A PSEUDOSUCHIAN REPTILE FROM ARIZONA

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INTRODUCTION

IN THE COLLECTIONS OF the American Museum of Natural History there is the partial skeleton of a small reptile, collected by Barnum Brown, Llewellyn I. Price, and William B. Hayden in the upper Triassic sediments of northern Arizona during the autumn of 1929 and the late summer of 1930. The collecting of this specimen, which represents an unusually rare pseudosuchian, was greatly facilitated by the interest and assistance given to the Museum party by Mr. Hubert Richardson and his family, of Cameron, Arizona, to whom the Museum and the science of paleontology are deeply indebted. The specimen was brought to the Museum, where it was carefully prepared by Mr. Otto Falkenbach. This was a painstaking task, since the specimen is of rather small size and has delicate bones, but the work was completed by Mr. Falkenbach with his usual skill. Many of the bones were then drawn by the late Mr. Sydney Prentice of the Carnegie Museum of Pittsburgh. In addition to the drawings originally made by Mr. Prentice, additional figures have been recently prepared by Mr. John LeGrand and Mrs. Lois Darling of the Museum Illustrators Corps.

Owing to the exigencies of an extensive program, the specimen was never studied by Dr. Brown. It is the purpose of this present paper to describe the specimen in some detail and to compare it with related forms of comparable age from other regions. It represents a new element in the upper Triassic faunas of North America, and for this reason it is of particular importance. Also this is a reasonably complete skeleton, even though the skull is fragmentary and much of the tail is missing, and as such it adds some facts to our knowledge of the pseudosuchian reptiles.

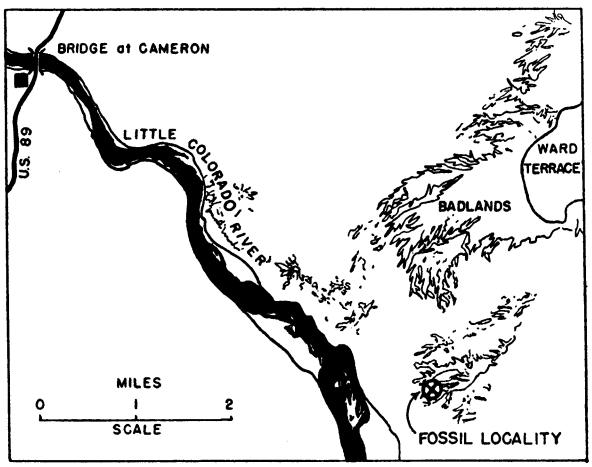


FIG. 1. Map of the region south and east of Cameron, Arizona, showing the locality at which *Hesperosuchus agilis* was discovered. This is the locality of the "Ward bone bed" near the old Tanner Crossing of the Little Colorado River.

The specimen was found about 6 miles southeast of Cameron, Arizona, near the old Tanner Crossing of the Little Colorado River, a locality that has yielded numerous remains of Triassic vertebrates in past years. It came from a level about 160 feet above the Moenkopi formation, which places it in the lower portion of the Chinle formation. In this region the Little Colorado River flows through a steep-walled canyon cut into the hard and very resistant Shinarump conglomerate and the heavy Moenkopi sandstones, the former above the latter. The Shinarump is rarely more than about 60 feet in thickness, and the

top of this conglomerate layer marks the edge of the canyon rim. The extensive badlands flanking the canyon are cut in the comparatively soft Chinle clays and sandstones, and it was from a clay facies of the Chinle that the skeleton was collected. From this same facies and not far distant there have been found a number of phytosaurs, including the gigantic skull and partial skeleton of *Machaeroprosopus gregorii* described by the writer a few years ago (Colbert, 1947). With the skeleton to be described in this paper were found various teeth and bones indicating several associated fishes and reptiles. These are discussed below.

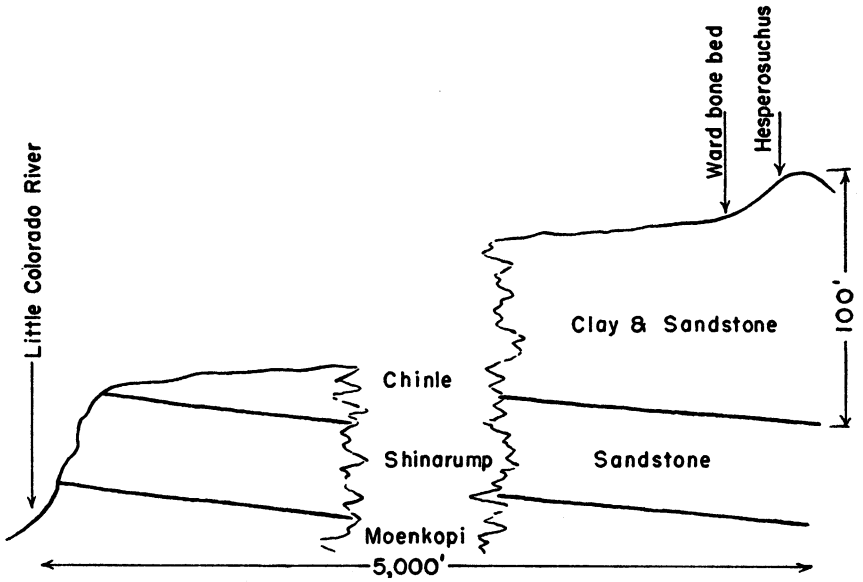


FIG. 2. Section showing the Triassic sediments along the Little Colorado River, about 6 miles southeast of Cameron, Arizona. The Ward bone bed and the *Hesperosuchus* locality are estimated to be about 100 feet, more or less, above the base of the Chinle formation. The locality is slightly less than a mile to the east of the Little Colorado River, which cuts a canyon in the Moenkopi and Shinarump.

SYSTEMATIC POSITION

CLASS REPTILIA

ORDER **THECODONTIA**

SUBORDER **PSEUDOSUCHIA**

FAMILY **ORNITHOSUCHIDAE**

Small pseudosuchians, lightly built and bipedal in posture. The limbs are slender, with the epipodials slightly longer than the propodials and with the hind limbs considerably larger than the fore limbs. Skull of rather generalized archosaurian type. The dermal plates are characteristically somewhat elongated.

HESPEROSUCHUS, NEW GENUS

TYPE SPECIES: *Hesperosuchus agilis*, new species.

DIAGNOSIS: The diagnosis is that given for the species, below.

Hesperosuchus agilis, new species

TYPE: A.M.N.H. No. 6758, a partial skeleton, consisting of the following elements: the fronto-parietal region of the cranial roof, much of the occiput, other skull fragments, posterior fragment of right maxilla, left premaxilla and maxilla, right quadrate, portion of an articular (?), a large portion of the left mandibular ramus, part of the right mandibular ramus, the first 10 presacral vertebrae, 24 additional partial vertebrae not definitely identifiable as to position, sacral vertebra, various fragments of vertebrae, various cervical and thoracic ribs, left scapula and proximal portion of coracoid, left humerus, left radius and ulna, proximal portions of metacarpals of right manus, left femur, a greater part of the left tibia, portion of left fibula, portions of right femur, proximal and medial parts of right tibia, proximal end of right fibula, three metatarsals, various phalanges, numerous fragments of foot bones and limb bones, several dorsal scutes. This material was associated and seemingly represents a single individual. In addition there are fragments of bones and teeth that may represent other individuals of the species under consideration, as well as other species of small reptiles.

HORIZON: Chinle formation, about 100 feet above the Shinarump conglomerate. Upper Triassic.

LOCALITY: About 6 miles southeast of Cameron, Arizona, on the north side of the Little Colorado River.

DIAGNOSIS: A large ornithosuchid with exceptionally well-developed and strong hind limbs and long, slender fore limbs. The bones of the skeleton are hollow. The fore limbs are much reduced as compared with the hind limbs, but there is a relatively large manus. Fore and hind feet with five digits. The vertebrae are amphicoelous, with the centra constricted in the middle, and with rather long vertebral spines lacking any expansions at their tops. The zygapophyses are long and oblique. The elongated scapula is strongly expanded dorsally. The fronto-parietal region of the skull is broad and very flat, and there is no pineal foramen. The narial opening seemingly is large, as is the antorbital opening and the orbit, and it is placed at the anterior extremity of the skull. The front of the skull is rather pointed. The skull as a whole probably is rather deep and narrow. There are perhaps 20 thecodont dentary teeth, and probably a similar number in the upper jaws. The third dentary tooth is enlarged, as are the third and fourth upper teeth, these latter probably being of premaxillary relationships. The teeth have anterior and posterior ridges, which are serrated. The anterior teeth are rather long and slender, but the posterior teeth are shorter and lanceolate in shape. There is a single row of dorsal scutes on either side of the midline, and the scutes are elongated.

DESCRIPTION AND DISCUSSION

General Considerations

THIS NEW ORNITHOSUCHID is on the whole a lightly built reptile with a delicate skeleton, yet even so it is among the largest members of the family. It is closely comparable to, but somewhat larger than, the type skeleton of *Ornithosuchus woodwardi*, and likewise than that of *Saltoposuchus longipes*. There is a second specimen of *Ornithosuchus*, described by Boulenger in 1903, that is much larger than the type specimen and also much larger than the specimen of *Hesperosuchus* here described. Also there is a single vertebra from northern Russia, described by von Huene in 1940 under the name of *Dongusia colorata*, which is much larger than any vertebra of *Hesperosuchus*. The *Dongusia* vertebra is characterized, among other things, by a well-developed hyposphene, so its assignment to the ornithosuchids can be questioned. Therefore, except for the second specimen of *Ornithosuchus*, *Hesperosuchus* is the largest of the known Ornithosuchidae.

The delicate nature of the skeleton is evident especially in the hollow construction of the bones, as can be seen particularly in the long limb bones and the vertebral centra. Hollow bones are typical of the small pseudosuchian thecodonts, and the character is carried over into the primitive coelurosaurian dinosaurs.

Hesperosuchus was obviously a dominantly bipedal reptile, as can be inferred from the large, strong hind limbs and the relatively slender and much smaller fore limbs. The disparity in size between the fore and hind limbs is not so great in this genus as it is in *Saltoposuchus*, as reconstructed by von Huene. However, the hind limbs are about equally large and strong in the two genera, in each of which the length of the extended hind limb is approximately equal to the length of the presacral vertebrae. A similar relationship holds in the genus *Pedeticosaurus*, described by van Hoepen from the Karroo beds of South Africa. Von Huene illustrates *Saltoposuchus* as walking with a quadrupedal gait as well as with a bipedal one, and it is probable that *Hesperosuchus* and *Pedeticosaurus* also utilized both the quadrupedal and bipedal types of locomotion. It is reasonable to think, however, that most of the progression of these reptiles was accomplished in the bipedal pose, and that the fore limbs and hands were used to a large extent for food gathering. In these animals the hand might have been useful for digging, for pulling down plants, for catching prey, and for defense.

The tail in *Hesperosuchus* must have been long, to serve as a counterbalance for the weight of the body. A complete series of caudal vertebrae is not preserved, so the length of the tail is conjectural. It has been restored with 45 caudal vertebrae, which would seem to be about the right number, if comparisons with other archosaurians are valid. Von Huene's restoration of *Saltoposuchus*, in which there are about 70 caudals indicated, seems excessively elongated.

The Skull, Jaws, and Dentition

It is unfortunate that the skull and mandible of *Hesperosuchus* are so imperfectly preserved. Enough bone is present to give some indication as to the structure of skull and jaws, but not enough is at hand to allow a detailed reconstruction. The reconstructed

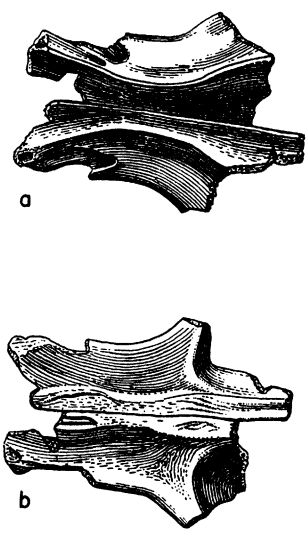


FIG. 3. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Portion of cranial roof. A. Dorsal view, B. Ventral view. Natural size.

skull and jaw shown in figure 12 is only an approximation, and much of it is of necessity conjectural.

One thing is certain, namely, that the skull roof was very similar in general form to that in *Ornithosuchus*. This is readily apparent from the comparative figure of fronto-parietal regions in the two general. In both of these forms the cranial roof was very flat, and there was a marked depression in the postorbital and frontal bones, in front of and lateral to the supratemporal fenestrae. There are no clear indications of sutures on the specimen from Arizona, but on the ventral surface there can be seen the channel against which the upper surfaces of the olfactory bulbs and the cerebral hemispheres were appressed.

The anterior portion of the skull is represented by three fragments—the left premaxilla and a part of the maxilla, an anterior portion of the right maxilla, and the posterior part of the right maxilla. There are no contacts between any of these fragments, so it is impossible to determine either the width of the skull in its front portion or the length of the upper tooth row.

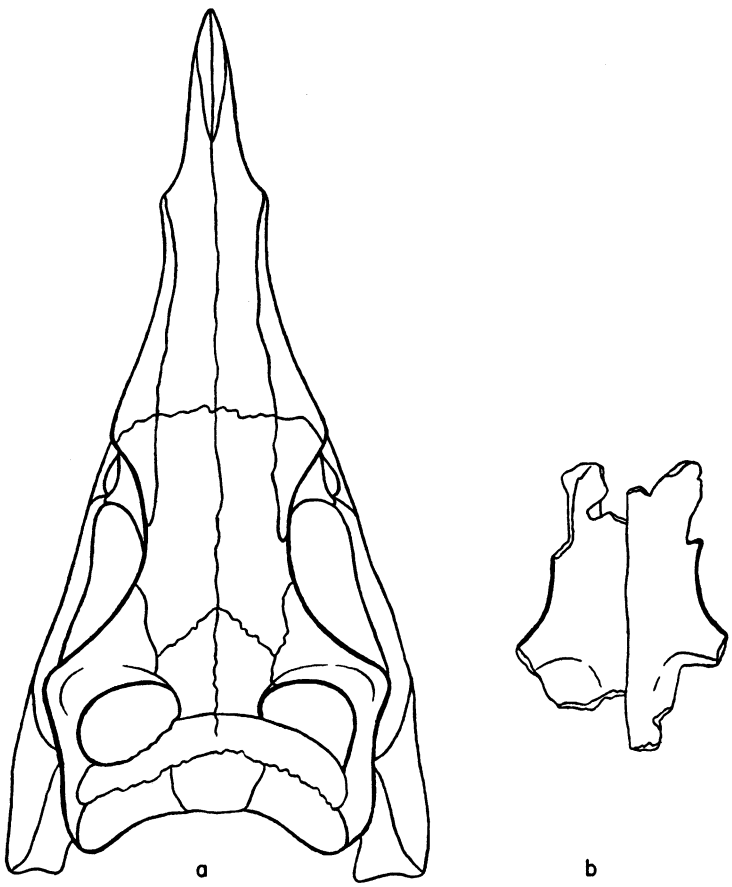


FIG. 4. Comparison in dorsal view of (A) skull of *Ornithosuchus woodwardi* Newton (after Newton) with (B) fragment of cranial roof of *Hesperosuchus agilis*, new genus and species. Both figures natural size.

The left premaxilla and maxillary fragment make up the largest of the three bone fragments here under consideration. It contains sockets for nine teeth, of which the first four are in the premaxilla. Behind the alveolus of the fourth tooth there is a junction between

the bony surfaces that is probably the premaxillary-maxillary suture. On the medial surface of this fragment there is a horizontal anterior bony shelf (the extension of the premaxilla to meet the same bone of the other side), and at the back this shelf terminates in a concave edge, obviously the anterior border of the internal nares. There is a dorsal smooth edge on the back portion of the maxilla, and this is evidently a portion of the lower border of the antorbital fenestra. The small posterior fragment of the right maxilla also shows a smooth dorsal edge, and this must be a continuation of the lower border of the fenestra. Evidently the antorbital fenestra in this reptile was very large, as it certainly is in *Ornithosuchus*.

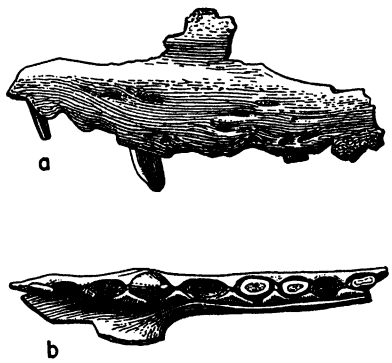


FIG. 5. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Portion of left premaxilla and maxilla. A. External lateral view. B. Crown view. Natural size.

The first premaxillary tooth is small and rather needle-like, while the teeth behind it were evidently progressively larger. The fourth tooth, which is present, is large and robust, possibly the largest of the upper tooth row. It is elliptical in cross section. *Ornithosuchus* is characterized by two large teeth in this region, indicated in Newton's figure as the first two maxillary teeth.

The maxillary teeth in *Hesperosuchus* are not particularly elongated but rather are of lanceolate shape and laterally much compressed. These teeth have well-defined anterior and posterior serrated cutting edges, along which the serrations are prominent, and run from the tip of the tooth down to the root.

It is not possible to make any definite statement as to the number of premaxillary and maxillary teeth. In the two fragments at hand there are 14 teeth, nine in the anterior fragment and five in the posterior one. It is obvious that a portion of the tooth row between the fragments is missing, while at least one or two teeth must have been present behind the last of the preserved teeth. Consequently it is quite possible that there were about 20 teeth in all in the upper tooth row, four in the premaxilla and about 16 in the maxilla.

Several pieces of bone represent the occipital portion of the skull in *Hesperosuchus*. Unfortunately there are no contacts between these various bone fragments, and for this reason an accurate picture of the occipital region cannot be drawn. On the other hand the bones preserved are sufficiently complete to give some idea as to the relationships of the elements in the back of the skull.

The basioccipital is typically archosaurian, with a rounded condyle, a rather elongated surface above it for the medulla oblongata,

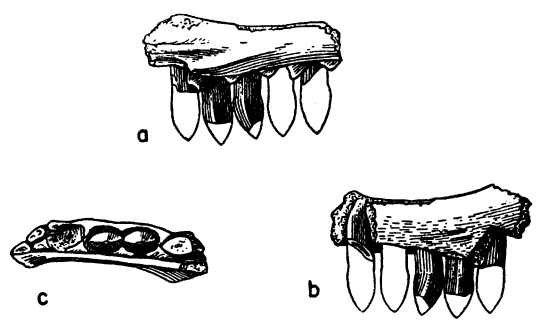


FIG. 6. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Portion of right maxilla. A. External lateral view. B. Internal lateral view. C. Crown view. Natural size.

and a deeply extended ventral plate. This form of basioccipital can be seen in the crocodilians and in extinct archosaurians such as the primitive theropod dinosaurs. In the ventral portion of the basioccipital, below the condyle, there is a small median pit, as there is in some of the dinosaurs. In the crocodilians this pit is resolved into a foramen transmit-

ting a median tube of a complexly expanded eustachian system, but in *Hesperosuchus* no such development is apparent.

On either side there is a long sutural surface between the basioccipital and the exoccipitals. The exoccipitals are relatively small, forming the lateral walls of the foramen magnum. Dorsally these bones terminate in a comparatively broad sutural surface for articulation with the opisthotics.

The opisthotics extend laterally and posteriorly in large, flaring paroccipital processes. One cannot be certain as to the correct position for these bones, but it would seem probable that they were directed rather strongly back, as they are in other thecodonts

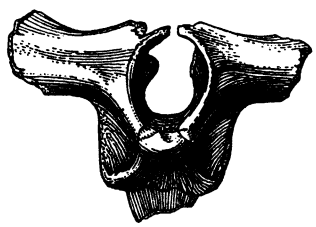


FIG. 7. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Occipital portion of the skull with the basioccipital and the exoccipitals; occipital view. Natural size.

such as the phytosaurs. Above and lateral to the foramen magnum the opisthotic becomes complex in form and is united by a strong suture to the similarly complex prootic, both bones forming the posterolateral walls of the braincase. In the specimens at hand there appear to be indications of some accommodation for the semicircular canals and other parts of the ear region on the inner surfaces of these bones.

There is a broad quadrate bone in the preserved materials of *Hesperosuchus*. This bone terminates in a laterally expanded but anteroposteriorly constricted articular surface. The surface is in fact composed of two parts, a smaller lateral portion and a larger medial portion. The entire articular surface, when seen from below, forms a gentle curve, convex anteriorly. On the front of the quadrate is a strong ridge, obviously to strengthen the joint between this bone and the braincase, but it is not possible to determine in just what manner the quadrate was joined to the rest of the skull.

One bone of uncertain relationships has here been tentatively identified as a ptery-

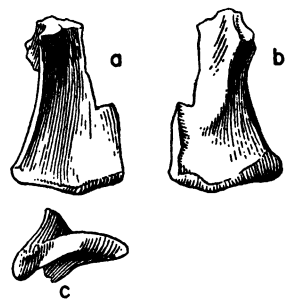


FIG. 8. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Right quadrate. A. Posterior view. B. Anterior view. C. Articular view. Natural size.

goid. A portion of it consists of a broad "wing" or flange, terminating in a somewhat rugose end. It seems quite possible that this may be the flange of the pterygoid that juts laterally from the median portion of the bone. If so, it

FIG. 9. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Portion of supposed pterygoid bone; ventral view. Natural size.

is probably the right pterygoid flange. This flange joins a complexly shaped portion that is very probably the median portion of the pterygoid, but of this latter region there is not enough preserved to determine with certainty its characteristics or relationships. It is evident, however, that there is a sutural connection running through the supposed median portion of the bone, and this may represent the union between the pterygoid and basisphenoid. This bone complex is of such problematical relationships and is so incompletely preserved that one cannot make any

very definite statements concerning it. It is illustrated by figure 9.

Of the two mandibular fragments preserved in *Hesperosuchus*, the fragment of the left side is the larger. It consists of the symphyseal portion of the ramus and the dentary back to and including the eighteenth tooth. The fragment from the other side of the jaw lacks its anterior and posterior portions and consists of a part of the dentary with 11 teeth, represented by the teeth themselves and by alveoli. The first tooth present is probably the fifth dentary tooth.

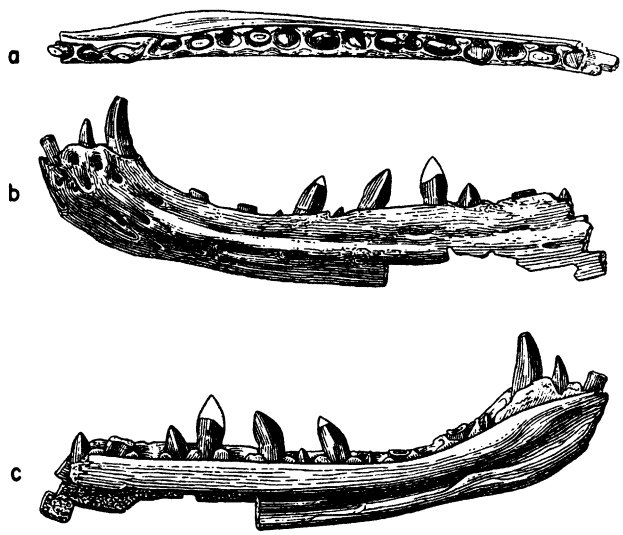


FIG. 10. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Portion of left dentary. A. Crown view. B. External lateral view. C. Internal lateral view. Natural size.

As seen in external lateral view the lower border of the ramus curves up sharply at the anterior end of the dentary. The entire symphyseal portion of the jaw is somewhat enlarged, indicating a considerable functional emphasis on the front part of the mandible in this reptile. Medially there is a deep Meckelian groove extending as far forward as the symphysis. This groove obviously was covered by the splenial, but in the material at hand this latter bone is not preserved.

The dentary teeth, like those of the upper jaw, are in general of lanceolate shape, compressed, and with serrated anterior and posterior edges. The fourth dentary tooth is elongated as compared with the others, and it bit up into a shallow depression on the premaxilla, immediately in front of the fourth premaxillary tooth. These two teeth can be compared with the enlarged teeth in the front of a crocodilian's jaws, especially the fourth upper and lower teeth. They must have been somewhat specialized in function, and, like the front teeth in the Crocodilia, they probably served for grasping and tearing. A somewhat similar arrangement is seen in other thecodonts. For instance, the anterior premaxillary and dentary teeth in the phytosaurs

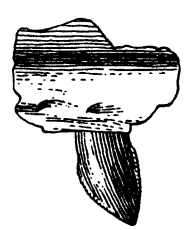


FIG. 11. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. A single tooth, enlarged, to show the serrated anterior and posterior ridges. Three times natural size.

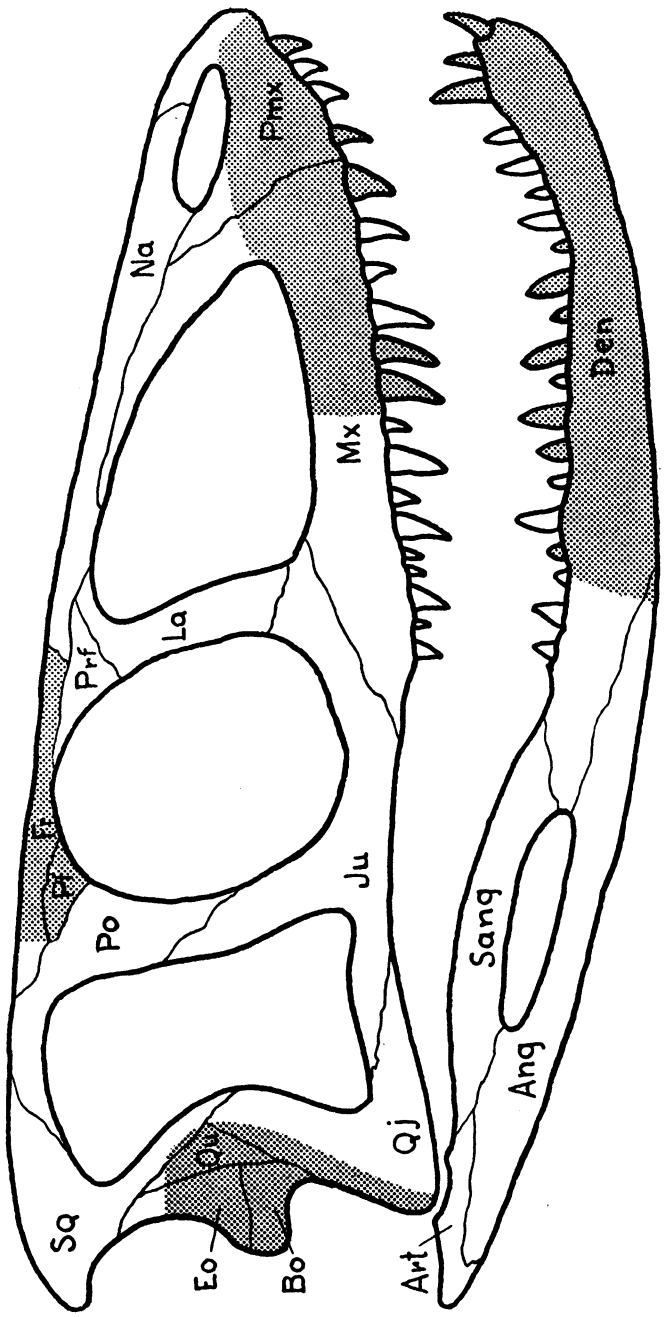


FIG. 12. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Restoration of the skull in lateral view. The hatched areas show the bone present; unshaded areas indicate restoration. Natural size. *Abbreviations:* ang, angular; art, articular; bo, basioccipital; den, dentary; eo, exoccipital; fr, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pf, postfrontal; pmx, premaxilla; po, postorbital; prf, prefrontal; qj, quadratojugal; qu, quadrate; sang, surangular; sq, squamosal.

are greatly enlarged, while in other ornithosuchids, especially *Pedeticosaurus* and *Ornithosuchus*, there is also an enlargement of certain teeth in the anterior part of the skull and mandible.

The left dentary shows in its posterior portion an alternation of teeth indicating replacement as frequently seen in the reptiles. The replacement of reptilian teeth has been studied by various authors, and has been recently described in a succinct manner by Romer, as follows:

"The teeth and tooth germs are present in two series, the 'odds' and 'evens' in each tooth row. One may find a condition in which, for example, in a given area of the jaw, the odd-numbered teeth are functional; between them, in place of the even-numbered ones, are sockets beneath which new teeth are in process of formation. Later this region may show a condition in which both sets of teeth are in place at the same time, but the odd set shows evidence of age and wear. Still a bit later, the odd-numbered teeth will drop out, leaving the even series the functional set, and so on. This neat device guarantees that at least half the teeth in any region will be functioning at any time" (Romer, 1949, p. 310).

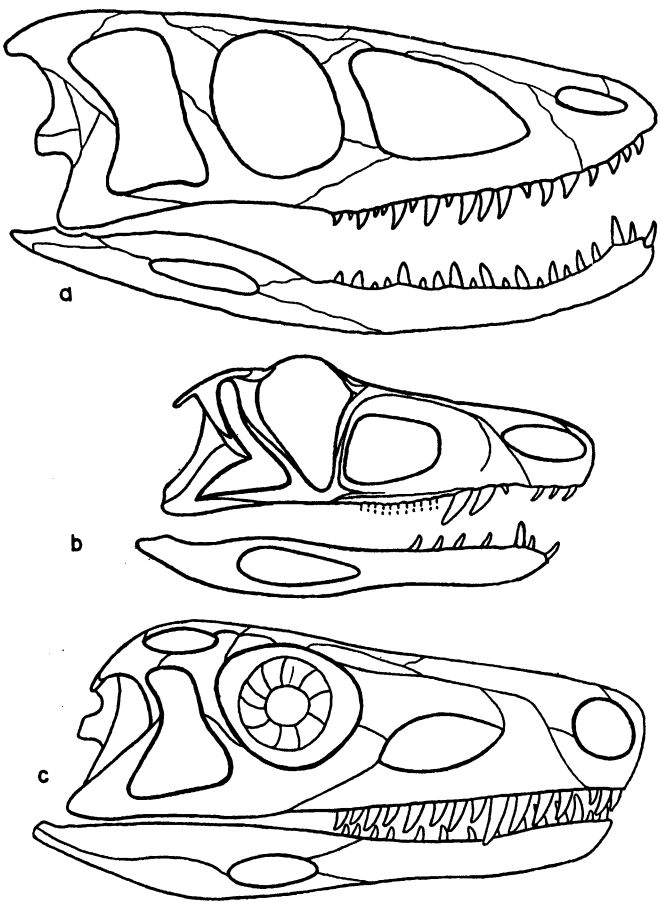


FIG. 13. Comparison of the skulls in lateral view. A. *Hesperosuchus agilis*, new genus and species. B. *Ornithosuchus woodwardi* Newton (after Newton). C. *Euparkeria capensis* Broom (after Broom). All figures one-half natural size.

In the specimen under consideration the tenth, twelfth, and fourteenth dentary teeth

are fully functional. The ninth, eleventh, and fifteenth teeth are beginning to erupt, while the thirteenth alveolus is empty. An erupting tooth was probably at one time present in the thirteenth alveolus but dropped out before the specimen became fossilized. This sequence of "odd" and "even" teeth can be seen in figure 10.

The Vertebrae and Ribs

The first seven presacral vertebrae of this specimen were preserved together in a block, in an articulated series. Thus there is no question as to their identities. As for the other vertebrae, it is difficult to be certain about their exact positions in the vertebral column. There is a well-preserved vertebra from about the middle of the presacral region which is quite possibly the eighth or ninth of the presacral series, while in addition there are four more centra that come from the posterior part of the presacral region. Finally, there are eight ends of centra that represent this number or fewer vertebrae from the middle and posterior portions of the presacral region. Thus there may be as many as 20 of the presacral vertebrae represented in the material at hand, possibly a few less.

One vertebra is present that can be identified as a sacral.

Three large centra, one with a fragment of another centrum attached to it, represents the anterior end of the tail. These may be the first four caudal vertebrae. These vertebrae are notable because of their robustness, especially when they are compared with the posterior presacral vertebrae. In addition there are 11 fragments of centra that represent caudal vertebrae farther back in the tail. It is therefore evident that portions of as many as 15 caudals may be present in the material at hand.

There is good reason to think that about 24 vertebrae comprised the presacral region of the column, that there were two sacrals, and, as mentioned above, perhaps 45 caudal vertebrae.

In general the vertebrae can be characterized as amphicoelous and very much constricted in the middle region of the centrum. The centra are elongated, so that in most cases the length of each centrum is about twice the diameter of its anterior articular surface. The anterior vertebrae have on the anterior border of each centrum a well-developed parapophysis, which together with the diapophysis on the strong neural arch above it serves for the articulation of the double-headed rib. The zygapophyses are greatly elongated, so that in lateral view they project far in front of and somewhat behind the anterior and posterior articular faces of the centra, to form strong interlocking elements for the vertebrae. In these anterior vertebrae the facets of the zygapophyses are strongly inclined. In the center of the neural arch is the fairly elongate and strong neural spine, which is of approximate uniform diameter throughout its length and is not expanded at the top.

The posterior presacral vertebrae differ

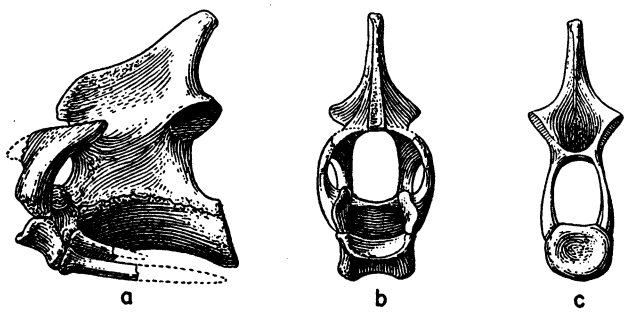


Fig. 14. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Atlas and axis vertebrae. A. Left lateral view. B. Anterior view. C. Posterior view. Natural size.

from the anterior ones in that the zygapophyses are not elongated, and they have the facets more nearly horizontal in position, while the rib articulations are entirely upon the neural arch. Of course the transition in these characters from front to back is gradual.

They are shorter than the presacral vertebrae, but the constriction of the centrum in each of these is much less extreme than is the case of the presacrals. Moreover, the articulating faces of the anterior caudals are large. There are large ventral facets for the chev-

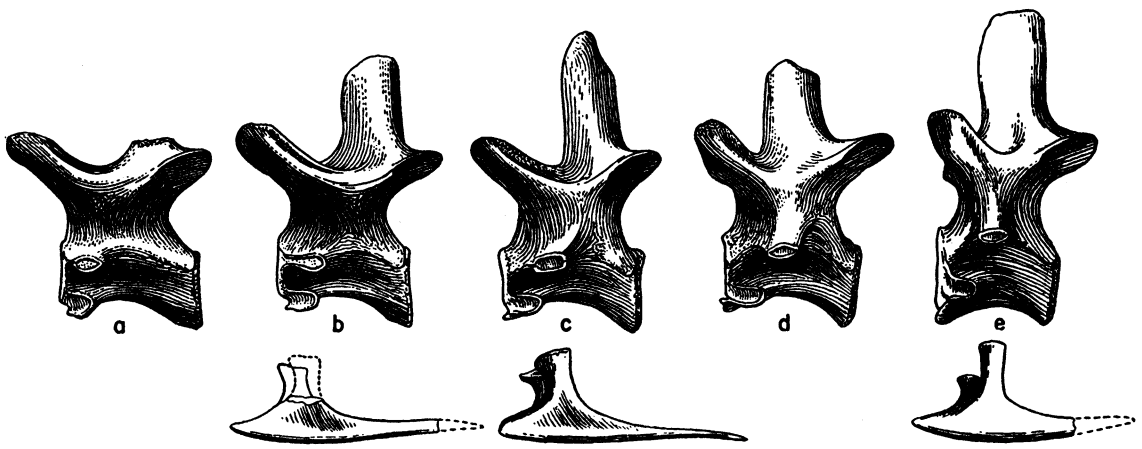


FIG. 15. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Presacral vertebrae and ribs, left lateral views. A. Third vertebra. B. Fourth vertebra. C. Fifth vertebra. D. Sixth vertebra. E. Seventh vertebra. All natural size.

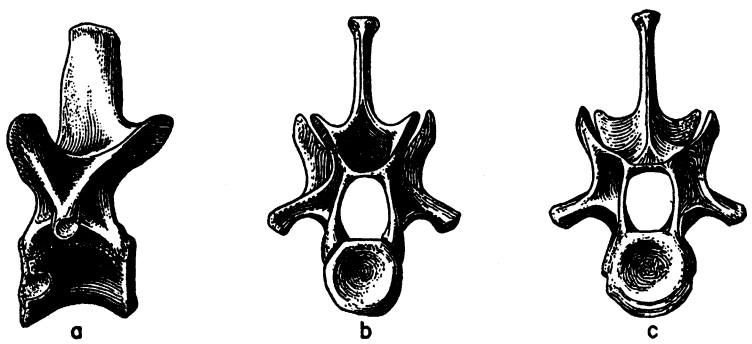
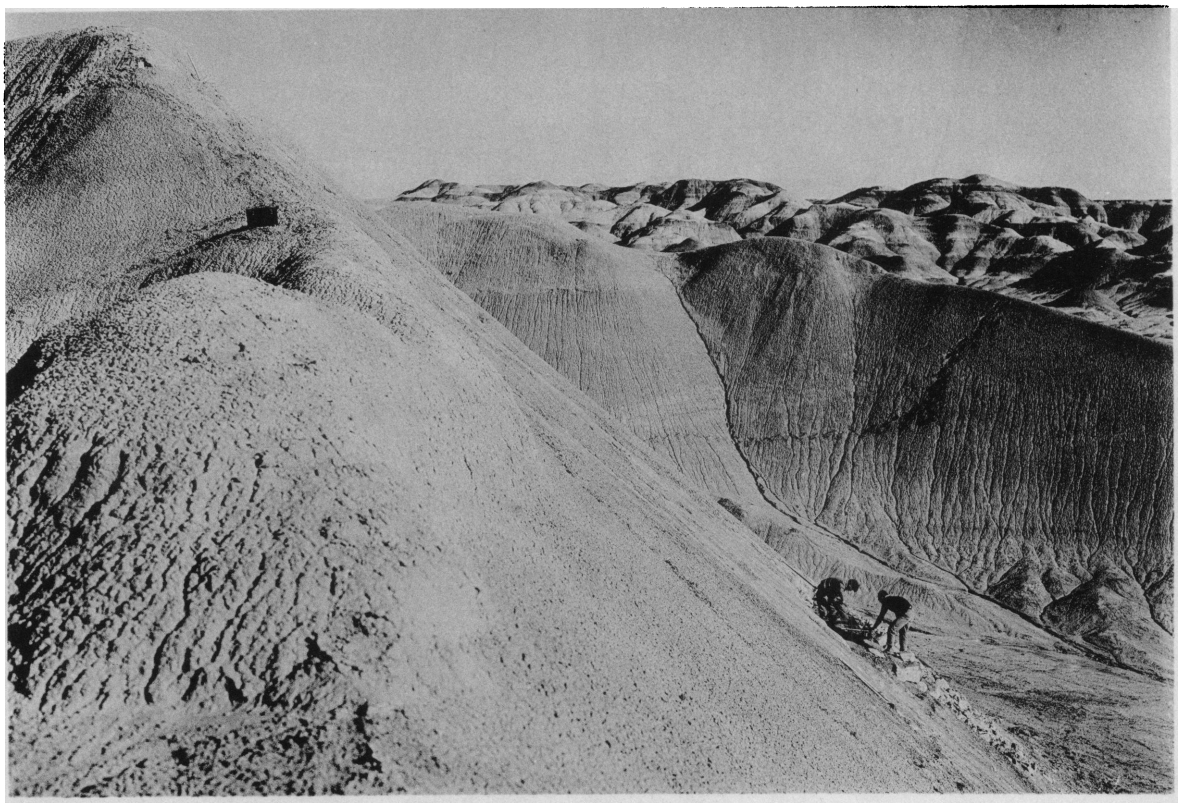


FIG. 16. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Eighth presacral vertebra. A. Left lateral view. B. Posterior view. C. Anterior view. All natural size.

A single sacral centrum is preserved. In general proportions it is similar to the last presacrals, but it is not constricted as they are. On its sides are large symphyseal surfaces to which there were attached at one time the transverse processes connecting the vertebra with the two ilia.

It was mentioned above that the anterior caudal vertebrae are comparatively heavy. rons. All in all this indicates that the tail was heavy and strong in its basal region. The more posterior caudal vertebrae are of course progressively smaller and more delicately built than are the anterior vertebrae. In all the caudals the articulating faces are rather higher than wide, as compared with the almost round faces of the presacral vertebrae.

The vertebrae of *Ornithosuchus*, as figured



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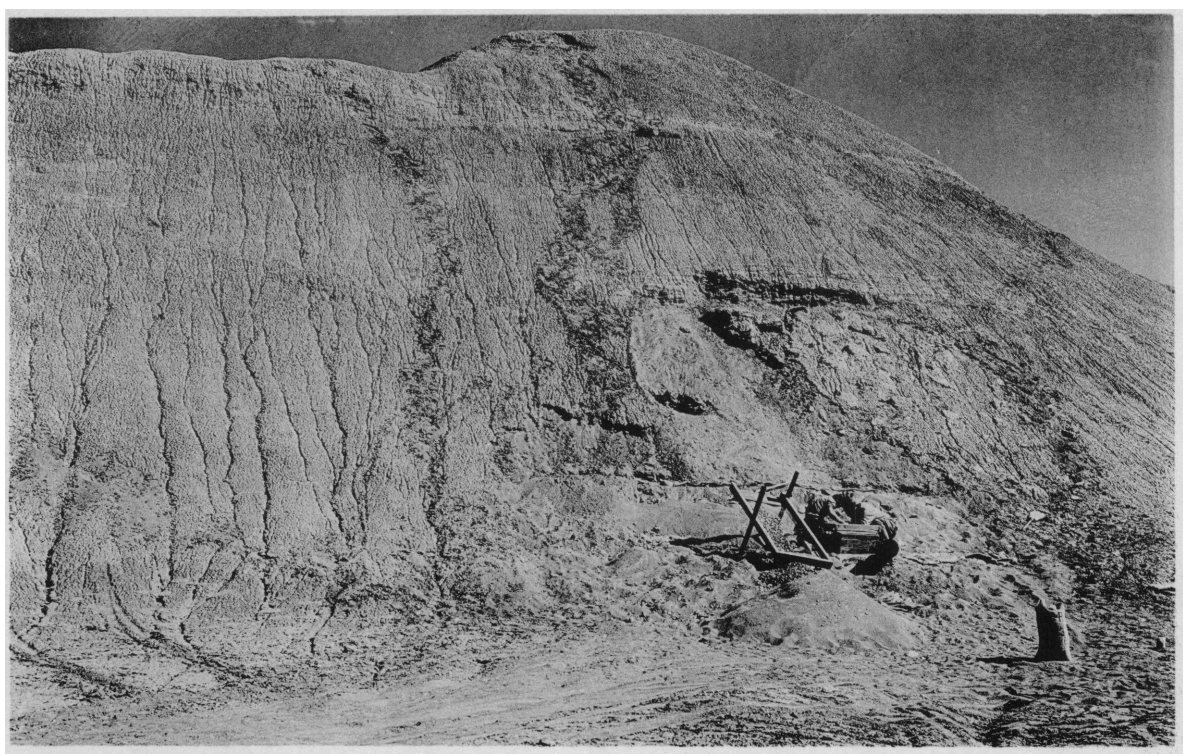
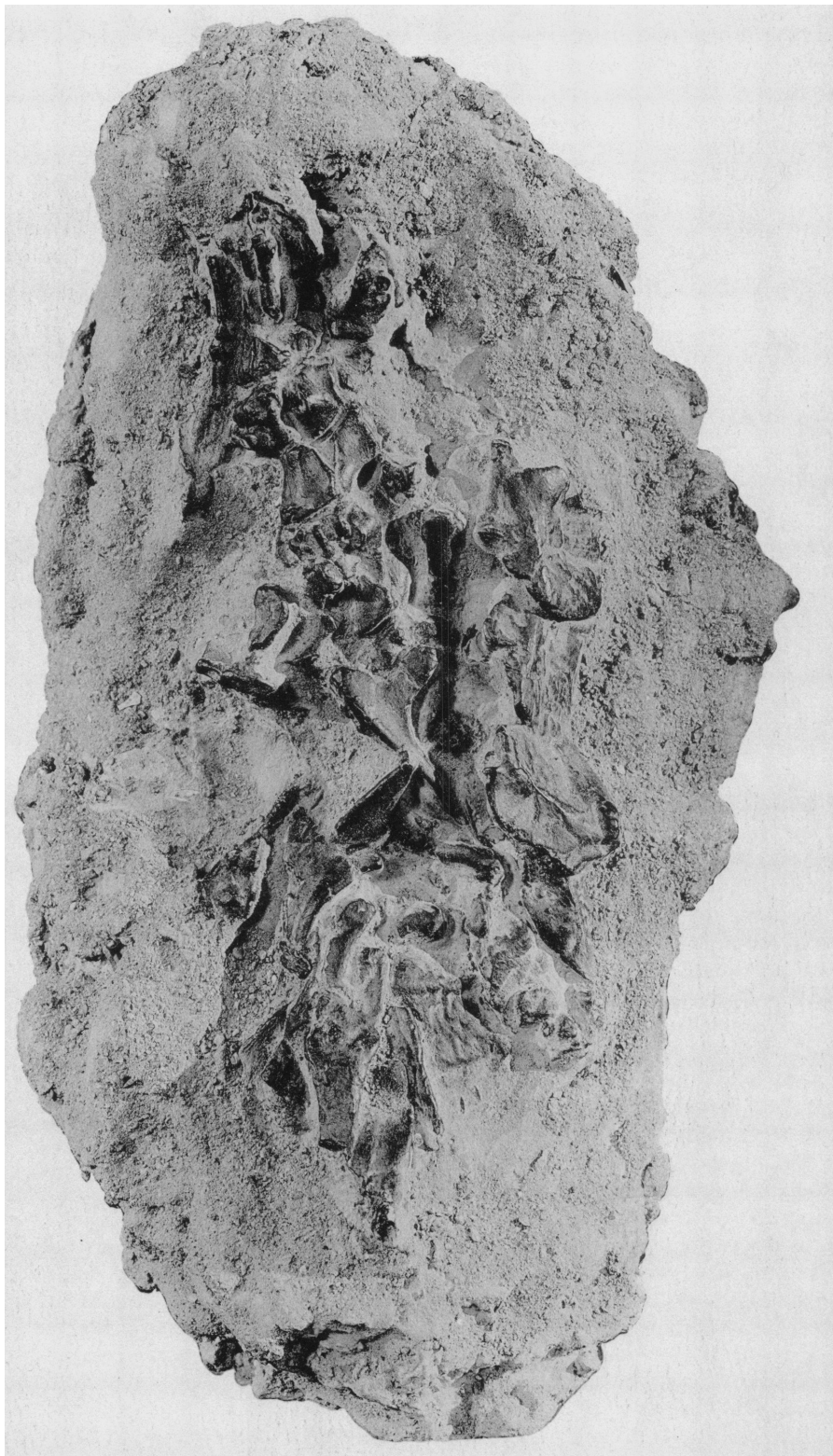


2

1. The *Hesperosuchus* site, southeast of Cameron, Arizona. Bones of *Hesperosuchus agilis* were found in place near the top of the hill, where a small shellac can is visible. The talus of the hill is being screened for other bones that have rolled down the slope. Bones of labyrinthodont amphibians and phytosaurs were found at the base of the hill. 2. Another view of the *Hesperosuchus* site, showing screening operations near the base of the hill



Associated anterior presacral vertebrae and scutes of *Hesperosuchus agilis*, new genus and species. These were the only bones found in association

by Newton, are generally comparable to those of *Hesperosuchus* but differ in that the centra are not so elongated, the spines are heavier, and the zygapophyses are shorter. *Erpetosuchus* seems to have high neural arches but relatively weak spines and horizontal zygapophyses of the usual sort.

istically double-headed. The first cervical rib, however, has a single head which articulates with a prominent facet on the centrum of the atlas. The axis bears two small facets, one on the centrum and one on the sutural border between centrum and neural arch, so it would appear that the rib articulating with this ver-

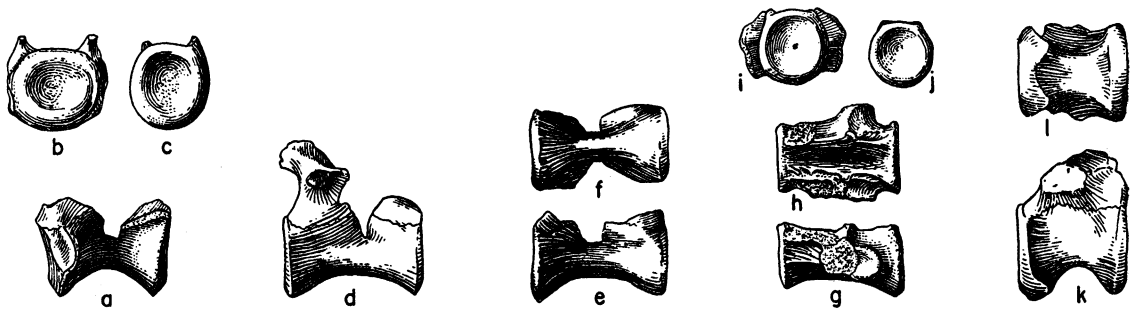


FIG. 17. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. A. Anterior posterior presacral vertebra, left lateral view. B. The same vertebra, anterior view. C. The same vertebra, posterior view. D. Posterior presacral vertebra, left lateral view. E. Posterior presacral vertebra, left lateral view. F. The same vertebra, ventral view. G. Sacral vertebra, right lateral view. H. The same vertebra, dorsal view. I The same vertebra, anterior view. J. The same vertebra, posterior view. K. Caudal vertebra, left lateral view. L. The same vertebra, ventral view. All natural size.

A much closer approximation in structure to the vertebrae of *Hesperosuchus* is to be seen in the genus *Saltoposuchus* as described and figured by von Huene. In *Saltoposuchus*, as in *Hesperosuchus*, the centrum is elongated, while in the presacral region the zygapophyses are elongated with oblique facets, and the neural spine is moderately long and uniformly proportioned. The same resemblances are to be seen between the presacral vertebrae of *Hesperosuchus* and those of *Pedeticosaurus*. The vertebrae in *Hesperosuchus* are somewhat larger than those of the European and South African specimens, but otherwise the resemblances are close, as can be seen from figure 18.

The genus *Parringtonia* from Africa has oblique zygapophysial facets as does *Hesperosuchus*, but the zygapophyses are not elongated. In the African genus the top of the neural spine is flattened and expanded in a manner somewhat similar to the spine of the phytosaurs, and therefore it is quite different in this respect from the spines of the several other ornithosuchids that are discussed here.

The ribs in *Hesperosuchus* are characteristically double-headed. The first cervical rib, however, has a single head which articulates with a prominent facet on the centrum of the atlas. The axis bears two small facets, one on the centrum and one on the sutural border between centrum and neural arch, so it would appear that the rib articulating with this vertebra had two small heads. From this point back, the two heads on each rib are strongly developed and widely spaced. In the anterior part of the presacral region the two rib heads articulate on a parapophysis, situated on the anterior border of the centrum, and a diapophysis, situated on the neural arch. This relationship holds at least as far back as the ninth presacral vertebra, but at some point behind this vertebra the relationship changes so that in the posterior region of the presacral series the articulations of both heads are entirely with the neural arch. Unfortunately not

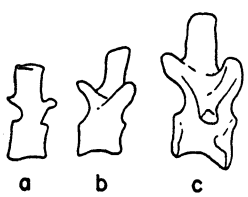


FIG. 18. Comparative figure of presacral vertebrae as seen in right lateral view. A. *Ornithosuchus* (after Newton). B. *Saltoposuchus* (after von Huene). C. *Hesperosuchus*. All one-half natural size.

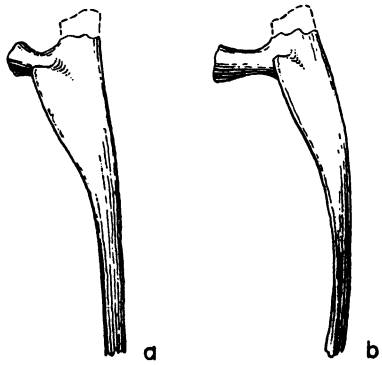


FIG. 19. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Proximal portion of left rib. A. Lateral view, showing development of flange on shaft. B. Oblique view. Natural size.

enough vertebrae are preserved to show this gradation, but it is reasonable to think that it was similar to that seen in other archosaurians and especially other thecodonts.

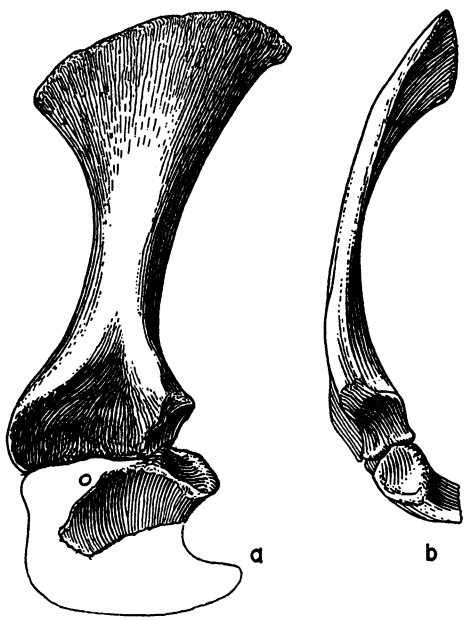


FIG. 20. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Left scapula and coracoid. A. External lateral view. B. Posterior view. Natural size.

Camp shows that in a phytosaur (*Machaeroprosopus*) the transition takes place at the eleventh presacral vertebra. On the tenth vertebra the rib articulations are borne by the centrum and the neural arch, respectively. On the eleventh vertebra the lower articulation is shared by centrum and neural arch, and the suture runs through the articular facet. On the twelfth vertebra both articulations are entirely upon the neural arch.

The cervical ribs of *Hesperosuchus* are strong in their proximal portions and taper to thin, delicate points distally. The dorsal ribs have shafts, of which the outer surfaces are flattened and broad.

THE PECTORAL GIRDLE AND FORE LIMB

Of the pectoral girdle, a complete left scapula and a portion of the left coracoid are preserved. It is probable that a clavicle and interclavicle were present in *Hesperosuchus*, as they are in other ornithosuchids, but there is no indication of these elements in the materials preserved. The clavicle and interclavicle may have been long, narrow bones, as they commonly are in other ornithosuchids and in other thecodonts.

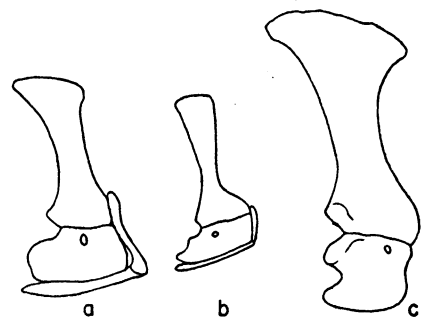


FIG. 21. Comparative figure of the right pectoral girdle as seen in external lateral view. A. *Saltoposuchus* (after von Huene). B. *Euparkeria* (after Broom). C. *Hesperosuchus*. All one-half natural size.

The scapula of *Hesperosuchus* is similar in form to the same bone in other genera of ornithosuchids. It is elongated and expanded both dorsally and proximally. The expansion at the upper end of the bone is quite pronounced, being more extreme than is the simi-

lar expansion in *Euparkeria* or *Ornithosuchus*. It is perhaps as great as the expansion of the upper part of the scapula in *Saltoposuchus*, as figured by von Huene, and in *Pedeticosaurus*. In *Hesperosuchus* the posterior border of the bone is relatively straight, while the anterior border is strongly concave—a result of the forward growth of the upper portion of the scapula.

At its lower end the scapula is not so much expanded as it is dorsally, but it is nonetheless strongly developed. There is a long border for articulation with the coracoid, of which latter bone only the proximal portion is preserved. On the basis of our knowledge of other ornithosuchids, it would seem likely that the coracoid in *Hesperosuchus* was a rather broad bone. The portion at hand does not contain a foramen.

Both scapula and coracoid have glenoid surfaces, and thus they shared in the articulation between the pectoral girdle and the humerus.

As seen from in front the scapula is a strongly curved bone, a function of its elongation and the necessity for such a long bone as this to fit the curve of the thorax.

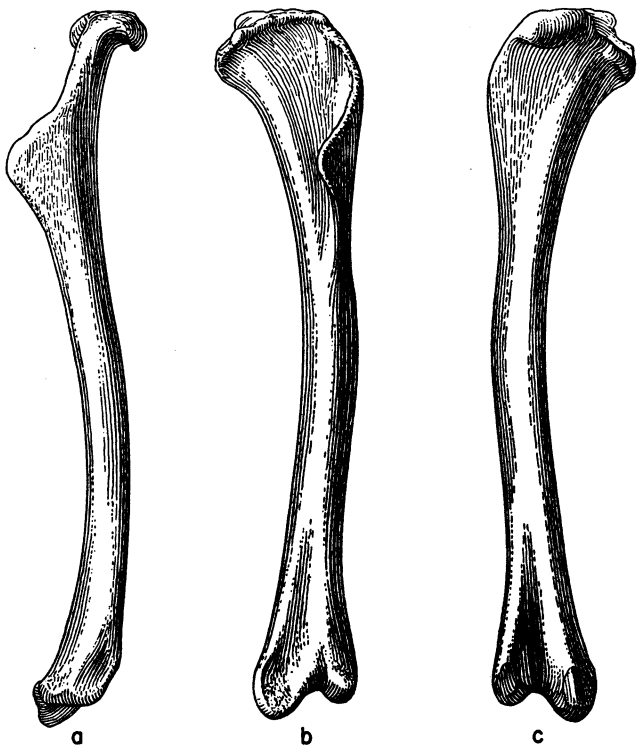


FIG. 22. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Left humerus. A. External lateral view. B. Ventral view. C. Dorsal view. Natural size.

The humerus and the radius-ulna of *Hesperosuchus* are slender, elongated bones of almost equal articular lengths. The similarity in length of the upper and lower arm in this genus can be compared with a like similarity in other ornithosuchids, such as *Ornithosuchus* as figured by Broom (1913), and *Pedeticosaurus*. In neither of these latter genera is the correspondence in length between the two segments of the arm so close as it is in *Hesperosuchus*. The humerus and the radius-ulna of *Hesperosuchus* are considerably longer than the scapula, as they are in *Pedeticosau-*

rus; whereas in *Ornithosuchus* they are somewhat shorter than the scapula, according to Broom's figure. The humerus of *Hesperosuchus* is about two-thirds of the length of the

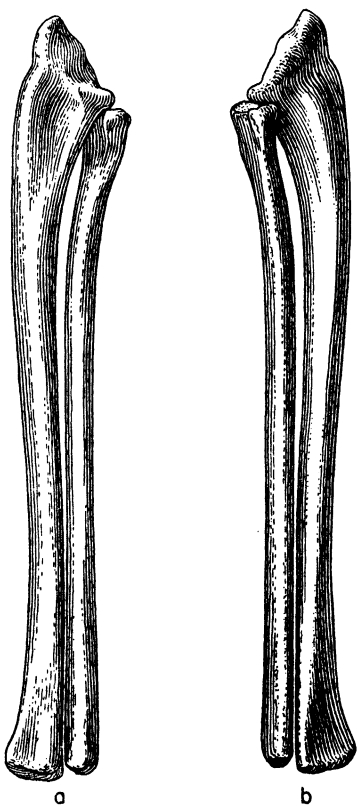


FIG. 23. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Left radius and ulna. A. Internal lateral view. B. External lateral view. Natural size.

femur, a proportion closely comparable to that characteristic of *Ornithosuchus* and *Pedeticosaurus*.

Although the humerus is slender, it is rather widely expanded at its proximal end, an expression of the large size of the articular surface. This part of the bone is also bent rather strongly mediad. There is a large pectoral crest that curves downward from the lateral surface of the bone and terminates in a pronounced point. The form of this bone is illustrated in figure 22.

The radius and ulna are rather straight bones, and are both very slender. The radius is slightly expanded at each end, for the accommodation of the articular surfaces. The ulna likewise is expanded at each end, but

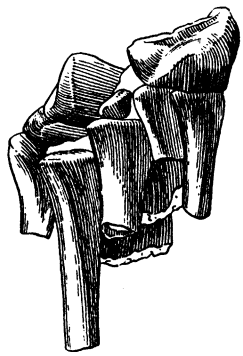


FIG. 24. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Left manus as found, showing the proximal ends of the metacarpals and certain carpal (?) bones; dorsal view. Natural size.

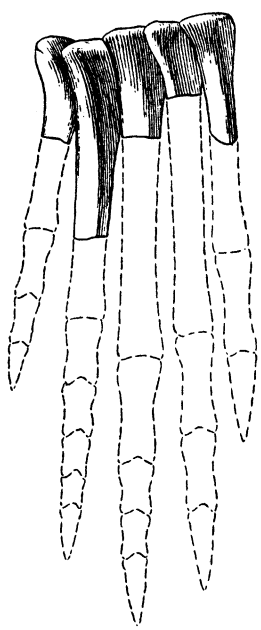


FIG. 25. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Left manus, restored; dorsal view. Natural size.

proximally the expansion is quite pronounced. There is a well-developed olecranon process.

The manus in *Hesperosuchus* is represented by the proximal ends of the metacarpals,

which were found fused to each other and to some other bone fragments, including the greater part of a tibia. Little can be said about the hand from the scanty material preserved. It seemingly was rather large, the length of the extended third digit probably being about as great as the length of the radius. There evidently were five well-developed digits.

The Pelvic Girdle and Hind Limb

There are no undoubted elements of the pelvic girdle present among the known materials of *Hesperosuchus*. There is a specimen that looks very much like an ilium, and one is almost tempted so to identify it. It shows a long extension of the bone that at first sight appears to be the posteriorly directed iliac crest. On one side this region shows a groove that might be an articular surface for the transverse processes of the sacral vertebrae. Below this groove the bone is thickened, and it bears facets of a sort that were at first considered as articulations for the ischium and pubis.

Under close examination, however, it cannot be considered the ilium of *Hesperosuchus*, for various reasons. It is much too small to have been a part of the pelvic girdle of the reptile here described. Moreover, the specimen is seen to consist of two bones, joined by a suture, this suture being interrupted by a rather large foramen. These characters exclude the specimen from classification as an ilium of *Hesperosuchus*, but one must admit that at the present time no definite identification for it can be reached.

A completely preserved and uncrushed left femur affords good evidence as to the form and the general characteristics of this bone in *Hesperosuchus*. It is long (as mentioned above, about a third again longer than the humerus), and it is heavy, indicating that the hind limb was indeed powerful in this pseudosuchian. In general form the femur is what one would expect in a reptile of this type. Proximally the bone is bent sharply mediad, for the articulation of the head within the acetabulum of the pelvis, a construction indicating that the hind legs were brought well beneath the body and that they were swung forward and backward in a rather straight line. There is a well-developed internal trochanter on the back of the bone, about a fourth of the length of the femur down the shaft from the head. Distally there are two large condyles for articulation with the tibia and fibula, and of these the external is the greater in size.

Fig. 26. Four aspects of problematical bone.

It would appear that the femur in *Hesperosuchus* is proportionally larger than the same bone in *Ornithosuchus* and *Pedeticosaurus*, and it is possibly comparable in comparative dimensions to the femur in *Saltoposuchus*. From the evidence of this bone in particular, but also from that of the other bones of the hind limb, it is obvious that *Hesperosuchus* was dominantly a bipedal animal, and it must have depended on the hind limbs for most of its locomotion.

There is no complete tibia or fibula present in the materials at hand. From the several portions preserved, however, it would seem that these bones were about equal to the femur in length—a relationship that is seen in

other ornithosuchids, such as *Pedeticosaurus* and *Saltoposuchus*. The tibia is a strong bone, as might be expected, expanded both proximally and ventrally for articulation with the femur and the pes, respectively. The fibula is a comparatively slender bone.

There are various isolated bones that obviously represent the hind foot of *Hesperosuchus*. With the materials at hand an attempt has been made to assemble a composite pes, which is illustrated in figure 31. There is no assurance, of course, that this pes is cor-

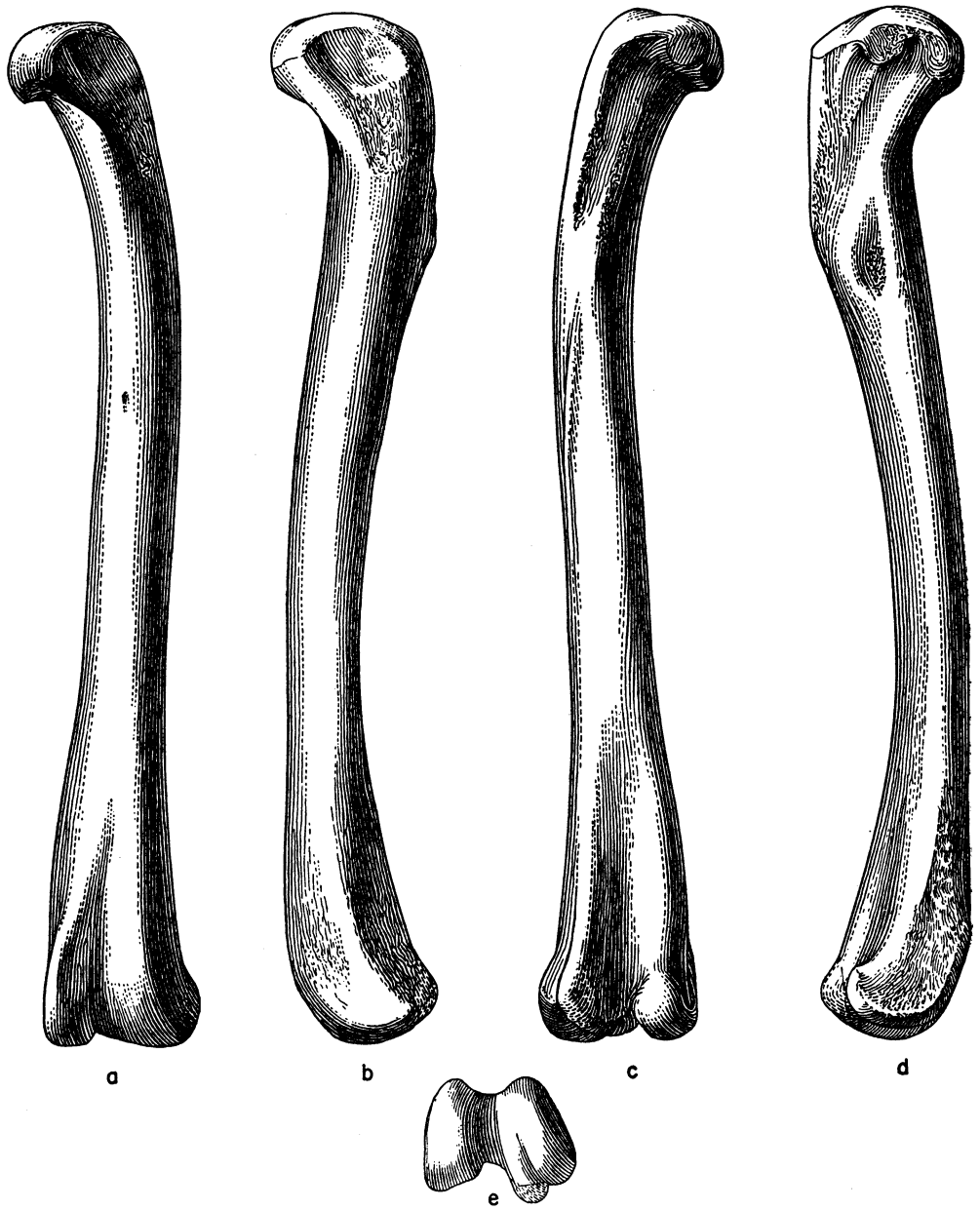


FIG. 27. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Left femur. A. Dorsal view. B. External lateral view. C. Ventral view. D. Internal lateral view. E. View of distal articular surface. Natural size.

rect in all details, but it is probably reasonably accurate. In making this composite pes, particular attention was given to the foot bones of *Ornithosuchus* as described and figured by Newton, to the pes in *Euparkeria* as described by Broom, and to the pes in *Pedeticosaurus* as figured by van Hoepen.

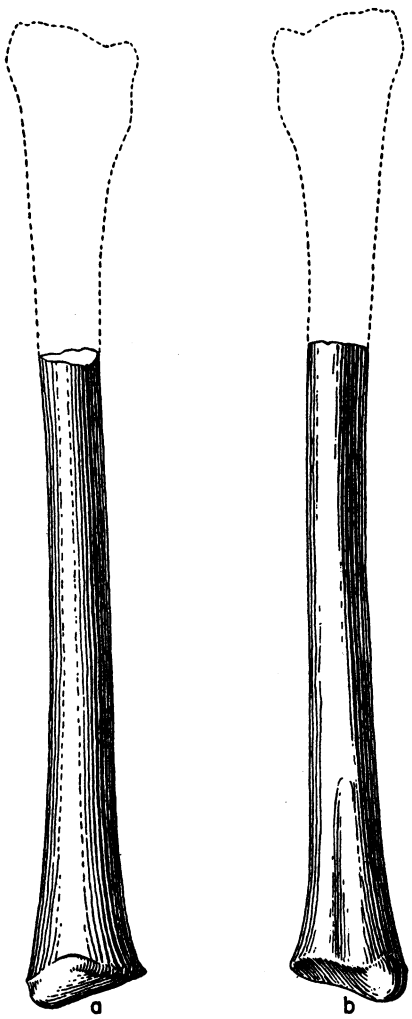


FIG. 28. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Distal portion of left tibia. A. Dorsal view. B. Ventral view. Natural size.

The two bones here figured as the second and fourth metatarsals are without much doubt correctly placed. There is some question as to the distal portion figured as a part of the third metatarsal and likewise of the proximal portion figured as a part of the fifth metatarsal. The phalanges available have been arranged in the order that seems most consistent with probabilities. As can be seen, there are no bones present that can be as-

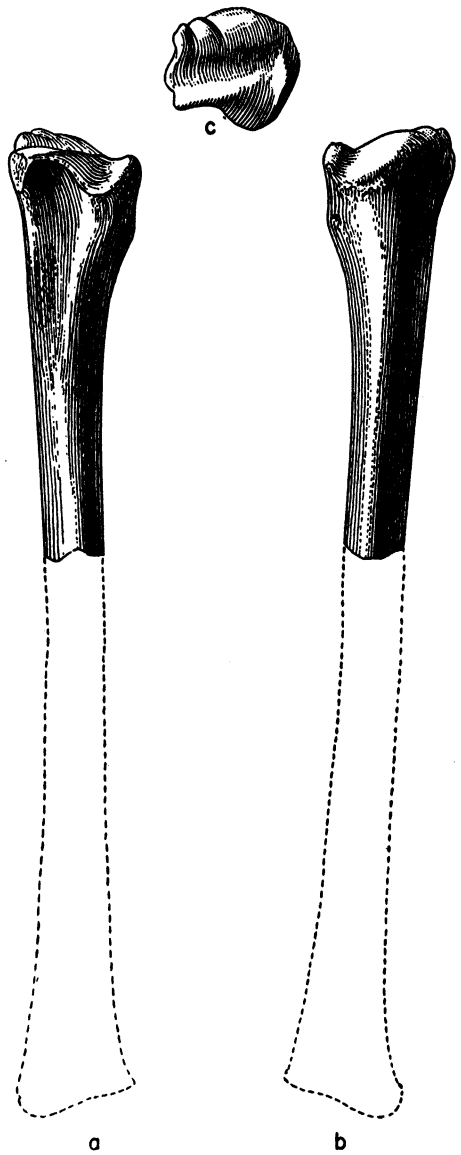


FIG. 29. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Proximal portion of right tibia. A. Ventral view. B. Dorsal view. C. Proximal articular surface. Natural size.

signed with any degree of certainty to the first digit. It should be pointed out also that no bones have been found from the tarsus.

This is a large pes, if correctly restored. The extended length of the third digit is approximately of the same length as the femur.

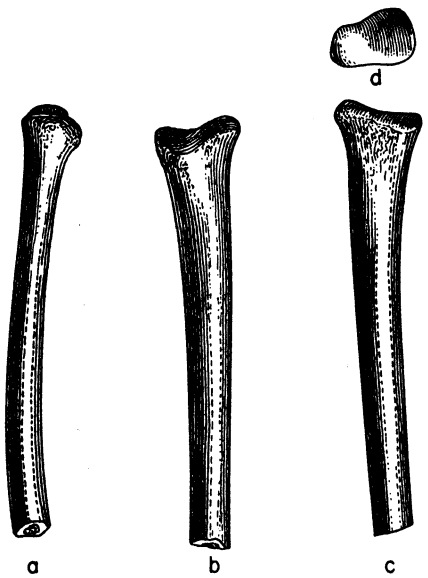


FIG. 30. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Proximal end of right fibula. A. Dorsal view. B. Internal lateral view. C. External lateral view. D. Proximal articular surface. Natural size.

It will be remembered that the tibia also is approximately equal to the femur, so the three major segments of the hind limb are thus essentially equal to one another in length. The individual bones of the foot are strong, as an adaptation for sustaining the shocks and stresses that go with rapid bipedal progression.

It would seem that the axis of the foot passed through the middle digit, but the two digits on either side are almost equal to it in size. Thus the three central digits of the foot formed the most important portion of that complex, and one can see how these three digits were to become the all-important part of the hind foot in many of the more advanced archosaurians, such as the dinosaurs. In addition to the middle toes, the first and fifth digits were probably well developed in *Hesperosuchus*, as they are in other ornithosuchids. The first toe in *Ornithosuchus* is very robust as compared with the other toes, and it has been so restored in *Hesperosuchus*. In *Ornithosuchus* and in *Euparkeria* there was in each case a fully developed fifth digit, and such has been indicated for *Hesperosuchus*. These pseudosuchians had not suffered the reduction of the fifth digit to a small, hook-like metatarsal that is so common in many of the thecodont reptiles. The fragment of bone shown as the proximal portion of this metatarsal is a flattened, slender bone, with a nar-

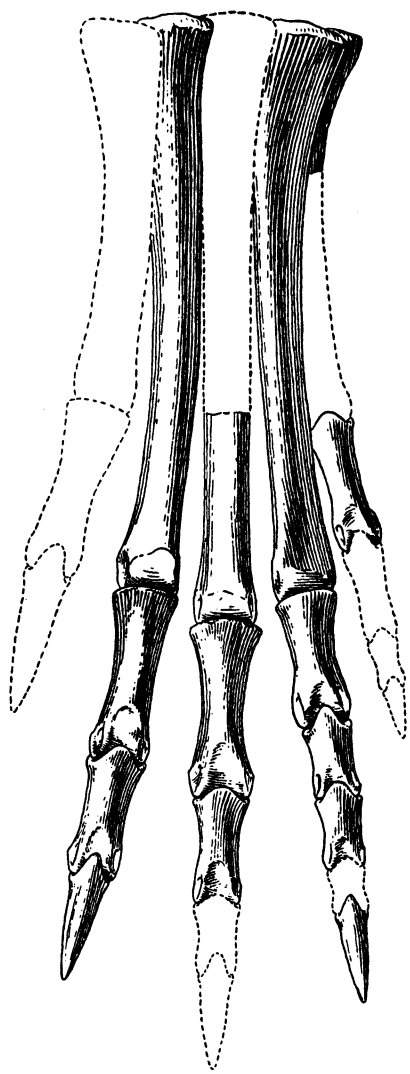


FIG. 31. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Left pes, restored; dorsal view. Natural size.

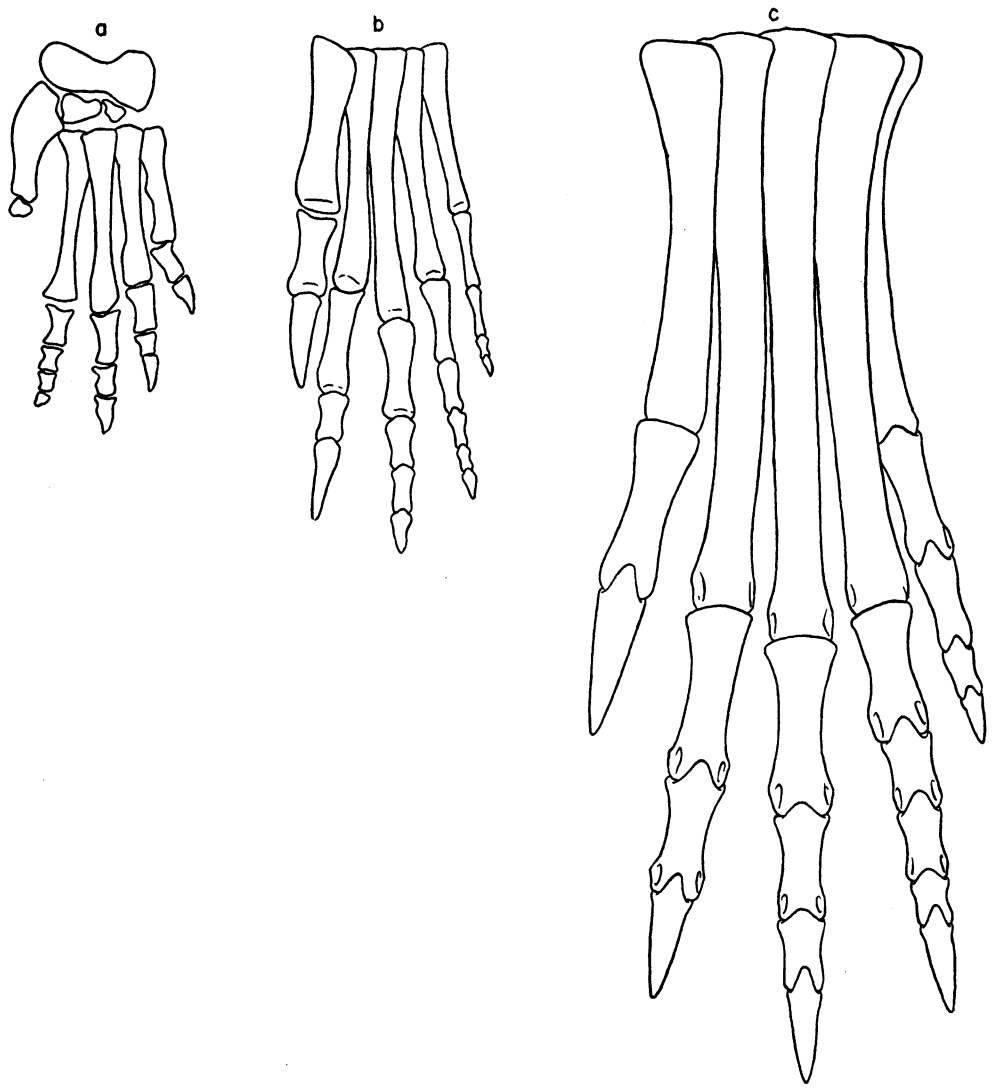


FIG. 32. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Comparative figure showing the pes in dorsal view. A. *Euparkeria* (right pes, after Broom). B. *Ornithosuchus* (left pes, after Newton). C. *Hesperosuchus*, left pes. All natural size.

row surface for articulation with the tarsus.

Two pointed ungual phalanges are present, and these have been placed at the terminations of the second and fourth digits. It is probable that all the ungual phalanges in the hind foot were well developed and pointed, with the middle three unguals approximately equal to one another in size, the first noticeably larger than these three, and the fifth much reduced.

The foot has been restored with a phalangeal formula of 2-3-4-5-4. Broom has indicated a formula of 2-3-4-5-3 for *Euparkeria*.

In order that the reconstructed pes of *Hesperosuchus* can be compared at this place with the hind feet in *Ornithosuchus* and *Euparkeria* the descriptions by Newton and by Broom are quoted. In addition, an outline drawing of the hind foot of *Hesperosuchus* and *Ornithosuchus* (this latter redrawn from the foot illustrated by Newton as *in situ*) is shown in figure 32.

"The *hind foot* of the left side is preserved in a most unexpected manner; but that of the right side, as well as the greater part of the right tibia and fibula, is wanting, and the position and direction of the pieces of the latter which are preserved make it very unlikely that any of the right foot-bones are mixed with those of the left; and further, the position and relations of the phalanges of each of the left toes show unmistakably that they belonged to one digit, and for the most part look as if they were still united by their decaying ligaments. There are five metatarsals, and these are numbered in the figure (Plate 56, fig. 2), in accordance with their gradually decreasing stoutness, but partly also on account of the number of phalanges in relation with them. Thus it will be seen that number 1 is the stoutest metatarsal, and number 5 the most slender. The second, third, and fourth metatarsals, however, are longer than the first or fifth. Metatarsal 1 has close to it two stout phalanges (a 1, a 2), the terminal one being ungual. Metatarsal 2 has three phalanges (b 1, b 2, b 3) close to its distal end, the last being ungual. Metatarsal 3 has no phalanges quite close to it, but it is evident from their size that the four rather smaller ones (c 1, c 2, c 3, c 4), which are close together, curled in a ring, belong to the third digit, the terminal phalanx of which was ungulate. Metatarsal 4 has near its extremity one phalange (d 1), while a little below this there are three small ones (d 2, d 3, d 4) in a series, and on the opposite block of stone, but continuing the series, is another very small one (d 5), making in all five phalanges to this fourth digit. In the cast figured metatarsal 5 has no phalanges near it, but, on the opposite block of stone, its counterpart is shown with two phalanges (e 1, e 2), in a line with it, but somewhat separated, and these are indicated in the figure by unshaded outlines. The second phalange of this fifth digit has an articular surface at its distal extremity, and consequently there must have been at least one other phalange. This foot, it will be seen, agrees with that of modern lizards in having five digits, and also in the number of phalanges in the first four digits, and probably in the fifth also; namely, in the first 2 phalanges, in the second 3, in the third 4, in the fourth 5, and in the fifth certainly 3, and very likely 4 phalanges" (Newton, 1894, pp. 597–598.)

"The metatarsals are all well developed, and the 5th has the peculiar Rhynchocephalian development. Of the others the 3rd is the longest. The 4th is slightly longer than the 2nd, and the 2nd considerably longer than the 1st. The 1st, 2nd, and 3rd digits have well-developed claws, but the 4th has the phalanges rather weak and the claw, if present, was very small. The 5th toe also has a small claw, though larger than that of the 4th. The digital formula is 2, 3, 4, 5, 3" (Broom, 1913b, p. 623).

The Dermal Armor

The thecodonts are characterized by well-developed dermal scutes, and such plates are characteristic of *Hesperosuchus*. Among the pseudosuchian thecodonts the ornithosuchids can be defined, among other characters, by their elongated and relatively narrow dorsal scutes. The plates of *Hesperosuchus* are in accord with this definition. These scutes, of which several are preserved, are somewhat longer than they are wide, and in this respect they resemble the dorsal scutes of *Erpetosuchus*, *Ornithosuchus*, *Saltoposuchus*, and *Pedeticosaurus*.

There is a series of scutes from the left side of the cervical region, which when found were preserved in a somewhat distorted sequence beside the vertebrae of the neck. These scutes, shown in figure 33, are roughly similar to one another in size and shape, except for the first one in the series. This first plate is considerably smaller than the others and is attenuated at the front. Probably it occupied a position on the neck directly behind the skull.

The other scutes have very straight medial edges, an indication that they were closely appressed to their opposites along the midline. Likewise the posterior borders are rather straight and form right angles with the medial borders. The external borders of the scutes are convexly curved. The anterior borders are strongly concave, or rather notched, and on the outside this border in each plate is extended forward to form a strong point. These points served as articulations between the plates, which overlapped one another like

shingles from front to back. This character, rather difficult to describe, is easily seen in the figure.

The under surfaces of the scutes are smooth, but the upper surfaces are strongly rugose. A pronounced longitudinal keel runs along the lateral part of each scute, and it divides the bone into two parts: a large, rectangular, flat medial portion, and a smaller, narrow lateral portion set at an angle to the medial portion.

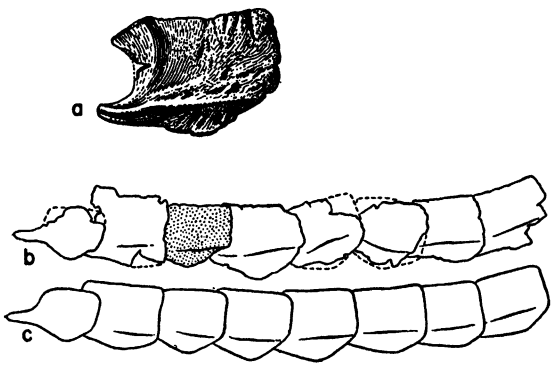


FIG. 33. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Dorsal scutes from the cervical region. A. Single scute, natural size. B. Series of eight scutes showing the position of the scute figured in A. C. The same series of scutes, restored. B and C one-half natural size.

Again, the figure illustrates this feature of each scute better than it can be described.

Evidently there was a single row of large dorsal scutes along each side of the midline in *Hesperosuchus*, as is characteristic of the ornithosuchids and of the pseudosuchians in general. The dermal armor in this reptile seemingly was not extensive, but it is quite characteristic, and it indicates, with so many characters of the skull and skeleton, that *Hesperosuchus* is closely related to *Ornithosuchus* and other genera comprising the family Ornithosuchidae.

THE RESTORED SKELETON

In figure 34 an attempt has been made to show a restoration of the skeleton of *Hesperosuchus* as it would appear in lateral view. It is realized, of course, that there are certain dangers in making this restoration, yet it is felt that enough material is present to justify the attempt. The restoration is made with a full realization that it is at best tentative, and that future discoveries may alter it materially.

Even though a considerable portion of the skeleton is missing, the parts present are for the most part crucial to give the basic information needed for an understanding of the skeleton as a whole. There is considerable conjecture in the restoration of the skull, as mentioned above, the length of the tail must be guessed at, the pelvis is completely restored, while certain details of the hands and feet are unknown. Most of the remainder of the skeleton, however, is restored on definite information gained from the materials at hand.

The skull is based on skulls of related ornithosuchids, especially *Ornithosuchus* and *Euparkeria*. Some indication of the size of the skull is shown by the materials preserved. Also these materials indicate that there was a large antorbital opening, as would be expected. The skull of *Hesperosuchus*, although lightly built, was evidently of rather large size as compared with the body. It is assumed that the tooth-bearing portion of the dentary, which is represented in the preserved portions of *Hesperosuchus*, is about half of the total length of the lower jaw. This is the proportion seen in *Euparkeria;* in *Ornithosuchus* the tooth row would seem to be somewhat more than half of the length of the lower jaw. Restoring the skull and mandible on the basis of this proportion makes the lower jaw longer than the femur by about a fourth of the length of the latter bone, which is essentially the relationship seen in *Ornithosuchus*. So far as can be judged from Broom's figures, the jaw of *Euparkeria* is even longer in proportion to the femur than it is in *Ornithosuchus*, or in this restored skull of *Hesperosuchus*. Therefore it is felt that the restoration of the skull and jaw to the size indicated is not out of line with other evidence concerning the ornithosuchid reptiles. Evidently these were large-headed animals.

In this respect they can be compared in a general way with the carnosaurian dinosaurs, which also had very large skulls. In both groups the animals were highly predaceous, bi-

TABLE 1

COMPARATIVE MEASUREMENTS (IN MILLIMETERS) AND RATIOS OF VARIOUS GENERA OF ORNITHOSUCHIDAE

	Hespero-suchus A.M.N.H. No. 6758	*Ornitho-suchus* from Newton	*Erpeto-suchus* from Newton	*Saltopo-suchus* from von Huene	*Pedetico-saurus* from van Hoepen
MEASUREMENTS					
Length of skull (premaxilla to quadrate)	145*e*[a]	111	78	135*e*	91
Length of presacral vertebrae	425*e*	240*e*	175*e*	285*e*	183*e*
Length of scapula	63	55	32	51	28
Length of humerus	94	57.5	38.5	—	50
Length of radius	87	47	28.5	—	43
Length of ulna	100	49	—	—	—
Length of metacarpal III	—	—	10.5	—	10
Length of manus	80*e*	—	20*e*	—	28
Length of femur	140	87	—	105	75*e*
Length of tibia	130*e*	—	—	90	67
Length of metatarsal III	80	36	—	69	28.5
Length of pes	150*e*	—	—	110[b]	63*e*
Length of an anterior presacral vertebra	18	12	7	12	9[c]
Breadth of centrum of same	10	—	—	—	—
Height of same	38.5	24	16	29	15[c]
RATIOS					
Skull/presacral vertebrae	34	46	—	47	50
Scapula/humerus	67	96	83	—	56
Radius/humerus	92	82	74	—	86
Metacarpal III/humerus	—	—	27	—	20
Femur/presacral vertebrae	33	36	—	37	41
Tibia/femur	93	—	—	86	88
Metatarsal III/femur	57	41	—	66	38
Humerus/femur	67	66	—	—	67
Fore limb/hind limb	62	—	—	—	59
Fore limb/presacral vertebrae	61	—	50	—	66
Hind limb/presacral vertebrae	99	—	—	107	112

[a] *e* indicates estimated measurements.
[b] Large basis of estimation.
[c] Posterior presacral.

pedal, and very active. It was advantageous for them to have large skulls, because this gave widely gaping jaws with which to attack and catch their prey. In this activity they must have used the grasping hands to aid the jaws. One might say that the two groups followed a similar pattern of adaptation—in the ornithosuchids on a small scale, in the carnosaurs on a giant scale.

Of course it was necessary for this relatively large skull to be light in both ornithosuchids and carnosaurs, so it was characterized by the development of large antorbital and postorbital fenestrae. Strength was thus preserved in the skull, but the weight was reduced, while sufficient areas for muscle attachments were retained. In the light of these considerations the skull of *Hesperosuchus* has been restored as being rather deep.

The size and depth of the skull of *Hesperosuchus* are indicated by the correlative evidence of the cervical vertebrae, which in this

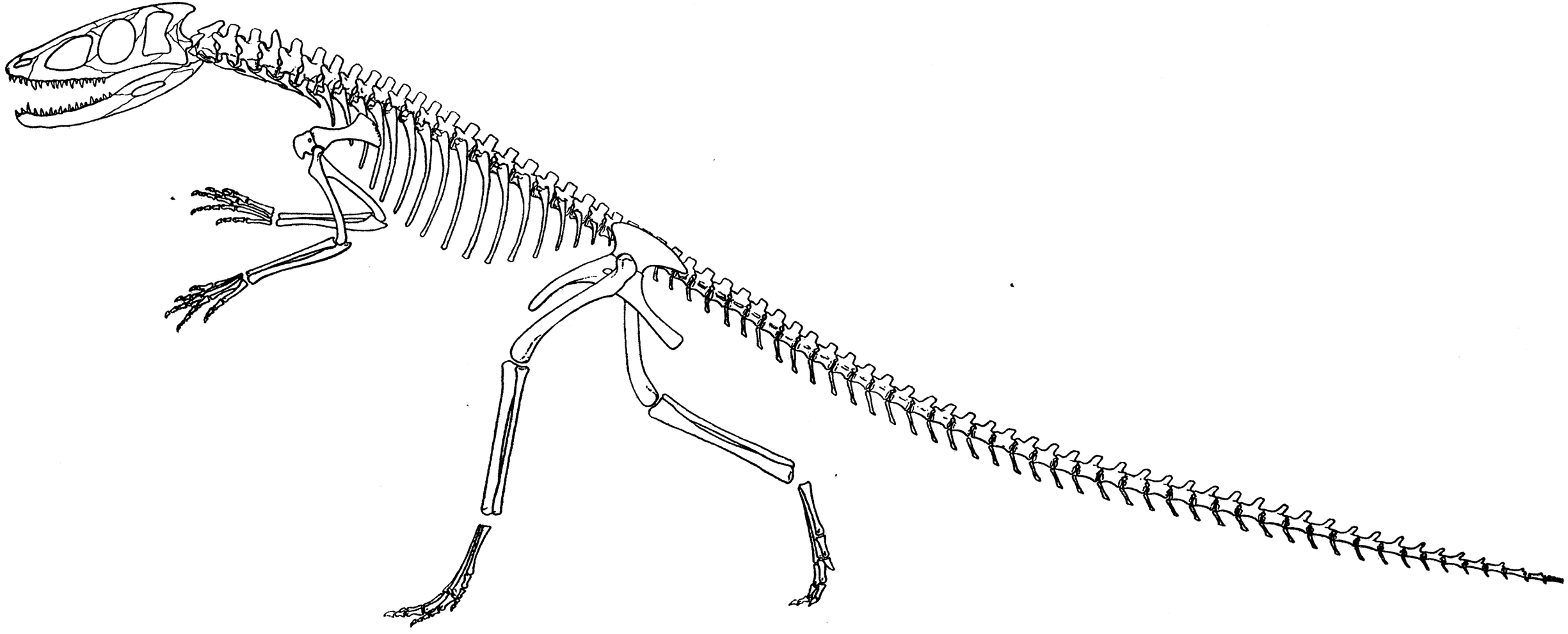


FIG. 34. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Restoration of the skeleton, lateral view. One-fourth natural size.

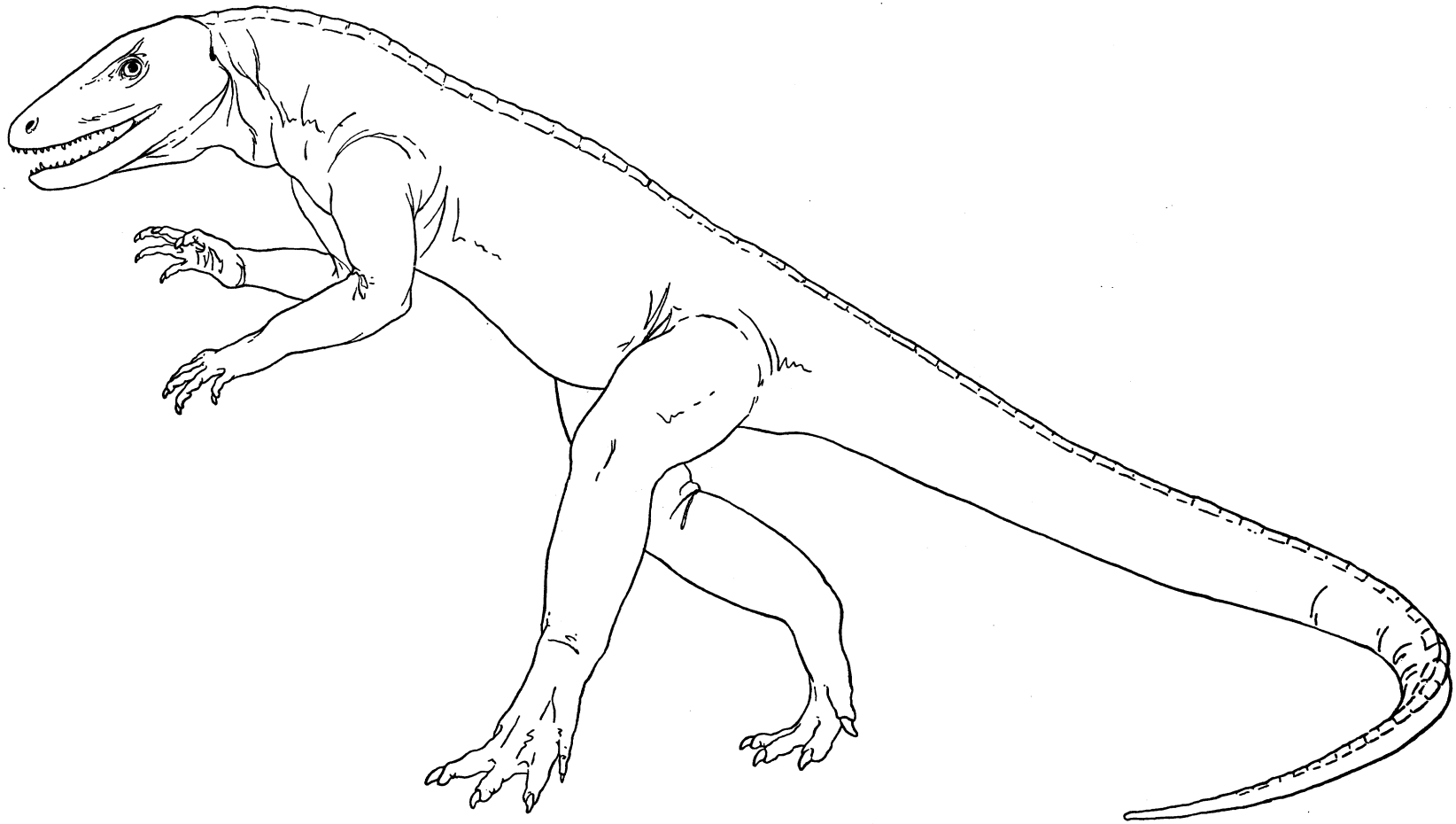


FIG. 35. *Hesperosuchus agilis*, new genus and species. A.M.N.H. No. 6758, type. Life restoration.

genus are quite large and strong. It is obvious that the neck was very powerful in relation to the size of the animal, as would be necessary for a large-headed reptile. Here again comparisons can be made with the carnosaurs, in which the neck was very strong. It is rather curious, however, that the neck in *Hesperosuchus* seems to be inordinately heavy as compared with the posterior part of the presacral series of vertebrae. There can be no doubt as to the relative lightness of the posterior presacrals, identifiable by their rib articulations, in comparison with the vertebrae of the neck. Of course it may be possible that more than one individual is represented in the material at hand, but the evidence of the limb bones seems to be against this.

The length of the tail is one of the biggest unknown quantities in this restoration of *Hesperosuchus*. In figure 34, 45 caudal vertebrae are shown, and it is felt that this number is rather conservative. There might have been 50 vertebrae or more, but it is really doubtful that there could have been as many as 70, the number indicated by von Huene in his restoration of *Saltoposuchus*. As restored the caudal series is about twice the length of the presacral series, and this would seem to be a fairly reasonable proportion.

The distal portion of the coracoid has been restored. No attempt was made to indicate a clavicle and interclavicle, although it is probable that these bones were present. Broom shows them in *Euparkeria*, and one would expect them in thecodont reptiles.

That there were five fingers in the hand is evident from the proximal portions of the metacarpals preserved. Unfortunately we have no information as to the number or size of the phalanges. In the restoration the normal reptilian number has been indicated, and the claws are shown as rather small. However, it is quite possible that some of the claws, particularly those of the first three digits, may have been enlarged. No attempt was made to restore the carpal bones.

The pelvis is completely restored and is based without much change on the pelvis of *Ornithosuchus*. For a bipedal, running animal, this type of pelvis is most suitable, since it is characterized by a long ilium and the elongated ischium and pubis.

The hind foot is fairly well known from the materials at hand, and its restoration can be regarded as reasonably accurate. No traces of tarsal bones were found, so this portion of the foot was left blank. It is probable, however, that there were a well-developed astragalus and calcaneum, and perhaps several other tarsal bones as well.

The individual bones of *Hesperosuchus* are delicate and fragile, but they combine to make an animal of some size. The skeleton as restored indicates a reptile about 5 feet in length, evidently capable of running with considerable speed and of preying on various other vertebrates that comprised the Chinle fauna. Figure 35 is an attempt to show very simply what *Hesperosuchus* might have looked like in life.

HESPEROSUCHUS AND THE CHINLE FAUNA

FROM THE FOREGOING DESCRIPTION and comparisons, epitomized by the reconstruction of the skeleton in lateral view (fig. 34), it is possible to obtain a fairly clear idea as to the general appearance of *Hesperosuchus*. This was a lightly constructed archosaurian, about 4 or 5 feet in length. It was habitually bipedal in gait, and the hind limbs were long and strong. The tail was long and attenuated and served as a counterbalance for the weight of the body. The fore limbs were small as compared with the hind limbs but were sufficiently large so that they formed efficient arms. The hands were adapted to grasping. The skull was armed with sharp teeth.

Evidently *Hesperosuchus* was a very active predator. It must have preyed upon small reptiles and amphibians, which it caught by virtue of its ability to move rapidly. This speed of movement was also an advantage to *Hesperosuchus* in escaping the large predatory reptiles that lived during upper Triassic times. The adaptations of this pseudosuchian would indicate that it was primarily an "upland" animal, living on firm, dry ground, where its ability to run fast would be most advantageous for survival. It would seem probable, however, that the land in northern Arizona during upper Triassic times was on the whole low and criss-crossed and dotted by numerous streams and lakes. Therefore *Hesperosuchus* was very likely never far from water, even though it held to firm ground as much as possible.

This is shown by the fossils found associated with the specimen. There are several "ganoid" scales, indicating a holostean fish of the genus *Semionotus* or *Lepidotus*. These were fresh-water fishes of the Triassic period, living in shallow streams and lakes. Also associated with *Hesperosuchus* are small stereospondyl vertebrae and some phytosaur teeth. These associations likewise indicate streams or lakes crossing a flood plain.

There are various small teeth, some amphibian, others of undoubted reptilian relationships, for which no definite identifications can be made. Some of these small teeth are certainly from *Hesperosuchus*, but there are others that probably indicate other types of small reptiles living in the Chinle fauna. Perhaps some of these teeth are from animals that *Hesperosuchus* fed upon. A small plant stem was also found.

The discovery of *Hesperosuchus* and of some of the fossils associated with it indicates that our knowledge of the Chinle fauna is far from complete. Much of what we know to date about the Chinle assemblage is based on rather large vertebrates. Thus the tetrapods in the Chinle fauna so far known are predominantly large phytosaurs and stereospondyl amphibians, large, armored pseudosuchians, and the large dicynodont *Placerias*. Even the dinosaur *Coelophysis*, though a small and primitive theropod, is a reptile 6 or 8 feet or more in length. The protorosaur *Trilophosaurus*, from the Dockum of Texas, is a long, lizard-like reptile some 6 or 7 feet in length. Consequently *Hesperosuchus* is the smallest of the known Chinle reptiles. There certainly must have been other reptiles in the Chinle fauna smaller than the pseudosuchian here described. Perhaps some of them may be found as a result of future exploration, but until they are we can feel reasonably sure that the picture we have of the Chinle fauna is a distorted one.

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