



The tarsus of erythrosuchid archosaurs, and implications for early diapsid phylogeny

DAVID J. GOWER

Department of Geology, University of Bristol, Wills Memorial Building, Queens Road, Bristol, BS8 1RJ, UK and Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Sigwartstrasse 10, D-72076 Tübingen, Germany

Received September 1994, accepted for publication February 1995

The morphology of the erythrosuchid ankle joint is reassessed. Two specimens, recently thought to have been incorrectly referred to *Erythrosuchus africanus*, are shown without doubt to belong to this taxon. Furthermore, the morphology is essentially similar to that of other early archosaurs. The tarsus of *Erythrosuchus* is poorly ossified and consists of a calcaneum, astragalus, and two distal tarsals. The calcanea of *Erythrosuchus*, *Vjushkovia triplicostata*, and *Shansisuchus shansisuchus* are all similar in being dorsoventrally compressed, possessing a lateral tuber, and lacking a perforating foramen. The astragalus of *V. triplicostata* is currently unknown. The astragalus of *Shansisuchus* is apparently unique in form. The erythrosuchid pes is therefore more derived than has been recently proposed. The tarsal morphology of several other archosauromorph taxa is reviewed and many details are found to be at variance with the literature. The plesiomorphic condition for the Archosauromorpha consists of four distal tarsals and a proximal row of three elements; two of which articulate with the tibia. These proximal elements are interpreted as the astragalus, calcaneum, and a centrale, and the same pattern is retained in the earliest archosaurs. This reassessed tarsal morphology has implications for the homology of the centrale and reconstruction of early diapsid phylogeny.

©1996 The Linnean Society of London

ADDITIONAL KEY WORDS:— Archosauromorpha – Erythrosuchidae – pes – morphology – homology – characters – synapomorphy.

CONTENTS

Introduction	348
Terminology	348
Abbreviations	349
Descriptive accounts	349
<i>Erythrosuchus africanus</i>	349
<i>Vjushkovia triplicostata</i>	358
<i>Shansisuchus shansisuchus</i>	360
Concluding remarks on the erythrosuchid pes	364
<i>Euparkeria</i>	365
<i>Proterosuchus</i>	366
Prolacertiformes	367
Rhynchosaurs	367
<i>Trilophosaurus</i>	368
Phylogenetic implications	368
Erythrosuchid ankle characters	368

Poorly defined/scored characters	368
Neglected characters	370
Acknowledgements	373
References	373

INTRODUCTION

Ankle morphology has been recognized as an important character, or suite of characters, in archosaur phylogeny. Interest was stimulated by Charig (1972) who noted that there are general trends in the evolution of the locomotor apparatus of early archosaurs which can be detected in changes in ankle morphology. Early work followed the format of producing complete archosaur phylogenies based only on a superabundance of discrete ankle 'types' (Cruickshank, 1979; Thulborn, 1980, 1982; Brinkman, 1981; Chatterjee, 1982; Cruickshank & Benton, 1985). With the integration of cladistic methodology in the study of archosaur phylogeny came a more holistic approach, but the information from ankle morphology was still largely based on identification of discrete ankle types (e.g. Gauthier, 1986; Benton & Clark, 1988). Recently (e.g. Sereno & Arcucci, 1990; Sereno, 1991), it has at last been accepted that discrete ankle types do not exist in such diversity and that the character changes occurring during the evolution of the hind limb are numerous and complex. Despite this realization, recent cladistic studies have strongly disagreed on the homology of various ankle characters and on how they should be defined and coded (e.g. Sereno, 1991; Parrish, 1993).

Rather sidelined during this debate has been the morphology of the erythrosuchid ankle. The ankle of this group of early archosaurs remains poorly known and controversial despite its potential importance. The aim of this work is to present detailed descriptions of all known erythrosuchid tarsi and to look at the phylogenetic implications of the morphology of the ankles of erythrosuchids and other early archosauromorphs.

Terminology

The terminology employed here for hind-limb orientation follows Rewcastle (1980), in envisaging a fully extended crus and pes with its long axis directed anteriorly, so that the tibia and first digit are medial and the fibula and fifth digit are lateral. The dorsal surface of the crus and pes then corresponds with the extensor surface. This unfortunately clashes with the terminology used in previous key studies of early archosaurian ankles (e.g. Cruickshank, 1979; Sereno, 1991), which adopted an essentially mammalian/avian terminology. The terminology used here corresponds to 'primitive' dorsal and ventral as defined by Romer (1922, 1923, 1942) and also, therefore, the terminology that is most commonly used in descriptions of the non-tarsal parts and musculature of the hindlimb of 'primitive' tetrapods. For example, the internal trochanter and intertrochanteric fossa are ventral and not posterior features. The terminology is further explained in Figure 1. The terminology adopted here requires renaming of certain features of the archosaur tarsus, including the astragalar 'anterior' hollow (dorsal hollow), 'posterior groove' (ventral), and separate 'dorsal' and 'ventral' calcaneal facets (proximal and distal respectively).

The use of the taxon Archosauria is applied throughout in its traditional concept,

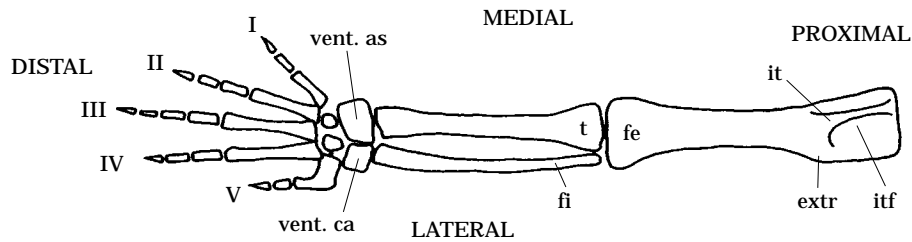


Figure 1. Ventral view of a fully anteriorly extended, right pelvic limb of a generalised, early archosauromorph reptile, explaining the orientation nomenclature used in text. extr = external trochanter; fe = femur; it = internal trochanter; itf = intertrochanteric fossa.

rather than in the crown-group concept, as advocated by Gauthier (1986). The less inclusive taxon referred to by Gauthier (1986) as the archosaurs is here called the crown-group archosaurs.

Abbreviations

Abbreviations used in more than one figure are as follows: as – astragalus, ca – calcaneum, cn – calcaneal notch, com – area of bone surface finished with compacta, ct – calcaneal tuber, dh – dorsal hollow, dt3/4 – distal tarsal 3/4, fi – fibula, gs – ventral groove system of astragalus, nan – non-articular notch, nf – nutrient foramen, pvg – proximoventral groove on calcaneum, s. – surface for articular with ..., t – tibia, roman numerals I–V – number of metatarsal/digit.

Institution names are abbreviated as follows: BMNH, British Museum (Natural History); BPI, Bernard Price Institute for Palaeontological Research, Johannesburg; DMSW, D.M.S. Watson Collection; GPIT, Institut und Museum für Geologie und Paläontologie, Universität Tübingen; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; NM, Nasionale Museum, Bloemfontein; PIAS, Paleontological Institute of the Russian Academy of Science, Moscow; SAM, South African Museum, Cape Town; UMCZ, University of Cambridge Museum of Zoology.

DESCRIPTIVE ACCOUNTS

Erythrosuchus africanus Broom, 1905

Erythrosuchus africanus from the *Cynognathus* zone of the Karoo of South Africa, is one of the most completely known early archosaur taxa. The history of knowledge concerning the ankle is complex. No ankle material is associated with the holotype, SAM 905 (Broom 1905, 1906), and Huene (1911) did not describe any tarsal material in his monograph on specimen BMNH R3592. Since then, however, two specimens have provided the focus for descriptive accounts (Huene 1915, 1920; Hughes, 1963; Cruickshank, 1978). These descriptions, particularly that of Cruickshank (1978), provided the basis for the analysis of the erythrosuchid ankle in the spate of publications on archosaur ankle types (Cruickshank, 1979; Thulborn,

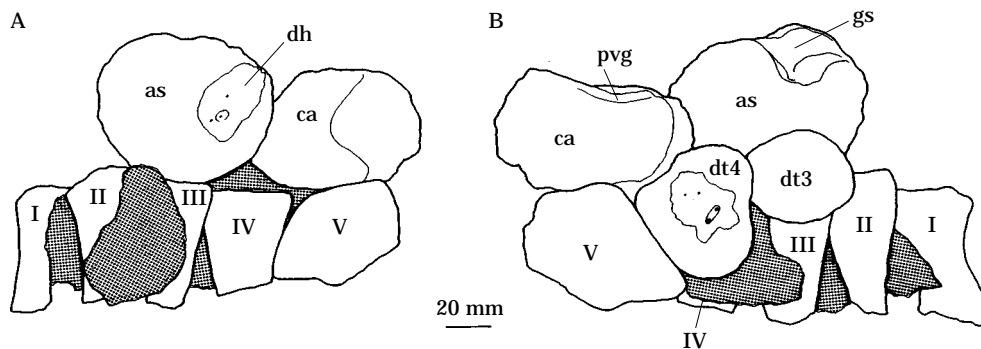


Figure 2. BMNH R3592, left tarsus of *Erythrosuchus africanus* during preparation. A, dorsal; B, ventral views.

1980, 1982). More recently Parrish (1986, 1992) has suggested that both of the specimens used for description do not belong to *Erythrosuchus* but possibly to a kannemeyeriid dicynodont. The evidence cited by Parrish (1992) is a mismatch between the size of the tarsals and the distal surface of the crus, and the absence of any features comparable to those seen on the tarsi of other early archosaurs. Parrish's suggestion has been followed by Sereno & Arcucci (1990) and Sereno (1991) in their tarsal-dominated phylogenies of basal archosaurs.

The material belonging to BMNH R3592 and BPI 2096 has been restudied allowing a detailed reassessment of the bones of contention.

BMNH R3592

The tarsus of BMNH R3592 (originally part of DMSW R525) was not described by Huene (1911) but was briefly sketched and described by the same author at later dates (1915, 1920). Hughes (1963), after fully preparing the same specimen in acid, presented a brief description as well as the first reconstruction of the ankle. Photographs were taken by Hughes during preparation, drawings of which are presented above (Fig. 2). The specimen consists of the left distal tibia and fibula, four tarsal elements and the proximal ends of all five metatarsals. Evidence that the tibia and fibula belong with this specimen comes from Watson's catalogue which reports that "The specimens are lower ends of the left tibia and fibula. The tarsus and metatarsals in articulation and the metatarsals of the other foot". The 'metatarsals' of the other foot are in fact metacarpals. The catalogue also reports that the specimen was found in 1911, at least 2 years later than the rest of BMNH R3592, although from exactly the same locality.

There is very strong evidence that this specimen is the ankle of *E. africanus*. Included as part of the original postcranial skeleton of BMNH R3592 is the proximal section of the right tibia and fibula still held together by matrix and incorrectly described by Huene (1911) as the left distal tibia and fibula. A short, homologous length of fibula shaft is presented in both the left distal section of DMSW R525, and the right proximal section of BMNH R3592. This covers the area of the characteristic roughened and slightly raised area for the insertion of the iliofibularis, and the two specimens show a very close match in form, size, and cross section — suggesting strongly that the distal fibula of DMSW R525 (found at the same time as

the rest of the R525 material) belongs to *E. africanus* (always assuming BMNH R3592 does).

The photographs of the unprepared material show that any disturbance of the elements during preservation was minimal, although the ankle was strongly flexed. The ventral view (Fig. 2B), in particular, shows the intimate articulation between the tarsals. The astragalus and calcaneum make contact and a large void is present on the medial side between the astragalus and the proximal surface of the first metatarsal, which does not articulate with any of the tarsals. There are two bones in the proximal row, the astragalus and calcaneum, and two distal tarsals. Compaction of the specimen during preservation may have exaggerated the definition of the articular surfaces identified on the elements.

Astragalus (Fig. 3)

Although previously described as a rough ovoid with only two notable features (Hughes, 1963; Cruickshank, 1978), the combination of acid preparation and the recording of pre-preparation position allows a more detailed description of the several articular surfaces. The greatest dorsal-ventral distance is approximately equal to the greatest medial-lateral distance. The various articular surfaces are only weakly separated from each other and the majority of the surface of the element is not fully finished with compacta.

Laterally there is a small, flattened, and essentially featureless surface for articulation with the calcaneum. There is no indication of a perforating astragalo-calcaneal canal, or of separate proximal and distal articular areas that would correspond to the 'dorsal' and 'ventral' areas identified in other early archosaurs by Sereno & Arcucci (1990) and Sereno (1991). Above this, only weakly separated from the articular surface for the calcaneum, and facing proximolaterally, is the astragalar facet for the fibula. This facet only occupies the dorsal part of the proximolateral face of the astragalus. Adjacent to this, and facing dorsomedially as well as proximally, is the articular surface for the tibia. This facet is not separated from that for the fibula by a non-articulating notch, such as is present in more plesiomorphic archosauromorph taxa including *Proterosuchus* (Sereno, 1991) and *Prolacerta* (Gow, 1975). The astragalar facet for the tibia is remarkable in being but less than one third of the area of the distal end of the tibia (see also Cruickshank, 1978). The distal end of the tibia of BMNH R525 is slightly crushed, but this has had only a minimal effect in any possible enlargement of the distal surface. A long narrow surface, distal and medial to the facet for the tibia, does not directly articulate with any other element. This is equivalent to the more elongated and distally directed area that in *Euparkeria* articulates with the metatarsals, and in *Proterosuchus* with the second distal tarsal (not the metatarsals as indicated in figure 3H of Sereno, 1991).

The distal surface of the astragalus is weakly tripartite. Dorsomedially there is a surface that contacts the third distal tarsal in the flexed ankle. Lateral to this is a small surface, weakly separated from the calcaneum facet, for articulation with the dorsal part of the proximal surface of the fourth distal tarsal when the ankle is flexed. The largest subdivision of the distal surface is ventrally positioned. Much of this area is probably non-articular, although in the extended ankle a small lateral part articulates with the proximal part of the peg of the fourth distal tarsal, and some of the medial part with the proximoverventral surface of the third distal tarsal. Well defined articular areas for the distal tarsals have not been identified on the astragali of other early archosaurs, and it is possible that these are only discernible in BMNH R3592 as a

result of the aforementioned compaction of the specimen. The whole of the undivided distal surface of the astragalus of other early archosaurs was referred to as the "distal roller" by Cruickshank (1979), and as the "articular surface for metatarsals" by Sereno (1991).

Surrounded by the dorsal edge of the articular surfaces described above, is a strongly defined depression surfaced with compacta. This is oval-shaped, contains a

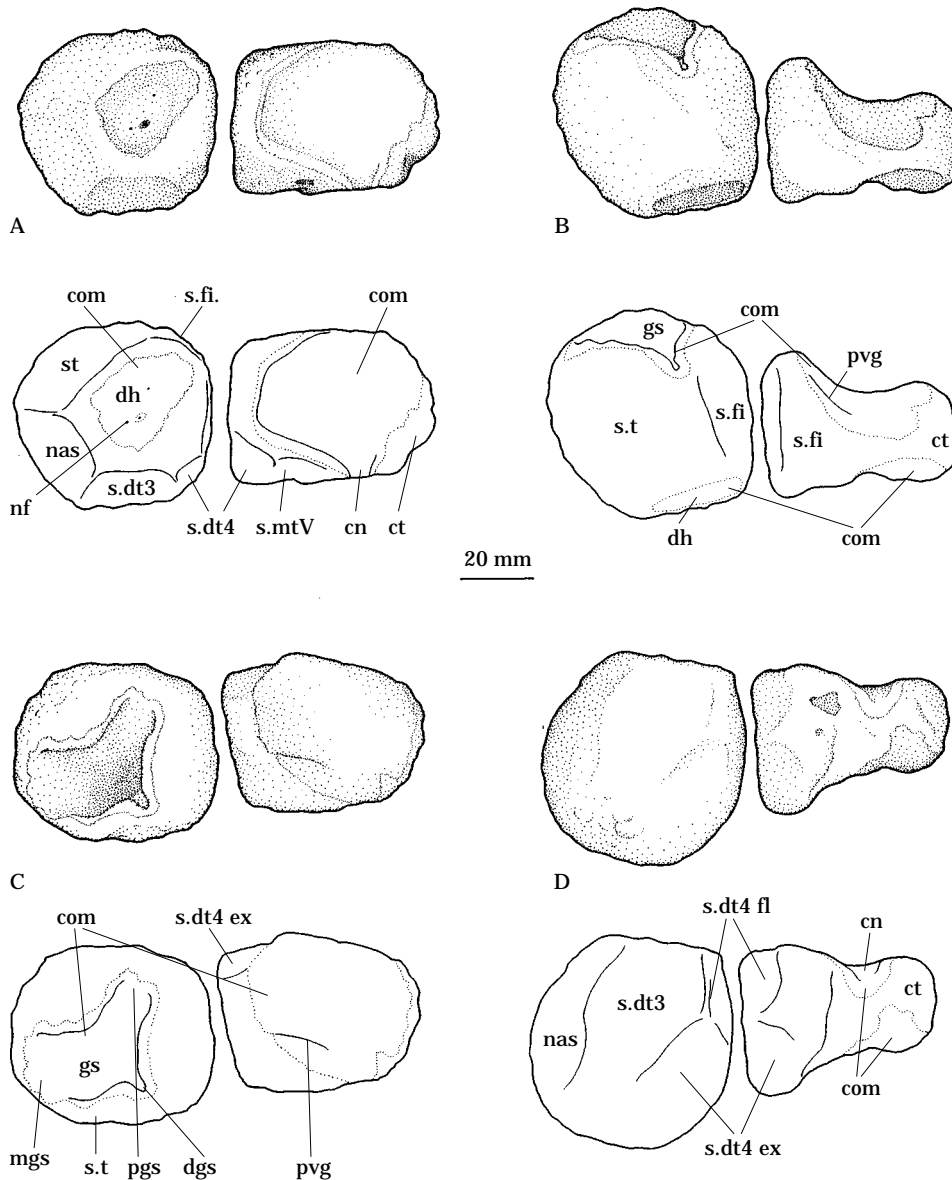


Figure 3. BMNH R3592, left astragalus and calcaneum of *Erythrosuchus africanus*. A, dorsal; B, proximal; C, ventral; D, distal views. dgs = distolateral branch of ventral groove system; mgs = medial branch; pgs = proximolateral branch; nas = non-articular surface.

number of nutrient foramina, and is clearly homologous with the 'anterior hollow' described for many archosaur taxa. It is here referred to as the dorsal hollow.

The ventral surface of the astragalus shows the other feature that is surfaced with compacta — a triangular depression harbouring a broad and approximately Y-shaped groove. This depression has been thought to represent all or part of the ventral ('posterior' of other authors) groove system (Cruickshank, 1978), although the homology and terminology of this feature have remained confused. In his description of the astragalus of *Proterosuchus*, Cruickshank (1979) described a Y-shaped set of grooves on the ventral surface. These consist of a broad shallow stalk, medially, and two lateral branches — a more proximal one confluent with the non-articular notch, and a more distal one leading to the perforating foramen. Cruickshank (1979) homologized these grooves with similar features present on the astragali of, among others, *Euparkeria*, *Chanaresuchus*, *Riojasuchus*, and *Crocodylus*. There is no non-articular notch in, for example, *Crocodylus* and this led Hecht & Tarsitano (1984) to reterm the three branches in this taxon as the astragalar fossa (notch branch), articulating channel branch (perforating foramen branch) and lesser groove (medial stalk). Other authors (e.g. Sereno, 1991) have used the term 'posterior groove' without explicit definition, but apparently equating it chiefly with the channel leading to the perforating foramen.

Cruickshank (1978, 1979) also equated the Y-shaped depression on the ventral surface of the astragalus of *Erythrosuchus* with the groove system of *Proterosuchus*. Referring to the distolateral branch, Cruickshank (1978) comments that "an indication of the astragalar component of the perforating foramen can be seen on the lateral surface" (see also Cruickshank's plate 3). As with the *Proterosuchus* grooves, the medial branch is the broadest and most shallow of the three, and the proximolateral branch does lie between the facets for the tibia and fibula, although without forming a full non-articular notch. I would therefore prefer to refer to the distolateral branch as the 'perforating foramen component of the astragalar groove system'. However, Cruickshank's (1978) interpretation of the homology of the groove and its various branches is supported here, although further investigation of this feature in other taxa is now desirable.

In that the distolateral branch of the groove does not lead to a perforating foramen, the proximolateral branch does not form a full non-articulating notch, and the medial branch is relatively short, this part of the astragalus of *Erythrosuchus* and *Euparkeria* are very similar. As a final note, a conspicuously deep fossa at the nexus of these grooves in *Erythrosuchus* is apparently absent in other archosauromorphs.

There is no intrinsic evidence that the astragalus of *Erythrosuchus* corresponds "to the lateral portion only of the proterosuchian equivalent" as concluded by Cruickshank (1979).

Calcaneum (Fig. 3)

The calcaneum is essentially dorsoventrally compressed, but with slightly expanded medial and lateral ends, and it has a laterally directed tuber. As with the astragalus, much of the surface of the calcaneum is not finished with compacta. The broad medial surface articulates with the astragalus. As with the corresponding area on the astragalus, this surface is rather flat and featureless. The medial end of the proximal surface bears a rounded, triangular shaped facet for the fibula. Distally there are smaller areas for articulation with the proximolateral surface of the fourth distal tarsal, and a larger, broad and roughened facet, which articulates with the

ventral part of the proximal surface of the fifth metatarsal when the ankle is flexed. The ventrally expanded part of the medial end of the calcaneum of *Erythrosuchus* is as deep distally as it is proximally. The proximal part of this expansion is not therefore drawn into a conical process as in the “posterior pyramid” or “pyramidal process” described for the calcanea of *Proterosuchus*, *Euparkeria*, and *Chanaresuchus* by Cruickshank (1979).

The dorsal face of the calcaneum is approximately rectangular in shape, shallowly concave, and largely surfaced with compacta. Distally, on this dorsal face, there is well defined notch which is clearly homologous with that seen in the same position on the calcaneum of *Proterosuchus* (Cruickshank, 1979). The notch lies between the dorsolateral extremity of the fifth metatarsal facet and the base of the calcaneal tuber.

Much of the ventral surface of the calcaneum is surfaced with compacta and near the proximal limit of this area, but still below the fibular facet, is a step-like groove. I refer to this here as the proximoventral groove, and have detected probable homologues in other erythrosuchids (see below), and possibly in *Proterosuchus* (pers. obs. of the well preserved calcaneum of IVPP 900002 found a weakly defined groove adjacent to the ventrodistal margin of the fibular facet). This feature might also be equivalent to the groove on the proximal surface of the calcaneum of *Euparkeria* (Cruickshank, 1979, unlabelled in Sereno’s 1991 figure 4G), and was possibly associated with soft tissue binding the fibula to the calcaneum. The calcaneal tuber is short, laterally directed, slightly ventrally expanded, and has a lateral face that lacks compacta.

The descriptions presented above contradict the idea (Parrish 1992) that the astragalus and calcaneum of BMNH R3592 and BPI 2096 bear little resemblance to the tarsi of other early archosaurs.

Fourth distal tarsal (Fig. 4)

The fourth distal tarsal is a short, triangular prism with a prominent ventral peg. There are three main articular surfaces. There is a small laterodistal surface for contact with the medial part of the proximal surface of the fifth metatarsal. Only a small dorsoproximal part of the broad medial surface forms an area for articulation with the third distal tarsal. The last major surface is composed of two parts; proximolaterally for the calcaneum and proximoventrally for the stragalus. The proximal surface of the peg is mostly a surface for contact with the astragalus, but the peg also extends ventrally between the astragalus and calcaneum. Ventrodistally, on the undersurface of the peg, the fourth distal tarsal is concave. This is the only well ossified surface of the element and it bears a number of nutrient foramina. The dorsal face of the element takes the form of an irregularly rounded area for articulation with the proximal surface of the fourth metatarsal.

Third distal tarsal

The third distal tarsal is the most featureless of all the tarsals and is considerably smaller than the fourth distal tarsal — approximately one third of the size. It is a roughened and ovoid bone lacking compacta on all surfaces. It has flattened proximal surface which articulates with the distal part of the astragalus when the ankle is flexed. There is a smaller convex surface, ventrally, which articulates with the astragalus in the extended ankle. Laterally there is a small area for contact with

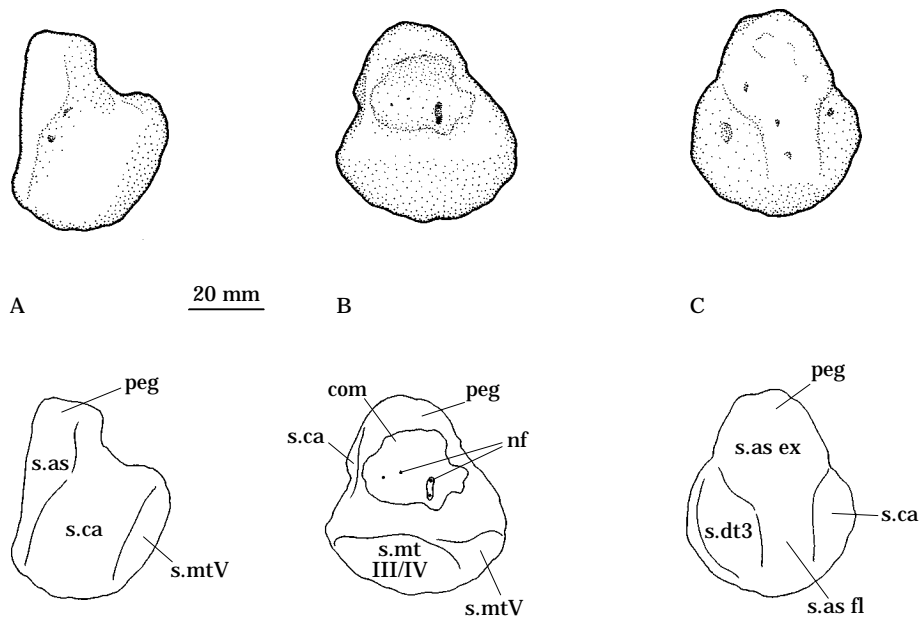


Figure 4. BMNH R3592, left fourth distal tarsal of *Erythrosuchus africanus*. A, proximomedial; B, ventrodistal; C, proximolateral views. ex, when the ankle is extended; fl, when the ankle is flexed; mt, metatarsal; peg, peg on distal tarsal 4.

the fourth distal tarsal. Dorsally the third distal tarsal contacted the proximal surfaces of the second and third metatarsals.

BPI 2096

BPI 2096 consists of the distal ends of the right tibia and fibula and the right pes (astragalus, calcaneum, two distal tarsals, and the nearly complete last four digits). It was discovered at the same locality as that yielding the ankle of BMNH R3592 (DMSW R525) and is of the same size as that specimen. It is thought (Cruickshank, pers. comm.) that the two specimens possibly represent the same individual, and the lack of any repetition in the preserved fragments of the right crus in these two specimens is consistent with this hypothesis. The specimen was described in detail by Cruickshank (1978) and a new reconstruction was presented. The specimen was mechanically prepared (Cruickshank, 1978) and photographic records were kept during this process.

This specimen supports and strengthens the conclusion that both it and 'DMSW R525' represent the ankles of *Erythrosuchus*. The distal ends of the tibia and fibula are extremely similar in form and preservation to those of DMSW R525. The photographic record of BPI 2096 during preparation demonstrates that these distal crus elements clearly belong with the ankle and foot elements. Any conclusions on possible postmortem displacement in this specimen obviously rely on the assumption that the tarsal elements of DMSW R525 are not significantly displaced.

The earliest stage of preparation that was recorded photographically is shown diagrammatically in Figure 5. At this stage there were four main pieces. The first is the distal end of the tibia, the astragalus, and third distal tarsal. The second comprises the fifth digit, fourth distal tarsal, and the calcaneum. The third piece consists of the

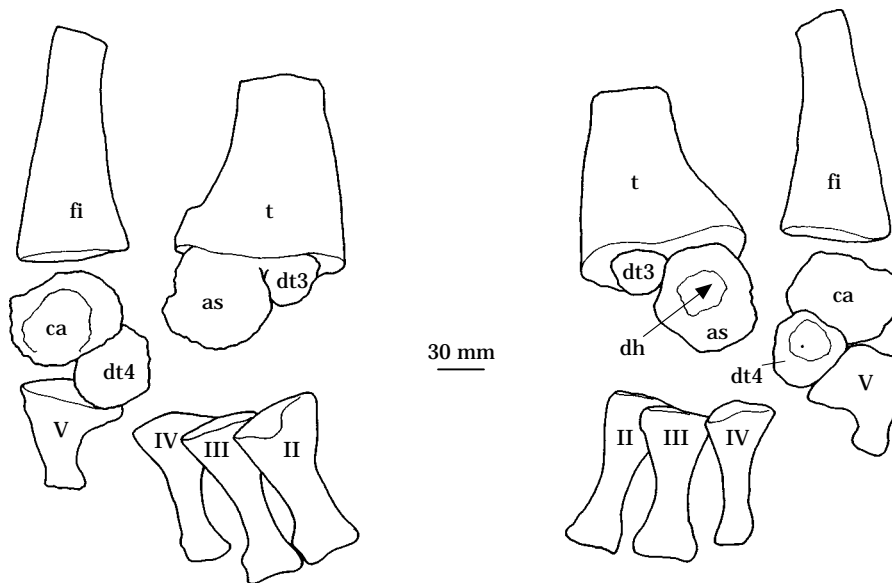


Figure 5. BPI 2096, right tarsus of *Erythrosuchus africanus* during preparation. A, dorsal; B, ventral views.

remaining preserved digits, and the fourth piece is the distal end of the fibula. Cruickshank (1978) reported that the tarsals had been “considerably disturbed during preservation”. The digits are preserved in a flexed state but remain in natural articulation. The calcaneum, metatarsal V and fourth distal tarsal do not appear to be dislocated. The astragalus, though preserved still contacting the distal surface of the tibia, has been rotated through 180° during preservation, with the distinctive dorsal hollow visible only in a ventral view of the distal end of the tibia. Also, the third distal tarsal is in contact with the distal surface of the tibia, mimicking a tibiale. There is no recorded information on the relative position of the four pieces of the specimens as listed above.

The small element in contact with the astragalus and distal surface of the tibia could alternatively be interpreted as a centrale — partly overcoming the problem of the size disparity between crural articular facets and those on the proximal tarsals noted by Parrish (1992). However, this would presuppose that the size disparity is a problem, and furthermore the evidence does not support it. There is no indication of preservational disturbance in the ankle of BMNH R3592, in which a centrale is not preserved. The rotation of the astragalus through 180° and loss of the first metatarsal and digit, provides direct evidence of the disturbance of the ankle elements of BPI 2096 during preservation. Additionally, the small element in question is very similar in size and shape to the third distal tarsal of BMNH R3592. Finally, identification of this element as a centrale does not really solve the ‘problem’ of tibia-proximal tarsal size disparity, because it and the astragalus together would still not match the much greater area of the distal surface of the tibia. A consideration of the available evidence leads me to identify this small tarsal element as a displaced third distal tarsal, rather than a centrale sharing support of the tibia as is seen in *Proterosuchus* (see below).

Because BMNH R3592 was acid prepared and apparently not disturbed during preservation, it remains the best specimen from which to describe the elements, and no more information can be added to the description of the tarsals given above. The metatarsals and digits are much more complete than BMNH R3592 and descriptions have been presented by Cruickshank (1978).

Reconstruction

A diagram of a reconstruction of the strongly extended ankle, based on the evidence presented above (Fig. 6), shows approximate spatial relations and articulations of the elements in one position only. This differs from previous reconstructions (Hughes, 1963; Cruickshank, 1978) in a number of important features. There is not a large gap between astragalus and calcaneum (although these elements may not have been in direct contact), the fibula articulates with the astragalus as well as the calcaneum, and the calcaneal tuber protrudes laterally beyond the fifth metatarsal.

The lack of any rotary joint between astragalus and calcaneum, and the plesiomorphic structure of the plate-like calcaneum with a laterally directed tuber, indicates that the ankle joint was mesotarsal. The astragalus and calcaneum would have been firmly attached to the crus and the main movement was between proximal and distal tarsals, but also between the tarsals and the closely overlapping proximal ends of the metatarsals.

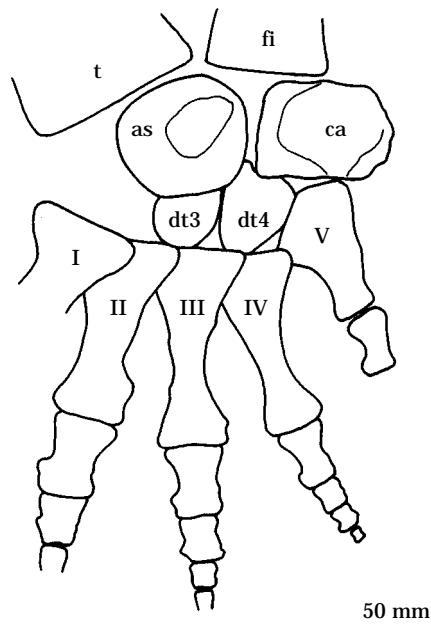


Figure 6. *Erythrosuchus africanus*, reconstruction of fully extended left pes in dorsal view.

The disparity in size between the distal surface of the tibia and the astragalar facet for the tibia, along with the generally poor ossification of the *Erythrosuchus* tarsus, led Brinkman (1981) to conclude that this form was aquatically adapted. The correlation between reduction in ossification and an aquatic existence has frequently been cited (Osburn, 1906; Williston, 1925; Romer, 1956). Coombs (1975, 1978) has shown, however, that a short metatarsus and reduced ossification can also be interpreted as graviportal adaptations (see also Thulborn, 1980) and, furthermore, that in deducing the habits of extinct forms, a consideration of the whole skeleton is often necessary.

Summary

This reassessment of the *Erythrosuchus* ankle highlights the importance of a number of factors in such a study

- (1) The use of articulated material, in providing direct evidence of the number and position of elements.
- (2) Recording the position of articulated elements during preparation/excavation.
- (3) Resisting the rejection of some material because at first glance the morphology does not fit accepted paradigms.

Vjushkovia triplicostata Huene, 1960

Vjushkovia triplicostata is a Russian erythrosuchid from the Yarenga Formation of the Southern Urals. The only description of *V. triplicostata* postcranial material was given in the type description by Huene (1960), but this did not include any description of tarsal material. Parrish (1992: 100) reported that the tarsus is "very similar to that of *Proterosuchus*, with a pair of concave/convex articulations between proximal tarsals, separated by a perforating canal and a broad, laterally directed calcaneal tuber". Parrish also reports (1993: 307) that the astragalar surface for articulation with the tibia is a "simply concave facet that faces proximomedially".

Following a re-examination of this material, it is clear that the two elements presumably taken by Parrish (1992) to be the astragalus and calcaneum, are in fact a complete right calcaneum (un-numbered), and an incomplete left calcaneum (PIAS 951/39) with the distal third eroded. Although the calcaneum of PIAS 951/39 is broken, the two elements correspond very closely in every possible comparative detail — size, shape, distribution of surfaces finished with compacta, position and form of the articular surfaces and features identified as the notch and proximoventral groove (Fig. 7). Despite their similar size, there is no information to confirm that they belong to the same individual. The metatarsals and phalanges of PIAS 951/39 include some left, but mostly right sided elements from apparently more than one individual, but further investigation is required to clarify how these elements relate to each other as well as to the rest of the extensive *V. triplicostata* postcranial material. No astragalus can be identified among any of the postcranial specimens.

Calcaneum (Fig. 7)

Apart from the obvious difference in size, the calcaneum of *V. triplicostata* is virtually identical to that of *Erythrosuchus* as described above. The element has the same proportions, and also only the dorsal and ventral faces are finished with

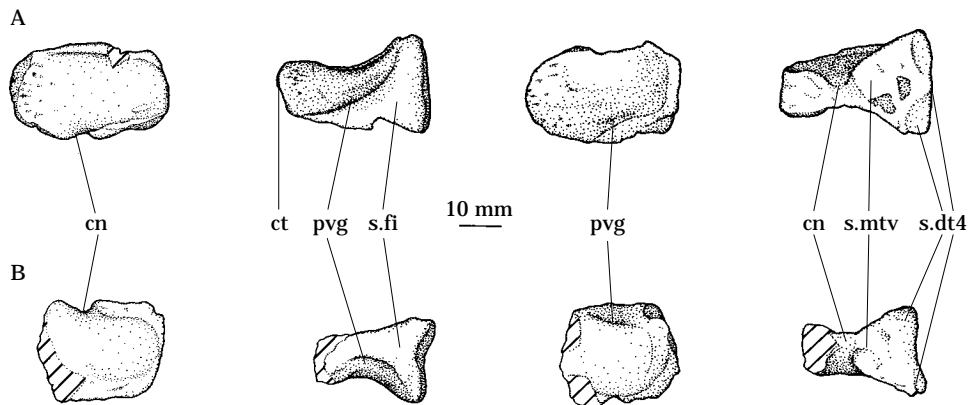


Figure 7. A, complete right (PIAS un-numbered) and B, incomplete left (PIAS 951/39) calcanea of *Vjushkovia triplicostata* in (from left to right) dorsal, proximal, ventral, and distal views. For ease of comparison, the incomplete specimen is rotated through 180°, i.e. its proximal edge is towards the bottom of the figure.

compacta. The surfaces for articulation with the astragalus, fibula, fourth distal tarsal (and fifth metatarsal?) all lack compacta, and are of the same form and in the same position as those on the calcaneum of *Erythrosuchus*. There is a clear notch on the dorsodistal edge and just below the facet for the fibula on the ventral surface is the proximoventral groove also described in *Erythrosuchus*. The medial end of the distal surface is better preserved in the right example, and it bears a very strong resemblance to that of *Erythrosuchus* in terms of the articular surfaces for the fourth distal tarsal and fifth metatarsal. The calcaneal tuber is again slightly expanded, laterally projecting, and the distal surface lacks compacta.

The articular surface for the astragalus is slightly concave in PIAS 951/39 and essentially flat in the unnumbered example. The less than ideal preservation of the PIAS 951/39 calcaneum, combined with a slight distal-proximal compression of the medial end of the unnumbered calcaneum, means that it would be unwise to attempt to interpret any medial surface detail. However, there is nothing to suggest that this surface was any more complex than that described for *Erythrosuchus*. There is no evidence for the paired concave/convex articulation with the astragalus described by Parrish (1992), and an ossified perforating canal was clearly absent. The extremely close similarity of these elements to the calcaneum described for *Erythrosuchus* provides reinforcement to the referral of BMNH R3592 (DMSW R525) and BPI 2096 to *Erythrosuchus*.

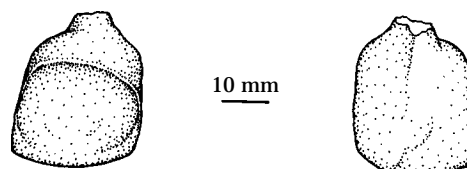


Figure 8. PIAS 951/39, possible fourth distal of *Vjushkovia triplicostata* in two views.

Distal tarsals

While no distal tarsals have been indisputably identified, there is, among the postcranial material, a small element (PIAS 951/39) bearing a superficial resemblance to the fourth distal tarsal of *Erythrosuchus*. This is shown in Fig. 8 and has a flattened quadrangular region, concave on one side, with an opposite surface that is roof-like in appearance. Towards one end of this latter surface is a slightly eroded conical projection. If this is the fourth distal tarsal, then the surface with the concavity might correspond to the slightly convex facet for the proximal surface of the fifth metatarsal on the fourth distal tarsal of *Erythrosuchus*. The roof-like surface and projection would then correspond to the facets for the calcaneum, astragalus, third distal tarsal and the posteroventral peg. Major differences to the fourth distal tarsal of *Erythrosuchus* are seen in the concavity, the quadrangular shape of the fifth metatarsal facet, the lack of a strongly concave and ossified area below the base of the peg and, finally, in the much smaller proportions relative to the calcaneum (always assuming the 'fourth distal tarsal' belongs to the same individual as either of the calcanea mentioned above).

Shansisuchus shansisuchus Young, 1964

Shansisuchus shansisuchus is an erythrosuchid from the Upper Ehrmayng Formation of China. Young (1964) described and figured some elements of the pes in his monograph. While this has remained the only descriptive account, there have been many interpretations based only on the information presented by Young (1964), such as Cruickshank (1978, 1979) and Thulborn (1980). Sereno & Arcucci (1990) and Sereno (1991) used the information presented by Young (1964) to represent the tarsal morphology of the Erythrosuchidae as a whole. Parrish (1992), though unable to study the material, believed the astragalus and calcaneum of *Shansisuchus* and the calcaneum of *Fenhosuchus* (there is some doubt about the taxonomic distinction of the two genera, and Parrish implies that at least the calcaneum of *Fenhosuchus* belongs an erythrosuchid or some other basal archosaur) to be morphologically similar to those of *Proterosuchus* and *V. triplicostata* — although the astragalus of *V. triplicostata* has been shown above to be unknown.

Most of the material described by Young (1964) was recently made available for this study. There are a number of problems associated with study of the material. None of the finds was articulated or even associated, and there does not appear to be any detailed record of them. The specimens are largely un-numbered, but mostly belong to field collection no. 56173. Young (1964) described four taxa from this material but there does not appear to be any strong evidence for the presence of two of these, *Shansisuchus heiyuekouensis* and *Fenhosuchus*. The final taxon, *Wangisuchus*, includes small and less common material, partly characterized by a calcaneum indicative of a rotary calcaneum-astragalus joint as in modern crocodiles (pers. obs., Parrish 1993).

The large size and number of the elements considered here, as well as the general similarity to the tarsi of early archosauromorphs, has led to the presumption that the material described below does belong to *S. shansisuchus*, the holotype of which is the skull roof IVPP 2503.

Astragalus (Fig. 9A–C)

The material includes three examples of an astragalus of a type which is presumed to represent *Shansisuchus*. There are the specimens shown by Young (1964: fig. 34A, B, = Figs 9A and B here) and one which was unfigured (Fig. 9C here). Those elements described by Young as the astragali of *Fenhosuchus* and *Wangisuchus* (Young, 1964; Figs 48G and 34D respectively) could not be located at the time of this study. The three specimens show a variety of states of preservation. Two of the similarly sized specimens are from the same side (Young, 1964: fig. 34A, B). One of these (Young, 1964: fig. 34B) is incomplete with its broad end concave from erosion. The third example is from the opposite side. It is less well preserved and appears crushed when compared to the other two.

The most completely preserved and apparently least crushed example is here used for description (Fig. 9A). There are problems in describing the morphology of this astragalus because it is disarticulated and very different from the only other known erythrosuchid astragalus. It is an elongate, flattened bone, with one end broadened and the other end narrower but taller. One of the two broad surfaces shows one oblique and one transverse groove leading to a small depression which divides the surface into three areas. The opposite surface shows a triangular depression at the broad end, which is flanked on either side by a smooth, convex area and a scoop-like concavity.

Young (1964) orientated the astragalus with the 'oblique ridge' side uppermost and the broad end lateral. This made the examples in his figure 34A and B both from the left side and led him to describe a convex lateral end which would articulate with a concave calcaneal surface. This interpretation is not accepted here. While the two good examples are accepted as left astragali, the conclusion here is that the broad end is medial, the oblique ridge remains proximal but the dorsal edge is now straight in proximal view. This interpretation makes the overall form of the astragalus more similar to that seen in many archosaurs (e.g. *Proterosuchus*, *Euparkeria*, *Crocodylus*).

The proximal surface as described above is divided into three areas. The largest of these is the medially located and broadly triangular facet for the tibia. Laterally this is bordered by the prominent oblique ridge. Centrally there is a concavity that is U-shaped in cross section. This broad groove is here interpreted as being a possible homologue of the non-articular notch seen between the tibia and fibula facets in *Proterosuchus* (Serenó, 1991) and other early archosauromorph taxa, but absent in *Erythrosuchus*. This notch is laterally bordered by a transverse ridge and lateral to this is the astragalar component of the facet for the fibula. It is uncertain how far laterally this surface extended because it does not seem to be particularly well separated from the facet for the calcaneum. The facet for the calcaneum is slightly convex but simple, with no indication of a perforating canal, nor of the presence of discrete proximal and distal facet components.

The non-articular notch continues in a ventral and medial direction onto the ventral surface. Laterally and just below the ventrodiscal edge of the notch is a small, but well-defined concavity which seems to have an open mediolateral end. This feature, much less obvious in the less well preserved examples, is tentatively interpreted as a possible part of the ventral groove system. Ventrodistally, beneath this concavity, is the scoop-like concavity which communicates with the medially positioned, roughened triangular depression. The most strongly defined border to this depression is at its dorsal margin where there is a clear groove. The whole of the dorsodistal edge of the astragalus forms a regular hemicylindrical facet, the 'distal

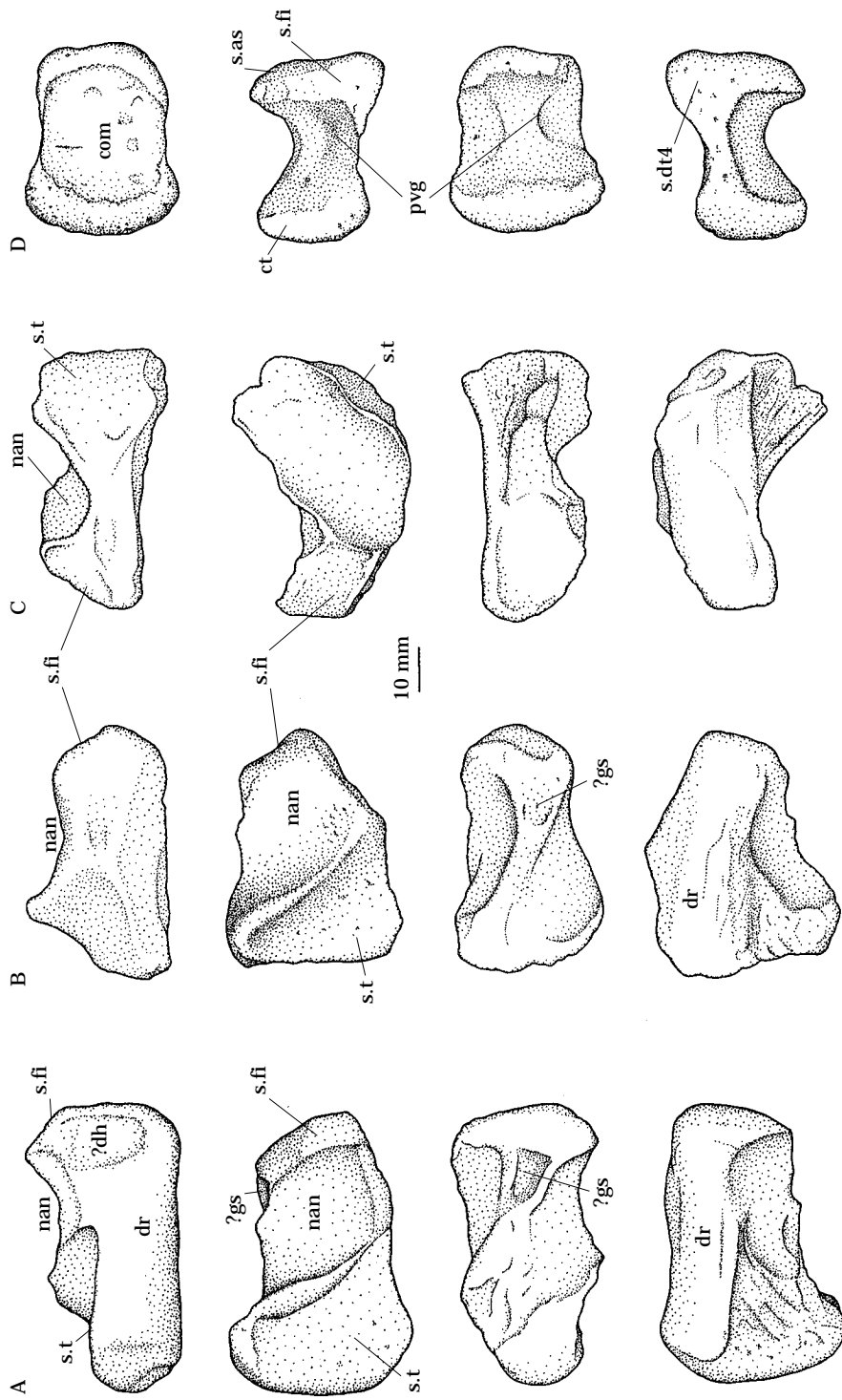


Figure 9. IVPP field collection number 56173, *Shansisuchus shansisuchus*. Left (A, B) and right (C) astragali and right calcaneum (D) in (from top to bottom) dorsal, proximal, ventral, and distal views. dr = distal roller; ?gs = possible groove system of astragalus.

roller', for articulation with the third distal tarsal and either metatarsal I or, if present, the first/second distal tarsals. Laterodistally this facet curves around to the surface for articulation with the calcaneum, and the resulting rounded corner would probably have articulated with the fourth distal tarsal.

In dorsal view, the astragalus bears a superficial resemblance to that of *Chanaresuchus* (Cruickshank, 1979; Sereno, 1991). The distal edge is relatively straight and, proximally, the medial border of the fibula facet is defined by a tall ridge. However there are obvious differences in the presence of a non-articular notch, and the absence of a well defined dorsal hollow. The latter is a consistent and obvious feature of the astragalus of many archosauromorph taxa, including *Erythrosuchus*. The shallow concavity at the lateral end of the dorsal face of the best preserved example may be a weakly formed equivalent, but it is hardly apparent in the other two examples. At a first glance, the only alternative candidate for the dorsal hollow would be the incised, narrow depression described above as a possible part of the ventral groove system. However, careful consideration of all features shows that this interpretation is not the most parsimonious when compared to the astragalar morphology of other, related taxa. The interpretations above, though problematic, are currently the best available — fitting in terms of the overall form and in the position of the oblique ridge, non-articular notch, and distal roller. Possible components of the ventral groove system of the astragalus described above, however, bear little resemblance to those in *Erythrosuchus*, *Proterosuchus*, and *Euparkeria*. The non-articular notch apart, it is not possible to identify structures equivalent to the small ventrolateral concavity, triangular distal depression, and scoop-like concavity in these other taxa. Finally, it should be borne in mind that there is no guarantee that the element described above is the astragalus of *Shansisuchus*.

Calcaneum (Fig. 9D)

Young (1964) mentioned thirteen calcanea as being present among the material assigned to *Shansisuchus*. He figured five in his figure 35A–E and two calcanea referred to *Fenhosuchus* (mentioned by Parrish, 1992) are shown in figures 35 F and 34 C. Of the specimens referred to *Fenhosuchus*, Young's figure 34 C, is inseparable from many of the specimens referred to *Shansisuchus*. Furthermore, the specimen figured as a possible calcaneum of *Fenhosuchus* (Young's figure 35 F), is in fact a disarticulated basioccipital (the rounded fibula facet of Young being the basioccipital component of the occipital condyle), probably also belonging to *Shansisuchus*. The best preserved example (Young, 1964, fig. 35 A) is figured here (Fig. 9D) and provides the basis of the description presented below.

In overall form, the calcaneum of *Shansisuchus* bears a very strong resemblance to the calcanea of *Erythrosuchus* and *V. triplicostata* described above (and this possibly casts doubt on the 'astragalus' being that of *Shansisuchus*). The calcaneum is a dorsoventrally compressed element, with only the dorsal and ventral surfaces finished with compacta. In dorsal view, the notch on the dorsodistal edge can be clearly identified. A small triangular facet for the fibula is located at the medial end of the proximal surface. A concavity distal and ventral to the facet for the fibula is interpreted as a homologue of the similar, but slightly more proximally positioned and smaller 'proximoventral groove' described for *Erythrosuchus* and *V. triplicostata*. A broad and roughened facet at the medial end of the distal surface is for articulation with the fourth distal tarsal and possibly the fifth metatarsal. Medially the surface for articulation with the astragalus is like that of *Erythrosuchus* and *V. triplicostata*, in that

it is a broad, but essentially flat and featureless surface — not concave as stated by Young (1964). As with the calcanea of *Erythrosuchus* and *V. triplicostata*, there is no indication of a perforating canal. The tuber is clearly a laterally projecting feature.

The main differences between the calcaneum of *Shansisuchus* and that of the two taxa described above lie in the proportions of the various parts of the element. In dorsal and ventral views, the greatest proximodistal length of the lateral end of the calcaneum of *Shansisuchus* is greater than that of the medial end, whereas they are subequal in *Erythrosuchus* and *V. triplicostata*. In proximal or distal view there is a stronger 'waist' and the free end of the tuber is more strongly expanded. Obviously these three differences are intimately connected.

Distal tarsals

Young (1964) briefly described, but did not figure, thirteen elements identified as the distal tarsals of *Shansisuchus shansisuchus*. An examination of these elements shows them to be essentially featureless spheres of bone. Until articulated specimens are found, their referral to *Shansisuchus*, let alone their identification as distal tarsals, must remain in doubt. Even if Young is correct in his identification, the fact that they are disarticulated and essentially featureless means that they currently provide no information about the number or form of the distal tarsals in *Shansisuchus*.

Digits

There is a large amount of disarticulated material which is thought to represent the digits of the pes of *Shansisuchus*. As Young (1964: 143) himself points out, his reconstructions of the digits are "extremely conjectural". Despite this, reading of Young's text has obviously not always accompanied the use of his figures as Cruickshank (1978: 175) and Sereno & Arcucci (1990: 26) utilized information from Young's reconstruction in inferring phylogenetic relationships. No conclusions can currently be drawn on the phalangeal 'formula' or relative sizes of the digits.

Concluding remarks on the erythrosuchid pes

(1) BMNH R3592 (DMSW R525) and BPI 2096 possibly come from the same animal and, contrary to recently published views, both represent the pes of *Erythrosuchus*.

(2) The erythrosuchid calcaneum exhibits a consistently similar morphology in all three taxa for which this element is known — plate-like form, a lateral and slightly expanded tuber, poorly finished surface except on the dorsal and ventral faces, dorsodistal notch, proximoventral groove, no perforating canal, simple and essentially flat surface for articulation with astragalus.

(3) The astragalus of *Vjushkovia triplicostata* is unknown. The astragalus of *Erythrosuchus* is characterized by being sub-spherical, having a surface generally lacking compacta, being much smaller than the distal end of the tibia, possessing a ventral groove system equivalent to that of *Proterosuchus* and *Euparkeria*, and in bearing a number of contiguous, featureless, articular surfaces for the fibula, tibia, calcaneum, and distal tarsals. The astragalus of *Shansisuchus*, if correctly identified, is very different in being elongated, lacking a well defined dorsal hollow, retaining a non-articular notch, and in having an apparently incomparable groove system.

(4) An articulated pes is known only for *Erythrosuchus*. There are two elements in the proximal row; two in the distal — distal tarsals three and four; a hooked fifth metatarsal; digit three is longer than four. The phalangeal formula is ?, 3, 4, ?5, (1).

(5) All known erythrosuchid tarsi clearly possessed a functionally mesotarsal joint and did not have a crurotarsal joint.

Euparkeria Broom, 1913

During the course of this study, the tarsus of *Euparkeria* was briefly examined. The examination of specimens GPIT 1681/1, SAM 6049, SAM 5867 and SAM un-numbered (Ewer, 1965: fig. 30), has warranted a number of comments on the conclusions made by previous studies.

(1) The non-articular notch on the proximoventral surface of the astragalus does not extend far enough forward to lie between the facets for the tibia and fibula (pers. obs.; Sereno, pers. comm.). This is contrary to Sereno & Arcucci (1990) and Sereno (1991), who list absence of non-articular notch as a synapomorphy of Proterochampsidae + crown group archosaurs.

(2) Sereno (1991) describes and figures a division of the lateral surface of the astragalus into discrete dorsal and ventral (i.e. proximal and distal) articular facets for the calcaneum. There is no indication of this on the specimens examined in this study.

(3) Parrish (1993: 291) is mistaken in his criticism of Sereno's (1991) observation of the distribution of contiguous calcaneal facets for fibula and distal tarsal four. These facets are clearly separated by a non-articulating surface in *Euparkeria* (pers. obs., Cruickshank 1979: fig. 7c, Sereno, 1991: fig. 4).

(4) There is a distinctive depression at the medial end of the tibial facet of the astragalus that is figured, but neither labelled nor described by Cruickshank (1979: fig. 6c), and completely omitted by Sereno & Arcucci (1990) and Sereno (1991), although all three of these studies figured the same specimen (UMCZ T692 — not examined during this study). It is uncertain whether this depression, well defined in SAM 6049, is at all equivalent to one of Parrish's (1993) two synapomorphies of Aetosauria + Rauisuchia, defined as a "prominent posteromedial excavation that forms a posteriorly directed concavity" on the tibial facet of the astragalus. In view of the fact that Parrish (1993: 299) also identifies this feature in ornithosuchids, and scores it as present in *Pseudhesperosuchus* (1993: table 2), this character clearly requires further investigation.

(5) Ewer's discussion of postmortem changes occurring in the tarsus of *Euparkeria*, and her subsequent functional conclusions warrant further attention. Specimen SAM 6049 is fully prepared so that any postmortem movement cannot be assessed here. Ewer's observations of the un-numbered SAM specimen figured by Broom (1913) are incorrect. The astragalar facet for the calcaneum identified by Ewer is, in fact, the astragalar facet for the fibula. Ewer's astragalar facet for the fourth distal tarsal, and marked on SAM 6049 with a dot in her figure 32, is the facet for the calcaneum. This correction renders the tarsus of *Euparkeria* much more similar in form to that of, for example, *Proterosuchus*, with the astragalar facets for the fibula and tibia approximately at a right angle to each other. Thus Broom's specimen, at least, does not support Ewer's conclusion (1965: 426) that disturbance of the tarsal elements

after death suggests that the calcaneum is functionally associated with the foot. It can only be concluded that the astragalus was well bound to the tibia. These conclusions of Ewer were perpetuated in the partly crocodyloid 'duplex' ankle type of Thulborn (1980). Reliance on postmortem movement aside, the morphological evidence strongly suggests that, as in *Erythrosuchus*, the ankle joint was mesotarsal (see also the discussion of calcaneal tuber alignment given below).

Proterosuchus Broom, 1903

Interpretations of the tarsus of *Proterosuchus* (= *Chasmatosaurus*) have had a long and interesting history in the literature. Since originally being described by Broom (1932), the proximal row has created controversy in terms of the number of elements articulating with the crus and their terminology. This is shown in Table 1.

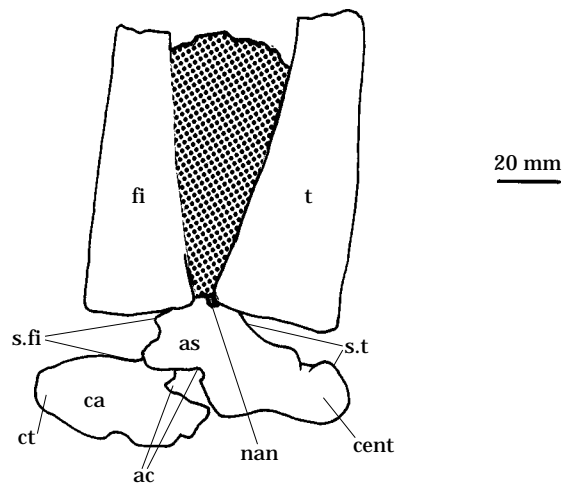


Figure 10. NMC 3016, distal right crus and proximal tarsals of *Proterosuchus* in dorsal view. ac = astragalocalcaneal canal; cent = centrale.

TABLE 1. Table showing variation in the literature on the observation of the number and terminology of the elements in the proximal row of the tarsus of *Proterosuchus*. Abbreviations are as follows: Ast=astragalus; Calc=calcaneum; Int=intermedium; Tib=tibiale; Cent=centrale

Author	Prox row	Terminology used		
		Ast	Calc	Medial element
Broom, 1932	3	Int	Calc	Tib
Schaeffer, 1941	2	Ast	Calc	Cent
Hughes, 1963	2	Ast	Calc	Cent
Romer, 1956	3	Ast	Calc	Cent
Cruickshank, 1972	3	Int	Calc	Ast
Carroll, 1976	2	Ast	Calc	Cent
Cruickshank, 1979	?	Ast	Calc	Cent

Sereno & Arcucci (1990), Sereno (1991), and Parrish (1993) all addressed the astragalus and calcaneum out of context of the whole ankle. A re-examination of specimens of *Proterosuchus* (particularly NM QR1484, shown in Fig. 10) has shown that the distal surface of the tibia clearly articulates with both the astragalus and the medial element (and that this medial element articulates firmly with the astragalus). Based on *Captorhinus*, Peabody (1951) provided evidence for the presence of a tibiale in primitive reptiles. This observation was supported by Hughes (1968) in a description of rhynchosaur tarsi, in which three proximal elements are found. Cruickshank (1972, 1979) claimed to be following Hughes' conclusions but, by misinterpreting the medial element as an astragalus and not a tibiale, he confused the terminology further. Carroll (1976a) refused to accept the conclusions of Hughes (1968), but his argument was not entirely convincing, and he also reconstructed the tarsus of *Proterosuchus* with only two elements articulating with the crus. Hughes' arguments were correct, based on the results presented by Peabody (1951) and a belief that *Captorhinus* exhibited the primitive reptile condition. Recently, however, Rieppel (1993) has demonstrated that there is no evidence for the presence of a true tibiale in the tarsus of any extant reptile, and that Peabody (1951) was incorrect in his observation of a tripartite astragalus in *Captorhinus*. Furthermore, Rieppel believes that even extinct reptiles did not possess a true tibiale and that the ossification of the astragalus from a single centre is an amniote synapomorphy. The work of Rieppel, combined with a knowledge of the situation in immediate neodiapsid outgroup taxa (where a single centrale is present medially and the proximal row consists of only two elements), suggests that the proximomedial element articulating with the tibia, in *Proterosuchus*, should be currently termed a centrale. This is discussed in further detail below.

Prolacertiformes

Gow (1975) described the tarsus of *Prolacerta* as consisting of a proximal row of three elements articulating with the crus and three distal tarsals. His reconstruction, however, does not clearly show the tibia contacting the centrale. A re-examination of this material (BPI 2675) supports Gow's description. A 'peg' on the proxiomedial element intimately articulates with a 'socket' on the medial edge of the astragalus (Gow, 1975: figure 33C) and when articulated, the tibia slightly overlaps the medial end of the astragalus to partially contact this element. This is strikingly similar to the condition seen in *Proterosuchus*.

Rieppel (1989) described the tarsus of *Macrocnemus* from a number of specimens and reported that the tibia articulates with both the astragalus and a proximomedial element. For the same reasons presented in the discussion of the tarsus of *Proterosuchus*, the proximomedial element in prolacertiform archosauromorphs is here termed a centrale, as it was by both Gow (1975) and Rieppel (1989).

Rhynchosaurus

Hughes demonstrated that there are three elements articulating with the crus in the rhynchosaurus *Stenaulorhynchus*, *Scaphonyx*, and *Howesia*, and he identified these as intermedium, fibulare and tibiale. The same arrangement has been described for

Paradapedon (Chatterjee, 1974), *Mesosuchus* (Carroll, 1976a), *Hyperodapedon* (Benton, 1983) and *Rhynchosaurus* (Benton 1990), but with the use of a different terminology — astragalus, calcaneum, and centrale. There were also probably three elements articulating with the crus in *Noteosuchus*, despite the reconstruction shown by Carroll (1976a). Here these three elements are termed astragalus, calcaneum and centrale.

Trilophosaurus Case, 1928

The tarsus of *Trilophosaurus* is known from well preserved and articulated material. The tarsus is very similar to that of *Proterosuchus*, with four distal tarsals, and a calcaneum with a perforating foramen and laterally directed tuber. A proximomedial element articulates firmly with the medial surface of the astragalus, and together they present a neatly defined facet for articulation with the distal end of the tibia. The description and reconstruction of the ankle of *Trilophosaurus* by Gregory (1945), strongly suggest that this proximomedial element articulates with the tibia. Following the reasoning presented above, and the apparent position of *Trilophosaurus* within the Archosauromorpha (Benton, 1984, 1985; Evans, 1988; Laurin, 1991), this element is here termed a centrale.

PHYLOGENETIC IMPLICATIONS

The results of this reassessment and description of early archosauromorph ankle material have important implications for phylogeny. The following discussion is divided into groups of characters: (1) those important because of the verification of the erythrosuchid tarsus, (2) those poorly defined or scored in other studies, and (3) those previously or most recently neglected.

Erythrosuchid ankle characters

Sereno & Arcucci (1990) and Sereno (1991), uncertain about the association of the ankle material referred to *Erythrosuchus*, used only information obtained from Young's (1964) figures and descriptions of the tarsal and pedal elements of *Shansisuchus* to represent the Erythrosuchidae as a whole. They present six synapomorphies of *Euparkeria* + Proterochampsidae + crown-group archosaurs. Three of these synapomorphies are based on tarsal and pedal characters — the loss of a bony astragalocalcaneal canal, absence of ossified distal tarsals 1 and 2, and pedal digit 4 significantly shorter than 3. Information presented above shows that these characters, at least, have a broader distribution, and are also present in erythrosuchids.

Poorly defined/scored characters

(a) Parrish (1993), defines his character 1 as calcaneal tuber aligned laterally (0) or with some posterior (ventral here) deviation (1). In scoring this character, he lists *Proterosuchus* as showing the primitive condition, but *Euparkeria* the derived.

Furthermore, Parrish includes the derived condition as a synapomorphy of *Euparkeria* + Proterochampsidae + crown-group archosaurs. As well as being rather loosely defined (even *Proterosuchus* and *Prolacerta* show *some* ventral deviation of the calcaneum relative to the long axis of the astragalus), it is suggested here that the important character transition is in the calcaneum becoming functionally part of the pes, as in crocodiles, and not whether the angle of the tuber axis differs by a few degrees. There is no evidence in *Euparkeria*, or apparently proterochampsids, of any development of a crocodile-like ankle joint. The tarsi of these forms have an essentially laterally directed calcaneal tuber, and they lack both a rotary astragalus-calcaneum joint and a specialised calcaneal condyle for articulation with the fibula (pers. obs., Cruickshank, 1979; Sereno, 1991). Reconstructions exaggerating any posterior deviation of the calcaneum in *Euparkeria* (Bonaparte, 1975; Brinkman, 1981; Parrish, 1986) are unjustified based on my examination of articulated and disarticulated material.

(b) Parrish's (1993) character 3 is "hemicylindrical facet on calcaneum for articulation with astragalus". He claims that this is modified from Sereno (1991), but Sereno lists no such character. He might possibly be referring to Sereno's character 8 (discussed as character 7 in the text), "hemicylindrical calcaneal condyle for articulation with fibula". If so, Parrish is mistaken in identifying such a facet in *Euparkeria* and listing it as a synapomorphy of *Euparkeria* + Proterochampsidae + crown-group archosaurs. Further confusion arises because Parrish (1993: 292) also addresses the presence of this same specialised condyle ("wheel-like process") as part of his separate character 12. Parrish's character 3 is therefore erroneous or in need of clarification.

(c) One of Sereno's (1991: character 9) proposed synapomorphies of his Crurotarsi has the derived state "tuber shaft proportions broader than tall". Parrish's (1993) character 4 is listed as being modified from Sereno (1991). Parrish follows Sereno's character state definitions, apart from omitting 'shaft', in his appendix (1993: 308), but reverses them in his main text (1993: 289 and table 1). He also disagrees with Sereno's interpretation of the proportions in *Euparkeria*, and lists the derived state as a synapomorphy of *Euparkeria* + Proterochampsidae + crown-group archosaurs (1993: 289). A number of points require discussion.

Firstly, Parrish's (1993: 308) claim that Sereno's figure 4 shows a tuber wider than tall (= dorsoventral length greater than proximodistal length) is unjustified. The calcaneum of *Euparkeria* is only 'broader than tall' at its medial end, but this expansion is the "pyramidal process" (Cruickshank, 1979) and not part of the shaft of the tuber. Furthermore, I agree with Sereno (1991: 29) on the proportions of the tuber in the GPIT specimen (GPIT 1681/1, not 8694 as given by Sereno), and can report that the tuber is also 'taller' than 'broad' in SAM 6049. Secondly, Parrish (1993: 308) makes no discussion of his reinterpretation of the proterochampsid calcaneal tuber, for which he (1993: table 2) also contradicts Sereno. The calcaneal tuber of e.g. *Chanaresuchus* is clearly also 'taller than broad' (Cruickshank, 1979: fig. 10). Thirdly, Parrish's statement (1993: 308) that "thus the derived state for this character is either an archosaurian synapomorphy for Archosauria plus *Euparkeria* or it may have been derived independently in Ornithodira and *Euparkeria* plus Suchia, depending on the interpretation of the tuber in *Lagosuchus*" is both puzzling, and difficult to reconcile with his data matrix and phylogenetic hypothesis, irrespective of the problems described here. Finally, Sereno's more rigorously defined version of this character, in specifying the tuber shaft, is preferable when it comes to the calcaneal

tuber of e.g. *Crocodylus*, which has a broad shaft but a flared and 'tall' end. A rigorous definition of what constitutes the shaft of the tuber may also become necessary.

(d) *Erythrosuchus* is incorrectly scored as exhibiting the derived condition of character 12, "rotary crurotarsal proximal ankle joint" by Parrish (1993).

(e) Parrish's (1993) character 31, "three or more (plesiomorphic) or fewer than three (apomorphic) phalanges on digit V" is scored as derived for *Erythrosuchus*, when the only known fifth digit (BPI 2096) does not support this.

(f) Laurin's (1991) character 'J9', a synapomorphy of his Lepidosauromorpha, is listed as "Lepidosauriform ankle joint: the fourth distal tarsal has a ventromedial process that fits under the astragalus medial to the calcaneum-fourth distal tarsal articulation.". This character, the ventral peg, is an important component of the mesotarsal ankle joint (Rewcastle, 1980), and is shown above to be present in erythrosuchid archosauromorphs. It is also present in more plesiomorphic archosauromorph taxa such as rhynchosaurs (Hughes, 1968).

(g) Parrish (1993: 288) states that he avoided the ordering of character state acquisition in his phylogenetic analysis. A closer examination of his character definitions indicates that in two instances concerning tarsal morphology, this is not the case. Parrish employs two characters that address the nature of the astragalus-calcaneum articulation. His character 12 is absence/presence of a rotary joint, while character 13 is absence/presence of a 'crocodile-normal' rotary joint. Additive binary coding of these two characters (that are not independent) shows that he has effectively ordered a single multistate character with a transformation series of: no rotary joint – rotary joint – 'crocodile-normal' rotary joint. In Parrish's analysis, the only taxon exhibiting the intermediate state is *Riojasuchus* (incorrectly scored as possessing a 'crocodile normal' joint in Parrish's data matrix), so that he has inadvertently assumed that the 'crocodile normal' joint is twice as many steps away from the plesiomorphic condition than is the 'crocodile-reversed' one. This might have implications for Parrish's hypothesis that the 'crocodile-reversed' ornithosuchids are the sister group to all archosaurs with a 'crocodile-normal' joint — particularly in light of the fact that a monophyletic Ornithosuchidae + Suchia required only a single additional step in Parrish's analysis (1993: 304).

Additionally, additive binary coding of his two obviously linked characters (1 and 9) that address the angle of calcaneal tuber projection, shows that he has effectively ordered a single multistate character, with a transformation series of: lateral – posterolateral – posterior tuber alignment. This in itself might not be a problem, but it is apparently unintentional.

Neglected characters

(a) Sereno & Arcucci (1990), Sereno (1991) and Benton & Clark (1988) use the absence of distal tarsals 1 and 2 as a derived condition but all of these authors and Parrish (1993) neglect the presence/absence of the centrale.

(b) It has been shown above that in many archosauromorph taxa, the tibia articulates with a proximomedial element as well as the astragalus. It is argued here that this element should be termed centrale rather than tibiale. It is realized that this interpretation relies partly on the acceptance of hypothesized phylogenetic relationships of, for example, *Petrolacosaurus* (as the most plesiomorphic diapsid, e.g. Evans, 1988, and clearly having a centrale that does not contact the tibia, as well as

lacking a tibiale, Reisz, 1981), as well as Rieppel's (1993) conclusions on tarsal homology. This solution, however, currently seems more parsimonious than the theoretical 'refragmentation' of a composite astragalus (possibly composed of at least a fused tibiale and intermedium — something yet to be convincingly demonstrated) and loss of the centrale, occurring somewhere at the base of the Diapsida. The homology of the particular centrale retained in these derived reptiles, in terms of correspondence with the several centralia seen plesiomorphically, is not discussed here.

Rieppel (1993) suggests that in basal amniotes the tibia articulates with the astragalus only, and that no amniote possesses a true tibiale. It is of great interest, therefore, to discover at what level of generality within diapsids a centrale is incorporated into the functional proximal row, topologically mimicking the tibiale of amniote outgroups.

The centrale-tibia articulation is seen in *Proterosuchus*, *Trilophosaurus*, prolacertiforms, and rhynchosaurs, but not in the neodiapsid outgroup taxon Araeoscelida (Reisz, 1981; Vaughn, 1955). Other contenders for sister group to the neodiapsids, the millerettids, also appear to lack any centrale-tibiale articulation (*Broomia* Thommasen & Carroll 1981, but perhaps less clear in *Milleropsis* Gow 1972). Broom (1921) and Hughes (1968: 477) identified three elements in the proximal row of *Youngina*, but the loss of this specimen (Gow, 1975) means that this cannot currently be verified. Although its presence has not been reported in other lepidosauromorphs and immediate neodiapsid outgroups, figures and reconstructions of the tarsi of some of these taxa suggest that a reassessment of this material might be worthwhile (e.g. *Thadeosaurus* Currie & Carroll 1984, *Saurosternon* Carroll 1975, *Galesphyrus* Carroll 1976b, *Claudiosaurus* Carroll 1981). Other taxa, such as the younginiforms *Kenyasaurus* (Harris & Carroll, 1977) and *Hovasaurus* (Currie, 1981) appear clearly to lack any centrale-tibia articulation. Some taxa present more of a problem; specimens of the neodiapsid outgroup taxon *Coelurosauravus*, for example, either show a clear lack of centrale-tibia articulation (Carroll, 1978) or suggest that a reassessment is necessary (Evans & Haubold, 1987). Benton (1990) includes the presence of three proximal tarsals as a synapomorphy of the Rhynchosauria. It is shown here that this character has a much wider distribution than this among diapsids.

Although there is still uncertainty over the distribution of this character and the relationships of some of the taxa in question (for example, compare Laurin 1991 with Evans 1988 in terms of the monophyly and composition of the Lepidosauromorpha), it might currently be concluded that significant contact between the tibia and centrale is a synapomorphy of at least the Archosauromorpha. Loss of the centrale is a possible synapomorphy of the group Erythrosuchidae + *Euparkeria* + Proterochampsidae + crown group archosaurs. Loss of an ossified pedal centrale is paralleled in the Lepidosauria (Gauthier, Estes & de Queiroz 1988). Loss of the perforating astragalocalcaneal canal in this group is also paralleled in the Lepidosauria. Adult lepidosaurs differ from archosauromorphs in having a fused astragalus and calcaneum. The distribution of these characters among several of the taxa discussed here is summarized in Figure 11.

Recent cladistic analyses of archosaur phylogeny have been dominated by information obtained from tarsal and pedal morphology in the relevant taxa. In Sereno & Arcucci (1990) these characters total some 16 out of 34. Similar proportions are present in Sereno, 1991 (15 out of 36) and Parrish, 1993 (16 out of 42). There is little evidence that possible functional links between many of these

characters, or possible redundancy through repetition (e.g. posterior deviation of calcaneal tuber and other aspects of a functionally crocodyloid ankle) has been investigated. For example, of Sereno's (1991: 27–31) nine synapomorphies of the Crurotarsi five are drawn directly from the astragalus and calcaneum and a further one (character 6) might be associated with the ankle joint. Four of these characters (8–11) could all be considered to be functionally interdependent within a 'crurotarsal' joint (see also Parrish 1993: 307). Because the derived states in all four characters have the same distribution, this could be considered equivalent to giving the character 'presence of crocodyloid joint' a relative weighting of $\times 4$. It should be remembered that the type, number and weighting of characters used in phylogenetic analysis can greatly affect the results obtained. Satisfactory *a priori* character discussion and definition is obviously detailed and problematic work, but it may prove necessary in resolving differences between phylogenetic hypotheses, such as those postulated by Sereno (1991) and Parrish (1993). Finally, it might be noted that "Crurotarsi" (Sereno & Arcucci, 1990) is something of a misnomer (see also Charig,

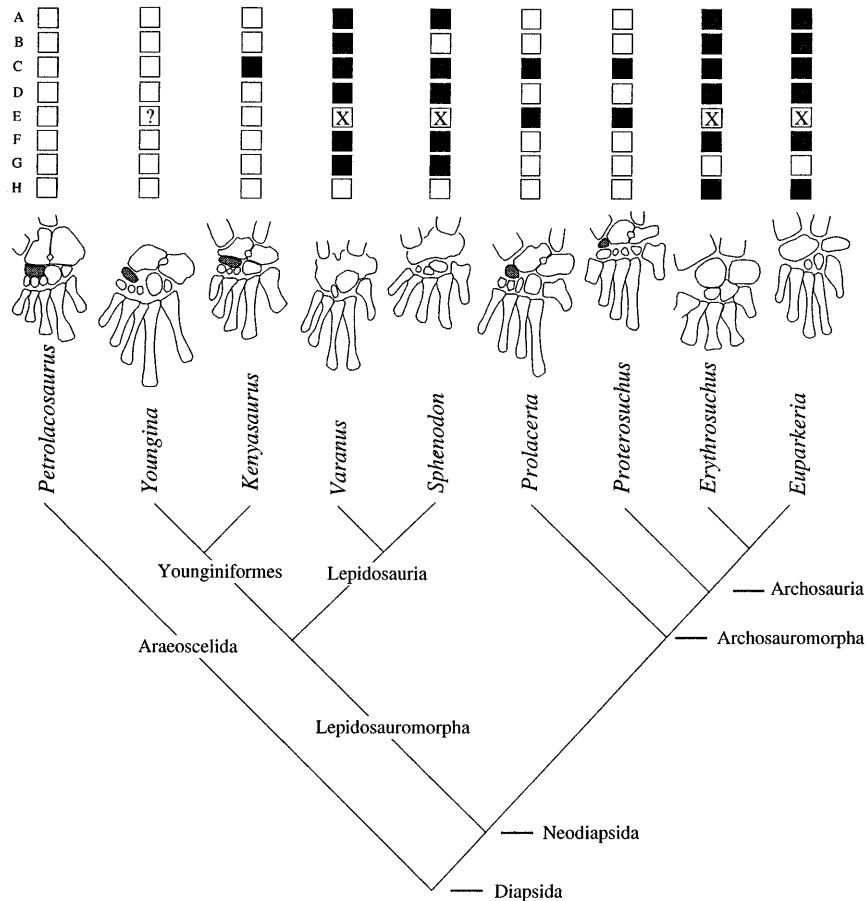


Figure 11. Left distal crus, tarsus and metatarsus in a selection of diapsid taxa discussed in text. Centrale, where present, is shaded. Filled boxes indicate the distribution of a selection of characters: A, loss of first distal tarsal; B, loss of second distal tarsal; C, loss of fifth distal tarsal; D, loss of centrale; E, presence of tibia-centrale articulation; F, loss of astragalocalcaneal canal; G, presence of fused astragalus and calcaneum; H, metatarsal III longer than IV. ? = state unknown, X = inapplicable character.

1993: 49), in that the main ankle joint in these forms is not between the crus and proximal tarsals, but between the crus + astragalus and the calcaneum + foot.

Phylogenetic reconstruction needs to be based on sound information gained from detailed morphological investigation, rather than the morphological information being a side product in a search for synapomorphies. The detailed morphological study presented here suggests that a number of fallacies regarding early archosaur ankles might not have been perpetuated if as much research effort had been directed towards such studies as there has been to the recent cladistic analysis of archosaur phylogeny. It is hoped that this study has demonstrated that, despite many years of focused attention, there are still many unanswered questions concerning archosauriform tarsal morphology. It is also hoped that, in future, as much attention will be paid to all other parts of the skeleton, avoiding the mistakes of the tarsal studies, and leading to a greater understanding of the relationships of these taxa.

ACKNOWLEDGEMENTS

I am indebted to Barry Hughes for help, encouragement, and for making me think. I am extremely grateful to Arthur Cruickshank and Barry Hughes for lending me photographs and notes on the unprepared specimens of *Erythrosuchus*, and for discussing ideas. Staff at the Bernard Price Institute, Johannesburg; the South African Museum, Cape Town; the Natural History Museum, London; the Palaeontological Institute, Moscow; and the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing are thanked for their hospitality and for access to material. I particularly thank Andrei Sennikov, with whom I also discussed the *V. triplicostata* tarsus. Reviews of earlier manuscript drafts by M.J. Benton, B. Hughes, J.M. Parrish, and P.S. Spencer all significantly improved this paper. This work was supported in part by NERC grant G9/1569 and a Royal Society European Fellowship.

REFERENCES

- Benton MJ. 1983.** The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London (B)* **302**: 605–720.
- Benton MJ. 1984.** The relationships and early evolution of the Diapsida. *Symposium of the Zoological Society of London* **52**: 575–596.
- Benton MJ. 1985.** Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* **84**: 97–164.
- Benton MJ. 1990.** The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. *Philosophical Transactions of the Royal Society of London (B)* **328**: 213–306.
- Benton MJ, Clark JM. 1988.** Archosaur phylogeny and the relationships of the Crocodylia. In: Benton MJ, ed. *The Phylogeny and Classification of the Tetrapods*. Oxford: Clarendon Press, 295–338.
- Bonaparte JF. 1975.** The family Ornithosuchidae (Archosauria: Thecodontia). *Colloque international de la Centre National Recherche Scientifique* **218**: 485–502.
- Brinkman D. 1981.** The origin of the crocodyloid tarsi and the interrelationships of thecodontian archosaurs. *Breviora* **464**: 1–23.
- Broom R. 1903.** On a new reptile (*Proterosuchus fergusi*) from the Karoo beds of Tarkastad, South Africa. *Annals of the South African Museum* **4**: 158–164.
- Broom R. 1905.** Notice of some new fossil reptiles from the Karoo beds of South Africa. *Records of the Albany Museum* **1**: 331–337.
- Broom R. 1906.** On the remains of *Erythrosuchus africanus*, Broom. *Annals of the South African Museum* **5**: 187–196.
- Broom R. 1913.** On the South African pseudosuchian *Euparkeria* and allied genera. *Proceedings of the Zoological Society of London* **1913**: 619–633.

- Broom R. 1921.** On the structure of the reptilian tarsus. *Proceedings of the Zoological Society of London* **1921**: 143–155.
- Broom R. 1932.** On some South African pseudosuchians. *Annals of the Natal Museum* **7**: 55–59.
- Carroll RL. 1975.** Permo-Triassic 'lizards' from the Karoo. *Palaeontologia Africana* **18**: 71–87.
- Carroll RL. 1976a.** *Notesuchus* — the oldest known rhynchosaur. *Annals of the South African Museum* **72**: 37–57.
- Carroll RL. 1976b.** *Galesphyrus capensis*, a youngid eosuchian from the *Cistecephalus* zone of South Africa. *Annals of the South African Museum* **72**: 59–68.
- Carroll RL. 1977.** The origin of lizards. *Linnean Society Symposium Series* **4**: 359–396.
- Carroll RL. 1978.** Permo-Triassic 'lizards' from the Karoo System. Part II. A gliding reptile from the Upper Permian of Madagascar. *Palaeontologia Africana* **21**: 143–159.
- Carroll RL. 1981.** Plesiosaur ancestors from the Upper Permian of Madagascar. *Philosophical Transactions of the Royal Society of London (B)* **293**: 315–383.
- Case EC. 1928.** A cotylosaurian from the Upper Triassic of western Texas. *Journal of the Washington Academy of Science* **18**: 177–178.
- Charig AJ. 1972.** The evolution of the archosaur pelvis and hindlimb, an explanation in functional terms. In: Joysey KA, Kemp TS, eds. *Studies in Vertebrate Evolution*. Edinburgh: Oliver and Boyd, 121–151.
- Charig AJ. 1993.** Recently proposed phylogenetic analyses of the Triassic Archosauria: a critical comparison and evaluation, facilitated by a simple technique for the modification of conflicting dendrograms. *Paleontologia Lombarda della Società Italiana di Scienze Naturali e del museo Civico di Storia Naturale di Milano Nuova serie* **2**: 45–62.
- Chatterjee S. 1974.** A rhynchosaur from the Upper Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London (B)* **267**: 209–261.
- Chatterjee S. 1982.** Phylogeny and classification of thecodontian reptiles. *Nature* **295**: 317–320.
- Coombs WP. 1975.** Sauropod habits and habitats. *Palaeogeography, Palaeoclimatology, and Palaeoecology* **17**: 1–33.
- Coombs WP. 1978.** Theoretical aspects of cursorial adaptations in dinosaurs. *Quarterly review of biology* **53**: 393–418.
- Cruickshank ARI. 1972.** The proterosuchian thecodonts. In: Joysey KA, Kemp TS, eds. *Studies in Vertebrate Evolution*. Edinburgh: Oliver & Boyd, 89–119.
- Cruickshank ARI. 1978.** The pes of *Erythrosuchus africanus* Broom. *Zoological Journal of the Linnean Society* **62**: 161–177.
- Cruickshank ARI. 1979.** The ankle joint in some early archosaurs. *South African Journal of Science* **75**: 168–178.
- Cruickshank ARI, Benton MJ. 1985.** Archosaur ankles and the relationships of the thecodontian and dinosaurian reptiles. *Nature* **317**: 715–717.
- Currie PJ. 1981.** *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. *Palaeontologia Africana* **24**: 99–168.
- Currie PJ, Carroll RL. 1984.** Ontogenetic changes in the eosuchian reptile *Thadeosaurus*. *Journal of Vertebrate Paleontology* **4**: 68–84.
- Evans SE. 1988.** The early history and relationships of the Diapsida. In: Benton MJ, ed. *The Phylogeny and Classification of the Tetrapods*. Oxford: Clarendon Press, 221–260.
- Evans SE, Haubold H. 1987.** A review of the Upper Permian genera *Coelurosauravus*, *Weigeltisaurus* and *Gracilisaurus* (Reptilia: Diapsida). *Zoological Journal of the Linnean Society* **90**: 275–303.
- Ewer RF. 1965.** The anatomy of the thecodont reptile *Euparkeria capensis* Broom. *Philosophical Transactions of the Royal Society of London (B)* **248**: 379–435.
- Gauthier JA. 1986.** Saurischian monophyly and the origin of birds. *Memoirs, California Academy of Sciences* **8**: 1–55.
- Gauthier JA, Estes R, de Queiroz K. 1988.** A phylogenetic analysis of Lepidosauromorpha. In: Estes R, Pregill G, eds. *Phylogenetic relationships of the lizard families*. Stanford, California: Stanford University Press, 15–98.
- Gow CE. 1972.** The osteology and relationships of the Milleretidae (Reptilia: Cotylosauria) *Journal of Zoology* **167**: 219–264.
- Gow CE. 1975.** The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana* **18**: 89–131.
- Gregory JT. 1945.** Osteology and relationships of *Trilophosaurus*. University of Texas Publications No 4401: 273–359.
- Harris JM, Carroll RL. 1977.** *Kenyasaurus*, a new eosuchian reptile from the Early Triassic of Kenya. *Journal of Paleontology* **51**: 139–149.
- Hecht MK, Tarsitano SF. 1984.** The tarsus and metatarsus of *Postosuchus* and its phyletic implications. In: Rhodin AGJ, Miyata K, eds. *Advances in Herpetology and Evolutionary Biology*. Cambridge, Massachusetts: Harvard University Press, 332–349.
- Huene Fv. 1911.** Über *Erythrosuchus*, Vertreter der neuen Reptil-Ordnung Pelycosimia. *Geologische und Paläontologische Abhandlungen* **10**: 1–60.
- Huene Fv. 1915.** On reptiles of the New Mexican Trias in the Cope collection. *Bulletin of the American Museum of Natural History* **34**: 485–507.
- Huene Fv. 1920.** Osteologie von *Aëtosaurus ferratus* O. Fraas. *Acta zoologica* **1**: 465–491.
- Huene Fv. 1960.** Ein grosser Pseudosuchier aus der Orenburger Trias. *Palaeontographica (A)* **114**: 105–111.
- Hughes B. 1963.** The earliest archosaurian reptiles. *South African Journal of Science* **59**: 221–241.
- Hughes B. 1968.** The tarsus of rhynchocephalian reptiles. *Journal of Zoology* **156**: 457–481.

- Laurin M. 1991.** The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. *Zoological Journal of the Linnean Society* **101**: 59–95.
- Osburn RA. 1906.** Adaptive modifications of the limb skeleton in aquatic reptiles and mammals. *Annals of the New York Academy of Science* **16**: 447–482.
- Parrish JM. 1986.** Locomotor adaptations in the hindlimb and pelvis of the Thecodontia. *Hunteria* **1**: 1–35.
- Parrish JM. 1992.** Phylogeny of the Erythrosuchidae (Reptilia: Archosauriformes). *Journal of Vertebrate Paleontology* **12**: 93–102.
- Parrish JM. 1993.** Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. *Journal of Vertebrate Paleontology* **13**: 287–308.
- Peabody FE. 1951.** The origin of the astragalus of reptiles. *Evolution* **5**: 339–344.
- Reisz RR. 1981.** A diapsid reptile from the Pennsylvanian of Kansas. *Special publications of the Museum of Natural History, University of Kansas* **7**: 1–74.
- Rewcastle SC. 1980.** Form and function in lacertilian knee and mesotarsal joints; a contribution to the analysis of sprawling locomotion. *Journal of Zoology* **191**: 147–170.
- Rieppel O. 1989.** The hind limb of *Macrocnemus bassanii* Nopsca (Reptilia, Diapsida): development and functional anatomy. *Journal of Vertebrate Paleontology* **9**: 373–387.
- Rieppel O. 1993.** Studies on skeleton formation in reptiles. IV. The homology of the reptilian (amniote) astragalus revisited. *Journal of Vertebrate Paleontology* **13**: 31–47.
- Romer AS. 1922.** The locomotion apparatus of certain primitive and mammal-like reptiles. *Bulletin of the American Museum of Natural History* **46**: 517–606.
- Romer AS. 1923.** Crocodilian pelvic muscles and their avian and reptilian homologues. *Bulletin of the American Museum of Natural History* **48**: 533–552.
- Romer AS. 1942.** The development of tetrapod limb musculature — the thigh of *Lacerta*. *Journal of Morphology* **71**: 251–298.
- Romer AS. 1956.** *Osteology of the Reptiles*. Chicago: The University of Chicago Press.
- Schaeffer B. 1941.** The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bulletin of the American Museum of Natural History* **78**: 395–472.
- Sereno PC. 1991.** Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology Memoirs* **2**: 1–53.
- Sereno PC, Arcucci AB. 1990.** The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **180**: 21–52.
- Thommasen H, Carroll RL. 1981.** *Broomia*, the oldest known millerettid reptile. *Palaeontology* **24**: 379–390.
- Thulborn RA. 1980.** The ankle joints of archosaurs. *Alcheringa* **4**: 261–274.
- Thulborn RA. 1982.** Significance of ankle structure in archosaur phylogeny. *Nature* **299**: 657.
- Vaughn PP. 1955.** The Permian reptile *Araeoscelis* restudied. *Bulletin of the Museum of Comparative Zoology* **113**: 305–467.
- Williston SW. 1925.** *The Osteology of the Reptiles*. Cambridge: Harvard University Press.
- Young CC. 1964.** The pseudosuchians in China. *Palaeontologia Sinica* **151**: 1–205.