THE ANATOMY OF
THE TRIASSIC THEROPOD
Syntarsus rhodesiensis
(Saurischia : Podokesauridae)
and a consideration of its biology

by

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ABSTRACT

The osteology of the Upper Triassic podokesaurid Syntarsus rhodesiensis is described, based on a series of 30^+ individuals representing all skeletal elements, recovered since the description of the holotype (Raath, 1969). A brief account of the geology of the finds is given, with an attempt at a reconstruction of the palaeoenvironment. The excellence of preservation of the bones has permitted an attempt at the restoration of soft tissues including the brain, cranial nerves, main cranial blood vessels and the musculature of the jaws, neck and limbs. Histological sections of limb bones have shown that the compact bone was highly vascular, and this, together with the structure of the brain, palaeoenvironmental considerations, social behaviour and group structure, leads to the conclusion that Syntarsus was an endothermic homeotherm inhabiting a hot arid region at the end of the Triassic, with a social organisation into "flocks" in which females predominated numerically. Clear evidence of sexual dimorphism is presented.

Syntarsus is reconstructed as a bipedal, saltatorial predator which differs in subtle, but probably generically significant, characteristics from the closely related North American genus, Coelophysis.

Its anatomy characterises it as a medium-sized agile animal with a highly kinetic skull; incipiently opposable pollex in the raptorial manus; highly cursorial hindlimb; and with features in the dentition and hallux which suggest a grooming function.

It is concluded that the Triassic coelurosaurian stock provided an advanced and well adapted base from which the successful coelurosaur radiation into the later Mesozoic sprang, and that this stock was physiologically pre-adapted for the emergence of the avian (and possibly the pterosaur) lineages in the Jurassic.

CONTENTS

1. INTRODUCTION

Dinosaur remains were first found in Rhodesia in 1914 on farms in the Bubi District, some 40 km northeast of Bulawayo (Maufe, 1916). Since that time many more dinosaur-bearing sites have been found in the country, and Bond (1973 : 87-96) gives a comprehensive account of the history of dinosaur palaeontology in Rhodesia up to 1973, listing the fossils recovered together with a record of the localities concerned.

Bond's paper was finalised prior to the discovery, late in 1972, of the rich fossiliferous deposits in the Forest Sandstone of the Chitake River on which the major part of this study is based.

It has been shown that the Forest Sandstone of Rhodesia correlates with the Stormberg Series of the Republic of South Africa, probably with the upper part of the Red Beds of that Series (Bond, 1973 : see especially his Table VI). Thus the Forest Sandstone is Upper Triassic in age (see e.g. Bond, 1955). Bond (1973) has suggested that the aridity reflected in the lithology of the Middle and Upper Forest Sandstone, and paralleled in the (apparently younger) Cave Sandstone of South Africa, set in earlier in the north (Rhodesia) than in the south (South Africa). This seems plausible in view of the drifting of the African continent at the time (McElhinny, Briden, Jones & Brock, 1968).

It is from Forest Sandstone and its stratigraphic equivalents that all specimens of *Syntarsus* have been recovered. The type specimen came from the limited, but highly productive, exposures in the Kwengula stream on Southcote Farm at 19°58'S; 28°24'35"E (Raath, 1969 and Plate 3c). Until this discovery in 1963, the only vertebrates recovered from the Rhodesian Upper Triassic sites were thecodontosaurid prosauropods (*sensu* Charig, Attridge & Crompton, 1965). The holotype of Syntarsus was nearly complete, lacking only the skull, neck, and parts from the right side which had been removed by erosion. This specimen was described and named Syntarsus rhodesiensis, gen. et. sp.nov. and referred to the coelurosaurian family Podokesauridae (Raath, 1969). Ostrom (1976a) includes it it the family in/ Procompsognathidae, a synonym of Podokesauridae. It constituted the first record of the Coelurosauria in the African Triassic (Colbert, 1958; Charig et al., 1965 : 217; Raath, 1969) the only other African coelurosaurs having been recovered from the Jurassic beds of Tendaguru, Tanzania (Janensch, 1920, 1925) and the lower Cretaceous of north Africa (Romer, 1966; Taquet, 1977).

At the time of excavating the type specimen of Syntarsus in 1964 and 1966, several other blocks of bone-bearing matrix were collected from sites close to the type site. On later preparation one of the blocks proved to contain fragmentary remains of a second specimen intermixed with the bones of a thecodontosaurid probably referrable to Massospondylus harriesi.

In 1968 the writer and Mr. D.F. Lovemore discovered fossiliferous Triassic beds in the Zambezi valley (16°13'S; 30°06'E) some 450 km northeast of the type locality in Nyamandhlovu, and a preliminary account of these beds was given by Raath, Smith & Bond (1970), in which the local occurrence of Massospondylus harriesi was reported. Because of the presence of this characteristic fossil of the Forest Sandstone the authors concluded that the Maura River beds represented a local facies of Forest Sandstone equivalent in age to the Southcote Farm bone-bearing deposits. From the new localities several partial skeletons have been collected, most of them well preserved and articulated. The majority represent thecodontosaurids, including forms other than M. harriesi. An account of the varied and relatively rich Maura River fauna will be prepared in due course. Two finds in these deposits are relevant to the present investigation. The first is an isolated and almost perfect femur of an adult Syntarsus and the second the pelvis and hind limbs of a juvenile, in which the material is not quite so well preserved.

In 1972 the writer re-examined some exposures of Triassic sandstone which had been recorded, but not visited, by Bond (1965), and in the exposures in the Chitake River (approx. 16°07'S; 29°30'E) found an extremely rich deposit of exquisitely preserved bones of Syntarsus (Table 1) representing a substantial number of individuals and a range of ontogenetic stages. Furthermore, this bone-bed produced well preserved elements of the skull as well as cervical vertebrae, both of which had been deficient in the holotype (Raath, 1969).

Syntarsus is thus known to occur in three areas in Rhodesia (Fig. 1), and together with Massospondylus, with which it has always been found in close association, seems to provide a reliable marker for Upper Triassic (Rhaetian?) terrestrial deposits in Rhodesia.

One other discovery relevant to this investigation is of a few well preserved fossil footprints found in a red aeolian sandstone on Spring Grange Farm in the Bubi district - the "cradle ground" of dinosaur studies in Rhodesia. The blocks on which the prints are impressed were collected in 1915 by Mr. G. Mitchell for use as paving stones around the farm homestead. The presence of the prints was not suspected until recently when the present owners of the farm, Mr. and the late Mrs. E. Rushmore, noticed them one evening when the sun was at a low angle showing the dimpled impressions of the prints clearly shadowed. These prints were described by the writer (Raath, 1972) and it was concluded that they belonged to Syntarsus. The prints (Plate 31) naturally assume significance in any consideration of the locomotion of Syntarsus.

Considering the all-too-familiar and common situation in palaeontology where a handful of isolated and eroded scraps of bone herald the birth of a new vertebrate taxon, Syntarsus seems to be the product of almost unbelievable good fortune. Relatively few dinosaurian taxa in the museum collections of the world can be represented by material of such quantity and quality. These facts alone provide an eloquent justification for the study reported here. The newly discovered material of the Chitake River deposit meant that the description of the holotype (Raath, 1969) could be extended and the deficiencies made good, particularly with regard to the skull and neck. The structure and variability of the entire skeleton could be studied not only in terms of individual variation and of changes related to growth and maturation, but also in terms of demonstrable sexual dimorphism. Much of the variability could be clearly linked to the differentiation of former soft tissues, which opened up an additional line of investigation into aspects of the soft anatomy of Syntarsus. In turn this has led to a consideration of some aspects of the physiology and biology of the animal, providing some insight into its role as a living participant in those events that took place at the close of the Triassic in Rhodesia.

When material as good as that of Syntarsus is found, common sense demands that it be studied from all possible angles. One of these avenues of study must inevitably be the possible evolutionary significance of the taxon concerned. Because it stands at or near the root of the theropod radiation in the Triassic, Syntarsus deserves close scrutiny in this respect. Because it is represented by such abundant, complete and well preserved material, Syntarsus should perhaps be regarded as a "standard" against which to compare new discoveries of Triassic and later theropods. Detailed knowledge of its skeleton provides knowledge of the basic skeletal adaptation from which sprang the most persistent and perhaps most successful of all dinosaurian lineages, the Coelurosauria, and the Syntarsus material has been particularly amenable to the following studies which have been intended to yield this information.

2. MATERIALS AND METHODS

PREPARATION AND RECORDING OF DATA

The lithological nature of the Forest Sandstone permitted simple mechanical preparation in most instances. Most of the work was carried out using a light hammer and masonry nails in conjunction with an electric engraving tool for roughing out the specimens. Fine work was carried out under a low power binocular microscope, picking at the matrix with steel dress-maker's pins held in a pin vice. Excellent results were produced by wetting the matrix with isopropyl alcohol, which has the advantages of penetrating well, softening the matrix while also improving contrast between bone and matrix, yet evaporating and drying quickly. The softened matrix is easily removed by pin or blade.

Occasional "nodules" cemented by calcite were encountered in the blocks of matrix. Initial tests with dilute (5% -10%) acetic and formic acid were discontinued when it was found that the bone was attacked almost as rapidly as the calcitic cement. Patient picking with the pin remained the most reliable and most readily controlled technique in these cases.

The Chitake and Maura River specimens which bore the manganese-rich encrustations responded, with difficulty, to preparation with tungsten-carbide tipped points in the vibratory engraving tool, or by light hammer-and-nail percussion. Wetting with isoproply alcohol enhanced the cleavage between the encrustation and the bone surface in several cases, allowing substantially large pieces of the encrustation to be "peeled" off the bone after being loosened by a carefully judged sharp tap on the masonry nail by the hammer. This technique produced very satisfactory results where the bone surface was smooth, but bones having roughened or scarred surfaces almost invariably suffered some damage because of loss of the outer bone laminae which parted away with the encrustation.

Experimentation with other methods of removing this encrustation, preferably by chemical means, will be pursued because of the prospects of excellent preservation of surface texture and detail on the enclosed bone which is so effectively protected from damage by the very resistant manganese jacket.

During preparation, all newly exposed surfaces of bone were immediately coated with a thin solution of "Glyptal" G1276 cement in lacquer thinners, applied by brush. This solution has excellent properties in that it penetrates very readily, dries and sets rapidly, and is outstanding as a bonding agent. Damaged bones were repaired either with a more viscous solution of "Glyptal" or, more normally, with a cement of celluloid dissolved in acetone. Both of these adhesives share the properties of rapid setting and strong bonding while being also readily soluble in their respective solvents for later correction of faults or deficiencies in repairs.

Some of the very light and fragile isolated elements (e.g. maxillae, pterygoids, quadrates) presented special problems in their removal from the matrix. Early attempts at preparation of such bones consisted of exposing one surface of the bone in the matrix block and then coating it with an application of polyester resin. When this had set the opposite side was prepared and the whole bone removed, held together by the strong bed of resin. The principal disadvantage of this technique is the thickness of the dried resin coat, which tends to obliterate or obscure bone surface details, and the great difficulty of its later removal should this prove necessary. These disadvantages were considered to outweigh the advantages of support and strength, and the method was discontinued. It was considered preferable to repair preparation damage after removal of these delicate elements.

Each of the fossiliferous matrix blocks from the Chitake River was marked with a locality code number, and as bones were prepared and removed they were individually numbered in waterproof black ink with the same code number to identify the block from which they came. Associated elements, in which there was no doubt of their association, were suffixed with additional serial numbers to record this fact. Bones were not assigned catalogue numbers immediately because it was clear that some elements, probably from different matrix blocks, could be associated later as the remains of a single individual. Where this proved possible, the specimens were given the same catalogue number. Doubtful cases, and those that could not be associated at all, were given individual catalogue numbers and remarks about their probable or suspected associations were recorded in the catalogue.

Data on each catalogued specimen were recorded on data cards and measurements were recorded on separately filed data sheets which make provision for "minimum essential" records. All measurements were taken with Vernier callipers to the nearest millimetre, except where stated otherwise.

Specimens consisting of several elements whose association was proven, or acceptably probable, were recorded on diagrammatic "skeleton templates" (e.g. Fig. 2) to give an immediate visual impression of their degree of completeness.

Most of the drawings of bones in this study are based on tracings from photographs which provided the basic outline or shape of the element, preserved the correct proportions and provided an immediate and accurate scale. Relief and other details were then added by shading, adopting the normal convention of light direction from the upper left corner of the illustration.

CASTS AND RECONSTRUCTIONS

Bone Casts

The study of limb musculature was facilitated by manipulation of an articulated pelvis and hindlimb, and an articulated forelimb, which were cast in polyester resin using silicone rubber moulds of the appropriate elements of the type specimen where bone associations were beyond dispute. The techniques employed in preparing the moulds and casts have been described in detail by J.C. Taylor of the Queen Victoria Museum (unpublished MS). Silicone rubber moulds have many widely acknowledged advantages, including the precise reproduction of surface detail combined with negligible shrinkage or distortion. Thus the casts which they produce are reliable as to dimensions, proportions and surface architecture. The resultant casts of limb elements were articulated by drilling and wiring the joints.

Casts of various bones also served to provide otherwise inaccessible information, short of mutilating the actual specimens, such as in sectioning to observe shapes and outlines at various points.

Endocranial Cast

Silicone rubber was also used to obtain the endocranial cast on which the reconstruction of the brain is based (Fig. 21), by simply pouring it into the braincase of the specimen, and removing it by careful manipulation after it had set.

Articulated model of Skull

The study of cranial kinesis was aided by an articulated model of the skull based on the drawings in Fig. 3. The model (Plate 4) was cut from hardboard via an intermediate drawing prepared by enlarging the working drawing through a short-throw epidiascope onto a screen. Actual cranial articulations were represented on the model by pivot holes or grooves (for sliding articulations) held by machine screws and nuts. The complex squamose articulation of the lachrymal, jugal and maxilla was represented by a strong elastic band. The model was fixed to a base-board by screws through the "fixed" segment (i.e. the "braincase").

Flesh restorations

A life-size, free-standing flesh restoration of Syntarsus was prepared in 1975 by Mr. T.W. Coffin-Grey and his team of Technicians at the National Museum, Bulawayo, under my direction. It was based largely on drawings of the type specimen in which the unknown skull and neck had been reconstructed before the Chitake River material had been studied. Several modifications of the same moulds produced a number of individuals, two of which were incorporated into a "habitat" display in the Geological Gallery of the National Museum (Plate 5a). These restorations are questionable in the details of size and proportions of the head and neck, and, in my opinion, in posture.

A later attempt at a flesh restoration (Frontispiece and Plate 5b) by Mr. L.J. Penny of the Queen Victoria Museum is, in my view, more successful in reflecting my own ideas of the posture, proportions and appearance of the animal (see also Fig. 35). It is based on a study of all of the known material and, being a scale model (approx X 0,3), it does not suffer the disadvantages of "emphasised errors" that afflict the life-size model.

Both reconstructions referred to above will be clothed in feathers, reflecting my views on the integument of Syntarsus.

The life-sized models were used in attempting to calculate the bodyweight of adult Syntarsus by submersion in a water bath to measure volumetric displacement, and then calculating the mass by multiplying by the average flesh specific gravity figure given by Colbert (1962a).

REGISTRATION AND STORAGE OF MATERIAL

In the following account specimens referred to by numbers with the prefix QG are catalogued and stored in the collections of the Queen Victoria Museum, Salisbury, Rhodesia.

In some of the photographs illustrating this study some specimens bear numbers prefixed CT6. This is a locality and matrix-block code recorded in the main catalogue of the Queen Victoria Museum department of palaeontology.

ABBREVIATIONS

A list of abbreviations used in the figures is given at the front of the accompanying volume of illustrations.

Other abbreviations used are:

AMNH	American Museum of Natural History, New York, U.S.A.
QG	Queen Victoria Museum, Salisbury, Rhodesia.

3. GEOLOGICAL SETTING AND THE NATURE OF THE PALAEOENVIRONMENT

All of the known Syntarsus-bearing localities are in the fine-grained, pale, buff Forest Sandstone. At the Southcote locality the sandstones are massive and show no obvious signs of bedding other than dune-bedding (Raath, Smith & Bond, 1970). Both the Chitake and Maura river localities are in sandstones which are generally pinker in colour than those at Southcote, and at both places large scale dune-bedding is evident. These latter two localities contain relatively common but localised lenses of current-bedded coarse sediments (Plate 1a) including marly layers, which are regarded as representing localised waterholes and pans in an otherwise arid, dune-covered environment. The two "wetter" localities lie to the north of the former "Lomagundi Highlands"(Bond, 1970) remnants of which crown the southern rim of the Zambezi Valley escarpment today.

In the Maura River area, the Upper Karroo rocks have been shown to be approximately 650 m thick (Raath et al., 1970). Their thickness in the Chitake River area is not known, but the field indications suggest that bone occurs through a vertical range comparable with the estimated 200 ft (70 m^+) on the Maura.

As at the Maura River, the Chitake River sandstones are overlain, apparently conformably, by a boulder conglomerate consisting of rounded gneissic boulders up to 1 m in diameter in a maroon sandy matrix and the beds dip $10^\circ - 15^\circ$ to the south southwest. Within 300 m of the Chitake Syntarsus locality several post-Karroo faults are visible (Plate 1b) which cut both the conglomerates and the Karroo sandstones, with throws as small as 15 cm and greater than 20 m.

The former existence of water bodies at the Chitake and Maura localities is shown by the current-bedded lenses and marly layers, associated with concentrations of iron staining in the sandstones.

It is suggested that the manganese-rich layer which encrusts and stains so many of the bones (Plate 2) may be a result of bacterial action in a water body. In the Southcote Farm occurrences (Nyamandhlovu), where there is no existing evidence of standing water (see e.g. Attridge, 1963), no manganese-rich encrustation has been found on any of the bones to the writer's knowledge. Ten km south-east of Southcote, in the Lukwe River exposures of Forest Sandstone (approx. 20° 00'S; 28° 30'E), manganese encrusted bones are known (K.R. Robinson, pers. comm.).

It is suggested that the manganese encrustation may have been produced by the action of micro-organisms such as members of the Chlamydobacteriales - especially Leptothrix (see e.g. Brock, 1970; Hawker & Linton, 1971). These bacteria are generally associated with fresh-water bodies with a high content of decomposing organic matter. Leptothrix is known to remove iron and manganese from its surroundings by oxidation and to precipitate the oxides in its enclosing sheath. The concentration of decomposing carcasses of Syntarsus in the Chitake waterhole would have provided ideal conditions for the action of these and similar microbes, and the bones might well have provided attachment surfaces for a very substantial microbial population resulting in the often surprisingly thick (up to 15 mm) encrustations. The fact that many of the bones are also iron-stained conforms with this suggestion of microbial precipitation.

The prosauropod-rich fossil deposits on the Maura River, from which only two Syntarsus specimens have been recovered, are even more ubiquitously manganese-encrusted than the Chitake bones. Similar indicators of water action (current bedding; coarse, gritty sediments; marly layers) are present at this locality but over a considerably wider area than at the Chitake River site, suggesting the presence of a larger waterhole. Presumably the more permanent waterbody would have provided more favourable conditions for the bacteria and other manganese/iron-depositing microbes, resulting in more even and complete utilisation of the available organic resources and attachment substrates, resulting in turn in a greater and more universal deposition of manganese oxides on the bones. In the Chitake deposits, unlike those on the Maura, manganese is not confined to the bones but occurs also as rare free nodules in the sandstones.

At both the Southcote and Maura River localities prosauropods (of several taxa including Massospondylus) greatly outnumber coelurosaurs (represented by Syntarsus). The Chitake locality is remarkable in that this situation is completely reversed and indeed the main site, which has produced 26 (minimum) Syntarsus individuals, has not produced a single prosauropod bone to date. Yet prosauropods, again representing several taxa including Massospondylus, are relatively common in the surrounding sediments within 30 m of the Syntarsus quarry. The only non-Syntarsus remains recovered from this particular site to date include an unidentified reptilian tooth, an osteoderm of an unidentified vertebrate and a few fragmentary jaws of small sphenodontids (to be described elsewhere by Dr. C.E. Gow and the writer).

The Chitake Syntarsus remains have all come from a small area measuring, as exposed, only 3,3 m along the bedding plane with a total measurable thickness of 30 cm (Plate 3a). Within this confined area the bones of Syntarsus accumulated in an incredible tangle (Plate 3b) with dissociated free elements intimately intermixed with articulated partial skeletons. The surprisingly negligible degree of damage to very delicate bones indicates that the process of accumulation and concentration of the bones could not have been violent.

Thus, transport into the pan by flooding rivers can be discounted as an agent of accumulation in this case. If water washed isolated bones into the basin it can only have been as a result of gentle transport such as might obtain through shallow "sheet flow" over the surface. It seems more plausible to suggest that the bones have been minimally transported, and that the animals therefore died in the pan or at its edge. Gentle currents within the pan might thereafter have tended to concentrate and mix the bones to produce the observed admixture combined with minimal damage.

The absence of prosauropods from the pan is surprising because of their predominance within the pan sediments on the Maura River and their presence in the near vicinity of the Chitake "palaeopan". The Maura situation indicates that prosauropods were attracted to water. The Chitake situation suggests that they avoided the water. This paradox is probably explained by the fact that Syntarsus was undoubtedly the most advanced local vertebrate predator of the times and that its concentration as a group around the small waterbody was sufficient to deter the less agile, cumbersome and inoffensive prosauropods from approaching the pan. The absence of the remains of aquatic vertebrates from the pan sediments implies that the waterbody was too ephemeral for the establishment of an aquatic vertebrate fauna (fish, amphibia, etc.). Had the pan been more permanent it is difficult to explain why the local prosauropods did not continue to use it, and die in it, following the demise of the Syntarsus group.

That the Chitake Syntarsus assemblage represents a single group of contemporaries is difficult to prove, but it is strongly suggested by the concentration of bones which are not separated vertically by any sedimentary layers which would indicate the passage of time. Although the great majority of bones lay parallel to the bedding plane, some long bones were entombed in a more upright attitude intersecting the bedding plane at an angle. The high quality of preservation of all bones in the assemblage is comparable throughout with only very minor variations, indicating that the conditions of burial and fossilisation were the same for all.

The Chitake bone site has some of the hallmarks of a classical "predator trap" (see Dodson, 1976, for a discussion of predator traps), in which the number of predators in a deposit exceeds the number of potential prey individuals. It is unusual mainly in that it is *deficient* in prey, except perhaps for minor items such as the sphenodontids.

An explanation for the Chitake concentration of *Syntarsus* might be sought in terms of the studies of Shipman (1975) on the taphonomic consequences of varying degrees of drought. Shipman describes three stages of drought (mild, severe and extreme) based on observations in Ethiopia in 1973. Persistent phase III (extreme) drought can result in permanent alteration of the environment into desert. Presumably, in an existing desert droughts can exhibit related, but relatively more severe, progressive phases. Features of phase II drought noted by Shipman (1975) are: (1) since many animals die of starvation rather than of thirst, they are buried close to major water sources; (2) the age distribution of individuals killed by the drought is indicative of catastrophic mortality (mild [Phase I] drought culls young individuals, while animals dying in severe [Phase II] drought are likely to be in their prime); (3) skeletons tend to be preserved articulated because of an observed tendency for carnivores to prefer soft flesh to bones under these circumstances, and because the dry environment dries the body tissues which helps to keep joints intact; (4) animals of disparate habitat preference are found associated, because of their dependence on the water source.

Clearly the Chitake situation is not directly comparable with Shipman's study in that the environment was apparently already a true desert, and admixture of "animals of disparate habitat preference" is remarkable chiefly because of its near absence. While the occurrence of fair numbers of well articulated partial skeletons agrees with Shipman's checklist, the abundance of dissociated elements does not. On the evidence available it seems that the majority of the animals which died at the Chitake pan were "animals in their prime". While immature animals and very large (? old) adults were present, the majority appear to have been mature adults, based on size-frequency analysis of the available sample of femora (Fig. 18).

Consideration of the concentration of bones, completeness of individual elements, uniformly high quality of preservation, absence of signs of transport or erosion, absence of alternating fossiliferous and sterile layers, absence of remains of sympatric taxa known to be present in the area, and the age composition of the assemblage (agreeing as it does with Shipman's, 1975, observations) leads to the conclusion that the Chitake bone bed represents the results of a single event; that the animals belonged to a single group, the members of which met their end within a short span of days or, perhaps, weeks.

Although not specifically studied or measured at the time of collection, the bony elements in the Chitake Syntarsus locality did not show any obvious preferred orientation, other than generally lying parallel to the surface, and it is therefore not possible at this stage to decide whether any water in the pan was still or flowing. The general shape of the basin (Plate 3a) suggests that it was simply a shallow, small pan. Sufficient of the deposit remains for bone orientation and current flow analyses to be carried out at a future date.

From the information available, the environment of Syntarsus seems to have been a hot, dry desert containing scattered pans and oases probably connected to seasonal drainage lines. The fine-grained character of the sandstones at all localities suggests that they are the products of "winnowing" by the prevailing winds, and the only occurrences of coarse or gritty sediments are associated with the higher energy systems of aqueous deposition in the pans or streams of the times.

There is virtually no information available on the nature of the vegetation of the times. Only at the Maura River localities is there any suggestion of plant remains (Raath, et.al., 1970: 4) and even these remain doubtful. On the face of it, though, the pans and oases would seem to be the most logical places for reasonable stands of vegetation to develop. Prosauropods are generally considered to have been herbivores (see e.g. Romer, 1956; Attridge, 1963; Charig et al., 1965), and they would simply not inhabit areas deficient in their food requirements. Pans and oases would therefore attract prosauropods, if not because of their drinking needs then certainly because of their need for food. Syntarsus, being predatory, would in turn be attracted to the pans for the same reasons. Some of the prosauropod skeletons at the Maura River localities have small, recurved, serrated teeth lying loose in the sediments around them, and it seems clear that these are the teeth of scavengers broken while feeding on the available carcasses. All of the teeth recovered in these oases are incomplete, lacking their roots, which suggests that they broke during use. Furthermore, many of the teeth are very reminiscent of the teeth of Syntarsus, suggesting that it may well have been the principal scavenger. This interpretation seems plausible in explaining the ratio of "prey" to "predator" in the Maura River deposits, but it fails to provide an adequate explanation of the Chitake *Syntarsus* concentration. Further investigation of this curious situation is clearly called for.

4. OSTEOLOGY

THE SKULL

Blocks of sandstone from the Chitake River locality (Queen Victoria Museum locality code CT6) have yielded many cranial bones, most of which were found disarticulated and isolated. A few specimens demonstrate articulations between adjacent bones, but in no case is it possible to study the whole skull in articulation. It is clear that the majority of cranial articulations were loose schindyleses or arthrodia (tongue-and-groove or lap-joints) arguing strongly for the existence of extensive cranial kinesis in the Syntarsus skull (Table 15). Only in the region of the braincase are the articulations of the familiar interdigitating type and sufficiently strong and tight to ensure their preservation post mortem.

Individual elements are extremely delicate and lightly built, apart from the braincase where the bones are more robust, particularly in the occipital region. In spite of their delicate nature many of the Chitake specimens are surprisingly well preserved and they show even the most delicate and fragile end processes. They thus permit detailed examination of the methods of articulation between many adjacent elements.

Amongst the specimens recovered so far are the remains of at least eight braincases, representing a considerable age-range of individuals.

One cranial element not yet identified with any confidence is the vomer in the palate, and no epipterygoid has been located.

The reconstruction of the skull (Fig. 3) and its dimensions (Table 2) represent a mature animal, and the reconstruction is based in the main on the following specimens:

QG 193 : braincase; frontoparietals; articulation of postorbital
and squamosal; mandible.

QG 193, QG 194, QG 195, QG 196, QG 197: braincase and endocranium.
QG 265: length of pterygoid.
QG 194: quadrate/pterygoid.
QG 235, QG 241: pterygoid/ectopterygoid; palatine.
QG 202: articulations of nasal, maxilla and premaxilla, tips of jaws (Plate 6).
QG 193, QG 202: nasal/maxilla.
QG 193, QG 278: articulations of prefrontal, lachrymal and jugal.
QG 307: mandible (especially coronoid).

In the presentation that follows a general description of the skull will be given first, followed by description of the individual elements.

Description of the whole cranium (Fig. 3a-d)

The skull is lightly built and consists largely of slender arcs of bone bordering cavities and vacuities.

Side view (Fig. 3a)

The cranium is long and shallow, being more than three times as long as its greatest depth in the region of the braincase. The subcircular orbit and triangular antorbital vacuity are prominent openings in the lateral surface, and the lower temporal opening behind the orbit is tall, narrow, and V-shaped. The upper temporal opening is scarcely visible in side view since it opens directly dorsally, and it is subcircular in shape. The elliptical external naris is subterminal. Bordering these openings, the slender cranial bones describe graceful arcs which give the cranium a very light and fragile appearance. The tooth row extends back to the hind border of the antorbital vacuity, and there is a slight degree of heterodonty in the teeth, the premaxillary teeth being more slender, less recurved and more nearly circular in cross section than the flattened, recurved and serrated maxillary teeth. There is also a short diastema between the premaxillary and maxillary teeth.

The external naris is bordered by the premaxilla, maxilla and nasal, and the loose sliding articulations between these bones suggest a substantial capacity for movement on the part of the premaxilla, extending forwards and downwards in protraction, and sliding back and upwards in retraction. The possible significance of this mobility is discussed below in the section on Cranial Kinesis (p.168ff.).

The antorbital vacuity is bordered only by the maxilla and the lachrymal. The lachrymal forms a slender vertical post dividing the orbit from the antorbital vacuity, and articulates with the small, flattened prefrontal in the anterodorsal corner of the orbit.

The postorbital bar consists of the crescentic postorbital and the jugal. The two bones have a long sliding mutual contact, and they share equally in the formation of the hind margin of the orbit.

The upper temporal opening is bounded laterally by the postorbital and squamosal. These articulate in a tapering tongue-and-groove joint, and the squamosal houses the head of the quadrate in a shallow cup on its ventral surface and sends a slender process ventrally to meet part of the quadrate lateral wing. The quadrate condyle lies at about the level of the tooth row, and the quadrate shaft is vertical below, so that the lower temporal opening shows the typically archosaurian V-shape in its hind margin. The squamosal and quadrate both contribute to the formation of an otic notch.

The occipital condyle is visible in side view in the upper half of the posterior plane of the skull.

The ventral pterygoid flanges project below the general plane of the skull base.

Dorsal view (Fig. 3b)

In dorsal view the skull is nearly rectangular from the occiput to the level of the lachrymal, and then it tapers evenly to the slender snout. The premaxillae are slightly flared ventrally, but are nearly vertical dorsally. The nasals extend back to the region of the anterior orbital border, and each encompasses a narrow opening which seems to be bordered laterally by the lateral spur of the nasal, the lachrymal, and the prefrontal. In no case can this narrow accessory cranial opening be demonstrated with absolute certainty, but the nature of the swollen lateral margin of the lachrymal combined with its slightly concave inner border, and the known shape of the hind portion of the nasal, make the presence of such a nasal fenestra highly probable.

The skull table narrows slightly at the mid orbital point and then flares posteriorly to the region where the postorbital articulates.

The nearly circular upper temporal openings are rather small and are bordered anteriorly by the frontals, medially and posteriorly by the parietals, and laterally by the postorbitals and squamosals.

The prominent paroccipital processes and the condyle are the major features in the occipital region in dorsal view.

Palatal View (Fig. 3c).

The palate is remarkably delicate and abounds in squamose articulations between its constituent elements. It consists principally of a median pair of struts reaching from the neurocranium to the tip of the snout, with marginal elements restricted to the hind end. The struts are made up of the elongated pterygoids which are fairly broad transversely at the posterior end, vaulted for much of their length, and which narrow to vertical blades anteriorly. These narrow points articulate with the ventral premaxillary spurs (which probably represent short rod-like vomers fused to the premaxillae) at a level deep to the small palatine processes of the maxillae (= maxillary ramps).

The hind part of the palate is broad, consisting of the flared pterygoid ventral wings which protrude below the tooth line, and which, together with the small ectopterygoids and elongate palatines, form the roof of the palatal vault to the jaw margins. Small triangular postpalatine fenestrae remain between the palatines and the ectopterygoids. Between the pterygoids medially and the maxillae laterally lies a pair of long and narrow openings in the palate which evidently are the true internal nares. Posteriorly the air duct is extended by the vaulted roof formed of the palatines which directs the air down at the posterior end of the palate in what seems to function as an incipient secondary palate.

A long and very narrow median interpterygoid vacuity runs the entire length of the palate.

At a slightly deeper level, the sharply pointed parasphenoid rostrum (cultriform process) reaches forward to a point near the front border of the orbit.

The thin, vertical quadrate wings of the pterygoid cover the medial wings of the quadrate, and the prominent quadrate condyles mark the widest part of the skull in ventral view.

The occipital condyle, paroccipital processes, basal tubera of the basioccipitals and basipterygoid processes, partly gripped by the basal articulations of the pterygoids, are all prominent features of the braincase region in ventral view.

Occipital View (Fig. 3d).

The hind end of the skull is nearly rectangular, with the angular postorbitals marking the upper lateral angles, and the quadrate condyles the lower lateral angles. Below the level of the quadrate condyles the ventral pterygoid flanges protrude a short distance. The quadrate passage, bordered laterally by the quadrate and medially by the braincase wall, is prominent in occipital view.

The foramen magnum and condyle lie just in the upper half of the hind surface of the skull. The laterally directed paroccipital processes are prominent features, nearly bisecting the hind surface of the skull. In most cases the paroccipital processes protrude laterally at right angles to the saggital plane, but in skull QG 194 they dip slightly down, making an angle of approximately 30° to the horizontal. Directly above the foramen magnum, on either side of the median ridge, lie the small atlantal facets.

Description of the whole Mandible (Fig. 3 e,f).

The light mandible is long and very slender, swollen in the region of the mandibular fossa, and bears a well developed retro-articular process for the insertion of the depressor mandibulae muscle. The symphysis between the two rami was evidently rather loose, since no distinct symphysial suture is noticeable in any of the specimens collected.

In lateral view (Fig. 3e) the moderately large external mandibular fossa shows as a longitudinal tapering opening, while in internal view the large and elliptical adductor fossa and long tapering Meckelian canal are prominent features.

Only the articular bone, and, to a lesser extent, the dentary show any degree of robustness. The remainder of the jaw elements are thin plates of bone which ensheath the Meckelian canal and overlap their neighbours in loose squamose articulations.

Description of individual elements of the cranium

Premaxilla and vomer (Fig. 4 f,g; Plate 7 a,b; Table 3)

The premaxilla is small, rounded towards the front, and ends in two tapering processes posteriorly which mark the anterior embayment of the external naris. The lower of these processes probably incorporates the vomer. The specimens in which both premaxillae are present and articulated show that the snout was very narrow above, flaring slightly towards the alveolar border ventrally. The dorsal edge of the bone bears a slight lateral rim which extends back onto the process which articulates with the anterior end of the nasal, riding over the latter. The lateral rim terminates at the front in a small lateral dimple situated directly above the second tooth alveolus.

There are four premaxillary alveoli, and the premaxillary teeth are noticeably smaller and more slender than those in the maxilla; they are nearly circular in cross section and are unserrated.

The ventral posterior spur, forming the anteroventral border of the naris, articulates with the maxilla in a sliding union which is limited laterally by a downward triangular flange on the premaxilla at the root of the spur, immediately behind the last premaxillary alveolus.

The medial surface of the premaxilla is smooth and nearly flat, forming a large surface for articulation with its fellow, devoid of any trace of interdigitating sutures to bind the two sides firmly together. The significance of this, and of the tapering processes bordering the naris, will be discussed in the section on Cranial Kinesis (p.155ff).

QG 246 shows what appear to be sutures at the base of the ventral posterior spurs, and it seems possible that part of each spur is composed of a short rod-like vomer which fuses early in life with the premaxilla.

Maxilla (Fig. 4 a,b; Plate 7 a,b; Table 3)

One (QG 194) is complete, and several others (notably QG 208) are nearly so. The bone is deeply incised behind into two processes forming all but the posterior border of the large antorbital fenestra. The upper ramus, which articulates with the nasal along its length and with the lachrymal at its posterior end, is shorter and more gracile than the lower dentigerous ramus.

The maxilla is delicately constructed of a very thin sheet of bone reinforced by thin longitudinal ridges at its edges. Just above the alveolar border, on the lateral (labial) surface, the thin lateral ridge extends from near the oblique groove of the jugal facet at the posterior end almost the entire length of the lower ramus. It swings dorsally opposite the second or third alveolus to form the reinforcing ridge of the upper ramus. The broad surface of bone, bounded anteriorly by this curved segment of the ridge and posteriorly by the antorbital fenestra, is characteristically sculptured into upper and lower shallow depressions, the upper being larger and slightly deeper than the lower, and the two separated by a shallow rounded ridge which is confluent with the thickened border of the antorbital fenestra. The anterior end of the maxilla tapers forward into a thin and narrow palatal process which articulates with the premaxilla in the sliding manner mentioned in the description of the latter bone. In lateral view there is a distinct notch at the base of this maxillary ramp reflecting the fact that it arises dorsal to the level of the tooth row. The alveoli are masked by a longitudinal flange on the labial side of the alveolar border.

In medial view the only notable features of the maxilla are the premaxillary ramp arising above the third or fourth alveolus and protruding anteriorly, and the alveoli themselves with well developed interdental plates. Specimen QG 194 shows 19, or possibly 20, alveoli.

Nasal (Fig. 4c,d; Table 3).

In QG 194 both nasals are preserved, lying crossed one over the other. The narial processes at the anterior ends of each are damaged. Details of the articulations around the naris are preserved in QG 202, and the most complete nasal is QG 193, which also preserves the correct contour of the bone.

The nasals are exceptionally thin (0,5 - 1 mm) and it is indeed surprising that any have survived. Viewed from above the nasal is elongate and narrow, tapering gradually towards the front. In no case is the posterior edge preserved intact. The medial border is straight and only slightly strengthened by a weakly developed longitudinal ridge. It met its fellow on the other side in a simple edge-to-edge articulation.

The lateral edge is also nearly straight, but it bows very slightly laterally around mid-length. Immediately medial to the bowed area is a very shallow longitudinal sulcus.

Near the anterior end the nasal forks to send down a process which forms the posterodorsal border of the naris, and a forwardly projecting spike which articulates with the premaxilla and contributes to the formation of the upper border of the naris. The ventral narial process is grooved on its hind edge for reception of the upper edge of the maxilla. The medial rim of the groove continues posteriorly to form a thin lamina on the ventral surface of the nasal, and disappears near the posterior end. Presumably this lamina was concerned with articulation of the maxilla along its length. The lamina lies directly beneath the sulcus visible on the dorsal surface.

At the posterior end the nasal is broad medially and overlies the anterior end of the frontal in a thin and mobile squamose articulation forming the frontonasal hinge. Laterally it is emarginate to produce a long and narrow opening bounded on the lateral edge by a short sharp spur.

In lateral view the nasal (QG 193) is gracefully sigmoidal, turned slightly up towards the rear and down towards the front in the region of the naris.

Frontal (Fig. 5 a,b,f)

The frontals are long and relatively narrow, being broadest immediately behind the orbits, in the region of articulation with the postorbitals. Dorsoventrally the bone is thin, being strengthened along the saggital suture by a narrow and low ridge on the ventral surface which serves to increase the surface area for the simple edge-to-edge union of the two frontals in the midline.

In dorsal view the upper border of the orbit shows as a shallow lateral embayment which flares posteriorly. This flared area forms the forward boundary of the upper temporal arch and bears a depressed area posterolaterally from which part of the temporal musculature took origin. Otherwise the dorsal surface of the frontal is flat, rising slightly in the region of the upper margin of the orbit.

In ventral view of the paired frontals (skull QG 193) the smooth bulbous twin depressions of the cerebral hemispheres are clearly visible, narrowing anteriorly to the midorbital narrowest point and then opening out again into the elongated olfactory bulb depressions. Grooves for the olfactory nerves extend beyond the olfactory bulb cavities to the anterior edge of the frontals, and are confluent with similar grooves on the ventral surface of the nasals.

The orbital cups are separated from the forebrain depressions by rounded ridges of bone defining the dorsomedial arcs of the orbits.

The orbital margin is interrupted near its anterior end, opposite the depression for the olfactory bulb, by a short longitudinal lateral groove which receives a tongue from the prefrontal.

Similarly, at the posterior end of the orbital margin, the frontal bears an oblique dorsoventral groove laterally which receives a corresponding anterior tongue from the postorbital.

The frontoparietal suture arises at the hind end of the postorbital slot in the frontal and extends transversely across the temporal muscle fossa. It turns anteriorly as it climbs to the skull roof, thus forming a suture which is bowed forward in the midline.

Parietals (Fig. 5 a,b,c,f: Table 3)

The parietals are short and fused, firmly sutured to the frontals, broad anteriorly and (especially) posteriorly where they flare abruptly into the parietal flanges of the occipital region. The side walls of the parietals drop away almost vertically from the nearly flat dorsal parietal table. Narrow ridges of bone mark the apex of the temporal fossae on either side of the table, and at the posterior end the ridges turn laterally and become confluent with the dorsal rim of the parietal flange on either side.

The parietal table is short and narrow, and slightly sunken in the midline. At the posterior end it rises slightly to meet the parietal flange.

The parietal flanges crowning the occiput are thin vertical sheets of bone which protrude laterally and articulate with the supraoccipitals and partly with the dorsal edge of the paroccipital processes of the exoccipitals. The dorsal edge of the parietal flange overhangs the occipital plane very slightly, demarcating two distinct fossae, one on either side of the supraoccipitals above the foramen magnum.

On the side wall of the brain case the parietal articulates with the laterosphenoid, prootic and opisthotic in order posteriorly. Skull QG 194 shows a small foramen near the anterior end of the parietal-laterosphenoid suture which presumably transmitted one of the smaller cranial blood vessels, most probably the dorsal head vein (Fig. 5a; 24b).

Prefrontal (Fig. 4 s,t).

The best preserved prefrontal available for examination is from the left side (QG 193). It has a flat rhomboidal dorsal surface with a thickened lateral rim. The medial edge is thin and, at the posterior end where it articulates with the frontal, it bears a tongue of thin bone which meets the corresponding surface of the frontal. Anterolaterally the bone bears a depressed surface which articulates with the posteromedial angle of the lachrymal, and a thin vertical process descends from here to lie closely appressed to the medial surface of the vertical ramus of the lachrymal. The vertical process of the preserved prefrontal is not complete, but it seems improbable, because of its extreme thinness, that it could have been much longer than as preserved in QG 193. This process gives rise to a thin lamina which swings dorsally and posteriorly to support the posterior part of the bone from below, and the lamina also serves to round off the anterodorsal border of the orbit.

Lachrymal (Fig. 4 k,l).

There are three more or less complete lachrymals, the best preserved being QG 193. It is a slender L-shaped bone whose arms are supported by very thin laminae. The upper horizontal arm, which contributes to the formation of the upper border of the antorbital fenestra with the maxilla, is T-shaped in section towards the rear and flattens out to a very thin vertical lamina towards the front. The anterior tip, which articulates with the hind end of the upper ramus of the maxilla, is slightly forked. The lower ramus, which projects vertically down, is rather more complicated in construction. From a broad but thin upper end it tapers distally and then expands abruptly at the distal (ventral) end into an elongated vertical foot which articulates with the posterior end of the lower ramus of the maxilla. On the posterior face of its vertical ramus the lachrymal bears a blind-ending groove which presumably is concerned with housing the lachrymal duct.

The medial surface of the lachrymal is relatively simple. A shallow groove traverses the length of the anterior face of the vertical ramus.

From the position of the articulation facets of lachrymal with maxilla it seems clear that these are the only bones which border the elongated, triangular antorbital fenestra.

A fragment of a larger lachrymal (QG 230) shows a more acute angle between the rami than the right angle of QG193.

Postorbital (Fig. 4 o,p)

The postorbital is represented by several specimens and between them they show all details of the structure. QG 193 is one of the best preserved.

It is triradiate, with the anterior arm tapering forward to end in a delicate and complex tongue which articulates in a corresponding lateral groove in the frontal; a short and tapering arm which projects to the rear and slides into a corresponding V-shaped groove at the anterior end of the squamosal; and a curved and tapering ventral arm which meets the postorbital ramus of the jugal in a relatively long but simple lap joint.

On the medial surface the anterior and ventral arms are strengthened by a curving ridge of bone.

On the lateral surface, in the region where the three arms meet, there is a slight anteroposterior ridge which shows a variable degree of surface ornamentation, and which protrudes very slightly into the hind margin of the orbit.

Jugal (Fig. 4 u)

The bone here identified as the jugal (e.g. QG 278) is long, very thin and asymmetrically forked at the posterior end to form an inclined dorsal arm, and a posterior prong. Neither of the rami of the fork is complete. The bone is almost totally devoid of surface features, with the exception of a supporting ridge along the lateral edge of the lower border. The ridge terminates at the anterior end in an oblique dorsoventral groove which articulates with the groove at the posterior end of the lower maxillary ramus, and which is covered by the foot of the lachrymal.

The postorbital ramus of the jugal bears a facet on its anterior face on which the jugal ramus of the postorbital articulates to complete the narrow postorbital bar.

There is no recognisable facet for articulation with the ectopterygoid on the medial surface.

Squamosal (Fig. 4 m,n).

Fragments of at least 11 squamosals have been recovered. The best preserved is QG 193 (R).

The squamosal is also essentially triradiate, with anterior posterior and ventral arms.

The dorsal surface is domed, falling away posteriorly to a shallowly concave facet which faces obliquely posteriorly and medially and articulates with the anterior surface of the paroccipital process. Anteriorly the dome falls away to form a thin tongue bearing a lateral groove which tapers towards the rear and into which fits the tapered posterior process of the postorbital. The dorsal surface is lightly ornamented. On the medial side the dorsal dome sends forward a thin flange of bone to contact the lateral flange of the parietal, lying on the anterior face of the latter.

The ventral process, which meets the quadrate, is incomplete in the specimens at hand. It was evidently moderately short and thin and applied to the surface of the lateral wing of the quadrate near the quadratojugal. There is a deep pocket on the anterior surface of the ventral process where it arises from the dorsal dome, and in the corresponding position on the posterior surface is another pocket, or notch, which distorts the line of the medial edge of the ventral process. The head of the quadrate articulated in this posterior pocket.

Quadrate (Fig. 4 j)

Several quadrates from either side are preserved and two of them (QG 194, QG 235) are nearly perfect and retain the quadratojugal attached. The quadrate is a relatively large bone with a stout ventral shaft which bears the asymmetrical, paired transverse terminal condyles for articulation of the lower jaw. Above the shaft lie two broad but thin vertical expanses (or wings) of bone - one directed parasaggitally, and the other, which bears the quadratojugal, directed more laterally. These two plates of bone unite in an acute angle and the line of union is supported posteriorly by a thickened ridge of bone. In medial view the quadrate is distinctly bowed forwards, producing the characteristic V-shaped posterior notch of archosaurs. It is on the medial surface that the squamous quadrate ramus of the pterygoid is applied, and a light scar of articulation can be seen in this position on the medial quadrate wing in the region of its ventral origin.

The lateral wing of the quadrate is perforated by the quadrate foramen near the edge where it articulates with the quadratojugal.

The head of the quadrate is a dorsal, rounded condyle which fits into the pocket on the lower posterior surface of the squamosal. The ventral process of the squamosal lies along the anterior surface of the lateral wing of the quadrate.

Quadratojugal (Fig. 4 j)

Apart from those still attached to QG 194 and QG 235, there is another well preserved and isolated quadratojugal (QG 193), from the right side. It is L-shaped, consisting of an extremely thin and rather narrow vertical arm which articulates with the lateral wing of the quadrate, and a more slender horizontal arm which tapers anteriorly and bears a shallow lateral groove near its anterior end. The posterior process of the jugal would have articulated in this groove.

Scleral plates (Fig. 3)

Several isolated scleral plates have been recovered, and these are composed of extremely thin quadrangular plates which are constricted below, giving a broad upper plate and narrower lower plate. The size is very variable, presumably related to size and age of the individual concerned, and the largest are three preserved in association with part of a large lower jaw (QG 208). One of these sclerals has the following dimensions :

greatest width	9,4 mm
least width	5 mm
greatest depth	8 mm

Palatine (Fig. 4 h,i)

Parts of six palatines are preserved but none is complete. The best preserved of the six is QG 241, from the left side. In ventral view the bone is relatively broad at the posterior end and it bears an acute embayment marking the anterior margin of the postpalatine fenestra. The bone has a straight lateral edge where it meets the maxilla. Medially it bears a large embayment which has a reinforced rim, and an extremely thin vaulted roof. This probably represents the lateral border of the large median palatal fenestra or choana.

In dorsal view the straight lateral edge is reinforced by a shallow ridge, and the remainder of the bone is rather dimpled and folded. This seems to represent the true topography of the bone, and not an artifact of post mortem compression or distortion, as it is also reflected in the other specimens of the palatine collected.

The vaulted roof of the palatine extends medially to stop just short of the midline and evidently forms a respiratory duct to channel air towards the back of the buccal cavity. At the posteromedial end of the palatine, in dorsal view, a long scar of articulation with the lateral wing of the pterygoid can be seen.

Pterygoid (Fig. 4 e; 6)

The pterygoid is represented by several fragmentary specimens but a few (e.g. QG 235 and QG 265) are extraordinarily well preserved. It is an extremely long, fragile and complex bone whose palatal and quadrate rami lie in different planes and meet in the area of the notch for the basal articulation.

The quadrate ramus is a crescentic thin plate of bone which covers nearly all of the medial surface of the medial wing of the quadrate. It is an otherwise featureless part. Anteriorly, the quadrate ramus contributes to the formation of the basipterygoid notch, a backwardly facing and deep dorsoventral groove which holds the basipterygoid process of the basisphenoid. The inner lip of the notch is a small, rounded and thin plate of bone from the palatal ramus of the pterygoid. The palatal ramus is well vaulted posteriorly, and bears a strengthened rim in the region of the basipterygoid notch which develops a "pocket" immediately ahead of the notch. In this region it also flares ventrally. Only in QG 265 is the anterior part of the palatal ramus reasonably preserved, and even here it is incomplete, consisting principally of the long and fragile thickened medial border, with traces only of the paper-thin lateral sheets which would have formed much of the bony roof of the mouth. In another specimen (QG 263) portions of the palatal rami from either side are preserved, and these indicate that the pterygoids were separated along their length by a narrow interpterygoid fissure. The pterygoids from either side might have met anteriorly in the region of the internal nares.

The anterior end of the palatal ramus is a thin beam which would have articulated with the "vomer" (on the premaxilla) laterally. Despite the lack of much of the lateral bony sheet of the palatal ramus it seems certain that the bone was narrow.

The ventrally flared wing at the posterior end, in the region of the basipterygoid notch, marks the area of articulation of the ectopterygoid. The two bones articulate in a complex manner which will be described in the following section.

Ectopterygoid (Fig. 4 q,r; 6)

Six well preserved ectopterygoids are present, the most complete being QG 235. It is a small hook-shaped bone with a fairly broad but thin medial wing (the pterygoid flange) and a robust hook curving laterally and then posteriorly from about the middle of the pterygoid flange. This hook thins into a vertical plate laterally which articulates with the jugal.

The pterygoid flange is variable in shape being relatively simple in QG 194, which is small in the series, and more complex in QG 235, which is large, but both bear a deep "pocket" on the ventral surface. QG 235 (left) shows that articulation with the palatine ramus of the pterygoid was accomplished by means of a "double-overlap" between the two bones (Fig. 6). The ventral flange of the palatine ramus of the pterygoid is stepped midway between the ventral and dorsal margins. Beneath this step the ventral half of the ectopterygoid is applied to the lower (or buccal surface) of the pterygoid. Above the step the positions are reversed and the ectopterygoid lies above the pterygoid. Such an articulation gives strength in the vertical plane, so that the two bones are held firmly together during any pitching movement (e.g. when biting). However, it does permit some movement of the bones relative to each other in the following directions :

a) side-to-side (i.e. yawing, or rotation about a vertical axis)

b) fore-and-aft (i.e. sliding, to a limited degree, over each other).

When the pterygoid and ectopterygoid are so articulated it is seen that the ventral pocket of the ectopterygoid becomes confluent with that of the pterygoid to form a relatively large and discrete triangular concavity at the posterior end of the buccal cavity (Fig.6). This "carnosaurian pocket" as it might be described (since it is also found in tyrannosaurids) is said to be absent from Coelophysis (Ostrom, 1969b), a close relative of Syntarsus. Its possible function is discussed in the section dealing with jaw musculature (p.112).

Occiput (Fig. 3 d; 5 c; Table 3)

The occipital surface is roughly quadrangular with the sides interrupted by the protrusion of the paroccipital processes. The dorsal angular contour is provided by the thin parietal flanges resting on the supraoccipitals and the paroccipital processes.

The supraoccipital is median in position and forms an inverted triangular prominence above the foramen magnum, flanked on either side by relatively deep fossae for the insertion of the rectus capitis posterior muscle (see p. 117). In the midline the supraoccipital bears a sharp ridge. Sutural details between supraoccipital and exoccipitals are not clear, but symmetrical cracks in this vicinity in two specimens (QG 193, QG 194) suggest that the supraoccipital did not reach the foramen magnum and was excluded from it by the exoccipitals, which themselves contribute to the formation of the median ridge.

The lateral muscle fossae are bounded on the exoccipitals by sharp ridges of bone but these fade out on the parietal flanges.

The exoccipitals extend into the paroccipital processes which reach laterally and slightly posteroventrally. The processes are anteroposteriorly thin and bear bluntly rounded tips.

The foramen magnum is subcircular and its lateral walls are notched at the level of the mid-point of the paroccipital processes for the exit of the first free spinal nerve. Directly above it, beside the median ridge, lie the small triangular atlantal facets.

The rounded hemispherical condyle is composed entirely of basioccipital and in QG 194 the basioccipital-exoccipital suture just enters the floor of the foramen magnum.

Lateral to the foramen magnum and condyle the ventral parts of the occiput are deeply excavated forming a blind pocket on either side. These pockets are bounded by the ventral margin of the paroccipital processes above, the lateral wall of the exoccipital laterally, and part of the lateral wall of the foramen magnum plus the basioccipital medially. From these pockets issue three small foramina on each side which transmitted the branches of the Hypoglossal nerve.

The basioccipitals swell ventrally to form the rounded basal tubera in combination with the basisphenoid.

The occiput is considerably narrower ventrally than dorsally. In lateral view of the whole occiput the condyle is the most prominent feature, and the occipital plane slants anteriorly to the skull roof dorsally, and drops to the basal tubera ventrally.

Side wall of the braincase (Fig. 5a)

Laterosphenoid (Fig. 5a)

The laterosphenoid is relatively small and shows two principal surfaces in side view - the first being an almost triangular lateral face which articulates dorsally with the frontal and parietal, and ventrally with the prootic, and the second facing obliquely forward into the orbital region. Near its ventral end this anterolateral face of the laterosphenoid is notched for the passage of the substantially large Optic nerve. Immediately behind the Optic nerve notch the bone bears a groove for the transmission of the deep opthalmic branch of the Trigeminal nerve. The groove communicates below with the large trigeminal notch in the upper border of the prootic, and shallows and disappears just above the level of the notch for the Optic nerve. Behind the trigeminal groove the laterosphenoid bears a short ventral flange (forming the hind wall of the groove) which also guided the mid-cerebral vein from its foramen in the laterosphenoid-prootic suture on its downward and backward course over the prootic.

The ventral portions of the anterolateral face of the laterosphenoids from either side meet in the midline immediately above the pituitary fossa, but they diverge away from each other dorsally, leaving the front of the braincase uncovered by bone.

Prootic (Fig. 5 a)

The largest of the bones constituting the lateral wall of the braincase, the prootic has a complex shape and articulates with the following bones : laterosphenoid, parietal, opisthotic and basisphenoid-parasphenoid. It contributes to the formation of several foramina for cranial nerves and blood vessels, as well as forming part of the wall of the auditory meatus, and of the pituitary fossa.

Its surface is depressed posteriorly near its sutural union with the parietal flange and the opisthotic. This concavity is bordered by a diagonal ridge which runs from the anterodorsal corner of the bone (where the foramen for the mid-cerebral vein is situated) to the most posterior point of the interdigitating suture with the opisthotic, and it bears the shallow groove in which the mid-cerebral vein (and twigs of the carotid) ran down and back from the foramen. Immediately ahead of the mid-cerebral vein foramen the upper edge of the prootic is very deeply notched for the passage of the Trigeminal nerve (principally the maxillary [V_2] and mandibular [V_3] branches, the opthalmic branch [V_1] exiting more dorsally at the junction of laterosphenoid and prootic as described above). Just below the ventral border of the trigeminal notch in skull QG 194 there is a horizontal longitudinal groove which reaches from the anterior edge of the bone to the posterior end near the prootic-opisthotic suture. Towards the rear end of this groove is a small foramen. In skull QG 193 the groove is absent in front of the foramen, and the foramen itself is markedly larger than in QG 194. The foramen evidently transmitted the Facial nerve. The anterior part of the groove probably carried a twig of the stapedial branch of the internal carotid, branching off near the carotid foramen which lies below the Facial nerve foramen. The ventral border of the prootic is rounded anteriorly where it overhangs and partly encloses the "parabasal canal" or channel which carried the palatine artery, the lateral head vein and the palatine branch of the Facial nerve. The fenestra ovale perforates the prootic posteriorly in a deep concavity and it is separated from the fenestra rotunda below by a short, low, and exceedingly thin sheet of bone whose relationships are not clear. It appears to be separate from the prootic, being held by the latter in a groove in the dorsal wall of the meatus and it seems probable that it may be an outgrowth of the basisphenoid. Anteriorly the prootic turns sharply in towards the midline and meets its fellow to form the dorsum sellae, or hind wall of the deep pituitary fossa. This wall is perforated on either side of the median suture by a small foramen which transmitted the Abducens nerve. From the level of the Abducens foramina (as shown in skull QG 194) the ventral part of the pituitary fossa is built of basisphenoid/parasphenoid. It would seem that the foramina in fact pierce the wall of the pituitary fossa on the line of the prootic-basisphenoid suture.

Opisthotic (Fig. 5 a,d)

The opisthotic forms part of the prominent paroccipital processes. It meets the parietal flange above in a narrow long contact, and articulates with the prootic in front and the basisphenoid below. There is no clear suture between the opisthotic and basisphenoid, although a sediment-filled line in QG 194 (which might be simply a crack) suggests that it ran for a short distance along the roof of the meatus and then turned vertically down the hind wall of the meatus to define a ventral spur on the opisthotic. The intimate contact of the opisthotic and the exoccipital in forming the paroccipital process is also devoid of visible sutures.

Basisphenoid/Parasphenoid (Fig. 5)

In none of the specimens to hand are these two bones visibly separated and so they will be described together.

Presuming the posterior end of the basisphenoid to be as described under the opisthotic, the basisphenoid forms much of the thin posterior wall of the auditory meatus, and probably gives off the thin plate described above which separates the fenestra ovale from the fenestra rotunda. At the upper hind end of the very deep, slit-like concavity which bears the fenestra rotunda there is another foramen which transmits the Glossopharyngeal, Vagus and Accessory nerves plus the jugular vein. These nerves leave the internal surface of the braincase through a well defined vagal fissure which slopes obliquely near the floor of the brain case.

The ventral posterior part of the basisphenoid, below the level of the meatus, contributes to the formation of the swollen basal tubera of the basioccipital, whose rounded surfaces are rather rugose.

From the basal tubera the basisphenoids extend forwards, forming the floor of the meatus and the ventral part of the side wall of the braincase. The wide "parabasal canal", carrying the palatine artery, lateral head vein, and the palatine branch of the Facial nerve, emerges from the basisphenoid in the region of the rounded ventral margin of the prootic, near the floor of the pituitary fossa.

Anterior to the opening of the canal on either side the basisphenoids flare in a wide arc to form the protruding basipterygoid processes. These processes project ventrolaterally, and they recurve slightly at their ends. The facets for articulation in the pterygoid cups are clearly marked and rather long mediolaterally. Anterior to the basipterygoid processes the basisphenoid/parasphenoid reaches forward to form the long tapering parasphenoid rostrum which bears a shallow longitudinal sulcus on its dorsal surface, and a very deep longitudinal sulcus ventrally. The rostrum reaches well beyond the orbits but in no case is it complete at its tip.

In ventral view, the paired elements are firmly united and reinforced with a transverse bar between the basal tubera and a transverse sloping plate of bone between the basipterygoid processes. Otherwise the ventral surface is longitudinally sulcate, and at the posterior end, arising from the bar between the basioccipital tubera, a short median spur of bone reinforces the cranial floor.

The endocranial floor and side walls (Fig. 5 d)

Two damaged braincases (QG 195, QG 196) and the well preserved QG 193 together show most of the internal details of the endocranium. The most notable features are : the deep subarcuate or floccular fossae associated with the auricular lobes of the cerebellum, lying opposite the level of origin of the paroccipital processes; the median ridge in the floor of the endocranium, on either side of which branches of the Abducens nerve travel forwards to mount the hind wall of the pituitary fossa and then penetrate it through the foramina described earlier; and the oblique and rather long vagal fissures near the posterior end of the endocranial floor.

The opening of the trigeminal notch on either side lies in a shallow depression which suggests that Syntarsus had well developed Gasserian ganglia.

Immediately below the trigeminal notch lies a twin foramen, part of which divides within the substance of the cranial wall. The anterior opening transmitted the stem of the Facial nerve. The hinder opening turns back in the bone and further divides, one branch opening to the lateral surface in a small foramen below and behind the external Facial foramen, and the other turning forward again to travel in a short bony canal which soon opens into the wide parabasal canal. The latter openings evidently housed branches of the internal carotid artery.

The vagal fissures slope obliquely below the subarcuate fossae, and lie on the line of the basisphenoid-basioccipital suture as shown in specimen QG 196. A further sloping ridge of bone, forming the hind border of the vagal fissure, separates it from the three separate foramina for the Hypoglossal nerve which open laterally on the basioccipital. Just above the opening for nerves IX to XI (i.e. the upper hind end of the vagal fissure) a further sediment-filled foramen is present in QG 196 which seems to end in the otic capsule and might therefore represent the conduit for the Auditory nerve.

Description of individual elements of the mandible (Fig. 3 e,f; Plate 8 a.b.c).

Many isolated portions of lower jaws have been recovered showing exquisite details of bone architecture in several cases. Some of the more fragile elements lack parts, but in general the lower jaw can be reconstructed with considerable confidence.

Dentary

The dentary is a long and slender beam bearing the alveoli in a shallow sulcus dorsally and the Meckelian canal as a long and tapering furrow on the medial surface. The Meckelian canal ends at the anterior end of the bone, and flares posteriorly in the region of the adductor fossa. On the lateral surface the bone is grooved for most of its length and the groove fades out in the region of the seventh alveolus. Ahead of this point the lateral surface bears a number of pits in a line, each pit associated with an alveolus. There are up to 25 alveoli in the dentaries recovered.

At the posterior end the dentary is an extremely thin vertical sheet of bone, and in no case is it entire in this region.

Angular

The angular is a narrow triangular bone which is thickened ventrally, broad and sheet-like anteriorly where it overlaps the dentary, and it tapers to a point posteriorly where it meets the prearticular and surangular. Its curving dorsal rim forms the lower border of the external mandibular fossa. The bone is otherwise featureless except for the narrow but robust medial rim which buttresses the ventral edge, and near the posterior end the scar of articulation with the prearticular is evident.

Surangular

The surangular is a complex bone which forms most of the border of the external mandibular fossa and its dorsal edge is bowed up in this region. Anteriorly it tapers to a spike which articulates with the dentary, bearing a long tapering groove on the dorsolateral surface which evidently received a corresponding spur from the hind end of the dentary although such a spur is not preserved in any specimens to hand. Medially the anterior spike of the surangular is also grooved for articulation with the coronoid. The upper surface of the bone is robust and smoothly rounded transversely.

The hind border of the external mandibular fossa is formed by a thin sheet of bone which falls from a longitudinal ridge along the jaw margin. In this ventral region the surangular is extremely delicate and fragile, and details of the shape of the bone have been lost.

The posterior end of the bone forms an almost flat shelf upon which the articular rests. The lateral surface is shallowly grooved and it continues back to form part of the retroarticular process.

The medial surface of the bone is deeply bayed, forming the wall (perforated by the external mandibular fossa) of the adductor fossa. It is reinforced in the region of its union with the articular by a short transverse spur. The upper surface, forming the jaw margin, is deeply grooved below.

Articular (Plate 8 c)

The articular is a small but robust flat bone which bears a ventral ridge, and a complex series of depressions on the upper surface concerned with jaw articulation and the insertion of jaw muscles. The glenoid consists of a pair of asymmetrical concavities, the medial larger than the lateral, in which the quadrate condyles articulate.

Immediately behind the medial glenoid fossa is a short transverse groove bounded posteriorly by a shallow ridge. This ridge also forms the front border of the gently concave upper surface of the retroarticular process, which tapers back to a dilated, blunt, roughened tip.

Prearticular

The prearticular is a long delicate bone consisting of expanded sheet-like ends joined by a curved rod-like central shaft. It is deeply embayed on its dorsal margin, which forms the lower border of the adductor fossa, and is gently bowed along its ventral margin.

Posteriorly a slender strip of the bone is closely applied to the medial surface of the articular, forming the medial surface of the retroarticular process.

Anteriorly, immediately ahead of the adductor fossa, the bone bears a slight marginal rim on its medial surface, bounding a shallow plane over which the splenial lies. This anterior dorsal edge of the bone partly covers the coronoid.

Coronoid

The coronoid is represented by a single imperfectly preserved specimen (QG 307). All that remains is a thin triangular plate of bone lying in the groove along the medial surface of the upper arm of the surangular, with an emarginate ventroposterior border which rounds off the anterior corner of the adductor fossa.

Splenial

The splenial is also a thin vertical plate of bone with a slightly thickened ventral rim and a gently emarginate upper surface which, together with the prearticular, contributes to the lower margin of the adductor fossa.

Posteriorly the bone tapers over the prearticular, presumably ending in a curved point, but these details are not preserved. Nor are details preserved anteriorly where the bone would have covered part of the Meckelian canal.

The splenial lies entirely over the anterior part of the prearticular, resting in the plane bounded by the dorsal rim which was described in the section dealing with the latter bone.

Dentition and tooth replacement (Fig. 7)

The dentition of *Syntarsus* shows minor heterodonty in that the anterior teeth (especially on the premaxilla) are different in shape from the posterior teeth and are devoid of serrations. All of the teeth are recurved to a greater or lesser degree, and they are laterally compressed - again to a variable degree.

Premaxillary teeth (Plate 9a)

There are four premaxillary alveoli in all premaxillae collected, with the possible exception of one (QG 254) which shows what might be a fifth, or it might equally be an artifact of preparation. The alveoli are subcircular in section, and those of the left side of QG 245 have the following dimensions :

Alveolus	1.	maximum	2,5 mm	minimum	2,0 mm
	2.		3,3		3,0
	3.		2,7		2,0
	4.		3,5		2,2

The premaxillary teeth are long, subcircular in section, only slightly recurved at the tip, and bear no serrations. The teeth protrude up to 7,7 mm from the jaw margin in QG 245, and 6 mm + in

QG 246, where they are still implanted in the jaw. However, most premaxillae in the collection lack teeth in their alveoli. In a few cases small replacement teeth can be seen in the otherwise empty alveoli. The fourth alveolus on each side is situated beside the ventral vertical flange which limits premaxillary movement on the maxillary ramp.

Maxillary teeth (Plate 9b)

The number of alveoli in the maxilla varies between 19 (QG 194) and 21 or 22 (QG 206). All of the maxillary alveoli, with the possible exception of the first, are considerably longer than broad, reflecting the fact that the teeth are strongly compressed laterally, being on average 2,3 times longer than broad. They are strongly recurved and sharp, both at the tip and along the serrated anterior and posterior edges. In all cases where functional maxillary teeth are preserved implanted the apex of the tooth lies well behind the hind margin of its alveolus, as noted by Ostrom (1969 b) in Deinonychus. Indeed, in those cases where replacement teeth are beginning to emerge, it almost seems that the tooth is growing out towards the rear, so sharp is the backward inclination of the tooth apex.

The fine serrations run the entire length of the erupted posterior edge, and also show over a variable length of the anterior edge to the apex. The number of serrations on the posterior edge of the maxillary teeth averages in excess of 50 in teeth protruding 12,7 mm or more beyond the jaw margin. One isolated tooth in the collection has dimensions of 4,2 mm x 1,8 mm x approximately 11 mm erupted height, and shows distinct signs of wear at the blunted apex. This tooth, otherwise clearly recognisable as a maxillary, has lost all serrations - presumably through wear.

Dentary teeth

Few dentary teeth are preserved implanted. Those that are represent the hinder "cheek-teeth" and are in all respects comparable with maxillary teeth. The number of dentary alveoli cannot be determined accurately because in no case to hand is the dentary known to contain the entire tooth row. QG 193 and QG 305 are the best preserved and they bear 20 + alveoli and 25 respectively. The latter is most probably close to a complete count. The alveoli at the front of the dentary are subcircular in section, rather like the premaxillary alveoli, and they are also smaller than the hinder alveoli, suggesting that the dentary bore teeth similar to those of the premaxillae at the front.

This suggestion is supported by the conditions seen in QG 202 where at least the first two dentary teeth are slender, subcircular, slightly recurved and devoid of serrations.

The first dentary alveolus opens obliquely forward on the front surface of the bone, suggesting a tendency towards procumbency of the first pair of teeth.

Fig. 7 shows diagrammatically the stages of tooth replacement represented in the specimens of maxilla examined.

The pattern of replacement is essentially identical to that described by Edmund (1960) in Coelophysis and Velociraptor, and using his techniques of analysis on three maxillae (QG 206, QG 209, QG 213) it can be shown that at least four replacement waves are in operation in the jaw at any one time. In the juvenile QG 213, in which the 15 preserved alveoli occupy only 62 mm of jaw length, five waves of replacement can be identified (Fig. 7). The result is that no more than two adjacent alveoli would ever be served by teeth which were not yet sufficiently large to be functional.

The leading edges of the replacement waves are close together in Syntarsus, rather like the condition noted in Coelophysis by

Edmund (1960), comparable stages being separated by 7 alveoli in both QG 213 and Coelophysis (AMNH 7252, see Edmund, 1960: Fig. 39 a).

Hyoids (Plate 10).

Slender angled rods were recovered which clearly represent the second cornua of the hyoid apparatus, which, as Romer (1956) notes, are "always well developed and generally well ossified" in reptiles. The second cornua correspond to the first cerato-branchials, and these are now known in several dinosaurian genera (see, e.g. Gilmore, 1920; Colbert, 1945; Romer, 1956; Ostrom, 1961; Bidar, Demay & Thomel, 1972). Colbert (pers. comm.) informs me that they are also known in Coelophysis.

The Syntarsus hyoids were found loose and disassociated except for a pair which were closely associated with skull QG 193, to which they are presumed to have belonged.

In some cases the angle at midlength is rather sharp (QG 244) but it may vary to a gentle and slight curve. The larger specimens, notably the QG 193 pair, bear a short lateral spur at the apex of the angle. There is no evidence preserved to elucidate their orientation or position in relation to the rest of the skull.

Comparison of the skull with other Theropods (Table 2).

Descriptions of coelurosaurian skulls are seldom detailed or complete, which is understandable in view of their notorious fragility. This hampers critical comparisons, but in the light of what is known, Syntarsus shows no startling deviations from the "standard" characters of the coelurosaur skull (Romer, 1956). It is small, relatively low, the snout is slender, and the jaws are long. The orbit is large and provided with a scleral ring. The teeth are pointed and recurved. The cranial bones are, with very few exceptions, delicate.

One of the most detailed and useful descriptions in recent years of the skull of a small theropod is that by Ostrom (1969b) of the Lower Cretaceous Deinonychus. Ostrom compares the ratio of skull length to presacral length in several theropod genera (p. 16) with the following results :

Ornithomimus	0,15
Coelophysis	0,23
Ornitholestes	0,24
Allosaurus	0,28
Deinonychus	0,35 - 0,40
Tyrannosaurus	0,41

Although the presacral series of Syntarsus is known only in part the calculations given in Table 4 give a skull/presacral ratio of approximately 0,35.

Deinonychus has a skull which is clearly more robust in proportions, shorter faced, deeper and wider than that of Syntarsus. Apart from the orbit, the other fenestrations in the Deinonychus skull are proportionately smaller than those of Syntarsus. Syntarsus does not show the development of accessory antorbital fenestrae as seen in Deinonychus, later carnosaurs and sauropods, but the undulating and dimpled wall of the maxilla ahead of the antorbital fenestra might possibly represent an incipient stage in the development of these accessory apertures. Photographs of the skull of Coelophysis, kindly supplied to me by Dr. E.H. Colbert, show undulations and depressions in the maxilla which are identical to those of Syntarsus.

Syntarsus retains a loosely articulated premaxilla which has a sliding articulation with the maxilla. Elsewhere in this study it is suggested that premaxillary mobility had assumed a specialised function in Syntarsus. In general, though, it seems to represent the persistence of a primitive archosaur feature since a basically similar arrangement has been demonstrated by Gow (1970) in Euparkeria, and Cruickshank (1972) notes that in the Lystrosaurus-zone Proterosuchus "the premaxillae are subject to displacement". Dr. E.H. Colbert (pers. comm.) informs me that Coelophysis also has a loosely articulated premaxilla. In contrast, later forms such as Deinonychus (Ostrom, 1969b) and Dromaeosaurus (Colbert & Russell, 1969), have premaxillae which are suturally bound to the maxillae.

The suggested fusion of the short and rod-like vomer to the premaxilla in Syntarsus seems to represent a departure from the situation in those early theropods where this region is adequately known. Colbert (pers. comm.) believes that the vomers of Coelophysis contacted the narrow palatal processes of the maxillae, probably in a fused union. Details remain unclear in both forms.

The number of premaxillary teeth seems to be constant in Syntarsus. Eight specimens examined all show four alveoli on each side (doubtfully five in QG 254). This compares with four in Deinonychus (Ostrom, 1969b) and four to five in Coelophysis (Colbert, pers. comm.) Maxillary tooth counts in Syntarsus vary from 19 to 22, which is similar to Coelophysis (Ostrom, 1969b).

The ventroposterior border of the external naris of Syntarsus is formed partly by the premaxilla and partly by the maxilla. The nasal does not reach down as far as this, and is confined to the upper quadrant of the naris.

An unusual feature in the skull of Syntarsus is the presumed presence of a nasal fenestra in the region of the frontal/nasal articulation. It is tempting to think of this area as the housing of some sort of secretory gland, and there is ample room for such a structure in the smooth cavity formed by the skull roof and the inner walls of the prefrontal and lachrymal (Fig. 3; 4 k,s). Its position is quite different from that normally occupied by the salt glands of birds, and perhaps of Sphenosuchus (Walker, 1972: Fig. 5 c). Colbert's reconstructions of the skull of Coelophysis show no such feature (Colbert, pers. comm.). It should be emphasised that the presence of this fenestra in Syntarsus is speculative, but it is strongly indicated by the configuration of the adjoining bones (Fig. 3, 4).

The lachrymal of Syntarsus is "normal" for small theropods (Colbert, pers. comm.; Ostrom, 1969b) but it bears an unusual ventral end which is expanded and covers the jugal-maxilla junction in squamose fashion. The lower end also reaches the level of the toothrow at the jaw margin. Colbert (pers. comm.) thinks the same might be true of Coelophysis, and Ostrom (1969b: Fig. 10 a) depicts the jugal of Deinonychus bearing a facet for the lachrymal in a similar position. The distal end of the Deinonychus lachrymal is unknown (Ostrom, 1969 b). The lachrymal of Compsognathus corallestris (Bidar, Demay & Thomel, 1972) is very similar in shape and surface architecture to that of Syntarsus, but the lower end evidently did not reach the level of the tooth row.

The external rugosity and sculpturing on the postorbital of Syntarsus is evidently a common feature, shared with such dissimilar forms as Ornithosuchus (Walker, 1964), and Deinonychus (Ostrom, 1969 b).

The ventral arm of the squamosal of Syntarsus seems unusual in that it lies medial to the quadrate lateral wing. Romer (1956) notes that this arm of the squamosal, together with the quadratojugal, generally covers the quadrate laterally. Syntarsus thus has a quadrate which is broadly exposed laterally, and its ventral squamosal arm certainly did not reach down to the quadratojugal. As discussed in the section on cranial kinesis, this arm of the squamosal probably functions as a protractor stop in *Syntarsus*.

A tongue-and-groove articulation between the postorbital and squamosal is a common feature among theropods such as *Deinonychus* (Ostrom, 1969 b), *Coelophysis* (Colbert, pers. comm.), *Allosaurus* (*Antrodemus*) and *Tyrannosaurus* (Gilmore, 1920). *Syntarsus* also shares this feature.

The streptostylic quadrate of *Syntarsus* rests with its distal end vertical (Fig. 3). The upper end, or head, rests in a cup on the under surface of the squamosal and partly on the opisthotic. This is in contrast to the situation noted by Walker (1972) in *Sphenosuchus* and the crocodiles where the quadrate has moved forward away from contact with the opisthotic and onto the prootic, but it agrees with the normal condition in theropods.

The quadratojugal is tightly bound to the quadrate in *Syntarsus*. Its relationship to the quadrate is either unclear or unknown in *Coelophysis* and *Deinonychus*. In *Deinonychus* it has a "clasping junction" with the jugal (Ostrom, 1969 b: 24). This is similar to the situation in *Syntarsus*, although in this case the articulation is loose and relatively long, evidently permitting a few millimetres of telescoping between the two bones. The jugal articulates in a similar "ramp-and-runner" telescoping fashion anteriorly with the maxilla in *Syntarsus*. This amount of free play in the postorbital portion of the skull has not been reported in dinosaurs hitherto as far as I am aware, but A.D. Walker (in. litt.) has noted a comparable situation in *Sphenosuchus*.

The palatal reconstruction of *Syntarsus* must be regarded as tentative in view of present incomplete knowledge of the pterygoids ahead of the basipterygoid articulation, and of the palatines and the vomers. Future refinement of the reconstruction is likely to affect mainly the configuration of these bones. The preserved width of the palatines makes it highly improbable that they could have lain further forward than the position given in Fig. 3 c because of the narrowness of the snout. However it must be conceded that their orientation remains doubtful. As reconstructed, the palate shows elongated lateral openings which occupy the position of the "traditional" internal nares, and a posterior median large opening, split by the pterygoids, which bears more of the stamp of the choana. Perhaps this apparent anomaly can be explained by the presence of a membranous roof covering the anterior openings in life, thus channelling the air back to the choana near the back of the mouth. This interpretation suggests that Syntarsus had an incipient secondary palate. It seems probable to the writer that the condition in Deinonychus parallels that in Syntarsus and that the "subsidiary palatine fenestra" (Ostrom, 1969b: 28) is, in reality, the choana. Von Heune (1926) has reported what seems to be an incipient secondary palate in Plateosaurus, a Triassic prosauropod.

The pterygoid of Syntarsus is very long, accounting for 70% of the skull length from the posterior end of the quadrate wing to the vomer articulation. In Deinonychus the pterygoid is approximately half the length of the skull (Ostrom, 1969 b), while in Coelophysis it is probably slightly less than half the skull length as calculated from unpublished drawings kindly supplied by Dr. E.H. Colbert.

The presence of the "carnosaur pocket" on the pterygoid and ectopterygoid is shared by Syntarsus, Deinonychus, Dromaeosaurus and later carnosaurs, but Ostrom (1969 b) notes that it is absent from Coelophysis. The double-overlap articulation of the ectopterygoid with the pterygoid in Syntarsus seems to be a unique feature. It is suggested that this is associated with snout-tip mobility.

There are few descriptions of well preserved theropod braincases with which to compare *Syntarsus*. *Dromaeosaurus* (Colbert & Russell, 1969), is extensively co-ossified in this region, but there is a large measure of agreement between the descriptions of this form and of *Syntarsus*. The main differences lie in the greater width of the braincase of *Dromaeosaurus* and the fact that each branch of the Trigeminal nerve exits independently in this genus. Both forms have large and prominent floccular (or subarcuate) fossae in the otic region, those of *Syntarsus* being evidently somewhat more pronounced than those of *Dromaeosaurus* as judged from Fig. 7B in Colbert & Russell (1969). In both of these genera, and in *Ceratosaurus* (Gilmore, 1920) and *Stenonychosaurus* (Russell, 1969) the cerebral hemispheres lay directly above the pituitary fossa.

Colbert & Russell (1969) record a mesokinetic hinge in *Dromaeosaurus* between the frontals and parietals. In *Syntarsus* the kinetic hinges lie between the parietal and occiput, and at the frontal and nasal articulation (Fig. 32).

The exoccipitals of *Dromaeosaurus* are widely separated above the foramen magnum, whereas in *Syntarsus* they are in contact and the supraoccipital is isolated to a dorsal median position. *Coelophysis* retains postparietal fenestrae in the occiput while in *Syntarsus* this area is walled over by the parietal flanges.

The only noteworthy features in the mandible of *Syntarsus* are the configuration of the articular surfaces, and the fact that the external mandibular fenestrae are noticeably larger than those shown in unpublished drawings of *Coelophysis* supplied by Dr. Colbert. The articular cotyli are very similar to those of *Ichthyornis* figured by Gingerich (1972 : Fig. 2, compare with Plate 8 c) who notes that this genus has "paired oblique cotyli (which) differ from the transverse articular cotyli of mosasaurs and other reptiles". In contrast, the retroarticular process of *Syntarsus* is long, unlike *Ichthyornis* or *Deinonychus*, but resembling that of *Coelophysis*.

Syntarsus shows no signs of the dental asymmetry recorded in *Dromaeosaurus* (Colbert & Russell, 1969), and *Deinonychus* (Ostrom, 1969 b). Serrations are distributed on the anterior and posterior edges of the teeth, covering nearly all of the posterior erupted edge and about the apical $\frac{1}{3}$ of the anterior edge. However, the premaxillary teeth are unserrated.

Ostrom's (1969 b) comment that premaxillary-maxillary tooth counts may have specific or even generic significance is not supported by this study since it is seen that *Syntarsus* and *Coelophysis* are identical in this respect, *Syntarsus* tending only to be slightly more constant in the premaxillary count of four while *Coelophysis* evidently varies from four to five.

The length of the tooth row is very different in the two genera. In *Coelophysis* the upper tooth row is more than 60% of basal skull length (Table 2, but see Ostrom, 1969 b) while in *Syntarsus* it is only 45% (estimated) of basal skull length.

The ratios of skull height to skull length for several theropod genera have been recorded by Ostrom (1969 b) and are repeated here as percentages, with *Syntarsus* included for comparison :

Saurornithoides	24%
SYNTARSUS	27%
Velociraptor	29%
Coelophysis	32%
Deinonychus	34%
Ornitholestes	35%
Dromaeosaurus	40%

Gorgosaurus	40%
Allosaurus	47%
Tyrannosaurus	47%

The figure quoted for *Coelophysis* must be regarded as approximate since Colbert (in. litt.) has noted its remarkable variation in adult skull length.

In its close similarity to *Coelophysis* in most respects, *Syntarsus* is properly regarded as a "podokesaurid" (Ostrom, 1976 a, includes both genera in the Procompsognathidae). The variations noted in the comparison of the skulls of the two genera seem significant but no more so than is to be expected of distinct but related genera in the same family. *Syntarsus* is evidently more specialised in the skull than is *Coelophysis*. Regrettably no analysis is available of cranial kinesis in *Coelophysis*, but *Syntarsus* seems relatively advanced in this respect - particularly in terms of its suggested premaxillary mobility. Its retention of the lizard-like amphikinetic condition, on the other hand, is primitive. Specialization is also evident in the reduction in length of the tooth row, and the sharp flexure of the brain axis in the braincase, probably associated with cerebellar enlargement. In spite of these specializations, which must surely be associated with improved predatory abilities and associated refinements of posture and balance to improve agility, *Syntarsus* shows surprisingly little tendency towards binocular vision. The orbits, although large, are lateral, and the bowing outwards of the lachrymal/prefrontal area must have effectively denied frontal binocular vision.

VERTEBRAL COLUMN (EXCLUDING THE SACRUM)

Cervical vertebrae and ribs (Plate 11, 12)

The length of the neck of Syntarsus is augmented by "cervicalization" of a few anterior dorsals, and elongation of the mid-cervicals. At each end the neck is composed of vertebrae with short centra and the pronounced sigmoid flexion of the neck takes place in these areas through inclined articular faces on the centra. Centrum length increases progressively to the sixth cervical and then drops more sharply to the cervicodorsal transition (Fig. 8).

From the axis backwards the cervicals are strongly keeled ventrally, the keel fading in the cervicodorsal transition area from cervical 8. The mid-cervicals bear prominent pleurocoels and they are amphicoelous. The zygapophyses are elongate, the postzygapophyses extending back substantially beyond the zygapophyseal articular facets in what might be termed "epipophyses" (Ostrom, 1969 b). The axis and the cervicodorsals bear relatively high neural spines, but otherwise the cervicals are very low-spined.

In several cases, particularly in those specimens regarded as representing mature individuals, the scars of interspinous ligaments and other soft tissues are well marked.

Cervical ribs were certainly present from the third cervical, but there is some doubt about their presence on the atlas or axis since no clear articular facets can be found. The ribs articulate in a characteristically low position on the anterior rim of the centrum, and in mature animals the ribs fuse with the centrum. The ribs are exceptionally long and lie parallel to the axis of the neck. In several specimens they overlap at least the next two vertebrae behind and produce a lateral "bundle" of three or four slender rib shafts on each side of the midregion of the neck (Plate 11 d).

Atlas (Plate 12 a, b; Table 5)

The best preserved specimen (QG 176) is complete, although the individual components were found disarticulated, and it represents a mature animal.

The atlas intercentrum is wedge-shaped, bearing a bevelled surface which faces forward and upwards and which articulated with the occipital condyle. The hind surface is transversely slightly convex for articulation with the saddle-like articular face of the axis. It is outlined by a rugose rim which represents the margin of the articular capsule. The ventral surface is flattened and lacks a keel. Dorsolaterally the intercentrum bears a small depression on each side which represents the surface for articulation of the atlas neural arch. The lateral surface is rugose and this probably marks the origin of the rectus capitis anterior muscle. The neural arch is divided into separate left and right elements, each of which bears a dilated ventral end with a terminal elliptical facet for articulation with the intercentrum. Immediately above this articular pedicel the neural arch widens and thins into a curved short lamina protruding forward to articulate with the skull beside the foramen magnum. Rising relatively steeply behind the atlantal "prezygapophysis" the neural arch tapers to a sharp spur pointing dorsally and posteriorly. At midlength it bears the atlantal postzygapophysis on an elliptical prominence which is nearly vertical and faces in towards the midline. Although the thin medial margins of the atlas neural arches are damaged it seems unlikely that there was much in the way of dorsal roofing to the atlas complex, leaving the spinal cord rather unprotected by bone dorsally in the postoccipital region. The economy of bone and the lack of tight articulations in this area would favour a high degree of mobility of the head on the neck and the lack of a bony roof to the neural canal would pose no great threat to the nerve cord since the area is deeply buried below the occipital musculature and is further protected by the relatively high axis neural spine immediately behind.

The atlas centrum fuses with the axis in mature individuals to form an odontoid process, and for this reason it will be described with the axis.

Axis (Plate 12, c,d,e; Table 5)

The axis is short, its centrum being approximately twice as long as high, and it is sharply keeled ventrally. The anterior surface of the centrum in young individuals is characterized by a flat vertical surface immediately below the neural canal on which the odontoid (= atlas centrum) rests. Below the flattened area, which occupies slightly more than half the area of the anterior centrum face, the centrum is concave and the atlantoaxial intercentrum fuses with this surface in mature individuals. With the odontoid and atlantoaxial intercentrum in position the anterior face of the centrum presents a transverse saddle-shaped articular area bounded above by the odontoid and below by the sharp rim of the crescentic atlantoaxial intercentrum. This saddle-shaped surface articulates with the atlas intercentrum.

The odontoid itself has a flat dorsal surface forming part of the floor of the neural canal, and its anterior surface is rounded. Laterally it bears a shallow pit on either side which may have housed an atlantoaxial ligament.

The joint capsule is demarcated by a relatively wide rugose zone extending from the level of the lower part of the odontoid around the lower half of the centrum. At its upper end this rugose zone is interupted by a small depression on the lateral surface of the centrum which evidently represents the cervical pleurocoels present in the remainder of the cervical series.

The hind face of the axis centrum is concave.

The neural arch is fused to the centrum in mature animals, but the suture between arch and centrum is clearly visible in immature individuals. The prezygapophyses are elliptical surfaces on the neural canal lateral wall situated adjacent to the anterior margin of the arch. They are not borne on elongate processes and their articular facets face laterally and very slightly upwards.

The neural spine is tall, thin and blade-like, the highest point being towards the rear. Its dorsal outline is rounded and posteriorly it divides and drops to join the postzygapophyses which bear long epipophyses.

The postzygapophyseal facets are slightly concave. Their edges meet medially above the neural canal and they delimit a deep concavity above them which housed the point of attachment of the interspinous ligament.

The lack of any clear articular facets for ribs suggests that the axis was devoid of these structures, which would further enhance mobility of the skull on the neck.

Third cervical

Behind the axis the cervicals are essentially similar in that they are elongate, bilaterally compressed, low spined, variably amphicoelous, and bear cervical ribs as well as having long pre-and postzygapophyses. However the third cervical merits individual description because of its very pronounced difference in the angular inclination of the anterior and posterior faces of the centrum (Table 5). This is associated with the pose of the head on the neck and is of value in reconstructing the living posture of the animal (Fig. 35).

The third cervical is extremely waisted, to the extent that the centrum consists of little other than the articular faces connected by the keel, and the lower edge of the keel is a straight line. The anterior face is almost square because the parapophysis for the rib tuberculum lies near the lower lateral edge of the centrum, thus drawing it out into a corner on each side. This end of the centrum is only slightly concave, while the posterior face is deeply concave. The two articular faces are inclined on the centrum to different extents.

The neural arch is considerably shallower than that of the axis, and the neural spine consists of a uniformly low sharp blade between the bases of the zygapophyses.

The prezygapophyses are elongate and the large elliptical articular facets cover a large area of the dorsomedial surfaces of the protruding processes which reach well beyond the anterior end of the centrum. A thin lamina, which acts as a ventral buttress for the prezygapophysis, slopes down and back to lie beside the centrum as a nearly vertical wing. A short ventral spur from this lamina reaches almost to the parapophysis forming the diapophysis for the rib capitulum. The two rib articulations are narrowly separated and both lie very near the anterior edge of the centrum. Both are elliptical convexities. A deep pocket lies immediately behind the parapophysis on the centrum. The lateral lamina fades posteriorly. Below it on the centrum, partly protected by the diapophysis, is a shallow longitudinal pleurocoel.

Posteriorly the postzygapophyses protrude back and extend as the epipophyses, to produce a considerable overlap with the prezygapophyses of the succeeding vertebra. A shallow but relatively long lateral groove, which effectively marks the boundary between zygapophysis and epipophysis, probably carried a tendon associated with the cervical musculature. The area below the postzygapophysis is deeply embayed to accept the prezygapophysis of the next vertebra. The centrum bears another shallow elongate pleurocoel towards the hind end.

Mid-cervicals (4-7) (Plate 11 a,b; Table 5)

The mid-cervicals differ from the third principally in their greater length, less pronounced differences in the angular inclination of the anterior and posterior centrum faces, more pronounced posterior pleurocoels, more substantial mid portions of the centrum (although still sharply keeled), gently emarginate outline of the keel ventrally, and more pronounced downward sweep of the lateral arch lamina (or "transverse process") bearing the diapophysis, with an associated greater tendency for the cervical rib to fuse with the vertebra.

Vertebral length increases to the sixth, which is the longest (centrum nearly four times as long as high), and decreases thereafter.

Posterior cervicals (8-10) (Plate 11 a,c)

Abrupt changes take place after the seventh cervical which affect the length of the centrum (Fig. 8; Table 5), degree of waisting, and the whole appearance of the neural arch.

The seventh cervical is substantially longer than the eighth. The eighth bears a more robust centrum with a much reduced keel. The parapophysis still lies in the low, characteristically "cervical" position on the edge of the intervertebral joint capsule which is marked by pronounced striations and rugosities on the centrum divided laterally by short longitudinal grooves concerned with the neck muscles.

The neural arch of the eighth cervical is markedly shorter and higher than that of the seventh. The zygapophyses are relatively short and scarcely protrude beyond the centrum face. The diapophysis is elevated onto a transverse process similar to that of a dorsal vertebra, although it tilts down laterally, and it is supported by a system of buttresses below in the same way as in the dorsals. The postzygapophyses bear large facets which curve medially to produce incipient hyposphene-hypantrum articulations.

Flanking the neural canal immediately below the postzygapophyses are small ridges of bone whose function seems to have been to limit hyperflexion of the cervicodorsal transition zone. A small medial ridge forming the edge of the prezygapophysis of the preceding vertebra engages this posterior ridge as it slides down the postzygapophyseal facet in flexion, thus preventing "kinking" of the neck with the attendant threat to the nerve cord.

Most marked is the shortness and robustness of the neural spine, heavily scarred at its apex with rugose excrescences and similarly scarred and rugose on its anterior and posterior surfaces between the divergent pre-and postzygapophyses.

All of these changes are carried a stage further in the ninth and tenth cervicals which are recognisable as cervicals only because of their "cervical" parapophyses and their narrow and low neural spines.

The cervical ribs vary from the elongate and thin anterior elements with closely spaced capitulum and tuberculum and a short anterior spur to the more conventional "dorsal" type of rib in the cervico-dorsal transition area (Plate 13). Cervicodorsal ribs bear widely separated capitulum and tuberculum and the shafts are robust, relatively long and strongly raked or inclined posteroventrally, rather than lying along the vertebral axis, as do the anterior cervical ribs. Specimen QG 173, a juvenile, shows that the cervicodorsal ribs have enormous heads for the size of the animal (Plate 11 c). The extraordinarily large isolated ribs recovered evidently belong to this region (cervicals 9 and 10) of the axial skeleton of mature animals. Widely divergent capitular and tubercular facets would be required to articulate with the low parapophyses and high diapophyses characteristic of these transitional vertebrae.

With the migration of the parapophysis up the centrum on the succeeding dorsal vertebrae the rib head becomes less distinctly yoke-shaped, the articular facets become smaller and the tuberculum assumes the "shoulder-like flange" shape described in the type specimen (Raath, 1969: 5).

Dorsal vertebrae, ribs and gastralia (Fig. 9,10; Plate 13 ; Table 6)

It was suggested in the description of the holotype that *Syntarsus* had a presacral vertebral count of 23, consisting of 10 cervicals and 13 dorsals (Raath, 1969) as is commonly found in other theropods (Osborn, 1917; Gilmore, 1920; Colbert, 1964; Ostrom, 1969 b). No single specimen in the collection can prove this point, but detailed study of regions which overlap in several specimens now available tends to confirm the suggestion. The principal clue concerns the position of the parapophysis in relation to the centrum (of cervicals) or the transverse process (of dorsals).

In a recent redescription of *Allosaurus* it is reported that the transition from cervicals to dorsals is rather gradual, (Madsen, 1976) which conflicts with Gilmore's (1920) statement that the change is "abrupt". Madsen had access to a much larger series of specimens than Gilmore, and his statements can thus be regarded as more firmly based. Madsen's conclusion that *Allosaurus* (= *Antrodemus* Leidy) has only 9 cervicals and 14 dorsals does not really affect the argument as the total presacral count remains constant at 23, while cervico-dorsal transitional vertebrae might function equally well as "cervicals" or "dorsals".

The transition from cervical to dorsal is relatively abrupt in *Syntarsus* in that the last cervical (C10) has the parapophysis still in direct contact with the centrum while on the first dorsal it is lifted onto the neural arch clear of the centrum. Otherwise the first two dorsals resemble the last two cervicals in most respects : short centra; relatively high and narrow (anteroposteriorly) neural spines; swollen rugose apex of neural spine; flat anterior and posterior surfaces of the neural spine which bore the strong interspinous ligaments; and well developed transverse processes.

Centrum length increases, as does the anteroposterior width of the neural spine, from dorsal 3 backwards. The height of the neural spine remains almost constant in the dorsal series.

The narrowness of the neural spines on the first two dorsals is related to the apparent "cervicalization" referred to above, in that these two vertebrae are functionally part of the base of the neck where maximum bending takes place, and wide neural spines would obstruct such bending. A similar situation obtains in the "cervicodorsal" (= C10) of Deinonychus (Ostrom, 1969 b: Fig. 31), and this genus has a pronounced "goose-neck" pose.

Several juvenile specimens in the collection have disassociated centra and neural arches. Although Madsen's (1976) point is noted that the hormone relaxin might cause disarticulation in these and other normally coalesced bones in a reproductively active adult female, the size of the disarticulated Syntarsus vertebrae shows that they are from juveniles. The centroneural suture visible in these disassociated specimens is intricate. On each side the suture consists of closely spaced serrations, which interdigitate with their counterparts borne on the gently bowed up walls of the neural canal. The number of serrations per side varies between 15 and 20. At mid centrum length a deeper notch on each side of the neural canal interdigitates with a correspondingly large "tooth" in the middle of the neural arch. The mid notches in the centrum seem always to be associated with a pair of small tubercles in the wall of the neural canal, one on either side adjacent to the notch. The floor of the neural canal is also deepest at this point.

In all of the dorsal vertebrae the transverse processes are backswept, as described in the type (Raath, 1969). In the anterior dorsals the transverse processes lie almost horizontally, but from the sixth dorsal back they are tilted up at a slight angle. The anterior dorsals (D1 to D3/D4) bear the parapophysis on the side of the neural arch and they are situated near the front edge of the arch. From dorsal 4 back the parapophysis is borne on a short pedicel which is initially connected to the transverse process above it by a thin lamina of bone, but from dorsal 7 posteriorly it reaches the level of the transverse process and then migrates progressively outwards along the process as described in the type. Even in young, immature individuals the dorsal vertebrae show hyposphene - hypantrum articulations (Fig. 10) and the vertical faces of the centra show that there was very little flexion in the trunk region. The hyposphene - hypantrum articulations would tend to make the trunk function as a relatively rigid integrated arch.

Ribs and gastralia (Fig. 11; Plate 13,14)

Apart from remarking on size of the cervicodorsal ribs there is little to add to the description of the ribs previously given (Raath, 1969). There is little doubt that the ribs were raked back in the living animal, giving a slender thorax and trunk. It seems likely that the large cervicodorsal transitional ribs may have served as strong attachment points for some of the superficial muscles of the trunk, probably the serratus muscles in particular.

Although slender bony shafts regarded as representing gastralia have been recovered from the Chitake River deposits, complete ventral "baskets" have not been found,other than in the type (Raath, 1969) and nothing further can be added to the description previously given (Fig. 11; Plate 14).

Caudal vertebrae and chevrons (Plate 15, Table 7)

Many isolated caudal vertebrae have now been recovered, a large number representing immature animals with centra and neural arches dissociated. In these latter cases the isolated centra are readily recognised : cervical centra, apart from their utterly characteristic shape and proportions, are keeled ventrally; dorsal vertebrae lack any such ventral ornamentation or feature; and caudal centra are longitudinally grooved ventrally to guide the caudal blood vessels along the lower surface of the tail series.

The anterior caudals agree with the description of the first caudal of the holotype (Raath, 1969). One feature to be added to the description is the presence of hyposphene-hypantrum articulations between anterior caudal vertebrae. These articulations are lost by the mid regions of the tail.

The mid-caudal vertebrae are characterized by sharply uptilted transverse processes which protrude laterally, are not backswept, and which are broader distally than proximally (i.e. they flare laterally). The neural spines of the mid-caudals lie far back on each vertebra, almost directly above the postzygapophyses. The centra in this region are slightly procoelous.

Beyond the mid-region of the tail the vertebrae become elongated, mainly because of the reduction in diameter of the neural arch and a reduction in diameter of the centrum, rather than because of any elongation of the centrum. In fact, the centra actually decrease in length. The prezygapophyses are very long, and the postzygapophyses comparatively shorter. Along either side of the neural arch runs a longitudinal ridge which seems to represent the vestigeal remnant of the transverse process.

The terminal caudals are delicate, slender, long and almost devoid of processes except for vestigeal pre - and postzygapophyses. In <u>Syntarsus</u> the tail ends in a "whip-lash".

Chevrons (Plate 15 c)

Contrary to the statement in the description of the holotype (Raath, 1969), the chevrons of *Syntarsus* do, in fact, reduce progressively to terminal skid-like structures. It cannot be established in which region of the tail this occurs, but it seems that it might be in the terminal third of the tail. *Allosaurus* shows similar skid-like chevrons from a point just after mid-tail length (Madsen, 1976).

PECTORAL GIRDLE AND FORELIMB (Fig. 12,13,14; Plate 16,17, 18; Table 8)

Colbert (pers.comm.) has noted extraordinary variability in the length of the arm of Coelophysis. Although the length of Syntarsus arm elements does vary the variation is not excessive. The largest elements in the collection are up to 25% longer than the corresponding elements of the type. The most noteworthy forelimb variation in Syntarsus lies in the proportions and robustness of the bones. It is tempting to regard this as a brachial reflection of sexual dimorphism in the same way as the clear dimorphism of the femur described later. That this seems to be so is shown by the holotype, whose humerus is "robust" and it is associated with a very clearly robust femur. It appears that robustness of the humerus, which is a consequence mainly of strong muscle scarring, is a function both of age and of sexual characteristics in much the same way as is true of the femur.

Scapulocoracoid (Fig 12; Plate 16; Table 8)

Fusion of the scapula and coracoid, which was noted in the type (Raath, 1969), is evidently a function of age. Several specimens show a clear suture between the two elements, and others which are clearly juvenile show that the two bones were easily dissociated postmortem. In articulated specimens the junction of scapula and coracoid on the edge opposite the glenoid is fragile and usually damaged, but it seems likely that a shallow notch marked this position. None of the new specimens shows the presumed "suprascapula" described in the holotype (Raath, 1969), and it seems that this was an artifact of distortion.

The coracoid bears a relatively small coracoid foramen which passes obliquely from the lateral surface to the medial surface.

It is situated in the middle of the coracoid plate near the scapulocoracoid suture, and runs dorsoventrally on its path through the coracoid.

Ahead of the glenoid, on the lower posterior edge of the coracoid lateral surface, there is a pronounced tubercle (Fig. 12) in all specimens including juveniles. The tubercle defines the front boundary of a small, concave, posterolaterally facing rugose facet which lies between the tubercle and the glenoid. This corresponds in position with the "biceps tubercle" of Deinonychus (Ostrom, 1974 a) and its function will be considered in the section on forelimb musculature. In the type description this tubercle was described as : "......a slightly rugose elliptical surface which lies at the lower posterior end of the coracoid" (Raath, 1969 : 7). The scapulocoracoid is regarded as having been suspended almost horizontally in life (see section 6 and Fig. 34).

Humerus (Fig. 13; Plate 16, 17)

The principal variations affecting the humerus concern the development of the deltopectoral crest, the breadth of the head and distal condyles, and the degree of muscle scarring. Some specimens are short and blocky, with a broad head, broad distal condyles, large deltopectoral crest and heavy muscle scars, while others are long, slender and almost devoid of scars. The humerus of juvenile specimens is especially gracile while the humerus of the holotype is robust.

Presuming that the broad-headed, robust elements represent an exaggerated condition over the normal, they are used here to refine the description given by Raath (1969).

The broad head (Fig. 13, Plate 17) is particularly thickened in the medial half, which is evidently the main articular region.

Medial to this area is a shallow notch let into the corner, which is itself bordered medially by a rugose rounded tubercle.

The head thins laterally and joins the deltopectoral crest which runs down the lateral side of the bone and ends abruptly halfway down the shaft. The distal half of the deltopectoral crest has an apical thickened rim which is rugose for muscle insertion. Various other scars of muscle origin and insertion are evident on both the palmar and anconal surfaces of the humerus and an account of these scars together with the muscles concerned will be given in the section on forelimb musculature.

"Robust" humeri have the distal condyles for the radius and ulna starkly outlined by a rim, and well finished in smooth bone.

Two nutritive foramina can be seen in the humerus, one proximally on the anconal surface just below the medial tubercle (in a position very similar to the pneumatopore of the avian humerus) and the other on the medial surface of the humerus shaft opposite the end of the deltopectoral crest.

Radius and ulna (Fig. 14)

The radius bows out consistently in all specimens available for study. This gives the forearm considerable girth and also allows for the pronation which characterizes the normal position of the wrist. The capacity for supination seems to have been limited by the nature of the antebrachial articulation on the humerus.

The proximal end of the radius is held in a shallow depression on the lateral surface of the ulna immediately in front of the olecranon.

The ulna varies in its degree of development of the olecranon process, most specimens having it very well developed, deep and robust, and others having almost no recognisable olecranon.

None of the specimens now in the collections can confirm the true nature of the bone described as the "flexor sesamoid" at the carpus of the type (Raath, 1969). Its proper identity and relationships must therefore remain uncertain for the present.

Carpus and manus (Fig. 14; Plate 18)

A few isolated small discoid bones have been recovered which are probably carpals, the only ones confidently identifiable being two radiales. These two bones (Fig. 14) confirm the peculiar crescentic nature of the radiale in the carpus of the type (see especially Galton, 1971: Fig. 3I,J). The carpus of the type is slightly damaged and it is therefore not possible to clarify precisely the carpal structure at this stage. Gilmore (1920) reports that *Antrodemus* (= *Allosaurus*) has five or six carpals. *Syntarsus* seems to have six (Raath, 1969). Galton's (1971) statement that the carpus lacks well defined articular surfaces proximally is not supported in the light of the new material, at least as far as the radiale is concerned. This bone is smoothly concave proximally and convex distally where it articulates with the large convex bone representing fused distal carpals I and II. The implication is that the wrist was capable of substantial movement on the ends of the radius and ulna. However, because of the inclination of the articular surfaces of these two bones towards the flexor surface, Galton is probably correct when he suggests that the wrist was not capable of much extension, and that hyperextension of the digits compensated for this weakness (Galton, 1971). Furthermore it appears that *Syntarsus* was capable of only limited intracarpal movement, and that the major articulation between forearm and hand was epicarpal, as noted by Madsen (1976) in *Allosaurus*. Raath (1969) reported that the type specimen of *Syntarsus* was preserved with the hand strongly flexed on the forearm.

There is little to add to Galton's (1971) redescription of the manus, except to draw attention to the fact that the subterminal phalanges of each digit are the longest. This seems to establish a trend in Triassic coelurosaurs which is also seen in Ornitholestes from the upper Jurassic (see Osborn, 1917: Fig. 3) and reached an extreme in the Cretaceous Struthiomimus. Apart from the specialisation of its enormous claws, the same is true of the enigmatic theropod Deinonychus from the early Cretaceous (Ostrom, 1969 b: Fig. 63) which seems to combine so many features characteristic of both coelurosaurs and carnosaurs.

PELVIC GIRDLE AND HINDLIMB (INCLUDING THE SACRUM) (TABLES 9, 10)

The specialisation in the hindlimb constitutes one of the most notable features of Syntarsus and the genus was in fact named on the basis of one particular specialised feature reported in the type, the fusion in the tarsal region (Raath, 1969). In discussing the type it was conceded that the discovery of other specimens might demolish the taxonomic significance of this feature (Raath, 1969 : 22) and this prediction has been largely borne out by the Chitake River discoveries. However, while apparently losing its significance as a diagnostic feature of the genus, it has assumed a new significance. Colbert has commented on the variable degree of skeletal fusion in Coelophysis (cited by Raath, 1969), which he thought might reflect adult sexual dimorphism. The evidence offered by the new material seems to demonstrate such dimorphism beyond doubt for Syntarsus, although the functional significance of the two main variants remains far from clear.

There is unequivocal evidence of bimodal variation in the femur (Fig. 15, 16, 17; Plate 22, 23; Table 9), but the situation as it affects other limb elements is not so clear. Reference has already been made to similar variation in the humerus. It is possible that variation seen in the pelvis (involving broader and narrower variants) might be linked to femoral dimorphism, but insufficient specimens are available with the critical bones articulated to decide the question.

Sacrum and pelvis (Fig. 17; Plate 19, 20; Table 10)

Several specimens in all states of preservation, from fragmentary to perfect, are now available for study. Some represent mature adults with the bones firmly fused together (Plate 19 a) while others represent immature individuals in which the bones are dissociated (Plate 19 b).

Mature pelvises confirm the general description given for the holotype (Raath, 1969). In front of the acetabulum the first two sacral vertebrae are simple and very like the posterior dorsals. They lack complex sacral ribs and retain relatively simple blade-like transverse processes. The centra fuse together on maturity and there is a corresponding but variable tendency for the transverse processes and neural spines to coalesce into continuous sheets of bone running the length of the sacrum. Fused sacral neural spines are invariably topped by a longitudinal swollen rim along the length of the continuous blade.

The hind sacrals (3, 4 and 5) are more complex and contribute to the peculiarly constructed hind sacrum described in the holotype, where the continuous dorsal "roof" (formed by fused transverse processes) covers deep ventral intervertebral pits visible only from below. These pits represent the spaces between the true sacral ribs which fuse together in complex fashion, giving great rigidity and strength to the girdle behind the acetabulum.

Isolated hind sacral centra of juvenile specimens show the large scars for articulation of the sacral ribs at the anterior and posterior corners of the centrum, leaving smooth, curved lips between them on each side which serve as the exits for lateral nerves (Plate 20). The characteristic sacral rib scars on these centra identify them immediately and they are very closely comparable with the sacral centra of true carnosaurs such as <u>Allosaurus</u> (Madsen, 1976 : Plates 24-28). The isolated juvenile centra also show that the lumen of the neural canal varies within the sacrum, being wider in sacral 4 than in sacral 5. This is presumably related to incipient development of a sacral neural swelling or plexus so characteristic of ornithischians and sauropods and which inspired the much-quoted verse by Bert L. Taylor :

"..... You will observe by these remains
The creature had two sets of brains
One in his head (the usual place),
The other at his spinal base.
Thus he could reason a priori
As well as a posteriori......"

The pelvis itself is remarkably constant in shape, but the availability of isolated elements now enables each pelvic element to be examined in detail.

The front border of the ilium does not end in a gentle rounded curve as figured by Raath (1969 : Fig. 4). Instead, the lower part of the front border projects forward slightly and is also very slightly reflected. In this respect the ilium is reminiscent of that of tyrannosaurids (Plate 19 b, cf. Osborn, 1917 : Plate XXVII). Lateral flaring of the ilium behind the acetabulum varies. The majority of pelvises from mature adults are broadly flared as in the type, while others are more slender. Whether this reflects true dimorphism or is simply a result of individual variation or compression is not possible to state at this stage of the study. Juveniles tend to show narrow pelvises with relatively unflared ilia. The hood-like roof over the acetabulum is consistently well developed in both juveniles and adults. In this respect, and in respect of the flaring of the ilium referred to above, Syntarsus evidently departs quite markedly from Coelophysis (Colbert, pers. comm.), but compares quite well with Elaphrosaurus (Janensch, 1925 and Fig. 34).

On the medial surface of the ilium, which was not available for study in the type specimen because of extensive fusion, there are few features except for scars associated with the articulation of sacral ribs and transverse processes (Plate 19c). The finely striated scars of muscular aponeuroses and other connective tissues are also visible on both the inner and outer surfaces of the ilium, even in juveniles.

Disarticulated immature pelvic elements also offer an opportunity to study the details of articulations between ilium, pubis and ischium. The pubic peduncle of the ilium terminates in a double-socket arrangement in which an upper concavity faces anteroventrally, while the lower faces ventrally. The two sockets are separated by a transverse ridge. The corresponding surface of the pubis is reversed in that two convexities articulate in the sockets and a groove accepts the ridge from the ilium. The effect on articulation is to provide a coarse interdigitation which provides a strong joint yet is loose enough to permit growth.

The ischiadic peduncle is less complex. It consists of a single concavity in the lower posterior surface of the ilium whose anterior lip projects down as a spike. The corresponding surface of the ischium bears a deep socket which accepts the iliac spike while its hind border projects to fit snugly into the socket on the ilium. The ilium-ischium articulation contributes to the formation of the flattened projecting facet in the hind wall of the acetabulum which interrupts its otherwise circular outline. This facet might be termed a "pseudoantitrochanter", since it articulates with a "pseudotrochanter" on the femur (Fig. 17) both of which appear to be analogues (or, perhaps, even homologues) of the comparable structures in birds.

The articulation of the pubic and ischiadic portions of the puboischiadic plate below the midpoint of the acetabulum is a relatively simple, sinuous, edge-to-edge union.

The pubis unquestionably bears two perforations in the puboischiadic plate, as shown in the type (Raath, 1969 : Fig. 4). The upper perforation is much smaller and elliptical, while the lower is large and subcircular (Plate 19). The distal end of the pubis bears no great expansion or foot, and is merely gently rounded off.

The ischium consistently shows the small backward spike on the puboischiadic plate, figured by Raath (1969 : Fig. 4), which is very like a similar projection in the ischium of Allosaurus (Madsen, 1976: Plate 48). The distal end of the ischium is moderately dilated and rounded, but is flat on the medial surface where it contacts its fellow.

Femur (Fig. 15, 16, 17, 18; Plate 21, 22, 23; Table 9)

The wealth of femoral material now available and the absolutely clear and consistent dimorphism of this bone demands a reconsideration and amplification of the description given by Raath (1969). Femora are consistently either "gracile" or "robust" (Fig. 15; Plate 22). The femur of the holotype represents a robust specimen. The two types are differentiated on the following grounds :

	Robust		Gracile
1	Greater trochanter bulbous and rugose	1	Greater trochanter flat and smooth
2 *	Lesser trochanter broad and shelf-like	2	Lesser trochanter narrow and crest-like
3	"Obturator Ridge" present in association with "pseudo-trochanter"	3	"Obturator Ridge" absent
4	Posterior femorotibialis region outlined by heavy scar	4	Posterior femorotibialis region not scarred

5	Insertion pit for caudifemoralis brevis crescentic, rugose, short and sharply rimmed	5	Insertion pit for caudifem. brev. elliptical, smooth, elongate and not sharply rimmed
6	Distal patellar ridge rugose, not sharp.	6	Distal patellar ridge smooth and sharp-edged.

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* It should be pointed out that this trochanter was wrongly identified as the "Greater trochanter" by Raath (1969). See Fig. 15 for an explanation of the trochanteric development in *Syntarsus*.

The lesser trochanter of gracile femora is very similar to the lesser trochanter of *Allosaurus* (Madsen, 1976 : Plate 50) and *Ceratosaurus* (Gilmore, 1920 : Fig. 64). The recently discovered femur of *Deinonychus* shows a peculiar development of a "posterior trochanter" high up on the posterolateral surface of the femur which Ostrom (1976 a) believes was the insertion of a powerful and specialised ischiotrochantericus muscle. *Deinonychus* apparently lacks a fourth trochanter (Ostrom, 1976 a).

All of the specializations in the two femoral variants of *Syntarsus* appear to be related to muscle development, the robust forms being substantially more muscular than the gracile forms. This raises questions of function which will be pursued below in the section on locomotion.

The gracile-vs-robust differences hold good irrespective of size in mature individuals (Fig. 16; Table 9). No robust forms are known amongst the femora of juveniles, which is to be expected if the specializations are associated with secondary sexual characters which would only develop and manifest themselves in animals reaching maturity.

In the description of the holotype it was noted that the medial border of the head of the femur is slightly downcurved at its lower end (Raath, 1969 : 16). This downturned "hook" is now known to be part of a posteriorly reflected groove which traverses the head dorsoventrally on the posteromedial surface. In the section on hindlimb muscles it is suggested that the medial hook and the dorsoventral groove are associated with ligaments and capsular tissues in the acetabular joint capsule. Deinonychus has an identical feature on the femur (Ostrom, 1976 a).

On the anterior surface of the femoral shaft, lateral to the caudifemoralis brevis insertion pit, is a nutritive foramen which receives a branch from a shallow groove running down the apex of the anterior surface of the femur for more than half its length distally (Fig. 15). It is presumed that this groove carried a branch of the femoral artery. The only noteworthy addition to the description of the distal end of the femur is the fact that the patellar surface, which carried the large combined crural extensor tendon, is bordered medially by a sharp rim (sharper in gracile femora than in robust) and the medial surface of the femur in this area is a concave sweep lying above the medial condyle. This curved depression might have provided the distal area of insertion of the adductor femoris muscle.

Tibia, fibula and tarsus (Plate 24, 25, 26; Table 10)

The fusion in the tarsal region described in the type (Raath, 1969) is now known to be variable (Plate 25). In general, smaller individuals do not show the fusion of astragalocalcaneum to the tibia, and the astragalus and calcaneum themselves - although clearly always tightly fitted together and functionally united - are not necessarily co-ossified.

Juveniles have a distinct circumferential groove around each end of the long bones suggesting the possession of growth epiphyses.

A juvenile right tibia (QG 691) demonstrates all of the essential features of tibia construction and also gives new information on the articulation of the tibia and proximal tarsals prior to fusion in adults (Plate 26).

The bone is slender, anteroposteriorly slightly flattened over most of its length beyond the cnemial crest, and noticeably bowed out towards the fibular side. The head is flattened and smooth on the medial surface, and the cnemial crest is strongly reflected laterally - i.e. towards the fibular side. This produces a hook-like appearance of the cnemial crest when viewed from above and the bone surface in the concave face of the hook is smooth and polished. It is suggested that the ambiens tendon rode in this trough on its course across the knee. The front face of the cnemial crest, which rises slightly above the level of the tibial condyles, forms a relatively broad tuberosity and curves outwards in the parasaggital plane. The "triceps femoris" (= iliofemoralis, sartorius and ambiens muscles) plus the femorotibialis inserted onto the tuberosity so formed. The inner tibial condyle lies slightly higher than the outer, but otherwise the two are comparable in dimensions.

A short distance distal to the head on the lateral side a very narrow flange arises and runs distally for a few centimetres. The proximal end of the fibula is retained behind this flange in articulation.

The distal end of the tibia which articulates with the astragalus (and partly with the calcaneum) is notched to receive the astragalus ascending process. The notch is excavated from the anterior side and is triangular in shape, deepest laterally and shallowing medially.

The posterior face of the tibia is plain distally and it protrudes further laterally than the anterior face. It is this small lateral protrustion that articulates in a short extension of the astragalar groove onto the calcaneum.

The distal end of the tibia cannot be considered adequately without including a discussion of its articulation with the tarsus. The description of the type tarsus (Raath, 1969) errs in exaggerating the "interlocking" of the tibia with the astragalocalcaneum. The lower end of the tibia does not lie as deeply embedded in the astragalus as indicated in the figure (Raath, 1969 : Fig. 6), nor does the ascending process of the astragalus engage the tibia in quite so well-defined a groove (Plate 26 e). The loose tarsal elements now available, together with the juvenile tibiae, show that the astragalus, with calcaneum loose in juveniles and fused in mature specimens (Plate 25, 26) is practically identical with that of Coelophysis (cf. Welles & Long, 1974 : Fig. 2). On a visit to Flagstaff in 1970 I had the opportunity to examine a few tarsi of Coelophysis with Dr. E.H. Colbert, and was forcibly struck by the similarity of structure between that genus and Syntarsus. Perhaps the major noticeable difference is a tendency for the ascending process in Syntarsus to be transversely broader than in Coelophysis and not quite so spike-like. However, this might well be accounted for by individual variation within each of the genera, as we did not examine a series of each sufficient to clarify any such details. The series of Syntarsus astragali now available shows some variation in this respect but spike shapes are rare.

Using the criteria of Welles & Long (1974 : Table on p.193) a dissociated juvenile astragalus and calcaneum (QG 816) gives the following values :

Height : breadth ratio (astragalus + calcaneum)	54
Height : breadth ratio (astragalus only)	62
Dip of medial edge of ascending process	ca.24°

It should be noted that the dimensions quoted for Syntarsus by Welles & Long (1974 : 193) do not agree with those given by Raath (1969 : Table 10), which would have a considerable effect on the indices they calculate for this genus. The values obtained from QG 816, however, do not alter their categorization of the Syntarsus tarsus as "Ceratosauroid" (Welles & Long, 1974).

The separate astragalus is deeply grooved behind the ascending process to form the cotylus housing the tibia. The cotylus has two main depressions, a smaller medial one which slopes down slightly to the flat medial side and a larger lateral one which continues for a short distance onto the inner posterior surface of the calcaneum. The front wall of the lateral cotylar depression is almost vertical, rising up to the apex of the ascending process which lies opposite the deepest part of the lateral cotylar depression.

In unfused tarsi only two distal tarsal bones exist, one being the characteristic and ubiquitous distal tarsal 4 figured by Raath (1969 : Fig. 6 b) and the other a central element which articulates predominantly with metatarsal III (Fig. 19; Plate 26) and is identified as distal tarsal 3. Fused tarsi retain only distal tarsal 4 as a free element, and distal tarsal 3 is fused to the lower proximal end of metatarsal III, with a related tendency for the proximal ends of metatarsals II and III to fuse as recorded in the type (Raath, 1969).

Ostrom (1969 b) records two free distal tarsals (III and IV) in Deinonychus, and Madsen (1976) the same number in Allosaurus.

On reaching maturity, substantial fusion evidently takes place between the crus, tarsus and metapodials of Syntarsus, as described in the type (Raath, 1969). Generally, fusion in the tarsal region is to be seen in large individuals which bear heavy muscle scarring. Whether the fusion is merely a function of age, or is related to sexual dimorphism, cannot be clarified at present. That the type specimen shows tarsal fusion, yet is not amongst the largest of the specimens available for study, suggests that fused tarsi and robust femora go together.

The fibula, as noted above, does not articulate exclusively with the calcaneum but wraps around part of the tibia distally and also just shields the lateral edge of the astragalar ascending process (Plate 26 a).

Pes (Fig. 19, 20; Plate 27)

The proximal metatarsal profile is shown in Fig. 19 a. Metatarsal III is the deepest and metatarsal II and IV wedge in on either side to produce a compact metapodial unit proximally. The proximal part of metatarsal III, on which rests the flattened tarsal 3, projects below the plantar plane of the metatarsus forming a robust central boss (or "hypotarsus") for metatarsal extensor tendon insertion (Fig. 19 a). Metatarsal V, although splintlike and reduced, is robustly constructed and scarred from the insertion of stressed tissue, and it is thought that its protrusion from the proximal end of the metatarsus (via the notch in distal tarsal 4) served as an analogue of a "calcaneal tuber" in that it acted as an additional extensor lever on the foot.

Metatarsals II and IV are slightly curved so as to diverge from the central toe distally, and their articular surfaces are somewhat rounded to enhance the capacity for toe-splay recorded by Raath (1969; 1972). That of digit IV seems to permit a wider (but variable) angle of splay than digit II.

The small articulated pes QG 164 (Plate 27) confirms the general structure of the foot described in the holotype (Raath, 1969; and Fig. 20). Digit I could not have touched the ground in life in the steeply digitigrade or "gralligrade" (Smith, 1967) pose of the animal. The presence of a well developed abductor tubercle at the proximal end of phalanx Ii in mature specimens, (Fig. 20) as well as the rounded articular surface of the metatarsal, suggests that this small digit retained a specialised function in life. Its use as a grooming accessory seems quite feasible.

All phalanges, except those of digit I, bear crescentic depressions distally on their upper surface which function to limit hyperextension of the digits.

Claws from the pes are readily distinguished from those of the manus by their flatter, much less trenchant curves and their flattened plantar surfaces. Their flexor tubercles are also less bulbous than in the claws of the manus.

BONE HISTOLOGY (PLATE 28)

Thin sections of several Syntarsus bones were prepared for microscopic study, three of which are shown in Plate 28, two being transverse sections and one a longitudinal section (all of the tibia). Other specimens were submitted to Dr. A. de Ricqles of the University of Paris for section and study. I am grateful to Dr. de Ricqles for the following report :

> "I have had time to study only the largest bone - femur diaphysis. Bone histology is well preserved.
>
> There is a clear contrast between the dense cortex and the medullar part of the bone : in fact the medullar cavity is hollow and seems to be completely devoid of bony trabeculae. In this respect the bone structure is not unlike what is found in birds and pterosaurs, as well as many mammals, very unlike crocodilian bone and, with the strong thick cortex, would distinctly point towards a good and firm adaptation to fully terrestrial habits. Only a small amount of endosteal bone lines the periphery of the medullar cavity. This would indicate that - at least at this transverse section - centrifugal erosion related to overall bone growth in width was beginning to slow down or stop. This suggests in turn, that the animal had already completed most of its growth.
>
> The cortical bone tissue is very homogeneous. It is entirely built of variations of "fibro-lamellar" tissues, with very abundant vascularization. The tissue is mainly of a plexiform pattern but, in some places, it gradually changes into a less orderly reticular pattern. Those patterns are well known among archosaurs.

A reticular pattern is often found among pterosaurs, while sauropods and theropods often show plexiform bone (see, for instance, Madsen (1976) on Allosaurus). There is no evidence at all of any kind of cyclical deposition. On the contrary, the whole thickness of the cortex seems to have been deposited in a continuous, non-stop process. Evidence from modern mammals indeed demonstrates that plexiform and similar patterns of bone are deposited continuously and quickly. There is some Haversian substitution within the cortex, with formation of "Haversian systems" or secondary osteones, but this process is very weak.

The general structure of the cortex would indicate that this animal enjoyed fairly rapid and continuous (not cyclical) growth. There are some indications of changes in the rate of bone deposition at the periphery of the cortex, so growth was possibly still active. Again, the poor amount of Haversian substitution would suggest that the individual's age was possibly rather low.

All-in-all, comparative histological data suggest to me that this animal was fully terrestrial, enjoyed rapid, continuous growth which was still just active at the time of its death and that it was, for all these reasons, a "subadult" individual, not yet fully grown. Its pattern of bone, as indicated by the primary bone tissue in the cortex, is found in the modern world among endotherms only, such as ostriches and artiodactyls. It is thus my opinion that histological data are accordant with the interpretation that Syntarsus had the same pattern of growth and dynamics as are seen in those animals, and, for this reason, was possibly also an endotherm like those modern animals".

The tibial sections illustrated here (Plate 28) support most of de Ricqles' conclusions, particularly with regard to the fibro-lamellar and dense pattern of vascularization. However, several sections of bones, notably of the tibia (Plate 28 c), ribs and metatarsals, show a surprising degree of osteoporosis, always near the endosteal margin in those tibial sections which show it (See discussion on p. 202). Also, several sections show a variable degree of peripheral lamellation, both at the periosteal and endosteal margins. In a few cases, especially the tibia, there are more or less concentric rings within the cortex. The possible significance of these features is discussed below in the section on physiology.

5. ASPECTS OF THE SOFT ANATOMY OF SYNTARSUS

Many of the bones show such clear indications of parts of the soft anatomy of Syntarsus that it was considered essential to attempt to reconstruct these tissues in relation to the skeleton. The indicators consist of muscle scars, striations associated with fascias and aponeuroses, grooves and foramina transmitting nerves and vascular vessels, and, of course, the endocranium yielding information on the brain.

CRANIAL SOFT ANATOMY

An endocranial cast and the brain (Fig. 21; Plate 29; Table 11)

Specimen QG 193 permitted an incomplete endocranial cast to be taken in silicone rubber. It is incomplete in that its limits in the orbital region are unknown since the brain was not enclosed by bone in these parts. However, the entire roof of the endocranium and the floor from the pituitary fossa backwards are known, thus giving an indication of the size and shape of the brain (Plate 29; Table 11). From this cast an attempt has been made to reconstruct the brain itself (Fig. 21).

The most notable feature of the whole brain is its strong flexure into an angular sigmoidal shape. The result of this is that the cerebral hemispheres come to lie directly above the pituitary, the optic lobes are displaced ventrally, and the cerebellum stands erect, partly covering the midbrain and the medulla.

Flexure of the Syntarsus brain is just as pronounced as that in the brain of Ceratosaurus (Gilmore, 1920: Plate 36 (1, 2)).

The QG 193 brain cast (delimited, for the purposes of this discussion, by the foramen magnum posteriorly and the anterior end of the olfactory bulbs anteriorly)has the dimensions given in Table 11.

The olfactory bulbs are long and thin, and the impressions of the Olfactory nerves in the lower surface of the frontals indicate that they were moderately large, as is also true of the olfactory tracts running back from the bulbs to the cerebral hemispheres. The latter taper forwards to join the olfactory tracts, and fill the endocranial roof. Flanking the cerebral hemispheres and olfactory tracts on either side are traces of a small cranial blood vessel - probably a branch of the internal carotid (? ethmoid artery).

A shallow depression on the inner surface of the laterosphenoid marks the position of the optic lobes of the midbrain, which are displaced ventrally and laterally from their more normal position in reptiles.

The large and prominent auricular lobes of the cerebellum (Fig. 5 d) lie above the level of the dorsal surface of the medulla and behind the optic lobes, indicating that the cerebellum was enlarged and probably erect, occupying the hind part of the endocranium. Shallow bilateral bulbous prominences in the parietals at the hind end of the skull roof delimit the posterior ends of the cerebral hemispheres, the upper curves of the optic lobes and the dorsal limit of the cerebellum behind the cerebral hemispheres.

The medulla is sharply flexed in the region of the midbrain-hindbrain transition, so that the Trigeminal nerve arises at a level somewhat higher than the more posterior cranial nerves. The root of this nerve is very stout, and is rivalled in size only by the Olfactory and Optic nerves. The root of the Facial nerve lies below and behind the Trigeminal on the lateral surface of the medulla.

A low and oblique ridge on the lateral wall of the medulla marks the position of the vagal fissure which transmits the Glossopharyngeal, Vagus and Accessory nerves, although the roots of each are not individually identifiable in the ridge.

On the dorsolateral surface of the medulla near the foramen magnum, a nerve root marks the origin of the Hypoglossal nerve which divides into three branches on its way through the braincase wall.

On the ventral surface of the medulla, in the region of the vagal fissure, a pair of ridges runs forward tracing the course of the Abducens branches which climb the hind wall of the pituitary fossa and enter it via twin foramina.

Little can be said of the pituitary itself since only the floor and hindwall of the fossa were ossified. Judging by the size of that part of the fossa which is preserved it must have been relatively large, and it must have borne a long stalk joining it to the diencephalon.

The roughly trimmed endocranial cast, truncated at its exit from the foramen magnum and just in front of the cerebral swellings displaces 10 ml of water. It is not possible to determine in detail the extent to which the brain filled the endocranium, nor, consequently, the amount of dura mater which cushioned the brain. The impression of the blood vessel traces in the frontals, lateral to the cerebral hemispheres, together with the smooth but distinct concavities indicating clearly the positions of such structures as the optic lobes, Gasserian ganglia, auricular lobes, and Abducens nerves suggest that the cavity was well filled with brain tissue.

The cerebellar region, however, suggests the presence of a considerable amount of dura mater since it seems doubtful that cerebellar tissue would have occupied the very narrow space from behind the level of the auricular lobes to the occipital wall.

Comparison of the brain with other forms

In comparing the brain of *Syntarsus*, dinosaurs and the surviving archosaur derivatives feature prominently in the reckoning. The crocodiles show few advances over what might be termed a "typically reptilian" brain but such advances as are present suggest development along lines comparable with those which ultimately produced the brain of modern birds (Edinger, 1951). The crocodilian brain shows minimal flexure; the optic lobes occupy a dorsal position; the cerebellum is not enlarged and it bears small flocculi or auricular lobes; on the other hand, the olfactory bulbs are well developed (Colbert, 1946 : Plates 14, 15).

Hadrosaurs have an almost crocodile-like brain which is "typically reptilian in form" (Ostrom, 1961), and shows little flexure.

Amongst the theropods endocranial casts are known in several genera (Colbert, 1962 b) and the cast of *Ceratosaurus* from the Jurassic Morrison Formation shows several features which are comparable with those of *Syntarsus* (cf. Gilmore, 1920 : Plate 36). Here the cerebral hemispheres are clearly better developed than in *Syntarsus*. The olfactory bulbs are enormously developed. There are indications of a similar narrowing to a thin ridge in the cerebellar compartment behind the large auricular lobes, and thus the cerebellum might also have been erect in *Ceratosaurus*.

Russell(1969 : Fig. 3) shows a reconstruction of an endocranial cast of *Stenonychosaurus* from the Late Cretaceous of Canada. This also bears a close similarity to the brain-cast of *Syntarsus* in dorsal view except that the cerebral hemispheres of *Stenonychosaurus* show greater transverse enlargement, and the cerebellar region is not so narrow posteriorly. The optic lobes are clearly displaced laterally and ventrally. *Stenonychosaurus* retains well developed olfactory bulbs, and, like Syntarsus, preserves traces of the lateral blood vessel running from the region of the olfactory bulbs to the cerebral hemispheres.

Regrettably, the endocranium is unknown in the closely related Coelophysis (Colbert, pers. comm.) because of extreme crushing of all the material examined so far.

Several of the noteworthy features of the Syntarsus brain (viz. flexure; size of auricular lobes; erect cerebellum; ventrolateral displacement of optic lobes) are reminiscent of similar features in the brains of birds. Edinger (1951) points out than an "avian shape" of the brain also developed in the other flying branch of the archosaurs, the Pterosauria, and she cites the following as avian features: cerebrum larger than any other portion of the brain; well developed cerebellum which is lobulated and in contact with the occipital wall of the braincase; ventrolateral displacement of the optic lobes; sharp flexure of the brain axis in marked contrast to the crocodilian or other reptilian brain. In some of these features the Triassic Syntarsus has evidently not yet reached a truly avian grade in that its cerebral hemispheres are not greatly expanded and its cerebellum was probably not in direct contact with the occipital wall. The degree of lobulation, if any, cannot be determined. It therefore becomes highly desirable to compare the brain of Syntarsus with the brains of fossil birds, but such a comparison is largely frustrated by few and equivocal specimens representing the fossil birds.

Edinger's (1926) study of Archaeopteryx led her to conclude that although the cerebrum filled its cavity the optic lobes still occupied a dorsal position and the cerebellum did not overlap the optic lobes as in later birds. On the other hand, in a more recent study, Jerison (1968 : 1381) concludes that the brain is "clearly avian in external form and intermediate between bird and reptile brains with respect to size", and shows that the cerebral hemispheres were enlarged and that the optic lobes were displaced ventrolaterally. Although the endocranium of *Archaeopteryx* is visible with any clarity only in dorsal view, and thus flexure cannot be observed directly, displacement of the optic lobes suggests that the brain axis was flexed in a manner comparable with *Syntarsus*.

Jerison's (1968) study of the brain of *Archaeopteryx* now establishes that a Triassic coelurosaur (*Syntarsus*) had a brain already essentially like that of the Jurassic *Archaeopteryx*, a form long regarded by many avian systematists as the "oldest certain bird" (Brodkorb, 1971).

Edinger (1951) re-assessed the material available for study of the brain characteristics in the Cretaceous birds *Hesperornis* and *Ichthyornis* and showed clearly that Marsh's (1880) claim that the brains were "reptilian" is spurious. Indeed, both genera had brains which were essentially avian. In *Ichthyornis*, a "dent" in the dorsal outline of the endocranium is regarded as indicating a position of contact between the cerebellum and the cerebral hemispheres (Edinger, 1951). A similar dent in the skull of *Syntarsus* reinforces the suggestion that the cerebellum was erect and at least partially or nearly in contact with the cerebral hemispheres (Fig. 21).

As Edinger (1951) points out, the dominant senses in birds are sight and equilibrium, while smell is insignificant. The great development of the auricular lobes of the cerebellum in *Syntarsus* show that critical powers of maintenance of balance and sustained muscular control, which are centred in the cerebellum (Bellairs, 1969; Pearson, 1972) were very well developed. The substantial size of the Optic nerve, and the size of the optic lobes suggest that *Syntarsus* also had acute visual powers. The size of the orbit (Fig. 3 a) supports this conclusion. However, smell was clearly not an insignificant sense in Syntarsus, nor in other theropods like Ceratosaurus and Stenonychosaurus, as shown by the relatively large size of the olfactory bulbs (Fig. 21, Plate 29).

The fact that pterosaurs also have a well developed cerebellum (Edinger, 1951) indicates the importance of this organ in animals which have evolved highly specialised and advanced methods of locomotion involving refined neuromuscular co-ordination. It seems fair to suggest that strong flexure of the brain axis is directly related to enlargement of the cerebellum and cerebral hemispheres to accommodate the enlarged structures without unduly elongating the braincase.

An attempt to calculate the brain - body weight ratio of Syntarsus has been made. The life-sized, flesh-restored model of an adult Syntarsus, described above, was used. Its volume was ascertained by measuring the volume of water it displaced when immersed, giving a figure of 11,9 l. This figure, multiplied by Colbert's (1962 a) figure of 0,9 for the average specific gravity of land-living animals yields a body weight of 10,71 kg. Thus Syntarsus appears to be comparable in weight with some of the larger living raptorial birds (Brown & Amadon, 1968). Colbert (1962 b) estimates the weight of Coelophysis at "no more than forty or fifty pounds". As noted by Raath (1969), Syntarsus and Coelophysis agree very closely in bodily dimensions, so that the two genera should presumably agree also in body weight. Colbert (1962 b) gives no indication of the method by which his estimate for Coelophysis was arrived at, but it has often been stated in the literature that Coelophysis was "lightly built". In my opinion Colbert has overestimated the body weight of Coelophysis.

The trimmed Syntarsus endocranial cast displaces 10 ml of water, and this multiplied by the 0,9 specific gravity estimate (see also Russell, 1969) gives an approximate brain mass of 9,0 g.

Thus an approximate brain-to-body weight ratio for Syntarsus can be calculated as 0,084%. Even allowing a fair margin for error, this would put Syntarsus in a category close to the lower range of living birds (Jerison, 1968; Russell, 1969; see also Fig. 22).

In his calculations of dinosaur brain weights, Jerison (1969) used half the endocast volume to obtain the brain weight, accepting an assumption by earlier workers that the dinosaur brain filled only half of the brain case. The evidence in Syntarsus indicates that, on the contrary, the brain filled almost all of the cavity (certainly a good deal more than half) and so to use only half the endocast volume in calculating brain weight would be meaningless. However, in Fig. 22 (adapted from Jerison, 1968 : Fig. 2) both the "full" brain weight of Syntarsus and half of this value are plotted, the lower weight placing Syntarsus just within the upper range for reptiles and the more likely upper weight placing it in a position intermediate between reptiles and birds, as Jerison (1968) found to be true of Archaeopteryx.

Cranial nerves (Fig. 5, 23)

All of the cranial nerves whose foramina are preserved have been identified in the Syntarsus braincase and the restoration of the cranial nerves (Fig. 23) is based largely on specimensQG 193 and QG 194. This information is summarised below.

I	Olfactory:	as described in the section on the brain, this nerve was stout and it entered the olfactory bulb just ahead of the orbit.
II	Optic:	recognisable only by the large notch in the front face of the laterosphenoid, suggesting that it was stout and well developed.

III Oculomotor and IV Trochlear: no traces are preserved since they traversed an unossified part of the skull.

V Trigeminal: a very large nerve which left the skull via the large trigeminal notch. A depression in the braincase wall in this vicinity suggests the presence of a substantial Gasserian ganglion, and from it the trigeminal issued in two major branches : the deep ophthalmic (V^1) which exited dorsally through a groove which scarred the laterosphenoid; and a lower branch which split on emerging from the trigeminal notch into the maxillary (V^2), and mandibular branches (V^3). The maxillary branch ran directly forward lateral to the hypophyseal stalk and below the Optic nerve. The mandibular branch turned and ran obliquely out down and back to the lower jaw.

VI Abducens: a small nerve which arose from the ventral surface of the medulla and ran forward, flanking a shallow median ridge in the braincase floor, to ascend the front wall of the braincase and emerge into the pituitary fossa through a pair of small foramina in the hind wall of the fossa. From here the nerve would have turned dorsally on its path to the eye muscles.

VII Facial: the size of this nerve was evidently variable because its foramen in skull QG 193 is nearly twice the diameter of that in QG 194 although the two skulls are of comparable size. On emerging from its foramen the nerve split into two branches, one (the palatine branch) turning down to travel in a shallow groove which runs into the wide and deep parabasal canal and thence forward to the palate; and the second branch turning back in a groove which is confluent with the groove carrying blood vessels over the surface of the prootic, and then evidently looping behind the stapès to form the Chorda tympani (or hyomandibular branch). No trace of the course of this branch of the Facial is preserved after leaving the otic region.

VIII Auditory (or Acoustic): only in QG 196 is there any indication of the conduit for this nerve into the otic capsule. Even this presumed nerve foramen may be simply an artifact of post mortem damage.

IX Glossopharyngeal, X Vagus, and XI Accessory: these nerves emerge from the skull through the elongated vagal fissure. No traces of their course beyond this exit can be discerned, nor can individual exits be identified.

XII Hypoglossal: this nerve is presumed to have emerged through three separate foramina in the deep lateral pockets on either side of the occipital condyle. No further trace of its course to its destination is preserved.

Major cranial blood vessels (Fig. 24)

One would not normally expect to be able to study such detailed features as the course of blood vessels in the remains of an Upper Triassic vertebrate. However, the preservation of the Rhodesian Syntarsus material makes an attempt possible, at least to a limited degree. As noted above in the description and interpretation of the endocranial cast, a trace is preserved on either side of the cerebral hemisphere impressions on the frontal which might represent one of the small arterial twigs of the carotid passing forward to the snout, probably the ethmoid artery.

For the clearest evidence of the paths of major blood vessels, the braincases of QG 193 and QG 194 are unsurpassed. Although the interpretation presented here can be regarded as no better than tentative, the pattern of vascular supply depicted in Fig. 24 seems to fit the presence and distribution of traces on the skull very well, and it is furthermore in broad agreement with what is known in living reptiles (Ostrom, 1961; Romer, 1956).

Cranial veins (Fig. 24 b)

Skull QG 194 shows a foramen situated on the laterosphenoid-parietal suture which leads into the cranial cavity immediately below and behind the articular groove for the postorbital. This foramen is interpreted as transmitting the dorsal head vein which collects blood from the occipital region and side of the braincase and empties into the temporal sinus (see Romer, 1956 : Fig. 28).

In the lower and hind portions of the braincase, there is evidence of the paths taken by tributary branches of the jugular vein. The anterolateral wall of the pituitary fossa is notched on either side, with the notch partly protected behind by a rounded curving flange on the prootic, forming a smoothly curved groove which is confluent with the parabasal canal. The lateral head vein, draining the orbital sinus, would have passed down from the sinus into this groove and then round into the parabasal canal on its way to join the jugular. En route backwards it would have been joined by the mid-cerebral vein which emerged fron the cranial cavity through the forwardly directed foramen immediately behind the exit for the deep ophthalmic branch (V^1) of the Trigeminal nerve. On emerging, the mid-cerebral vein turned down and back in the shallow groove over the prootic to join the main root of the jugular vein as it emerged through the jugular foramen in the region of the auditory meatus.

Cranial arteries (Fig. 24 a)

The course of the internal carotid and its main branches can be reconstructed in greater detail than is possible with the jugular and its tributaries.

On reaching the region of the auditory meatus the internal carotid would have split, giving off a major side-branch, the stapedial artery. This branch ran a short way along the groove shared with the mid-cerebral vein and Facial nerve (see Fig. 5 a). It soon divided to produce three branches (Romer, 1956): the mandibular artery, which swung down in a shallow groove on the surface of the prootic to enter the parabasal canal; the inferior orbital artery, which in the case of QG 194 ran in a horizontal groove over the prootic to pass lateral to the pituitary gland; and the superior orbital artery, which probably also followed the sloping groove on the prootic dorsally with the other structures (veins and nerve branches).

The main branch of the internal carotid, after the division of the stapedial artery, dived into the parabasal canal, which it shared with the mid-cerebral vein and the palatine branch of the Facial nerve. It seems that a further small branch of the carotid divided off between the front of the auditory meatus and the Facial nerve foramen to enter a small foramen in this region which in turn issues into the parabasal canal.

In the vicinity of the pituitary fossa, the carotid gave off a further branch which entered the fossa through a foramen situated deep in its floor. From this point of division forward, the main branch would have constituted the palatine artery. The branch entering the fossa would have formed the cerebral artery which probably gave off a median horizontal branch to travel forward in the median dorsal sulcus of the parasphenoid rostrum as the median palatine artery.

Passing dorsally with the hypophyseal stalk, the cerebral artery would have divided to form the cranial and caudal branches of the basilar artery below the brain. No trace of the course of the cranial branch is preserved. However, the hind wall of the pituitary fossa bears a concave dorsal rim which suggests that the caudal branch bore on this rim in its path back below the medulla.

Jaw musculature (Fig. 25)

Syntarsus had a well differentiated and powerful jaw musculature, and most of the normally occurring components can be accounted for in the two skulls which preserve the relevant areas (QG 193, QG 194). Its jaw musculature was evidently more "complete" in terms of the classifications of Lakjer (1927) and Säve-Söderbergh (1945) than that of the Ostrich, Struthio (Webb, 1957). Much of the account that follows is based on the study of hadrosaurian jaw muscles by Ostrom (1961), and the agreement between the theropod, Syntarsus, and the hadrosaurs is close, indicating consistent conservatism in the jaw musculature. The principal differences can probably be attributed to the kinetic condition of the skull of Syntarsus as opposed to the akinetic hadrosaurian skull. Clues for muscle origins and insertions were sought in areas that were rugose, bounded by ridges, or bearing some other scar or feature likely to be associated with muscle masses.

The adductor mandibulae externus group

Three divisions of the adductor externus group can be recognised, at least by their areas of origin :

i) add. ext. superficialis

This takes origin in a position very like that described by Ostrom (1961) in the hadrosaurs, in a triangular depression facing laterally on the squamosal just ahead of the jugal process. It could not have been a particularly powerful muscle, but its proximal parts would have rounded off the lateral temporal contour in the region of the upper hind corner of the lower temporal fenestra.

ii) add. ext. medialis (= add. ext. medius of Säve-Söderbergh 1945)

Its origin lies close to that of the superficialis but on the medial surface of the squamosal where another deep recess or "pocket" (i.e. the lower surface of the domed squamosal roof ahead of the jugal process) provides accommodation for the muscle head. It too, was relatively small.

iii) add. ext. profundus

This was a relatively powerful muscle which took origin mainly on the parietal, filling most of the hind area of the upper temporal fenestra. It lay medial to the add. ext. medialis, and its fibres probably arose on the anterior wall of the parietal flange, the parietal part of the braincase sidewall, and probably even on the lateral surface of the concave and slightly dimpled posterior half of the prootic.

All three of these parts of the adductor mandibulae externus would have inserted in the large adductor fossa in the medial side of the mandible, with fibres of the superficialis and medialis portions probably also inserting along the dorsal narrow surface of the surangular above the fossa, as in Alligator and Sebecus (Colbert, 1946).

The adductor mandibulae internus group

This muscle generally has two major components, the m. pseudotemporalis and the m. pterygoideus:

i) m. pseudotemporalis

Säve-Söderbergh (1945) points out that in sauropsids the m. pseudotemporalis has two portions, and there is evidence that this was true of Syntarsus. The superficialis portion originated on the anterior half of the upper temporal fenestra, with fibres arising on the temporal shelf of the frontals (just medial to the postorbital groove), the lateral wall of the parietal, and probably also the laterally facing wall of the laterosphenoid. This last area is defined by a low, curving ridge which follows the suture between parietal and laterosphenoid in the upper portion and between pro-otic and laterosphenoid in the lower portion, ending in the region of the trigeminal notch.

The profundus portion evidently originated on the anterior face of the laterosphenoid above and lateral to the groove of the branch V^I of the Trigeminal nerve, thus retaining its correct position relative to the Trigeminal branches to be classified as an "internus" muscle.

Clearly the m. pseudotemporalis was large and powerful as it is in most sauropsids, where it is generally the most powerful of the mandibular adductors (Ostrom, 1961).

Its insertion would have been in the large adductor fossa together with the adductor externus.

ii) m. pterygoideus (m. pterygo-mandibularis of Säve-Söderbergh, 1945)

The origin of this muscle in tetrapods is evidently variable, originating on the pterygoid, ectopterygoid and maxilla in hadrosaurs (Ostrom, 1961), and on the palatine and pterygoid in the Ostrich, where it is described as the most powerful of the adductors (Webb, 1957). In some birds part of its origin is also on the neurocranium (Säve-Söderbergh, 1945). An obvious feature in the palate of Syntarsus and of several other theropods (Ostrom, 1969 b; Colbert & Russell, 1969) is the "carnosaur pocket" on the ventral surface of the rear end of the pterygoid.

In Syntarsus the "carnosaur pocket" is also contributed to by the ectopterygoid, and it is suggested that this pocket is the area of origin of part of the pterygoideus. The pocket is a depressed roughly triangular area (Fig. 6) outlined with a thickened rim, and it faces medially. This proposed position of the pterygoideus lies slightly anterior to the more conventional part described below and the two parts probably shared a common insertion on the mandible. Part of the insertion would have been in the classical position, wrapping round the mandible to insert along the lateral mandibular surface in the region of the retroarticular process. It seems probable that some fibres of this muscle also inserted on the inner surface immediately below the adductor fossa. Contraction of the muscle would have produced powerful adduction of the jaws and retraction of the palate.

A narrow surface on the curving posteroventral border of the pterygoid-ectopterygoid pocket marks what was probably the origin of the other head of the m. pterygoideus which retained the conservative relationships of the muscle, inserting in the classical wrap-around manner on the retroarticular process in association with the head just described.

The adductor posterior

This muscle was evidently short but well developed in Syntarsus. Its origin was on the relatively broad anterior surface of the quadrate shaft, possibly reaching up into the extensive area enclosed by the lateral and medial wings of the quadrate. Its insertion on the mandible was on the hindmost part of the adductor fossa on the front face of the surangular immediately in front of the articular. The space available suggests that this was a thick bellied, short muscle but it is not clear whether its insertion was split by the intercalation of the insertion of the m. pseudotemporalis, as in Alligator (Colbert, 1946). Since the skull was clearly kinetic, one may expect some differentiation or splitting of this muscle (Ostrom, 1961) but the extent to which this has taken place in Syntarsus is not clear.

The constrictor dorsalis group

Two of the major components of this group can be considered in Syntarsus - the m. protractor pterygoidei, and the m. levator pterygoidei.

i) m, protractor pterygoidei

In Sphenodon this muscle originates on the ventrolateral surface of the prootic (Ostrom, 1962). In Syntarsus there is a relatively wide flat surface on the prootic below the Trigeminal notch, and ahead of the Facial nerve foramen, bounded below by the parabasal canal and in front by the edge of the pila antotica. This area is probably the origin of the protractor pterygoidei. Its fibres would have run posterolaterally and nearly horizontally back to insert on the quadrate wing of the pterygoid, spilling over also onto the medial surface of the quadrate itself. The area of origin is very similar to that described by Bock (1964) in birds.

ii) m. levator pterygoidei

In Sphenodon the levator pterygoidei originates on the cartilaginous orbitosphenoid (Ostrom, 1962). Säve-Söderbergh (1945) points out that in some Sauropsida the origin of this muscle often lies close to that of the protractor pterygoidei - just ahead of the latter. A convenient surface for its origin in Syntarsus lies on the side walls of parasphenoid rostrum. Its insertion would have been on the dorsal surface of the pterygoid, and in Syntarsus this area is probably identifiable in a longitudinally slightly concave surface immediately ahead of the basal articulation with the basisphenoid, just medial to where the pterygoid dips down to form its ventral wing which protrudes into the palatal plane. Contraction of the muscle would have tended to raise the palate, pulling it forward at the same time.

There are no clear traces of the m. levator bulbi - the third major component of the constrictor dorsalis group.

The intramandibularis muscle

In view of the large open adductor fossa on the medial mandibular surface, and the long internal channel within the mandible leading to the exposed Meckelian canal, it seems certain that Syntarsus bore a well developed intramandibularis muscle. This muscle is associated with an extension forward of the site of operation of some of the mandibular adductors (Colbert, 1946), in response to lengthening of the jaw.

The depressor mandibulae

The origin of this muscle is difficult to define. It may have been on the paroccipital process (where it would be expected) near its lateral extremity, possibly with some fibres originating on the anteroventral edge of the paroccipital process.

Its insertion on the retroarticular process of the mandible is clearly marked as a depressed triangular area on the upper surface, directly behind the glenoid of the articular, extending back onto the rugose posterior extremity of this process.

m. intermandibularis

No clear evidence of the intermandibularis muscle is preserved. This muscle, which is a superficial component of the constrictor ventralis group, generally attaches to the lower margin of the mandible and inserts on a midline aponeurosis to form a transverse sheet of muscle which assists in swallowing (Ostrom, 1961).

Hyoid muscles

Because of the presence of well developed hyoids it can be confidently asserted that Syntarsus bore a well developed hyoid musculature, but no evidence of the origins, insertions, or relationships of these muscles is discernible.

Axial muscles of the occiput and neck

Muscles inserting on the cranium (Fig. 26 b, Table 12)

Ostrom (1961) carried out a detailed analysis of axial muscle scars on the occipital surface of hadrosaur skulls in which he was able to demonstrate a generally close similarity with the arrangement found in modern sauropsids such as Sphenodon and Ctenosaura. A similar examination of the Syntarsus occiput (based on QG 193 and QG 194) shows a comparably conservative pattern of axial muscle insertions on the back of the skull (Fig. 26 b).

Each of the more prominent features noted on the occipital surface seems to be concerned in some way with muscle insertion. In the interpretation that follows the muscle terminology of Ostrom (1961) will be followed.

ligamentum nuchae

This powerful ligament attaches on the midline near the dorsal surface of the skull. In Syntarsus it evidently inserted on the bulbous median supraoccipital, lying well above the foramen magnum in the vicinity of what is described below. as part of the metakinetic joint.

m. spinalis capitis

Originating on the neural spines of the posterior cervical and cervicodorsal vertebrae, this muscle must insert in a dorsal position to permit the passage of the shorter occipital muscles (Ostrom, 1961). In the hadrosaurs the spinalis capitis seems to have inserted near the midline beside the nuchal ligament (Ostrom, 1961). The same seems to be true of Syntarsus which has a small triangular area on each lateral face of the median supraoccipital which is the probable area of insertion of the spinalis capitis.

m. longissimus capitis

This muscle, which originates on the prezygapophyses of the fourth cervical vertebra, typically divides into three parts (Ostrom, 1961) :

a) pars articulo-parietalis: inserts high on the occipital plane, and is evidently variably represented in reptiles. In Syntarsus it probably inserted on the fairly deep depressions formed on the occipital face of the parietal flanges which rest on the paroccipital processes. The large area available for its insertion suggests that it was a well developed muscle inserting in a broad arc above the m. rectus capitis posterior (see below). Its function is to rotate and turn the head laterally, and its reconstructed size suggests that this was an important head manoeuvre in Syntarsus.

b) pars transversalis capitis: there is some doubt about the respective insertions of this and the obliquus capitis muscle, both of which function to rotate and turn the head, and both of which insert wide of the midline on the paroccipital processes. There are two fairly clearly demarcated surfaces on the paroccipital process which must be related to these two muscles. One is a rather small triangular facet near the lateral end of the process, facing directly back, and the other is a long triangular area with its base near the foramen magnum, tapering laterally. The surface faces back and somewhat dorsally. In view of the generally larger size of the obliquus capitis, and its description as "the largest of the reptilian abductor muscles" (Ostrom, 1961), it has been interpreted as having inserted on the inner of the two facets with a wide lateral extent of insertion, and exerting its pull on a more robust part of the paroccipital process. The pars transversalis capitis, therefore, is reconstructed as having lain lateral to it, inserting near the end of the paroccipital process.

c) pars transversalis cervicis: this muscle inserts on a "spheno-occipital tubercle" below the foramen magnum in Sphenodon (Ostrom, 1961). In Syntarsus the homologous position would be on the rugose ventroposterior surface of the basioccipital basal tubera, providing a relatively small area of insertion on either side.

m. rectus capitis posterior

This is one of the two most powerful occipital muscles and its insertion is clearly demarcated in depressions above and lateral to the foramen magnum in hadrosaurs (Ostrom, 1961). In Syntarsus it was clearly equally powerful as it has left sharp and prominent pockets above the foramen magnum which are visible in every occiput available for examination irrespective of size (= age).

Like the next described, this muscle originates on the broad expanse of the axis neural spine.

m, obliquus capitis magnus

The obliquus capitis was evidently relatively large, and, as discussed under the pars transversalis capitis, it probably inserted lateral to the foramen magnum on the paroccipital process. With the transversalis capitis it produces lateral turning of the head, and has its origin on the atlas-axis complex (Ostrom, 1961), probably principally from the large lateral surfaces of the neural spine and postzygapophyses of the latter bone.

m. rectus capitis anterior

This is a powerful ventral flexor of the head (Ostrom, 1961) which functions with the pars transversalis cervicis (and possibly with the m. iliocostalis capitis, which cannot be identified with any confidence in Syntarsus). It probably inserted in the deep lateral pockets lying below the inner parts of the paroccipital process from which the three branches of the Hypoglossal nerve emerge. The available area suggests that the rectus capitis anterior was a powerful muscle.

Its origin probably lay on the centra of the anterior cervicals.

Cervical axial muscles which do not reach the cranium (Fig. 26 a, Table 12)

Attachment scars preserved on the cervical material has allowed an attempt at reconstructing some of the more important cervical muscles which do not reach the skull (Table 12). The dearth of studies of this kind in other dinosaurs means that the present attempt must be regarded as purely tentative and speculative (Fig. 26 a). It is based largely on an analysis of the musculature in the domestic turkey, Meleagris gallopavo, by Harvey, Kaiser & Rosenberg (1968). In order to avoid confusion in muscle terminology, I have used the same nomenclature as that used by Harvey et al. (1968) to whom reference should be made for a table of synonymy. The analysis that follows is in no way exhaustive.

m. longus colli dorsalis

In the turkey this muscle originates on the dorsal parts of the neural spines of the first and second "thoracic" (= dorsal) vertebrae, together with the origins of the m. biventer cervicis (= m. spinalis capitis of Ostrom, 1961). The thickened and highly rugose corresponding parts of the Syntarsus cervicodorsals (C8 to ? D2) suggest a similar origin. From here anterior slips pass to the postzygapophyses of successively anterior vertebrae, and in Syntarsus the long epipophyses offer ideal points of insertion. Anterior to the eighth or ninth cervicals, the m. longus colli dorsalis becomes tendinous, inserting on the axis in the turkey. In Syntarsus the deep pocket on the posterior side of the axis neural spine, between the postzygapophyses, probably represents the point of insertion. The long tendon also sends back short caudal slips which insert on the postzygapophyses of the third to seventh cervicals. Again in Syntarsus the epipophyses seem to represent the insertion areas of these slips.

The function of the posterior cranially directed slips would be to elevate the neck, drawing it into a more nearly vertical pose. The anterior caudally directed slips would function to straighten the anterior parts of the neck and to elevate the head.

m. longus colli ventralis

In the turkey this complex muscle originates on the centra of the vertebrae at the base of the neck (cervicals 13, 14 and "thoracic" 1 in the case of the medialis portion) and slips insert individually along the cervical ribs and centra of the cervical vertebrae cranially. Several tendons develop in association with this muscle, and the centra of cervicals 8 and 9 in Syntarsus bear smooth grooves immediately below the parapophyses which seem in the right position to have transmitted these tendons.

The action of the m. longus colli ventralis is antagonistic to the m. longus colli dorsalis in that it extends the neck and thereby lowers the head.

mm. obliqui colli

These are short lateral oblique muscles which originate caudally and insert cranially between cervical vertebrae. In the turkey they originate on the transverse processes and they insert on the postzygapophyses of the receiving vertebrae. The most anterior representative originates on cervical 6 and inserts on cervical 3. Posteriorly the slips span one intervening vertebra as follows:

Origin	Insertion
C6	C3
C8	C6
C9	C7
C10	C8
Dorsal 1	C8

A similar situation seems to have obtained in Syntarsus since cervical 8 retains a recognisable epipophysis on the postzygapophysis, whereas in C9 this feature is lacking. Therefore it seems that the insertion of C10 and D1 was shared by C8 in Syntarsus as in the turkey.

The muscle functions to turn the neck laterally, or to raise the head if the slips contract together.

mm. interspinales craniales

These short interspinal muscles run from the anterior face of the neural spine to the posterior face of the next anterior neural spine at the base of the neck in the turkey. The broad and rugose anterior and posterior faces of the neural spines of cervicals 8 and 9 and dorsal 1 suggest that the same occurred in Syntarsus.

Their action is to flex the neck dorsally and thereby to lift the head.

mm. intertransversales

In the turkey these short lateral muscles originate in the region of the parapophysis and diapophysis of one vertebra and insert on the caudal face of the same region in the next vertebra cranially. On Syntarsus it seems likely that the lateral pleurocoels may have housed the bellies of these muscles, and that the relationships were comparable with the turkey.

The action of these muscles is to turn the neck laterally.

MUSCLES OF THE FORELIMB (Fig. 27, 28; Table 13)

Compared with the muscles of the tetrapod hindlimb, those of the forelimb have apparently received relatively little attention except in birds. A detailed treatment of tetrapod forelimb muscles is given by Romer (1922) as part of a work which concerns itself with locomotion in primitive amphibia and reptilia of the Carboniferous and Permian, and which refers to previous work on forelimb musculature. Romer's analysis, supplemented by the work of Fisher (1946) on the locomotor apparatus of New World vultures and Ostrom's (1974 a) on Deinonychus has formed the basis of what follows. In general, Fisher's terminology is followed. I have also relied heavily on information extracted from detailed and very helpful correspondence with Dr. A.D. Walker of Newcastle-upon-Tyne bearing on archosaurian forelimb musculature.

The heavily muscle-scarred humeri in the collection of Syntarsus material have greatly facilitated this attempt at forelimb muscle reconstruction. However, it must be accepted that this attempt is tentative and offered to promote debate on the musculature of a part of the vertebrate body often ignored. The same principles of muscle location have been applied here as in the hindlimb and other muscle analyses. Table 13 summarises the forelimb muscles located with some degree of confidence in Syntarsus.

Axial muscles

It appears that there are three major axial muscles attaching to the forelimb, the latissimus dorsi, the pectoralis and the serratus. Probably at least one other modified axial muscle attached to the girdle, the levator scapulae. This muscle might have arisen from the dorsal fascia near the midline and inserted along the dorsal (or morphologically anterior) edge of the scapula.

m. latissimus dorsi

The latissimus dorsi, arising from the neural spines of the dorsal vertebrae, inserted on the anconal surface of the humerus. Just medial to the top of the deltopectoral crest and distal to the rounded head of the humerus is a fairly large triangular area, outlined by scars in robust humeri (Fig. 13) which is interpreted as the insertion of the latissimus dorsi. The function of this muscle is to retract and elevate (abduct) the humerus. Its relatively short moment arm shows that its contraction would produce rapid movement of the humerus.

m. serratus

The extent to which the serratus might have been differentiated into separate heads is unknown. It is presumed that the muscle originated on the thoracic ribs, as is normal (Romer, 1922; Fisher, 1946) and the large anterior ribs of the cervicodorsal transition area seem to provide convenient points of origin for the muscle. It evidently inserted on the medial surface of the scapulocoracoid in the region of the striations seen near the line of junction of its two constituent bones. This muscle is the main anchor of the scapulocoracoid.

m. pectoralis

This muscle would have been one of the main humeral adductors, pulling it in toward the chest. In vertebrates possessing a sternum the pectoralis originates from it. In the absence of an ossified sternum the origin of the pectoralis in Syntarsus might have been from ribs, gastralia or even from soft tissues (e.g. rectus abdominis) in the anterior trunk region. It inserted apically on the large deltopectoral crest, spilling over slightly onto the inner surface of the crest. Robust, muscle-scarred humeri again show a distinct scar in this region which can only be for the pectoralis.

Appendicular muscles on the palmar surface of the humerus

m. supracoracoideus and m. scapulohumeralis

It has already been suggested that the latissimus dorsi exerted some abductive force on the humerus. However, the major abductor seems to have been the supracoracoideus. This muscle originates on the outer surface of the coracoid. Ostrom (1974 a) shows it as occupying a large area dorsal to the coracobrachialis in Deinonychus. Walker (pers.comm.) is of the opinion that the supracoracoideus occupied a larger area of origin in Deinonychus than shown by Ostrom (1974 a), to the extent that it incorporated the coracoid foramen. Adjacent to this muscle, situated principally on the scapula where it meets the coracoid, Walker (pers.comm.) places the scapulohumeralis muscle. In Syntarsus the scapulocoracoid is "dished" on the lateral surface in this region, but there are no scars of attachment to identify individual muscles. Romer (1922) shows that the scapulohumeralis (anterior) and supracoracoideus are closely related muscles which originate near each other and also insert proximally near the head of the humerus on the anconal surface. Ostrom (1974 a) notes that Deinonychus bears a small but distinct tubercle laterally adjacent to the humeral head which he considers to be the insertion point of the supracoracoideus. Syntarsus has a similar tubercle which probably served the same function. The insertion of the scapulohumeralis, if it existed, cannot be defined. Romer (1922) has drawn attention to the fact that the scapulohumeralis is missing in crocodiles.

m. coracobrachialis and m. biceps

The origin of the coracobrachialis and of the coracoidal head of the biceps has aroused a vigorous debate recently. Ostrom (1974 a) has identified a small tubercle in Deinonychus on the lateral surface of the coracoid near the glenoid as the "biceps tubercle", from which he suggests the coracoidal head of the biceps originated. Walker (in litt) has challenged this interpretation, stating that the coracoidal origin of the biceps in reptiles is consistently at the medial edge (= anterior, in a nearly horizontal bone) of the coracoid, sandwiched between the coracobrachialis complex and the supracoracoideus. Ostrom has cited his interpretation as part of his evidence for a coelurosaurian ancestry of birds (Ostrom, 1973, 1974 c, 1975 a, 1976 b,c). Walker (in litt.) has shown that a wide range of archosaur derivatives bear a tubercle in a comparable position (allowing for the great expansion anteriorly of the coracoid of Deinonychus), including prosauropod dinosaurs, thecodonts and phytosaurs. He argues compellingly that, since all living reptiles have the coracoidal head of the biceps originating in a conservative position, it is reasonable to expect dinosaurs to agree, and unreasonable to shift the origin in dinosaurs on the slender grounds presently available. He goes on to suggest that the "biceps tubercle" represents the point of origin of a tendon associated with the coracobrachialis brevis and that the coracobrachialis longus occupied the small disc-like area normally present between this tubercle and the glenoid.

Syntarsus does little to resolve this debate, but tends to support Walker's contention. Accepting that the main area of origin of the coracobrachialis (brevis) is on the distal half of the coracoid, and presuming that its insertion in Syntarsus fills much of the area on the palmar surface of the humerus bounded laterally by the deltopectoral crest, as in other tetrapods (Romer, 1922; Fisher, 1946), Walker's interpretation fits adequately. In Syntarsus the tubercle (Fig. 12) and ventrally directed (morphologically posteriorly directed) rugose facet are clearly part of the same unit and the facet faces directly into the vacant space on the humerus. If the biceps originated in the conservative position, as Walker advocates, then its coracoidal head (or tendon) would have to dive deep beneath the coracobrachialis complex to reach the medial side of the humerus where its humeral origin should be. Syntarsus bears a smooth oblique groove adjacent to the glenoid, formed partly by the lip of the glenoid and partly by the border of the coracobrachialis facet, in just the right position to guide the biceps round.

The actions of these muscles would be : coracobrachialis - strong protraction of the humerus; biceps - protraction and some adduction of the humerus, together with flexion of the forearm.

Fisher (1946) has noted that in New World vultures part of the coracobrachialis anterior muscle originates fleshily from the long head of the biceps, suggesting a close relationship between these two muscles.

The humeral portion of the biceps probably originated on the palmar medial edge of the humerus, bounded laterally by the coracobrachialis. One possible facet of origin of this muscle is the small tubercle on the palmar surface opposite the presumed insertion of the subcoracoideus on the anconal surface. In birds the biceps occupies a similar position on the humerus (Fisher, 1946), and extends distally along the bicipital crest. The medial edge of the humerus of Syntarsus shows a weakly developed crest which probably served the same function.

The distal insertions on the antebrachium are difficult to determine. A rugose scar on the ulna of some specimens, just below the pit housing the head of the radius, is here regarded as the biceps insertion. Whether the tendon split to insert on both radius and ulna, as it does in birds, cannot be clarified.

m. brachialis

The palmar surface of the humerus bears a shallow triangular depression at its distal end which must have housed the origin of the short brachialis muscle. Romer (1922) notes that in primitive reptiles the brachialis and biceps usually share a common insertion, usually on the ulna.

Appendicular muscles on the anconal surface of the humerus

m. deltoideus and m. humeroradialis

The deltoideus muscle arises broadly from the outer surface of the scapula blade. Its insertion on the humerus seems to be indicated by a narrow curved area on the lateral wall of the deltopectoral crest near its apex. Immediately adjacent to this scar in robust humeri is another larger and more heavily scarred area occupying most of the delto pectoral crest lateral wall. Whether this represents differentiation of the deltoid into major and minor portions cannot be decided. Such differentiation and gross size would indicate the deltoid to be a very powerful humeral retractor, which seems logical in terms of the proposed ripping function of the manus of Syntarsus.

In Allosaurus Madsen (1976) has identified as the "humeroradialis" a small but pronounced scar in a position comparable with the lower end of the larger of the two deltoid scars in Syntarsus. It seems doubtful that the humeroradialis should be excessively developed in

Syntarsus yet so reduced in Allosaurus, whose limb proportions are not that drastically different from Syntarsus. Romer (1922) states that the brachio-(humero-)radialis is found in mammals, Sphenodon, some lizards and the crocodile, and not elsewhere. Syntarsus probably lacked this muscle, but if this was so it is difficult to determine the muscle responsible for the scar in Allosaurus. It would be a forearm flexor.

m. subcoracoideus

The subcoracoideus arises on the medial surface of the coracoid, presumably anterior to the insertion of the serratus. Its insertion on the humerus of birds is on the proximal surface of the internal tuberosity. Syntarsus bears a well-defined insertion facet in this vicinity, on a tuberosity marked off from the head of the humerus by a shallow notch at the medial corner. It is presumed that this is where the subcoracoideus inserted and that the tuberosity is therefore homologous with the internal tuberosity of the avian humerus.

The main function of the subcoracoideus seems to be to adduct and slightly rotate the humerus abaxially. Fisher (1946) lists it as a humeral retractor in New World vultures.

?m. proscapulohumeralis

In birds, other smaller muscles insert near the internal tuberosity on the anconal surface, the principal one being the small proscapulohumeralis, originating on the scapula immediately adjacent to the glenoid. The shallow notch mentioned above which lies lateral to the internal tuberosity on the Syntarsus humerus bears two clearly defined facets, one facing directly medially, and the other anconally. It is possible that an equivalent of the proscapulohumeralis inserted here. Its function would be weak retraction of the humerus.

m. triceps

Whether or not Syntarsus bore a scapular head of the triceps is impossible to determine. Its origin on the humerus seems to have been fleshy and large, occupying almost all of the medial half of the anconal surface and separated from the latissimus dorsi insertion by a thin ridge in robust humeri.

Its distal insertion was clearly tendinous onto the olecranon process. Its main function would have been powerful extension of the forearm.

Muscles originating on the humeral epicondyles

Syntarsus has clear scars of attachment on the ectepicondyle and entepicondyle which undoubtedly provided origins for the muscles normally associated with movements of the forearm and manus, namely the supinator and extensors of the forearm and manus arising from the ectepicondyle above and lateral to the radial condyle, and the pronator and flexors from the entepicondyle above and medial to the ulnar condyle. The strong pronator probably inserted on the radius proximally on the rugose tubercle which tops the slight crest in front of the cotylus of the radius. The supinator was probably reduced because of the small degree of supination possible at the carpus and proximally at the elbow.

Manus muscles

With regard to details of muscles in the manus, little can be said. It is clear that the digits had well developed flexors and extensors on account of the size and development of the flexor and extensor tubercles on the phalanges. The pollex was also equipped with a strong abductor attaching to the lateral tubercle proximally on phalanx Ii. It presumably, therefore, also bore an antagonistic adductor although no definite scar is preserved in any of the specimens available.

MUSCLES OF THE HIND LIMB (Fig. 29, 30; Table 14)

Romer's pioneering studies of crocodilian (1923 a) and saurischian (1923 b) pelvic musculature have for long been the starting point of any limb muscle reconstructions in vertebrate palaeontology. However, those studies are confined to analyses of the muscles of the hip and thigh, and reconstructions of the muscles of the lower leg in fossil species, especially dinosaurs, are rare. While Romer's conclusions on saurischian pelvic musculature (Romer, 1923 b) are readily applicable to the pelvis and hindlimb of *Syntarsus*, and form the basis of the analysis that follows, the excellence of preservation of the *Syntarsus* material demands that an attempt be made to provide as complete an account as possible of hind limb musculature in this genus. Studies of avian limb muscles by Fisher (1946), Berger (1952) and Cracraft (1971) have been used to supplement Romer's work and to extend the analysis to the lower leg of *Syntarsus*.

Muscle positions have been determined according to the location of scars of origin and insertion on the bones coupled with a comparison against the published descriptions to identify the muscles so located. Many of the muscles reconstructed can be located with considerable confidence, while others are less certain and some cannot be placed at all. In the latter cases the lack of clues as to sites of origin and insertion might reflect the fact that the muscles arose or inserted on soft tissues, such as joint capsular tissues, or composite aponeuroses such as are known in the knee region of birds (Cracraft, 1971).

Table 14 summarises the identification and location of the muscles treated in this section.

The well-preserved *Syntarsus* material available has permitted comparisons between the bones of adult and juvenile specimens, as well as between the sexes on the basis of the "robust" and "gracile" femora described above. The robust femora show very clear and well developed muscle scars, particularly near the proximal end of the bone, and femoral sites of origin and insertion are reconstructed largely on the basis of these bones because they are regarded as showing an "exaggerated" muscle condition. In general the proximal parts of the gracile femora are rather featureless. Muscle terminology will follow Romer (1923 b) except where otherwise stated.

Axial muscles of the pelvic region

Few details are evident which might help to locate insertions of the axial muscles on the pelvis. Clearly the dorsal trunk and tail muscles occupied the troughs above the transverse sheet formed by the fused sacral transverse process on either side of the median longitudinal sacral neural blade, and fibres from these muscles (m. dorsalis trunci and m. dorsalis caudae) would have inserted along the sacral neural blade and the inner edge of the iliac crest on either side. There is no mid-length constriction of the sacrum by the ilia in Syntarsus such as there is in larger theropods, e.g. Antrodemus (Gilmore, 1920), Tyrannosaurus (Romer, 1923 b) and in birds, so that there was no clear separation of trunk and caudal portions of the dorsal axial muscles.

Ventrally the axial musculature would have consisted of the m. obliquus abdominis externus, m. obliquus abdominis internus, m. transversus abdominis, m. rectus abdominis, and the m. ilioischiocaudalis (Romer, 1923 a,b). The obliquus externus might have inserted tendinuously onto the pubis near the origin of the m. ambiens, and a shallow depression below the rugose ambiens scar on the pelvis of QG 1 might mark this insertion; by virtue of its association with the m. rectus abdominis it might have inserted also along the lateral edge of the pubic apron. The m. obliquus abdominis internus might itself have inserted on the pubis distal to the rectus abdominis, and the transversus abdominis probably inserted with the rectus on the cartilaginous pubic extension as in crocodilia (Romer, 1923 a). The extent of the pubic cartilage in Syntarsus is unknown.

The femoro-acetabular joint capsule

All of the robust femora show a distinct rugose scar encircling the head just distal to the articular surface which is taken to represent the limit of the joint capsule (Fig. 15). Ventromedially the capsule scar lies on the apex of the medial "hook" of the femoral head, which was evidently concerned with the transmission of capsular ligaments attaching the femur to the acetabulum. Galton (1969; Fig. 8 B) records a similar ligament in Hypsilophodon, an ornithopod. In Syntarsus the ligament arose from a smooth surface defined by a low rim on the medial surface of the femur at the junction of the head and neck, with the medial "hook" bordering it medially. Evidently it then turned back to climb the posterior surface of the femoral head in the longitudinal trough bounded medially by the "hook" to emerge at the articular surface of the head. This portion of the femoral head protrudes slightly through the inner opening of the acetabulum and it is uncertain whether the ligament attached to the inner surface of the acetabular rim or to the centrum of sacral vertebra 3, opposite which it lies.

Evidence of a second ligament on the femoral head is seen in a shallow dimple on the anterior face of the neck, within the limits of the joint capsule. In the articulated state this ligament scar faces the roof of the acetabulum where a corresponding shallow pit probably marks its pelvic attachment. Its dorsal and anterior femoral attachment suggests that this ligament is the homologue of the avian teres ligament, and that therefore the posterior ventral one which runs in the trough of the medial femoral hook should be the homologue of the posterior acetabular ligament in birds (Cracraft, 1971).

The joint capsule scar, from its position adjacent to the attachment of the posterior acetabular ligament, rises along the posteriomedial rim of the femoral hook and then passes transversely across the posterior ligament trough, dividing the latter into upper and lower halves. This feature, however, applies only to robust femora, and the gracile elements show no such transverse division of the trough. The capsular scar continues transversely across the hind surface of the femoral neck to the upper end of the oblique trochanter for the pubioischiofemoralis externus muscle (= obturator ridge of birds) which develops only on robust femora. It moves around the lateral side of the neck proximal to the bulbous trochanter for the pubioischiofemoralis internus (= greater trochanter) and then in a gentle arc across the anterior surface of the neck to complete the circle in the vicinity of the medial femoral hook. In its path across the anterior surface of the neck the capsular boundary incorporates the teres ligament pit within the joint capsule.

The degree of scarring on robust femora suggests that the capsular tissues were well developed and tough, and subject to substantial stresses in operation. Although on gracile femora it is more difficult to trace the boundary of the joint capsule, it is possible to make out features on the exceptionally well-preserved juvenile femur of QG 691 which agree very closely with the path of the capsule boundary on robust femora. The differences between robust and gracile forms therefore seem to be related to differences in degree of development of fibrous and muscular tissues.

Appendicular muscles

Table 14 lists the muscles which have been located and identified in a "traditional" sequence, based largely on Romer (1923 a) for the thigh muscles. In the descriptive sequence that follows the muscles have been grouped into functional associations concerned mainly with propulsion and recovery.

1) Propulsive muscles of the hind limb

Propulsion in the hind limb cycle comprises four major activity components which should really be considered with reference to the foot as the "fixed" segment in contact with the ground and the other leg segments moving relative to it, finally transmitting propulsion to the body via the acetabulum. However, it seems traditional to consider leg movements in a proximal-to-distal sequence, and viewed in this light the four main propulsive components are: retraction of the femur; extension of the crus; extension of the metatarsus; and flexion of the toes.

A) Retractors of the femur

i) m. caudifemoralis longus et brevis

The main retractor force seems to have been provided by the powerful caudifemoral muscles. M. caudifemoralis longus (= m. coccygeofemoralis longus of Romer, 1923 a) originated on the lower surface of the transverse processes, centra and possibly the chevrons of the caudal vertebrae in the proximal and middle portions of the tail. The bulky and fleshy belly of this muscle would have provided much of the bulk of the tail, and would have contributed therefore to the counterweight function of the tail in the bipedal stance of Syntarsus. The muscle inserted by means of a narrow tendon in a well defined depression on the posteromedial surface of the femoral shaft in the region of the fourth trochanter. The inserting tendon seems to have borne a small accessory tendon which split off at the point of insertion and ran distally down the medial surface of the fourth trochanter in a short and shallow groove on its way to its insertion on the head of the fibula (Fig. 31). This small accessory tendon is present also in lizards and birds (Galton, 1969).

The m. caudifemoralis brevis (= coccygeofemoralis brevis of Romer, 1923 a) was also a powerful and fleshy muscle but it was much shorter than m. caudifemoralis longus. Its origin was on the broad undersurface of the sacrum and ilium behind the acetabulum, and it inserted by means of a powerful tendon in a crescentic depression anterior to the longus insertion on the medial surface of the femur in the vicinity of the fourth trochanter. This muscle clearly did not insert onto the fourth trochanter itself, the insertion lying substantially forward of the ridge of the trochanter.

The fact that neither part of the caudifemoral musculature inserted on the fourth trochanter probably explains the small size of this structure in Syntarsus when compared with its massive crest-like form in prosauropods or pendent form in Ornithischia.

In retracting the femur from the resting position the caudifemoralis longus has the more advantageous moment arm, and the brevis probably came into play near the terminal stage of retraction to give an additional powerful boost at the moment of "lift-off" of the body. Its short moment arm would also serve to produce fast movement of the distal parts of the leg.

ii) m. adductor femoris

The m. adductor femoris seems to have arisen fleshily from the lateral surface of the puboischium beneath the acetabulum. In this region the puboischiadic plate is slightly concave. Its origin was bounded anteriorly by the superficial fibres of the m. puboischiofemoralis externus near the thyroid and obturator fenestrae, and posteriorly probably by the origin of the m. flexor tibialis internus. It is not possible to determine whether the adductor was divided into several heads. It inserted fleshily along the distal half of the posteromedial femoral surface. Near the internal condyle of the femur a fairly deep and curved groove probably represents the distal limit of the adductor insertion.

Contraction of the muscle would exert a strong retractor force on the femur, and would also tend to pull the distal end in towards the midline, thus causing adduction.

iii) <u>m. ischiotrochantericus</u>

It is difficult to define the origin or insertion of this muscle. It seems possible that it originated on the dorsolateral surface of the ischiadic shaft as Romer (1923 b) suggested for saurischia. An elongated and smooth surface exists in this region which could have given origin to the muscle. Its insertion is regarded as having been tendinous around the posterolateral surface of the femoral neck, lying in a trough between the greater and lesser trochanters. Its contraction would have produced a small retractor force as well as some lateral rotation of the head of the femur.

B) Extensors of the crus

Three of the major tibial extensor muscles are two-joint muscles arising on the pelvis and inserting on the cnemial crest of the tibia via the patellar tendon with no fibres passing to the intervening femur. The three are m. iliotibialis, m. sartorius and

m. ambiens, otherwise known collectively as the "triceps femoris".

i) m. iliotibialis

As in crocodilia (Romer, 1923 a) and those saurischia studied (Romer, 1923 b), the iliotibialis seems to have arisen by aponeurosis from the crest of the ilium along its length forming a broad but relatively thin sheet of muscle which invested most of the other muscles of the outer surface of the thigh on its course to the patellar tendon.

ii) m. sartorius

In Romer's (1923 b) analysis the equivalent of this muscle is treated as part of the m. iliotibialis, with which it is undoubtedly closely associated. However, in Syntarsus and several other theropods it seems to have had a distinctive and fleshy origin from the lower forward projection at the anterior end of the ilium (Plate 19 b). For this reason it is treated as a separate muscle and given the name which has been applied to it by Galton (1969) in ornithopods, and by several authors in birds (e.g. Berger 1952; Cracraft, 1971; Fisher, 1946). From its fleshy origin on the lower anterior flange of the ilium, the sartorius ran to the knee to join the patellar tendon.

iii) m. ambiens

The m. ambiens was evidently relatively well developed with its origin in an elliptical and rugose depression on the lateral surface of the pubis directly ahead of the acetabulum and lying above and in front of the obturator and thyroid fenestrae. The ambiens ran down the front of the thigh to join in the formation of the patellar tendon. Part of its tendon probably also crossed the knee laterally to merge at the knee with the aponeuroses of origin of the long digital flexor muscles, as occurs in birds (Cracraft, 1971).

The three extensors of the tibia described above probably shared a common insertion onto the cnemial crest of the tibia via the robust patellar tendon, with part of the ambiens tendon probably crossing over the knee joint. The patellar tendon inserted on the hook-shaped tuberosity at the apex of the cnemial crest which protrudes laterally, and fascia probably continued down the crest to the point where it fades into the tibial shaft. The well developed and high cnemial crest provides a relatively long moment arm for the force developed by the concerted contraction of this muscle group, plus the m. femorotibialis described below, resulting in powerful extension of the lower leg as part of the propulsive stroke.

iv) m. femorotibialis

As in other archosaur derivatives (Crocodilia, Romer, 1923 a; Saurischia, Romer, 1923 b; Ornithischia, Galton, 1969; and birds, Cracraft, 1971) this muscle was well developed and divided into three heads. In Syntarsus the three heads arose fleshily from the medial, posterior, and lateral surfaces of the femoral shaft. The medial head arose from the mid section of the shaft below the caudifemoral insertions and above the adductor insertion. Distally it swept round the front of the femoral shaft to join the patellar tendon. It was demarcated from the lateral head by a groove running down the anterior surface of the femoral shaft which probably housed part of the femoral artery.

The lateral head had a more extensive fleshy origin than the medial head, extending from the edge of the lesser trochanter proximally, to well beyond the middle of the shaft distally before it too joined the patellar tendon on the anterior surface. A foramen pierces the femur near the front border of the area of origin of the lateral head a centimetre or two distal to the lesser trochanter, Lying as it does adjacent to the arterial groove just described this foramen is regarded as being a nutritive foramen for transmission of a branch of the femoral artery to the interior of the femur.

The posterior head was very powerfully developed and arose from a sharply defined rectangular area on the posterior femoral surface, delimited above and on either side by ridge-like muscle scars. The upper ridge is confluent laterally with the lesser trochanter for the m. iliofemoralis. The medial ridge forms the fourth trochanter, and the lateral ridge separates the areas of origin of the posterior and lateral heads of the m. femorotibialis. It runs down the posterolateral edge of the femur about the same distance as the fourth trochanter on the posteromedial edge, gradually fading distally. At about shaft midlength the posterior surface of the femur "twists" to face posterolaterally. It seems that this "twist" allowed the posterior head of the m. femorotibialis to run round onto the anterior surface to join the patellar tendon. It is also from this point, extending distally on the posteromedial surface, that the m. adductor femoris is thought to have inserted.

The description of the three femorotibialis heads given above applies particularly to robust femora, where the degree of muscle scarring is great. The gracile femora in the collections show few of the scar features, the only one consistently present being the posteromedial ridge which equates with the fourth trochanter.

The tibial extensor complex described above would tend to neutralise a small flexor force imparted by the gastrocnemius because of its partial origin on the femur; the moment arms of the femoral origins of the gastrocnemius are very small, and the femorocrural flexor force must have been minimal.

C) Extensors of the metatarsus

i) m. gastrocnemius

The most powerful single metatarsal extensor is the m. gastrocnemius, as is true of all limbed land-dwelling tetrapods. Details of its origin are not entirely clear in Syntarsus but it seems to have had areas of origin on the external and internal femoral condyles, from the popliteal fossa at the distal end of the femur, and from the medial surface of the cnemial crest of the tibia. The slips of origin from the femoral condyles seem to have been tendinous and they have left roughened scars on the condylar surfaces. The scars consist of an outer one on the lateral face of the external condyle behind the presumed origin of the m. tibialis anterior slip (see below), and an inner one on the medial face of the internal condyle distal to the curved trough of insertion of the m. adductor femoris.

A popliteal origin is shared by part of the gastrocnemius and the long digital flexors in some birds (e.g. Cracraft, 1971) and it seems probable that the same was true of Syntarsus. The deep popliteal fossa of the Syntarsus femur provides ample room for such muscle origins but no individual scars can be made out which would assist in detailed determination of individual muscle origins. In some specimens a low transverse ridge divides the popliteal space into upper and lower portions, which may be concerned with the origin of muscle complexes. If this is so, one would expect the upper portion to house the gastrocnemius origin since this muscle lies superficial to the deeper layer of toe flexors.

The portion of the gastrocnemius which has its origin on the medial surface of the cnemial crest has left a concave scar near the apex of the crest proximally.

The individual components of origin would have combined immediately distal to the knee on the posterior surface of the crus to form a thick-bellied (and most probably pennate) muscle. The muscle belly would have narrowed distally and concentrated into the powerful Achilles tendon. This tendon crossed the plantar surface of the intratarsal joint to insert on the well developed "hypotarsus", or ventral bony tubercle, at the proximal end of the metatarsus formed chiefly under metatarsal III and probably also onto the protruding proximal end of metatarsal V. The distribution of low ridges and striations on the ventral surface of metatarsals II, III and IV suggest that the gastrocnemius insertion extended beyond the "hypotarsus" in a plantar fascia as well. As stated earlier, this muscle, as well as being the main foot extensor, also exerted a slight femorocrural flexor force.

ii) m. peroneus longus et brevis

These muscles originated on the anterior face of the crus, in association with the tibialis anterior. They should be therefore, a priori, flexors of the metatarsus. However, their tendons of insertion pass laterally across the intratarsal joint in birds to become confluent with the tendon of m. flexor perforatus digiti III (Fisher, 1946, Berger, 1952; Cracraft, 1971), and to be associated with the tibial cartilage. Since the m. peroneus longus seems to be concerned with flexion of the toes, it seems that it must have an accessory action in extending the metatarsus. This point cannot be checked in Syntarsus, but it is presumed that the same conditions obtained.

The origins of the peroneus longus and brevis cannot be separated in Syntarsus and it seems probable that the two were indistinguishably united in their origin along the anterior surface of the crus, extending down the narrow space between tibia and fibula. Proximally the peroneus longus seems to have had a substantial part of its origin on the anterior and anterolateral surface of the fibula, adjacent to the fibular flange on the tibia. Distally the muscle would have narrowed into a tendon of insertion which crossed the intratarsal joint via the transverse or annular ligament (see below under m. tibialis anterior) to insert with the equivalent in <u>Syntarsus</u> of the avian flexor perforatus digiti III as mentioned above. The peroneus brevis also crossed the intratarsal joint but it may have inserted on the equivalent of the avian tibial cartilage (Cracraft, 1971).

iii) m. plantaris

The plantaris is also uncertain in <u>Syntarsus</u>. Proximally on the posteromedial surface of the cnemial crest, behind the gastrocnemius origin and below the scar of what is taken to represent the medial knee joint ligament, is a triangular smooth area which agrees with the area of origin of this muscle in birds (Cracraft, 1971). It presumably inserted, as in birds, by means of a tendon into the cartilage of the intratarsal joint (= tibial cartilage of birds). In the absence of the cartilage this point cannot be clarified.

The function of the plantaris in birds is debatable (Cracraft, 1971). It has been included with the metatarsal extensors because of its posterior position on the crus and the belief that its insertion was on the plantar surface of the intratarsal joint.

D) Digital Flexors

The long toe flexors also exert varying degrees of extension on the metatarsus. As indicated earlier, details of the origins of some of the digital flexor muscles in the popliteal area of the femur cannot be made out except to say that they would have to lie deep to the popliteal origin of the gastrocnemius. For this reason the following toe flexors are grouped together and assigned a general "popliteal origin" :

m. flexor digiti II
m. flexor digiti III
m. flexor digiti IV
m. flexor hallucis longus.

Because of the reduction of digit I in Syntarsus it is unlikely that m. flexor hallucis longus would have been as greatly developed as it is in birds. However, the well formed (though reduced) and complete digit with a small flexor tubercle on the claw shows that the flexor muscle must indeed have been present. The remaining flexors in this group presumably exhibited the conservative relations of these muscles in limbed tetrapods.

Only the m. flexor digitorum longus can be described with some confidence as to its origin. On the posterior surface of the fibula at the proximal end is a short posterior spur which borders a shallow depression on its ventrolateral surface. This depression evidently represents the proximal origin of m. flexor digitorum longus on the fibula externally with further fibres emanating from the deep fossa on the medial surface of the fibula head and from the adjacent tibial shaft. On the medial fibular surface the flexor origin is bounded above by the insertion of the popliteus. The gastrocnemius would have covered all of the digital flexors, lying as they did deep to that muscle.

The long tendon of the flexor digitorum longus passed across the intratarsal joint and presumably divided in conventional fashion to send branches to the flexor tubercles of the claws of digits II, III and IV. The action of this muscle is to flex the toes simultaneously, in contrast to the independent toe flexors grouped together above.

In their flexing action all of the digital flexors would also have contributed to extension movements of the metatarsus.

2) Recovery muscles of the hind limb

Recovery of the limb at the end of the propulsive phase of the cycle can also be resolved into four main activity components which are the opposite of the propulsive actions, namely : protraction of the femur; flexion of the crus; flexion of the metatarsus; and extension of the toes.

The set of recovery muscles is neither as differentiated nor as strongly developed as is the propulsor set. Because recovery is an action which prepares the limb for the next propulsive stride but is not itself concerned with moving the relatively great bulk of the body, this is understandable.

A) Protractors of the femur

Most of the crural extensors must have exerted some protractive forces on the femur - e.g. m. iliotibialis, m. sartorius, and m. ambiens. Indeed the femoral protractor moment arms of each of these muscles was long so that the forces developed must have been considerable and Romer (1923 a) groups them together as the "Extensor femoris". These forces must have been counteracted by the femoral retractors during propulsion or else the propulsive power stroke would have collapsed through protraction of the femur. This probably also explains in part the great development of the m. femorotibialis which extended the crus without imparting any protractive pull on the femur.

The principal protractor muscles seem to have been the m. puboischiofemoralis internus and externus.

i) m. puboischiofemoralis internus

In Crocodilia this muscle arises from the lower surface of the transverse processes of the posterior dorsal vertebrae and from the inner surface of the ilium (Romer, 1923 a). The same seems to have been true of Syntarsus and the preacetabular projection of the ilium flares ventrally to accommodate the belly of this muscle. The pubic peduncle of the ilium is also shallowly and smoothly grooved to carry the inserting tendon to the femur. The insertion is interpreted as having been on the bulbous and heavily scarred greater trochanter of robust femora, wrapping around part of the lateral and posterior face of the femoral neck immediately distal to the joint capsule. In gracile femora the same position is represented by a flattened and slightly expanded surface on the lateral side of the neck onto which the tendon inserted.

In an adult specimen, such as QG 1, the moment arm of this muscle is not long - only about 2 cm - but the thick belly must surely have developed great power in its contraction. Contraction of the muscle, in addition to causing protraction of the femur, would also cause the femur to rotate medially on its axis - turning the knee in toward the midline.

ii) m. puboischiofemoralis externus

The origin of this muscle is not clear except in so far as it was probably associated with the posterior surface of the pubic apron up to the obturator fenestra in the pubis. This area of origin would have been bounded posteriorly by the origin of the adductor femoris.

The belly of m. puboischiofemoralis externus travelled caudally medial to the femur and has been restored as inserting tendinously on the posterior face of the femoral neck on the oblique ridge-like trochanter seen in robust femora and which is here regarded as the homologue of the "obturator ridge" of birds (Cracraft, 1971). Like the puboischiofemoralis internus this muscle would have had a short protractor moment arm of about 2 cm but its bulk would have developed great power. Because of its posterolateral insertion from the medial side its contraction would have caused the femur to rotate laterally, tending to turn the knee outwards and thus acting antagonistically to the inward pull of the puboischiofemoralis internus while simultaneously protracting the femur.

Gracile femora lack the "obturator ridge" and bear no clear indication of the insertion of this muscle.

iii) m. iliofemoralis

This muscle had a large fleshy origin from most of the concave lateral surface of the ilium bounded above by the aponeurosis of the m. iliotibialis, behind by the crural flexor origins, and ahead by the origin of the m. sartorius. Its short belly evidently narrowed rapidly into a tendon which passed over the rounded and smooth "roof" of the acetabulum to insert tendinously on the lesser trochanter situated laterally near the head of the femur.

In specimens with robust femora the tendon was enormous and strap-like, inserting into the massive rugose shelf which occupies the lateral surface at the junction of the neck and shaft of the femur. Gracile femora, on the other hand, bear only a short and narrow spur in the corresponding position, situated rather more anterolaterally, which projects up toward the ilium. Here the inserting tendon was clearly smaller and narrower, but the insertion was nevertheless strong.

Perhaps the principal action of the m. iliofemoralis was abduction of the femur, acting as the main antagonist of the m. adductor femoris. In the resting position the muscle has virtually no femoral protractor moment arm, but its abductor moment arm is relatively long (approx. 3 cm). In the latter stages of femoral protraction by the puboischiofemoral muscles, the iliofemoralis orientation is improved with respect to protraction and it thus probably assisted in the terminal stages of femoral protraction.

It probably also caused a slight inward rotation of the femur.

B) Flexors of the crus

As mentioned above, some of the force of the gastrocnemius and the digital flexors must have tended to flex the crus because the origins of those muscles cross the knee joint. However, since their crural flexor moment arms are short, and since they were undoubtedly amply opposed by the great forces of the crural extensors during propulsion, these tendencies to flex the crus can be disregarded.

The major crural flexors, with large fleshy bellies, powerful tendinous insertions and long moment arms were unquestionably the m. iliofibularis and the two principal components of the flexor tibialis complex.

i) m. iliofibularis

The origin of the iliofibularis is not entirely clear but it probably arose from a quadrangular and rather rugose platform on the lateral surface of the ilium at the posterior end of the pelvis. The m. flexortibialis externus probably shared this area of origin with the iliofibularis. The rugosity of the surface on the pelvis of QG 1 suggests a tendinous or aponeurotic origin which then developed into a bulky fleshy belly. Forming a substantial part of the bulk of the proximal thigh, the m. iliofibularis would have narrowed distally into a powerful inserting tendon which attached laterally to the fibula at the distal end of the fibular crest. The anterior edge of the crest in this region is slightly thickened and rugose and slightly reflected laterally. Behind it on the lateral surface of the fibula is a shallow depression. All of these features are regarded as being involved with the insertion of the iliofibularis.

The tendon of the muscle probably passed through a ligamentous sling or "biceps loop" as in birds (Fisher, 1946; Berger, 1952; Cracraft, 1971), but no clear attachment scars for such a sling can be demonstrated on the bones. However, since, in some birds at least, this loop is intimately associated with the tissues of origin of other leg muscles, such as the gastrocnemius, ambiens, etc. (Berger, 1952), it is not surprising that the existence of the loop cannot be clearly demonstrated. If the tendon of the ambiens crossed the knee in Syntarsus, as is proposed in this study, it would have been associated with the attachment of the iliofibularis sling on the fibular side of the knee.

Judging by the scar of its insertion on the fibula, the iliofibularis was a powerful crural flexor.

ii) m. flexor tibialis internus

Evidence for the origin of part of this muscle exists in a small circular rugosity immediately behind the acetabulum on the lateral surface of the base of the ischium. The size and nature of the scar suggest a tendinous origin.

The flexortibialis internus probably joined the flexortibialis externus to share a common tendinous insertion on the tibia.

iii) m. flexortibialis externus

As noted above, this muscle seems to have arisen on the quadrangular platform at the rear of the ilium near the m. iliofibularis. Its origin was restricted and might therefore have been tendinous or aponeurotic, since in other forms - notably the birds - this muscle is a powerful crural flexor with a bulky belly.

The common tendon of insertion of this muscle and the flexor-tibialis internus probably attached to the medial surface of the cnemial crest near its apex, inserting into the pit in this position in association with the origin of part of the gastrocnemius.

C) Flexors of the metatarsus

If the peroneus complex inserted on the ventral surface of the metatarsus with the digital flexors, as is the case in birds, then the only metatarsal flexor muscle of particular note is the m. tibialis anterior.

m. tibialis anterior

In birds a slip of this muscle originates on the femur from a pit on the external condyle (Fisher, 1946; Berger, 1952; Cracraft, 1971). Much the same seems to have been true of Syntarsus where a small rugosity on the anterolateral edge of the patellar groove at the extreme distal end suggests the origin of this slip. From its origin this portion of the muscle traversed the knee joint to join the remainder of the tibialis anterior, after passing through the laterally facing longitudinal hook of the cnemial crest. The greater part of the tibialis anterior had a fleshy origin from the broad concave surface of the tibia between the cnemial crest and the fibula, with fibres extending some distance down the shaft before concentrating into the powerful and long inserting tendon.

At the distal end of the tibia, immediately proximal to the astragalocalcaneum, the front surface is heavily scarred in adult specimens and the scarring is taken to represent a strong transverse or "annular" ligament which held the tibialis anterior tendon close to the tarsal joint in this region. The ligament attached to the tibia on a broad ridge at the anteromedial corner of the distal end, and to the flared base of the fibula, leaving a trough between them through which the tendon passed together with the tendon of the extensor digitorum longus.

The insertion of the tibialis anterior was onto the proximal end of the metatarsus immediately after emerging from the transverse or annular ligament. In this region the metatarsals are shallowly excavated on their dorsal surfaces to provide a wide depression when articulated together. The tendon opened out to insert in the depression by a strong fascia which also covered much of the dorsum of the metatarsus, helping to keep the metatarsals tightly bound together and functioning as a unit.

D) Digital extensors

m. extensor digitorum longus

Distal to the fibular flange near the proximal end of the tibia is a depressed area bounded laterally by the highest parts of the fibular crest. This is interpreted as the proximal limit of the area of origin of the m. extensor digitorum longus. Fibres of this muscle probably originated fleshily to the point where the fibular crest fades imperceptibly into the fibular shaft, at which point they converged into the long inserting tendon. The tendon traversed the tarsal joint beneath the transverse or annular ligament, together with the tendon of the tibialis anterior, and divided over the dorsum of the metatarsus, sending branches to digits II, III and IV to insert on the extensor tubercle at the base of each claw.

Contraction of this muscle, apart from its obvious effect in extending the central toes, assisted in flexing the metatarsus.

m. popliteus

The popliteus is one of two muscles remaining to be considered of those that can be located in the hindlimb of Syntarsus. Its presumed origin was fleshy from the posterior surface of the tibial head immediately distal to the knee in a depression between the two tibial condyles. It was a very short muscle which inserted on the medial face of the fibula head in a relatively smooth small area immediately proximal to the upper limit of the m. flexor digitorum longus. Its contraction would have pulled the fibula more closely to the tibia, and possibly slightly backwards. Its function is not clear, and Cracrfat (1971) suggests that in the domestic pigeon, Columba livia, it may have some effect in controlling knee-joint extension.

m. abductor hallucis

The other of the two muscles located is what must be termed the m. abductor hallucis. This was an extremely short but obviously well developed muscle which arose on the medial surface of the distal third of metatarsal I, principally from a tubercle protruding medially just proximal to the articular surface. It inserted on a corresponding medial tubercle at the proximal end of the first phalanx (Fig. 20). Its action would have been to produce a medial swing or abduction of the hallux, causing it to diverge away from the rest of the foot.

Muscles not located with certainty in Syntarsus

Part of the difficulty encountered in this anyalysis of Syntarsus limb muscles involves the equivocal nature of some of the presumed areas of origin. Insertion areas are generally less difficult to define because so many of the insertions were tendinous and left clear scars. Associated with the problem of identifying muscle origins is the problem of gauging the possible degree of differentiation of each muscle into a number of separate heads. Only when there is clear or strongly suggestive evidence of such a differentiation in Syntarsus has this been taken into account in the reconstruction (e.g. puboischiofemoralis externus; iliotibialis and "sartorius"). Of the total list of "possible" muscles compiled from Romer (1923 a,b), Fisher, (1946), Berger (1952), Galton (1969) and Cracraft (1971) the following have not been located with certainty :

i) m. puboischiotibialis. In crocodilians this reduced muscle appears to be part of the flexortibialis complex (Romer, 1923 a). It might have been present in Syntarsus, originating from the ample space of the puboischiadic plate but it cannot be demonstrated. It is lost in birds (Galton, 1969), which might equally well have been the case in Syntarsus.

ii) Short digital flexors, extensors, abductors and adductors. Although such muscles must have been present, their origins are not marked in any of the specimens to hand, but the following comments are relevant :

a) the m. extensor hallucis longus can be recognised only in its point of insertion on the extensor tubercle on the claw of the reduced digit I.

b) the m. flexor hallucis brevis might have arisen along the medial surface of metatarsal II, or even on the presumably cartilaginous proximal portions of the reduced metatarsal I near the origin of m. abductor hallucis to insert on the ventral surface of the proximal end of the first phalanx.

c) both digits II and IV evidently bore abductor (? and adductor) muscles. The proximal end of the first phalanx of each bears a rugose scar on its abaxial surface onto which such abductors would have inserted. The evidence of toe splay in the footprints attributed to Syntarsus (Raath, 1972 and Plate 31) supports the existence of these muscles. Neither the abductor nor adductor muscle origins can be located.

d) the m. extensor brevis digiti IV and the m. extensor proprius digiti III cannot be located.

e) the m. lumbricalis, arising and inserting on soft tissues as it is known to do in birds (Cracraft, 1971), cannot be located.

6. ASPECTS OF THE FUNCTIONAL ANATOMY AND BIOLOGY OF SYNTARSUS

The quality of the Syntarsus material and the opportunities that it has offered for reconstruction and study of some of the soft tissues has prompted, in turn, a desire to look at Syntarsus as a living, moving animal. In the following sections consideration is given to some of the anatomical specializations discussed in the preceeding sections, in relation to their significance in the animal's biology.

CRANIAL KINESIS (Fig. 32; Plate 4; Table 15)

Several factors point to a kinetic skull in Syntarsus: the fact that tightly bound sutures are rare except in the braincase, while moveable joints of several kinds are common (Fig. 3, 4); that, as a consequence of the loose articulations, the majority of the cranial elements were recovered disassociated; and the differentiation of the jaw musculature showing clearly the presence of the protractor pterygoidei, and pointing to the presence of the levator pterygoidei.

The mobile skull articulations have been grouped into four main categories (Table 15) according to the joint type, with an arbitrary "mobility rating" assigned to the joints. Those rated "very mobile" have design features which permited a great deal of movement between the participating elements; in some cases the actual amount of movement may have been restricted by the presence of stops associated with the joints. Those rated "intermediately mobile" were largely governed by the limitations of bone deformation and connective tissue elasticity. The "least mobile" joints are those which articulated through complex tongue-and-groove articulations or which are considered to have been tightly bound by inelastic connective tissues.

Several important recent reviews of cranial kinesis in various living animal groups (Simonetta, 1960; Frazzetta, 1962; Bock, 1964) underline the difficulties of any clear interpretation of the sequence and details of movement in the kinetic mechanism, and of the functional significance of these movements. Most workers agree that kinesis is concerned with an elevation of the snout region of the skull often coupled with depression of the lower jaws, either through mechanical coupling, as in some birds (Bock, 1964), or via neuromuscular pathways.

Three different kinds of kinetic joint are generally recognised, depending on their location in the skull (Frazzetta, 1962):

i) a prokinetic joint, which lies in front of the eyes

ii) a mesokinetic joint, which lies between the frontals and parietals

iii) a metakinetic joint, which lies between the parietals and the occiput.

Animals possessing a single kinetic joint are described as monokinetic, and those with two are amphikinetic, regardless of which two kinetic joints are associated.

Syntarsus certainly possessed a prokinetic joint in the form of a frontonasal "hinge" (Fig 32; Plate 4), but it seems likely that it also had a (?) vestigeal metakinetic joint similar to that described by Frazzetta (1962) in Varanus, where the hinge lies on the exoccipitals and the parietal rides over the supraoccipital during the kinetic cycle. This suggestion is supported by the fact that the articulations between the frontoparietal-plus-laterosphenoid units and the prootics consist of relatively broad surfaces which meet edge-to-edge and which are devoid of interdigitating sutures, resulting in the postmortem disassociation of the skull roof from the braincase in several specimens collected. The parietal flanges resting on the paroccipital processes are very thin walled, especially at their distal (articulatory) margins, suggesting that a limited degree of bone deformation was possible here.

The frontonasal hinge, or prokinetic joint, consists of the squamose overlap of thin flat terminal surfaces on the frontals and nasals immediately in front of the orbits, forming a transverse zone of deformable bone which acts as the hinge.

In terms of Frazzetta's (1962) analysis, the "fixed" occipital segment in Syntarsus consists of the occiput below the parietals, together with the sidewall of the braincase (below and behind the laterosphenoids) and the basal portions of the braincase and parasphenoid rostrum (Fig. 32).

The maxillary segment consists of the following units :

i) parietal unit, comprising the skull roof between the two kinetic hinges and made up of parietals, frontals, laterosphenoids, upper temporal arches and prefrontals;

ii) quadrate unit on each side consisting of the streptostylic quadrate with the adnate quadratojugal;

iii) basal unit on each side comprising the pterygoid, ectopterygoid, palatine and vomers, and including the jugals laterally;

iv) muzzle unit, comprising the lachrymals, maxillae and premaxillae. The premaxillae seem to constitute a separate unit, because they appear to have been moveable relative to the rest of the muzzle unit, but since this movement was probably minor in nature it is treated here as part of the muzzle unit. The minor independent mobility of the premaxillae will be discussed separately below.

The mandible bears an intramandibular joint whose axis lies in the region of the front margin of the external mandibular fenestra.

The bones in this region (angular, dentary, splenial, prearticular, coronoid) are very thin broad expanses of bone which meet in squamose overlaps, walling the lumen of the meckelian canal internally. The joint so formed would allow movement in a vertical and a horizontal plane by sliding and flexing actions respectively, thus permitting a modification of the gape, and buckling outwards of the mid portions of the mandibular rami as noted by Frazzetta (1962) in Varanus.

Muscles associated with cranial kinesis

Although all of the jaw musculature would have been involved in some way with the kinetic movements of the skull, certain elements of the musculature can be regarded as playing a primary role in the two main movements, protraction and retraction.

Principal protractors

The two muscles principally concerned with protraction are the protractor pterygoidei and the levator pterygoidei (Frazzetta, 1962). In Syntarsus the former exerts a forward pull on the quadrate and pterygoid relative to the braincase, while the latter, reconstructed as originating on the lateral walls of the parasphenoid rostrum, pulls up and forward on the palatal roof. Because of their orientation, from a medial origin to a lateral insertion, both muscles also exert a pull towards the midline on contraction.

Dr. A.D. Walker (pers.comm.) suggests that in Sphenosuchus the depressor mandibulae muscle is also a powerful protractor, because of its steep insertion on the retroarticular process below the level of the jaw articulation. In Syntarsus it is unlikely that this muscle could have been responsible for any initiation of protraction, but its contraction may have assisted protraction in the terminal phases with the jaws open. In this situation the streptostylic quadrate would already have rotated forward, and the inclination of the thrust of the articular cotylus on the quadrate condyle in consequence of depressor mandibulae contraction would push the distal end of the condyle further forward. Thus, in Syntarsus, protraction by the depressor mandibulae, if it operated at all, seems to have operated only at extreme protraction combined with maximum gape.

Principal retractors

The powerful jaw adductors and the pterygoideus muscles are the main retractors. As in Varanus (Frazzetta, 1962) retraction and closing of the jaws seem to have been linked in Syntarsus.

The pterygoideus bellies pull back on the palate relative to the "fixed" lower jaw (anchored at the quadrate-articular joint), which tends to restore the palate to the resting position causing the pterygoids to splay laterally by riding along the facets of the basipterygoid processes. At the same time they pull up on the mandible in conjunction with the adductors, closing the jaw. The adductor muscles, originating as they do in the temporal region, also pull back on the mandibles (because of their insertion at a point substantially forward of the origin of the intramandibular muscle), and pull down on the "parietal unit", thus restoring the metakinetic hinge to rest.

The kinetic mechanism

Manipulation of an articulated hardboard model (Plate 4) of the skull of Syntarsus demonstrates the main movements of the kinetic mechanism (Fig. 32). Basically the mechanism consists of a quadric-crank (Frazzetta, 1962) at the rear end of the skull which, when deformed, operates a push rod system which modifies the attitude of the anterior end of the upper jaw. In combination with depression or elevation of the mandible, this affects the gape of the jaws and modifies the profile outline of the skull. Although most of the kinetic movements operate in a parasaggital plane, there are some components which operate transversely. The transverse movements are subtle and difficult to analyse in detail, and they were not reproduced in the hardboard model. Description of these transverse movements in what follows is based solely on direct observation of the bones, while analysis of the parasaggital movements is based on direct bone observation and manipulation of the model.

The kinetic mechanism can be resolved into two main components which are defined according to the path of the thrust. The first is the marginal thrust path, and the other the axial thrust path.

Marginal thrust path

This is the principal component which acts in a "conventional" way. Movement is initiated by the protractor pterygoidei muscle pulling forward on the quadrate whose lower end rotates forward because the quadrate head pivots in the "fixed" squamosal cup. Because of the contact of the quadrate wing of the pterygoid with the quadrate, the pterygoid is also thrust forward. The consequential events along the palate are the same as those to be described under the axial thrust path, and they will be followed in that section.

Along the jaw margin, rotation of the quadrate carries with it the adnate quadratojugal which thrusts on the jugal. The grooved articulation between quadratojugal and jugal suggests that some telescoping between the two elements took place here, to compensate for an alteration in alignment of the two bones which would have threatened to break a rigid joint under tension. The jugal in turn thrusts on the maxilla, with similar compensation for tension provided by the sliding grooved joint between them. This joint is also covered squamosely by the foot of the lachrymal, which, in conjunction with the connective tissues at this point, would have assisted in preventing lateral buckling. The thrust is transmitted by the maxilla to the tip of the snout where the maxillae and premaxillae are locked together by the ramp-and-spur mechanism. Protrusion of the snout is resisted by its roof formed of the nasals, so that the forward thrust is resolved into a lifting, rotating component about the frontonasal hinge and the metakinetic hinge at the occiput. Thus the gape of the jaw is widened. Measurements from the articulated model indicate that the gape of the mandible, from rest, where the mouth is closed, to extreme protraction, is improved by about 10%, compared with a 15% wider gape reported by Bellairs (1969) in Varanus. Combined, as it is, with opening of the lower jaw by contraction of the depressor mandibulae muscle, kinetic muzzle protraction seems to be concerned with feeding activity.

The push-rod mechanism operating along the margin of the jaw is delicate. Unlike the rods in birds, which, although slender, are subcircular in section and therefore less vulnerable to tensional forces, the marginal elements in Syntarsus are bilaterally thin and relatively deep. They are thus relatively strong in the vertical plane, because of their depth, but vulnerable to tension and buckling in the horizontal plane, because of their thinness.

The main transmission of thrust along the marginal path causes subsidiary shifts in bone articulations through the abundant mobile articulations between skull elements. Thus, as the quadrate foot rotates forward, pushing the jugal via the quadratojugal, the upper arm of the jugal must move relative to the descending arm of the postorbital, the latter bone being "fixed" to the parietal unit.

Provision is made for this adjustment in the curved, sliding articulation between postorbital and jugal. Similarly, the lachrymal must pivot on the prefrontal when the snout lifts. Its lower end moves forward with the transmission of thrust from the jugal to the maxilla, and, since it is firmly united with the upper ramus of the maxilla dorsally, its anterior arm is lifted. The expected position of the pivot is indicated by a smooth, rounded surface of articulation on the reduced prefrontal which mates with a corresponding polished surface on the lachrymal. This lachrymal-prefrontal pivot area lies in line with the axis of the frontonasal hinge, as would be expected for it to work.

Opening of the metakinetic hinge at the occiput is accomplished by a continuation of the thrust forces via the frontals (pushed by the nasals, lachrymals and prefrontals) and parietals, deforming the thin parietal flanges which rest on the paroccipital processes and causing the skull roof to lift slightly.

Axial thrust path

The second component of the kinetic mechanism is axial, along the palate to the snout tip. The axial transmission unit seems to have been capable of operating "passively" (in concert with the marginal unit) or "actively" (independently of the marginal unit).

As noted in the section on the marginal path, contraction of the protractor pterygoidei, in pulling the quadrate forward, brought with it a forward pull on the quadrate wing of the pterygoid. Because the muscle pulls obliquely in toward the midline and slightly upward, the pterygoids converge and lift, guided by the inclination of the articular surfaces of the basipterygoid processes which are gripped by the articular grooves on the pterygoid. Thrust is transmitted along the pterygoids, affecting the ectopterygoids and palatines along the way. The ectopterygoids articulate laterally with the jugals, which are simultaneously in motion because of marginal thrust. The palatines tend to be "wedged" laterally by the pterygoids, and it seems probable that the initial medial convergence of the hind parts of the pterygoids compensates for this wedging tendency. The nature of the pterygoid-palatine articulation is not known in detail, but the delicate, wafer-thin nature of the bones in their mutual articular regions suggests that the union was squamose and mobile. This would also tend to counteract any wedging force on the palatines. The slender, rod-like anterior ends of the pterygoids transmitted the thrust forwards, probably to the posterior spur (? vomer) on each premaxilla. Details are again unclear because no pterygoid collected to date is undamaged in this region. Furthermore, doubt about the identity of the vomer hinders a clear elucidation of relationships at the anterior tip of the palate. If, as has been suggested above, the vomers are fused and represented by the premaxillary spurs, then the logical path of thrust would be along the pterygoid (which is re-inforced along the medial edge by a ridge which continues forward as the anterior spike), to the vomer and thence to the premaxilla. At the snout tip the resolution of the forward thrust into the posterodorsal force which opens the kinetic hinges combines the transmissions from both the axial and marginal paths.

The "active", or independent, mobility of the palate seems to have been initiated by the levator pterygoidei muscle which evidently played only a subsidiary or accessory role in the "passive" sequence. On its contraction, the pterygoids are pulled forward, upward and inward because of the alignment of the muscle. Because the protractor pterygoidei is thought to be relaxed in this phase, the quadrate wing of the pterygoid is permitted to slide forward relative to the stationary quadrate.

Transmission of thrust along the palate is now the same as in the "passive" sequence, but the elements of the jaw margin(quadrate, quadratojugal, jugal, maxilla) are stationary. The consequence of thrust at the snout tip now is to unlock the ramp-and-spur mechanism between the premaxilla and maxilla, allowing the premaxilla to protrude and dip by riding along the maxillary ramp. The loose, curved groove-and-runner articulations between the nasals and premaxillae permit the protraction of the premaxillae by sliding. One consequence of this movement would be to deform and slightly enlarge the opening of the external naris, but the effects would be slight and presumably permitted by loose soft tissues in the area.

Retraction

Retraction of the protracted snout, and restoration of the kinetic hinges to the closed resting position is accomplished by the jaw closing muscles, the adductors and the pterygoideus complex. Because of their origin far back on the skull and their postulated insertion via the intramandibularis far forward in the lower jaw, the adductors exert a backward pull on the lower jaw on contraction. Apart from closing the jaw this force also pulls back on the foot of the quadrate because of its articulation with the mandible. The effect is to draw back the marginal elements of the upper jaw which are part of the marginal thrust path, thus closing the metakinetic hinge and restoring the deformable zone of the prokinetic hinge. Unloading of elastic ligaments probably assisted in this restoration to rest. The same backward pull would initiate retraction of the protracted palatal elements, but contraction of the pterygoideus would exert a powerful and direct backward pull on the palate, causing the pterygoids to draw back until stopped by the limits of the basipterygoid facets, at the same time reversing the protractor wedging effect by pulling laterally on the pterygoids because of the inclination of the muscle, and because of the inclination of the basipterygoid facets. The basipterygoid processes also guide the pterygoids ventrally in conjunction with contraction of the pterygoideus. This action is antagonistic to the effects of contraction of the levator pterygoidei during protraction.

Comparison with other forms

Few detailed studies of cranial kinesis in fossil forms exist against which to compare Syntarsus apart from the exhaustive studies by Dr. A.D. Walker of the vestigeal kinesis in the young of Sphenosuchus, a pseudosuchian from the South African Upper Triassic. I am grateful to Dr. Walker for permitting me to use his as yet unpublished detailed findings in the following comparison.

The kinetic mechanisms of the two genera are comparable and similar in many respects. Notable differences include -

1) Walker's conclusion that the depressor mandibulae muscle is the main initiator of protraction in Sphenosuchus, because of the inclination of the quadrate and the design of the retroarticular process of the mandible. It is doubtful that the depressor mandibulae performed in this way in Syntarsus except in the terminal phases of opening the mouth to its extreme limits.

2) The forward shift of the head of the quadrate in Sphenosuchus to occupy a position similar to that in birds and crocodilians in which it articulates with the pro-otic (rather than the opisthotic) and squamosal (Walker, 1974). The quadrate head in Syntarsus articulates normally. Walker (in litt.) has noted mobile cranial articulations in Sphenosuchus, several of which are similar to those in Syntarsus,

notably: sliding through a short arc between jugal and postorbital; telescoping between quadratojugal and jugal; tongue-and-groove sliding joint between the front end of the jugal and the rear end of the maxilla; sliding contacts between the nasals and the frontals, lachrymals and prefrontals (Sphenosuchus differs slightly from Syntarsus in that the latter's nasals and frontals are regarded as forming a "hinge" of thin, deformable squamose bone, whereas Walker believes the maxillae of Sphenosuchus hindered hinging so that kinesis was achieved by sliding between the mobile nasals and the fixed frontals). The main kinetic pivot in Sphenosuchus lies far back in the temporal region (Walker, in litt.) in a position comparable with the metakinetic hinge of Syntarsus. Walker is of the opinion that the quadratojugal, jugal and maxilla in Sphenosuchus probably did not contribute much to active transmission of thrust, but permitted it to take place by not hindering the main thrust transmitted along the palate.

Walker believes that stretched ligaments played an important role in retraction and restoring the kinetic components to rest in Sphenosuchus, with an obvious concomitant advantage in economy of energy. The same is most probably true of Syntarsus, although it is difficult to prove the presence of the necessary ligaments. Moreover it seems that the muscular arrangements in Syntarsus allowed for both protraction and retraction. Since kinesis in Sphenosuchus is vestigeal (Walker, 1974) and demonstrable only in juvenile specimens, while in Syntarsus it is fully developed and functional in adults, it follows that Syntarsus should have more direct and specialised adaptations in its jaw musculature to allow its operation. The proposal of independent mobility of the snout tip via levator pterygoidei action also suggests that Syntarsus was highly specialised in its kinetic mechanism.

Colbert & Russell (1969) have examined kinetic articulations in the Upper Cretaceous theropod Dromaeosaurus from the Oldman formation of North America. In this genus the single kinetic hinge is mesokinetic, lying between the frontals and parietals, as opposed to the amphikinetic condition in Syntarsus with its pro-and metakinetic hinges. Moveable joints between elements in Dromaeosaurus are otherwise similar to those in Syntarsus, but Dromaeosaurus apparently had no independent mobility of the premaxilla.

The question of kinesis in Archaeopteryx is evidently much in dispute. Bock (1964) believes that Archaeopteryx was mesokinetic with a streptostylic quadrate, but he cites the differing views of other students such as Simonetta, who believes that it was akinetic. With the poor material available for study in the critical regions of Archaeopteryx, it is likely that this debate will persist until better specimens are found. Regrettably de Beer's (1954) analysis of Archaeopteryx does little to assist in this debate.

In Ostrom's (1969 b) detailed description of the osteology of Deinonychus he notes that most cranial elements were recovered disarticulated and suggests that the skull "was........probably highly kinetic", without elaborating on the possible mechanism. The sutural joint between premaxilla and maxilla in Deinonychus shows that independent premaxillary mobility did not exist in this genus, but other potentially loose sliding articulations are evident in Ostrom's reconstruction of the skull (Ostrom, 1969 b: Figs. 4, 5) similar to those found in the skull of Syntarsus.

Russell (1969) has shown that interdigitating sutures in the skull roof of the Cretaceous theropod Stenonychosaurus precludes operation of a mesokinetic hinge, but the paucity of available material does not permit analysis of possible alternatives.

Galton (1974) has considered the evidence for kinesis in the lower Cretaceous ornithopod Hypsilophodon and finds it equivocal. As Galton points out, there are indications in the skull that it might conceivably have been kinetic, but the function of kinesis in a herbivore is a puzzle.

The Cretaceous bird Hesperornis has a streptostylic quadrate but no kinetic hinge (Gingerich, 1973). However, Gingerich notes that the maxilla could probably be moved fore-and-aft, driven by the streptostylic quadrate, over a few millimetres.

It seems that Syntarsus has capitalised on a primitive design feature of many archosaurs in developing the mobility in its premaxilla. A comparable but less advanced ramp-and-spur articulation between the premaxilla and maxilla can be seen in such diverse forms as the thecodonts Euparkeria and Proterosuchus, and the prosauropod dinosaur Massospondylus (C.E. Gow, pers. comm.). Cruickshank (1972) has noted that several of the known specimens of Proterosuchus show displaced premaxillae and other indications of loose articulations between bones of the snout. These might be related to snout mobility, and the premaxillary "rostrum" of proterosuchian thecodonts looks like an ideal anatomical forerunner of the mobile Syntarsus snout-tip (see e.g. Cruickshank, 1972: Fig. 2). Colbert (pers. comm.) reports loose articulations between the premaxillae and adjacent bones in the American theropod Coelophysis which is clearly closely related to Syntarsus. It is thus possible that premaxillary mobility was fairly widespread amongst early archosaurs. Its function seems to have been involved with minor manipulations at the front of the jaw, perhaps in picking up small food morsels, manipulation of food within the mouth, preventing escape of live small prey from the mouth, etc. In Syntarsus the mechanism seems to have evolved to a specialised condition and I suggest that, in addition to the more "expected" functions outlined above, Syntarsus might have employed this specialisation for grooming or preening. The difference between the teeth at the tip of the jaw and those behind is probably related to cranial kinesis, and is presumably involved to some extent with the feeding activities of the animal. The mobile snout, capable of sliding protraction and retraction, might have functioned as a "rake" to gather and orientate food debris in the mouth, or to carry out minor manipulations within the mouth. The lack of serrations indicates that they were not concerned with the slicing of meat, and their slender build suggests that their normal use in feeding was for gripping and slight manipulation of the food, but not for vigorous biting. The procumbent nature of the first dentary tooth is exaggerated in the right ramus of QG 303, where the tooth apex points almost directly forward. This exaggeration is comparable with the apparent sharp backward inclination of the more posterior teeth in their early stages of eruption.

Combined with the procumbent anterior dentary teeth, the minor "combing" action of the rake-like premaxillary teeth (nearly straight, sub-circular in section, not serrated) would have been an ideal grooming aid. Elsewhere in this study it is suggested that Syntarsus had a feathered integument and the premaxillary preening action would have been useful in this regard.

Function of cranial kinesis in Syntarsus

Apart from the proposed grooming function noted above for the independent premaxillary mobility, kinesis in Syntarsus must be related to feeding. Bellairs (1969) notes that in lizards it is important in alighment and occlusion of the teeth, and that it acts as a damper when the jaws of a carnivore are snapped shut. Bellairs cites the view of Dr. P. Robinson that kinesis in lizards also permits the lower jaw to move back and forth (because of the rotation of the streptostylic quadrate) without necessitating palatal movements, which Robinson believes helps to pull prey into the mouth. Similarly, Gans (1961) (cited by Bellairs, 1969) suggests that streptostyly helps in what he terms "inertial feeding", by which the prey remains stationary while the jaws are quickly opened, protracted and snapped shut repeatedly, thus progressively shifting the prey back for swallowing.

Syntarsus was clearly carnivorous; the nature of the teeth and the bony stomach contents of the type specimen leave no doubt of this. Perhaps in snatching small vertebrates, such as lizards, from the desert sands Syntarsus "struck" with its long and mobile neck, and a non-rigid skull with a capability to dissipate the shock of the strike would have been very necessary. The kinetic capability (in both the upper and lower jaws) would also be of advantage in clamping tightly on anything in the jaw, allowing some "give" to protect delicate cranial bones against damage. Thus, if the pterygoideus muscles contracted tetanically, the rear portions of the jaw adjacent to the articulation would clamp strongly, thus increasing the gripping ability of the teeth at the front or middle sections of the jaw without threatening to break the forward elements. As noted in the section on cranial osteology, the pterygoid-ectopterygoid articulation is complex and so arranged that movement between the two bones is possible fore and aft, and by yawing, but any biting movement locks the two together to function as a single unit. It thus seems that the accessory head of the pterygoideus muscle proposed here, which fills the carnosaur pocket made up of pterygoid and ectopterygoid, is the "big bite muscle" of Syntarsus.

The premaxillary mobility in Syntarsus, apart from its probable usefulness in preening, would have been useful in feeding in allowing the animal to pick soft tissues off a carcass while scavenging by allowing the tips of the jaws to nip together and pull away the morsel.

MOVEMENTS OF THE HEAD

The well developed axial muscles inserting on the occiput are shown in Fig. 26 b. The most prominent are the rectus capitis posterior above and lateral to the foramen magnum, and its antagonist the rectus capitis anterior on either side on the condyle. The former produces an elevation of the head and maintains it in its normal pose on the column; the latter produces flexion of the skull on the neck. The extension and flexion movements of the head are assisted by the pars articulo-parietalis of the longissimus capitis (which itself seems to have been well developed), the spinalis capitis, the nuchal ligaments, and the pars transversalis capitis. The long skull makes extension a more critical requirement than flexion to maintain the essentially horizontal pose of the head. It is possible that the lack of post-temporal fenestrae, such as are found in the allied Coelophysis (Colbert, pers. comm.), is related to possession of strong cranial extensors by Syntarsus. In locomotion these muscles would have assisted in maintaining balance by critical adjustments in the position of the skull and neck so as to maintain the correct centre of gravity. Many modern birds use the neck and skull in this way, and the movements are especially noticeable in ground dwelling cursorial birds such as the ostrich, Struthio, particularly when cornering at high speed. Furthermore, extensor forces would be necessary to counteract the inertial forces of the head in a hopping animal (such as Syntarsus) each time it landed.

The head-turning muscles (obliquus capitis and pars transversalis capitis of the longissimus capitis) show that lateral turning movements of the head were important and that these were not accomplished merely by bending of the neck in long-necked forms as noted by Ostrom (1961) in his discussion of hadrosaur cranial muscles. No doubt cumulative deflections in the cervical vertebrae would have helped in such bending in Syntarsus.

That the cranial extensors and the nuchal ligaments were strong is shown by several specimens from the Chitake deposits which exhibit marked opisthotonus of the neck. This feature is well known in long-necked fossils, especially those in sediments which indicate some degree of aridity. The drying of the ligaments leads to shortening and consequent traction of the extremities toward the resistant bulk of the body. The type specimen of Syntarsus was not opisthotonically contorted (Raath, 1969) although it was found perfectly articulated in aeolian sandstone representing a very arid regime. Even the ribs were supported in perfect articulation with the trunk vertebrae and such delicate structures as the carpus and gastralia were intact. All of this suggests burial of the specimen under a load of sediment before desiccation or decomposition had begun, and this is probably attributable to the shifting desert sands which could have covered the carcass in short order.

MANUS MOVEMENTS

Galton (1971 a) has shown that the pollex (referred to as "hallux" by Galton) of Syntarsus articulated on asymmetrical distal condyles on metacarpal I producing a flexion arc of the pollex which brought its claw tip in towards the axis of the manus, thus confirming Raath's (1969) suggestion that the pollex was opposable to some degree. Galton has also drawn attention to the remarkable capacity for hyperextension in the manus, allowing the first phalanges of the digits to extend until the digits protrude almost at right angles from the extensor surface of the hand. The significance of this capability in hand movements is not readily understood, but Galton suggests that it was to compensate for a limited capacity for extension at the wrist of Syntarsus. While extension of the manus at the wrist might well have been very limited, flexion was not. The proximal carpals have concave surfaces which articulate with the distal ends of the ulna and (especially) the radius, and the rounded articular ends of these bones are inclined to the palmar surface so as to favour flexion. Furthermore, the small, rounded sesamoid-like bone found at the wrist of the type is on the flexor surface, and, as suggested in the description of the type, may have developed in a strong flexor tendon (Raath, 1969). If Galton's proposal is correct, the combination of digital hyperextension with powerful carpal-plus-digital flexion suggests an adaptation for strong scratching or ripping with the relatively strong trenchant claws of the manus. The opposability of the pollex suggests also an ability to grasp, perhaps to pick up morsels of food torn from a carcass by the scratching and ripping action. The limits which Galton (1971 a) noted in the degree of opposability of the pollex show that the grasping ability of Syntarsus was not such as to allow a strong grip, but it was surely sufficient to manipulate pieces of meat, or to hold small prey animals which were incapable of putting up much of a struggle. The localised group of small bones found within the body cavity of the type and interpreted as stomach contents (Raath, 1969) supports the suggestion that Syntarsus preyed on small vertebrates, as do the isolated Sphenodontid remains recovered from the Syntarsus bed on the Chitake, while the broken Syntarsus-like teeth found near prosauropod skeletons in the Maura River deposits suggests that Syntarsus also utilised carrion. In the deserts in which Syntarsus lived a wide range in food preference would clearly have aided survival. However, it seems that Syntarsus must have been an obligate, if catholic, carnivore; the only known moderate-sized vertebrate herbivores of Forest Sandstone times, the prosauropods, bore gastroliths to deal with their fibrous plant foods (Raath, 1974) since their rather feeble dentition was evidently not equal to the task.

POSTURE AND LOCOMOTION

Posture

Syntarsus was an obligate biped. The long slender legs, short arms, short trunk and long tail all speak eloquently of bipedal grace and agility (Fig. 35). The obviously powerful and differentiated hindlimb musculature leaves little doubt of its propulsive capabilities. Equally, the short and slender arms and the hands armed with their raptorial trenchant claws and partly opposable thumbs leave little doubt of their use as organs of prehension rather than of locomotion. In this connection Galton (1971) was able to state : "This (study of theropod hands) leave Syntarsus as the only theropod described to date in which the hallux (sic) was opposable........".

Yet it is insufficient merely to characterize Syntarsus as a biped. The wealth of detail available in the recovered material deserves and demands a more detailed consideration of the posture of the animal. In recent years this aspect of the reconstruction and restoration of fossil forms has been re-examined in detail by several palaeontologists, notable amongst whom are R.T. Bakker, P.M. Galton, B.H. Newman, J.H. Ostrom and A.D. Walker. Careful study of articular surfaces and the mutual relationships of bones has shown that long-standing and widely accepted restorations of even the most famous dinosaurs (e.g. Tryannosaurus, Newman, 1970, fide Desmond, 1975) are faulty.

The principal structure about which to begin a reconstruction of the stance and pose of a biped is clearly the hindleg. It is largely on the restored attitude and suspension of the hind leg that the pose of the remainder of the body depends. In Syntarsus the attitude of the femur is readily established. Manipulation of the femoral head in the acetabulum, so that the "pseudotrochanter" articulates convincingly with the "pseudoantitrochanter", shows that the femur was held sloping forward, down and cocked laterally to clear the side of the trunk. Articulation of the tibia on the femoral condyles causes the tibia to incline in towards the midline and to slope backwards. Thus the heels are brought under the belly and the metapodials slope fairly steeply down to the toes in contact with the ground. This gives Syntarsus a steeply digitigrade, almost "gralligrade" (Smith, 1967), pose of the limb, and a narrow track.

The next major consideration is the attitude of the vertebral column supported on the legs. The pelvis, connecting the anterior and posterior parts of the column to the supporting limbs, is especially worthy of attention. Again, the most convincing pelvic articulation with the leg in Syntarsus is provided when the pelvis is maintained horizontally, perhaps even dipping very slightly down in front. This in turn leads to a reconstruction of the trunk column as a practically horizontal unit, balancing the almost upright neck at its anterior end. The sigmoid curve of the neck, with its sharp bends at the upper end carrying the horizontal skull and at the cervicodorsal transition, is preserved in several articulated specimens in the collection, and is confirmed by the wedge-shape of the centra of vertebrae from these regions.

The root of the tail in the holotype has a peculiarity in that it kinks slightly upward on the sloping face of the last sacral vertebra. Distally the tail curves down towards the ground and ends in a slender "whiplash".

The rib cage was evidently quite strongly raked, as judged from the excellently preserved dorsal series of the type and confirmed by other articulated specimens in the collection. On this cage, shallow anteriorly and deepening posteriorly towards the pelvis, the arm was suspended by the pectoral girdle. The scapulocoracoid was preserved in a shallowly sloping, almost horizontal, attitude in the type, and this was evidently its natural attitude. If the slope is steepened, the contour of the bone does not fit the contour of the rib cage so neatly, and, more importantly, the (?) coracobrachialis tubercle and facet distal to the glenoid is fouled when the humerus protracts, which would prevent the hands from reaching the mouth.

The animal was narrow across the chest and trunk, and rather "slab-sided". Thus the picture which develops of Syntarsus at rest is as shown in Fig. 35 and the Frontispiece.

Corroboration for this type of stance and posture in a theropod is derivable from several sources. Ostrom's (1969 b) reconstruction of Deinonychus serves as a convenient and well-analysed model. Ostrom notes that the anterior dorsal vertebrae of Deinonychus bear clear scars of attachment of strong interspinous ligaments which act as tension members to prevent sagging in a vertebral column held horizontally. He also shows that the sigmoid curve of the neck is inconsistent with the notion of a sloping thoracic column. Similar comments apply to Syntarsus on both counts. Furthermore, Syntarsus has well-developed hyposphene-hypantrum articulations between the vertebrae of the trunk and those of the anterior portion of the tail, which make the prospect of sagging or vertical dislocation of the horizontal segmented series even more remote.

The incorporation of possibly two dorsal vertebrae into the bending mechanism at the base of the neck effectively shortens the trunk of Syntarsus, conferring a considerable advantage on a biped concerned with maintaining balance about the hip. The ratio of trunk length to hindlimb length has long been accepted as an index of bipedalism.

Table 16 (adapted from Galton, 1971 b) shows where Syntarsus stands in relation to other known bipeds in regard to this index, and other skeletal ratios.

The upward kink at the root of the tail suggests that the tail might have been used during locomotion as a dynamic stabilizer and counterbalance, in much the same way as the highly specialized, stiffened tail of Deinonychus (Ostrom, 1969 b), or the tail of Tyrannosaurus (Newman, 1970 fide Desmond, 1975) and other recently restudied dinosaurs, both saurischian and ornithischian. However, there is no trace in Syntarsus of the ossified caudal tendons found in many of these other dinosaurs.

Locomotion

How did Syntarsus, as a biped, move? Two principal alternatives must be considered. Either it moved by alternating strides of the legs, or else it hopped saltatorially in kangaroo fashion. The distinction, on anatomical grounds, between these two means of locomotion is by no means clear cut. Howell (1944) expressed the opinion that the differences were slight and probably dependent chiefly on the functioning of the nervous system. He noted that certain American birds within the same family differ in their choice of locomotor style on the ground, some hopping and others striding. Amongst African birds differences are often to be found within the same genus - e.g. the hornbill genus Tockus, in which the Yellowbilled Hornbill, T. flavirostris, habitually walks when on the ground while the Grey Hornbill, T. nasutus, habitually hops.

Howell (1944) listed a number of specializations which he regards as characterizing modern mammalian saltators (e.g. kangaroos, jerboas, gerbils, kangaroo rats, springhares, etc.) :

i) extreme lengthening of the hindlimb, particularly the distal segments;

ii) reduction in the number of digits in the foot;

iii) fusion of metatarsals;

iv) shortening of the body;

v) lengthening of the tail, which generally develops a hairy terminal tuft;

vi) fusion of some cervical vertebrae in some forms;

vii) lengthening of the ear pinna, or enlargement of the bulla.

It is also clear from Howell's analysis that most of the obligate bipedal saltators of the modern world live in arid, semi-arid or sandy areas.

In terms of Howell's criteria, Syntarsus fits with regard to hindlimb length, digital reduction, metatarsal fusion, trunk shortening, tail length and environmental type. But it must be conceded that, on these anatomical grounds, almost all other bipedal dinosaurs would qualify as well. Thus the question of whether or not Syntarsus bears any particular anatomical specializations consistent with, or directly indicative of, saltation must be considered. The anatomical structures relevant to locomotion are chiefly :

i) limb design and suspension

ii) musculature

iii) specializations to cope with shocks and stresses in the rest of the body supported by the legs.

Naturally, footprints and (especially) trackways could be particularly helpful in deciding the type of locomotion used.

In terms of limb design and suspension Syntarsus has some extraordinary specializations which have been described elsewhere in this study. The pelvic girdle itself, the crucial link structure between the body and its propulsive mechanism, is an impressive example of structural design for maximal strength coupled with minimal weight (Plate 30). The girdle is supported by structures which seem to be tension and compression members to safeguard against buckling, distortion or fracture. Along the top, running the length of the girdle, is a double-channel arrangement consisting of the iliac crests on either side of the central coalesced spinal blade. Each of the crests, and particularly the central one, is reinforced by a dilated rim at its free-standing edge. Between the roughly parallel crests the channel floor is provided by the coalesced transverse processes forming a continuous thin sheet of bone on either side.

The acetabular cup is small in diameter, deep and protected dorsally by the projecting lip or "roof". This forms an enarthrodial joint with the femur to give great mechanical strength and weight-bearing potential (Thulborn, 1975).

The walls of the acetabulum, formed partly by each of the three bones participating in the pelvis, are strong. Even in immature individuals, in which coalescence has yet to take place, the articulation between the elements is complex and strong (Plate 19 b).

Behind the acetabulum the pelvis and sacrum form a compact, light, but very robust box-like structure (Plate 30). The dorsal roof is composed of coalesced transverse processes, and the side walls are formed by the curved iliac blades. The floor of the box is symmetrically perforated and is buttressed by longitudinal and transverse bony struts, the most rigid of which is the axial unit formed by the coalesced sacral centra. The outer parts of the floor of the box provide the broad surfaces of origin for the powerful caudifemoralis brevis muscles.

Beneath the sacropelvic box the continuous puboischiadic plate seems to form a tie beam to prevent tension spreading of the pelvic arch under load.

The complexity of the pelvic structure behind the acetabulum, and the extent to which the pelvis flares transversely in this region, seems to be a major point of difference between Syntarsus and Coelophysis (Colbert, pers. comm.).

The limb bones, especially the femur, are notably specialised for bipedal locomotion. Robust femora demonstrate an extraordinary degree of muscularity and the clear scars of capsular tissues at the sites of limb joint capsules indicate that the joints were strongly braced by tough connective tissues. The tarsal joint is effectively reduced to a simple hinge because of the loss of freely articulating tarsalia through fusion. The hind end of the metatarsus, with the protruding proximal end of metatarsal V and the extensor boss (or "hypotarsus") below the proximal end of metatarsal III, provides evidence of its use as a strong extensor lever of the foot (Fig. 19 a).

Limb musculature in Syntarsus, as already described (Fig. 29), is well differentiated and powerful, particularly with regard to propulsive muscles (caudifemoralis, "triceps femoris" and gastrocnemius) and the main recovery muscles (puboischiofemoralis, iliofemoralis and crural flexors). All of the recovery muscles have relatively short moment arms, which indicates that they effect rapid recovery since a small amount of contraction produces a great amount of movement at the distal ends of the bones on which they insert.

Amongst specializations to cope with shocks and stresses in the rest of the body may be listed the hyposphene-hypantrum articulations betwen dorsal vertebrae (Fig. 10) and in the anterior 1/3 of the tail, the lightly built kinetic skull (Fig. 3), and the abdominal "basket" of gastralia (Fig. 11; Plate 14).

As reported by Raath (1972), footprints attributable to *Syntarsus* are also now known (Plate 31).

The evidence of the footprints apart, all of the above-listed features of *Syntarsus* are *a priori* simply specializations for bipedalism and not especially or conclusively indicative of any particular *type* of bipedalism.

In the hope of gaining some idea of the skeletal distinctions, if any, between closely related striders and hoppers, prepared skeletons of two species of the hornbill genus *Tockus* were examined - *T. flavirostris*, which strides, and *T. nasutus* which hops. Selected dimensions and ratios of the pelvis and hindlimb are given in Table 17. Bearing in mind that this comparison is coarse and empirical in that it is based not on a series of each species but is restricted to a single unsexed specimen of each, its value is dubious. However, it is interesting to note that the most marked apparent differences lie in the proportional relationships between the pelvis and femur. The ilium appears to be slightly longer, and substantially broader behind the acetabulum in the hopping form than in the strider.

As mentioned earlier, the only available direct clue to locomotion in *Syntarsus* lies in the footprints attributed to it by Raath (1972). The main block, QG 91 (Plate 31), contains two clear prints of a closely comparable size which fit the dimensions of the adult foot of *Syntarsus* very well. The two prints lie close to each other, are level with each other, and are comparable in all of their observable features. There is no clear indication to show whether these are the prints of a single animal, or the fortuitous juxtaposition of the prints of two different animals. Because of their general similarity in shape, size, angle of toe splay, and depth of claw marks, Raath (1972) regarded them as belonging to one individual. If this interpretation is correct, the question of whether the prints represent a strider standing at rest, or a hopper in motion remains to be answered. The strider notion can probably be discounted on the following grounds : when a "normal bipedal strider", such as man, stops walking his feet come to rest beside each other, much as might conceivably be the case in the QG 91 prints. However, when walking resumes the two feet behave differently. The first foot to move is passively lifted; the centre of gravity of the body is tilted forward and the airborne foot checks the forward momentum when it next lands on the ground; the second foot now thrusts on the ground to accelerrate the foot through for the second step; and so on. Each print on each side will thereafter show signs of thrust at the toe, but the resting prints will show thrust signs in only one, i.e. the print of the second foot to move. A bipedal hopper coming to rest will also stop with its feet beside each other. However, when the next hop occurs, *both* of the resulting prints will show signs of thrust. It is therefore of interest to note that both prints in the QG 91 block show what are regarded as signs of thrust in that both prints are deeper at the front and the claws of the toes appear to have "slipped" or scratched backwards into them both (Plate 31).

This evidence, combined with the evidence of the strongly muscular hindlimb and the broad and rigid pelvis, makes hopping in *Syntarsus* an attractive feasibility. It is tempting to consider the differences in the pelvis between *Coelophysis* and *Syntarsus* as reflecting differences in the locomotor style by analogy with the hornbills.

What remains a puzzle is the meaning of the differences between robust and gracile limbs. Since the distinction between the two types manifests itself at maturity it seems logical to regard it as an expression of a secondary sexual characteristic. The robust and more muscular limbs are the logical choice for bipedal hopping. But what, then, of the gracile limbs? It is inconceivable that the two sexes should have had differing locomotor styles. It is conceivable that the greater muscularity of robust limbs may be related to an aspect of physical exertion peculiar to one sex, and a number of possibilities come to mind such as intra-specific fighting, courtship display, or perhaps even nest preparation. In this regard it is pertinent to recall Howell's (1944) remark that : "It is probably not the easy movements of everyday life that are chiefly instrumental in shaping the muscular and osseous pattern, but the critical potential that is usually held in reserve". On this basis it is feasible that the periodic exercise of the "critical potential" represented an exaggerated modification of the "easy movements of everyday life", resulting in an exaggerated expression of the more normal features of the musculoskeletal system. Thus possession by only one sex of robust limbs does not by itself preclude the possibility of saltation by gracile individuals of the opposite sex.

That saltation had developed in vertebrates by the Triassic is shown by a growing number of finds of hopping trackways in the geological record. One such find in 1963 by Dr. K.L. Tinley (pers. comm.) was of a small pigeon-sized bipedal track in the Cave Sandstone (Upper Triassic) of the Giant's Castle Reserve in Natal, South Africa. This find was briefly reported by van Dijk (1966). That a dinosaur was responsible for the Giant's Castle trackway seems very probable. Dinosaurs owe much of their success to the perfection of bipedalism in the Triassic (Bakker, 1968; Thulborn, 1975), and the best of the Triassic bipeds (perhaps the only obligate bipeds) known to date are coelurosaurian theropods such as Syntarsus.

A search of the quarry from which the QG 91 footprints were recovered unfortunately produced no trackway. A trackway could very probably have clinched the question one way or the other.

Dawson & Taylor (1973) have studied the energetic costs of hopping in kangaroos and they show that it is energetically a surprisingly inexpensive means of travelling at high speeds. At 18 km/h and faster it is less costly than quadrupedal running, but at slower speeds the energy costs are higher in comparison. Much of the advantage of this type of locomotion seems to depend on energy storage and recovery in elastic ligaments and in tendons (Dawson & Taylor, 1973). Over a measured threefold increase in speed oxygen consumption (and thus energy expenditure) of the kangaroos was found to remain relatively constant, and it was noted that speed varied according to the distance covered per hop rather than the frequency of hopping. Dawson & Taylor (1973) commented : "It is difficult to understand why large hopping herbivores are found only in Australia, since hopping appears to be such an inexpensive way to travel at high speeds".

Syntarsus might represent one non-herbivore which capitalized on the advantages under environmental conditions at least as demanding as those which face the saltatory inhabitants of modern arid regions.

The advantages of bipedalism as a means of locomotion lie mainly in the greater speeds that can be achieved and in greater manouverability, with freeing of the hands as an important corollary. In an active predator hands freed from the duties of locomotion are potentially a considerable asset in feeding. The advantages of bipedal saltation seem to lie largely in the realm of energy conservation at higher speeds (Dawson & Taylor, 1973), and in dodging ability (Bartholomew & Caswell, 1951). Harrison (1976) cites the conclusion of Driver and Humphries that a measure of unpredictability in behaviour helps an animal to escape capture by a predator. The sudden and often erratic leaps of a saltator could certainly confuse a potential predator(Bartholomew & Caswell, 1951), and saltation in Syntarsus might thus have conferred advantage not only in speed coupled with energy conservation, but also in evading attack. It would thus have conferred advantages on Syntarsus on two main counts : hunting ability, and a better ability to avoid falling prey itself to other predators.

Although the question of the type of locomotion used by Syntarsus cannot be settled conclusively at this stage, the weight of the arguments which can be brought to bear on the question seems to me to lean in favour of bipedal saltation.

SEXUAL DIMORPHISM AND NOTES ON BEHAVIOUR

Attention has been drawn repeatedly in this study to bimodal variation in the femur, and possibly in other bones of Syntarsus (humerus, tibia and tarsus). The two principal variants are robust and gracile femora (Plate 22). The differences seem to develop and become manifest at the threshold of maturity, and an explanation for this which springs most readily to mind is that the differences are related to secondary sexual characteristics. As Ager (1963 : 71) notes: "After eating, the most widespread habits among modern animals are those concerned with sex, and there is no reason to suppose that this did not raise its allegedly ugly head millions of years before Freud. Clearly if we are to regard our fossils as once-living creatures, considerations of sex must arise, and many palaeontologists have suggested sexual dimorphism to explain pairs of contemporaneous fossils with slight, but non-gradational differences".

The variation is not related to size as is demonstrated by the femur of the holotype (QG 1), which is robust and 208 mm long, while the femur of QG 76 is gracile and comparable in length at 201 mm, a length difference of only 3,4%. While there are few (9) complete femora whose overall length can be measured, there is a reasonable sample (18) of well preserved femoral heads from which dimensions can be taken (Table 9). The most marked observable differences lie in the much greater trochanteric development in the robust femora than in the gracile. To illustrate the bimodality, the breadth of the lesser trochanter (= iliofemoralis trochanter) of a selection of femoral heads was plotted against the maximum transverse breadth of the femoral head (Fig. 16). It is noteworthy that the gracile portion of the graph includes very small individuals (e.g. QG 691) whereas robust individuals only appear once the femoral head has reached a breadth of 28 mm or more. The graph also suggests that robust specimens grew to a larger absolute size than gracile specimens (QG 726, which is the largest of the robust femora recovered, has a head 15% wider than that of QG 739, which is the largest of the gracile femora).

In the section dealing with locomotion it is argued that robustness may be related to a specific physical activity peculiar to one sex, such as intraspecific fighting, courtship display or nest preparation. Perhaps another possible alternative is a special hunting responsibility to provide for developing young.

Thus it becomes desirable to try to establish which sex is represented by which type of femur. The general observable tendency among vertebrates is for males to be larger and generally more muscular than females. However, there are many exceptions to this generalization, so that merely to declare the robust individuals to be male would be facile and insupportable on reasonable grounds.

The recovered sample of femora, being the largest sample of a readily identifiable bone with distinctive features, was analysed to arrive at an estimate of the minimum number of individuals represented, and to obtain an estimate of the ratio of robust to gracile individuals in three "age classes" based primarily on size (Table 18). Again the contention that robustness develops at or near maturity is borne out, in that none of the "juveniles" are robust, but the split takes place amongst "sub-adults", with gracile forms predominating. By the time full adulthood is reached the ratio has swung slightly in favour of the robust forms. The sample represented in the collection is unlikely to be random in that the conditions prevailing at the time of death might have selected against one particular section of the population, e.g. females reluctant to desert distressed young.

If this were so, it would be expected that females would predominate amongst the adults in the collection, which would suggest that the robust forms are females.

Alternatively, if the sample is random and normal, a sex ratio that favours one sex implies that it is a population with a considerable breeding potential and that females should be the sex predominating numerically. This would also tend to identify the robust forms as females.

It is by no means biologically unknown for females to be larger and generally more powerfully built than males of the same species. Indeed, it is the general rule amongst raptorial birds (Brown & Amadon, 1968). However, in these birds it is also a general rule that male and female pair for life, so that the sex ratio would be expected to be parity. A sex ratio favouring females is expected amongst gregarious animals where mature males are polygamous and tend to collect "harems" (e.g. amongst the antelope and many bird genera). Whether or not Syntarsus was gregarious cannot be established with certainty, but the concentration in the restricted Chitake River pan deposit, which is practically devoid of the remains of any other species, together with the fact that a wide range of growth stages is represented, points at least to some sort of group activity, if not strict gregariousness. Ostrom (1972 a) was able to establish the fact of gregarious behaviour in some species of bipedal dinosaurs on the basis of analyses of fossil trackways, and he cautioned that accumulations of the bones of a single species at one locality (e.g. the Coelophysis accumulation at Ghost Ranch in New Mexico) did not necessarily mean that the animals had been behaving gregariously.

The intense concentration of the Syntarsus bones, both vertically and laterally, within the limits of a very shallow and restricted basin strongly suggests that the death of the group was caused by a single event, and that no great span of time is involved. The animals died together, probably within days or weeks, and the constantly shifting desert sands drifted over the carcasses to bury them and fill the interstices between the bony elements. If this concentration of bones simply represents a "group activity" rather than "herding habits" (Ostrom, 1972 a) why is it that the Syntarsus group seems to have been so successful in excluding other animals from utilising the pan? On the face of it it seems more reasonable to suggest that the group was behaving in truly gregarious fashion, and that the "flock" (for want of a better term) perished together at the shrinking pan which they collectively defended against the other water-seeking animals in the area, after having exhausted the available food resources within reach of the pan.

Ostrom (1969 b) has suggested that Deinonychus hunted in packs because the remains of perhaps as many as five individuals were preserved together in association with the fragmentary remains of a medium size ornithopod, thought to be the prey animal. Similar group hunting behaviour has been proposed for other theropod genera (reviewed by Dodson, 1976). Thus a growing body of evidence is accumulating to show that many dinosaurs had the nervous equipment to permit sophisticated social behaviour and that herding was probably a characteristic common to several genera. Syntarsus seems to have been such a gregarious form.

The evidence seems to suggest that the larger females were the ones burdened with the responsibility of tending and providing for the young and, perhaps, of scraping and preparing nests in the desert sands at breeding time - providing the physical demands on the musculo skeletal system which resulted in the manifestation of robustness in their bones.

One other aspect of behaviour in Syntarsus on which a few comments can be offered concerns predation. The type specimen contained fragmentary small bones which have been interpreted as stomach contents (Raath, 1969) because they lay within the limits of an undisturbed skeleton. The prey animal is not identifiable because of the degree of comminution of the bone, but it was clearly a small vertebrate perhaps of lizard size. Amongst the concentrated bones at the Chitake site are a few vertebrate remains representing forms other than Syntarsus. One element which is readily recognisable is a series of small jaws bearing four or five apparently acrodont teeth. These remains are of sphenodontids (to be described elsewhere by Gow and Raath)but there is no direct evidence that they were the prey of Syntarsus, although their mere presence establishes them at least as potential prey animals. The same remarks apply to the other odd bones, one evidently an osteoderm and three looking rather like part of a sacrum consisting of three or four coalesced vertebrae. The general shape, proportions, texture and fragility rule them out as Syntarsus bones, and their identity for the present must remain unsettled.

Elsewhere in this paper it has been noted that teeth resembling those of Syntarsus have been found in association with prosauropod skeletons, particularly at the Maura River localities. Some of the prosauropods, such as Massospondylus, are quite large and bulky and it seems doubtful that even an adult Syntarsus could have killed one unaided. For this reason the notion that it hunted gregariously is more plausible than any idea of solitary pursuit of large prey. However, it is also very possible that the prosauropods were utilized as carrion by Syntarsus, in which case active predation is not at issue.

THE PHYSIOLOGY OF SYNTARSUS

A burgeoning volume of literature has emerged within the last decade on the question of the physiology of fossil forms, especially the dinosaurs - with authors such as Bakker (1968, 1971 a,b,c, 1972, 1974, 1975), Bakker & Galton (1974), de Ricqles (1969, 1972a, b, 1974), Dodson (1974), Jensen (1969), Ostrom (1969 a, 1973, 1974 b,c, 1975 a,b, 1976 b) and Russell (1965) arguing in favour of the possession by dinosaurs of high energy metabolism and endothermic homeothermy and others such as Axelrod & Bailèy (1967), Bennett & Dalzell (1973), Bennett (1974), Feduccia (1973, 1974) and Thulborn (1973, 1975) arguing against.

The heat of the debate has all but matched the heat of the title of a recent book by Desmond (1975) in which the major contributions on the topic have been reviewed in eminently readable form. Desmond's review settles strongly in favour of the proponents of endothermic homeothermy (i.e. a metabolism in which the constancy of a high body temperature is maintained by physiological processes depending only indirectly on an external source of heat), and he has drawn severe criticism for his "partisan views" by several reviewers (see e.g. the anonymous review by "B.C." in Geological Mag. 113 (3); 1976). Briefly, the main arguments advanced to support the proposal that dinosaurs were endotherms include : the erect gait of dinosaurs which is paralleled in the modern world only amongst birds and mammals - which are endotherms; predator/prey ratios, calculated from museum collections with an assessment of any bias shown by field collectors, which suggest that a small standing crop of predators subsisted on a proportionately much larger standing crop of prey (i.e. predator/prey ratios comparable with those in modern mammalian communities); and the histology of dinosaur bone, which is highly vascular, often extensively remodelled by Haversian modification, and is also paralleled today only in the bone of mammals and birds.

To the proponents of dinosaurian endothermy, the inferences are clear: the attributes enumerated for dinosaurs are found in combination today only in the birds and mammals, all of which are endothermic homeotherms as defined by de Ricqles (1974); thus, dinosaurs can be presumed to share the same fundamental physiological adaptation which is peculiar to these two groups of vertebrates - namely, "warm bloodedness".

The opponents of this view doubt the correlation of erect limbs and parasaggital gait with endothermy, and have cast justifiable doubt on the validity of predator/prey ratios calculated in the manner described. It has also been questioned whether highly vascular, remodelled, "fibrolamellar bone" (de Ricqles, 1974) can be regarded as any measure of physiological sophistication in terms of thermoregulatory ability. For example, Currey (1962) interpreted the similarity of "laminar bone" in a prosauropod dinosaur (unidentified), a dicynodont and a cow as indicating that they are all herbivores because of what is known of the cow, and inferred for the other two.

Ostrom (1974 b) feels that the question of the nature of dinosaur physiology is beyond proof. However, it remains true that investigations along histological, anatomical and palaeoecological lines do, in the opinion of several authors, point to some sort of endothermy in dinosaurs.

The question as far as this study is concerned is : to what extent can Syntarsus contribute to the debate? The only direct clues are

i) joint anatomy and limb suspension
ii) footprints
iii) bone histology.

As far as joints and limbs are concerned it has been shown in this study that Syntarsus is an advanced biped and that it may well have been saltatorial. The evidence of the footprints, if correctly interpreted, supports this view. Study of Syntarsus bone histology shows that its compact bone was highly vascular and subject to some degree of Haversian remodelling, and that it agrees very closely with the "plexiform" variant of fibrolamellar bone defined by de Ricqles (1974 : Fig. 2). This all suggests (but does not prove) that Syntarsus had an advanced physiological pattern. One of the functions of intense vascularization of bone is to provide for the improved recycling of mineral ions in the body of a vertebrate (Currey, 1964; Amprino, 1967). Part of the physiological purpose of the recycling is to make available the ions (including phosphates) required for the body's metabolic processes, including its bioenergetic needs. Ectothermic vertebrates (such as fish, amphibia and "classic" reptiles) have, with very few exceptions, bone which is very poorly vascularized (Enlow & Brown, 1956, 1957, 1958), and in some cases the bone is even devoid of vascularization internally. These animals also have a low metabolic rate. Endothermic vertebrates (mammals, birds), on the other hand, are known to have high metabolic rates and are also the only known vertebrates (apart from dinosaurs and pterosaurs) to have characteristically highly vascular and extensively remodelled Haversian bone. On the face of it, bone vascularity and metabolic rate seem to be linked. The few "classic" ectotherms which do possess reasonably vascular bone, such as some of the large sea turtles and some highly active fish (cited by de Ricqles, 1974), are rather atypical in that they have a higher level of normal activity than their more "normal" relatives. Thus they have an incipient homeothermy, because of the production of body heat by their more sustained activity, which de Ricqles terms "ectothermic homeothermy". The histological structure of their bone is comparable in several respects with that of endothermic homeotherms (de Ricqles, 1974), and they seem, therefore, to be "the exceptions that prove the rule" - i.e. activity levels and the consequent levels of bodily heat production are reflected in the histological pattern of the bone.

On palaeoecological grounds, the indications also lean, in my opinion, in favour of homeothermy in Syntarsus. The environment in which it lived was arid and hot. At the time Rhodesia lay in the heart of the supercontinent of Gondwanaland, itself still linked to Laurasia, but there is some debate about the amount of land lying east of the African coast at the time (see reconstructions in King, 1961 and Cox, 1973). It formed part of what King (1961) terms "de Almeida's great desert", and, as King said, a weather forecast in those days would have been distressingly monotonous : "warm to hot with bright sunshine; rain not expected". He might have added that it would be cold at night. Cox (1973) shows Rhodesia to occupy his palaeolatitude band F(10° - 30°S), so that its position was tropical to subtropical and not greatly different, latitudinally, from the present.

Because of its central intracontinental position, Rhodesia and adjacent areas suffered a dry tropical climate resulting in a desert environment. A modern analogy can presumably be drawn with the Kalahari desert in Botswana, but the scale of the Triassic desert and its attendant climatic rigours were magnified by the sheer size of the landmass and the (presumably) greater distance from the moderating effects of the palaeocoast. As with modern tropical inland deserts, daily and seasonal climatic fluctuations could be expected to be severe. The high daytime temperatures would quickly have dropped after nightfall because of high terrestrial radiation from the bare, sandy land surface unhampered by cloud blankets; seasonal fluctuations would also be high (see Logan, 1968, for an account of desert climatology).

How is an animal the size and shape of Syntarsus equipped to deal with these circumstances? Anatomically it does not bear any obvious adaptations or specializations for burrowing, which is a common strategy adopted by many small animals, both endothermic and ectothermic, to escape extremes of both heat and cold. Its size alone makes burrowing improbable. Other traditional and widespread behavioural tactics for avoidance of temperature extremes (especially high temperatures) are: shadeseeking; wading and bathing; nocturnal behaviour patterns; and aestivation.

Little can be said of shade-seeking by Syntarsus, because knowledge of the vegetation of the time is scanty indeed. Besides, as Smith (1968) points out, an essential characteristic of the desert environment is the sparsity or absence of vegetation. Reasonable stands of vegetation are to be expected around reasonably permanent waterbodies, and indeed one of the few pieces of possible evidence of plants associated with the Rhodesian dinosaur deposits comes from the Maura River localities (Raath et al., 1970).

Syntarsus seems to have been water-dependent - at least to some degree - and presumably would have taken the opportunity to wade and bathe in the pans from which it obtained drinking water. However, it seems unlikely that an animal which is, in any case, clearly adapted for life on dry land and which lived in a desert would have adopted wading or bathing as its principal thermoregulatory tactic.

The question of whether Syntarsus was nocturnally or diurnally active is moot. Its orbit is substantially broader, but no deeper than that of Coelophysis (Colbert, pers. comm.) and the evidence for large "nocturnal" eyes is slim. Besides, the mere fact of nocturnality would not by itself eliminate the need to contend with high temperatures at mid-day, nor would it ease the problems of coping with extremes between daily high and low temperatures.

Faced with these apparent limitations in its ability to combat stresses of temperature (mainly high temperatures) Syntarsus as a naked ectotherm seems particularly vulnerable. Its slender and long legs, neck and tail and its "slab-sided" trunk give it a high surface-to-volume ratio which seems to equip it best for heat-exchange capabilities which would serve its interests least and aggravate its distress by rapid heat gain during periods of high ambient temperature and rapid heat loss during periods of low ambient temperature.

It seems, therefore, logical to argue that Syntarsus solved the problem by physiological means, i.e. by endothermic homeothermy. A high metabolic rate and its attendant production of body heat may seem paradoxical as a means to escape heat stress, but it has been shown that a high "thermostat setting" in birds and mammals lowers the gradient between body temperature and air temperature, so that the animal does not incur excessive heat loads and is faced with the problem of cooling by only a few degrees to maintain an acceptable body temperature. In many cases, especially in birds, the excess may be stored, to be dissipated in the cooler hours of the day when ambient temperatures have dropped. Thus, those birds show diurnal fluctuations of body temperature which may vary by as much as 2° to 4°C (Dawson & Bartholomew, 1968) above their normal high body temperature. Evaporative cooling helps to limit the amount of excess heat stored, but by thermostatic adaptation to hyperthermia the critical need for evaporative cooling is reduced, thus economising in water utilization by the bird. Some birds, including many that are desert residents, will also use gular fluttering to increase evaporation, and thus to increase the evaporative cooling effect at ambient temperatures near the upper limit of tolerance. One of the birds most successful at conquering its heat problems in hot arid areas is the Ostrich, Struthio camelus, which, by "appropriate adjustment of its evaporative cooling,.....maintains a body temperature of 39,3°C.....even at ambient temperatures as high as 51°C" (Dawson & Bartholomew, 1968). It is also pertinent to note that the Ostrich, unlike most other birds, erects its feathers to combat heat. Erection of the feathers increases the insulating layer of air between the feather surface and the skin and is a tactic normally adopted by birds to combat cold. However, as Crawford & Schmidt-Nielsen (1967, cited by Dawson & Bartholomew, 1968) point out, insulation influences the rate, and not the direction of heat flow. It is thus just as effective in excluding heat as in retaining it. Thus the feathers can function as "heat shields" owing to their low conductance combined with the insulating layer of of air which they trap adjacent to the skin.

Regal (1975) has proposed a model for feather evolution in which he has demonstrated the importance of heat-shielding properties of enlarged reptilian scales. He concludes that the first feathers (or "protofeathers") which evolved from reptilian scales were already pennaceous, or vaned, to preserve their heat shielding qualities. Indeed, Regal suggests that the complex interlocking mechanism of barbs and barbules which characterizes the vane of a modern pennaceous feather was an early development out of homologues of the setae of modern reptilian scales. This mechanism maintained the continuous, but flexible, vane surface whose function was initially (in Regal's view) to exclude heat from the animal's body. Thus, Regal (1975) favours the view that feathers evolved initially in response to the thermoregulatory need to exclude excess heat, being thereafter available for selective modification which led ultimately to the evolution of the avian wing.

This brief discussion of insulation and thermoregulation has been introduced to show what seems to be a plausible thermoregulatory alternative for Syntarsus. Several workers now believe that the primary and original role of feathers was in thermoregulation, although it remains true that several others believe that feathers evolved in relation to the aerodynamics of flight (see e.g. Parkes, 1966). A structure as versatile in its potential as a feather, once evolved, is thereafter available for selection for a variety of specializations, the most spectacular of which has been the production of the aerofoil surface of the avian wing.

The idea of a feathered integument among theropod dinosaurs is not new, and has gained ground since Ostrom's (1970, 1972, 1973, 1974, 1975, 1976) re-evaluations of the Jurassic Archaeopteryx in which he has shown that, but for its feathers, Archaeopteryx is a coelurosaurian dinosaur (see also Romer, 1966). Indeed, he has noted (1975 a) that this was precisely the case with the fifth known specimen of Archaeopteryx, reported by Mayr (1973, fide Ostrom, 1975 a) which was for twenty years believed to be a small specimen of the coelurosaurian Compsognathus because it lacked the vital clue of distinct feather impressions. The idea has been promoted by Bakker (e.g. 1971, 1975) who expresses the view that birds inherited fully erect locomotion and high levels of continuous activity from their advanced archosaur predecessors, and that the early appearance of feathers enabled them to exploit their high activity patterns in the context of small body size and insulation enabling them to occupy hitherto under-exploited niches. Thulborn (1975), although sceptical about the idea of endothermic homeothermy in dinosaurs, concurs with the idea of a dinosaurian ancestry of birds, probably from a coelurosaurian stock. Thulborn dismisses endothermy on the grounds that the advanced enarthrodial hip joint of dinosaurs, leading to an erect stance and gait, was, by itself, sufficient to ensure the success of dinosaurs without invoking an advanced physiology. If the improved limb suspension and gait were not to allow for rapid reactions and more advanced and sustained patterns of activity, what was their advantage? If they *did* favour substantially greater activity levels, particularly amongst the predaceous carnivores of the time, what physiological mechanism provided the necessary quantities of energy "on tap" to satisfy the energetic demands of the new levels of sustained activity? Homeothermy frees an animal from direct dependence on external sources of heat to bring the body up to "working temperature", and insulatory devices coupled with behavioural and physiological adaptations allow the animal to limit fluctuations in body temperature about the optimum. This in turn allows those animals to remain active for longer periods during the day regardless of ambient temperature. It is now known that several archosaurians or their derivatives possessed dermal specializations, including the lower Triassic pseudosuchian *Longisquama* (Sharov, 1970), the pterosaur *Sordes* (Sharov, 1971) and, of course, *Archaeopteryx* itself. It is generally conceded that a close relationship exists between reptilian scales and feathers, and Maderson (1972 b) has shown how the elaborate and elongate scales of *Longisquama* might have given rise to a "proto feather". Regal's (1975) study examines the same problem from a different viewpoint. Since the *Longisquama* specialization was already present by Lower Triassic times it is surely conceivable that an elaboration of the basic design into a thermoregulatory insulator could have taken place by the Upper Triassic when Syntarsus lived, and that possession of this enormous advantage permitted an otherwise structurally ill-equipped animal to exploit the hot deserts of Triassic Rhodesia very effectively.

There is no direct evidence for a feathered integument in Syntarsus, but one feature which is worth considering a little further in this context is the degree of osteoporosis and the circumferential rings seen in some of the microscopic sections of Syntarsus bone. In a paper which seems to have been largely overlooked, Meister (1951) described histological changes which affected the long bones (especially the tibiotarsus) of moulting birds. He noted that birds which underwent a catastrophic moult, notably ducks and geese, showed a characteristic and extensive osteoporosis which invaded the bone cortex centrifugally from the endosteal surface. Following moult, bone reconstruction began by Haversian deposition which progressively obliterated the osteoporotic spaces by filling them with secondary bone, leaving a characteristic zone of altered bone which was clearly delimited from the unaffected outer layers of the bone cortex. With subsequent endosteal bone growth this would tend to isolate more or less clearly defined "zones" within the bone cortex which could be taken to represent successive moults.

The conditions seen in the osteoporotic tibial sections in Syntarsus (described on p. 96) agree, in broad terms, with Meister's (1951) findings. It could, of course, be argued that other factors - such as the need for calcium in egg production by mature and reproductively active females - could have been responsible for withdrawing material from the bone. The question cannot be settled conclusively one way or the other, but it is worthy of note that during the egg production cycle modern birds show a quite different set of changes in the bone (Bloom, Bloom & McLean, 1941; Taylor & Belanger, 1969). Additional *medullary* bone is laid down as trabeculae in preparation for egg shell formation and withdrawn as shell formation progresses. It might be that the thinning of the cortex of pneumatic avian bones would render them vulnerable if too much material was withdrawn from the bone wall itself, although Meister's (1951) study shows that many modern birds do indeed survive such a condition in their lives in connection with their normal moult patterns.

In terms of the present argument it is proposed that one of the most crucial features of bird evolution, the appearance of feathers or feather-like structures, had already taken place by the late Triassic-fully fifty or sixty million years before *Archaeopteryx* in the Kimmeridgian. Thus, although this conclusion does not pre-empt the need for Ostrom's (1975 b) search for a direct ancestor for *Archaeopteryx* amongst Jurassic theropods, it does help to negate Broom's (1913) and Heilmann's (1926) views that the theropods were too specialized or too late to be ancestral to *Archaeopteryx*.

It is not my purpose to claim direct avian descent from *Syntarsus*. The specializations in *Archaeopteryx* in its quadrate position, palate construction, forearm and girdle, and possession of an ossified furcula (? = clavicle), probably reduce (but, in my opinion, do not rule out) the likelihood of a direct connection. The point is that a great span of geological time exists between *Syntarsus* and *Archaeopteryx* in which these modifications could take place. In each respect *Syntarsus* is more generalized than *Archaeopteryx*, reflecting its more primitive and conservative nature consistent with its geologically earlier existence. But the basic "patent" seems, on circumstantial grounds, to have been already present in *Syntarsus* and its close Triassic theropod relatives. The demands for neuromuscular co-ordination resulting from its style of locomotion endowed

Syntarsus with an enlarged cerebellum and a flexed brain axis providing the foundation on which the avian brain could be built. The exigencies of its environment and its need to contend with them, as well as its energetic requirements in living the life of a fleet and active predator, endowed it with an ability to maintain a high metabolic rate and a stable body temperature, both of which are pre-adaptive for avian physiology. "Plasticity" in some parts of the skeleton of coelurosaurian theropods, for example the enormous variability in arm length between such forms as *Syntarsus*, the Jurassic *Compsognathus corallestris* (Bidar, *et al*. 1972), and the Cretaceous *Ornithomimus* (Osborn, 1917), seems to have provided natural selection with a range of selective options which probably explains the extraordinary success of the coelurosaurs - persisting from the Triassic at least to the Cretaceous.

7. THE TAXONOMIC STATUS AND EVOLUTIONARY POSITION OF SYNTARSUS.

Repeated comparisons in this study of the Rhodesian Syntarsus against the American Coelophysis have shown close correspondence between the two in many general respects (see e.g. Tables 2, 16 and Fig. 33). Indeed, even the conditions of burial and preservation, where in each case a group of individuals was preserved concentrated in a small area, are surprisingly similar (Table 19). Because of doubts about the validity of the taxon Syntarsus which arise as a result of this close similarity, it is desirable to compare Syntarsus and Coelophysis in detail. In the absence of a detailed description of the Coelophysis series now available, such a comparison is partially frustrated. However, Dr. E.H. Colbert of the Museum of Northern Arizona, Flagstaff, the leading authority on Coelophysis, has been immensely kind and helpful in checking queries raised by the writer on detailed points of comparison between the two genera. From his comments and from remarks scattered in the literature it has been possible to draw up a table highlighting those features in which the two genera differ (Table 19). The table omits what would be a tedious list of similarities since the object of this part of the study is to attempt to test the validity of generic separation of the two forms, and is thus more concerned with differences which could be regarded as specific or generic than with similarities.

Apart from the very clear sexual dimorphism of the femur of Syntarsus, which has not been reported in Coelophysis, the main differences seem to lie in the skull (occipital region, palate, antorbital area, and perhaps in the extent of cranial kinesis) the vertebrae (length of the neck, hyposphene-hypantrum articulations), and the hindlimb (flaring of the ilium, number of pubic foramina, length of pubis, extent of co-ossification, and degree of muscularity which influences the form of the femoral trochanters).

Few of the differences are especially impressive or clearcut (Fig. 33), and several must be treated with caution as being rather subjective because of the limitations of the crushed Coelophysis skeletons and uncertainty as to the limits of individual variation in Syntarsus. In many respects it is ironic that the data which the Coelophysis specimens can supply, especially with regard to skeletal ratios and proportions because of their beautiful articulation and completeness, cannot be matched or checked in the largely dissociated Syntarsus specimens, while conversely the exquisite preservation of detail in the individual Syntarsus elements cannot be matched in the crushed, fractured and distorted bones of the Coelophysis specimens.

For the time being, therefore, Syntarsus and Coelophysis are separated on the grounds summarised in Table 19, and it is considered reasonable to uphold the distinction between the two at generic level until a more exhaustive and detailed comparison is possible.

There is no doubt that Syntarsus was the local equivalent of the American Coelophysis, being a medium-sized, gregarious, agile and fleet predator and scavenger. These small Triassic podokesaurids (=procompsognathids) are part of a ubiquitous terrestrial fauna, which included "sauropodomorph" prosauropods (sensu Charig et al., 1965), and which is now known from the Upper Triassic of most continents (see e.g. Charig et al., 1965; Romer, 1966).

Of immediate concern as far as the evolutionary position of Syntarsus is concerned, is the occurrence of other coelurosaurs in the late Jurassic of East Africa (Janensch, 1920, 1925). Elaphrosaurus bambergi is the best known of these animals from the Tendaguru beds of Tanzania described by Janensch (1920, 1925), and Tacquet (1977) notes that the genus Elaphrosaurus also occurs in the Upper Cretaceous (? Aptian) of Niger in West Africa.

Janensch (1925) noted the similarity between the vertebrae of Elaphrosaurus and those of such animals as Procompsognathus and Podokesaurus (= Coelophysis) of the Upper Triassic, particularly with regard to the form of the transverse processes. Both of the latter genera belong to the same family as Syntarsus (Podokesauridae /= Procompsognathidae/). Furthermore, the descriptions and illustrations of the pelvis and sacrum given by Janensch (1925), and presented here in Fig. 34, reveal some noteworthy similarities with Syntarsus. This is especially true in the form of the ilium, which is flared posteriorly in both forms, and both bear a well-developed projecting roof or hood over the acetabulum. Janensch (1925) noted that the lower surface of the sacrum behind the acetabulum was perforated by foramina, which recalls the condition in Syntarsus (Raath, 1969: Fig. 4 e). He also noted that the iliac crests in Elaphrosaurus rose to the same height as the coalesced sacral neural blade, which is also true of Syntarsus. It is clear from Fig. 34 that Elaphrosaurus possessed a "pseudantitrochanter" in the acetabulum as well developed as that of Syntarsus.

The ischia of the two genera differ considerably, especially in the extent of the distal expansion in Elaphrosaurus, but both seem to possess the small backwardly projecting spike at the rear end of the puboischiadic plate.

Limb proportions differ between the two genera, Elaphrosaurus having a tibia relatively longer than Syntarsus (Elaphrosaurus tibia = 115% of femur length; Syntarsus = 107%). Elaphrosaurus is also considerably larger in absolute terms than Syntarsus and considerably later in geological time. On the basis of similar specialisations in pelvic construction, however, it seems that the two genera were related. The femur of Elaphrosaurus, although more markedly curved in its sigmoidal form than that of Syntarsus, is nevertheless similar in respect of the shallow fourth trochanter, and the similarity in form of the lesser trochanter, or iliofemoralis trochanter, to that of the gracile form of Syntarsus. In the tibia, the two genera are also similar in general build, particularly in their sharing of a very similar longitudinal flange proximally for retaining the fibula. They differ in the greater distal breadth of the Elaphrosaurus tibia.

According to Janensch's (1925) reconstruction of Elaphrosaurus it has proportionally much shorter toes than Syntarsus, in this respect foreshadowing the condition seen in ornithomimids (Osborn, 1917). Indeed Janensch (1925) drew particular attention to the structure of the proximal ends of the metatarsals as articulated in Elaphrosaurus and remarked on their suitability as a precursor for the type of proximal metatarsal specialisation seen in Ornithomimus where the proximal end of metatarsal III is attenuated and "squeezed in" between II and IV.

In the description of the holotype of Syntarsus (Raath, 1969) it was remarked that the presence of coelurosaurs in the late Triassic of Africa provided a stock from which the late Jurassic elaphrosaurs of East Africa might have arisen. This cursory comparison of Syntarsus with Elaphrosaurus suggests that a direct evolutionary link between them is not beyond possibility. It also appears to provide a link between the Podokesauridae (= Procompsognathidae) of the Triassic and the Coeluridae of the Jurassic, if Janensch's (1925) assignment of Elaphrosaurus to the latter family is correct.

It is beyond the intention or scope of this study to delve deeply into the evolutionary history of the saurischian dinosaurs and to evaluate the role played by the coelurosaurs in that history.

Nevertheless, a few general remarks are warranted. It has been proposed in this study that *Syntarsus* (and probably other podokesaurids) had already achieved endothermic homeothermy by the upper Triassic. It has been suggested, following Regal's (1975) reasoning, that the selective forces leading to insulation of the integument by means of feathers included the need to *exclude* the excess environmental heat of the hot Triassic desert days. It has been noted that, once insulation and endothermy were achieved, the insulating mechanism would also function to *retain* the body heat of an endotherm when the temperature gradient was reversed, as it would have been both daily and seasonally. The physiology of these animals therefore permitted the successful exploitation of relatively small body size enabling them to occupy niches not available to their larger relatives and previously occupied by animals of a lower physiological grade (e.g. pseudosuchians and other "lower" reptiles). Their physiological sophistication and its consequent wide latitude in potential activity cycles and patterns, niche choice and exploitation, and general advantage over animals not similarly endowed, would undoubtedly have opened up to them rich evolutionary possibilities. Ostrom's views on bird origins (synthesised in his 1976 b paper) show that coelurosaurs probably played a central role in the evolution of birds during the Jurassic. The advanced physiology proposed for Triassic coelurosaurs (at least for *Syntarsus*) was preadaptive for the avian condition and the insulating feathers in pre-avians would have been available for selective modification into the aerofoil of the avian wing.

Another member-group of the archosaurian lineage which possessed a sophisticated physiology, insulation, and specialised means of locomotion in the Jurassic was the highly successful and diverse

Order Pterosauria. The recent discovery of a "woolly" pterosaur, Sordes (Sharov, 1971) establishes beyond doubt an insulatory covering for this animal. The actual nature of the integumentary covering is not entirely clear but, since the animal was derived from the archosaurs, it seems reasonable to suggest that the "wool" was produced by specialised and highly modified feather-like structures, or "filoplumes". It is thus not inconceivable that a branch of the coelurosaurs, or some near relative, might have played a part in the emergence of the pterosaurs some time during the early Jurassic. The fact that the known Triassic coelurosaurs are all short-armed does not invalidate this suggestion, as the later undoubted coelurosaurs, Ornithomimus, Compsognathus corallestris, and others, bore what must have been secondarily elongated forelimbs. Elongation of the digits in particular is a noteworthy feature in Ornithomimus, and it is a digit which provides the skeletal support for the wing of the pterosaur. However, one major difficulty in the way of a coeluorsaur - pterosaur lineage is the fact that the wing-supporting digit in the pterosaurs is digit IV, whereas the coelurosaurs are notable for extreme reduction of this very digit (see e.g. Fig. 14 h,i).

Whatever their detailed role (if any) in the evolution of these highly modified, specialised and successful groups, the coelurosaurs as a group clearly played an interesting and important role in the biological events of the unfolding Mesozoic. As the most persistent and ubiquitous of all dinosaurs their success in comparison with their fellows was unparalleled.

8. SUMMARY

The occurrence of the coelurosaurian theropod, Syntarsus, at three localities in Rhodesia is recorded. All finds were in the middle-upper horizons of the Forest Sandstone (Upper Triassic). The most recent discovery, on the Chitake River (Zambezi Valley, 16° 07'S; 29° 30'E), consisted of the highly concentrated remains of at least 26 individuals, both adult and immature, within the confines of a small depression interpreted as having been an ephemeral water-hole in the otherwise hot arid environment.

Manganese-rich encrustations around the bones, as well as the localised occurrence of coarse, gritty, and current-bedded lenses with marly layers, are regarded as evidence of the former existence of small, ephemeral freshwater bodies in which the action of Chlamydobacteriales precipitated manganese salts around the bones at two of the three localities.

The osteology of the delicately constructed skull is presented in detail. The skull was "normal" for a coelurosaur, being relatively long, shallow and sharp-snouted. Apart from the braincase, most cranial articulations provide evidence of extensive cranial kinesis. The skull differs from the skull of the closely related American genus Coelophysis mainly through closure of the post-parietal fenestrae by flanges from the parietals; the presence of nasal fenestrae; an increase in size of the antorbital fenestrae; reduction in size of the ectopterygoid which has also achieved a complex "double-overlap" articulation with the pterygoid in the palate, both bones contributing to the formation of a "carnosaur pocket" at the rear end of the palate; specialisation in the squamosal-quadrate articulation whereby the quadrate comes to lie lateral to the squamosal descending arm;

and the presence of interdental plates in the jaws.

Apart from the premaxillary and anterior dentary teeth, which are subcircular in section, small, and unserrated, the teeth are laterally compressed, recurved, sharp-pointed and serrated, confirming that Syntarsus was carnivorous. Rapid alternate replacement of the teeth took place so that up to five waves of replacement were operative in the jaws at any one time.

A scleral ring of plates was present in the orbit, and the hyoids were well developed.

The vertebral column bears specialisations in each main section, the cervicals being short at each end of the neck, and wedge-shaped in these places to permit sigmoidal "goose-neck" bending, while the mid-cervicals are elongate - the sixth being the longest. Cervical ribs are long and slender rods which collect in "bundles" of up to four or five rib shafts lying parallel with, and lateral to, the vertebral column. The hindmost cervical ribs, at the cervicodorsal transition, bear enormous heads and are long-shafted. All cervical centra are keeled ventrally.

The anterior dorsals are shortened, wedge-shaped, and contribute to the bending mechanism at the base of the neck. Migration of the parapophysis from the centrum onto the transverse process and then laterally along the transverse process is confirmed. All members of the dorsal series possess well developed hyposphene-hypantrum articulations. An abdominal "basket" of gastralia was present, evidently consisting of 13 paired series of gastralia.

The caudal series is long, the suggestion that it consists of 40 vertebrae as deduced in the holotype being neither confirmed nor negated by the new material. The anterior caudals retain hyposphene-hypantrum articulations, and chevron bones are present between the vertebrae over most of the length of the tail, the hindmost chevrons being reduced to small "skids". The mid-and hind-caudals are elongate and slender. Tail length accounts for approximately half of the axial length of the entire animal.

The forelimb is approximately half of the length of the hindlimb, and appears to exhibit sexual dimorphism similar to that noted in the bones of the hindlimb. This dimorphism in both limbs is reflected in robustness of the bones concerned as a consequence of extreme muscle scarring; in the forelimb it is mainly the humerus that is affected. One of the nutritive foramina in the humerus occupies a position similar to that of the pneumatopore in birds. The degree of development of the olecranon process on the ulna varies considerably. No confirmation is available for the existence of a rounded "pisiform" bone at or near the carpus as noted in the holotype. Of the carpalia only the crescentic radiale is individually recognisable in the collection. The metacarpals and digits confirm Galton's conclusion that digit I was opposable.

In the pelvis and hindlimb the specialisations due to sexual dimorphism are most clearly observable, affecting the pelvis, femur and tarsal joint. The femur is especially dimorphic, showing a "robust" and a "gracile" form in which the development of the femoral muscle trochanters is influenced to produce bimodal variation. Femoral dimorphism is consistent beyond a certain minimal size, indicating that its onset is linked with maturity and that it is therefore a sexual character. The pelvis varies mainly in the extent of bone co-ossification and the degree of flaring of the ilium behind the acetabulum. The tarsal area varies in the extent of fusion between astragalus and calcaneum both with each other and with the distal end of the tibia. The interlocking, prior to fusion, of the (? immature) tibia with the ascending process of the astragalocalcaneum is not as intimate as described in the holotype.

Two pubic foramina are consistently present in the puboischiadic plate, and neither the pubes nor the ischia end in great distal expansions. The anterior end of the ilium bears a ventral projection for the sartorius muscle.

In the tarsus distal to the astragalocalcaneum, juveniles bear two free tarsal elements, 3 and 4. At maturity tarsal 3 fuses onto metatarsal III, but 4 remains free. Metatarsal III has an enlarged tubercle ventrally at the proximal end which appears to be a homologue of the avian hypotarsus. Digits II and IV are capable of splaying laterally from the central, and longest, digit III.

In its entire skeleton Syntarsus shows the characteristics of a medium-sized, lightly built, agile bipedal predator. Its vertebral formula is: ce 10:d 13:s 5:ca?40. The phalangeal formula of the manus is 2:3:4:1:-, and of the pes 2:3:4:5:0.

Microscopic sections of the bone show that it was highly vascularized in a dense fibro-lamellar pattern. A variable degree of Haversian remodelling is evident, and considerable osteoporosis near the endosteal margin is noteworthy in some sections from the tibia.

An attempt has been made to reconstruct some of the soft tissues, including the brain, cranial nerves, major cranial blood vessels, and muscles of the jaws, occiput, neck, forelimb, and hindlimb. In respect of the brain the major conclusions are that it was incipiently avian in construction with pronounced flexion, ventrolateral displacement of the optic lobes, and possession of a cerebellum at least partially erect. It retained relatively small cerebral hemispheres and large olfactory bulbs. The brain: body weight ratio of 0,84% puts it close to the value for living ratite birds and intermediate in position between the reptiles and birds, as is true of Archaeopteryx. Brain weight was calculated by volumetric displacement of a trimmed endocranial cast in silicone rubber, and body weight is based on the volumetric displacement of a life-size model.

Jaw muscles in Syntarsus were well differentiated and powerful. The mandibular adductors filled the temporal openings and inserted far forward on the lower jaw via the adductor fossa and the intramandibularis muscle. The pterygoideus muscle seems to have been differentiated into at least two heads, one originating in the "carnosaur pocket" on the palate. The levator and protractor pterygoidei were the principal muscles initiating protraction in the kinetic cycle of the Syntarsus skull (which could have increased the gape of the jaws by up to 10%) while the depressor madibulae, mandibular adductors and pterygoideus were concerned with retraction to rest. The levator pterygoidei was evidently capable of driving the palatal elements to produce independent though small "groping" movements of the premaxillae, which were capable of sliding to-and-fro on the narrow palatal processes of the maxillae. The skull of Syntarsus was amphikentic, with one kinetic joint situated between the parietals and exoccipitals, and the other between the frontals and nasals.

Cranial and cervical muscles were rather conservative in their development and differentiation. The development of "epipophyses" on the pre-and postzygapophyses of the cervical vertebrae seems to have been concerned with the origin and insertion of some cervical muscles, and the rugose apices and front and rear faces of the neural spines were similarly concerned with the attachment of muscles and interspinous ligaments.

The forelimb musculature of Syntarsus is notable for the development of the coracobrachialis muscles on the coracoid, the coracobrachialis brevis originating by tendon from a tubercle ahead of the glenoid (following the reasoning of Dr. A.D. Walker). The pectoralis, deltoideus and biceps muscles were all well developed and have left prominent attachment scars on the humerus, especially in "robust" forms. The strongly (though variable) developed olecranon process indicates powerful development of the triceps muscle. Pronation of the forearm and flexion of the wrist was favoured over supination and extension, and the muscle scars reflect this differential development. Specialisation of the phalanges permitting hyperextension of the fingers evidently compensated for limited extension at the wrist.

The hindlimb musculature was very well developed and powerful, especially in those muscles which acted in propulsion of the body ("triceps femoris", femorotibialis, caudifemoralis longus and brevis, gastrocnemius). The tendon of the ambiens muscle seems to have crossed the knee via the proximal hook on the tibia. Recovery muscles were less powerfully developed, although the puboischiofemoralis group (externus and internus) were evidently bulky and attached to the femur by strong tendons. Powerful insertion scars on the femur are distinguishable for the following muscles: puboischiofemoralis internus and externus; iliofemoralis; femorotibialis; caudifemoralis longus and brevis; and the adductor. It is chiefly these muscle scars that produce the pronounced dimorphism of the femur that is interpreted as representing sexual dimorphism. The great muscularity of the hindlimb together with the evidence provided by fossil footprints referred to the genus, suggest that Syntarsus was a bipedal saltator and that the "robust" form performed additional exertions which produced the pronounced specialisations in the pelvis and femur associated with the musculature. These activities are thought to have been related to courtship display, nest preparation, and special responsibilities for feeding of the young. For these reasons, and because robust individuals predominate in the collection - yet in the company of juveniles and mature gracile forms - the "robust" forms are interpreted as females (cf. birds of prey?).

Specialisations in the skeleton which point to bipedal hopping include: a relatively short neck and trunk; small acetabulum with tightly fitting femoral head; hyposphene-hypantrum articulations in the dorsal series and proximal caudal vertebrae; abdominal basket of gastralia; co-ossification in the pelvis and the tarsal and metapodial regions to prevent rupture and dislocation of the elements; and extreme development of the femoral retractor muscles with an accompanying specialisation of the nerve supply via the large ventral perforations in the ventral surface of the hind sacrum.

Because of its advanced postulated method of locomotion it is considered unlikely that the metabolism of Syntarsus can have been comparable with that of reptiles in the traditional sense. The advanced development of the brain and the histology of the bones also lead to this conclusion. The arid, hot environment of the times and its intracontinental position suggest that Syntarsus and its contempories were subject to extreme fluctuations in daily and seasonal temperatures. It is argued that on the basis of its build, surface: volume ratio, nervous and muscular specialisations, and evidently gregarious habits, its physiology was advanced and able to cope adequately with its environmental stresses and at the same time to permit it to lead an active life as the principal known terrestrial vertebrate predator of the times in this region. It is argued that it was in fact an endothermic homeotherm. It is proposed that its integument was clothed in "feathers", which developed initially in response to the need to exclude excess environmental heat (acting as "heat shields" as proposed by Regal), but which had the additional advantage of retaining body heat when the temperature gradient reversed. This argument envisages endothermic homeothermy as being already present in the late Triassic and providing a physiologically preadapted stock from which the "birds" of the Jurassic (such as *Archaeopteryx*) might have evolved.

Finally, consideration is given to the validity of the taxon *Syntarsus* because of its close similarity in many respects to *Coelophysis* Cope, 1889, which has taxonomic priority. It is concluded that the differences in the skull, vertebrae, pelvis, and limbs justify generic separation of the two forms pending a detailed description of the extensive *Coelophysis* material available against which to compare *Syntarsus*.

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THE ANATOMY OF
THE TRIASSIC THEROPOD
Syntarsus rhodesiensis
(Saurischia : Podokesauridae)
and a consideration of its biology

by

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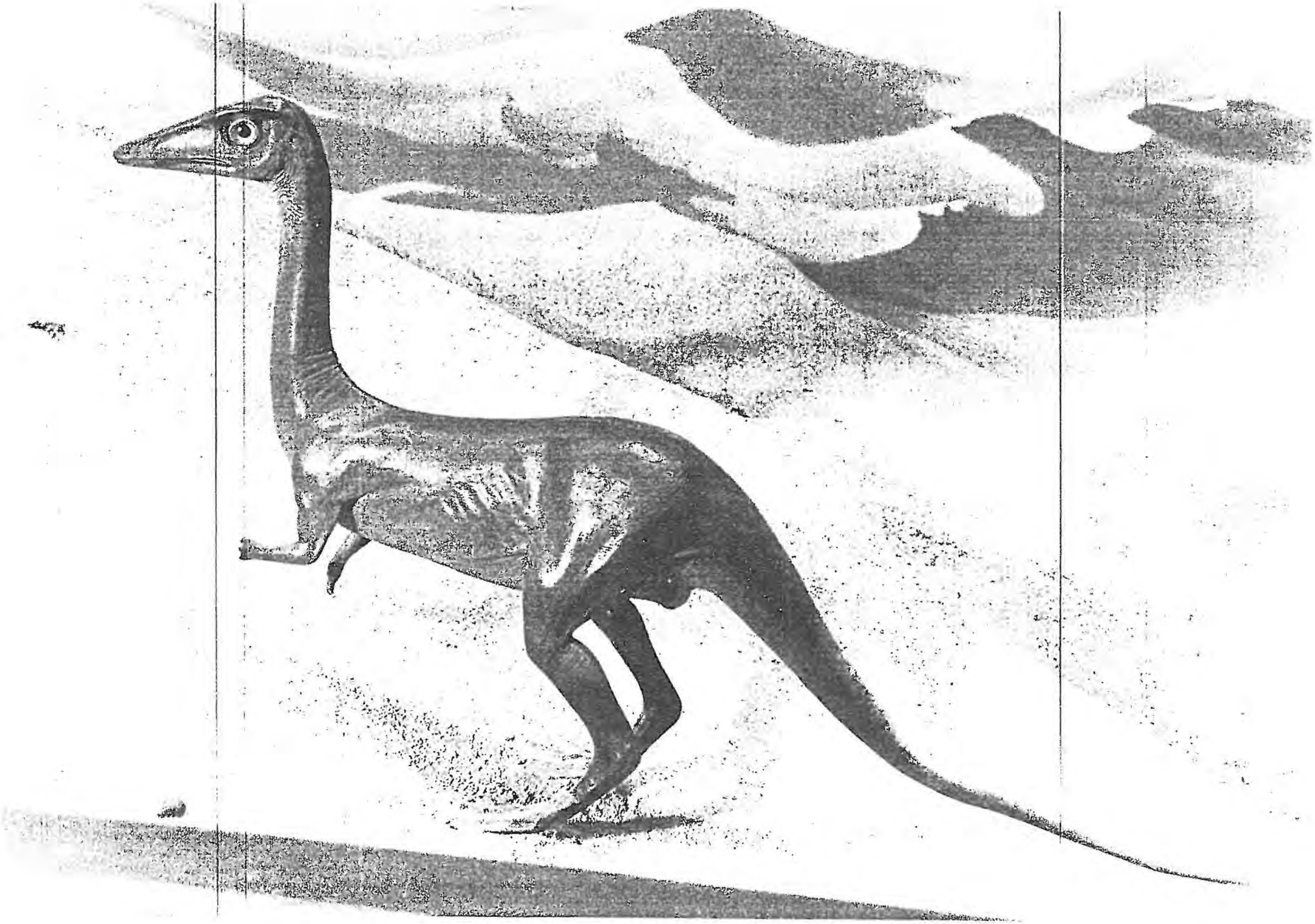
Dissertation presented in the Department of Zoology and Entomology, Rhodes University, for the degree of Doctor of Philosophy

VOL. II

1977

Frontispiece   *Syntarsus rhodesiensis*: scale model by Mr. L.J. Penny,
Queen Victoria Museum. (Original approx. $\frac{1}{3}$ scale)



LIST OF ABBREVIATIONS USED IN THE FIGURES

I - XII cranial nerves (N.B. Roman numerals also refer to metapodials and digits, as will be clear from the context):

I	Olfactory		
II	Optic		
V	Trigeminal	V^1	deep ophthalmic br.
		V^2	maxillary br.
		V^3	mandibular br.
VI	Abducens		
VII	Facial	VII^1	palatine br.
		VII^2	hyomandibular br. ("chorda tympani")
VIII	Auditory (Acoustic)		
IX	Glossopharyngeal		
X	Vagus		
XI	Accessory		
XII	Hypoglossal		

a	angular
abh	abductor hallucis muscle
add	common insertion of adductor muscles
adf	adductor fossa
adfm	adductor femoris muscle
adp	adductor posterior muscle
aem	adductor externus medialis muscle
aep	adductor externus posterior muscle
aes	adductor externus superficialis muscle
alig	annular ligament
alv	alveolus
amb	ambiens muscle -
aof	antorbital fenestra
ar	articular

artic.	articulation (preceded by name of articulating bone)
astc	astragalocalcaneum (fused)
aul	auricular lobe

bacd	caudal branch of basilar artery
bacr	cranial branch of basilar artery
bart	basal articulation of palate and braincase
bi	biceps muscle
bo	basioccipital
bpt	basipterygoid process
br	brachialis muscle
bs	basisphenoid
bt	basal tubera of basisphenoid
bv	blood vessel

c	coronoid
ca	cerebral artery
caps	joint capsule scar
cb	coracobrachialis muscle
cbb	coracobrachialis brevis muscle
cbl	coracobrachialis longus muscle
cbr	cerebral hemisphere
cfb	caudifemoralis brevis muscle
cfl	caudifemoralis longus muscle
ch	choana
cm	complexus muscle
con	condyle
cor	coracoid
corf	coracoid foramen
cp	cultriform process
crb	cerebellum
ct	centrum

d	dentary
dc	dorsalis caudi muscle
dhv	dorsal head vein
dia	diastema
dige	digital extensor muscle(s)
digf	digital flexor muscle(s)
dipo	diapophysis
dl	deltoideus muscle

dm	depressor mandibularis muscle
dpc	deltopectoral crest
dt	dorsalis trunci muscle
ec	ectopterygoid
ecco	ectepicondyle
edl	extensor digitorum longus muscle
emf	external mandibular fossa
en	external naris
enco	entepicondyle
eo	exoccipital
f	frontal
fdl	flexor digitorum longus muscle
fib	fibula
flf	floccular fossa
fm	foramen magnum
fo	fenestra ovalis
fte	flexortibialis externus muscle
fti	flexortibialis internus muscle
ftm	femorotibialis muscle
fr	fenestra rotunda
gl	glenoid fossa
gstm	gastrocnemius muscle
hs/ha	hyposphene-hypantrum articulation
ht	"hypotarsus"
ic	foramen for internal carotid
ica	internal carotid artery
icm	interspinales craniales muscle
idp	interdental plates
ilfb	iliofibularis muscle
ilfm	iliofemoralis muscle
im	intertransversales muscle
inm	intramandibularis muscle
int	internal tuberosity
ioa	inferior orbital artery

iptv	interpterygoid vacuity
istr	ischiotrochantericus muscle
itm	iliotibialis muscle

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j	jugal
jv	jugular vein

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l	lachrymal
lca	longissimus capitis muscle (pars articuloparietalis)
lcd	longus colli dorsalis muscle
lcta	longissimus capitis muscle (pars transversalis capitis)
lctb	longissimus capitis muscle (pars transversalis cervicis)
lcv	longus colli ventralis muscle
ld	latissimus dorsi muscle
lhv	lateral head vein
lign	ligamentum nuchae
lpt	levator pterygoidei muscle
ls	laterosphenoid
lsc	levator scapulae muscle
ltf	lower temporal fenestra

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m	maxilla
mcv	mid cerebral vein
mda	mandibular artery
mds	median dorsal sulcus
mec	meckelian canal
med	medulla
mpa	median palatine artery
mt	metatarsal
mvs	median ventral sulcus
mxr	"maxillary ramp" (Palatal process of maxilla)

n	nasal
na	neural arch
nc	neural canal

nf	nasal fenestra
ns	neural spine
nuf	nutritive foramen

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ob	olfactory bulb
obc	obliquus colli muscle
obt	obturator ridge
oc	otic capsule
ocm	obliquus capitis magnus muscle

ol	optic lobe
op	opisthotic
or	orbit

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p	parietal
pa	palatine artery
pap	parapophysis
pat	patellar tendon
pbc	parabasal canal
pem	pectoralis muscle
pife	puboischiofemoralis externus muscle
pifi	puboischiofemoralis internus muscle
pit	pituitary gland
pitf	pituitary fossa
pits	pituitary stalk
pl	palatine
pli	posterior acetabular ligament
plt	plantaris muscle
pm	premaxilla

po	postorbital
pop	popliteal muscle
popr	paroccipital process
pozp	postzygapophysis
ppt	protractor pterygoidei muscle
pr	prootic
pra	prearticular
prf	prefrontal
prl	peroneus longus muscle
pro	pronator muscle
ps	parasphenoid
psh	proscapulohumeralis muscle
pst	pseudotemporalis muscle
pt	pterygoid
ptga	part of pterygoideus muscle originating in "carnosaur pocket"
ptgb	part of pterygoideus muscle inserting in "wrap-round" on mandible

ptv	palatal vacuity		

q	quadrate	qj	quadratojugal
qcp	quadratocranial passage	qpt	quadrate process of pterygoid
qf	quadrate foramen		

rap	retroarticular process	rcp	rectus capitis posterior muscle
rca	rectus capitis anterior muscle		

sa	surangular	soa	superior orbital artery
sart	sartorius muscle	soc	supraoccipital
sbc	subcoracoideus muscle	sp	splenial
sc	scleral plate	spc	spinal cord
scap	scapula	spca	spinalis capitis muscle
scm	supracoracoideus muscle	sq	squamosal
sl	sling for iliofibularis muscle	sta	stapedial artery
		sup	supinator muscle
sm	serratus muscle		

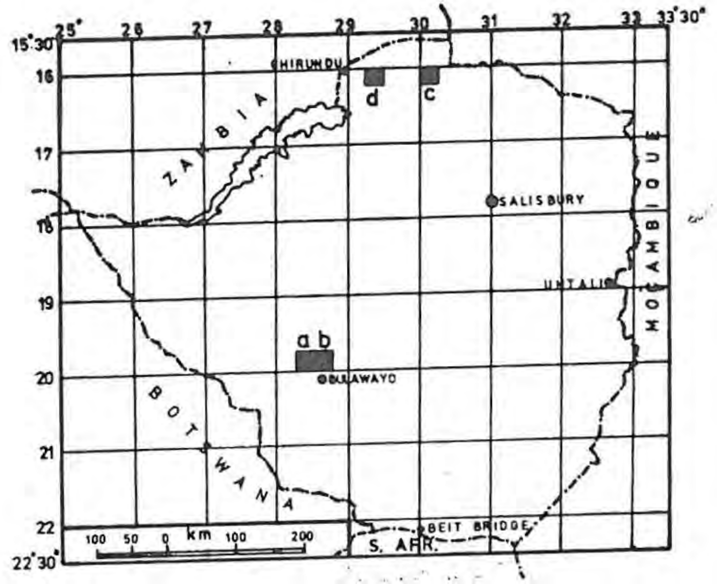
T4	fourth trochanter	tam	tibialis anterior muscle
Tg	greater trochanter	te	teres ligament
Tl	lesser trochanter	ten	tendon (followed by muscle abbreviation)
Tps	pseudotrochanter		
Tpa	pseudantitrochanter	tr	triceps muscle
ta4	tarsal 4		

utf	upper temporal fenestra		

v	vomer	vf	vagal fissure

Fig. 1. Map of Rhodesia showing $\frac{1}{4}^{\circ}$ squares (shaded) in which _Syntarsus_ localities are situated:

- a - holotype locality(see detail - map A: holotype site arrowed and marked "type")
- b - footprint locality
- c - Maura River localities (see detail - map C: fossil sites arrowed; _Syntarsus_ site marked "Synt"
- d - Chitake River localities (see detail - map D: fossil sites arrowed and identified with CT locality codes; _Syntarsus_ site = CT6)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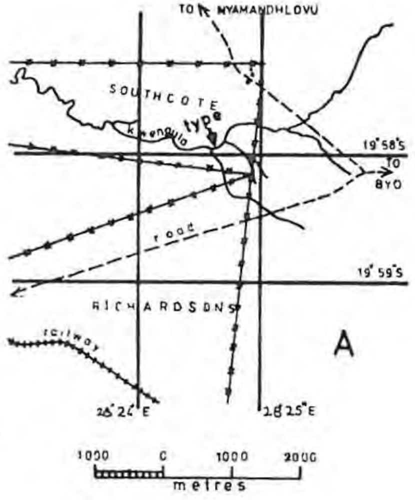
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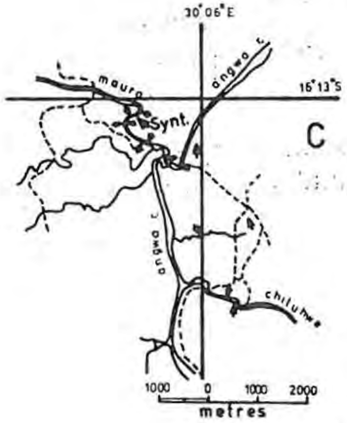
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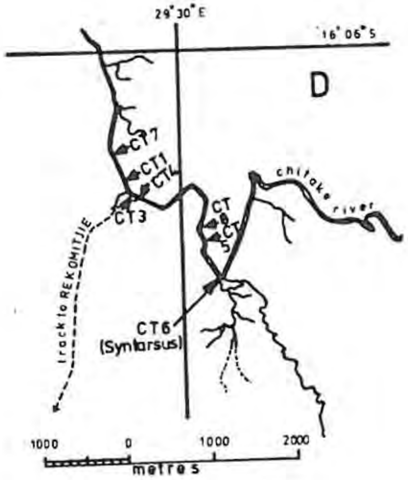
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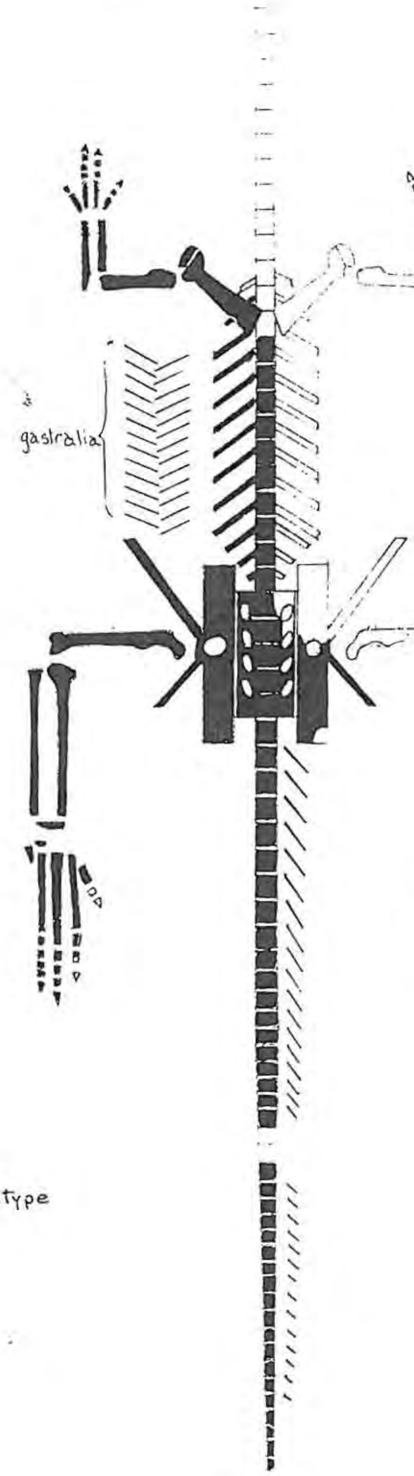
Fig 2. Syntarsus rhodesiensis: schematic skeleton "template" representing holotype: material recovered shaded black



QG 1

SYNTARSUS holotype
(Nyamandhlovu)

Fig. 3. *Syntarsus rhodesiensis*: reconstruction of skull

a - lateral view of cranium
b - dorsal view of cranium
c - palatal view of cranium
d - occipital view of cranium
e - lateral view of mandible
f - lingual view of mandible

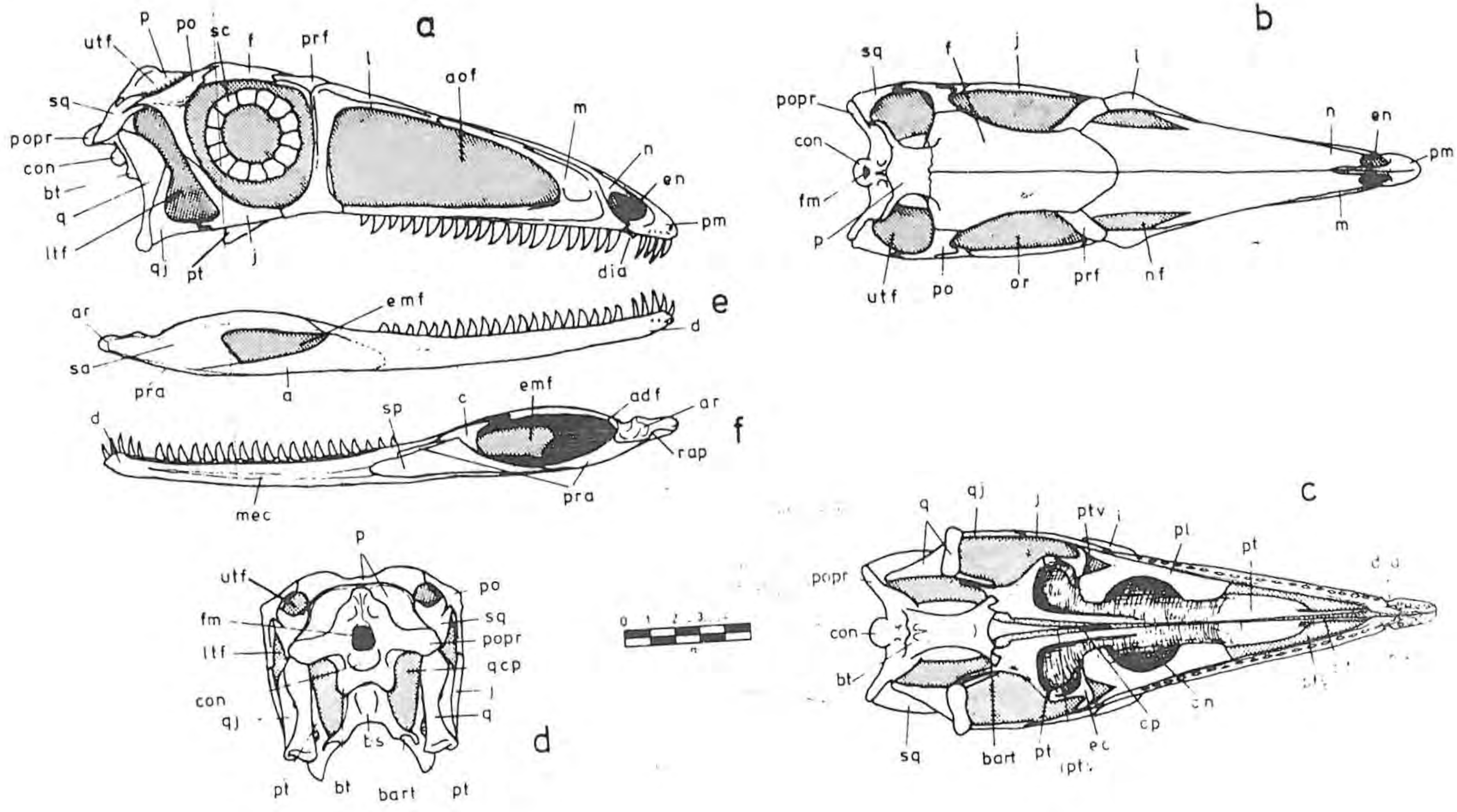

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Fig. 4. *Syntarsus rhodesiensis*: individual cranial elements

a - lateral view L. maxilla (QG 194)
b - medial view R. maxilla (based on QG 210)
c - dorsal view R. nasal (QG 193)
d - medial view R. nasal (QG 193)
e - palatal view L. pterygoid (based on QG 235, QG 265)
f - lateral view L. premaxilla (? + vomer) (based on QG 249, QG 254)
g - medial view L. premaxilla (? + vomer) (based on QG 249, QG 254)
h - dorsal view L. palatine (QG 241)
i - palatal view L. palatine (QG 241)
j - lateral view R. quadrate + quadratojugal (QG 194)
(a - j drawn to common scale)
k - medial view L. lachrymal (based on QG 193, QG 234)
l - lateral view L. lachrymal (based on QG 193, QG 234)
m - lateral view R. squamosal (based on QG 193, QG 194)
n - medial view R. squamosal (based on QG 193, QG 194)
o - medial view R. postorbital (based on QG 193, QG 287)
p - lateral view R. postorbital (based on QG 193, QG 287)
q - dorsal view R. ectopterygoid (QG 194)
r - palatal view R. ectopterygoid (QG 194)
s - lateral view L. prefrontal (QG 193)
t - dorsal view L. prefrontal (QG 193)
u - lateral view R. jugal (QG 278)
(k - u drawn to common scale)

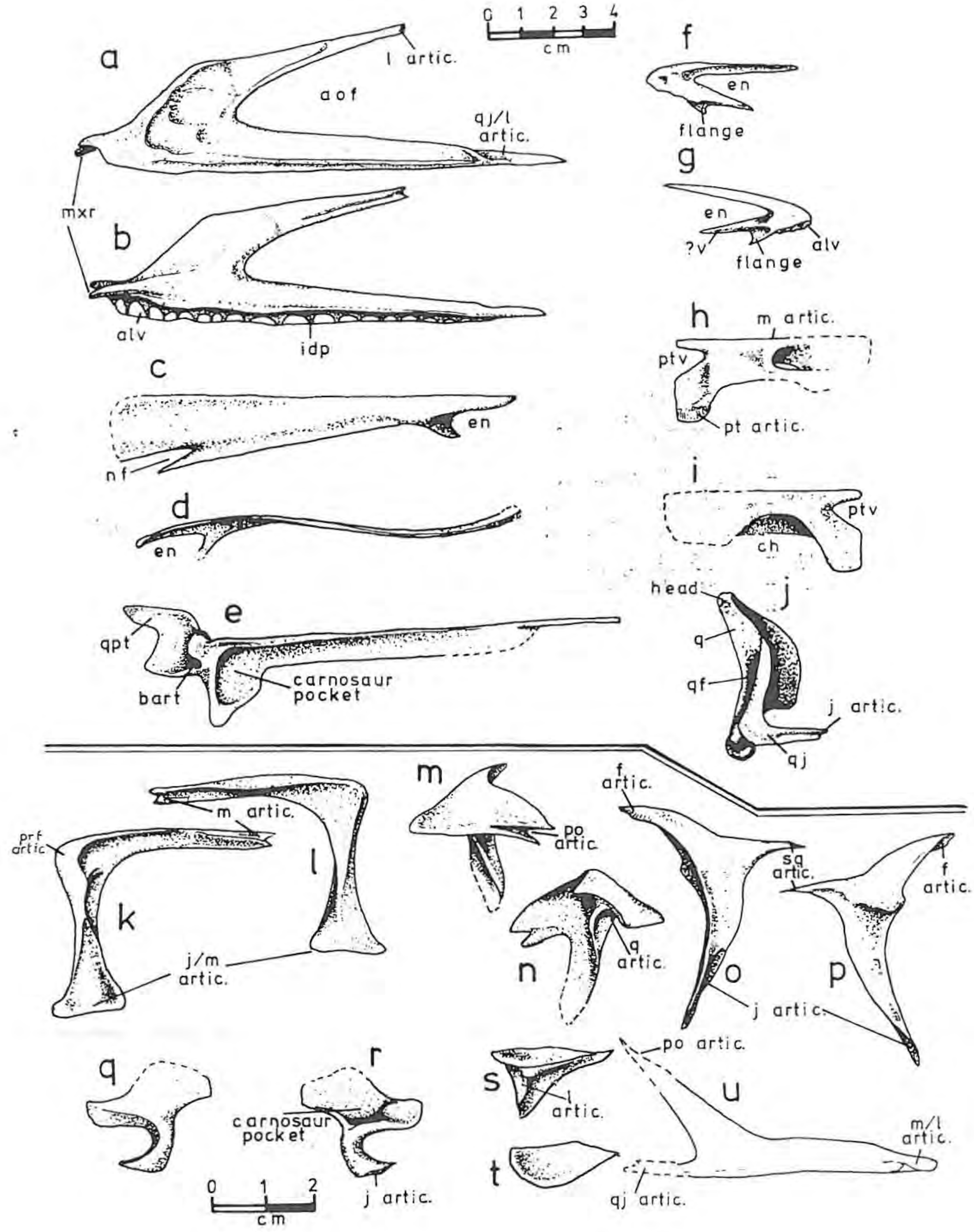
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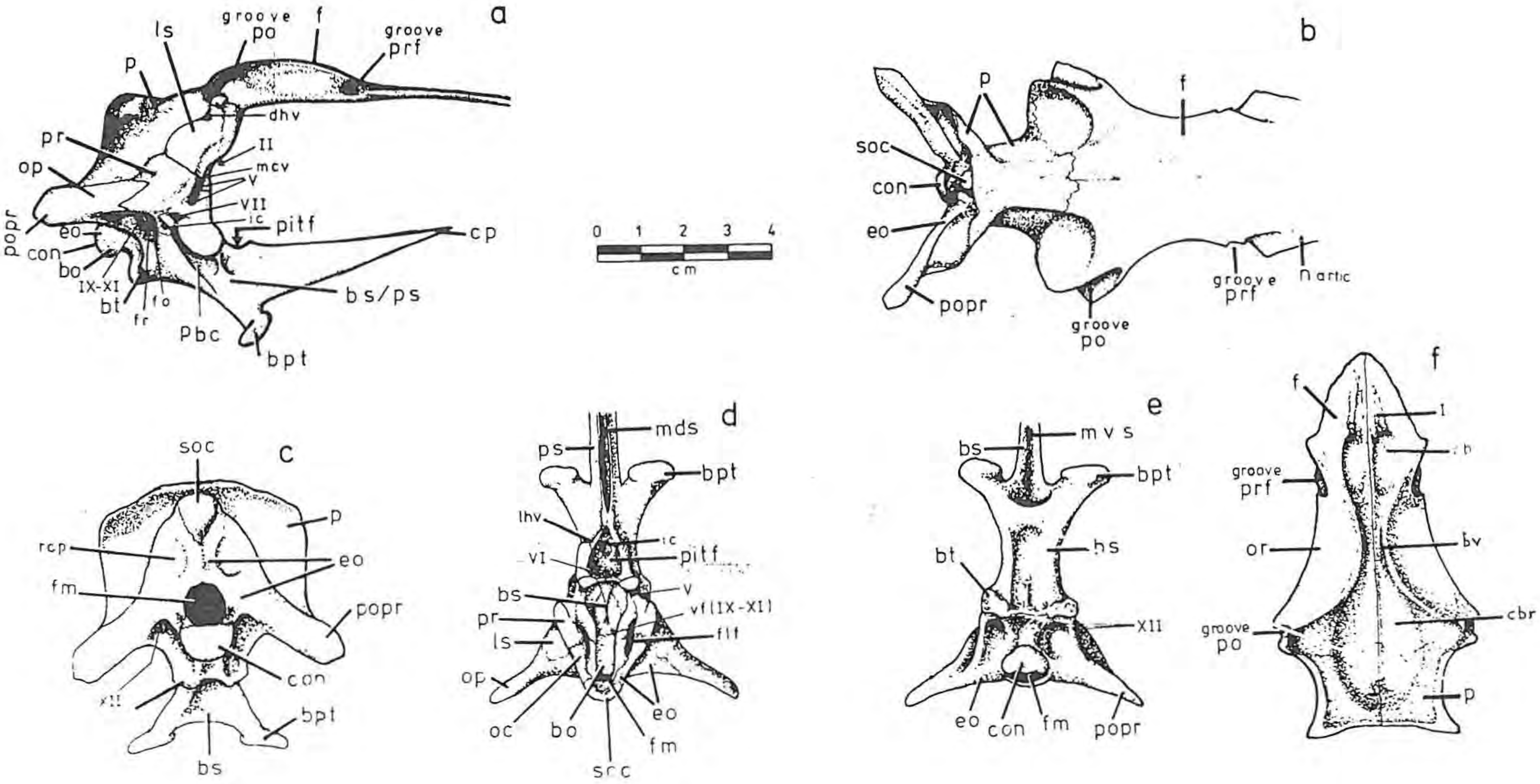
Fig. 5. *Syntarsus rhodesiensis*: braincase and skull roof, excluding lateral elements

a - lateral view of braincase (frontals attached)
b - dorsal view (frontals attached)
c - occipital view (cf. Fig. 3d where lateral elements are included)
d - endocranial floor and side walls, dorsal view
e - cranial base, ventral view
f - ventral view of frontals and parietals in articulation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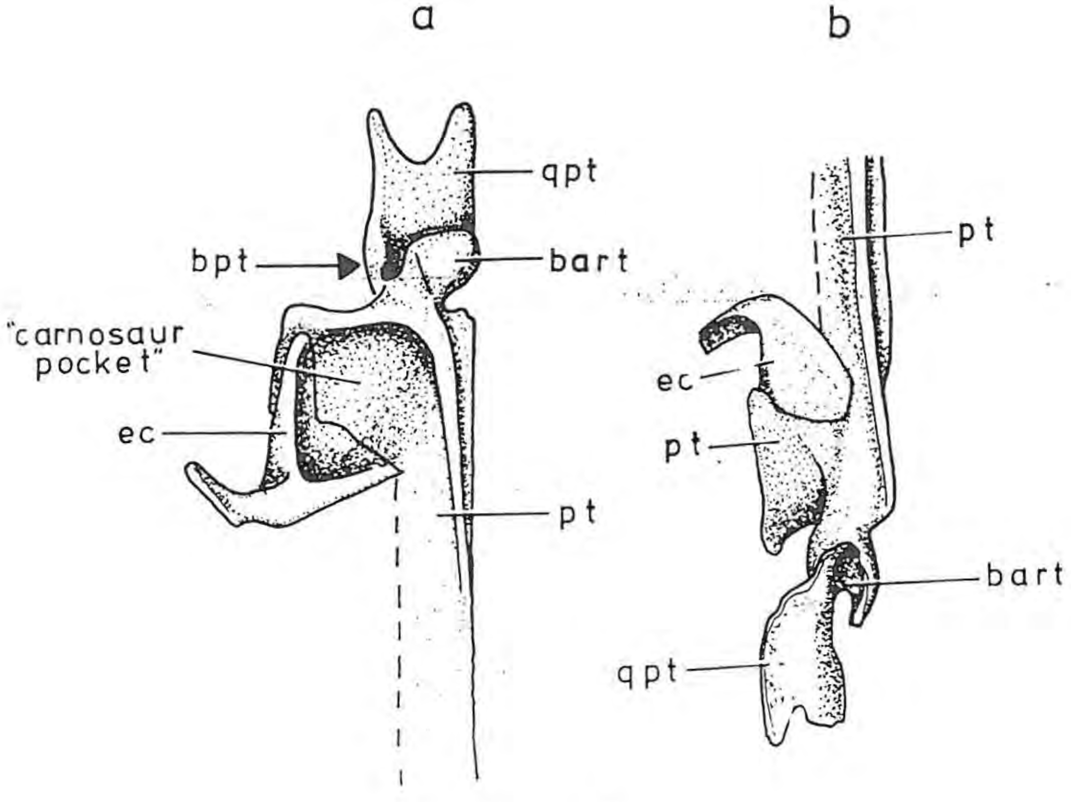
pitf
bs
V
vf(IX-XI)
pr
flt
ls
op
oc
bo
eo
fm
soc
e
bs
mvs
bpt
bt
hs
XII
eo
con
fm
popr
f
f
I
groove
prf
or
bv
groove
po
cbr
p

Fig. 6. *Syntarsus rhodesiensis*: pterygoid and ectopterygoid articulation (based on QG 235)

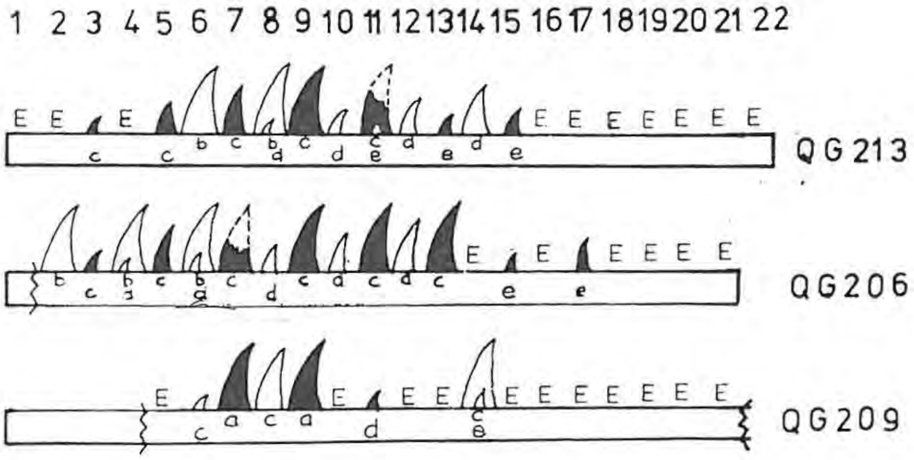
a - palatal view (note "carnosaur pocket")
b - dorsal view

(arrow marked *bpt* indicates grooved cup within which basipterygoid process articulates)

Fig. 7. *Syntarsus rhodesiensis*: tooth replacement in maxillae (diagrammatic)
Alternate tooth positions shaded black, except where replacement teeth occupy the same position. Successive tooth generations labelled a, b, c .....
E - empty alveolus


a
b
qpt
bpt
bart
"carnosaur pocket"
ec
pt
pt
ec
pt
bart
qpt

6


1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
E E E E E E E E E E E
c c b c b a c d c e d e d e
QG 213
E E E E E E E
b c b a c b a c d c d c d c e e
QG206
E E E E E E E E E E E E
c a c a d c e
QG209

7

Fig. 8. Syntarsus rhodesiensis: centrum length of cervical and dorsal vertebrae plotted against position in vertebral column (Numbers refer to specimen catalogue numbers without QG prefix)

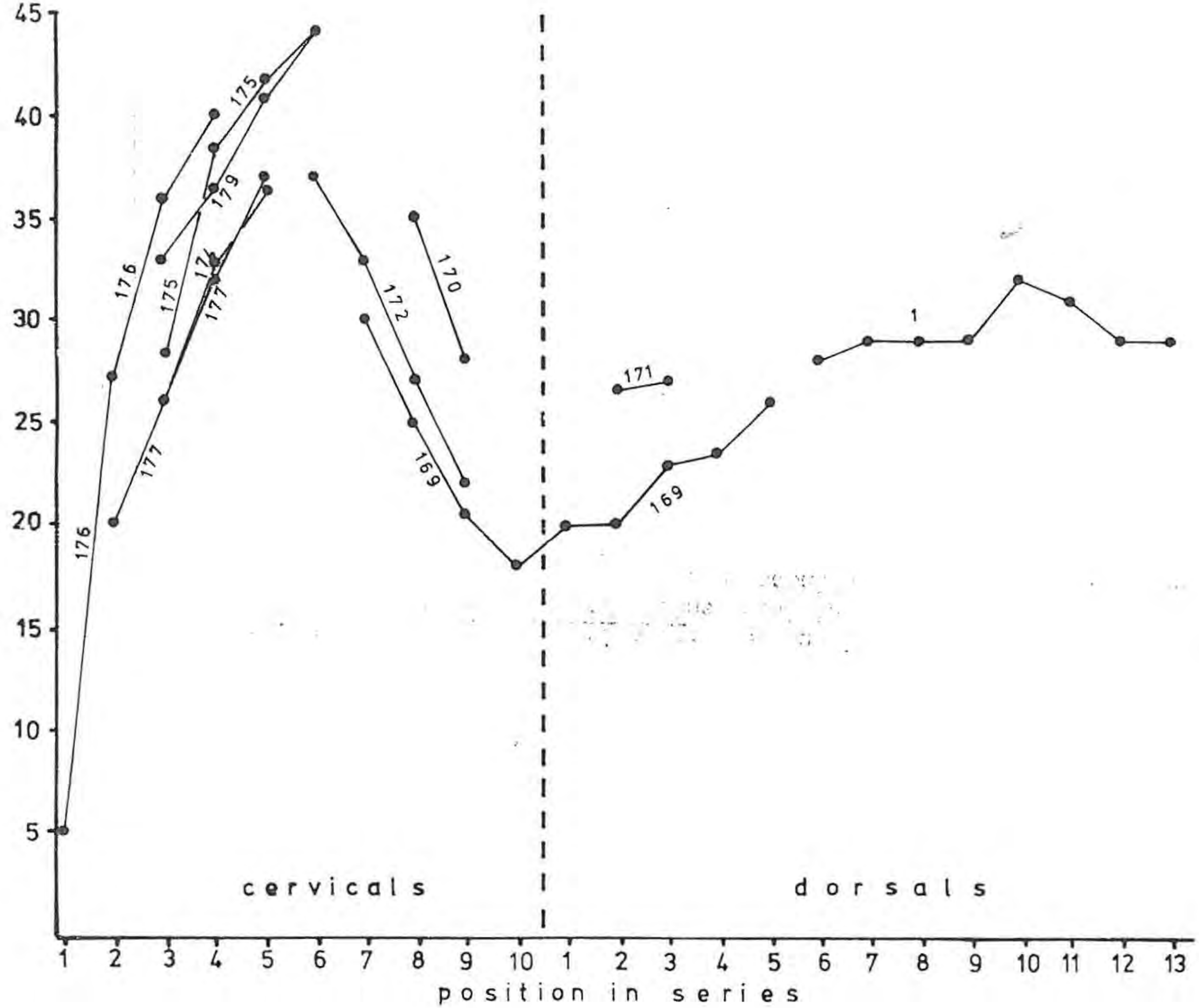
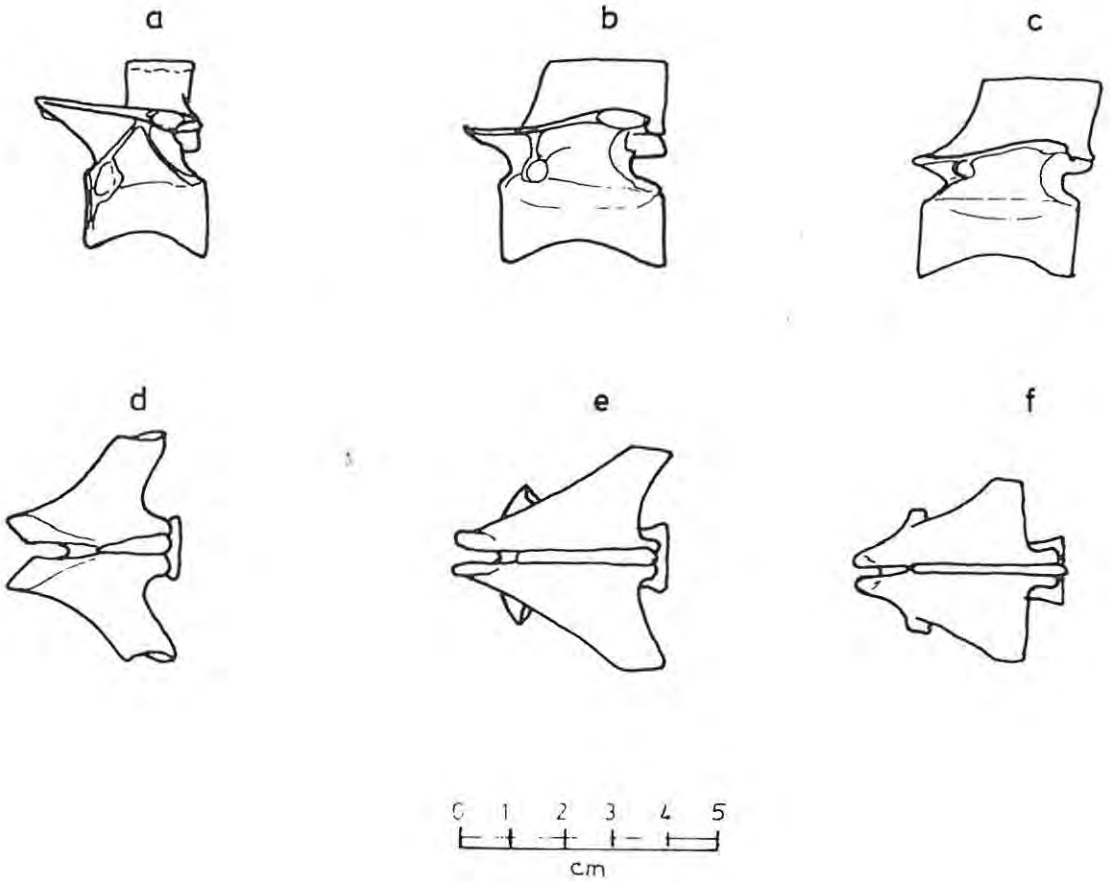

45
40
35
30
25
20
15
10
5
176
176
175
175
179
174
177
177
172
170
169
171
169
1
cervicals
dorsals
1
2
3
4
5
6
7
8
9
10
1
2
3
4
5
6
7
8
9
10
11
12
13
position in series

Fig. 9. Syntarsus rhodesiensis: dorsal vertebrae

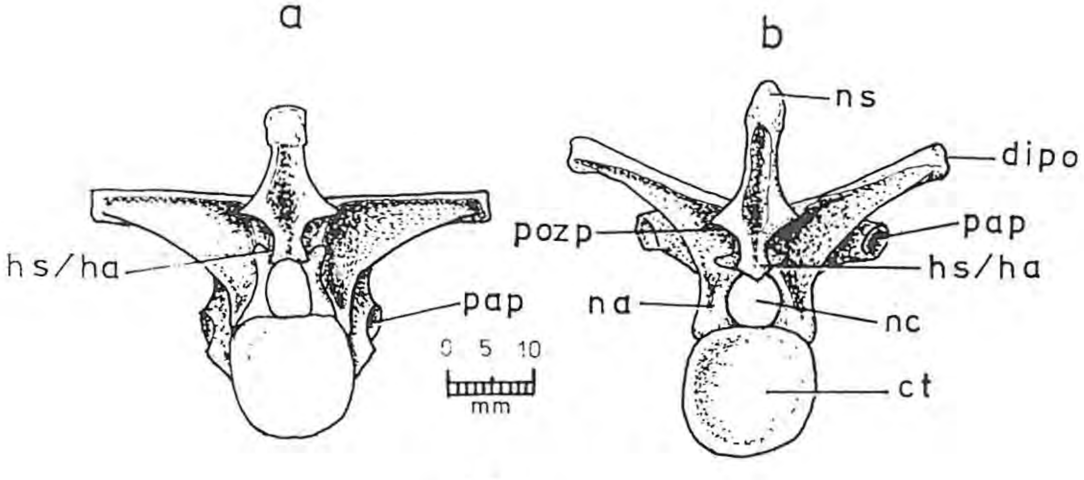
(a - c left lateral view)
(d - f dorsal view)
a,d - dorsal 2 (QG 180)
b,e - dorsal 5 (QG 406)
c,f - dorsal 7 (QG 408)

Fig. 10. Syntarsus rhodesiensis: hyposphene/hypantrum **articulations** on dorsal vertebrae

a - posterior view of 2nd dorsal (QG 180)
b - posterior view of 5th dorsal (QG 406)


a
b
c
d
e
f
0 1 2 3 4 5
cm

9


a
b
ns
dipo
pozp
pap
hs/ha
hs/ha
na
pap
nc
0 5 10
mm
ct

10

Fig. 11. *Syntarsus rhodesiensis*: gastralia

a - gastralia as preserved in the holotype (QG 1) with stomach contents shaded black (cf. Plate 14)

b - diagrammatic reconstruction of gastralia "basket" ("internal view" as in (a))

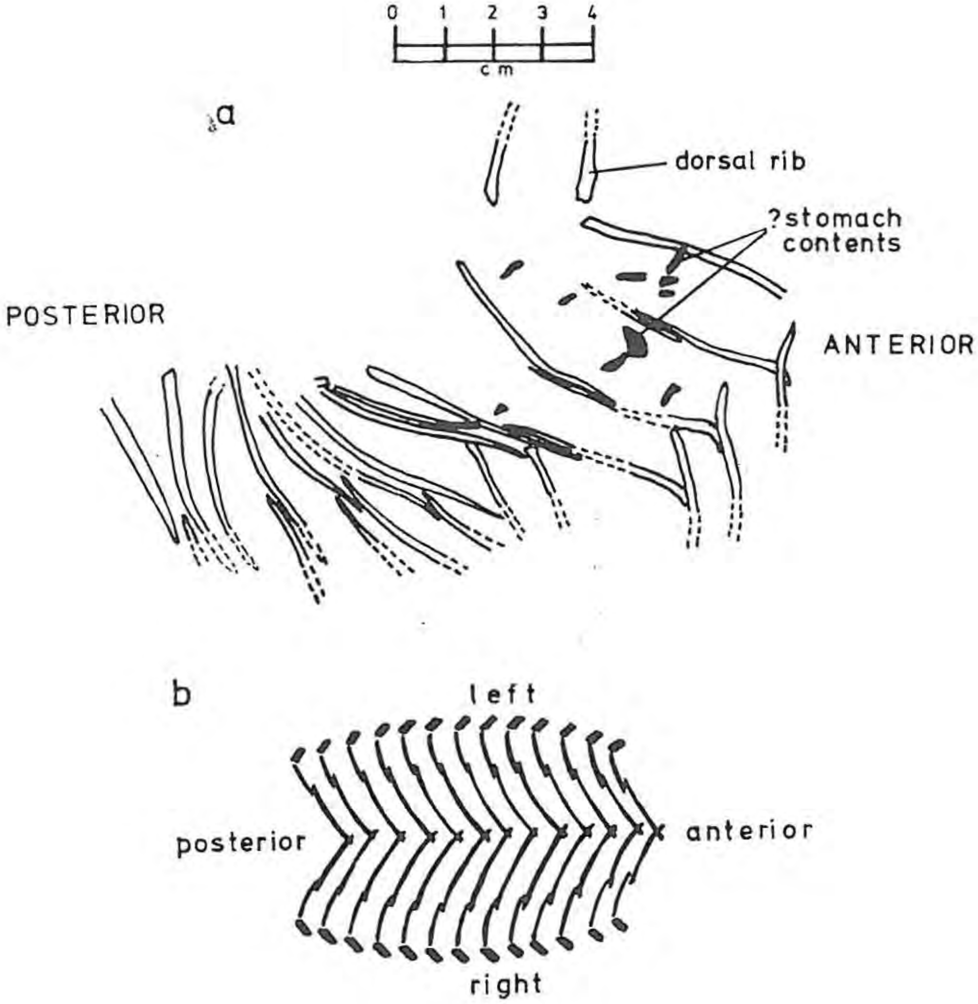

0 1 2 3 4
cm
a
dorsal rib
?stomach contents
POSTERIOR
ANTERIOR
b
left
posterior
anterior
right

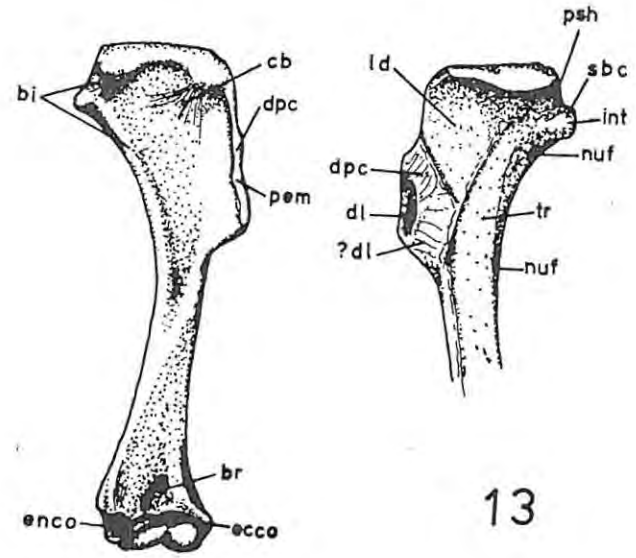
Fig. 12. *Syntarsus rhodesiensis*: L. scapulocoracoid, lateral view (based on QG 193)

Fig. 13. *Syntarsus rhodesiensis*: L. humerus (based on QG 514)

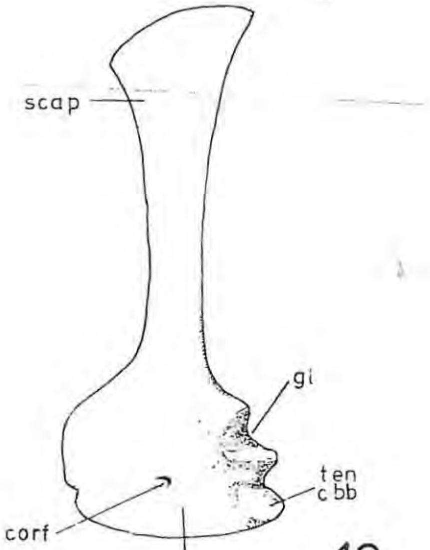
left: palmar view
right: anconal view of upper portion

Fig. 14. *Syntarsus rhodesiensis*: forearm elements

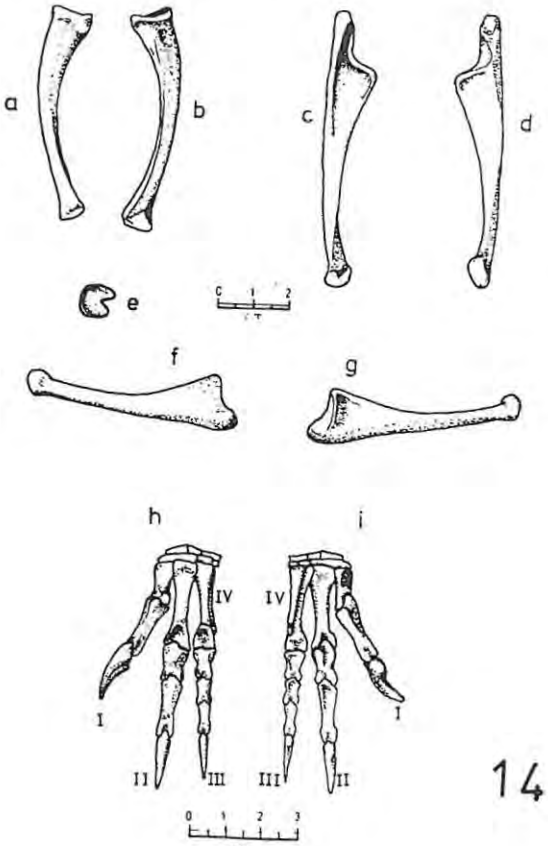
a,b: L. radius (a - lateral view; b - medial view) (QG 1)
c,d: L. ulna (c - medial view; d - lateral view) (QG 1)
e: R. radiale, proximal surface (QG 687)
f,g: R. ulna with short olecranon (f - medial view; g - lateral view) (QG 563)
h,i: L. carpus and manus (h - anconal view; i - palmar view) (QG 1)


psh
bi
cb
dpc
pem
br
enco
ecco
ld
sbc
int
nuf
dpc
dl
tr
?dl
nuf

13


scap
gl
ten
c bb
corf
cor

12


a
b
c
d
e
0 1 2
cm
f
g
h
i
IV
IV
I
I
II
III
III
II
0 1 2 3
cm

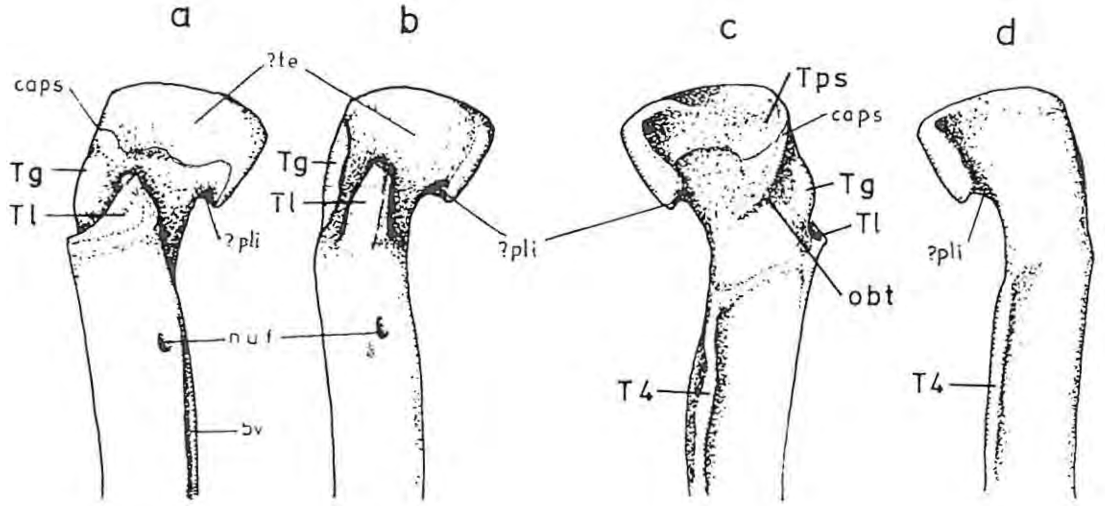
14

Fig. 15. Syntarsus rhodesiensis: heads of robust and gracile femora

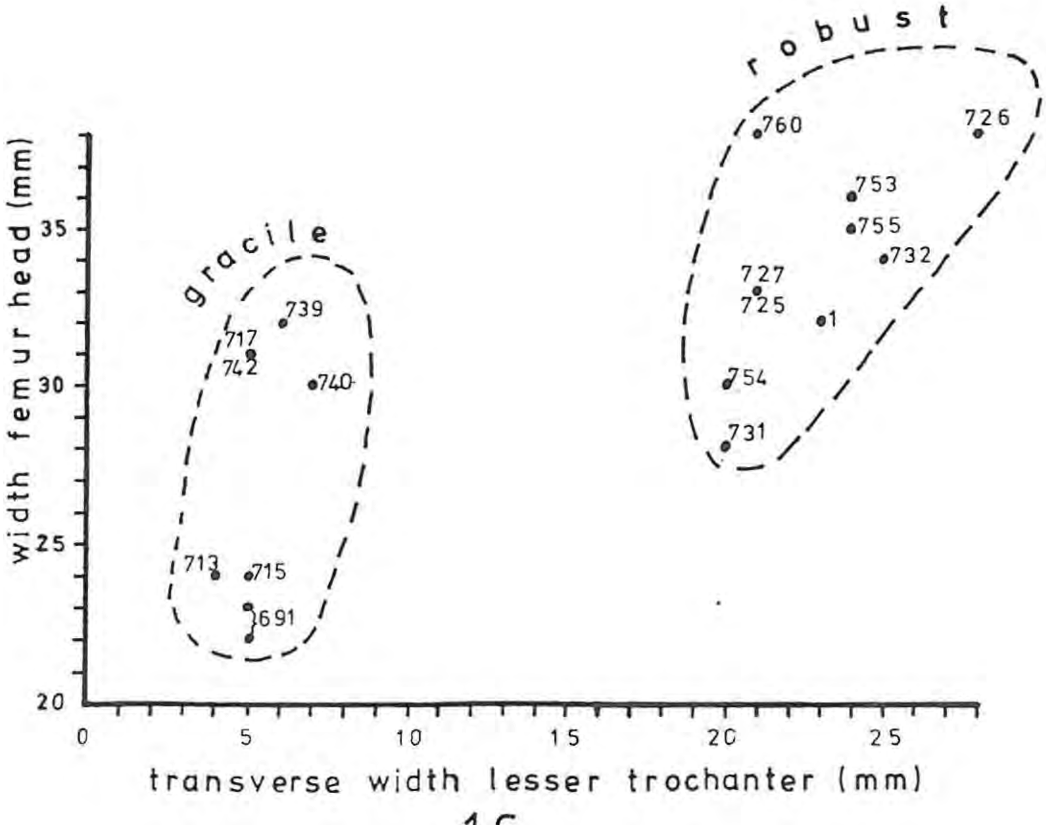
a,c: robust R. femur (a - anterior surface; c - posterior surface)

b,d: gracile R. femur (b - anterior surface; d - posterior surface)

Fig. 16. Syntarsus rhodesiensis: graph of femur head width plotted against transverse width of lesser trochanter, to show dimorphism


a
b
c
d
caps
?te
Tg
Tl
?pli
nuf
bv
Tps
caps
Tg
Tl
obt
T4
?pli
T4

15

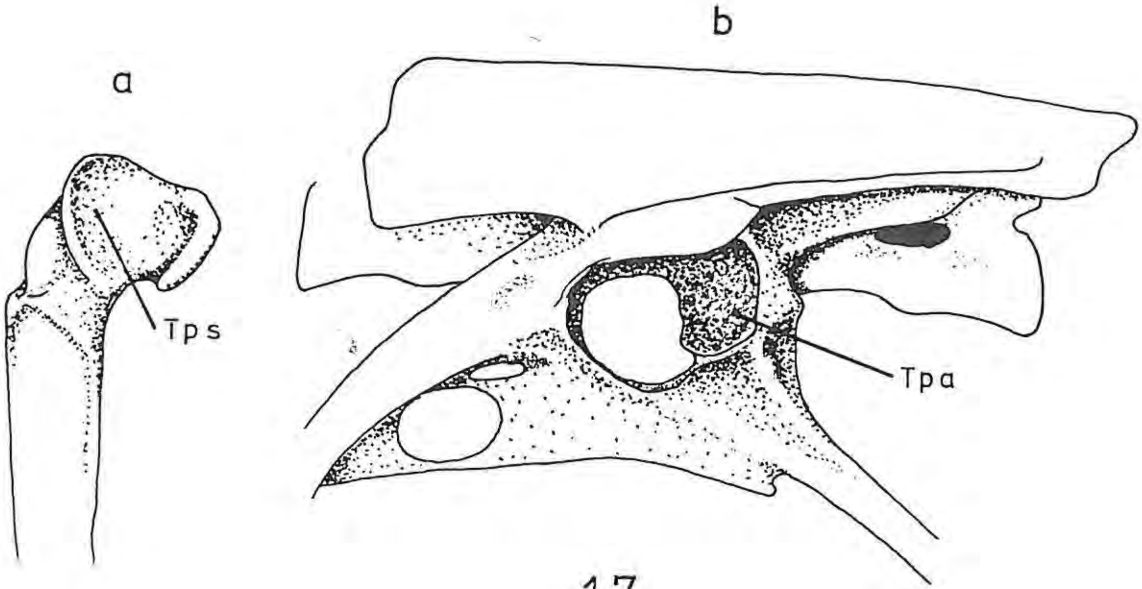

robust
gracile
width femur head (mm)
transverse width lesser trochanter (mm)
20
25
30
35
0
5
10
15
20
25
717
742
739
740
713
715
691
760
726
753
755
732
727
725
1
754
731

16

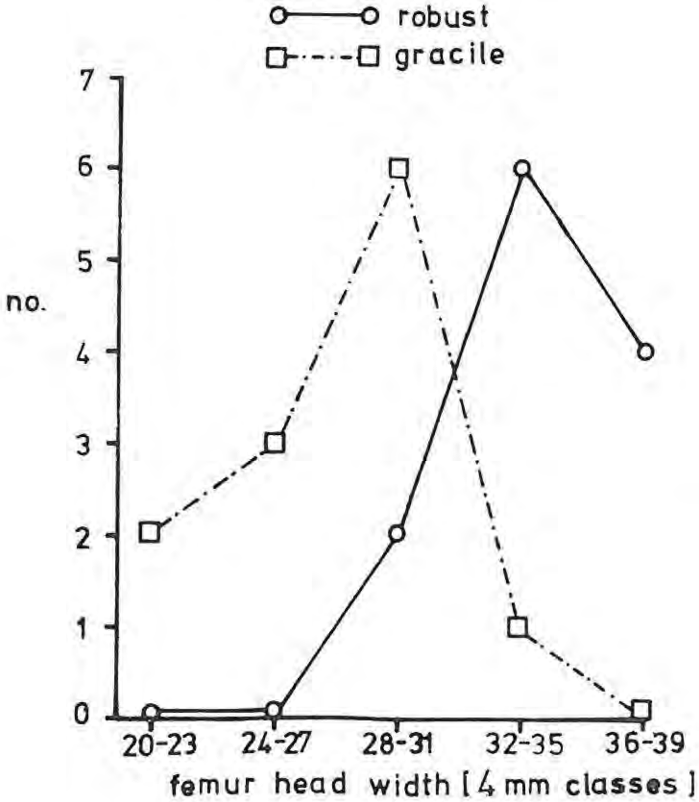
Fig. 17. Syntarsus rhodesiensis:

a - posterior view of proximal end, left femur
b - left side view of acetabular region of pelvis:to show "pseudotrochanter" and "pseudantitrochanter"

Fig. 18. Syntarsus rhodesiensis: size:frequency distribution of the heads of femora in the sample from the Chitake River locality


a
b
Tps
Tpa

17


robust
gracile
no.
7
6
5
4
3
2
1
0
20-23
24-27
28-31
32-35
36-39
femur head width [4 mm classes]

18

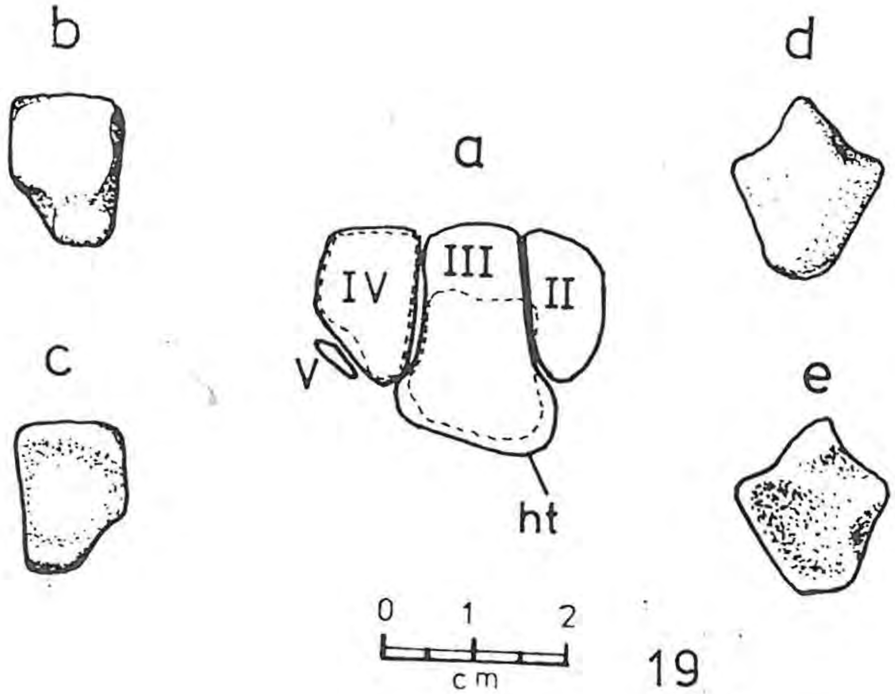
Fig. 19. Syntarsus rhodesiensis: tarsal region

a - metatarsal profile (positions of distal tarsals 3 and 4 dashed), left pes (QG 768)
b,c - R. distal tarsal 4 (b - distal surface; c - proximal surface)
d,e - R. distal tarsal 3 (d - proximal surface; e - distal surface) (QG 846)

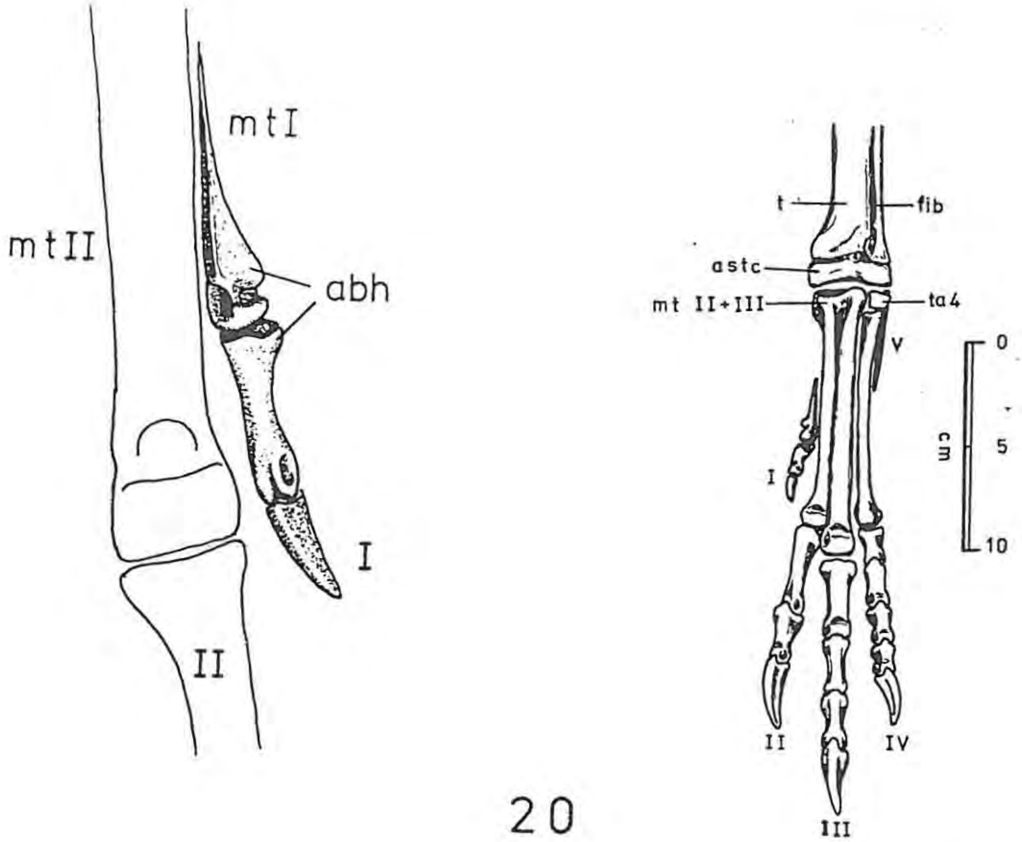
Fig. 20. Syntarsus rhodesiensis: pes

left: detail of digit I to show abductor hallucis tubercle

right: L. pes of holotype, dorsal view


b
d
a
III
IV
II
V
c
e
ht
0
1
2
cm

19


mtI
mtII
abh
I
II
t
fib
astc
mt II+III
ta4
V
0
cm
5
10
I
II
IV
III

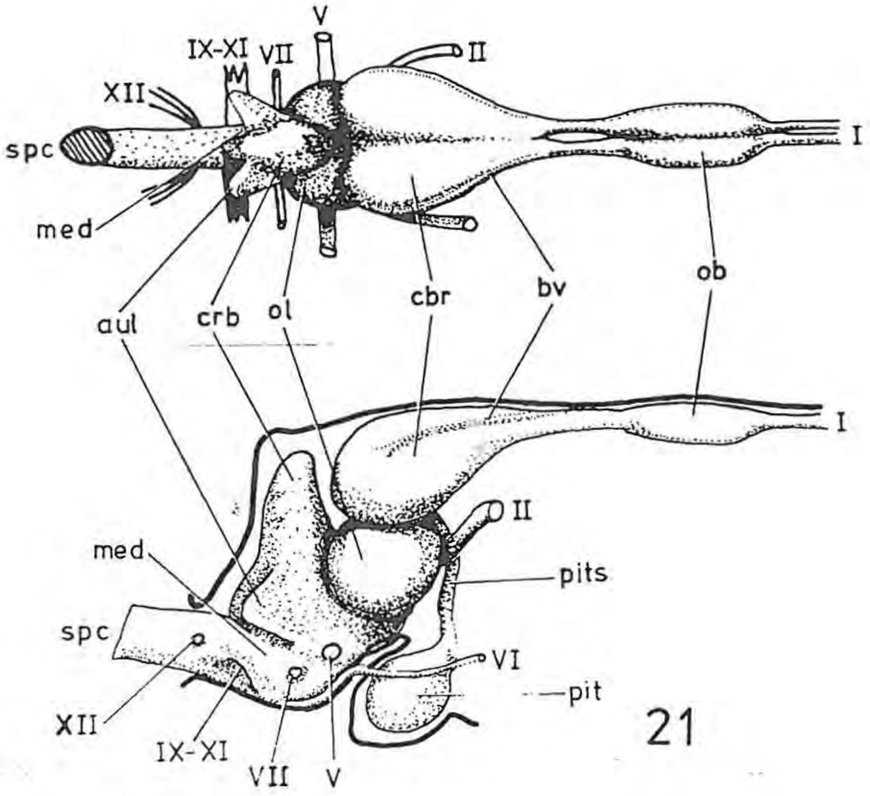
20

Fig. 21. *Syntarsus rhodesiensis*: restoration of brain

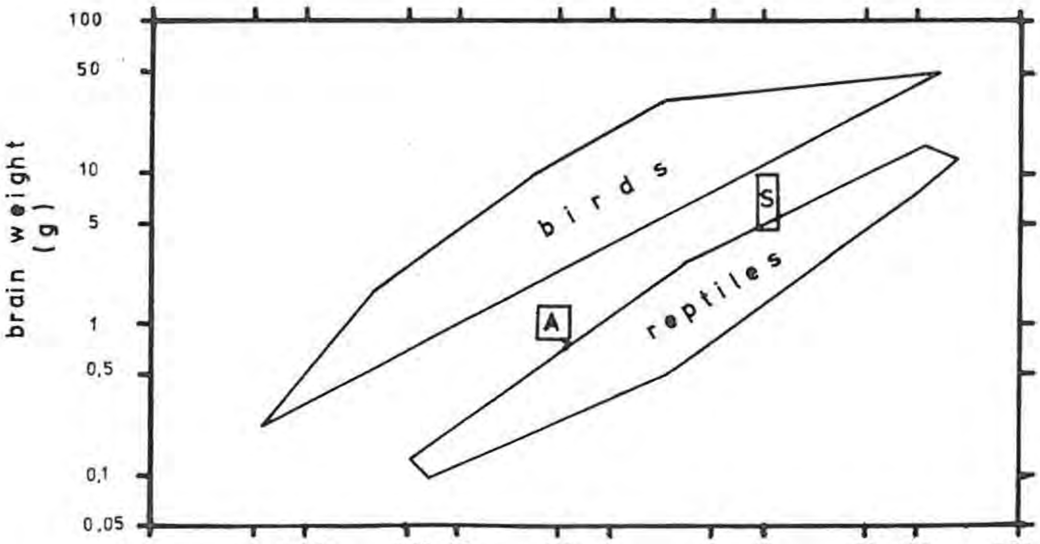
above - dorsal view

below - right lateral view (limits of endocranium outlined)

Fig. 22. Brain and body weight relationships in living birds and reptiles, compared with *Archaeopteryx* (A in square) and Syntarsus (S in oblong). (Adapted from Jerison, 1968: Fig. 2)


V
IX-XI
VII
II
XII
spc
I
med
aul
crb
ol
cbr
bv
ob
I
II
med
pits
spc
VI
pit
XII
IX-XI
VII
V

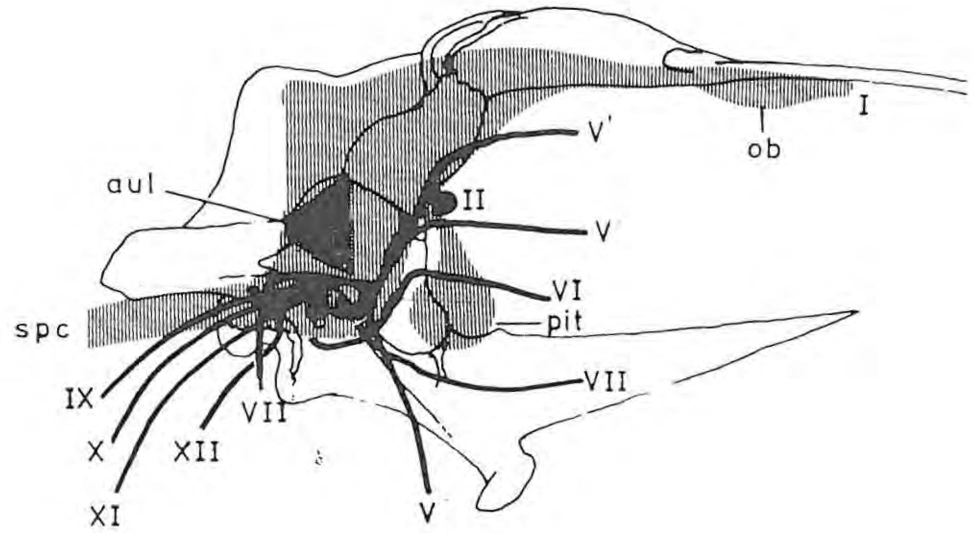
21


brain weight (g)
100
50
10
5
1
0,5
0,1
0,05
birds
reptiles
S
A
0,001
0,005
0,01
0,05
0,1
0,5
1
5
10
50
100
500
body weight (kg)

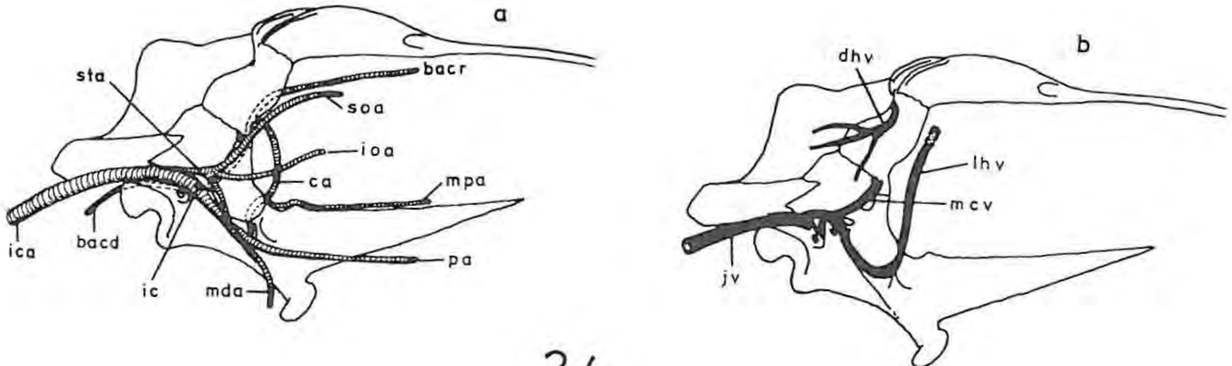
22

Fig. 23. *Syntarsus rhodesiensis*: restoration of cranial nerves (limits of endocranium shaded)

Fig. 24. *Syntarsus rhodesiensis*: restoration of major cranial blood vessels
a - arteries
b - veins


V'
I
ob
aul
II
V
VI
spc
pit
IX
VII
VII
X
XII
XI
V

23

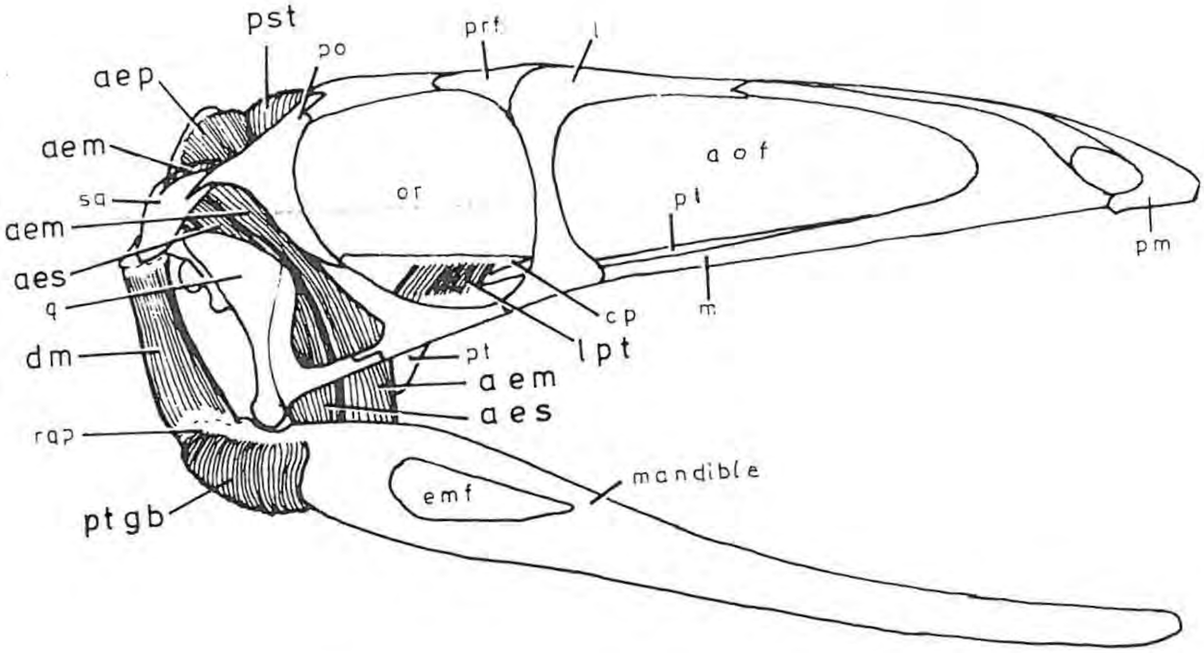

a
sta
bacr
soa
ioa
ca
mpa
ica
bacd
pa
ic
mda
b
dhv
lhv
mcv
jv

24

Fig. 25. *Syntarsus rhodesiensis*: restoration of jaw muscles

above : lateral view

below : internal view


pst
po
prf
l
aep
aem
sa
aem
aes
q
dm
rap
ptgb
or
aof
pt
pm
m
cp
lpt
pt
aem
aes
mandible
emf

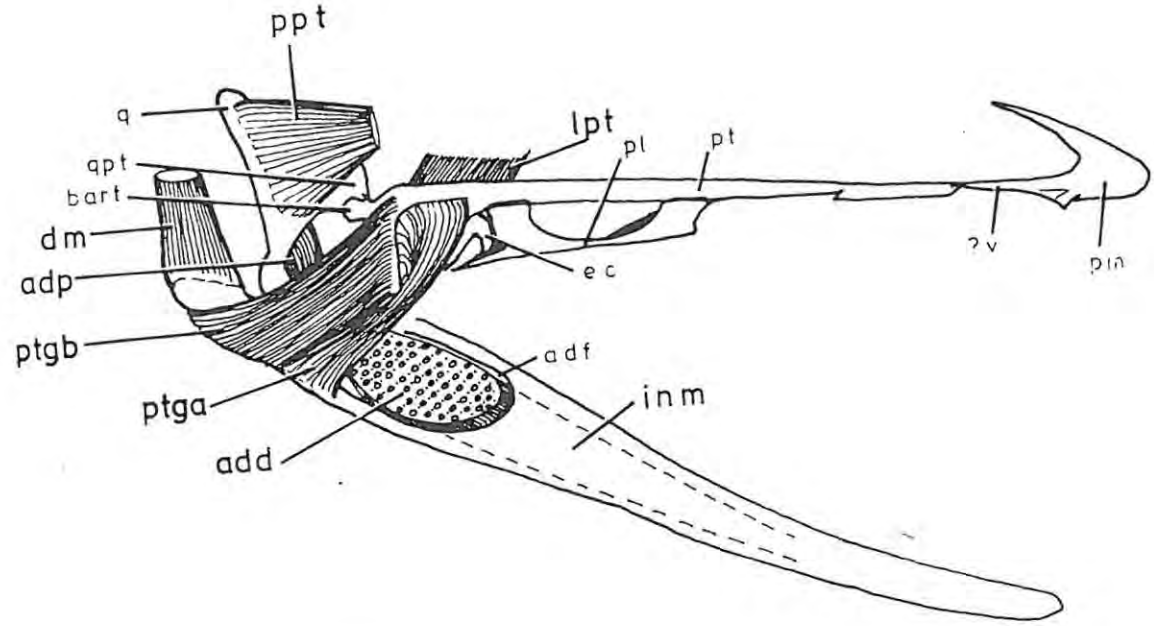

ppt
q
qpt
bart
dm
adp
ptgb
ptga
add
lpt
pl
pt
ec
adf
inm
?v
pm

Fig. 26. Syntarsus rhodesiensis: restoration of cervical muscles

a - lateral view

b - muscle insertions on occiput

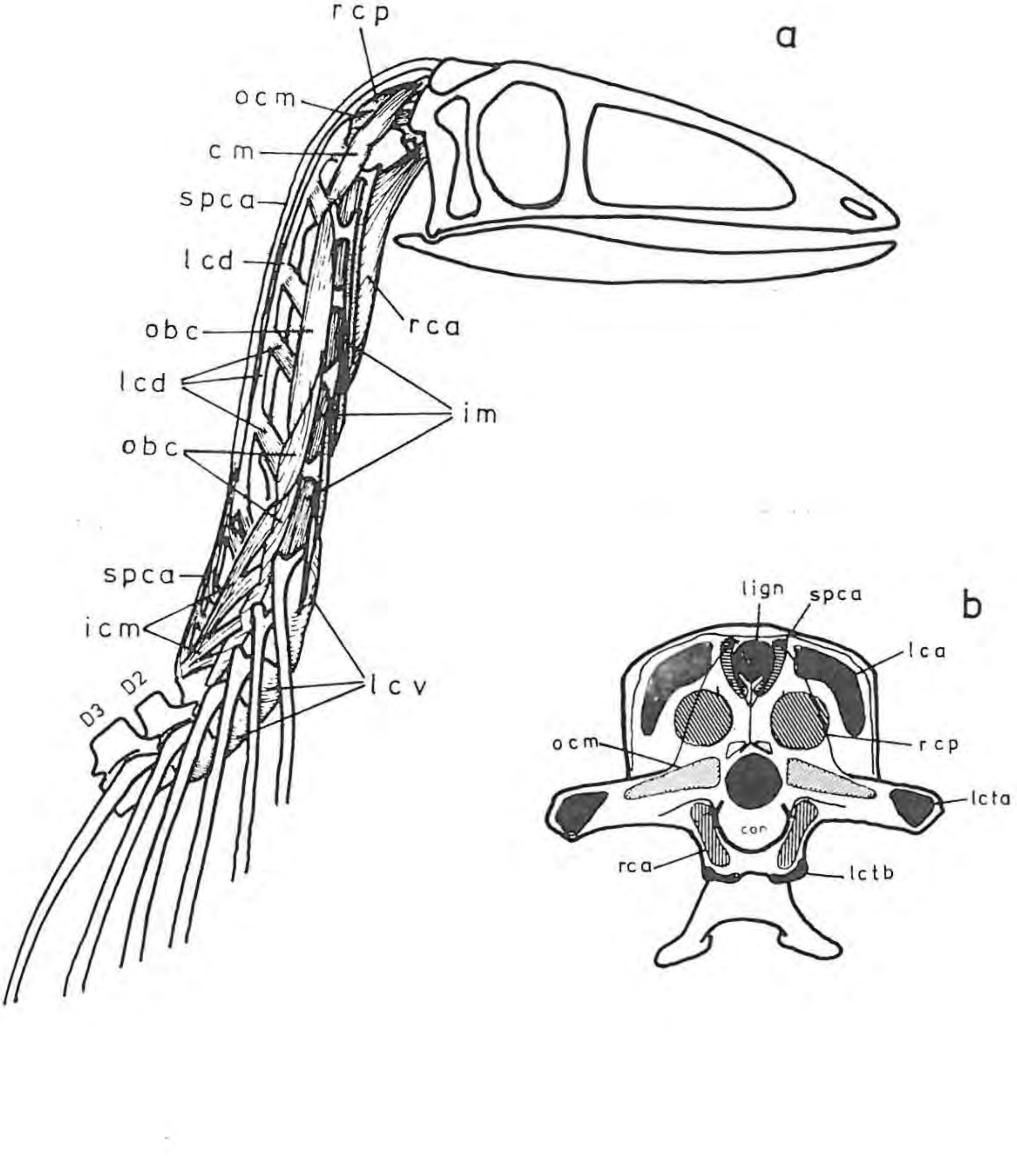

a
rcp
ocm
cm
spca
lcd
obc
lcd
obc
spca
icm
D3
D2
rca
im
lcv
b
lign
spca
lca
rcp
ocm
lcta
con
rca
lctb

Fig. 27. *Syntarsus rhodesiensis*: restoration of forelimb musculature

a - lateral view

b - semi-schematic section viewed from in front

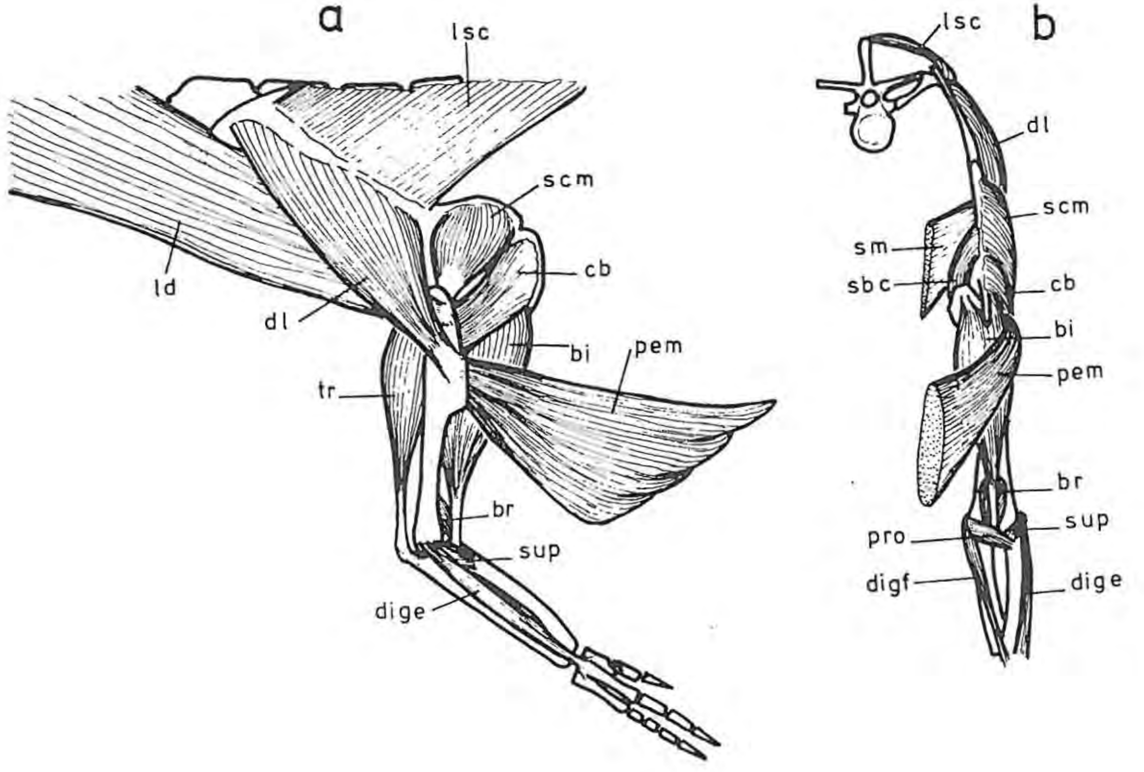

a
lsc
scm
cb
bi
pem
ld
dl
tr
br
sup
dige
b
lsc
dl
scm
sm
sbc
cb
bi
pem
br
sup
pro
digf
dige

Fig. 28. Syntarsus rhodesiensis: muscle attachments (dashed) on forelimb bones:

a – c scapulocoracoid (a – posterior; b – lateral; c – medial)
d – g humerus (d – palmar; e – anconal; f – lateral; g – medial)
h,k radius (h – lateral; k – medial)
i,j ulna (i – lateral; j – medial)

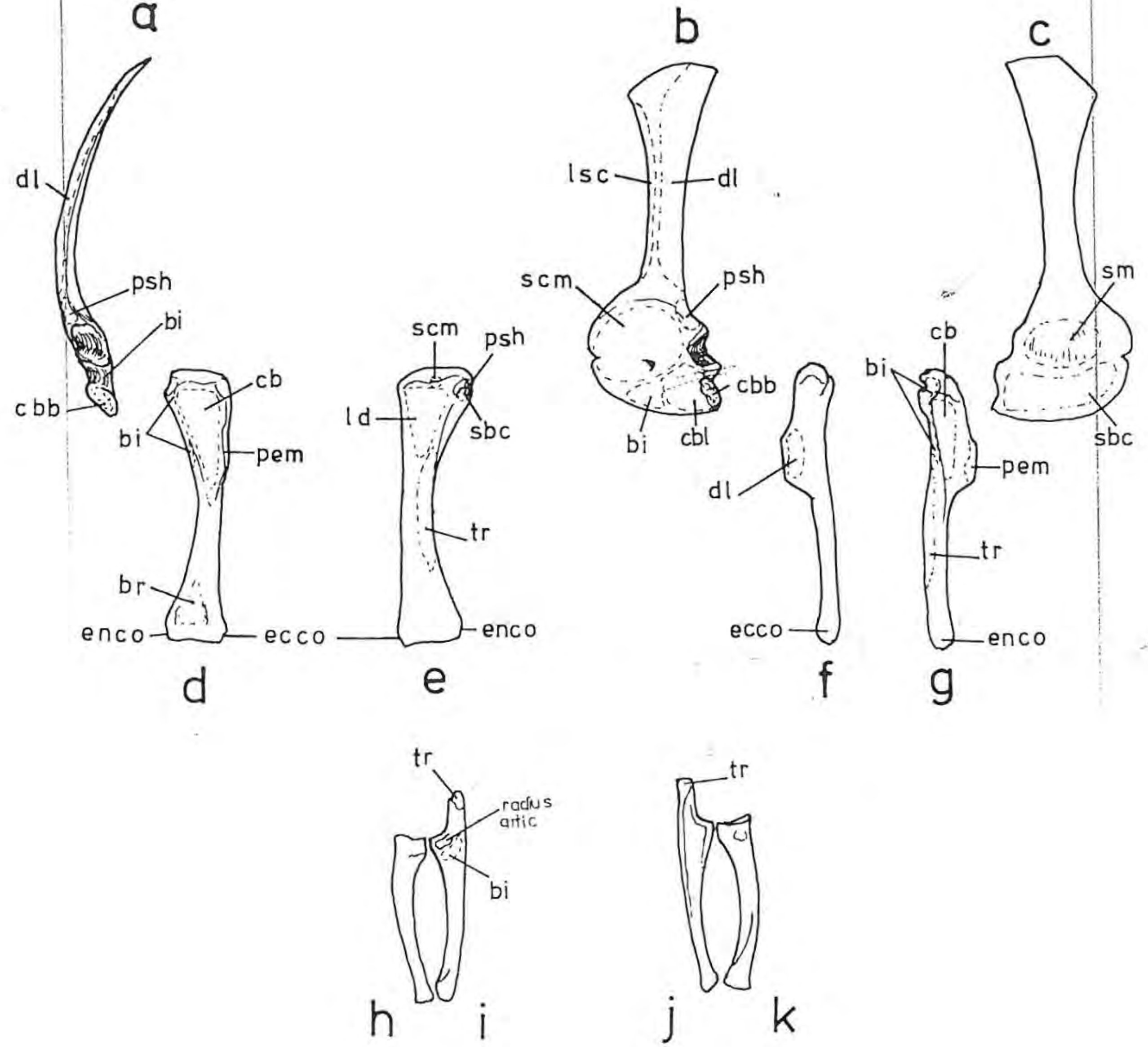

a
dl
psh
bi
cbb
b
lsc
dl
scm
psh
cbb
bi
cbl
c
sm
sbc
d
cb
bi
pem
br
enco
ecco
e
scm
psh
ld
sbc
tr
ecco
enco
f
dl
ecco
g
cb
bi
pem
tr
enco
h
i
tr
radius artic
bi
j
k
tr

Fig. 29. Syntarsus rhodesiensis: restoration of hindlimb musculature
a - semi-diagrammatic section, posterior view
b - semi-diagrammatic section, anterior view
c - side view mainly of superficial muscles
d - schematic restoration of musculature

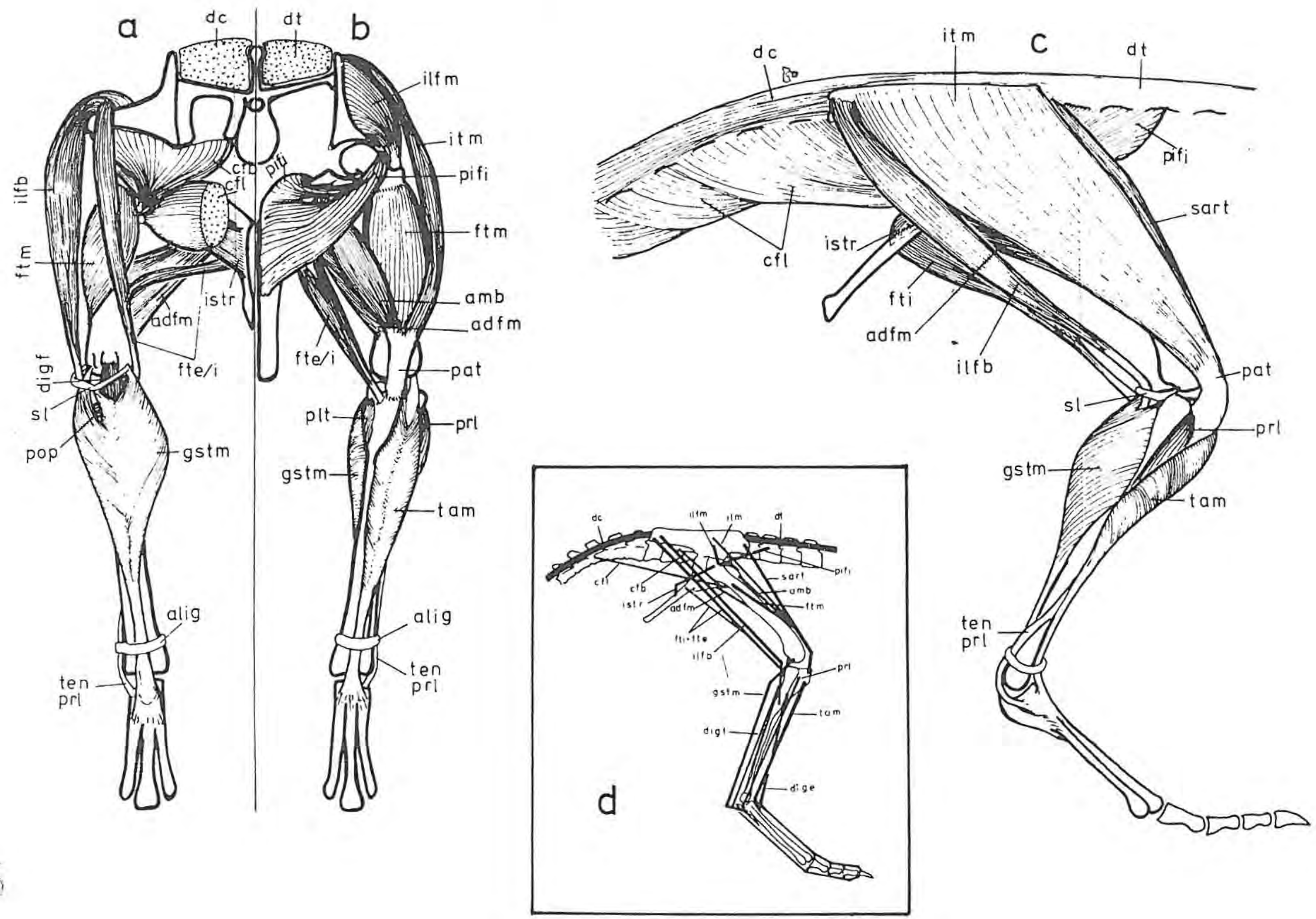

a
b
c
d
dc
dt
ilfm
itm
pifi
ftm
amb
adfm
pat
prl
tam
alig
ten prl
plt
gstm
fte/i
istr
cfb
cfl
pifi
ilfb
ftm
adfm
fte/i
digf
sl
pop
gstm
alig
ten prl
dc
itm
dt
pifi
sart
cfl
istr
fti
adfm
ilfb
pat
sl
prl
gstm
tam
ten prl
dc
ilfm
itm
dt
pifi
sart
amb
ftm
cfl
cfb
istr
adfm
fti-fte
ilfb
prl
gstm
tam
digf
dige

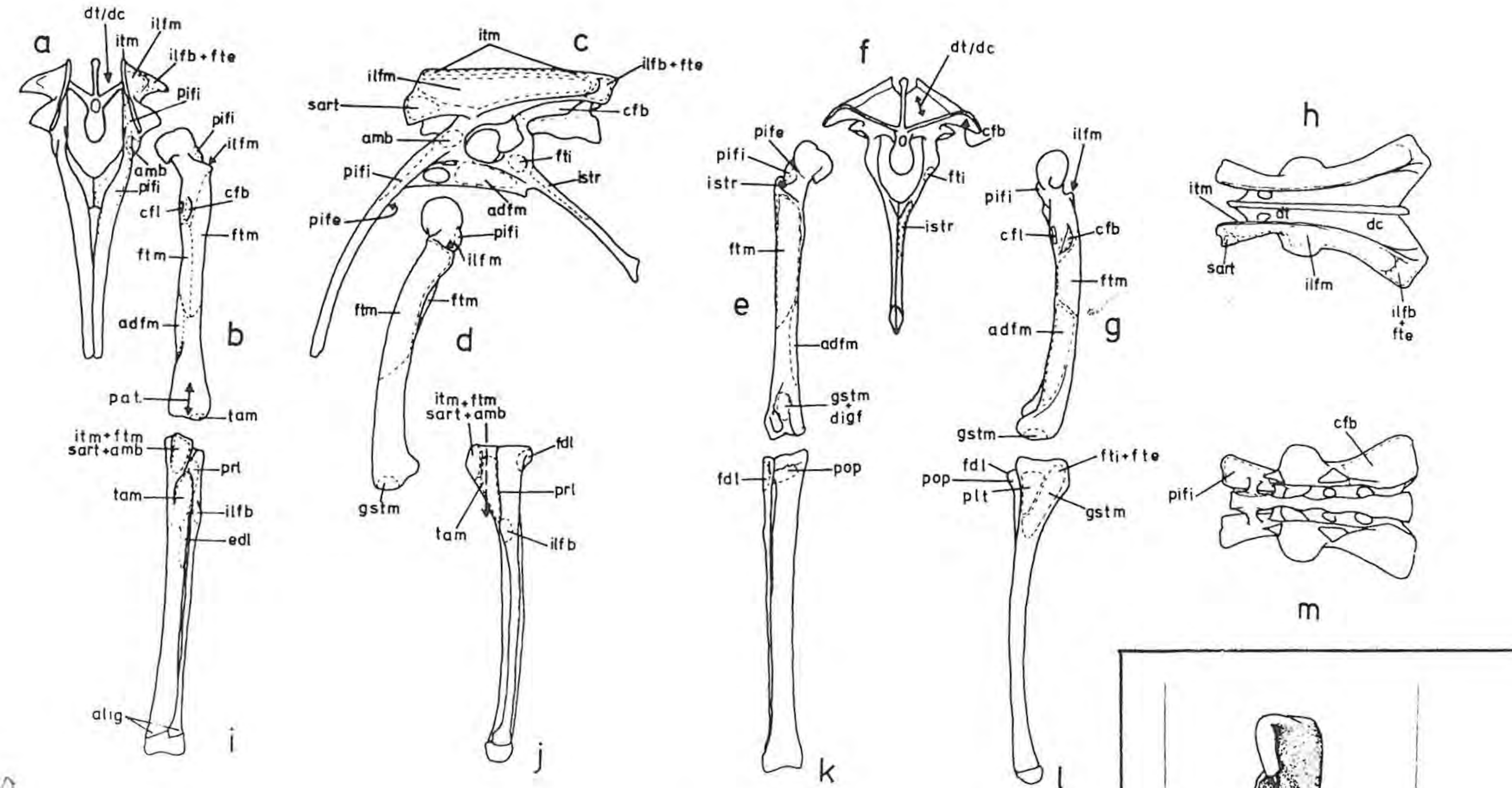
Fig. 30. *Syntarsus rhodesiensis*: muscle attachments (dashed) on hindlimb bones:

a,c,f,h,m - pelvis (a - anterior; c - lateral; f - posterior; h - dorsal; m - ventral [pubes + isc removed])

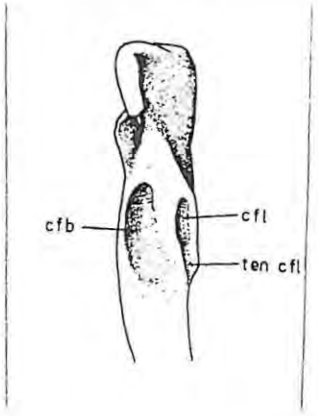
b,d,e,g - femur (b - anterior; d - lateral; e - posterior; g - medial)

i,j,k,l - tibia, fibula (i - anterior; j - lateral; k - posterior; l - medial)

Fig. 31. *Syntarsus rhodesiensis*: medial view of proximal end R. femur (QG 745) to show groove for accessory tendon of caudifemoralis longus muscle


a
dt/dc
itm
ilfm
ilfb + fte
pifi
amb
pifi
b
pifi
ilfm
cfb
cfl
ftm
ftm
adfm
pat.
tam
c
itm
ilfm
ilfb + fte
sart
cfb
amb
fti
pifi
istr
adfm
pife
d
pifi
ilfm
ftm
ftm
gstm
e
pife
pifi
istr
ftm
adfm
gstm + digf
f
dt/dc
cfb
fti
istr
g
ilfm
pifi
cfl
cfb
ftm
adfm
gstm
h
itm
dt
dc
sart
ilfm
ilfb + fte
i
itm + ftm
sart + amb
prl
tam
ilfb
edl
alig
j
itm + ftm
sart + amb
fdl
prl
tam
ilfb
k
fdl
pop
l
fdl
pop
plt
fti + fte
gstm
m
cfb
pifi

30


cfb
cfl
ten cfl

31

Fig. 32. Syntarsus rhodesiensis: schematic representation of resting and protracted states in the cranial kinetic cycle

a,b - side view; c,d - palatal view
a,c - resting; b,d protracted (in d, note how palatal elements move medially to close interpterygoid vacuity)

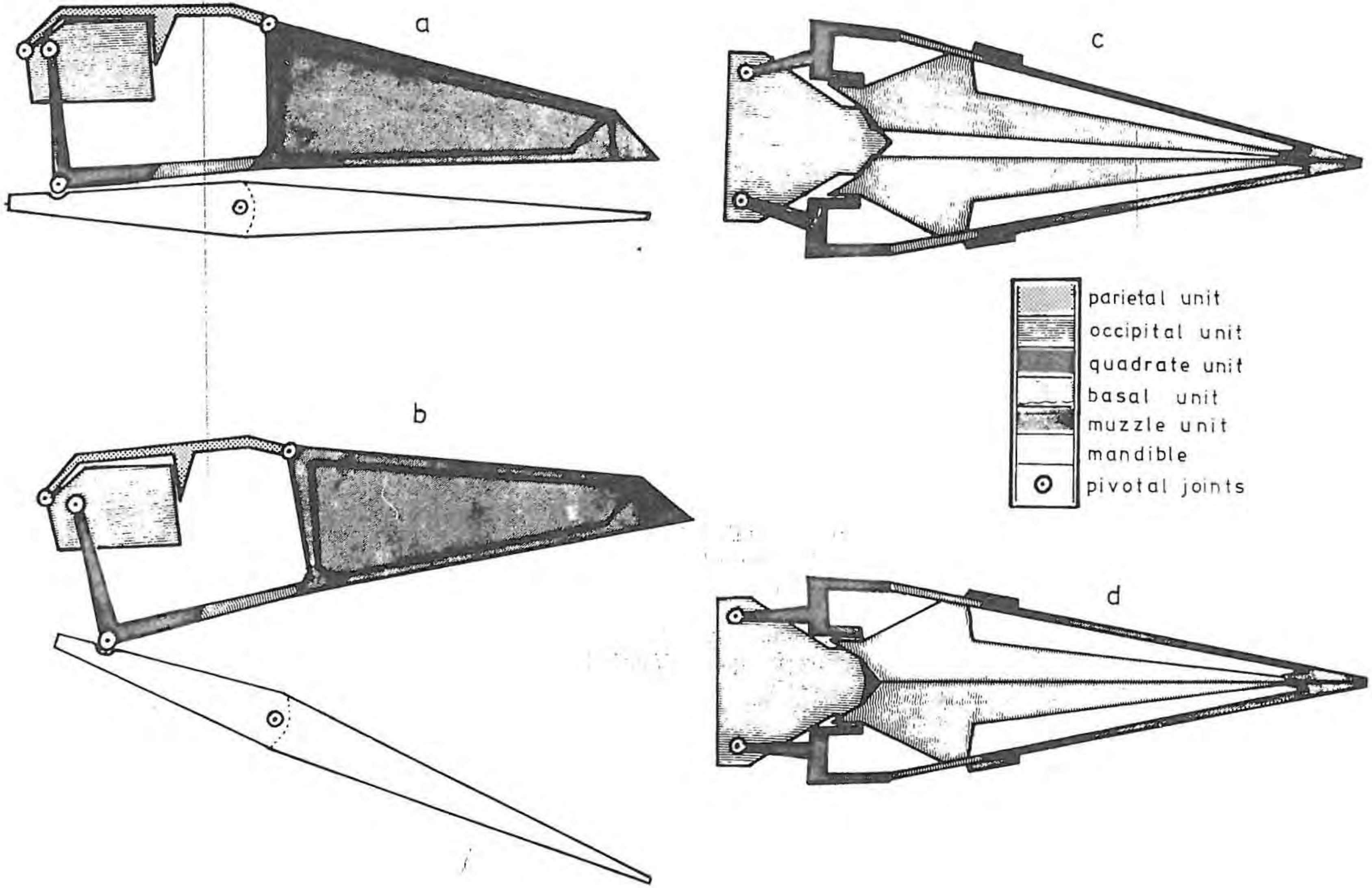
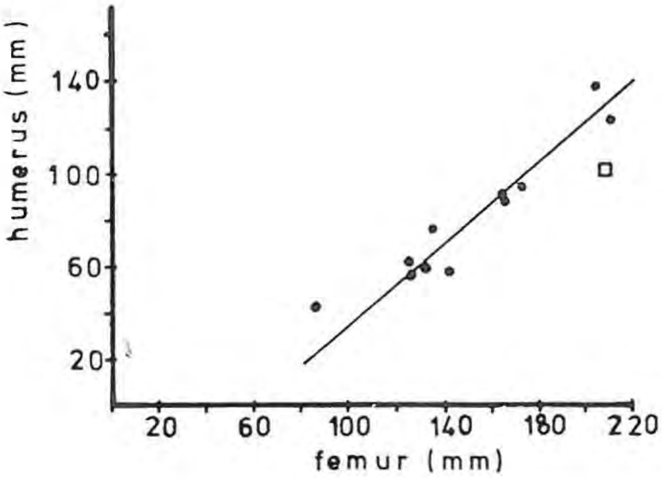
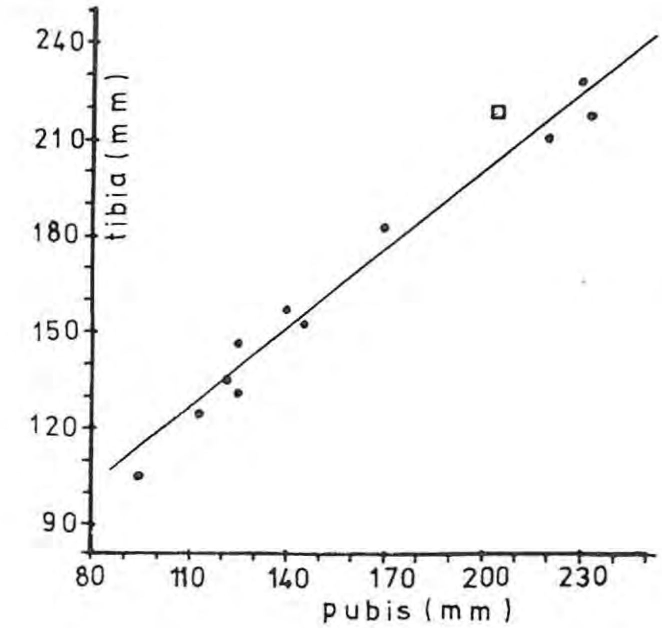

a
b
c
d
parietal unit
occipital unit
quadrate unit
basal unit
muzzle unit
mandible
pivotal joints

Fig. 33. Graphs of limb bone proportional relationships (adapted from Colbert & Baird, 1958)

dots - Coelophysis
open squares - Syntarsus (holotype)


humerus (mm)
140
100
60
20
20
60
100
140
180
220
femur (mm)


tibia (mm)
240
210
180
150
120
90
80
110
140
170
200
230
pubis (mm)

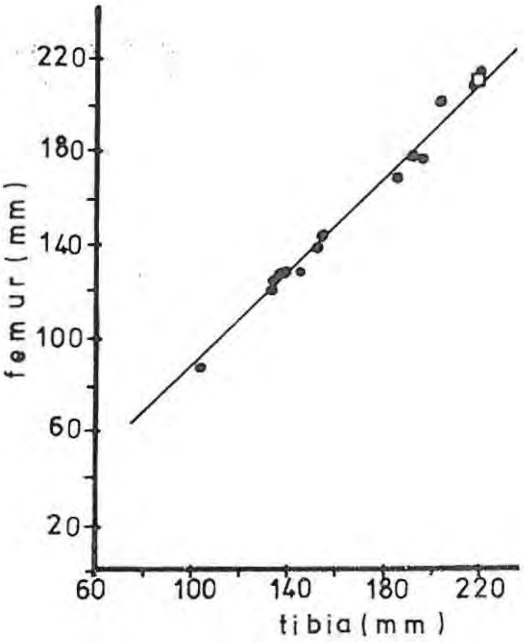

femur (mm)
220
180
140
100
60
20
60
100
140
180
220
tibia (mm)

Fig. 34. Pelvis of theropods in lateral (a - c); dorsal (d - f) and posterior (g - i) views

a,d,g - *Coelophysis* (information from unpublished preliminary drawings by courtesy of Dr. E.H. Colbert)
b,e,h - *Syntarsus* (holotype, adapted from Raath, 1969)
c,f,i - *Elaphrosaurus* (modified and corrected for distortion, from Janensch, 1925)

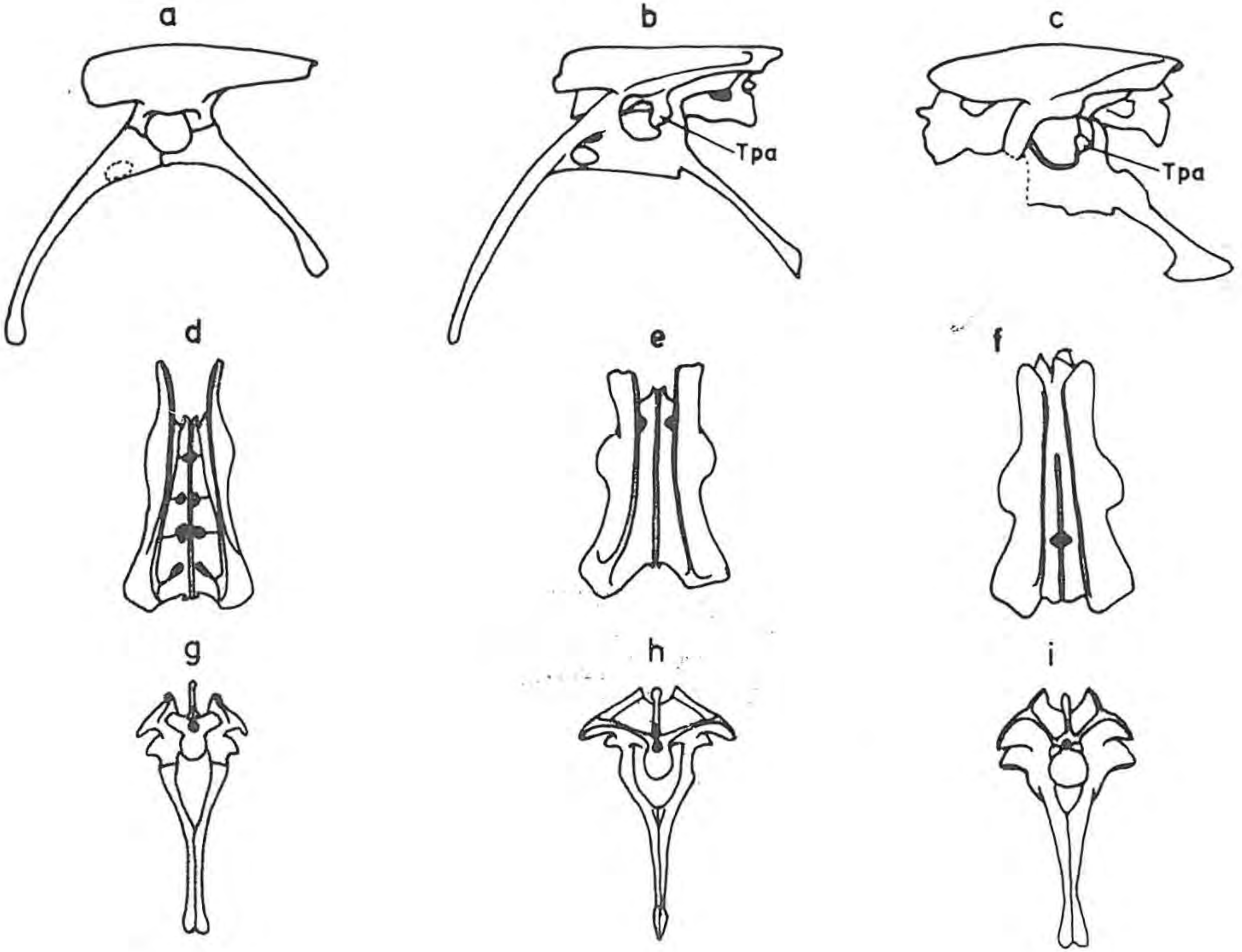

a
b
c
Tpa
Tpa
d
e
f
g
h
i

Fig. 35. *Syntarsus rhodesiensis*: reconstruction of the skeleton

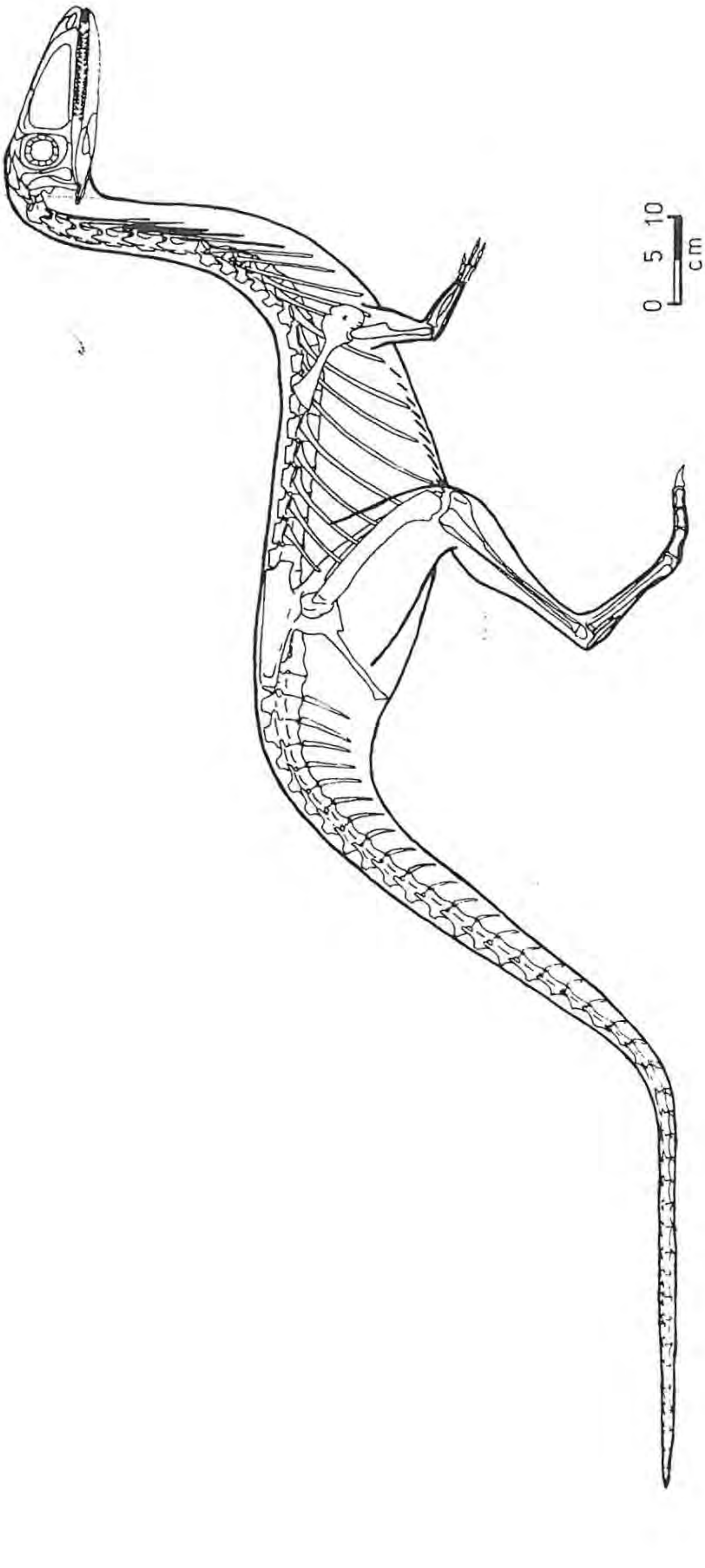
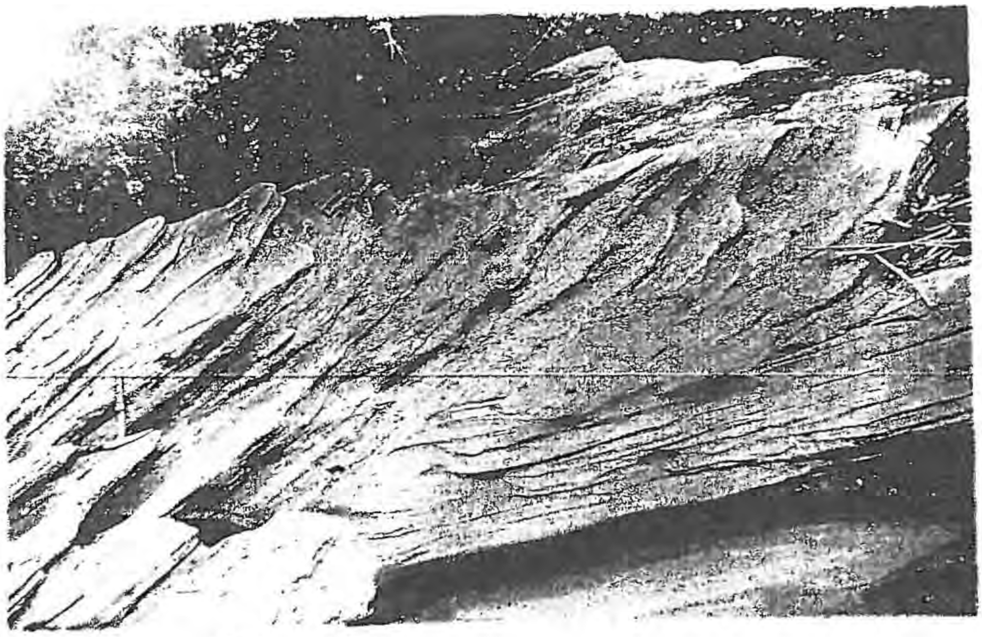

0 5 10
cm

Plate 1.

a - current-bedded, gritty sandstone in the Maura River area

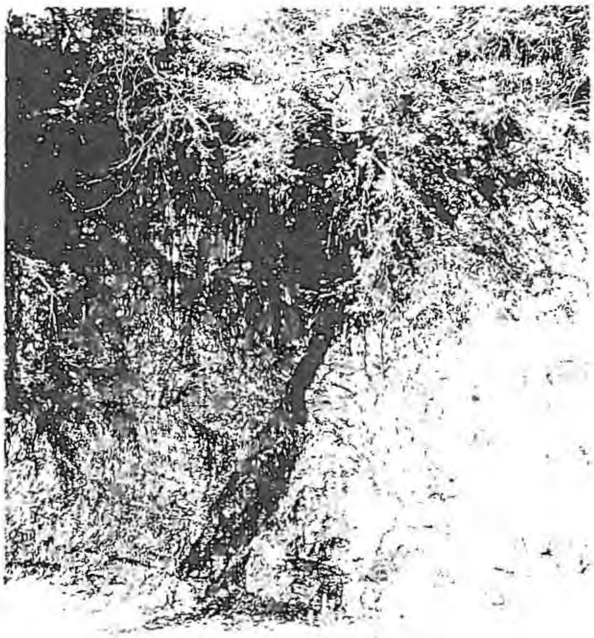
b - post-Karroo fault cutting Forest Sandstone and overlying conglomerates in the Chitake River area (downthrown conglomerate to left)

Plate 2. Manganese encrustation (black) around bones, as found in the Maura River and Chitake River localities

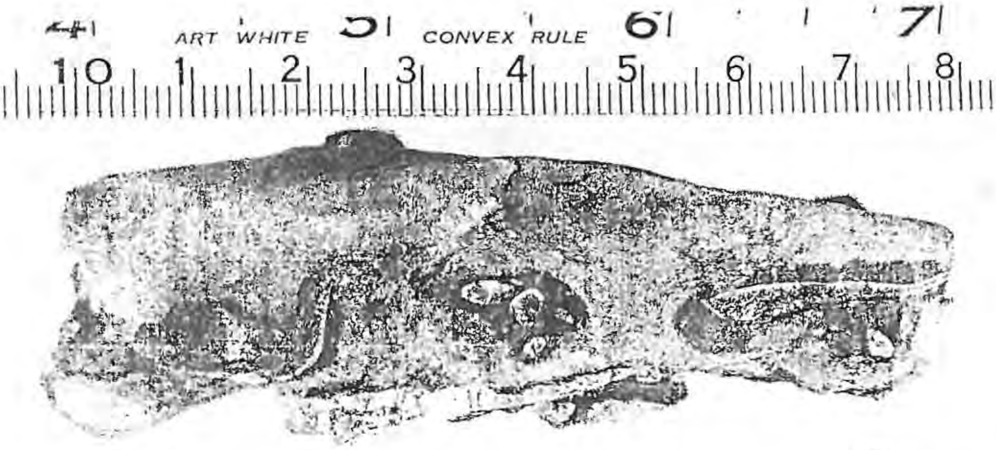


a

1



b

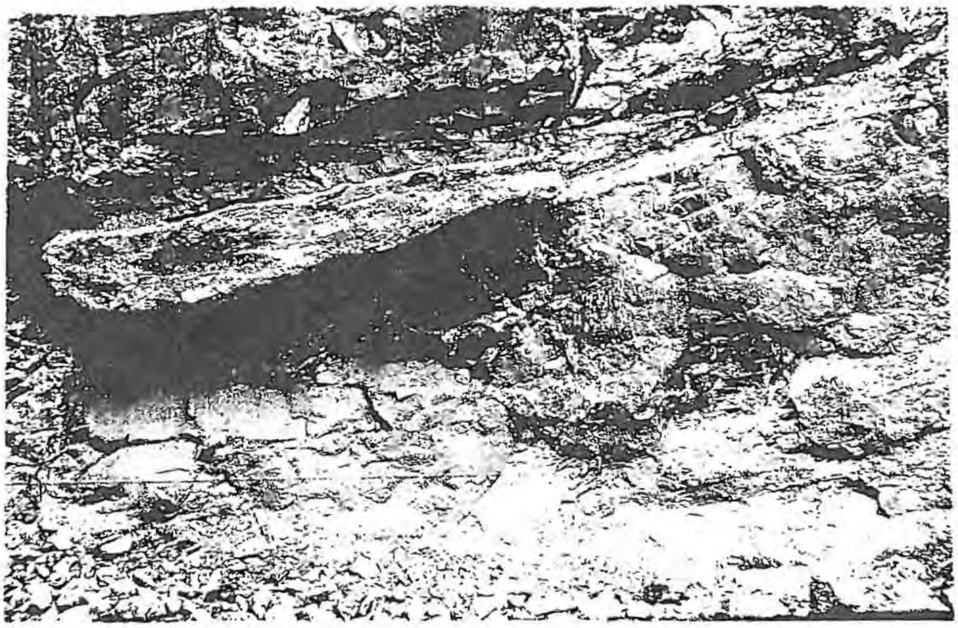


2

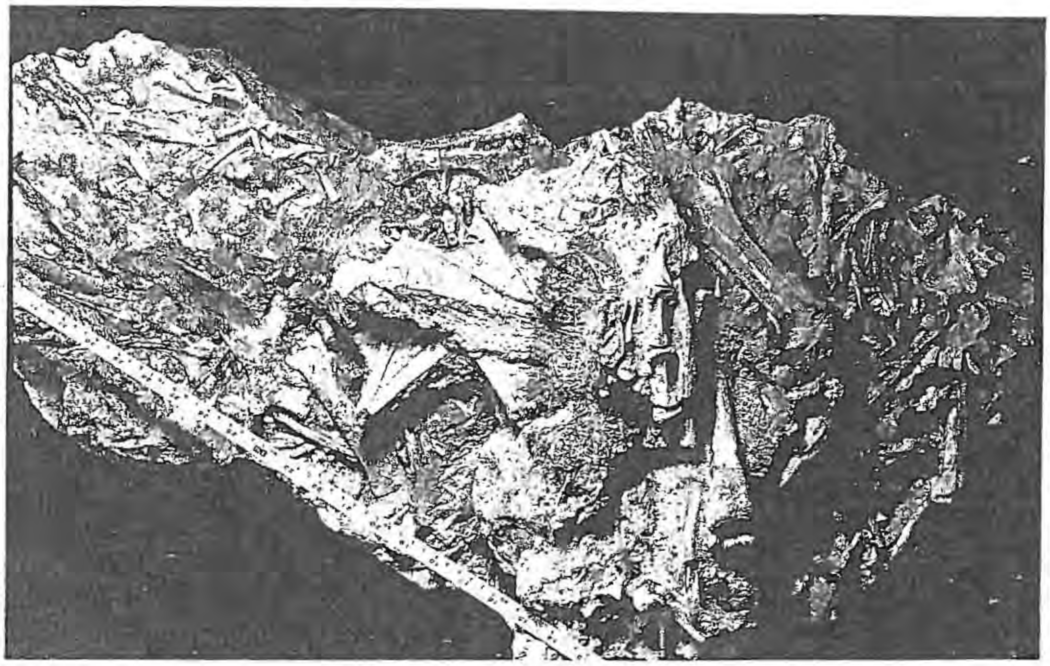
Plate 3. a - the lens in the Chitake River from which the concentrated _Syntarsus_ remains were recovered

b - a portion of a block of Chitake River matrix showing the concentration and mixing of _Syntarsus_ remains

c - the holotype of _Syntarsus_ (QG 1) _in situ_ on Southcote Farm, prior to excavation (scale in inches)



a



b

c

Plate 4. Articulated hardboard model of skull used in elucidating cranial kinesis

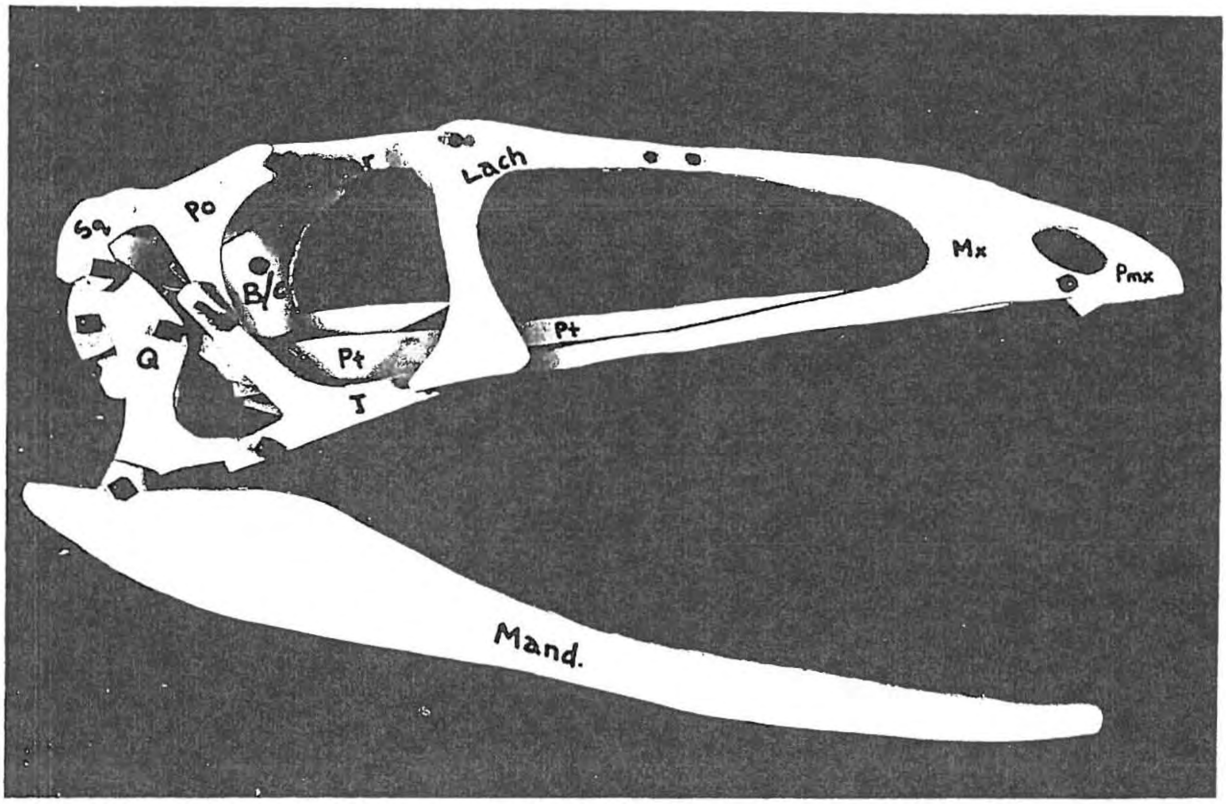
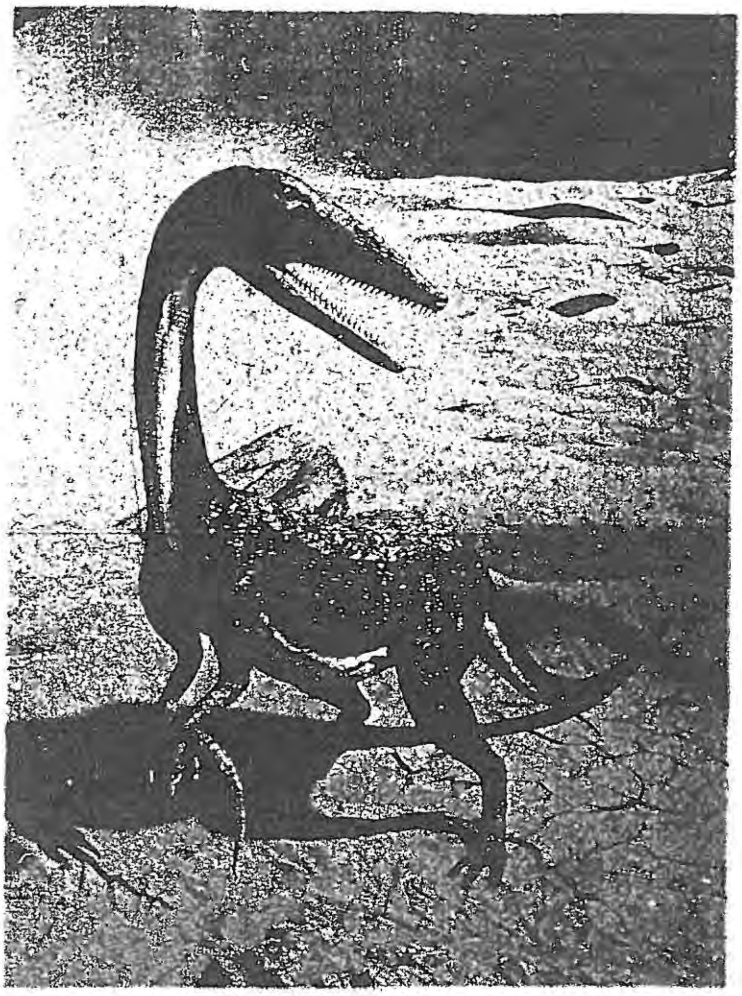

Sq
Po
Lach
Mx
Pmx
B/c
Pt
Pt
Q
J
Mand.

Plate 5. Flesh restorations of Syntarsus

a - life size model in National Museum, Bulawayo (modelled by Mr. T.W. Coffin-Grey)

b - scale models in Queen Victoria Museum, Salisbury (modelled by Mr. L.J. Penny)



a

b

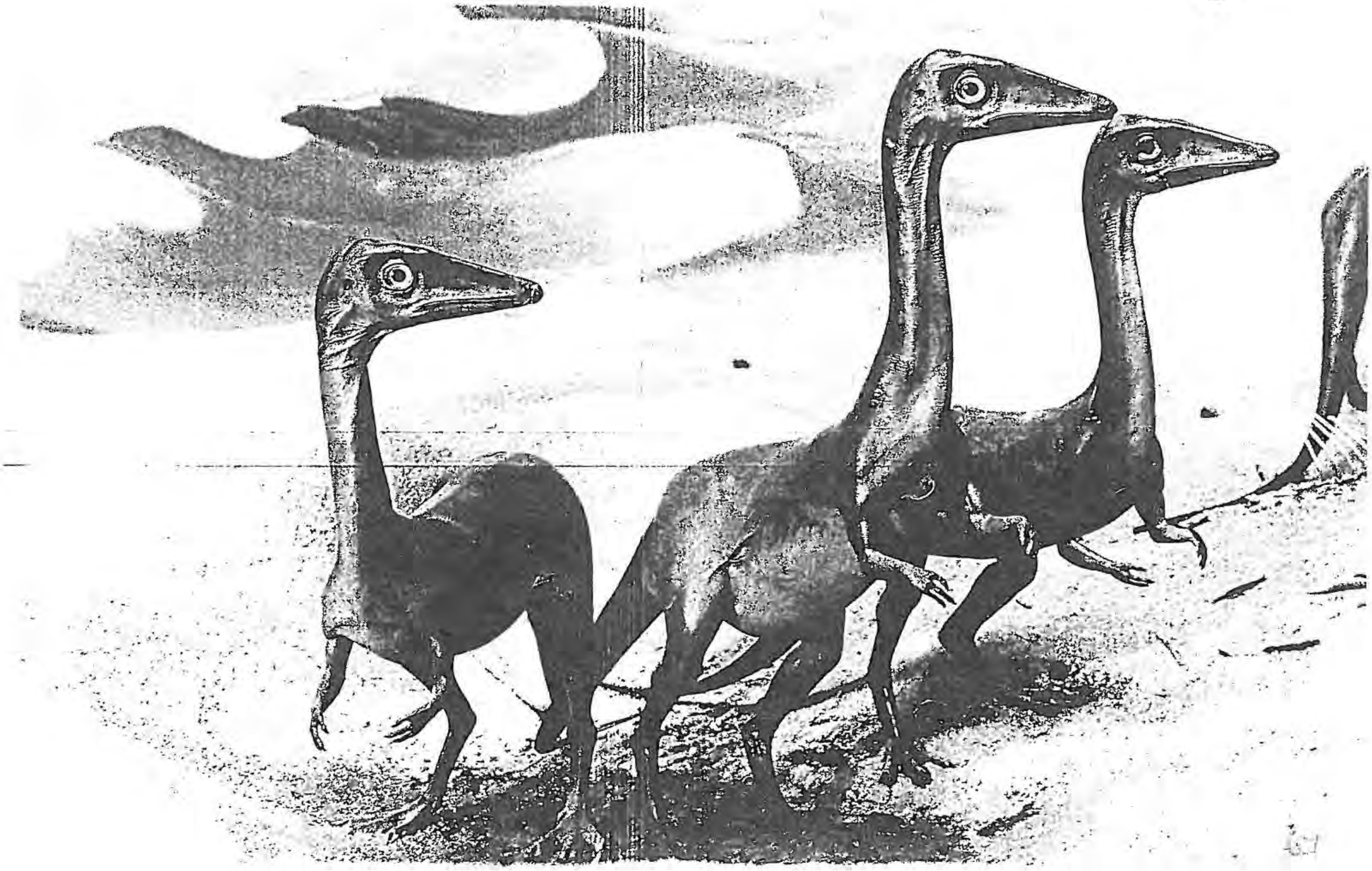


Plate 6. Syntarsus rhodesiensis: the crushed left snout of a juvenile (QG 202)

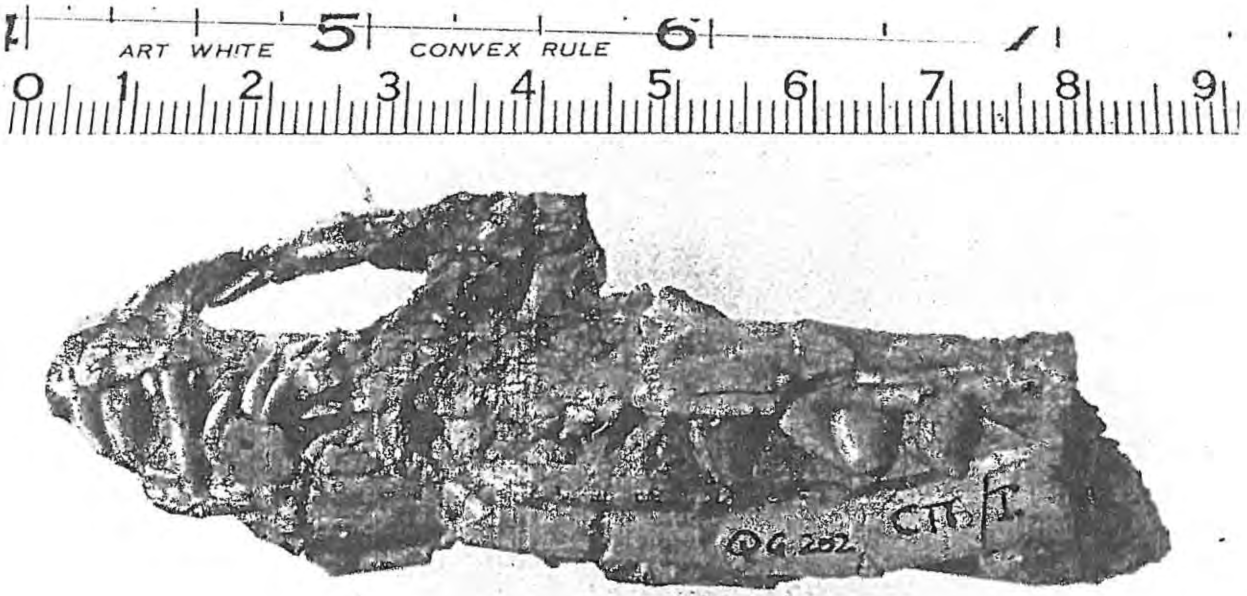
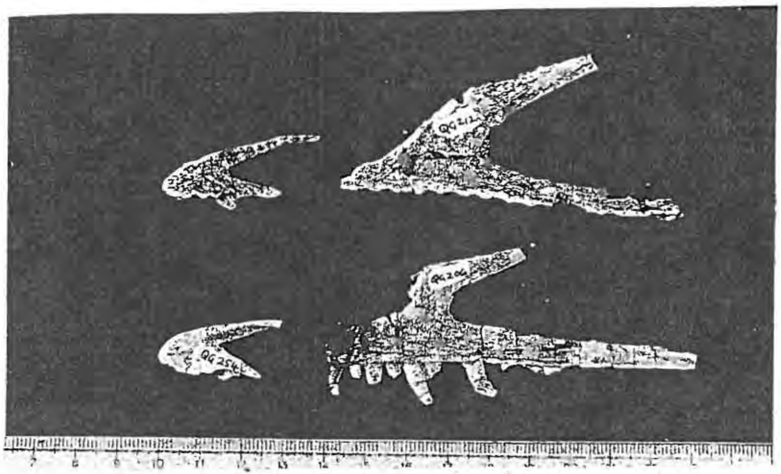
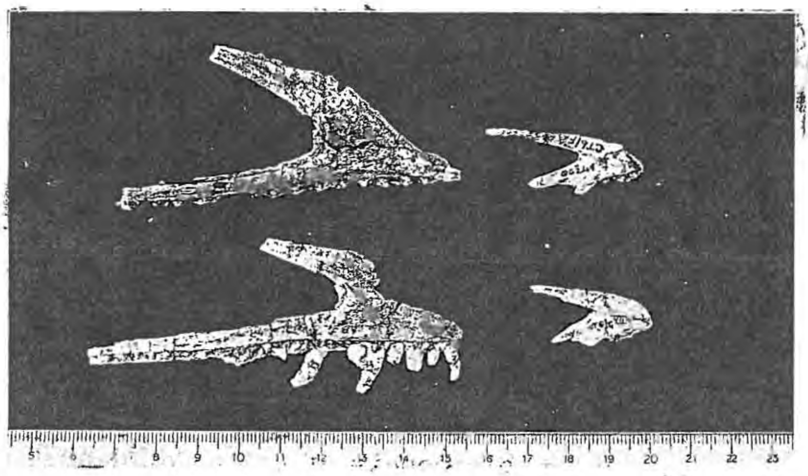
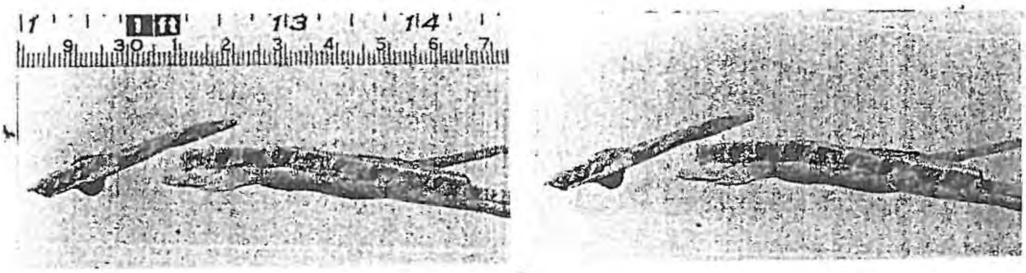

4 ART WHITE 5 CONVEX RULE 6 7
0 1 2 3 4 5 6 7 8 9
@G.202
CT6/I

Plate 7. *Syntarsus rhodesiensis*: maxilla and premaxilla

a - L. lateral view (premaxillae to left, maxillae to right)
b - L. medial view (maxillae to left, premaxillae to right)
c - stereopair of L. premaxilla and maxilla (alveolar view)
d - stereopair of articulated premaxillae (alveolar view)


a


b


c

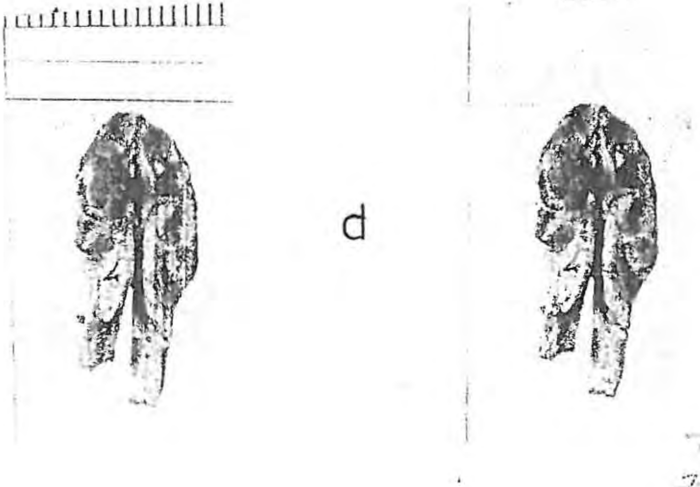
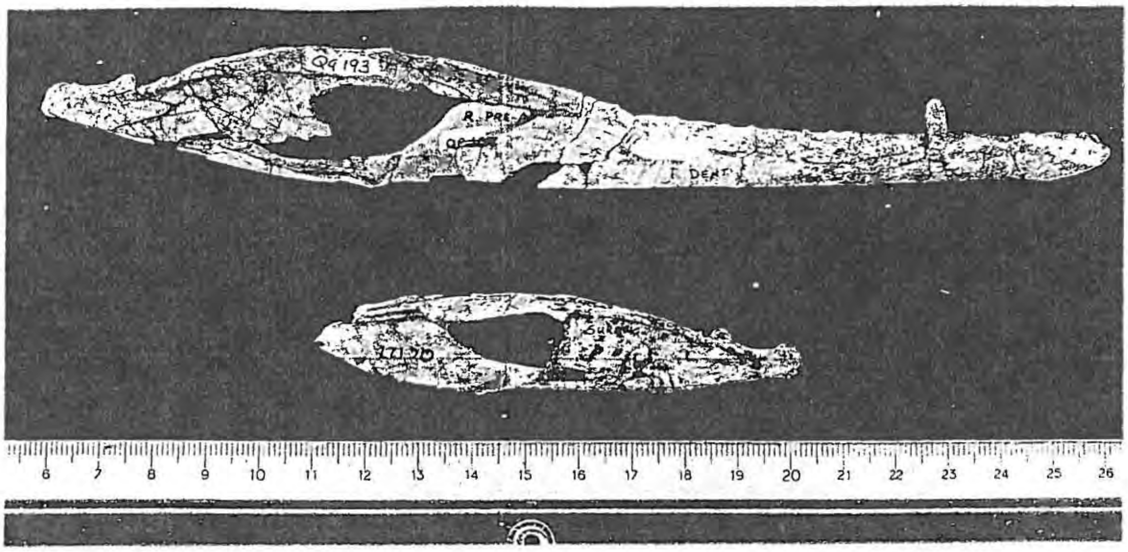

d

Plate 8. *Syntarsus rhodesiensis*: mandible

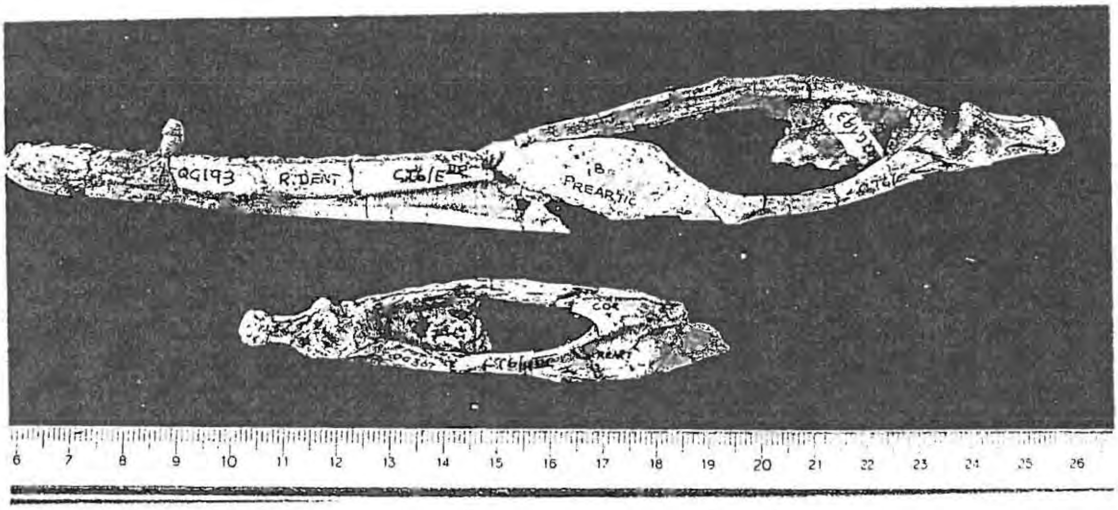
a - lateral view (above R. mandible, below hind part of L. mandible)

b - medial view (above R. mandible, below hind part of L. mandible)

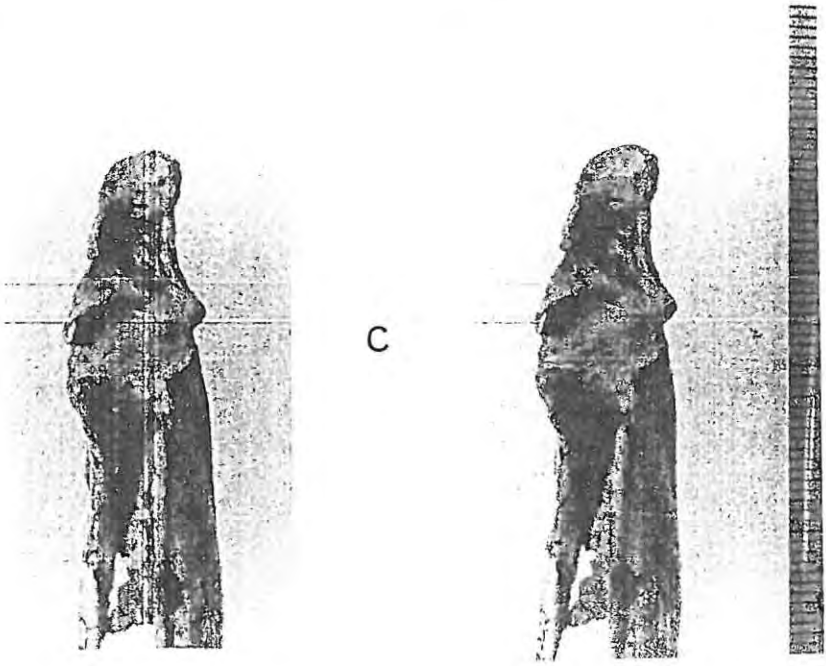
c - stereopair of posterior and of L. mandible, dorsal view


QG193
R. PRE-A
R. DENT
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26

a


QG193
R. DENT
PREARTIC
COR
PREART
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26

b



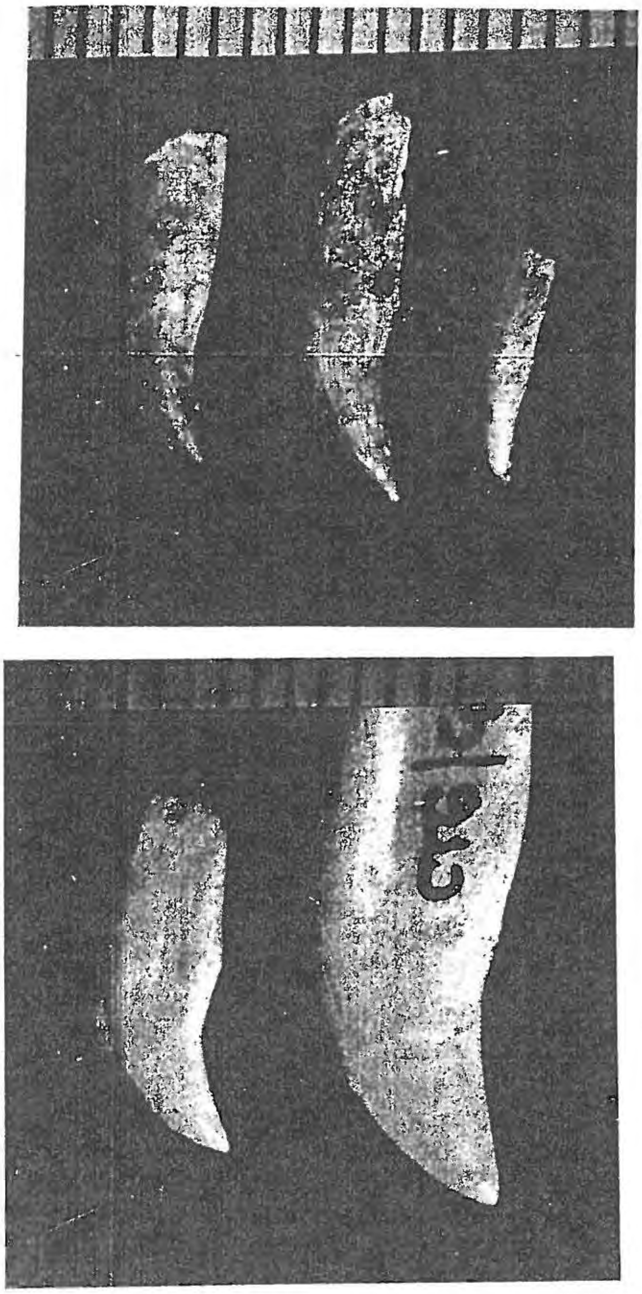
c

Plate 9. Syntarsus rhodesiensis: photomicrographs of teeth

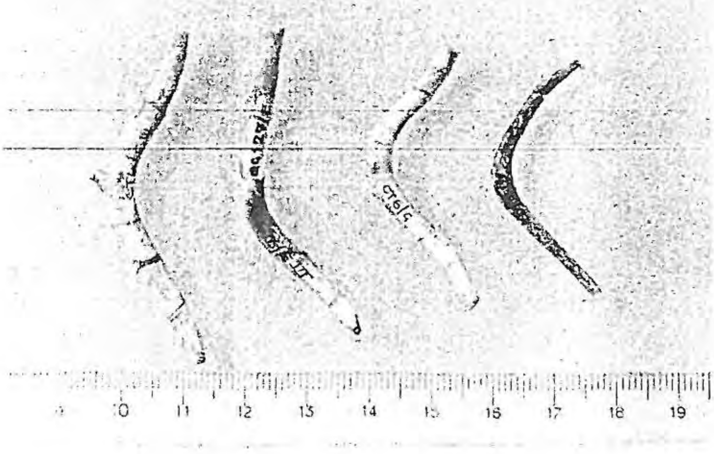
a - premaxillary

b - maxillary
(scale in mm)

Plate 10. Syntarsus rhodesiensis: hyoids (scale in cm/mm)



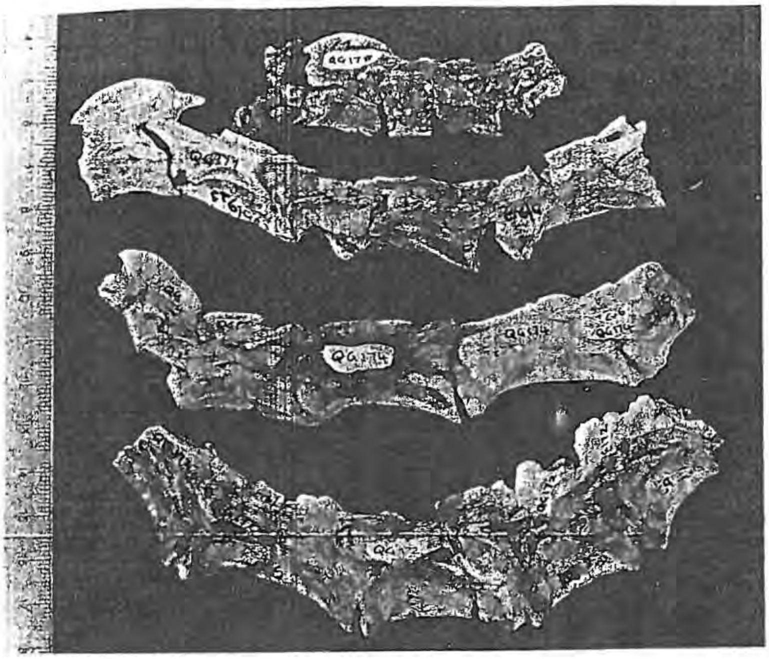
9



10

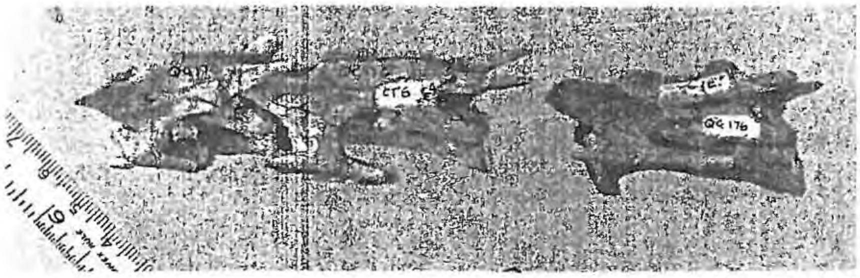
Plate 11. *Syntarsus rhodesiensis*: cervical vertebrae

a - articulated cervical series
b - anterior cervicals (left side)
c - cervicodorsal transition
d - "bundle" of cervical rib shafts from mid neck



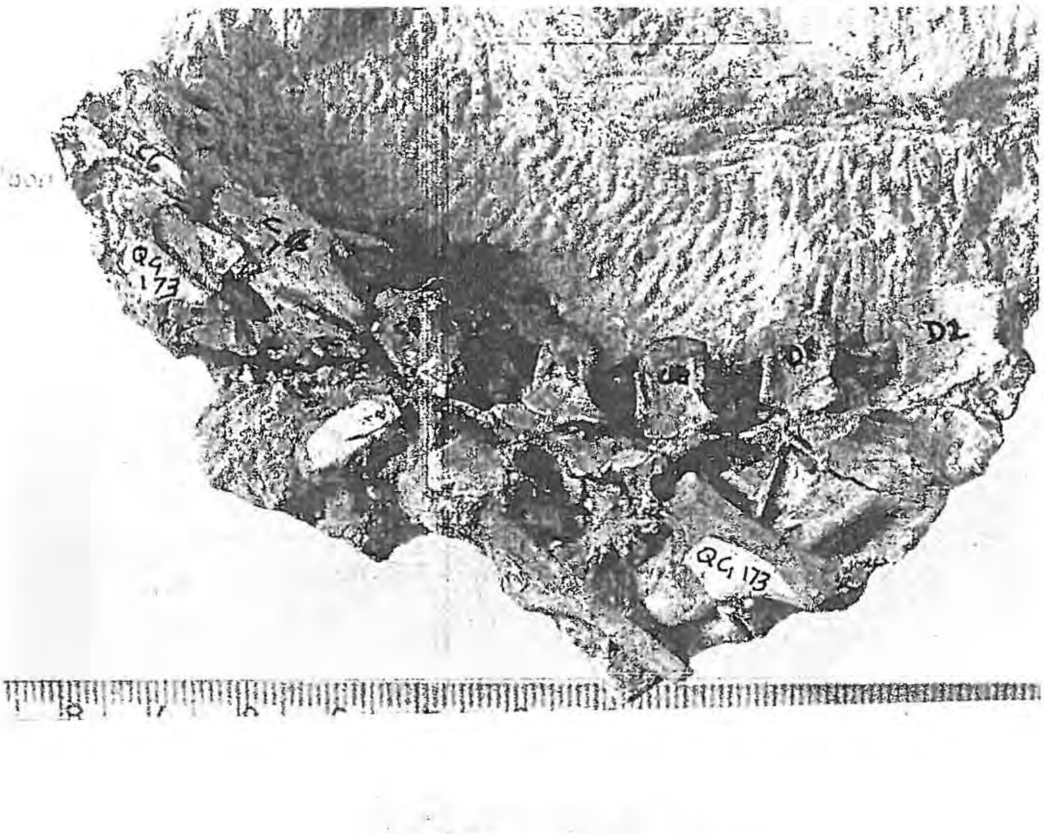
QG174
CT6
QG174

a



CT6
QG176

b



C6
C4
QG 173
C8
D1
D2
QG 173

c

QG423
CT6/G

d

77

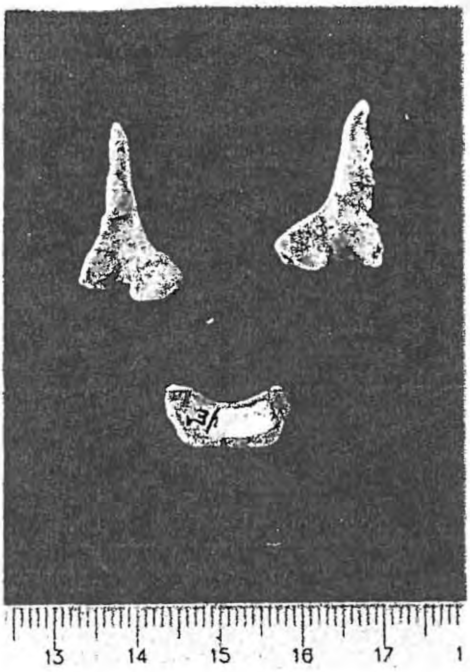
Plate 12. *Syntarsus rhodesiensis*: atlas and axis

a,b - atlas (a - intercentrum in anterior view, neural arches internal)

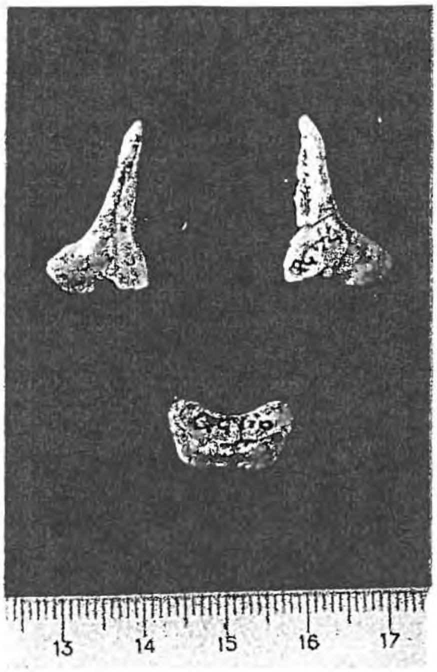
(b - intercentrum in posterior view, neural arches lateral)

c-e - axis (c - anterior view; d - left lateral view;

e - posterior view)



a



b

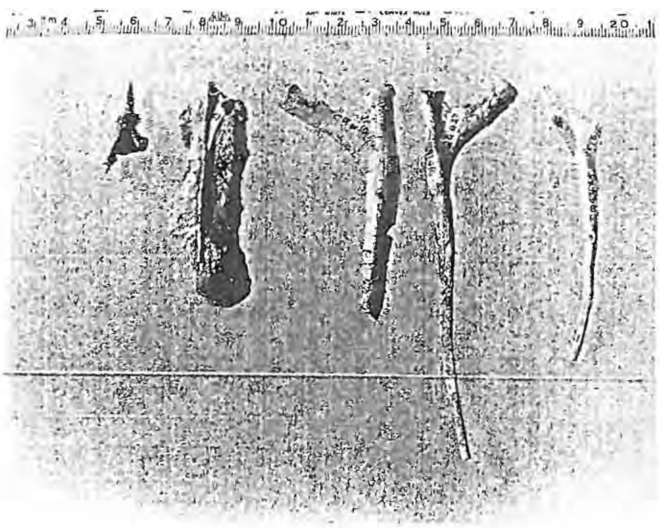
c

d

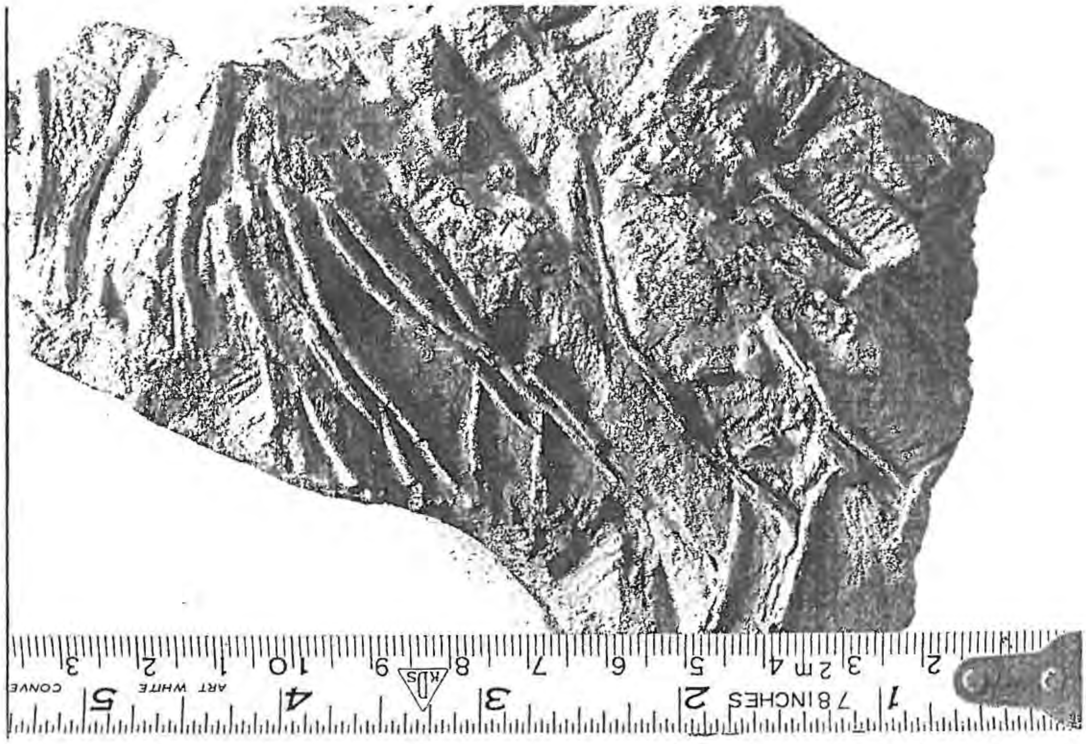
e

Plate 13. Syntarsus rhodesiensis: ribs
from left: cervical (head only), cervical, cervicodorsal, cervicodorsal, dorsal

Plate 14. Syntarsus rhodesiensis: gastralia
a - as recovered in holotype (cf. Fig. 11a)
b - detail of presumed stomach contents (area dotted)

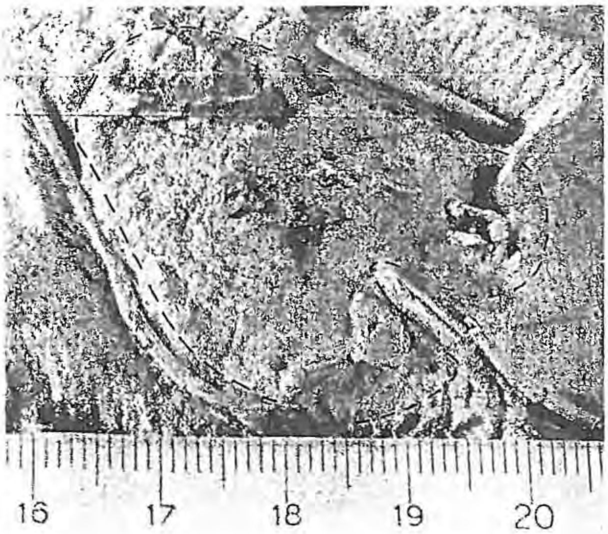


13



a

14



b

Plate 15. <u>Syntarsus rhodesiensis</u>: caudal vertebrae and chevrons

a - proximal caudal series from holotype (L. side view)
b - mid and posterior caudals
c - chevrons (note "skid" shape of last 3 to right)

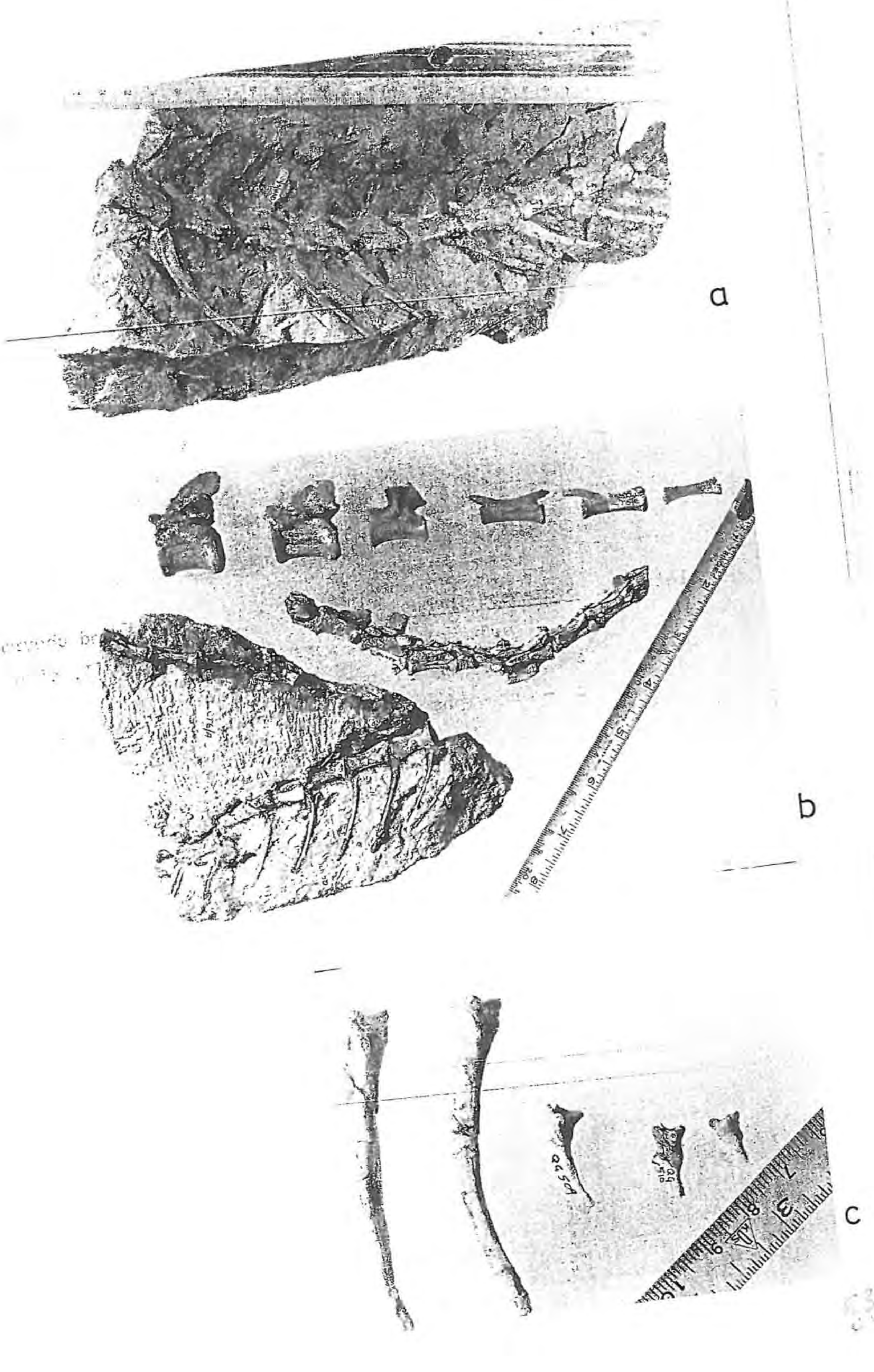
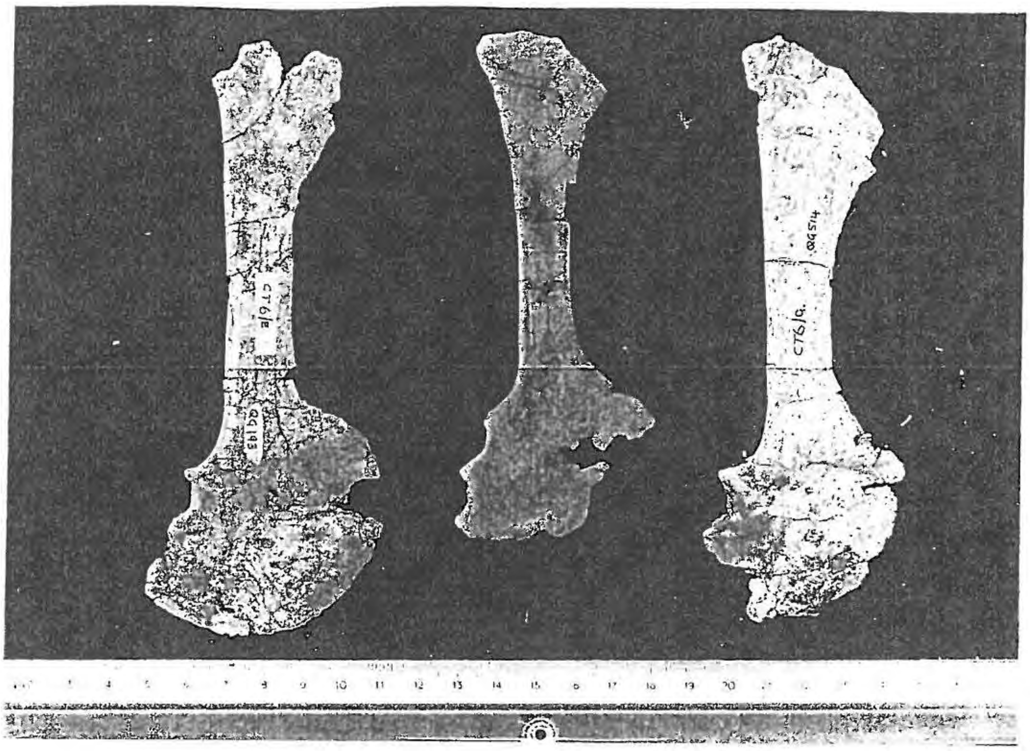

a
b
c

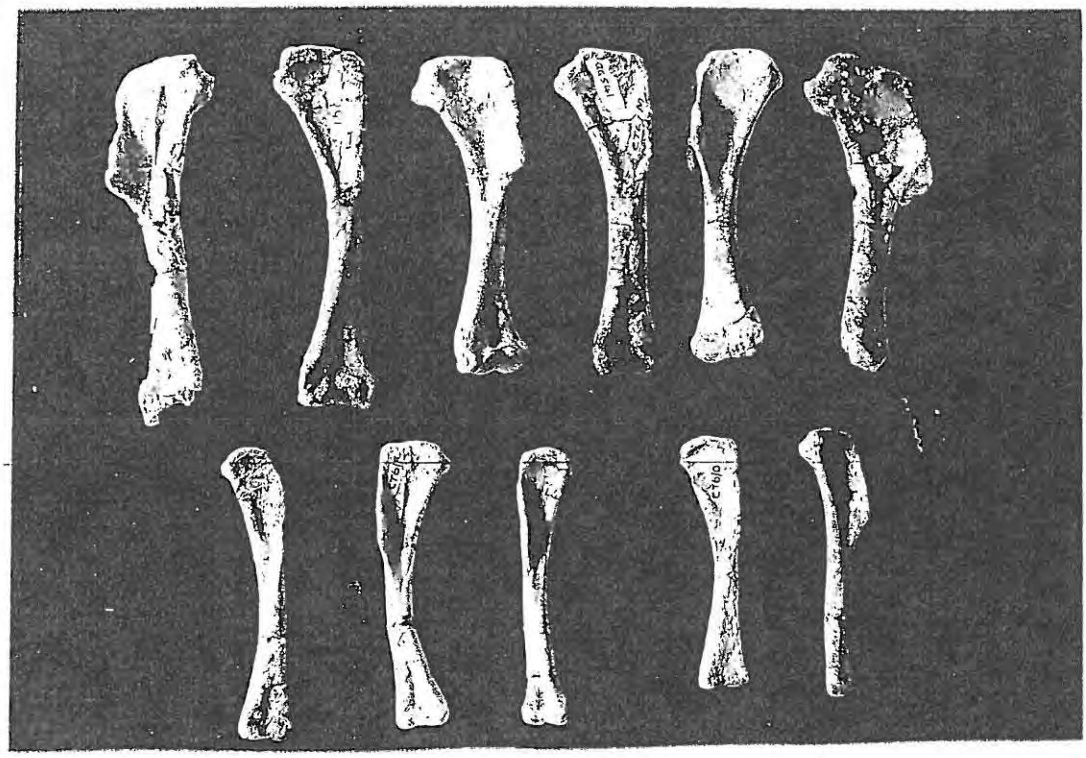
Plate 16. <u>Syntarsus rhodesiensis</u>: forelimb elements

a - scapulocoracoids (lateral, medial, lateral views)

b - series of humerus in palmar view (upper row - "robust", lower row - "gracile")



a



b

Plate 17. Syntarsus rhodesiensis: proximal end of "robust humerus" to show muscle scars (cf. Fig. 13)

a - palmar surface

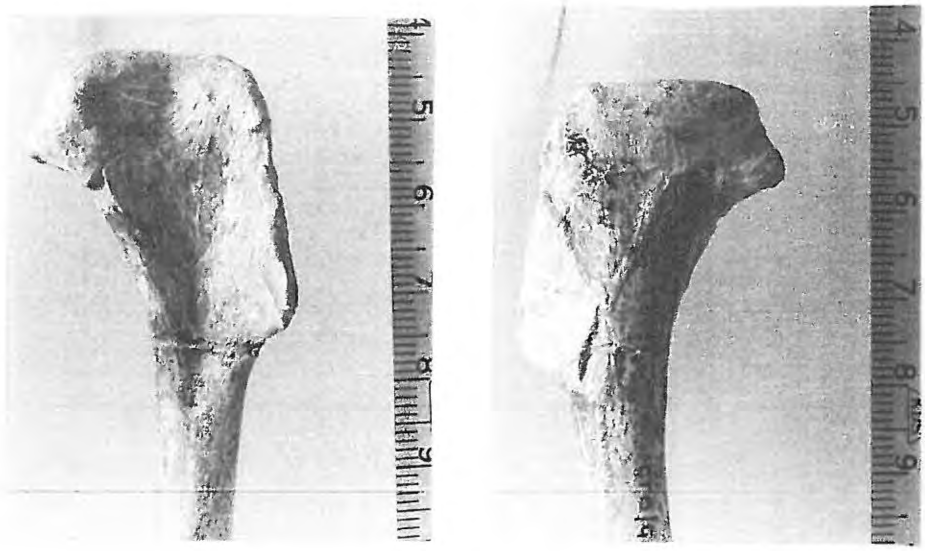
b - anconal surface

Plate 18. Syntarsus rhodesiensis: manus

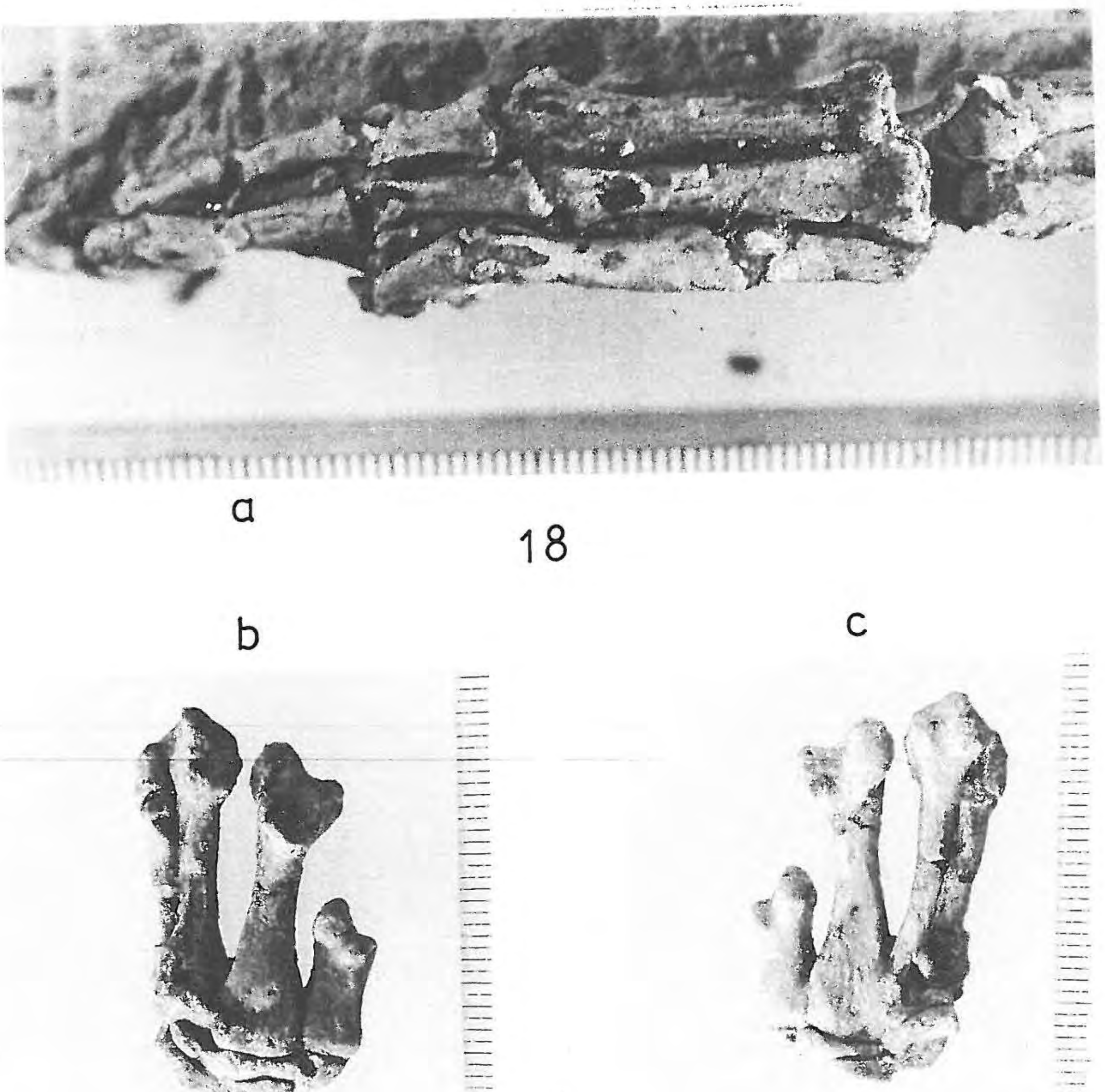
a - anconal view of articulated R. manus of juvenile (QG 577)

b - L. carpus and metarcarpals, articulated (anconal view) (QG 1)

c - L. carpus and metacarpals, articulated (palmar view) (QG 1)



a 17 b



a

18

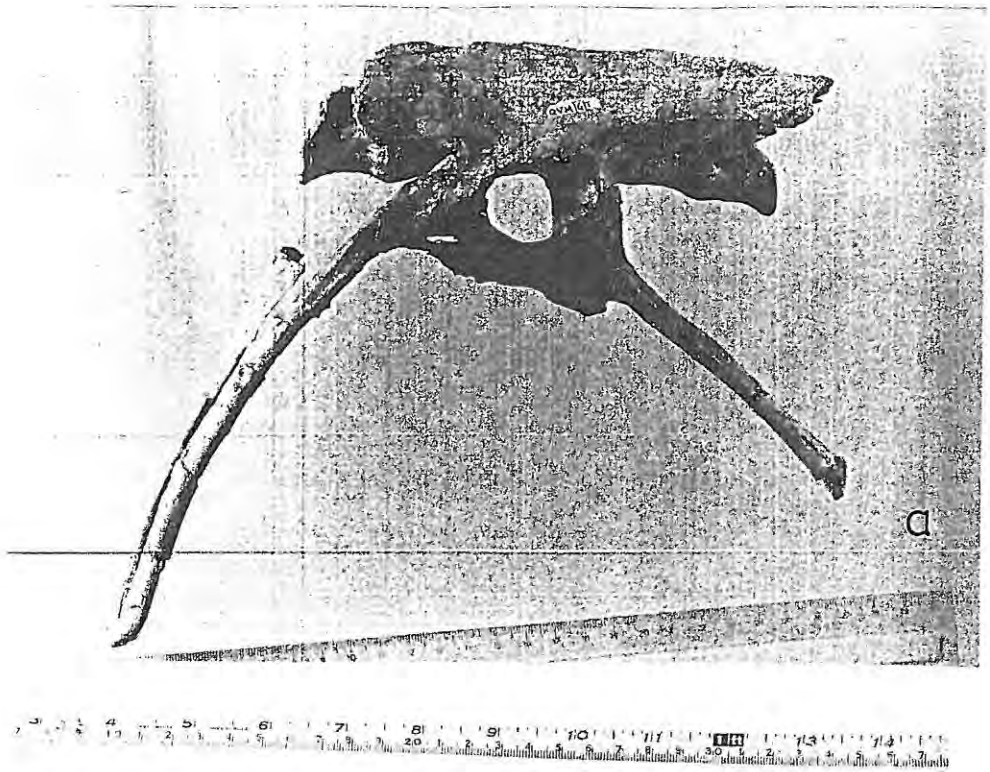
b c

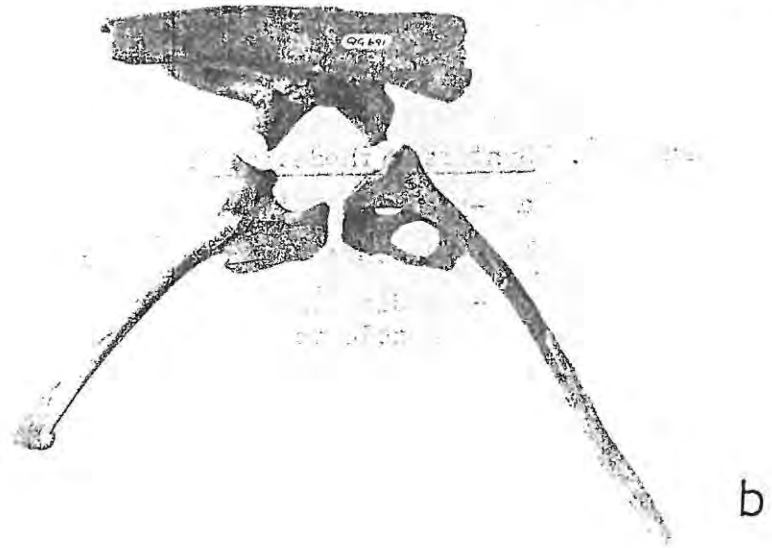
Plate 19. Syntarsus rhodesiensis: pelvis

a - adult (holotype QG 1) (left)

b - juvenile (QG 691) (right)

c - medial view of QG 691 R. ilium to show sacral rib and muscle scars


a
1 ft


b

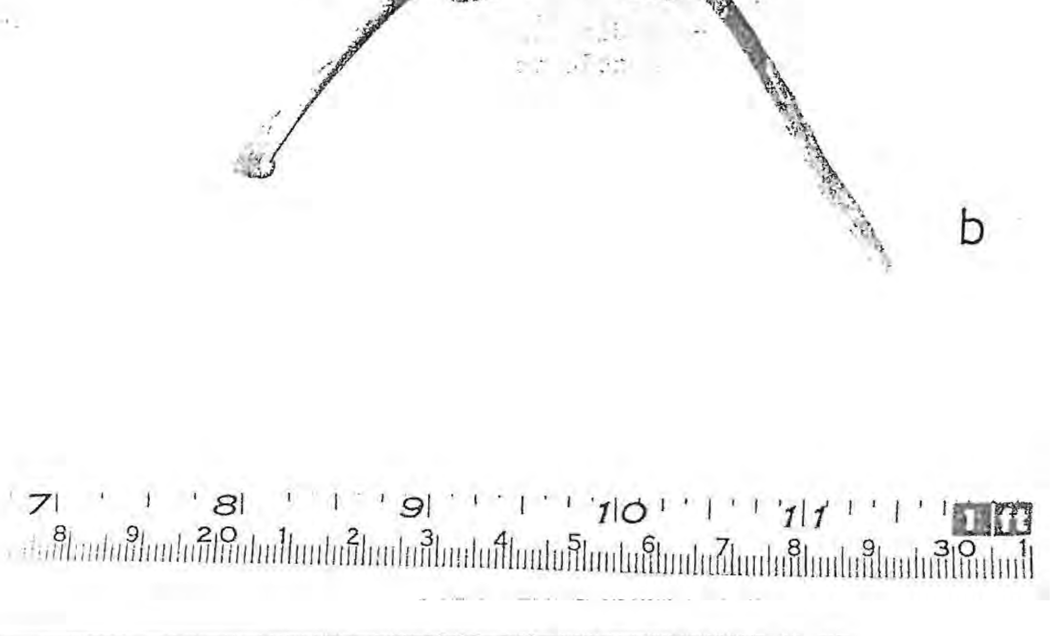

1 ft
c

Plate 20. Syntarsus rhodesiensis: sacral vertebrae (centra only) in dorsal view (note large scars of **sacral ribs**)

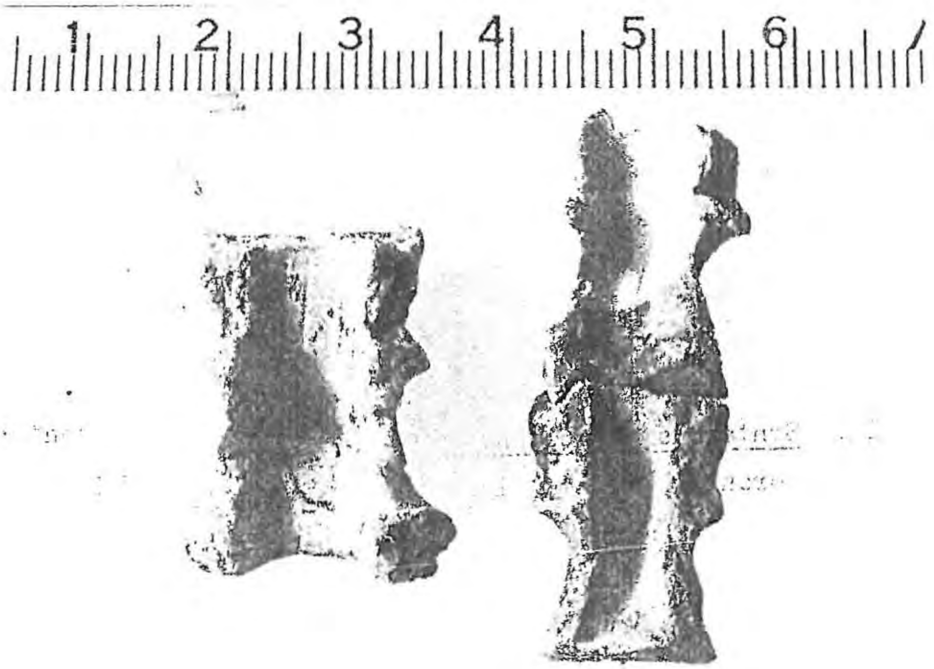
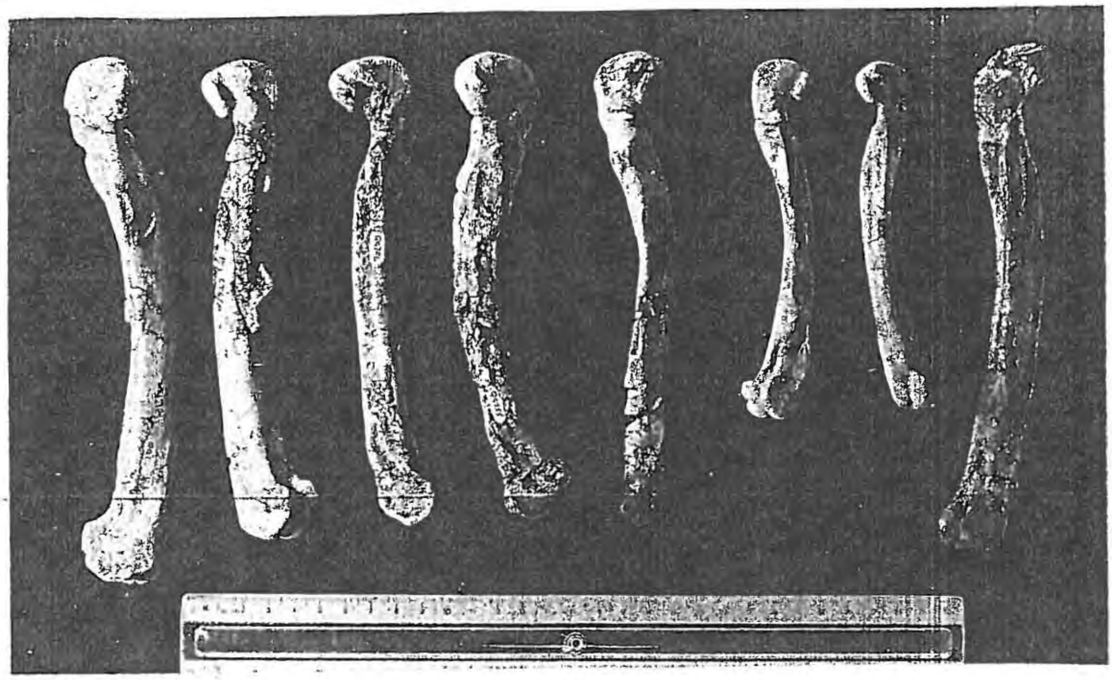

1
2
3
4
5
6
7

Plate 21. Syntarsus rhodesiensis: femora

a - series of femora

b - (l-r) lateral, anterior, posterior and medial views of R. femur of gracile "juvenile" (QG 691)



a

b

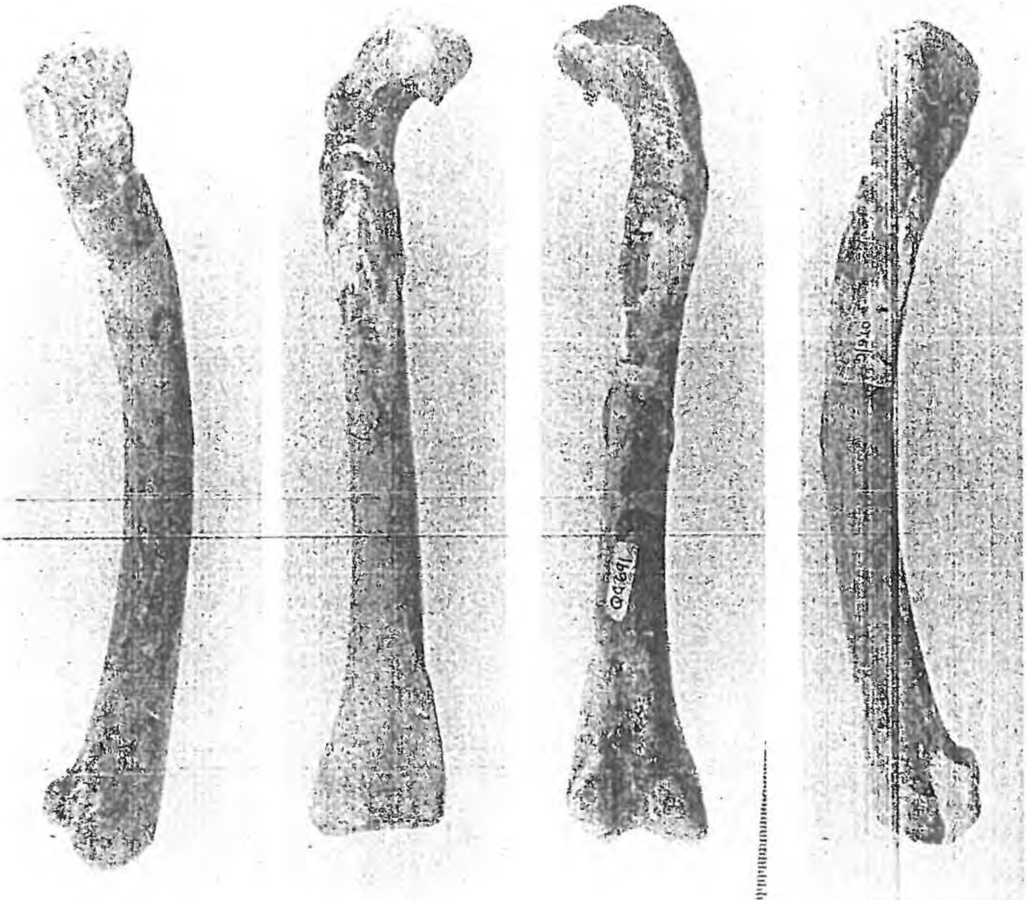


Plate 22. *Syntarsus rhodesiensis*: robust and gracile femora

a,c,e,g - gracile

b,d,f,h - robust

a,g - medial view, showing caudifemoralis muscle insertion tendon scar (a - left femur; b - right femur)

c,d - anterior view, showing lesser trochanter (tip broken in c). (c - left femur; d - right femur)

e,f - posterior view, showing greater trochanter and obturator ridge (e - left femur; f - right femur)

g,h - dorsal view at proximal end, showing form of lesser trochanter (protruding to right) (both left femur

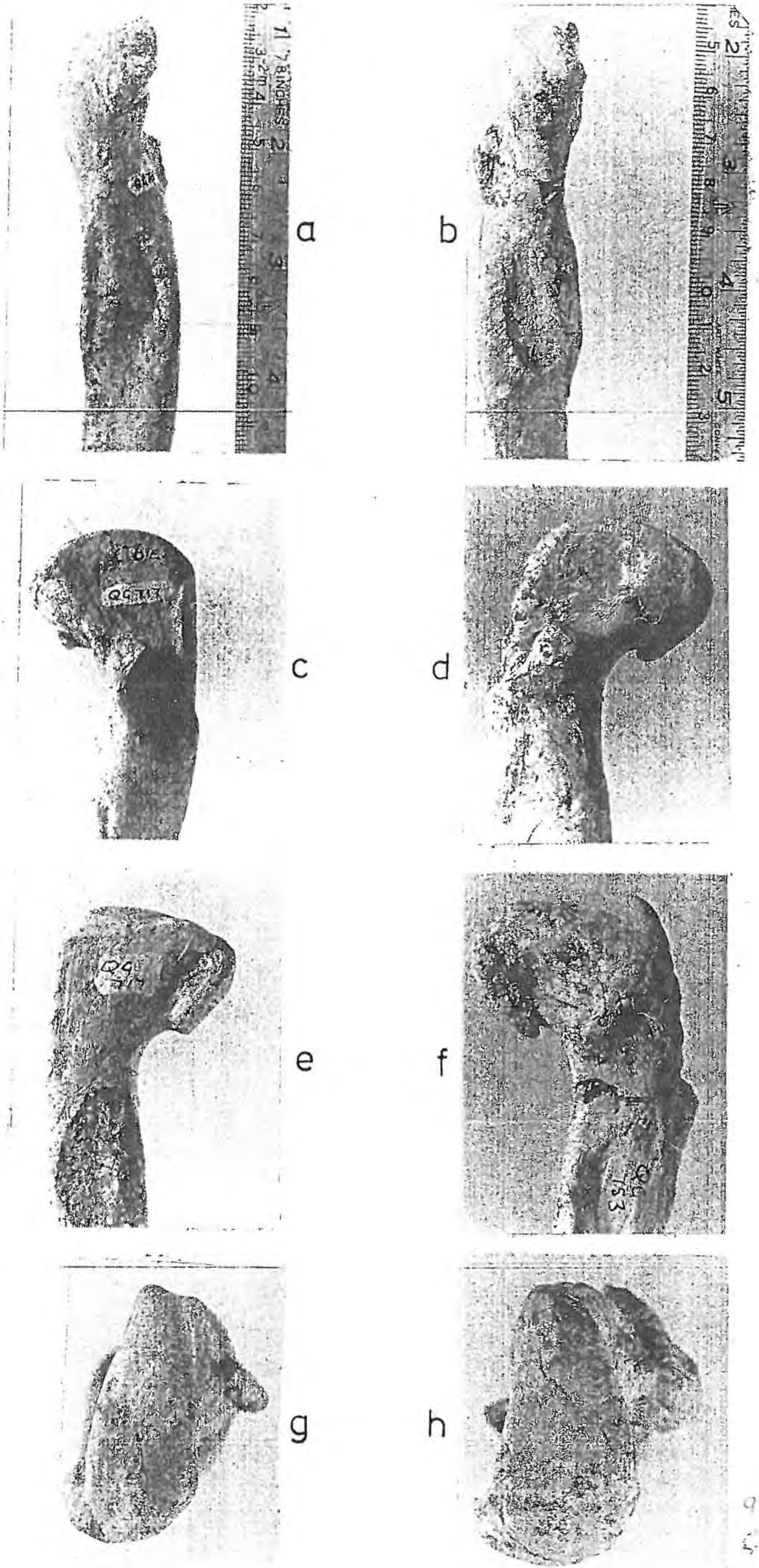
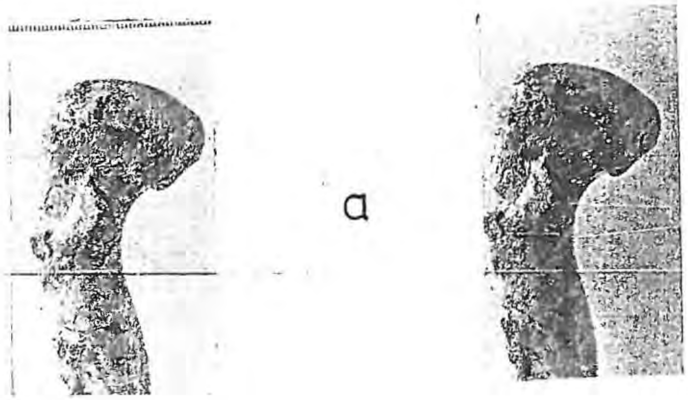
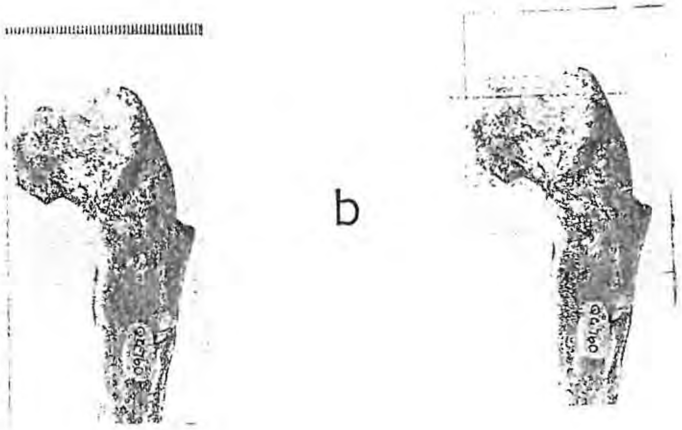

a
b
c
d
e
f
g
h
QG 753

Plate 23. <u>Syntarsus rhodesiensis</u>: stereopairs of femoral heads

a - anterior surface, robust right femur
b - posterior surface, robust right femur
c - anterior surface, gracile left femur



a



b

c

Plate 24. *Syntarsus rhodesiensis*: series of tibia (some with fused astragalocalçaneum) and fibula

Plate 25. *Syntarsus rhodesiensis*: tarsal elements
upper two rows - astragalus, calcaneum
third row - distal tarsal 4
lowest row - distal tarsal 3


CT6/E
Q4805
CT6/L
Q4807
10
11
12
13
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

24

25

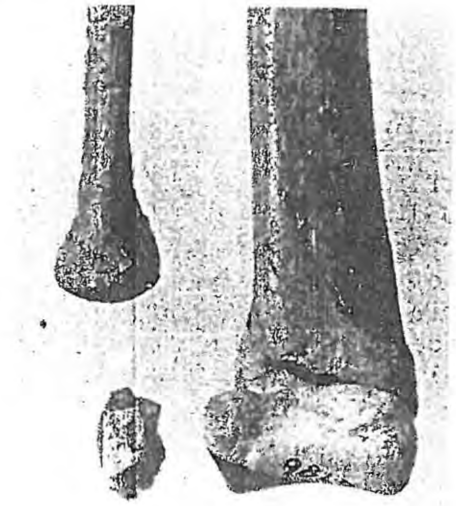

Q4816
CT6/F
Q4831
CT6/M
Q4837
CT6 LL
CT6/E
Q4 820
CT6/E
Q4825/D
CT6/E
Q4834
Q4847
CT6/F
Q4848
Q4 838
Q4853
7
8
9
10
11
12
13
14
15

Plate 26. <u>Syntarsus rhodesiensis</u>: tarsal region of juveniles

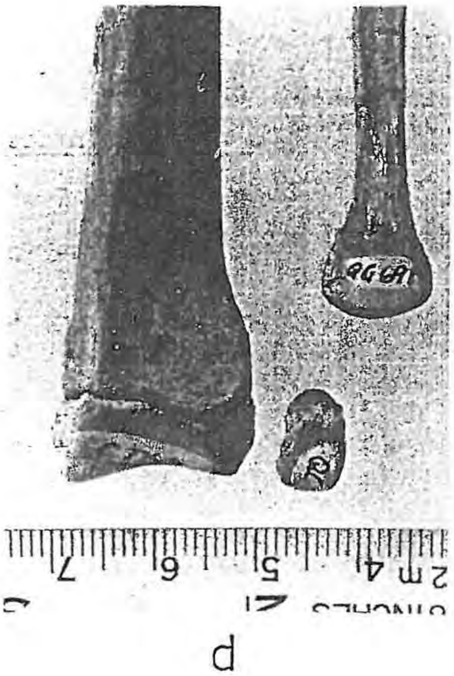
- a - anterior view of articulated L. crus, tarsus and metapodials (QG 768)
- b - disarticulated R. tibia (anterior view) with dorsal view of R. astragalus and calcaneum
- c - anterior view of R. tibia with articulated (unfused) astragalus, separate calcaneum, lateral view of distal end of fibula (QG 691)
- d - as for c, opposite views (QG 691)
- e - stereopair dorsal view of astragalus and calcaneum shown in b (note ascending process)

a

b



c



d

e

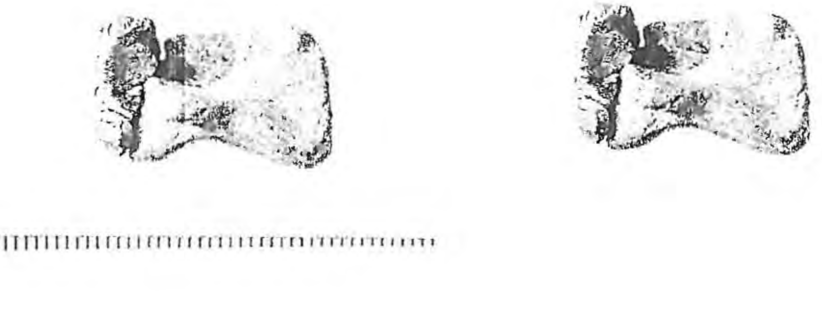


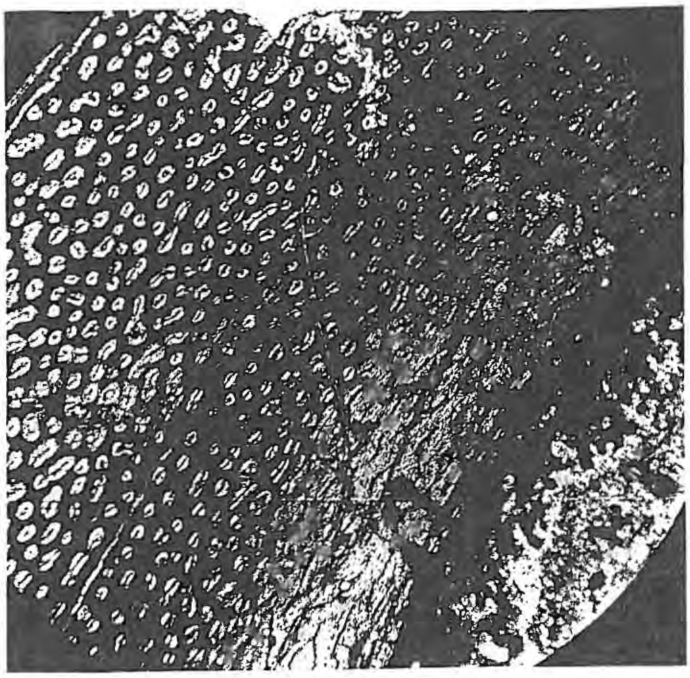
Plate 27. Syntarsus rhodesiensis: dorsal view of articulated L. pes of juvenile (QG 164) (spur protruding beside metatarsal II is the reduced metatarsal I; digit I just visible below Mt II near distal end)

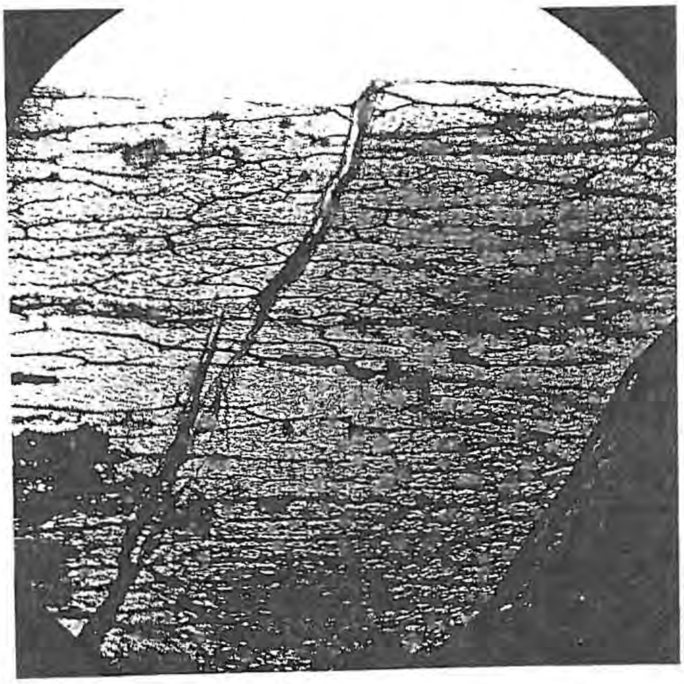
Plate 28. <u>Syntarsus rhodesiensis</u>: histological sections of tibia

a - transverse section (endosteal surface lower right)

b - longitudinal section (periosteal surface, above, lost)

c - transverse section (note osteoporosis) (endosteal surface below)


a


b

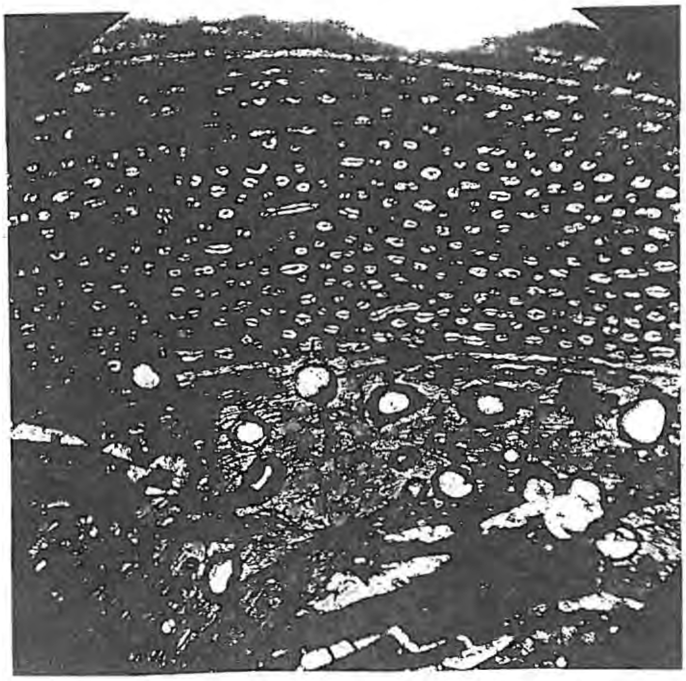
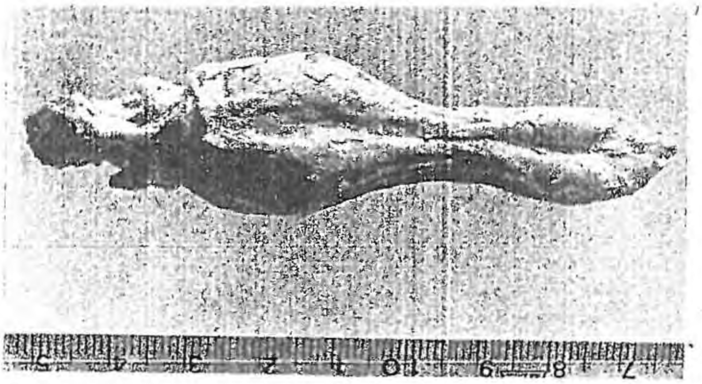

c

Plate 29. Syntarsus rhodesiensis: dorsal view of endocranial cast in silicone rubber from skull QG 193

Plate 30. Syntarsus rhodesiensis: stereopair of ventral surface of sacrum, with ilia attached and pubes and ischia removed (cast taken from QG 1) (Note broad caudifemoralis shelf behind acetabulum and perforations for sacral lateral nerves)



29

30

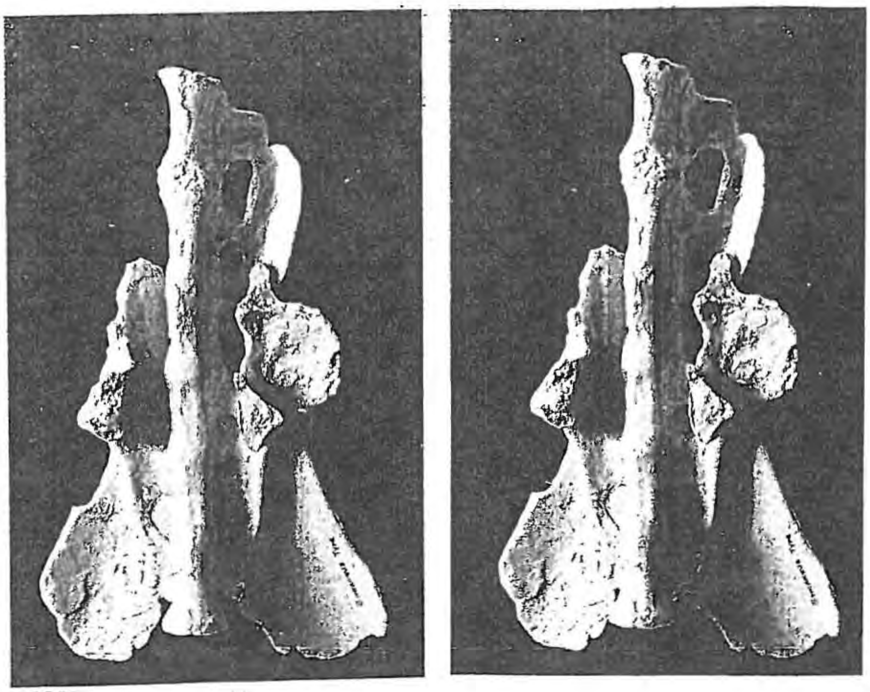


Plate 31. Footprints attributed to Syntarsus: toe impressions of II and III of left foot visible at left edge of block; right print complete (QG 91)

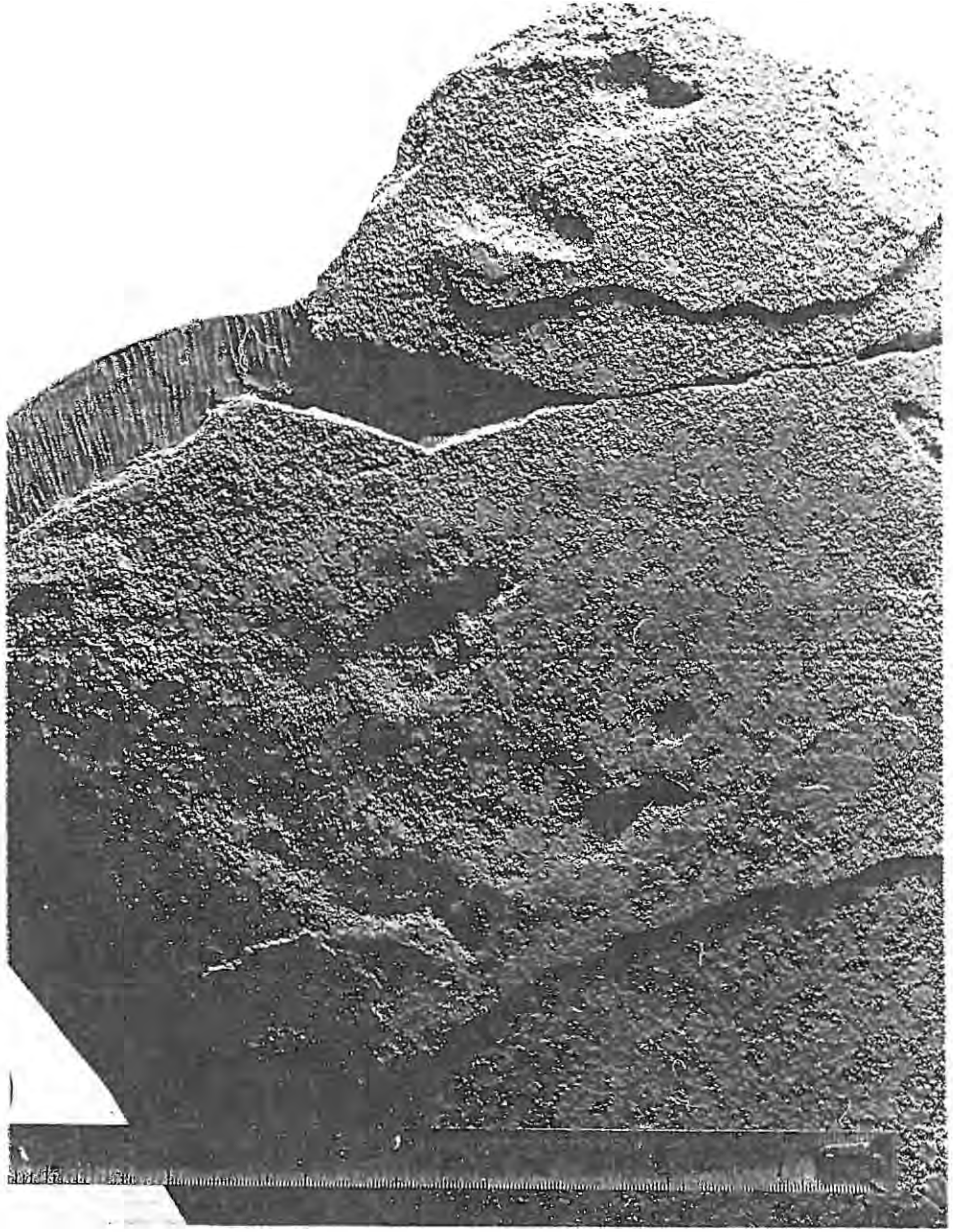


TABLE 1. *Syntarsus rhodesiensis*: summary of material available

LOCALITY	CATALOGUE NO.	NATURE OF MATERIAL				
SOUTHCOTE FARM Nyamandhlovu 19° 58'S; 28° 24'E.	QG 1	HOLOTYPE. Articulated postcranial skeleton including: dorsal vertebrae, ribs, gastralia, caudals, chevrons, complete L. girdle and forelimb, complete pelvis and sacrum, partial R. hindlimb, complete L. hindlimb. "Robust" form.				
	QG 3A	TOPOTYPE. Material isolated and fragmentary, including: cranial (squamosal, lachrymal, dentaries) and postcranial (cervical, dorsal, sacral and caudal vertebrae, ribs, chevrons, femoral heads, tibial head) elements. "Robust" form.				
MAURA RIVER 16° 13'S; 30° 06'E.	QG 45	Juvenile. Fragmentary articulated postcranial elements, including: sacrum and ilia, R. femur, L. femur, L. tibia and pes, and indet. fragments. "Gracile" form.				
	QG 76	Almost perfect L. femur. "Gracile" form.				
CHITAKE RIVER 16° 07'S; 29° 30'E.	QG 124,) QG 164,165) QG 169 –) 1103	Concentrated remains of at least 26 individuals. Counts below are based on best representatives of prepared material. Including "Robust" and "Gracile" forms:				
		CRANIAL		POSTCRANIAL		UNPREPARED
		Premaxilla (+ vomer?)	21	Cervical vertebrae	77	12 blocks of matrix containing abundant remains
		Maxilla	31	Cerv. ribs	7++	
		Nasal	13			
		Frontal	19	Dorsal vertebrae	36	
		Parietal	21	(centra only)	82	
		Prefrontal	7	Dorsal ribs	38+	
		Lachrymal	13	Sacrum/pelvis	10+	
		Postorbital	10	Sacral centra	7	
		Jugal	2			
		Squamosal	11	Caudal vertebrae	120	
		Quadrate	19	(centra only)	45	
		Quadratojugal	3	Chevrons	37++	
		Palatine	6			
		Pterygoid	8	Scapulocoracoid	22	
		Ectopterygoid	6	Humerus	22	
				Ulna	8	
		Braincase/occiput	5	Radius	10	
		Dentary	21			
		Angular	15	Manus(± complete)	8	
		Surangular	11	Manus elements	Many	
		Articular	18	Femur	34+	
		Prearticular	11	Tibia	23+	
		Coronoid	1	Fibula	18+	
		Splenial	11	Astrag./calc.	12+	
		Scleral plates	Few	Tarsal 4	23	
		Teeth	Many	Pes elements	Many	

TABLE 2. Theropod skull dimensions

*SOURCE REFS.	1	2	3, 5	4	5	6	5	7	5
DIMENSION (mm)	Syntarsus	Coelophysis	Deinonychus	Compsognathus corallestris	Ornitholestes	Ornithomimus	Dromaeosaurus	Allosaurus	Velociraptor
Greatest skull length	220	220	310	c115	127	238	234	760	168
Greatest skull width	80	72	150				109	310	
Greatest skull height	60	60	115	c40	50		95	320	45
Upper tooth row length	100	135	160	c30	51		106	400	78
Orbit height	48	40	75	25	30	c50	c43	175	
Orbit width	45	30	45	25	35	60	41	110	38
Lower Temp. Fenestra height	45	40	80		30	c34	210		
Lower Temp. Fenestra width	8	15	?35		15	c10	c40	70	
Upper Temp. Fen. width (transverse)	20	15					c26	100	
Upper Temp. Fen. length (ant/post)	25	30			24		43	80	17
Antorbital Fenestra height	40	28	60	10	22		c25	160	
Antorbital Fenestra length	95	60	90	15	21		32	160	35
Lower jaw length	235	218	317		138	210	213	790	168
Dentary tooth row length	120	140	138	28	40		88	290	73
Greatest depth lower jaw	26	25	58		24	35	40	150	22
Depthlower jaw (ant. end)	8	8	?18		10	18	20	60	

*Source : 1 - reconstructions based on QG 193 and several others

2 - calculated from figure based on AMNH 7224 - Colbert, pers. comm.

3 - Ostrom, 1969: Figs. 4,5

4 - Bidar, Demay & Thomel, 1972 (calculated from Fig.)

5 - Colbert & Russell, 1969: Table 1

6 - Osborn, 1917 (calculated from Fig.)

7 - Madsen, 1976 (calculated from Fig.)

TABLE 3. *Syntarsus rhodesiensis*: measurements of selected cranial elements

Measurement (mm)	Specimen No.	QG 193	QG 194	QG 195	QG 196	QG 197	QG 202		QG 245	QG 246	
	Side						L	R		L	R
Braincase:											
Length paroccipital process (from border of foramen magnum)		24	21		20						
Max. diameter foramen magnum		10	13	10		9					
Min. diameter foramen magnum		9	5	7		7					
Max. width across parietal flanges			c34								
Skull depth (parietals to basioccip. tubera)			45								
Max. diameter condyle (transverse)		10	10	9	10	9					
Min. diameter condyle (saggital)		6	7	5	6	6					
Condyle to end of basipterygoid process		43	42	37	39	39					
Basioccip. tubera to end basipter. proc.		33	30	28	29	28					
Max. width across basioccip. tubera		20	c17	17	18	c15					
Max. width across basipter. proc.		31	c25	28	31	c24					
Min. temporal width		25	17								
Interorbital width (min.)		23	20								
Maxilla											
Length upper ramus		c70	107								
Length lower ramus			145								
Height antorbital fenestra		c20	28								
Number of alveoli		10^+	19								
Premaxilla											
Length upper ramus							29	28			
Length lower ramus							20		28		
Height of triangular flange									3	4,5	5
Number of alveoli							4		4	4	4
Nasal											
Overall length		109^+	108^+								
Maximum breadth		15	18								
Breadth at mid-length		14	13^+								
Breadth at naris		7	9								

TABLE 4. Syntarsus rhodesiensis: principal skeletal dimensions and ratios (based mainly on holotype QG 1)

	Element or portion	Length (mm)		Ratio (expressed as % of part with which compared)
AXIAL	Skull	220	PRESACRAL 632 mm	c f. Total axial = 11%; c f. Presacral = 35%
	Cervical series	270		c f. Total axial = 13%; c f. Presacral = 43%) c f. total
	Trunk series	362		c f. Total axial = 18%; c f. Presacral = 57%) axial = 31%
	Sacrum	148		c f. Total axial = 7%; c f. Presacral = 23%; c f. caudal = 15%
	Caudal series	1020		c f. Total axial = 51% c f. Presacral = 161%
	TOTAL AXIAL	2020		
FORELIMB	Humerus	100		c f. Total forelimb = 42%
	Radius	61		c f. Total forelimb = 26%
	MC II	26		c f. Radius = 43% c f. Humerus = 26%; c f. total forelimb = 11%
	Digit: II i	13		c f. Total forelimb = 20%
	II ii	17		
	II iii	19		
	TOTAL FORELIMB	236		c f. Total hindlimb = 35%
HINDLIMB	Femur	208	F+T+MT 563 mm	c f. Total hindlimb = 31%; c f. Tibia = 93%; c f. F+T+MT = 37%
	Tibia + astrag.	223		c f. Total hindlimb = 33% c f. F+T+MT = 40%
	MT III	132		c f. Tibia = 59%; c.f. Femur = 63%; c f. F+T+MT = 23%
	Digit: III i	37		c f. Total hindlimb = 17%
	III ii	29		
	III iii	24		
	III iv	22		
	TOTAL HINDLIMB	675		c f. Total axial = 33%; c f. Presacral = 107%

MEASUREMENT (mm)	SPECIMEN NO.	QG 178			QG 176				QG 177					QG 179						QG 170		QG 172				QG 169								
	NO. IN SERIES	1	2	3	1	2	3	4	1	2	3	4	5	1	2	3	4	5	6	? 8	? 9	6	7	8	9	7	8	9	10	D1	D2	D3	D4	D5
Centrum: maximum length				25,5		27	36	40		20	26	32	37			33	36,5	41	44	35	28	37	33	27	22	30	25	20,5	18	20	20	23	23,5	25,
minimum length				25		23,5	35	40		19	26		37			31	36,5	40	42	35	28													
minimum transverse width				3,5		6,5		6,5		4	2	3	3,5							5	6													
height anterior face				6,5		10,5	8			10			8			7	8,5			14,5	15													
width anterior face				7		12	9	11,5		10			9							18	18													
inclination anterior face				16°			19°	23°			35°		24°			36°	30°	20°		2°	7°													
height posterior face						11		11		9		8,5	9		10	9	11	12,5		16	15													
width posterior face				12,5		10,5	12	12		8,5		8,5	9,5							15,5	14													
inclination posterior face				13°		15°	18°	14°		16°	12°	8°	19°			8°	20°	17°		15°	3°													
median ventral keel				+		+	+	+		+	+	+	+			+	+	+	+	+	+													
Greatest length (prezygs.-postzygs.)			22,5	40		31	47,5	61		26,5	38	44	47,5		26,5	45	56	58	59		29													
Max. width across prezygapophyses			7,5	12,5	16	10		16,5		9		13,5	14,5								22,5													
Max. width across postzygapophyses			12	13		17	18,5	18			14	14	13,5							21	17													
Overall depth (apex of spine to mid-centrum)				17	27	28,5	22,5	20		25	17	12	18,5			23	20	21		34	36													
Anteroposterior length neural spine			18	16		26	22	26		24		22,5	25		27	20		22,5		12	9					17,5	10,5	18	9	12	12	16,5	17,5	17
Height neural spine (from roof neural canal)			7			15,5				12,5										18	17,5													
Neural canal max. diameter (anterior)					11	5				7										6														
Neural canal max. diameter (posterior)					11	5				6,5																								
Greatest length atlas neural arch		13,5			22				17					19																				
Greatest width atlas neural arch		5			10				8,5					10																				
Maximum diameter odontoid		7			8,5				9																									
Minimum diameter odontoid		5			4,5				4																									
Max. diamoter atlas intercentrum		9			15																													
Length atlas intercentrum		3			5																													

TABLE 5. Syntarsus rhodesiensis: measurements of cervical vertebrae

TABLE 6. Syntarsus rhodesiensis: measurements of dorsal vertebrae

MEASUREMENT (mm)	SPECIMEN NO.	QG 1 - Holotype								QG 396	QG 180	QG 171		QG 405	QG 406	QG 408			QG 413	
	NO. IN SERIES	6	7	8	9	10	11	12	13	1	2	2	3	6	5	6	7	8	Post dorsals	
Centrum: length		28	29	29	29	32	31	29	29	23,5	22	26,5	27	29	29		27,5		26,5	25
height anterior face		12	11						14	12	13	14	14	14	14,5	14	13		12	15
width anterior face		14	15						13	18	18	11,5	11	13	15	13	12,5		14	15,5
minimum breadth at mid centrum		7					8			6	6	5,5	6,5	6	6,5	6	7		8	8,5
height posterior face										13	13,5	13,5	12	13,5	15		14		16	16
width posterior face										14	14	11,5		12	14,5		13,5		16	15,5
Length transverse process (lateral)											22		13	20	22,4	19	14,5	15	15	13,5
Length neural spine (ant/post)							24	25			13	26	26,5	24	22	25	26	25		
Height neural spine (from roof of neural canal)							14				17			19,5	20	19	17,5	18		

MEASUREMENT (mm)	SPECIMEN No.	QG 1						QG 445 (Adult)					QG 453 (Juv.)							QG 481 (Adult)				QG 501			QG 509	
	POSITION IN SERIES	Anterior		Mid		Posterior		Anterior caudals					Mid caudals							Posterior caudals				Chevrons			Chev.	
		1	10	14	26	32	39																					
Centrum: length		24,5	27	27,5	26,5	27,5	22	27,5	28	27	28	28	20,5	21	21	20	20	21	21	27	29	29,5	29					
height anterior face		20						19	18,5	18	17,5	16								9	8,5	8,5	7,5					
width anterior face		17,5			9			18	15	14	13	12,5	8	6,5	6	6,5		7	5,5	8,5	9	8,5	8					
minimum breadth at mid centrum		10,5			6,5			11	9	9	8	8,5								5,5	6	5	5					
height posterior face		18,5	13					19,5	18	17,5	16,5	15,5								9,5	8	8,5	7,5					
width posterior face					8,5			16	14	13,5	12	12				7		6	5	9	9	8	7,5					
Length transverse process (lateral)		36						29	29	28,5	26,5																	
Length neural spine (ant/post)								23	21,5	20																		
Height neural spine from roof of neural canal										20																		
Chevron: length																								63	64,5	60	14	11
breadth at intercentrum																								10	11,5		8	7,5

TABLE 7. Syntarsus rhodesiensis: measurements of caudal vertebrae and chevrons

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TABLE 8. Syntarsus rhodesiensis: measurements of forelimb and girdle elements

MEASUREMENT (mm)	Specimen No.	QG1	QG 514	QG 563	QG 517	QG 550	QG 524	QG 193	QG 512
	Side	L	R	R	L	R	R	R	L
SCAPULA/CORACOID:									
Greatest length		129	153+					157	121
Length (scap. only)					80				
Length (cor. only)									
Width prox. end scap.		32+	45						29
Max. width cor.			53					63	34+
Glenoid thickness		9	10,5		7,5		9	11,5	9,5
Min. width scap. shaft		13	16,5		8,5		13	16	13
Max. thickness scap. shaft		7,5	7,5		5,5		7,5	7,5	7
Height pre-glenoid tubercle		10						10	9,5
HUMERUS:									
Greatest length		100	102		74,5	76,5	87		
Proximal width		25	27		18	15,5	24		
Max. thickness head		8	11		6,5	6	7		
Condylar width		22			14	13,5	20,5		
Length deltopectoral crest		30+	46		33,5	34,5	39		
Height delt/pect crest (from anconal surface)			22,5		12,5	12,5	19,5		
ULNA/RADIUS:									
Ulna length		77	71	60					
Length olecranon (from anterior face)			11	5					
Height cotylus frontface (from anconal surface)			20	16,5					
Max. diameter distal end			11,5	9,5					
Radius length		61	62,5	54					
Max. diameter prox. end			13	10,5					
Max. diameter dist. end		10	11	8,5					

TABLE 9. *Syntarsus rhodesiensis*: measurements of the femur

MEASUREMENT (mm)		SPECIMEN CATALOGUE NUMBERS																																				
	SPECIMEN NO.	QG1	QG3A	3A	726	755	732	733	753	725	760	729	727	731	754	716	756	76	740	739	743	714	717	742	745	738	744	715	713	691	691	734	757	747	723	746	748	722
	SIDE	L	L	R	L	R	L	L	R	L	R	L	L	L	R	R	L	L	R	R	R	L	L	R	R	R	R	L	L	L	R	L	R	R	L	R	R	L
OVERALL LENGTH		208				185								189	186			201							172^{+}	192				199	142							
MAXIMUM WIDTH HEAD Medial surface to greater trochanter		32	35		38	35	34	34	36	33	38	36	33	28	30		32		30	32	30	29	31	31		30	24	24	24	23	22							
MAXIMUM THICKNESS HEAD Anteroposterior		15	19	18	15	17	17	16	16	15	16	15	15	15	15	14	15	12	14	15	14	12	13	13		12	10	12	10	10	11							
MINIMUM DEPTH HEAD At Teres ligament "hook"		20	23	23	23	23	22	20	23	20	21	20	19	19	20	20	20		18	18		17	20	19		19	14	15	12	13	13							
PRESENCE(+) OR ABSENCE(-) OF "OBTURATOR RIDGE"		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	-	-	-			-	-	-	-	-	-	-	-	-							
PRESENCE(+) OR ABSENCE(-) OF BULBOUS GREATER TROCHANTER		+	+	+	+	+	+	+	+	+	+	+	+	?	?	+	?	-	-	-			-	-	-	-	-	-	-	-	-							
BREADTH OF ILIOFEMORALIS TROCHANTER (= lesser troch.) along lateral border		23			28	24	25		24	21	21		21	20	20			4	7	6			5	5	5			5	4	5	4							
PROXIMAL END TROCH. 4 FROM PROXIMAL SURFACE HEAD		44			45	‾43	41		42	36	40		34	38	35		41	38										30	28	28	27							
DISTAL END TROCH. 4 FROM PROXIMAL SURFACE HEAD		74			78^{+}		72		77	68	75		65	71	69		70	70										60		55	50							
MAXIMUM THICKNESS(anteroposterior) SHAFT AT MID TROCH. 4		19			23	23	22		21	21	21		18	17	19		18	20					18		16			15		14	13						15	
GREATER DIAMETER of m. caudifem. longus TENDON SCAR		11			17		11		11		13						14	22							12			19		11	12							
LESSER DIAMETER OF m. caudifem. longus TENDON SCAR		3			4		5		5		4						4	3							4			3		3	3							
GREATER DIAMETER OF m. caudifem brev. TENDON SCAR		21			24		22		23		21		21		22		21	30					28		22			20		17	20							
LESSER DIAMETER OF m. caudifem brev. TENDON SCAR		7			10		8		9		10		8		6		13	9					9		9			7		6	5							
MIDLENGTH SHAFT DIAMETER Transverse		21			18	16				18			14		13		15	15							14			12		10	11					14	12	
MIDLENGTH SHAFT DIAMETER Anteroposterior		18			22					20			16		17		17	18							16			13		13	12					15	14	
MAXIMUM TRANSVERSE WIDTH OF ROTULAR SURFACE		25													19			22							18	21				15	18		24	13	15		18	17
MAXIMUM DISTAL TRANSVERSE Width across condyles		28				34												25							29	28				21	23	33	37	17	22		25	25
MAXIMUM DISTAL LATERAL THICKNESS(ant.surface to apex fibular condyle)		29				28												24							28	27				20	20		24	21	20		21	
MAXIMUM DISTAL MEDIAL THICKNESS(ant.surface to apex internal condyle)		26				25									25										22	24				18	16	29	23	17	18		19	18
AGE A = adult SA = "sub-adult" J = juvenile		A	A	A	A	A	A	A	A	A	A	A	A	SA	SA	SA	? SA	A	A	A	A	SA	A	A	J	SA	J	J	J	J	J			J	J			

TABLE 10. <u>Syntarsus rhodesiensis: measurements of hindlimb elements and pelvis (for femur see Table 9)</u>

MEASUREMENT (mm) — Specimen No.	QG 1	QG 691	QG 696	QG 803	QG 805	QG 762	QG 770	QG 816	QG 785	QG 786	QG 781
Side	L	R		L	L	R	R	L	R	R	R
PELVIS:											
Ilium length (upper edge)	148	122	148								
Depth preacetabular process	36,5	31	43,5								
Breadth "caudifemoralis shelf"	31	20									
Length pubis (from il/pub-suture)	204										
Length ischium	130	125,5									
"Pseudantitrochanter" thickness	22,5	17,5	21								
Max. diameter of large fenestra	c23	15,5	22								
Max. diameter of small fenestra	10										
FEMUR: (see Table 9)											
TIBIA FIBULA AND ASTRAGALO-CALCANEUM:											
Tibia + astragalocaneum	223			214	216		210				
Tibia only		156		205	207	179					
Tibia-breadth head	21	18			24	18	25,5				
Tibia-condyles to cnem. crest	40	27			40,5	28					
Tibia-thickness ambiens groove	11,5	7			13	7,5					
Tibia-breadth distal end (excl. astrag/calc)	24	19,5		28	25						
Breadth astragalo-calc.	29			33	31						
Astragalus-height ascending process								12	14,5	13	19,5
Astragalus-transverse breadth								20	23	20,5	26
Astragalus-medial thickness								6,5	7	6,5	8
Calcaneum-transverse breadth								6		6	8
Calcaneum-lateral thickness								8		8	11,5
Fibula length	208	152		194	201		197				
Fibula-breadth head	25	18			28,5	18,5	22				
Fibula-breadth distal flare	15,5	11		12,5	15		15				

TABLE 11. *Syntarsus rhodesiensis*: measurements of an endocranial cast taken from QG 193

	mm
Overall length (from foramen magnum exit to front end of olfactory bulbs - straight line)	72
Overall length - measured over curves	93
Length olfactory bulb	16
Maximum width olfactory bulb	6
Length olfactory tract (hind end of bulb to front end cerebrum)	c.16
Length cerebral hemispheres	c.23
Maximum width cerebral hemispheres	c.22
Depth of brain cavity (cranial roof to floor of medulla)	30
Length of medulla (foramen magnum to wall of pituitary fossa)	19
Width of medulla	9
Transverse width between apex of auricular lobe, L. and R.	13
Height of "cerebellum compartment" (dorsal surface of medulla to cranial roof)	17

TABLE 12. *Syntarsus rhodesiensis*: cranial and axial cervical muscles

NAME OF MUSCLE	ORIGIN	INSERTION	ACTION

NAME OF MUSCLE		ORIGIN	INSERTION	ACTION
after Harvey et al (1968)	After Ostrom (1961)			
m. biventer cervicis	m. spinalis capitis	Neural spines of cervicodorsals by aponeurosis	Dorsally and medially on occiput	Raises head; dorsal flexion of neck to sigmoid curve
m. complexus	m. longissimus capitis	Prezygapophyses of ? cervical 4 possibly also atlas and C3	Occiput in dorsal (pars articulo-parietalis): lateral (pars transversalis cervicis) on occiput	Dorsal flexion and lateral turning of head
m. rectus capitis dorsalis	m. rectus capitis posterior	Neural spine of axis	Pockets laterally on occiput above foramen magnum	Dorsal flexion of head
	m. obliquus capitis magnus	? Lateral surface of axis neural spine	Paroccipital process lateral to foramen magnum	Lateral turning of head
? m. rectus capitis lateralis and ventralis	m. rectus capitis anterior	Ventrally on centra of anterior cervicals (?3-6)	Below foramen magnum ? in deep lateral pockets	Powerful ventral flexion of head
m. longus colli dorsalis		Neural spines of cervicodorsalis together with m. biventer cervicis	Cranial slips: epipophyses of cervicals 10-7 caudal slips: from tendon to epipophyses of cervicals 3-8	Cranial slips: elevate neck Caudal slips: elevate head
m. longus colli ventralis		Ventrally on centra of cervico-dorsals	Centra and cervical ribs of more anterior cervicals	Ventral flexion of neck, reducing sigmoid curve
m. obliquus colli		"Transverse process" C 6 C 7 C 8 C 9 C 10 Dorsal 1	Tendons ? on epipophyses C 3 C 5 C 6 C 7 C 8 C 8	Lateral movement of neck If all contract together neck flexes dorsally
m. interspinales craniales		Front face of neural spine D 1 C 10 C 9 C 8	Hind face of neural spine C 10 C 9 C 8 C 7	Assist in elevation of neck
m. intertransversales		Cranial face of parapophysis/diapophysis area C 10 C 9 C 8 C 7 C 6 C 5 C 4	Caudal face of parapophysis/diapophysis area, ? and lateral pleurocoels C 9 C 8 C 7 C 6 C 5 C 4 C 3	Lateral bending of neck

TABLE 13. *Syntarsus rhodesiensis*: forelimb muscles

MUSCLE GROUP	NAME OF MUSCLE	ORIGIN	INSERTION	ACTION
AXIAL MUSCLES	Latissimus dorsi	Neural spines of dorsal vertebrae	Anconal surface of humerus, medial to deltopectoral crest on triangular site	Retractor and abductor of humerus
	Serratus	Cervicodorsal and dorsal ribs	Medial surface of scapulocoracoid	Anchors scapulocoracoid
	Pectoralis	? Ribs, gastralia and soft tissues in anterior trunk region	Apex of deltopectoral crest on humerus, extending onto inner surface of crest	Main adductor of humerus
MUSCLES ON PALMAR SURFACE OF HUMERUS	Supracoracoideus	Outer surface of coracoid, over a wide fleshy area	Small tubercle on lateral anconal surface near head of humerus	Major abductor and protractor of humerus
	(Scapulo-humeralis)	?	?	(? missing)
	Coracobrachialis	Medial edge of coracoid adjacent to glenoid - partly from tubercle	Palmar surface of upper half of humerus, bounded by deltopectoral crest	Strong protraction of humerus
	Biceps	Anterior edge of coracoid (between coracobrachialis and supracoracoideus) and medial side of humerus shaft on palmar surface	? on rugose scar on ulna, adjacent to radius facet	Some protraction and adduction of humerus, and strong flexion of forearm
	Brachialis	Shallow triangular depression at distal end of palmar surface of humerus	? with biceps on ulna	Flexion of forearm
MUSCLES ON ANCONAL SURFACE OF HUMERUS	Deltoideus	Fleshy from outer surface of scapula blade	Narrow curved area on lateral wall of deltopectoral crest near its apex	Powerful abductor and retractor of humerus
	(Humeroradialis)	?	?	(? missing)
	Subcoracoideus	Medial surface of coracoid, ? anterior to serratus	Tuberosity on proximal inner "corner" of humerus	Adductor and rotator of humerus
	Proscapulohumeralis	? Scapula, adjacent to glenoid	Two small facets near subcoracoideus insertion on proximal inner "corner" of humerus	Weak retractor of humerus
	Triceps	(? Scapula) and most of medial half of anconal surface of humerus - near lat. dorsal insertion	By tendon onto olecranon of ulna	Powerful extensor of forearm
MUSCLES ON EPICONDYLES OF HUMERUS	Supinator and Distal extensors	(Ectepicondyle of humerus above (and lateral to radial condyle	Extensor tubercles on phalanges and carpals	Reduced supination, strong distal extension
	Pronator and Distal flexors	(Entepicondyle of humerus, above (and medial to ulnar condyle	Flexor tubercles on phalanges and carpals	Strong pionation and distal flexion

TABLE 14. Syntarsus rhodesiensis: hindlimb muscles

NAME OF MUSCLE	ORIGIN	INSERTION	NOTES
Dorsal axial muscles Dorsalis trunci } Dorsalis caudae }	Neural spines and dorsal surface of transverse processes of dorsal and caudal vertebrae	Neural spines, dorsal surface of sacrum and inner rim of ilium above sacrum	No mid pelvic constriction into clearly trunk and caudal components
Ventral axial muscles Obliquus abdominis ext. } Obliquus abdominis int. } Transverse abdominis }	"Lumbodorsal fascia" anterior to pelvis	Pubis lateral edge, the transversus inserting with the rectus	
Rectus abdominis Ilioischiocaudalis	- Sternal area and long ribs - Centra and lower surface T.P. of caudal vertebrae	- Pubis - Posterior rim of ilium, sacrum and ischium	
ILIOTIBIALIS	Narrow and aponeurotic from dorsal rim of ilium along its length	Apex of cnemial crest via the "patellar tendon"	
SARTORIUS	Fleshy from the anteroventral projection of the pre-acetabular ilium	With iliotibialis via the "patellar tendon" to cnemial crest	
AMBIENS	Tendinous from rugosity on pubis immediately ahead of acetabulum	With iliotibialis, etc. to cnemial crest via "patellar tendon" and tendon crosses knee to digital flexors	As in birds, part of the Iliofibularis sling (=biceps loop) was probably associated with the ambiens tendon at the knee
FEMOROTIBIALIS	Three heads arising on femoral shaft (i) medial surface of femur distal to caudifem (ii) lateral surface distal to Iliofemoralis trochanter (iii) posterior surface, defined by ridges in "robust"	With iliotibialis, etc. to cnemial crest via "patellar tendon"	
ILIOFIBULARIS	Posterolateral shelf of ilium	Rugose depression on fibula, distal to head, on lateral surface	The long tendon of the Iliofibularis passed through the "Iliofibularis sling" (biceps loop) on its path to its insertion
PUBOISCHIOFEMORALIS INTERNUS	Centra and lower surface of transverse processes of posterior dorsals, and from inner surface of anterior part of ilium; portions also from anterior face of pubic apron	Bulbous trochanter adjacent to joint capsule scar on lateral surface of femoral neck (? = greater trochanter)	
ILIOFEMORALIS	Fleshy from most of concave lateral surface of ilium	Shelf like trochanter minor (robust forms) or blade-like trochanter minor (gracile forms) on lateral surface of femur at base of neck	
ISCHIOTROCHANTERICUS	Dorsolateral surface of ischium shaft along its length, ? by aponeurosis	Lateral surface of femoral neck, proximal to iliofemoralis and distal to puboischiofemoralis int.	
FLEXORTIBIALIS INTERNUS	Tendinous from rugose area on lateral surface of ischium immediately behind acetabulum,? also from vent surf of prox ½ of ischium shaft	Proximal medial surface of cnemial crest by tendon which inserts in a depression and is associated with the gastrocnemius origin	
FLEXORTIBIALIS EXTERNUS	Possibly from posterolateral shelf of ilium, which it shares with iliofibularis	? inserts with flexortibialis internus by common tendon	
ADDUCTOR FEMORIS	Fleshy from lateral surface of puboischiadic plate below acetabulum	Fleshy along distal $^2/_3$ of posteromedial surface of femoral shaft, between medial and posterior heads of femorotibialis ? curved area near lat condyle	
PUBOISCHIOFEMORALIS EXTERNUS	From posterior (ventral) face of pubis in the region of obturator fenestra, fleshy	Diagonal trochanter adjacent to joint capsule on posterior face of femoral neck (? = "obturator ridge" of birds)	
CAUDIFEMORALIS LONGUS	Fleshy from centra and lower surface of transverse processes of proximal/mid-caudal vertebrae	Tendinous to lateral surface of fourth trochanter, inserting into a rugose elliptical depression	Several specimens (especially QG 745) show a groove running distally from the insertion, which may be for an accessory tendon to the head of the fibula
CAUDIFEMORALIS BREVIS	Large and fleshy from the ventral surface of the sacrum and ilium (="brevis shelf") behind the acetabulum	Powerful tendon to medial surface of femoral shaft ahead of caudifem. long. crescentic depression	
TIBIALIS ANTERIOR	Probably two heads - one small and tendinous from small depression on femoral external condyle; and main head fleshy from cnemial crest (lateral surface and tibial shaft	Narrowed to strong tendon which ran down anterior face of tibial shaft and held to the bone distally by a strong annular ligament, to insert on metatarsals	The insertion appears to have been by broad aponeurosis at the proximal end of the metatarsus
EXTENSOR DIGITORUM LONGUS	Fleshy from anterior surface of tibial shaft beside m. tibialis anterior, distal to fibular flange on tibia	Base of claws of digits II, III, IV by tendon which passes across tarsal joint with tibialis anterior via annular lig.	The long tendon of m. extensor digitorum longus has left a longitudinal shallow groove on the tibia, adjacent to the fibula, in several specimens
PERONEUS LONGUS) PERONEUS BREVIS)	Separate origins for the longus and brevis cannot be identified The composite muscle seems to have had a fleshy origin on the anterolateral surface of the fibular head, with fibres arising on the distal shaft	The common tendon ran down the anterior tibial surface, in a groove bordered by the fibula to emerge through the tarsal annular ligament to insert on the metatarsals, ventrally	It cannot be seen whether part of the insertion was on a tibial cartilage; th main insertion was presumably to the "hypotarsus" or in confluence with digital flexor tendons as in birds
GASTROCNEMIUS	Probably three heads - i) from base of external condyle of femur; ii) from proximal lateral face of cnemial crest; and iii) from curved trough proximal to internal condyle of femur. ? also from popliteal fossa	Powerful tendon (Achilles) which inserted on a well-developed "hypotarsus" principally under MT III	The m. plantaris was probably closely associated. The insertion of the tendon distally seems to have involved a broad and powerful fascia on the sole of the foot
PLANTARIS	Fleshy from posteromedial surface of proximal end of tibia, below and behind one head of m. gastrocnemius	Sharing common tendon of insertion with m. gastrocnemius, ? mainly to the tibial cartilage	In the absence of the tibial cartilage, the insertion point is uncertain
POPLITEUS	Fleshy from the depression between the tibial condyles on the posterior tibial surface	Medial surface of fibular head on a small backward projection	
FLEXOR DIGITI II } FLEXOR DIGITI III } FLEXOR DIGITI IV }	In the absence of clear scars of origin it is presumed that the long digital flexors originated from popliteal area or from the tissues of the knee joint capsule and the complex aponeuroses associated with the knee, as is the case in birds	The long tendons of insertion would have inserted on the appropriate digits, on the ventral (flexor) surface, but the degree to which they mutually joined, perforated or ensheathed each other cannot be determined	
FLEXOR DIGITORUM LONGUS	Fleshy from depressed area on backward projection of fibular head, with other fibres fleshy from posterior surface of tibia	Long composite tendon reaching digits II, III and IV	
FLEXOR HALLUCIS LONGUS	Probably as for other digital flexors, by aponeurosis from knee joint	Tendon to flexor boss at base of hallux claw	
ABDUCTOR HALLUCIS	Medial surface of distal ½ of MT I, from tubercle	Medial tubercle at prox. end of phalanx I	

TABLE 15. *Syntarsus rhodesiensis*: cranial kinetic articulations

JOINT TYPE	ARTICULATING ELEMENTS	MOBILITY RATING 1 = very mobile 2 = intermediate 3 = scarcely mobile
PIVOTAL JOINTS (ROTATORIA)	Quadrate head in squamosal socket	1
	Lachrymal on prefrontal	1
	Parietals on exoccipitals	2
SLIDING JOINTS (ARTHRODIA)	Premaxilla with nasal, and on maxilla	1
	Jugal on maxilla	1
	Jugal on postorbital	1
	Pterygoid on basipterygoid process (= basal articulation)	1
	?Ectopterygoid with jugal	?2
SQUAMOSE JOINTS	Nasal on frontal (frontonasal hinge)	1 – 2
	Lachrymal with jugal and maxilla	1
	Ectopterygoid with pterygoid	1 – 2
	Pterygoid with palatine	?3
	Pterygoid (quadrate wing) with quadrate	2 – 3
TONGUE - AND - GROOVE JOINTS (SCHINDYLESES)	Prefrontal and frontal	3
	Postorbital and frontal	3
	Postorbital and squamosal	2
	Quadratojugal and jugal	1

71 125

TABLE 16. Comparative skeletal indices (adapted from Galton, 1971)

* SOURCE REF.	TAXON	Length femur (mm)	$\frac{T}{F}$	$\frac{T+MT}{F}$	$\frac{MT}{F}$	$\frac{MT}{T}$	$\frac{F}{Tr}$	$\frac{HL}{Tr}$
1	Ornitholestes	207	0,77	1,33	0,57	0,73	0,66	1,52
2	Coelurus	207	0,77	1,33	0,57	0,74		
1	Coelophysis	209	1,07	1,67	0,60	0,56	0,47	1,20
3	Syntarsus (type)	208	1,07	1,71	0,63	0,59	0,57	1,55
4	Compsognathus	110	1,23	1,96	0,74	0,60	c0,67	c1,98
2	Elaphrosaurus	529	1,15	1,89	0,74	0,64		
1	Struthiomimus	480	1,12	1,90	0,77	0,68	0,71	2,58
5	Deinonychus	336	1,14	1,63	0,49	0,45	?0,78	c2,05
6	Archaeopteryx (A)	58	1,38	2,14	0,76	0,55		
6	Archaeopteryx (B)	51	1,37	2,04	0,67	0,49		
6	Archaeopteryx (C)	58	1,38	2,10	0,72	0,53		
6	Archaeopteryx (D)	c54	c1,48	c2,37	0,89	0,60		
7	Allosaurus	810	0,90	1,31	0,41	0,45	0,65	1,49
1	Gorgosaurus	1040	0,96	1,53	0,57	0,59	0,57	1,52

Abbreviations:
T - tibia; F - femur; MT metatarsal III;
Tr - trunk; HL - hindlimb (=F+T+MT);
A - London specimen; B - Berlin specimen;
C - Solnhofen specimen; D - Teyler specimen.

* Sources:
1 - Galton, 1971
2 - Janensch, 1925
3 - Raath, 1969 and this study (see Table 4)
4 - Bidar, Demay & Thomel, 1972
5 - Ostrom, 1969; 1976
6 - Ostrom, 1972
7 - Madsen, 1976

22 12 6

TABLE 17. Bone dimensions and ratios in congeneric Hornbill's: *Tockus nasutus* (which hops) and *T. flaviventris* (which strides)

	T. nasutus (hops)		T. flaviventris (strides	
Dimension	mm	as % Femur	mm	as % Femur
Length femur	37	100	41,5	100
Max. diameter head	3	8,1	3	7,2
Max. length ilium	34	91,9	36	86,8
Breadth pelvis across acetabulum	14,5	39,2	14	33,7
Breadth pelvis anterior end	15	40,5	14,5	34,9
Breadth pelvis posterior end	21	56,8	17,5	42,2
Length tibiotarsus	55	148,6	64	154,2

TABLE 18. Syntarsus rhodesiensis: femur sample analysis by "age-classes" and by morphological form

LOCALITY	FORM	AGE CLASSES						TOTALS FOR LOCALITY (Minimum)
		ADULT		SUB ADULT		JUVENILE		
		L/R	MIN	L/R	MIN	L/R	MIN	
SOUTHCOTE FARM	Robust	L 2 R 1	2	L 0 R 0	–	L 0 R 0	–	2
	Gracile	L 0 R 0	–	L 0 R 0	–	L 0 R 0	–	
	Min. Sub Total		2		0		0	
MAURA RIVER	Robust	L 0 R 0	–	L 0 R 0	–	L 0 R 0	–	2
	Gracile	L 1 R 0	1	L 0 R 0	–	L 1 R 1	1	
	Min. Sub Total		1		0		1	
CHITAKE RIVER	Robust	L 9 R 3	9	L 2 R 2	2	L 0 R 0	–	26
	Gracile	L 1 R 7	7	L 4 R 1	4	L 3 R 4	4	
	Min. Sub Total		16		6		4	
	Totals per age class (Min.)		19		6		5	30

TOTAL MINIMUM INDIVIDUALS

TABLE 19. Comparison of the genera Coelophysis and Syntarsus

		Coelophysis Cope, 1889	Syntarsus Raath, 1969
Geological Formation(s) from which recovered		Petrified Forest member, Chinle Formation, New Mexico, U.S.A. Portland Arkose, Newark Group, Connecticut, U.S.A.	Forest Sandstone (Stormberg), Karroo Formation, Rhodesia
Localities		Ghost Ranch, New Mexico Mt. Holyoke, Connecticut Middletown, Connecticut	Southcote Farm, Nyamandhlovu Maura River ± Angwa River confluence Chitake River
Geological Age		Upper Triassic (Norian - Rhaetian)	Upper Triassic (?Rhaetian)
Sedimentological and taphonomic notes		New Mexico quarry: Lowland silts ("Low-lying tropical land of many lakes and rivers. Coniferous forests covered the higher ground, while the edges of the waterways were fringed with ferns", Colbert, 1974). Many articulated skeletons (24+) concentrated in small area (c·10m x 10m), all ages represented. Connecticut: Alluvial shales and silts (Colbert & Baird, 1958). Isolated single occurrences; one an articulated partial skeleton, the other exocasts of bones of an articulated partial specimen. Footprints associated (Grallator) in Connecticut.	Localities in aeolian sandstone associated with local occurrence of water bodies. Southcote Farm: Two isolated specimens; one nearly complete (holotype), the other fragmentary and dissociated. Maura River: Two isolated fragmentary specimens. Chitake River: Many individuals (26+) representing all ages, and in all stages of dissociation and articulation. Footprints from Nyamandhlovu sandstone referred
CONTRAST OF SKELETAL FEATURES	SKULL	Skull height:length ratio 32% (but very variable)	Skull height:length ratio 27% (variability not known)
		Postparietal fenestrae persistent	Postparietal fenestrae absent
		Basisphenoid ? shorter than Syntarsus (Colbert)	
		Ectopterygoid rather large and platelike (Colbert) not articulating in "double-lap" with pterygoid	Ectopterygoid smaller, hook-like, articulating in "double-lap" with pterygoid
		"Carnosaur pocket" in palate absent (Ostrom)	"Carnosaur pocket" present
		Choanae lateral, elongate, near anterior end	Choanae medial, subcircular, far back in mouth
		Sq. descending arm covers q. laterally	Sq. descending arm covered by q.
		Nasal fenestrae absent	Nasal fenestrae ? present
		Antorbital fenestra smaller; 27% skull length	Antorbital fenestra larger; 43% skull length
		Upper tooth row longer; 60%+ skull length	Upper tooth row shorter; 45% skull length
		Lower tooth row longer; 64% mandible length	Lower tooth row shorter; 51% mandible length
		Skull: presacral length ratio 23% (variable)	Skull: presacral length ratio 35% (variability not known)
		Interdental plates absent	Interdental plates present
		Extent of kinesis unknown	Skull extensively kinetic, amphikinetic, premaxilla independently mobile
	VERTEBRAE	Last cervical keeled (v. Huene, 1932)	All cervicals (except atlas) keeled
		Fusion of sacral neural spines variable, ? function of sexual dimorphism (Colbert)	Sacral neural spine fusion certainly seen in "robust" forms, variability not known
		Hyposphene-hypantrum articulations not reported	Hyposphene-hypantrum articulations present in dorsal series and anterior caudals
	FORELIMB	Forelimb length ca.50% of hindlimb length (forelimb length variable -? sexual dimorphism, Colbert)	Forelimb length ("robust" form) 35% of hindlimb length (variability not known)
		Humerus:femur length ratio (ave.) 62%	Humerus:femur ratio 48%
		Humerus:tibia length ratio (ave.) 57%	Humerus:tibia ratio 45%
		Digit IV reduced, but ? not as much as Syntarsus	Digit IV greatly reduced, not showing in life
	HINDLIMB	Fusion between astragalocalcaneum and crus not reported	Fusion between astragalocalcaneum and crus common in "robust" adults
		Only one pubic foramen (obturator) reported (v.Huene, 1932)	Two pubic foramina present
		Ilium not laterally flared posteriorly	Ilium broadly flared posteriorly ("robust" form), but ? variable
		Pubis and ischium expanded at distal ends (Colbert)	Pubis blunt ending but not expanded, ischium minimally expanded
		Pubis length equal to, or longer than, femur	Pubis length shorter than femur
		Greater trochanter crest-like	Greater trochanter crest-like in gracile forms, shelf-like in "robust" forms
		Remaining femoral trochanters not dimorphic	Remaining femoral trochanters markedly dimorphic