Huene, shows a striking accord with the tibia of the Upper Cretaceous titanosaurs. The proximal articulating surface of the Stagonosuchus fragment is quite flat and lies very obliquely to the longitudinal axis of the bone, being higher in front than behind; the anteromedial corner of the head is produced into an anteriorly directed ridge which extends down the head as far as the beginning of the shaft, a groove running lateral to it. The whole tibial head projects strongly anteriorly, while in Mandasuchus it projects posteromedially.

Dermal scutes.

Dorsal scutes, present in Mandasuchus, have not been found in Stagonosuchus. The expanded nature of the apices of some of its neural spines might nevertheless indicate that such scutes were also present in the latter genus.

Summary.

Stagonosuchus is much larger than Mandasuchus and its vertebrae and limb-bones are relatively shorter and stouter. The inferred presence of cervical intercentra in Stagonosuchus is another noteworthy difference. But, if the extraordinary fragments which von Huene ascribed to the radius and the tibia of his animal be set aside, - and they are indeed puzzling, - then it is true that the rest of the skeleton shows a striking similarity to that of Mandasuchus. Vertebral column, humerus and pelvis agree in detail as well as in general form. In the vertebral column the following common peculiarities may be instanced:

i) Elongation of the cervicals.

ii) Presence of a ventromedial keel in the axis and following vertebra, but not in the others.

iii) Presence of a muscle-process above the post-zygapophysis of the third cervical.

iv) Beginning of ventral furrows and haemapophysial facets at approximately the same positions in the tails of the two animals.

v) Presence of a pre-neural spine in the mid- and/or distal caudals.

Thus, from the nature of the post-cranial endoskeleton, it cannot be doubted that there is a close relationship between the two genera, and henceforth also between _Stagonosuchus_ and the South American _Prestosuchus_. This is in accordance with the findings of von Huene, who concluded that _Stagonosuchus_ was "ein ostafrikanischer Stagonolepide aus nächster Verwandtschaft der gleichaltrigen südamerikanischen Rauisuchinae, doch grösser als diese und im einzelnen abweichend". But, if _Prestosuchus_ and _Mandasuchus_ are no longer to be considered as members of the Stagonolepidae, then neither is _Stagonosuchus_; it may be placed with the former genera in the new family Prestosuchidae. The diagnostic feature of that family, the dermal armour, is unknown in _Stagonosuchus_, but its presence may be inferred with confidence. The peculiar radius and tibia may denote some particular specialisation in the animal's mode of life.

vii) Comparison with Spondylosoma and with other supposed saurischian remains from Brazil

Spondylosoma absconditum von HUENE (1935-1942) is a supposed saurischian from the upper Rio do Rasto Beds of Brazil. Mandasuchus, although a pseudosuchian, seems to resemble Spondylosoma very closely; a detailed comparison of the two genera has therefore been made. (See also Plates 51-53).

The Spondylosoma material discovered consists only of two teeth, nine vertebrae, complementary portions of two scapulae, the proximal parts of a humerus and a pubis, and the distal end of a femur; the distal end of a radius may also belong to this genus. Several individuals are represented even among this small quantity of material, for one tooth and one vertebra were found in localities separate from each other and from that in which the rest of the bones were found; while even the major find comprises vertebrae which are not of commensurate size. Von Huene has no proof that the girdle- and limb-bones are correctly associated with the eight vertebrae, but considers it probable on grounds of propinquity, absence of other fossils (except for Stahleckeria and one cynodont canine tooth), size, and manner of preservation.

The anterior half of a cervical centrum and a supposed tibia without a distal end, found in the same beds and described in the same section, are merely referred to "Saurischier".

Size.

The Spondylosoma material is derived from individuals which are of about the same size as the Mandasuchus type-specimen (no. 11b), and which must therefore be much smaller than the largest Mandasuchus (specimen no. 63).

Teeth.

The teeth of Spondylosoma, like those of Mandasuchus, are laterally compressed so that the base is oval in section. The lightly recurved crown tapers regularly to a point, and its sharp anterior and posterior borders bear "Palisadenkerbung" - rectangular crenulations.

Vertebral column.

Cervical and anterior dorsal region. (Plate 51).

In the form and position of their rib-facets and supporting buttresses, the two "cervical" vertebrae of Spondylosoma (according to von Huene, a posterior cervical and the probable penultimate) correspond most closely with the last cervical vertebra and the first dorsal of Mandasuchus; they will therefore be compared with these. (It is difficult to determine whether the Spondylosoma vertebrae are consecutive or not; the zygapophyses do not fit together properly, but a certain amount of distortion may have taken place). The following characters are common to both pairs of vertebrae. The parapophysis is borne at the anteroventral corner of the centrum, and the downwardly directed diapophysis is borne entirely on the neural arch; the diapophysial buttresses and the pleural concavities (except the superior) are moderately well developed. (In the cervical vertebrae of Mandasuchus, except the last, they are not developed at all). The anteroventral lamella runs towards the anterior border of the centrum and does not connect with the parapophysis. In the anterior vertebra of each pair the anterodorsal buttress runs only to the root of the prezygapophysis, in the posterior vertebra almost to its end. The vertebrae are also alike in more general characters; in both genera the centra are strongly constricted, rounded beneath (in Spondylosoma there is a very faint short median ridge at the front end of each centrum) and weakly amphicoelous, and the zygapophyses are very similar.

There is a marked difference, however, in the degree of elongation of the centra in these two pairs of vertebrae. The following figures are the ratios of the length of each centrum to its mean diameter, those for specimen no. 11b being only very approximate because of the poor preservation of these particular vertebrae in that individual:

		anterior vertebra (Ce8?)	posterior vertebra (D1?)
Mandasuchus	type-specimen (no. 11b)	1.46	1.21
	specimen no. 13	1.33	1.11
Spondylosoma		2.05	1.70

It is apparent that these vertebrae are very much more elongated in _Spondylosoma_ than in either of the East African specimens. This need not indicate a greater elongation of the neck region relative to other parts of the body, for the vertebrae from other regions of the column are also longer and more slender in _Spondylosoma_ than in _Mandasuchus_. In this connexion it will be relevant to compare the length of each centrum with that of a typical dorsal centrum from the same (in _Spondylosoma_, probably the same) animal:

	anterior vertebra (Ce8?)	posterior vertebra (D1?)
Mandasuchus type-specimen (no. 11b)	1.21	1.00
Spondylosoma	1.37	1.24

From this it would appear that, even allowing for the generally more slender nature of Spondylosoma, the vertebrae of this region are more elongated in that animal than in Mandasuchus; this is presumably for incorporation in a longer functional neck.

It should be remembered that other cervical vertebrae of Mandasuchus, anterior to those under discussion, are elongated to a much greater degree; they are up to one and a half times as long as a typical dorsal.

Another difference between the genera lies in the form of the neural spines of these vertebrae; although just as long antero-posteriorly, those of Spondylosoma are relatively much higher and more slender than those of Mandasuchus and lack the flattened and expanded tops. The top is somewhat thickened, however, especially its front part in the spine of the posterior vertebra.

Dorsal region.

Four dorsal vertebrae of _Spondylosoma_ are available for study. Von Huene describes them as the "probable first" (the isolated vertebra), an "anterior", a "middle" and a "posterior" dorsal. Their centra are constricted and weakly amphicoelous, those of the "first" and "posterior" vertebrae being very lightly saddle-shaped behind; their sides are hollowed out at the base of the neural arch.

The supposed first dorsal vertebra compares best with the third dorsal of _Mandasuchus_; it is, however, badly preserved. The elongation ratio of the centrum is greater than in the _Mandasuchus_ vertebra (_Mandasuchus_ specimen no. 13 - 1.12, _Spondylosoma_ - 1.39), and the centrum differs also in that it is weakly keeled. In both vertebrae the large parapophysis lies with its upper border just below the level of the threshold of the neural canal; and the powerful diapophysis, projecting almost horizontally, is broken off to show a quadrangular transverse section. All four supporting buttresses are present, the two ventral being short; the anterior, posterior and inferior pleural concavities are deep. Other differences lie in the facts that the postzygapophyses do not project behind the centrum of the _Spondylosoma_ vertebra, and that the base of the neural spine is axially shorter in the latter.

The "anterior" dorsal vertebra of Spondylosoma is badly preserved, with the transverse processes and the neural spine entirely lacking. The prezygapophyses are very small and the inward inclination of their facets is only slight. They project but very little in front of the centrum; the postzygapophyses, on the other hand, project behind for a considerable distance.

The "middle" dorsal vertebra of Spondylosoma consists only of a badly preserved centrum.

The "posterior" dorsal vertebra is well preserved and compares closely with the middle dorsals of Mandasuchus, exactly with none but perhaps best with the supposed eleventh. The Spondylosoma vertebra is a little more elongated and the hollowing at the base of the neural arch is not so well marked. In both genera the para- and diapophysis are borne upon the neural arch and each bears a roughly oval facet; the diapophysis projects further than the parapophysis and is connected to it by a short anteroventral lamella. (Von Huene notes that the transverse process of the Spondylosoma vertebra is strongly reminiscent of that of the posterior dorsals of Rauisuchus). Posteroventral and posterodorsal buttresses are also present in both reptiles, but there is no trace of an anterodorsal buttress. The anterior pleural concavity appears in neither vertebra; the posterior and inferior pleural concavities, on the other hand, are present in both, the latter well developed. The pit-like superior pleural concavity, present in all the Mandasuchus vertebrae of this region, is absent in the Spondylosoma vertebra. The prezygapophyses of the latter incline only slightly inwards and do not project in front of the centrum (in Mandasuchus they do project); they are rounded beneath and there is a gap between them. In both genera a weak hyposphene lies beneath the post-zygapophyses (this cannot be seen in the supposed eleventh dorsal of Mandasuchus, perhaps because of poor preservation, but is shown particularly well by the supposed thirteenth dorsal); and this, together with the postzygapophyses, projects behind the centrum. From the tip of the hyposphene horizontal ridges run forwards to the roof and side-walls of the neural canal; these diverge anteriorly in Spondylosoma and probably did likewise in the less well preserved supposed thirteenth dorsal of Mandasuchus. The neural spine appears to have been similar in the two animals, with a perpendicular anterior edge; that of the Brazilian vertebra is broken off near its base.

Sacrum. (Plate 53).

The Spondylosoma material includes three sacral vertebrae. Von Huene takes one of these to be a first sacral; he assumes another to be the second sacral of the same individual, for, although markedly different in form, it is of much the same size as the first and the two fit well together. The other vertebra must come from a smaller animal because of its size and more slender build; it resembles the large second and could conceivably be another second sacral, but there are small differences and von Huene thinks it more likely to be a third.

The Mandasuchus material, on the other hand, includes only one sacral vertebra. A broad comparison with Spondylosoma (see Chapter 3, Section a), Sub-section ii) above) shows that this is probably the second of two. Under these circumstances, detailed comparison of the sacral vertebra of Mandasuchus with those of Spondylosoma will be restricted to the second and supposed third sacral vertebrae of the latter animal.

The centra of the sacral vertebrae of Spondylosoma are a little longer and more constricted than that of the sacral of Mandasuchus, but resemble it in being rounded beneath. Their articulating faces are slightly concave (the posterior face of the second appears to be deeply so, but this could well be artificial); the Mandasuchus centrum is almost amphiplatyan. In all three vertebrae the rib is attached to the upper part of the centrum and the neural arch (a little higher in Mandasuchus than in the Brazilian animal) and occupies about three-quarters of the length of the centrum, lying nearer to its anterior end. It is bordered below by a slightly swollen suture, which, in Spondylosoma, converges forwards towards the mid-line. In the second sacral of Spondylosoma there are, beneath this swollen suture, two concavities on either side; the hinder of each pair is much the larger. Such hollows are very weakly developed in the supposed third sacral and virtually absent in Mandasuchus. In all three vertebrae the base of the rib projects more or less horizontally; its strongly built ventral portion is directed obliquely forwards (less so in the second sacral of Spondylosoma than in the other two vertebrae) and the dorsal portion forms a long narrow plate which turns obliquely backwards at an angle of some 20 to 30 degrees to the transverse plane. This dorsal part is relatively more powerful in the supposed third than in the second sacral of

Spondylosoma, and in Mandasuchus is thinner and nearly twice as broad as in either of the Brazilian vertebrae. The two parts of the sacral rib are in virtual juxtaposition in Mandasuchus, rather further apart in the supposed third sacral of Spondylosoma, and widely separated in the second sacral of that animal; there is an oblique bony connexion between them, broad enough to assume the form of a thick lamella in the last vertebra mentioned. In the supposed third sacral of Spondylosoma, just as in the Mandasuchus vertebra, the sharp anterior border of the dorsal part of the rib curves round towards the root of the prezygapophysis, and there is a hollow beneath it; in the second sacral of Spondylosoma the rib has no form of connexion with the prezygapophysis. There is also, in the supposed third sacral of Spondylosoma (and to a lesser extent in the second) a hollow underlying the dorsal part of the rib posteriorly; the Mandasuchus vertebra is not well enough preserved to show this feature, but it does not seem likely that it was present.

According to von Huene (op. cit., pp. 251-252), "Diese Art von Sacralrippen stimmt mit primitivem Saurischiern überein und unterscheidet sich grundsätzlich von Thecodontiern, bei denen die erste Sacralrippe nach vorn, die zweite nach rückwärts gerichtet ist und beide auch oben sich distal sehr breit pilzförmig ausdehnen."

The prezygapophyses are badly preserved in the Mandasuchus sacral, but they seem to have been far more widely separated from each other than is the case in either Spondylosoma vertebra. There was certainly a wide basin between them, as in the other reptile, and they certainly projected forwards beyond the centrum. The postzygapophyses are broken off in Mandasuchus, but it seems probable that, like those of the second sacral of Spondylosoma, they did not project behind the centrum. The neural spine is broken off in the Mandasuchus vertebra and in the supposed third sacral vertebra of Spondylosoma; it would appear that in both Spondylosoma vertebrae the spine extended further forwards (almost reaching the level of the front of the centrum in the second sacral) and was considerably stouter than in Mandasuchus.

Scapula. (Plate 52).

The scapulae of Mandasuchus and of Spondylosoma are very similar. That of Spondylosoma is of about the same size and massiveness as that of the type-specimen of Mandasuchus (no. 11b), but it is decidedly more slender, being only approximately two-thirds as wide at corresponding points. The _Spondylosoma_ scapula is also slightly less inflected in the transverse plane than is that of the East African animal; and the inflexion takes place by a gradual curvature rather than, as in _Mandasuchus_, by a fairly sharp bend in the scapula at a distance from the glenoid fossa equal to about a quarter of its own length. The upper end of the scapula appears to have been bent backwards rather less in _Spondylosoma_, and the muscle-process on the posterolateral edge of the bone, just above the glenoid, was either absent or (as the condition of the surface seems to indicate) has been broken off in preparation.

Von Huene writes of the _Spondylosoma_ scapula (op. cit., p. 254), "Diese Scapulagestalt......ist leicht mit Saurischiern, kaum mit Pseudosuchiern in Einklang zu bringen."

Humerus.

The proximal end of the humerus which von Huene refers to _Spondylosoma_ is badly weathered and scarcely merits description; von Huene remarks that it recalls that of _Procerosuchus_, though clearly distinct therefrom. Its actual outline is very different from that of the head of the Mandasuchus humerus, but it could well have resembled it closely before weathering; there is no positive feature to suggest that the two bones differed much. In both genera the deltopectoral crest lies at the same angle to the proximal expansion, and in both the margins of the deltopectoral crest and of the processus latissimi dorsi are inclined at the same angle to the axis of the shaft. Most important of all, the Spondylosoma humerus shows the high position of this broad deltopectoral crest, in which respect it resembles Mandasuchus and other pseudosuchians and differs from all other known saurischians.

The shafts of the humeri, like those of the other major limb-bones of both genera, are hollow and thin-walled.

Pubis. (Plate 51).

The pubes of Mandasuchus and Spondylosoma are remarkably alike. That of Spondylosoma is somewhat more robust; unfortunately it is incomplete, for only the proximal part is preserved (probably rather more than half), and the surface of the proximal end is badly weathered. In both animals the acetabular region is expanded in the parasagittal plane; and its posteroventral extension, which presumably bore the ischiadic articulating surface, is broken off. Just in front of this break is the obturator foramen; the fragile plate of bone which bordered it ventrally is also broken away in every case. At a distance from the proximal end of about one-quarter the length of the whole bone the plane of its greatest extension is suddenly twisted from parasagittal to horizontal (that is, horizontal if the downwardly directed natural orientation of the pubis be neglected), the sharp ventral edge turning obliquely inwards and upwards towards its fellow. Beyond the point of torsion the two pubes differ slightly. That of Spondylosoma consists essentially of a flat plate, thickened laterally and becoming thinner medially, and with the thickened lateral margin produced into a strong downwardly projecting ridge; thus the posterior broken surface presents an L-shaped section, the under-surface of the pubic blade is transversely concave, and it has a right-angled dorsolateral edge. This ridge, and therefore also the concavity and the right-angled edge, are much less developed in Mandasuchus. The two prominent muscle-processes on the lateral surface of the proximal part of the bone are also much less developed in Mandasuchus than in Spondylosoma.

Von Huene believed that the upper part of the proximal end of the Spondylosoma pubis, including its thickest portion, served for articulation with the ilium; this cannot be doubted. The lowermost portion of the end is clearly broken off and it must also be true that the pubis extended further in a posteroventral direction to meet the ischium. Between these two parts lies a section of the end which von Huene thought to be a natural surface and which, according to him, must therefore form part of the sub-acetabular surface; that is, the acetabulum was perforated. The writer cannot agree that this section shows a true unweathered surface; laterally it may be natural, but medially it is definitely weathered. Even if the lateral side is natural, this region could have formed part of the acetabulum as in Mandasuchus, where a sector of the acetabular surface is clearly defined on the proximal end of the pubis in a precisely corresponding position. The important question is: did the articulating surface for the ilium extend down the medial side of this portion to meet that for the ischium (as in Mandasuchus) or was the whole width of the portion free of any articulation whatsoever? If the former, then the acetabulum was closed; if the latter, then it was open. The weathered condition of the surface does not allow of any definite conclusion on this point, but the great resemblance of the *Spondylosoma* pubis to that of *Mandasuchus* in almost every other essential, as indeed of the whole skeleton, must indicate the probability that it also resembled it in this; in other words, that the acetabulum was closed.

Femur.

The distal end of the femur of *Spondylosoma* does not differ significantly from that of *Mandasuchus*. (Unfortunately the distal ends of both femora of the *Mandasuchus* type-specimen are corroded or incompletely ossified). In *Spondylosoma*, however, there is a slight longitudinal hollowing on the outer side of the fibular condyle, absent in *Mandasuchus*, and the inter-condylar groove on the posterior surface is better developed. Both bones have hollow shafts, that of *Spondylosoma* being a little more slender at a comparable distance from the end.

Dermal scutes.

Dorsal scutes, present in *Mandasuchus*, have not been found in *Spondylosoma*, where their absence would appear to be confirmed by the lack of flattening and expansion of the tops of the neural spines.

Radius of (?)Spondylosoma.

A small, badly preserved and rather featureless fragment was described by von Huene as the distal end of a radius, probably belonging to Spondylosoma. The end-surface is flattened, but its outline is much more elongate than that of the presumed distal end of the supposed Mandasuchus radius. It does not come from the same excavation as the Spondylosoma type-material; moreover, it is too small to have belonged to such a large animal.

Cervical vertebra of "saurischian".

This fragment, from yet another excavation, is the anterior half of the centrum of a cervical vertebra. It was referred by von Huene to a saurischian - probably a coelurosaur, perhaps an animal similar to Spondylosoma in general form - because of its obviously elongated nature. It comes from an animal larger than Spondylosoma and of about the same size as the largest specimen of Mandasuchus (no. 63). In actual fact it compares quite closely with the fourth or fifth cervical of the latter animal. The centrum is constricted below and its anterior face is moderately concave. There is a slight but well defined ventromedial ridge (very faint in Mandasuchus), on either side of which lies a large parapophysis at the anteroventral corner of the centrum. The ventral surface of the centrum is lightly concave between the ridge and the parapophysis.

"Tibia of saurischian". (Plate 52).

Von Huene described a small bone as a tibia without a distal end, very probably belonging to a saurischian much smaller than Spondylosoma; he noted that it resembled the tibia of a coelurosaur particularly closely, and was broader and more differentiated than that of a Thecodont. It was from the same excavation as the cervical vertebra mentioned above.

This bone is quite unlike the tibia of Mandasuchus; but the form of its proximal end is virtually indistinguishable, in every detail, from that of the supposed "proximal end of the ulna" of the Mandasuchus type-specimen, no. 11b. (This latter is a little larger; it is not certain that it is indeed the ulna of the type-specimen - see description in Chapter 3 above, - but it is much too small to be part of the tibia, which is already present and is of a totally different shape. On the other hand, it is possible that this supposed Mandasuchus ulna is in fact the proximal end of the tibia of the much smaller pseudosuchian specimen no. 11a). The supposed ulna of the smallest specimen of *Mandasuchus* (no. 13) is rather similar to that of the type-specimen, but does differ in certain respects. It differs from the Brazilian "tibia" in the same way as from the type-specimen; also in that the shaft (which is not preserved in the type-specimen) is flattened and lightly grooved on both sides. The shaft of the Brazilian bone is neither flattened nor grooved and bears a small muscle-process on the side which von Huene calls posterior. All these bones have thin walls.

The systematic position of *Spondylosoma*.

Spondylosoma has always been described as a saurischian; von HUENE (1939c) placed the genus in the Coelurosauria, albeit tentatively, while ROMER (1945) assigned it to the Prosauropoda as a member of the family Thecodontosauridae. The vertebrae do indeed resemble those of prosauropods. But the individual bones of *Spondylosoma* have now been compared in detail with those of *Mandasuchus*, a genus which is quite clearly a pseudosuchian; a striking resemblance between the genera has been established in every case, and there can be no reasonable doubt that they are closely related.

These facts appear less inconsistent if it be remembered that Mandasuchus may be considered as "an advanced pseudosuchian whose form shows certain saurischian trends" (p. 218 above). It is now suggested that, in fact, both Mandasuchus and Spondylosoma represent a grade of evolution intermediate between Pseudosuchia and Saurischia, for each shows a combination of the characters of the two groups. Mandasuchus is nearer than Spondylosoma to other known pseudosuchians and is therefore more primitive, while Spondylosoma is nearer to the saurischians and is therefore more advanced.

The only "pseudosuchian" characters retained by Spondylosoma are (probably) the closed acetabulum and, on the humerus, the high position of the apex of the deltopectoral crest. Characters in which the genus differs from Mandasuchus and which indicate a closer relationship to the saurischians are:

i) The greater elongation of the neck, probably including more vertebrae.

ii) The probable incorporation of a third vertebra in the sacrum.

iii) The more slender and slightly less inflected form of the scapula.

iv) The probable absence of dermal armour, as shown by the form of the neural spines.

An interesting similarity of rather doubtful significance is the presence of a hyposphene in the dorsal vertebrae of both genera.

The fact remains that the distinction between the Pseudosuchia and the Saurischia is based, quite arbitrarily, upon the nature of the acetabulum. If this distinction be maintained, then Mandasuchus, which has an imperforate acetabulum, is a pseudosuchian. The condition in the Spondylosoma pelvis, and hence the systematic position of the reptile, cannot be determined conclusively because of the incomplete nature of the remains. A fenestrated acetabulum might be expected in Spondylosoma because of the rather more advanced character of the skeleton; von Huene thought that a perforation was indicated by the shape of the proximal end of the pubis (see above). But a comparison of the pubes of Mandasuchus and Spondylosoma shows neither any essential difference between them nor, in the case of Spondylosoma, any real evidence for von Huene's previous belief in the presence of an acetabular fenestration. Because of the great similarity of the two pubes it seems highly probable, though not absolutely certain, that the acetabulum of Spondylosoma was closed, and that the animal should therefore be considered as a pseudosuchian. Further, in view of the great similarity in the whole osteology of Mandasuchus and Spondylosoma (as far as they are known), it seems desirable to include the latter in the same family of the Pseudosuchia as the former - the Prestosuchidae - despite its apparent lack of the diagnostic feature of that family, the dermal armour. It may best be regarded as an advanced member of the family which, tending rather more than Mandasuchus towards the Saurischia, seems to have acquired an even longer neck and to have lost its armour entirely.

The Prestosuchidae appear to form an evolutionary series leading from the Pseudosuchia to the Saurischia through forms like Mandasuchus and Spondylosoma. The question of which particular saurischians are most directly concerned is considered in the following Sub-section.

The systematic position of the other "saurischian" material from Brazil.

It should be noted that, apart from Spondylosoma, the only material from the upper Rio do Rasto Beds which has been ascribed to the Saurischia (namely, the cervical vertebra and the "tibia") compares well with _Mandasuchus_ and could be derived from related pseudosuchians.

viii) The Prestosuchidae and the Saurischia

It has already been shown that the Prestosuchidae, although pseudosuchians, resemble the saurischians in several respects; their more important differences and resemblances have been enumerated above (see Sub-sections i) and vii) of this Section). It is also apparent that _Prestosuchus_, _Mandasuchus_ and _Spondylosoma_ form an evolutionary series connecting the typical Pseudosuchia with the Saurischia. The Saurischia of the Upper Trias are numerous and varied, although remains which can be referred to that order with certainty have not been found in older beds. It might therefore be relevant to enquire whether the Prestosuchidae give indications of differentiation towards any particular group of these Upper Triassic Saurischia.

The saurischians of the Upper Trias - indeed, all saurischians - are clearly divisible into two great sub-orders. These are the comparatively small and lightly built coelurosaurs and the generally much larger and heavier pachypodosaurs. The pachypodosaurs of the Trias include the carnosaurs and the prosauropods; the carnosaurs, like the coelurosaurs, survived throughout the Mesozoic, while the prosauropods did not continue as such beyond the Trias but gave rise to the gigantic sauropods of the Jurassic and Cretaceous (in contrast to which all other saurischians are sometimes classified as "theropods"). The anatomical features characteristic of these various taxonomic groupings have been listed by von HUENE (1932, 1948).

In their tendency towards large size, in the serrated nature of their teeth, and in the detailed osteology of their vertebrae, girdles and limbs - in the short anterior spine of the ilium, for example, - the Prestosuchidae resemble the pachypodosaurs rather than the coelurosaurs; and of the pachypodosaurs they resemble the prosauropods rather than the carnosaurs. The prosauropods include four families. Only two of these, the Thecodontosauridae and the Plateosauridae, merit special attention, for they occur throughout the Upper Trias and are fairly widely distributed; the other two, the Plateosauravidae and the Melanorosauridae, are confined to the uppermost Trias of South Africa and are less primitive in form, the latter family probably being the point of origin of the sauropods. Von HUENE (1907-1908) gives an excellent description of the characters of the Plateosauridae, detailed yet concise (although at that time no genus was known other than Plateosaurus itself); a great number of these characters, too numerous to mention individually, are also typical of the Prestosuchidae.

In the same publication von Huene proceeds to list the differences between the Plateosauridae and the Thecodontosauridae. Most of these are not well marked and few are of use in the present problem; the build of the skeleton is altogether very similar in the two families. The Thecodontosauridae are smaller than the Plateosauridae, being of no great size (this could account for some of the other differences), and they are generally of very slender build. The limbs, however, are powerful; these animals seem to have been semi-quadrupedal in habit, while the Plateosaurids were undoubted bipeds. All the vertebrae are elongated to a greater extent in the Thecodontosaurids. The fore-limb epipodials are relatively longer in that family; the pubic plate is narrower and thicker distally; the ischium (at least in the oldest species) is built so that, in contrast to the condition found in the Plateosauridae, the peduncle is directed more strongly backwards than downwards, and its distal end is relatively broader; and, in the femur, the lower end of the fourth trochanter is above the middle of the bone. The simplest distinction, according to von Huene, is between the proximal ends of the tibiae of the two families; but here his description is rather difficult to understand.

Thus it would appear that the Prestosuchidae could have been close to the line of descent of both the Thecodontosauridae and the Plateosauridae, if not indeed their direct ancestors. This cannot be true unless the "Upper Bone Bed" of Tanganyika and the upper Rio do Rasto Beds of Brazil are a little older than those in which these earliest prosauropods occur.

Plateosaurus itself is a European genus and has been known for many years; several species have been described in a number of papers, of which by far the best is a very complete description by von HUENE (1926a). In recent years YOUNG has described two more genera from the Red Beds of Yunnan, China; these are Lufengosaurus (1941a, 1947, 1951) and Yunnanosaurus (1942, 1951) and have also been very fully described. The five genera included in the less well known Thecodontosauridae are Thecodontosaurus, Yaleosaurus ("Anchisaurus"), Dromicosaurus, Gyposaurus and Massospondylus; descriptions of these are collected in von HUENE's monograph on the Saurischia (1932). Since then another species of Gyposaurus, G. sinensis, has been described by YOUNG from Yunnan (1941b, 1948, 1951).

ix) Comparison with Parringtonia

Parrington's Ruhuhu collection of 1933 included a small pseudosuchian from the "Upper Bone Bed" (specimen no. 68a). This was described by von HUENE (1939b) as Parringtonia gracilis; he noted that it had similarities with the Ornithosuchidae, within which family it was provisionally included by ROMER (1945). Since it is one of the only two genera of pseudosuchian already described from the "Upper Bone Bed", it was suspected that it might prove to be related to Mandasuchus or might even represent an immature individual of that genus. A comparison with *Mandasuchus*, summarised below, has shown these suspicions to be totally unfounded.

The recognisable remains of *Parringtonia* consisted only of a maxilla, eleven vertebrae (many incomplete), a scapula, part of an ischium and dermal scutes. The writer has also found two small, badly preserved sacral vertebrae among the large fragments of a *Stenaulorhynchus* which comprise the greater part of field-collection no. 68; by their size it is plain that they form part, hitherto undescribed, of the *Parringtonia* type-skeleton.

Size.

The smallest known specimen of *Mandasuchus* (no. 13) is about twice as large as *Parringtonia* in its linear dimensions.

Maxilla.

The maxillae alone are sufficient to distinguish the genera at a glance. In *Mandasuchus* the posterior part of the bone consists of a stout dentigerous bar, bearing at least nine alveoli behind the anterior border of the antorbital vacuity; in *Parringtonia*, on the other hand, there are only three alveoli below the antorbital vacuity, and behind those the maxilla is very broad and flat. Other contrasting characters of the Parringtonia maxilla include the apparent shortness of the snout; the sloping nature of the lateral wall; the axial elongation of the transverse section of the ascending process; the vertical wall within the antorbital vacuity, formed from a posterior prolongation of the ascending process; the well developed flange at the base of the tooth row (produced anteriorly into a palatine wing); and the small foramen between this flange and each alveolus.

The teeth of Parringtonia are not preserved.

Vertebral column.

Pre-sacral region.

Von Huene described an "isolated" neural arch as possibly belonging to the fourth of the preserved pre-sacral vertebrae of Parringtonia. Removal of all the matrix from the centrum and the neural arch in question has now confirmed that they fit together perfectly.

In all those vertebrae of Parringtonia in which the parapophysis is preserved it lies at the height of the middle of the neural canal.

The pre-sacral vertebrae of Parringtonia differ from those of Mandasuchus in that their centra taper ventrally to a weak median ridge, are virtually platycoelous, and have no lateral hollowings. Diapophysial buttresses are absent except in the mid-dorsal region, where a strong anteroventral buttress connects para- and diapophysis. Further, the thin-walled neural canal of Parringtonia is relatively much larger, nearly as large as the centrum; the prezygapophyses do not project forwards beyond the centrum, the postzygapophyses project correspondingly further backwards; both pairs of zygapophyses project more strongly sideways; and the neural spine, which is placed further back than in Mandasuchus, is relatively more expanded above.

Sacrum.

The sacrum of Parringtonia was not described by von Huene. The two small vertebrae subsequently discovered among the Stenaulorhynchus fragments of field-collection no. 68 were not well preserved, and attempted preparation with acetic acid was unsuccessful. The following facts may nevertheless be of interest.

The two vertebrae are closely apposed. Both centra are roughly 9mm. long; the more anterior is about 8mm. high and 9mm. wide, the other 7mm. high and 8mm. wide. They are thus a little shorter than the dorsals, from which they differ also in being rounded beneath. The transverse processes are single and comparatively massive (it is upon this alone that these vertebrae are designated as sacrals) and are attached to the anterodorsal part of the centrum and to the side of the neural arch. The more anterior vertebra retains the base of the neural spine; this is set well back on the neural arch and is axially rather narrow.

Caudal region.

The second and third of the preserved caudals of Parringtonia bear a low raised ridge running longitudinally along the middle of the groove on the ventral surface; this is not known in Mandasuchus. Only one neural spine is preserved complete in Parringtonia, and differs from that of a Mandasuchus caudal in that its dorsal surface is expanded and very concave.

Scapula.

The scapulae also are very distinct in the two genera. The most striking difference is that, in Parringtonia, a powerful vertically placed ridge projects laterally from the narrowest part of the outer surface of the bone, just above the point of inflexion; this is presumed to be the muscle-process for the levator scapulae internus, and is absent in Mandasuchus. The scapula of Parringtonia also differs from that of Mandasuchus in that it is more strongly inflected in the transverse plane; the anterior edge of the blade is relatively less sharp; the upper part of the blade curves forwards rather than backwards; the lateral surface of the bone is concave above the articulation (for the insertion of the trapezius muscle); and the scapular portion of the glenoid facet is higher and narrower.

Ischium.

It is difficult to conceive that the Parringtonia fragment can indeed be the proximal end of an ischium, for there does not appear to be any part of the acetabular surface present upon it. Even if it were, it seems more likely that it would be the right than the left, for the ischium is usually thicker posterodorsally than anteroventrally.

Dermal scutes.

The dorsal scutes of Mandasuchus and Parringtonia resemble each other in so far as they are longitudinally ridged and arranged tile-wise. Those of Parringtonia, however, are more or less square in outline, lacking both the anterior spine and the posterior notch, and their external surfaces are deeply sculptured. They differ also in that the only scute preserved complete is appreciably longer than any of the vertebrae.

x) Comparison with other pseudosuchians

Other pseudosuchians may give indications of relationship to Mandasuchus and must be considered briefly in that connexion.

Chasmatosaurus and its allies.

Chasmatosaurus and Chasmatosuchus from the lowermost Trias are the oldest pseudosuchians known, and as such should receive special attention.

Three species of Chasmatosaurus have been described from widely separated localities, all from rather incomplete specimens and each associated with Lystrosaurus. These are the type-species, C. vanhoepeni HAUGHTON from South Africa (1924a; von HUENE, 1926b; BROOM, 1932b; BROILI & SCHRÖDER, 1934); C. yuani YOUNG from Sinkiang (1936); and C. indicus von HUENE from the Panchet Beds of Bengal (1942a).

This last is based on "dicynodont" vertebrae described by HUXLEY (1865) and LYDEKKER (1885); teeth described by Huxley as those of a new genus Ankistrodon (=Epicampodon LYDEKKER) were also referred to the species.

The related Chasmatosuchus von HUENE (1940b) is from Zone V (Benthosuchus zone) in the basal Trias of Northern Russia. The material, consisting only of a lower jaw fragment, nine vertebrae and two tibiae, represents several individuals and at least two species.

Two other skulls from South Africa also appear to belong within this group. One of these, Proterosuchus BROOM (1904) must be a little younger than Chasmatosaurus, although still Lower Triassic, for it occurs in the Procolophon zone; the other, Elaphrosuchus BROOM (1946) was found in rocks of unspecified age.

According to von HUENE (1936a,b, 1948), these genera constitute a family of their own, the Proterosuchidae; but ROMER (1945) places them with Erythrosuchus in the Erythrosuchidae.

The marginal teeth of Chasmatosaurus are very like those of Mandasuchus; the anterior serrations are worn down gradually as the teeth become older, first to a smooth edge and then to an even surface. (The teeth of Chasmatosuchus, as far as can be judged from replacing teeth, differ in being relatively broader and not at all recurved). In manner of insertion, however, there is a clear distinction: the teeth of Mandasuchus are thecodont, while those of Chasmatosaurus and its allies are acrodont, at least when mature. Broom noted that in Proterosuchus "The immature teeth have distinct sockets, but in the old teeth the roots seem to be united with the bone." The value of this difference in the nature of the tooth insertion is not easy to determine; von Huene regards acrodonty as a "Palaeozoic" character, while Romer considers it specialised. It is indeed true that all archosaurs later than Proterosuchus are typically thecodont, the teeth having long roots which are sunk into alveoli; but Broom's observations on Proterosuchus lead to the conclusion reached by Broili and Schröder, that this character is probably of little taxonomic value.

Chasmatosaurus also recalls Mandasuchus in the form of its cervical vertebrae. The axis is very like that of Mandasuchus; it bears a narrow longitudinal keel beneath and has a strikingly long, hatchet-shaped neural spine which is lower and thinner in front than behind. This close similarity, however, is probably of no special significance, for the form of this element seems to vary but little; Broili and Schröder pointed out the great resemblance of the axis of Chasmatosaurus to that of the Lower Permian Ophiacodon, so far removed from it in time. The remaining cervicals show an interesting similarity to those of Mandasuchus (and a difference from those of most other pseudosuchians) in that they possess elongated centra, the third cervical being longer than the axis; other resemblances include such progressive changes along the series as the gradual disappearance of the ventro-medial keel, the increase in the distance between the parapophysis and the mid-line, and the strengthening of the diapophysis. Cervical ribs of rather similar form are present in both genera, but they are more slender in Chasmatosaurus. The only really significant difference lies in the fact that intercentra other than the axial are present in Chasmatosaurus; the first four cervical vertebrae certainly have them, and perhaps other pre-sacrals too. This indicates the essentially more primitive nature of the genus.

The last cervical vertebra and the first dorsal of Chasmatosuchus are much like the corresponding vertebrae of Mandasuchus, especially in the detailed arrangement of the diapophysial buttresses and the pleural concavities; they differ, however, in their possession of a well marked ventromedial ridge. The more posterior dorsals of Chasmatosaurus are again very similar to those of the East African reptile, except in that no hyposphene has been observed in the former genus; von Huene notes this as a difference between these animals and Dongusia.

The caudal vertebrae of Chasmatosaurus and Chasmatosuchus also bear a strong resemblance to the caudals of Mandasuchus. They have one unusual characteristic, however, in that there are deep grooves on the neural arch, behind the prezygapophyses and on either side of the anterior part of the base of the neural spine. These are barely indicated on the few well preserved neural arches of the Mandasuchus tail.

The limb-bones of Chasmatosaurus, while generally similar, are distinctly stouter than those of Mandasuchus; of the former, Young remarks that they show a decided analogy with the limb-bones of the pelycosaur Varanosaurus. On the other hand, the lengths of the limb-bones relative to the length of a typical dorsal vertebra are alike in the two reptiles. It may be noted that Young's descriptions of limb-bones, much better preserved than those described by Broom, appear to have invalidated Broili and Schröder's earlier conception of Chasmatosaurus as an animal of crocodile-like proportions. The tibia of a specimen of Tomistoma measured by the writer was 3.5 times as long as the centrum of a mid-dorsal vertebra of the same animal, while corresponding figures for Chasmatosaurus yuani and Mandasuchus are 5.5 and 5.9 respectively. Similarly, the ulna of Tomistoma was found to be 2.8 times as long as a mid-dorsal centrum; the corresponding figure for Chasmatosaurus is 3.7, and in Mandasuchus, where no complete fore-limb epipodial is known, the length ratio of humerus to femur suggests a figure of 4.1. Thus it would seem that the limbs, especially the hind-limbs, were relatively much longer in Chasmatosaurus and Mandasuchus than in a modern crocodile.

The coracoid foramen appears to have been large in Chasmatosaurus and small in Mandasuchus. It is probably not true of the radius of Mandasuchus that its distal end is expanded, as has been recorded of that of Chasmatosaurus. The ilium of Mandasuchus differs from that of the earlier beast in its well defined acetabulum with a clearly marked supra-acetabular crest, in the presence of an anterior spine, and in the stoutness and slightly greater relative length of the posterior spine. The fibula of _Chasmatosaurus_ differs also in the absence of a prominent trochanter near its proximal end.

Dermal scutes, found in _Mandasuchus_, are not known in _Chasmatosaurus_ and its allies. The degree of completeness of the Sinkiang animal is such that, had dermal scutes indeed been present, it is hard to imagine that not one would have been preserved. On the other hand, the figures of the dorsal vertebra of the Bengal _Chasmatosaurus_ show a neural spine with a somewhat flattened and expanded top; this may be an indication of the presence of armour.

The close similarity of the vertebral columns and the more general similarity of the limb-bones indicates some sort of relationship between _Chasmatosaurus_ and _Mandasuchus_. _Chasmatosaurus_ is the more primitive, as might be expected; this is clearly shown by the presence of post-axial intercentra in its neck, by the stouter build of its limbs, and perhaps by the acrodont insertion of its teeth. It is nevertheless improbable that the one descended directly from the other. As pointed out by Broili and Schröder, certain characters of the skull of Chasmatosaurus, such as the overhanging premaxillary beak and the lack of a pineal foramen (present in the later Erythrosuchus) show that the animal was considerably specialised in certain directions. At the same time, lack of knowledge of the skull of Mandasuchus means that the possibility of its descent from a Chasmatosaurus-like reptile cannot be precluded entirely.

Dongusia.

Dongusia occurs in Zone VI (Capitosaurus zone) of the North Russian Trias. This zone is probably of Lower Triassic age, being equivalent to part of the Cynognathus zone of the South African Karroo (WATSON, 1942); Dongusia must therefore be a little younger than Proterosuchus. The genus is known only from one large and extremely well preserved anterior dorsal vertebra described by von HUENE (1940b); ROMER (1945) has assigned it provisionally to the Ornithosuchidae.

This vertebra bears a striking and detailed resemblance to the anterior dorsals of Mandasuchus, in particular to the supposed fourth dorsal of specimen no. 63; the presence of a hyposphene may be noted in both genera. Minor differences of the Dongusia vertebra include the slightly greater relative length of the centrum: the presence of a ventromedial keel; the fact that the postzygapophyses do not project behind the centrum; and the presence of a vertical longitudinal strip lying in a median furrow on the hinder margin of the neural spine. In Mandasuchus the articulating faces of the centra fit closely together and leave no spaces for intercentra; but von Huene's illustration of the Dongusia vertebra in lateral view gives the impression that such gaps may have been present.

The resemblance to Mandasuchus is so marked that descent of the latter from Dongusia or from an ally thereof appears distinctly possible. However, no conclusions should be based upon the characters of a single vertebra, for they might well be proved fallacious by subsequent finds of new material.

Erythrosuchus.

This large pseudosuchian from the Cynognathus zone was first described by BROOM (1906), a preliminary account having been published by the same author a year earlier; and a more detailed description was given later by von HUENE (1911a). According to ROMER (1945), the genus is the type-genus of the family Erythrosuchidae; but according to von HUENE (1936a,b) it is the only genus of that family.

Von Huene opines that Erythrosuchus lived much of its life in water as a sort of "reptilian hippopotamus"; thus it seems to be specialised in a manner otherwise unknown among the Pseudosuchia, its proportions being quite unlike those of other supposedly semi-aquatic members of the sub-order (such as Typothorax). It is certainly very different from Mandasuchus and could hardly have been ancestral to that form. Erythrosuchus possessed a large head, a very short neck and short limbs; most of the bones, while of the general pseudosuchian type, are correspondingly very short and massive. The cervical vertebrae are exceptionally short in the axial direction, having narrow neural spines which are thickened but not broadened above; the presence of intercentra is indicated and denotes the primitive nature of the creature. Dermal armour is unknown, except perhaps for one small bone which Broom believed to be a dermal ossification.

Euparkeria and Browniella.

BROOM (1913a) differentiated a new genus of Thecodont (Euparkeria) from the material previously described by WATSON (1912) as the new rhynchocephalian Mesosuchus; development of one block had revealed an almost perfect skull of the former reptile. A more detailed description of Euparkeria was given in a later paper (BROOM, 1913b), in which another (apparently) closely allied genus was distinguished as Browniella. The blocks containing the skeletons have meanwhile undergone further preparation; more information has been given by HAUGHTON (1921), who has referred nearly all the supposed Browniella material back to Euparkeria. The Browniella type-specimen thus consists of nothing more than an isolated femur.

Broom wrote that the skeletons were "discovered in Upper Triassic beds" (of the South African Karroo), but this appeared to be incorrect; they were in fact from the Cynognathus zone and therefore of about the same age as Erythrosuchus. Perhaps Broom meant Upper Beaufort.

Both these genera are included by ROMER (1945) in the family Ornithosuchidae; but von HUENE (1936a,b, 1948) restricts the latter term to the Upper Triassic genera, placing these Lower Triassic forms in the separate family Euparkeriidae.

The single femur described as Browniella can hardly be considered. Euparkeria is a small reptile and seems to occupy a fairly central position within the Pseudosuchia, most of its characters being typical of the sub-order and rather unspecialised. The osteology is nowhere described as completely as might be wished - in particular, the vertebrae and dermal armour are dismissed in a few lines and are not figured at all, - but the animal does not seem to possess any feature which might preclude the possibility of its being ancestral to any of the three important pseudosuchian families of the younger Triassic beds, namely the Prestosuchidae, the Stagonolepidae and the Ornithosuchidae. The resemblance to the last named is especially close. That Euparkeria is nevertheless comparatively primitive is shown by its possession of palatal (probably pterygoid) teeth.

Other characters of Euparkeria which should be noted include: marginal teeth just like those of Mandasuchus; apparently twenty-six pre-sacral and two sacral vertebrae; comparatively short cervical centra; a secondary shoulder girdle; a slender humerus with a short deltopectoral crest in a high position and without indication of any ectepicondylar foramen or groove; epipodials which are a little shorter than the propodials; a typical pseudosuchian ilium with a large closed acetabulum, a short anterior spine, a long posterior spine and serrations across the dorsal margin; a rather short and broad pubis with a considerably thickened outer border passing almost directly downwards and with two pubic foramina (Haughton seems dubious about this last point); a long and slender but plate-like ischium; a femur with a slight sigmoidal curvature and a well marked trochanter borne posteromedially about one-third of the way down the bone; and paramedian pairs of dermal ossifications arranged along the back from the head to at least well down the tail, corresponding to the vertebrae in number and position and, although of an unspecified shape, about twice as long as broad.

The Ornithosuchidae.

The Lower and Middle Triassic forms which ROMER (1945) has included within this family have already been considered above, for their membership of the family is open to doubt. The Upper Triassic forms, on the other hand, include the type-genus of the family, Ornithosuchus NEWTON (1894; BOULENGER, 1903; BROOM, 1913b) from the Elgin Sandstone; Saltoposuchus von HUENE (1921) from the Keuper of Württemberg; and Hesperosuchus COLBERT (1947) from the Chinle formation of Arizona. Often included with these is Erpetosuchus NEWTON (1894; BROOM, 1913b) from the Elgin Sandstone; and Dyoplax O. FRAAS from the Keuper of Germany, referred to above on p. 250, may also belong here.

These reptiles seem to be modified in the same general direction as the contemporaneous coelurosaurs and carnosaurs, but they are much smaller than most of the Saurischia. The second specimen of Ornithosuchus woodwardi (=O. taylori BROOM) is the largest Ornithosuchid known and must have been about six feet long; Hesperosuchus is the next largest (four or five feet long, according to Colbert); and some of the others can have been no bigger than large lizards, with skulls only three or four inches in length. All these creatures, especially Saltoposuchus and Hesperosuchus, closely parallel their saurischian cousins in many of their adaptations, and in the general build of their girdles and slender limbs approach more closely to the Saurischia than do Mandasuchus and its allies. Examples may be cited. All the Ornithosuchids possess elongated vertebral centra, and Hesperosuchus resembles Mandasuchus and the Saurischia in having the cervical centra longer than those of the dorsal region. Ornithosuchus and Saltoposuchus, but probably not Hesperosuchus, have three sacral vertebrae instead of two, and in Ornithosuchus the second and third of these seem to have been firmly united. While the Ornithosuchids show a general archosaur character in that the bones of the fore-limb are only about two-thirds as long as the corresponding bones of the hind-limb, there is a tendency for the epipodials to become as long as the propodials or even longer; this tendency is not fully developed in <u>Ornithosuchus</u>, but in <u>Hesperosuchus</u>, where the tibia and the fibula seem to have been about as long as the femur, the radius and the ulna are a little longer than the humerus. Broom remarks that the scapula of <u>Ornithosuchus</u> "differs from that of <u>Euparkeria</u> in being.......much more Dinosaurian in appearance", and that the general appearance of the humerus of the same animal with its well developed deltopectoral crest "suggests a comparison with that of the Theropoda." The humerus of <u>Hesperosuchus</u> is indeed quite unlike that of most other pseudosuchians, for it is exceptionally slender, bears a deltopectoral crest whose apex is situated well below the proximal end of the bone, and has no epicondylar foramina or grooves. In <u>Ornithosuchus</u> the ilium has a fairly large anterior spine, and the pubis is "essentially similar to that of <u>Euparkeria</u>, but much more elongated" (BROOM, op. cit.). The femur of <u>Hesperosuchus</u> has a definite head turned in at an angle to the shaft, a moderately large fourth trochanter and very well developed distal condyles.

Unlike the Saurischia, however, and like the

Prestosuchidae, the Ornithosuchidae are characterised by the presence of dermal armour in the form of two paramedian dorsal rows of scutes, each overlapping the scute behind it and each divided externally by a longitudinal keel. These nevertheless differ from those of the Prestosuchidae in certain important respects. They seem to correspond with the vertebrae in number and position (except in the distal part of the tail of _Saltoposuchus_, where von Huene reports two pairs of scutes per vertebral segment); the keel is nearer the outer than the inner margin; the plates are usually of a fairly simple quadrate outline with a straight posterior border (those of _Saltoposuchus_ and _Hesperosuchus_ have an anterior spine which served for articulation with the preceding plate as in _Prestosuchus_ and _Mandasuchus_, but, being continuous with the longitudinal keel, this is situated much more laterally than in those genera); and their outer surfaces are usually heavily sculptured. (It may be noted that Colbert's description of the Ornithosuchidae as being characterised by elongated and relatively narrow scutes is not strictly correct; the scutes are sometimes more or less isodiametric, as on the trunk of _Ornithosuchus taylori_, or even broader than long, as on the neck of the same reptile). Another difference between the Ornithosuchidae and the Prestosuchidae lies in the fact that, in the former family, the tops of the neural spines of the vertebrae are never much flattened or expanded for the support of the dorsal scutes; those of Hesperosuchus are not expanded axially and only a very little transversely. Indeed, the neural spines of the Arizona reptile are quite unlike those of Mandasuchus, for their anterior and posterior margins ascend vertically and almost parallel to each other.

Other "pseudosuchian" (as contrasted with "saurischian") characters may be noted in the Ornithosuchidae; for instance, a secondary shoulder girdle is known in Ornithosuchus, Saltoposuchus and Erpetosuchus, and in Hesperosuchus there is a well developed olecranon on the ulna.

An interesting similarity to the Prestosuchidae lies in the presence of a pre-neural spine in some of the caudals of Saltoposuchus.

As already shown, Mandasuchus appears to lie on or near the line of ancestry of the pachypodosaurs; and it can hardly be ancestral to the Ornithosuchids if that is indeed the case. Both the Prestosuchidae and the Ornithosuchidae could nevertheless be derived from a common ancestor in the Lower Trias, perhaps a creature rather similar to Euparkeria.

Specialised or poorly known pseudosuchians.

Certain pseudosuchians need not be considered in the present work, for they are either too specialised in certain directions or else too poorly known.

In the former category may be placed those pseudosuchians which tend towards the crocodiles in their structure. These include only one genus, Sphenosuchus HAUGHTON (1915, 1924b; von HUENE, 1925; BROOM, 1927) from the Red Beds of the South African Karroo; for, although van HOEPEN (1915) described Pedeticosaurus from the Cave Sandstone of the Orange Free State as a pseudosuchian, ROMER (1945) considers the reptile to be a true crocodilian. Another highly specialised pseudosuchian is Scleromochlus WOODWARD (1907; BROOM, 1913b) from the Elgin Sandstone; this little animal was evidently adapted to a leaping mode of progression, perhaps even to simple gliding. Romer lists it as another Ornithosuchid.

Recently described and inadequately known pseudosuchians include Anisodontosaurus and Arizonasaurus, both described by WELLES (1947) from the upper Moenkopi formation of Arizona, and Cerritosaurus PRICE (1946) from the supposed Upper Trias of Brazil.

b) TELEOCRATER

i) General discussion

First impressions of this genus are rather puzzling, for a vertebral column of saurischian type appears to be associated with an ilium and a collection of limb-bones belonging to a pseudosuchian. The vertebrae resemble those of a coelurosaur very closely; they are long, especially the anterior cervicals, and are generally lightly constructed. But the acetabulum is almost certainly closed; the humerus has a supinator process and an ectepicondylar groove; the femur is without a well defined head set at an angle to the shaft and without a fourth trochanter; the tibia is shorter than the femur; and the fibula bears a lateral trochanter. The question now arises as to whether the association of these bones is justified by the evidence available.

Only one good specimen of _Teleocrater_ is known, and it must be admitted that this specimen (no. 48b) was found in a heterogeneous field-collection. The the reptile material found with it, however, consisted only of the proximal part of a rib (probably of a dicynodont), part of an unidentified sacrum which is too large to belong to _Teleocrater_, and perhaps a pair of very large bones whose affinities are highly problematical. The remaining bones, all of which have been referred to the type-specimen of Teleocrater tanyura, are all of undoubted archosaur origin and of commensurate size. It seems most unlikely that twenty-eight vertebrae belonging to a saurischian, without any corresponding limb-bones, would be found together with nine well preserved pseudosuchian girdle- and limb-bones lacking any corresponding vertebrae, the dimensions of the two sets of bones being strictly comparable.

A caudal vertebra found with the second specimen of Teleocrater is far too large to belong to it. This field-collection (no. 53) otherwise includes two vertebrae of much the same size as those of the type-specimen, one being of a characteristic form and almost identical with one vertebra of the latter; and with them, again of comparable size, is the distal part of a typically pseudosuchian humerus.

Thus it would seem that each of the two specimens described as Teleocrater consists of the remains of only one individual and is not an adventitious mixture of two. The genus must be referred to the Pseudosuchia because of the apparently closed acetabulum. Although some form of dermal armour is borne by nearly every other pseudosuchian described, neither of these specimens includes any dermal scutes; this evidence is quite negative, however, for the type-specimen also lacks the top of every neural spine (with the possible exception of one) and the second specimen is too incomplete to be considered.

The ilium and limb-bones of _Teleocrater_, although typically pseudosuchian in form, show no especial similarity to those of any one pseudosuchian described hitherto. In point of fact they are not widely different from those of _Mandasuchus_, despite the great differences in the vertebrae of the two reptiles. On the other hand, the vertebral column _does_ resemble that of a particular coelurosaur, namely _Coelophysis_; this animal is discussed in greater detail immediately below.

ii) Comparison with Coelophysis

Coelophysis is a coelurosaur of the family Podokesauridae and occurs in the Upper Triassic of New Mexico and Texas. Some very incomplete material, first described by COPE (1887a) as two new species of *Coelurus*, was later re-described in greater detail (1887b) as three new species of *Tanystrophaeus*; and in yet another publication (1889) COPE proposed the name *Coelophysis* for the specimens, pointing out their differences from the two previously mentioned genera and from *Megadactylus*. None of these descriptions is illustrated, and the species seem to be distinguished by size alone.

Von HUENE (1906, 1915) provided the first illustrations of the material and supplemented the earlier descriptions; he refers to the genus also in his monograph on the Saurischia (1932). New and better material, mostly of the vertebrae, was described by CASE (1922, 1927, 1932). Even so, our knowledge of the osteology of the genus as published remains very incomplete, and is further confused by the fact that some of the specimens referred to *Coelophysis* are quite obviously different from others.

However, an extensive find of *Coelophysis* has now been made at Ghost Ranch, New Mexico, in clays of the Chinle formation; an account of the expedition is given by COLBERT (1947). The discovery consisted of a large mass of intertwined, completely articulated skeletons in stream-bottom sediments; eighteen skulls were visible on the surface alone. Apart from a few scattered phytosaur bones, the material consisted almost exclusively of Coelophysis. A description of this material will certainly make Coelophysis the best known of the primitive saurischians, and comparison with Teleocrater and other genera will be facilitated.

There is a general resemblance between Teleocrater and Coelophysis in the hollow, thin-walled nature of their bones.

Size.

Teleocrater is a little smaller than an average specimen of Coelophysis.

Vertebral column.

The vertebrae of both animals are long and slender, especially in the neck and tail, and their centra are usually amphicoelous.

Cervical region.

The presumed affinity of the two genera is based very largely upon the similarity of the first preserved vertebra of Teleocrater (described as a supposed anterior cervical, "CeA") to one of Cope's original vertebrae, described by von HUENE (1906, 1915) as the axis of Coelophysis longicollis; and, to a much lesser extent, to the cervical vertebrae described by CASE (1922, 1927).

Von Huene's axis resembles the Teleocrater vertebra in its extreme elongation and in the marked and asymmetrical concavity of its ventral profile, the apex of which lies in front of the middle of the vertebra. It seems that in both animals the anterior face of the centrum must have lain more dorsally than the posterior, showing that the head was carried above the level of the body. There is a further resemblance in the nature of the ventral surface of the centrum: concave or flattened in front between a pair of sharp edges, bearing a medial ridge in the middle part (much longer in Coelophysis), and rounded behind. The posterior face is roughly circular and fairly deeply concave in both genera. The most striking similarity, however, lies between the flange-like diapophyses and zygapophysial ridges of the two vertebrae, giving them both a highly characteristic appearance. The detailed arrangement of the flanges and ridges is almost exactly the same; in Coelophysis, just as in Teleocrater, the base of the broken-off diapophysis forms a broad plate which is directed obliquely downwards and outwards and which is continued posteriorly into a posteroventral buttress; but its origin is situated more dorsally in Coelophysis, upon the side of the neural arch instead of upon the centrum, and a small canal which remains between this and the wall of the neural canal has not been observed in the East African vertebra. The broken-off base of the neural spine is axially short in both vertebrae, its length being rather less than half the length of the centrum in Coelophysis.

The most anterior of the series of vertebrae described by CASE (1922, 1927) is thought to be the fourth or fifth cervical. This centrum and the three which follow it seem to be relatively shorter than that of the Teleocrater anterior cervical, the first being the longest; the asymmetry of the ventral profile (the anterior face of the centrum lying more dorsally than the posterior) is nevertheless well marked. The ventral face of the centrum is broader anteriorly, nearly flat in front and rounded behind, but without trace of a median keel or ridge. The flange of the diapophysis is borne on the centrum as in Teleocrater, but is restricted to its anterior half, and the ridges to the zygapophyses are not developed as in that genus. The zygapophysial facets are almost horizontal in the first two of the preserved vertebrae while in the Teleocrater vertebra they lie obliquely; and the thin floor between the widely divergent post-zygapophyses (not preserved in Teleocrater) is peculiar in that it bears two low ridges running nearly parallel to the zygapophyses themselves.

The only other vertebra of Teleocrater which has been assigned to the cervical region ("CeB") is rather incomplete and is probably from the posterior part of the neck; it is much shorter than the supposed anterior cervical yet longer than the other pre-sacrals. Indeed, its characters (as far as they are known) are similar to those of Case's last cervicals or anterior dorsals, but it differs from those in that the anterior face lies more dorsally than the posterior. It otherwise compares best with Case's sixth or seventh vertebra (ninth or tenth, or tenth or eleventh cervical) in that the parapophysis is a distinct facet in the anteroventral corner of the centrum, and in the presence of incipient ventral diapophysial buttresses.

Dorsal region.

The dorsal vertebrae of both reptiles are still slender and rather elongated but become a little stouter towards the sacrum. There is also a resemblance in the gradual change in position of the parapophysis. In this respect "DC" parallels Cope's eighth vertebra, "DD" and "DE" his ninth, tenth and eleventh (where the parapophysis has reached the level of the top of the centrum and forms a distinct projecting peg); all more posterior vertebrae of Coelophysis bear but a single rib-facet on the transverse process. Further, the more anterior members of each series have slender and well developed diapophysial buttresses, deep pleural concavities, and oblique zygapophysial facets; in Coelophysis the latter become horizontal again towards the end of the series. The neural spines of the posterior cervicals and of all except the last few dorsals of Coelophysis appear to have been greatly elevated, with spinal buttresses fore and aft; towards the sacrum they probably became thicker and shorter and their apices became heavier. None of the neural spines is preserved in Teleocrater. A more detailed comparison of the genera is not possible.

Caudal region.

There is also a general similarity between the caudal vertebrae of the two genera. Those of Coelophysis are best known from a long series from Texas described by CASE (1932), the most anterior of which is either the first caudal or lay not very far behind it. Their centra are elongated and contain a large thin-walled central cavity. They differ from the Teleocrater caudals, however, in that there appear to be no facets or intervertebral spaces for haemapophyses (although Case opines that chevrons would most certainly be expected), and their ventral surfaces are rounded without trace of longitudinal grooves or ridges; from the tenth preserved vertebra backwards the centra are almost cylindrical. In Teleocrater only the last four of the fifteen caudals preserved possess rounded ventral surfaces without haemapophysial facets. In both genera, however, the centra are weakly amphicoelous; the flattened transverse processes, the bases of which are axially long in the anterior caudals, diminish down the series and eventually disappear; the zygapophyses remain, even in the smallest vertebrae, and the anterior pair project in front of the centrum; and the neural spines, which also diminish down the series until they disappear, have an anterior edge which rises obliquely backwards and a posterior edge which rises almost vertically.

Other single caudals described by von HUENE (1906) appear to be rather different from those described by

Case; the larger ones resemble the Teleocrater caudals in having haemapophysial facets, and their articulating surfaces are barely perceptibly concave. They are moderately long or even very elongated, the actual length decreasing distally but the elongation ratio increasing; proper transverse processes are absent, but there are long projecting longitudinal ledges on the sides of the vertebrae, more strongly formed in the smaller members. These differences indicate that Case's material may be wrongly referred to the genus Coelophysis.

Ilium.

Here the two genera are utterly different. The acetabulum of Coelophysis is widely perforated (according to von Huene, relatively far more widely in C. willistoni than in C. longicollis); it has a broad roof and a very prominent supra-acetabular crest, and the short, thick and widely separated pre- and post-acetabular processes bear the pubic and ischiadic articulations respectively. In Teleocrater, on the other hand, the acetabulum is almost certainly closed. Another important difference lies in the form of the anterior spine; in Coelophysis this is typically coelurosaurian, being long and very broad, while in

Teleocrater it is extremely short. The posterior spine of the *Coelophysis* ilium is even longer than the anterior and is also rather broad; its outer surface is very slightly convex, and its inner surface bears a high, vertical medial crest near its lower edge. The posterior spine is broken off in *Teleocrater*, but it seems probable that it was also long, and the beginning of a strong medial crest is preserved.

CASE (1927) described an isolated ilium from Texas, of much the same size as that of *Coelophysis longicollis* but "somewhat different in form." This is in fact very different and cannot possibly be referred to that genus; it is rather similar to that of *Teleocrater*, although about twice as large. Part of the acetabulum is broken away, but, judging from Case's figures, it could have been complete; the perforation, if any, must have been small. There is an extremely short anterior spine and a comparatively long, very heavy posterior spine bearing a high medial crest.

Hind-limb.

Femur.

The femora differ chiefly in that the head is strongly bent towards the medial side in *Coelophysis* but not at all in Téleocrater. The Coelophysis femur is very slender and about as long as five dorsal vertebrae; the shaft is almost straight, and an external trochanter is present at the point of flexure of the head. The Teleocrater femur, on the other hand, is more powerfully built but is relatively even longer, as long as six or seven anterior dorsal vertebrae; the shaft is sigmoidally curved and there is no external trochanter. The two bones resemble each other only in the absence of a properly developed fourth trochanter and in the form of the broadened, club-shaped distal end with its weakly developed condyles.

Tibia.

Cope's determination of the "proximal extremity of the tibia of Coelophysis bauri" seems to be regarded somewhat sceptically by von HUENE, who remarks (1915) that the fragment "differs essentially from the Pachypodosauria." There is not the remotest resemblance to the tibia of Teleocrater.

Fibula.

The proximal end of the fibula of Coelophysis is described as being but little expanded; in this respect it differs from Teleocrater.

<u>Summary</u>.

The similarity between <u>Teleocrater</u> and <u>Coelophysis</u> is confined to their vertebral columns; the few possible comparisons of their girdle- and limb-bones indicate that their appendicular skeletons are essentially different. This similarity of the vertebrae is, in general, no greater than might be expected between any two coelurosaurs. There is, however, the particularly close resemblance of the anterior cervicals, with their highly elongate centra and characteristic flanges; this form is most unusual, yet almost identical in the two genera. It is difficult to imagine that such an extraordinary type of vertebra can have been evolved twice, quite independently, in comparatively unrelated animals.

iii) <u>The new family Teleocrateridae</u>

<u>Teleocrater</u>, although classified as a pseudosuchian on the nature of its acetabulum, is clearly quite distinct from all other pseudosuchians described hitherto; it may well lie on or near the line of ancestry of <u>Coelophysis</u> and its allies. <u>Teleocrater</u> must therefore represent a new family of the

Pseudosuchia, for which the name Teleocrateridae is proposed.

Definition.

Pseudosuchians of moderate size in which the vertebral column is like that of the Coelurosauria: the vertebrae are long and generally lightly constructed, the anterior cervicals are especially long and bear a characteristic arrangement of flanges and ridges. The appendicular skeleton, on the other hand, is typically pseudosuchian in form, the acetabulum being almost certainly closed; the humerus has a supinator process and ectepicondylar groove; the ilium has a short anterior spine; the femur has no well defined head and no fourth trochanter; the tibia is shorter than the femur; and the fibula bears a lateral trochanter.

Since only one genus of the family is known at present, the diagnosis of that genus (p. 177) is equally valid for the family.

c) GENERAL TAXONOMICS

The two new pseudosuchians described above, Mandasuchus and Teleocrater, are both from the "Upper Bone Bed" of Tanganyika and share a common tendency to resemble the Saurischia to an unusual extent; this tendency, especially in Teleocrater, is more pronounced in the vertebral column than in the girdle- and limb-bones. The two genera are nevertheless strikingly different from each other; while the characters of Mandasuchus (and of other Prestosuchids) are generally reminiscent of those of the pachypodosaurs, Teleocrater is very like the coelurosaurs in some aspects of its osteology. Indeed, if nothing were known of Mandasuchus except its vertebral column, it might well be regarded as a primitive prosauropod; the vertebrae of Teleocrater, on the other hand, would almost certainly have been assigned to the Coelurosauria if it had not been for the conflicting evidence afforded by the ilium and limb-bones.

It thus appears that, while both Mandasuchus and Teleocrater possess appendicular skeletons of the general pseudosuchian type, their vertebral columns are specialised in different directions - that of Mandasuchus towards the Pachypodosauria, that of

<u>Teleocrater</u> relatively further in the direction of the Coelurosauria. These facts lead to some rather interesting conclusions. First, that in saurischian evolution specialisation of the vertebrae preceded specialisation of the limbs. Secondly, that the Pseudosuchia were themselves differentiated into pachypodosaur-like types and coelurosaur-like types at the time when these beds were laid down; and it is not unreasonable to suppose that the Pachypodosauria originated from the former (the Prestosuchidae) and the Coelurosauria from the latter (the Teleocrateridae), both sub-orders being descended, not necessarily from the genera described, but at least from hypothetical unknown members of those families. In other words, the Saurischia (if these be defined from the Pseudosuchia by their possession of an acetabular fenestration) are unlikely to be of monophyletic origin from the latter group. This view is supported by the fact that the Pachypodosauria and the Coelurosauria do not seem to have any common feature of taxonomic value which is shared neither by their pseudosuchian ancestors nor by their crocodilian, pterosaurian or ornithischian cousins.

Independent origin of the Pachypodosauria and of the Coelurosauria from the Pseudosuchia would imply that perforation of the acetabulum had occurred independently in the first two groups. (It should be noted that the evidence afforded by Teleocrater, considered quite alone, is sufficient to establish this fact; for, if the similarity between the vertebral columns of Teleocrater and Coelophysis is not to be regarded as an almost incredible example of convergence, then it must be presumed that Teleocrater lies on or near the coelurosaur line of evolution before the fenestration of the acetabulum yet after the divergence of the pachypodosaur stock). "Perforation" of the acetabulum signifies nothing more than that a portion of the cup-shaped socket has failed to ossify; this is presumably connected with the fact that the femur thrusts upwards instead of inwards when the thigh is placed more vertically. Such perforation has occurred independently, and not necessarily in a homologous manner, in four of the five great groups of archosaurs derived from the Thecodontia - the Crocodilia, the Saurischia, the Ornithischia and the birds. Since it has certainly occurred four times, there seems to be no reason why it should not have done so five times or even more often.

It might therefore be argued that such a variable feature as the nature of the acetabulum ought not to be used to distinguish the groups, and that the definition of the Saurischia should be revised to allow the inclusion of forms with closed acetabula. Mandasuchus and Spondylosoma might then be regarded as very primitive pachypodosaurs having closed acetabula and certain other "pseudosuchian" features; Teleocrater would be a primitive coelurosaur, also with a closed acetabulum; and it would no longer be necessary to postulate a diphyletic origin for the Saurischia if it were supposed that all these genera were derived from a common ancestor among the older Pseudosuchia. It is, however, difficult to find another character upon which to base the arbitrary distinction between the Pseudosuchia and the Saurischia; and the probable conclusions reached above must be allowed to stand.

Apropos of this, it has sometimes been suggested (e.g., by von HUENE, 1921) that short cervical vertebrae are characteristic of the Pseudosuchia. This does not in fact appear to be the case. Elongated cervical vertebrae are found in the earliest pseudosuchian known (Chasmatosaurus from the Lower Trias), in four "Upper Bone Bed" and upper Rio do Rasto pseudosuchians (Stagonosuchus, Mandasuchus, Spondylosoma and Teleocrater), and in the Upper Triassic Hesperosuchus. Elongation of the cervical vertebrae may even be a primitive character for this sub-order.

It has also been suggested, albeit rather vaguely (e.g., by ROMER, 1945), that the Ornithosuchidae are ancestral to the Saurischia. Although these little pseudosuchians do indeed show many saurischian-like characters, it does not seem possible that this should be correct. All the Ornithosuchids described (except for the very poorly known <u>Dongusia</u> and <u>Parringtonia</u>, whose membership of this family is highly dubious) are of certain Upper Triassic age; and, as pointed out above, the Saurischia are already numerous and varied in the Upper Trias. In fact, the better known Ornithosuchids are found together with saurischians in the very same rocks: <u>Ornithosuchus</u> and <u>Erpetosuchus</u> with <u>Saltopus</u> in the <u>Stagonolepis</u> Sandstone of Scotland, and <u>Saltoposuchus</u> with <u>Procompsognathus</u> in the Stubensandstein of Germany. (For the purposes of this discussion the Lower Triassic <u>Euparkeria</u> and <u>Browniella</u> are not considered as Ornithosuchidae, although included within the family by ROMER, 1945; von HUENE - 1936a,b, 1948 - prefers to place them in the separate family Euparkeriidae).

5. DESCRIPTION AND COMPARISON OF MORE INCOMPLETE ARCHOSAUR MATERIAL FROM THE RUHUHU VALLEY

a) SPECIMEN NO. 11a

Field notes.

This specimen is the small pseudosuchian mentioned above as being included among the material found mixed with that of the Mandasuchus longicervix type-specimen (no. 11b) in locality B5 at Irundi; the bones are associated together on grounds of commensurate size. It resembles specimen no. 11b in being of a whitish colour and generally well preserved.

Material available.

Lower jaw: right articular and much of the surangular.

Vertebrae: 5, including 1 mid-dorsal, 2 possible posterior dorsals or pygals, 1 possible sacral and 1 caudal.

Humerus: right, lacking central part of shaft.

Femur: distal part of left.

End of small unidentified limb-bone.

Lower jaw. (Plate 42).

This fragment is 70mm. long as preserved. It consists only of the right articular together with a considerable portion of the surangular; the badly preserved mess of bone at the anterior end of the surangular may also include part of the coronoid.

The articular is equilaterally triangular in transverse section, with a horizontal upper surface and with lateral surfaces which face obliquely downwards and meet in a ridge below; it is 32mm. long and tapers from a width of 19mm. in front to a rounded but narrow posterior end. Just behind the front edge of the upper surface is the broad transverse groove which served for articulation with the quadrate, and behind this lies another narrower groove; between the latter and the posterior end a strong muscle-process rises dorsally and a little inwards. This is 6mm. high but may be incomplete, and the upper (broken?) surface measures 8mm. axially and 2mm. transversely. The inner surface of the articular is almost plane, but a process whose broken-off base is 10mm. long and 4mm. high projected medially from the middle of its upper margin. The outer surface is largely covered by the surangular, which extends to within 4mm. of the posterior end of the former and also bears a medially directed flange covering the anterior face of the articular. The surangular plate overlying the outer surface of the articular is prolonged anteriorly beyond the latter, and its upper margin in this region bears a horizontally situated lateral extension; the plate becomes wafer-thin below, the horizontal extension becomes thinner laterally, and the free borders of both are everywhere incomplete. The anterior end of the fragment is very badly preserved and affords no information whatsoever.

Vertebral column.

Table of principal measurements. See overleaf.

Mid-dorsal vertebra. (Plate 42).

This vertebra ("A") lacks the ends of the right diapophysis, of both prezygapophyses and of the left postzygapophysis, and the top of the neural spine. It is otherwise well preserved.

The centrum is rather long, nearly half as long again as its own mean diameter. Its middle is constricted below and at the sides, and the floor of the neural canal is deepened a little within the vertebra. Ventrally it is rounded, even slightly flattened. The end-faces are slightly broader than high and moderately concave.

The rib-processes are borne high on the sides of the neural arch; the parapophysial and diapophysial no. 11a - TABLE OF PRINCIPAL MEASUREMENTS OF THE VERTEBRAE (millimetres)

	A	B	C	D	E
Centrum:					
length below	15	15	17	15	14
anterior height	10	12	10	12	11
anterior width	11	14	12	14	12
posterior height	10	12	10	13	11
posterior width	11	13	11	14	11
mean diameter	$10\frac{1}{2}$	13	11	13	11
elongation ratio	1.43	1.15	1.55	1.15	1.27
minimal transverse thickness	6	8	7	10	7

facets are just contiguous but are still quite separate, forming a "spectacles"-shaped rib-articulation. This character indicates the position of the vertebra as being somewhere behind the middle of the dorsal region, yet not immediately pre-sacral. The parapophysis projects 3mm. laterally at the level of the middle of the neural canal; the oval facet measures 5mm. by 2mm., its longer axis being inclined upwards and backwards. The diapophysis projects further (7mm.) and its facet, measuring 4mm. by 2mm., is behind and above that of the parapophysis, and lies more horizontally; the whole transverse process projects directly laterally, neither forwards nor back, neither up nor down. There are no diapophysial buttresses or concavities, but a deep hollow underlies the transverse process. Traces of the neurocentral suture are visible, but its exact course is not distinct. The postzygapophyses bear obliquely inclined facets which project behind the centrum, and the deep cleft of the posterior spinal concavity lies between them. The neural spine rises vertically above the posterior part of the vertebra; it is broken off at a height of 5mm. above its base, and the broken surface measures 10mm. by 2mm.

Possible posterior dorsal or pygal vertebrae.

These two vertebrae, "B" and "C", are rather different from each other and must be described separately.

"B". (Plate 42). Of the transverse processes, only the bases remain in this vertebra; and the whole of all four zygapophyses and of the neural spine is missing.

The centrum of this vertebra resembles that of the mid-dorsal described above except in that, while of the same length, it is rather stouter. Little can be made of the form of the transverse process except that it lies in the middle of the vertebra at the level of the neural canal, has a horizontal upper surface, and is supported by a short stout buttress running downwards and forwards.

"C". (Plate 42). This vertebra lacks all trace of the transverse process on the right side, while on the left only the weathered base is present. The prezygapophyses, the end of the right postzygapophysis and the upper part of the neural spine are also missing.

The centrum is longer than any other of this specimen and is comparatively more slender; it does not otherwise differ from those described above. Nothing can be made of the form of the transverse process beyond its horizontal, rather anterior position and the absence of diapophysial buttresses. The postzygapophyses and neural spine bear a general resemblance to those described in the mid-dorsal vertebra above; the base of the neural spine is slightly longer.

Possible sacral vertebra. (Plate 42).

Only the centrum and the bases of the transverse processes remain in this vertebra ("D"). It is tentatively described as a sacral for its centrum, while of the same length as in most of the other vertebrae, is considerably stouter and is much less constricted in the middle; and the base of the transverse process, lying at the level of the base of the neural canal, is relatively massive.

Caudal vertebra. (Plate 42).

This vertebra ("E") lacks the ends of the transverse processes, the tips of the prezygapophyses and of the right postzygapophysis, and most of the neural spine.

The centrum generally resembles the others of this specimen. It is slightly shorter, however, and has a flattened ventral surface with ridges leading posteriorly to small, not very well preserved haemapophysial facets; and both end-faces are rather more deeply concave.

The transverse process has a short, slender base placed horizontally and a little behind the middle of the vertebra at the level of the middle of the neural canal; it is unsupported by buttresses. The zygapophyses appear to have been small and placed close together, and the neural spine seems also to have been small and posterior in position.

Humerus. (Plate 43).

The two expanded ends of the right humerus are preserved but the shaft is missing.

The proximal end is weakly convex above and concave below; the end-surface is 29mm. long and has a maximal width of 8mm., but both pre-axial and post-axial margins approach each other distally so that the bone is only 10mm. broad and 7mm. thick where the shaft is broken off 29mm. below the end. The end-surface is convexly arched and extends further down the pre-axial than the post-axial side. The pre-axial face is flat and bears a slight downwardly projecting deltopectoral crest, while the post-axial is broadly ridged.

The shaft of the bone was hollow, with walls approximately 1mm. thick.

The distal end is expanded post-axially; it is 9mm. broad and 6mm. thick where the shaft is broken off 28mm. from the end, and measures 23mm. by 9mm. at the end-surface. The latter, which seems to be not quite complete, is partly divided into radial and ulnar condyles; the radial is the larger of the two. On either side of the expanded end there is a slight depression between the ridges which run down the pre-axial and post-axial borders to the radial and ulnar condyles respectively; that on the posterodorsal side is the better developed. Although the distal end of the pre-axial surface is damaged, it seems fairly certain that there was no ectepicondylar groove.

<u>Femur</u>. (Plate 43).

The distal part of the left femur is preserved, the length of the curved fragment being 44mm. Its general form closely resembles that found in other pseudosuchians; it is expanded like a club and has a flattened anterior surface and a broadly grooved posterior surface. The completely ossified end-surface is flat and bounded anteriorly by a low ridge; it is partly divided by the posterior groove into tibial and fibular condyles, the latter being the larger. The whole end-surface is 24mm. long and reaches a maximum width of 18mm. across the fibular condyle.

Unidentified limb-bone. (Plate 43).

This small fragment is 27mm. long. The end-surface is roughly rectangular (12mm. by 6mm.) and the bone tapers down into a hollow shaft, egg-shaped in transverse section, measuring 6mm. by 5mm. where broken off. One of the expanded surfaces is weakly convex, and one of the "lateral" surfaces has well defined edges where it meets those adjacent. It is possible that this fragment belongs not to specimen no. 11a but to the hand or foot of specimen no. 11b, the type-specimen of *Mandasuchus longicervix*.

Comparisons and affinities.

If this small archosaur is to be compared with others from the "Upper Bone Bed", comparison with the even smaller *Parringtonia* is obviously desirable. The only elements common to both specimens, however, are the vertebrae; and it is immediately apparent that the two animals are quite distinct. The mid-dorsal vertebra of specimen no. 11a differs from the dorsal vertebrae of Parringtonia in that the centrum is slightly flattened below (instead of tapering ventrally to a median ridge) and has more deeply concave ends; a slight lateral hollowing is present, the parapophysial facet is elongated instead of round, the neural canal is comparatively small, the prezygapophyses do not project so far laterally and the postzygapophyses not so far behind the centrum. The "possible sacral" vertebra of specimen no. 11a is as long as the dorsals rather than shorter, and its end-surfaces are fairly deeply concave instead of being almost flat. The proximal caudal of the present specimen has very small haemapophysial facets, while that of Parringtonia bears exceptionally large ones; the transverse process is relatively more slender than in the latter animal and the neural spine seems to have been inclined backwards instead of rising vertically.

Comparison with Mandasuchus is suggested by a superficial resemblance to that genus. The mid-dorsal vertebra of specimen no. 11a compares fairly closely with, say, the supposed thirteenth dorsal of the M. longicervix type-specimen; the former is much smaller and has a relatively longer centrum with rather deeper hollowings in its end-surfaces, a more elongated parapophysial facet, and a diapophysis in a much higher position so that its upper surface is level with the zygapophysial facets. The "possible posterior dorsal or pygal" vertebrae of the present specimen are not strictly comparable with any Mandasuchus vertebrae known, although "B" shows certain resemblances to the supposed second caudal of the type-specimen. The "possible sacral" vertebra of specimen no. 11a has a centrum which is much less constricted than that of the Mandasuchus type-specimen and is also distinguishable by its concave ends. The caudal vertebra differs from the possible sixth caudal of the Mandasuchus type-specimen in having a concave posterior face; the Mandasuchus vertebra has a posterior face which is convex and saddle-shaped.

The form and proportions of the humerus are much the same in specimens nos. 11a and 11b; but the deltopectoral crest is inclined more steeply downwards in the former animal, and, most important of all, there appears to be no ectepicondylar groove. The outlines of the distal ends are therefore rather different. The distal ends of the femora are very similar in the two animals; the end-surface is completely ossified in specimen no. 11a.

The only lower jaw with which that of this specimen may be compared is the fragment preserved in <u>Rauisuchus</u>; this also includes the prearticular. A fair degree of resemblance exists. In this connexion the following points from von Huene's description should be noted:

i) The articular is bent medially relative to the surangular and projects inwards.

ii) The articulating surface of the articular is badly shattered and the medial part seems to be pressed down out of its original position.

iii) The surangular, which adheres laterally to the articular, extends forwards with its upper end horizontal; the upper edge forms a horizontal surface, of which the side-ridges project laterally and medially.

iv) The posterior point of the surangular is near the hinder end of the articular.

Specimen no. 11a does not appear to belong to any genus described; yet only the absence of the ectepicondylar groove on the humerus prevents its reference, if not to <u>Mandasuchus</u> itself, at least to some allied genus at present unknown. It may be described as "Pseudosuchian gen. et sp. indet."

b) SPECIMEN NO. 14a

Field-collection no. 14 was found in locality B5 at Irundi; it includes, in addition to specimen no. 14a, a quantity of material which appears to belong to *Stenaulorhynchus* (specimen no. 14b), and perhaps other material which belongs to neither of these.

Specimen no. 14a is very poorly preserved, but three small distal caudal vertebrae and the proximal ends of three larger haemapophyses are easily recognisable. Other fragments which seem to be of the same texture and commensurate size include the end of a limb-bone, but their condition is such that no description can be given. The bones are very soft and of a whitish colour.

Vertebrae.

One of these (Plate 44) is almost complete, lacking only the left postzygapophysis and part of the neural spine; but it is badly weathered in every part.

The centrum is 20mm. long below; it is 11mm. high and 11mm. wide in front, and 10mm. high and 11mm. wide behind. It is constricted below and at the sides (minimal transverse thickness 6mm.), and the hinder face bore large haemapophysial facets. A low raised ridge, on either side of which is a light groove, runs along the middle of the ventral surface. The end-surfaces are fairly deeply concave.

The transverse process, of which only the base remains, was a small projection in the middle of the vertebra at the level of the base of the neural canal. The prezygapophyses, as preserved, do not project in front of the centrum; the postzygapophyses, on the other hand, do project behind the centrum. All that can be discerned of the neural spine is that it is small and situated far back.

Another vertebra consists only of the centrum and the anterior part of the neural arch, including the prezygapophyses. The dimensions of the centrum are almost exactly the same as those given immediately above, and the form of the vertebra is also very similar. The floor of the neural canal is not deepened within the centrum.

A third, smaller vertebra seems to have possessed a ventromedial keel and no transverse process, but otherwise does not merit description. The centrum is 19mm. long and of approximately 8-9mm. mean diameter.

Haemapophyses.

The proximal end of one haemapophysis (Plate 44) is fairly well preserved, the length of the fragment being 24mm. The two rami unite at a distance of 10mm. from the articulating surfaces. The latter are roughly egg-shaped and are not united by a bridge; but, since each extends towards its fellow, it seems probable that a bridge was present and has been broken away. Further, since the transverse span of the whole articulation is 14mm., it is apparent that the haemapophysis was connected to a vertebra considerably larger than those described above. Each ramus is somewhat flattened from side to side and has a fairly sharp anteroventral margin; where the two rami unite, these ridges also unite to form a median ridge on the anteroventral side of the shaft, while the posterodorsal side bears a median groove. The shaft, the central part of which is filled with spongy bone, is thus heart-shaped in transverse section; at the broken surface it measures 7mm. from front to back and 7mm. from side to side.

Two other similar fragments are present, but are too badly preserved to warrant description.

Affinities.

The vertebrae of this specimen resemble no others described from the "Upper Bone Bed" except the second and third of the preserved caudals of Parringtonia. The two larger vertebrae are of exactly the same proportions as the smallest Parringtonia vertebra, although roughly twice as large, and the only discernible differences in form lie in the almost flat end-surfaces of the centrum and slightly higher position of the transverse process in the latter animal. Two particular resemblances are the presence of large haemapophysial facets, directed very steeply downwards, and of a low raised ridge running along the middle of the groove on the ventral surface; this latter feature has been observed in no other "Upper Bone Bed" archosaur. This specimen might therefore represent an animal akin to Parringtonia but considerably larger.

c) SPECIMEN NO. 50b

Field notes.

This specimen was found in B36, Parrington's new locality near Mkongoleko. Specimen no. 50a, found with it, consists of the two ends of a cynodont femur (cf. Scalenodon?). The yellowish-brown bones were surrounded by a hard greenish matrix which contained many calcite crystals; preparation with acetic acid proved effective.

Material available.

Vertebrae: parts of at least 6, including 3 dorsals and 3 sacrals; together with 2 ends of centra which could belong to these or to other vertebrae.

Humerus: right, lacking distal end.

Vertebral column.

Table of principal measurements. See overleaf.

Dorsal region.

Mid-dorsal vertebrae. (Plates 45 and 46). One of these consists of a complete centrum bearing the sides of the neural arch and the weathered lower parts of the bases of the transverse processes. Another consists of the anterior half of a centrum and neural arch, together with the bases of the transverse processes no. 50b - TABLE OF PRINCIPAL MEASUREMENTS OF THE VERTEBRAE (millimetres)

Centrum:	mid-dorsals			sacrals		
	whole	half	end	S1	S2	S3
length below	38	-	-	-	39	38
anterior height	31	33	29	-	30e	32
anterior width	28	31	30	-	32?e	31
posterior height	31	-	-	-	32	34
posterior width	29	-	-	-	30	34
mean diameter	30	32	29½	-	31	33
elongation ratio	1.27	-	-	-	1.26	1.15
minimal transverse thickness	17	20	-	-	-	24

(e - estimated)

and the prezygapophyses. The third includes only the front end of a centrum, showing the beginning of the anteroventral buttress on the right side.

The complete centrum is longer (by 27%) than its own mean diameter. All the centra are constricted below and at the sides, and the floor of the neural canal is deeply excavated within each vertebra. The centra are rounded beneath, the whole one with a faint median ridge; the form of their moderately concave end-surfaces is variable, probably because of weathering. The broken centra are seen to be hollow.

The lateral longitudinal depression between the centrum and the neural arch is fairly well developed. The complete centrum bears a weathered parapophysis, the lower edge of which is level with the base of the neural canal and lies some 5-6mm. behind the anterior face of the centrum; its facet is directed obliquely outwards and downwards. An anteroventral buttress extends obliquely upwards and backwards from this to the origin of the diapophysis, situated high on the side of the neural arch and a little in front of the middle of the vertebra. A posteroventral buttress passes backwards and slightly downwards from the diapophysis to die out 13mm. in front of the posterior face of the centrum. A deep hollow underlies the diapophysis. In the half-centrum the broken-off base of the transverse process begins just below the level of the base of the neural canal and 7mm. behind the front of the centrum, whence it extends upwards and backwards, at first obliquely and then less steeply. In the third fragment the slender anteroventral buttress begins at the level of the base of the neural canal, 7mm. behind the front of the centrum. The prezygapophyses of the half-centrum are small, close together (transverse span 20mm.), and not very obliquely inclined; a deep gap between them may well be natural and could have received a hyposphene from the preceding vertebra. The beginnings of anterior spinal buttresses are indicated.

Sacrum.

The supposed order of succession of the three vertebrae is based on a comparison with Spondylosoma. If this be correct, then the articulation between the second sacral vertebra and the third is smaller (32mm. by 30-31mm.) than that behind the third (34mm. by 34mm.) The correctness of the order adopted, while still open to some measure of doubt, nevertheless tends to be confirmed by the fact that the fit of the articulating faces between these two centra is better than it would be if the succession were reversed; and further confirmation stems from the presence in the supposed second sacral vertebra and the absence in the supposed third (exactly as in Spondylosoma) of concavities underlying the rib-sutures.

Supposed first sacral vertebra. (Plates 45 and 46). This is represented only by a fragment of the right side: the prezygapophysis, that part of the centrum which lies immediately beneath it, and the whole of the sacral rib.

The rib is situated anteriorly on the upper half of the centrum and the side of the neural arch, and has a swollen suture at its base; the whole rib is directed obliquely outwards and downwards. Seen from the front, it is much broader distally (46mm.) than at its base (21mm.). The lower (parapophysial) part is massive and club-shaped distally, being thickened towards the front so that its anterior face is strongly convex. The distal facet for the ilium is consequently enormous; it measures 29mm. from top to bottom and 23mm. from front to back. The ventrolateral corner bears a backwardly directed facet (15mm. by 13mm.) which presumably articulated with a forward extension of the second sacral rib. The upper (diapophysial) part of the rib is directed a little obliquely forwards; it is as long as the lower part, its dorsolateral corner lying 50mm. from the junction of the neural arch with the anterior face of the centrum. Its upper surface is fairly flat and of almost constant width (about 11mm.), and is joined to the lower part of the rib by a stout wall. Its front edge is sharp in its distal and middle portions, but fades out towards the base of the rib; the anterior surface of the rib is more or less flat proximally and deeply concave distally. The hinder edge of the upper surface also forms a backwardly projecting shelf, beneath which the posterior surface of the rib is concave proximally and broad and flat distally. The distal surface of the diapophysial part of the rib forms an upward extension of the great iliac facet formed by the parapophysial part; dorsally it curves towards the front. The prezygapophysis bears an almost horizontal facet, and does not extend forwards as far as the plane of the front of the centrum, to which it is connected by a sharp vertical ridge at the side of the neural canal.

Supposed second sacral vertebra. (Plate 45). This vertebra consists of the right half of the centrum (split more or less sagittally, but with the hinder face entire) together with the base of the sacral rib.

The centrum closely resembles the mid-dorsal centrum described above in both size and form; it is, however, less constricted below, and there is no trace of a ventromedial ridge. The ends of the centra are moderately concave, and the posterior face is elliptical in form, being rather higher than wide.

The base of the lower part of the sacral rib lies well forward on the side of the upper part of the centrum; its anterior margin lies only 3mm. behind the front of the latter, while its posterior margin lies 15mm. in front of the back of the vertebra. This base is bordered below by a swollen suture, beneath which are two light concavities. The base of the upper part of the rib originates from the side of the neural arch and is also preserved, together with a portion of its dorsal surface; it is continuous with the base of the lower part directly beneath it and is axially narrower (respective widths 11mm. and 21mm.). The dorsal surface is produced forwards and backwards into horizontal shelves as in the first sacral rib, but is much broader than in the latter (20mm.). The total height of the base of the sacral rib is 30mm. There is a large hollow behind the rib, at the side of the neural arch and below the postzygapophysis (not preserved); and a short, stout horizontal buttress runs forwards from near the posterodorsal corner of the centrum to the base of the sacral rib, separating this hollow from the hinder of the two concavities mentioned above.

Supposed third sacral vertebra. (Plate 45). The whole centrum is present, together with the sides of the neural arch and the bases of the lower parts of both sacral ribs.

This centrum, while of the same general type as its predecessor, differs in being far more massive. Its length and the dimensions of its anterior face are much the same as in the supposed second sacral, but the almost circular hinder face is larger and there is very little lateral constriction.

The rib extends further ventrally than that of the supposed second sacral, while its base is more central in position; at its widest point it is 20mm. across, and it lies 6mm. and 12mm. from the front and hinder faces of the centrum respectively. There are no hollows in the side of the centrum beneath the suture. The lower part of the rib was thicker than the upper, and seems to have been directed forwards.

Fragmentary vertebral material.

The complete end of a centrum and a fragment of another are also preserved. The former is 31mm. high and 33mm. wide.

Humerus. (Plate 47).

The right humerus lacks its distal end. The fragment as preserved is 126mm. long.

The pre-axial and post-axial sides of the proximal region are expanded into a deltopectoral crest and a processus latissimi dorsi respectively. The former is remarkable in that its apex is situated a considerable distance below the proximal end of the bone (54mm. from the highest point on the head); further, while its major part is directed obliquely downwards and forwards, this extreme apex is bent straight forwards again. The crest is slender below the apex, its margin forming a fairly sharp edge; above the apex the pre-axial margin gradually increases in thickness and meets the broad proximal end-surface of the bone at its highest point. The proximal end-surface is more or less flat and measures 51mm. by 20mm.; its post-axial end forms the apex of the processus latissimi dorsi, much more proximal in position than the apex of the deltopectoral crest.

The processus latissimi dorsi nevertheless extends as far down the shaft as the deltopectoral crest, about 75mm.; its lateral border is thick and rounded. Seen from above, the shaft is 16mm. across and 15mm. thick at its narrowest point; it begins to expand again before the place where it is broken off. The broken surface measures 25mm. by 17mm. and shows that the bone is hollow, with walls approximately 3mm. thick; if its form is truly indicative of the plane of expansion of the distal end, then the humerus is hardly twisted at all. A square-cut edge separates the pre-axial surface of the shaft from the dorsal surface, and extends up on to the dorsal surface of the proximal expansion as far as the level of the apex of the deltopectoral crest.

Comparisons and affinities.

Dorsal vertebrae.

The form of the mid-dorsal vertebrae, as far as can be judged from such imperfectly preserved fragments, differs from that found in *Mandasuchus* only in that a faint ventromedial ridge is present. The whole vertebra, however, is relatively longer; its elongation ratio (1.27) is about the same as that of an approximately corresponding centrum from the much smaller Mandasuchus longicervix type-specimen, and considerably greater than that of a mid-dorsal centrum of specimen no. 63 (1.03), which latter is of equal length (38mm.) but much stouter (mean diameter 37mm. instead of 30mm.).

Sacrum.

The form of the sacrum shows a great resemblance to that of the Brazilian archosaur Spondylosoma absconditum von HUENE. A detailed comparison of the two sacra is given below. (See also Plate 53).

Size. Specimen no. 50b seems to have been of about the same size as Spondylosoma; the length of the centrum of the supposed second sacral is a little more than that of the corresponding centrum in Spondylosoma, but the 50b centrum is slightly lower. The length and height of the supposed third centrum are appreciably greater in specimen no. 50b; but it will be remembered that the third sacral vertebra of Spondylosoma belongs to a different individual, smaller than the type-specimen. A comparison of the respective elongation ratios is not significant:

	specimen no. 50b	Spondylosoma
S2	1.26	1.12
S3	1.15	1.22

<u>First sacral vertebra</u>. The similarity here is particularly close. The sacral ribs resemble each other in their anterior position, the swollen sutures around their bases, and the downward direction of the whole rib. The parapophysial part is broadly expanded distally in both animals, the axial length of the distal end being the same; but its lower surface, rounded in specimen no. 50b, is more or less flat in <u>Spondylosoma</u> and the distal end therefore appears less thick. The backwardly directed facet is not present in the Brazilian animal. The diapophysial part of the rib is directed slightly forwards in both beasts; in <u>Spondylosoma</u>, however, it is comparatively narrow and weakly developed, and it is broken off short so that the backwardly projecting shelf cannot be seen. The sharp front edge, on the other hand, continues upwards and forwards towards the base of the prezygapophysis in <u>Spondylosoma</u>, leaving a deep hollow beneath it. In neither animal are the prezygapophyses much inclined to the horizontal; those of <u>Spondylosoma</u> differ in projecting a little in front of the centrum, and they seem to be closer together.

<u>Second sacral vertebra</u>. The <u>Spondylosoma</u> centrum is a little shorter and much more constricted in ventral view than that of specimen no. 50b; its

posterior face, being a little higher and much wider, is almost isodiametric. (Its extraordinarily deep concavity may well be artificial). The base of the sacral rib is in about the same position, being perhaps a little lower on the centrum and a little further back in Spondylosoma. The two concavities underlying the swollen suture on each side are rather better developed in the Brazilian reptile, where the upper part of the rib is narrower and the hollow behind the rib virtually absent (so that the buttress beneath it appears less prominent).

Third sacral vertebra. The centra are much alike as far as they are preserved. The concavities beneath the rib-sutures, entirely lacking in specimen no. 50b, are virtually absent in Spondylosoma too.

Humerus.

The humerus, as already indicated, is remarkable for its possession of a deltopectoral crest extending far down towards the shaft. This character distinguishes the specimen from Spondylosoma, in which the humerus, though badly weathered, clearly shows the high position of the deltopectoral crest. Specimen no. 50b thus appears to resemble the Saurischia more closely than does Spondylosoma in this respect.

Conclusions.

In summary, it may be said that this specimen shows great similarities to the Prestosuchidae, especially Mandasuchus and Spondylosoma; and that, in particular, it resembles Spondylosoma (the most advanced of the Prestosuchidae) in its possession of a sacrum composed of at least three vertebrae and in the exact form of those vertebrae. Other characters indicating its advanced nature are its fairly large size; the hollow, lightly constructed nature of its bones; the possession of dorsal vertebrae which, for their size, are more elongated than those of any other known Prestosuchid; and, placing it even closer to the Saurischia than Spondylosoma, the possession of a humerus with the apex of the deltopectoral crest lying well below the proximal end. Whether or not this creature possessed an open acetabulum is at present unknown; it shows no "pseudosuchian" characters whatsoever, but in view of its marked resemblances to the more advanced Prestosuchids it may perhaps be described as "Prestosuchid gen. et sp. indet." It seems to represent the most advanced archosaur known from these beds.

d) SPECIMENS NOS. 52a, 52c, 52d and 52e

Field-collection no. 52 was found in locality B9/2 between Kihoho and Mkongoleko. Specimen no. 52a consists of two very large teeth; specimen no. 52b is a dicynodont centrum; specimen no. 52c is an elongated caudal centrum; and specimens nos. 52d and 52e are the distal parts of two small left femora. The state of preservation is variable.

i) Specimen no. 52a

This consists of two extremely large teeth. One (Plate 44) is well preserved and is 52mm. long. The whole tooth is flattened from side to side and has sharp anterior and posterior cutting edges bearing fine perpendicular serrations (about 2 to the millimetre). The base measures 21mm. by 15mm. and shows a central pulp cavity measuring 11mm. by 5mm. Distally the tooth tapers to a point and is recurved to a moderate extent; a lateral curvature of the distal third is probably artificial.

The other tooth is yet larger (68mm. long and possibly incomplete) but is very badly preserved. It is less curved than that described above but seems to have been of the same general type.

The size and form of these teeth render it probable that they belong to some large archosaur; they are not too large to have belonged to a Stagonosuchus or even to a large Mandasuchus.

ii) Specimen no. 52c

This is a well preserved caudal centrum 31mm. long (Plate 44). The anterior face is 14mm. high and 15mm. wide; the posterior face is 14mm. high and 16mm. wide; the centrum is therefore 2.07 times as long as its own mean diameter. It is a little constricted below and at the sides (minimal transverse thickness 9mm.), but for most of its length its borders are straight; there is no deepening of the floor of the neural canal. The posterior face bears haemapophysial facets. The ventral surface shows two light longitudinal ridges, and there are two similar ridges in the middle of each side of the centrum. The end-surfaces are moderately concave.

Enough is preserved to show that there was no transverse process but only a downwardly facing shelf running the length of the vertebra at the base of the neural arch. A shallow groove lies beneath it.

The form of this vertebra, especially the absence of any deepening of the floor of the neural canal and the lack of a transverse process, indicates that it comes from the distal region of the tail. The relatively large size and elongated nature of the centrum suggest a probable archosaur origin - possibly from the same animal as the two large teeth described above (specimen no. 52a). It is, however, more elongated than any known vertebra of Mandasuchus.

iii) Specimen no. 52d

This fragment (Plate 44) is the well preserved distal part of a small left femur, showing the typical curvature, and is 46mm. long. The anterior surface is flat; the posterior bears a wide groove at its distal end, and this divides the end-surface into the larger fibular condyle above and the smaller tibial condyle below. A ridge above the groove runs down to the fibular condyle. The end-surface measures 17mm. dorsoventrally and 13mm. across the fibular condyle. The shaft, where broken off, measures 9mm. by 7mm. and bears a light ridge on its posterodorsal surface; it is hollow, with walls about 1mm. thick.

The form of the distal end is very similar to that found in Teleocrater, but the shaft does not seem to be flattened as in that animal and the bone is very much smaller. It seems probable that this specimen is derived from a small pseudosuchian of uncertain affinities.

iv) Specimen no. 52e

This fragment, 54mm. long, is also the distal part of a small left femur, but is very badly preserved. Except in that it is larger, it bears a general resemblance to specimen no. 52d described above; the end-surface is 22mm. long and measures 14mm. across the fibular condyle.

e) SPECIMEN NO. 53b

This specimen (Plate 48) is the single caudal vertebra mentioned above as being found with the second specimen of Teleocrater tanyura (no. 53a, to which it is far too large to belong) in locality B9/2 between Kihoho and Mkongoleko. It is well preserved; only the ends of the prezygapophyses and the upper part of the neural spine are missing.

The centrum is 40mm. long below; it is 24mm. high and 27mm. wide in front, and 24mm. high and 28mm. wide behind. Its elongation ratio is therefore 1.54. It narrows rapidly just behind the anterior end (minimal transverse thickness 18mm.) and then becomes thicker again towards the back. The lower edge of the hinder face bears well defined haemapophysial facets; except for a pair of short light ridges running towards these facets, the underside of the centrum is smoothly rounded. The centrum is moderately amphicoelous.

The transverse process lies just behind the middle of the vertebra at the junction of the centrum and the neural arch; it is a small but stout thorn-like projection 5mm. long, somewhat flattened dorsoventrally and supported by faint oblique buttresses radiating from its base. The prezygapophyses are very stout and, even broken off as they are, project well beyond the front of the centrum; no basin lies between them. The postzygapophyses are small and set close together, with their facets placed almost vertically and directed outwards; they project a short way behind the centrum. The stout, axially short neural spine is set far back and rises almost vertically; its thick and rounded anterior edge is situated directly above the transverse process, while its narrow posterior edge ascends from between the bases of the postzygapophyses (spinal buttresses and concavities are absent). It is broken off some 14mm. above its base; the broken surface is 14mm. long and has a maximal breadth of 8mm.

This vertebra shows no great similarity to any other described from the "Upper Bone Bed". The elongation of the centrum and the fact that it is certainly derived from an exceptionally large animal nevertheless tend to indicate an archosaur origin.

f) SPECIMEN NO. 58

This large mid-cervical vertebra (Plates 49 and 50) was found alone in locality B12 at Mkongoleko/Njalila. It is well preserved except in that it has been subjected to strong lateral compression; the sides of the neural arch have been crushed in so that the lumen of the neural canal is virtually occluded, and the whole vertebra has been distorted so that the various processes on its left side seem to lie more dorsally than the corresponding processes on the right. The only parts broken off are the end of the right postzygapophysis and the anterodorsal corner of the neural spine.

The centrum is 61mm. long below; it is 40mm. high and 37mm. wide in front, and 43mm. high and 38mm. wide behind. Thus it is 1.54 times as long as its own mean diameter. Seen from the side, it is much constricted beneath, the highest point of its ventral margin being nearer the front than the back; and it is also much constricted laterally, the minimal transverse thickness being 16mm. The ventral surface is rounded, with a slight tendency towards flattening, and its anterior third bears a light median ridge. The anterior face seems to be weakly concave; the posterior face is more deeply so and is roughly circular in outline. Both faces lie obliquely relative to the axis of the centrum; in other words, the anterior face is situated more dorsally than the posterior if the vertebra be orientated with these faces vertical.

A deep longitudinal depression lies on each side of the vertebra between the centrum and the neural arch; the latter projects sideways well beyond the centrum in the middle of the vertebra. The parapophysial facet is 11mm. high and 8mm. wide and lies on the anterior margin of the centrum, just above the ventral corner; the distance between the two parapophyses, seen from below, is 32mm. The diapophysis lies higher on the centrum, 4mm. behind its anterior margin and 6mm. above the parapophysis; it is very short and projects obliquely downwards and outwards, terminating in a facet 6mm. high and 9mm. wide. A ridge runs back from this facet along the side of the vertebra and above the lateral longitudinal depression. The zygapophyses are exceptionally large and powerful and project well in front of and behind the centrum respectively; a deep cleft separated the postzygapophyses, and what appears to be a large but badly crushed hyposphene lies beneath them. (This latter could be an artifact due to the crushing). An ascending ridge runs backwards on either side of the neural arch to become the outer border of the postzygapophysis. The left posterior spinal buttress bears a small but prominent backwardly directed muscle-process 7mm. above the facet of the postzygapophysis. The neural spine is high and slender, rising 79mm. above the top of the centrum; its anterior margin begins between the origin of the prezygapophyses (there being no anterior spinal buttresses) and slopes upwards and forwards, while its posterior margin, formed by the union of the posterior spinal buttresses, rises almost vertically. The spine is thus axially longer at its dorsal surface (length estimated at some 50mm.) than at its base. The dorsal surface is flat but not expanded at all, its greatest transverse width being 7mm.

This vertebra resembles the mid-cervicals of Mandasuchus. The centrum is of about the same proportions as the fourth and fifth cervicals of specimen no. 63 and is about 1.23 times as large, but the lateral constriction is more marked and the parapophyses are relatively further apart than in those vertebrae; this may indicate a slightly more posterior position. One particular similarity between the specimens lies in the presence of the muscle-process on the back of the postzygapophysis. The chief differences lie in the form of the neural spine. This is relatively higher in the present specimen, where its height (measured from the top of the centrum) is much greater than the length of the centrum; in Mandasuchus the height of the neural spine is either approximately equal to the length of the centrum (as in specimen no. 13) or even appreciably less (as in specimen no. 11b). Further, the dorsal surface of the neural spine is not expanded as in the Mandasuchus type-specimen, its greatest transverse width being no more than in one particular cervical of the comparatively tiny specimen no. 13; this probably indicates that there was no dermal armour protecting the back of the neck. (Saurischians are characterised by their lack of such expansions, but their cervical neural spines are usually low). Other differences lie in the absence of anterior spinal buttresses, and, if natural, in the presence of a hyposphene.

It is perhaps best to designate this vertebra as "Prestosuchid gen. et sp. indet." It could well have belonged to the advanced genus of Prestosuchid which is represented by specimen no. 50b described above;

there is, however, no evidence either for or against such a hypothesis, and this vertebra is certainly derived from a substantially larger animal.

g) SPECIMEN NO. 69a

Field-collection no. 69 was found on the surface in locality B15/2 at Mkongoleko/Njalila. It includes the distal part of a small right humerus (specimen no. 69a), the eleventh or twelfth pre-sacral vertebra of a Stenaulorhynchus (specimen no. 69b), and a number of unidentified fragments.

The distal part of the humerus (Plate 48) is very similar to that of specimen no. 11a described above. It is a little smaller, but rather more of the shaft is preserved so that the fragment is in fact longer (31mm.) than that of specimen no. 11a. The hollow shaft is 6mm. broad and 5mm. thick where broken off, and the end-surface measures 21mm. by 9mm. There is scarcely any depression on the anteroventral side of the bone. An ectepicondylar groove is definitely absent.

This specimen is almost certainly derived from a smaller animal belonging to the same genus, and possibly to the same species, as specimen no. 11a; that is, to a pseudosuchian of indeterminate genus and species.

h) SPECIMEN NO. 71

Field-collection no. 71 comprises only one small right humerus found in locality B15/3 at Mkongoleko/ Njalila. This bone, though complete, is not well preserved.

The humerus (Plate 48) is 58mm. long. It resembles that of specimen no. 11a but is smaller and more delicately constructed. The proximal end-surface is 23mm. long and its greatest width is 5mm. The pre-axial face of the proximal end is flat and bears a low deltopectoral crest projecting downwards; the post-axial border forms a fairly sharp ridge. The shaft is 6mm. across and 5mm. thick at its narrowest point. The distal end, expanded in a plane which lies at about 45 degrees to the plane of the proximal expansion, is very poorly preserved; the end-surface measures 18mm. by 7mm., the depression on the posterodorsal surface is well developed while the anteroventral surface is almost flat, and there is no ectepicondylar groove.

This specimen may also belong to the same indeterminate genus of pseudosuchian as specimen no. 11a.

j) SPECIMEN NO. 107

This very large posterior dorsal vertebra (Plate 50) was found isolated in locality B30 between Mdongossi and Ndembe. It lacks the right diapophysis and part of the parapophysis, the postzygapophyses and the neural spine.

The centrum is 48mm. long below; it is 51mm. high and 47mm. wide in front, and 52mm. high and 48mm. wide behind. Thus its length is very slightly less than its own mean diameter. It is much constricted below and at the sides, the minimal transverse thickness being 19mm.; the lower surface is smoothly rounded. The anterior face is very lightly concave, the posterior almost flat.

There is a deep depression in the side of the vertebra between the centrum and the neural arch. The transverse process is borne on the side of the latter at the level of the neural canal and projects outwards and slightly forwards and downwards. Its anterior (parapophysial) part may be complete on the left side. The posterior (diapophysial) part lies behind the parapophysial and a little more dorsally, and it projects further; it has a smooth dorsal surface and terminates in a facet 18mm. long and 9mm.

high whose furthest point is 34mm. from the mid-line. This facet is separated from the parapophysial facet by a constriction. The diapophysis is supported from below by a very short, stout posteroventral buttress, between which and the parapophysis is a deep inferior pleural concavity underlying the transverse process. The posterior margin of the diapophysis forms a sharp ridge which is continued backwards towards the (missing) postzygapophysis. The anterior opening of the neural canal is 14mm. high and 20mm. wide. The prezygapophyses are massive and their facets, separated by a median gap, are rather obliquely inclined towards each other; while they project a very short way in front of the centrum, their transverse span (36mm.) is less than the width of the centrum. The anterior margin of the neural arch on each side forms a sharp ridge running up from the top of the centrum to just below the prezygapophysial facet. A shallow basin lies between the prezygapophyses.

The form of this vertebra closely resembles that of a posterior dorsal vertebra from the type-specimen of Mandasuchus longicervix (no. 11b); the supposed thirteenth dorsal of the latter affords a good comparison. Specimen no. 107 is approximately twice as large in its linear dimensions and shows certain differences in its proportions; thus the centrum is not elongated relative to its own mean diameter, its articulating faces are higher than wide, and the neural canal is relatively much smaller. Such differences, however, may be attributed to the difference in absolute size, and the vertebra may be described as "cf. Mandasuchus". The animal to which it belonged must have been exceptionally large for a pseudosuchian and probably measured nearly two metres from the tip of the snout to the sacrum, perhaps four metres with the tail.

6. REVIEW AND LIST OF THE ARCHOSAUR FAUNA OF THE RUHUHU VALLEY

All material described from the "Upper Bone Bed" and referred by previous authors to either the Pseudosuchia or the Saurischia must be reviewed in the light of the present work. Such material has already been catalogued in the Introduction (Chapter 1, Section c). The only two archosaur genera named from the Bed hitherto - Stagonosuchus and Parringtonia - have been discussed in Chapter 4 and will not be considered here.

1. "Stenaulorhynchus stockleyi" HAUGHTON (1932).

This new genus and species of rhynchosaur was founded on the proximal half of a right humerus. Other fragments of humeri and femora were referred correctly to the same species, but von HUENE has already shown by his work on Stenaulorhynchus (1938b) that the rest of the material was of an archosaur nature.

a) Dorsal vertebrae. Four posterior dorsal vertebrae were found, three attached by matrix to a femur of Stenaulorhynchus and one in isolation. Haughton tentatively concluded that these three vertebrae belonged together with the femur, and was much puzzled by the archosaurian nature of the former and the evidently rhynchosaurian affinities of the latter. The centra are described as not quite so long as high, not quite so wide as high, much constricted and lightly amphicoelous. The para- and diapophysis are distinct and carried on the neural arch; the former lies at the height of the neural canal and the latter is short. The articular facet of the prezygapophysis is inclined to the horizontal at an angle of about 30 degrees and does not project anteriorly beyond the centrum. The neural spine is broken off in every case.

Von HUENE (1939b) describes these vertebrae as anterior dorsals of a typical pseudosuchian; and he compares them, with their "spectacles"-shaped rib-articulations and short diapophyses, to the vertebrae of Rauisuchus and Prestosuchus.

In the nature of the centrum and rib-articulations the figured vertebra resembles also the posterior dorsals of Mandasuchus. (In the type-specimen of Mandasuchus, no. 11b, the centra are considerably smaller and relatively longer; but in the largest specimen, no. 63, they are of about the same size as in Haughton's specimen and approximately as long as high). On the other hand, if Haughton's illustration is accurate, the form of the zygapophyses and of the base of the neural spine is quite unlike that of any other pseudosuchian known. The prezygapophysis and the base of the neural spine seem to form a more or less continuous ossification without a deep bight separating them in lateral view; and the post-zygapophysis appears to be overhanging, for it juts downwards from the base of the neural spine and is separated from the neural arch by a wide gap. The affinities of these vertebrae must therefore remain obscure for the present.

b) Skull fragment. This consists only of the anterior tooth-bearing portions of the maxillae of a narrow-snouted Thecodont, lying so close together that only a deep and very narrow groove is left between them on the palatal side. The alveoli are longer than broad, large and deep. The teeth are oval in section with a coarsely serrated anterior edge; the posterior edge does not seem to be serrated. From the upper border of the bone a strong bar passes obliquely upwards and backwards; behind it lay the antorbital vacuity.

Von HUENE (1939b) remarks that this fragment must belong to a pseudosuchian related to the animal whose vertebra was figured by Haughton (see a) above), but probably to a substantially larger beast. The narrowness of the snout and the consequently presumed elongation of the skull are said to indicate a pseudosuchian rather than a carnosaur or a coelurosaur. Von Huene also suggests that the fragment may have belonged to Stagonosuchus. This suggestion is presumably based only on its great size; even so, it does not appear to be large enough to be derived from an animal as large as either of von Huene's specimens. It is true that large archosaurs other than Stagonosuchus were present in the Manda Beds. For example, in the Parrington collection there are two giant teeth - specimen no. 52a - and a large isolated posterior dorsal vertebra - specimen no. 107, q.v., - which latter has a centrum about twice as high as that of a vertebra from the same region of the Mandasuchus type-specimen; it is not impossible that Haughton's skull fragment should belong to such an animal. In a later publication (1940a) von Huene states that both skull fragment and vertebrae (see a) above) are derived from a small Stagonolepid related to the Brazilian Rauisuchus.

The fragment seems to differ from the maxilla of the <u>Mandasuchus</u> <u>longicervix</u> type-specimen (no. 11b) and that of specimen no. 77a, described by von Huene as "Saurischian gen. et sp. indet." (see 5. below). It is approximately twice as large in its linear dimensions, and must therefore have belonged to an animal considerably larger than the largest known specimen of <u>Mandasuchus</u> (no. 63). The form of the antorbital vacuity in Haughton's specimen is such that its anteroventral corner forms a fairly sharp angle; the ascending process of the maxilla is broken off much lower down in specimens nos. 11b and 77a, but in both the anteroventral corner of the antorbital vacuity seems to have been broadly rounded. Moreover, in Haughton's fragment that part of the maxillary surface which borders the antorbital vacuity seems to lie more or less horizontally, while in specimen no. 77a (and to a much lesser extent in specimen no. 11b) it slopes obliquely downwards and outwards or forwards and outwards (see von Huene's figure). Further differences between the fragments are shown by Haughton's observations - if the latter be correct - that a portion of the jugal seems to lie on the upper edge of the maxilla right at the front of the antorbital vacuity, and that the posterior borders of the teeth in his specimen are not serrated.

2. "Stenaulorhynchus major" HAUGHTON (1932).

The distal halves of a left and a right humerus from different localities were referred by Haughton to a new species of Stenaulorhynchus.

Von HUENE (1939b) showed that these fragments actually belong to the large pseudosuchian Stagonosuchus nyassicus from the same region.

3. "Thecodontosaurus(?) alophos" HAUGHTON (1932).

a) Cervical vertebrae. Two anterior cervical vertebrae were found, the longer being the better preserved. The centrum is between three and four times as long as high and is deeply excavated beneath in lateral view. Its ventral face is hollow between the parapophyses; behind this is a short flattened area which passes back into the rounded hinder half of the centrum. The ends are lightly concave, the posterior hollowing being the deeper. The parapophysis is an elongate knob stretching back from the ventral side of the lower quadrant of the anterior face and sinking into the body posteriorly by a short keel. The diapophysis is a downwardly directed flange lying wholly in the anterior half of the centrum, its outer edge being in the plane of the middle of the body. From its anterior end a sharp ridge passes upwards and forwards to the underside of the prezygapophysis. The neural canal is wider than high at its anterior end. The prezygapophysial facet projects in front of the centrum and is only slightly inwardly inclined. The postzygapophysis does not project behind the centrum. The neural spine has a long narrow base, but its upper part is broken off.

Haughton refers these two cervical vertebrae and the two associated dorsals (see b) below) to a small theropod, noting that they "show considerable similarity with those of the Thecodontosauria (sic), particularly with that described as _Coelophysis collis_", but that they differ in the absence of a ventromedial keel. He therefore places them temporarily in the genus _Thecodontosaurus_ under the new specific name _T. alophos_.

Von HUENE (1939b) agrees that the elongation of the vertebrae indicates a saurischian, but remarks that the size and the high neural spine definitely exclude reference to the genus _Thecodontosaurus_. He also suggests (1939b, 1940a) that the figured vertebra could be associated with his "saurischian" maxilla (see 5. below) on grounds of commensurate size.

A certain resemblance exists between the vertebra figured by Haughton and the supposed anterior cervical vertebra of the type-specimen (no. 48b) of Teleocrater. Haughton's specimen, as is evident both from his own remarks and from his drawings, was not adequately prepared, and the Teleocrater vertebra is badly damaged at the front. Haughton's specimen nevertheless seems to differ only in the following particulars, some of which may be artificial:

i) It is considerably larger and relatively shorter, the centrum being 73mm. long and 23mm. high posteriorly (corresponding figures for Teleocrater vertebra 53mm. and 14mm.).

ii) There is no ventromedial ridge, of which there is a trace in Teleocrater.

iii) There is no posteroventral prolongation of the diapophysial ridge as in Teleocrater.

iv) There does not appear to be a ridge running obliquely backwards and slightly downwards from the prezygapophysis as in Teleocrater.

v) The postzygapophysial facet faces downwards rather than obliquely outwards as in Teleocrater, in which latter animal it also projects a very short distance behind the centrum.

vi) The posterior excavation of the neural arch for the exit of the spinal nerve is hardly indicated. (Artificial?).

vii) The anterior spinal buttresses appear to show a marked lateral convexity in anterior view.

viii) The neural spine rises more steeply behind. (Artificial?).

Many of these slight differences, if natural, could be attributed either to differences in age or to intra-regional variations within the vertebral column. It may therefore be concluded that these vertebrae could belong to _Teleocrater_ or to a somewhat larger related genus.

b) _Dorsal vertebrae_. These are also two in number and incomplete. The centrum of the better preserved is about one and a half times as long as high, evenly constricted in the middle, without a ventromedial keel or ridge and lightly amphicoelous. The anterior face is squarish in outline, the posterior rounded. The parapophysis is short and lies at the height of the threshold of the neural canal, obliquely before and beneath the diapophysis.

These vertebrae agree well with the anterior dorsals of Teleocrater except in that they are larger and relatively shorter (elongation ratio of Teleocrater centra 1.60 to 1.94).

4. "Theropod gen. et sp. indet." HAUGHTON (1932).

This is represented by an isolated dorsal vertebra lacking diapophyses and neural spine. The centrum is a very little longer than high, moderately constricted, without a ventromedial ridge and with lateral hollowing; the posterior margin projects further downwards than does the anterior, and both faces are almost flat. The parapophysis is near the anterior border and lies on the neurocentral suture, about one third of its surface being formed by the centrum. All four diapophysial buttresses and the anterior, inferior and posterior pleural concavities are well developed; the anteroventral buttress runs to the parapophysis. A rounded ridge connects the upper surface of the parapophysis with the under-surface of the prezygapophysis, and there is a shallow groove between this ridge and the margin of the neural canal. The facets of the prezygapophyses are inclined at about 30 degrees to the horizontal. Both pre- and postzygapophyses project beyond the centrum. The posterior spinal concavity is deep.

Haughton compares this vertebra with the fourth and fifth dorsals of Plateosaurus. Von HUENE (1939b) agrees that the vertebra is "unzweifelhaft" the anterior dorsal of a saurischian; in a later publication (1940a) he suggests that it may be related to the prosauropod Massospondylus.

The vertebra compares very closely in size and form with the supposed fourth dorsal of the largest specimen of Mandasuchus (no. 63), in which the centrum is about as long as high. (In the smaller specimens of Mandasuchus it is relatively longer). There seems to be no reason why Haughton's vertebra should not be referred to this genus.

5. "Saurischian gen. et sp. indet." von HUENE (1939b).

This left maxilla (no. 77a in the Parrington collection) was described while still in the matrix. The matrix has now been removed by a combination of mechanical preparation and the acetic acid technique, the latter being particularly successful. Certain of von Huene's observations on the teeth and their alveoli now appear to be not quite correct, and other features of the fragment have come to light. Moreover, a review of its systematic position appears to be necessary.

Von Huene observed that the teeth had fallen out except for one indistinct stump. Dissection has now revealed large stumps in the 4th and 7th of the preserved alveoli and the remains of unerupted teeth in the 9th, 11th and 13th. These teeth bear a close resemblance to those of Mandasuchus; they are strongly compressed, recurved, and have sharp anterior and posterior borders, the former at least being crenulated. It is untrue that each individual alveolus is broader in its anterior part than in its hinder part, and that the anterior edges of the teeth are rounded (although they may have become so later through wear). It is also untrue that the broadest tooth is that which lies directly below the posterior end of the ascending process, and that the two teeth in front of that tooth are broader than most of the others. Further, there appear to be no grounds for von Huene's observation on this jaw, "Sie kann nicht von einem Pseudosuchier kommen, da die Zahnalveolen alle klein sind und dicht stehen." In the same paper he declares, "Diese Maxilla muss also einem grossen Tier, und zwar eher einem Coelurosaurier als einem Carnosaurier angehören," and "Die Zähne sind relativ kleiner und zahlreicher als bei anderen bekannten Coelurosauriern der Trias, und sehr viel zahlreicher als bei Carnosauriern."

The further preparation of specimen no. 77a showed a series of foramina on the lateral surface of the bone, apparently alternating with the alveoli; their openings are directed slightly downwards. The dorsal surface of the posterior part of the maxilla bears a deep groove which becomes shallower anteriorly and eventually fades out a short distance behind the ascending process; this is bordered laterally by a thin vertical wall which forms a dorsal extension of the lateral surface of the maxilla and which becomes higher behind. The jugal may have fitted into this groove. The maxilla itself tapers considerably towards its hinder end. A break through the bone at the level of the eighth preserved alveolus shows that the latter is very deep (14mm.), reaching to within 4mm. of the dorsal surface.

The specimen compares closely in both size and form with the left maxilla of the Mandasuchus longicervix type-specimen (no. 11b). It is better preserved anteriorly, two more alveoli being indicated, but lacks one alveolus preserved at the hinder end of the type-specimen. As mentioned above, the two specimens have similar teeth; and the alveoli of each correspond exactly, even to their individual variations in size and shape along the length of the maxilla. For example, the distance from the front of the most anterior complete alveolus in specimen no. 11b to the back of the last but one complete alveolus - that is, including nine alveoli, - is 78mm., and the corresponding distance in specimen no. 77a is the same. Since there is no doubt that Mandasuchus is a pseudosuchian, von Huene's reason for referring specimen no. 77a to the Saurischia (see above) is thus rendered invalid.

However, the two maxillae are not exactly alike. In crown view, the maxilla of specimen no. 77a is barely perceptibly curved into an S-shape; while the left maxilla of specimen no. 11b shows a much greater curvature, with the outer surface concave beneath the antorbital vacuity and the hinder end of the maxilla directed somewhat laterally. This hinder end is bent slightly downwards in specimen no. 77a and is not so in no. 11b. Both these differences in curvature could have been caused by distortion. The following characters of specimen no. 77a, however, definitely distinguish it from specimen no. 11b:

i) That part of the surface of the maxilla which borders the antorbital vacuity slopes downwards and outwards or forwards and outwards; the antorbital vacuity thus appears to have two more or less parallel margins, an outer below an inner. (The outer margin may correspond to the ledge noted by von Huene on the maxilla of _Rauisuchus_).

ii) The lateral wall is less deep posteriorly.

iii) The series of foramina is nearer the dorsal margin of this wall in the posterior part of the maxilla.

iv) The groove for the jugal is better defined.

v) The shelf medial to the tooth row is better developed.

Despite these minor differences, a comparison of the two specimens leads to the conclusion that specimen no. 77a does not represent a saurischian but that, in all probability, it belongs to another species of _Mandasuchus_.

6. "cf. _Thecodontosaurus_" BOONSTRA (1953).

This single vertebra is described as a fairly small anterior caudal with a centrum 40mm. long, 34mm. high and 28mm. wide, and lacking the upper part of the neural spine. Unfortunately it is not figured.

On grounds of size alone it could well belong to either a large *Mandasuchus* or a small *Stagonosuchus*.

The complete archosaur fauna of the Ruhuhu Valley as known at present is conveniently summarised in the following list:

A. Family PRESTOSUCHIDAE:

1. *Stagonosuchus nyassicus* von HUENE
   - 2 specimens in Tübingen (type-specimens)
   - 2 distal halves of humeri in South Africa ("*Stenaulorhynchus major*" HAUGHTON)

   Stagonosuchus tanganyikaensis BOONSTRA
   - 1 humerus in South Africa (type-specimen)

   cf. *Stagonosuchus*?
   - 1 skull fragment in South Africa ("*Stenaulorhynchus stockleyi*" HAUGHTON)

2. *Mandasuchus longicervix* gen. et sp. nov.
   - specimen no. 11b (type-specimen)
   - no. 13 (smaller)
   - no. 63 (larger)

   Mandasuchus sp. indet.
   - specimen no. 77a (maxilla, "saurischian gen. et sp. indet." von HUENE)

1 dorsal vertebra in South Africa ("theropod gen. et sp. indet." HAUGHTON)

cf. Mandasuchus

specimen no. 107 (very large posterior dorsal vertebra)

3. Prestosuchid gen. et sp. indet.

specimen no. 50b (dorsal vertebrae more elongated than in other Prestosuchids; sacrum of at least three vertebrae very like that of Spondylosoma; more advanced type of humerus)

specimen no. 58 (large mid-cervical vertebra with neural spine higher than in Mandasuchus and not expanded above; possibly from same genus as specimen no. 50b, but no evidence either for or against)

B. Family ORNITHOSUCHIDAE?

4. Parringtonia gracilis von HUENE

specimen no. 68a (type-specimen)

cf. Parringtonia

specimen no. 14a (3 small distal caudal vertebrae, 3 larger haemapophyses)

C. Family TELEOCRATERIDAE:

5. _Teleocrater_ _tanyura_ gen. et sp. nov.

specimen no. 48b (type-specimen)

no. 53a

cf. _Teleocrater_

4 vertebrae in South Africa ("_Thecodontosaurus_(?) _alophos_" HAUGHTON)

D. Family ?

6. Pseudosuchian gen. et sp. indet.

specimen no. 11a

no. 69a (distal part of humerus)

no. 71 (humerus)

7. Pseudosuchian gen. et sp. indet.

4 vertebrae in South Africa (2 individuals, "_Stenaulorhynchus_ _stockleyi_" HAUGHTON)

E. ALSO:

specimen no. 52a (2 very large teeth with serrated edges)

specimen no. 52c (elongated caudal centrum)

specimen no. 52d (distal part of small femur)

specimen no. 52e (distal part of small femur) ?

specimen no. 53b (large caudal vertebra) specimen no. 77c (11½ consecutive small dorsal vertebrae)

1 large anterior caudal vertebra in South Africa ("cf. Thecodontosaurus" BOONSTRA)

7. REVIEW OF THE FRAGMENTARY ARCHOSAUR REMAINS FROM THE MALERI BEDS OF INDIA

The whole of the material listed below was described by von HUENE (1940c), and must be reviewed in the light of the present work.

1. Pseudosuchian gen. et sp. indet. (Form No. 1).

a) Skull fragment. This consists only of part of a maxilla showing five empty alveoli and a small portion of the premaxilla. Von Huene compares it with the skull fragments of the Brazilian *Prestosuchus chiniquensis* and of "*Stenaulorhynchus stockleyi*" HAUGHTON.

b) Cervical vertebra. This vertebra, which lacks zygapophyses and neural spine, is neither elongated nor shortened, the centrum being approximately as long as high and lightly amphicoelous. There is a high ventromedial keel; the parapophysis is situated some distance above the ventral margin of the centrum; and the diapophysis is not supported by buttresses, but has an anteroventral lamella running into the anterior margin of the centrum. The vertebra seems to be a posterior cervical (or anterior dorsal); the lack of elongation and the presence of a high keel show that it cannot represent a species of Mandasuchus (or, for that matter, of Teleocrater). But long cervical vertebrae without ventromedial keels are not invariably characteristic of the Prestosuchidae, and the possibility that this vertebra may be derived from a short-necked genus of that family, such as Prestosuchus itself, cannot be precluded.

c) Caudal vertebra. This vertebra, also lacking zygapophyses and neural spine, is rather longer than high, flatly rounded beneath and with two distinct and well developed haemapophysial facets. There is no transverse process; hence the vertebra must come from a fairly distal part of the tail. Its affinities remain uncertain.

2. Pseudosuchian gen. et sp. indet. (Form No. 2).

This is represented by the distal ends of two very small femora. Each is bent strongly downwards from the longitudinal axis of the whole bone. The condyles are indistinct and are separated by a faint furrow, and there is a small groove on the lateral side of the fibular condyle.

3. "Coelurosaur gen. et sp. indet." ("Form No. 1").

a) Dorsal vertebra. This vertebra is very slender, the centrum being twice as long as high. (The dorsal buttresses, zygapophyses and the top of the neural spine are broken off). The centrum is rounded beneath and lightly amphicoelous. Both ventral buttresses are indicated; they are short, begin high up, and are not steeply inclined. The parapophysis lies on the anteroventral buttress at just half the height of the neural canal; the latter is very large relative to the size of the vertebra. The diapophysis, the buttresses and the base of the neural spine are all very thin. Von Huene notes a great resemblance to the dorsal vertebrae of *Coelophysis longicollis* COPE, and a lesser resemblance to those of *Thecodontosaurus polyzelus* HITCHCOCK. He therefore ascribes this vertebra and the femur (see b) below) to a small coelurosaur, probably a member of the Podokesauridae.

An even greater resemblance, however, is to the anterior dorsal vertebrae of *Teleocrater tanyura*, which latter are of about the same size (length of Maleri vertebra 30mm., length of vertebra "DE" of specimen no. 48b 28mm.). The only observable differences in the Indian specimen are the slightly higher origin of the ventral buttresses and the rather narrower posterior notch for the exit of the spinal nerve. That the Maleri vertebra actually represents a pseudosuchian closely allied to *Teleocrater* seems highly probable.

b) Femur. Von Huene remarks that the distal third of a straight, very slender and thin-walled femur "considering its size and shape could well go together with the vertebra just described." Comparison with the *Teleocrater* type-specimen, however, shows that this femur is in fact far too small; for, while the Maleri vertebra is a little larger than those of *Teleocrater*, the Maleri femur is only about half as large as that of the East African reptile (diameter of distal end 18mm. in Maleri femur, 36mm. in *Teleocrater*). Other differences are to be seen in the Indian bone. The anterior surface is slightly convex; the furrow on the posterior surface between the ridges running down to the condyles is much larger and deeper; the outline of the distal end is more nearly isodiametric; and the articulating surface itself is more rounded. It therefore seems unlikely that this femur is correctly associated with the vertebra, nor do there appear to be any particular grounds for considering the former to denote the presence of a saurischian.

4. Coelurosaur gen. et sp. indet. (Form No. 2).

This is represented only by the extreme proximal end of a small hollow tibia. There is no resemblance to the tibial head of either Mandasuchus or Teleocrater, for the articular face is rather slender in shape and is bent laterally above the cnemial crest. Von Huene compares it with the tibia of the coelurosaur Dolichosuchus cristatus (von HUENE 1932), for in this tibia and in Dolichosuchus there is a lateral longitudinal ridge descending from the articular face below the border between the cnemial crest and the lateral condyle.

This tibia must indeed come from an animal about twice as large as "Form No. 1", considering the latter to be represented by the femur. On the other hand, it is of about the same size as the tibia of Teleocrater and could therefore belong with the vertebra of "Form No. 1", which is but little larger than the Teleocrater vertebrae. The difference in form, however, leads to the conclusion that such an association would be incorrect. There seems to be no reason to deny von Huene's assertion that this tibia probably indicates the presence of a coelurosaur, perhaps related to the Podokesauridae.

5. "Prosauropod cf. Massospondylus sp."

One complete dorsal centrum was referred to a member of the Thecodontosauridae, probably to the genus Massospondylus. Two similar half-centra were also found. The centrum is about one and a quarter times as long as high, is moderately constricted, rounded beneath and lightly amphicoelous. There are lateral hollowings and the neural canal is much deepened within the centrum.

This differs from the dorsal centra of the type-specimen of Mandasuchus only in its greater size and in that it is a little less constricted below. In actual size it agrees well with the largest specimen of the East African reptile (no. 63); in which, however, the dorsal centra are relatively shorter (length and height approximately equal). The Indian vertebra could well have belonged to an animal closely related to Mandasuchus, and therefore to a pseudosuchian.

8. STRATIGRAPHICAL IMPLICATIONS

NOWACK (1937) subdivided the "Upper Bone Bed" of Tanganyika upon its lithology; while BOONSTRA (1953) considered that its faunal assemblage was related to a large part of the South African fauna, beginning at the top of the *Cisticephalus* zone and continuing right up to the Red Beds of the Stormberg. (The rather inadequate grounds for Boonstra's opinions were, presumably, his very doubtful identification of *Lystrosaurus* in the Bed and his identification of a single caudal vertebra as "cf. *Thecodontosaurus*"). But it would appear that, in actual fact, not enough vertebrate material has yet been described or identified from the various localities of the "Upper Bone Bed" to enable it to be determined whether the Bed represents one or several distinct fossiliferous horizons. (A list of localities of apparent "Upper Bone Bed" age, together with lists of the specimens found in each, is given in Appendix IV). The "Upper Bone Bed" must therefore be treated at present as a single stratigraphical unit. Similar considerations apply to the other insufficiently well known beds, such as the upper Rio do Rasto, which enter into the following discussion.

HAUGHTON has already suggested (1932) that the fauna of the "Upper Bone Bed" may be closely correlated with that of the upper Rio do Rasto Beds of Brazil; and, consequently, that these deposits may be homotaxial. (Some authorities prefer to restrict the use of the name "Rio do Rasto" to the lower beds, the age of which is upper Permian, and to refer to the Triassic sediments as the Santa Maria formation. The more conventional term, however, will be employed throughout this discussion). Von HUENE (1939c, 1940a especially) has elaborated this view, basing his arguments partly upon the similar constitution of the two faunas and partly upon the anatomical resemblances of the East African members of the various groups to their South American counterparts. He describes both faunas as 'Faunen "gemischten" Charakters' or "Mischfaunen", defining such a "mixed" fauna as one which contains the earliest saurischians together with the last of the therapsids, namely dicynodonts and cynodonts (although, of course, mammal-like reptiles survive in younger beds as ictidosaurs). The similarity in the constitution of the two faunas extends also to the presence of rhynchosaurs and pseudosuchians and to the apparent absence of phytosaurs and ictidosaurs in both; the only differences lie in the presence of a procolophonid (Candelaria PRICE, 1947) and the apparent absence of labyrinthodonts in the South American beds. Even the latter difference may well be fortuitous, since a brachyopid stereospondyl of about the same age occurs elsewhere on the continent (Pelorocephalus, described by CABRERA, 1944, from Argentina). Von HUENE himself (1938b) had already described the East African rhynchosaur Stenaulorhynchus in great detail and had followed Haughton in pointing out its close relationship to the South American Cephalonia and Scaphonyx, although he opined that it was substantially more primitive than either of these. A fragment of a very large dicynodont skull from the "Upper Bone Bed", recalling that of Kannemeyeria, was mentioned by HAUGHTON (1932) and, to von Huene as to him, seemed to resemble that of the Brazilian Stahleckeria. (Since then von HUENE has described further Ruhuhu dicynodont material from the Tübingen collection - 1942b). Of the East African pseudosuchians, von Huene commented that Stagonosuchus was very like the Brazilian Prestosuchus, both being large Stagonolepids, while the skull fragment and vertebrae described by HAUGHTON (1932) must have come from a small Stagonolepid related to the Brazilian Rauisuchus.

As far as cynodonts were concerned, von HUENE had at this time very little Ruhuhu material upon which to base his comparisons; although he later (1950) described the material available in the Tübingen collection. Since then CROMPTON has described new cynodonts from the much better material in the Parrington collection (1955, in press); he has shown that these are more closely related to the cynodonts of the upper Rio do Rasto Beds than to any others, thus confirming Haughton's and von Huene's conclusions.

Further positive evidence for the view that the "Upper Bone Bed" of Tanganyika and the upper Rio do Rasto Beds of Brazil are homotaxial is provided by the conclusions on the systematic position of Mandasuchus reached above. Four genera of pseudosuchians are considered to belong to the same newly constituted family (Prestosuchidae) on the grounds of close anatomical resemblance; of these, Stagonosuchus and Mandasuchus are from the "Upper Bone Bed" and Prestosuchus and Spondylosoma are from the upper Rio do Rasto Beds. The resemblance of the new genus Mandasuchus to the two South American genera is particularly close, and it might be claimed with some justification that the comparison is more striking than that between any other pair of animals from the two deposits. No remains have been described from any other beds which could be assigned to the Prestosuchidae with any degree of certainty.

No animal resembling Teleocrater has been described from the upper Rio do Rasto Beds.

A considerable quantity of seemingly good dicynodont material from the "Upper Bone Bed" remains in the Parrington collection; its preparation, description and comparison with Stahleckeria are awaited with interest, for such a comparison may well provide further confirmation of the homotaxial nature of the two beds in question.

This confirmation of the close resemblance of the two faunas, taken in conjunction with the apparent absence of similar faunas and of many of their component elements in beds of equivalent age in the Northern Hemisphere, lends further support to the hypothesis that terrestrial animals were able to migrate directly between Africa and South America at that particular time. This does not, of course, necessarily mean that the two continents were then united or lay adjacent to each other, having since drifted apart; the connexion may have been through an isthmus or an island chain.

It seems impossible at present to reach any conclusion as to whether the "Upper Bone Bed" and the upper Rio do Rasto Beds are of exactly the same age or whether one is a little older than the other, especially as it may yet be shown that either or both represent more than one horizon. As mentioned above, von Huene considers the East African rhynchosaur Stenaulorhynchus to be more primitive than the South American Cephalonia and Scaphonyx; but, as he himself has pointed out and as ROMER (1952) has also declared, "the degree of specialization of a rhynchosaur type gives little indication of its stratigraphic position." Further, if an attempt were made to place the various Prestosuchids in some sort of evolutionary progression based on their osteological characters, the most logical sequence would pass from Prestosuchus (from Brazil) to Mandasuchus (Tanganyika), then to Spondylosoma (Brazil) and finally to specimen no. 50b (Tanganyika).

The rocks of the South African Karroo, geographically not far distant from Tanganyika, appear to indicate continuous continental deposition throughout the Trias. There is, however, no "mixed" fauna of the "Upper Bone Bed" type; and neither the Prestosuchidae nor the Teleocrateridae (nor, for that matter, the Stagonolepidae) is represented among the archosaurs found there. The Upper Beaufort Series, lying beneath the almost barren Molteno Beds, contain primitive pseudosuchians which are quite distinct and generally more primitive; these are *Chasmatosaurus* from the *Lystrosaurus* zone, *Proterosuchus* from the *Procolophon* zone, *Elaphrosuchus* from some unspecified horizon in one of these two zones, and *Erythrosuchus*, *Euparkeria* and *Browniella* from the *Cynognathus* zone. That part of the Stormberg Series which lies above the Molteno Beds, on the other hand, contains many more archosaurs of a more advanced nature. The advanced crocodile-like pseudosuchian *Sphenosuchus*, the early crocodilian *Erythrochampsa* and numerous saurischians occur in the Red Beds; two more early crocodilians (*Pedeticosaurus*, sometimes described as a pseudosuchian, and *Notochampsa*), other saurischians and the doubtful ornithischian precursor *Geranosaurus* occur in the Cave Sandstone. Further, while the beds beneath the Molteno Beds contain abundant dicynodonts and cynodonts, these groups are absent from the beds above, in which ictidosaurs are the only mammal-like reptiles known. It would therefore seem, as originally proposed by Haughton and as frequently suggested by von Huene, that the pseudosuchian-containing faunas in the "Upper Bone Bed" of Tanganyika and in the upper Rio do Rasto Beds of Brazil correspond to the gap in the South African faunal succession which occurs in the Molteno Beds; and consequently that the particular horizons of these East African and South American beds in which pseudosuchians are found are contemporaneous with at least a part of the Molteno Beds.

It has been shown that the nature of the respective pseudosuchian faunas of South Africa, Tanganyika and Brazil indicates a far stronger faunal connexion between Tanganyika and Brazil than between Tanganyika and South Africa in that part of the Trias which is under discussion. The similar observations of earlier workers on both the rhynchosaur and cynodont faunas are thus confirmed independently. But it must also be pointed out that the Tanganyikan and Brazilian animals lived at a particular time when conditions of deposition in South Africa seem to have been unfavourable to the preservation of tetrapod remains; that similar animals may in fact have lived in South Africa at that time and left no trace of their presence; and that it would therefore be dangerous to draw any far-reaching palaeogeographical conclusions from these observations.

In the South African Karroo, von HUENE (1940a) regards the Lystrosaurus and Procolophon zones as Lower Triassic in age, the Cynognathus zone as Middle Trias, and the Molteno Beds as part of the Upper Trias. Thus, since the "Upper Bone Bed" and the upper Rio do Rasto Beds are considered to be homotaxial with the Molteno Beds, these are also of Upper Triassic age, and therefore equivalent to the Lettenkohle and Lower Keuper of Europe; and, according to von HUENE (1939c, 1940a), all these beds (except, of course, the Molteno) share the common peculiarity of containing the earliest known saurischian remains. WATSON, on the other hand (1942), prefers to consider the whole of the Upper Beauforts, up to and including the Cynognathus zone, as Lower Trias (correlated with the European Bunter), taking the Molteno Beds as Middle Trias (European Muschelkalk), and leaving only the beds above the Molteno as Upper Trias (European Keuper; plus, perhaps, Rhaetic). As far as can be judged from his paper, Watson bases this correlation entirely on the occurrence in the Cynognathus zone of typical Capitosaurus and Trematosaurus, which, since they are good "time-markers" and are also found in the "Middle" Bunter of Bernberg and in the Russian Zone VI, must certainly indicate a pre-Muschelkalk age for the zone. ROMER (1945, 1952) adopts Watson's view and, in his "Classification of Vertebrates", lists the genera from the "Upper Bone Bed" and upper Rio do Rasto Beds as Middle Triassic; Spondylosoma is included as the only Middle Triassic saurischian. Von HUENE later (1950) suggested that the "Upper Bone Bed" might be either upper Middle Trias or lower Upper Trias. The opinions of earlier workers on the age of these various beds may also be cited; BROOM (1932a) followed Du Toit in regarding the Molteno Beds as Upper Triassic or Rhaetic, while HAUGHTON (1932) considered the "Upper Bone Bed" as certainly Triassic, probably Upper Triassic.

In actual fact it now seems that there is no real evidence for the presence of true saurischians in either the "Upper Bone Bed" or the upper Rio do Rasto Beds. In the former, both the maxilla described by von Huene as "saurischian gen. et sp. indet." and the vertebra described by Haughton as "theropod gen. et sp. indet." have been referred to the pseudosuchian genus Mandasuchus; the vertebrae described by Haughton as "Thecodontosaurus(?) alophos" have been compared with those of the pseudosuchian Teleocrater; while the vertebra described by Boonstra as "cf. Thecodontosaurus" seems to be too nondescript to be assigned to either the Pseudosuchia or the Saurischia with any certainty. In the Brazilian beds, it has been shown that Spondylosoma is, in all probability, an advanced member of the pseudosuchian family Prestosuchidae and not a saurischian, and that the isolated cervical vertebra and isolated "tibia" also referred to the Saurischia by von Huene may be the cervical vertebra and the ulna of this or of related Prestosuchids. No other supposed saurischian material has been recorded from either bed. However, it must be borne in mind that, while there is no real evidence for the presence of archosaurs with open acetabula in these beds, archosaurs which show other "saurischian" characters are certainly present. In this connexion Spondylosoma from the South American beds and the even more advanced specimen no. 50b from the East African beds should be noted especially; the latter has three sacral vertebrae and the deltopectoral crest extending far down the humerus, and appears to represent the most advanced type of archosaur known from rocks of Molteno age.

The lack of certain evidence for the presence of saurischians sensu stricto in the "Upper Bone Bed" of

Tanganyika and in the upper Rio do Rasto Beds of Brazil indicates a Middle Triassic rather than an Upper Triassic age for these deposits. This supports Watson's view that the Molteno Beds, with at least a part of which the Tanganyikan and Brazilian archosaur localities seem to be homotaxial, are of Middle Triassic age. It would nevertheless appear that the differentiation of the pseudosuchian stock into coelurosaur-like types (such as <u>Teleocrater</u>) and pachypodosaur-like types (such as <u>Mandasuchus</u>) was already well under way at that time.

Further confirmation of the Middle Triassic age of these rocks is given by the fact that dicynodonts, present therein, are not known to occur elsewhere in beds of supposed Upper Triassic age (excepting the large, extremely specialised North American <u>Placerias</u>); while cynodonts are not known elsewhere from beds above the Lower Trias. In fact, there seems to be no certain evidence for the existence of "Mischfaunen" (in which therapsids and true saurischians occur simultaneously) in any part of the world. Even in North America possible evidence of such "mixed" faunas is found in three places only. In the Chinle Beds of St. John's, Arizona (of which the Upper Triassic age does not appear to be in doubt because of the presence of phytosaurs), the dicynodont *Placerias* is present in association with supposed coelurosaur vertebrae (CAMP 1933) which have yet to be described; in the Upper Trias of Phoenixville Tunnel, Pennsylvania, dicynodont teeth have been found together with teeth described by Cope as *Thecodontosaurus gibbidens*; and in the Popo Agie Beds near Lander, Wyoming, dicynodont remains (probably *Placerias*) have been found with primitive phytosaurs, though not with saurischians. As von HUENE himself remarks (1940a), "......in Nordamerika nur an wenigen Stellen des grossen Kontinents dieser Zeit Theromorphen sich mit Sauromorphen mischen und in Europa fast gar nicht." The faunal assemblage of the Upper Trias of Elgin, for example, includes a coelurosaur (*Saltopus*) but no therapsids.

Another fauna which von HUENE discusses in this connexion but which cannot be considered as a "Mischfauna" is that which he described from the Maleri Beds of India (1940c), and of which the archosaur content has been reviewed above (Chapter 7). Some of the animals had been described by LYDEKKER (1885) and HAUGHTON (1932) had mentioned the probability of their correlation with the reptiles from the "Upper Bone Bed"; FOX (1931) had correlated the Maleri Beds with the Molteno and Red Beds, giving all these a Middle Keuper age, while he considered the Rio do Rasto Beds to be somewhat earlier but also Keuper. The constitution of this Maleri fauna differs from that of the two already discussed in that phytosaurs are present while therapsids (as far as is known) are entirely absent; von HUENE (1940a) suggested that the latter difference might be due to local variations in distribution. Labyrinthodonts are present as in East Africa. The Maleri rhynchosaur _Paradapedon_ is described as being intermediate in nature between the East African _Stenaulorhynchus_ and the South American forms. The archosaur remains are very fragmentary. Among those assigned to the Pseudosuchia there is a skull fragment compared by von Huene with the skull fragments of the Brazilian _Prestosuchus_ and of the Tanganyikan "_Stenaulorhynchus stockleyi_" HAUGHTON, and a single cervical or anterior dorsal vertebra which might well come from a short-necked Prestosuchid. The material ascribed to the Saurischia includes a dorsal vertebra compared by von Huene with those of _Coelophysis_ and (less closely) _Thecodontosaurus_, and which he therefore considered to indicate the presence of a coelurosaur, probably a member of the Podokesauridae; but, as shown above, there is an even greater resemblance to the anterior dorsal vertebrae of the East African pseudosuchian Teleocrater. The distal third of a small femur associated (probably incorrectly) with this vertebra could be either pseudosuchian or saurischian, but is too nondescript to be referred to either group with certainty. The dorsal centra from Maleri which von Huene described as "Prosauropod cf. Massospondylus sp." are likewise very similar to those of the East African pseudosuchian Mandasuchus. Thus the only supposed saurischian remains from Maleri which cannot be compared with pseudosuchian remains from elsewhere consist of one small hollow tibia of which only the extreme proximal end is preserved; von Huene compared it with the tibia of the coelurosaur Dolichosuchus and asserted that it probably indicated the presence of a coelurosaur, perhaps related to the Podokesauridae.

The existence of a faunal connexion between the Maleri Beds on one hand and the "Upper Bone Bed" and upper Rio do Rasto Beds on the other cannot be denied; but it seems to be far less close than the relationship of the two latter beds to each other. The apparent absence of therapsids, the undoubted presence of phytosaurs and the possible presence of true saurischians would seem to indicate a slightly younger age for the Indian deposits. It should be noted that the labyrinthodonts which they contain are metoposaurs, known only from the Upper Trias in other parts of the world; and it may be that these beds are of early Upper Triassic age. It is hoped that the "Upper Bone Bed" labyrinthodonts in the Parrington collection will be described in the near future so that the necessary comparisons may be made.

The apparent absence of phytosaurs in the "Upper Bone Bed" and in the upper Rio do Rasto Beds cannot be taken as evidence of their Middle Triassic age. The typical phytosaurs are unquestionably a characteristically Upper Triassic group (ROMER, 1945, describes the solitary Lower Triassic genus, Mesorhinus from the Middle Bunter of Germany, as ".......poorly known.......relatively primitive....... may be leading back toward the more generalized thecodont type"), but they seem to be lacking entirely in the rocks of Gondwanaland; so that even in the South African Karroo, where richly fossiliferous rocks of indubitable Upper Triassic age are abundant, phytosaurs are unrepresented.

With the adoption of Watson's and Romer's view that the beds in question are of Middle Triassic age, the present work has the further implication that, since <u>Spondylosoma</u> is no longer considered to be a saurischian, it is removed from the somewhat anomalous position of being the only known genus of saurischian in the Middle Trias.

9.

SUMMARY

1. The Triassic material collected by Parrington in 1933 in the Ruhuhu Valley of Tanganyika has been examined for the remains of archosaur reptiles.

2. Two new archosaurs are described from the "Upper Bone Bed" - Mandasuchus longicervix gen. et sp. nov. from three specimens, and Teleocrater tanyura gen. et sp. nov. from two. Skull material is poor or absent, but the post-cranial material is good.

3. Detailed comparisons are made between these new reptiles and other archosaurs. Both Mandasuchus and Teleocrater show differing combinations of characters, some of which have hitherto been regarded as typical of the Pseudosuchia and others of the Saurischia. It is therefore concluded that the distinction between these two naturally continuous groups can no longer be based on a whole series of opposing features. If a purely arbitrary separation is to be effected on a single diagnostic character, then that which is usually chosen may well be retained: a closed acetabulum indicates a pseudosuchian, an open acetabulum a saurischian. Both Mandasuchus and Teleocrater have closed acetabula and are therefore pseudosuchians.

4. Comparison with other pseudosuchians shows that the closest resemblance exists between Mandasuchus and the Brazilian Prestosuchus from the upper Rio do Rasto Beds; the only important difference between the genera is that the cervical vertebrae of the former are elongated while those of the latter (as far as is indicated by the scanty remains available) are not. It is proposed that a new family, the Prestosuchidae, be erected to include these genera. The diagnostic features of the family are enumerated; the most characteristic is the nature of the dermal armour, which clearly distinguishes members of the family from those of the related Stagonolepidae. The Prestosuchidae are found in the Middle Triassic of Gondwanaland and the Stagonolepidae in the Upper Triassic of Laurasia.

5. The Rio do Rasto pseudosuchian Rauisuchus, formerly placed with Prestosuchus in a special sub-family of the Stagonolepidae (Rauisuchinae) and later, still with Prestosuchus, in a separate family (Rauisuchidae), differs from Prestosuchus in certain important respects and should not be considered a member of the same family; its resemblance to Prestosuchus is much less close than that of the latter to Mandasuchus. Rauisuchus nevertheless has affinities with the

Prestosuchidae. It would seem that its true systematic position cannot be determined more certainly until the arrangement of its several different types of dermal plate becomes known.

6. The pseudosuchian Stagonosuchus from the "Upper Bone Bed" of Tanganyika is also a Prestosuchid and not a Stagonolepid. Certain peculiarities of its osteology are more strongly reminiscent of Mandasuchus than of any other animal. The dermal armour is unknown, but its presence may be inferred with confidence.

7. Mandasuchus also bears a close resemblance to the Rio do Rasto archosaur Spondylosoma, hitherto supposed to have had an open acetabulum and consequently to have been a saurischian. It is now shown that there are no good grounds for considering the acetabulum of Spondylosoma to have been open. It is therefore proposed, because of its great similarity to Mandasuchus, that Spondylosoma should be removed from the Saurischia and placed in the Pseudosuchia; and, despite its apparent lack of dermal armour, in the family Prestosuchidae. The neck of Spondylosoma is more elongated than that of Mandasuchus. Only two other fragments of Rio do Rasto material have been ascribed to the Saurischia hitherto; and these also seem to have Prestosuchid affinities.

8. The Plateosauridae and Thecodontosauridae (and perhaps other pachypodosaurs) appear to have arisen from the Prestosuchidae through forms like Mandasuchus and Spondylosoma. Prestosuchus, Mandasuchus, Spondylosoma and Plateosaurus represent the grades of an evolutionary series leading from a typical pseudosuchian to a typical prosauropod saurischian.

9. Teleocrater has an unusual type of vertebral column with greatly elongated cervicals; it is quite unlike the vertebral column of any other pseudosuchian described, but closely resembles that of the North American coelurosaur Coelophysis. Nevertheless it has a closed acetabulum and limb-bones like those of other pseudosuchians. If classified as a member of the Pseudosuchia, Teleocrater must represent an entirely new family within that sub-order, the Teleocrateridae, whose origins remain obscure and from which at least some of the coelurosaurs - Coelophysis and its allies - appear to be derived.

10. From the conclusions reached in the two preceding paragraphs, it appears unlikely that the Saurischia can be of monophyletic origin if the distinction between the Pseudosuchia and the Saurischia be maintained on the condition of the acetabulum.

11. It is suggested that a short neck is not, as previously supposed, a typical pseudosuchian character. Elongated cervical vertebrae are found in the earliest pseudosuchian known (Chasmatosaurus from the Lower Trias), in four "Upper Bone Bed" and upper Rio do Rasto pseudosuchians (Stagonosuchus, Mandasuchus, Spondylosoma and Teleocrater), and in the Upper Triassic Hesperosuchus.

12. It is considered improbable that the Ornithosuchidae are ancestral to any of the main lines of saurischian evolution, for well developed saurischians are contemporaneous with them.

13. The more incomplete remains of other archosaurs from the "Upper Bone Bed" are described and their affinities discussed.

14. The archosaur fauna of the "Upper Bone Bed" is reviewed and listed. It is shown that all the material previously ascribed to the Saurischia may be confidently referred to either Mandasuchus or a Teleocraterid.

15. The fragmentary archosaur remains from the Maleri Beds of India are also reviewed. The material previously ascribed to the Saurischia (except for one insignificant fragment) compares closely with either

Mandasuchus or Teleocrater and could well be derived from related pseudosuchians.

16. Not enough vertebrate material has yet been described or identified from the various localities of the "Upper Bone Bed" of Tanganyika to enable it to be determined whether the Bed represents one or several distinct fossiliferous horizons.

17. The similarity of the pseudosuchian faunas of the "Upper Bone Bed" of Tanganyika and of the upper Rio do Rasto Beds of Brazil supports the view that these beds are homotaxial; it also supports the hypothesis that there was some form of land connexion between Africa and South America when the beds were laid down, rendering possible the direct migration of terrestrial animals between the continents. The observations of earlier workers, based on the nature of the rhynchosaur and cynodont faunas, are thus confirmed independently.

18. The South African Karroo, in which no Prestosuchid or Teleocraterid is known to occur, contains more primitive pseudosuchians below the almost barren Molteno Beds and more advanced archosaurs above them. This supports the view that the horizons of the "Upper Bone Bed" and of the upper Rio do Rasto Beds which contain pseudosuchians of these families are contemp-

oraneous with some part of the Molteno Beds. There appears to be a far stronger faunal connexion between Tanganyika and Brazil than between Tanganyika and South Africa in that part of the Trias which is under discussion.

19. The lack of evidence for the presence of saurischians in the "Upper Bone Bed" of Tanganyika and the upper Rio do Rasto Beds of Brazil supports the view that their archosaur localities, and hence the Molteno Beds also, are of Middle Triassic rather than Upper Triassic age. It would nevertheless appear that the pseudosuchian stock was already differentiated into coelurosaur-like types and pachypodosaur-like types when these beds were deposited.

20. There is no certain evidence for the co-existence of therapsids and saurischians in any deposit.

21. The fauna of the Maleri Beds of India, while bearing a certain resemblance to those of the "Upper Bone Bed" of Tanganyika and the upper Rio do Rasto Beds of Brazil, appears slightly younger and may indicate an early Upper Triassic age for the Maleri Beds.

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APPENDIX I.

METHOD OF RE-NUMBERING INDIVIDUALS IN MULTIPLE FIELD-COLLECTIONS

The original field-numbers assigned by Parrington have been retained throughout.

A number without a suffix indicates that all the material given that number in the field appears to be derived from a single animal, or that there is no available evidence to the contrary.

A number with an alphabetical suffix indicates that the material given that number in the field appears to be derived from more than one animal. The suffixes "a", "b", "c" and so on indicate the various animals to which material can be assigned with a reasonable degree of confidence; the suffix "u" indicates unsorted or indeterminable material.

APPENDIX II.

LIST OF SUSPECTED DIAPSID MATERIAL IN THE 1933 COLLECTION,

including also other material found in the same field-collections

Field-no.	Locality	identified as:
2	B5	*Stenaulorhynchus stockleyi* in quantity
6	B5	*Stenaulorhynchus* in quantity
11a	B5	small pseudosuchian gen. et sp. indet.: articular region of lower jaw, 5 vertebrae, proximal and distal ends of humerus, distal part of femur, end of a smaller limb-bone
11b	B5	*Mandasuchus longicervix* gen. et sp. nov., type-specimen
11c	B5	large animal: 5 unrecognisable fragments
12	B5	dicynodont, to which one small centrum from 11 may belong
13	B5	*Mandasuchus longicervix* in quantity
14a	B5	cf. *Parringtonia*: 3 small distal caudal vertebrae, 3 larger haemapophyses
14b	B5	*Stenaulorhynchus* in quantity; may contain 14a and 14u
48a	B9/1	large labyrinthodont in quantity
48b	B9/1	*Teleocrater tanyura* gen. et sp. nov., type-specimen
48c	B9/1	dicynodont: proximal part of rib

Field-no.	Locality	identified as:
48u	B9/1	problematical bones of large animal, part of unidentified sacrum
50a	B36	cynodont cf. *Scalenodon*?: femur without shaft
50b	B36	Prestosuchid gen. et sp. indet.: 6 incomplete vertebrae, proximal part of humerus
52a	B9/2	archosaur: 2 very large teeth with serrated edges
52b	B9/2	dicynodont: centrum
52c	B9/2	archosaur: elongated caudal centrum
52d	B9/2	pseudosuchian: distal part of small femur
52e	B9/2	pseudosuchian?: distal part of small femur
53a	B9/2	*Teleocrater tanyura*: 2 vertebrae, distal part of humerus, end of a smaller limb-bone
53b	B9/2	large archosaur: caudal vertebra
58	B12	Prestosuchid gen. et sp. indet.: large mid-cervical vertebra
61a	B15/1	*Stenaulorhynchus*: right maxilla, caudal vertebra and claw
61b	B15/1	dicynodont: 5 vertebrae
61u	B15/1	?: collection of phalanges and claws

Field-no.	Locality	identified as:
63	B15/2	Mandasuchus longicervix in quantity
67	B15/2	Stenaulorhynchus in quantity
68a	B15/1	Parringtonia gracilis von HUENE, type-specimen (including 2 sacral vertebrae not described hitherto)
68b	B15/1	Stenaulorhynchus in quantity; may contain 68a and 68u
68u	B15/1	limb-bone and other fragments, some possibly belonging to 68a
69a	B15/2	small pseudosuchian gen. et sp. indet. cf. specimen no. 11a: distal part of humerus
69b	B15/2	Stenaulorhynchus: 11th or 12th pre-sacral vertebra
69u	B15/2	remainder of surface collection: unidentified fragments
71	B15/3	small pseudosuchian gen. et sp. indet. cf. specimen no. 11a: humerus
72u	B11	Stenaulorhynchus and dicynodont in quantity, unsorted
73	B11	Stenaulorhynchus in quantity
77a	B17	"saurischian" maxilla fig. von HUENE (Mandasuchus sp. indet.)
77b	B17	dicynodont in quantity; may contain 77a and 77c
77c	B17	small archosaur: 11½ consecutive dorsal vertebrae (too small to belong to 77a)

Field-no.	Locality	identified as:
106	B29	rhynchosaur: 2 humeri, and a femur perhaps differing from that of Stenaulorhynchus (?)
107	B30	very large Prestosuchid cf. Mandasuchus: posterior dorsal vertebra
112a	B29	Stenaulorhynchus left maxilla fig. von HUENE
112b	B29	Scalenodon angustifrons fig. CROMPTON
112c	B29	Scalenodon angustifrons fig. CROMPTON
112e	B29	Scalenodon sp. indet. fig. CROMPTON
112f	B29	Scalenodon sp. indet. fig. CROMPTON
119a	B29	diapsid: tiny short-snouted skull, thecodont dentition
119b	B29	Scalenodon angustifrons fig. CROMPTON
119u	B29	Scalenodon sp. indet.
120a	B29	Scalenodon angustifrons fig. CROMPTON
120b	B29	Scalenodon angustifrons (PARRINGTON), type-specimen
120c	B29	diapsid?: 2 small mandible fragments
120d	B29	Scalenodon sp. indet. fig. CROMPTON
120e	B29	Scalenodon sp. indet. fig. CROMPTON

Field-no.	Locality	identified as:
123	B29	*Stenaulorhynchus* right maxilla fig. von HUENE
125	B29	*Stenaulorhynchus*: 7 vertebrae and right femur (latter larger than von Huene's largest)

APPENDIX III.

LIST OF FOSSILS FROM THE "UPPER BONE BED"

This list includes:

i) all valid species named from the Bed,
ii) all valid genera of which no species have been named or determined, and
iii) all larger groups of which no genera have been named or determined.

Thus, although some specimens have been described as "*Scalenodon* sp. indet." and another as "cf. *Teleocrater*", these are not mentioned because the species *S. angustifrons* and *T. tanyura* have been named. Similarly no reference is made to the various specimens described as "pseudosuchian gen. et sp. indet." because several pseudosuchian genera have been named.

RHYNCHOSAURS:

Stenaulorhynchus stockleyi HAUGHTON emend. von HUENE

PSEUDOSUCHIANS:

Stagonosuchus nyassicus von HUENE
Stagonosuchus tanganyikaensis BOONSTRA
Mandasuchus longicervix CHARIG

Parringtonia _gracilis_ von HUENE

Teleocrater _tanyura_ CHARIG

DICYNODONTS:

Dicynodon _njalilus_ von HUENE

Aulacephalodon(?) sp. indet.

Eocyclops(?) sp. indet.

Kannemeyeria sp. indet.

Lystrosaurus sp. indet.

CYNODONTS:

Aleodon _brachyrhamphus_ CROMPTON

Cricodon _metabolus_ CROMPTON

Scalenodon _angustifrons_ (PARRINGTON)

Theropsodon _njalilus_ von HUENE

Trirachodon sp. indet.

cf. _Gomphodontosuchus_ _brasiliensis_ von HUENE

cynosuchid gen. et sp. indet.

AMPHIBIANS:

labyrinthodonts gen. indet.

FISHES:

hybodont gen. indet.

dipnoans gen. indet.

MOLLUSCS:

gastropod gen. indet.

Unio karrooensis COX

PLANTS:

Rhexoxylon tetrapteridoides

APPENDIX IV.

LIST OF LOCALITIES OF APPARENT "UPPER BONE BED" AGE, TOGETHER WITH LISTS OF THE SPECIMENS FOUND AT EACH

"P." denotes a specimen in the Parrington collection;

"B.", "H." and "v.H." denote specimens described by Boonstra, Haughton and von Huene respectively.

B5 - IRUNDI (according to Stockley's map, in the Kingori Sandstones)

Stenaulorhynchus stockleyi	P. 2	
Stenaulorhynchus sp. indet.	P. 6	
	P. 14b	
Mandasuchus longicervix	P. 11b	type-specimen
	P. 13	fig.
cf. Parringtonia	P. 14a	fig.
pseudosuchian gen. et sp. indet.	P. 11a	fig.
dicynodont gen. et sp. indet.	P. 12	
Scalenodon sp. indet.	P. 1	fig. CROMPTON
?	P. 4	
?	P. 8	
?	P. 9	
?	P. 10	
?	P. 11c	
?	P. 15	

B8 - near KIHOHO HILL (according to Stockley's map, in unidentified strata; but according to his list, in the Kingori Sandstones)

dicynodont gen. et sp. indet.	H.	fig. HAUGHTON as "cf. *Titanosuchus* sp."
dicynodont sp. indet.	H.	

B9 - between KIHOHO and MKONGOLEKO (according to Stockley's map, in unidentified strata)

Teleocrater tanyura	P. 48b	type-specimen	(B9/1)
pseudosuchian	P. 53a	fig.	(B9/2)
pseudosuchian?	P. 52d	fig.	(B9/2)
archosaurs	P. 52e		(B9/2)
	P. 52a	fig.	(B9/2)
	P. 52c	fig.	(B9/2)
	P. 53b	fig.	(B9/2)
dicynodont gen. et sp. indet.	H.		
	P. 48c		(B9/1)
theriodont gen. et sp. indet.	P. 52b		(B9/2)
labyrinthodont	P. 56		(B9/3)
?	P. 48a		(B9/1)
?	P. 48u		(B9/1)
?	P. 51		(B9/2)
	P. 55		(B9/2)

B10 - MKONGOLEKO/NJALILA (according to Stockley's map, in the Manda Beds)

Stagonosuchus nyassicus	H.	fig. HAUGHTON as "*Stenaulorhynchus major*"

B11 - MKONGOLEKO/NJALILA (according to Stockley's map, in the Manda Beds)

Anthodon minusculus	B.	(probably from "Lower Bone Bed"; labelling error)
Stenaulorhynchus stockleyi	H.	type-specimen
Stenaulorhynchus sp. indet.	B.	
	P. 72u	
	P. 73	
Stagonosuchus tanganyikaensis	B.	type-specimen
cf. *Stagonosuchus*?	H.	fig. HAUGHTON as "*Stenaulorhynchus stockleyi*" skull fragment
Mandasuchus sp. indet.	H.	fig. HAUGHTON as "theropod gen. et sp. indet."
pseudosuchian gen. et sp. indet.	H.	fig. HAUGHTON as "*Stenaulorhynchus stockleyi*" vertebrae
archosaur	B.	described BOONSTRA as "cf. *Thecodontosaurus*"
Aulacephalodon(?) sp. indet.	B.	
Kannemeyeria sp. indet.	B.	
Lystrosaurus sp. indet.	B.	
dicynodont gen. et sp. indet.	P. 72u	
Cricodon metabolus	P. 74	type-specimen, CROMPTON
Trirachodon sp. indet.	B.	

B12 - MKONGOLEKO/NJALILA (according to Stockley's map, in the Manda Beds)

Prestosuchid gen. et sp. indet.	~~P. 58~~	~~fig.~~
?	P. 59	
?	P. 60	
?	P. 62	
gastropod	P. 70	

B13 - MKONGOLEKO/NJALILA (according to Stockley's map, in the Manda Beds)

Dicynodon sp. indet.	H.	
dicynodont gen. et sp. indet.	P. 64	
cynodont gen. et sp. indet.	P. 65	

B15 - MKONGOLEKO/NJALILA (according to Stockley's map, in the Manda Beds)

Stenaulorhynchus sp. indet.	P. 61a		(B15/1)
	P. 67		(B15/1)
	P. 68b		(B15/1)
	P. 69b		(B15/2)
Mandasuchus longicervix	P. 63	fig.	(B15/2)
Parringtonia gracilis	P. 68a	type-specimen, von HUENE	(B15/1)
pseudosuchian gen. et sp. indet.	P. 69a	fig.	(B15/2)
	P. 71	fig.	(B15/3)
pseudosuchian gen. et sp. indet.	H.	described HAUGHTON as "*Stenaulorhynchus stockleyi*" isolated vertebra	
dicynodont gen. et sp. indet.	P. 61b		(B15/1)
	P. 66		(B15/1)
?	P. 57		(B15/1)
?	P. 61u		(B15/1)
?	P. 68u		(B15/1)
?	P. 69u		(B15/2)

B17 - between MATAMONDO and LINYANYA (according to Stockley's map, in the "Lower Bone Bed")

Mandasuchus sp. indet.	P. 77a	fig. von HUENE as "saurischian gen. et sp. indet."
archosaur	P. 77c	
dicynodont gen. et sp. indet.	P. 77b	

B22 - below MADAMBASI RIDGE, near KETEWAKA RIVER (according to Stockley's map, in the Manda Beds)

Eocyclops(?) sp. indet.	H.	

B24 - TUMBAKO RIVER, south-east of KISAURA (according to Stockley's map, in the Manda Beds)

dicynodont gen. et sp. indet.	H.	

B26 - GINGAMA, south of RUHUHU RIVER (according to Stockley's map, in the Manda Beds)

cf. Gomphodontosuchus brasiliensis	P.136	fig. CROMPTON
labyrinthodonts	P.135	
	P.138	
hybodont	P.141	
dipnoan	P.137	

B27 - GINGAMA, south of RUHUHU RIVER (according to Stockley's map, in the Manda Beds)

cf. Teleocrater	H.	fig. HAUGHTON as "Thecodontosaurus(?) alophos"

B29 - between GINGAMA and TSCHIKONGE (according to Stockley's map, in the Manda Beds)

Stenaulorhynchus sp. indet.	P.112a	fig. von HUENE
	P.123	fig. von HUENE
	P.125	

cf. *Stenaulorhynchus*	P.106	
Stagonosuchus nyassicus	H.	described HAUGHTON as "*Stenaulorhynchus major*"
diapsid	P.119a	
diapsid?	P.120c	
Aleodon brachyrhamphus	P.113c	type-specimen, CROMPTON
	P.134a	fig. CROMPTON
Scalenodon angustifrons	P.120b	type-specimen, CROMPTON (formerly *Trirachodon angustifrons* PARRINGTON)
	P.110a	fig. CROMPTON
	P.111b	fig. CROMPTON
	P.111c	fig. CROMPTON
	P.112b	fig. CROMPTON
	P.112c	fig. CROMPTON
	P.113d	fig. CROMPTON
	P.119b	fig. CROMPTON
	P.120a	fig. CROMPTON
	P.122	
	P.129a	fig. CROMPTON
	P.131	fig. CROMPTON
	P.134b	fig. CROMPTON
Scalenodon sp. indet.	P.104	fig. CROMPTON
	P.110b	fig. CROMPTON
	P.110c	
	P.110u	
	P.112e	fig. CROMPTON
	P.112f	fig. CROMPTON
	P.112u	
	P.113u	
	P.119u	
	P.120d	fig. CROMPTON
	P.120e	fig. CROMPTON

"Group C Gomphodont"	P.111a	fig. CROMPTON
	P.113a	fig. CROMPTON
	P.113b	fig. CROMPTON
	P.114	
theriodont gen. et sp. indet.	P.118	
?	P.124	
?	P.130	
?	P.133	
labyrinthodonts	H.	
	P.115	
	P.116	
dipnoan	P.105	
<u>Unio</u>	P.117	
	P.126	

<u>B30</u> - between MDONGOSSI and NDEMBE (according to Stockley's map, in the Manda Beds)

cf. <u>Mandasuchus</u>	P.107	fig.
theropod(?) gen. et sp. indet.	H.	
dicynodont gen. et sp. indet.	H.	
<u>Unio</u>	P.108	

<u>B36</u> - near MKONGOLEKO (Parrington's new locality)

Prestosuchid gen. et sp. indet.	P. 50b	fig.
cf. <u>Scalenodon</u>?	P. 50a	
?	P. 49	

<u>NJALILA</u> (B10-B15, but which not specified)

<u>Stenaulorhynchus</u> <u>stockleyi</u>	H.	
<u>Stagonosuchus</u> <u>nyassicus</u>	v.H.	type-specimens (2 different localities)

Dicynodon njalilus	v.H.	type-specimen
Theropsodon njalilus	v.H.	type-specimen
gomphodonts gen. et spp. indet.	v.H.	
cynosuchid gen. et sp. indet.	v.H.	

VARIOUS LOCALITIES

Stenaulorhynchus stockleyi	B.	
cynodonts gen. et spp. indet.	v.H.	
Unio karrooensis	described BROILI & SCHROEDER	
Rhexoxylon tetrapteridoides	described COX, type-specimen	
	described WALTON	

Also on Stockley's map and within the Manda Beds are the localities B14, B23, B25 and B28; and within unidentified strata is the locality B7. No bones collected at these sites have been described.

According to Stockley all the other localities lie in the "Lower Bone Bed", except B34, which is in the Ruhuhu Beds.

Ph. D. Dissertation 2873

Illustrations

to

NEW TRIASSIC ARCHOSAURS FROM TANGANYIKA

including

Mandasuchus and Teleocrater

a dissertation submitted for the degree of

Doctor of Philosophy in the University of Cambridge

by

A.J. Charig, M.A., Emmanuel College

INDEX OF CONTENTS

NOTES

All drawings and photographs are in their natural size (except in Plate 26, where they have been enlarged four times).

The following conventions have been employed in the drawings:

i) A broken line indicates a broken edge.

ii) A dotted line indicates a reconstructed edge, the reconstruction appearing reasonable but being unsupported by direct evidence.

iii) Cross-hatching indicates a broken surface.

iv) Stippling indicates unfinished bony surfaces, including some articulating surfaces. These, however, have not been stippled in every case; where unfinished bone constitutes a considerable part of the illustration (as, for example, in anterior and posterior views of the vertebrae) the stippling has been omitted for the sake of clarity. (In Plate 1 stippling has been used to indicate the teeth).

There has been no correction for distortion, except where especially indicated, for the bones are rarely distorted to any appreciable degree. Small breaks in natural edges have not been shown where the presence of a continuous edge may be inferred with a reasonable degree of probability, and other artifacts have been ignored.

Where each of a pair of bones, or each of the sides of a vertebra, is more complete than the other in some respect, the left has been restored from the right or _vice versa_; this has usually been done without indication in the legend. Where both bones of a pair are more or less equally well preserved that of the left side has usually been figured. To facilitate comparison, _all_ vertebrae have been drawn from the left (except the isolated vertebra specimen no. 53 in Plate 49, which, being exceptionally distorted, has been illustrated from both sides). Thus, where the right side of a vertebra is the more complete, the original drawing has been made of that side and then reversed. Consequently, in all drawings of vertebrae and neural spines in lateral view, and also in those in ventral and dorsal view, the anterior end is to the left. Likewise, where it is desirable to figure two bones together in their supposed natural relative orientation (as, for example, scapula and coracoid), and where one is better preserved on the left side and the other on the right, then the drawing of one of them (usually the right) has been reversed so that both bones of the same side can be figured.

The photographs of *Spondylosoma* and other Rio do Rasto material were made and are reproduced by kind permission of Professor Baron von Huene of Tübingen.

PLATE 1

Mandasuchus longicervix gen. et sp. nov.:
type-specimen (no. 11b)

All illustrations in natural size.

Left maxilla:

A. Lateral view.
B. Medial view.
C. Ventral (crown) view.
D. Dorsal view.

Right dentary:

E. Lateral view.
F. Medial view.
G. Dorsal (crown) view.
H. Ventral view.

Teeth are indicated by stippling.

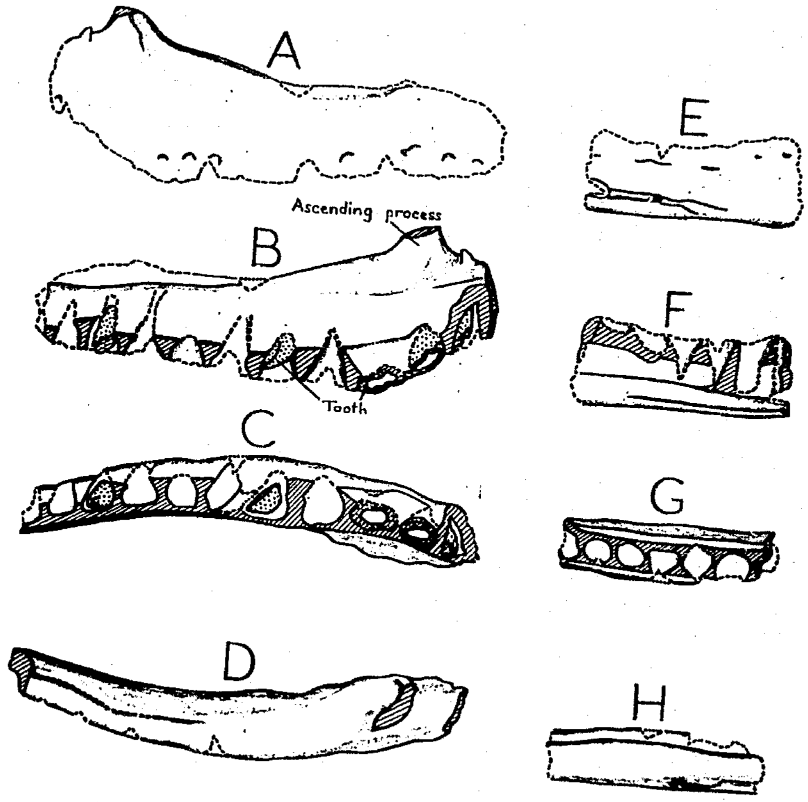


PLATE 2

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Vertebrae in left lateral view:

Ce2. Axis, with reconstruction of odontoid and intercentrum.

Ce3-Ce8. Cervical vertebrae (Ce6 with dermal scutes in situ on neural spine).

D1-D6. Dorsal vertebrae (D6 with part of capitulum of rib).

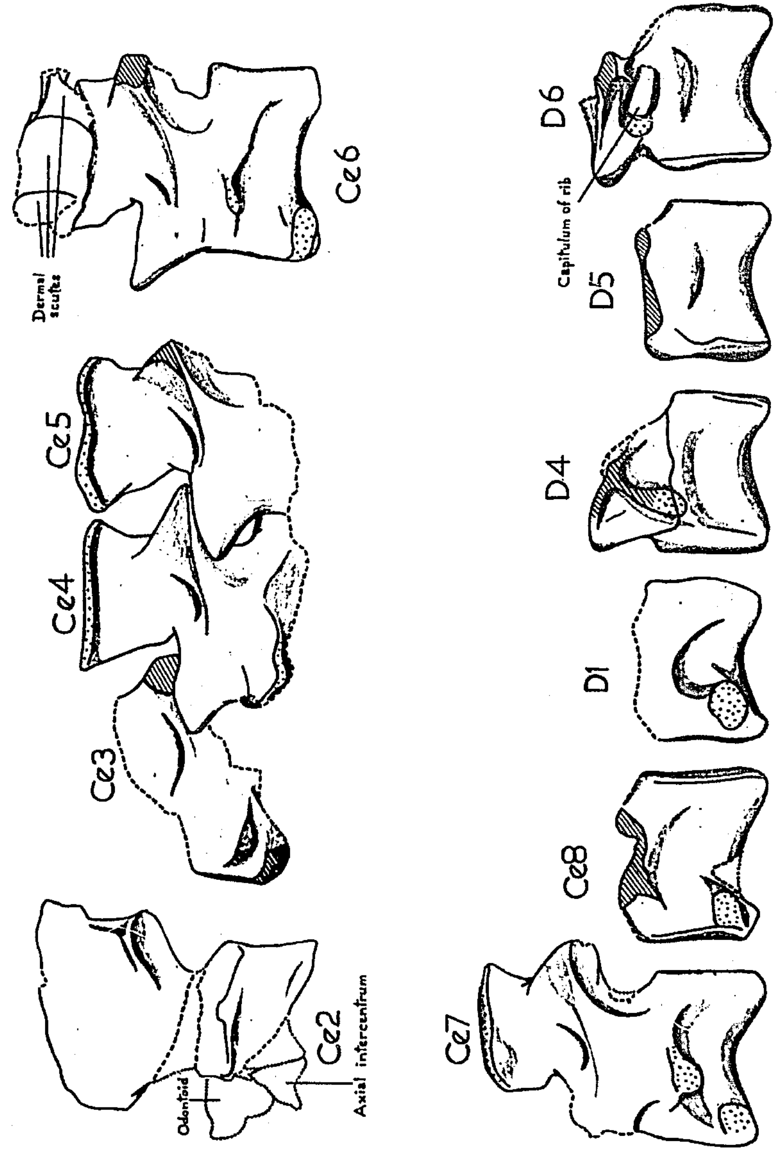


PLATE 3

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Vertebrae in left lateral view:

D7–D17. Dorsal vertebrae.

S2. Sacral vertebra, supposed second.

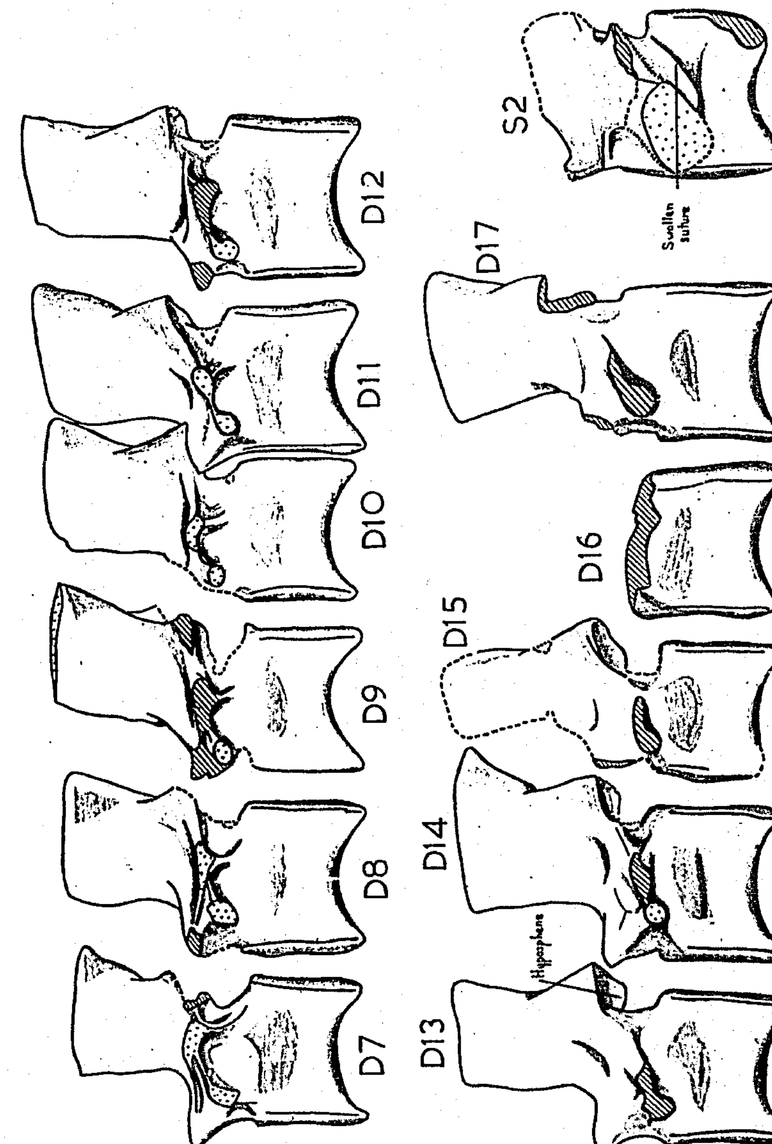


PLATE 4

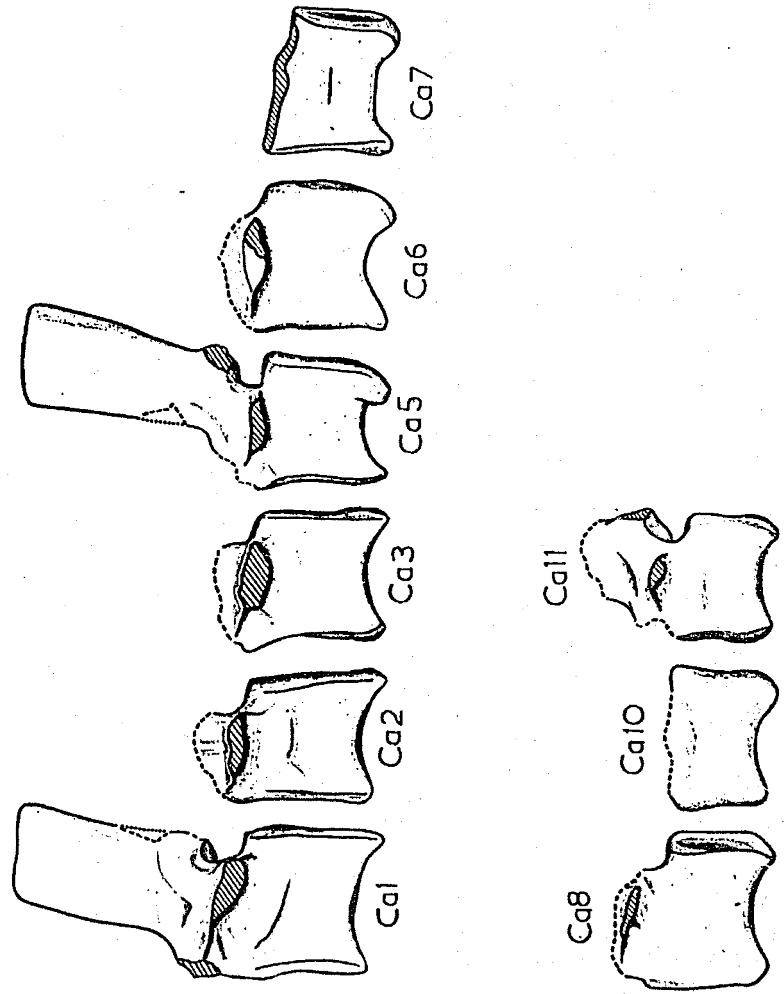
Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Vertebrae in left lateral view:

Ca1-Ca11. Caudal vertebrae. (From Ca5 onwards the positions in the column assigned to the vertebrae are only conjectured and are not based on any substantial evidence).



<u>PLATE 5</u>

<u>Mandasuchus</u> <u>longicervix</u> gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Vertebrae in ventral view:

Ce2.	Axis.
Ce6–Ce8.	Cervical vertebrae.
D1–D15.	Dorsal vertebrae (D6 with part of capitulum of rib).

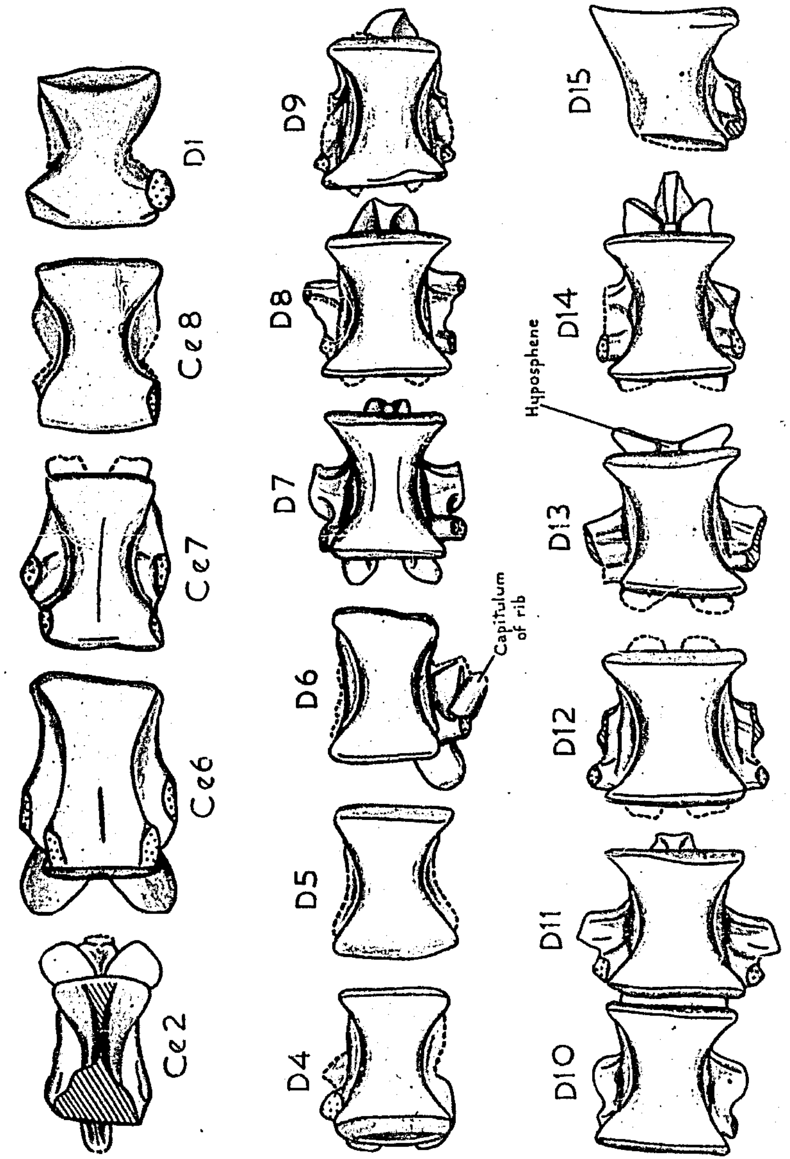


PLATE 6

Mandasuchus longicervix gen. et sp. nov.:
type-specimen (no. 11b)

All illustrations in natural size.

Vertebrae in ventral view:

- D16, D17. Dorsal vertebrae.
- S2. Sacral vertebra, supposed second.
- Ca1–Ca11. Caudal vertebrae. (From Ca5 onwards the positions in the column assigned to the vertebrae are only conjectured and are not based on any substantial evidence).

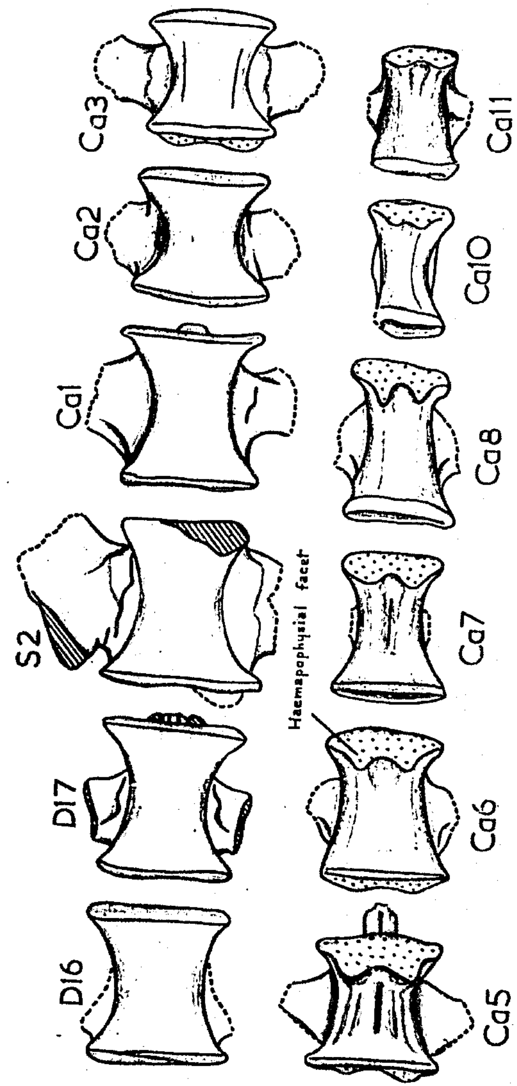


PLATE 7

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Vertebrae in dorsal view; in some cases only the tops of the neural spines are shown:

Ce2.	Axis.
Ce4–Ce7.	Cervical vertebrae.
D7–D17.	Dorsal vertebrae.
S2.	Sacral vertebra, supposed second.
Ca1–Ca11.	Caudal vertebrae. (From Ca5 onwards the positions in the column assigned to the vertebrae are only conjectured and are not based on any substantial evidence).

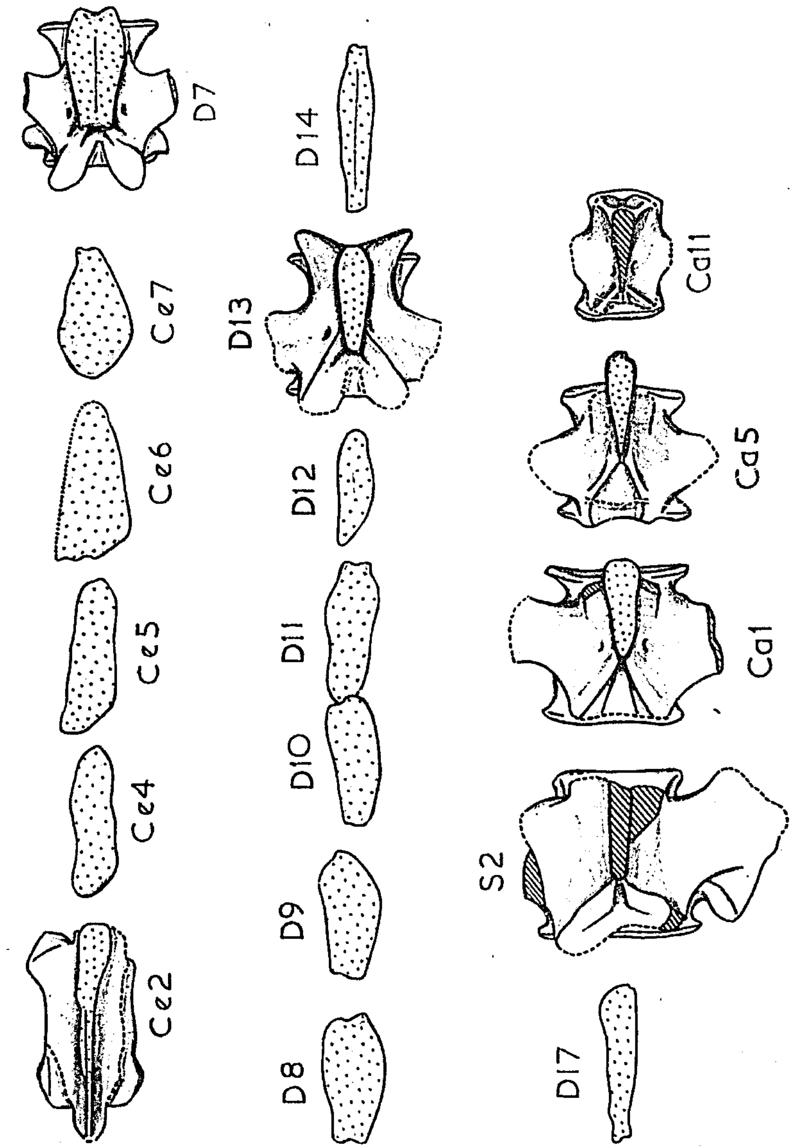


PLATE 8

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Vertebrae in (above) anterior and (below) posterior view:

Ce7. Cervical vertebra, supposed seventh.

D7, D13. Dorsal vertebrae.

S2. Sacral vertebra, supposed second.

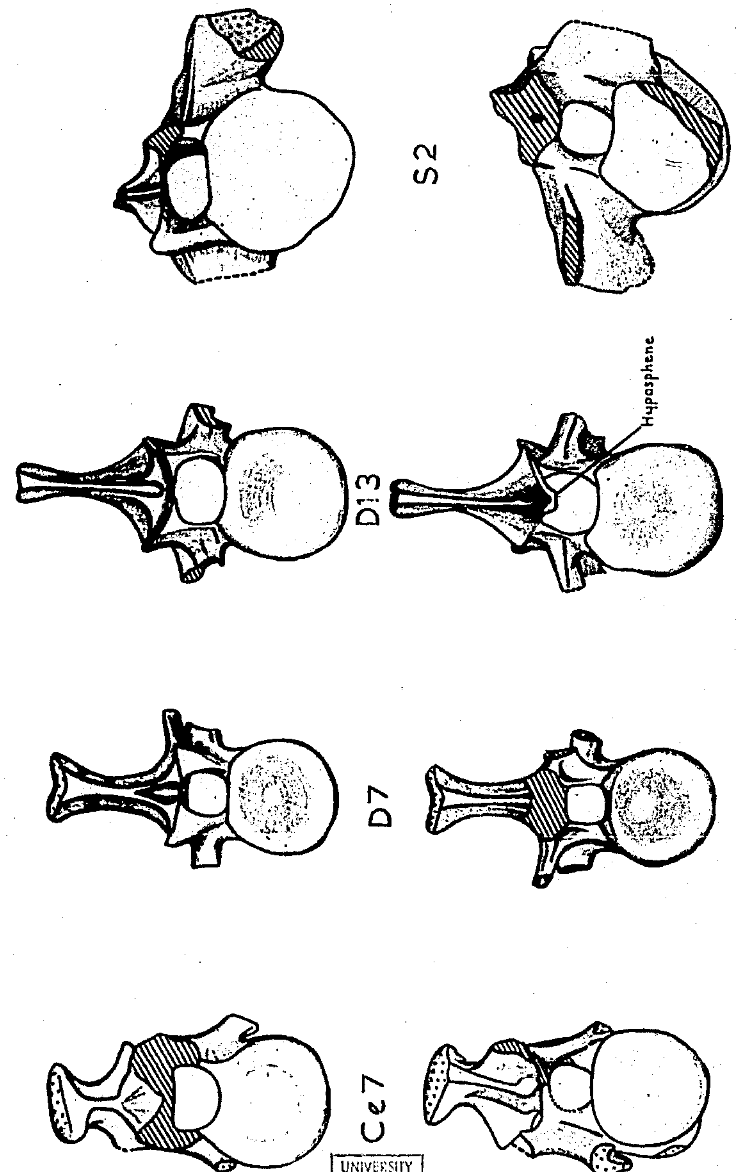


PLATE 9

<u>Mandasuchus</u> <u>longicervix</u> gen. et sp. nov.:
type-specimen (no. 11b)

All illustrations in natural size.

Vertebrae in anterior view:

Ca1–Ca11. Caudal vertebrae. (From Ca5 onwards the positions in the column assigned to the vertebrae are only conjectured and are not based on any substantial evidence).

Vertebrae in posterior view:

Ca1'–Ca11'. Caudal vertebrae.

Dorsal rib, fragment of shaft:

A. Outer view.

B. Inner view.

C. Anterior or posterior view.

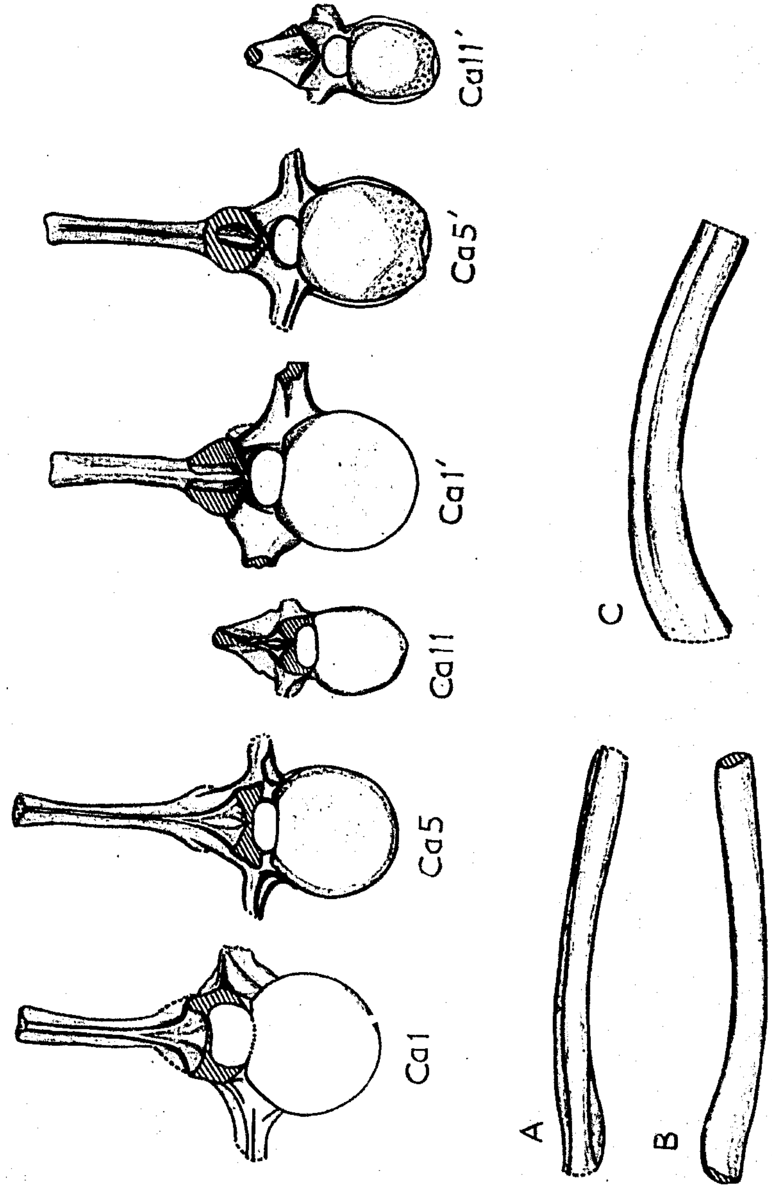


PLATE 10

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Left scapula and coracoid:

A. Lateral view.

B. Medial view.

C. Posterior view.

Left scapula:

D. Articulating surface for coracoid.

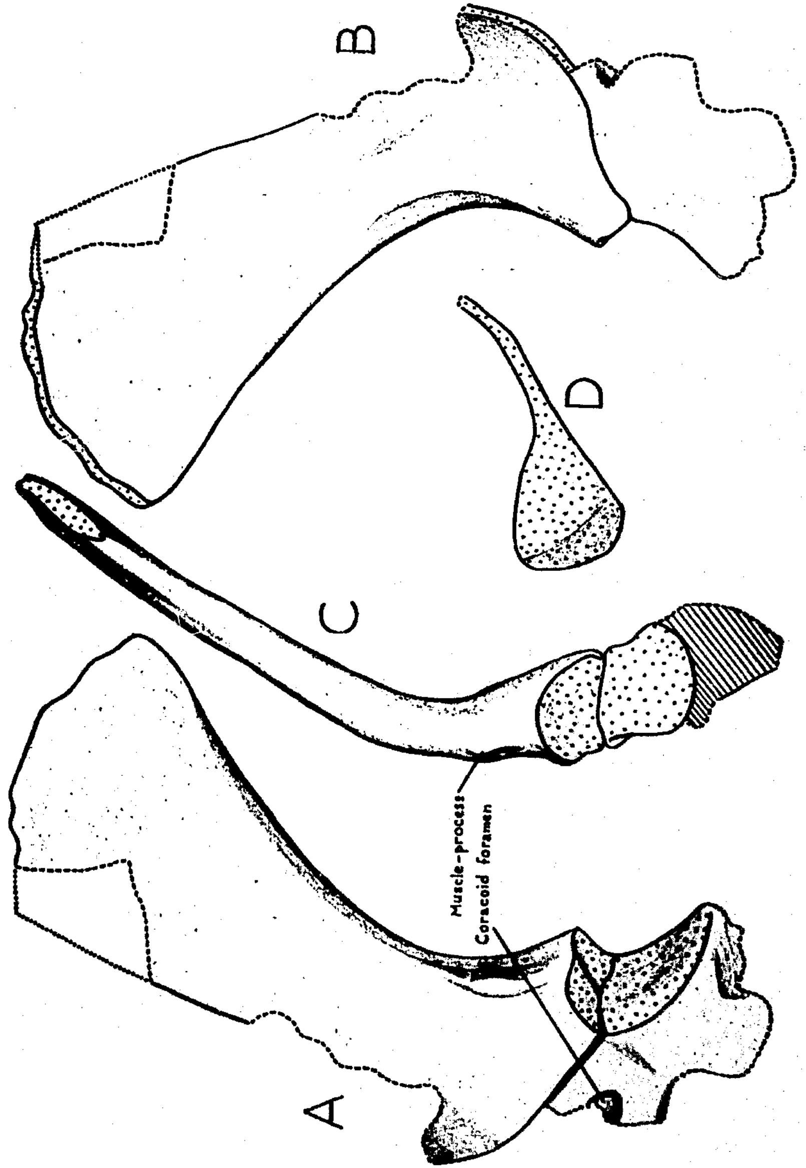


PLATE 11

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Right humerus:

A. Pre-axial view.

B. Post-axial view.

C. Anterior view. (slightly ventral).

D. Posterior view (slightly dorsal).

E. Ventral view.

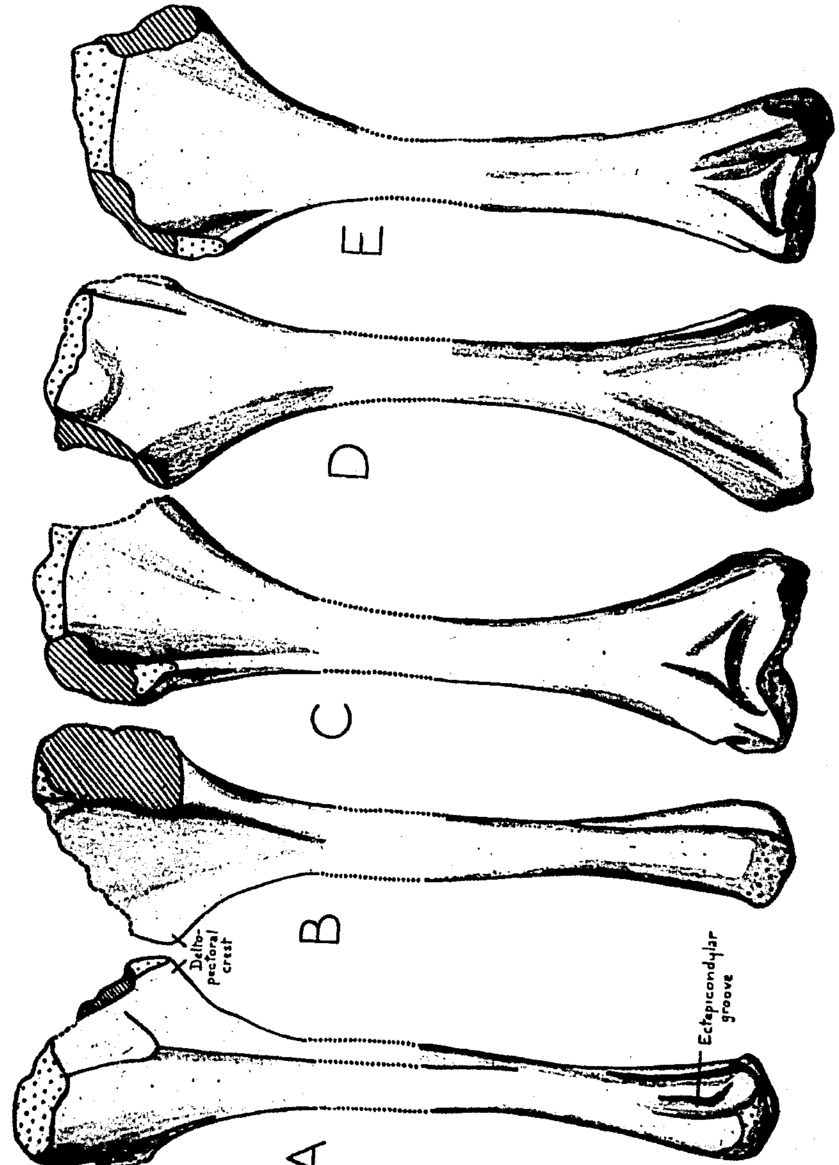


PLATE 12

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Right humerus:

A. Proximal end.

B. Distal end.

Right(?) radius, proximal part with outline of more distal part restored from its fellow:

C. Anterior(?) view.

D. Posterior(?) view.

E. Lateral(?) view.

F. Medial(?) view.

G. Proximal end.

Right(?) ulna:

H. Anterior(?) view.

J. Posterior(?) view.

K. Lateral(?) view.

L. Medial(?) view.

M. Proximal end.

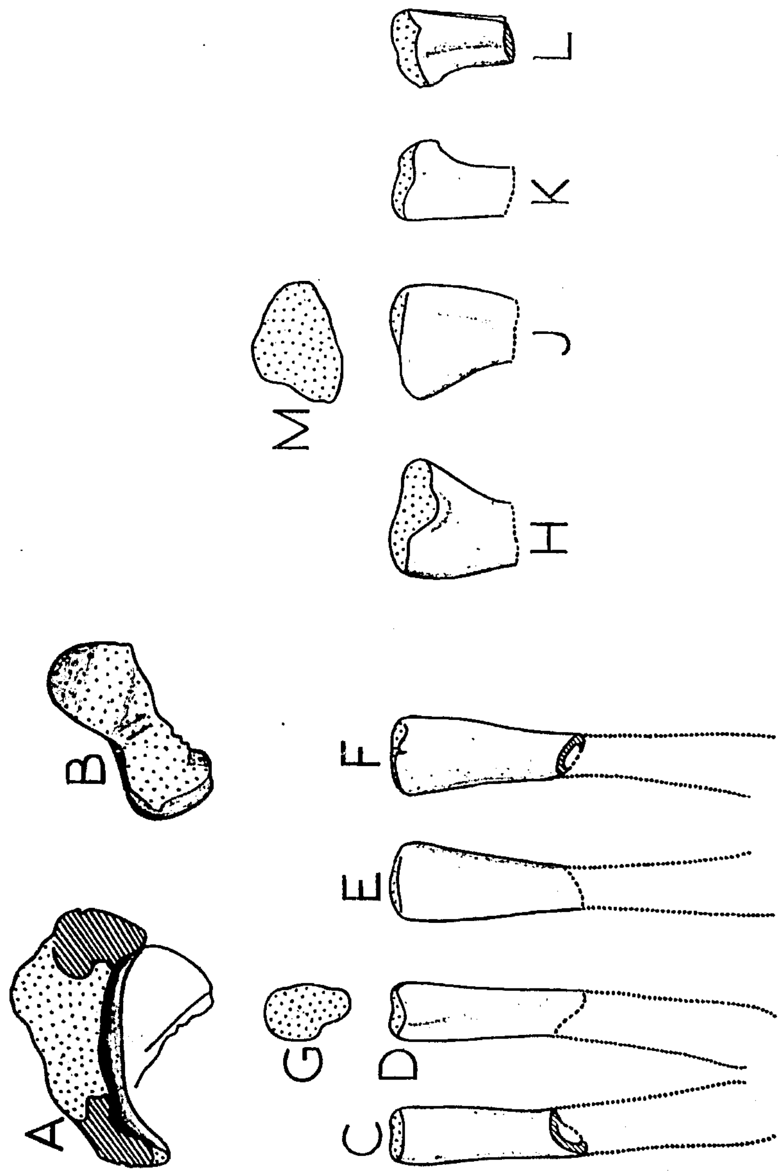


PLATE 13

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

Natural size.

Left side of pelvic girdle in lateral view.

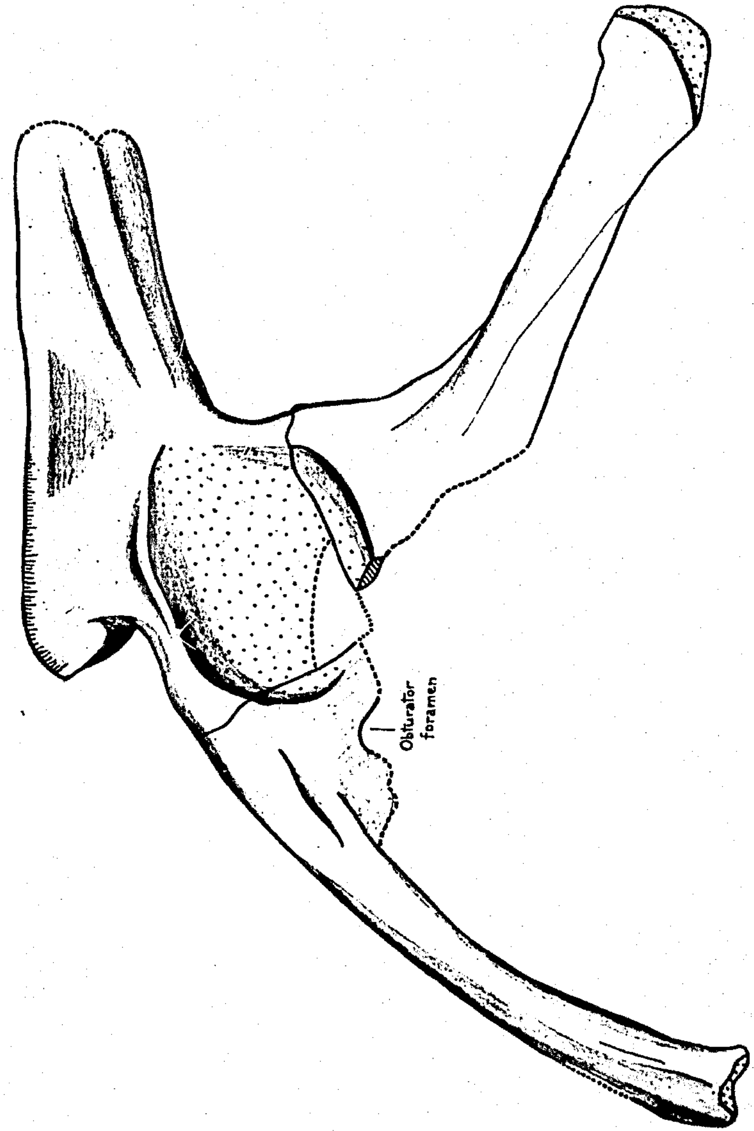


PLATE 14

<u>Mandasuchus</u> <u>longicervix</u> gen. et sp. nov.:

type-specimen (no. 11b)

Natural size.

Left side of pelvic girdle in medial view.

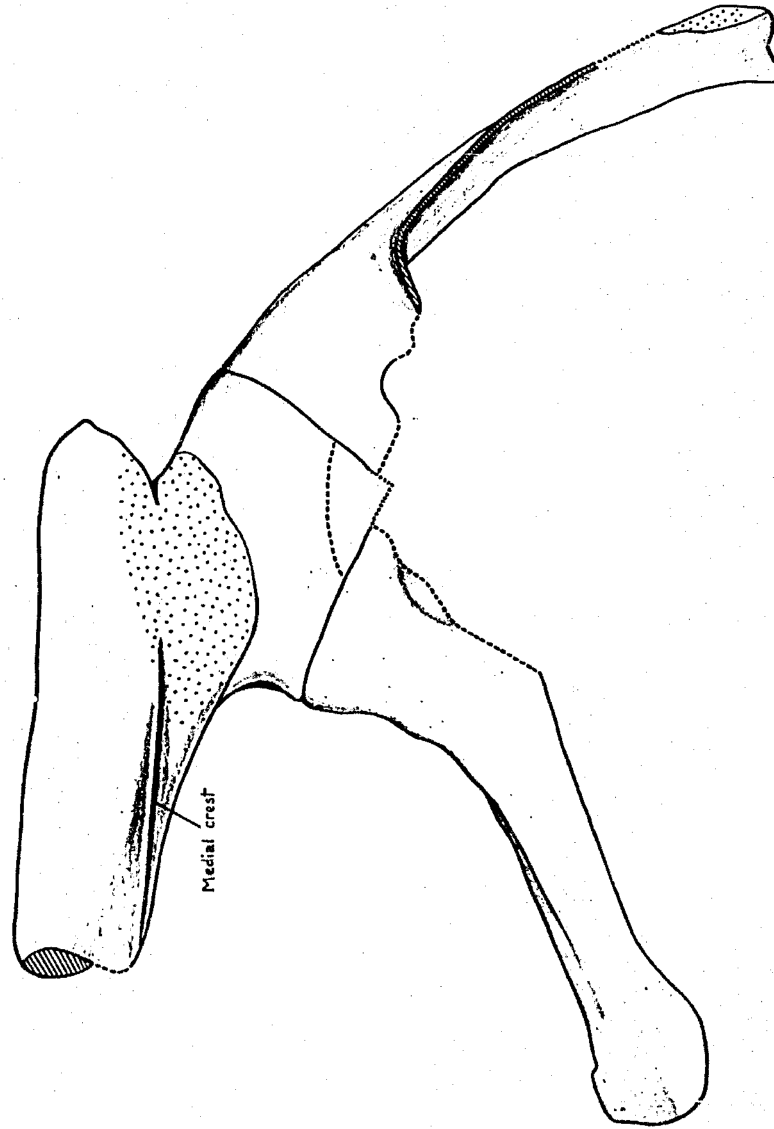


PLATE 15

Mandasuchus longicervix gen. et sp. nov.:

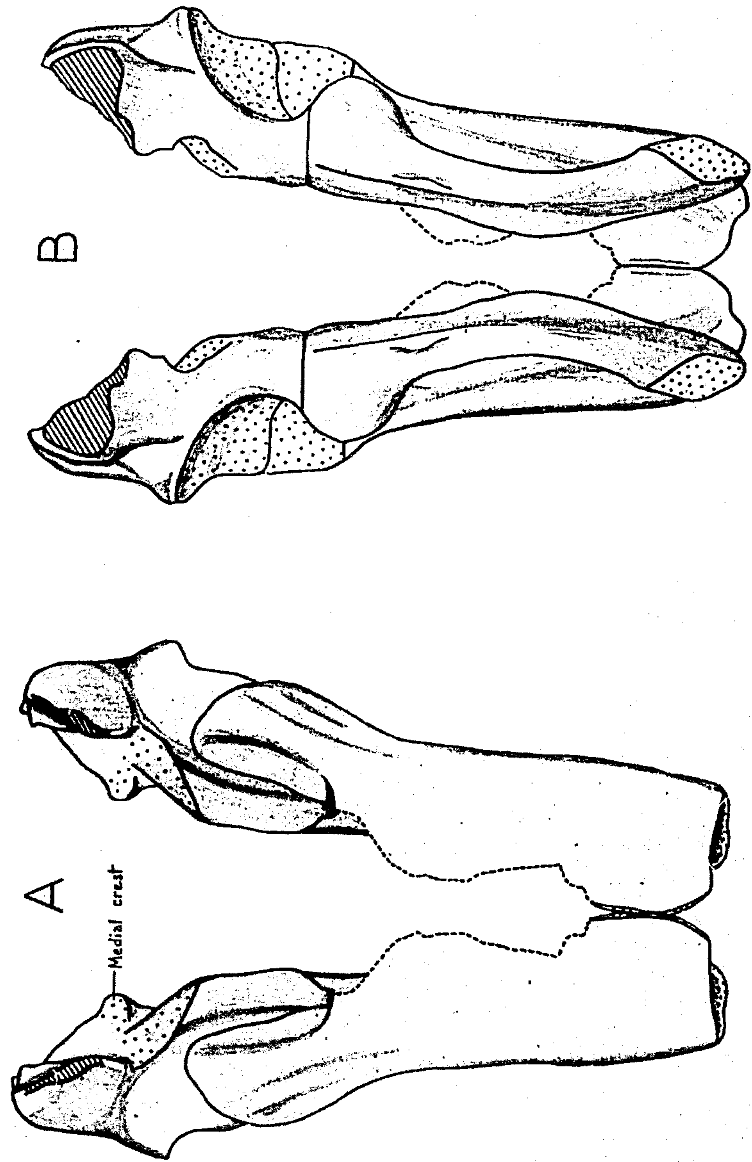
type-specimen (no. 11b)

Both illustrations in natural size.

Pelvic girdle, the two halves re-assembled:

A. Anterior view.

B. Posterior view.



<u>PLATE 16</u>

<u>Mandasuchus</u> <u>longicervix</u> gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Left side of pelvic girdle:

A. Dorsal view.

B. Ventral view.

C. Distal end of pubis.

D. Ilium, articulating surface for pubis.

E. Pubis, articulating surface for ilium.

F. Ilium, articulating surface for ischium.

G. Ischium, articulating surface for ilium.

H. Distal end of ischium.

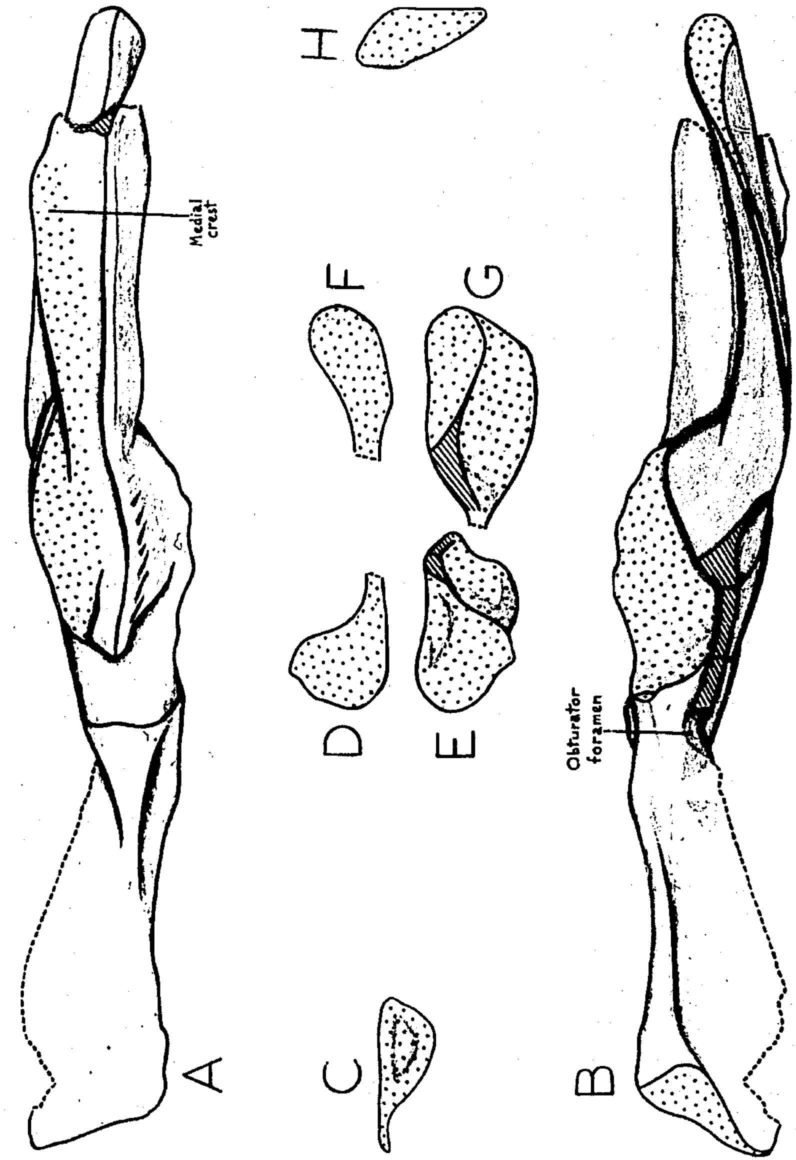


PLATE 17

Mandasuchus longicervix gen. et sp. nov.: type-specimen (no. 11b)

All illustrations in natural size.

Left femur:

A. Pre-axial (anteroventral) view.

B. Post-axial (posterodorsal) view.

C. Proximal end.

D. Distal end (as preserved).

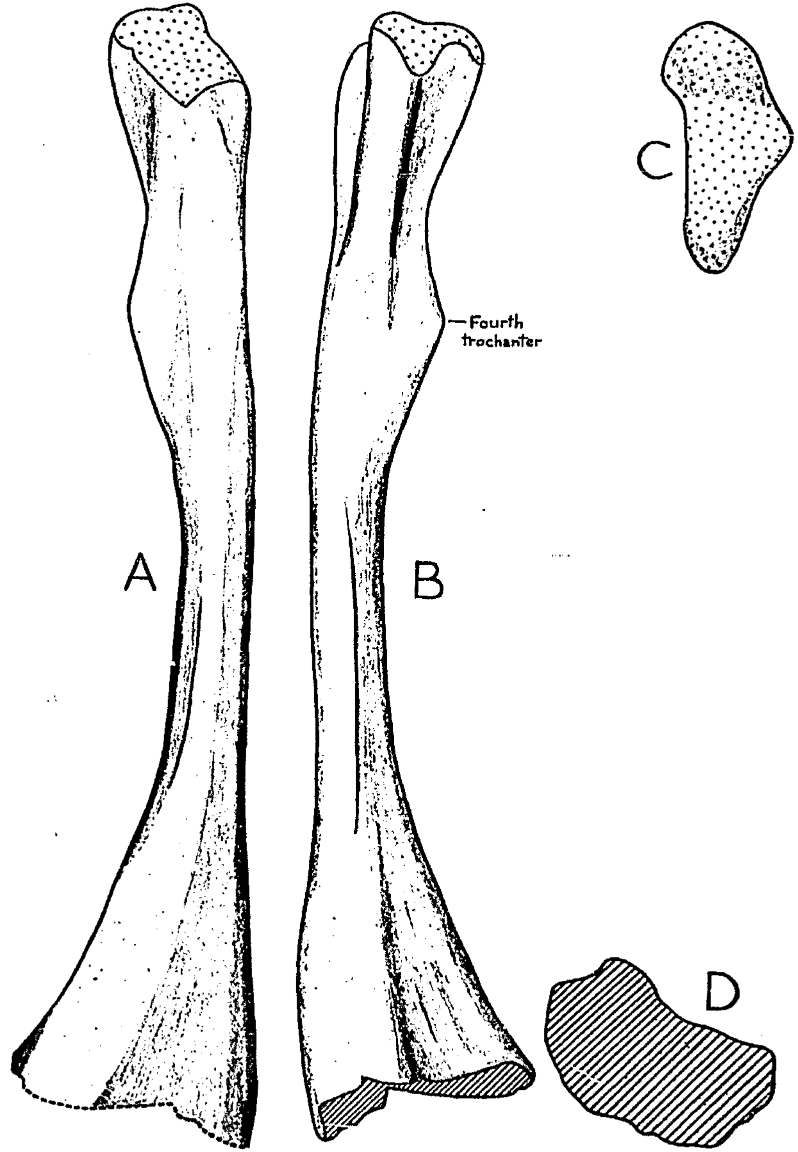


PLATE 18

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

Both illustrations in natural size.

Left femur:

A. Dorsal view (slightly anterior).

B. Ventral view (slightly posterior).

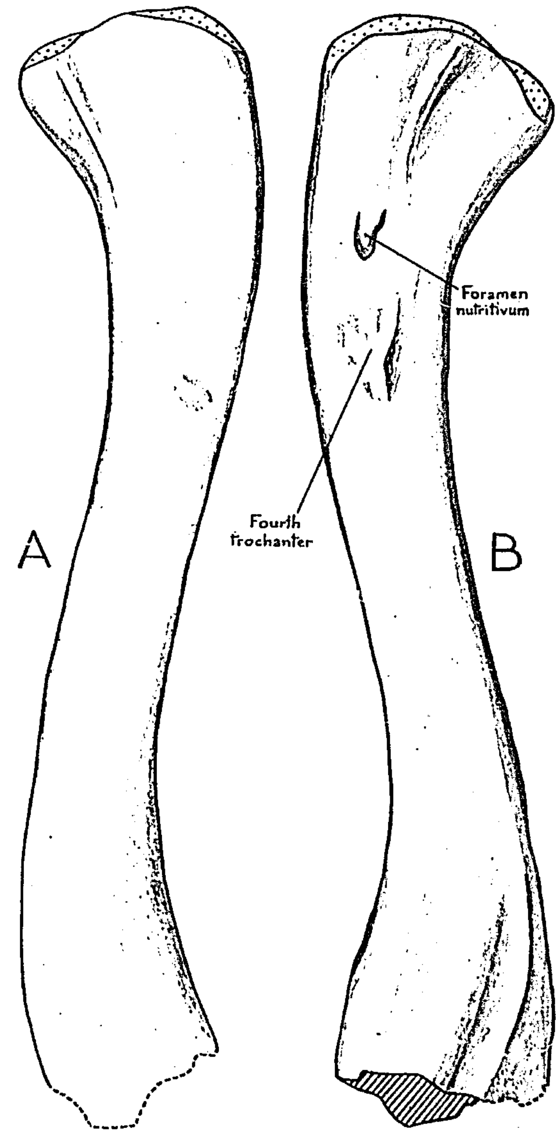


PLATE 19

<u>Mandasuchus</u> <u>longicervix</u> gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Left tibia, proximal end reconstructed from right:

A. Anterior view.

B. Posterior view.

C. Proximal end.

D. Distal end.

Right fibula:

E. Anterior view.

F. Posterior view.

G. Proximal end.

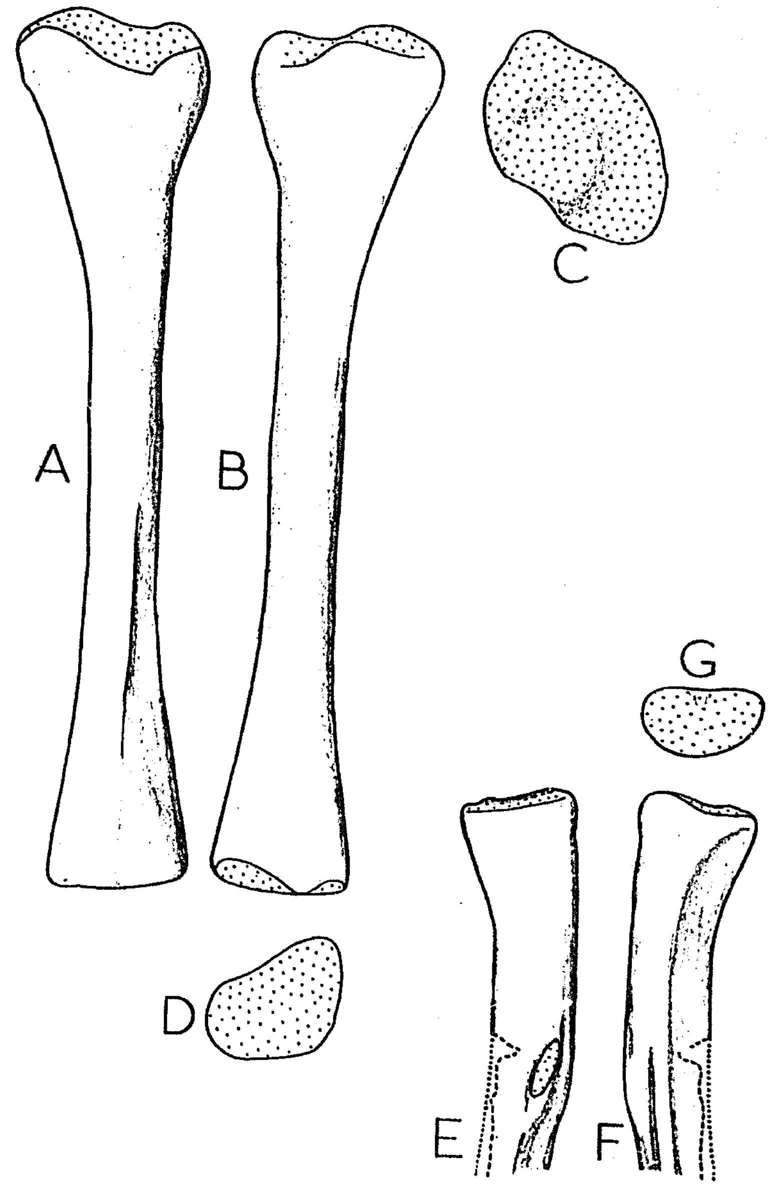


PLATE 20

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Left tibia, proximal end reconstructed from right:

A. Posterolateral view.

B. Anteromedial view.

Right fibula:

C. Lateral view.

D. Medial view.

Possible metatarsal:

E-H. Four views.

J. Proximal end.

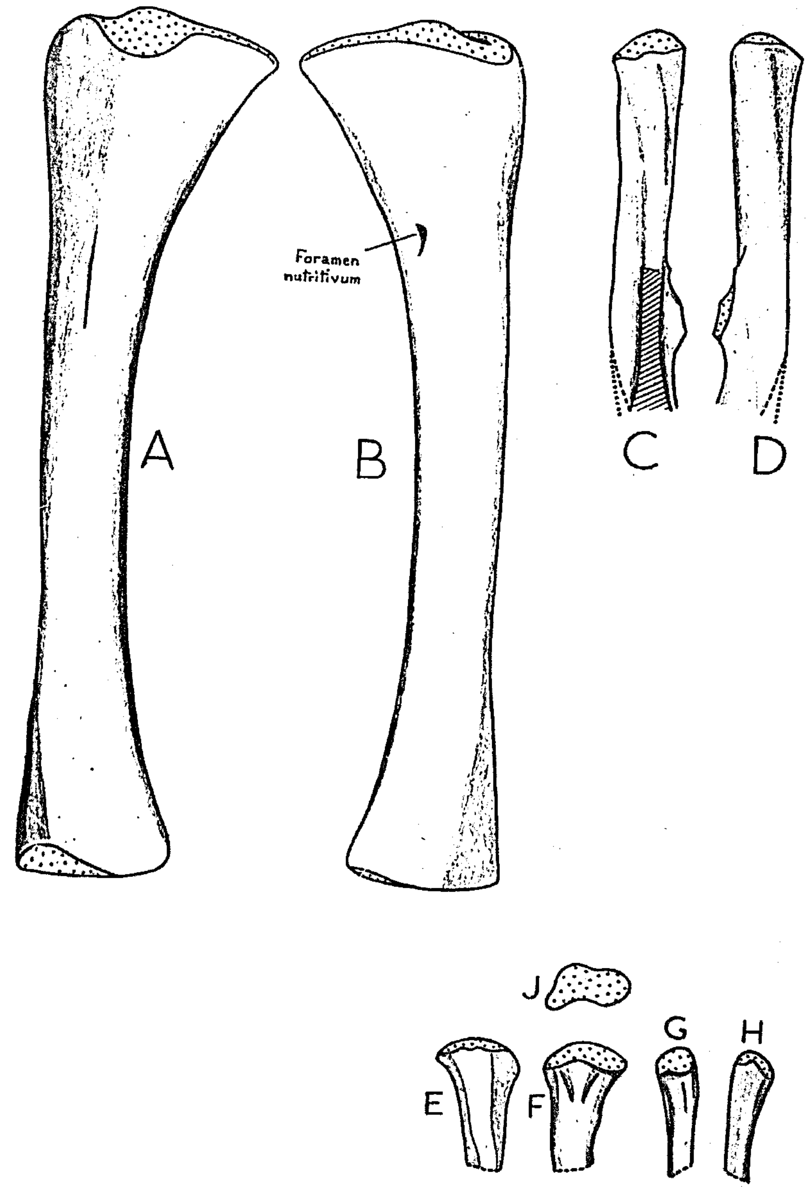


PLATE 21

Mandasuchus longicervix gen. et sp. nov.:

type-specimen (no. 11b)

All illustrations in natural size.

Dermal scutes in outer (dorsolateral) view:

Ce6. Those in situ upon the neural spine of the supposed sixth cervical vertebra; from the right paramedian row.

P, Q. Isolated fragments from the right paramedian dorsal row.

R, S. Isolated fragments from the left paramedian dorsal row.

Dermal scutes in inner (ventromedial) view:

P', Q', S'. Isolated fragments (corresponding to P, Q & S above).

Dermal scutes in posterior view:

Q", S". Isolated fragments (corresponding to Q & S above).

Reconstruction of part of the left paramedian dorsal row of dermal scutes:

T. Outer (dorsolateral) view.

U. Inner (ventromedial) view.

V. Transverse section.

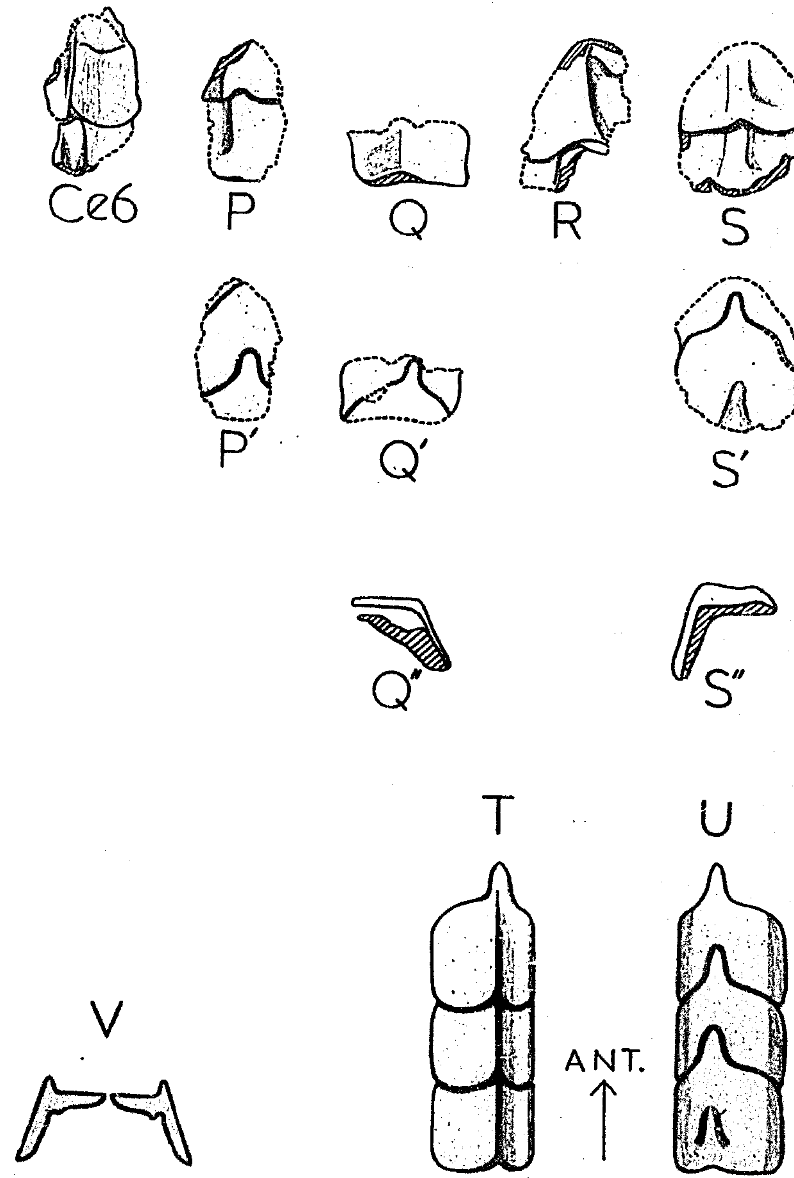


PLATE 22

Mandasuchus longicervix gen. et sp. nov.:

specimen no. 13

All illustrations in natural size.

Right maxilla (with fragment of unidentified bone adhering to its lateral surface):

A. Lateral view.

B. Medial view.

C. Ventral (crown) view.

D. Dorsal view.

Vertebrae in left lateral view:

Ce2. Axis with rib.

Ce3-Ce8. Cervical vertebrae.

D1-D5. Dorsal vertebrae.

X, Y. Possible middle dorsal vertebrae.

Z. Possible caudal vertebra.

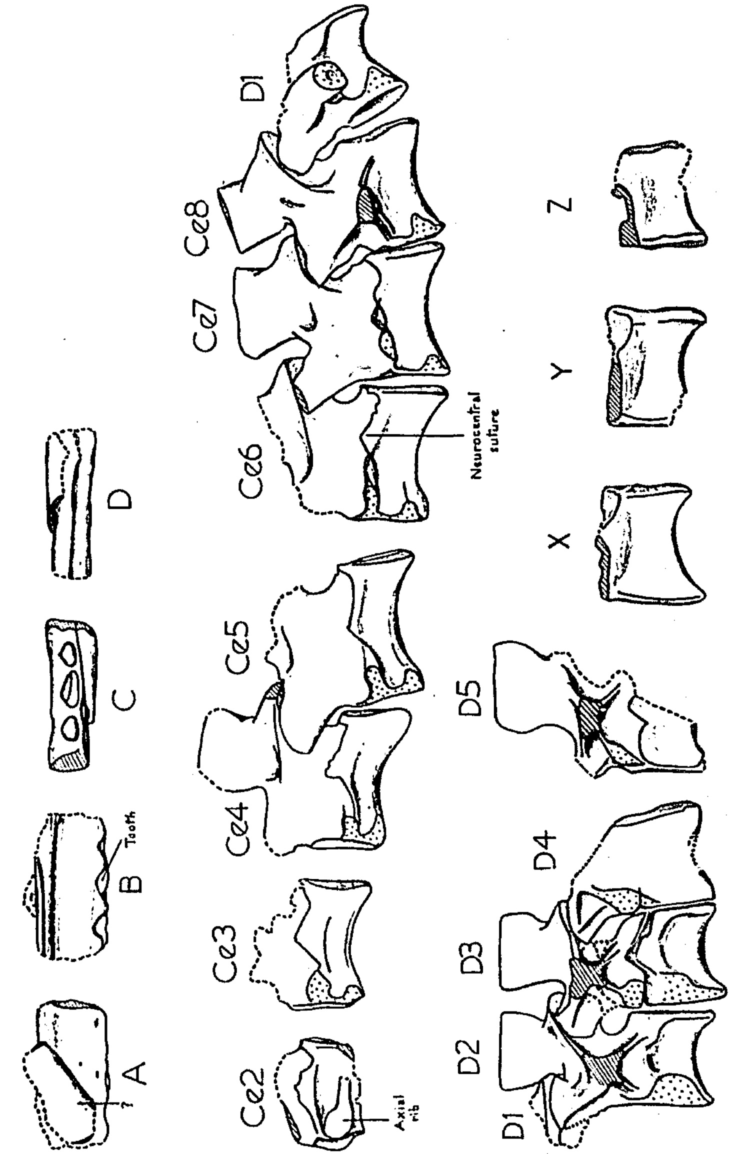


PLATE 23

Mandasuchus longicervix gen. et sp. nov.:

specimen no. 13

All illustrations in natural size.

Vertebrae in ventral view:

- Ce2. Axis with rib.
- Ce3-Ce8. Cervical vertebrae.
- D1-D5. Dorsal vertebrae.
- X, Y. Possible middle dorsal vertebrae.
- Z. Possible caudal vertebra.

Vertebrae in dorsal view; in some cases only the tops of the neural spines are shown:

- Ce4'-Ce8'. Cervical vertebrae.
- D2'-D5'. Dorsal vertebrae.

Vertebrae in anterior view:

- Ce4a. Cervical vertebra, supposed fourth.
- D2a. Second dorsal vertebra.

Vertebra in posterior view:

- Ce4p. Cervical vertebra, supposed fourth.

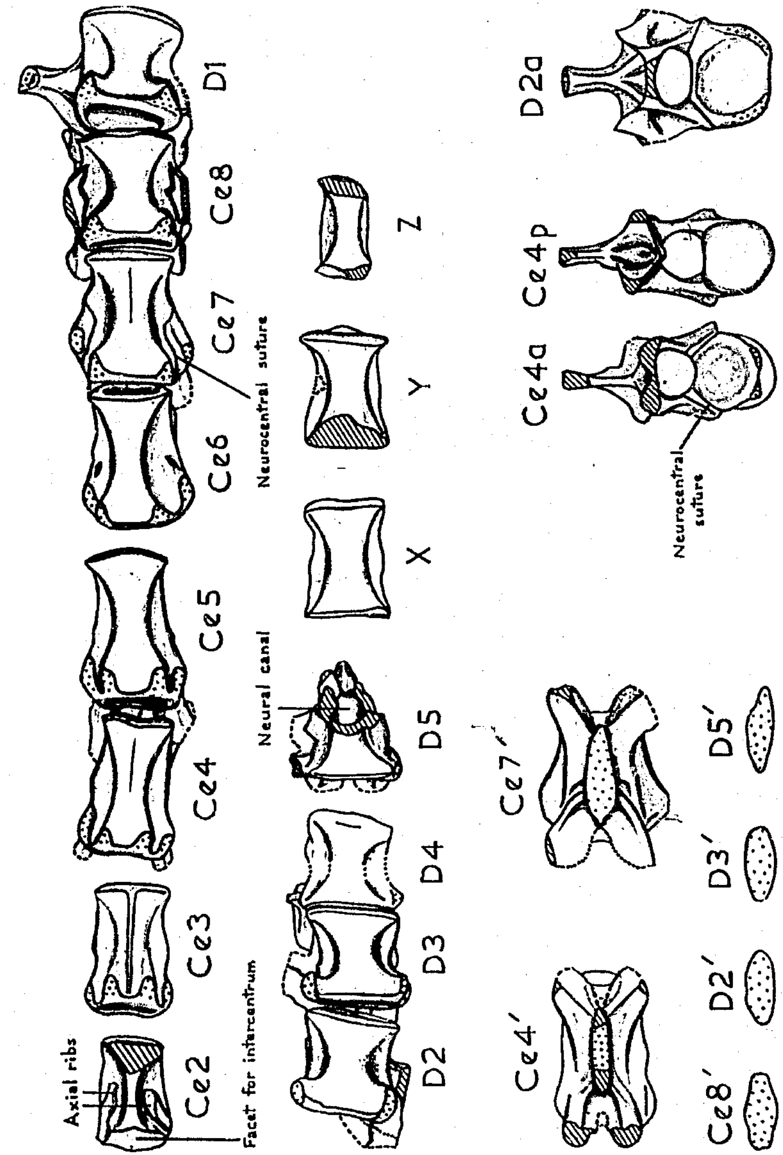


PLATE 24

Mandasuchus longicervix gen. et sp. nov.:

specimen no. 13

All illustrations in natural size.

Left scapula and coracoid (coracoid reversed from right):

A. Lateral view.

B. Medial view.

C. Posterior view.

Left scapula:

D. Articulating surface for coracoid.

Left coracoid (reversed from right):

E. Articulating surface for scapula.

Left humerus:

F. Pre-axial view.

G. Post-axial view.

H. Anterior view (slightly ventral).

J. Posterior view (slightly dorsal).

K. Proximal end.

L. Distal end.

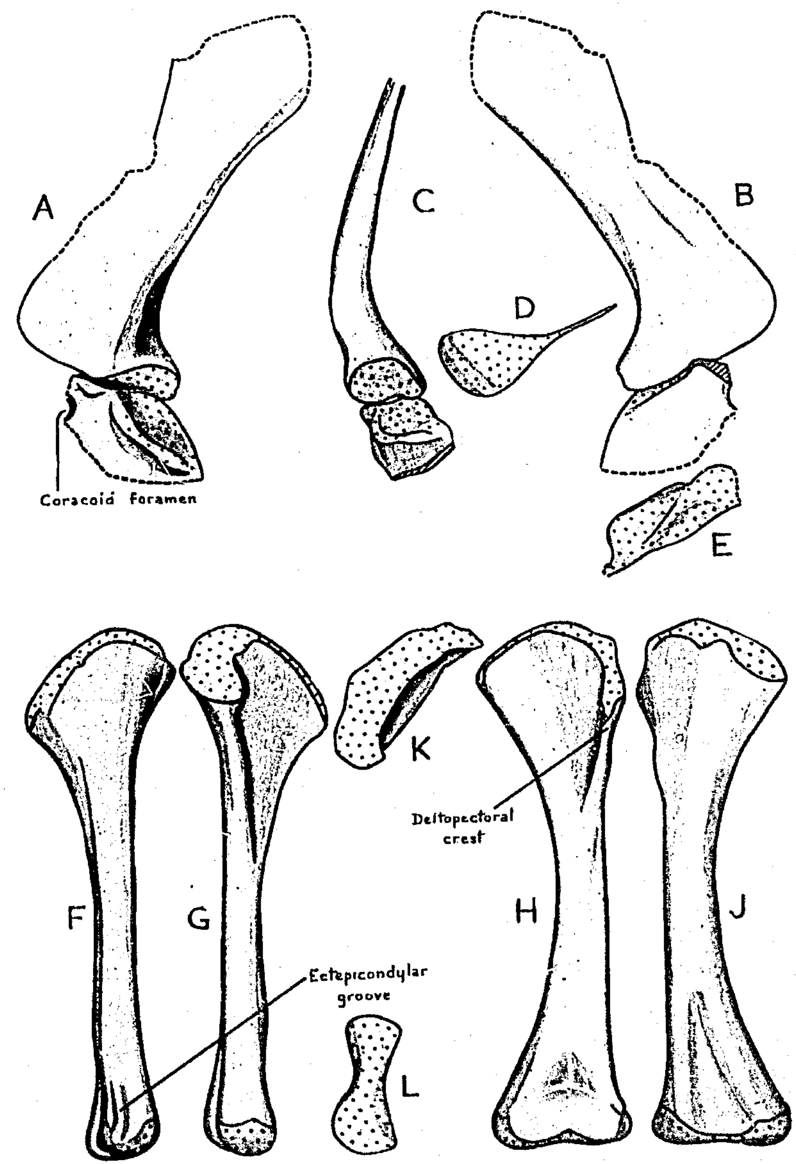


PLATE 25

Mandasuchus longicervix gen. et sp. nov.:

specimen no. 13

All illustrations in natural size.

Left humerus:

A. Ventral view.

Left(?) radius, proximal part:

B. Anterior(?) view.

C. Posterior(?) view.

D. Lateral(?) view.

E. Medial(?) view.

F. Proximal end.

Radius, distal part:

G–K. Four views.

L. Distal end.

Left ulna:

M. Anterior view.

N. Posterior view.

P. Lateral view.

Q. Medial view.

R. Proximal end.

Dermal scutes in transverse section:

S, T. Isolated fragments.

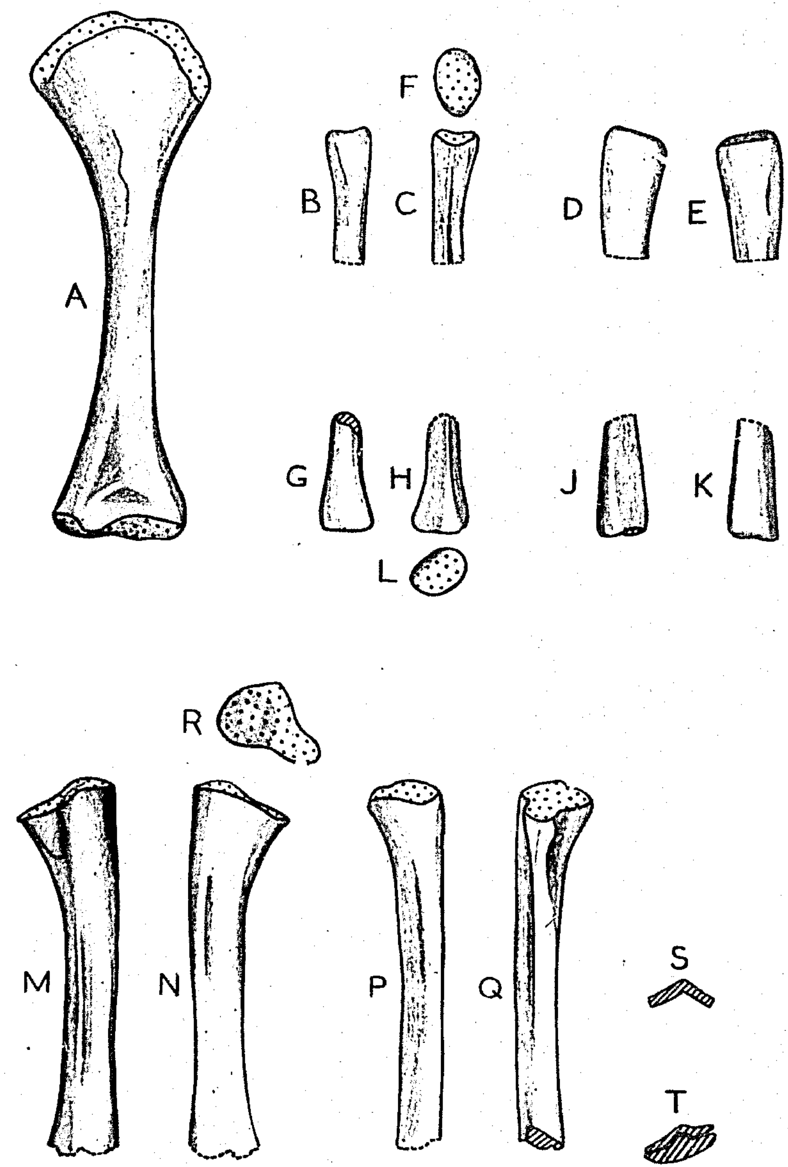


PLATE 26

<u>Mandasuchus</u> <u>longicervix</u> gen. et sp. nov.:

specimen no. 13

Both illustrations four times natural size.

Dermal scutes, prepared and embedded in a transparent block of synthetic resin:

A. Outer view.

B. Inner view.

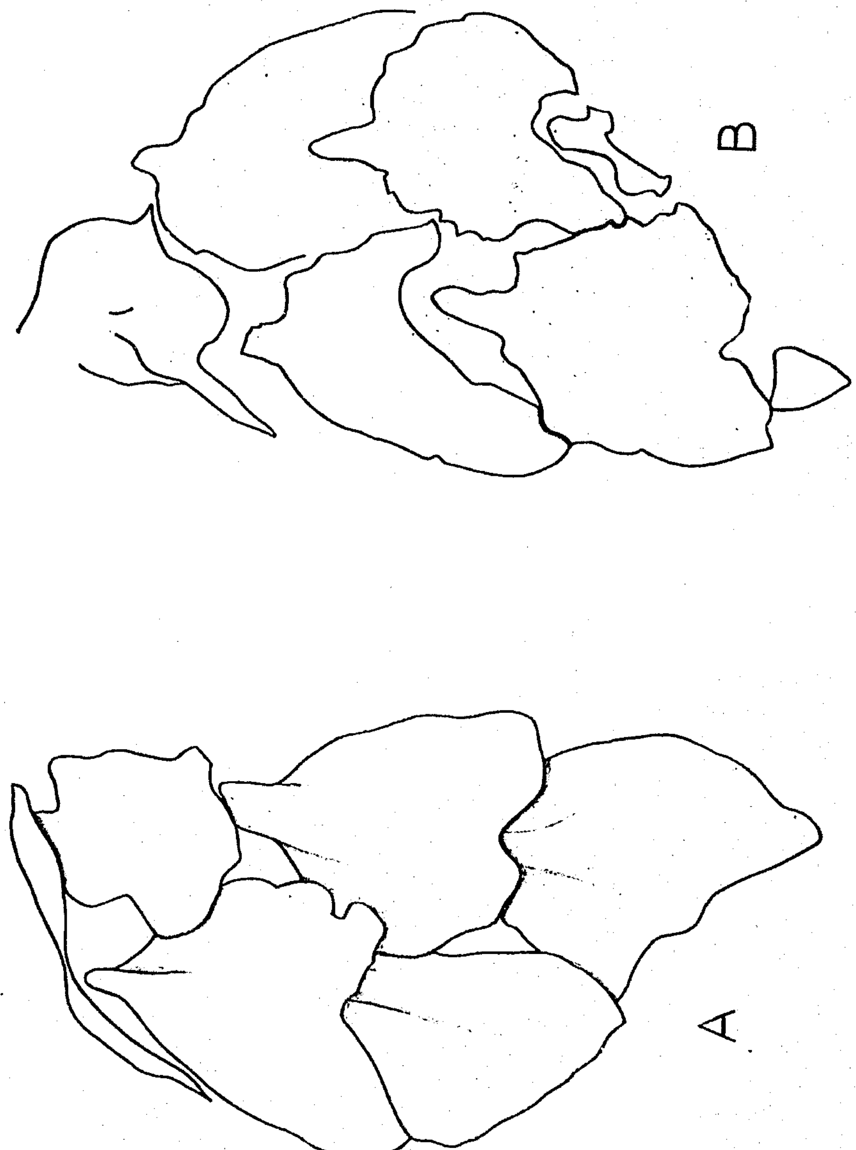


PLATE 27

<u>Mandasuchus</u> <u>longicervix</u> gen. et sp. nov.:
specimen no. 63

All illustrations in natural size.

Cervical vertebrae:

Ce2-Ce8. Left lateral view, with odontoid and axial intercentrum. (Neural arch of axis reconstructed).

Ce2'-Ce8'. Ventral view, with odontoid and axial intercentrum; fifth cervical vertebra with reconstructed outline of rib of left side. This illustration is semi-diagrammatic; the whole neck has been straightened, each centrum is seen from an angle normal to its own longitudinal axis, and no attempt has been made to show the zygapophyses.

A. Odontoid, axial intercentrum and reconstructed axis in anterior view. (Odontoid moved slightly to animal's right to centralise it and correct post-mortem displacement).

B. Reconstructed axis in posterior view.

C. Odontoid, axial intercentrum and centrum of axis after removal of part of capitulum of axial rib from parapophysial facet. (Right side reversed).

D. Neural spine of axis, dorsal view.

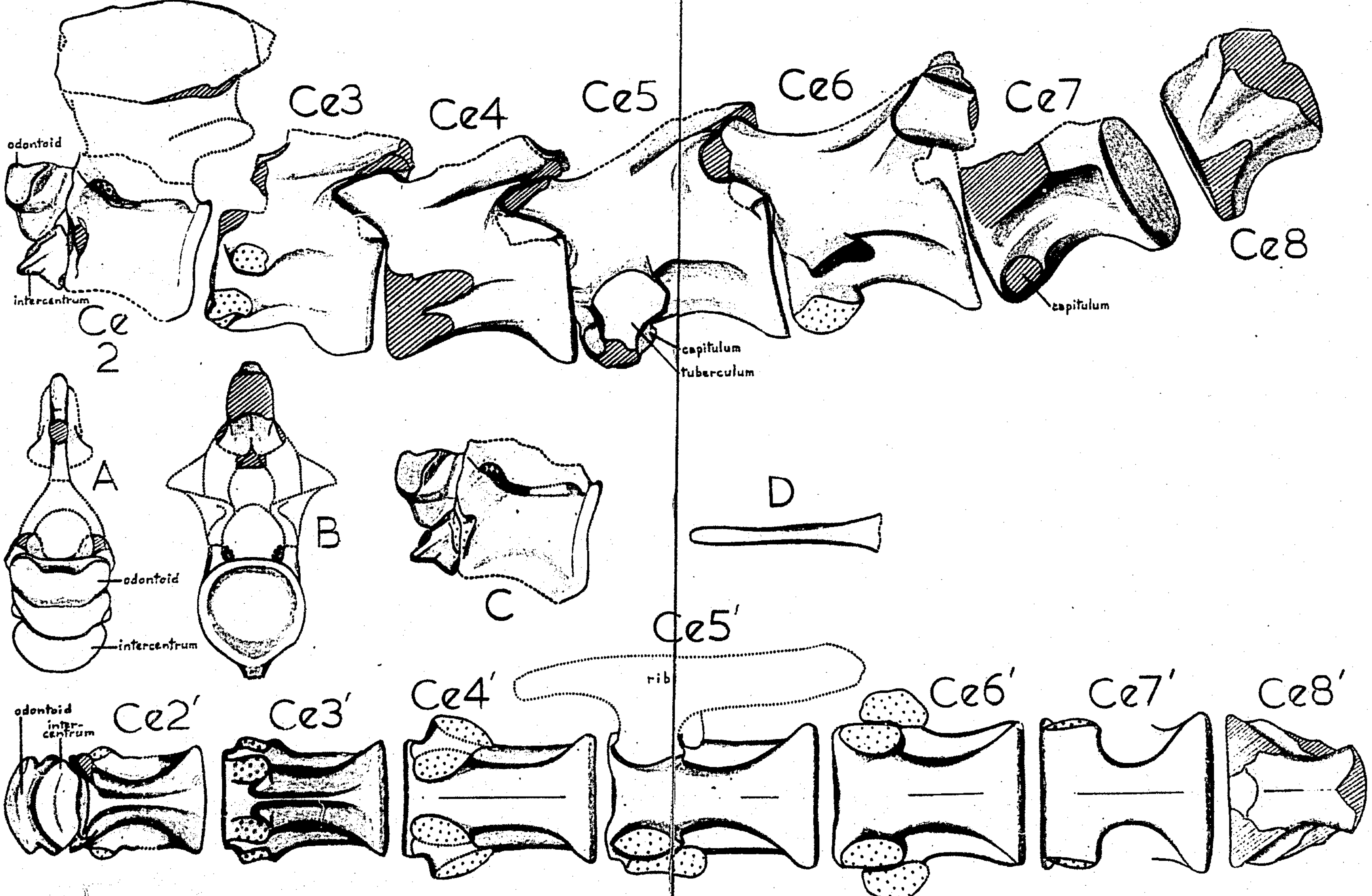

odontoid
intercentrum
Ce
2
Ce3
Ce4
Ce5
Ce6
Ce7
Ce8
capitulum
tuberculum
capitulum
A
odontoid
intercentrum
B
C
D
Ce5'
rib
odontoid
inter-
centrum
Ce2'
Ce3'
Ce4'
Ce6'
Ce7'
Ce8'

PLATE 28

Mandasuchus longicervix gen. et sp. nov.:

specimen no. 63

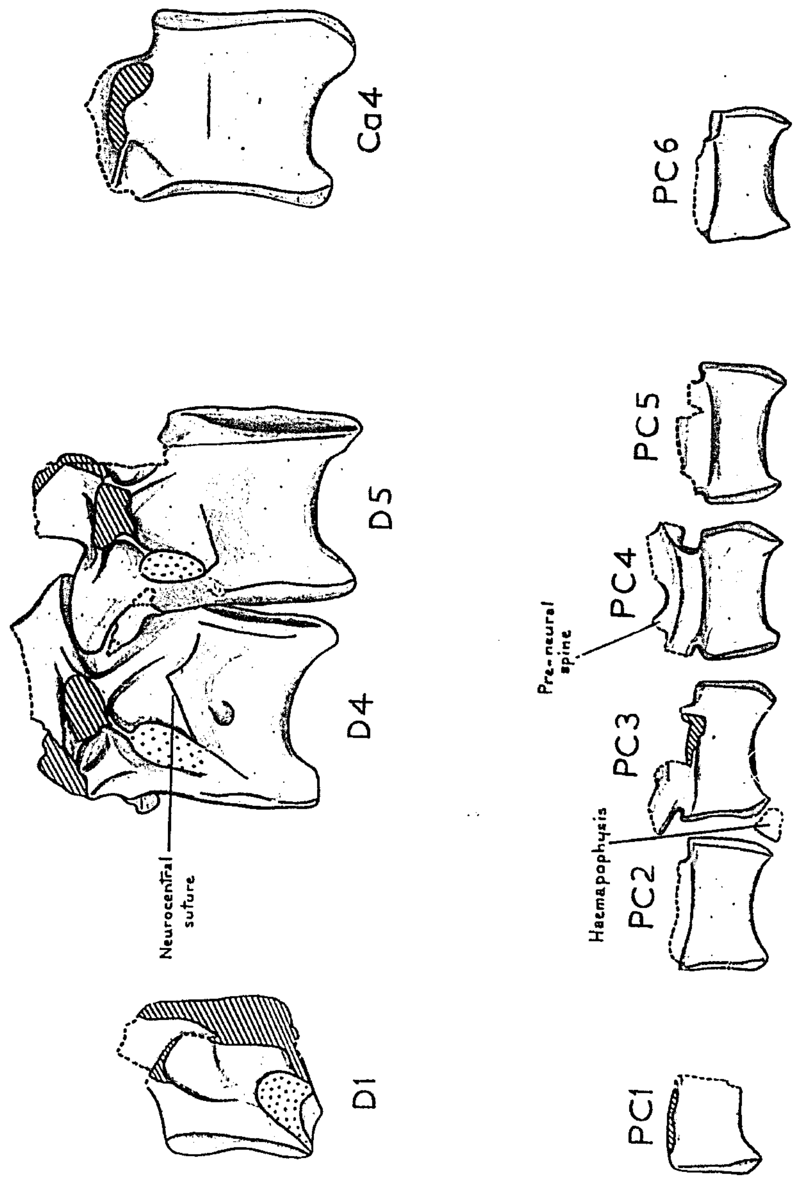
All illustrations in natural size.

Vertebrae in left lateral view:

D1-D5. Dorsal vertebrae.

Ca4. Caudal vertebra, possible fourth.

PC1-PC6. Distal caudal vertebrae (the proximal end of a haemapophysis between PC2 and PC3).



29

PLATE 29

Mandasuchus longicervix gen. et sp. nov.:

specimen no. 63

All illustrations in natural size.

Vertebrae in ventral view:

- D4, D5. Dorsal vertebrae.
- Ca4. Caudal vertebra, possible fourth.
- PC1–PC6. Distal caudal vertebrae (the proximal end of a haemapophysis between PC2 and PC3).

Vertebra in dorsal view:

- PC4'. Distal caudal vertebra.

Vertebra in anterior view:

- PC4a. Distal caudal vertebra.

Vertebrae in posterior view:

- D4'. Dorsal vertebra, supposed fourth.
- PC4p. Distal caudal vertebra.

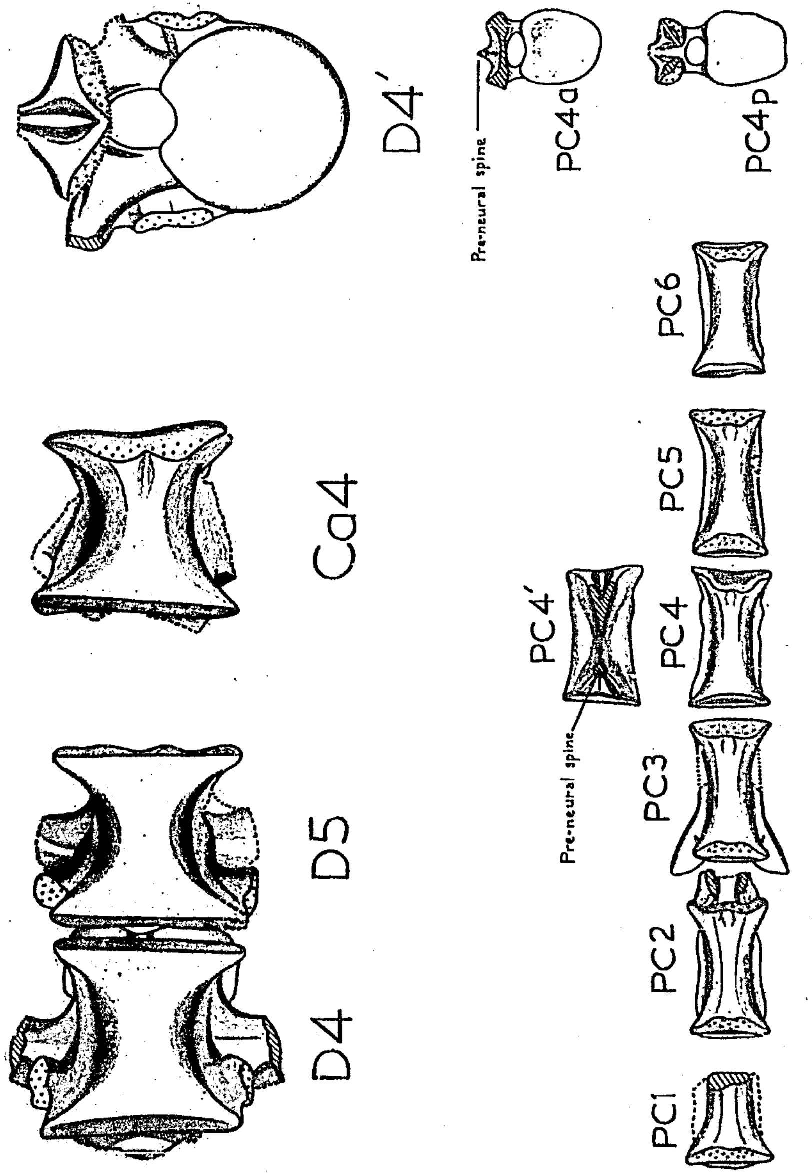


PLATE 30

Mandasuchus longicervix gen. et sp. nov.:

specimen no. 63

All illustrations in natural size.

Cervical ribs of left side, capitulum and tuberculum reconstructed on middle rib:

A. Dorsolateral view.

B. Ventromedial view.

C. Internal view.

D. External view.

Dorsal rib of right side:

E. Anterior view.

F. Posterior view.

G. Dorsal view.

H. Ventral view.

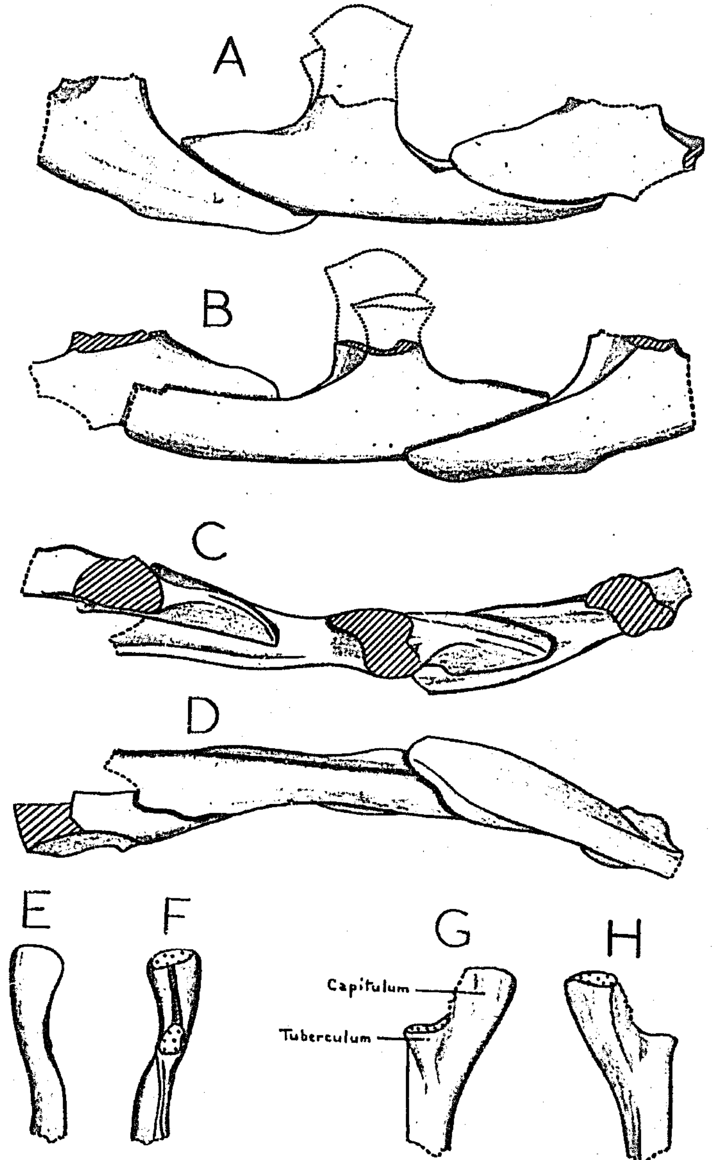


PLATE 31

Mandasuchus longicervix gen. et sp. nov.:

specimen no. 63

All illustrations in natural size.

Left side of pelvic girdle:

A. Lateral view.

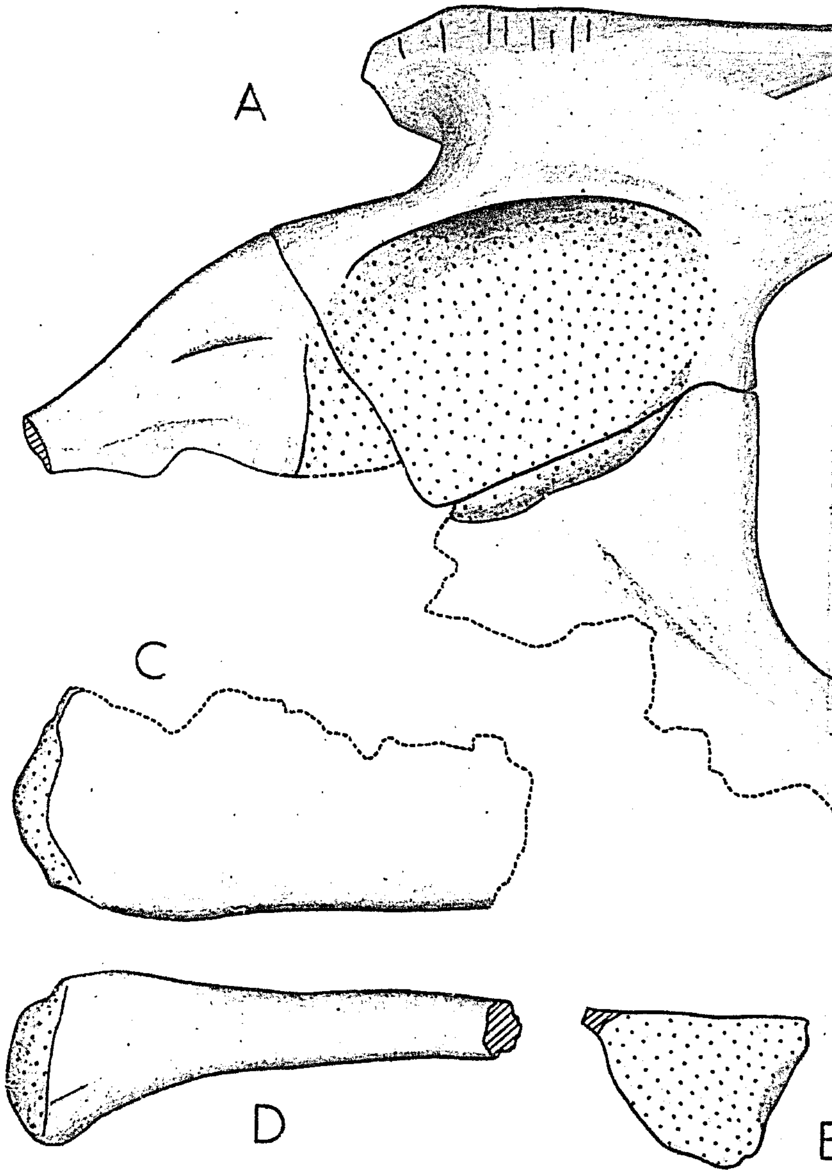
B. Posterior view.

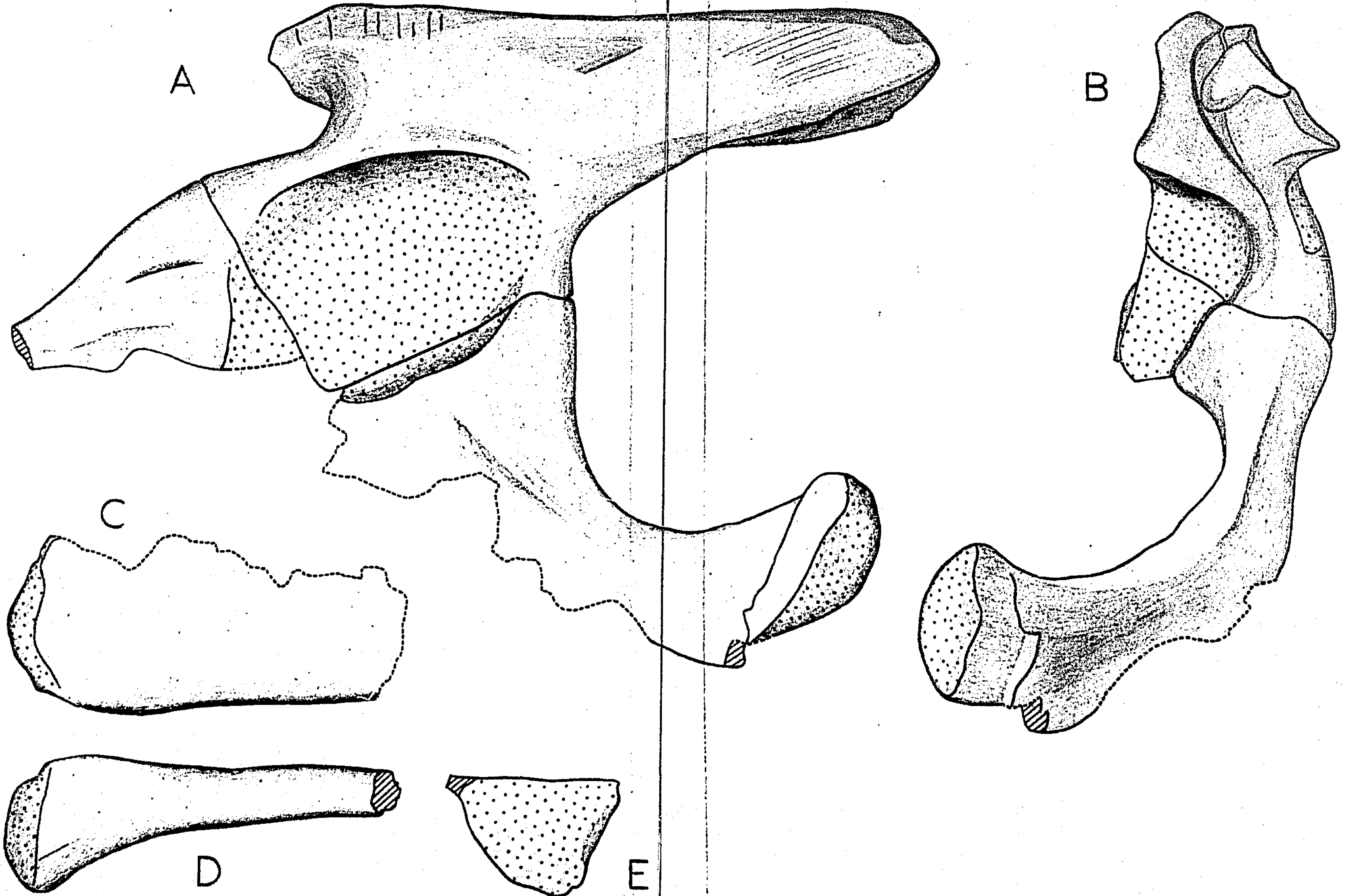
Detached distal part of left pubis:

C. Anterodorsal view.

D. Lateral view.

E. Distal end.




A
B
C
D
E

<u>PLATE 32</u>

Mandasuchus longicervix gen. et sp. nov.:

specimen no. 63

All illustrations in natural size.

Left fibulare:

A. Anterior view.

B. Posterior view.

C. Lateral view.

D. Medial view.

E. Dorsal view.

F. Ventral view.

Fragment of dermal scutes:

G. Outer view.

H. Inner view.

J. Lateral view.

Another fragment of dermal scutes:

K. Outer view.

L. Inner view.

M. Posterior view.

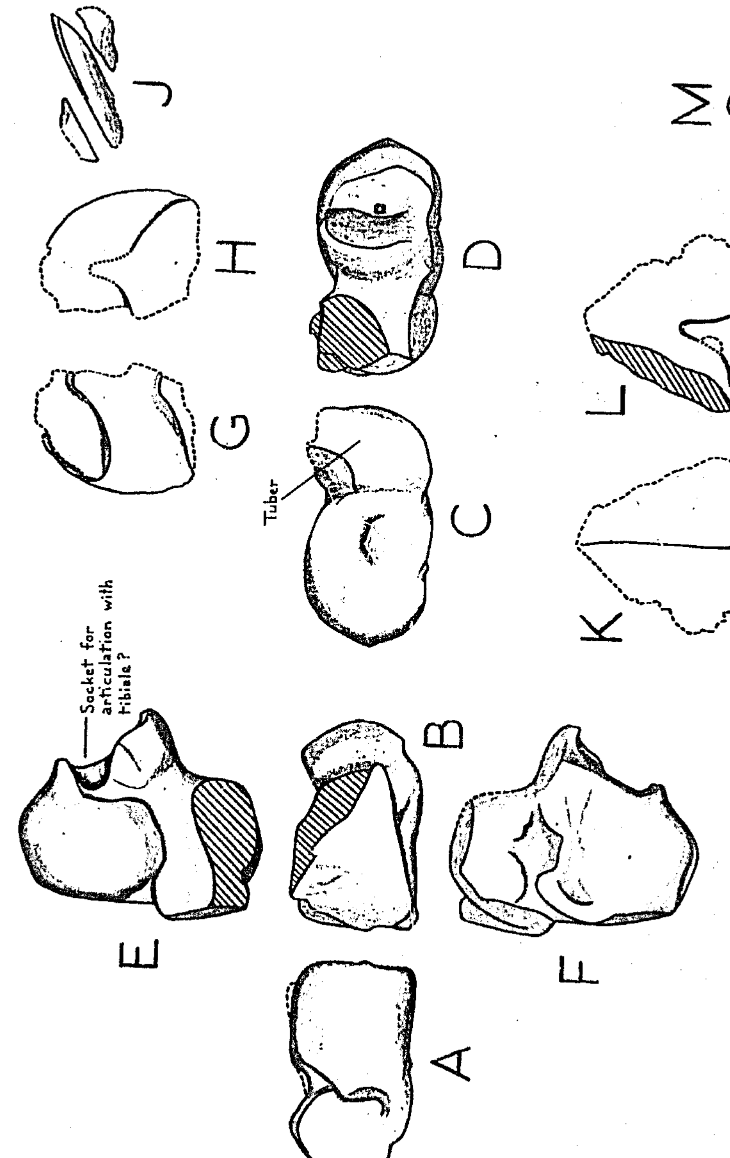


PLATE 33

Teleocrater tanyura gen. et sp. nov.:

type-specimen (no. 48b)

All illustrations in natural size.

Vertebrae in left lateral view:

CeA, CeB.	Cervical vertebrae.
DA-DH.	Dorsal vertebrae.
DI-DK.	Posterior dorsal or pygal vertebrae.
CaA-CaO.	Caudal vertebrae.

The vertebrae have been lettered alphabetically in what appears to be the most likely order of succession; missing vertebrae are not considered.

33

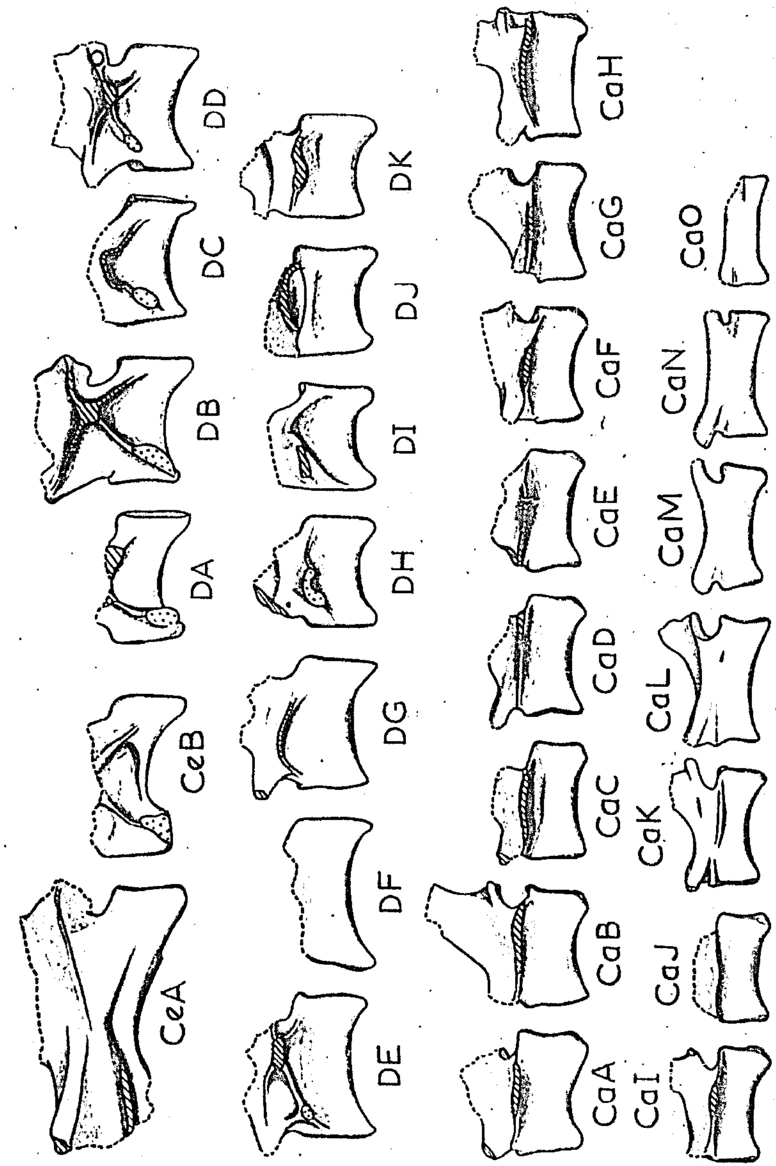


PLATE 34

Teleocrater tanyura gen. et sp. nov.:

type-specimen (no. 48b)

All illustrations in natural size.

Vertebrae in ventral view:

CeA, CeB.	Cervical vertebrae.
DA–DH.	Dorsal vertebrae.
DI–DK.	Posterior dorsal or pygal vertebrae.
CaA–CaO.	Caudal vertebrae.

The vertebrae have been lettered alphabetically in what appears to be the most likely order of succession; missing vertebrae are not considered.

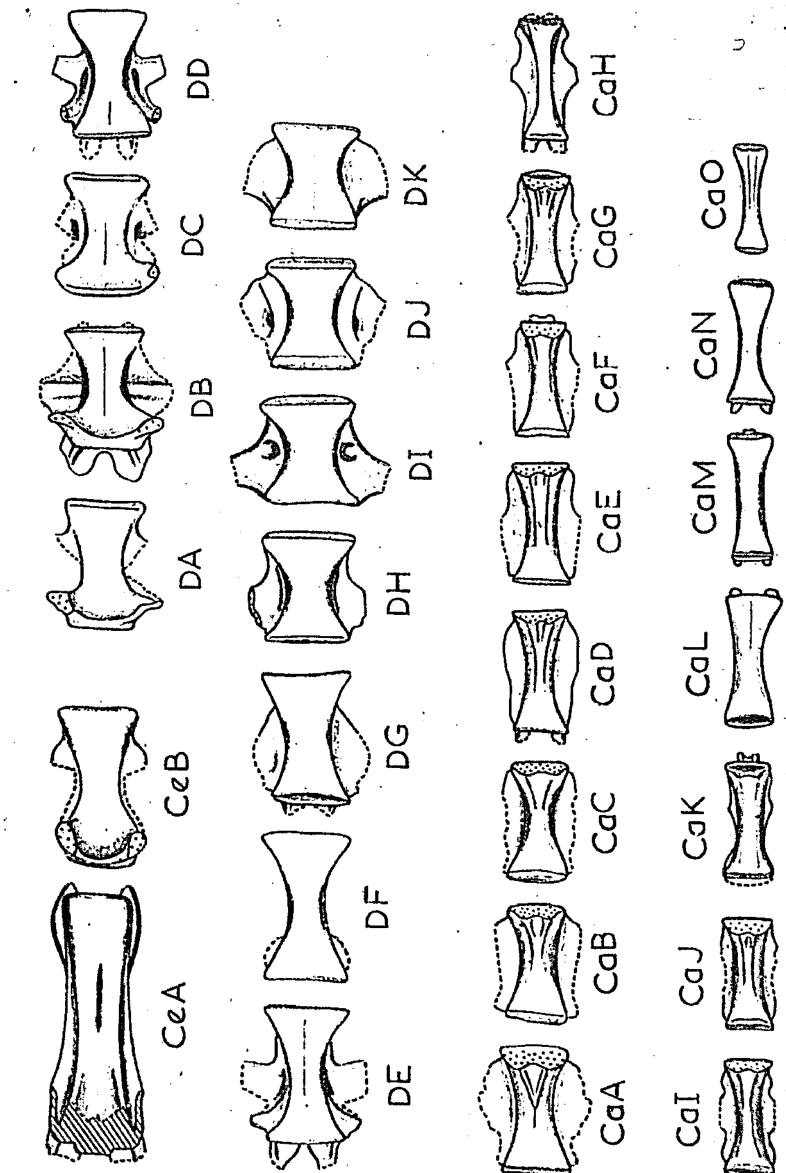


PLATE 35

Teleocrater tanyura gen. et sp. nov.:

type-specimen (no. 48b)

All illustrations in natural size.

Vertebrae in dorsal view:

- CeA. Cervical vertebra, supposedly anterior.
- DB-DG. Dorsal vertebrae.
- DK. Posterior dorsal or pygal vertebra.
- CaD-CaO. Caudal vertebrae.

Vertebrae in anterior view:

- CeA'-CeB'. Cervical vertebrae.
- DA'-DH'. Dorsal vertebrae.
- DI'-DK'. Posterior dorsal or pygal vertebrae.
- CaA'-CaE'. Caudal vertebrae.

The vertebrae have been lettered alphabetically in what appears to be the most likely order of succession; missing vertebrae are not considered.

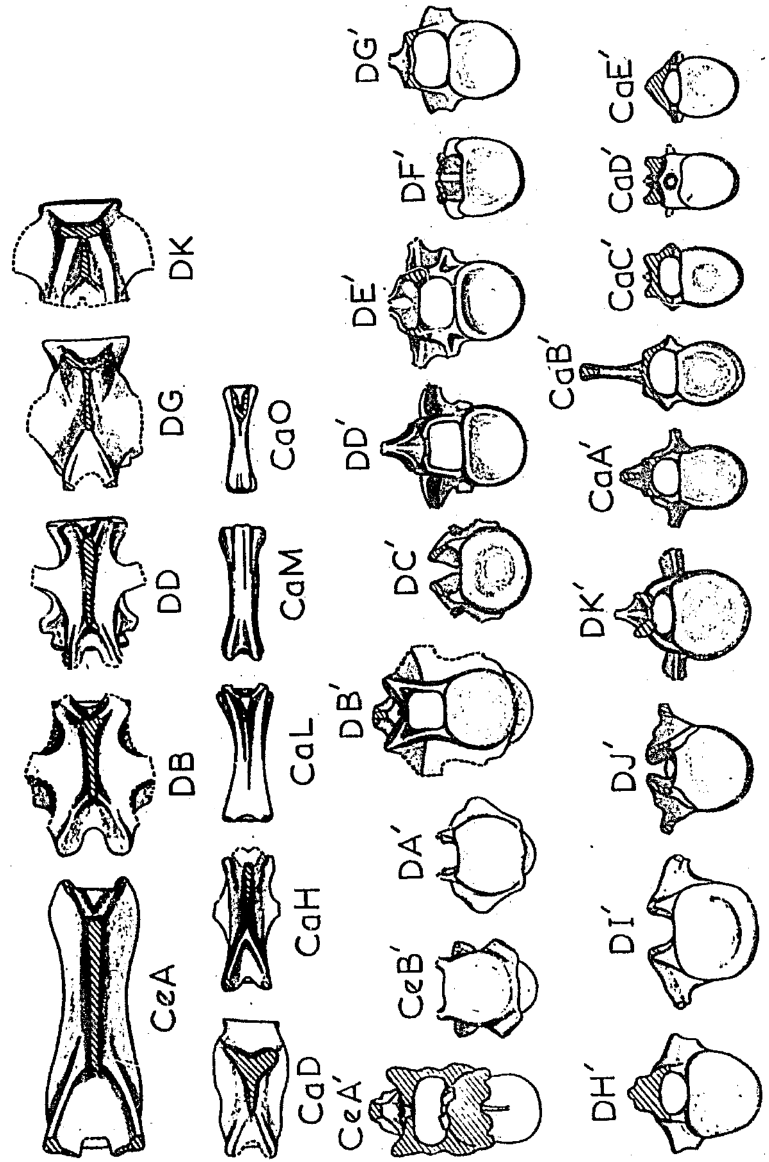


PLATE 36

Teleocrater tanyura gen. et sp. nov.:

type-specimen (no. 48b)

All illustrations in natural size.

Vertebrae in anterior view:

CaF'-CaO'. Caudal vertebrae.

Vertebrae in posterior view:

CeA-CeB. Cervical vertebrae.

DA-DH. Dorsal vertebrae.

DI-DK. Posterior dorsal or pygal vertebrae.

CaA-CaO. Caudal vertebrae.

The vertebrae have been lettered alphabetically in what appears to be the most likely order of succession; missing vertebrae are not considered.

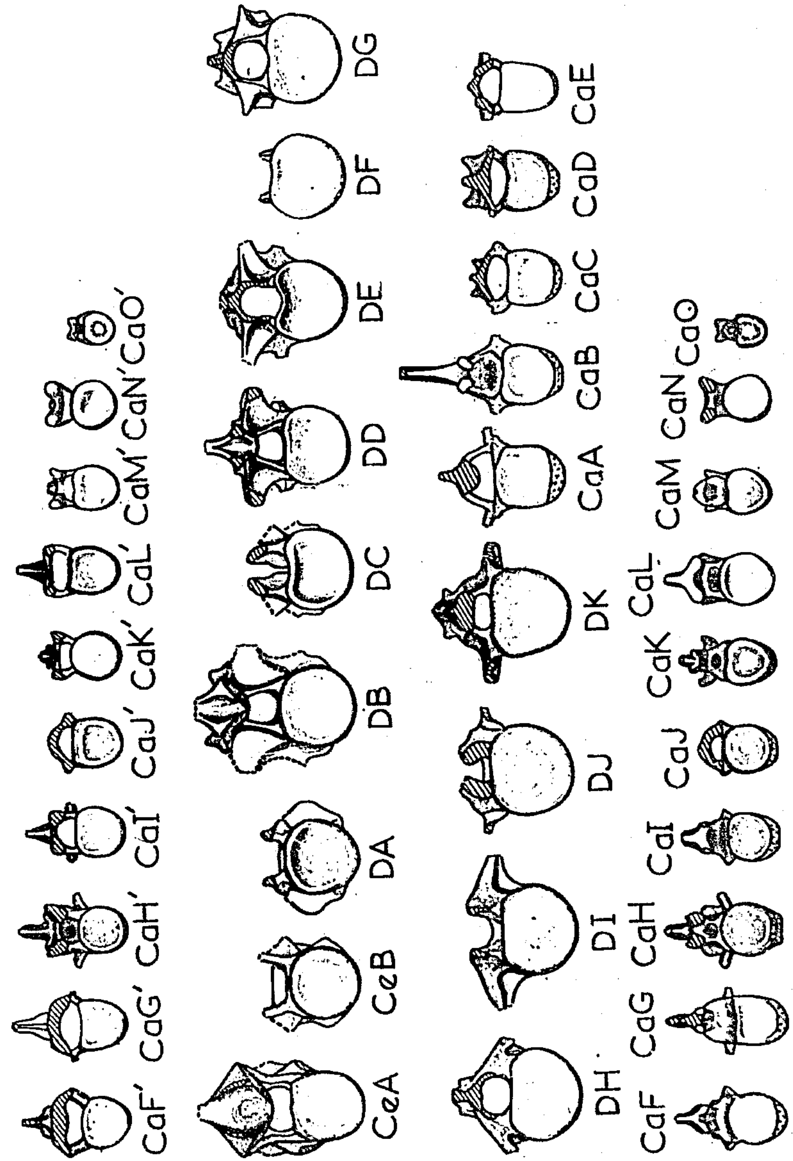


PLATE 37

Teleocrater tanyura gen. et sp. nov.:

type-specimen (no. 48b)

All illustrations in natural size.

Dorsal rib:

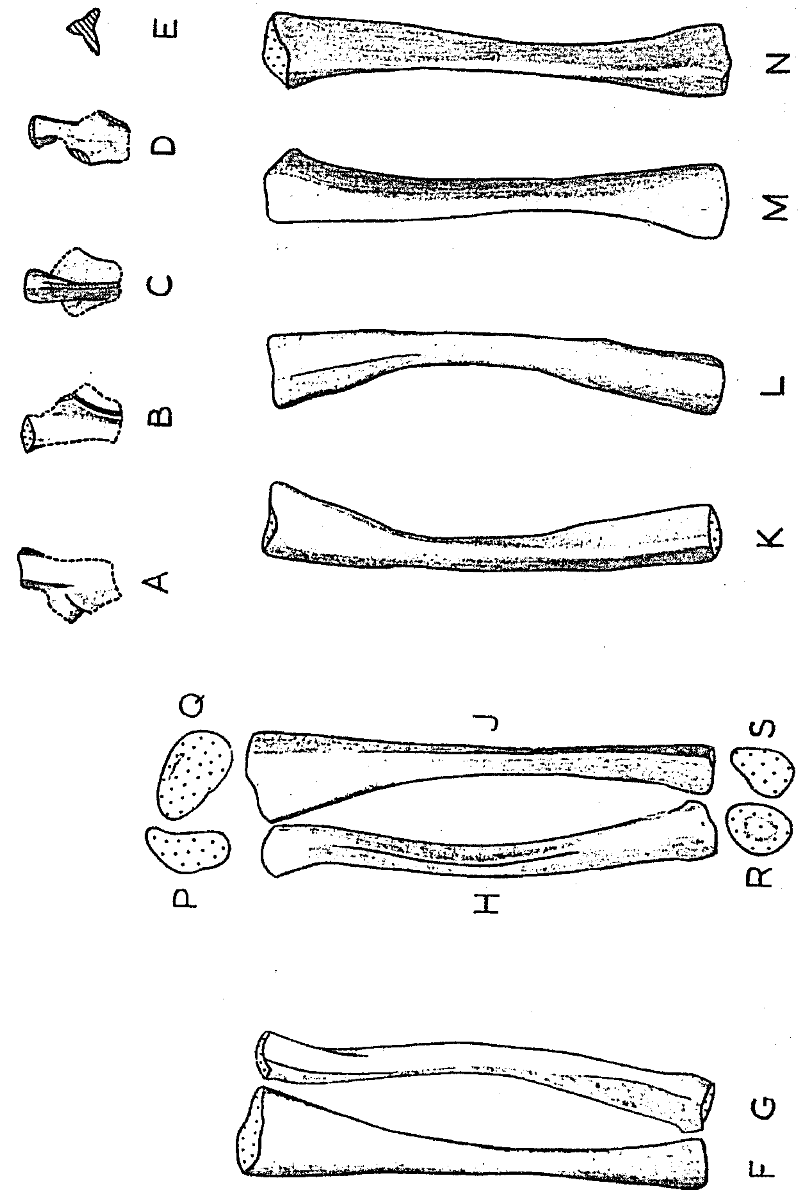
- A–D. Four views.
- E. Broken end.

Right radius:

- G. Anterior view.
- H. Posterior view.
- K. Lateral view.
- L. Medial view.
- P. Proximal end.
- R. Distal end.

Right ulna:

- F. Anterior view.
- J. Posterior view.
- M. Lateral view.
- N. Medial view.
- Q. Proximal end.
- S. Distal end.



<u>PLATE 38</u>

<u>Teleocrater</u> <u>tanyura</u> gen. et sp. nov.:
type-specimen (no. 48b)

All illustrations in natural size.

Left ilium:

A. Lateral view.

B. Ventral view.

C. Medial view.

D. Anterior view.

Left femur:

E. Pre-axial (anterior) view.

F. Post-axial (posterior) view.

G. Proximal end.

H. Distal end.

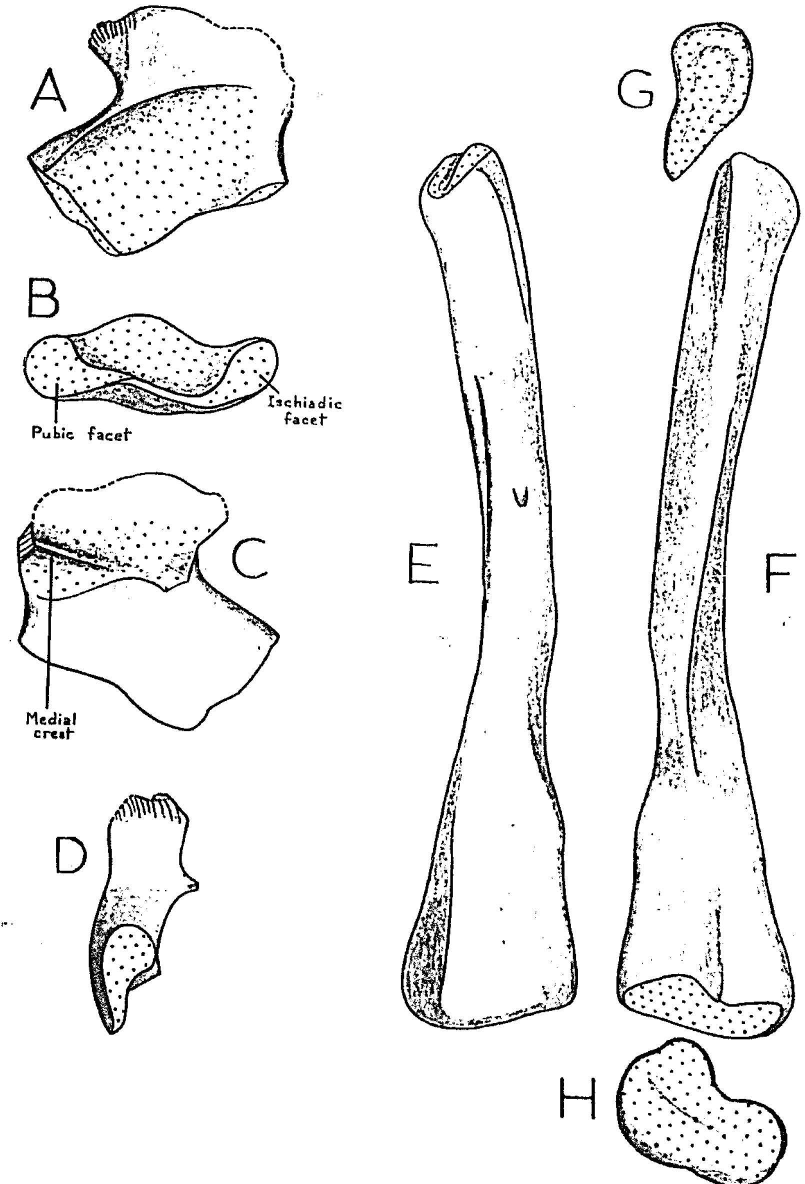


PLATE 39

Teleocrater tanyura gen. et sp. nov.:
type-specimen (no. 48b)

All illustrations in natural size.

Left femur:

A. Dorsal view (slightly anterior).

B. Ventral view (slightly posterior).

Left tibia:

C. Anterior view.

Left fibula:

D. Anterior view.

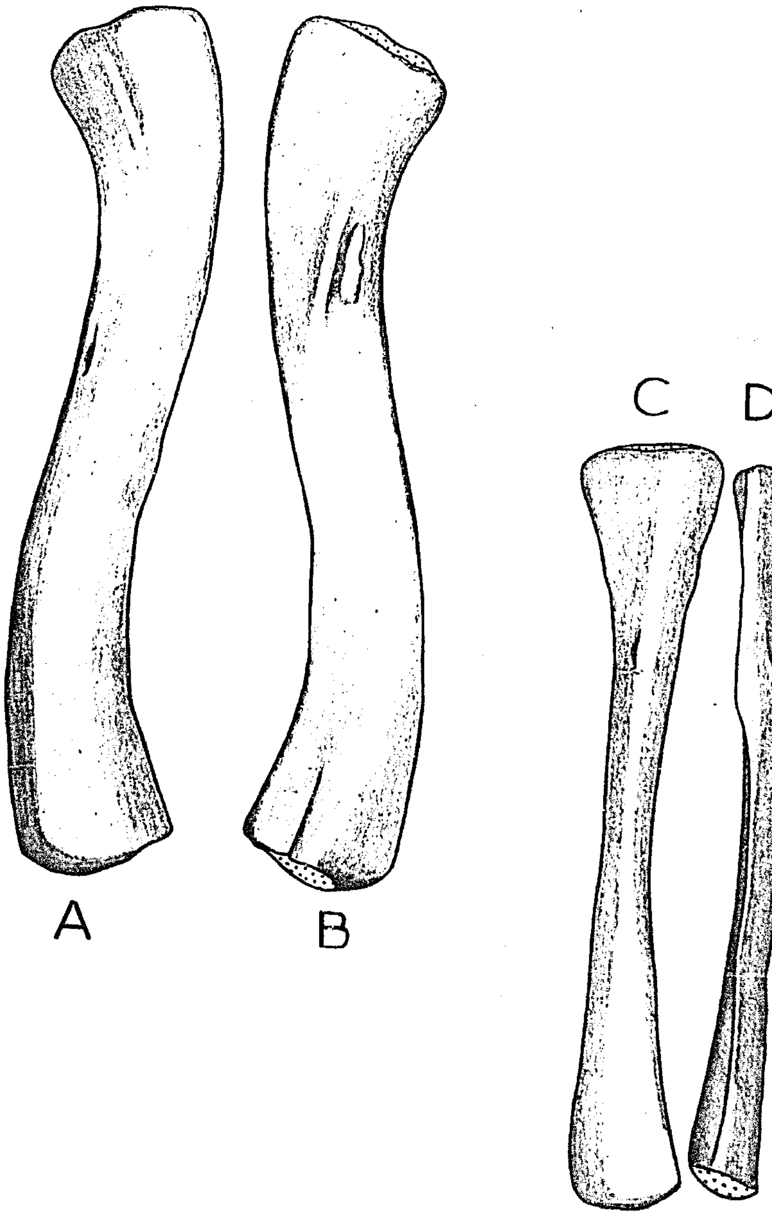


PLATE 40

<u>Teleocrater</u> <u>tanyura</u> gen. et sp. nov.:

type-specimen (no. 48b)

All illustrations in natural size.

Left tibia:

B. Posterior view.

C. Posterolateral view.

D. Anteromedial view.

H. Proximal end.

K. Distal end.

Left fibula:

A. Posterior view.

E. Lateral view.

F. Medial view.

G. Proximal end.

J. Distal end.

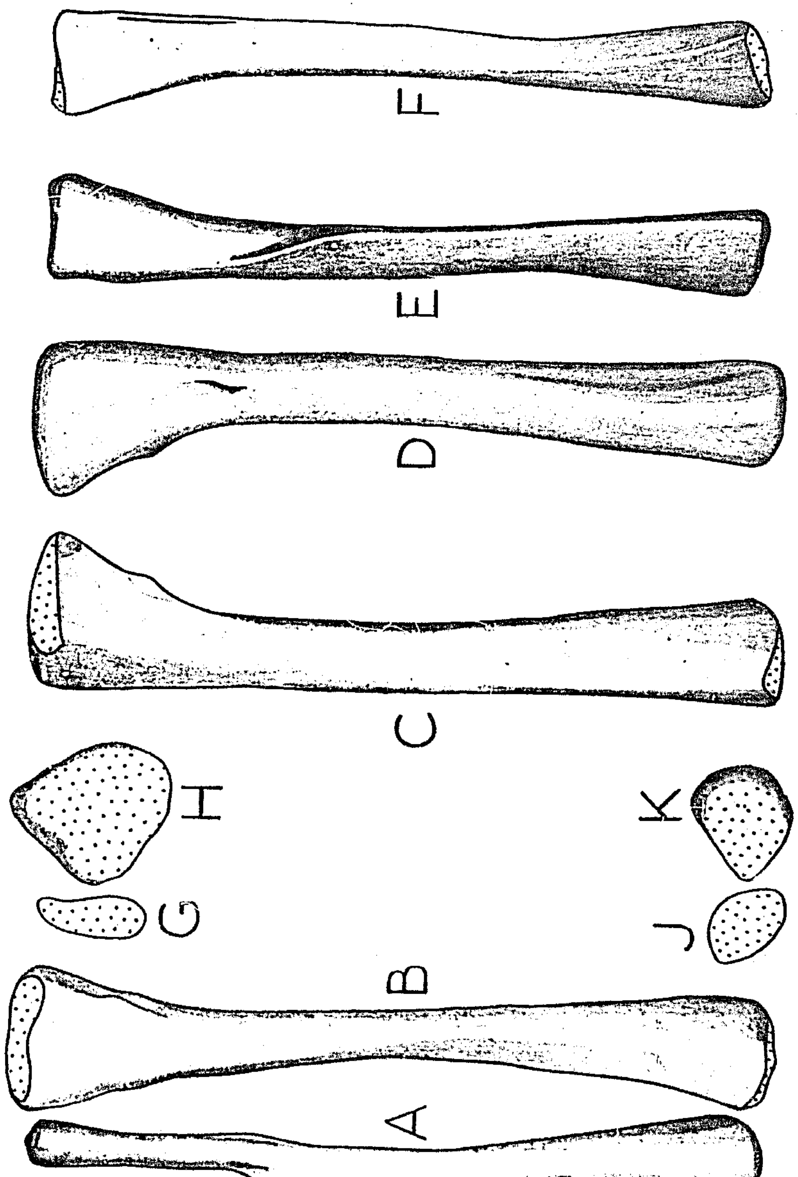


PLATE 41

Teleocrater tanyura gen. et sp. nov.:

specimen no. 53a

All illustrations in natural size.

Vertebrae in left lateral view:

A. Dorsal vertebra, supposedly anterior.

B. Posterior dorsal or pygal vertebra.

Vertebrae in ventral view:

A'. Dorsal vertebra, supposedly anterior.

B'. Posterior dorsal or pygal vertebra.

Vertebrae in anterior view:

Aa. Dorsal vertebra, supposedly anterior.

Ba. Posterior dorsal or pygal vertebra.

Vertebrae in posterior view:

Ap. Dorsal vertebra, supposedly anterior.

Bp. Posterior dorsal or pygal vertebra.

Left humerus:

C. Pre-axial view.

D. Post-axial view.

E. Anteroventral view.

F. Posterodorsal view.

G. Distal end.

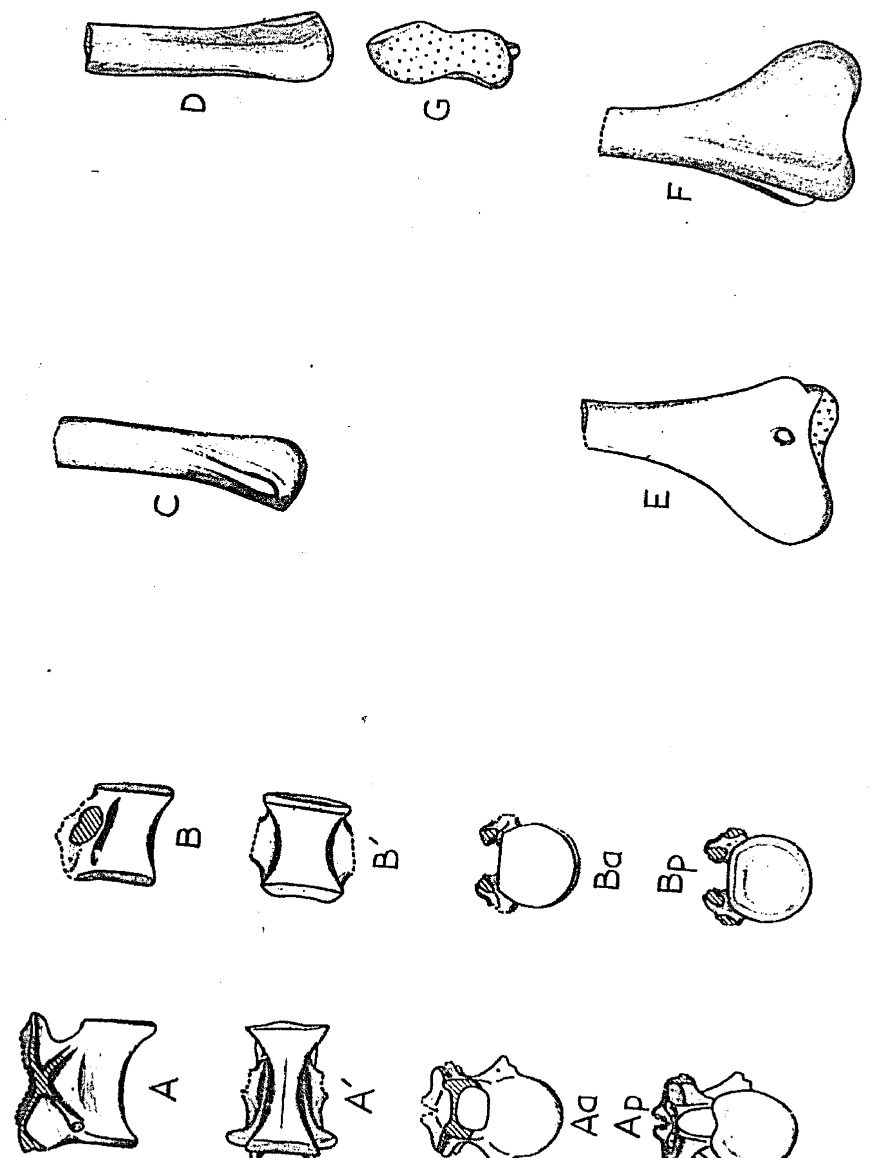


PLATE 42

Pseudosuchian gen. et sp. indet.:
specimen no. 11a

All illustrations in natural size.

Right side of lower jaw:
- P. Lateral view.
- Q. Medial view.
- R. Dorsal view.
- S. Ventral view.
- T. Posterior view.

Vertebrae in left lateral view:
- A. Dorsal vertebra.
- B, C. Posterior dorsal or pygal vertebrae.
- D. Sacral vertebra.
- E. Caudal vertebra.

Vertebrae in ventral view:
- A'. Dorsal vertebra.
- B', C'. Posterior dorsal or pygal vertebrae.
- D'. Sacral vertebra.
- E'. Caudal vertebra.

Vertebrae in dorsal view:
- A". Dorsal vertebra.
- E". Caudal vertebra.

Vertebrae in anterior view:
- Aa. Dorsal vertebra.
- Ea. Caudal vertebra.

Vertebrae in posterior view:
- Ap. Dorsal vertebra.
- Ep. Caudal vertebra.

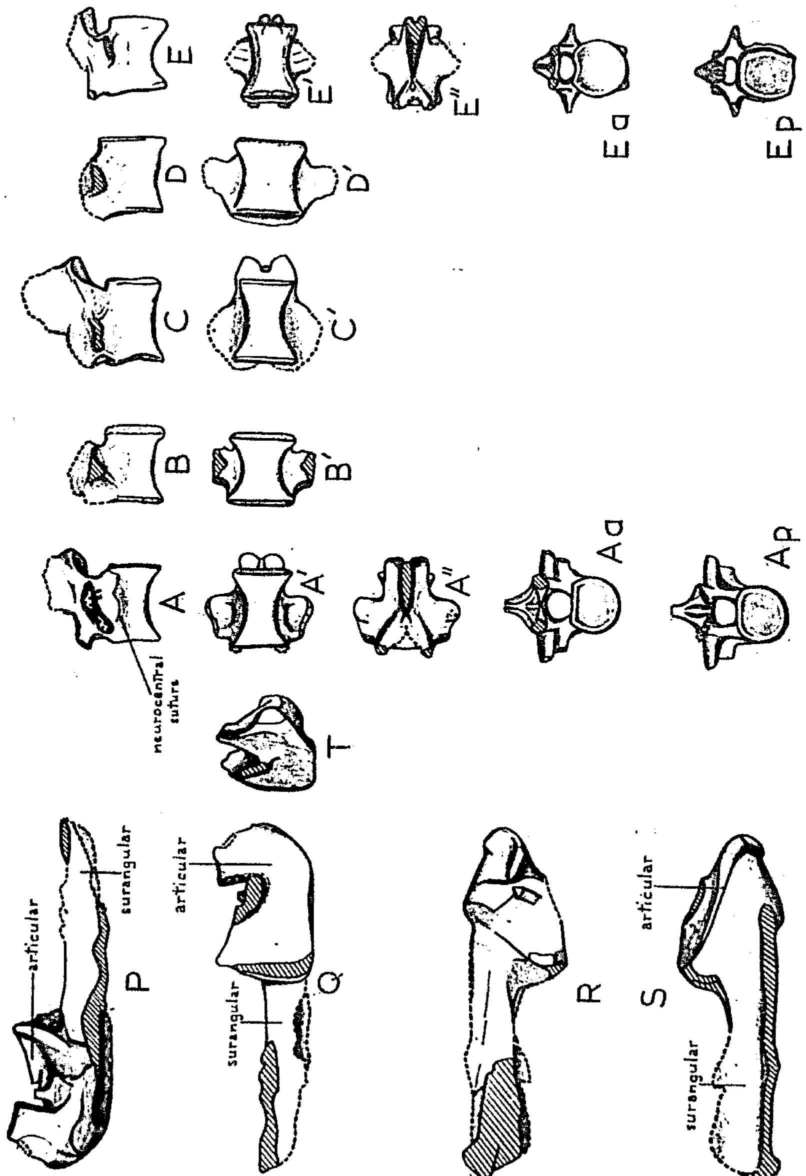


PLATE 43

Pseudosuchian gen. et sp. indet.:

specimen no. 11a

All illustrations in natural size.

Right humerus, proximal part:

A. Pre-axial view.
B. Post-axial view.
C. Anteroventral view.
D. Posterodorsal view.
E. Proximal end.

Right humerus, distal part:

F. Pre-axial view.
G. Post-axial view.
H. Anteroventral view.
J. Posterodorsal view.
K. Distal end.

Left femur:

L. Anterior view.
M. Posterior view.
N. Dorsal view.
P. Ventral view.
Q. Distal end.

Unidentified limb-bone:

R-T. Three views.
U. End-surface.

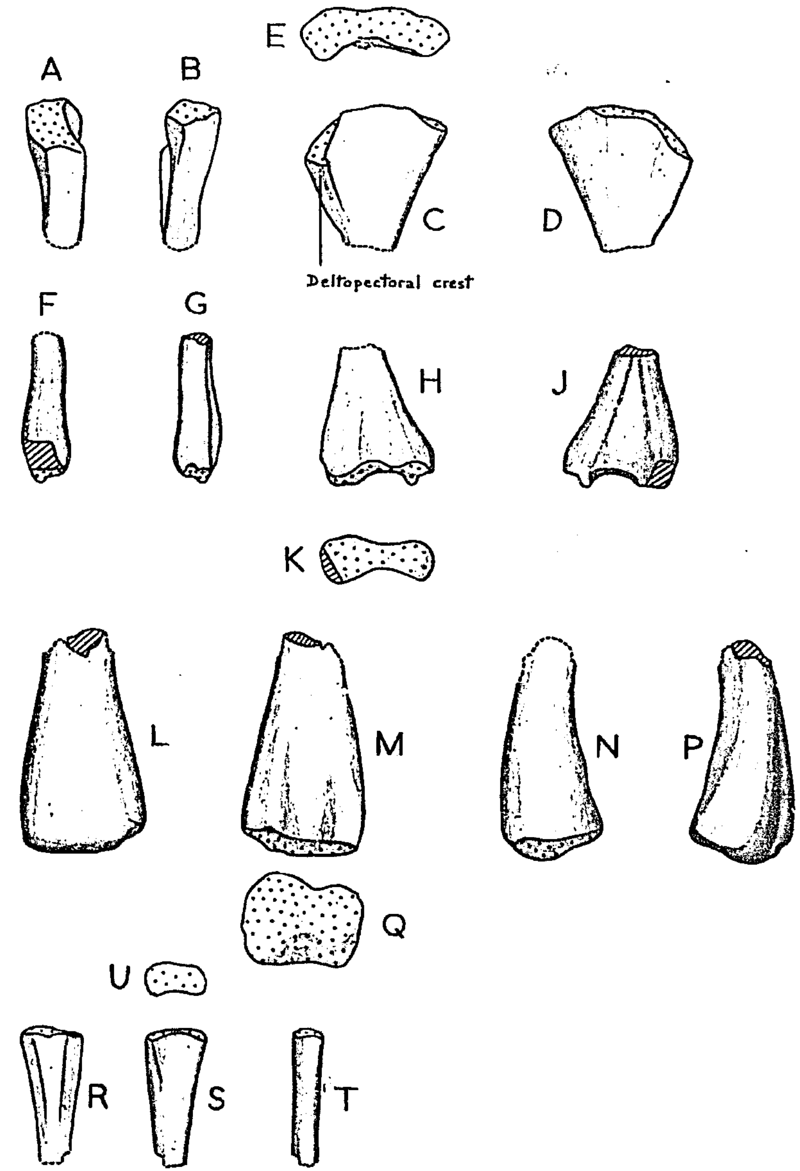


PLATE 44

All illustrations in natural size.

Pseudosuchian cf. Parringtonia:
specimen no. 14a

Caudal vertebra:
- A. Left lateral view.
- B. Posterior view.
- C. Ventral view.
- D. Dorsal view.

Haemapophysis:
- E. Anteroventral view.
- F. Posterodorsal view.
- G. Left lateral view.

Archosaur gen. et sp. indet.:
specimen no. 52a

Tooth:
- H. Lateral or medial view.
- J. Anterior view.
- K. Terminal view of root.

Archosaur gen. et sp. indet.:
specimen no. 52c

Caudal vertebra:
- L. Left lateral view.
- M. Anterior view.
- N. Ventral view.

Pseudosuchian gen. et sp. indet.:
specimen no. 52d

Left femur:
- P. Anterior view.
- Q. Posterior view.
- R. Dorsal view.
- S. Ventral view.
- T. Distal end.

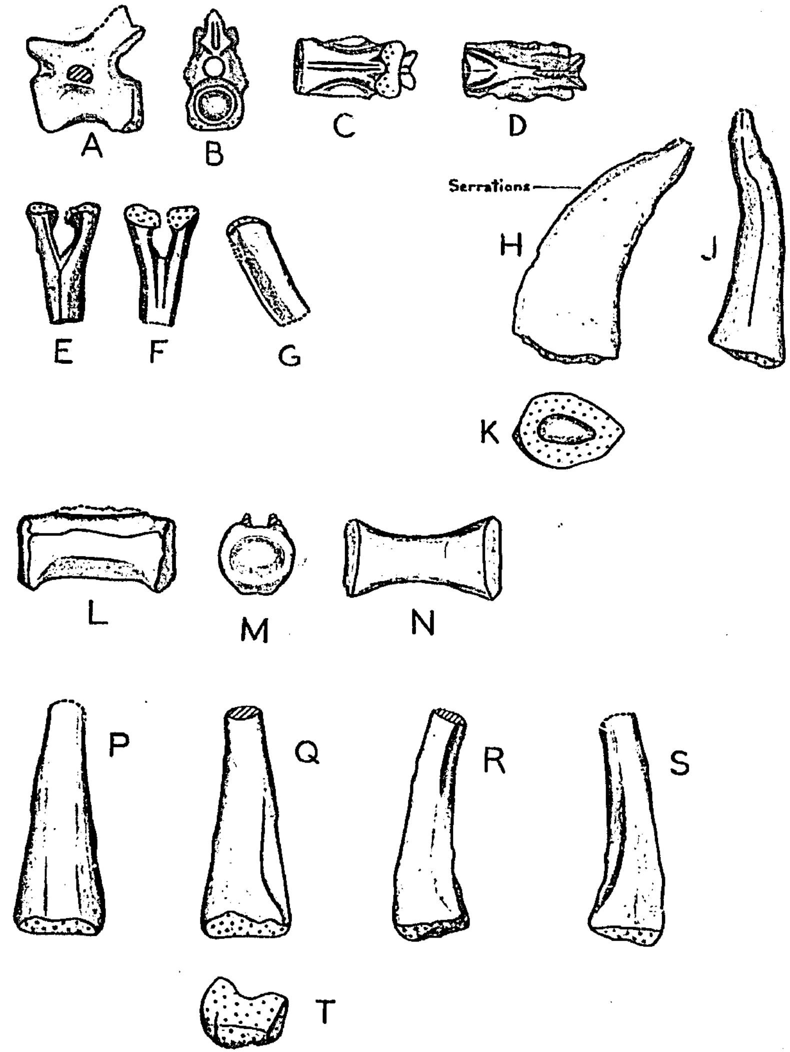


PLATE 45

Prestosuchid gen. et sp. indet.:

specimen no. 50b

All illustrations in natural size.

Vertebrae in left lateral view:

DA, DB. Mid-dorsal vertebrae.

S1-S3. Sacral vertebrae. (S1, which consists of little more than the right sacral rib, has been reversed).

Vertebrae in ventral view:

DA', DB'. Mid-dorsal vertebrae.

S2', S3'. Sacral vertebrae.

Vertebra in dorsal view:

S1'. First sacral vertebra. (Right sacral rib reversed).

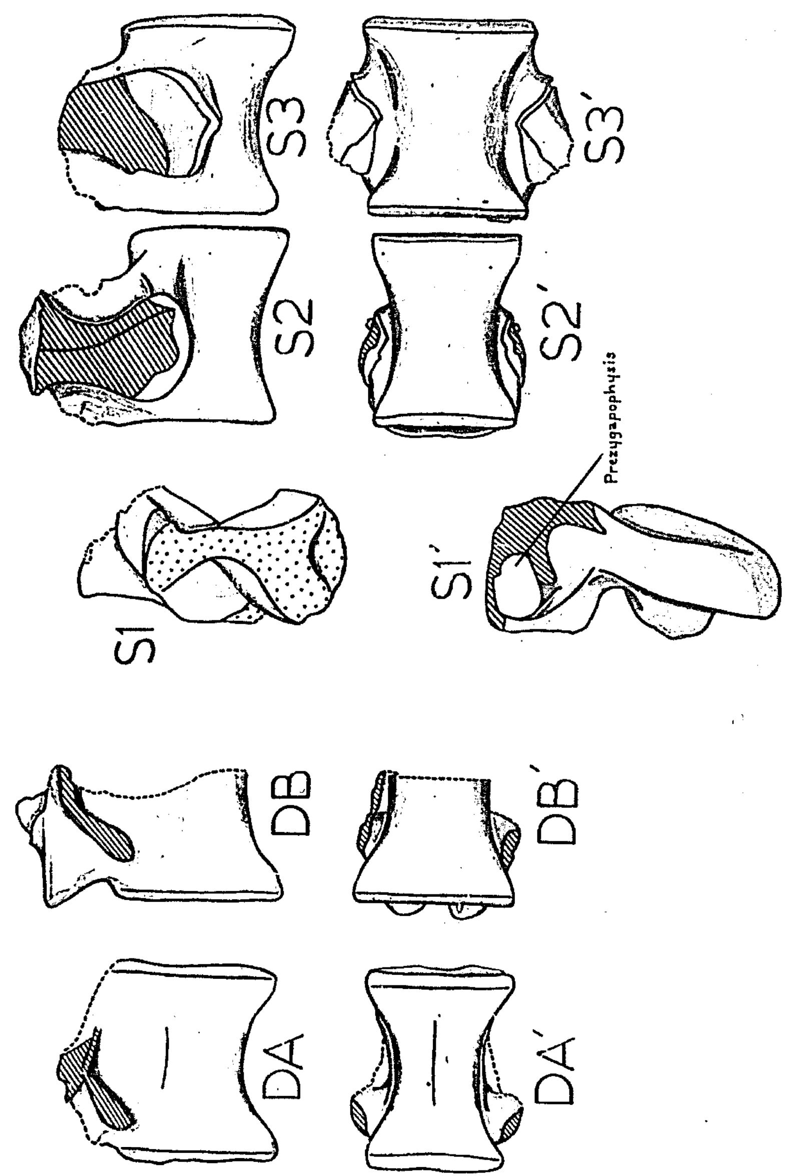


PLATE 46

Prestosuchid gen. et sp. indet.:

specimen no. 50b

All illustrations in natural size.

Vertebrae in anterior view:

A. Mid-dorsal vertebra (corresponding to DB in Plate 45).

B. First sacral vertebra, with centrum reconstructed.

Vertebra in posterior view:

C. First sacral vertebra, with centrum reconstructed.

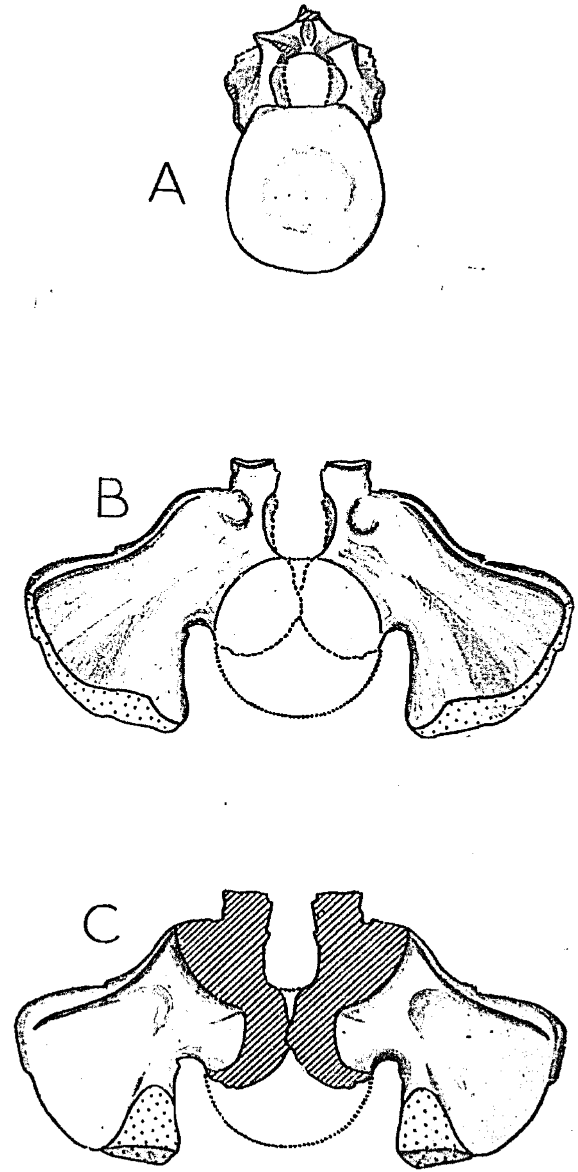


PLATE 47

Prestosuchid gen. et sp. indet.:

specimen no. 50b

All illustrations in natural size.

Right humerus:

A. Pre-axial view.

B. Post-axial view.

C. Ventral view.

D. Dorsal view.

E. Proximal end.

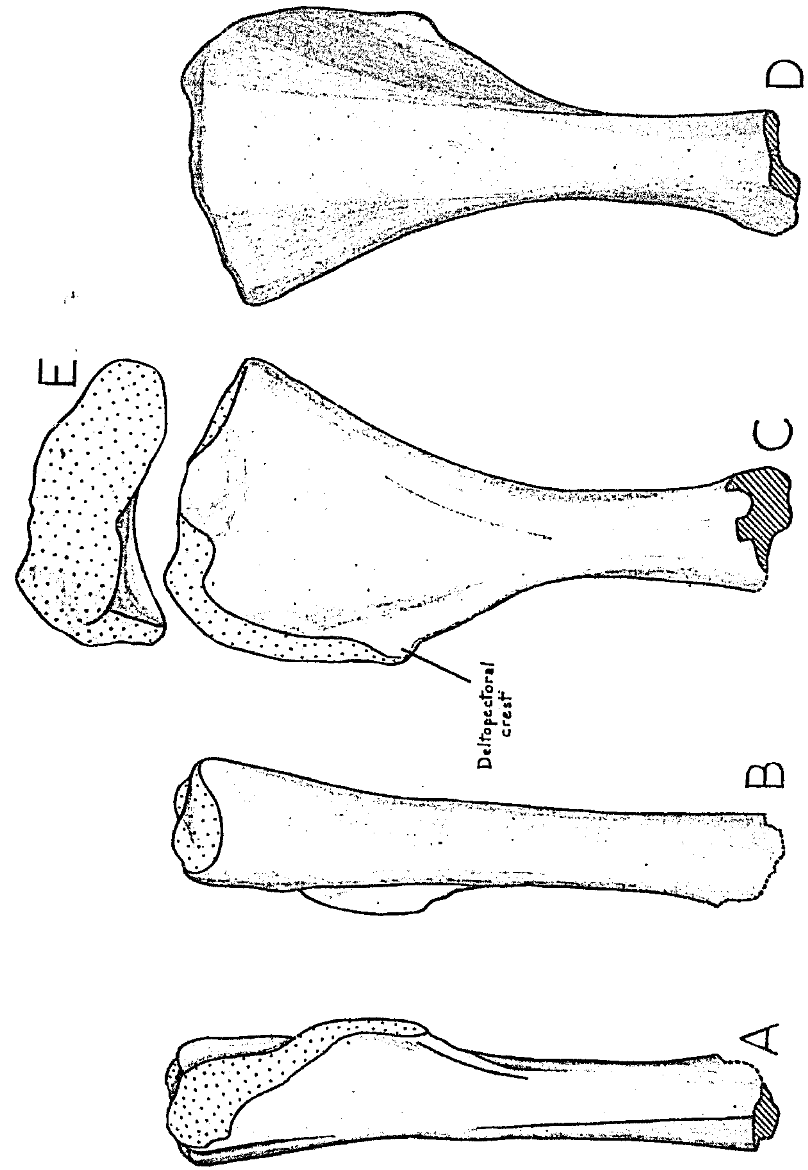


PLATE 48

All illustrations in natural size.

Archosaur gen. et sp. indet.:

specimen no. 53b

Caudal vertebra:

A. Left lateral view.
B. Posterior view.
C. Ventral view.
D. Dorsal view.

Pseudosuchian gen. et sp. indet.:

specimen no. 69a

Right humerus:

E. Pre-axial view.
F. Post-axial view.
G. Anteroventral view.
H. Posterodorsal view.
J. Distal end.

Pseudosuchian gen. et sp. indet.:

specimen no. 71

Right humerus:

K. Pre-axial view.
L. Post-axial view.
M. Ventral view.
N. Dorsal view.
P. Proximal end.

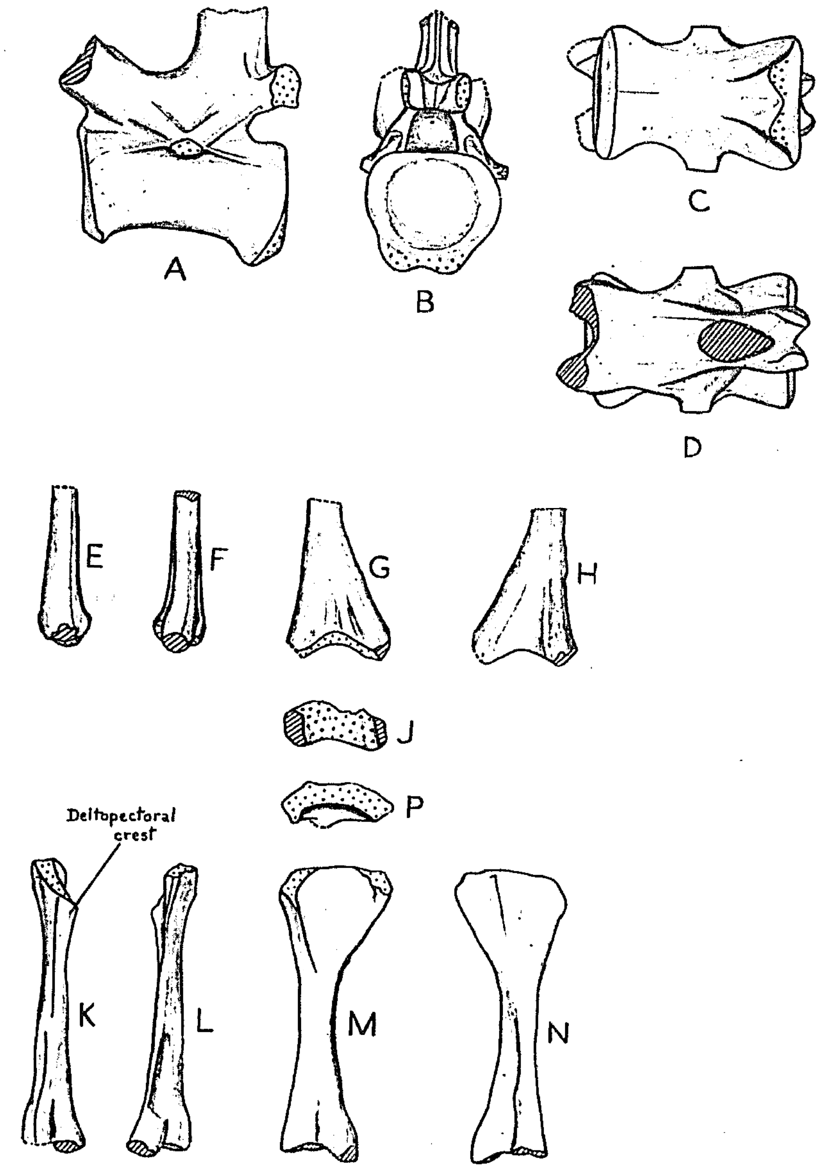


PLATE 49

Prestosuchid gen. et sp. indet.:

specimen no. 58

All illustrations in natural size.

Mid-cervical vertebra:

A. Left lateral view.

B. Right lateral view.

C. Anterior view.

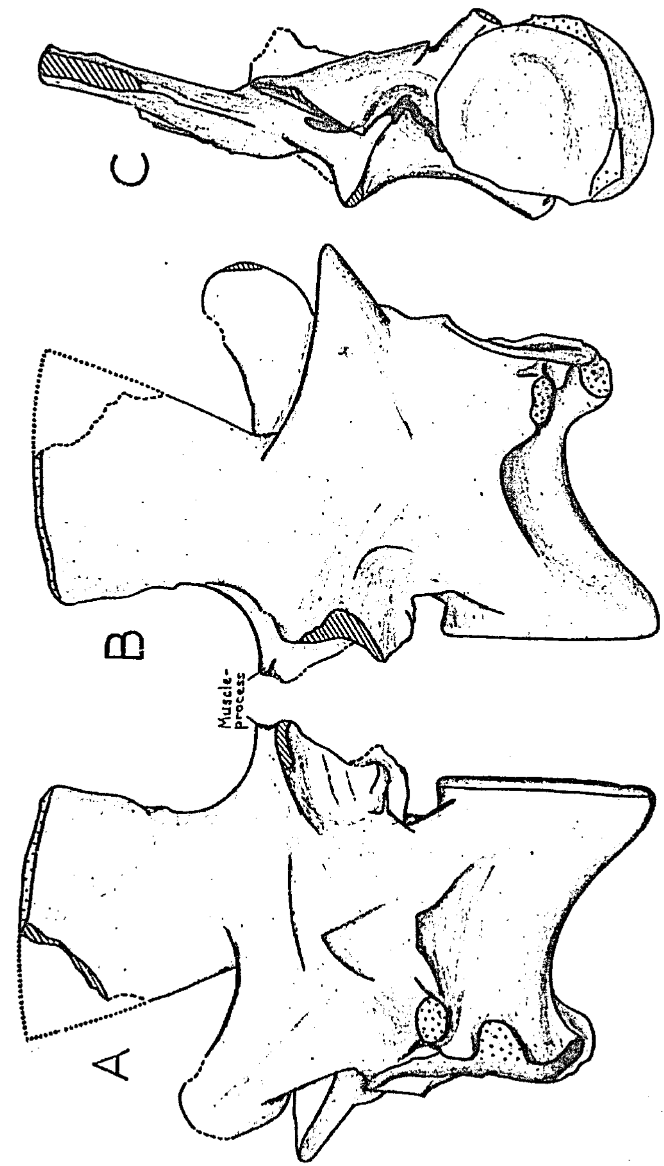


PLATE 50

All illustrations in natural size.

Prestosuchid cf. Mandasuchus:

specimen no. 107

Posterior dorsal vertebra:

A. Left lateral view.

B. Anterior view.

C. Ventral view.

D. Dorsal view.

Prestosuchid gen. et sp. indet.:

specimen no. 58

Mid-cervical vertebra:

E. Ventral view.

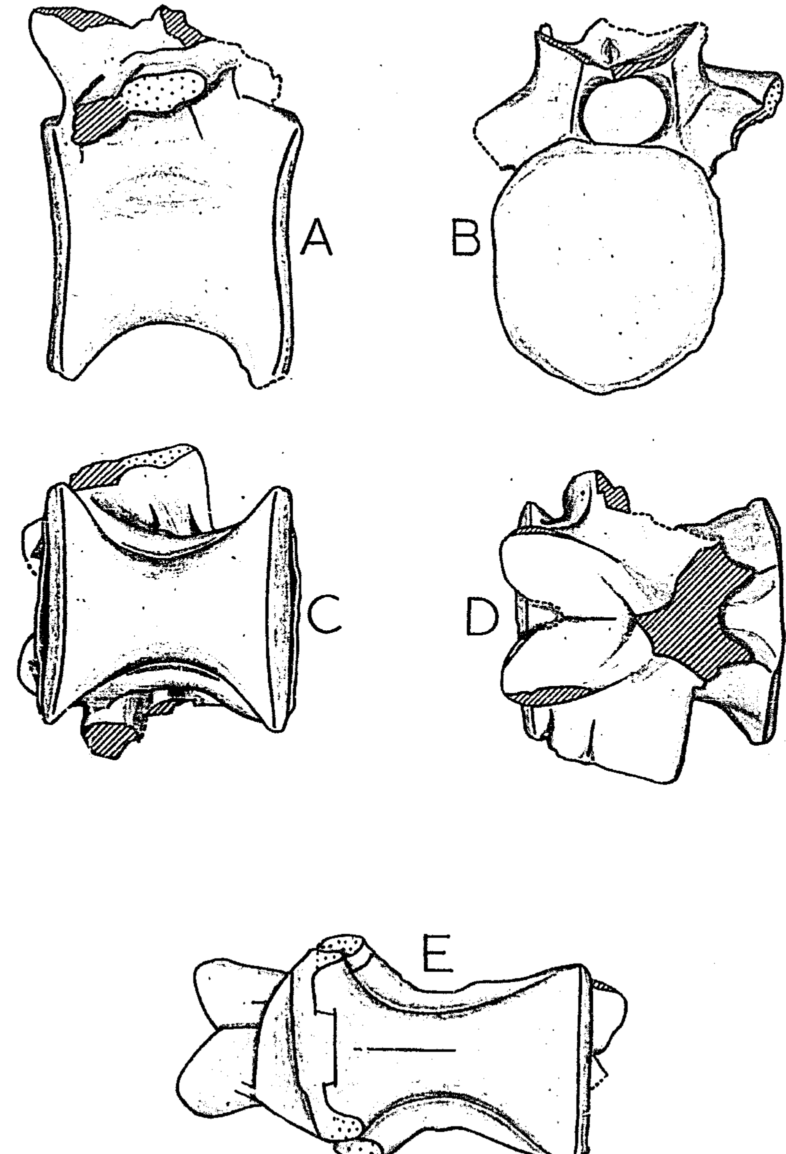


PLATE 51

Mandasuchus and Spondylosoma

All photographs in natural size.

Left, vertebrae in left lateral view:

Above. Last cervical (supposed eighth) and first dorsal vertebra of Mandasuchus longicervix (specimen no. 13).

Below. Posterior cervical vertebra of Spondylosoma absconditum.

Right, right pubis in ventromedial view:

Left. Mandasuchus longicervix (type-specimen, no. 11b).

Right. Spondylosoma absconditum.

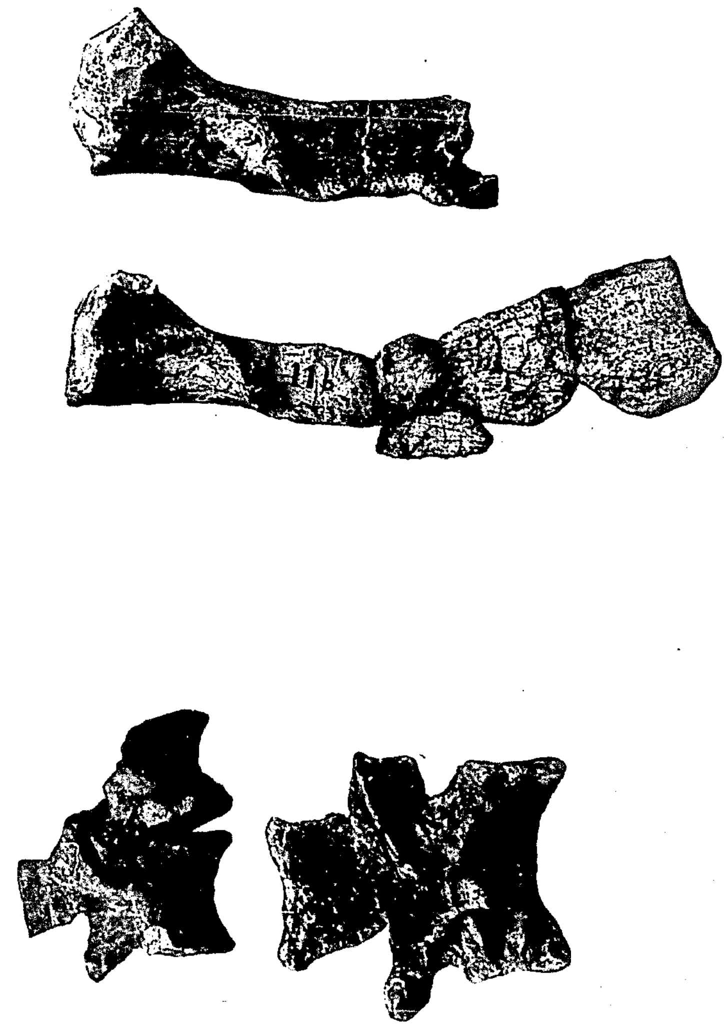


PLATE 52

Mandasuchus and Rio do Rasto "saurischians"

All photographs in natural size.

Left, scapulae in posterior view:

Left. Right scapula of Mandasuchus longicervix (type-specimen, no. 11b).

Right. Lower part of right scapula and upper part of left scapula of Spondylosoma absconditum.

Right, proximal end of ulna:

Left. Right ulna of Mandasuchus longicervix (type-specimen, no. 11b).

Right. "Tibia of saurischian" von HUENE.

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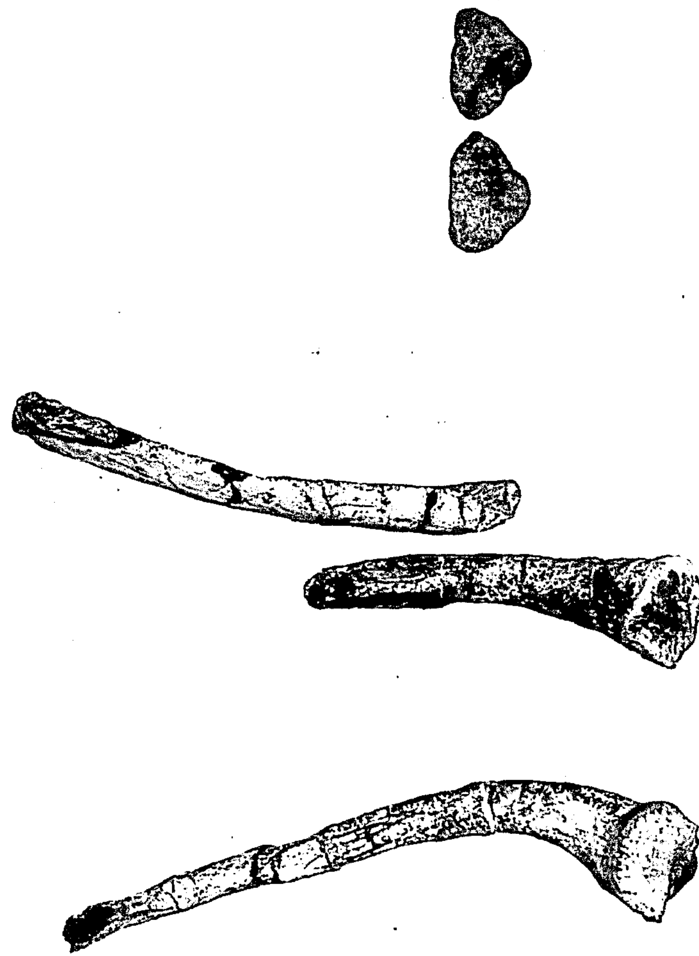

PLATE 53

Spondylosoma and specimen no. 50b

All photographs in natural size.

Sacral vertebrae.

Above, first sacral vertebra in right lateral view:

Left. Spondylosoma absconditum.

Right. Specimen no. 50b (consists of little more than the sacral rib).

Below, second sacral vertebra from below and a little to the right:

Left. Spondylosoma absconditum.

Right. Specimen no. 50b.