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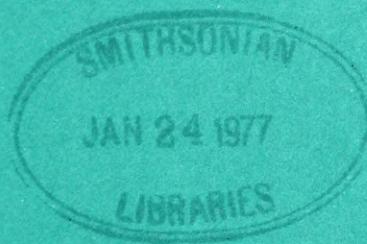
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ANNALS

OF THE SOUTH AFRICAN
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CAPE TOWN



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- FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. — *Archs Zool. exp. gén.* 74: 627-634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. — *Ann. Mag. nat. Hist.* (13) 2: 309-320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. — *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.
- THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. — *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

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NOTEOSUCHUS—THE OLDEST
KNOWN RHYNCHOSAUR

By

ROBERT L. CARROLL

Cape Town

Kaapstad

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NOTEOSUCHUS—THE OLDEST KNOWN RHYNCHOSAUR

By

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(With 12 figures)

[MS accepted 5 May 1976]

ABSTRACT

Noteosuchus colletti, known from a single specimen from the base of the *Lystrosaurus* zone in South Africa, is the oldest known rhynchosaur. The postcranial skeleton closely resembles that of *Mesosuchus* and *Howesia*. The tarsal elements resemble those of later rhynchosaurs and demonstrate that the bones identified as intermedium and tibiale by Houghton, Von Huene and Hughes are homologous with the astragalus and centrale of other primitive reptiles. The tarsus of *Noteosuchus* is nearly identical to that of the primitive archosaur *Proterosuchus*, but this may not be indicative of close relationship. It is probable that the rhynchosaurs had a long period of evolution prior to their appearance in the Lower Triassic. Early Triassic rhynchosaurs show no significant similarities with primitive squamates.

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INTRODUCTION

The late Permian and early Triassic mark a time of major radiation among diapsid reptiles, comparable with that which took place among placental mammals in the late Cretaceous and early Tertiary, although far less well documented. All three living diapsid orders—Crocodylia, Squamata and Rhynchocephalia—are known by the end of the Triassic, and the thecodont ancestors of the crocodiles and ancestral lizards are known from the late Permian. Rhynchocephalians are reported from the *Cynognathus* zone, in the upper portion of the Lower Triassic. The modern family Sphenodontidae is represented only by one or two jaws, but the presumably closely related rhynchosaurs are known from several nearly complete skeletons.

It is generally accepted that the Permo-Triassic eosuchians represent a primitive stage in evolution, antecedent to the modern diapsid orders, although Romer (1966, 1971) has maintained that archosaurs had a separate origin from more primitive reptiles.

Although archosaurian features have been cited in the eosuchian genus

Heleosaurus (Carroll 1976a), and the earliest lizards retain many eosuchian features (Carroll 1975), the specific relationships between these advanced groups and their eosuchian predecessors have not been established. The well-known rhynchosaurs from the *Cynognathus* zone, *Mesosuchus* and *Howesia* (Broom 1906; Haughton 1921, 1924a) are also clearly distinct from the primitive eosuchian pattern in their specialized dentition and foot structure. Determination of the specific ancestry of rhynchosaurs requires the knowledge of earlier, more primitive members of this group.

NOTEOSUCHUS—A FORGOTTEN RHYNCHOSAUR

The oldest known form attributed to the rhynchosaurs was described by Watson (1912) and Broom (1925). It is from Grassy Ridge, Cape Province, at the very base of the *Lystrosaurus* zone (J. Kitching, pers. comm.)—the lowermost

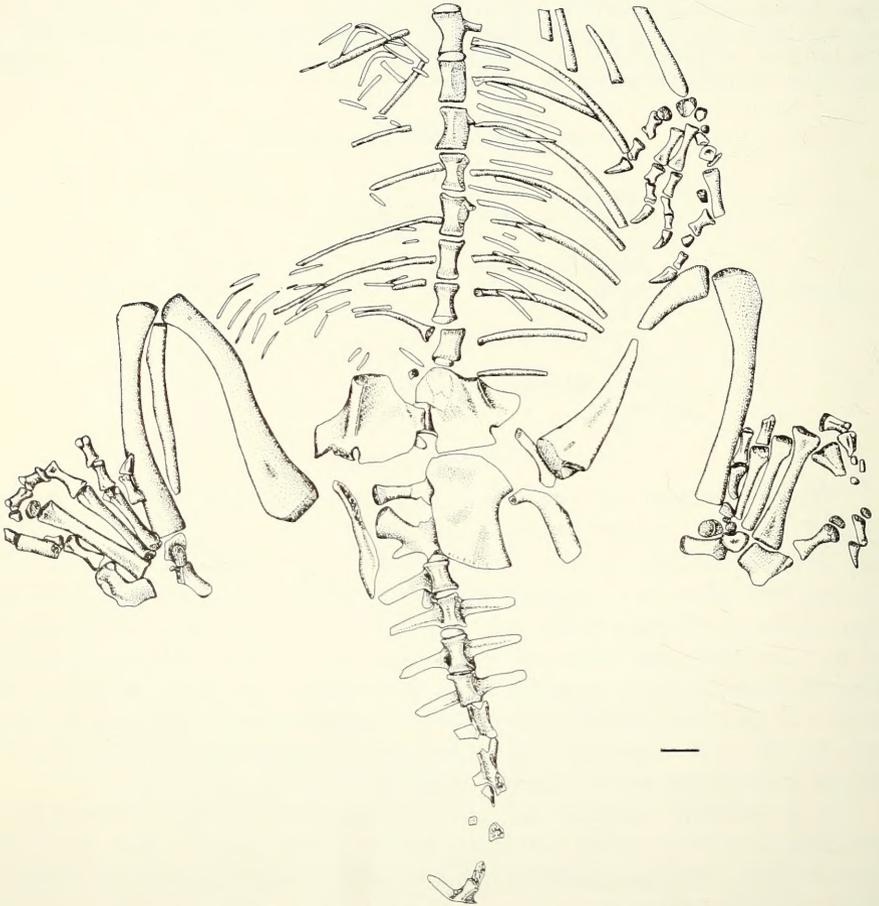


Fig. 1. *Noteosuchus colletti*, type, Albany Museum 3591; ventral view; $\times 0,5$.

Triassic. Watson originally designated the single known specimen (Albany Museum, Grahamstown, 3591) as *Eosuchus colletti*, in analogy with *Mesosuchus*. Broom subsequently recognized that this name was preoccupied, and so termed the genus *Noteosuchus*. It is clear from Broom's (1914) original definition of the Order Eosuchia that it was based on *Youngina*, and that Watson's genus had no relevance to the group. Despite these early descriptions and the clear indication that *Noteosuchus* was a rhynchosaur, most if not all recent references (Romer 1956, 1966; Kuhn 1969) list *Noteosuchus* as an eosuchian rather than a rhynchosaur. Although some doubt might be cast on the inclusion of this specimen among the Rhynchosauridae *sensu strictu*, it is certainly not an eosuchian, if the pattern of *Youngina* can be taken as representative of this group.

Identity of this specimen as a rhynchosaur is subject to question because of the absence of the skull. Comparison with specimens of *Howesia* and *Mesosuchus* in the South African Museum reveals no significant differences in the postcranial skeleton. *Howesia* and *Mesosuchus* are currently being studied by M. E. Malan, who published a preliminary report in 1963. Her work will provide a much more complete understanding of the skeleton of these early rhynchosaurs. Despite the general similarity of these forms to *Noteosuchus*, it seems valuable to publish a complete description of this genus, since it is by far the oldest known rhynchosaur. The excellent preservation provides a strong basis for evaluating the pattern in early rhynchosaurs and for comparison when possible antecedent forms are discovered. Modern techniques of preparation and casting enable a much more thorough description than was possible for Watson or Broom.

DESCRIPTION

MATERIAL AND METHODS

The type of *Noteosuchus colletti* is preserved in a roughly circular block of waterworn limestone, termed a 'nodule' by early describers. The block was broken into three large pieces, one ventral and two dorsal, divided along the line of the neural spines. Small fragments at the junction of the blocks are now missing. The posterior portion of the skeleton is present, including portions of both hands, eleven trunk vertebrae, the pelvic girdle and rear limbs, and much of the tail, curled around the front of the block (Figs 1-5). Broom suggested that the break at the front of the block was still fresh, and indicated the necessity for hunting further for the anterior portion of the skeleton. Sixty years later such a search would still be worth while.

Very little effort was made to prepare the specimen by either Watson or Broom, aside from splitting the blocks. Nearly all the exposed bones were split in approximately equal parts so that only an occasional trace of original bone surface was visible. It might have been possible to glue the blocks together and prepare away the matrix, either mechanically or with acetic acid. Because the matrix was exceedingly hard and the bone comparatively soft, it was decided rather to remove the bone mechanically. This resulted in the exposure of

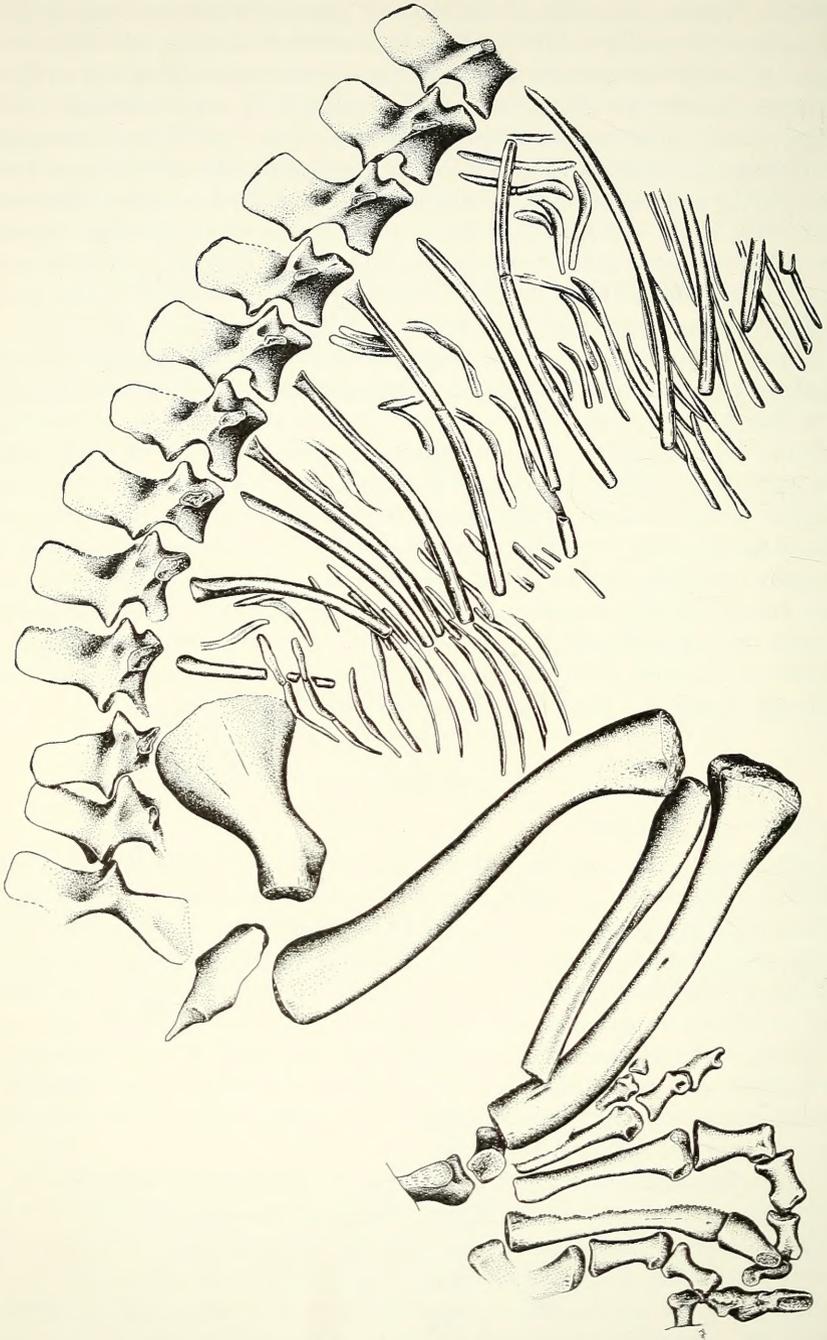


Fig. 2. *Noteosuchus*, dorsal view of right side; vertebrae are drawn in lateral view, although they are preserved in their natural orientation; $\times 1$.

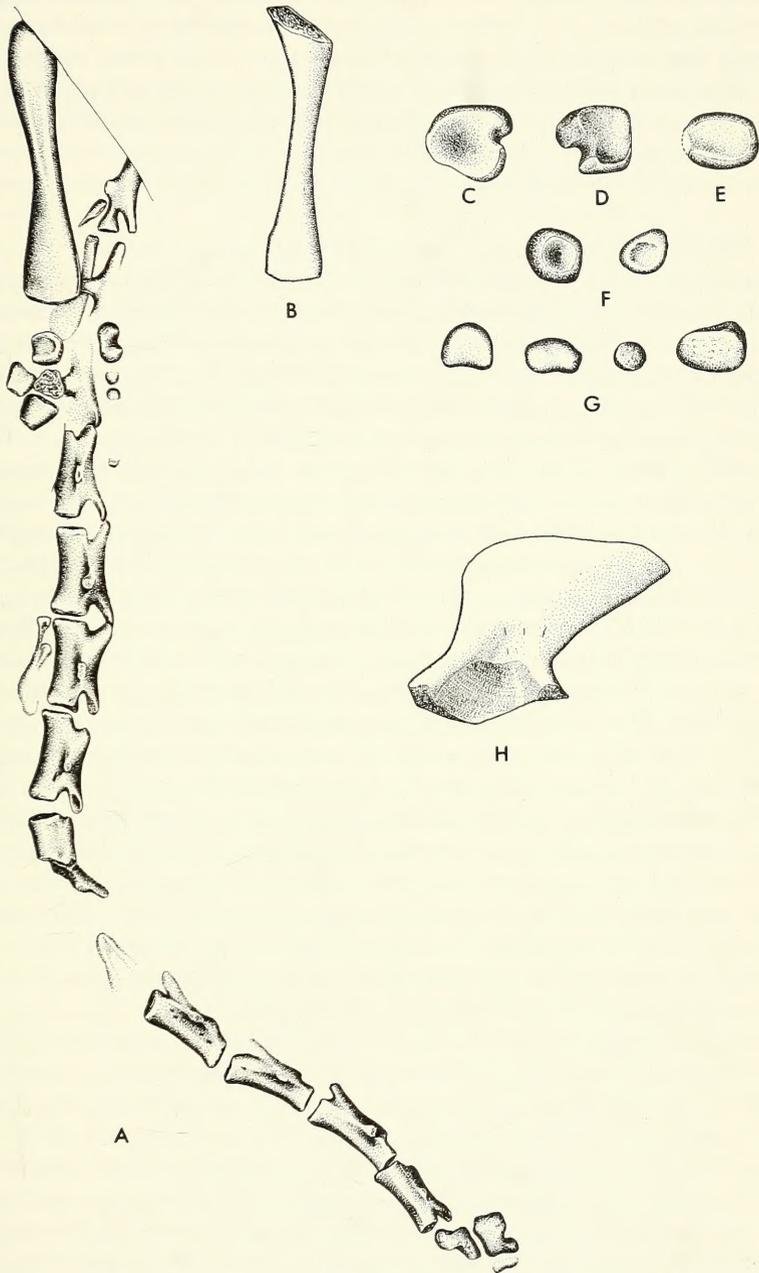


Fig. 3. *Noteosuchus*. A. Right ulna, carpals and tail, printed in approximately their natural relationship to the remainder of the skeleton illustrated on the facing page; $\times 1$. B. Left ulna, drawn from counterpart block; $\times 1$. C.-G. Carpals, drawn from ventral block except for ?radiale (tentative identification: C. ulnare; D. intermedium; E. radiale; F. centralia; G. distal carpals 1-4); $\times 2$. H. Left ilium, drawn from ventral block; $\times 1$.

extremely high fidelity moulds of both dorsal and ventral surfaces. These were cast with liquid latex. It is from these casts that the drawings have been made. Although the skeleton as a whole is flattened into a single plane, the individual bones are almost undistorted. Much greater detail has been exposed by this method of preparation than is evident in most contemporary fossils prepared by more orthodox methods. Where practical, casts of the dorsal and ventral surfaces of individual bones have been joined together to form three-dimensional replicas.

VERTEBRAE AND RIBS

Eleven vertebrae are present anterior to the sacrum. They have tall rectangular spines, moderately well-developed transverse processes and non-notochordal but shallowly amphicoelous centra. As has been noted in some other primitive tetrapods (Vaughn 1970), there is a noticeable dimorphism of the neural spines. The width of the spines is alternately wide and narrow throughout the sequence preserved. The transverse processes show progressive shortening and thickening toward the sacrum. They shift gradually from the level of the zygapophyses toward the lower half of the centrum. The zygapophyses are nearly horizontal and set close to the midline. In the typical younginid eosuchians *Youngina* and *Galesphyrus*, the neural arches are wide, the neural spines short, the zygapophyses laterally placed and the centra notochordal (Gow 1975; Carroll 1976b).

The two sacral vertebrae resemble those more forward except that the sacral ribs are fused to the transverse processes. The proximal caudal vertebrae can be seen in the ventral block, but beyond the third this portion of the dorsal surface has been lost. Ventrally, the first eight caudals are seen in sequence; all bear short ribs fused to the transverse process and extending straight laterally. The tail intersects the margin of the block at the level of the eighth caudal. A more posterior segment of the tail can be seen at the anterior edge of one of the dorsal blocks. Fourteen vertebrae are present, extending back toward the rear limbs. The intervening portion of the tail presumably had wrapped around the front of the body, but is missing from the blocks as preserved. This would suggest a tail length of 40–50 segments. The posterior caudals are long and narrow, with little development of the neural arch. Long narrow lateral processes are evident in this series. No tail-break mechanism can be seen.

Small crescentic intercentra are present throughout the preserved portion of the trunk and between the first three caudals. More posteriorly, haemal arches are visible. There is no evidence for rib articulation on the trunk intercentra.

The distal ends of three anterior ribs are seen at the margin of the block. The shafts are quite wide and flattened. Nearly complete ribs are visible adjacent to all the preserved trunk and sacral vertebrae. The articulating surfaces are rarely well exposed, but they appear to have two heads, fairly widely spaced, as in more primitive reptiles. The shafts are long and widely oval, rather than round. There are two pairs of sacral ribs, both fused to the vertebrae. The more anterior has the articulating surface only slightly expanded from the shaft. The second appears to be bifurcate, with a large anterior articulating surface and a narrower

posterior process. This pattern is repeated in later Rhynchocephalia, and is also evident in the early archosaur *Proterosuchus* (Cruickshank 1972). In the first eight caudals there are short ribs, indistinguishably fused to the transverse processes. The first extends posteriorly at a slight angle. The remainder are set at right angles to the axis of the tail. Their length gradually decreases to the edge of the block.

FORELIMB

Nothing of the pectoral girdle is visible. Unfortunately, the trunk is not preserved far enough anteriorly to determine whether or not there may have been a sternum (a hallmark of sphenodontids in contrast to rhynchosaurs).

Neither humerus is preserved, but portions of both left and right limbs and hands are in place. What is preserved of the forelimb is much smaller than the rear. The ulna and radius are approximately 60 per cent the length of the tibia, and very slim. The distal articulating surface of the radius is circular, and oriented at right angles to the shaft. The distal end of the ulna is flattened in the plane of the carpus. The articulating surface is in the shape of a broad arc.

From the two sides of the animal, most of the carpus and manus is represented. The carpal elements, although individually well preserved, are difficult to identify or reconstruct in the absence of better known material of related genera, since they are badly disarticulated.

Of the left wrist, eight carpals can be seen in either the dorsal or ventral blocks (Fig. 3). It may be that only four of the five distal carpals are preserved since the fifth metacarpal is not evident, although other elements of the fifth digit are present. The right hand is much less well preserved, but one of the carpals appears to have a different configuration than any of those evident on the left side. It is probable that there are four or five proximal carpals. There are six proximal carpals, including the pisiform, in most primitive reptiles. None of the elements preserved resembles a pisiform, nor is any bone to be seen in the area normally occupied by the pisiform. Two of the carpals are considerably larger than the others, have a considerable area of finished bone, and are deeply notched on one margin. Comparison with other primitive reptiles suggests that these may be ulnare, intermedium or laterale centrale. The bone represented only from the right wrist is also relatively large, with much finished surface; it is roughly triangular in outline. It might be the radiale. The remaining elements are approximately circular in outline, and have little finished bone surface. If the pisiform is absent in the fossil or not present in the living animal, two of the remaining elements are presumably centralia. The bones represented as distal carpals in the restoration (Fig. 6B) are arranged according to the pattern in other primitive reptiles, with the fourth the largest.

Apart from the loss of the fifth metacarpal, the hand is apparently represented in its entirety on the left side. The first metacarpal is only about half the length of the second, after which the length increases only slightly in the third and fourth. The more distal elements are just slightly shorter. The proximal



Fig. 4. *Noteosuchus*, dorsal view of left side of skeleton; $\times 1$.

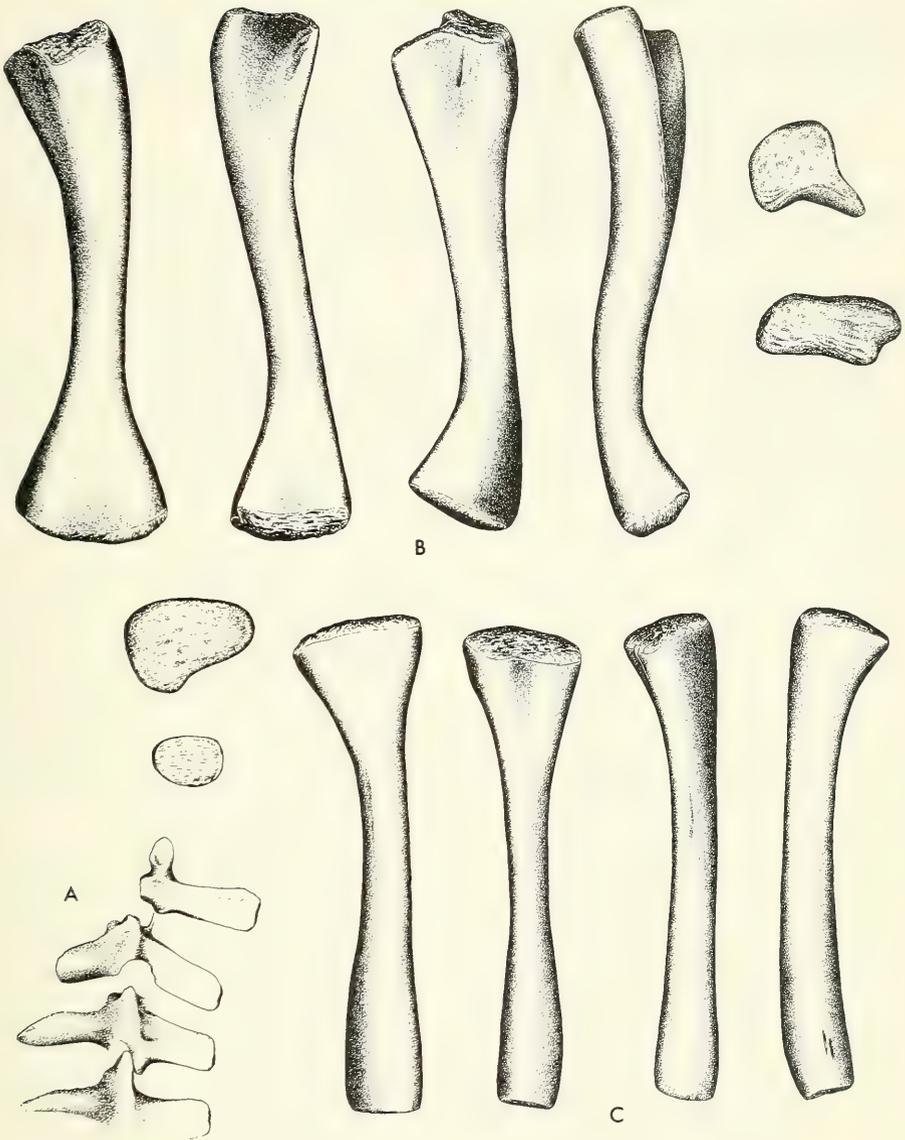


Fig. 5. *Noteosuchus*. A. Proximal caudal vertebrae drawn in approximately their natural relationship to the remainder of the skeleton illustrated on facing page. B. Left femur in dorsal, ventral, anterior, posterior, proximal and distal views. C. Left tibia in extensor, flexor, medial, lateral, proximal and distal views. All $\times 1$.

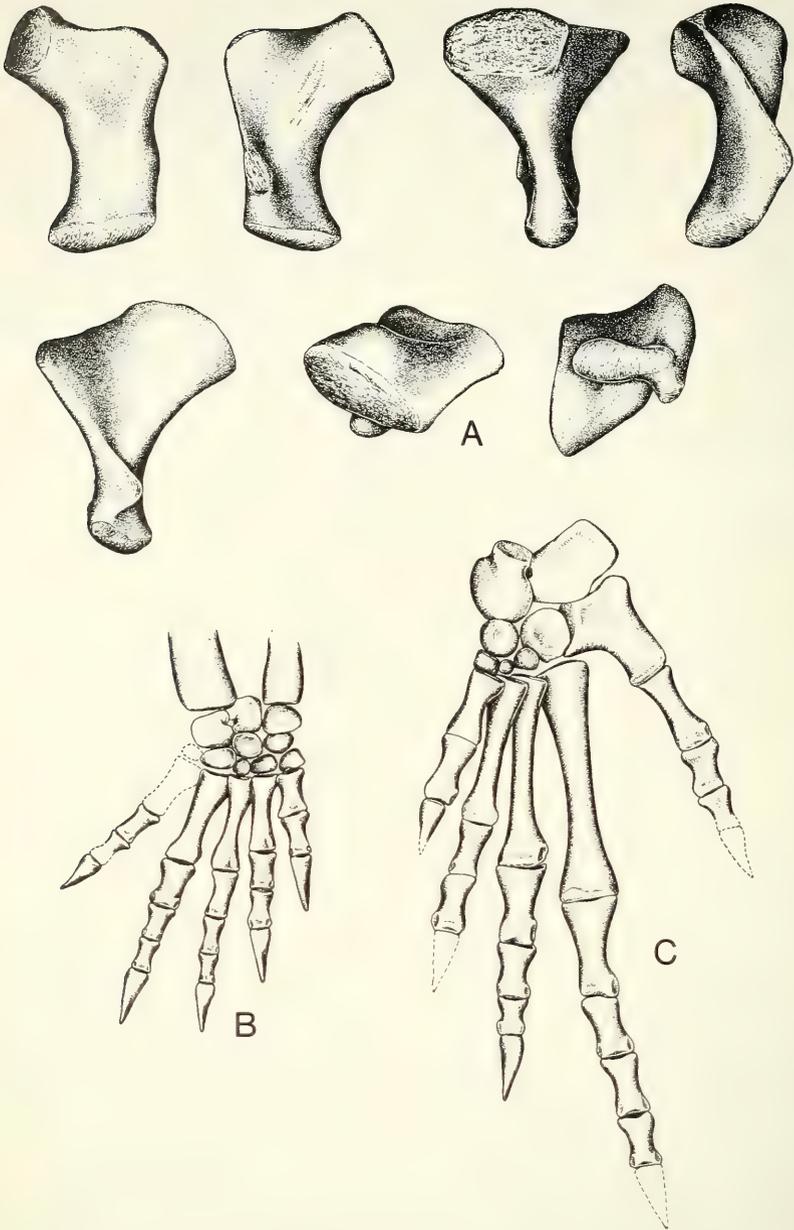


Fig. 6. *Noteosuchus*. A. Left fifth metatarsal in dorsal, ventral, medial, lateral, ventrolateral, proximal and distal views; $\times 2$. B. Right hand in dorsal view; $\times 1$. C. Left foot in dorsal view; $\times 1$.

phalanges are all of approximately the same length, roughly that of the first metacarpal. The unguals are long, fairly sharp, and somewhat recurved. Longitudinal grooves along the ventral margin demarcate the base of a tubercle for the attachment of the flexor tendon. Digits one, two and three definitely have a phalangeal count of two, three, four. The fourth also appears to have only four, although the slight displacement of the bones indicates the possibility that one more might have originally been present. An element adjacent to the fourth metacarpal is probably a phalanx from the fifth digit, from which another proximal and the ungual phalanx are preserved.

PELVIC GIRDLE AND REAR LIMB

The pelvic girdle is of the primitive plate-like appearance seen in eosuchians, other primitive rhynchosaurs and proterosuchian archosaurs. There may be a slight down-turning of the pubis, but this is difficult to ascertain as a result of the manner of preservation. There is certainly a prominent pubic tubercle. There is a small obturator foramen at the posterior margin of the pubis, but no development of the thyroid fenestra. The pubis and ischium both meet their counterparts

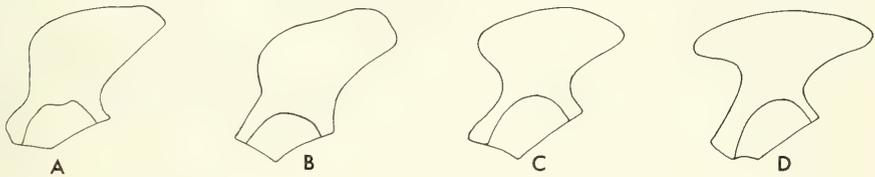


Fig. 7. Ilii of rhynchosaurs, reduced to a common size. A. *Noteosuchus*. B. *Howesia*. C. *Stenaulorhynchus*. D. *Paradapedon*. (B.–D. from Chatterjee 1974.)

along the full length of their medial margins. The ilium closely resembles that of *Mesosuchus*, in having a broad blade and narrow anterior and posterior ridges surrounding an essentially circular acetabulum. Chatterjee (1974) has illustrated a series of ilia from more advanced rhynchosaurs, which show progressive anterior extension of the blade. In *Noteosuchus*, the anterior margin is nearly vertical. The pubis and ischium appear to contribute equally to the acetabulum, in contrast to the condition in *Proterosuchus*, in which the pubis is excluded. Except for its smaller size, the ischium is almost identical with that of *Proterosuchus*.

The bones of the rear limb (Fig. 5) resemble those of *Howesia* and *Mesosuchus* in their length and proportions. They are much slimmer than those of *Proterosuchus*. In anterior or posterior view, the femur is notably sigmoidal in configuration, as is that of *Mesosuchus*. The proximal articulating surface is a flat, nearly square area, which is continuous with an internal trochanter that nearly doubles the thickness of the end of the bone. This structure is continuous with the anterior surface of the femur, and tapers gradually toward the middle

of the shaft. The intertrochanteric fossa is short without a definite distal limit. There is no adductor crest.

The tibia is approximately 90 per cent the length of the femur. There is a large, more or less triangular, proximal articulating surface, and no cnemial crest. The shaft rapidly narrows to an oval cross-section, and then very gradually thickens toward a flat, circular, distal articulating surface. The fibula is a slim, flattened bone with a small oval articulating surface proximally and a larger, flattened area distally. Distally, the bone is no wider than the tibia, in contrast to that of *Galesphyrus*.

The feet of the only specimen of *Noteosuchus* are particularly well known. Although somewhat disarticulated, the individual elements are perfectly preserved, retaining their original three-dimensional configuration. There is little difficulty in restoring the natural arrangement of the foot. Its elements are figured individually and in articulation in Figures 6 and 12. The general configuration is comparable to the tarsus of later rhynchosaurs recently reviewed by Hughes (1968). Before detailed description of the feet is possible, a very serious question of the homology of the units must be settled. Romer (1956) and Schaeffer (1941) identify the proximal elements in the tarsus of rhynchosaurs as astragalus, calcaneum and centrale—the elements present in the vast majority of primitive reptiles. Hughes (1968), in his recent consideration of the rhynchocephalian foot, identifies the centrale as a tibiale and the astragalus as an intermedium. No centrale is recognized. This identification has been followed by Cruickshank (1972) and Chatterjee (1974).

If comparison is made with *Galesphyrus* or other primitive reptiles (Fig. 10), acceptance of Hughes's identification of the proximal elements in rhynchosaurs indicates very significant differences. The astragalus must be assumed to revert to a more primitive state in which the intermedium and tibiale are not co-ossified, a condition not seen in any other reptile. Presumably, the proximal centrale, a third bone which was incorporated into the astragalus of primitive reptiles (Peabody 1951), remains with one or the other of the two recognized elements. At the same time, the distal centrale is presumably lost or incorporated in some other area of ossification.

In fact, there is a considerably easier way of looking at the changes in the proximal series. Rather than both losing the distal centrale and breaking down the astragalus into its primitive components, one need only enlarge the distal centrale from the condition seen in *Galesphyrus* and incorporate it more closely with support of the tibia. The element termed 'intermedium' by Hughes is in fact structurally and functionally completely comparable with the astragalus of *Galesphyrus*, captorhinomorphs and other primitive reptiles. In all these forms there are large but distinctly separate facets for articulation with the tibia and fibula. The so-called tibiale of rhynchosaurs has the same relationship to the astragalus and to the first three distal tarsals as has the centrale of all primitive reptiles.

Despite their obvious homology, the relationship of the astragalus with the

calcaneum in *Noteosuchus* and the shape of the calcaneum are distinctly advanced over the pattern of eosuchians (Carroll 1976*b*) and completely comparable to that seen in more advanced Triassic rhynchosaurs. The astragalus has a well-developed peg which overrides the medial end of the calcaneum, and the latter bone has a distinct lateral tubercle. The centrale is a smaller, nearly spherical bone with no finished surface. It is not as closely integrated with the astragalus as it is in middle and late Triassic rhynchosaurs. Although the pattern of the proximal tarsals can be derived from that seen in eosuchians, no known eosuchian specifically presages this condition. There is no fifth distal tarsal. The fourth

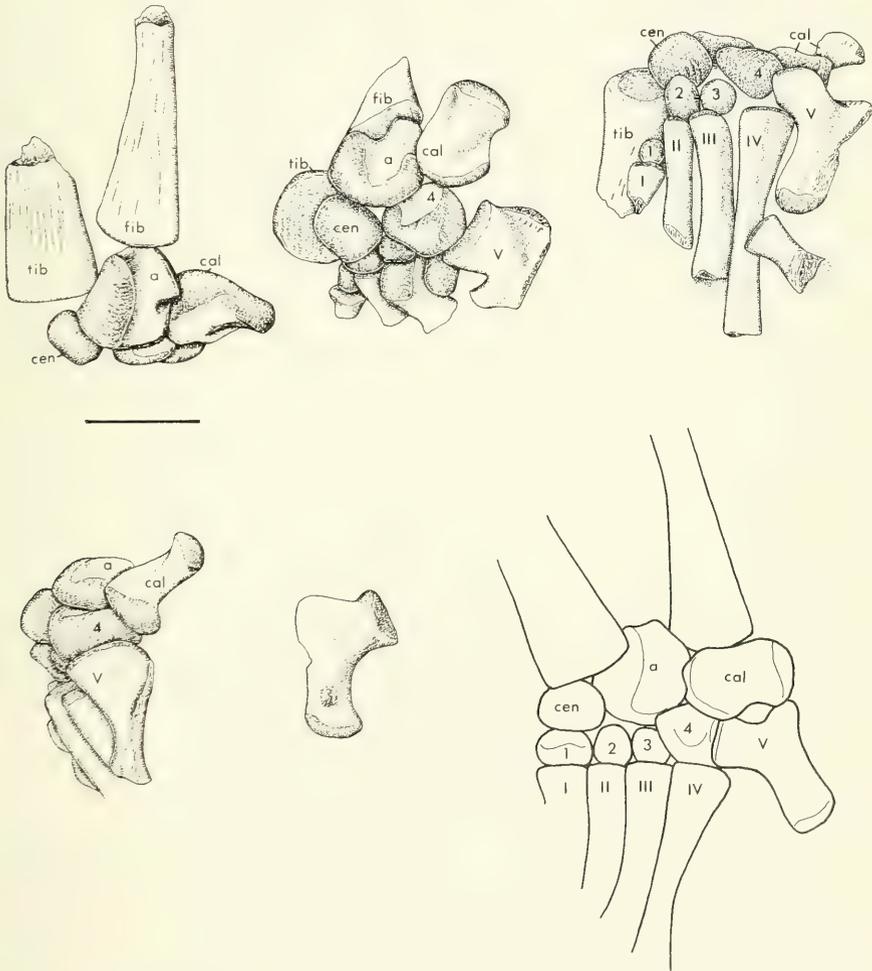


Fig. 8. Right foot of *Howesia*, South African Museum 5886, in various views; fifth metatarsal in ventral view; restoration of foot; $\times 1.5$. Abbreviations: a—astragalus; cal—calcaneum; cen—centrale; fib—fibula; tib—tibia; 1, 2, 3, 4, 5—distal tarsals; I, II, III, IV, V—metatarsals.

distal tarsal is a large, flat, quadrangular bone, supporting principally the calcaneum. The second and third distal tarsals are much smaller, essentially spherical elements. The first distal tarsal is a larger oval bone, articulating with almost the entire proximal end of the first metatarsal.

The lateral margins of the proximal end of the first four metatarsals overlap each other in succession. The length of the metatarsals increases steadily from the first to the fourth. All are approximately twice as long as their counterparts in the forelimb. The fifth metatarsal (Fig. 6) is shorter than all but the first and exhibits all the characteristics cited by Robinson (1975) as typifying the hooked condition in lepidosaurs. The proximal end of the shaft angles sharply medially and presents a very large articulating surface to the fourth distal tarsal. There is no articulating surface between the fourth and fifth metatarsals. Laterally, the proximal end of the bone has a distinct outer process. The dorsal surface of the shaft is evenly convex from side to side throughout its length. Ventrally, the lateral margin is projected as a distal plantar tubercle. There appears to be a smaller medial tubercle as well. The distal articulating surface forms a broad arc on which the digit could rotate widely.

The proximal phalanges are all considerably shorter than their corresponding metatarsals; those of the first two digits are considerably smaller than the rest. The length of the remaining phalanges diminishes gradually. The ungual of the first digit is seen on the right side; two on the left are probably from digits three and four. As in other rhynchosaurs, there is apparently still the primitive reptilian phalangeal count of 2, 3, 4, 5, 4.

Large but fairly typical reptilian ventral scales can be seen among the ribs.

M. E. Malan, who is currently studying the rhynchosaurs from the *Cynognathus* zone—*Howesia* and *Mesosuchus*—kindly gave the author permission to prepare and illustrate the feet of these forms (Figs 8–9). They show a striking similarity to the feet of *Noteosuchus*. Except for the definite identification of a first distal tarsal and elimination of the possibility of a separate medial centrale beneath the astragalus, little modification of the reconstruction of *Howesia* given by Broom (1906) is required. Additional preparation has shown that most of the elements are larger than he had estimated; consequently, all the bones are more closely fitting. The relatively small size of the centrale and its separation from the astragalus reflect the more primitive condition of this genus in comparison with the Middle Triassic forms described by Hughes.

Mesosuchus is slightly closer to the pattern of the later forms. Hughes has admitted some difficulty in interpreting the drawing of *Mesosuchus* provided by Houghton (1921, plate 3 (fig. 6)). Further preparation of this specimen (Fig. 9B) demonstrates an anatomy very similar to that of *Howesia*. The element identified as intermedium is actually the lateral portion of the astragalus; the presumed break from the more medial area is simply the sharp change in angle at the level of the raised articular facet for the tibia. The elements shown by Houghton and Hughes as fused calcaneum and tibiale are clearly separable into astragalus and centrale. Although definitely not fused, the centrale shows a more intimate

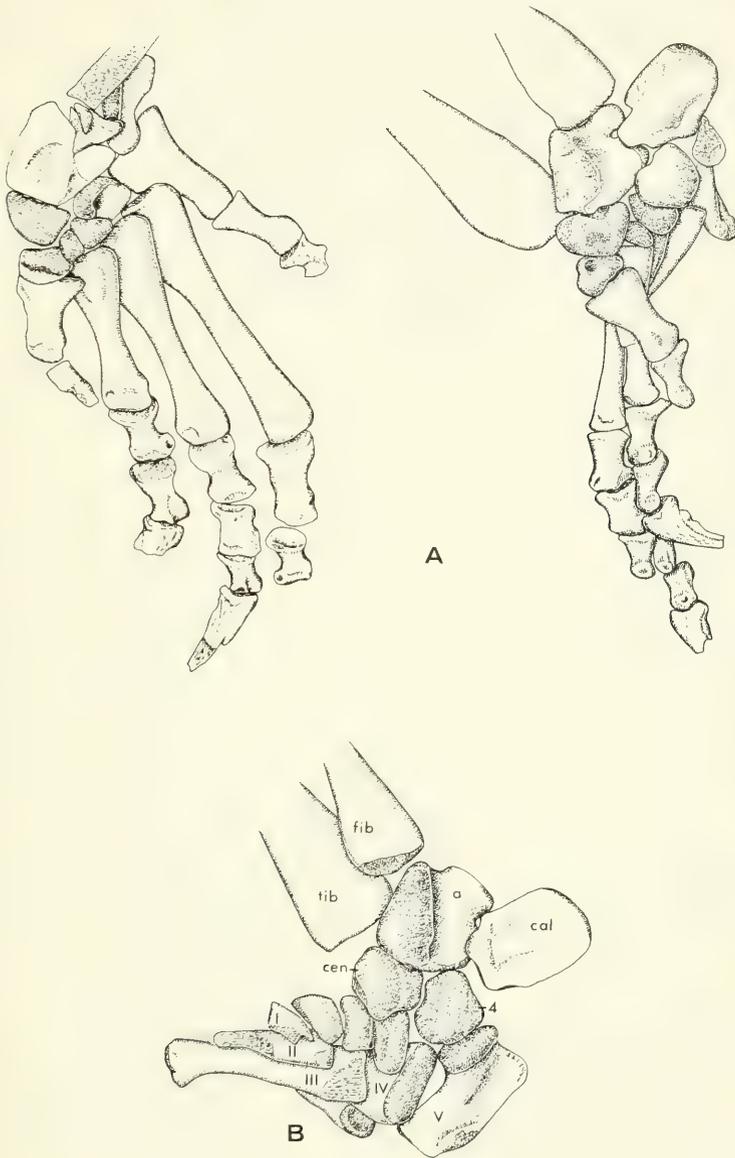


Fig. 9. *Mesosuchus*. A. South African Museum 7416, left and right feet. B. South African Museum 6046, right foot. All $\times 1.5$. Abbreviations as for Figure 8.

association with the astragalus than is seen in *Howesia*. The left and right feet of *Mesosuchus* are fairly well preserved in a second specimen, South African Museum 7416 (Fig. 9A), confirming the pattern shown in the earlier described ankle and providing additional information concerning the metatarsals and phalanges.

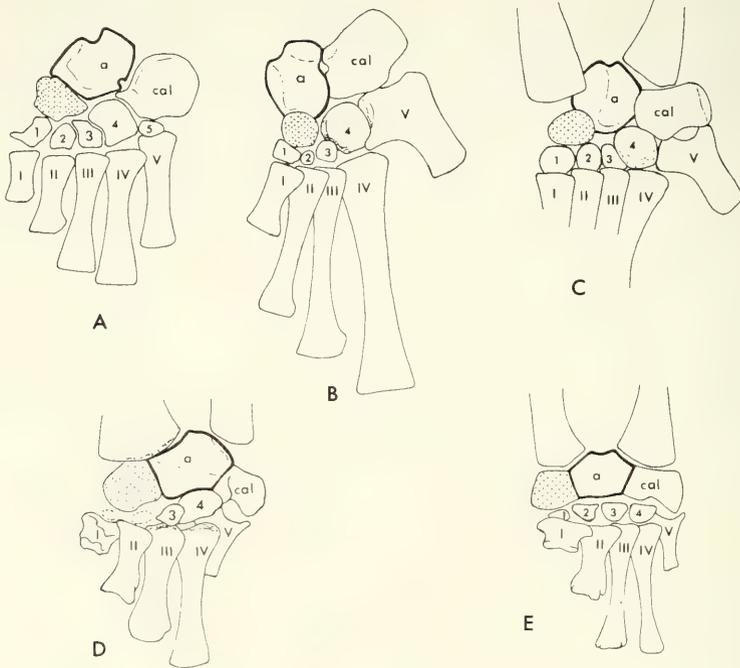


Fig. 10. Tarsals of diapsids. A. *Galesphyrus*; $\times 1,5$. B. *Noteosuchus*; $\times 1$. C. *Howesia*; $\times 1$. D. *Stenaulorhynchus*; $\times 0,25$ (from Hughes 1968). E. *Paradapedon*; $\times 0,25$. Astragalus is heavily outlined, centrale is coarsely stippled. Abbreviations as for Figure 8.

DISCUSSION

Comparison of all known elements of the skeleton of *Noteosuchus* with those of the slightly younger rhynchosaurs *Howesia* and *Mesosuchus* shows extremely similar patterns. Specimens of all three genera are of nearly equal size and degree of ossification, further emphasizing their anatomical similarity.

Despite the absence of the skull and anterior trunk region, *Noteosuchus* may be included in the same family with considerable assurance. It is not possible, however, to determine whether or not generic distinction from both younger genera is justified.

Assignment of *Noteosuchus* to the Rhynchosauridae extends the known range of the family to the very base of the Triassic. Unfortunately, *Noteosuchus*

provides little if any more specific information regarding the origin of the rhynchosaurs. Eosuchians from earlier beds are either much more primitive, e.g. *Youngina* (Gow 1975) and *Galesphyrus* (Carroll 1976*b*), or specialized in a totally different manner, e.g. *Heleosaurus* (Carroll 1976*a*), and the Tangasauridae (Haughton 1924*b*; Piveteau 1926) and Paliguanidae (Carroll 1975, 1977). One must assume a considerably earlier separation of rhynchosaurs from the ancestral eosuchian stock. The description of a primitive diapsid from the Upper Pennsylvanian (Reisz 1975) indicates that rhynchosaurs could have diverged from the basic eosuchian stock long before their fossils are first known in the Lower Triassic.

A further comparison of *Noteosuchus* and other primitive rhynchosaurs that bears investigation was made by Cruikshank (1972). In describing the archosaur *Proterosuchus* he stated (p. 116), 'it is possible that *Proterosuchus* represents a slightly modified carnivorous rhynchocephalian'. Cruikshank stressed the similarity of the feet of these forms. This was emphasized by his acceptance of Hughes's terminology of the proximal units asfibulare, intermedium and tibiale. More detailed illustrations of the feet of *Proterosuchus* and *Noteosuchus* (Figs 11–12) show how close the resemblance is. Comparisons are particularly striking between the astragalus and calcaneum, both of which exhibit considerable complexity.

The elements in *Proterosuchus* are approximately 50 per cent larger than those of *Noteosuchus*, and there are some differences in proportions, but hardly more than might be expected in different species within a genus or even different-sized individuals in a single species. Functionally, they must have been nearly identical. One difference which does appear significant is the configuration of the facet of the astragalus that articulates with the tibia. In *Proterosuchus* it is very broad and flat, but in *Noteosuchus* and also *Mesosuchus* and *Howesia* it is narrower and distinctly convex.

In *Proterosuchus* and early rhynchosaurs, the centrale is a large, essentially spherical bone, with no area of finished surface, that shares with the astragalus support of the tibia. The fourth distal tarsal is a larger element that is notched to receive the much smaller third distal tarsal. The second distal tarsal is much smaller, but the first is comparable in size to the centrale. The metatarsals (notably the hooked fifth) and the phalanges are similar in all significant respects, although the fifth digit appears to have one more phalanx in *Noteosuchus*.

Despite the general similarities of the postcranial skeleton between *Proterosuchus* and *Noteosuchus*, and the striking similarities of the tarsus, a number of specific differences can be cited:

1. Exclusion of the pubis from the acetabulum by the ilium in *Proterosuchus* but not *Noteosuchus*.
2. Sharp posterior angle of the iliac blade in *Proterosuchus* in contrast with a rounded margin in *Noteosuchus*.
3. Three-part division of the posterior sacral rib in *Proterosuchus*, in contrast with two parts in *Noteosuchus*.

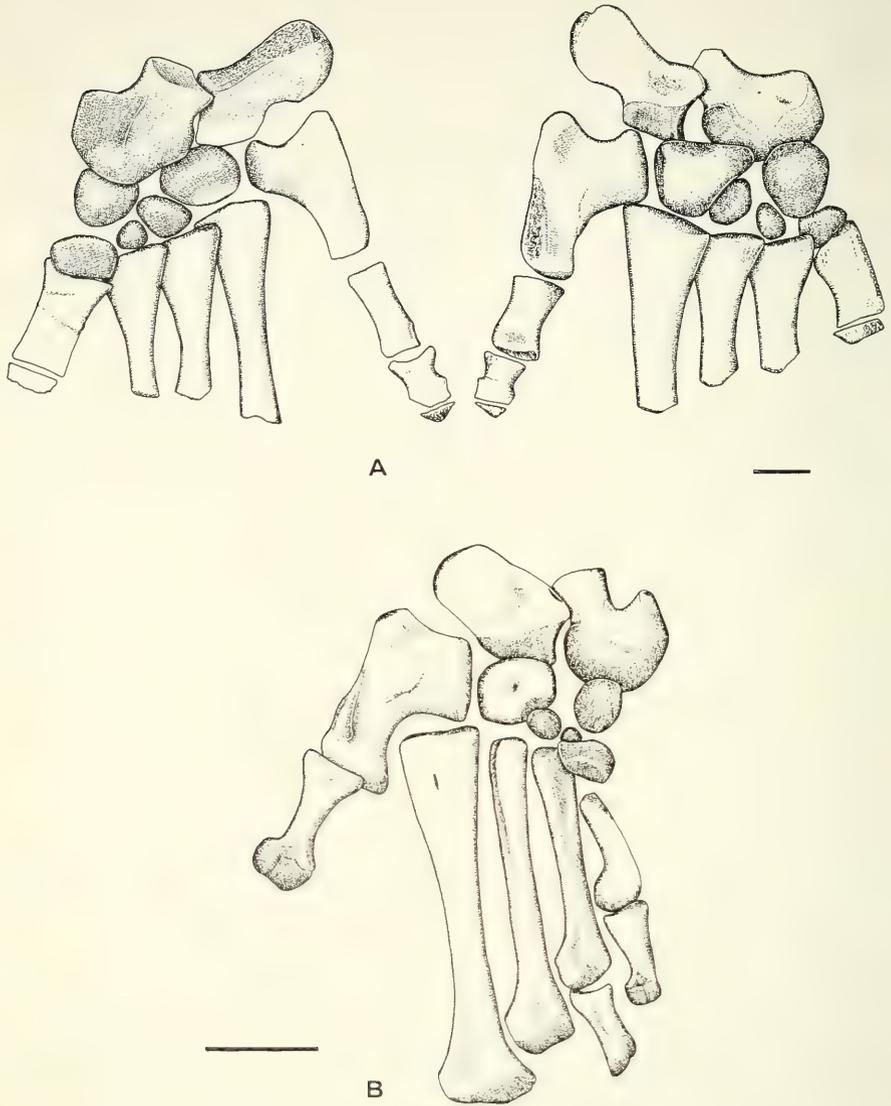


Fig. 11. A. *Proterosuchus*, dorsal and ventral views of the left foot; $\times 0,75$. B. *Noteosuchus*, ventral view of left foot; $\times 1,5$.

4. Proportionately heavier limb bones in *Proterosuchus*, corresponding to the greater size of the adult.

It is difficult to evaluate the relative significance of the head and the post-cranial skeleton in establishing phylogenetic relationships, although in practice more importance is nearly always given to cranial remains. In view of the constancy of important cranial features among both primitive thecodonts (Ewer 1965; Cruickshank 1972; Hughes 1963) and rhynchosaurs (Malan 1963; Chatterjee 1974), it seems probable that the similarities in foot structure in

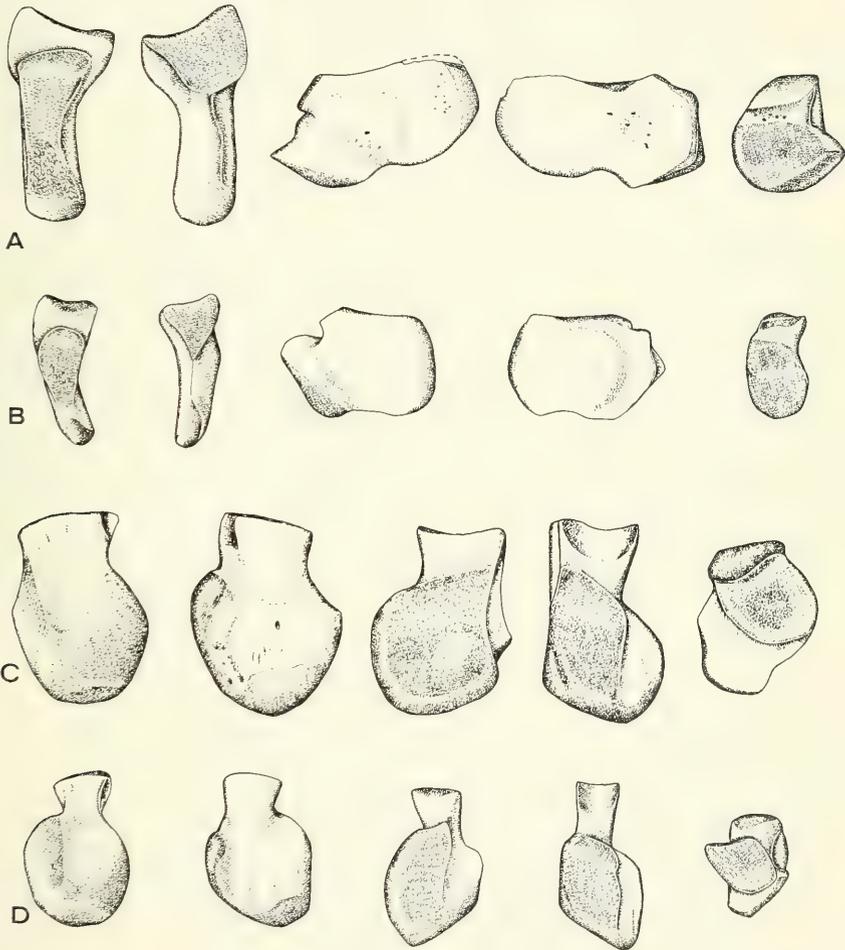


Fig. 12. Proximal tarsals of a rhynchosaur and an archosaur. A. *Proterosuchus*, left calcaneum in proximal, distal, dorsal, ventral and medial views; $\times 0,75$. B. *Noteosuchus*, left calcaneum in same views; $\times 1,5$. C. *Proterosuchus*, left astragalus in dorsal, ventral, medial, lateral and proximal views; $\times 0,75$. D. *Noteosuchus*, left astragalus in same views; $\times 1,5$.

primitive rhynchosaurs and *Proterosuchus* are a result of convergence of this particular feature, rather than being indicative of close relationship. In the absence of knowledge of the specific ancestors for either rhynchosaurs or *Proterosuchus*, this cannot, however, be stated with great confidence.

There are also a number of points of similarity between the postcranial skeleton of *Noteosuchus* and that of *Prolacerta*, recently described by Gow (1975). The shapes of the sacral ribs and the ilium are essentially the same, and the femur shows a comparable twisting. However, the greater length of the tibia and fibula, relative to the femur, provides a simple way of differentiating these forms. The foot of *Prolacerta* shows a comparably hooked fifth metatarsal. Material of both *Prolacerta* and rhynchosaurs demonstrates the difficulty of assigning late Permian and early Triassic diapsids to either the Lepidosauria or the Archosauria, as distinguished by Romer (1956).

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6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family *Nuculanidae*

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers, date and geographical positions.

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.



ROBERT L. CARROLL
NOTEOSUCHUS—THE OLDEST
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