A Revision of the Jurassic Reptile Hallopus victor (Marsh), with Remarks on the Classification of Crocodiles

A. D. Walker

Phil. Trans. R. Soc. Lond. B 1970 **257**, 323-372
doi: 10.1098/rstb.1970.0028

A REVISION OF THE JURASSIC REPTILE *HALLOPUS VICTOR* (MARSH), WITH REMARKS ON THE CLASSIFICATION OF CROCODILES

By A. D. WALKER
Department of Geology, University of Newcastle upon Tyne

(*Communicated by T. S. Westoll, F.R.S.—Received* 30 *July* 1969)

[Plate 72]

CONTENTS

The unique holotype of *Hallopus victor* (Marsh), from the Upper Jurassic of Garden Park, Colorado, is redescribed. The bones previously identified as pubes (Marsh 1890) or ischia (von Huene 1914) are regarded here as the left radius and ulna, and the 'ulna' and 'radius' of previous workers are considered to be the left radiale and ulnare. Marsh's identification (1890) of the ischium and his orientation of the scapula and femur (1896) are upheld. The presence of a humerus on the larger slab is confirmed.

Hallopus is interpreted as a highly specialized, cursorial crocodilian, with slender, hollow bones, a greatly elongated radiale and ulnare, and a roller-like joint between these and the metacarpals. The manus is pentadactyl with a symmetrical distribution of lengths about the central axis and some proximal wedging-out of the metacarpals. The iliac blade is elongated and resembles that of *Orthosuchus*, the ischium is reminiscent of that of *Protosuchus*. The femur has a lesser trochanter, a fourth trochanter and a 'pseudointernal' trochanter, but no greater trochanter. The tibia is longer than the femur. The tarsus is basically crocodilian in pattern, but greatly compressed and specialized. The first metatarsal is reduced to an elongated splint, permanently recessed into metatarsal II. Metatarsals II to IV are symmetrical in length with III longest, metatarsal V is reduced, pointed, and lacks phalanges. The interpretation put forward provides a consistent explanation of the peculiarities of the skeleton of *Hallopus* as a variant on the basic crocodilian plan.

The details of the articulation of the carpal and tarsal joints are described as far as preservation permits, and possible movements are considered. The carpometacarpal and tarsal joints are simple hinges, but the proximal carpal joint appears to have been relatively immobile and the elongation of the radiale and ulnare is viewed as a device to compensate for the increase in length of the tibia. The femur has an off-set, ball-like head and evidently moved essentially in a parasagittal plane. The pes is functionally tridactyl, with the metatarsals locked together proximally. It is concluded that both fore- and hind-feet were digitigrade during movement, although in a stationary pose the metatarsus may have been in contact with the ground. Some aspects of the pelvic and hind-limb musculature are briefly discussed. Functional analogies from the locomotory point of view are limited by the lack of cursorial quadrupedal archosaurs for comparison. It is concluded that a hare-like bounding gallop was the most probable type of fast locomotion in *Hallopus*.

Vol. 257. B. 816. (Price £1. 9*s*.; U.S. $3.80) 29 [Published 26 February 1970

Although no skull bones have been identified, evidence from the postcranial skeleton is adduced to show that *Hallopus* is of pedeticosaurid descent. The relationships of early crocodilomorphs are discussed, and it is deduced that two basic stocks diverged from a common ancestry during the middle part of the Trias. These two groups are included in an expanded Order Crocodylomorpha. The Suborder Crocodylia has the Triassic Stegomosuchidae as its radicle and contains 'normal' crocodiles (including the Sebecosuchia but not the Baurusuchidae). The suborder Paracrocodylia is proposed for mainly cursorial forms, to include the infraorders Pedeticosauria, Baurusuchia and Hallopoda. Diagnoses for these groupings are presented. An origin for both stocks from a form close to *Cerritosaurus* is postulated. *Erpetosuchus* and *Dyoplax* are not now regarded as crocodilomorphs.

The possibility of an early cursorial phase in crocodilian evolution is briefly discussed, and it is tentatively suggested that the gallop occasionally observed in young crocodiles (Cott 1961) may be a relic of a primitive type of locomotion in the group. The significance of this to the emergence of the crocodilian type of shoulder-girdle is considered.

1. INTRODUCTION

The unique specimen of *Hallopus victor* has always been something of a puzzle to palaeontologists. Many of the bones are incomplete, nothing of the skull is identifiable, even the horizon of the specimen has been disputed. Yet I believe it provides sufficient evidence to indicate its systematic position with some certainty, and also displays a remarkable example of convergence, in a reptile, towards a mammalian type of limb structure and locomotion.

The specimen was discovered in April 1877 near Canyon City, Colorado, and was described by Marsh in September of the same year (1877) as *Nanosaurus victor*. The horizon was said in this paper to be 'probably Jurassic, but possibly in the lower part of the Dakota Group' (i.e. early Cretaceous). As usual, Marsh was reticent about the locality, simply giving the 'Rocky Mountains'. Later (1881) Marsh separated the species from *Nanosaurus* (type species *N. agilis* Marsh) and based upon it the new genus *Hallopus*. Nomenclatorially, therefore, the specimen should be referred to as *Hallopus victor* (Marsh). In the 1881 paper the specimen is said to come from Colorado.

In later publications Marsh (1881, 1891) successively lowered the horizon from which *Hallopus* supposedly came, so that a basal Jurassic, or possibly Upper Triassic age, was finally assigned to it. This position has been generally accepted. However, in a paper which has often been overlooked, Schuchert (1939) gives circumstantial evidence which makes it very difficult to avoid the conclusion that the first statement of horizon given by Marsh was correct, that is, near the top of the Morrison formation. A consequence of this is that the strata termed by Marsh (1891) the 'Hallopus Beds', probably do not contain *Hallopus*.

Marsh's first description (1877) of the specimen is very short, without figures. The animal is said to have been 'about as large as a fox' and is simply stated to be a 'small Dinosaur'.

In 1881 the peculiarity of the calcaneum is noted, and taken to indicate 'a foot especially adapted for leaping'. The genus was made the type of a new family, the Hallopodidae, placed by itself in the new Suborder Hallopoda of the Order Dinosauria. Later (1882, 1890) Marsh was less certain of its dinosaurian nature, concluding (1890, p. 417) 'the Hallopoda at present may be regarded as an order of Dinosaurs standing more apart from typical forms than any other'. The size is now given as that of a rabbit. In 1895, however, he regarded *Hallopus* as a link between typical dinosaurs, with which he believed it agreed in the 'true Dinosaurian pelvis, with the pubic bone taking part in the open acetabulum' and the more primitive forms *Aetosaurus*, *Alligator* and *Belodon*, which also have a calcaneal heel. In this paper and in 1896, the Suborder Hallopoda is retained within the dinosaurian Order Theropoda.

The specimen was first properly described by Marsh (1890) with a figure of the left hind-limb.

This description and figure were repeated later with the addition of a plate (1896, Pl. VI) showing, in outline, the restored fore- and hind-limbs, with their girdles. Von Huene & Lull (1908) gave a revision of the species with the addition of some details. The most notable changes are the suggestion of a third sacral vertebra, the inversion of the scapula, and the interchange of the pubes with the ischia. This paper contains many minor inaccuracies, of which the accidental transposition of 'right' for 'left' in several places is the most baffling. Von Huene (1914) gave essentially the same interpretation, repeating the earlier figures and adding a plate showing the two blocks for the first time. This paper is more comprehensive than that of Von Huene & Lull, and most of the internal inconsistencies have been removed, so that it alone will be referred to in the present account. Von Huene considered *Hallopus* to be a primitive coelurosaur, which by virtue of its caudal vertebrae, scapula, hand and pubis stood nearest to the Pseudosuchia. In this view, and also no doubt in the identification of the pubis, he was certainly influenced by Williston (1905) who was strongly in favour of allocating an Upper Triassic age to the Hallopus Beds.

Since 1914, no detailed re-examination of the specimen has been made. In systematic works *Hallopus* appears as a coelurosaur, primitive in retaining a calcaneal heel. Romer (1956) places it with *Procompsognathus* (in which, however, the calcaneum is not preserved) in the Hallopodidae, and gives the age as Upper Triassic or Lower Jurassic. De Lapparent & Lavocat (1955) took note of Schuchert's paper and allied *Hallopus* with the Upper Jurassic *Compsognathus* in the Compsognathidae. The most recent classification by Romer (1966) puts it, with reserve, in the Coeluridae, as Upper Jurassic.

My interest in *Hallopus* arose in the first place from its apparent similarity to *Saltopus* from the Lossiemouth Beds (Upper Triassic) of the Elgin area. Study of *Hallopus*, however, soon dispelled the notion of a close relationship between it and *Saltopus*. The latter has three sacral vertebrae, a long slender pubis and ischium, a non-elongate carpus, and a calcaneum with reduced heel, and is clearly a primitive coelurosaur.

2. The horizon of *Hallopus*

Schuchert (1939) presented a convincing case for an Upper Jurassic age for *Hallopus*, i.e. from near the top of the Morrison formation. His argument depends upon certain letters from Baldwin, a collector employed by Marsh, to Marsh himself. There are, however, certain inaccuracies and inconsistencies in Schuchert's paper which still leave one uncertain as to the exact locality of the specimen. It is difficult to reconcile some of the statements made by him with those of Osborn & Mook (1921). Thus Schuchert assumed that the 'little knoll or tent-shaped point' mentioned by Baldwin as the place of origin of *Hallopus*, is a small hill known as 'The Nipple' at the edge of the escarpment of the Morrison formation at Garden Park, Colorado. Schuchert seems also to assume that the 'large bones' which were being excavated a few metres away just above the *Hallopus* level by a party of Cope's collectors, were the type of *Camarosaurus supremus* Cope. According to Osborn & Mook (1921), however, this specimen came from Cope Quarry no. 1, some 460 m to the south-west of The Nipple. The dates of collection of *Hallopus* (about 15 April 1877) and the type of *Camarosaurus supremus* (not known with certainty but probably some time in March 1877, according to Osborn & Mook) agree closely, and support Schuchert's assumption to this extent, but of course this would mean that The Nipple is not the *Hallopus* locality, which would have to be close to Quarry no. 1. This seems unlikely. Another difficulty is that in one letter Baldwin states that the *Hallopus* level is 9 m below the top of the 'low red point', and in another 4.5 m below the apex. Schuchert (1939, p. 25) however, chose as the horizon of *Hallopus* a band of brown nodules only 1.5 m below the summit, from the section at The Nipple given by Mook in Osborn & Mook (1921).

Baldwin did not collect the specimen himself, but acquired it for three dollars from a 'Curiosity shop' in Colorado Springs, having heard of the discovery of a supposed fossil 'bird' some days previously. The actual collectors, according to one of the letters quoted by Schuchert, were John Jennings and S. C. Robinson. These were local men, like Baldwin, and, being collectors, were probably well known to him. At any rate Baldwin visited the spot himself soon afterwards in the hope of finding more material, and was able to give precise information to Marsh as to the horizon and locality of the specimen.

Although there is thus some slight doubt as to whether the locality is in fact The Nipple, from the general sense of Baldwin's statements it is clear that the horizon is in the lower part of the 6 m or so of red strata which cap the Morrison formation in this area. These beds are variously described as 'brown clay', 'chocolate-coloured shale' and, by Baldwin, 'red sandstone' and 'solid red rock'. According to Schuchert (1939), a possible reason why Marsh, in spite of clear evidence from Baldwin, in later papers placed the horizon much lower, was that he was unaware of the existence of red beds in the Morrison formation, and therefore assumed that the specimen must be Triassic or early Jurassic in age. It may be added that the high degree of specialization attained by the skeleton is consistent with an Upper Jurassic assignment.

3. PRESERVATION AND PREPARATION

The specimen (Yale Peabody Museum no. 1914) consisted originally of two slabs (figures 1 and 2) of which the smaller only partly counterparts the larger. The bones, when clean, are white, in a matrix of reddish brown, fine-grained, muddy sandstone with mudstone or shale fragments embedded in it. These are especially numerous on the back of the larger slab. It does not seem correct to describe the slabs as a nodule, as Schuchert does (1939, p. 25). At some time the smaller slab has been trimmed on three sides. Two small pieces of the trimmings have been retained, of which the larger is devoid of bone. The smaller piece, which fits on to the smaller slab at a narrow contact behind the tarsus, has part of a bone which might conceivably be from the skull, but most of its boundaries are uncertain and I have been unable to identify it.

A very thin calcite vein runs straight across both slabs, perpendicular to their contact surfaces. This vein passes lengthways through the left tibia, astragalus and calcaneum, and provides a useful reference line for transferring measurements and angles from one slab to the other. Part of its surface has been exposed in the smaller slab, extending medially from the calcaneal heel; this appears as a light coloured area resembling bone in figure 19, plate 72.

The bones have suffered two phases of damage. In the first phase the pubic and ischiadic peduncles of the right ilium were largely broken away. The anterior half of the left ilium, the bowl-like antero-ventral part of the scapula, and some of the proximal portion of the ischium, were also lost, to name the most conspicuous damage. The fragments do not seem to be present on the slabs, so that a phase of transport apparently occurred, or, more probably, the action of a predator or scavenger was involved. Later, some parts of the skeleton were subjected to decay *in situ*. For example, the anterior point of the right ilium is joined on to the body of the bone by a very slender bridge and the second sacral rib of the left side is prolonged backward as a narrow, almost invisible, strip of bone. Obviously, these could not have survived transport. Unfortunately, some of the joint-surfaces have been attacked by this process.

The limb-bones are all very hollow, the cavities being filled with a deep-red fine powder. The amount of crushing which they have undergone is usually not great, however, and their original form has, on the whole, been very well maintained. The joint-surfaces, where preserved, are pink in colour and the bone has a soapy texture. This is probably due to the fact that the originally cartilage-covered surfaces took up the red haematite stain more readily.

Preparation has mainly been directed towards elucidation of points of detail. Most time has been spent on the left tarsus and metatarsus, the carpus and manus, and the proximal ends of the femur and tibia. The possibility was considered of removing the matrix entirely from behind the ankle joint so that this could be seen clearly without needing to rotate the block from side to side, but in order to afford some measure of protection to this fragile and unique structure, a thin pillar has been left supporting the calcaneum. A new aperture was cut between tibia and metatarsal II, to prove continuity of metatarsal I.

The vibro-tool has been extensively employed, with the use of mounted needles for fine details. The siliceous nature of the matrix soon takes the point off any needle, making preparation time-consuming.

4. Identification of bones present

It should be stated at the outset that radiography has revealed no trace of bones other than those which are exposed on the surface of the blocks.

A diagram combined from both slabs, showing the layout of the bones, proved to be of no help in suggesting identifications—the arrangement appears to be random, apart of course, from those elements which are still articulated. Many other identifications, apart from those discussed below, have been considered for some of the bones, but there is space only to deal with the most plausible suggestions. In the following discussion numbers in parentheses refer to the bones as shown in figures 1 and 2.

No elements of the skull have been identified. Certain fragments near the *right tibia* (21) and in one of the smaller pieces may be such however. The vertebral column is represented by the *sacrum* (1) consisting of two co-ossified vertebrae, and a small number of *mid-caudals* (2). A few *ribs* (3) and one *chevron bone* (4) are also present.

In identifying the bone adjacent to the left tibia as a *scapula* (5), I am following previous authors. This element cannot be a limb-bone, since all these are, as Marsh pointed out (1877) hollow with thin walls, whereas the bone in question is thin, flattened and lacks a lumen. Ilium and ischium (see below) are ruled out, and pubis would seem to be the only other likely alternative. The bone does bear a superficial resemblance to a crocodilian pubis, but it is broader and more flattened than any of this type with which I am acquainted (all known crocodilian pubes have a rod-like shaft), and the forking of the 'proximal' end also rules out this identification. It is manifestly not a dinosaurian pubis, and, since the possibility of a Triassic age for *Hallopus* cannot be entirely excluded, it may be added that it is quite unlike a thecodont pubis and shows, in addition, no indication of the 'twist' which occurs in pubes of that type. I cannot accept, however, that the forked end is the upper one, as von Huene (1914) has it. This end is too thick and peculiar in shape to be the dorsal end of a scapula; the thin, expanded opposite end, on the other hand, is just what one would expect. One then has to account for the lack of a glenoid and the forked lower termination. It is pointed out that in many (if not all) archosaur scapulae, there is a relatively thin, bowl-like excavation in front of the glenoid which, if broken away, would yield an appearance very much like this bone. The scapula of *Pedeticosaurus* from the Cave Sandstone (Upper Trias) of South Africa (van Hoepen, 1915, Pl. XIII, and this paper, figure 8) is particularly instructive in this connexion. The specimen is stated to be mainly an impression of the right side of the skeleton. Clearly, in this instance, the medially curving bowl-like part of the scapula has been removed in the counterpart (unfortunately missing) and the bone appears very similar to that which is here identified as the scapula of *Hallopus*. Also, as noted above, other bones of *Hallopus* have clearly suffered damage during a phase of transport or predation; the loss of this part of the scapula could thus be explained.

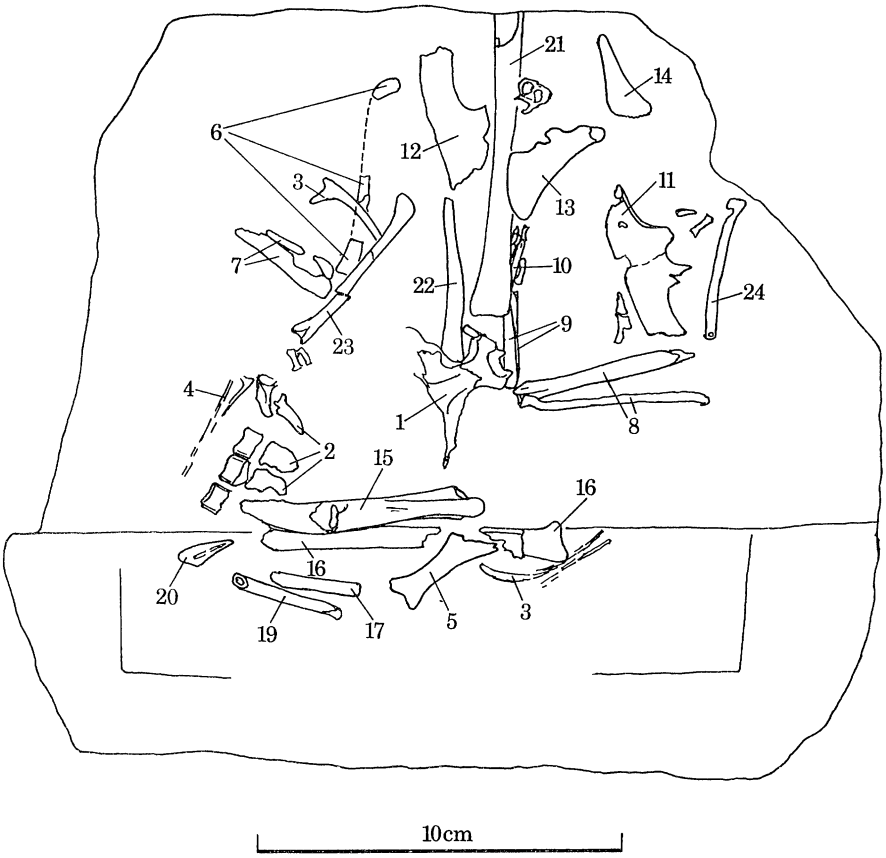


FIGURE 1. *Hallopus victor* (Marsh). The larger block (magn. × $\frac{1}{2}$) showing the arrangement and identification of the bones. The horizontal line represents the calcite vein in this and in figure 2. For key to figures 1 and 2 and abbreviations, see pull-out, p. 372.

The *humerus* (6) is a somewhat elusive bone; indeed its presence remained unnoticed by the writer for a considerable length of time. The existence of a humerus was, however, mentioned by Marsh, who devoted three sentences to its description, as follows (1890, p. 416): 'The humerus is slender, with a strong radial crest. The shaft is very hollow, with thin walls, and the cavity extends almost to the distal end. The latter is but little expanded transversely.'

Marsh also figured the bone in question (1896, Pl. VI). Von Huene was unable to recognize a humerus, and stated that Marsh had referred to a small impression near the right tibia, although Marsh did not make any statement about the position of the humerus on the blocks. This impression von Huene believed to be part of the pubis. There is, however, adjacent to the proximal ends of the right radius and ulna (7) at the edge of the smaller slab, a short portion of one end of a hollow bone (6). This I had been inclined to regard as a damaged vertebra, until further preparation showed that this could not be the case. On fitting the smaller slab in place over the larger, it can be seen that the impression of one side of this piece of bone is present in the larger slab. Beginning 13 mm away, and in line with the axis of the bone, the (here uncounterparted) surface of the larger slab shows the straight impression (7 mm in length) of part of the shaft of a bone. 21 mm beyond this impression again and in line with it there was originally a small portion of bone embedded in the matrix near the left ilium (12). These three areas (6) are extremely inconspicuous when the larger slab alone is examined, and their significance not at all apparent. After removal of the small area of bone from the larger slab with a needle, and the taking of a cast from the resulting three impressions plus the radius and ulna, no doubt is left that these impressions (and of course the hollow distal end in the smaller slab) are of the 'missing' humerus. Comparing the cast with the small slab, it can be seen that the proximal end of the radius is almost in contact with the outer (radial) condyle of the humerus, and the ulna has slipped a little distance away from the humerus, but the sigmoid notch is still opposite the position of the trochlear articulation on the latter. The orientation with regard to the radius and ulna (7) thus confirms the identification and, further, shows that these three elements are of the right side. The full length of the humerus is thus determined at 54 mm, since part of the head is preserved. This is longer than the measurement of 40 mm obtained from Marsh's figure, but agrees well in proportion with the length of the left radius and ulna, which are more complete than those of the right side. The reason for the discrepancy may be that Marsh had loose portions of the right humerus which have since become lost; that (not surprisingly) he did not recognize the impressions on the larger slab; and that the portions of the bone which he did have were incomplete. He would also be predisposed to think of the humerus as a short bone, because of the shortness of the supposed 'radius' and 'ulna'.

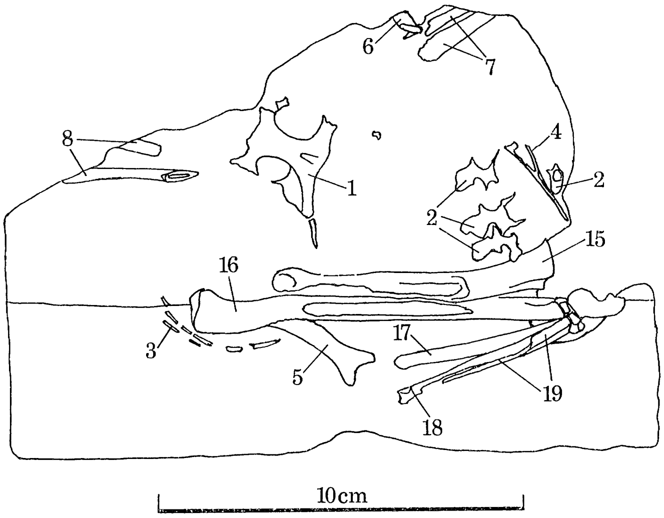


FIGURE 2. *Hallopus victor* (Marsh). The smaller block (magn. $\times \frac{1}{2}$) showing arrangement and identification of the bones. The calcite vein shows how the two blocks fit together.

The identification of the humerus in fact provided a striking example of verified prediction. Before the presence of this bone was suspected, four estimates of its length had been made, using the lengths of the radius-ulna and scapula in *Hallopus* compared with these elements and the humerus of *Pedeticosaurus* and *Hesperosuchus*, assuming a close relationship between these three forms. These four values are 55, 56, 58 and 54 mm, averaging 56 mm.

The identification of the radius and ulna is closely connected with that of the radiale and ulnare. The elements which I take to be the *left radius* and *ulna* (8) are those which Marsh took to be pubes, and which von Huene believed to be ischia, while I identify as the left *radiale* and *ulnare* (9) the two bones which previous workers have regarded as ulna and radius, respectively.

It seems unnecessary to argue at length against the identification of the radius and ulna as ischia or pubes: the mere fact of their unequal thickness is sufficient to dispose of these suggestions. The proximal end of the ulna is not as expanded as in the restorations of Marsh (1896) and von Huene (1914) and the distal end shows none of the characteristics one would expect in a pubis or ischium. Since the question of the systematic position of *Hallopus* depends to a considerable extent upon the correct identification of these elements, it is necessary to give the reasons for these new determinations in some detail.

(*a*) The distal ends of the radius and ulna (8) converge and meet; the end of the ulna is nearly in contact with the proximal end of the radiale (9) ('ulna' of previous authors) and the three bones have the appearance of a natural joint held together by decaying connective tissues.

(*b*) The radius and ulna agree in thickness with the corresponding bones of the right side, whose identification is discussed above.

(*c*) The shape of the ulna, although a little crushed proximally, agrees excellently with those of *Ornithosuchus* and *Hesperosuchus* (Colbert 1952, Fig. 23*a*). In addition to having the usual gentle sigmoid curvature which one naturally associates with this element, the shape of the distal end is particularly important. In *Hallopus* the distal end of the ulna has a shallow longitudinal groove along the medial side which dies out gradually on the shaft, and the posterior side of the distal end has a small pit. These features give the ulna some resemblance to a metatarsal; however, in metatarsals the corresponding groove (in this case on the dorsal side) is short and clearly defined both from the shaft and from the distal articular surface, and the lateral ligament-pits are larger. In addition, the ulna, which is 49 mm long (and was originally longer proximally) could only be compared on thickness grounds with metatarsal II. The latter is 46 mm long in the left foot, is thinner than the ulna and differs from it considerably in the shape of the proximal end. The flat distal termination of the *Hallopus* ulna also rules out identification as a metatarsal. Comparison with casts of the right ulna of *Ornithosuchus* (Walker 1964, Fig. 9) in which the longitudinal groove is for the reception of the radius, demonstrates a striking similarity between this ulna and the bone here identified as the ulna of *Hallopus*. Furthermore, the radius in *Hallopus* converges distally upon the ulna and, although damaged, part of it still rests in the longitudinal groove. The orientation of the ulna, as determined from the above comparisons, is such as to identify it as an element of the left side seen in posteromedial view in the larger block.

(*d*) Leaving out of consideration the bones dealt with immediately above, the 'radius' and 'ulna' of previous authors (i.e. the ulnare and radiale) (9) are, although complete, shorter and noticeably thinner than the incomplete right radius and ulna (7).

(*e*) These two bones (9) also differ very much morphologically from them and from the usual shapes of the radius and ulna in reptiles. They are, for example, in contact by means of a flange throughout their length and terminate distally in a transverse roller-joint; proximally the 'ulna' extends sideways to form a 'stop' for the shorter 'radius' in a manner which is much more like that of a crocodilian radiale than a normal ulna.

(*f*) If the above elements are really the radius and ulna, then the carpus is represented merely by a doubtful meniscus. On the other hand, if the carpus is essentially crocodilian, in spite of the great elongation of the proximal elements, then the reduction or loss of the distal carpals is not surprising, since they are very thin and disk-like in all crocodiles.

(*g*) Again, the 'radius' is very short compared with the length of the right humerus—25.5 mm/54 mm or 47 %. Only one coelurosaur, namely *Compsognathus*, is known to approach this low ratio with about 60 % (data from plaster cast). One of the chief characteristics of *Hallopus*, indeed, as formerly interpreted, has been the very short fore-limb compared with the hind-limb, based upon the identification of the bones (9) as radius and ulna.

(*h*) Further preparation of the manus has proved the presence of all five metacarpals, and that these (and also the bones I take to be the radiale and ulnare) are seen mainly from the posterior, or ventral side. Unfortunately, insufficient phalanges are present to determine which is the medial or lateral side by means of the formula, and the metacarpals are symmetrical as to lengths. However, if the radiale and ulnare are correctly identified, then they must be of the left side, since the radiale must lie to the medial side. This is in complete agreement with the identification and orientation of the radius/ulna (see above). It should be made clear that although the radiale and ulnare are above said to be seen from the posterior aspect, in order to see them clearly the block has to be tilted, otherwise they are partly concealed by the right tibia (21) and sacrum (1). When the ulna is seen in postero-medial view, as in a 'normal' view of the slab, the radiale, ulnare and hand are seen from a similar, but slightly more medial, aspect. The proximal wrist-joint has, however, been flexed back to less than 90 degrees.

Thus consistency of interpretation of these two segments of the limb has been attained by considering each segment independently.

The only question which might arise in relation to the *right ilium* (11) is that of orientation. This hardly needs to be raised, since the pointed end of the blade (away from the ulna) is obviously anterior, but the long posterior extent of the second sacral rib agrees well with the similar post-acetabular extension of the ilium. As von Huene (1914) has noted, the ilia complement each other and the full rear extent of the blade has to be obtained from the *left ilium* (12).

The distal end of the *pubis* may possibly be represented by a triangular area of impression (14) close to the ischium, but no great weight can be placed upon this identification.

For the identification of the *ischium* (13) I return to that of Marsh (1890, p. 416). Von Huene (1914) regarded this bone as a pubis, since he thought that a rod-like pubis and a plate-like ischium were irreconcilable, and believed that he could identify an obturator foramen in the proximal part of the bone. As to the latter point, the borders of this embayment are nowhere finished and it is a much shallower feature than von Huene's Fig. 54 implies; the figure is also misleading in the apparent narrowness of the bone. The width is also sufficient to rule out identification as a scapula, also taking into account the shape of the expanded end, which would have to be the upper one. I think the question of its being a coracoid, even a crocodilian coracoid, can be excluded. I fail to see how the bone could be regarded as a pubis, since there is no indication of the type of symphysis which occurs in such a bone. It is manifestly very different from the types of pubis found in typical dinosaurs. In primitive saurischians, as in some thecodonts, the pubis is long and plate-like, with the symphysis along the medial edge and a proximal 'twisted' zone where the plate changes its orientation. There is no sign of these features in this particular bone, and the 45° angle which the edge in contact with the tibia makes with the longest edge (which would have to be lateral) is also out of keeping with a plate-like pubis. It can, in fact, only be interpreted as a pubis by assuming strong proximal crushing (of which there is no trace) and by taking great liberties in restoration. On the other hand, there is a close resemblance to the ischium of the primitive Upper Triassic crocodile *Protosuchus* (Colbert & Mook 1951, Pl. 13, Fig. 1) and Marsh himself (1890) noted a crocodilian resemblance.

The *femur* (15) is clearly the bone lying alongside the left tibia (16), but opinions have differed as to whether it is right or left and which end is proximal. Comparison of Marsh's text-figure (1896, Fig. 3) of the limb as it occurs, with his restoration (Pl. VI, Fig. 2), shows that he has placed the end nearest the proximal end of the tibia, which one would naturally think of as distal, in the acetabulum although he does not mention this. Von Huene (1914) reversed this orientation. Further preparation of the bone shows that the end nearest to the proximal end of the tibia has a ball-like head projecting medially from the shaft and a system of trochanters is present at this end. Marsh's orientation is thus confirmed. In fact, one has a natural tendency, because of the orientation of the tibia and metatarsus in the smaller slab, to view the femur in an inverted and reversed position. When turned round, the natural curvatures of the bone and the beginning of the condyles (one of which is von Huene's 'trochanter major') are much more readily recognized. It is thus an odd but incontrovertible fact that the femur, although of the left side and belonging to the tibia with which it is in contact, has been reversed end-for-end.

The *left tibia*, *tarsus* and *metatarsus* are unmistakeable (16 to 20). Preparation has revealed a splint-like metatarsal I and a small medial distal tarsal in addition to the elements previously known. Most of the *right tibia* (21) is present, somewhat crushed, in the larger slab. I agree with von Huene (1914) that it shows the posterior side but I think it is clear that the distal end is missing, not the proximal. By its side less than half of the *right fibula* (22) is preserved, in medial aspect. Again I differ from von Huene in regarding this as the proximal portion. It has certain quite characteristic, though subtle curvatures and it seems to me that Marsh was quite right in saying (1890) that it 'tapered much from above downward', since the facet on the astragalus for its distal end is very small. It was this facet that he evidently had in mind when he said that the bone 'was' complete.

Two detached *metatarsals* are present. One of these (23, near the right radius and ulna) is 50 mm long. Preparation has exposed the typical condyles at the distal end. From the length, and the impression of the proximal end, this is evidently metatarsal III of the right foot, as von Huene identifies it. The other metatarsal (24) is incomplete, its (?) proximal end having apparently been destroyed to get at the proximal end of the ulna. I removed some matrix from the (?) distal end, exposing a curious notch. This end is evidently much too slender to be the proximal end of a pubis as the notch might suggest, and since the bone is otherwise very like the other metatarsals, it seems probable that the notch is due to damage or decay. The identification suggested is as metatarsal IV of the right foot, since metatarsal II is thicker in the shaft. The identification of the distal end is to some extent supported by the presence of one or two ill-preserved phalanges near to it.

5. Description of *Hallopus*

Vertebral column

Unfortunately, no recognizable presacral vertebrae are preserved. I believe that Marsh was correct in assuming that the *sacrum* (figure 3*a*) consisted only of the two co-ossified vertebrae as preserved, although von Huene (1914) though it necessary to add on a hypothetical third sacral because of the long iliac blade. The sacrum is seen from above in the smaller slab and the shape of the second sacral rib identifies the posterior end; the upper parts of the neural arches and spines are embedded in the larger slab. Much damage has been done to the sacrum and the centra are crushed; the first sacral rib of the right side extends farther from the mid-line than the left, and its distal end is more complete, showing more of the backward curvature at the beginning of the expansion. The breadth across the first sacral ribs must have been considerably more than 26 mm. The length of the combined vertebrae is 22 mm. The left second sacral rib is more complete than the right. Its posterior end is prolonged backward and outward as a thin strip of bone, previously unremarked, but continuous in the counterpart (larger slab). The end of this strip is 19 mm from the mid-line, giving 38 mm for the maximum preserved breadth of the sacrum. It is reasonable to suppose, as did von Huene (1914), that the sacral ribs originally expanded anteriorly and posteriorly to join each other at a firm contact. The length of the articular area on the left side is now 31 mm, and allowance for the anterior expansion of the first sacral rib suggest an original length of about 34 mm. It seems unnecessary to postulate a missing third sacral vertebra, in spite of the great length of the iliac blade (49 mm). The fact that the two sacrals are firmly co-ossified (indeed no trace of suture can be made out) suggests that they were the only two present. If there was a third sacral, why is it not co-ossified with them? Sacral ribs do not always extend the full length of the blade, but in fact the long second sacral rib (articular surface still 20 mm long) agrees with the long backward extension of the ilium and, assuming that the junction of the ribs was over the middle of the acetabulum, this rib would leave only 5 or 6 mm of the blade unsupported at the rear end. It is, in fact, difficult to 'fit in' an additional sacral vertebra of commensurate size with the two already present.

Four *vertebrae* are preserved in series near the left femur. The most anterior of these, which has lost the neural arch, is overlain by the distal end of the femur; the fourth is tipped up obliquely. Part of another vertebra may be present between this and metatarsal III of the right foot. These vertebrae (figure 3*b*) are small compared with the sacrum (centra 7 mm long) and although they show little sign of chevron-facets, the first of the series shows traces of the ventral groove characteristic of caudals. They have evidently been crushed laterally, hence their flattened appearance, and the ends of the centra are not well preserved. The neural spines are tall, confirming the impression that they are caudals, but their small size suggests that they are not from immediately behind the sacrum. The transverse processes, which are broken off or inaccessible, are evidently placed well above the neurocentral suture. Another broken vertebra of similar size lies on the opposite side of the chevron-bone in the smaller slab. This too is poorly preserved and has lost both transverse processes. What appear to be parts of two centra are exposed near the upper margin of the right ilium.

Fragments of a few *ribs* are present. The best of these (3), which crosses the isolated metatarsal III, is evidently an anterior dorsal, with well-separated heads. Other fragments near the proximal end of the left tibia show that the ribs were hollow. The single *chevron-bone* (4) preserved, below the caudal vertebrae, is evidently too wide proximally to have come from the same part of the column and must be one of the most anterior of these elements.

Shoulder girdle

The *scapula* (figure 3*c*) measures 29 mm along the side presumed to be posterior, that is, nearer to the proximal end of the left tibia. The bone is thickened at the lower end and forks in an almost symmetrical manner, presumably due to the loss of the thin, concave area in front of the glenoid (see above). The blade is thin and flattened and expands dorsally. This end is incomplete but probably little is missing. It is impossible to say whether the bone is from the right or left side.

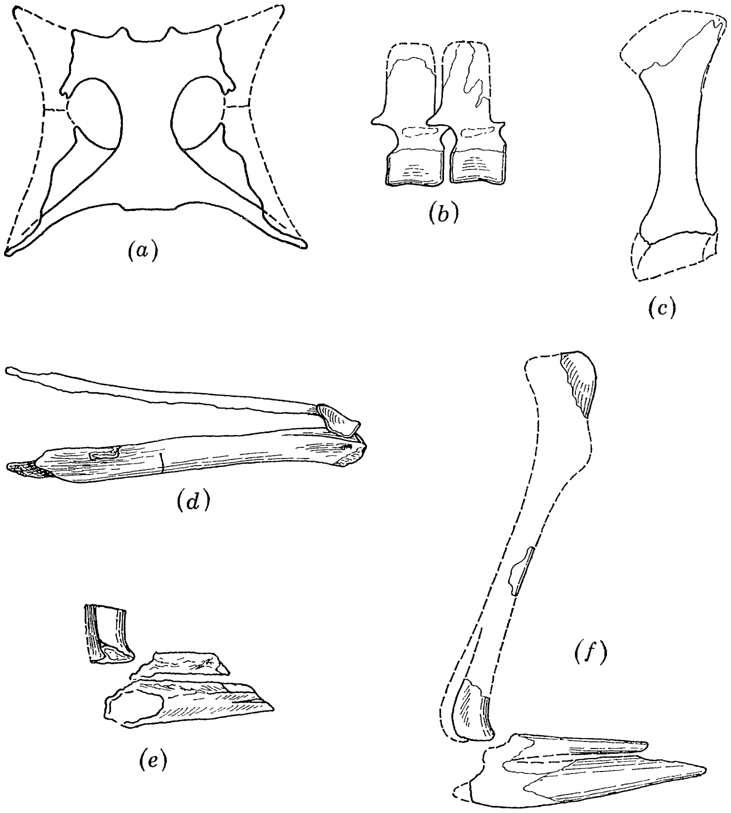


Figure 3. *Hallopus victor* (Marsh). (*a*) Sacrum with outline of sacral ribs restored; (*b*) two of the caudal vertebrae; (*c*) scapula restored as from the left side; (*d*) left radius (mainly an impression) and ulna in posterior and slightly medial view, from larger slab; (*e*) distal end of right humerus, proximal ends of radius and ulna from smaller slab; (*f*) right humerus, radius and ulna combining evidence from both slabs and from a cast from larger slab. In (*e*) and (*f*) the humerus is seen in lateral and partly posterior view (magn. × 1).

Fore-limb

The right *humerus* (figure 3*e*, *f*) is represented by three areas of impression in the larger slab and the distal end in the smaller slab. As preserved, it measures 54 mm, but a millimetre or two may be missing from the imperfect distal end. The cast from the larger slab shows the bone in postero-lateral aspect, that is, the deltopectoral crest is turned down into the 'matrix'. In the actual block, of course, the crest was turned up 'into the air', hence its absence. In the smaller block, the distal end is turned somewhat on its long axis to present a postero-lateral view, thus agreeing with the orientation deduced from the cast. Only a small part of the rounded head of the bone is preserved, but this evidently includes most of the articular area. The distal portion (6 mm wide) is somewhat crushed and displays a hollow cross-section. There is little in the way of transverse expansion, as Marsh (1890) noted, but the condyles curve forward and there is a groove running down between them, both in front and behind.

The right *radius* and *ulna* (figur 3*e*) are incomplete distally and most of the bone has been broken away. The radius is about 3 mm thick, the ulna about 5 mm. The olecranon process seems to have been short, but by combining both slabs it can be proved to have extended at least up to the adjacent metatarsal, giving a preserved length of 32 mm for the right ulna.

The left radius is mainly in the smaller slab. The shaft is oval in cross-section, measuring *ca.* 3.5 by 2 mm. It expands towards the proximal end; although the latter is incompletely preserved, careful examination shows that it is actually reached at the edge of the smaller block. The damaged distal end is level with that of the left ulna (figures 3*d*, 4) in the larger block, giving a total length of 50 mm. This is confirmed from the ulna, whose somewhat crushed and incomplete proximal end is evidently curving up towards the coronoid process. The preserved length of the ulna is 49 mm; at its most slender portion (about one-third of its length from the distal end) it is *ca.* 4 mm in maximum diameter. The distal end curves slightly laterally and is apparently rather square in cross-section, but the postero-lateral edge is drawn out to form a flange so that the posterior width appears to be greater than it actually is. The medial side bears a shallow groove which dies out proximally. The distal termination is flat and rectangular. Between this surface and the medial groove there is a small concave area facing ventromedially. The posterior surface of the distal end is gently concave, with a sharp edge between it and the medial groove.

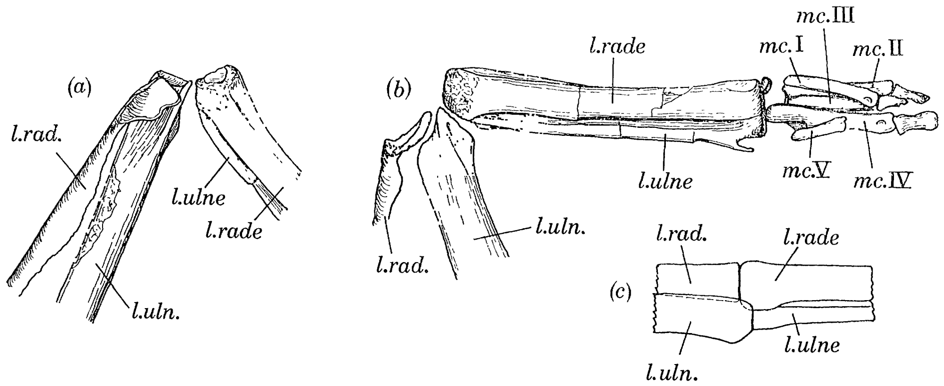


FIGURE 4. *Hallopus victor* (Marsh). (*a*) Distal ends of left radius and ulna and proximal ends of radiale and ulnare. The radius mainly an impression, the ulna seen in medial view, the radiale and ulnare in oblique proximo-. posterior view; (*b*) oblique view of ends of left radius and ulna, with left carpus and manus in posterior view; (*c*) restored diagrammatic posterior view of left proximal carpal joint (magn. $\times 1\frac{1}{2}$).

The left *radiale* and *ulnare* (figure 4, and figure 14, plate 72) are straight bones, mainly seen from behind, measuring 29 and 25.5 mm respectively. The radiale is a stout element, with a square proximal end which expands laterally to act as a partial 'stop' for the ulnare. Unfortunately the proximal articular surface is not fully preserved, but a small portion of it is flat. The shaft of the radiale is a little deeper (3 mm) from front to back than transversely (2.5 mm). It expands and thickens distally along with the ulnare, to form a transverse, roller-like surface, 6.5 mm wide. The ulnare tapers gradually proximally until its posterior surface forms a thin edge; the anterior side, however (embedded in the block) expands medially to form a flange which is in contact with the radiale throughout its length. The ulnare thus has an L-shaped cross-section, forming a longitudinal channel along the posterior surface at the junction of the two bones. The proximal end of the ulnare has also suffered damage and detailed preparation shows that a splinter of bone has been lost from the lateral side of the thin edge alluded to above.

Articulation of the proximal carpal joint and comparison with the crocodilian type

In spite of their great elongation, the similarity of the proximal carpals of *Hallopus* to those of crocodiles suggests that the proximal carpal joint should be capable of interpretation by comparison with the crocodilian type. This can be done satisfactorily, although there are certain differences.

In modern crocodiles (Romer 1956, Fig. 183) the ulna extends beyond the radius, meeting the ulnare and also having a rather flat medial contact with the radiale. The radius does not meet the ulnare, nor does it meet the ulna distally. The radiale is more massive than the ulnare and acts as a partial proximal 'stop' for it so that the ulnare wedges in between the radiale and the ulna. The axis of the carpus and manus diverges laterally from that of the radius-ulna. Some dorso-ventral bending at the joint is permitted, but flexion is limited by the pisiform which bears against a postero-lateral flange near the distal end of the ulna.

In *Hallopus* the radiale is also the stouter of the two bones. Its proximal articular surface appears to have been flat and at right angles to the shaft. Only a fragment of the distal end of the radius is preserved, and nothing of the distal articular surface. The preservation of the proximal end of the ulnare does not of itself permit one to decide whether it met the ulna, or whether the 'stop' formed by the radiale interposed between them. However, several lines of evidence combine to suggest that the former alternative applied.

(*a*) The breadth of the radiale plus ulnare as now preserved is 5 mm, contrasting with a width of 6 mm at the distal end of the humerus and 6.5 mm at the carpo-metacarpal 'roller'. It seems reasonable, on structural grounds, to assume a similar width at the proximal carpal joint also, which would imply a long, and therefore mechanically weak, lateral extension of the radiale to form the 'stop'.

(*b*) One would expect the contact between the ulna and ulnare to be maintained—assuming the usual crocodilian type to be primitive.

(*c*) The concave area ventro-medially placed at the distal end of the ulna is obviously comparable to the ulna/radiale contact in a 'normal' crocodile, and thus indicates a 'step' in the joint surface from radius to ulna.

It is therefore concluded that the basic crocodilian arrangement obtained, with the ulna extending a little way beyond the radius to meet the ulnare. The radius and ulna were closely appressed distally, with the radius fitting into a groove in the medial side of the ulna. The flat articular surfaces are disposed at right angles to the long axes of the epipodials and proximal carpals, with little or no freedom of movement being possible. Two further aspects of the joint emphasize its immobility. First, the interlocking effect of the broader proximal end of the radiale, which meets the ulna as well as the radius, and, secondly, the fact that the joint surface 'steps down' from radius to ulna. The medial and lateral portions of the joint are thus not on the same transverse axis. Also, the small size of the postero-lateral flange on the ulna suggests that the pisiform was small (no trace of it is preserved). A large pisiform presumably indicates a strong leverage exerted by the flexor carpi ulnaris, and conversely in the case of a small pisiform. Probably significant to the question of mobility at the joint is the shallowness of the concave surface behind the distal end of the ulna, compared with the pulley-like grooving for the flexor tendons in a Recent crocodile. This suggests that no appreciable amount of extension took place at the joint.

The breadth of the distal end of the ulna (including the concave area) is 3 mm, and, if the joint was originally about 6 mm wide, the contribution of the radius must have been about the same. The antero-posterior dimension, from the evidence of the ulna and radiale, is 3.5 mm. The width of the flat surface on the distal end of the ulna is about 2 mm, indicating 4 mm for the proximal breadth of the radiale, which is in fact the maximum breadth preserved.

The proximal carpal joint (figure 4*c*) of *Hallopus* thus differed from that of a modern crocodile in its immobility. At first inspection, the latter also appears, from its interlocking nature, to be immobile. However, the lateral deflexion of the long axis of the carpus and manus relative to that of the antebrachium has the important result of counteracting the 'stepped' effect of the longer ulna, permitting bending to take place about an oblique axis through the distal ends of the radius and ulna. This may perhaps be a secondary device to free an originally fixed joint.

Manus

The carpo-metacarpal joint (figure 4*b*, and figure 14, plate 72) has suffered *in situ* decay, making interpretation a little difficult. On the lateral side, it is clear that the distal end of the ulnare and the proximal end of metacarpal IV have been eaten into by this process. A narrow groove runs transversely across part of the roller surface from this area, but is also clearly due to decay. The proximal end of metacarpal IV is still in contact with the 'roller' at the junction of radiale and ulnare. The presence of a ligament-pit, and the shape of the distal end of this metacarpal and its phalanx show that it has been rotated about its long axis and now presents the medial aspect. (This explains why there appears to be insufficient room at the joint for metacarpals I to III.) The lower (i.e. plantar) portion of its proximal end has been removed, apparently after rotation occurred, since the decayed area is continuous with that on the ulnare. Significantly, the proximal end of metacarpal V, which is obviously incomplete, begins opposite the end of the decayed portion of metacarpal IV. This suggests that *in situ* decay has affected this metacarpal also, and that it would be incorrect to 'close it up' to the ulnare.

The outer metacarpals have been mentioned first, since the above points bear upon the situation in metacarpals I to III. These three appear to form a unit, but I think this is misleading, due to the fact that they now end proximally at the same distance (2 mm) from the radiale. During preparation, it was found that what appeared to be the proximal end of metacarpal I was a composite, and included another metacarpal which crossed beneath it. The distal end of this was exposed near the right tibia. This bone is certainly metacarpal II, and the next lateral metacarpal is thus metacarpal III. Metacarpals I to III have also been rotated, as a group, so that they show a partly medial view, but the rotation has been less, at least in the case of metacarpal II, than in IV. (Metacarpal I is a special case.) Medially, in contact with the end of the radiale is a small fragment of bone. (It should be explained, in case anyone should in future be misled, that a tiny corner of this fragment came off during cleaning and was replaced.) The problems are (*a*) whether this fragment represents the carpus, and (*b*) whether metacarpals I to III should be 'closed up' or not. The following points are relevant: (i) Examination of the proximal ends of metacarpals II and III suggests that they also have been corroded—the canaliculate interior of the bone is exposed. (ii) The gap at their bases is continuous with the transverse groove noted above. (iii) Metacarpal II expands proximally from between I and III in such a way as to suggest that it originally continued across the gap into the fragment touching the radiale. It is therefore concluded that these metacarpals are essentially in their correct positions, and that the fragment adjacent to the radiale is the proximal end of metacarpal II.

Metacarpal I is 8.5 mm long, but if, as seems likely, its proximal end is missing, it originally measured 10.5 mm. It tapers proximally and evidently had a reduced area of contact with the radiale. This end appears to have a bevelled-off lateral surface against metacarpal II such that it was held permanently somewhat flexed, with the distal condyles turned a little laterally (in this latter point it is very like metacarpal I of a modern crocodile). There is a dorso-medial ligament pit at the distal end; one incomplete phalanx, 3 mm long, is present. Metacarpal II is now 10 mm long, originally probably 12 mm. It also has an incomplete phalanx, 3.5 mm long. Metacarpal III begins to wedge out proximally; like metacarpal I, it evidently had a reduced contact with the wrist, but probably still met the latter. Distally it descends below the phalanges of the other metacarpals and is inaccessible to the preparator. Metacarpal IV is 12 mm long and retains one phalanx of 4 mm length, seen in medial view. Metacarpal V is incomplete distally; allowing for the gap of 2 mm proximally, its length must have been at least 7.5 mm. The distal end of this metacarpal is at a higher level in the matrix than the others, and it swings behind metacarpal IV in an almost symmetrical relationship to metacarpal I.

Articulation of the metacarpals

The fourth metacarpal now meets the radiale as well as the ulnare but, when rotated into its correct attitude, it would take up less room proximally and there is sufficient space on the ulnare to accommodate it and metacarpal V. The first three metacarpals must also be rotated to a slightly less extent and moved laterally. Metacarpal I may have tapered out before reaching the radiale, or perhaps just met it. Metacarpal III seems to be wedging out rapidly in ventral view, but the proximal end shows that this is not so great as it seems and the bone probably still met the radiale.

After rotation into their original attitudes, the proximal ends of metacarpals I to III would overlap each other in such a way as to confirm that this is a left manus, seen from below.

Pelvic girdle

The right *ilium* (figure 5*a*) is the better preserved of the two, but to get the full length of the blade it is necessary to combine it with the left ilium (figure 5*b*). As von Huene (1914) points out, the right ilium has an anterior point. Detailed preparation shows that this is joined by a mere filament to the rest of the bone. A small pit in the lateral surface at the anterior end seems to be a secondary feature (possibly a tooth-mark). The lower surface of the anterior end of the blade extends about 4 mm medially. The posterior end is a flat sheet of almost constant depth, which curves markedly down posteriorly. A squeeze from the right ilium shows the beginning of this downward curvature also. The total length is 49 mm. The right ilium, which is mainly seen in lateral view, possibly shows the junction of the articular areas for the two sacral ribs above the centre of the acetabulum where the bone has come away, but, as it is cracked down the middle, it is difficult to be sure of this. The ischiadic peduncle has a jagged broken termination and it is clear that both it and the pubic peduncle were originally longer. There was probably a more pronounced anterior sinus, also. The left ilium mainly shows the impression of the inner surface, covered by a film of bone, and lacks the anterior end. There is a slight notch in the acetabular part of the left ilium at the same distance (14 mm) below the upper margin as the marked notch in the right ilium, but the differences in detail suggest that this notch does not actually represent the acetabular perforation, but is due to the breakage of the thin acetabular wall. The thickened supra-acetabular rim is assumed to have lain not far above this notch in the right ilium.

An elongated triangular impression near the proximal end of the ischium might possibly be the distal end of a *pubis*.

The *ischium* (figure 5*c*) is a thin, flattened bone, with a slightly thickened postero-dorsal border. The proximal corner is more massive and appears to represent the peduncle for the ilium, although slightly eroded. The expanded ventral portion, in contact with the tibia, has a slightly irregular edge and may possibly have been a little larger originally, but the amount lost cannot have been great. It is difficult to decide from which side of the pelvis the bone comes; I am inclined to think it is a left ischium, in lateral view.

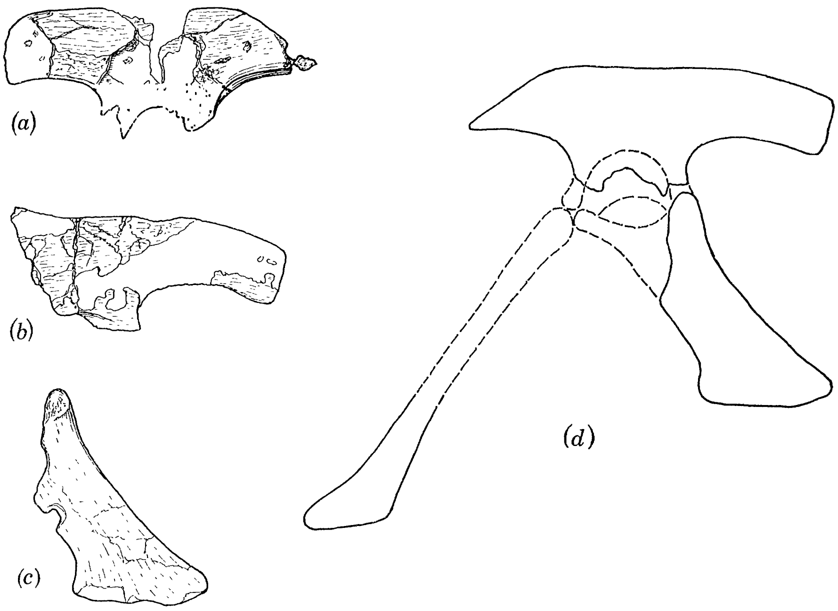


FIGURE 5. *Hallopus victor* (Marsh). (*a*) Right ilium, lateral view; (*b*) left ilium, lateral view; (*c*) ischium; (*d*) restoration of the pelvis (magn. × 1).

Hind-limb

The left *femur* (figure 6, and figure 15, plate 72) shows the medial view of the proximal half in the larger slab, and the lateral view of the distal portion in the smaller slab. The impression of the medial surface continues proximally in the smaller block and, to prove the orientation of the femur beyond doubt, I removed the remaining bone from the proximal end, since this area was impossible to prepare positively.

The resulting latex cast shows that the femur has a ball-like head projecting dorso-medially, well set off from the shaft. Preparation of the larger slab exposed a lesser trochanter arising as a thin ridge from the lateral side of the shaft a little way down from the head. The shaft becomes gradually modified proximally below the head to form a ventro-lateral ridge, which is quite distinct from the head itself. Unfortunately the proximal end of the ridge proved to be damaged. Although there is evidence of lateral compression of the femur, this is clearly insufficient to account for the presence of this ridge. For convenience, the ridge is here termed the 'pseudo-internal trochanter', since it appears to have been for the attachment of the pubo-ischio-femoralis externus muscle, but it is not in the normal position of an internal trochanter. The fourth trochanter can be recognized on the bone, but more clearly in the cast from the smaller slab (figure 6*h*), as a low, narrow ridge arising from the ventro-medial border of the shaft, alined towards the head, and about 31 mm from the latter. Immediately above it on the medial surface is a shallow depression for the insertion of the caudifemoralis longus. The proximal half of the shaft is almost straight, but distally it is arched dorsally. The beginning of the condyles, and the intercondylar groove, are preserved at the distal end. The cross-section of the eroded termination shows that some oblique compression has occurred. The lateral condyle is the more complete, and it is only necessary to restore the rounded anterior contour of this to obtain the original length of the bone—80 mm.

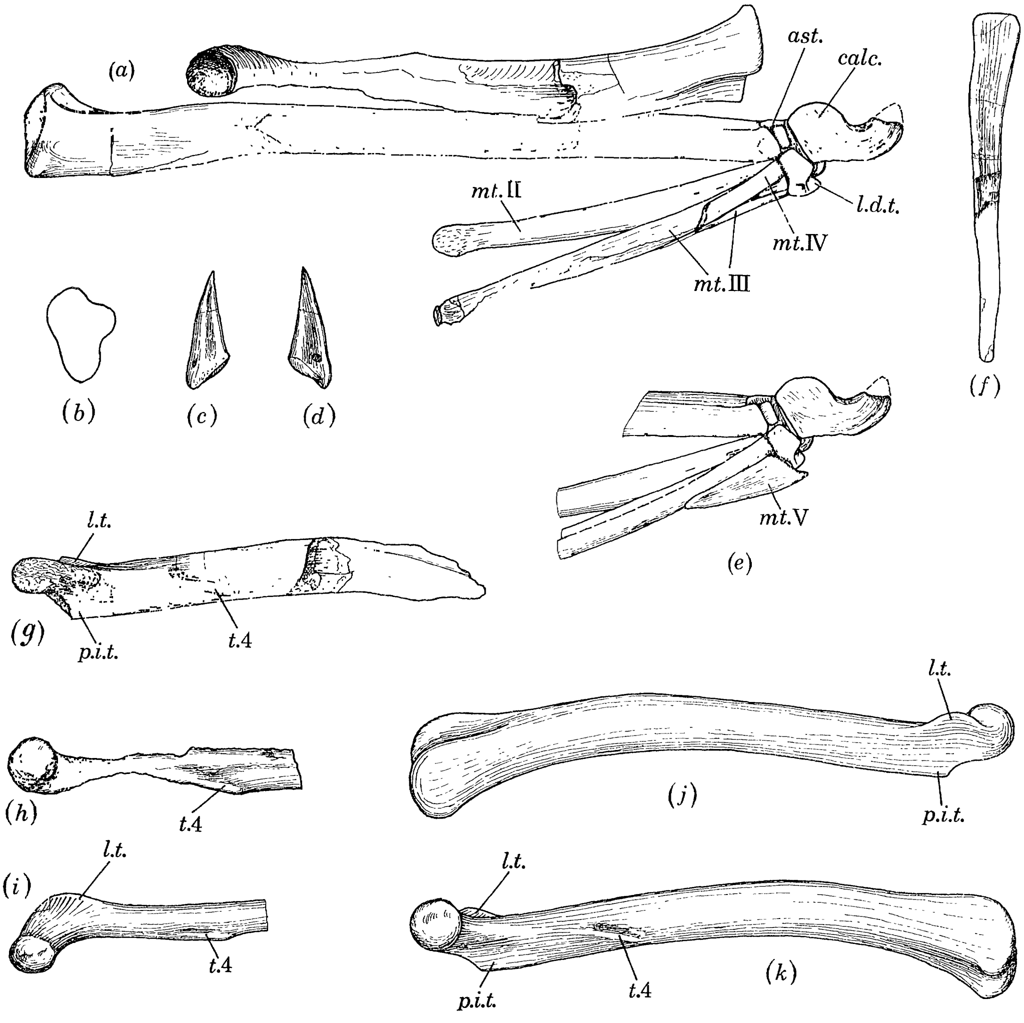


FIGURE 6. *Hallopus victor* (Marsh). (*a*) Left femur, tibia, tarsus, and metatarsus, as preserved, the proximal half of the femur as an impression; (*b*) outline of proximal end of tibia, anterior end downward; (*c*) dorsal and (*d*) ventral view of metatarsal V; (*e*) tarsus and metatarsus with metatarsal V in presumed original position; (*f*) proximal half of right fibula, medial view; (*g*) medial view of left femur as preserved in larger slab; (*h*) cast of proximal half of same from smaller slab; (*i*) upper view of proximal end, combined from cast and bone; (*j*) lateral and (*k*) medial views of restored femur (magn. × 1).

The left *tibia* (figures 6 and 7) has a long, slender, cylindrical shaft. This is slightly crushed laterally, beginning at about one-third the way up from the distal end. The maximum effect occurs in an area *ca.* 13 mm from the proximal end and terminates at a prominent transverse crack a few millimetres further up. Beyond this point the distortion decreases and the proximal termination seems little affected. The proximal end is obtained by combining a cast from the larger slab with the actual bone in the smaller slab, which has lost a little of its lateral edge. The proximal outline is triangular, with a slight lateral notch marking the position of a faint groove on the lateral surface, presumably for the fibula. The articular surface slopes down a little laterally as it does in a crocodile. Anteriorly there is a narrow cnemial crest which is probably accentuated by crushing; posteriorly the head of the bone overhangs and there is a small concave area below this.

The distal end is broadened transversely, measuring 9.5 by 5 mm. The astragalus is firmly attached at this end. The medial side of the tibia descends a little farther than the lateral side, with a convex surface received into a corresponding concavity on the astragalus, which rises up in front of it. The lateral side of the distal end is obliquely bevelled-off at an apparently flat surface which faces postero-ventrally and a little medially. The posterior surface above the astragalus is slightly concave.

About 45 mm of the proximal end of the right *fibula* is present in the larger slab, showing the medial side (figure 6*f*). The proximal portion is longitudinally concave. 15 mm below the head a slight convexity of the anterior margin probably indicates the position of insertion of the iliofibularis muscle on the lateral side. Distally the bone tapers to a width of 2.5 mm at the broken end.

The *tarsus* (figure 7, and figures 16 to 19, plate 72) is beautifully preserved and, although basically conforming to the crocodilian pattern, it is very much compressed from side to side with consequent modification of the crocodilian plan. The *astragalus* is a relatively large bone, occupying the whole width of the tarsus, 9.5 mm wide by 9 mm high posteriorly. Its anterior face is largely hidden by the distal tarsals and metatarsals, but ventro-medially it is quite flat.

The proximal surface rises dorso-laterally to meet the tibia at the bevelled off area noted above, and the rectangular dorsal apex of the astragalus enters the hollow at the back of the tibia. The shallow facet for the distal end of the fibula is placed on the posterior surface of the dorso-lateral process, so that, as Marsh noted (1890) the distal end of the fibula lay behind the tibia. Below the dorso-lateral process is a deep recess which obviously, as in the crocodile, received the 'lip' of the calcaneum and acted as an anterior stop for it when the metatarsus was flexed. Below the recess the laterally-projecting 'peg' of the astragalus is fully exposed, due to the calcaneum having rotated too far backward. Part of the roller surface on the posterior and ventral surface of the 'peg' is preserved laterally, but more medially a groove runs vertically across the base of the 'peg' and enters the recess above it. The bone here has a damaged appearance and, coupled with the lack of an articular area which is demanded by the adjacent surface on the calcaneum, it is thought that the vertical groove is a secondary feature, perhaps produced during the first preparation of the specimen. On the lateral side the astragalus interposes between the tibia and the calcaneum, and astragalus, calcaneum, and lateral distal tarsal form essentially one flattened lateral surface. The dorso-lateral process of the astragalus has a ventral articular surface for the calcaneum which is gently concave from front to back and which also curves in a quarter-circle medially and ventrally. On the medial side of the astragalus is a large, shallow pit, probably for a ligament of the joint-capsule. The convex, somewhat cone-shaped articular surface for the metatarsals and distal tarsals faces as much downwards as forwards, and gives way abruptly in front to a flat surface. A curious feature of this articular surface is that it trends, as a whole, anteromedially at 45° to the transverse axis. That this is not due to rotation of the tibia about its long axis is shown by the attitude of the proximal end of the bone, and by the nature of the 'peg and socket' articulation between astragalus and calcaneum. A slight groove runs transversely across the laterally tapering portion of the articular surface.

The *calcaneum* is extremely compressed. Its maximum length is 15 mm. The dorsal articular surface for the lateral process of the astragalus and the distal end of the fibula is semicircular in longitudinal profile, very narrow, and curved in the form of a quadrant in transverse section with the convexity on the medial side. Part of this area has probably been lost at a point where it is now very narrow, adjacent to the astragalar 'peg'. Within the back of this semicircular arc, on the medial side, is located the socket for the 'peg'. Medially the transversely disposed concave area which met the roller-surface on the 'peg' has been left lightly covered with matrix, in order to avoid damage to its dorsal 'lip'. In upper view the calcaneal heel contracts at first gradually in width backwards, and then rapidly so that the distal 4 mm is only 2 mm thick. This distal portion forms a dorsally directed process which, as shown by a curved line of bone remaining in the larger slab, rises 2 mm above the point at which it is broken off in the smaller slab. The lateral surface of the calcaneum is flattened, with a gentle longitudinal concavity in the lower part. Below this there is a slightly out-turned rim which continues back along the lower and posterior edges of the tuber. This rim is the expression of a ventrally projecting thin

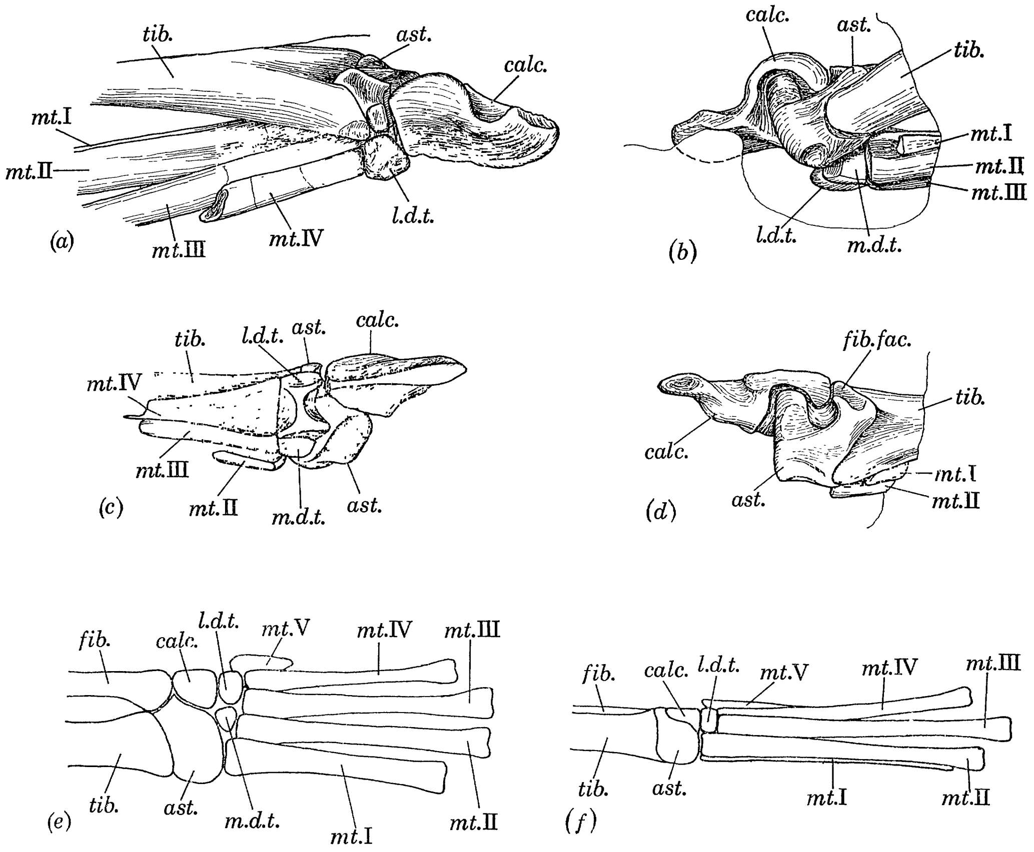


FIGURE 7. (*a*) to (*d*) *Hallopus victor* (Marsh). Left tibia, tarsus and metatarsus: (*a*) oblique lateral view, tibia and astragalus seen partly from behind; (*b*) oblique medial view; (*c*) lower view, normal to the metatarsals, the astragalus in antero-ventral view; (*d*) posterior view of tibia and astragalus, upper view of calcaneum (magn. × 1½). (*e*), (*f*) diagrammatic anterior views of tarsus and metatarsus: (*e*) in a modern *Alligator*; (*f*) in *Hallopus*. It is uncertain whether the medial distal tarsal would be visible in (*f*).

ridge which is actually a forward continuation of the narrow posterior end of the tuber. The anterior surface of the calcaneum is bevelled off at a flat surface inclined at *ca.* 60° to the long axis. This surface also faces slightly laterally.

The *medial distal tarsal* is a small rectangular element pressed against the flattened medial side of the lateral distal tarsal. Distally it meets metatarsal III, and proximally it has a slightly concave, oblique articular surface for the astragalus; this area probably continued on to the adjacent corner of the lateral distal tarsal.

The *lateral distal tarsal* is a large, irregular bone 6 mm across. The lower surface has an H-shaped ridge-system, the cross-bar of the H running transversely. The more lateral of the parallel bars of the H, now a little degraded, runs backward and was obviously continuous with the ventral ridge on the calcaneum. The posterior portion of the H encloses a concavity which was continuous on to the lower surface of the calcaneum when the two bones were closed up to each other. The anterior part of the H likewise borders a concavity which continues distally on to the lower surface of metatarsal IV, where it dies out. The medial boundary of this area is formed by the projecting lower edge of metatarsal III. The medial parallel bar is a thick ridge which projects backward, continuing the line of the oblique articular area on the medial distal tarsal. Proximally there is a flat surface laterally for contact with the calcaneum. This surface faces a little medially, matching the inclination of the corresponding surface on the calcaneum. Distally almost the entire surface meets metatarsal IV, at least on the ventral surface, but there is a very small contact with metatarsal III. Owing to the inverted L-shaped cross-section of the proximal end of this metatarsal, however, there is an exchange of roles dorsally. The lateral distal tarsal is somewhat wedge-shaped, being narrower antero-posteriorly on the dorsal side.

Preparation of the proximal end of metatarsal II revealed a thin splint of bone lying in a longitudinal recess in its medial side. The proximal 2 mm or so of the recess is empty where the bone has at some distant time broken away. During exploration for metatarsal I a curious thin edge of bone, less than 1 mm thick, was discovered lying parallel to the medial side of metatarsal II and separated from it by a thin layer of matrix. The extreme slenderness of this edge, and its inaccessibility in the angle between tibia and metatarsus, prevents further exposure. This strip is clearly not part of metatarsal II, the medial surface of which is undamaged. Its significance was not at first appreciated, until it was realized that it actually represents an exceedingly slender metatarsal I, and a new aperture was cut between metatarsal II and the tibia, proving the continuity of the strip with the proximal splint. Distally the strip continues as far as preparation is allowed by the condylar expansion of metatarsal II. Thus metatarsal I is represented by a mere splint, apparently continuously recessed into the medial side of metatarsal II and almost equal in length to it.

Metatarsal II is 46 mm long and is the stoutest of the three main metatarsals, but proximally it develops a triangular or inverted L-shaped cross-section, which originally fitted closely against metatarsal III. The proximal end has a slightly concave, triangular articular area to which metatarsal I evidently contributed a very small, dorso-medial corner. Since this articular area does not now meet the articular area on the astragalus, and furthermore since it lies 2 mm distal to the articular surface on the medial distal tarsal, it is assumed that metatarsal II requires to be moved proximally by this amount. This assumption is further supported by the fact that the thin ventral proximal edge of metatarsal II is now well separated from metatarsal III, and the longitudinal lateral recess which received that metatarsal has been exposed by the upward movement of the distal end of metatarsal II. The dislodgement of this metatarsal is probably due to the overclosing of the crurometatarsal angle which has occurred. The relatively broad dorsal surface of the proximal end of metatarsal II seems to require some degree of lateral overlap over the medial distal tarsal. Whether the latter appeared at all in dorsal view cannot be decided, because of the acute angle between tibia and metatarsus.

The distal condyles of metatarsal III can be made out in broken section in the smaller block. The length is thus determined at 50 mm. Proximally this bone also has an inverted L-shaped cross-section, with a narrow ventral edge, the transverse arm of the L being sunk into the upper surface of metatarsal IV. The reverse relationship holds with the proximal end of the latter, which however is ventrally much broader, since the dorsal width of metatarsal III is reduced by the overlap of metatarsal II. The lateral side of metatarsal III is almost complete in the smaller block, so that it is clear that the more ventral of the two metatarsals seen in the larger block is metatarsal IV, since this lies directly alongside metatarsal III. The distal end of metatarsal IV shows the beginning of the downturn of the lateral condyle, and, allowing 2 mm for the missing portion, one obtains a length of 43 mm for this bone.

Metatarsal V is 14 mm long and 5 mm broad at the proximal end. Without entering into all the details, comparison with the corresponding metatarsal of a small *Alligator* suggests the following homologies. The longest edge is morphologically lateral, and the surface originally exposed in the larger slab is dorsal. In the crocodile, there is a definite free posterior edge on metatarsal V, between the lateral margin and the articular area for the lateral distal tarsal; in *Hallopus* this is represented only by the acute posterior angle. The dorsal surface is divided into two areas set at an obtuse angle to each other. The broader, more medial of these, bears a shallow discontinuous longitudinal groove. The adjacent area faces dorso-laterally (conventionally speaking), and has a small pit at its rear end. Ventrally there is a deeper longitudinal groove which emerges distally on the medial side of the point, forming a curved surface in the latter. The ventral groove is bordered laterally by a ridge which runs out to form the thin, chisel-like distal point, a small part of which was lost on removal from the block. The proximal end, apart from a small lateral ridge, is mostly taken up by a low, convex articular surface which faces (conventionally) slightly downward.

The original position of metatarsal V in the larger block was with the dorsal surface facing medially (with respect to the tarsus), the proximal end very close to the lateral distal tarsal and the proximal end of metatarsal IV, and the distal point directed towards the femur at an angle of 27° to the calcite vein. The bone was removed from the slab, in order to determine, by direct fit, its original disposition. The following considerations governed the attitude finally adopted: (*a*) the chisel-like distal tip with concave surface on one side must have tapered out against the side of metatarsal IV, against which it fits very well; (*b*) there is no sign, on metatarsal IV or the lateral side of the lateral distal tarsal, of any articular area for the proximal end of metatarsal V; (*c*) the lateral side of the concave ventral area shared by metatarsal IV and the lateral distal tarsal provides a suitable location for this articulation, and also homologizes well with the crocodilian arrangement. A good fit is obtained with metatarsal V in this position (figure 6*e*), assuming that the bone has been rotated about its long axis, such that the morphologically 'lateral' edge is slightly more medial than the 'medial' edge, the narrow 'dorsolateral surface' facing ventrally, and the 'dorsal' surface facing ventro-laterally. This leaves room for a reduced plantar aponeurosis ventrally in the space between metatarsal V and metatarsals III and IV, and for the flexor tendons to pass over the transverse ridge on the lateral distal tarsal.

In the above position, metatarsal V compares well with the attitude of the tapering, pointed fifth metatarsal in *Procompsognathus* (von Huene 1921) and *Saltopus*. Up to a point, there is a functional analogy between these coelurosaurs and *Hallopus*.

Articulation of the tarsus and metatarsus

From the preceding description it will already be evident that the ankle-joint of *Hallopus* is of a thoroughly crocodilian type. The astragalus is immovably united with the tibia; the calcaneum, on the other hand, forms a unit with the distal tarsals and the foot, which rotates around the peg-and-socket joint between the astragalus and the calcaneum. The striking difference from the crocodilian type is in the great compression of the tarsus; this is discussed further below. In order to restore the tarsus of *Hallopus* to its natural arrangement the following changes must be made. The calcaneum has been rotated too far backwards, so that the astragalar peg is fully visible and the dorsal articular area now lies entirely behind the lateral process on the astragalus. In addition to rotating the calcaneum forwards, its rear end must be moved 2 or 3 mm medially, and the bone as a whole must also be slightly rotated clockwise about its long axis (viewed from behind), in order to place the peg in its socket. At present there is a slight gap between the flat articular surfaces on the calcaneum and the lateral distal tarsal, and these diverge at 15°. Correction of the divergence places the calcaneal heel in line with the metatarsus. The proximal end of metatarsal II must be moved back 2 mm, the angle between it and metatarsals III and IV eliminated, and its lower edge placed in contact with that of metatarsal III. When this is done, the proximal articular surface passes continuously from metatarsal II to the medial distal tarsal and probably to the proximo-dorsal side of the posterior projection on the lateral distal tarsal. The obliquity of this surface matches that on the lower side of the astragalus and it is only necessary to open out the crurometatarsal angle and move the metatarsus plus the distal tarsals back a little in order to obtain the correct articulation between them.

It is clear that the interlocking of the proximal ends of the metatarsals allowed of no relative movement between them. Metatarsal II, although slightly longer (46 mm) than metatarsal IV (43 mm) was functionally its equal in length, because its proximal end met the astragalus, whereas the lateral distal tarsal interposes in the case of metatarsal IV. The obliquity of the medial articular surface on the astragalus may perhaps be explained by comparison with the pulley-like articular surfaces which occur at various joints, e.g. the distal end of the tibia in birds or between metatarsals and phalanges in general. These presumably act as lateral stabilizers. This may also have been the function in the presumably digitigrade *Hallopus* where, owing to the retention of the roller-joint laterally (which needs must be disposed transversely), only 'half a pulley' is developed.

Derivation from the crocodilian type

In the crocodilian tarsus (figure 7*e*) the first metatarsal is the stoutest; it has a large proximal articular surface which meets the astragalus directly. Metatarsal II meets the medial distal tarsal but not the astragalus, and the two distal tarsals alternate in position between the proximal ends of metatarsals II to IV. In *Hallopus* (figure 7*f*), it is as if the compression of the joint has caused the metatarsals to move medially. Metatarsal I has been reduced to a splint, probably however retaining a tiny contact with the astragalus. The second metatarsal now meets the astragalus directly, but its proximal surface is narrow ventrally and it lies alongside the medial distal tarsal which contributes a greater area to the articulation, at least on the ventral side. Metatarsals III and IV abut directly against the distal tarsals at a broad, flat surface. It is understandable that, with the retention of a crocodilian type of ankle-joint along with the development of a functionally tridactyl foot, the more medial side of the pes should be reduced. This follows naturally from the lateral position of the peg-and-socket joint and the fact that the calcaneum, distal tarsals and metatarsals function as a unit in crocodiles. It is to be expected that the lateral side of the tarsus would assume greater importance in the transmission of stresses, especially since, as seems probable, *Hallopus* was digitigrade.

In crocodiles the dorso-lateral process of the astragalus partly overlies the upper articular surface on the calcaneum, but the lateral position of the fibular contact with the calcaneum prevents it from appearing in lateral view. Due to the great lateral compression of the calcaneum in *Hallopus*, however, the dorso-lateral process entirely covers the narrow upper articular surface of the calcaneum and appears laterally as a small rectangular process. The area for the distal end of the fibula, instead of being laterally placed, is now entirely on the posterior surface of the dorso-lateral process—as indeed it must be, otherwise the fibula could not have made contact with the calcaneum. This may also be an adaptation to digitigrady.

The secure interlocking of the proximal ends of the metatarsals follows naturally from the lateral tilting commonly found in these elements. It is noteworthy that the direction of overlap on the dorsal surface is lateral in all three major metatarsals, and there is even a hint of this in the first metatarsal.

TABLE 1. MAIN MEASUREMENTS OF *HALLOPUS*

		mm
scapula, height above glenoid	preserved	29
scapula, height above glenoid	estimated at	31
right humerus, length		54
left radius		50
left ulna	preserved	49
left radiale		29
left ulnare		25.5
metacarpal I, left		10.5
metacarpal II, left		12
metacarpal III, left	estimated at	14
metacarpal IV, left		12
metacarpal V, left	preserved	7.5
ilium, blade length (combined from both)		49
right ilium, across ‘neck’		15

		mm
right ilium, maximum preserved height		17
ischium, maximum preserved length		34
left femur, preserved length		76
left femur, estimated original length		80
left tibia length		102
metatarsal I, left	exposed	40
metatarsal II, left		46
metatarsal III, left		50
metatarsal IV, left	estimated at	43
metatarsal V, left		14
metatarsal III, right		50
metatarsal IV, right	preserved	40

6. AFFINITIES OF *HALLOPUS*

In view of the identifications give above, it is clear that *Hallopus* is not a coelurosaur. The elongated radiale and ulnare and the form of the ischium rule out this possibility; on the other hand, these characteristically crocodilian features suggest the direction in which the affinities of *Hallopus* lie. In the following comparisons, only those forms which are generally agreed to be crocodiles will first be considered. These include *Protosuchus*, from the Dinosaur Canyon Sandstone of Arizona, *Notochampsa* and *Erythrochampsa* from the Cave Sandstone and Red Beds respectively of South Africa, and *Orthosuchus* from the Red Beds of Lesotho. All these are Upper Triassic in age.

The sacrum in *Hallopus* consists of but two vertebrae, a character universal throughout the Crocodylia. In being wider than long, and in the consequent broad separation of the iliac blades, it is most uncoelurosaurian, but again in this it agrees with the crocodilian (and also of course the thecodont) type.

The scapula is not particularly like those of *Protosuchus* and later crocodiles, but it does resemble the scapulae of a certain group of Triassic reptiles, about which varying opinions have been expressed. These are further discussed below. The humerus, radius and ulna are neutral with regard to crocodilian affinities.

The elongated radiale and ulnare are particularly indicative of crocodilian relationships. One would scarcely imagine that this peculiar and uniquely crocodilian character had evolved on more than one occasion. It is significant that in the primitive Triassic crocodilian *Protosuchus* (Colbert & Mook 1951, Fig. 9) the radiale and ulnare are more slender elements than in a modern crocodile and the radiale is actually longer than the metacarpals. According to Haughton (1924), the radiale in *Notochampsa* also is slightly longer than the longest metacarpal. The hand in *Hallopus* is very small compared with the foot; this, however, is also the case in *Protosuchus*.

The ilium of *Hallopus* does not appear at first to be particularly crocodilian in type. In *Protosuchus*, however, the blade is elongated, with an anterior point, and there is a long, down-curving posterior extension. According to Colbert & Mook (1951) the iliac crest is 'turned sharply outward'. Whether or not this out-turning is due to crushing, if the upper part of the blade were rotated into the vertical plane, there would be a close resemblance to the ilium of *Hallopus*. More recently Nash (1968, Fig. 7) has figured the ilium of *Orthosuchus*. This is even more like *Hallopus*, in having a vertical blade with a long pointed anterior extension. The ilium of *Erythrochampsa* has not been figured, but Haughton (1924) describes it as having a long dorsal border and a 'long preacetabular portion with a bluntly pointed extremity'. Thus it appears that the primitive crocodilian ilium had an elongated blade conforming rather closely in shape to that of *Hallopus*. In both *Protosuchus* and *Orthosuchus*, however, the blade is lower than in *Hallopus*.

The ischium of *Hallopus* is crocodilian in shape as Marsh (1890) remarked. It resembles that of *Protosuchus* quite closely (Colbert & Mook 1951, Pl. 13, Fig. 1).

The femur is more specialized proximally than is the case in typical crocodiles, but the acquisition of trochanters due to the changed attitude of the bone relative to the pelvis does not rule out a crocodilian heritage. The distal arching of the bone and the shape of the condyles are, in fact, quite similar to the condition in *Protosuchus* (Colbert & Mook 1951, Pl. 11, Fig. 1).

Since there is little doubt that *Hallopus* is Upper Jurassic in age, the crocodilian nature of the ankle-joint acquires greater significance, it being unlikely that at that epoch such a joint would be possessed by anything other than a true crocodile. Moreover, we may note that the calcaneal tuber is elongated in *Protosuchus*, and the proximal end of metatarsal I seems, from the figure (Colbert & Mook, Fig. 12) to be slightly reduced compared to that of metatarsal II. The authors also state that metatarsal II meets the astragalus but, since the medial distal tarsal is not present, this may not have been the case.

The retention of the first metatarsal in *Hallopus*, as a splint subequal in length to the second metatarsal and permanently attached to it, indicates derivation of the foot from a type which had four elongated subequal metatarsals, such as is found in *Protosuchus*, *Erythrochampsa*, and the vast majority of crocodiles.

Typical crocodiles have a well-developed system of dorsal, and in some cases also ventral scutes. The lack of these in *Hallopus* may be due to the incompleteness of the material; on the other hand, loss of armour in a lightly built, cursorial reptile would not be surprising.

Thus, in those skeletal characteristics which are of positive significance, i.e. the carpus, ilium, ischium, tarsus and metatarsus, a crocodilian heritage is definitely indicated. The nature of the sacrum is of slightly less weight, but, taking into account the near-certainty of an Upper Jurassic age, an archosaur sacrum composed of two vertebrae could at this time only belong to a crocodile. Other characters of *Hallopus*, not typically crocodilian, can reasonably be attributed to the adoption of a cursorial gait and consequent changes in the pelvic musculature. These include the great elongation of the radiale and ulnare, increase in height of the iliac blade, development of an offset head and a lesser trochanter on the femur, functionally tridactyl pes, and loss of armour. Questions such as bipedality or quadrupedality, digitigrady or plantigrady, are postponed to a later section.

While concluding that *Hallopus* is closely related to the Crocodylia and shows evidence of derivation from a type postcranially very like *Protosuchus* and *Orthosuchus* (whether the Protosuchia be regarded as divisible into one family or two is immaterial to the present discussion), it is thought that these forms did not provide the actual stock from which it came. Before elaborating upon this point further it is necessary to insert some discussion of a number of Upper Triassic genera whose affinities have been disputed. A detailed consideration of previous views will not be entered into here, since it is believed that these are largely invalidated by certain new interpretations now to be put forward. The genera in question are *Pedeticosaurus* (van Hoepen 1915) from the Cave Sandstone of South Africa, *Sphenosuchus* from the underlying Red Beds, *Hesperosuchus* (Colbert 1952) from the Chinle Formation of Arizona, *Saltoposuchus* (von Huene 1921) from the Stubensandstein of Germany, and *Platyognathus* (Simmons 1965) from the Dark Red Beds of the Lower Lufeng Series, Yunnan, China.

Sphenosuchus (figure 12*c*) has been re-examined by the author and a redescription is in preparation. Some of the more important points arising from the revision are as follows. The external nares are probably not confluent as has sometimes been thought (Haughton 1924; von Huene 1925), but are believed to have been separated by ascending processes from the premaxillae, as Broom (1927) suggested. They are nearly terminal but laterally facing. There is a deep notch between premaxilla and maxilla, which received a large mandibular tooth. The teeth have cylindrical roots and compressed, lanceolate crowns, much like those of *Hesperosuchus*. The prefrontals send ventromedial processes within the orbits which meet in the mid-line but which do not touch the upper surface of the palate. The basal region of the pterygoid is complex and has a medial pterygoid flange as well as the usual lateral one. The large basipterygoid process is bifid and the parabasal process of the pterygoid (Walker 1964, p. 74) is fused to its medial ramus. The braincase has to some extent been misinterpreted by Haughton (1924). Further preparation has revealed many more details, including the complete laterosphenoids. The basisphenoid is a remarkable structure, with a rectangular 'window' passing completely through transversely. There is a supradentary in the lower jaw and the splenial enters into the symphysis. The 'radius' and 'ulna' of von Huene (1925) are elongated metatarsals; I to IV are subequal in length, but metatarsal I is slender and the pes was functionally tridactyl. Metatarsal V is unknown. The tarsus is not preserved but the distal end of the tibia shows on the lateral side a flat, postero-ventrally-facing facet like that on the tibia of *Hallopus*. It is thus reasonable to assume that the tarsus was crocodilian. Contrary to previous accounts, a few dorsal and ventral scutes are preserved.

Crocodilian features of *Sphenosuchus* include the following:*

(*a*) Ventro-medial processes of the prefrontals meeting in the mid-line.

---

* Since this paper was written, several other crocodilian features have been recognized in the skull of *Sphenosuchus*. The most important of these is the structure of the otic region.

(*b*) Reduction of the preorbital fossa.

(*c*) Arrangement of the bones around the lateral temporal fossa. The squamosal has a long posterior overhang and entirely lacks a descending process alongside the quadrate. The latter is inclined forwards and the quadratojugal runs upwards as a parallel-sided strip along its ventro-lateral edge. The quadratojugal is almost entirely lateral in exposure, and the jugal has a long contact with it.

(*d*) Loss of the postfrontals (or fusion with postorbitals).

(*e*) Narrow supraoccipital, which enters the post-temporal fossa.

(*f*) Fusion of the basal articulation.

(*g*) A transverse sinus passing through the basisphenoid.

(*h*) Beginnings of a eustachian system and some pneumatization of the skull.

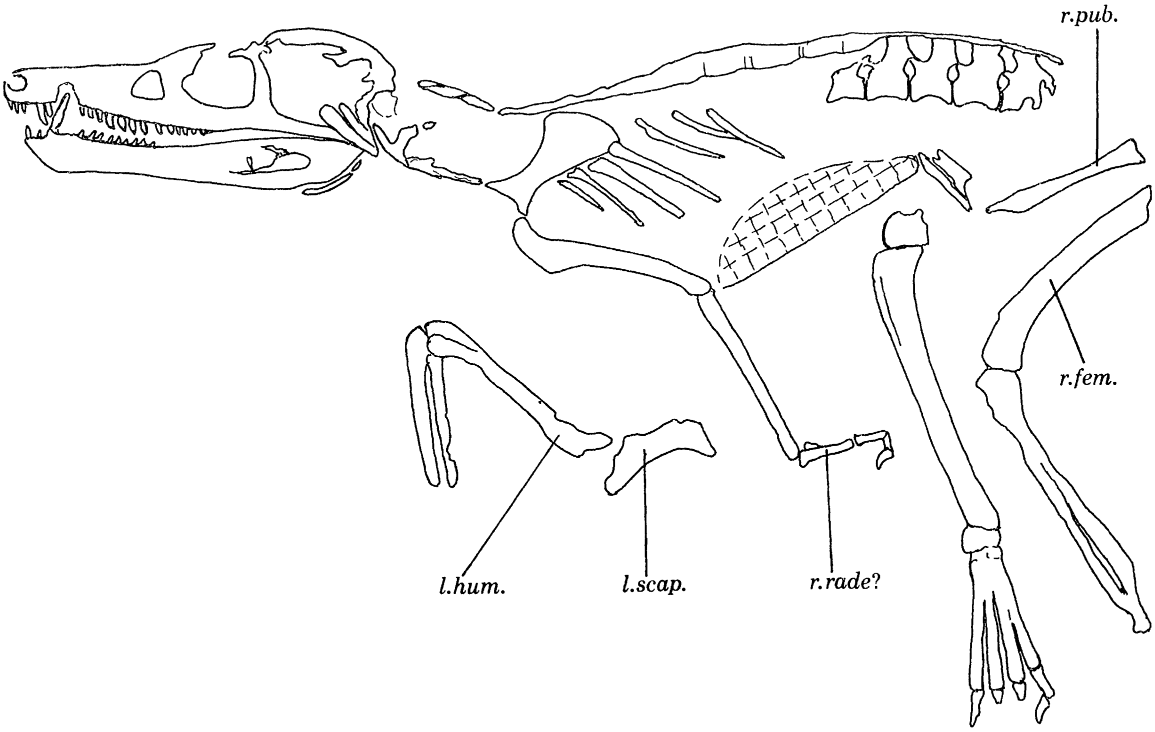


FIGURE 8. *Pedeticosaurus leviseuri* van Hoepen. Traced (with minimum of interpretation) from van Hoepen (1915, Pl. XIII). The original specimen is preserved mainly as an impression of the right side; the left scapula and fore-limb have been displaced downwards, the left hind-limb is in advance of the right, and the right pubis lies above the right femur (magn. *ca.* × ½).

(*i*) An enlarged mandibular tooth bites into a notch between premaxilla and maxilla.

(*j*) Elongation of the coracoids and, probably, loss of clavicles.

(*k*) Crocodilian tarsus (by inference from the tibia).

(*l*) Four subequal elongated metatarsals.

(*m*) Dorsal and ventral scutes.

Unfortunately the radius, ulna, carpus, manus, pelvis and femur are unknown.

Pedeticosaurus (figure 8) is related to *Sphenosuchus* by the position of the external naris, the reduced, posteriorly placed preorbital fossa, and the shape of the orbit with its forwardly inclined postorbital/jugal bar. A small portion of the inwardly directed process of the prefrontal appears to be preserved (van Hoepen 1915, Pl. XIII). The lateral temporal fossa is of similar shape and size and the quadratojugal is wedged in obliquely between jugal and quadrate. The more slender appearance of the rear end of the jugal in *Pedeticosaurus* is probably due to the fact of its being preserved as an impression of the outer surface; there is an external ridge in this region in *Sphenosuchus*. The jaw is of similar shape (by comparison with *Sphenosuchus* it is seen that the articular region is missing in *Pedeticosaurus*) and a large dentary tooth enters a gap in the upper tooth row. It seems likely that this gap, in *Pedeticosaurus*, actually represents the premaxilla/maxilla junction (although van Hoepen placed this contact further forward), so that the premaxilla bears three small and two large teeth and the maxilla fourteen small teeth. Many of the teeth seem to have lanceolate crowns like those of *Hesperosuchus*, but this is a point not mentioned by van Hoepen, who simply says that they are thecodont. The premaxilla of *Sphenosuchus* appears to have three small teeth followed by a larger tooth, but the preservation is not good. The maxilla has about 13 teeth, but these and the dentary teeth are, on the whole larger than those of *Pedeticosaurus*. The scapula is of similar shape in the two genera and there are four subequal, elongated metatarsals in *Pedeticosaurus* also. Dorsal and ventral scutes are present. It seems to me that van Hoepen was correct in his identification (as the left scapula) of the bone adjacent to the left humerus (see figure 8). This element is too long in comparison with the right scapula to be a coracoid as Haughton (1924) suggested; furthermore, a reversed tracing of it superimposes very well on the right scapula. I believe the lower edge in the figure to be posterior and the dorsal end to be adjacent to the left humerus. Nevertheless, it is extremely probable, by comparison with *Sphenosuchus* and *Platyognathus*, that the coracoid of *Pedeticosaurus* was elongated and crocodilian affinities are further enhanced by the nature of the pubis in *Pedeticosaurus*. This is rod-like, with a slightly expanded proximal end, very much as in *Protosuchus*, *Orthosuchus* and *Erythrochampsa* (Haughton 1924).

Van Hoepen interpreted the elongated element distal to the right radius of *Pedeticosaurus* as a metacarpal and stated merely that 'the carpus seems to have been very small' (1915, p. 85); no trace of it can be seen in the plate. It is here suggested that this elongated element is actually the radiale. The right scapula and fore-limb are preserved as impressions, seen from the medial side. The radiale would thus interpose between the radius and the first digit and the latter would, as seen here, be comprised of a metatarsal and two phalanges, the terminal one ungual. The remaining digits of the right manus are probably still present, but lying deeper within the matrix. There is a small impression in the position of a pisiform at the proximal end of the radiale. Unfortunately, van Hoepen appears to have made a slight error in the measurement of this element. Comparison of the proportion which it bears to other parts of the skeleton suggests a length of 13 mm, not 10 mm as he states. The difference is small but significant in relation to limb-elongation in this group. I estimate metacarpal I at 7 mm. The first metacarpal might, on this interpretation, appear to be very short, being about one-quarter the length of the longest metatarsal, but it is not greatly different from the proportion in *Protosuchus*; in *Hallopus* this ratio is one-fifth (see table 2). The proportion of the assumed radiale to the radius in *Pedeticosaurus* is only a little greater than in *Protosuchus* or *Alligator*. Again, in *Protosuchus* the radiale is about half as long again as the first metacarpal; in *Hallopus* it is nearly three times as long. In *Pedeticosaurus*, as now interpreted, it is nearly twice as long. This degree of elongation is in keeping with the intermediate position of *Pedeticosaurus* between *Protosuchus* and *Hallopus* in respect of limb elongation.

Pedeticosaurus differs from *Sphenosuchus* in details of the dentition, the lower skull with a longer premaxilla, and skeletal proportions.

Colbert (1952) figured a portion of the skull roof amongst the remains of *Hesperosuchus*. This he compared (his Fig. 4) with the skull of *Ornithosuchus*. It is apparent, though, that no valid comparison can be made in this way, since there is no sign in the *Hesperosuchus* fragment of the fronto-parietal sutures or of the postorbitals, which should be present. It is necessary to point out that the legends to Colbert's Fig. 3 have been transposed: his Fig. 3*a* is evidently the lower view of the fragment as it bears a pair of notches for the reception of the prefrontals and, as Colbert notes, is traversed by the usual channel for the olfactory tracts. This being so, his Fig. 3*b* is the dorsal view, which shows a conspicuous median longitudinal ridge. This is an unusual structure in reptiles, indeed another example does not readily come to mind—with the significant exception of *Sphenosuchus*, in which the configuration of the upper surface of the frontals is closely similar to the *Hesperosuchus* fragment (figure 9). The latter is thus composed only of the frontals, and the postero-lateral surfaces represent in large part the articular areas for the postorbitals. The portion of upper jaw (Colbert, Fig. 5) shows no suture between premaxilla and maxilla and it may be that this fragment is entirely maxilla, in which case the bone has a long extension in front of the preorbital fossa. The jaw shape is reminiscent of those of *Sphenosuchus* and *Pedeticosaurus*.

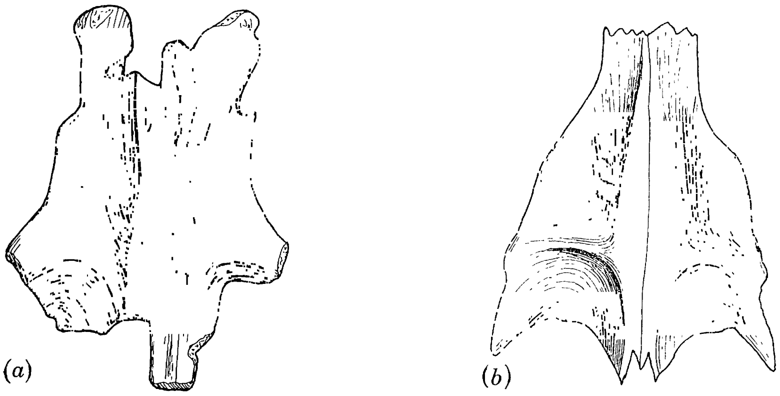


FIGURE 9. The upper surface of the frontals in (*a*) *Hesperosuchus*, after Colbert (1952) (magn. × 1.4); (*b*) *Sphenosuchus* (magn. × 1).

Colbert (1952, Fig. 26) also figured a 'problematical bone'. Dr K. A. Kermack informs me (personal communication) that this is virtually identical with the coracoid of a crocodilian which he collected from one of the Triassic fissures of Glamorgan (see also Kermack 1956). I think that once this identification has been pointed out, its correctness is self-evident. The coracoid of *Hesperosuchus* agrees in type with that of *Sphenosuchus* but is not as elongated; the scapula and slender limb-bones are closely similar to those of *Pedeticosaurus*. The pelvis again is unknown. Paired dorsal scutes, at least, are present.

Saltoposuchus is at present being studied by Dr Krebs and will not therefore be commented upon in detail, except in so far as is necessary to justify its inclusion within the group under discussion. Of the disarticulated skull bones, the 'lachrymal' (von Huene 1921, Pl. I, Fig. 9) is extremely like the jugal of *Sphenosuchus* and *Pedeticosaurus*. The 'ischium' (von Huene's Fig. 18) is unusual in the depth of the undercut below the 'iliac peduncle' and von Huene mentions (p. 355) and illustrates a flat surface bevelling off the 'peduncle' postero-dorsally. It seems likely that this bone is actually a left coracoid of *Sphenosuchus* type, the flat surface representing the lower part of the glenoid, and the supposed acetabular surface being the thickened posterior portion of the sutural surface for the scapula such as is commonly developed. There is a well-developed flat facet at the distal end of the tibia (von Huene, Pl. III, Figs. 9 and 14) and the curvatures of this element agree well with the tibia of *Sphenosuchus*. The calcaneum (von Huene, p. 347) is described as 'remarkably crocodile-like with a large tuber'. There are four elongated, subequal metatarsals (von Huene, p. 348). A paired series of dorsal scutes is present.

Von Huene (1921, Fig. 19) also described a pubis of non-crocodilian type as that of *Saltoposuchus longipes*. In another place (p. 335), however, he notes that the remains include parts of three skulls for only two postcranial skeletons and (p. 336) he allocates one of these sets of skull-bones to a saurischian 'which has great similarity to *Procompsognathus triassicus*'; the latter is a coelurosaur which was described by von Huene in the same paper on material from the same or a proximate horizon in a nearby quarry. Since the pubis (p. 355) occurs isolated on a separate block from the 'ischium', and since it also resembles that of *Procompsognathus* closely, there is a strong possibility that it, too, is coelurosaurian. It may be noted that several bones allocated to *Aetosaurus crassicauda* by von Huene (1921) are actually of a coelurosaur closely related to *Procompsognathus* (Walker 1961). These include a pubis very like the one figured.

Simmons has recently (1965) described new material of the formerly problematical *Platyognathus*. He concludes by placing the genus in a new family of Pseudosuchia, the Platyognathidae, while recognizing that this occupies 'a taxonomic position intermediate between the Pseudosuchia and Protosuchia'. It seems to me, however, that the resemblances between *Platyognathus* and *Pedeticosaurus* are much greater than Simmons has realized. The muzzle in each is low and acutely triangular in profile. There is a long premaxillary area between the external naris and the diastema (both differ from *Sphenosuchus* in this), and in each the preorbital fossa is set far back, close to the orbit. The distance from snout-tip to diastema is less than that from the diastema to the beginning of the preorbital fossa; this is not the case in *Orthosuchus*. The jaw shape is also very similar in both. It is almost possible to superimpose Simmons's Fig. 8A over the skull of *Pedeticosaurus* in van Hoepen's plate (1915, Pl. XIII). It may perhaps be doubted, in view of the situation formerly reported in *Sphenosuchus* and the very slender anterior border of the naris in *Pedeticosaurus*, whether the external nares in *Platyognathus* are really confluent. Unfortunately the rear half of the skull is unknown in *Platyognathus*. Simmons states (p. 40) that the dental patterns of *Platyognathus* and *Pedeticosaurus* are dissimilar. Assuming that the diastema in *Pedeticosaurus* marks the suture between premaxilla and maxilla, this statement does not seem to be borne out by the facts. In *Pedeticosaurus* (van Hoepen 1915) the premaxilla bears three small and two large teeth and the maxillary teeth, 14 in number, are said to be 'all small and diminish gradually in size going backwards'. The dentary has two small teeth at the symphysial end, followed by a large tooth, a gap, and then 'ten uniform small teeth, diminishing in size backwards'. (There may well have been more than this, seeing that the posterior maxillary teeth appear to be unopposed.) In *Platyognathus*, according to Simmons, the premaxilla has four subequal teeth, the first two being anteriorly directed, the postdiastemic (i.e. maxillary) teeth 'are immediately less robust and become progressively smaller backward'. The first two dentary teeth are small and 'are followed by larger and more erect teeth'. Posteriorly the teeth are smaller. The overall pattern is thus similar in the two forms.

The scapula of *Platyognathus* has an expanded blade like that of *Pedeticosaurus*; the coracoid is elongated and more like that of a modern crocodile than is that of *Protosuchus*. There is a distinct resemblance to the scapula and coracoid of *Orthosuchus* (Nash 1968). The pelvic girdle and limbs are unknown. The dermal armour is closely comparable to that developed in

Pedeticosaurus, with a paired row of dorsal scutes extending on to the tail and eight longitudinal rows of rectangular scutes below the belly in both animals.

The evidence presented above is considered sufficient to justify the conclusion that *Sphenosuchus*, *Pedeticosaurus*, *Platyognathus*, *Hesperosuchus* and *Saltoposuchus* are closely related genera which may, for the convenience of the present discussion, be placed in the family Pedeticosauridae (van Hoepen 1915, p. 87). No evidence is known to the author which positively contradicts this assignment. It is difficult, because of incomplete knowledge of all these forms, to give a list of characters common to them all. Since the purpose of the present discussion is to establish the probability that *Hallopus* has descended from this group, only postcranial characters will be considered in the present section, and the broader question of the relationship between the Pedeticosauridae and 'true' crocodiles is deferred until later. As these genera are deemed to be closely related, it is regarded as legitimate to assume that a synthesis of characters may be made from them. Thus in *Pedeticosaurus* the coracoid is unknown, and the tarsus indistinct. Comparison with other members of the family, however, implies that both of these were of crocodilian type. If the interpretation suggested above is correct, the proximal elements of the carpus are considerably elongated. It is particularly unfortunate that nothing more of the pelvis has been recovered in any of these reptiles, but the crocodilian nature of the postcranial skeleton and the resemblance of the pubis of *Pedeticosaurus* to those of *Protosuchus*, *Orthosuchus* and *Erythrochampsa* suggests that, when ultimately found, the ilium and ischium will also prove to be of protosuchian type. It is not impossible that *Erythrochampsa* itself is a pedeticosaurid, in fact.

The scapula of *Hallopus* most resembles that of *Hesperosuchus*, in which the narrow part of the blade is longer than in *Pedeticosaurus*. The preserved parts of the humerus also agree well. The gentle sigmoid curve of the ulna compares satisfactorily, and the slight concavity at the posterior side of the distal end (Colbert 1952, Fig. 23*a*) is mirrored in *Hallopus*. The distal end of the radius is slightly shorter than that of the ulna. The femur of *Hallopus* is derivable from that of *Hesperosuchus* in the following manner. In *Hesperosuchus* the femur (which is closely similar to that of a present-day crocodile) has a vertically elongated proximal articular surface, the narrow lower end of which lies at the termination of a ventrally projecting ridge running back from just below the fourth trochanter. In crocodiles the puboischiofemoralis externus muscle attaches along the flat lower surface of this ridge. When, in the *Hallopus* line, the femur became movable only in the fore-and-aft-plane and, as a consequence, developed an offset head, the ventrally projecting ridge became separated from the head and was, so to speak, 'left behind' on the shaft and its abrupt posterior termination ceased to be part of the articular surface. The formation of a lesser trochanter is also a necessity when the hind-limbs are held close to the mid-line of the body—the iliofemoralis which attaches to it prevents the body falling over sideways when the contralateral hind-foot is off the ground.

A flat, postero-ventrally-facing facet on the lateral side of the tibia is characteristic of pedeticosaurids (although it occurs also in stagonolepids). This is a more definite feature than the less well-defined, but generally similar, area in modern crocodiles. The resemblance between *Sphenosuchus* and *Hallopus* in this character is very marked and the author has had the benefit of being able to compare them directly. It probably denotes a firmer fixation of the astragalus in relation to cursorial habits. As noted above, the foot of *Hallopus* was derived from a type which originally had four subequal elongated metatarsals. This pattern is present at least in *Pedeticosaurus*, *Sphenosuchus* and *Saltoposuchus* among the Pedeticosauridae. Furthermore, the first metatarsal of *Sphenosuchus* is very slender and there is little doubt that the pes was functionally tridactyl (digits II to IV); it provides a pattern from which the pes of *Hallopus* could readily have been derived.

A principal reason for considering that *Hallopus* is a descendant of the Pedeticosauridae is the tendency towards elongation of the limbs shown in varying measure by all members of the family (except *Platyognathus* in which the limbs are unknown), but particularly by *Pedeticosaurus* and *Hesperosuchus*. Table 2 shows various limb ratios in *Hallopus* and other forms. The agreement between *Hallopus* and the pedeticosaurids is striking and not only provides strong evidence of affinity but reinforces the correctness of the interpretation offered for the scapula and forelimb of *Hallopus*. It also argues against the possibility of a fortuitous association of more than one type of reptile on the *Hallopus* slabs. The rather shorter distal segments of the limbs, particularly the crus, in *Protosuchus*, assuming this form to be typical of the Protosuchia, and the slenderness of the limbs in pedeticosaurids, are the main points of difference between these two groups. An interesting point which emerges is the persistence of the two-thirds proportion between humerus and femur which survives in the primitive coelurosaur *Saltopus*. This ratio also obtains in the stagonolepids and in *Ornithosuchus*, and is evidently a primitive archosaurian character.

Table 2. Comparison of proportions of crocodilomorphs ahd coelurosaurs

	Hallopus	*Pedeticosaurus*	*Hesperosuchus*	*Protosuchus*	*Alligator* (juv.)	*Saltopus*	*Procompsognathus*	*Coelophysis*	*Compsognathus*
scapula (height above glenoid)/radius (%)	62	65	60	73	77	—	130+	*ca.* 145	141
scapula/humerus	57	56	55	58	53	—	—	*ca.* 105	85
scapula/femur	39	42 (37)	37	38	47	—	42+	*ca.* 66	46
humerus/femur	67	76 (67)	67	66	85	66	—	44–57	54
radius/femur	62	65 (57)	62	52	57	45	33	*ca.* 46	33
radius/humerus	92	86	92	79	67	70	—	*ca.* 73	*ca.* 60
radiale/radius	58	30	—	27	26	small	small	small	small
metacarpal I/radius	21	16	—	20	25	20	—	—	—
metacarpal I/metatarsal III	20	25	—	29	31	13	—	—	—
tibia/femur	125	101 (90)	93	83	82	120	116	117–107	116
metatarsal III/tibia	50	43	62	46	58	58	64	59–56	62
humerus + radius + radiale/ femur + tibia	74	80 (75)	—	72	87	*ca.* 50	—	*ca.* 50	*ca.* 40
hum. + rad. + radiale + McI/ fem. + tibia + MtIII	62	70 (66)	—	64	75	< 43	—	—	< 39

Data from Colbert (1952, 1962, 1964), Colbert & Mook (1951), van Hoepen (1915), and von Huene (1921); for *Compsognathus* from a cast. Figures in brackets for *Pedeticosaurus* are for a femur length of 75 mm.

In *Hallopus* the tendency of the pedeticosaurids towards limb elongation has been taken much further with the elongation of the tibia and, to some extent, the metatarsus. This elongation of the tibia has been compensated in the fore-limb by the elongation of the radiale and ulnare (see table 2) such that the ratio: humerus + radius + radiale/femur + tibia remains essentially the same as in *Pedeticosaurus* and *Protosuchus*.

7. Restoration and functional aspects of the skeleton

Restoration of *Hallopus* is hampered by the lack of information concerning the skull and vertebral column. It seems legitimate to assume that these portions of the skeleton were not greatly different from the pattern seen in the Pedeticosauridae, and van Hoepen's description and plate (1915) of the skeleton of *Pedeticosaurus* itself (figure 8) has been particularly useful in suggesting the general proportions of skull and different segments of the vertebral column which might have obtained in *Hallopus*.

In *Pedeticosaurus* the femur is between seven and eight times the length of a dorsal vertebra, in *Protosuchus* the ratio is a little over eight times. In the latter the dorsals are a little shorter than the sacrals. Both these methods of calculation agree in suggesting 10 mm for the lengths of the dorsal vertebrae of *Hallopus*. On the basis of similar comparisons, a skull-length of 90 mm, a presacral length of 210 mm and a glenoid-acetabular distance of 180 mm are arrived at. The preserved caudal vertebrae, although rather small, still have tall neural spines and transverse processes set well above the neuro-central sutures. This implies that they are from the middle of a rather long tail. Van Hoepen estimated that the tail in *Pedeticosaurus* (a long section of which is preserved) was 'probably longer than the body with the skull'. This proportion would make the total length of *Hallopus* 620 mm (or 2 feet).

The humerus of *Hallopus* seems to have resembled that of *Hesperosuchus* very closely. The distal end is narrow in both, with a deep posterior groove. Taken with the short olecranon process of the ulna, this presumably indicates that the forearm was capable of extension into line with the humerus. The proximal carpal joint has been discussed in some detail above (see §4), where it was concluded that little or no movement was possible. Thus it seems that the elongation of the mesopodials was essentially a device to increase the effective length of the antebrachium and it would be incorrect to compare them with the cannon-bone of a cursorial mammal (as I was at first inclined to do). The comparison with mammals would also imply that there were five functional segments in the forelimb of *Hallopus* compared with four in the hind-limb, and with four in digitigrade mammals. This also seems unlikely. Nevertheless, a certain 'springiness' at the joint in question may have been permitted, otherwise it is difficult to see why the mesopodials should have elongated to the extent that they have done. One would have thought that it would have been simpler and stronger to elongate the fore-arm instead.

The carpo-metacarpal articular surface is a transverse roller-joint which permitted movement only in the vertical plane. The relatively long, slender metacarpals and the analogy with modern crocodiles suggest that the fore-foot was digitigrade. This conclusion is supported by the symmetrical distribution of lengths of the metacarpals about the central axis, and the attitude of metacarpals I and V in the fossil. These converge distally behind the central metacarpals, and the proximal end of metacarpal I is faceted against metacarpal II as if carried in a permanently flexed attitude. Its condyles are turned a little laterally as in a Recent crocodile. Digits 1 and 5 thus seem to have functioned as lateral stabilizers, touching the ground behind and to the side of digits 2 and 4.

The derivation of the femur of *Hallopus* from a type like that of *Hesperosuchus* has been dealt with above (see p. 353). The *Hallopus* femur which at first appears to be *sui generis*, is thus readily obtainable from a crocodilian type. Presumably M. puboischiofemoralis externus inserted on to the lower edge of the pseudointernal trochanter, which corresponds to the flattened downward-facing area for its insertion in the crocodile femur. There is a certain resemblance also to the bird femur, in which the same muscle ('obturator externus') attaches to the lateral side of the ventrally projecting ridge below the great trochanter. In the bird, however, the ridge is more proximally placed, directly opposite the head of the bone. The longer area of insertion in *Hallopus* indicates a more powerful development of the muscle, similar to that in crocodiles.

The position of the lesser trochanter is like that of coelurosaurs, megalosaurids and *Ornithosuchus*. Its significance has already been mentioned.

The off-set head of the femur and the development of a lesser trochanter show that movement of this bone was essentially restricted to the parasagittal plane. The lack of a greater trochanter is notable, and, since this point is of some significance in determining the pose of the hind limbs, it deserves some discussion. In the dinosaurs, as Romer has shown (1923*a*; 1927, p. 230), M. puboischiofemoralis internus 2 arose from the centra and lower surfaces of the transverse processes of the posterior dorsal vertebrae and passed directly backward below the preacetabular process of the ilium to insert on the greater trochanter of the femur. Because of the proximal projection of this trochanter, the lever action of this muscle is only really effective when the femur is directed mainly downward (assuming that the vertebral column is horizontal). This being so, it seems to follow that the failure to develop a greater trochanter in *Hallopus* indicates that the femur was not habitually held in this attitude, but moved through a more forwardly directed arc. In order to avoid too great a height at the sacrum relative to the glenoid, such a pose is almost inescapable.

The details of the articular surfaces at the ankle-joint have been described above (see §4). All that is necessary here is to emphasize that movement was limited to the vertical plane. The oblique articular surface at the lower end of the astragalus probably acted as a medial stabilizer in the same manner as the pulley-like surface at the distal end of the bird tibia; because of the retention of the peg-and-socket joint between astragalus and calcaneum a similar area could not develop laterally in *Hallopus*. The amount of extension possible at the metatarsus is indicated by the length of the convex upper surface of the calcaneum in relation to that below the dorsolateral process of the astragalus, less what should be allowed for the small fibular contact which prolonged the latter backward. An arc of opening of the tibia-metatarsus angle between 40 and 140° is implied from observation of these areas. This is in agreement with the antero-ventral position of the medial articular area on the astragalus.

The indications are that *Hallopus* was digitigrade in the hind-foot. The evidence for this is as follows: (*a*) The pes is functionally tridactyl, with the proximal ends of the metatarsals securely locked together (but diverging distally). Metatarsal III is longer than II and IV, which are effectively subequal. This metatarsus is similar to those of coelurosaurs and carnosaurs, in advanced members of which the three functional metatarsals are immobile with respect to each other, and also to that of birds, and is obviously a mechanically stable type. (*b*) The tibia is notably longer than the femur, a trait again characteristic of coelurosaurs and birds. (*c*) The great length of the pes. It is a reasonable assumption that the phalanges of digit 3 were, in sum, equal in length to the metatarsal. The total length of the foot would thus be equal to that of the tibia, which is itself very elongated. Since the evidence from the femur and ankle shows that the limb could only have moved in a fore-and-aft plane, it becomes virtually impossible for the foot, assuming plantigrady, to clear the ground during the recovery phase. Attempts to restore it in this attitude are quite unconvincing. (*d*) The calcaneal heel is very narrow and lacks the posterior groove present in typical crocodiles; it extends back in line with the metatarsus. It is thus likely that it functioned as a simple lever and was closely comparable in its action to that of a cursorial mammal. This point is dealt with further below. (*e*) The lower end of the fibula retained a small contact with the narrow dorsal articular area on the calcaneum. This extends the articular area below the dorsolateral process of the astragalus backward. The posterior, rather than lateral, position of the distal end of the fibula may have served to transmit stresses from the lateral side of the metatarsus-calcaneum to the knee more effectively in a digitigrade pose. There is otherwise no obvious reason why the fibula should not have tapered out before reaching the distal end of the tibia, in bird-like fashion, since the astragalus occupies the full width of the tarsus. There is thus little doubt that *Hallopus* was digitigrade in the pes, although it may have rested with the foot in a plantigrade attitude. The hind-limb as a whole thus fulfils the conditions for a cursorial animal laid down by Gray (1968, pp. 252–3).

Hind-limb musculature

In the absence of the pubis it is clearly not possible to make a full reconstruction of the pelvic musculature of *Hallopus*; however, it may be assumed that the pubis was long and rod-like, very much like that of *Protosuchus*, and some suggestions on certain aspects of the musculature may be put forward. Romer (1923*a*) has discussed the changes which have taken place in the pelvic musculature of saurischian dinosaurs, compared with primitive reptiles, consequent upon the changed attitude of the femur in bipedal locomotion. The ilium of *Hallopus* is fairly readily understandable in terms of his analysis. The high, elongated blade gave long areas of origin for the iliofemoralis and iliotibialis muscles, which were powerfully developed. These are important in bringing the knee forward and extending the tibia. The long posterior extension of the blade recalls the ilium of coelurosaurs, but differs slightly in its downward curvature. It does not seem likely that the backward extension owes its existence to any expansion of the caudifemoralis brevis, since the fourth trochanter on which this muscle inserts is inconspicuous. Rather, the ilium appears to have developed a larger area for the origin of part of the long flexors (flexor tibialis externus and flexor tibialis internus 2) and particularly, the iliofibularis. The explanation for the elongation of the posterior part of the blade in coelurosaurs and in *Hallopus* may be as follows. In forms with an elongated tibia and metatarsus, the caudifemorales are less effective in retracting the hind-limb because the fourth trochanter on which they insert is relatively nearer to the fulcrum (the acetabulum) than in carnosaurs. The long flexors plus the iliofibularis, inserting below the knee, are able to exert a greater leverage. The parallel may again be drawn with birds, in which the caudifemorales are weak and the fourth trochanter is absent, but iliofibularis ('biceps femoris') is well developed. In *Hallopus* the downward curvature of the rear end of the blade may indicate that the knee joint was on the whole more anteriorly directed than in the bipedal coelurosaurs, so that the long flexors from the end of the blade passed more obliquely downward and forward.

In the crocodilian tarsus, to quote Schaeffer (1941): 'the tendon of the relatively much larger fibular portion (of the gastrocnemius) passes directly over the tuber and is partially attached to it, although the actual insertion is into the plantar aponeurosis. The tibial head joins the fibular at the tuber, as does the long tendon of the flexor tibialis.' Because the calcaneum is functionally part of the pes, the tuber acts as a lever elevating the heel during propulsion. Some movement is permitted, however, between the calcaneum and the lateral distal tarsal. The tuber also projects downwards as well as backwards, relative to the axis of the metatarsus. The effect of this deviation is to increase the angle of application of the gastrocnemius tendon as it passes over the pulley-like groove at the back of the tuber, making its pull on the plantar aponeurosis more effective.

In *Hallopus*, on the other hand, calcaneum and lateral distal tarsal meet at perfectly flat surfaces, and no movement is possible between them. The calcaneum, distal tarsals and metatarsals are firmly consolidated into a rigid unit. The tuber calcanei is very narrow and it is quite clear that the gastrocnemius tendon did not pass over it. Also, the tuber projects directly backward in line with the axis of the metatarsus. It is evident that the gastrocnemius attached mainly to the ascending process at the distal end of the tuber, and the latter acted as a simple lever in comparable fashion to the calcaneum of mammals.

As discussed above, metatarsal V can be located satisfactorily alongside metatarsal IV, with its proximal articular surface lying against the lateral side of the ventral concavity shared by the lateral distal tarsal and metatarsal IV. This allows space for a reduced plantar aponeurosis such as one would expect in a form with a bird-like pes and a fully-developed 'Achilles tendon'. The transverse ridge on the lower side of the lateral distal tarsal, immediately proximal to this concavity, would have increased the angle of application of the tendon of the flexor digitorum longus as it passed over the ridge. It is thus analogous to the hypotarsus of the bird foot.

According to Schaeffer, the peroneus brevis in the alligator inserts mainly on the fifth metatarsal, and functions as an extensor (dorsiflexor). The position of this metatarsal in *Hallopus* mainly underneath metatarsal IV, would permit more efficient elevation of the consolidated pes by means of this muscle. The position and shape of metatarsal V is very similar in the coelurosaurs *Saltopus* and *Procompsognathus*, which have a general resemblance to *Hallopus* in hind-limb proportions.

The acquisition of limb specialization

It is helpful to compare *Hallopus* with *Protosuchus* and *Pedeticosaurus* in order to obtain some insight into the manner in which the specializations of *Hallopus* have arisen. There is little difference between these three in the humerus/femur, humerus/dorsal vertebra and femur/dorsal vertebra ratios (taking the dorsals in *Hallopus* as not very different in length from the sacrals). It is therefore difficult to assert that the proximal segments of the limbs have undergone any elongation or reduction. In table 2 van Hoepen's estimate for the length of the femur in *Pedeticosaurus* has been used, but if the femur was in fact longer (say 75 mm, which is quite probable) many of the values involving this element in table 2 would be even closer to corresponding ratios for *Hallopus* and *Hesperosuchus*. (As a corollary, the proximal end of the femur in van Hoepen's plate (see figure 8) would be well behind the proximal end of the pubis, implying that the latter was largely excluded from the acetabulum.)

The distal segments of the limbs are slightly elongated in *Pedeticosaurus* and *Hesperosuchus* with respect to *Protosuchus*. This involves the radius/humerus, radiale/radius and tibia/femur. The elongation is much greater in *Hallopus*; here it is the radiale which has lengthened to compensate for the long tibia, the radius proportion remaining as in the pedeticosaurids.

Protosuchus was probably plantigrade in the manus, to judge from the equality of lengths of the first four metacarpals (metacarpal V is unknown). The similarity of the low tibia/femur ratio to that of a modern crocodile implies that it was plantigrade in the pes. As Romer (1956) points out, the manus and pes have undergone some secondary elongation in modern crocodilians in relation to amphibious habits. This obscures the comparison of these regions with the fossil forms here under consideration. An index of the proportion between the effective lengths of the fore- and hind-limbs is given by humerus + radius + radiale/femur + tibia in the case of plantigrade forms, and to these may be added metacarpal I and metatarsal III respectively or possibly digitigrade forms (it would be preferable to use metacarpal III but this is unknown in *Pedeticosaurus*). The similarity between each of these ratios in *Protosuchus* and *Hallopus* reinforces the suggestion that the former was plantigrade in both the manus and the pes—since there is good evidence for digitigrady in both of these segments in *Hallopus*. An important further conclusion is that any possibility of bipedalism in any of these forms is firmly ruled out.

The values for *Pedeticosaurus* appear to differ a little from those for *Protosuchus* and *Hallopus* but, if one assumes, as before, that van Hoepen's estimate for the femur length was too low, the agreement becomes very good. Bipedalism is even less likely in *Sphenosuchus*, in which the scapula and humerus are a little larger in relation to the tibia than in other pedeticosaurids. The metatarsals in *Hesperosuchus* are abnormally large in relation to both femur and tibia, whereas all other known skeletal proportions agree well with *Pedeticosaurus*. The reason for this is not clear.

The question naturally arises as to whether the pedeticosaurids were plantigrade or digitigrade. Without detailed knowledge of the structure of the tarsus and pes in this group one cannot give a definite answer. The limbs are very slender and the bones hollow, nevertheless the shortness of the first digit of the manus and the lack of any tendency towards tridactyly in the pes implies that *Pedeticosaurus* at least was still plantigrade. On the other hand, in *Sphenosuchus* the pes is functionally tridactyl with metatarsal III half as long as the tibia, and metatarsal I is slender. The probability is that the pes was digitigrade in this form.

There is a certain degree of parallelism in the proportions and build of the hind-limb between *Hallopus* and coelurosaurs, although, of course the fore-limbs are reduced in the latter group. A major difference between them is the retention of a calcaneal heel in *Hallopus* and its absence in most coelurosaurs. The explanation of this lies in the structure of the tarsus. In crocodiles and, in a more intimate manner, in *Hallopus* (as in mammals) the calcaneum is functionally part of the foot. Its heel is therefore able to act as a lever in raising the metatarsus. In coelurosaurs, on the other hand, as in birds, the calcaneum is part of the crus. A calcaneal heel could not, therefore, act as a lever for the gastrocnemius, although it could increase the angle of application of any tendon which passed over it. This function is fulfilled by the tibial cartilage in birds. It is nevertheless odd, as Schaeffer (1941) points out, that dinosaurs have no indication of any structure that would increase the angle of application at the foot.

The question of whether the coelurosaurian tarsus can be derived from the crocodilian type is outside the scope of this paper. It may be noted, however, that *Saltopus*, from the Lossiemouth Beds (Upper Trias) is a coelurosaur in all ascertainable morphological features, including limb proportions, yet it possesses a small calcaneal tuber, a rather large lateral distal tarsal, and a dorsolateral process of the astragalus partly overlying the calcaneum.

Pose of the limbs and locomotion

The picture of *Hallopus* which emerges from the foregoing analysis is of a small, lightly built, agile reptile with elongated limbs. The carpus and tarsus are compressed and 'streamlined'. The manus is pentadactyl, the pes functionally tridactyl. Both were probably digitigrade. Comparison with other archosaurs is limited by the fact that *Hallopus* was specialized for rapid quadrupedal progression, whereas the predominant tendency in cursorial archosaurs was towards bipedalism (e.g. coelurosaurs and some ornithopods), with reduction of the fore-limbs and specialization of the hand for grasping. In making the restoration of the skeleton (figure 10) the chief difficulty encountered was the high position of the acetabulum in relation to the glenoid. This has not been resolved with complete satisfaction. Several alternative poses of the hind-limbs have been tried, with the knees more flexed, or the tibia/metatarsal angle less obtuse, but all proved unsatisfactory for a variety of reasons. The attitude shown represents the animal in a standing or slow walking pose. It is possible that when stationary the metatarsus would have been in contact with the ground. In rapid locomotion the fore-limbs would act

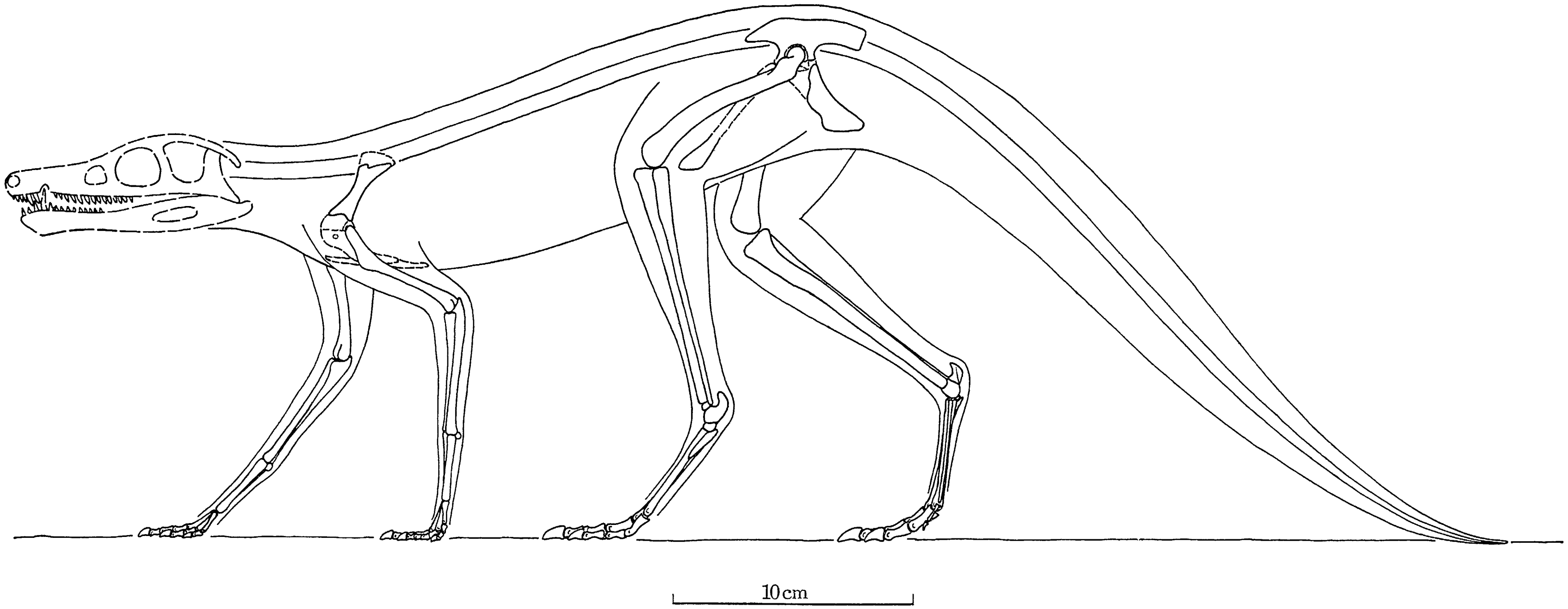


Figure 10. *Hallopus victor* (Marsh). Restoration of the skeleton in standing pose. (Skull hypothetical, based on *Pedeticosaurus*) (magn. × $\frac{1}{3}$).

more in the nature of struts, the fore-part of the body 'bouncing' off each in turn (or together) so that a longer stride would be attained by the fore-limbs than in the attitude shown. This would raise the glenoids a little and partly compensate for the longer hind-limbs. Probably a bounding or galloping type of progression like that of a hare or greyhound was well within its capabilities.

There is some similarity in proportions to *Scleromochlus*, a small archosaur from the Lossiemouth Beds. In this animal the radius is only slightly shorter than the humerus, the tibia is longer than the femur (108 %), and the first four metatarsals are fused and elongated (55 % of tibia length). The tarsus is crocodilian. The presacral vertebrae are, however, very short, and with the humerus/femur ratio at 61 % indicate a definite tendency towards bipedal hopping. It differs also from *Hallopus* in the normal, short carpus, and the coracoid (*pace* von Huene 1914) is not elongated. In addition, metatarsals I to IV are equal in length and thickness and form a rectangular surface which I believe may be interpreted as having had a 'snowshoe' effect to prevent the foot sinking into the dune sand which was the probable habitat. Some features of the skull of *Scleromochlus* (a highly specialized aetosauroid with both temporal fossae almost completely closed up) imply, by comparison with certain modern lizards, life in such an environment. The analogy with *Hallopus* is, therefore, limited from the functional aspect.

A major difficulty in comparing *Hallopus* with mammals is that the radiale-ulnare appears to have functioned essentially as an extension of the radius-ulna, and not as a separate segment analogous to the elongated metacarpus of cursorial forms. Although in mammals the radius may be considerably longer than the humerus, e.g. *Neohipparion* (130 %) or *Antilope* (126 %) (data from Gregory 1912), the radiale + radius/humerus ratio in *Hallopus* far exceeds these at 146 % (only the giraffe at 160 % is greater!). Furthermore, the types with an elongated radius (i.e. R/H > 100 %) dealt with by Gregory have the longest metacarpal (III) at least half as long as the humerus and in some cases exceeding the latter in length. The longest metacarpal of *Hallopus* is estimated with only a small margin of error at 26 % of the length of the humerus.

The best mammalian analogy available appears to be that of a hare (e.g. *Lepus timidus*). The radius is slightly longer than the humerus, and the manus is short (metacarpal III/humerus: 29 %) with a tendency to develop a roller-like joint at the proximal end of the carpus. The tibia is longer than the femur (110 %) and the effective length of the metatarsus (i.e. including part of the elongated tarsus to make the comparison valid) is 55 % of tibia length. The humerus/femur ratio at about 83 % is higher than in cursorial ungulates, and also of course than this ratio in *Hallopus*. However, the more elongated distal segment of the fore-limb in *Hallopus* makes up for this deficiency and there is an extremely close agreement between the values of humerus + radius + radiale/femur (166 %) in the reptile and humerus + radius/femur (167 %) in the mammal. Adding the tibia length to the femur gives 74 and 79 % respectively. (The greyhound differs in that the humerus/femur ratio is high (94 %), the radius is slightly shorter than the humerus and the metacarpal III/humerus ratio is relatively high at 40 %.) It seems not unlikely that the development of a mammal-like calcaneal lever in *Hallopus* is directly connected with a bounding gait. (It is interesting to recall that the name was coined to mean 'leaping foot' by Marsh (1881), although he believed that the apparently very short radius and ulna indicated *bipedal* jumping habits). However, the above analogy should obviously not be pressed too far; it is extremely unlikely that the posterior dorsal vertebrae of *Hallopus* were capable of as much dorso-ventral flexion and extension as in lagomorphs or mammalian carnivores and, in addition, the few preserved caudal vertebrae suggest the presence of a long tail. Thus it is uncertain whether the vertebral column would be capable of sufficient flexion, or short enough, to permit the hind-feet to pass the fore during the gallop. Naturally, in the absence of any presacral vertebrae no more can be said on this point.

Cott (1961) records that young Nile crocodiles gallop: 'The leg action is rapid, the crocodile bounding along like a squirrel, with a pitching motion of the body, and at an estimated speed of about 7 or 8 miles per hour'; 'Crocodiles seen galloping have all been small specimens measuring between about one and two metres in length'. The possible significance of the gallop in the emergence of the distinctive crocodilian type of shoulder-girdle is discussed further below.

8. THE CLASSIFICATION AND EARLY EVOLUTION OF CROCODILES

The outline of a proposed classification of crocodiles has been presented in a previous publication (Walker 1968) but there was not space at that time to set out the reasons for the arrangement suggested. It is desirable that this should now be done.

The description by Nash (1968) of *Orthosuchus* (figures 11 and 12) adds greater probability to the suggestions made by the author concerning the skull roof of *Protosuchus*, and reinforces the interpretation of *Stegomosuchus* as a crocodile. It should be made clear that the interpretation of the skull roof of *Stegomosuchus* was based largely on a cast from the counterpart slab. This cast gives the upper surface of the skull and dorsal armour, whereas Emerson & Loomis's original figure (1904) was of the lower slab, from which most of the bone had 'skinned off'. In Lull's plate (1953, Pl. VI), Fig. B is of the counterpart slab. *Orthosuchus* and *Stegomosuchus* (figure 11 *a*) resemble each other closely in the broad, flattened skull-table, although the sutures differ and the supratemporal fossae are very small in *Stegomosuchus*. In both there is a longitudinal rebate along the margin of the skull table, there are two supraorbital elements on each side, and a transverse flange crosses the rear of the skull. The skull roof is pitted in both forms. The nasals and frontals are paired, but the parietals are fused. Emerson & Loomis's figure (1904) of the cheek region is difficult to understand. They show *two* laterally directed temporal fossae behind the orbit, separated by a slender bridge of bone, but since there is an unmistakable supratemporal fossa on the skull roof this cannot be correct. Gilmore (1926, p. 339) suggested that the slender bar represents an inclined quadrate, the small triangular fossa above it being the auditory channel. Comparison of the casts of the upper and lower slabs suggests, however, that this slender 'bar' represents a smooth impression where the bone has come off the lateral flange of the squamosal in the lower block. Apart from this, the cast shows only a hint of a strongly inclined quadrate below the overhanging squamosal. By comparison with *Orthosuchus* and *Notochampsa* (von Huene 1925) it is a reasonable inference that there was a deep otic notch.

Postcranially *Stegomosuchus* is poorly known but other crocodilian characters include the broad, triangular apex of the scapula (Emerson & Loomis 1904, p. 379) and the presence of four subequal elongated metatarsals on the hind-foot, clearly seen in the cast from the dorsal slab. There are two sacral vertebrae. Careful comparison of the 'upper' and 'lower' casts suggests that the apparent lateral dorsal scutes are actually bent-down portions of the paramedian scutes as in *Protosuchus*. The resemblance of the dorsal armour is very close in these two genera (compare Colbert & Mook 1951, Pl. 11 with Lull 1953, Pl. VI).

It is an interesting commentary on the systematic position of *Stegomosuchus* that Gilmore

(1926, p. 340) placed *Hoplosuchus* from the Upper Jurassic in the family Stegomosuchidae of the Suborder Aetosauria, in spite of the many crocodilian characters of *Hoplosuchus* which he listed. He was impressed by the resemblances between the skulls and slender limbs of the two animals. *Hoplosuchus* is now classified as an atoposaurid crocodile; it may be, in consideration of the reduced supratemporal vacuities in *Stegomosuchus* and the atoposaurids, that Gilmore's assignment was a not unreasonable one, and that *Stegomosuchus* is close to the ancestry of that family.

In view of the interpretation of the radiale in *Pedeticosaurus* offered above, it is noteworthy that Gilmore failed to recognize this elongated element in *Hoplosuchus* but identified it as a metacarpal.

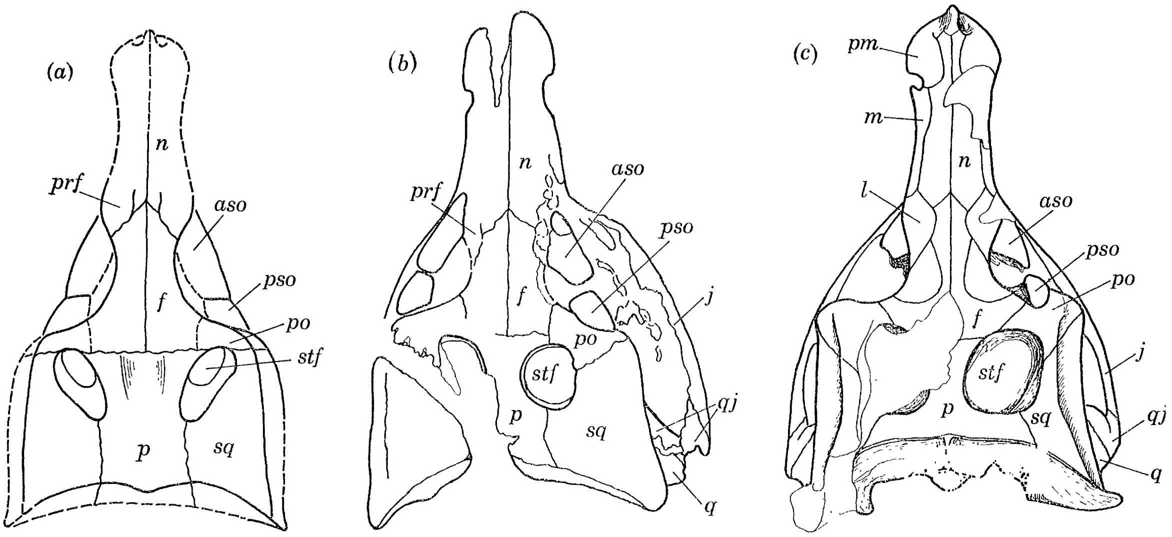


FIGURE 11. Dorsal views of the skulls of (*a*) *Stegomosuchus*, from casts (magn. × 1.5); (*b*) *Protosuchus*, traced from Colbert & Mook (1951, Pl. 12, Fig. 1) (magn. × *ca.* $\frac{2}{3}$); (*c*) *Orthosuchus*, after Nash (1968), (magn. × *ca.* $\frac{2}{3}$). The bone labelled '*l*' is perhaps the prefrontal.

The external nares lie at the extreme anterior end of the snout in *Orthosuchus*. In the restoration of the skull of *Protosuchus* I assumed that these structures faced upward and, since their borders are said (Colbert & Mook 1951, p. 158) to be not preserved, I allowed a greater length to the snout than in their restoration. This now seems unjustified in view of the similarity which has since emerged between the snout region (Colbert & Mook, Pl 12, Fig. 1) and that of *Orthosuchus* (see figure 11).

Protosuchus, *Orthosuchus*, *Stegomosuchus* and *Notochampsa* appear to be so similar in their skulls and the known features of their postcranial skeletons that they may be placed in the same family. As far as I am aware, the only major obstacle to this procedure is the possible absence of an otic notch in *Protosuchus*. Bearing in mind the condition of the skull as shown by Colbert & Mook's plates and the fact that this most important, indeed critical, region is not even mentioned in their description, I have yet to be convinced that the apparent absence of an otic notch is a real phenomenon. This is especially so in view of the remarkable similarity between *Orthosuchus* and *Protosuchus* in the dorsal aspect of the skull and jugal arcade (see figure 11, and compare Nash 1968, Fig. 1 with Colbert & Mook 1951, Pl. 12, Fig. 1). As has been pointed out (Walker 1968) the correct name for the family is Stegomosuchidae von Huene 1922.

Synthesis of characters from the various genera of the Pedeticosauridae gives the following as crocodilian:

Small, terminal external nares; reduced, posteriorly placed preorbital fossa; prefrontals meet in mid-line above palate; loss of postfrontals; parietals fused; squamosal with long, posterior overhang, without descending process; quadrate moderately inclined forwards; quadratojugal a parallel-sided strip mainly lateral in exposure, obliquely placed between quadrate and posterior process of jugal; plate-like occiput with narrow supraoccipital entering margins of small post-temporal fossae; secondary palate partly developed; fusion of basal articulation; initiation of a eustachian system; a transverse foramen through the basisphenoid; an enlarged mandibular tooth bites into a notch between premaxilla and maxilla; elongated coracoid; elongated proximal carpals; rod-like pubis; 'typical' crocodilian tarsus with calcaneal tuber; four elongated subequal metatarsals; dermal armour.

Whether *Platyognathus* merits recognition as the type of a separate family is difficult to decide. The dorsal vertebrae are described by Simmons (1965) as gently procoelous, a surprisingly advanced character, in contrast to the amphicoelous dorsals of *Orthosuchus*. The secondary palate of *Platyognathus* is said to be of mesosuchian type, but the precise meaning of this is not easy to ascertain. The vertebral column is not well known in other pedeticosaurids, but there is a short secondary palate in *Sphenosuchus*. A conservative course is therefore adopted here and only the family Pedeticosauridae is recognized.

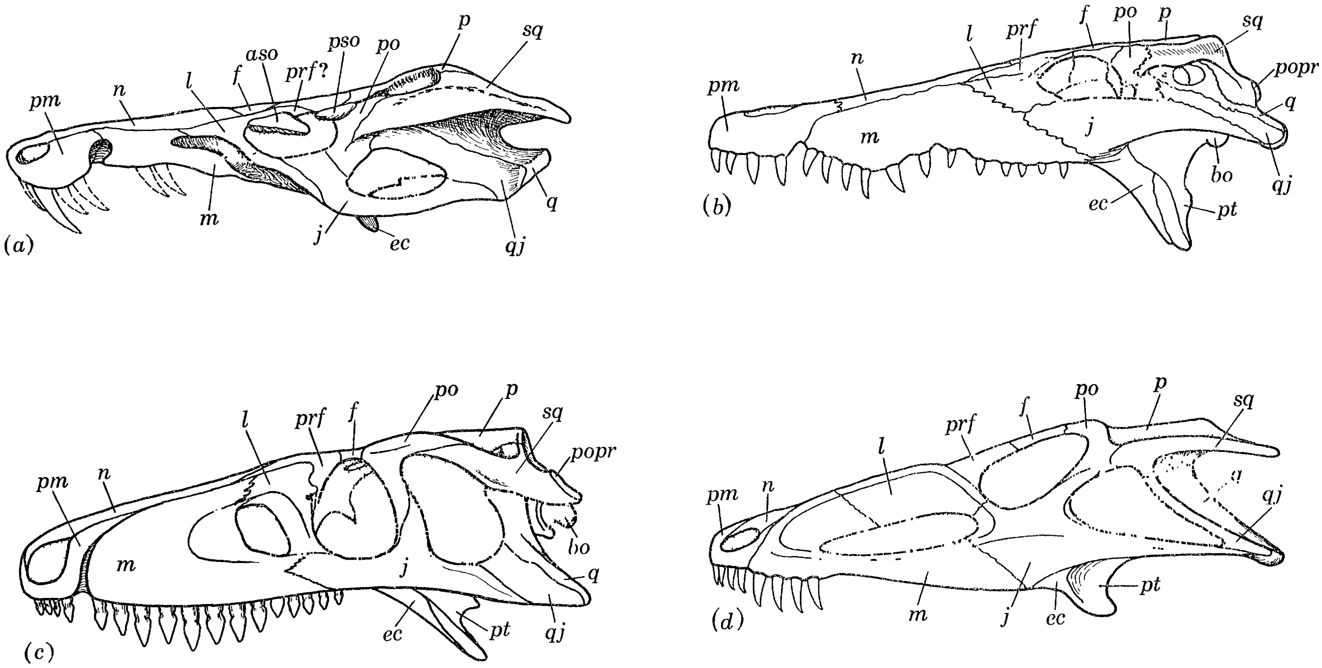


FIGURE 12. Side views of the skulls of (*a*) *Orthosuchus*, after Nash (1968), (magn. × ⅔); (*b*) *Crocodylus*, after Romer (1956); (*c*) *Sphenosuchus* (magn. × 0.42); (*d*) *Erpetosuchus*, natural size.

It is considered that the above assemblage of characters is sufficient to demonstrate that the pedeticosaurids are closely related to the 'true' crocodiles on the one hand, and distinct from thecodonts on the other. The nature of the postcranial skeleton is of particular importance in indicating crocodilian affinities. Such an assemblage of characters is surely unlikely to have arisen by parallel evolution. Nevertheless, there are other features which also imply that this group is not intermediate in position between thecodonts and 'true' crocodiles, but branched off at an early stage from a common ancestry with the latter. These features include the rather high postorbital region of the skull with large lateral temporal fenestrae, large supratemporal fenestrae (at least, in *Sphenosuchus*) and relatively primitive palate. Taking *Orthosuchus* as typical of protosuchian crocodiles, contrasting features to pedeticosaurids (figure 12) lie in the rectangular, flattened skull table, the strongly inclined quadrate and deep otic notch, small lateral temporal fossa and lower skull. Postcranially there is no convincing evidence of important morphological distinctions between the two groups. Pedeticosaurids appear to have been, on the whole, more cursorially-inclined animals but there are indications of such tendencies in *Protosuchus* and *Stegomosuchus* also.

While uniting these two groups within one Order, it seems more logical to place them in a larger grouping, the Crocodylomorpha, than to attempt to 'squeeze' the Pedeticosauridae into the current concept of the Order Crocodylia. This becomes even more difficult when the case of *Hallopus* is considered. Since the pedeticosaurids and 'true' crocodiles evidently represent a fundamental dichotomy of the crocodilian stock, a new subordinal category to rank co-ordinate with the Crocodylia is required. Nopcsa (1923) used the term 'Procrocodilia' as a suborder of Crocodylia to include the two families Sphenosuchidae and Erpetosuchidae. This is inappropriate since it implies an ancestral position for this group with respect to the Crocodylia, and also includes *Erpetosuchus* which I do not now regard as a crocodilian. The term Paracrocodylia is considered more suitable in its implications. Subdivision of the Suborder Paracrocodylia is necessary to give due weight to the differences between the highly specialized *Hallopus* and the pedeticosaurids. It also seems probable to the author that *Baurusuchus* is descended, independently of other crocodiles, from the Pedeticosauridae. The evidence for this is to be discussed shortly. The Suborder Paracrocodylia is therefore divided into the Infraorders Pedeticosauria (based on Pedeticosauridae van Hoepen 1915, which has priority over Sphenosuchidae von Huene 1922), Hallopoda (proposed as a suborder by Marsh 1881), and Baurusuchia (based on Baurusuchidae Price 1945).

The common ancestor of all crocodilomorphs might be expected to have possessed already all the essential postcranial characters of the Order—elongated coracoid and proximal carpals, rod-like pubis partly excluded from the acetabulum, 'typical' tarsus and four subequal long metatarsals, dermal armour. In the skull it would have had small, terminal nares, a reduced, posteriorly placed preorbital fossa, probably a rather high postorbital skull with a large lateral temporal fossa, a moderately inclined quadrate, squamosal without descending process, quadratojugal wedged in obliquely between jugal and quadrate, some development of a secondary palate, a rectangular skull table with supratemporal fossae of modest size, no postfrontals, narrow supraoccipital, and the squamosal/parietal sutures rather medially placed. *Cerritosaurus* (figure 13) from the Santa Maria formation of Brazil (Price 1946) fulfils many of these requirements, at least cranially, and seems to be close to the ancestral crocodilian (Walker 1968), but the nature of the external nares is an obvious specialization.

The tendencies towards cursorial adaptation indicated by the elongated proximal carpals in *Protosuchus* and *Notochampsa*, and the slender limbs of the latter and *Stegomosuchus*, together with the more obvious elongation of the limbs in pedeticosaurids and in *Hallopus*, raise the question as to whether other peculiarities of the crocodilian postcranial skeleton may not have arisen during an initial cursorial phase.

It seems possible that the elongated coracoid, loss of clavicles and peculiar pelvis of crocodiles may be of significance in this connexion. There is a certain resemblance between the low elongated blade of the ilium and the long, rod-like pubis of stegomosuchids and the corresponding

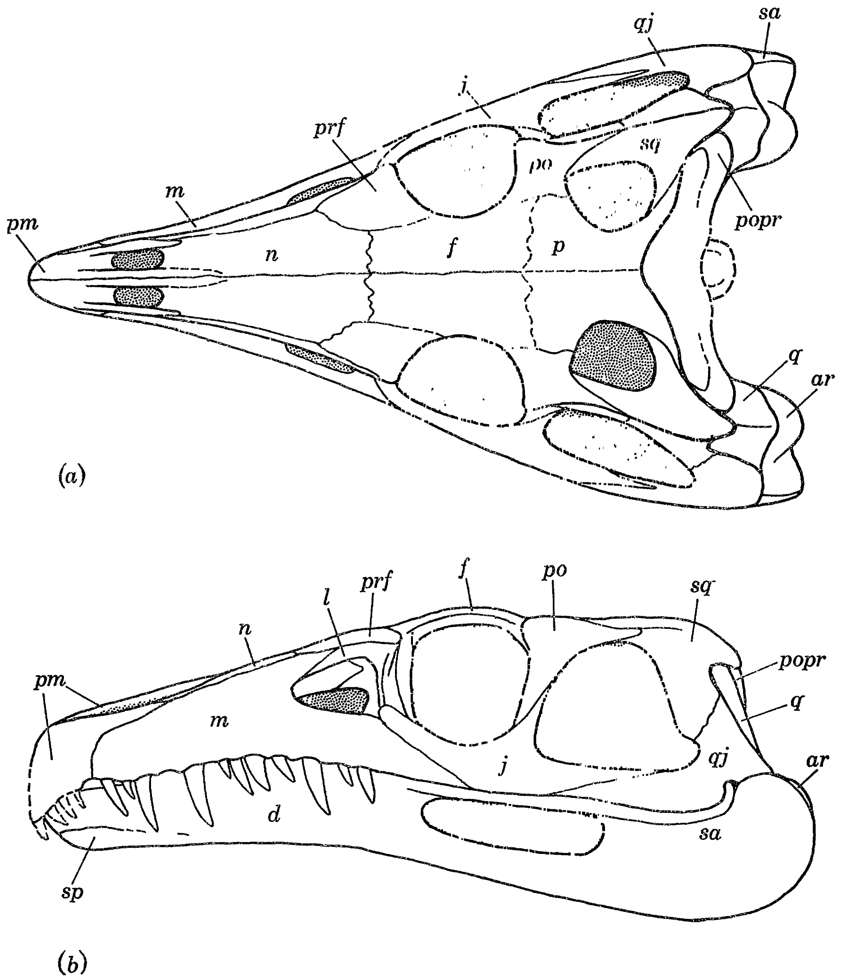


FIGURE 13. (*a*) Dorsal, and (*b*) side views of the skull of *Cerritosaurus*, after Price (1946), (magn. ×1.1).

bones of coelurosaurs, and the pelvic musculature must have been quite similar (Romer 1923*a*, *b*). However, in crocodiles the sacrum is relatively wide, whereas in archosaurs which show a tendency to bipedality, e.g. coelurosaurs, the sacrum becomes extremely compressed. The possibility arises that the peculiarities of the crocodilian shoulder-girdle may have originated in a galloping or bounding mode of progression. This seems to have been normal in *Hallopus* and by extension, in the pedeticosaurids which have a similar, but less extreme pattern of limb specialization. Von Huene indeed (1925, p. 314–315) suggested that forms like *Pedeticosaurus* were 'upright runners and jumpers' when they wished to move quickly, and Kermack (1956) postulated a terrestrial phase in the early history of the group. The words of Cott on the galloping of young Nile crocodiles have been quoted above and it is noteworthy that all the pedeticosaurids and stegomosuchids are of small size, with a skull length at a maximum of 18 cm. Obviously such a type of locomotion could hardly have arisen in a large, primitive archosaur but it may have done so in a small, lightly built form. The freeing of the shoulder-girdle by the loss of the clavicles would thus be analogous to the reduction or loss of these elements in jumping or galloping mammals, e.g. lagomorphs, carnivores, ungulates. The postero-ventral elongation of the coracoid probably had two main advantages. In the first place, it moved the glenoids farther apart, thus ensuring greater lateral stability when the fore-limbs met the ground (the elongated coracoids of frogs provide a parallel). Secondly, it afforded a more posterior origin for the pectoralis and coracobrachialis muscles. This is brought out by a comparison between the figures of the ventral musculature of *Sphenodon* and *Crocodylus* in Gregory & Camp (1918). In the crocodile, the pectoralis is entirely behind the glenoid and has an exceptionally long posterior area of origin from the sternal ribs. The more posterior position of the retractor muscles, inserting on the deltopectoral crest and ventral surface of the humerus, would have permitted a more effective, and longer, backward pull at the take-off of the fore-part of the body, which begins with the humerus extended downwards and perhaps forwards. (It is not possible to say whether there was one or two phases of suspension during the primitive gallop but, if there were only one phase, the shift in the musculature would have been equally effective during the 'closing-up' period, when the hind-limbs are brought up close behind the fore-limbs, preparatory to the jump.) Without this backward extension of the coracoid, a near-vertical attitude of the humerus would bring the bone too close to the areas of origin of these particular muscles for them to have much effect. The situation would thus be analogous to that demonstrated by Romer (1923*a*) for the shift in the ventral pelvic musculature of saurischian dinosaurs—in that case due to the femur having come to move in a near-vertical plane close to the pelvis. It is probably significant that in some primitive crocodilomorphs (*Hesperosuchus*, *Sphenosuchus*, *Protosuchus*), the coracoid is directed more posteriorly than ventrally. An analogy in broad terms may be drawn between the presumed action of the pectoralis and coracobrachialis muscles in a galloping crocodile and the same muscles in the flapping flight of a bird. The arrangement of the muscles is quite similar and, of course, the coracoid is elongated in the bird in a manner very much like that of the crocodile. In the bird the greatest muscular effort takes place during the downstroke of the humerus; in the crocodile, presumably during the backward stroke as the hind-limbs close up to the fore-limbs.

The resulting lateral position of the glenoid and the rearrangement of the ventral musculature at the shoulder girdle would then have been preadaptive for amphibious life, permitting greater efficiency of the use of the fore limbs in swimming, steering, slithering and 'fending-off' movements. Lateral migration of the glenoid has occurred in other aquatic reptilian groups, e.g turtles, nothosaurs, plesiosaurs. Modern crocodiles use only the tail for propulsion (Cott 1961), but presumably the limbs are used in steering; in the earliest amphibious members of the group the forelimbs may have played a more important role.

The secondary reduction of the length of the pubis (from the presumably primitive condition shown by *Protosuchus* and *Erythrochampsa*) and its gradual exclusion from the acetabulum may have been due to the flattening of the body and the adoption of the well-known sprawling habits of typical crocodiles.

If there be any validity in the above suggestion, then the gallop of young crocodiles preserves a very ancient type of locomotion.

Erpetosuchus (figure 12*d*), previously suggested (Walker 1968) as a crocodilomorph, is now thought to be a pseudosuchian at best only distantly related to crocodiles. The preorbital fossa is very large; the squamosal has a small descending process which meets the quadratojugal; the latter lies mainly behind the quadrate and appears laterally only as a thin edge and has but a short contact with the jugal; the basal articulation of the braincase is free. Removal of a flake of matrix proved that appearances were deceptive and that the coracoid is not constricted in the middle. In the left forelimb there is a gap between the distal ends of the radius and ulna and the carpus. This now seems to me to be due to the manus having been bent upward at right angles to the fore-arm and not to loss of the proximal elements of the carpus, as I formerly thought. (The right manus is disarranged and unclear.) The skull of *Erpetosuchus* is now considered to display a remarkable example of convergence towards the crocodilian condition in the attitude of the quadrate and formation of an otic notch, but a critical analysis shows that the details of the squamosal and quadratojugal are essentially pseudosuchian and can be distinguished from the pattern developed in the Crocodylomorpha. It is intended to re-describe *Erpetosuchus* more fully in the future. For the present *Erpetosuchus*, *Dyoplax* and, possibly, *Parringtonia* are placed in the family Erpetosuchidae Watson, 1917.

Proterochampsa from the Ischigualasto formation (probably early Carnian) of Argentina has been considered by Reig (1959) and Sill (1967) to be a primitive crocodilian. I have elsewhere (Walker 1968) suggested that this is not the case and Nash (1968) notes further differences between the skull of this form and those of stegomosuchids. Whether or not it be related to phytosaurs, it seems that the position of the choanae alone is sufficient to exclude it as a crocodilian ancestor.

Outline of classification

Order **CROCODYLOMORPHA** Hay, 1930 (*nom. correct.* herein, *pro* order Crocodilomorphi Hay 1930).

Archosauria with terminal external nares; preorbital fossa reduced or absent; prefrontals meet in mid-line above palate; no postfrontal; parietals fused; squamosal overhanging posteriorly in varying degree, in advanced forms meeting quadrate to enclose otic notch, without descending process towards quadratojugal; quadrate inclined forwards; quadratojugal a parallel-sided strip mainly lateral in exposure, having a good contact with the jugal; narrow supraoccipital entering post-temporal fossae; some development of a secondary palate; basal articulation fused; some development of a eustachian system; two sacral vertebrae; coracoid elongated, no clavicle; proximal carpals elongated; pubis rod-like; ankle-joint mesotarsal on medial side but crurotarsal on lateral side, calcaneum with tuber; four elongated subequal metatarsals (except in specialized marine forms); dermal armour present (except probably in *Hallopus*). ? M. Trias, U. Trias–Rec.

To the above should probably be added: acetabulum perforated, ischium with anterodorsally directed process excluding the pubis in varying degree from the acetabulum. However, the pelvis is largely unknown in the Pedeticosauridae.

Suborder **CROCODYLIA** Gmelin, 1788 (*nom. transl.* herein, *ex* order Crocodylia Gmelin, 1788)

Diagnosis as in Romer (1956) except that the Protosuchia are more primitive in certain details. Surangular straight and lower edge of mandible inclined upward behind mandibular fossa in nearly all forms. U. Trias–Rec.

DESCRIPTION OF PLATE 72

Hallopus victor (Marsh)

FIGURE 14. Posterior view of left radiale, ulnare and manus, with distal ends of radius and ulna seen obliquely. (× 2.)

FIGURE 15. Medial view of proximal portion of left femur, showing trochanters; scapula to right of femur. (× 1.)

FIGURE 16. Lateral view of distal end of left tibia, tarsus and metatarsus, with distal end of left femur in lateral view above. (× 2.)

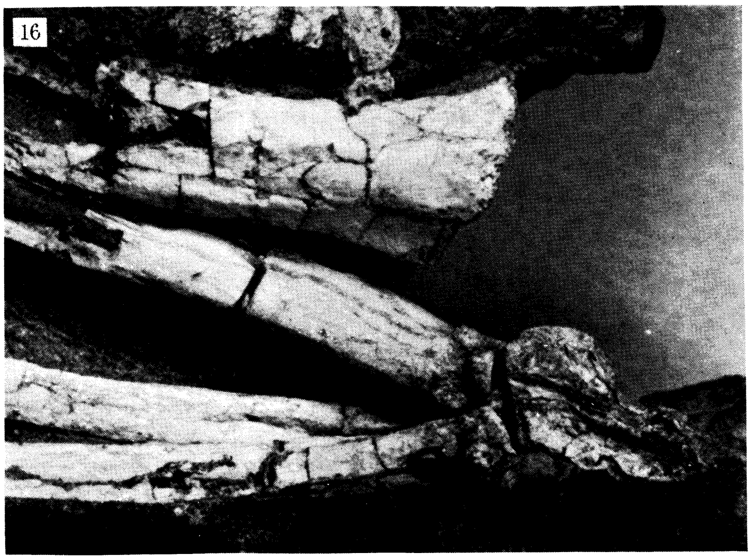
FIGURE 17. Oblique medial view of same. (× 2.)

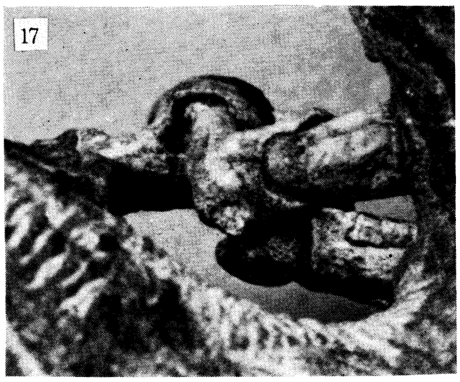
FIGURE 18. Lower view of same. (× 2.)

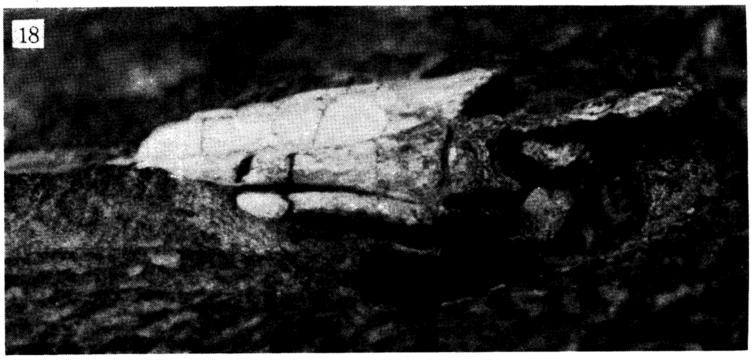
FIGURE 19. Posterior view of distal end of tibia and astragalus, upper view of calcaneum. (× 2.)

14


15


16


17


18


19


Figures 14 to 19. For legends see facing page.

Infraorder **PROTOSUCHIA** (*nom. transl.* Walker, 1968, *ex.* suborder Protosuchia Mook 1934)

Snout slender, moderately elongated; parietals fused; skull table flattened, rectangular, supratemporal fossae variable in size, no parietal crest; two supraorbital bones on each side; external nares terminal, separate; preorbital fossa reduced or absent; postorbital bar superficial; infratemporal fossa small, quadrate strongly inclined, otic notch deep (except perhaps in *Protosuchus*). Secondary palate formed by premaxillae and maxillae, primary palate vaulted; pterygoids and quadrates fused to braincase. Surangular straight, lower edge of mandible inclined upwards behind mandibular fossa. Vertebrae amphicoelous. Coracoid shorter than in later crocodiles. Radiale longer than metacarpals in at least two genera, metacarpals I to IV subequal (V poorly known), manus small. Ilium with elongated blade, pointed anteriorly; pubis at least partly excluded from the acetabulum by a process from the ischium. U. Trias.

Family Stegomosuchidae von Huene, 1922

Diagnosis as for the infraorder.

Genera: *Stegomosuchus* von Huene, 1922; *Notochampsa* Broom, 1904; *Erythrochampsa* Haughton, 1924; *Protosuchus* Brown, 1934; *Orthosuchus* Nash, 1968.

The only departures from the classification of more advanced Crocodylia given in Romer (1956) are as follows. The Suborders Mesosuchia, Eusuchia, Sebecosuchia and Thalattosuchia are reduced to the status of infraorders, coordinate with the Protosuchia, and the family Baurusuchidae is removed from the Sebecosuchia.

Suborder **PARACROCODYLIA** Walker, 1968

Diagnosis as for the Order, with the addition of: skull relatively high posteriorly; supratemporal fossae large, longer than wide; quadrate not greatly inclined; surangular arched dorsally, lower edge of jaw essentially straight; an enlarged dentary tooth bites into a notch between premaxilla and maxilla. U. Trias–U. Cret.

Infraorder **PEDETICOSAURIA** Walker, 1968

Diagnosis as for the suborder, with the addition of: preorbital fossa small, posteriorly placed on maxilla; postorbital bar inclined forward at top; infratemporal fossa large; otic notch not enclosed; secondary palate formed only by premaxillae and maxillae; limbs slender and elongated, limb-bones hollow; radiale longer than metacarpals; manus small; dermal armour present. U. Trias.

Family Pedeticosauridae van Hoepen, 1915

Diagnosis as for the infraorder.

Genera: *Pedeticosaurus* van Hoepen, 1915; *Sphenosuchus* Haughton, 1915; *Saltoposuchus* von Huene, 1921; *Platyognathus* Young, 1944; *Hesperosuchus* Colbert, 1952.

Infraorder **BAURUSUCHIA** Walker, 1968

Diagnosis as for Family Baurusuchidae Price, 1945, which is the sole family placed in this infraorder. U. Cret.

Infraorder **HALLOPODA** (*nom. transl.* Walker, 1968, *ex* suborder Hallopoda Marsh, 1881)

Scapula blade narrow; limb-bones hollow; proximal carpals greatly elongated, in contact throughout their length, proximal carpal joint apparently immobile but distally a roller-joint with the metacarpus, probably no other carpals; metacarpals I and III wedging out proximally, manus small, compressed; iliac blade long and high, curving down behind; femur with 'pseudointernal' trochanter and lesser trochanter, fourth trochanter an inconspicuous narrow ridge, head offset, subspherical; tibia and fibula very slender, longer than femur; tarsus greatly compressed, dorso-lateral process of astragalus visible in lateral view, distal end of fibula posterior to astragalus, calcaneum very narrow, with long tuber; lateral distal tarsal large; pes functionally tridactyl, metatarsals II–IV elongated, firmly fixed together proximally, metatarsal I a long slender splint recessed into metatarsal II, metatarsal V reduced, pointed. U. Jur.

Family Hallopodidae Marsh, 1881

Diagnosis as for the infraorder.

Genus *Hallopus* Marsh, 1877.

My thanks are due to Dr A. W. Crompton and Dr J. H. Ostrom for the loan of the specimen, to Dr Juliet Jewell for data on the hare and greyhound skeletons, to Sr J. F. Bonaparte for stimulating discussions on early crocodiles, and to Dr K. A. Kermack for permission to quote the observation on p. 351.

REFERENCES

Broom, R. 1927 On *Sphenosuchus*, and the origin of the crocodiles. *Proc. Zool. Soc. Lond.* pp. 359–370.

Colbert, E. H. 1952 A pseudosuchian reptile from Arizona. *Bull. Am. Mus. nat. Hist.* **99**, 565–592.

Colbert, E. H. 1962 *Dinosaurs: their discovery and their world.* London: Hutchinson and Co. Ltd.

Colbert, E. H. 1964 The Triassic dinosaur genera *Podokesaurus* and *Coelophysis*. *Am. Mus. Novit.*, no. 2168, 1–12.

Colbert, E. H. & Mook, C. C. 1951 The ancestral crocodilian *Protosuchus*. *Bull. Am. Mus. nat. Hist.* **97**, no. 3, 143–182.

Cott, H. B. 1961 Scientific results of an enquiry into the ecology and economic status of the Nile Crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Trans. zool. Soc. Lond.* **29**, iv, 211.

Emerson, B. K. & Loomis, F. B. 1904 On *Stegomus longipes*, a new reptile from the Triassic sandstones of the Connecticut Valley. *Am. J. Sci.* (4), **17**, 377–380.

Gilmore, C. W. 1926 A new aetosaurian from the Morrison formation of Utah. *Ann. Carneg. Mus.* **16**, 325–348.

Gray, J. 1968 *Animal locomotion.* London: Weidenfeld and Nicolson.

Gregory, W. K. 1912 Notes on the principles of quadrupedal locomotion and on the mechanism of the limb in hoofed animals. *Ann. N.Y. Acad. Sci.* **22**, 276–294.

Gregory, W. K. & Camp, C. L. 1918 Studies in comparative myology and osteology, no. III. *Bull. Am. Mus. nat. Hist.* **38**, 447–563.

Haughton, S. H. 1924 The fauna and stratigraphy of the Stormberg Series. *Ann. S. Afr. Mus.* **12**, 323–497.

Huene, F. von 1914 Beiträge zur Geschichte der Archosaurier. *Geol. paläont. Abh.* N.F. **13**, 3–53.

Huene, F. von 1921 Neue Pseudosuchier und Coelurosaurier aus dem Württembergischen Keuper. *Acta zool., Stockh.* **2**, 329.

Huene, F. von 1922 The Triassic reptilian order Thecodontia. *Am. J. Sci.* (5), **4**, 22–26.

Huene, F. von 1925 Die Bedeutung der *Sphenosuchus*—Gruppe für den Ursprung der Krokodile. *Z. indukt. Abstamm.-u. Vererblehre.* **38**, 307–322.

Huene, F. von & Lull, R. S. 1908 On the Triassic reptile, *Hallopus victor* Marsh. *Am. J. Sci.* (4), **25**, 113–118.

Kermack, K. A. 1956 An ancestral crocodile from South Wales. *Proc. Linn. Soc. Lond.* **166**, 1–2.

Lapparent, A. F. de & Lavocat, R. 1955 Dinosauriens, in *Traité de Paléontologie*, Tome V, 785–962, Paris: Masson and Cie.

Lull, R. S. 1953 Triassic life of the Connecticut Valley. *Bull. Conn. Geol. Nat. Hist. Surv.* no. 81, 13.

Marsh, O. C. 1877 Notice of some new vertebrate fossils. *Am. J. Sci.* (3), **14**, 249–256.

Marsh, O. C. 1881 Principal characters of American Jurassic dinosaurs. *Am. J. Sci.* (3), **21**, 417–423.

Marsh, O. C. 1882 Classification of the Dinosauria. *Am. J. Sci.* (3), **23**, 81–86.

Marsh, O. C. 1890 Distinctive characters of the Order Hallopoda. *Am. J. Sci.* (3), **39**, 415–417.

Marsh, O. C. 1891 Geological horizons as determined by vertebrate fossils. *Am. J. Sci.* (3), **42**, 336–338.

Marsh, O. C. 1895 On the affinities and classification of the dinosaurian reptiles. *Am. J. Sci.* (3), **50**, 483–498.

Marsh, O. C. 1896 The dinosaurs of North America. 16*th Ann. Rep. U.S. Geol. Surv.* (1894–95), 133–244.

Nash, D. 1968 A crocodile from the Upper Triassic of Lesotho. *J. Zool., Lond.* **156**, 163–179.

Nopsca, F. von 1923 Die Familien der Reptilien. *Fortschr. Geol. Palaeont.* **2**, 1–210.

Osborn, H. F. & Mook, C. C. 1921 *Camarosaurus*, *Amphicoelias*, and other sauropods of Cope. *Mem. Am. Mus. nat. Hist.* (n.s.), **3**, no. 3, 249–387.

Price, L. I. 1945 A new reptile from the Cretaceous of Brazil. *Notas prelim. Estud. Div. Geol. Miner. Bras.* **25**, 1–8.

Price, L. I. 1946 Sôbre um novo pseudosuquio do Triássico superior do Rio Grande do Sul. *Bolm. Div. Geol. Miner. Bras.* **120**, 7–38.

Reig, O. A. 1959 Primeros datos descriptivos sobre nuevos reptiles arcosaurios del Triásico de Ischigualasto. *Revta Asoc. geol. argent.* **13**, 257–270.

Romer, A. S. 1923*a* The pelvic musculature of saurischian dinosaurs. *Bull. Am. Mus. nat. Hist.* **48**, 605–617.

Romer, A. S. 1923*b* Crocodilian pelvic muscles and their avian and reptilian homologues. *Bull. Am. Mus. nat. Hist.* **48**, 533–552.

Romer, A. S. 1927 The pelvic musculature of ornithischian dinosaurs. *Acta zool. Stockh.* **8**, 225–275.

Romer, A. S. 1956 *Osteology of the reptiles*. University of Chicago Press.

Romer, A. S. 1966 *Vertebrate paleontology*, 3rd edn. University of Chicago Press.

Schaeffer, B. 1941 The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bull. Am. Mus. nat. Hist.* **78**, 395.

Schuchert, C. 1939 The geological horizon of the dinosaurs *Hallopus* and *Nanosaurus agilis*. *Am. J. Sci.* **237**, 19–26.

Sill, W. D. 1967 *Proterochampsa barrionuevoi* and the early evolution of the crocodilia. *Bull. Mus. Comp. Zool. Harv.* **135**, 415–446.

Simmons, D. J. 1965 The non-therapsid reptiles of the Lufeng Basin, Yunnan, China. *Fieldiana Geol.* **15**, 1–93.

Van Hoepen, E. C. N. 1915 A new pseudosuchian from the Orange Free State. *Ann. Transv. Mus.* **5**, 83–87.

Walker, A. D. 1961 Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Phil. Trans. Roy. Soc. Lond.* B **244**, 103–204.

Walker, A. D. 1964 Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Phil. Trans. Roy. Soc. Lond.* B **248,** 53–134.

Walker, A. D. 1968 *Protosuchus*, *Proterochampsa*, and the origin of phytosaurs and crocodiles. *Geol. Mag.* **105**, 1–14.

Williston, S. W. 1905 The *Hallopus*, *Baptanodon* and *Atlantosaurus* beds of Marsh. *J. Geol.* **13**, 338–350.

KEY TO FIGURES 1 AND 2

1	sacrum	13	ischium
2	caudal vertebrae	14	distal end of pubis?
3	rib	15	left femur
4	chevron-bone	16	left tibia
5	scapula	17	metatarsal II, left pes
6	right humerus	18	metatarsal III, left pes
7	right radius and ulna	19	metatarsal IV, left pes
8	left radius and ulna	20	metatarsal V, left pes
9	left radiale and ulnare	21	right tibia
10	left manus	22	right fibula
11	right ilium	23	metatarsal III, right pes
12	left ilium	24	metatarsal IV, right pes

EXPLANATION OF ABBREVIATIONS USED IN FIGURES

Skull

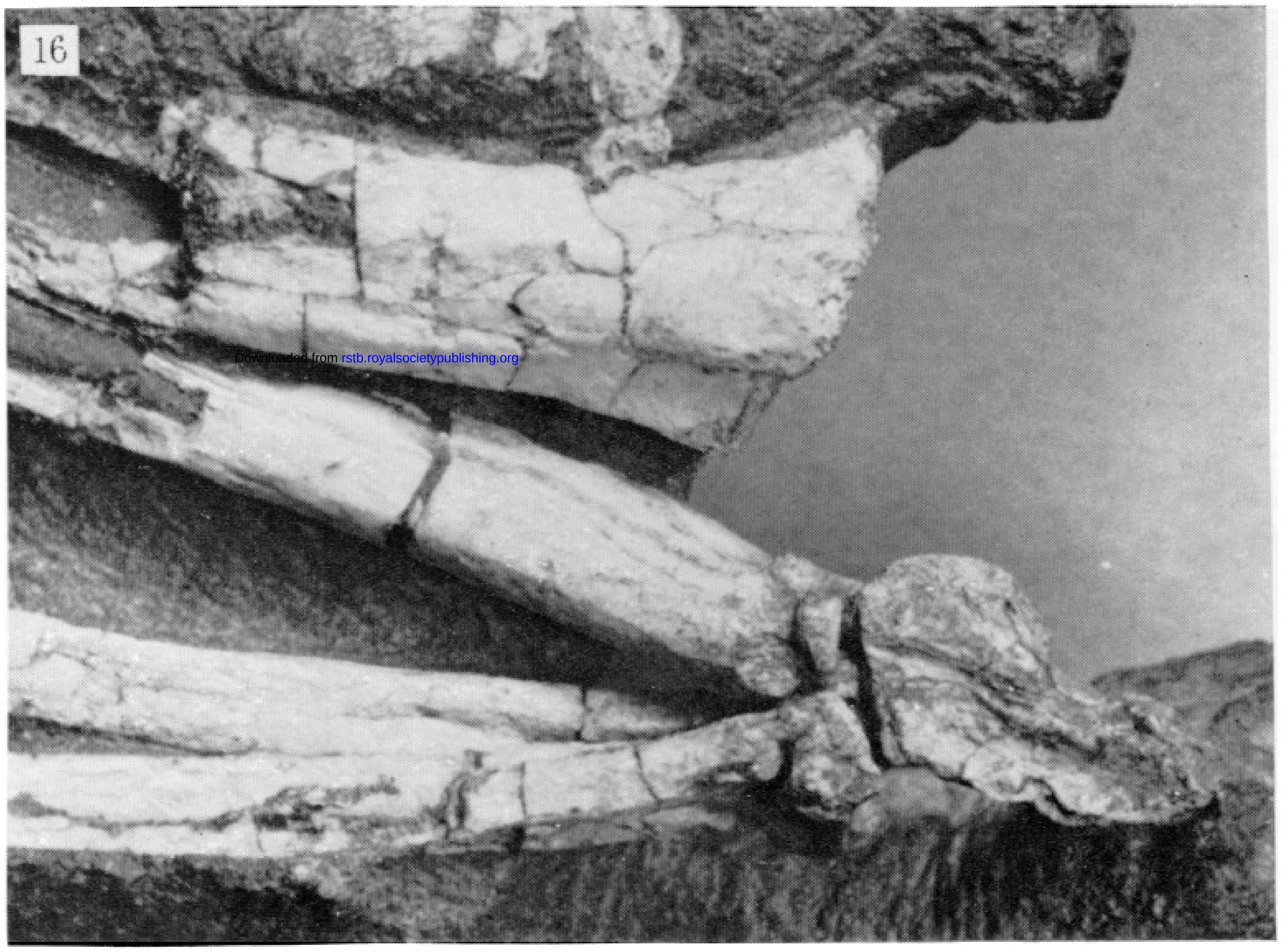
ar	articular	*pm*	premaxilla
aso	anterior supraorbital	*po*	postorbital
bo	basioccipital	*popr*	paroccipital process
bs	basisphenoid	*prf*	prefrontal
d	dentary	*pso*	posterior supraorbital
ec	ectopterygoid (transverse)	*pt*	pterygoid
f	frontal	*q*	quadrate
j	jugal	*qj*	quadratojugal
l	lachrymal	*sa*	surangular
m	maxilla	*sp*	splenial
n	nasal	*sq*	squamosal
p	parietal	*stf*	supratemporal fossa

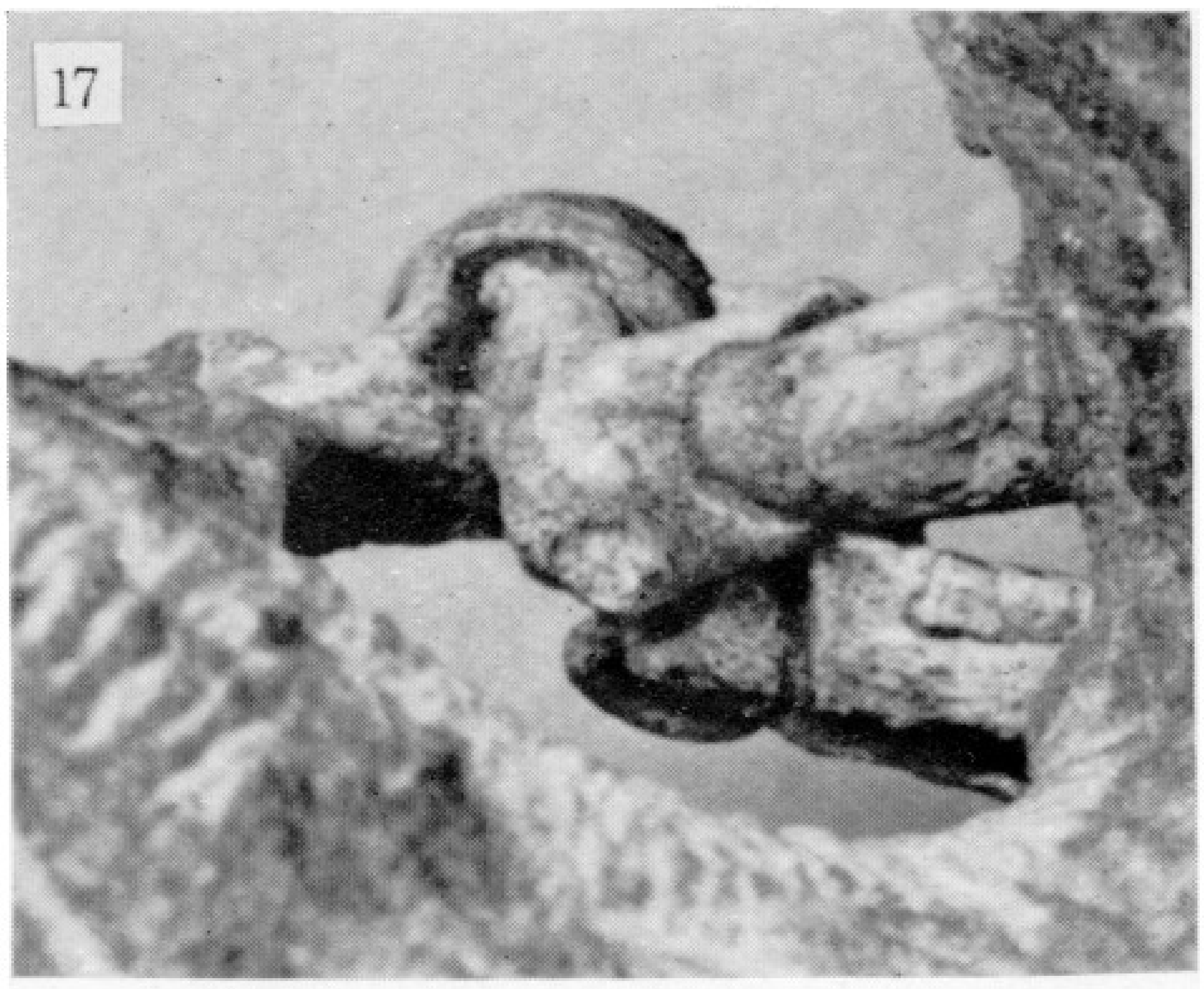
Postcranial skeleton

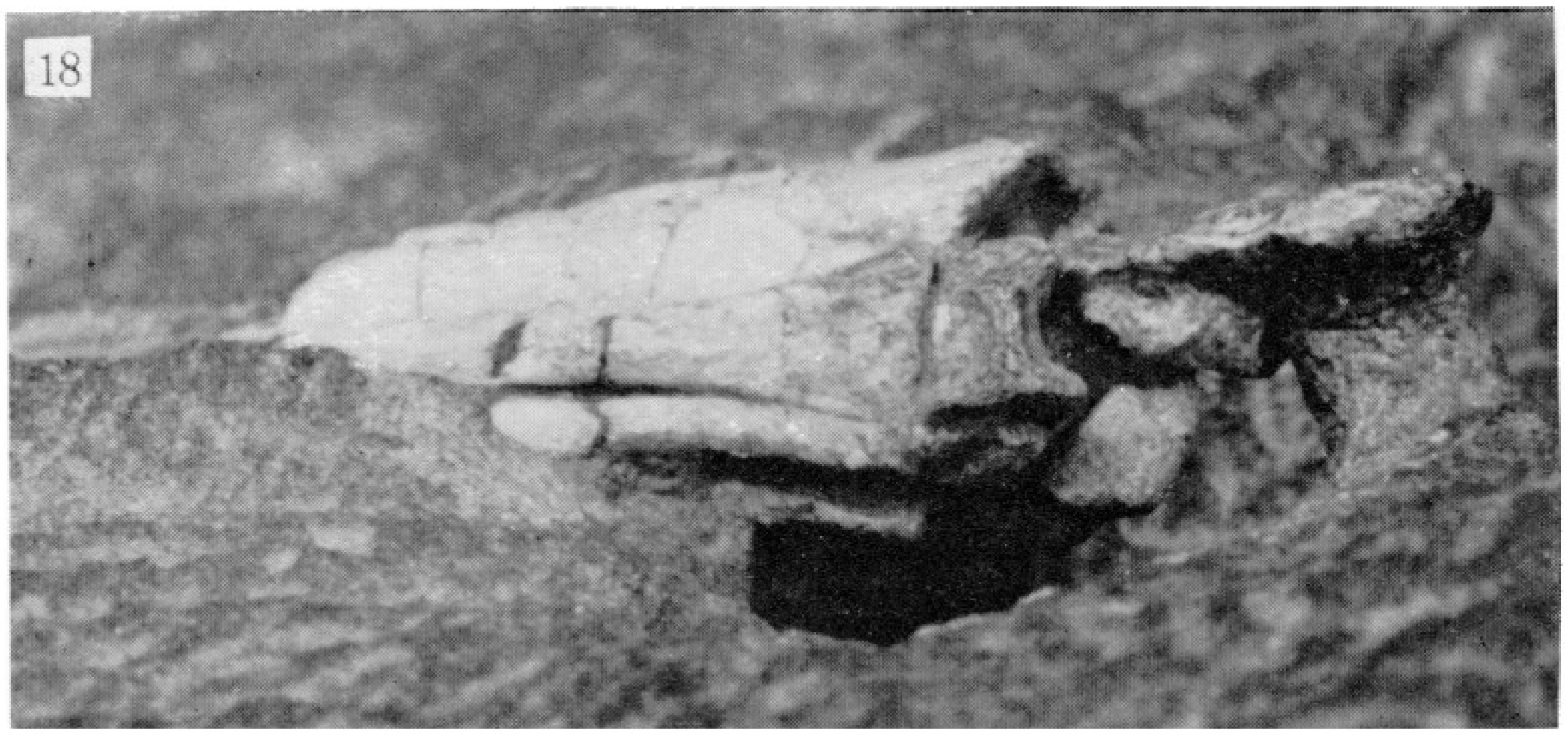
l.scap.	left scapula	*p.i.t.*	pseudointernal trochanter
l.hum.	left humerus	*t.4*	fourth trochanter
l.rad.	left radius	*tib.*	tibia
l.uln.	left ulna	*fib.*	fibula
l.rade	left radiale	*fib.fac.*	facet for fibula
l.ulne	left ulnare	*ast.*	astragalus
r.rade?	right radiale?	*calc.*	calcaneum
mc. I–V	metacarpals I–V	*m.d.t.*	medial distal tarsal
r.pub.	right pubis	*l.d.t.*	lateral distal tarsal
r.fem.	right femur	*mt. I–V*	metatarsals I–V
l.t.	lesser trochanter		

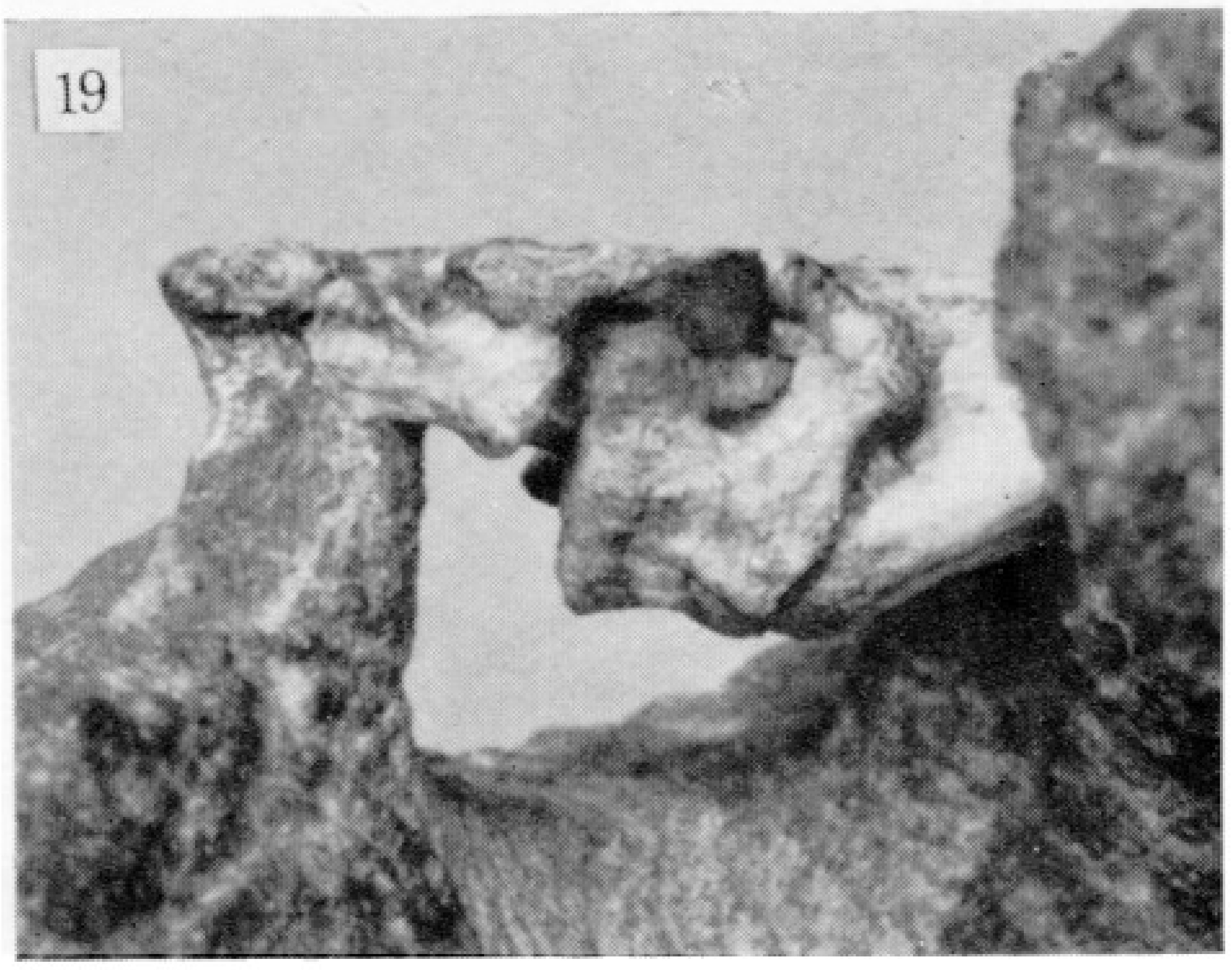

14


15


16


17


18


19

Figures 14 to 19. For legends see facing page.