THE ANCESTRAL CROCODILIAN
PROTOSUCHUS

EDWIN HARRIS COLBERT AND
CHARLES CRAIG MOOK

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INTRODUCTION

PROTOSUCHUS RICHARDSONI (BROWN) was described by Barnum Brown in 1933 upon the basis of materials that he discovered and collected in 1931. In the original description the name *Archaeosuchus richardsoni* was applied to the fossils under consideration, but since this generic name was preoccupied by *Archaeosuchus* Broom, 1905, it was replaced by Brown in 1934 by a new generic name. In his second contribution Brown established the family Protosuchidae, based upon the genus *Protosuchus*.

Since the appearance of the original description and the subsequent correction of the generic name little has been published about *Protosuchus*. A detailed description and discussion of *Protosuchus* is necessary for students of reptilian evolution, because this genus is certainly one of the very important genera of Mesozoic reptiles, essentially representative of the stem of all crocodilian evolution.

Originally Brown had intended to publish a detailed description of *Protosuchus*, but the pressure of other duties prevented him from carrying out the work, so that we are now presenting the first comprehensive study of the genus. We wish to express the debt that not only we but the paleontological world in general owes to Dr. Brown for having located and collected the materials of *Protosuchus* that form the subject of the present contribution.

A great deal of credit should go to Mr. Otto Falkenbach, who prepared the specimens for study. It was through his great skill as a preparator that the delicate bones were successfully exposed and made available for study and exhibition.

The drawings that illustrate this paper were made by Mr. John LeGrand, except for figure 3, which was made by Mr. John C. Germann, and figure 13, which was made by Mr. Owen J. Poe. The restoration illustrated in plate 15 was made by Mrs. Louise Waller Germann.

CIRCUMSTANCES OF DISCOVERY

The first fossils of *Protosuchus* were found in 1930 by a Navajo Indian northeast of Cameron, Arizona, and were shown by him to Mr. Hubert Richardson, proprietor of the famous trading post at Cameron. Richardson, a friend of Brown, informed the latter of this discovery, and arrangements were made for Brown to visit the locality the next year. Accordingly, Brown went to Arizona during the early part of the summer of 1931, making Cameron the headquarters for his work. He went to the locality where the bones had been found and worked there from June 4 to June 16.

As a result of his work four specimens were collected, all within about 20 feet of one another. These were the type skeleton, to be described below, A.M.N.H. No. 3024, and three partial skeletons, catalogued as A.M.N.H. Nos. 3025, 3026, and 3027. The fossils found by the Indian have been catalogued as A.M.N.H. No. 3028.

The specimens collected by Brown were sent to the Museum, and work was immediately commenced upon them by Falkenbach. At first the nature and relationships of the specimens were not clear, but as preparation proceeded it became increasingly apparent that these fossils were representative of an ancestral crocodilian. Their importance was thereby established, and Falkenbach continued his preparation of the materials with great skill and dispatch.

In the summer of 1934 Brown again visited the locality and collected two additional partial skeletons, the specimens that have been catalogued as A.M.N.H. Nos. 3056 and 3057.

In the meantime Mr. R. T. Bird of the American Museum of Natural History Paleontological Laboratory visited the locality in 1933, and again in 1938. Dr. S. P. Welles, in charge of a University of California field party, went to the locality in 1941, at which time he collected the partial skeleton described below, U.C.M.P. No. 36717.[1] Dr. Welles very kindly made arrangements for this specimen to be lent to us, and to him and the university we owe our sincere thanks.

Finally, one of us (Colbert) in company with Welles visited the locality in 1949, for the purpose of making stratigraphic ob-

[1] U.C.M.P., University of California Museum of Paleontology.
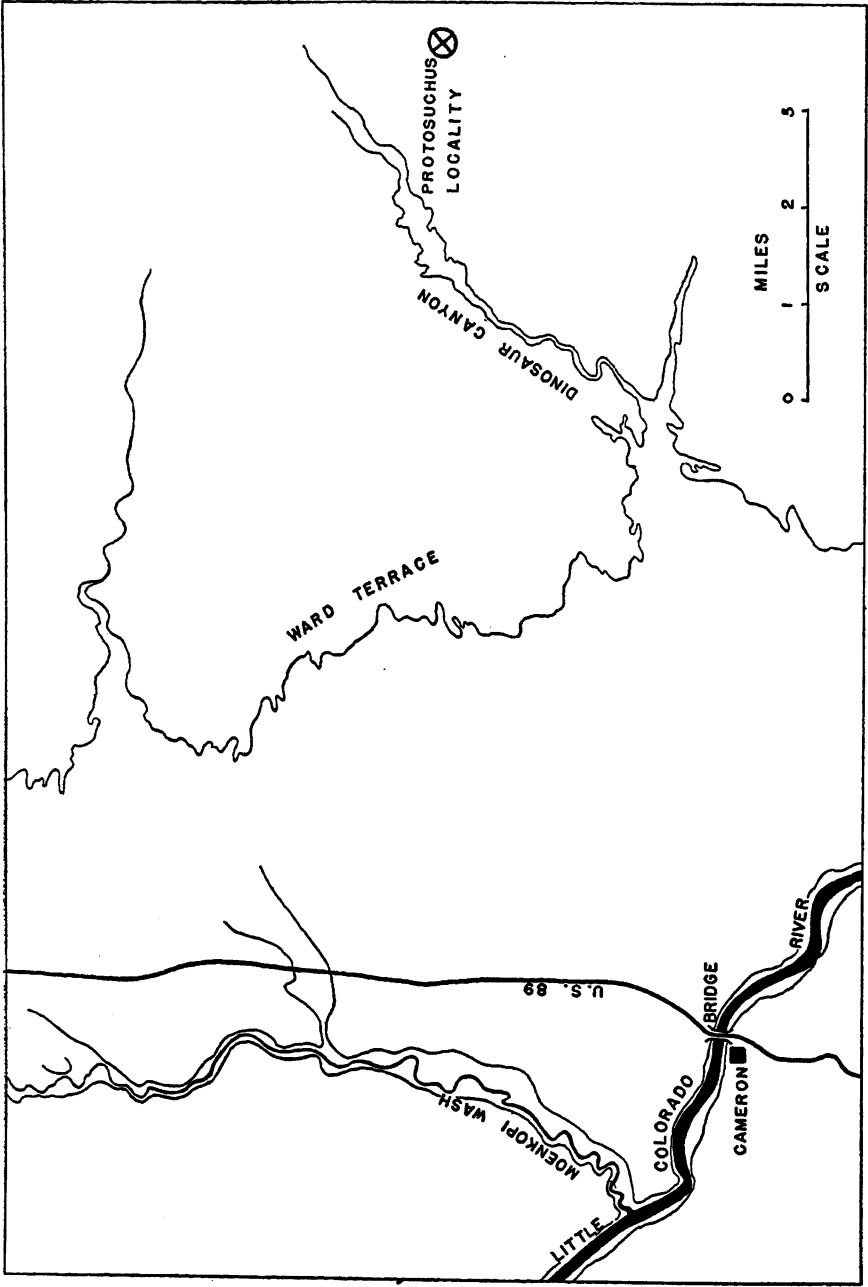
FIG. 1. Map of the region north and east of Cameron, Arizona, showing the locality at which the known materials of *Protosuchus richardsoni* were collected and the edge of Ward Terrace.

servations. The photographs of the locality published in this paper were made on the last trip.

It is to be hoped that additional materials of *Protosuchus* can be obtained in the future from the type locality. This place is not, however, easy to reach, and further collecting at the spot will require careful planning and considerable perseverance. Yet there is every reason to believe that future work in this region, if properly conducted and sufficiently protracted, will yield more fossils of *Protosuchus*, which are sorely needed. The present study, while based on fairly adequate specimens, is of necessity rather incomplete in some respects. None of our material is sufficient to give us, for instance, proper information as to the palate, and this is most important. Moreover, additional knowledge is desirable as to the front of the skull and jaws, the relationships of skull bones, and the dentition, while more data on certain parts of the postcranial skeleton would be most helpful.

STRATIGRAPHIC POSITION OF *Protosuchus*

The known materials of *Protosuchus* were found at a single locality, and most of these materials were recovered from a very circumscribed area. The locality is approximately 11 miles east by north from Cameron, Arizona, near the base of some prominent cliffs that rise from the plateau surface, known in this region as the Ward Terrace. A few miles to the north of the *Protosuchus* locality the Ward Terrace disappears, so that the entire stratigraphic sequence forms a single high cliff, constituting the southern limb of the great Triassic-Jurassic escarpment running north and west through northern Arizona and southern Utah. From the vicinity of The Gap to the head of Marble Canyon the escarpment is known as the Echo Cliffs, and beyond, on the western side of Marble Canyon and around the Paria Plateau into Utah, as the Vermilion Cliffs.

In the vicinity of Cameron there are about 800 feet of definite Chinle sediments between the heavy Shinarump sandstone at the base of the sequence and the surface of the Ward Terrace at the top of the sequence. These sediments are of various colors, purplish and gray and red, and they consist of alternating sandstones and clays. Consequently they make an extensive area of badlands to the north of Cameron, these badlands grading into the escarpment that runs up to the level of the Ward Terrace. Most of the Chinle vertebrates from this region have been found near the bottom of the sequence, in the lower 100 feet of sediments above the Shinarump.

The Ward Terrace is held up by three thin limestone layers, which in this desert region are resistant to erosion so that they form a very extensive, flat area capping the Chinle. From this flat surface there arise the orange red cliffs, from which the known materials of *Protosuchus* have been recovered. These cliffs are about 200 feet in thickness, and because of their brilliant color they have been described as "orange red" in some of the recent literature. Actually, by comparison with the Rock Color Chart distributed by the National Research Council, the color of this sandstone is seen to be a "moderate reddish brown," the hue, chroma, and lightness being 10 R 4/6.

In the bright desert sunshine, however, the terms of the Rock Color Chart seem all too moderate to express the impression of brilliance that one gets when viewing these cliffs. They are strikingly colored and highly cross-bedded and massive, and because of the physical features of the sandstone the cliffs weather into irregular surfaces and fantastic shapes. Commonly in front of the cliffs there are erosion remnants in the form of tall pillars, stacks, and pedestals. Under the microscope the sandstone forming these cliffs is seen to consist of well-rounded grains of quartz sand of rather uniform size.

The use of the name "orange red sandstone" for the sediments at the *Protosuchus* locality is not in accordance with standard American stratigraphic usage, and for this reason the above name, even though admittedly tentative, should be abandoned as soon as possible. As mentioned above, it has already found its way into the literature. In order to have a convenient name for the sandstone in which the *Protosuchus* materials were collected and to avoid any further usage of the term "orange red sandstone" it is hereby proposed that this stratigraphic unit be named the Dinosaur Canyon sandstone. The type locality is Dinosaur Canyon, which joins the valley of the Little Colorado River
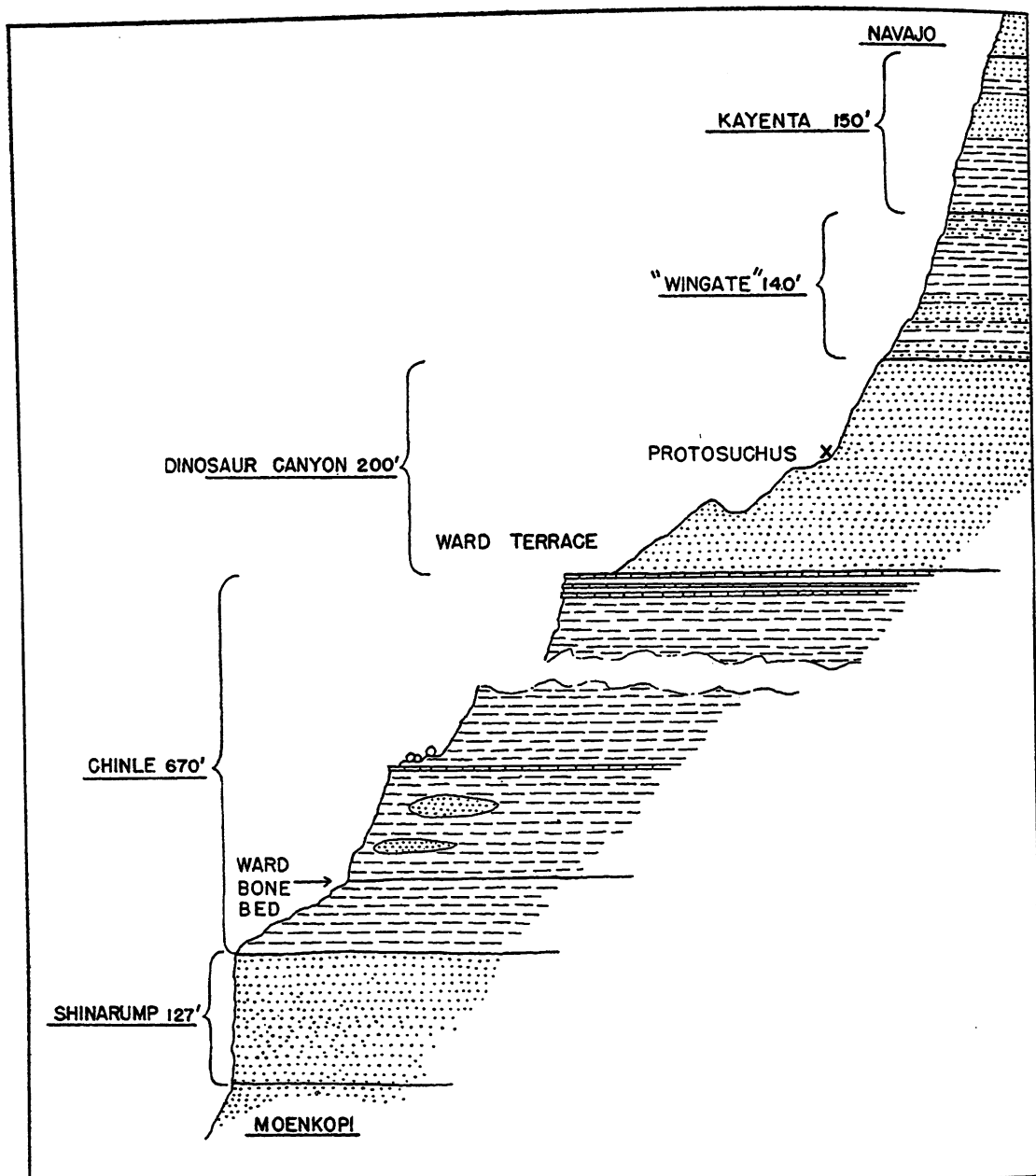
FIG. 2. Composite section of the Triassic and Jurassic sediments northeast of Cameron, Arizona. Measurements of the Shinarump and Chinle formations were made by S. P. Welles; those of the overlying formations, by Edwin H. Colbert.

to the east of Cameron, Arizona. From its entrance into the valley of the Little Colorado River, Dinosaur Canyon runs in a north-westerly direction. The *Protosuchus* locality is about 1 mile to the east of the canyon, some 5 or 6 miles up the canyon from the point of

its opening into the Little Colorado valley. The physical characteristics and the color of the Dinosaur Canyon sandstone are described in the preceding paragraphs.

The Dinosaur Canyon sandstone is rather extensively exposed to the north of the can-

yon itself. It forms striking badlands along the road from United States Highway 89 to Tuba City, especially in the eroded area where the road crosses Moenkopi Wash. It appears in the Echo Cliffs, which trend northward from the vicinity of Moa Ave to the head of Marble Canyon. For instance, these sediments can be identified at The Gap, Arizona. How much farther the Dinosaur Canyon sandstone is exposed it is difficult to say, but it is quite possible that these sediments run on into southern Utah.

Whether the Dinosaur Canyon sandstone is of Upper Triassic affinities or of Lower Jurassic relationships is a difficult problem, discussed below. Suffice it to say that there are cogent reasons, as stated in another paragraph, for associating the Dinosaur Canyon sandstone either with the Chinle formation below it or the supposed Jurassic sediments above. In correspondence and conversations with the authors, both Drs. C. L. Camp and S. P. Welles of the University of California have stated their belief that the affinities of this sandstone are with the overlying sediments. Both these authorities have done a great deal of work in northern Arizona, and their opinions on this problem are to be accorded much weight. They stress particularly the gradations of the sandstone into the overlying Jurassic sediments and the sharp lithologic break between the Dinosaur Canyon sandstone and the typical Chinle below it. Also, they cite the presence of *Protosuchus* as an argument in favor of the Jurassic age of this stratigraphic unit, since they regard the crocodilians by definition as having first appeared at the beginning of the Jurassic period.

As opposed to these considerations, one of us (Colbert) has found that whereas the Dinosaur Canyon sandstone does grade into the overlying sediments at the *Protosuchus* locality and while it is lithologically separated from the Chinle, there are localities in this general region where the opposite conditions hold true. For instance, the Dinosaur Canyon sandstone can be seen to differ from the sediments above it and to grade downward into the Chinle beneath it in the vicinity of The Gap. Moreover, at some localities the sandstone looks suspiciously similar to the upper portion of the Chinle formation, called Chinle A, as described by Gregory to the north in

the vicinity of Chinle trading post.

Above the Dinosaur Canyon sandstone cliffs at the *Protosuchus* locality are more cliff faces comprising about 300 feet of variegated sandstones and clays, the lower half of which can be regarded as representing a local facies of the so-called "Wingate"[1] in this area, and

[1] The use of the term "Wingate" is now in a hopeless state of confusion, owing largely to the paper published by Baker, Dane, and Reeside in 1947. In this contribution, in which they revised the correlations of Jurassic formations of the Colorado Plateau, they stated that the Entrada formation of Utah can be equated with the type Wingate of New Mexico. Moreover, they pointed out the probable fact that the "Wingate" of Utah, extensively exposed and mapped, is not the same as the type Wingate. Consequently, since they maintained that it would be "unfortunate and confusing" to replace the term "Wingate" as used for the Utah exposures, they proposed that this term be abandoned for the type Wingate, to be replaced by the name Entrada. Therefore, according to their usage the type Wingate loses its status, whereas the "Wingate" of Utah, for which there is no type locality of that name, becomes *the* Wingate.

This proposal violates the practice of priority as it is now well established in stratigraphic usage by American geologists. True, there are no international rules of stratigraphic nomenclature, but the rule of priority has been observed by stratigraphers in North America, and it is unfortunate that these authors should have abandoned the rule merely as a matter of convenience. It is obvious that there are much more extensive exposures named and mapped as "Wingate" in Utah than there are in the vicinity of the type locality at Fort Wingate, New Mexico. Nevertheless, if we are to retain any sanity and system whatsoever in our methods of stratigraphic nomenclature, it behooves us to adhere as strictly as possible to the rule of priority in the use of stratigraphic names, no matter what considerations of convenience may arise.

The type Wingate was named by Dutton in 1885, and since then the name has been in constant usage for the Jurassic rocks as exposed continuously from Fort Wingate westward into Arizona. This is *the* Wingate, and it must remain the Wingate. Exposures obviously of the same stratigraphic expression and age are found in other parts of New Mexico as well, especially around Zuni and to the north along the Chama River. The Entrada was named by Gilluly and Reeside in 1926 from Entrada Point, in the northern part of the San Rafael Swell, Utah. If the Entrada is equivalent to the type Wingate, as it probably is, the name Wingate still holds, and the later name must be considered as a synonym or a local term. If the so-called "Wingate" of Utah is different from the type Wingate, as it probably is, then it must be given a new name.

Since no new name has as yet been proposed for these Utah exposures, which incidentally extend into the northern part of Arizona, the name "Wingate" is being used here in quotation marks. The name is so used with an understanding that the rocks above the sandstone in which *Protosuchus* was found are probably different from the type Wingate of New Mexico.

the upper half as the Kayenta. This latter phase of sedimentation shows bright orange colors that approximate to some degree the colors of the "orange red" cliffs immediately above the surface of the Ward Terrace. Finally, above the Kayenta, as here designated, are sandstones that can be considered as of Navajo age, although here in their lower phases they do not show typical Navajo sedimentation.

One might regard the stratigraphic evidence as indicating that there was a gradual transition in northern Arizona and southern Utah from the Triassic into the Jurassic period, without the definite break between these periods that is seen in most regions where rocks of the two systems are exposed in sequence. This transition from the typical Chinle into Jurassic sediments can be followed along the Echo Cliffs and the Vermilion Cliffs, as far west as Zion Canyon, Utah.

Some additional evidence on this problem was recently received from Mr. Joseph Callahan of the University of Arizona, who made extensive field studies in northern Arizona during the summer of 1950. Mr. Callahan has kindly given us permission to publish some of his remarks: "One of the most important things that was established [during the past field season] was the presence of a thin pebble conglomerate which I believe represents a time plane, and which extends at least from Lee's Ferry to Ward's Terrace. This is located usually within 25 feet of the top of the uppermost limestone bed in the Chinle formation. This rock is from 6 inches to 2 feet in thickness, and is characterized by the presence of red chert pebbles throughout, with a matrix ranging from very fine to coarse sand. If this material can be found in other sections of the Plateau country, it will be a very good horizon marker and a place to end the Chinle and begin the upper formations. Also, immediately below this, in Moenkopi Wash, a channel was found that had been eroded in the underlying Chinle formation and was filled with boulders and cobbles. Perhaps this is the erosion interval that has been sought above the Chinle, and it may help to prove that the material above is of Jurassic age.

"I note that in your stratigraphic section [fig. 2] you end the Chinle on the top of the limestones. It is my belief that it would terminate some 25 feet above this point. The location of *Protosuchus* would then be in what I described in the field as 'Kayenta type' lithology. This is a field classification that was used because the lithology is definitely not Chinle type, nor is it Wingate type, but represents in every way the Kayenta formation. From trends that were established in the 'cliff Wingate,' with its marked thinning to the south until it is nearly unrecognizable in the Moenkopi Wash area, it is my opinion that somewhere to the south and west this cliff member vanishes and the Kayenta type is present throughout the entire section. This will have to be established when more field work has been done."

The preliminary phases of Callahan's work thus seems to indicate that the Dinosaur Canyon beds are definitely separable stratigraphically from the underlying Chinle, and that they are to be correlated with at least a part of the Kayenta formation. If this conclusion eventually proves to be valid, *Protosuchus* will then be removed from close association with the Chinle fauna. Whether it should be regarded as of late Triassic or early Jurassic age will still remain an unsettled question. Most authorities are inclined at the present time to consider the Wingate-Kayenta-Navajo sequence as representing the beginnings of Jurassic sedimentation in the southwest, but in a recent paper Heaton (1950) places the Wingate and the Kayenta in the Upper Triassic, although he regards the Navajo formation as of Jurassic age.

Unfortunately, as mentioned above, the evidence of *Protosuchus* is not definitive. There is nothing in the structural anatomy of this reptile to preclude its assignment either to the later phases of Triassic history or to the earliest stages of Jurassic time. Comparisons with early crocodilians from other parts of the world lead to some interpretations that are set forth below, but the interpretations are not absolute; they can be accepted or rejected largely according to the bias of the individual student. All that can be said at this place on the basis of stratigraphic evidence is that the age of *Protosuchus* is still an open question.

Taxonomic Position of *Protosuchus*

As was mentioned above, Brown established the family Protosuchidae as based upon his new genus *Protosuchus*. Subsequently, in 1945, Romer used the name Notochampsidae to include the genera *Protosuchus*, *Notochampsa*, *Erythrochampsa*, and, questionably, *Pedeticosaurus*, the latter three genera from the Stormberg series of the South African Karroo system.

The choice of the name Notochampsidae is unfortunate, since the relationships of the genus *Notochampsa* have been questioned. This genus was originally described by Broom in 1904 upon the evidence of two specimens which he assigned to two species. One of these, *Notochampsa istedena*, the type species for the genus, was found in the Cave sandstone of the Stormberg series, while the other, *Notochampsa longipes*, was collected from the underlying Red Beds. In 1924 Haughton came to the conclusion that the crocodilian relationships of *Notochampsa istedena* are open to question and that this species may actually be a pseudosuchian. In the type specimen, which is incompletely preserved, certain skull characters such as the divided external nares seem to indicate pseudosuchian relationships. The same is to be said with regard to the development of the fore limb. On the other hand, the general form of the scapula and coracoid, the latter an elongated bone that to a large degree forms a "mirror image" of the scapula, and the elongation of the radiale and ulnare are characters that appear to relate *Notochampsa istedena* to the crocodilians. Haughton concluded that this form was intermediate between the thecodonts and the crocodilians; to the present writers it seems logical to place this reptile among the crocodilians, as was done by Broom in 1927, as a very primitive member of the order. An opposite opinion was expressed by von Huene in 1925, when he indicated that *Notochampsa* should be placed among the pseudosuchians.

Haughton was so impressed by the crocodilian characters of the other notochampsid species that he removed it from the genus and created a new genus, *Erythrochampsa*, for it. *Erythrochampsa longipes* is without much doubt a crocodilian. This was the opinion of Broom in 1927, although previously, in 1925,

von Huene had placed this genus, together with *Notochampsa*, in the Pseudosuchia. Unfortunately the type lacks a skull, and those portions of the skeleton present are fragmentary. However, it is characterized by a very crocodilian-like pelvis, with the pubis excluded from the acetabular border. Moreover, the hind limb in this form shows crocodilian features.

Pedeticosaurus leviseuri, from the Cave Sandstones, is less definitely crocodilian than either *Notochampsa* or *Erythrochampsa*. It is hereby suggested that this genus should be placed among the pseudosuchians.

Thus the primitive crocodilians of Upper Triassic or Lower Jurassic age are *Protosuchus* of North America and *Notochampsa* and *Erythrochampsa* of South Africa. Whether or not these three genera should be placed in a single family is a question open to argument. This might be done, or it might be maintained that the two South African forms should be relegated to a family distinct from that in which the North American genus is contained. But if it is assumed that they do belong to a single family, and this is the classification that is used in the present paper, there still is no compelling reason why the earlier name, Notochampsidae, must be retained in preference to the name Protosuchidae.

The International Rules of Zoological Nomenclature do not apply to categories higher than the genus, so it is not necessary to follow the law of priority in the application of family names. However, in recent years authors have unofficially followed certain procedures with regard to the higher categories, and there has been an attempt on the part of many workers to develop some degree of uniformity of practice in the use of the names above generic rank. In his recent classification of mammals, Simpson (1945) drew up a list of principles (not a code) that he has followed in his treatment of the higher categories among the mammals. In this list of principles he recognizes the fact that when two or more names of correct derivation are available for a single group in one of the higher categories, the name with priority of publication should be used "unless there is strong contrary indication." He then goes on to show that disregard for the principle of

priority is justified when, among other things, the prior name is "based on a genus of doubtful pertinence to the group in question and a later name is based on a genus surely belonging to that group."

This is just the situation with regard to the present example. *Notochampsa* probably is a crocodilian; *Protosuchus*, on the other hand, is without doubt a crocodilian. For this reason the family name Protosuchidae is here regarded as the preferable one for the ancestral crocodilians of Upper Triassic or Lower Jurassic age. The classification of these early crocodilians can then be presented in the following manner:

Protosuchia
  Protosuchidae
    Protosuchus
    Notochampsa
    Erythrochampsa

SYSTEMATIC DATA, DIAGNOSIS, AND MATERIALS

PROTOSUCHIA

PROTOSUCHIDAE

PROTOSUCHUS Brown

Protosuchus Brown, 1934, Science, new ser., vol. 79, p. 80.

TYPE: *Protosuchus richardsoni* (Brown).

Protosuchus richardsoni[1] (Brown)

Archaeosuchus richardsoni Brown, 1933, Amer. Mus. Novitates, no. 638, p. 1.

Protosuchus richardsoni, Brown, 1934, Science, new ser., vol. 79, p. 80.

TYPE: A.M.N.H. No. 3024. An articulated skeleton, nearly complete.

HORIZON: Dinosaur Canyon sandstone, about 108 feet below the top of this unit at the type locality. Upper Triassic or Lower Jurassic.

LOCALITY: In the original description the locality is given as "fifteen miles northeast of Cameron, Arizona." The locality is more accurately designated as being 11 miles (by airline) east by north of Cameron. This locality is indicated on the accompanying map (fig. 1).

DIAGNOSIS: A small crocodilian, less than 1 meter in total length. The skull is short and the skull roof very flat. The upper temporal fenestrae are small, the orbits are placed laterally, and there are no preorbital fenestrae. There are probably four premaxillary teeth and about 13 maxillary teeth, while there are probably about 17 teeth in the dentary. The teeth are thecodont. There is a long diastema between the last premaxillary tooth, which is enlarged, and the first maxillary tooth. There are 24 presacral vertebrae, two sacrals, and about 35 caudal vertebrae. The vertebral centra are somewhat elongated, and the spines are strong but not very high. The pectoral girdle is pre-crocodilian in form, with the coracoid elongated and pierced by a coracoid foramen. The humerus is slender and slightly longer than the radius and ulna. The radiale and ulnare bones are fully as elongated as in modern crocodilians, and there are five digits in the manus. The pelvis is distinguished by the crocodilian-like,

[1] Named in honor of Mr. Hubert Richardson of Cameron, Arizona.

elongate pubis, the distal end of which participates in the acetabular foramen. The iliac crest is extended anteriorly to form a strong process above the anterior border of the acetabulum. The ischia are large and joined ventrally by a long symphysis. The femur is long, somewhat longer than the radius and ulna, and slightly curved, as in later crocodilians. The calcaneum and astragalus are large and well-developed bones, the latter being characterized by a very strong and expanded tuber. There are four functional digits in the pes, the fifth digit being reduced to the vestigial "hook" of the fifth metatarsal, so characteristic of archosaurians. There is a median row of large, rectangular, dorsal armor plates on either side of the midline, while the ventral surfaces of the belly and tail are protected by a full armor of small rectangular plates.

MATERIALS UNDER CONSIDERATION: A.M.N.H. No. 3024, the type, listed above.

A.M.N.H. No. 3025, left coracoid and portion of a right coracoid, left humerus, left scapula, part of a tibia (?), part of a left dentary (?), vertebrae, scutes, and miscellaneous fragments.

A.M.N.H. No. 3026, right radius and ulna and fragments of manus, ribs, scutes, distal portion of tibia, astragalus and calcaneum, fibula (?), various fragments not identified.

A.M.N.H. No. 3027, portion of the anterior region of a skull, crushed.

A.M.N.H. No. 3028, five fragments of limb bones (femora and tibiae). These were the first specimens of *Protosuchus* to be discovered.

A.M.N.H. No. 3056, part of pelvis, including both pubes and portions of ischia, proximal portion of left femur and complete right femur, a series of seven or more posterior presacral vertebrae.

A.M.N.H. No. 3057, a few associated skeletal bones.

U.C.M.P. No. 36717, a partial skeleton, including a left manus, left radius, left femur, tibia, fibula, and pes, a series of 14 or more presacral vertebrae with ribs, and scutes.

All these specimens came from the same locality and the same stratigraphic level as the type specimen.

DESCRIPTION AND DISCUSSION

SIZE

PROTOSUCHUS RICHARDSONI is a rather small reptile, and it certainly is small for a member of the Crocodilia. The total length of the type specimen is something under 3 feet, actually in the neighborhood of 800 millimeters. Of course this specimen may not represent a fully adult animal, but it is probably close to full size, as judged from the supplementary materials. None of the referred specimens is as large as the type, and some of them are noticeably smaller than the type. Consequently it can be inferred that in life *Protosuchus* was probably never much more than 3 feet, or 1 meter, in length.

SKULL

The skull, of which both the dorsal aspect and the palate are visible, is almost complete except for the anterior portion of the snout. The snout as preserved is relatively short, and one cannot be certain as to its original length. It was certainly somewhat longer than it is at present, because the preserved portion shows no indication of the border of the external narial aperture or apparently even of the posterior processes of the premaxillaries. The crushed nature of the specimen in this region makes determination of the latter point rather uncertain, but the expectation is that the snout was of moderate length. The snout is constricted, being considerably narrower at its base than the posterior portion of the skull. Moreover this constriction, which takes place just anterior to the orbits, is rather sudden. The cranial portion of the skull top resembles in shape the cranial table of later crocodilians, but probably it was less elevated above the level of the snout than is the case in the more advanced members of the order.

At first glance the skull of *Protosuchus* appears to be rather short in comparison with the total length of the body. Actually, the proportions of head to body in this primitive crocodilian are rather similar to what they are in the modern alligator, as can be seen by the following comparison:

	Proto-suchus	Alli-gator
Length of skull × 100 / Length of presacral vertebrae	46	47

The orbits are rather large, and they are directed outward and forward rather than predominantly upward as is the case in later crocodilians. The supratemporal fenestrae are much smaller than the orbits, irregular in shape, much nearer to each other than they are to the external border of the cranial table, and somewhat nearer than they are to the posterior border of the cranial table. The borders of these fenestrae are well preserved, and the lateral borders converge slightly forward. The lateral temporal fenestrae were very large, as large as or larger than the orbit. In the development of a small supratemporal fenestra and a large lateral temporal fenestra, *Protosuchus* shows the inheritance of what is essentially the primitive thecodont condition. In the Mesosuchia both temporal fenestrae became large, while in the Eusuchia there has been a reduction of the temporal openings, that of the upper one being a secondary reduction.

Unfortunately the preservation of the specimen is such that sutures on the skull cannot be determined very extensively. The one known skull of *Protosuchus*, the type specimen, while fairly complete and relatively uncrushed, is broken by innumerable cracks that traverse the surface of the bones in all directions. A few undoubted sutures can be made out, but in many instances it is difficult if not impossible to distinguish sutures from cracks. The accompanying drawings of the skull (figs. 5, 6) represent syntheses of all available evidence, including the collateral evidence from other genera. It should be recognized that some of the skull relationships shown on these drawings are only approximate and subject to change when more complete knowledge becomes available. This will explain the lack of any definite statements in the text with regard to certain bones of the skull and jaw.

In the first place it might be said that the surficial pitting of the skull bones is shallow and irregular. The frontal does not enter to form a border of the supratemporal fenestrae, while the parietal is distinctly in front of the fenestrae, giving this bone a contact with the postorbitals. The posterior external corner of the superior cranial surface extends slightly outward and considerably backward, giving the posterior border of the skull a
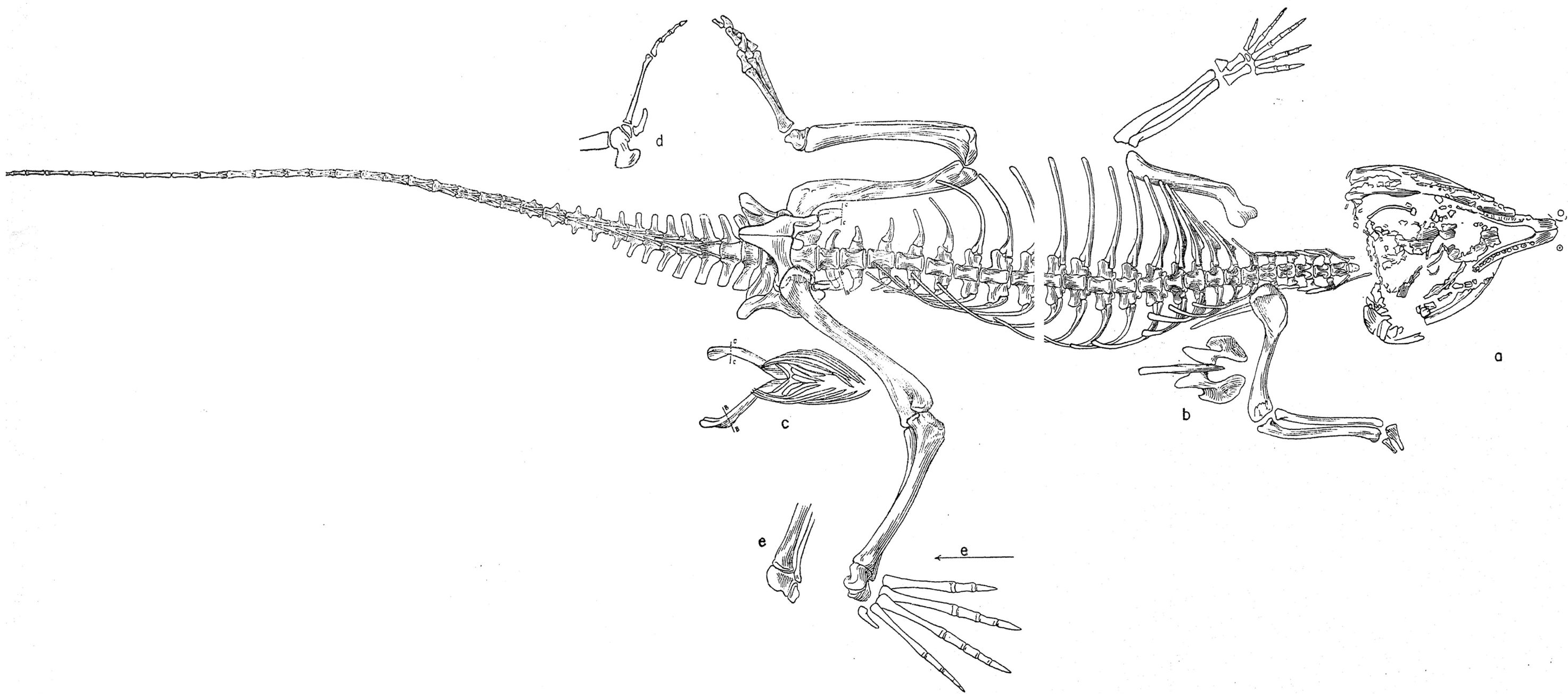
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Fig. 3. *Protosuchus richardsoni* (Brown). A.M.N.H. No. 3024, type. A. Ventral view of skeleton with dermal armor omitted. Right manus drawn as restored from U.C.M.P. No. 36717. Left pes also restored. B. Coracoids and sternum, shown to one side to reveal the vertebrae above them. C. Pubes and abdominal ribs, shifted to one side. D. External lateral view of right pes, behind the foot as it is drawn in place, to illustrate form of calcaneum and fifth metatarsal and the number of phalanges in fourth digit. E. Anterior view of left tarsus, with distal portion of tibia and fibula. One-half natural size. Drawing by John C. Germann.
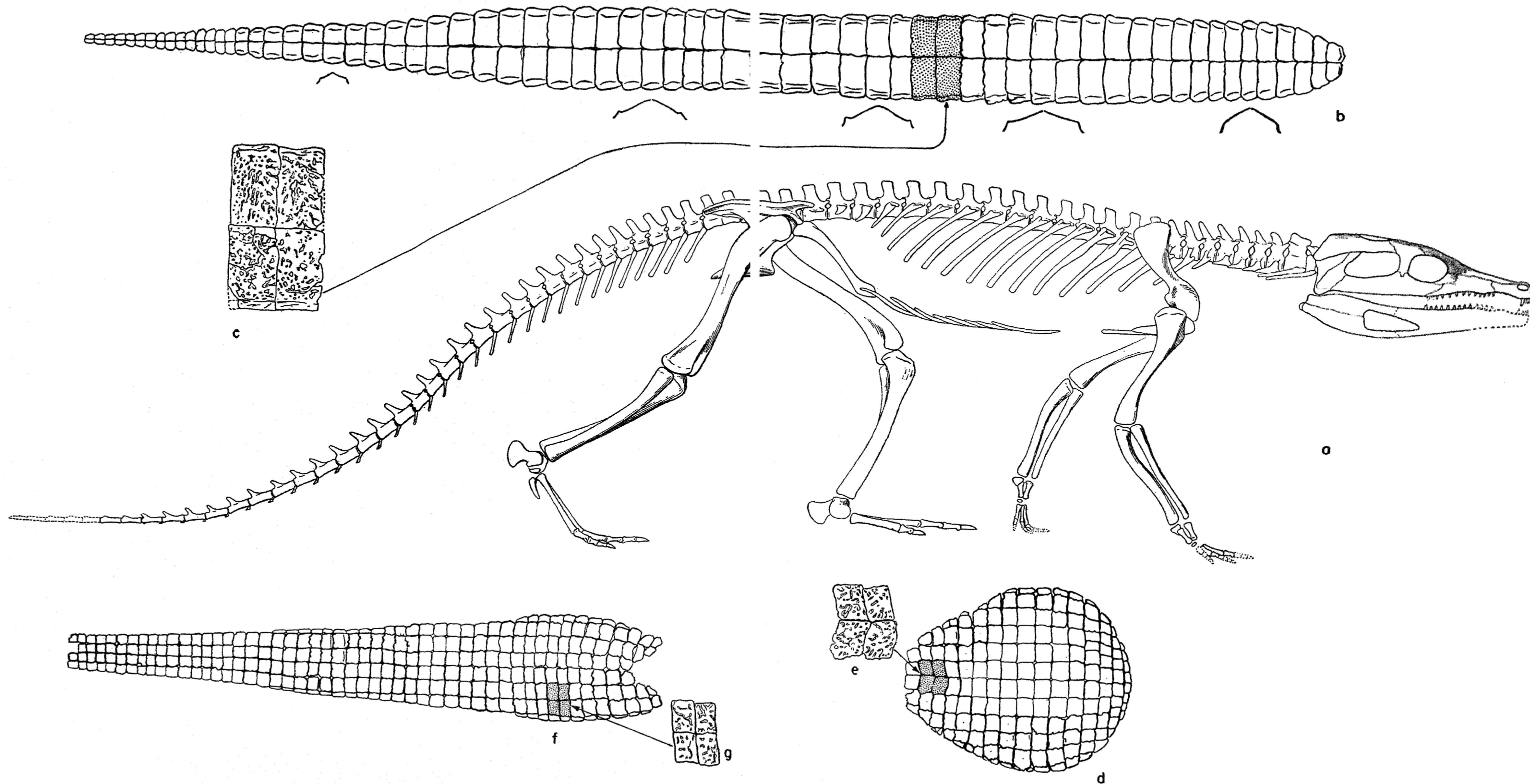
FIG. 4. *Protosuchus richardsoni* (Brown). A.M.N.H. No. 3024, type. A. Lateral view of skeleton, restored in normal walking pose; one-half natural size. B. Dorsal scutes, with cross sections showing position of dorsal surfaces of scutes at five points in series; dorsal view, one-half natural size. C. Enlarged view in detail of four scutes indicated by shading; dorsal view, natural size. D. Abdominal scutes; ventral view, one-half natural size. E. Enlarged view in detail of four scutes indicated by shading; ventral view, natural size. F. Scutes of ventral and lateral surfaces of tail; ventral view, one-half natural size. G. Enlarged view in detail of four scutes indicated by shading; ventral view, natural size.

definitely concave shape when seen from above.

Because of this expansion in the posterolateral portion of the skull roof the squamosal is extensively developed dorsally, as it is in the recent crocodilians. Indeed, the entire cranial table in shape and development is characteristically crocodilian, resembling very much the same area as seen in

sidered as a departure from the general crocodilian heritage.

The postorbital bar in *Protosuchus* is at the surface as would be expected in a primitive form, and not inwardly displaced as in the eusuchians. On the other hand, there is no evidence of a preorbital fenestra, so that *Protosuchus* was already completely crocodilian with respect to this character and
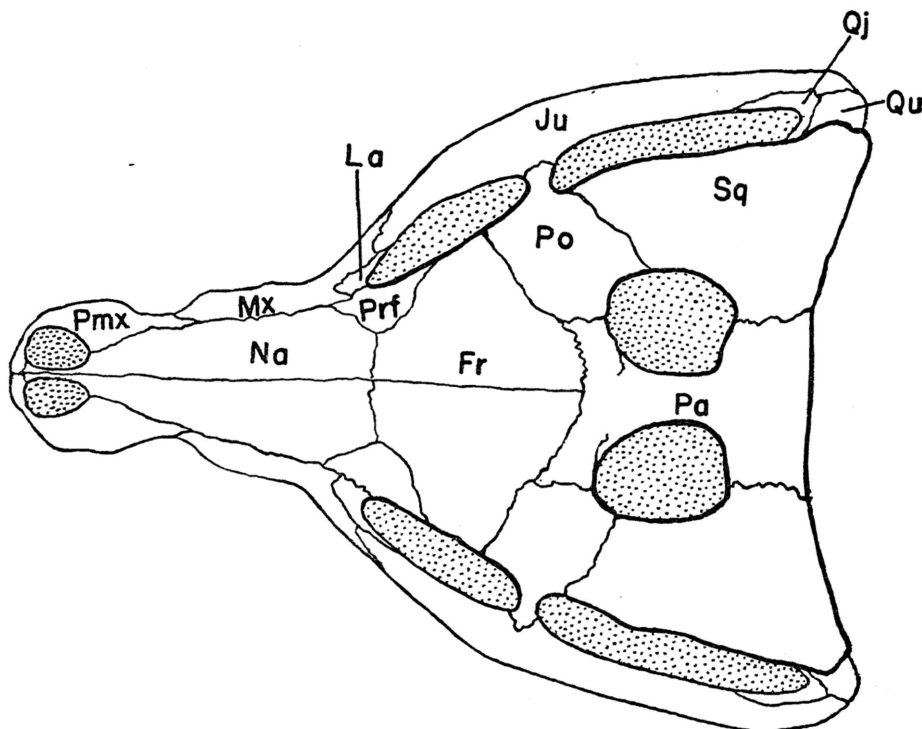

FIG. 5. *Protosuchus richardsoni* (Brown). A.M.N.H. No. 3024, type. Dorsal view of skull as restored, natural size. *Abbreviations*: Fr, frontal; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Pa, parietal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Qj, quadratojugal; Qu, quadrate; Sq, squamosal.

some Mesosuchia, in the Sebecosuchia as exemplified by *Sebecus*, and in the Eusuchia. It should be pointed out here that in certain mesosuchians such as the teleosaurs the enlargement of the supratemporal fenestra brings about a restriction of the dorsal surface of the squamosal in a way that is not typical of the crocodilians as a group. Perhaps in light of the development of the cranial table in *Protosuchus*, the enlarged supratemporal fenestra and the restricted squamosal of these mesosuchians should be con-

quite specialized over its thecodont ancestors.

The palate is crushed into the nasal passage and badly broken, so that it is difficult to interpret, but it seems probable that the palate extended well back towards the base of the snout. There is a rather large area of bone between the maxillary teeth, and this must be part of the two maxillaries, meeting on the midline of the palate. A median suture can be seen. This being the case, it seems probable that *Protosuchus* had a fairly well-developed secondary palate, very likely

similar to that in the Mesosuchia. Palatine fenestrae apparently were present, although their outlines are obscure. It appears that some of the anterior borders of the left opening can be seen, consisting of naturally rounded bone edges and not edges of crushed bone. The bones involved appear to be the maxilla anteriorly and the ectopterygoid postero-externally. The palatines appear to have been very short in the anteroposterior direction. The pterygoid region is too poorly preserved to permit description.

It was mentioned above that the snout as preserved is comparatively short, though

section, apparently subconic and acute. All the teeth have separate alveoli. Posterior to the eleventh alveolus the borders of the maxilla are not preserved.

Only a portion of the right mandibular ramus is preserved in the known material of *Protosuchus*, and this is attached to the skull of the type skeleton, A.M.N.H. No. 3024. There is little that can be said about this jaw. It shows the presence of a well-developed mandibular fenestra. At the back it appears that the lower jaw in *Protosuchus* lacked a marked prolongation of the angular and articular bones, as is so characteristic of the
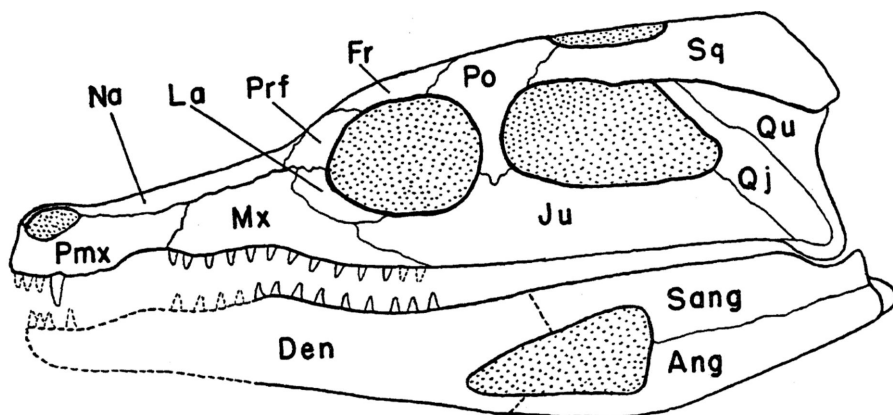

FIG. 6. *Protosuchus richardsoni* (Brown). A.M.N.H. No. 3024, type. Lateral view of skull as restored, natural size. *Abbreviations*: Ang, angular; Den, dentary; Fr, frontal; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Qj, quadratojugal; Qu, quadrate; Sang, surangular; Sq, squamosal.

some of its anterior portion is missing. There is reason to think that not much of the snout is absent in the type specimen of *Protosuchus*, this argument being based upon the presence of a large tooth at the front of the snout, as it is preserved. This tooth can be interpreted as the fourth tooth of the upper series (which is commonly enlarged in the crocodilians) and therefore of premaxillary relationships. Behind this tooth there is a remarkable edentulous section of the snout about 15 mm. long comparable to the notch in later crocodiles. Of the two tooth-bearing branches of the maxillary bones, the left has 11 tooth roots preserved, while the right is obscured by the ramus of the lower jaw. The teeth are small, circular or subcircular in horizontal

mesosuchians and eusuchians. Rather, the lower jaw is sharply truncated behind the glenoid, which means that the articular and angular bones were limited in their development, a condition similar to that seen in various thecodonts. This implies a relatively weak depressor mandibulae muscle.

VERTEBRAE

On the dorsal surface the vertebrae are hidden for the most part by the scutes, and even on the ventral surface some of the vertebrae are not visible. This is especially true of the caudal vertebrae. It has been possible, however, to remove three of the dorsal scutes in the middle portion of the presacral region, so that the upper portions of at least

some of the presacral vertebrae can be seen.

There appear to be 24 presacral vertebrae. In the cervical region fragments of the atlas and axis can be seen, while posterior to the axis the vertebrae are well preserved. The anterior cervical vertebrae are strongly keeled, the keels being set off sharply from the main bodies of the centra. The keels are slender in their mid-portions, but they are expanded at their posterior ends and even more so anteriorly, where the expansions assist in supporting the rib-bearing parapophyses. The keels become less strongly developed on the more posterior cervicals, so that on the ninth presacral vertebra the keel has completely disappeared. The cervical ribs are large and well developed.

The centra of the dorsal vertebrae immediately behind the cervical region are short anteroposteriorly, but they increase in length more or less regularly to the eleventh presacral vertebra, while from this point back to the sacrum they are of about equal length. The vertebral centra are fairly constant as to width through the middle region of the back, but towards the sacrum they become increasingly broad, so that the centrum of the last presacral vertebra is as broad as it is long. In the anterior portion of the vertebral series, the anterior faces of the centra are broader than the posterior ones, but towards the sacrum this relationship is reversed so that the posterior articulations are noticeably the broader. None of the centra have keels, much less hypapophyses in the anterior dorsal region, as is the case in many later crocodilians.

Protosuchus shows a resemblance to the later crocodilians in that the transverse processes are very wide throughout a great part of the dorsal region, and they bear the two articulations for the double-headed ribs. On the ninth, tenth, and eleventh presacral vertebrae the parapophyses are placed on the centra, but they show a progressive migration from the centrum up towards the transverse process, so that in the last of these three vertebrae the parapophysis is virtually contiguous with the transverse process. From this point back, the parapophysis becomes essentially an integral part of the transverse process, though even as far back as the fifteenth presacral vertebra it is still

recognizable. In the last few transverse processes of the dorsal series the parapophysis has completely lost its identity. Here is a close approach, as far back as early Mesozoic times, to the specialization of the transverse processes so characteristic of modern crocodilians. However, *Protosuchus* is more primitive than the modern forms in the expression of this character; the transverse processes are never so widely expanded as in modern crocodilians, and the parapophysial articulation is never so reduced.

The spines of the dorsal vertebrae are comparatively tall and compressed, and in proportions and structure appear to be very similar to the comparable spines in the modern crocodilians.

The two sacral vertebrae have the largest centra in the vertebral series, although the centrum of the last presacral approaches these two vertebrae in size. In the first sacral vertebra the anterior articulating face of the centrum is considerably larger than the posterior one, while in the second vertebra the reverse condition holds. This arrangement allows for a strong articulation between the sacrum and the presacral series in front and the caudal series behind. Since the sacral vertebrae are connected with the ilium by very broad transverse processes, the articution between the two vertebrae is of secondary importance.

The sacrum in *Protosuchus* shows a close approach to the characteristic crocodilian condition, in which the transverse processes of the posterior sacral are very greatly enlarged, to afford the principal binding of the ilium to the sacrum. It should be remarked, however, that there is a considerable enlargement of the transverse processes of the first sacral vertebra too, so that together the two sacrals are very strongly joined to the ilium throughout most of its length.

There are about 34 caudal vertebrae preserved, the total length of which is somewhat greater than the total length of the presacral series. The caudal series, from the fifteenth to the thirty-fifth vertebrae inclusive, has been broken away from the rest of the vertebral column and rotated, so that the posterior vertebrae (such as are visible) appear in side view on the ventral aspect of the skeleton.

The first four caudal vertebrae are visible from below, while a few posterior caudals are partially visible from the side, but except for these vertebrae the caudals are completely hidden by the encasing scutes of the tail. As might be expected, the anterior caudals have broad and short centra and long transverse processes, while the more posterior caudals have narrow, elongated centra with reduced transverse processes. In the posterior portion of the tail the caudals lack transverse processes, but are characterized by prominent zygapophysial buttresses. Chevrons are present throughout the caudal series, beginning with the articulation between the second and third caudal vertebrae. The anterior chevrons are quite large and robust.

RIBS

As mentioned above, the cervical ribs of *Protosuchus* are well developed. The first cervical rib, attaching to the atlas, is long and slender, and it has a single head, which is the condition seen in the modern crocodilians. The second cervical rib is also long and slender, and it has an expanded head. Whether or not it had a second articular surface as is the case in the recent crocodilians cannot be determined from the type specimen, but it is very probable that such was the case. The remaining cervical ribs are similar to those of modern crocodilians, each consisting of a widely separated head and tubercle, with a short but strong shaft.

The cervical ribs grade into those of the dorsal region, and these latter are long and slender. As in the modern crocodilians the thoracic ribs articulate completely upon the transverse processes of the vertebrae, with the exception of the most anterior ones in which the head of the rib articulates with a parapophysis located on the centrum. These ribs are double headed except for the most posterior ones of the series, in which there is a reduction of the rib tubercle. The slender shaft of the thoracic ribs is flanked by both anterior and posterior dorsal flanges, contrasting with the ribs of the modern crocodilians in which only anterior flanges are present.

The last four presacral vertebrae are free of ribs—again a resemblance to the modern crocodilians. To put it in another way, ribs

are present on all the vertebrae back to and including the twentieth.

In its ventral aspect the type skeleton of *Protosuchus* shows an accumulation of ventral ribs immediately in front of the pelvis. It seems probable that these are to some extent out of place, and in the normal condition would be distributed rather evenly along the ventral surface of the body.

PECTORAL GIRDLE

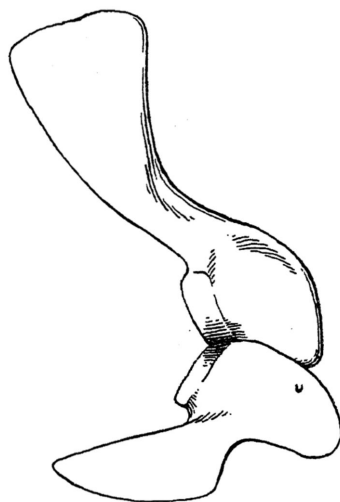The pectoral girdle of *Protosuchus* can be seen in the type specimen, while in addi-

FIG. 7. *Protosuchus richardsoni* (Brown). A.M.N.H. No. 3024, type. External lateral view of right scapula and coracoid, natural size.

tion there is a well-preserved coracoid in A.M.N.H. No. 3025. The girdle in this early crocodilian is surprisingly like that in the recent members of the order, which indicates that in the evolution of the Crocodilia there was an early and rapid specialization of the scapula and coracoid. These elements in *Protosuchus*, as in the more advanced crocodilians, are subequally developed, so that in lateral view they approximate mirror images of each other. In other words, the coracoid is enlarged, particularly by the growth of its distal portion, so that it approximates the scapula in size and shape. The effect is striking in modern crocodilians, but is less marked in *Protosuchus*, in which ancestral form the

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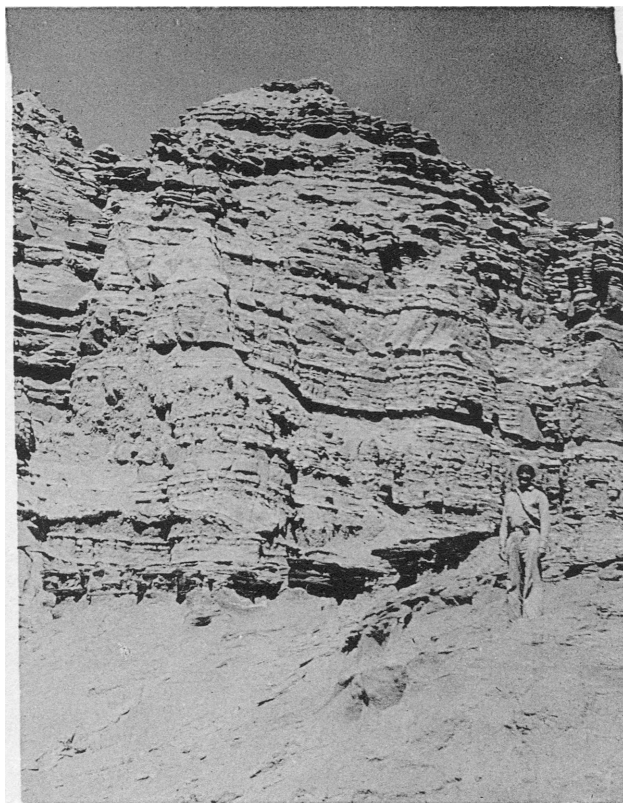
2

1. Dinosaur Canyon beds near the *Protosuchus* locality. The foreground, approx-imately the level at which *Protosuchus* was found, and the lower half of the cliff are composed of the Dinosaur Canyon beds. The upper portion of the cliff consists of Lower Jurassic sediments, commonly called "Wingate." 2. Dr. S. P. Welles of the University of California standing on the spot from which the type specimen of *Protosuchus* was collected

1

2

1. Contact of the Dinosaur Canyon sediments, above, and the Chinle formation, below, a few miles northwest of the *Protosuchus* locality. 2. The Triassic-Jurassic sequence in the vicinity of The Gap, Arizona. At the base is seen a small exposure of the Chinle, dipping beneath the Dinosaur Canyon sediments. Above the Dinosaur Canyon beds is the Lower Jurassic of this region
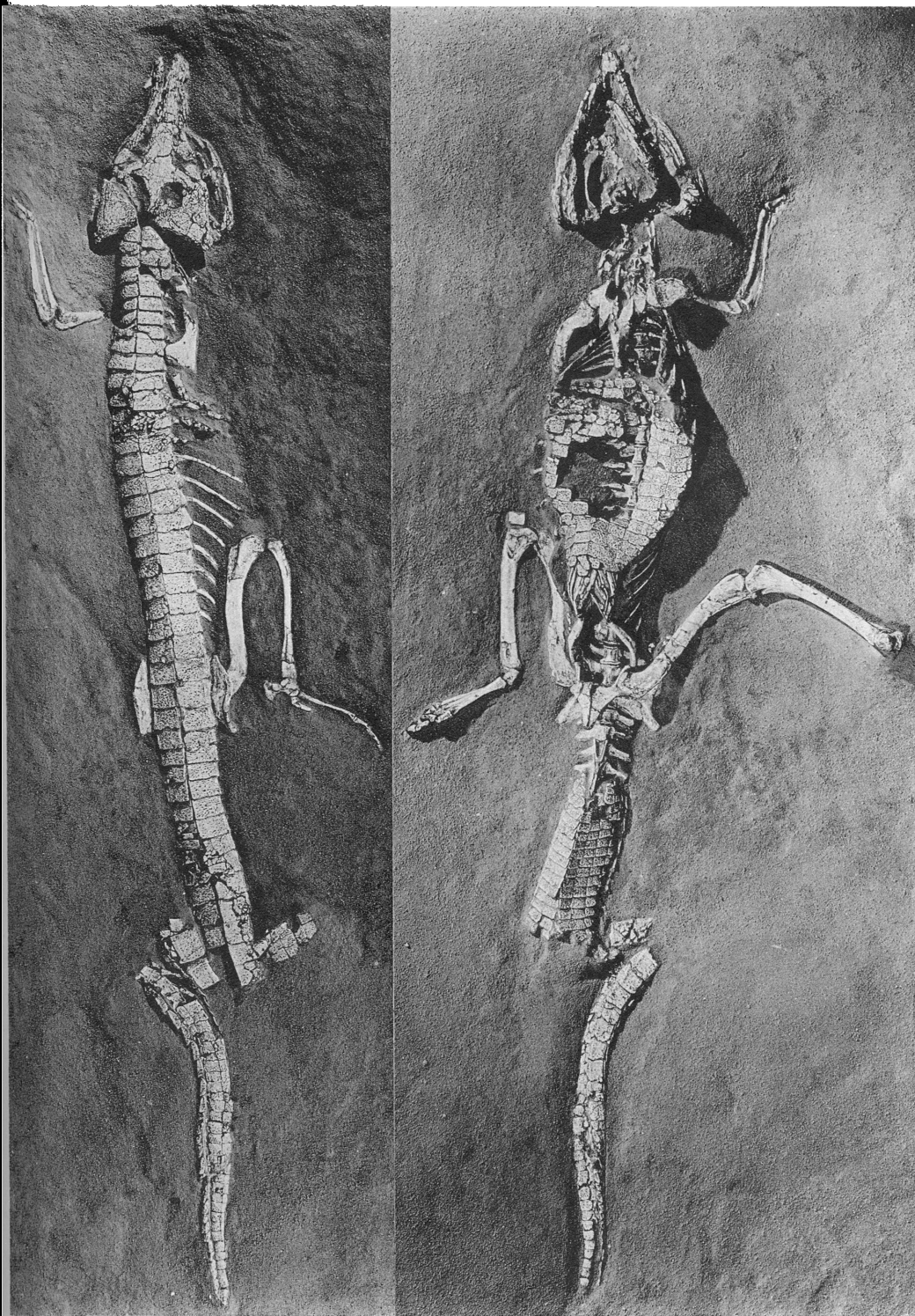
Protosuchus richardsoni (Brown). A.M.N.H. No. 3024, type. 1. Dorsal view of the skeleton as exposed in the matrix, one-fourth natural size. 2. Ventral view of the skeleton as exposed in the matrix, one-fourth natural size
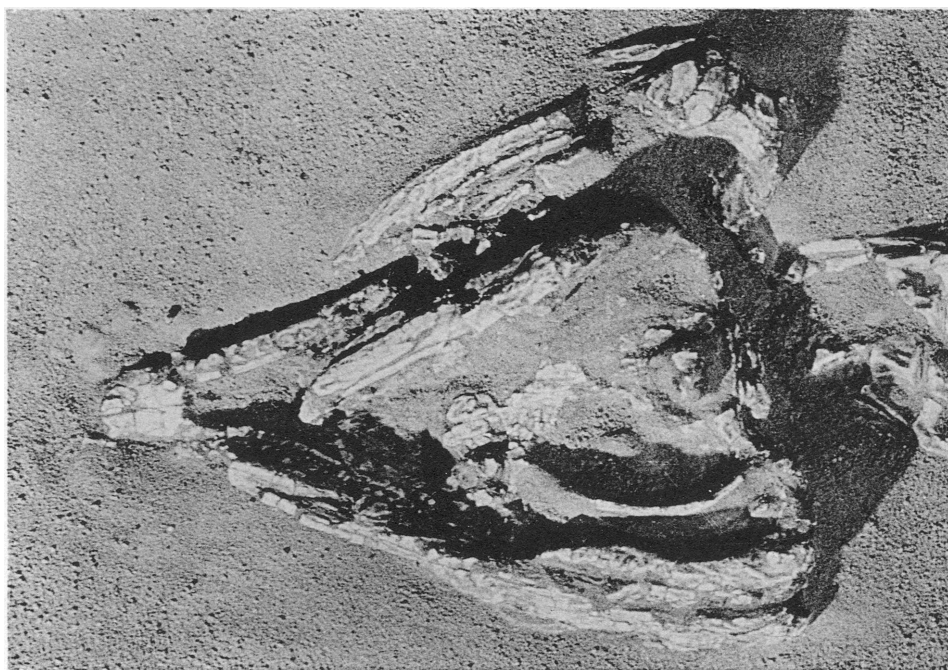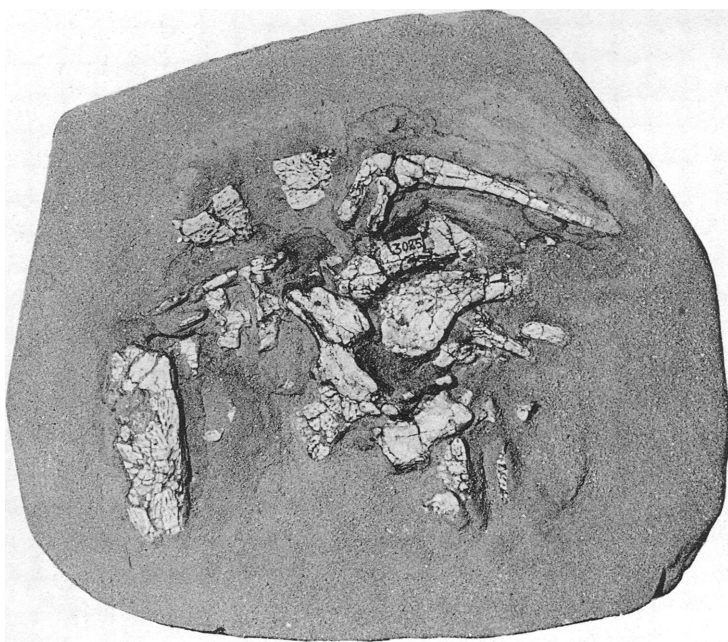
Protosuchus richardsoni (Brown). A.M.N.H. No. 3024, type. 1. Dorsal view of skull, natural size. 2. Ventral view of skull, natural size. This figure shows the fragmentary condition of the palatal region

1

2

Protosuchus richardsoni (Brown). 1. A.M.N.H. No. 3024, type. Oblique view, showing the articipation of the proximal end of the pubis in the acetabulum. This figure shows also the concentration of abdominal ribs at the distal end of the pubis. 2. A.M.N.H. No. 3025, referred specimen from the type locality, one-half natural size
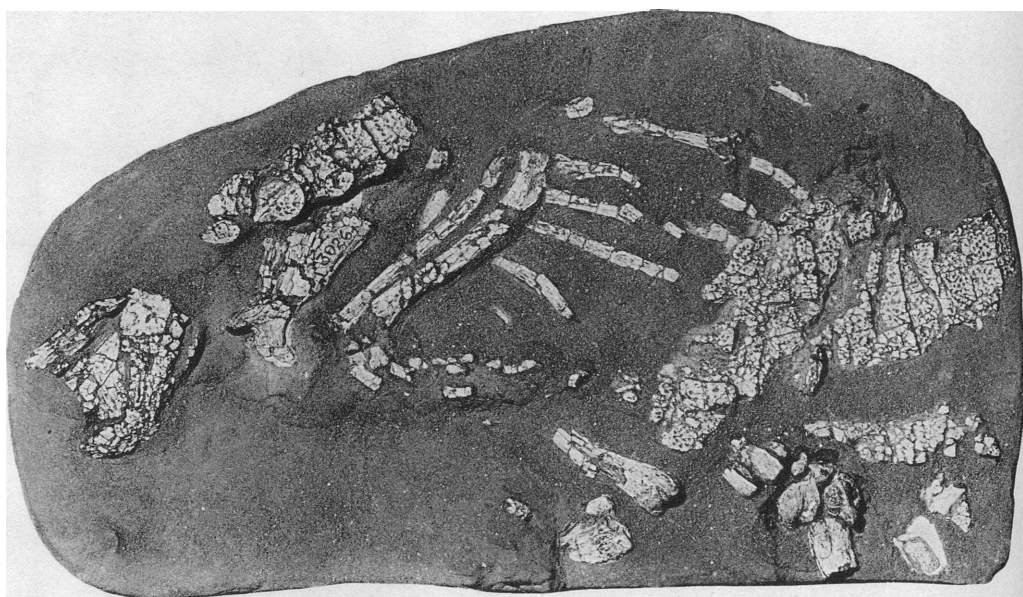
Protosuchus richardsoni (Brown). 1. A.M.N.H. No. 3026, referred specimen from the type locality, one-half natural size. 2. U.C.M.P. No. 36717, referred specimen from the type locality, partial skeleton, one-half natural size
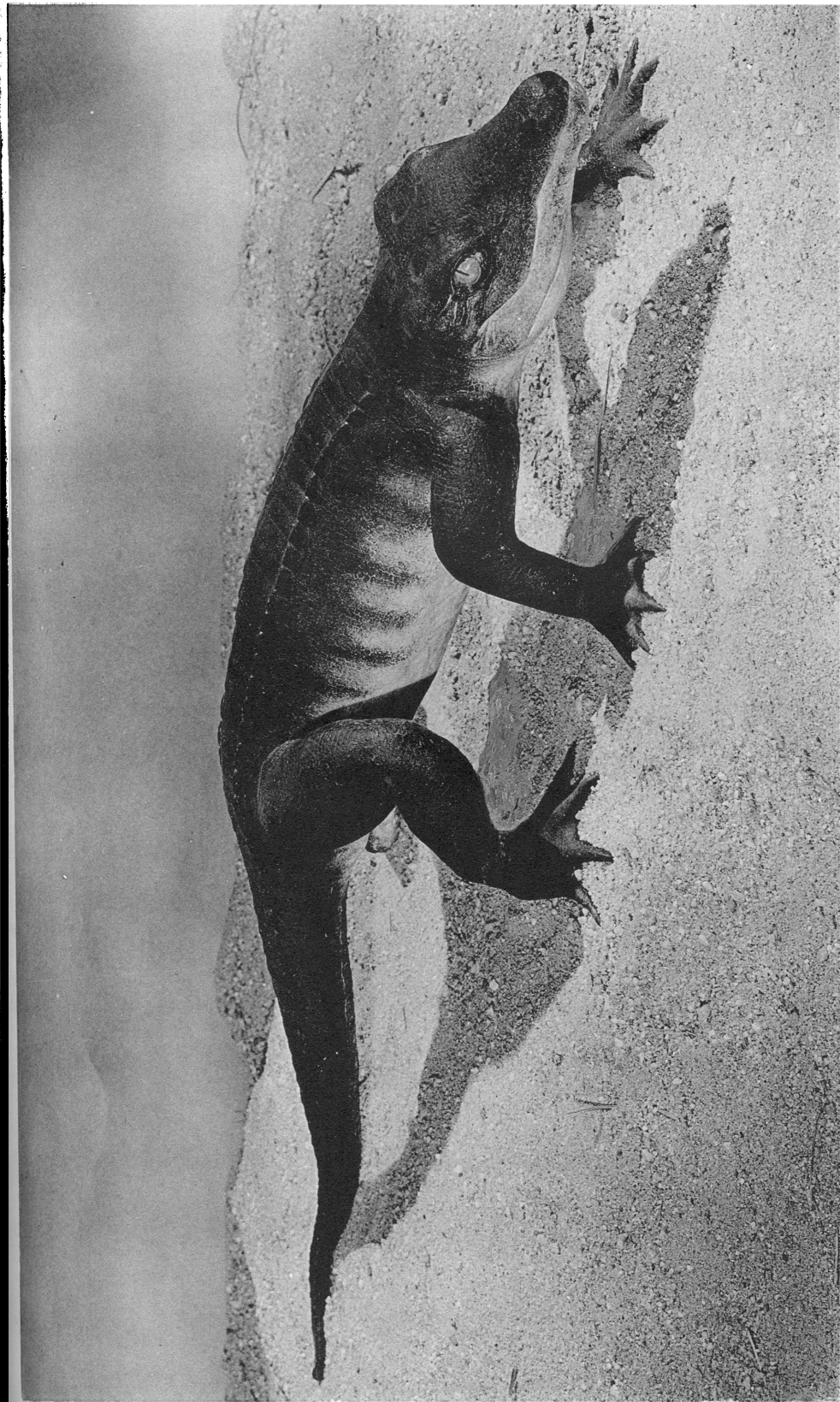
A restoration of *Protosuchus richardsoni* by Louise Waller Germann
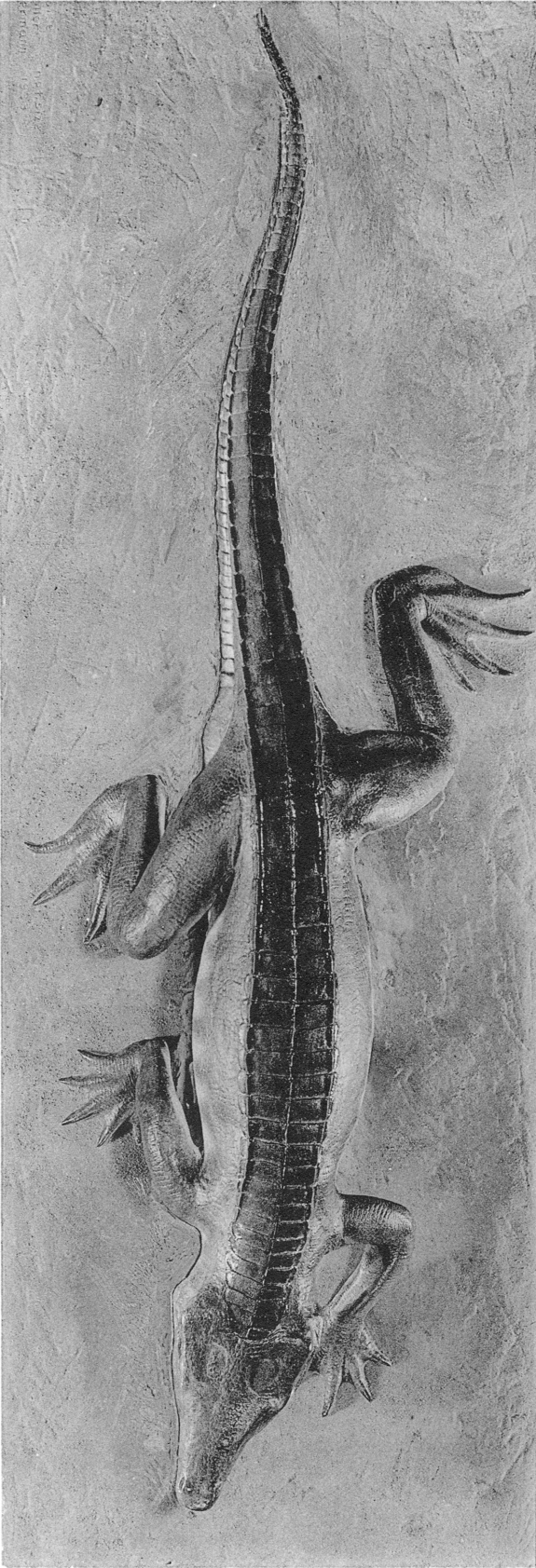
A restoration of *Protosuchus richardsoni* by Louise Waller Germann. 1. Dorsal view. 2. Lateral view

FIG. 8. Comparison of the scapula and coracoid. A. *Protosuchus*, a pro-
tosuchian. B. *Steneosaurus*, a mesosuchian, from Andrews (1913). C.
Alligator, a eusuchian. Not to scale.

coracoid is not so elongated as in the later
crocodilians, while its distal portion is less
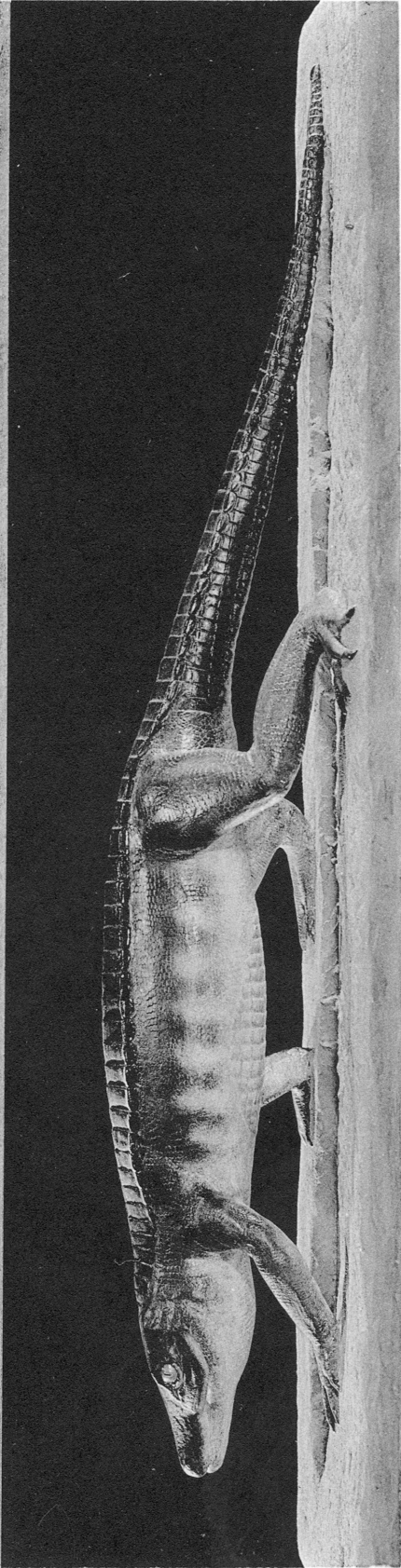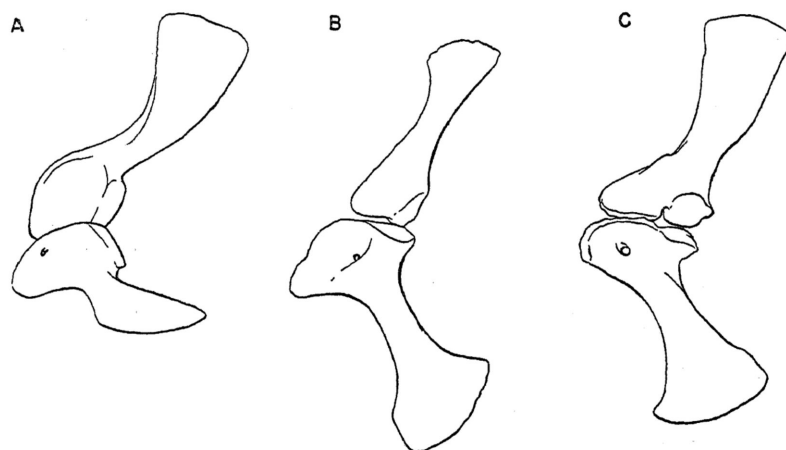blade-like than it is in recent genera. There
is a well-developed coracoid foramen.

The scapula is elongated, with a narrow,
distal blade. Both scapula and coracoid share
in the glenoid articulation.

There is a long, slender sternum between
the two coracoids.

FORE LIMB

The humerus resembles that of the later
crocodilians very closely in its form. As
compared with the humerus of living croco-
dilians the bone in *Protosuchus* is slender.
It is broadly expanded at the proximal end,
with a broad head and a prominent deltoid
crest. There is also a distal expansion of the
bone, for articulation with the radius and
ulna. As compared with living crocodilians
the humerus of *Protosuchus* is proportion-
ately short with reference to the femur, and
to the radius and ulna as well.

The radius and ulna are long and slender.
These bones are almost as long as the hum-
erus, which is a distinct contrast to the con-
dition in the recent crocodilians, in which the
radius and ulna are noticeably shorter than
the humerus. The radius is a straight, rod-
like bone; the ulna is curved, much as in the
modern crocodilians.

The fore foot of *Protosuchus* is, so far as can
be determined, completely crocodilian. It is

characterized especially by an elongated
radiale and ulnare, and these bones are pro-
portionately fully as elongated as they are in
the recent crocodilians. This is an interesting
development in *Protosuchus*, in line with
other characters of the skull and skeleton
that are surprisingly advanced in this genus.
It emphasizes the fact that *Protosuchus*, one
of the earliest and most primitive of the croc-
odilians and the archetype for a crocodilian
ancestor, is in many respects a completely
specialized crocodilian significantly removed
from its thecodont ancestry, and it demon-
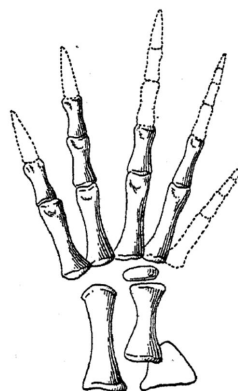strates the rapidity and thoroughness of the

FIG. 9. *Protosuchus richardsoni* (Brown). Res-
toration of right manus, based largely on U.C.M.P.
No. 36717. Dorsal view, natural size.

transition from thecodont to crocodilian in late Triassic and early Jurassic times.

In addition to the elongated radiale and ulnare the fore foot of *Protosuchus*, as shown by the University of California specimen, contains a fourth carpale and what appears to be a pisiform. There are no other carpal bones present, so that this limitation of the carpus to four bones foreshadows what was to become typical of the later crocodilians. In this specimen there are four metacarpals, but the phalanges are not completely preserved so that the phalangeal formula cannot

acetabulum, but it still abuts against both the ilium and the ischium. In the eusuchians, which represent the final step in this sequence, the anterior process of the ischium is enlarged to such an extent that it forms the entire articulation with the pubis, this latter bone being now completely separated from any contact with the ilium.

The pubis is elongated, with a rod-like shaft. Proximally the bone is curved, as seen in its ventral aspect, so that the proximal end of the bone is parallel to the axis of the body, while the main part of the shaft is directed
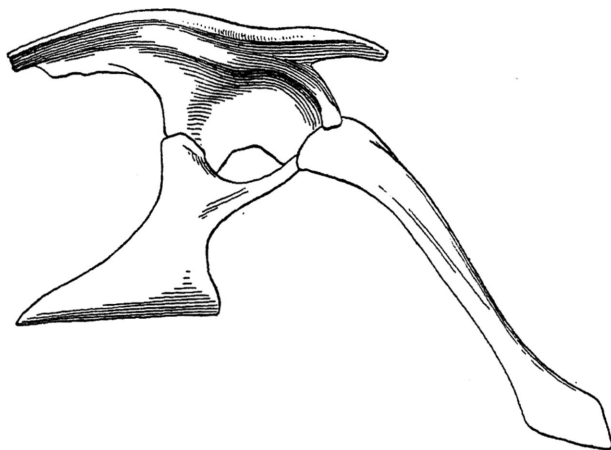

FIG. 10. *Protosuchus richardsoni* (Brown). A.M.N.H. No. 3024, type. External lateral view of right ilium, ischium, and pubis, natural size.

be given with certainty. It seems probable, however, that the formula was 2-3-4-5-3.

PELVIC GIRDLE

The pelvis of *Protosuchus* is in most respects crocodilian. It is more primitive than any other crocodilian pelvis, however, in that the pubis takes part in the acetabular border, whereas in other members of the order this bone is completely excluded from the acetabulum. Here we see the retention of a heritage from the earlier thecodonts, though one much modified, for the pubis is slender, and the proximal portion that forms a part of the acetabulum is small, as it is in the South African genus *Erythrochampsa*. This proximal end of the pubis is in contact with both the ilium and ischium. In the mesosuchians, *Steneosaurus* for instance, the proximal end of the pubis is entirely excluded from the

medially. The two pubes meet along the median line, and on each bone there is a flat, distal expansion.

The ilium is broad and low, with the iliac crest turned sharply outward. The posterior point of the ilium is produced backward to form a prominent extension of the bone, perhaps more markedly developed than in the modern crocodilians, while anteriorly the iliac crest is extended into a sharp point reaching as far forward as the transverse process of the last presacral vertebra. Here is a character that must be considered as rather specialized in such an early crocodilian as *Protosuchus*. This anterior extension of the iliac crest is retained in the mesosuchians, where it has been designated by Andrews as the anterior angle of the ilium. It is well developed in *Steneosaurus*. In the eusuchians the anterior angle of the ilium is suppressed,

and the front edge of the ilium is rounded.

The ischium in *Protosuchus* is rather similar to the same bone in recent crocodilians, but it shows a greater distal expansion, formed by a posterior prolongation of the bone along its symphyseal junction with the opposite ischium. Thus the two ischia are projected back into a point instead of being truncated as they are in the modern crocodilians. Anteriorly the ischium articulates with both the ilium and the pubis. The acetabulum is large and is formed mainly by the ischium and the ilium.

and development of the metatarsals. The hind foot is much larger in relation to the fore foot (or it might be better to say the fore foot is smaller in relation to the hind foot) than is the case in recent crocodilians, which is in harmony with the greater size disparity between fore and hind limbs in *Protosuchus* than in modern genera, a point that is discussed more fully below.

The calcaneum in *Protosuchus* is remarkable because of the very large size of the tuber. This part of the bone is proportionately much larger than the same process in
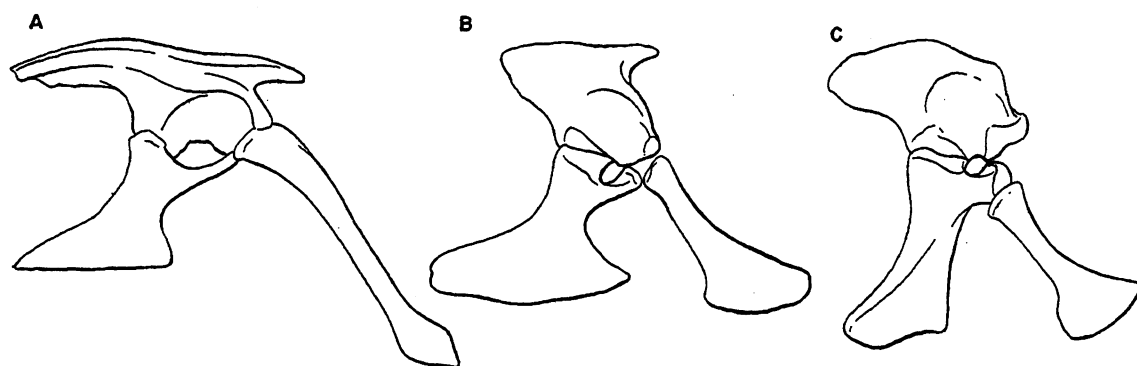

FIG. 11. Comparison of the pelvis. A. *Protosuchus*, a protosuchian. B. *Steneosaurus*, a mesosuchian, from Andrews (1913). C. *Alligator*, a eusuchian. Not to scale.

HIND LIMB

The femur in *Protosuchus* is a strong bone, and it resembles the femur in living crocodilians as to form and the position of the fourth trochanter. At the distal end the bone is perhaps bent slightly more towards the condyles than is the case in recent crocodilians. The head is well formed, and it is set at an angle to the shaft.

The tibia and fibula are long bones, somewhat longer in proportion to the femur than are the same bones in living crocodilians. Thus, these bones are only slightly shorter than the femur, whereas in recent genera the tibia and fibula are appreciably shorter than is the femur. These two bones are relatively slender, though strong.

Like the fore foot, the hind foot in *Protosuchus* is of an advanced crocodilian type. It is characterized by the specialized and enlarged calcaneum and astragalus in the tarsus, and by the crocodilian arrangement

recent crocodilians, and it is expanded at its free end into a large, rounded, pulley-like surface for the accommodation of the flexor tendons of the hind foot. This extreme development of the calcaneum in *Protosuchus* must have been correlated with significant adaptations for locomotion. Likewise the astragalus is very large, and it very likely represents a coössification of at least two tarsal elements, centrale and intermedium. It has a large facet for articulation with the tibia and an expanded convex surface for articulation with the first two metatarsals. The third and fourth metatarsals articulate with a rather square tarsal element that intervenes between these bones and the calcaneum. This is the bone sometimes called the cuboid in recent crododilians, but more properly to be regarded as the fourth reptilian tarsal or a fusion of the fourth and fifth tarsalia. All in all, the development and arrangement of the tarsals in *Protosuchus* are
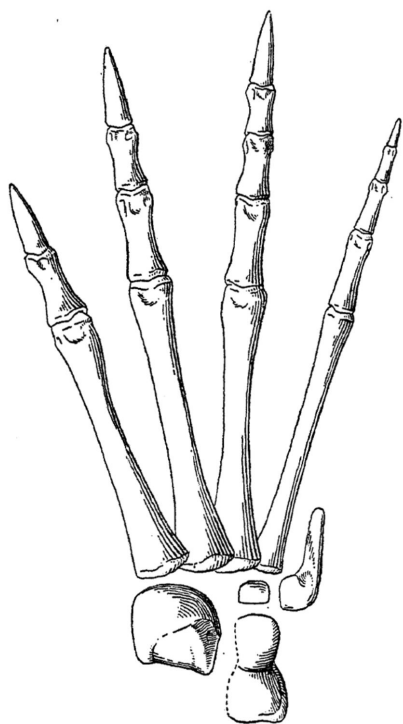
FIG. 12. *Protosuchus richardsoni* (Brown). A.M.N.H. No. 3024, type. Right pes, dorsal view, natural size.

very similar to what they are in recent crocodilians.

There are five metatarsals in *Protosuchus*, of which the fifth is reduced to a hook, as it is in the modern crocodilians. Here again we see an interesting early specialization in this primitive member of the order. True, the "shaft," or what remains of it, in the fifth metatarsal is relatively longer in *Protosuchus* than it is in recent crocodilians, but the difference is not great. The important fact is that already in this early crocodile there was suppression of the fifth digit to a mere remnant. It should be remembered, however, that a similar suppression of the fifth digit is characteristic of the thecodonts, so that what we see in *Protosuchus* is the heritage of a character that was passed along to most of the archosaurian reptiles.

The first four metatarsals are long and slender, and they decrease in weight and strength but not in length from the first to the fourth of the series. Proximally they overlap each other, the first over the second,

and so on, as do the metatarsals in other crocodilians.

The phalangeal formula for the first four digits is 2-3-4-4, as it is in modern crocodilians. The first three digits are clawed, while the fourth digit terminates in a tiny phalanx.

ARMOR

Protosuchus was a heavily armored reptile, and in this respect it shows the heritage of its thecodont ancestors. The crocodilians are also heavily armored reptiles, but it is safe to say that the armor of most of the crocodilians is not so extensively developed, nor is it relatively so heavy as the armor of *Protosuchus*. In this reptile there is a dorsal armor that runs along the middle of the back from the back of the skull to the end of the tail, and a ventral armor that covers the under surface of the body and the tail. The dorsal and ventral plates meet on the lateral surfaces of the tail, so that the tail is completely encased in armor plates. Such a strong development of the armor recalls certain thecodonts, such as *Aetosaurus* or *Stegomus*.

On the dorsal surface a double row of scutes extends the entire length of the vertebral column. The scutes correspond in number and position with the vertebrae beneath them. For instance the overlap of one scute over the next is located immediately above the vertebral spine. The first four pairs of scutes are much narrower anteriorly than posteriorly, but behind these scutes the remaining plates are all essentially rectangular. In the dorsal, lumbar, and sacral regions and well back on the tail the scutes are quite broad in comparison to their length, and only in the posterior part of the tail do the scutes approach a square shape, or even become slightly longer than they are broad.

Throughout most of its length the series of dorsal scutes shows on each scute a laterally placed keel, running anteroposteriorly. This keel, which is low, marks an axis, on either side of which the surfaces of the scute are at an angle to each other. In other words the lateral plate of each scute on the outer side of the keel is bent sharply downward, giving the effect of an independent lateral scute. It should be emphasized, however,

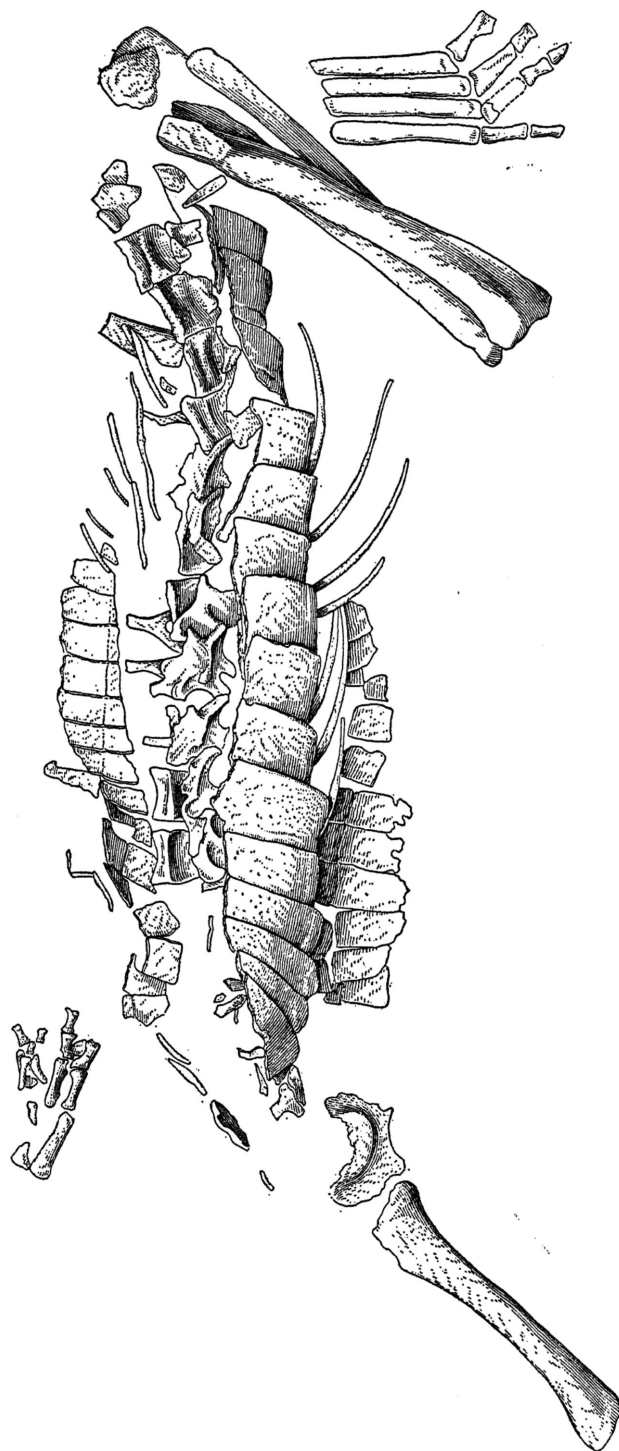Fig. 13. *Protosuchus richardsoni* (Brown). U.C.M.P. No. 36717, referred specimen. Dorsal view of partial skeleton, showing portions of dermal armor, dorsal vertebrae, left radius and left manus, left femur, tibia, fibula, astragalus, and pes. The drawing of the pes (in ventral view aspect) is shifted from its original position at the distal end of the tibia and fibula. Natural size. Drawing by Owen J. Poe.

that this lateral portion is an integral part of the scute.

The surface of each dorsal scute is rugosely pitted, except for the anterior margin that is overlapped by the preceding scute of the series. This "articulating surface" of the scute is relatively smooth, as might be expected.

The ventral scutes are well exposed on the belly and the tail. The armored area preserved under the thorax and abdomen is rather short anteroposteriorly and elliptical in extent. Along the midline this ventral armor extends from the region of the sternum to a point somewhat anterior to the distal ends of the pubes. The anterior transverse row of scutes consists of eight scutes, four on either side of the midline. The second transverse row contains 10 scutes, while the third has 12 scutes, six on either side of the midline. There are 12 scutes in the third to ninth transverse rows inclusive, and from the tenth row to the sixteenth, which is the last, the number decreases gradually to six, three on either side of the midline. Most of these scutes are rectangular in shape, and many of them, especially those near the midline, are essentially square. None of these scutes are keeled. Along the lateral borders of the armored area the scutes are quite small and somewhat irregular in shape, which indicates that the armor ended in about this position and was absent on the lateral surfaces of the body. The ventral scutes are rugosely and irregularly pitted, as are the scutes along the back.

On the ventral and lateral surfaces of the tail the scutes are essentially similar to the ventral scutes of the body region. As mentioned above, these scutes extend around the tail to meet the dorsal scutes, so that the entire caudal region is completely sheathed with armor. In the anterior caudal region there are eight scutes in each transverse row, four on either side of the midline, while through the middle part of the caudal region there are six scutes to each transverse row. In the posterior caudal region there are but four scutes to each transverse row. Approximately 50 transverse rows of ventral caudal scutes are preserved, but there is reason to think that several of the posterior rows are absent.

The ventral caudal scutes are rectangular, and those along the midline tend to be approximately square. As might be expected, these scutes are sculptured by coarse pitting.

Throughout a greater portion of the caudal region the ventral scutes are just half the length of the dorsal ones. Whereas the dorsal scutes are developed one to each vertebral segment, the ventral scutes are double this number, and in the lateral aspect where the dorsal and ventral scutes meet this two-to-one relationship is clearly seen. In the posterior part of the tail, however, the dorsal scutes become small, and here a one-to-one relationship between dorsal and ventral scute lengths is established. There is no appreciable diminution in the lengths of the posterior caudal vertebrae, so that in this region there are two dorsal as well as two ventral scute lenths to each vertebra.

FROM THE FOREGOING DESCRIPTION of the known materials of *Protosuchus* it is evident that this early crocodilian shows a mixture of characters, some of them directly inherited from thecodont ancestors, others of a specialized nature and clearly indicative of the adaptations that were to be typical of the crocodilians as an order. In other words there are seen in *Protosuchus* thecodont heritage characters and crocodilian habitus characters. Yet in spite of the admixture of these characters *Protosuchus* is quite obviously a crocodile; its specialized habitus characters make it so. To put it in another way, *Protosuchus* is a crocodilian that retains certain traces of its thecodont ancestry, which is not surprising since the remnants of some thecodont characters are to be seen in the latest and most advanced of the crocodilians.

Perhaps it will be useful here to enumerate the heritage and habitus characters seen in *Protosuchus*, and to discuss those characters that were touched upon in the description of the genus, in order that they can be emphasized and compared.

THECODONT HERITAGE

1. It is pointed out in the description that the orbits in *Protosuchus* are directed forward and outward, rather than upward as they are in most of the later crocodilians. In a majority of the crocodilians the skull is relatively quite broad and low, and it is this flattening of the skull that has resulted in the upward direction of the orbits in these forms. The skull in *Protosuchus* is not specialized in this respect, so that the orbits are oriented in the manner typical of most reptiles. It might be pointed out here that in the phytosaurs, thecodont reptiles that show a close parallelism to the crocodilians, the orbits are oriented in a "normal" manner, since the skull is rather deep. Also in the extinct crocodilian suborder, the Sebecosuchia, the orbits show this development, because these crocodilians are unique in having deep and rather narrow skulls.

2. In *Protosuchus* the upper temporal opening is smaller than the orbit, while the lateral temporal opening is very large. This is exactly the relationship seen in the the-codonts, so it can be assumed to be the primitive condition. In some of the mesosuchians both temporal fenestrae are large. In the eusuchians, on the other hand, the upper temporal opening is quite small, and since the eusuchians are of mesosuchian ancestry this probably is a secondary reduction of the upper opening.

3. The relationship of the bones of the skull roof in *Protosuchus* are the same as seen in the thecodonts. Likewise, these same relationships are seen in the more advanced crocodilians. Consequently, it is valid to conclude that we see here a general archosaurian condition, which is widely spread throughout the group.

4. The postorbital bar is at the surface, as it is in most reptiles. In the depression of the postorbital bar the eusuchians are specialized as contrasted with other crocodilians; in the mesosuchians, for instance, the postorbital bar is at the surface.

5. In *Protosuchus* it appears that the articular and angular bones of the lower jaw are not posteriorly extended as they are in later crocodilians. The lack of a posteriorly extended angle is common in the thecodonts —in the phytosaurs, for instance.

6. The dorsal vertebrae in *Protosuchus* are without hypapophyses, whereas in many crocodilians, especially the eusuchians, hypapophyses are commonly well developed. In this connection it should be said that the centra in *Protosuchus* show the primitive amphiplatyan condition, inherited from the thecodonts, and among the crocodilians carried on into the mesosuchians. It is only in the Suborder Eusuchia, the last and most specialized of the crocodilians, that the vertebrae are procoelous.

7. The development of the pubis in *Protosuchus* has already been described. We see here an almost ideal condition for an ancestral or stem crocodilian. The pubis has the crocodilian form, but its proximal end is still retained within the confines of the acetabulum. Here one can see the process of exclusion of the pubis from the acetabulum well under way, and from *Protosuchus* it is but a step to the mesosuchian condition, and from this, in turn, to the eusuchian condition.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) AND RATIOS

	Protosuchus richardsoni U.C.M.P. No. 36717	*Protosuchus richardsoni* A.M.N.H. No. 3024 Type	*Crocodylus porosus* (young) A.M.N.H. No. 69125	*Saltoposuchus longipes* (from von Huene)
Skull				
Length	—	113	190	—
Preorbital length	—	44	117	—
Postorbital length	—	69	73	—
Width at quadrates	—	86	78	—
Width at premaxillary-maxillary suture	—	18	26	—
Mandible				
Length	—	116	209	—
Vertebrae				
Presacral length	—	270	347	306
Sacral length	—	27	29	27
Caudal length	—	395[a]	605[b]	675[c]
Length of a middorsal centrum	7	12[d]	15[d]	—
Total height of a middorsal	19	19	27	—
Width across transverse processes of a mid-dorsal	—	27	50	—
Pectoral girdle				
Length of scapula	—	48	46	—
Length of superior border of scapula	—	28	16	—
Length of coracoid	—	25	42	—
Proximal anterior-posterior diameter of coracoid	—	22	20	—
Pelvic girdle				
Length of iliac crest	—	51	34	—
Height of ilium	—	19	23	—
Length of ischium	—	30	38	—
Length of ischial symphysis	—	29	22	—
Length of pubis	—	56	37	—
Length of pubic symphysis	—	11	19	—
Vertical diameter of acetabulum	—	14	14	—
Fore limb				
Length of humerus	—	66	77	40
Length of radius[e]	—	52	46	33
Length of manus	28	50	57	30
Length of radiale	9	14	10	—
Length of third digit	19	33	45	—
Hind limb				
Length of femur[f]	—	100	86	95
Length of tibia	57	83	64	111
Length of pes	46	80	100	120
Anterior-posterior length of calcaneum	—	19	16	—
Length of third digit	36	68	85	—

[a] 35 vertebrae.
[b] 37 vertebrae.
[c] 70 vertebrae.
[d] Sixteenth presacral.
[e] 61, in specimen A.M.N.H. No. 3026.
[f] 107, in specimen A.M.N.H. No. 3056.

TABLE 1—*Continued*

	Protosuchus richardsoni U.C.M.P. No. 36717	*Protosuchus richardsoni* A.M.N.H. No. 3024 Type	*Crocodylus porosus* (young) A.M.N.H. No. 69125	*Saltoposuchus longipes* (from von Huene)
RATIOS				
Presacral and sacral length	—	100	100	100
Caudal length	—	133	161	205
Length of fore limb	—	56	48	31
Length of hind limb	—	89	66	98
Length of femur	—	100	100	100
Length of tibia	—	83	74	117
Length of pes	—	80	116	126
Length of humerus	—	66	89	42
Length of radius	—	52	53	35
Length of manus	—	50	65	32

8. The reduced, hook-like, fifth metatarsal in *Protosuchus* is clearly the inheritance of a thecodont character. The bone is close to the thecodont condition, since it is not so reduced relative to the other metatarsals as it is in the later crocodilians.

9. In the development of the bony armor, *Protosuchus* is very thecodont-like. Indeed, the large size of the plates and their shape recall certain other thecodonts such as *Aetosaurus*, *Stegomus*, or *Typothorax*. The very large, transversely broadened dorsal plates, the heavy ventral armor, and the complete encasement of the tail are all characters whereby this genus can be compared closely with the thecodonts that preceded it. It should be mentioned that the armor in the mesosuchians approaches in its development that of *Protosuchus*.

CROCODILIAN HABITUS

1. The crocodilian shape of the skull roof in *Protosuchus* is indeed striking, and it immediately sets this skull apart from any thecodont skull. The frontal, parietal, postorbital, and squamosal bones are involved, and in all these bones there is a flattening, and in some cases a considerable amount of expansion, of the dorsal surfaces. The flattening and expansion of the bones dorsally are particularly noticeable in the squamosal and postorbital bones, and it is the development of these elements, as much as anything, that gives to the *Protosuchus* skull roof its characteristically crocodilian shape.

2. It appears that in *Protosuchus* there is no antorbital fenestra, and in this respect *Protosuchus* shows an early departure from the thecodont condition. In most of the archosaurians the antorbital fenestra is retained.

3. It is probable that *Protosuchus* had a mesosuchian type of palate, but on this point nothing definite can be said in the light of present knowledge. It is to be hoped that future discoveries will provide additional material that will make known, without any doubts, the form of the palate in this early crocodilian.

4. The extended transverse processes of the presacral vertebrae give the *Protosuchus* column a most distinctive crocodilian look. This is emphasized by the migration of the parapophyses onto the transverse processes in all but the most anterior of the dorsal vertebrae, so that the ribs articulate on the end of the processes. Such a rib articulation is distinctively crocodilian, and in its development *Protosuchus* is virtually as advanced as the eusuchians.

5. The enlargement of the transverse processes of the second sacral vertebra to form the principal connection between backbone and pelvis is a crocodilian character that is well developed in *Protosuchus*.

6. In the enlargement of the coracoid, *Protosuchus* shows an approach to the later crocodilians. However, whereas in some skull characters and vertebral characters *Protosuchus* is almost completely crocodilian, in

this particular character it shows a somewhat intermediate stage of development. In this respect the development of the shoulder girdle can be compared with the development of the pelvis in *Protosuchus*; it is almost crocodilian, but not quite so. The coracoid in *Protosuchus*, though enlarged, does not show the degree of specialization that makes it almost a mirror image of the scapula, as is the case in the eusuchians. The coracoid of the mesosuchians is approximately intermediate between that of *Protosuchus* and that of the eusuchians.

7. The elongated radiale and ulnare in the fore foot of *Protosuchus* represent a highly specialized crocodilian character, comparable in their high stage of development to such crocodilian features as the squamosal bone or the articulation of the ribs on the transverse processes. The limitation of the carpus to four bones is a characteristic crocodilian feature in *Protosuchus*.

8. The pelvis of *Protosuchus* has already been discussed. It was shown that this genus is remarkable by having crocodilian-like pubes, but with the pubes participating in the acetabular border. Except for this, however, the pelvis is very crocodilian in form. Indeed, the pelvis is specialized beyond the condition characteristic of other crocodilians

in that the iliac crest is expanded anteriorly. Thus the front of the iliac crest is extended forward to a point that reaches a position opposite the transverse process of the last presacral vertebra. No such development is seen, for instance, in the eusuchians, but it is present in the mesosuchians.

9. In the enlargement of the astragalus and the calcaneum, as in the form of the iliac crest, *Protosuchus* shows a crocodilian stage of development that goes beyond anything seen in other crocodilians. Thus these bones are proportionately larger than they are in other crocodilians, and in the calcaneum the tuber is proportionately very large. One must suppose that such specializations were correlated with the development of the leg and foot muscles, and were a function of the pose and the method of locomotion in this animal. This point is discussed below.

It may be helpful to list the salient heritage and habitus characters of *Protosuchus* (here essentially representative of the Protosuchia) as compared with the same characters in the Mesosuchia and in the Eusuchia. In this list crosses indicate that characters in the two higher suborders are essentially similar to those characters in the Protosuchia, while circles indicate specializations away from the protosuchian condition.

	PROTOSUCHIA	MESOSUCHIA	EUSUCHIA
Direction of orbits	x	o	o
Broad cranial table	x	o	x
Supratemporal fenestra smaller than orbit	x	x/o	x
Lateral temporal fenestra large	x	x	o
No antorbital fenestra	x	x/o	x
Postorbital bar at surface	x	x	o
Mandible without posteriorly produced angular	x	o	o
Anterior vertebrae without hypapophyses	x	x	o
Parapophyses on transverses processes	x	x	x
Second sacral enlarged	x	x	x
Coracoid enlarged, subequal to scapula	x	x	x
Elongated radiale-ulnare	x	x	x
Pubis participates in acetabular border	x	o	o
Ilium with anterior process	x	x	o
Enlarged calcaneum and astragalus	x	x	x
Very heavy armor	x	x/o	x/o

DISCUSSION OF LIMB PROPORTIONS

IN TABLE 1 an attempt is made to compare the various dimensions of *Protosuchus* with those of a modern crocodilian on the one hand and of a primitive thecodont reptile on the other. The skeleton of a young *Crocodylus porosus* was used, because it happened to be closely comparable in size to the *Protosuchus* skeleton and it was reasonably complete. *Saltoposuchus* as restored by von Huene was used as the thecodont because of its generally primitive structure. Unfortunately, it was not possible to obtain from von Huene's paper as many measurements as would have been desirable. It should be kept in mind, therefore, that some of the comparisons involve, so far as *Saltoposuchus* is concerned, a certain amount of conjectural evidence.

In figure 14, a comparison of vertebral lengths and limb lengths is made, with the presacral plus sacral length taken as unity. As can be seen, the difference between *Protosuchus* and *Crocodylus* as to caudal length is not great. The tail in *Saltoposuchus* seems to be excessively long, but this length is open to question, for von Huene has restored *Saltoposuchus* with 70 caudal vertebrae, as compared with about 35 or 40 in the crocodilian genera under consideration. There is reason to think that the vertebral count of the thecodont should be closely comparable to that for the crocodilians, in which case the tail length would also be more nearly that seen in the other two genera.

The point of particular significance here is the comparison of limb lengths in the genera being considered. As can be seen, the hind limb of the thecodont is longer than that of *Protosuchus*, although the difference between them is not great, while a considerable disparity is evident between *Protosuchus* and *Crocodylus* in the length of the hind limb. *Crocodylus* is a semi-aquatic reptile, while it is presumed that *Saltoposuchus* was strongly cursorial. Therefore, the proportions of the charts (figs. 14, 15) seem to indicate that *Protosuchus* was more of a running, land-living reptile than are the modern crocodilians.
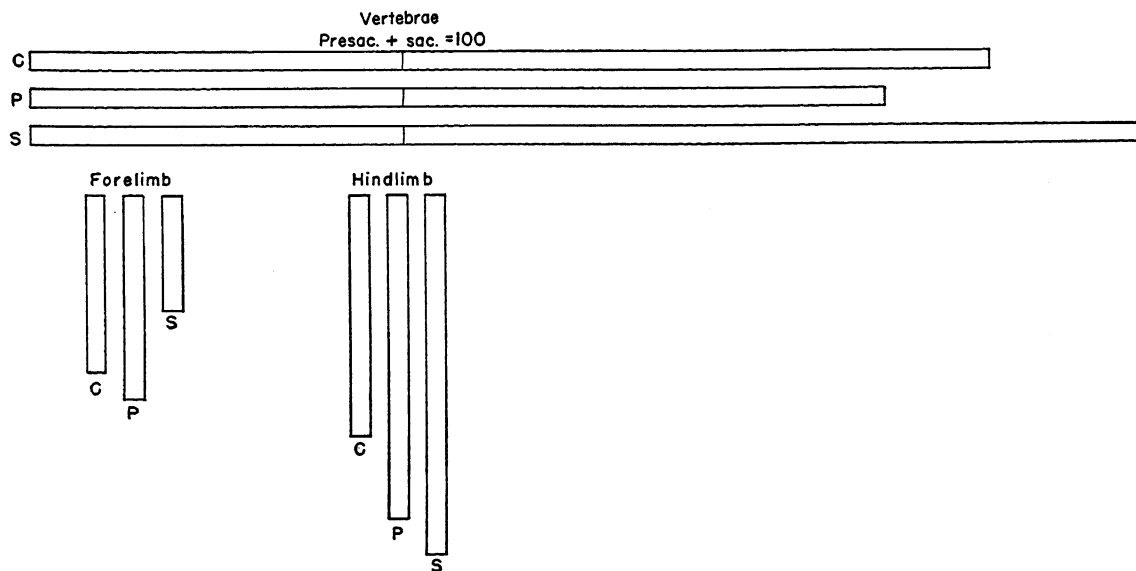
This conclusion is borne out by the com-

FIG. 14. Diagram to show proportional lengths of vertebrae, fore limbs, and hind limbs in three crocodilians. The presacral plus sacral length is taken as unity, and other proportions are scaled on this basis. *Abbreviations:* S, *Saltoposuchus*, a psuedosuchian; P, *Protosuchus*, a protosuchian; C, *Crocodylus*, a eusuchian. Measurements for *Saltoposuchus* taken from von Huene, 1921.

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parison of the fore limbs. Here a great disparity in length between the fore limb and the hind limb of the thecodont is indicated. This reptile probably walked and ran about in a predominantly bipedal pose, with the fore limbs functioning as grasping structures to aid in food gathering and the like. In *Crocodylus* the disparity between limb lengths is not so strong, even though it is marked, and we know that this animal is quadrupedal when it moves on land. *Protosuchus*, as can be seen, is more or less intermediate between the thecodont and the modern crocodilian. Obviously the front legs were already beginning to enlarge *vis-a-vis* the hind limbs, so that *Protosuchus* probably had a varied mode of locomotion, partially bipedal and partially quadrupedal. It was losing some of the primitive thecodont cursorial adaptations.

The comparison of the limbs in the three genera here being discussed is further illustrated by an analysis whereby not only the total lengths but also the various elements making up limb lengths are considered. This is shown in figure 15, in which the length of the femur is taken as the unit, and all other lengths are calculated relatively upon this basis. The diagram shows very strikingly the increase in length of the fore limb in whole and in its parts from the thecodont through *Protosuchus* to the modern crocodilian, and it shows conversely the reduction in length of hind limb through the same series. In this latter instance, however, the effect is masked to some degree by the fact that the hind foot of the modern crocodilian is elongated as compared with that of *Protosuchus*, the result of the aquatic adaptations in the later crocodilians. Indeed the pes in *Protosuchus* is relatively short as compared with elongated hind feet in both the thecodont and the modern crocodile. The elongated foot of the thecodont can be correlated with its cursorial mode of locomotion, while that of the recent crocodile, as mentioned, is to be correlated with its swimming habits. Therefore it would be logical to suppose that the shorter pes in *Protosuchus* is the expression of a mode of locomotion less cursorial than that of *Saltoposuchus* but less aquatic than that of *Crocodylus*.

Protosuchus AND THE THECODONTS

One is struck by the general similarity in appearance and adaptations between *Protosuchus* and the two thecodont genera *Aetosaurus* and *Stegomus*. Both of these Triassic genera show certain developments parallel to the primitive crocodilian from Arizona, and these can be outlined in a general way as follows.

Of the two thecodonts, *Aetosaurus* is roughly comparable to *Protosuchus* in size, while *Stegomus* is considerably smaller than the crocodilian. Both are especially like *Protosuchus* in the development of their dermal armor. *Aetosaurus* in particular was a heavily armored reptile, with large, transversely broadened, rectangular plates covering the back, one anteroposterior row on either side of the midline, and with smaller plates covering the under side of the body. *Stegomus*, too, had a dorsal armor of large,
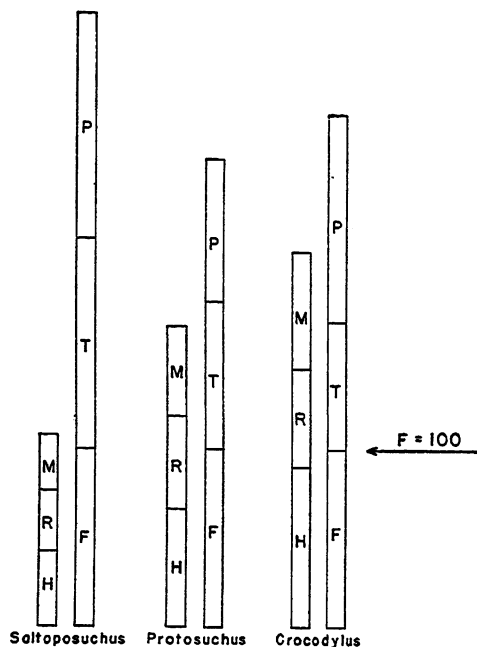

FIG. 15. Diagram to show the proportional lengths of limb segments in three crocodilians. The femoral length is taken as unity, and other proportions are scaled on this basis. *Saltoposuchus*, a pseudosuchian; *Protosuchus*, a protosuchian; *Crocodylus*, a eusuchian. *Abbreviations*: F, femur; H, humerus; M, manus; P, pes; R, radius; T, tibia.

transversely broadened, rectangular plates.

Since both of these reptiles were heavily armored, they were predominantly quadrupedal (perhaps even more so than was *Protosuchus*), but even though they were quadrupedal there is a disparity in size between the fore and hind limbs as in the crocodilian. Moreover, in *Aetosaurus* at least, the tuber of the calcaneum is elongated and enlarged at the end in a manner similar to that seen in *Protosuchus*.

retention in *Protosuchus* of basic thecodont characters or of parallelism. The development of a heavy dermal armor is one thecodont character that is especially striking. Evidently *Protosuchus*, *Aetosaurus*, and *Stegomus* were roughly similar to one another in their adaptations. They seemingly were land-living reptiles with, one might say, lizard-like habits. Perhaps they lived in such undergrowth as there was in those days and sought protection beneath rocky ledges and
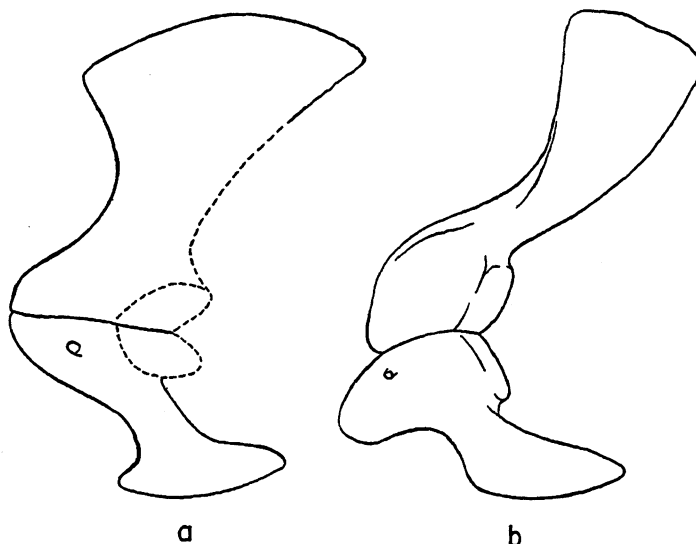

FIG. 16. Comparison of the shoulder girdles as seen in lateral view. A. *Notochampsa istedena* Broom, from Broom (1927). B. *Protosuchus richardsoni* (Brown). Not to scale.

Of course the skulls of these two thecodonts are quite different in details from the skull of *Protosuchus*. This latter shows the various adaptations that mark it as already a true crocodile, adaptations such as the flattening of the cranial table, the diminution in size of the upper temporal fenestra, and the complete suppression of an antorbital fenestra. In *Aetosaurus* and *Stegomus*, on the other hand, the skulls are thoroughly thecodont, with large temporal fenestrae and an antorbital opening.

Consequently it is evident that such resemblances as exist between these two thecodonts and *Protosuchus* are the results of the

other features. They were heavily armored because they lived in a world inhabited by highly predatory reptiles and amphibians of great size, animals such as the aggressive phytosaurs and the giant stereospondyls. For this reason they developed along parallel lines, but it must not be thought because of this that *Protosuchus* is any closer in its relationships to *Aetosaurus* and *Stegomus* than it is to other thecodonts. Indeed, when basic structural comparisons are made it is probably more valid to compare *Protosuchus* with a generalized and comparatively primitive thecodont such as *Saltoposuchus* than with these obviously specialized genera.

Protosuchus, Notochampsa, AND Erythrochampsa

At the beginning of this paper some general remarks are made as to the relationships of *Protosuchus*, *Notochampsa*, and *Erythrochampsa*, and varying opinions regarding the taxonomic positions of the last two genera as members of either the Thecodontia or the Crocodilia are cited. Some remarks are added here concerning certain comparisons that can be made between the three genera.

As pointed out above, it is the belief of the present authors that both *Notochampsa* and *Erythrochampsa* are crocodilians, and in this we follow the view set forth by Broom in 1927. This is in contradiction to von Huene's statement of 1925 that the two South African forms are thecodonts, to be included among the pseudosuchians.

Certainly *Notochampsa* is rather closely related to *Protosuchus*. A strong resemblance is to be seen between the two reptiles in the development of large, transversely broadened, rectangular dorsal plates, forming two matched rows, one on either side of the midline of the back. Similar plates were, of course, cited in the pseudosuchian genera, *Aetosaurus* and *Stegomus*, but in neither of these forms are the resemblances in the plates so close as are those between *Protosuchus* and *Notochampsa*. And this fact, taken in conjunction with other crocodilian characters in

a   b

FIG. 17. Comparison of the right carpus and manus as seen in dorsal view. A. *Notochampsa istedena*, Broom, from Broom (1927, reversed). B. *Protosuchus richardsoni* (Brown). Not to scale.

Notochampsa, seems to give weight to the view that the North American and South African genera are rather closely related.

For instance, the pectoral girdle of *Notochampsa* is definitely crocodilian. It can be compared closely with the girdle in *Protosuchus*; in both genera the coracoid is greatly enlarged and rather similar to the scapula in size and shape, a character that is quite typical of the more advanced crocodilians. Moreover, *Notochampsa* has greatly elongated carpals, as is the case in *Protosuchus*, and this indicates that these two genera not only are related but also are characterized by very definite crocodilian adaptations.

The resemblances between *Protosuchus* and *Notochampsa* are not so strong in the skull and mandible as they are in the postcranial skeleton. We see here without much doubt two separate genera, living on opposite sides of the earth, and it is in the skull that the generic differences should be most apparent. The skull of *Notochampsa*, though imperfectly preserved, is nevertheless complete enough to show that this was a fairly long-snouted crocodilian. *Notochampsa* shows a strong contrast in this respect to *Protosuchus*, which seems to have had a rather short snout. Moreover, the cranial roof in *Notochampsa* does not appear to be so completely flattened as is the same area in *Protosuchus*.

In certain respects, on the other hand, *Notochampsa* shows various general resemblances to *Protosuchus* and to other crocodilians in the anatomy of the skull. For instance, the squamosals, parietals, and frontals all are quite large in the South African form, as they are in the North American genus, while the squamosal has its posterior portion directed down and back, as is so characteristic of the crocodilians. In addition, the supratemporal fenestrae are rather small in both *Protosuchus* and *Notochampsa*, whereas in many of the early mesosuchians the fenestrae generally are large. This leads to the conclusion that the small fenestrae of the modern crocodilians are secondarily reduced to a condition similar to that of the primarily small fenestrae in the ancestral crocodilians.

Broom, in his original description of *Notochampsa*, indicated that the external nares were undivided by a central bridge of
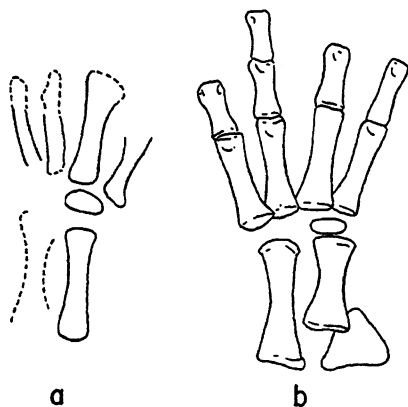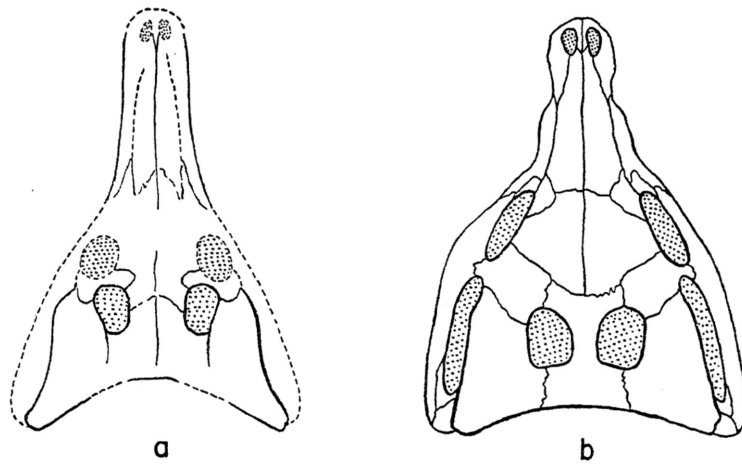
FIG. 18. Comparison of the skull as seen in dorsal view. A. *Noto-champsa istedena* Broom, from Broom (1927). B. *Protosuchus richardsoni* (Brown). Not to scale.

bone, a common character in the Mesosuchia and the Eusuchia. Subsequent development of the specimen has indicated, however, that there was very probably a bony septum, formed by extensions of the nasal bones, dividing the nares. Such a septum is to be seen in some modern crocodilians, especially the alligatorids. The evidence is not clear as to *Protosuchus*, but because of its general relationships to the South African genus a dividing septum has been indicated.

Certainly *Protosuchus* shows no indication of a preorbital vacuity, and in this respect *Notochampsa* probably resembles the North American form. Here again the evidence of the South African specimen is not clear, but Broom believes that there was no antorbi-

tal opening, despite the opinion of von Huene to the contrary. In view of other specialized crocodilian features in these two genera, one would expect that *Notochampsa* like *Protosuchus* was advanced in the suppression of the opening in front of the eye.

From this comparison it is evident that *Notochampsa* is similar to *Protosuchus* in many respects, and to us there seems little doubt but that, like the American form, it had progressed well along the adaptational trend towards the specialized crocodilians. Indeed the two genera show so many similarities, even though there are some differences of structure and proportion in their skulls, that it seems probable they should be placed in a single suborder, and possible
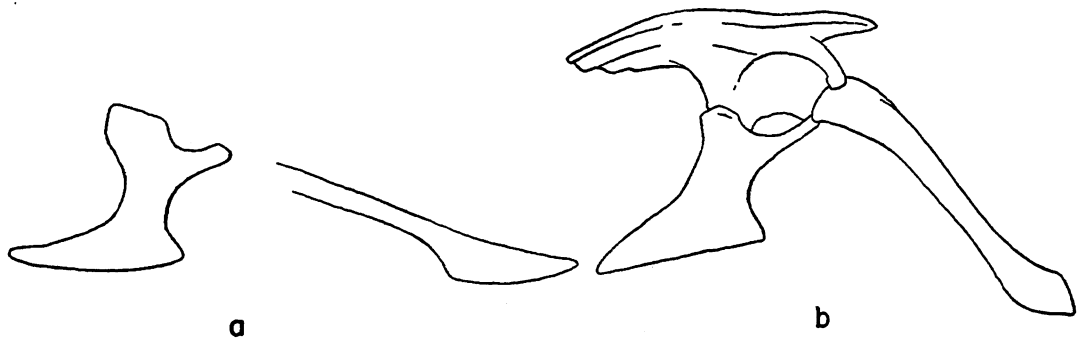

FIG. 19. Comparison of the pelvis as seen in right lateral view. A. *Erythrochampsa longipes* (Broom), from Broom (1927, reversed). B. *Protosuchus richardsoni* (Brown). Not to scale.

that they should be included within a single family, as is indicated above.

It is unfortunate that the pelvis and the hind limb of *Notochampsa* are at the present time unknown. These parts would help greatly in establishing the definitive position of the South African form. It is the opinion of the present authors that if and when the pelvis and hind limb of *Notochampsa* are found, they will be very similar to the same elements in *Protosuchus*.

We are fortunate in having knowledge of the pelvis and hind limb of *Erythrochampsa*, but we lack the skull. Some scutes are also known, and these according to Broom are similar to the scutes in *Notochampsa*. The pelvis of *Erythrochampsa* is definitely crocodilian, and so far as it is known, similar to the same structure in *Protosuchus*. The ischial symphysis is elongated as it is in *Protosuchus*, and as in *Protosuchus* this bone has a prominent anterior prong or process for articulation with the pubis. The pubis is an elongated, rod-like bone, expanded at its distal end into a spatulate-like plate. The proximal end of the bone is missing on both sides, but the evidence of the ischium indicates that the pubis was either completely excluded from the acetabulum or nearly so; in the latter case it would show the same relationships as are to be seen in *Protosuchus*.

Von Huene shows the pes in *Erythrochamp-*

sa as lacking tarsal bones and with the fifth metatarsal well developed and articulating with a large proximal phalanx. This would be a most unusual type of foot to be associated with such a crocodilian pelvis and femur as characterize this particular genus. On the other hand, Broom indicates that there were well-developed astragalar and calcaneal bones in *Erythrochampsa* and that the fifth metatarsal was reduced to the vestigial hook that is so characteristic of the crocodilians and many thecodonts. If Broom's evidence is correct, then *Erythrosuchus* is closely comparable in the structure of its hind limb and pes, as well as in its pelvis, to *Protosuchus*. *Pedeticosuchus* need not be considered in this comparison. It is so different from the other two South African genera that have been discussed, and from *Protosuchus*, that it can safely be regarded as a pseudosuchian, as suggested above.

From the foregoing comparison it can be seen that the genera *Protosuchus*, *Notochampsa*, and *Erythrochampsa* are all closely related to one another, and they can be considered as representing the first major step in the phylogenetic development of the crocodilians, located in such widely separated portions of the world as South Africa and the southwestern United States. Evidently the primitive crocodilians of early Mesozoic times were broadly distributed over the surface of the earth, and it would not be surprising to find representatives of the group in Upper Triassic or Lower Jurassic sediments of other continental regions.

In the Protosuchia the crocodilian habitus had been established. In the heavy dermal armor these animals preserved some of their thecodont heritage, but in many other respects, such as the development of the skull roof, the structure of the squamosal bone, the loss of the antorbital opening, the enlargement of the coracoid, the elongation of the radiale and ulnare bones, the shape of the ischium, the rod-like structure of the pubes, the incipient if not complete exclusion of the pubis from the acetabulum, the presence of a large astragalus and calcaneum, the hypertrophy of the calcaneal tuber, and the great reduction of the fifth digit of the pes, the Protosuchia were well on the way to being thorough crocodilians.
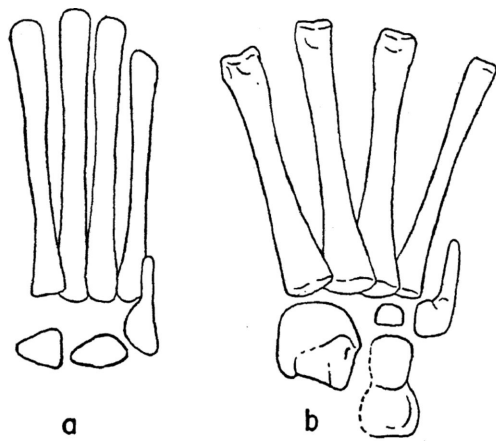

FIG. 20. Comparison of the right pes as seen in dorsal view. A. *Erythrochampsa longipes* (Broom), from Broom (1927, reversed). B. *Protosuchus richardsoni* (Brown). Not to scale.

Von Huene, and especially Broom, have suggested that the pseudosuchian genus *Sphenosuchus*, though probably not an actual pre-crocodile, shows many characters indicating it to be on a line of evolution trending in a general way towards the Crocodilia. These characters are evident in the skull and skeleton and have been outlined by Broom. In this genus the limbs were subequal in size; *Sphenosuchus* was losing the highly cursorial adaptations so typical of the more centrally placed thecodonts, genera such as *Saltoposuchus* which was utilized above to illustrate a rather generalized member of the order. Certainly it is logical to suppose that the early crocodilians were derived from some generalized thecodonts such as *Saltoposuchus*, through an adaptational line such as that represented by *Sphenosuchus*.

The age relationships of the Protosuchia are very much open to question. It is pointed out above that the stratigraphic position of *Protosuchus* can be variously interpreted, for this reptile can be considered as occurring in sediments of Upper Triassic age, intimately associated with the Chinle formation, or as preserved in sediments of Lower Jurassic age. The evidence in favor of either interpretation is not conclusive, and at the present time there seems to be no decisive manner in which the question can be resolved.

A somewhat similar uncertainty holds for the strata in which the two South African genera were discovered. *Notochampsa* is from the Cave sandstone, while *Erythrochampsa* is from the underlying Red Beds, and both of these horizons, together with the Molteno beds beneath the Red Beds, constitute the Stormberg series. The Stormberg series has been the basis of much stratigraphic controversy in the past. One school of thought regards these sediments as essentially of Lower Jurassic age, ranging from the Rhaetic into the Liassic. The other view is that the Stormberg series is entirely of Upper Triassic age.

The flora of the Molteno sediments has been cited as evidence in favor of a Rhaetic age for this lowest horizon of the Stormberg. However, according to Haughton, "the Rhaetic age assigned to the Molteno plant forms is based upon what is by no means clear

TABLE 2

UPPER TRIASSIC FAUNAS OF EUROPE, SOUTH AFRICA, AND NORTH AMERICA

Keuper	Stormberg Series	Chinle and Dockum Formations Newark Series
Europe	South Africa	North America
Pisces	Pisces	Pisces
Semionotus	*Semionotus*	*Semionotus*
Amphibia		Amphibia
Metoposaurs		Metoposaurs
Reptilia	Reptilia	Reptilia
Thecodontia	Thecodontia	Thecodontia
Staganolepids		Staganolepids
	Sphenosuchids	
Phytosaurs		Phytosaurs
Crocodilia	Crocodilia	Crocodilia
	Notochampsa	*Protosuchus*
	Erythrochampsa	(Dinosaur Canyon beds)
Saurischia	Saurischia	Saurischia
Coelurosaurs		Coelurosaurs
Carnosaurs	Carnosaurs	
Prosauropods	Prosauropods	Prosauropods
Plateosaurus	*Plateosaurus*	
Ictidosaurs	Ictidosaurs	Ictidosaurs
Dromatheres		Dromatheres
	Tritheledonts	

evidence and in view of recent discoveries the conclusion may need considerable revision . . . the undoubted association of *Glossopteris, Chiropteris, Pterophyllum, Callipteridium* and apparently *Rhexoxylon* with the typical Molteno genera *Baiera, Thinnfieldia,* and *Taeniopteris* give a very pronounced Keuper appearance to the flora" (Haughton, 1924, p. 490).

Haughton then goes on to point out the fact that "The vertebrates which it should be remembered come from still higher horizons, when studied in detail, also bear a Triassic aspect" (Haughton, 1924, p. 490). This is particularly apparent as regards the dinosaurs, *Euskelesaurus* and *Plateosaurus* in the lower Red Beds and *Thecodontosaurus, Massospondylus,* and *Gyposaurus* in the upper Red Beds and the Cave sandstones. All these are characteristic Upper Triassic types. Moreover, it should be pointed out that *Semionotus,* a distinctive Triassic holostean fish, occurs in the Cave sandstone. The evidence of these reptiles and of the fish indicates that the Stormberg series is approximately equivalent to the Keuper of Europe and the Upper Triassic of other regions. The argument that crocodilians indicate a Jurassic age, since by definition no crocodilians appeared prior to the Jurassic period, is hardly a valid one. It is being maintained here that the primitive crocodilians cannot be accepted as definitive regarding the age of the sediments in question; age determinations must rest upon other evidence.

The evidence for an Upper Triassic age for the Stormberg series suggests that a similar age may hold for the very puzzling sediments containing *Protosuchus* in Arizona. Since the African horizons are, on the basis of other vertebrates, probably Keuper in relationships, and since they contain crocodilians closely related to *Protosuchus,* it seems to the present authors that weight is added to the evidence that would place the Dinosaur Canyon beds in the Triassic rather than in the Jurassic sequence.

The general resemblances between the Upper Triassic faunas of North America, notably the Chinle, Dockum, and Newark assemblages, together with *Protosuchus* and the fauna of the Stormberg series of South Africa and the Keuper faunas of Europe, are shown in table 2.

SUMMARY

IN THIS PAPER there are presented a description in detail and a discussion of *Protosuchus richardsoni*, from the Dinosaur Canyon beds of northern Arizona. It is shown that the Dinosaur Canyon beds are intermediate in position between the typical Upper Triassic Chinle formation below, and the supposed Lower Jurassic sediments above. Consequently, the relationships of the Dinosaur Canyon beds and its contained fossils to the Triassic below or the Jurassic above are a question open to some differences of opinion.

Protosuchus is definitely a primitive crocodilian. It is small as crocodilians go, being about 1 meter in length. The skull is rather short and broad and quite crocodilian in many of its features. For instance, the skull roof shows a characteristic crocodilian arrangement of bones, with the squamosal, the parietals, and the frontals enlarged, and with the supratemporal fenestrae reduced in size. The top of the cranial region is quite flat, as is typical of many crocodilians. There is no antorbital fenestra, which is a character diagnostic for the crocodilians. In some respects, however, *Protosuchus* shows either primitive characters or special features in the skull. The orbit is directed more laterally than in most crocodilians. The snout is short, yet in the front part of the dental series there is a long diastema between the last premaxillary tooth, which is enlarged, and the first maxillary tooth, a most peculiar specialization for a crocodilian.

There seemingly are 24 presacral vertebrae in *Protosuchus*, a number similar to that for the crocodilians, while there are two sacrals and about 35 caudals. The vertebrae are platycoelous, and in the dorsolumbar and caudal regions they have somewhat elongated centra, while the spines are closely comparable in relative height and strength to the vertebral spines in other crocodilians. *Protosuchus* shows a definite advance towards the crocodilians in the extension of the transverse processes, to which the ribs are articulated by both head and tubercle in the region behind the neck.

The shoulder girdle is strongly crocodilian in that the coracoid is greatly elongated to such a degree that it is almost equal to the scapula in size. The bones of the leg are similar to those of the Crocodilia, and the radiale and ulnare in the carpus are elongated fully as much as they are in typical crocodilians of Mesozoic, Cenozoic, and Recent times.

The pelvis is characterized by the elongated, rod-like pubis, a crocodilian character, but proximally this bone participates in the acetabulum, whereas in later crocodilians it is completely excluded from the acetabulum. The ischium is large, and the two ischia are joined by an extensive symphysis. The ilium is elongated anteriorly to form a strong process above and in front of the acetabulum. As in the fore limb, the bones of the hind limb are very much like the same bones in other crocodilians. The astragalus and calcaneum on the tarsus are enlarged, and the latter bone is characterized by its large, expanded tuber. The fifth digit is reduced to a short, metatarsal hook, a character that is inherited by the crocodilians from their thecodont ancestors.

The body armor is heavy. On the back there is a double row of rectangular scutes running along the midline, while the belly and the ventral and lateral surfaces of the tail are protected by smaller rectangular scutes.

This array of characters indicates the strong crocodilian habitus of *Protosuchus*, for it is evident that in most respects this reptile is a true crocodilian. It does retain certain thecodont heritage characters, but these are quite secondary in importance as compared with the crocodilian features that typify the genus.

Such resemblances as are apparent between *Protosuchus* and the thecodonts, especially genera like *Aetosaurus* and *Stegomus*, are clearly due to the persistence in *Protosuchus* of basic thecodont heritage characters or to parallelism in evolution. On the other hand the resemblances between *Protosuchus* and the South African genera *Notochampsa* and *Erythrochampsa* are close and are based on the comparisons of crocodilian habitus characters. Therefore, *Protosuchus*, *Notochampsa*, and *Erythrochampsa* are without much doubt closely related, and are here considered as members of a single family and suborder of ancestral crocodilians.

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