

STUDIES OF THE PHYTOSAURS  
*MACHAEROPROSOPUS* AND  
*RUTIODON*

EDWIN HARRIS COLBERT

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*SOPUS* AND *RUTIODON*





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*PROSOPUS* AND *RUTIODON*

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## CONTENTS

GENERAL INTRODUCTION . . . . .	59
PART 1. A LARGE <i>Machaeroprotopus</i> FROM ARIZONA . . . . .	60
Introduction . . . . .	60
Description . . . . .	60
Taxonomy, Diagnosis, and Materials . . . . .	60
Skull . . . . .	61
Mandible . . . . .	63
Vertebrae . . . . .	64
Ribs . . . . .	64
Pectoral Girdle . . . . .	64
Pelvis . . . . .	64
Humerus . . . . .	65
Femur . . . . .	67
Feet . . . . .	67
Scutes . . . . .	67
Summary . . . . .	67
Species, Growth, and Sexual Dimorphism in the Chinle Phytosaurs . . . . .	67
Described Species and Skull Characters of Chinle Phytosaurs . . . . .	67
Size . . . . .	70
Robustness . . . . .	70
Crest on Rostrum . . . . .	70
Posterior Expansion of the Premaxillae . . . . .	71
Elevation of the External Nares . . . . .	72
Proportion of Prenarial Length to Length of Skull . . . . .	72
Shape of the Squamosal Process . . . . .	73
The Postorbital-Squamosal Bar . . . . .	73
Number of Teeth . . . . .	75
Spacing of Teeth . . . . .	75
Analysis of Skull Characters in <i>Machaeroprotopus</i> . . . . .	76
Skull Characters in <i>Machaeroprotopus</i> Compared with Growth Characters in the Alligator Skull . . . . .	76
PART 2. A MOUNTED SKELETON OF <i>Rutiodon</i> . . . . .	79
Introduction . . . . .	79
Skull and Mandible of <i>Rutiodon</i> . . . . .	80
Skull . . . . .	80
Mandible . . . . .	87
General Form and Proportions . . . . .	88
<i>Rutiodon</i> , Other Phytosaurs, and Crocodilians . . . . .	93
Remarks Concerning the Mounted Skeleton of <i>Rutiodon</i> . . . . .	94
BIBLIOGRAPHY . . . . .	95

## TABLES

1. Measurements (in Millimeters) and Indices of Skulls . . . . .	65
2. Measurements (in Millimeters), Ratios, and Indices of Skeletal Elements . . . . .	66
3. Interpretation of External Narial Development in the Chinle Phytosaurs . . . . .	71
4. Analysis of Skull Characters in <i>Machaeroprosoopus</i> . . . . .	76
5. Comparative Measurements of <i>Rutiodon</i> , Other Phytosaurs, and Certain Crocodilians . . . . .	91
6. Ratios and Indices of <i>Rutiodon</i> , Other Phytosaurs, and Certain Crocodilians . . . . .	92



## GENERAL INTRODUCTION

THE PHYTOSAURS are thecodont reptiles of Triassic age, remarkable particularly for the close parallelism which they show to the modern crocodilians. Or perhaps it might be better to say that the crocodilians show parallelisms with the phytosaurs, since the phytosaurs were first on the scene and set a pattern of reptilian adaptations which was subsequently imitated by the crocodilians. Indeed, the close parallelisms between certain genera in these two separate orders of reptiles constitute some of the finest examples of this phenomenon in the evolutionary record.

Consequently the phytosaurs have attracted the attention of various students in the past, and within recent years several comprehensive works on these reptiles have appeared, of which particular mention should be made of studies by von Huene, by Case, the monograph by McGregor (1906), and the splendid memoir by Camp (1930). In view of what has already been written about these long-extinct reptiles it might seem that additional contributions are not necessarily needed at the present time. However, some materials in the American Museum of Natural History have under scrutiny shown so many interesting points bearing upon the problem of phytosaurian adaptations and evolution that a paper describing and interpreting these materials is felt to be in order. These are the reasons for the present contribution.

This paper is in two parts. The first section is based upon a very fine and extraordinarily large skull, with certain associated skeletal

elements, of *Machaeroprotopus*, discovered and collected in Arizona by Messrs. Barnum Brown and R. T. Bird of the American Museum of Natural History. The second part deals with a new composite mount of *Rutiodon carolinensis*, as worked up by Mr. Charles Lang of the American Museum Paleontological Laboratory, in collaboration with the author, from materials collected by the late William Diller Matthew at Egypt, North Carolina, and originally described by James H. McGregor in 1906.

The drawings illustrating this paper were made by Mr. John C. Germann.

At this place I wish to acknowledge the many kindnesses extended to me by Prof. Charles L. Camp, the outstanding modern authority on the phytosaurs. With Professor Camp's permission I was allowed to study the fine series of *Machaeroprotopus* skulls in the University of California collections, including unpublished materials. In addition I had the privilege of discussing problems of phytosaurian evolution at some length with Professor Camp, and finally the opportunity of traveling with him over the area in Arizona from which the University of California collections were made.

The catalogued collections of various institutions are referred to with the following abbreviations:

- A.M.N.H., The American Museum of Natural History
- M.C.Z., Museum of Comparative Zoölogy, Harvard University
- U.C.M.P., University of California, Museum of Paleontology
- U.W., University of Wisconsin

## PART 1. A LARGE *MACHAEROPROSOPUS* FROM ARIZONA

### INTRODUCTION

THE SUBJECT OF THIS CONTRIBUTION is an extraordinarily fine skull and jaw of the parasuchian genus *Machaeroprosopus*, together with portions of the skeleton. The specimen, A.M.N.H. No. 3060, was discovered and excavated during the summer of 1936, by Messrs. Barnum Brown and R. T. Bird of the American Museum of Natural History, at the "Ward Fossil Locality," in the vicinity of the old Tanner Crossing and about 3 miles east of Cameron, Arizona. It is an especially large specimen—indeed it would seem to be the largest known phytosaur—and the skull is virtually complete and uncrushed, a rather rare occurrence in these ancient reptiles. For these reasons it is felt that this fossil merits a careful study and description, even though our knowledge of the genus has been fully and admirably elucidated by Camp (1930).

In the American Museum collections are several other specimens of *Machaeroprosopus*, which, needless to say, are much less complete and less perfectly preserved than the fossil listed above. These were found by Dr. Brown at various times in the course of his work in the Triassic of Arizona, and since these specimens came from localities not far distant from that at which No. 3060 was found, they will be used for any supplementary information that they may afford.

In the course of the study of these new phytosaurians it has been necessary to go into the questions of specific relationships, individual variations, and sexual dimorphism in the genus *Machaeroprosopus*. As a result of these correlative investigations certain remarks bearing upon them will be included in the present work, after the formal description of the specimen has been made.

### DESCRIPTION

#### TAXONOMY, DIAGNOSIS, AND MATERIALS

##### *MACHAEROPROSOPUS* MEHL

*Machaeroprosopus* MEHL, 1916, Bull. Univ. Oklahoma, new ser., no. 103, p. 5.

TYPE: *Machaeroprosopus validus* Mehl.

##### *Machaeroprosopus gregorii* Camp

*Machaeroprosopus gregorii* CAMP, 1930, Mem. Univ. California, vol. 10, p. 43.

TYPE: U.C.M.P. No. 27200, a skull with lower jaws, eight associated vertebrae, a femur, and three dermal scutes.

HORIZON: Upper portion of the Lower Chinle, estimated to be 300 feet above the base of the Chinle.

TYPE LOCALITY: Six miles southwest of Round Rock trading post and 3 miles southeast of Round Rock, northern Apache County, Arizona. U.C.M.P. Locality A272.

DIAGNOSIS: A very large member of the genus *Machaeroprosopus*. Anterior portion of the rostrum heavy, with a middorsal swelling of the premaxillary, which is continued as a crest back to the nasals. Tip of premaxillary expanded and carrying two enlarged teeth on either side. Alveolar border

of premaxillary expanded in its posterior portion and carrying several greatly enlarged teeth. Teeth large. Alveoli crowded, but with the septae retained. Posterior maxillary teeth beneath posterior border of antorbital fenestra. Nasals elongated. Squamosal with tip produced somewhat posteriorly, fairly deep but compressed. Parietals small, excavated posteriorly by the supratemporal fenestra, which is rather large and prominent as seen in a dorsal view. Postorbital bar thin. Internal nares directly beneath external nares. Symphysis long, its posterior border being opposite the thirty-third tooth in the dentary.

MATERIALS: A.M.N.H. No. 3060, skull and jaws, virtually complete and uncrushed; six vertebrae, which have been identified as follows: axis, third, fourth, fifth, and seventh cervicals, third dorsal; cervical rib and fragments of other ribs; left humerus, right ilium, ischium, and pubis, right and left femora; left ilium and ischium; dermal plates, probably from the throat region; various fragments. Chinle. From the Ward Fossil Locality, about 3 miles east of Cameron, Arizona. Brown and Bird, 1936.



The following specimens of the genus, not necessarily belonging to the species *Machaeroprotopus gregorii*, have been used for supplementary observations:

A.M.N.H. No. 3000, fragmentary skull and lower jaws. Chinle. From the "Blue Hills," 3 miles east of Cameron, Arizona. Brown, 1930.

A.M.N.H. No. 3001, various vertebrae, dermal plates, and foot bones. Chinle. Rock Crossing, 4 miles north of Cameron, Arizona. Brown, 1930.

A.M.N.H. No. 3002, portion of a skull vertebrae, and dermal plates. Chinle. Said to be from about 25 miles east [southeast?] of Cameron, Arizona. Brown, 1930.

A.M.N.H. No. 3003, portion of a skull. Chinle. Same locality as A.M.N.H. No. 3002. Brown, 1930.

A.M.N.H. No. 3004, plates. Shinarump conglomerate 100 feet above the Moencopi. About 6 miles east of Cameron, Arizona. Brown, 1930.

A.M.N.H. No. 6760, vertebrae. Chinle. Near Cameron, Arizona. Brown, 1930.

#### SKULL

As was mentioned in the introduction to this paper, the specimen with which we are concerned is of unusual size; in fact it is probably the largest phytosaur known at the present time. The skull is 1420 mm. (4 feet 8 inches) long from the back of the squamosals to the tips of the premaxillaries, a length that may be compared with the measurement of 1230 mm. for the type of *Machaeroprotopus gregorii*, and with 1243 mm. for the large skull and jaws from the Triassic of Texas, described by Case as the type of *Brachysuchus megalodon*. It would appear that the present specimen is larger than any phytosaurs known from the Triassic of the Old World.

**PREMAXILLARIES:** The premaxillary bones are large and heavy, and their lower borders form approximately one-half of the alveolar length. These bones are conspicuously expanded anteriorly, and dorsally they rise in their posterior region to help form the crest that runs from the narial openings along the dorsal midline of the snout. There are two greatly expanded teeth on either side in the tips of the premaxillaries, and behind these teeth there is a marked upswing of the alveolar border to form a notch for the reception of certain large dentary teeth. The posterior part of the alveolar border of the

premaxillary is expanded to contain enlarged teeth, and this gives to the lower border of the upper jaw its characteristic sinuosity.

**MAXILLARIES:** The maxillaries show the usual relationships with the premaxillaries, nasals, jugals, prevomers, palatines, and ectopterygoids. Laterally and posteriorly these bones show an expansion of their alveolar borders which accentuates the sinuous outline of the upper tooth row, already mentioned. The posterior portion of the lateral plate of the maxillary is deeply excavated by the antorbital fenestra.

The teeth are crowded in the premaxillary and maxillary alveoli, a circumstance owing in part to their relatively large size. This crowding certainly is not to be attributed to an unusual number of teeth, because the present specimen is closely comparable to other individuals of this genus with regard to tooth count. Thus, in this fossil there appear to be about 37 upper teeth on either side of the upper jaw, a condition that may be compared with 37 teeth in the generic type, *Machaeroprotopus validus*, with 41 teeth in the upper jaw of *Machaeroprotopus gregorii*, and with 41 in the upper jaw of *Machaeroprotopus adamanensis*, as figured by Camp. In the type of *Brachysuchus megalodon* there are about 47 upper teeth on either side. The teeth are heavy and robust, and the ones in the back of the maxilla have strong anterior and posterior keels.

**SEPTOMAXILLARIES:** As pointed out by Camp, the septomaxillae are large and elongated, inserting themselves between the premaxillaries and the nasals in the dorsal aspect, and forming most of the internarial septum. Camp has shown how these bones spread posteriorly on the ventral surface of the nasals in this genus.

**NASALS:** The nasals are large, extending anteriorly to a point opposite the front of the antorbital fenestra, posteriorly to a point in line with the fronts of the orbits, and laterally almost to the upper border of the antorbital fenestra. In some specimens of *Machaeroprotopus*, figured by Camp, the nasals reach the upper border of the antorbital fenestra, so this evidently is a variable relationship in the genus. The nasals in the present specimen are not elevated, which is taken as an indication that it was a male

specimen. Camp has shown that in about half of the known specimens of *Machaeroprotopus* the nasals are elevated to form a volcano-like eminence on the top of the skull, and this together with the slender snout of such forms in which it occurs is regarded by him as a female character. In the supposed males the nasals are not elevated and the snout is heavy. Case (1932, p. 77) disagrees with this opinion.

**LACRIMALS:** Of large size, the lacrimals are excavated in front by the posterior border of the antorbital fenestra and in back by the anterior border of the orbit.

**PREFRONTALS:** The prefrontals are thick bones forming a part of the orbital borders and occupying an anterolateral position in relation to the frontals.

**POSTFRONTALS:** Similar in size to the prefrontals, the postfrontals also form a part of the orbital border and are situated posterolaterally in relation to the frontals.

**FRONTALS:** The frontals are comparatively large and form the middle portion of the upper border of the orbit.

**PARIETALS:** As compared to the frontals, the parietals are small bones and are deeply excavated behind by the superior temporal openings. Posteriorly each parietal is produced back in a process that meets the supraoccipital below, while it joins with a forwardly extending process of the squamosal to form a long bar or brace that connects the occipital and squamosal regions of the skull.

**POSTORBITALS:** The postorbitals show the usual thecodont relationships; in each there are a posterior bar that unites with the squamosal and a ventrally directed process adjoining the jugal and lacrimal. The postorbital-squamosal bar is comparatively thin, in decided contrast with some of the other large members of the genus, notably the generic type, *Machaeroprotopus validus*. Owing to the comparatively thin postorbital-squamosal bar the supratemporal fenestra is broadly visible in a dorsal view of the skull, as is the case in the type of *Machaeroprotopus gregorii*. This condition may be compared with that of *Machaeroprotopus validus*, in which the postorbital-squamosal bar is so broad that it overlaps the supratemporal fenestra, hiding the opening in a dorsal view of the skull.

**JUGALS, QUADRATOJUGALS:** These bones together form the lower border of the lateral temporal fenestra, the latter bone, as is usual in this genus, being expanded into a broad, triangular plate.

**QUADRATE:** The quadrate, adjoining the posterior border of the quadratojugal, is transversely broad, and on its inner side it extends up to join the squamosal, while a forwardly produced wing meets the pterygoid.

**SQUAMOSALS:** Camp has devoted a considerable amount of attention to the squamosals in *Machaeroprotopus*, because he considers that the form of these bones is diagnostic for the several species that at the present time constitute the genus. In this present specimen the squamosal is produced backwardly as a broadly rounded tip, very similar to what it is in the type of *M. gregorii*, and to a lesser degree similar to the squamosal of *M. adamanensis*. It should be noted that Camp pointed out the similarity in shape between the squamosals in *M. gregorii* and *M. adamanensis*, so the present specimen would seem to fit in with previous evidence as to this character. In its entirety the squamosal is a complicated bone that has been fully described by Camp.

**TABULARS, INTERPARIETAL:** It is not possible, in the specimen now under consideration, to distinguish the tabulars, but it may be assumed that they are essentially as Camp has described them for the genus. According to Camp these bones are situated beneath the posterior processes of the parietals, and they form a portion of the deep median fossa which must have served for the insertion of the ligamentum nuchae. The median part of this fossa is occupied by the fused interparietals.

**SUPRAOCCIPITAL, EXOCCIPITALS:** In this genus the supraoccipital is located beneath the fused interparietals, in the median posterior fossa, and forms the dorsal border of the foramen magnum, while the exoccipitals form the lateral borders of the opening and cover its floor.

**BASIOCCIPITAL:** Also seen in the posterior aspect of the skull is the heavy basioccipital which is the major element of the occipital condyle. This strong bone, necessarily so because of its function as the articulation for a remarkably large and heavy skull, is



elongated and, as Camp has shown, is excluded from the foramen magnum by the exoccipitals above it. It shows the rather ventrally directed articulating surface characteristic of the genus, an indication that the head was generally carried in a horizontal or downwardly directed pose. A small notochordal pit pierces the center of the articulating surface.

**PROOTICS, OPISTHOTICS:** The opisthotics or paroccipitals are as Camp has described them for the genus—long bones, expanded posteriorly to articulate with the squamosal and quadrate. Anteriorly these bones have a broad contact with the supraoccipitals and the prootics, the latter elements forming the forward walls of the neurocranium.

**PARASPHENOID:** In this specimen the parasphenoid is readily visible as an elongated blade, rather compressed along its ventral edge and trough-shaped on its dorsal surface. Posteriorly it abuts against the basisphenoid and serves to enclose in part the hypophyseal pit. Anteriorly it is enfolded on either side by the vertical plates of the pterygoid-prevomer complex, which in this specimen are very high and prominent.

**PRESPHENOID:** The presphenoid, being a small element in *Machaeroprotopus*, is not well defined in the present specimen. Indeed, it may be missing altogether.

**BASISPHENOID:** This bone is typical of the genus—a heavy element forming a portion of the floor of the brain case. It has a strong sutural articulation with the basioccipital, while anteriorly it supports the expanded base of the parasphenoid.

**PREVOMER, PTERYGIDS, PALATINES, ECTOPTERYGIDS:** There is nothing in particular to say about these bones in the specimen under consideration. Together they form the palatal vault, which, as Camp has shown, is rather compressed along the region of the midline, as if there had been in life a cartilaginous floor that served in part to enclose the air passage. Camp has described the manner in which the pterygoids, prevomers, and palatines are intimately associated, extending up in the middle region of the skull as extensive and complicated vertical plates. So far as may be determined, the present specimen accords with the condition as described by Camp for the genus as a whole.

According to Camp the "Internal choanae are much larger than the external" in the genus *Machaeroprotopus*. The specimen under consideration does not accord with Camp's characterization in this regard. Whether the difference is of any importance so far as it affects Camp's suppositions as to the relationships of Jacobsen's organ and the course of the air passage is a question that can hardly be answered at the present time.

It might be said here that the anterior borders of the external nares are directly above the anterior borders of the internal nares, a characteristic relationship in the genus *Machaeroprotopus*.

#### MANDIBLE

The mandible of the American Museum specimen accords in most respects with the description given by Camp for the mandible of the genus *Machaeroprotopus*, as based upon the specimens he studied. A brief review of the form and disposition of the mandibular elements is presented in the following remarks.

**DENTARIES:** The dentaries are large and swollen at their tips to receive the enlarged terminal teeth. There are three of these on either side. Although the remainder of the dentary teeth are not so large as those at the tips of the bones, they are, nevertheless, very heavy and robust, and are crowded together in the bone. The dentaries extend far posteriorly so that the last alveoli are located well up on the coronoid process. Ventrally each dentary bounds the lateral sulcus.

In the dentaries there appear to be about 44 teeth on either side, a number that is somewhat intermediate between the count of 44 to 50 in the several specimens described by Camp (47–48 for *M. gregorii*), and the 40 teeth present in the dentary of *Machaeroprotopus validus*.

**SPLENIALS:** A major portion of the symphyseal junction is occupied by the very large splenials, which form much of the lingual surfaces and the ventral borders of the lower jaws. These bones also form the internal borders of the alveoli.

**SURANGULARS, CORONIDS:** Posteriorly the splenials articulate with the surangulars, each of which is large and forms the high coronoid

process for the attachment of the powerful capito-mandibularis muscles. Camp has shown that there were also coronoid bones in this genus but they are usually lost, as is the case in the present specimen.

**ANGULARS:** Beneath the surangulars are the elongated angulars. According to Camp these elements do not quite reach the posterior tip of the lower jaw in *Machaeroprotopus*, but in the present specimen they have every appearance of so doing. In fact, on the posterior surface of the process at the back of the lower jaw there is a distinct suture that seems to be the junction between the angular on the external surface of the ramus and the articular on the lingual surface.

**ARTICULARS:** The articulars are heavy elements, very broad, and rather deep. They form a wide glenoid to articulate with the broadened condyle of the quadrate. As Camp has shown, the outer portion of the glenoid is formed by the angular, there being a distinct groove that marks the junction of the articular and angular in the articulating surface. This present specimen shows the broken base of the posterior process of the articular, which was first noticed and described by Camp.

**PREARTICULARS:** The prearticulars are long bones above the angulars, on the lingual surfaces of the rami.

#### VERTEBRAE

As mentioned above (p. 60) there are six vertebrae associated with the skull under consideration, and these have been identified as the axis, the third, fourth, fifth, and seventh cervicals, and the third dorsal. Except for the axis, it is difficult to be absolutely certain as to the exactness of these identifications, but it is felt that they approximate as nearly as possible the correct positions. These are characteristic phytosaurian vertebrae. In each the centrum is characterized by its expanded concave articulating faces and its constricted middle portion. The neural spine is long, and expanded at the top, and there are long transverse processes from the neural arch, terminating in the diapophyses. The spine of the axis is large. All in all, these vertebrae accord with the descriptions given by Camp for the vertebrae of *Machaeroprotopus*.

#### RIBS

The ribs in this specimen are represented by a cervical rib and the proximal end of another with the capitulum and tubercle preserved. This latter is shown in plate 6.

#### PECTORAL GIRDLE

The only element of the pectoral girdle preserved in this specimen is a single clavicle, seemingly from the right side. This is a short, stout, and rather straight bone, the acromial end of which is sharply pointed. It resembles the same element in *Machaeroprotopus adamensis* as figured by Camp (1930, fig. 14) except that it is considerably straighter. The medial end of the bone is broken, but there is evidence that it terminated in a sort of hook-shaped knob, as was inferred by Camp from the material under his observation. The anterior border of the bone is flattened; the ventral surface contains a deep groove, the prominence of which may be due in some part to crushing. This bone is shown in plate 6.

#### PELVIS

Associated with the large skull of *Machaeroprotopus gregorii*, described above, were the pelvic bones of the right side, in an excellent state of preservation. Because of the importance of the pelvis in taxonomic and phylogenetic considerations of the reptiles these bones deserve some careful attention.

On page 77 of his monograph of 1930, Camp has made in tabular form a detailed comparison of the ilia in various genera of phytosaurs. As might be expected, the present specimen accords closely with *Machaeroprotopus* and *Clepsysaurus* in the characters of the ilium. Thus it shows the small muscular process on the anterior portion of the iliac crest, the long post-ilial process, the juncture of the ischio-pubic border beneath the pre-ilial notch, the short pre-ilial process, the somewhat upward bowing of the iliac crest just behind the pre-ilial process, and the inwardly bowed ischial suture, all of which are characters typical for *Machaeroprotopus*. This present specimen does differ, however, from the ilia described by Camp in two respects. In the first place the acetabulum is essentially round, so that

TABLE 1  
MEASUREMENTS (IN MILLIMETERS) AND INDICES OF SKULLS

	Total Length	Prenarial Length	Postnarial Length	Index: Postnarial Length to Total Length
<i>Machaeroprotopus</i>				
<i>gregorii</i> , A.M.N.H. No. 3060	1420	750	670	47
<i>gregorii</i> type, U.C.M.P. No. 27200	1230	671	559	46
<i>lithodendrorum</i> type, U.C.M.P. No. 26688	1215	660	555	46
<i>lithodendrorum</i> , U.C.M.P. No. 26719	965	546	399	42
<i>lithodendrorum</i> , U.C.M.P. No. 27179	815	510	305	37
<i>lithodendrorum</i> , U.C.M.P. No. 27181	678	419	259	38
<i>adamanensis</i> type, U.C.M.P. No. 26699	1095	618	477	42
<i>adamanensis</i> , U.C.M.P. No. 27007	951	570	381	40
<i>tenuis</i> type, U.C.M.P. No. 27018	819	513	306	37
<i>tenuis</i> , U.C.M.P. No. 27149	1169	628	541	46
<i>buceros</i> type, A.M.N.H. No. 2318	830	520	310	37
<i>validus</i> type, U.W. No. 3807	970	560	410	42
<i>Phytosaurus kappfi</i> <sup>a</sup>	690	420	270	47
<i>Mystriosuchus planirostris</i> <sup>a</sup>	785	560	225	28
<i>Rutiodon carolinensis</i>	715	470	245	33
<i>Paleorhinus bransonii</i> <sup>a</sup>	730	375	355	48
<i>Leptosuchus crosbiensis</i> <sup>a</sup>	810	450	360	44
<i>Brachysuchus megalodon</i> <sup>b</sup>	1266	714	552	44

<sup>a</sup> From Camp, 1930.

<sup>b</sup> From Case, 1929.

its height and length are about equal, as contrasted with the elongated acetabula seen in the University of California specimens of *Machaeroprotopus*. Secondly the pubic articular surface is definitely longer than the ischial, as contrasted with the equal surfaces seen by Camp. On the whole, the resemblances between this ilium, the ilium of *Machaeroprotopus adamanensis*, as figured by Camp, and the same element in *Clepsysaurus* as figured by Sinclair (1918), are very close.

The ischium of this specimen is seemingly a stockier, heavier element than it is in the type of *Machaeroprotopus adamanensis*. For instance, the ischium figured by Camp projects back considerably beyond the iliac crest, while the "neck" of that bone (the portion between the ilio-pubic sutures and the ischial symphysis) is indicated as being greatly constricted. In the present specimen, on the other hand, the posterior border of the ischium is apparently about directly underneath the back of the iliac crest, while the "neck" of the bone is relatively broad.

Further differences are to be seen in the pubis. In the present specimen it is noticeably a longer bone in relation to its height than is the case in the type of *Machaeroprotopus adamanensis*.

#### HUMERUS

Camp has shown that the width of the head of the humerus is very great in *Machaeroprotopus*, and such is the case in the specimen under consideration. The relationship of length divided by width of head is 2.3 in this specimen, as compared with L/W 2.5-3.0 for the genus *Machaeroprotopus*, according to Camp. Thus it can be seen that this animal had a great proximal expansion of the humerus, as might be expected in so large an individual. This specimen accords with Camp's descriptions in that the median portion of the head is high, while the deltoid crest is long. It is characterized by its very pronounced entepicondylar groove, a decided contrast to the implied condition for the material available to Camp. "The entepi-

condylar groove is less developed than in p. 81). This specimen appears to have a the European forms . . ." (Camp, 1930, groove as fully developed as in the European

TABLE 2  
MEASUREMENTS (IN MILLIMETERS), RATIOS, AND INDICES OF SKELETAL ELEMENTS

	<i>Machaeroprotopus gregorii</i> A.M.N.H. No. 3060	<i>Machaeroprotopus adamanensis</i> U.C.M.P. Nos. 26717, 26718	<i>Machaeroprotopus adamanensis</i> type From Camp, 1930
Humerus			
Greatest length	429	408	—
Width of head	172	140	—
Index: $W/L^a \times 100$	40	34	—
Femur			
Greatest length	522	492	—
Width of proximal end	136	132	—
Index: $W/L \times 100$	26	28	—
Ratio: L humerus/L femur	82	83	—
Pelvis			
Length	545	—	—
Height	358	—	—
Ilium			
Length of iliac crest	308	—	252
Height	177	—	158
Ischium			
Length	290	—	264
Breadth of "neck"	110 <sup>b</sup>	—	50
Pubis			
Length	250 <sup>b</sup>	—	200
Depth of pubic plate	165 <sup>b</sup>	—	140
Acetabulum			
Anterior to posterior length	135	—	160
Vertical height	148	—	110
Axis			
Total height	253	—	—
Transverse diameter of centrum	85	—	—
7th cervical			
Total height	298	—	—
Transverse diameter of centrum	83	—	—
3d dorsal			
Total height	250	—	—
Transverse diameter of centrum	86	—	—
Width across transverse process	237	—	—

<sup>a</sup> W, width; L, length.

<sup>b</sup> Approximate.



forms, and certainly more pronounced than in *Rutiodon*.

#### FEMUR

This bone is essentially as it has been described by Camp. It is a long and rather straight bone with a long fourth trochanter and well-developed distal condyles. The width of the head is contained in the length of the bone about 3.75 times, which accords with the condition typical for *Machaeroprosoopus*.

#### FEET

A single toe bone represents the foot in this specimen. It appears to be a phalanx, short and very broad proximally. It is shown in plate 6.

#### SCUTES

Various bony scutes were found associated with the skull and skeletal elements. There is a group of heavy articulated scutes, roughly hexagonal in shape and somewhat elongated. It is possible that these came from the region of the throat. In addition there are a few isolated scutes.

#### SUMMARY

In the foregoing description, the large *Machaeroprosoopus* in the American Museum

collections has been compared with various species of the genus, and especially with *Machaeroprosoopus gregorii*. An attempt has been made to show that the specimen under consideration resembles the type of this species, particularly as regards the great size, the heavy rostrum, the middorsal swelling of the premaxillary, the enlargement of the three posterior premaxillary teeth, the smallness of the parietals, and the form of the squamosals.

There is some difference between the two specimens as regards the number of teeth. Thus the 37 upper teeth and the 44 lower teeth (on either side) in the American Museum specimen may be compared with the 41 upper teeth and the 47 lower teeth in the type of *M. gregorii*. These discrepancies are not, however, considered to be of specific import. An examination of a series of *Alligator sinensis* skulls showed a variability of one or two teeth on either side in a total of 18 to 20; consequently a variability of three or four teeth in more than 40 need not be considered as inordinately large.

All in all, the resemblances are considered of sufficient importance to outweigh any differences which may be observable, and the new skull here described is therefore identified as *Machaeroprosoopus gregorii*.

### SPECIES, GROWTH, AND SEXUAL DIMORPHISM IN THE CHINLE PHYTOSAURS

#### DESCRIBED SPECIES AND SKULL CHARACTERS OF CHINLE PHYTOSAURS

We now come to the difficult question as to the interrelationships between, and the validity of, the several supposed species of Chinle phytosaurs belonging to the genus *Machaeroprosoopus*. Perhaps in this connection it might be well first to review briefly the somewhat involved taxonomic history of the genus and its included species, as it is known from the Chinle formation of northern Arizona and southern Utah.

The genus *Machaeroprosoopus* was created by Mehl in 1916, upon the basis of a new species from the Chinle of Arizona, described by him as *M. validus*. It was very unfortunate, to begin with, that Mehl chose the trivial name *validus* for his new form, since this name had already been used by Marsh for a phytosaur from Connecticut (*Belodon*

*validus* Marsh). It so happens that the Connecticut form is indeterminate, being based upon a single scapula, but the probabilities are overwhelmingly strong that it belongs to the genus *Clepsysaurus*, one of the two phytosaurian genera common in the Triassic of eastern North America. And to complicate matters still further, there is good reason to think, as has been shown by Colbert and Chaffee in 1941, that the name *Machaeroprosoopus* may be synonymous with *Clepsysaurus*. Therefore if the identity of *Machaeroprosoopus* with *Clepsysaurus* can be proved at some date in the future, then *M. validus* Mehl becomes invalid since it is a synonym of *Clepsysaurus validus* (Marsh). But until that time it may be advisable to regard *M. validus* Mehl as a good species, the type of the genus *Machaeroprosoopus*.

Still another complication is added to this

problem by the fact that Lucas in 1898 described a phytosaur from the Chinle formation of southern Utah, naming it *Heterodontosuchus ganei*. It is very probable that the type of this species, which is the forward part of a mandible, is generically and specifically the same as some of the material subsequently described under the name of *Machaeroprotopus*. If this could be proved, then the generic name given by Lucas in 1898 would have precedence over the name coined by Mehl in 1916, assuming of course that these phytosaurs of the west are generically distinct from *Clepsysaurus* of eastern North America. From all of this it can be seen that the situation with regard to the taxonomy of the phytosaurs of western North America is indeed confused, and difficult of solution. It is here proposed to avoid any further confusion of the problem by regarding *Heterodontosuchus ganei* as an indeterminate type, which in effect it is, thereby disregarding the name *Heterodontosuchus* as having any priority over *Machaeroprotopus*.

In 1887 Cope described a rather small phytosaur from the Triassic of New Mexico and named it *Belodon buceros*. Whether this type came from the Chinle or not is a question that cannot be decided upon the evidence extant, but perhaps for the purposes of this discussion it may be considered as probably a Chinle form. It certainly seems to be a distinct species of *Machaeroprotopus* if it is properly of this genus.

In 1920 Case described *Phytosaurus doughertyi* from the Dockum formation of Texas. This species possibly is referable to *Machaeroprotopus*, but it is outside the limits of the present discussion since it does not come from the Chinle formation. Likewise, *Machaeroprotopus andersoni*, described by Mehl in 1922, is not considered here since it comes from eastern New Mexico, also from the Dockum rather than from the Chinle formation.

There remain to be listed *Machaeroprotopus pristinus* (Mehl), described in 1928 under the generic name of *Pseudopalatus*, and a series of species described by Camp in 1930, namely, *M. zunii*, *M. adamanensis*, *M. gregorii*, *M. lithodendrorum*, and *M. tenuis*.

Upon the basis of this discussion the

phytosaurs of the Chinle formation may therefore be listed as follows:

*Machaeroprotopus* Mehl

Type of genus: *M. validus* Mehl, 1916

*M. buceros* (Cope), 1887

*M. validus* Mehl, 1916

*M. pristinus* (Mehl), 1928

*M. zunii* Camp, 1930

*M. adamanensis* Camp, 1930

*M. gregorii* Camp, 1930

*M. lithodendrorum* Camp, 1930

*M. tenuis* Camp, 1930

Is this multiplicity of species within a single formation, enclosed for the most part within an area that measures about 200 miles in either direction, to be justified upon the basis of critical taxonomic analysis? Do we see in the Chinle a series of species at different levels, representing a time sequence, or do we see rather a series of ascending variations within a single species, or at the most confined to two or three species? This is a problem to which various interpretations may be applied, depending to some degree upon the personal bias of the observer. It is a problem that already has been analyzed and discussed at some length and in a thoroughly objective manner by Camp in his monograph of 1930. However, a further analysis and discussion of the subject will be attempted at this time, since it is felt that additional material and some new methods of approach may be of aid in establishing, so far as possible, a solution of the problem upon as wide a basis as possible.

Camp analyzed a number of well-defined characters in the skull of *Machaeroprotopus* and decided that some of them could be correlated with age and growth in this genus, some with sex, some with taxonomic differences, and some with independent adaptive changes.

The characters correlated by Camp with growth and age were the ratio of the preaural region of the skull to the length of the skull, the posterior expansion of the premaxillary bones, the size of the antorbital fenestrae, and the spacing of the teeth.

The one character that he correlated with sex was the relative elevation of the external nares above the level of the skull roof.

Taxonomic characters established by Camp

were the shape of the squamosal bone, the development of a prenarial rostral crest and a correlated frequent swelling of the middle part of the premaxillae along their dorsal surfaces, and to some extent the number of teeth.

Finally, changes caused by independent adaptations in the skull were specified by

Camp as the depression of the supratemporal fenestrae and the correlative varying width of the postorbital bar.

These and certain other characters visible in the skull of the Chinle phytosaurs, such as size and robustness, can be analyzed either quantitatively or qualitatively. At this place, most of the characters mentioned above will

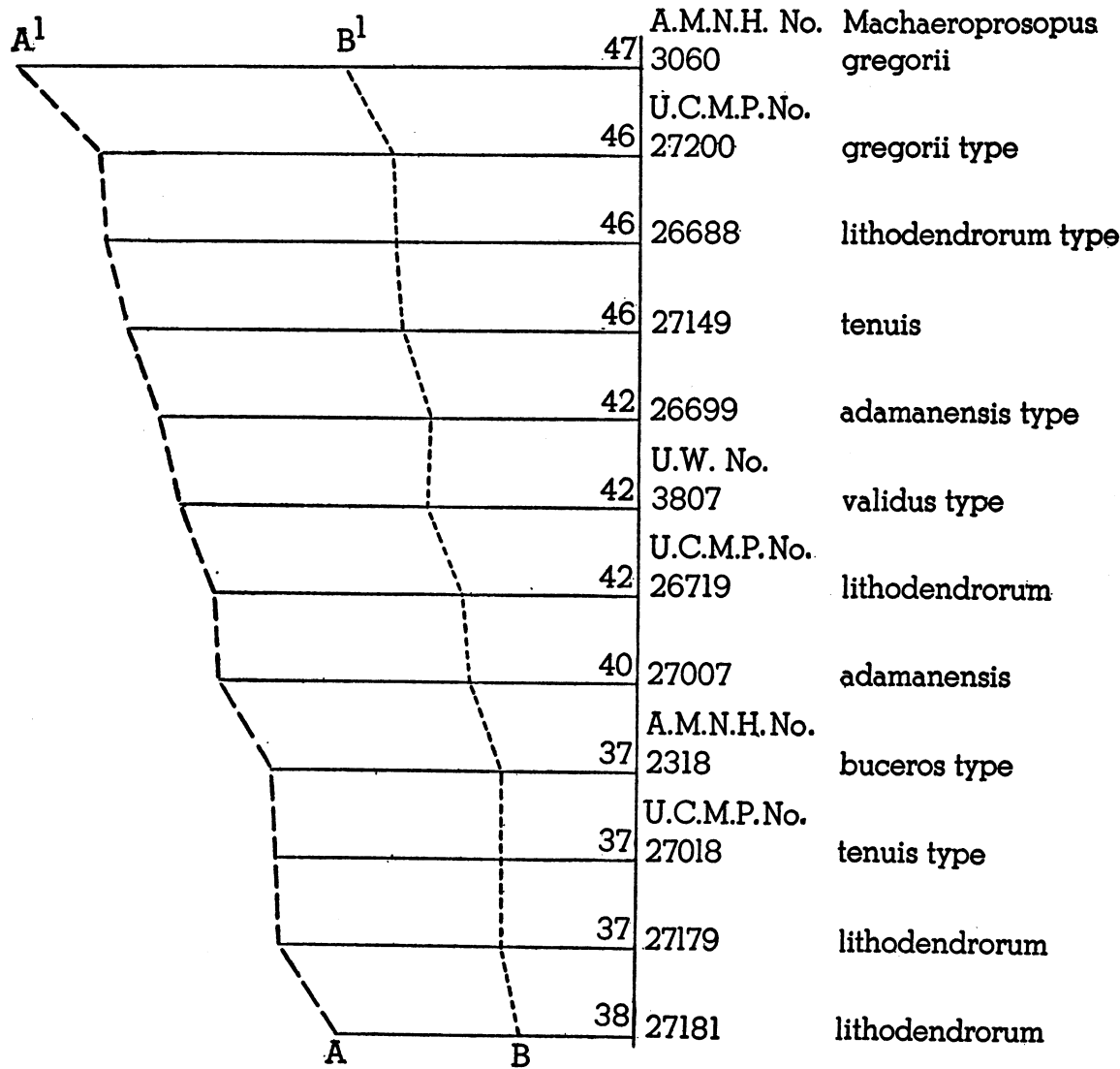


FIG. 1. Graph to show the comparative skull lengths, prenarial and postnarial lengths in various specimens of *Machaeropsopos*. The heavy dotted line (A-A¹) indicates the total skull length in the several specimens; the lighter dotted line (B-B¹) indicates the position of the external nares with regard to the total length of the skull. The portion of each solid line to the left of this light dotted line represents the prenarial length, that to the right the postnarial length. The figures give the ratio of postnarial length to total skull length in each specimen. Data on University of California specimens from Camp, 1930.

be so examined in an attempt to determine their value as indicators of growth or age, sex, and taxonomic differentiation.

#### SIZE

Generally speaking, size is of less taxonomic value in the differentiation of species of reptiles than other characters, for these animals do not have any definite limit to their growth. This is well illustrated by the graph (fig. 1) showing total length, prenarial and postnarial lengths in the Chinle phytosaurs. As will be seen by this graph, there is on the whole a random distribution of the several supposed species through the size range of *Machaeroprotopus*, indicative of the fact that in plotting the size of these reptiles we are dealing with growth factors rather than with taxonomic factors. One important exception to this generalization is to be seen in the case of *M. gregorii*, for there is good reason to think that this form attained greater dimensions in the adult than did any of the other Chinle phytosaurs. Also it might be mentioned that *M. zunii*, not shown on the graph, may have been a relatively small member of the genus. Except for these two forms, however, size as observed in the Chinle phytosaurs appears to be dependent upon the age of the individual, with little sexual or taxonomic significance.

#### ROBUSTNESS

Studies upon the unexcelled series of Chinle phytosaurs in the University of California collections indicate that general robustness of the skull probably is a sexual character in these extinct reptiles. Thus, the broad, heavy skulls are very probably those of males, while the more delicately proportioned skulls may represent the females. This observation seems to correlate reasonably well with the dichotomy of the series based upon the elevation of the external nares and the development of the dorsal rostral crest, to be discussed below. Of course it must be remembered that robustness is in part a factor of growth, and this possibility must be given its proper place in a comparison of the materials. For instance, in a given species, large females will show a greater robustness of structure than small males. However, an examination of some undescribed skulls at the University of Cali-

fornia, all certainly of one species, bears out the contention made above as to robustness as a general indication of sex in these phytosaurs.

#### CREST ON ROSTRUM

According to Camp, "Variations in the contour of the rostrum and the development of dorsal crests are puzzling." This is certainly true. Camp then goes on to cite the theory advanced by certain authors that the rostral ridges or crests are sexual, occurring in the males, absent in the females. This argument is refuted by Camp in the following words:

"We have, from the lower 275 feet of the Chinle, eight adult skulls which show the contour of the rostrum. None of these have elongated crests. Two from the lowest horizons have no crests. Six from the 200-275-foot levels have crests reaching only to the posterior alveolar borders of the premaxillaries. From the next 85 feet of sediments there are seven adult skulls in our collections. All these have elongate rounded crests extending to the tips of the premaxillaries. Above the 360-foot level there are two adult skulls, one of which *M. validus* has a short crest and the other *M. tenuis* a heavy, rounded snout without crests.

"One would infer from this that the development of the crest is a specific rather than a sexual character of adult skulls; that both males and females have it in some species and do not have it in others; and that there is no *pronounced* sexual dimorphism in *Machaeroprotopus*" (Camp, 1930, p. 28).

In the light of additional materials now available, a somewhat different interpretation may be applied to the development of the rostral crest in *Machaeroprotopus*. For instance, in materials identified as *Machaeroprotopus adamanensis*, *lithodendrorum*, and *tenuis* (some of the last as yet undescribed) there are found skulls either with or without the rostral ridge or crest. The presence or absence of the crest is the basic distinction that can be made in these materials. Naturally, in those skulls having the crest there are various phases of development, it being more completely formed in some than in others.

The rostral crest is found on skulls identified (by the development of the external

TABLE 3  
INTERPRETATION OF EXTERNAL NARIAL DEVELOPMENT IN THE CHINLE PHYTOSAURS

EXTERNAL NARES NOT ELEVATED	LENGTH OF SKULL	POSTERIOR EXPANSION OF PREMAXILLARIES
ROSTRAL CREST PRESENT		
Adult males		
A.M.N.H. No. 3060, <i>M. gregorii</i>	1420 mm.	Strong
U.C.M.P. No. 27200, <i>M. gregorii</i> <sup>a</sup>	1230	Strong
U.C.M.P. No. 26688, <i>M. lithodendrorum</i> <sup>a</sup>	1215	Moderate
U.C.M.P. No. 34246, [ <i>M. tenuis</i> ] <sup>b</sup>	1100	Strong
Young males		
U.C.M.P. No. 27288, not identified	1008	Moderate
U.C.M.P. No. 27007, <i>M. adamanensis</i>	951	Absent
U.C.M.P. No. 34250, [ <i>M. tenuis</i> ]	870	Moderate
U.C.M.P. No. 27179, <i>M. lithodendrorum</i>	815	Moderate
EXTERNAL NARES ELEVATED		
ROSTRAL CREST PRESENT		
Adult females		
U.C.M.P. No. 27149, <i>M. tenuis</i>	1169	Strong
U.C.M.P. No. 26699, <i>M. adamanensis</i> <sup>a</sup>	1095	Absent
U.C.M.P. No. 26719, <i>M. lithodendrorum</i>	965	Moderate
ROSTRAL CREST ABSENT		
Young females		
U.C.M.P. No. 34245, [ <i>M. tenuis</i> ]	1059	Absent
U.C.M.P. No. 34251, [ <i>M. tenuis</i> ]	1017	Absent
U.C.M.P. No. 34249, [ <i>M. tenuis</i> ]	865	Absent
U.C.M.P. No. 27018, <i>M. tenuis</i> <sup>a</sup>	819	Absent
U.C.M.P. No. 27181, <i>M. lithodendrorum</i>	678	Absent
U.C.M.P. No. 34228, [ <i>M. tenuis</i> ]	520 (est.)	Absent

<sup>a</sup> Type.

<sup>b</sup> The brackets indicate provisional identifications of specimens as yet undescribed. There is no doubt that these six specimens all belong to a single species.

nares, see below) as both male and female, which supports Camp's conclusion that this is not a sexual character in the adult skulls. Some of the smaller skulls, identified as young males, show the crest, but it is an interesting fact that the smaller skulls identified as females lack the crest. Therefore it is suggested here that the rostral crest is a growth character appearing in all of the adult skulls and in the young males but not in the young females. To some degree it is also a sex character of minor importance, in that if the above suggestion is correct, the young females lack the crest.

Of course conclusions based upon these observations are limited by the fact that in

the series of skulls available there were none representing really juvenile animals. It would be interesting to know whether or not all of the very young individuals lack the rostral crest; whether this was a character that appeared earlier in the males than in the females.

#### POSTERIOR EXPANSION OF THE PREMAXILLAE

Another character in *Machaeroprosoopus* that appears to be dependent upon the age and size of the individual is the posterior expansion of the premaxillary bones, a conclusion reached by Camp. In the description of the large skull preceding this discussion, it was noted that there is an expansion of the



alveolar border in the posterior part of the bone, accompanied by an enlargement of the teeth in this region. This is a character common to the large individuals of the genus, while in the smaller ones such an expansion is either absent or but feebly developed.

This expansion of the premaxillae closely parallels the development of the prenasal crest on the rostrum, discussed above, in that the expansion is found in virtually all the so-called males and the adult females, while it is not present in the young females. Thus, in table 3 it will be seen that the posterior portion of the premaxillae is expanded in all the supposed males except one young individual, U.C.M.P. No. 27007, and in two of the three supposed adult females. It is absent on all of the supposed young female skulls.

Consequently it may be assumed that the expansion of the premaxillary bones in their posterior part represents a character dependent upon age and size. Like the rostral crest, the expanded premaxillaries are in a minor way a sex character since they are not found in young female skulls. This character is of no taxonomic value.

#### ELEVATION OF THE EXTERNAL NARES

What would seem to be a rather clear-cut sex character in *Machaeroprotopus* is the degree of elevation of the external nares in relation to the bones around them. This was pointed out by Camp in his monograph, as follows:

"In about half of the known specimens, the nasals are elevated into narrow rims around the nares, which is presumably a female character" (Camp, 1930, pp. 93-94).

Case (1932, p. 77) did not agree with Camp, but the present study, during the course of which a series of more than 20 skulls of *Machaeroprotopus* was carefully examined, corroborates Camp's view as to the validity of the development of the external nares as an indication of sex. Briefly stated, it may be postulated that the males in this genus are those individuals in which the external nares are not conspicuously elevated above the level of the top of the skull, whereas the females are those individuals in which the nares are raised as a sort of crater-like structure, well above the

level of the top of the skull. This development of the nares can be used to some extent in conjunction with the development of the crest on the rostrum, discussed above, as an indication of the sex in any individual of *Machaeroprotopus*, and quite possibly in other genera of phytosaurs as well. Application of these criteria to a group of *Machaeroprotopus* skulls, all of which can be measured, yields the interpretation outlined in table 3.

As seen in table 3, there is good statistical support for the assumption that *Machaeroprotopus* shows sexual dimorphism in the development of the external nares. The degree of elevation of the nares is definitely not a growth factor, since both small and large phytosaurs show the two differing expressions of this character. Likewise, there are no indications that the character of low as against elevated nares is of taxonomic significance.

#### PROPORTION OF PRENASAL LENGTH TO LENGTH OF SKULL

This is a most interesting character to study in *Machaeroprotopus* because it lends itself so well to graphic or statistical analysis, as may be seen in Camp's monograph. Moreover, similar studies can be and have been made on some of the modern crocodiles, so that comparisons are possible.

The graph (fig. 1, see also Camp, 1930, table 3, fig. 27) shows very clearly that when a series of *Machaeroprotopus* skulls are arranged according to size, there is a gradual change in proportions of prenasal length to skull length, from the smallest to the largest specimens. Thus, in the series illustrated by the graph, it will be seen that the *relative* prenasal length is greatest in the smallest *Machaeroprotopus* skull, where it measures some 62 per cent of the total skull length, while it is smallest in the largest skull, where it measures only 53 per cent of the total skull length. To put it another way, in the smallest skull the rostrum is almost two-thirds of the total skull length, while in the largest skull it is little more than half of the total skull length. This means that there is a relative decrease in length of the prenasal region and a correlative increase in the length of the postnasal region in a series ranging from the

smallest to the largest individuals of *Machaeroprosoopus* available.

This progression may be shown by another method, namely, a scatter diagram as illustrated in figure 2. In this chart, skull lengths are plotted along the horizontal axis, while prenarial or snout lengths are plotted along the vertical axis. The striking character of this graph is the fact that all of the plotted points lie on or near a straight line that extends from the lower left- to the upper right-hand portion of the graph. This appears to be an approximation to the type of a regression line that might be expected in a simple isogonic growth series.

As a check against this graph similar plottings have been made for a sample of the modern alligator, *Alligator mississippiensis*, with results as shown in figure 3. Here the line connecting the points on the graph takes the form of a very gentle curve. It has been shown by Simpson (Simpson, 1939, p. 364) that the growth gradient for the American alligator approximates the formula for heterogonic growth,  $Y = bX^k$ , which when resolved numerically becomes  $Y = 0.187X^{1.215}$ . Therefore, although differences are apparent between the plotted growth gradient of the modern American alligator and the scatter diagram for the extinct phytosaur, the differences are mainly those of detail, and one cannot help but feel that perhaps the specimens from the Chinle formation represent, at least in part, ascending growth stages.

It might be said in this connection that there are inherent differences, aside from those of isogony or heterogony, between the growth of the phytosaur and of the alligator skull. In the phytosaur, as has been noted, there is a decrease of relative prenarial or snout length with increasing age and size, while in the alligator, on the other hand, there is an increase of the relative snout length with increase in size. In this respect, the extinct phytosaur *Machaeroprosoopus* resembles more closely the modern long-snouted crocodile of Africa, *Tomistoma*, in which there is a decided decrease in relative snout length during growth from the newly hatched individual to the adult.

From this discussion it is quite evident that the proportion of prenarial to skull length in

*Machaeroprosoopus* is the expression of a growth factor. It is not a sex character nor is it a character of taxonomic significance.

#### SHAPE OF THE SQUAMOSAL PROCESS

Camp has very rightly placed a great deal of emphasis upon the shape of the squamosal process as a character of real taxonomic significance in the study of *Machaeroprosoopus*. He has shown that this part of the squamosal bone changes from a relatively deep and narrow process in the specimens from the lowest horizons to a rather shallow but thick and somewhat pointed process in those specimens from the uppermost horizons of the Chinle formation. Consequently he regards his species *M. zunii*, *M. adamanensis*, *M. gregorii*, and *M. lithodendrorum* as an ascending series from the lower to the upper horizons of the formation. *M. tenuis*, at the top of the Chinle, is certainly quite distinct as to the shape of its squamosal process, but Camp does not place it in the series outlined above, but rather regards it as an invading form that came in to replace *M. lithodendrorum*. There can be no question as to the reality of the change in the shape of the squamosal process from the lower to the higher levels of the Chinle. Therefore this is a taxonomic character, representing either a series of species, as Camp has defined them, or a series of gradations within a species. The changes in the shape of the squamosal process cannot be correlated either with sex differences or with age differences in *Machaeroprosoopus*.

#### THE POSTORBITAL-SQUAMOSAL BAR

Camp has discussed the depression of the supratemporal fenestra posteriorly, and has shown that this development in *Machaeroprosoopus* probably represents an independent adaptive change correlated with an increase in size. However, as Camp has shown, the width of the postorbital-squamosal bar is a taxonomic character, in that those forms from the lower and middle part of the Chinle have a narrow bar while only those skulls from the uppermost horizons show the wide bar. Correlative with the shape of the bar is the exposure of the supratemporal fenestra as seen dorsally. In those forms with the

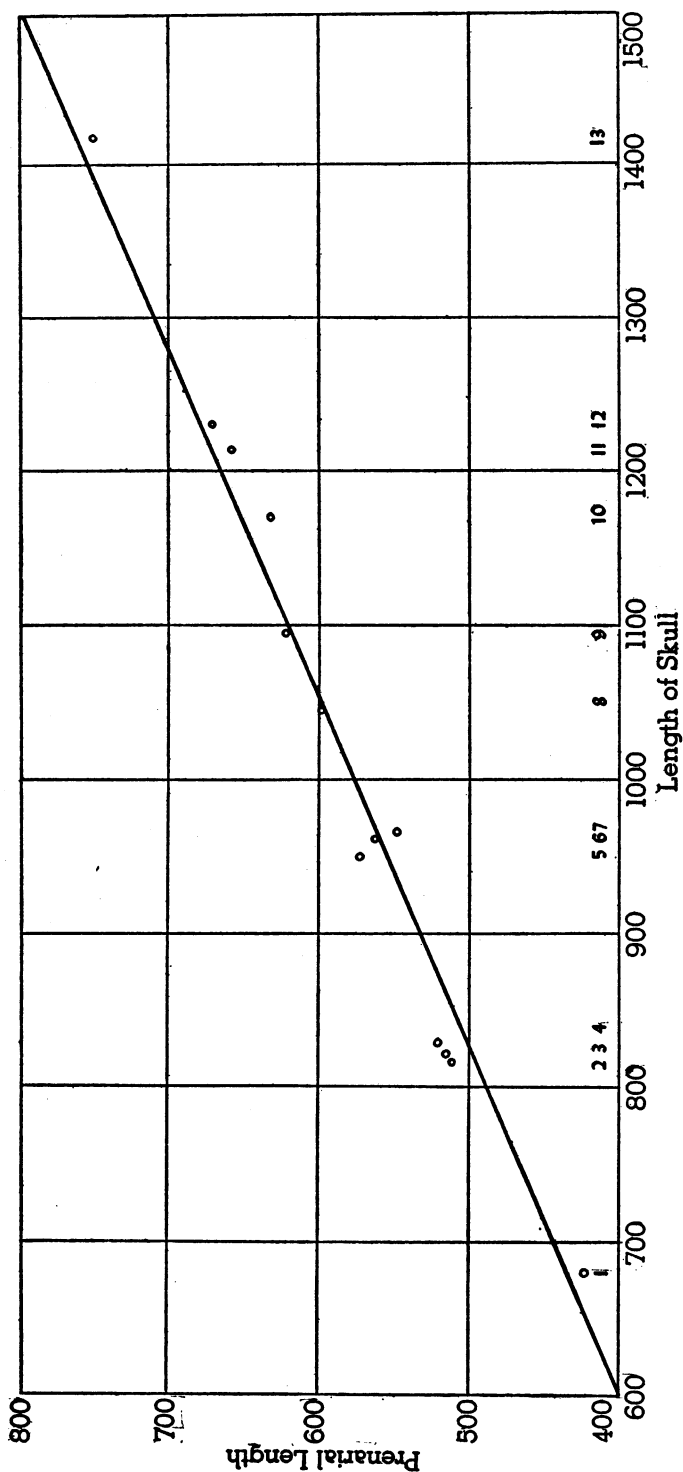
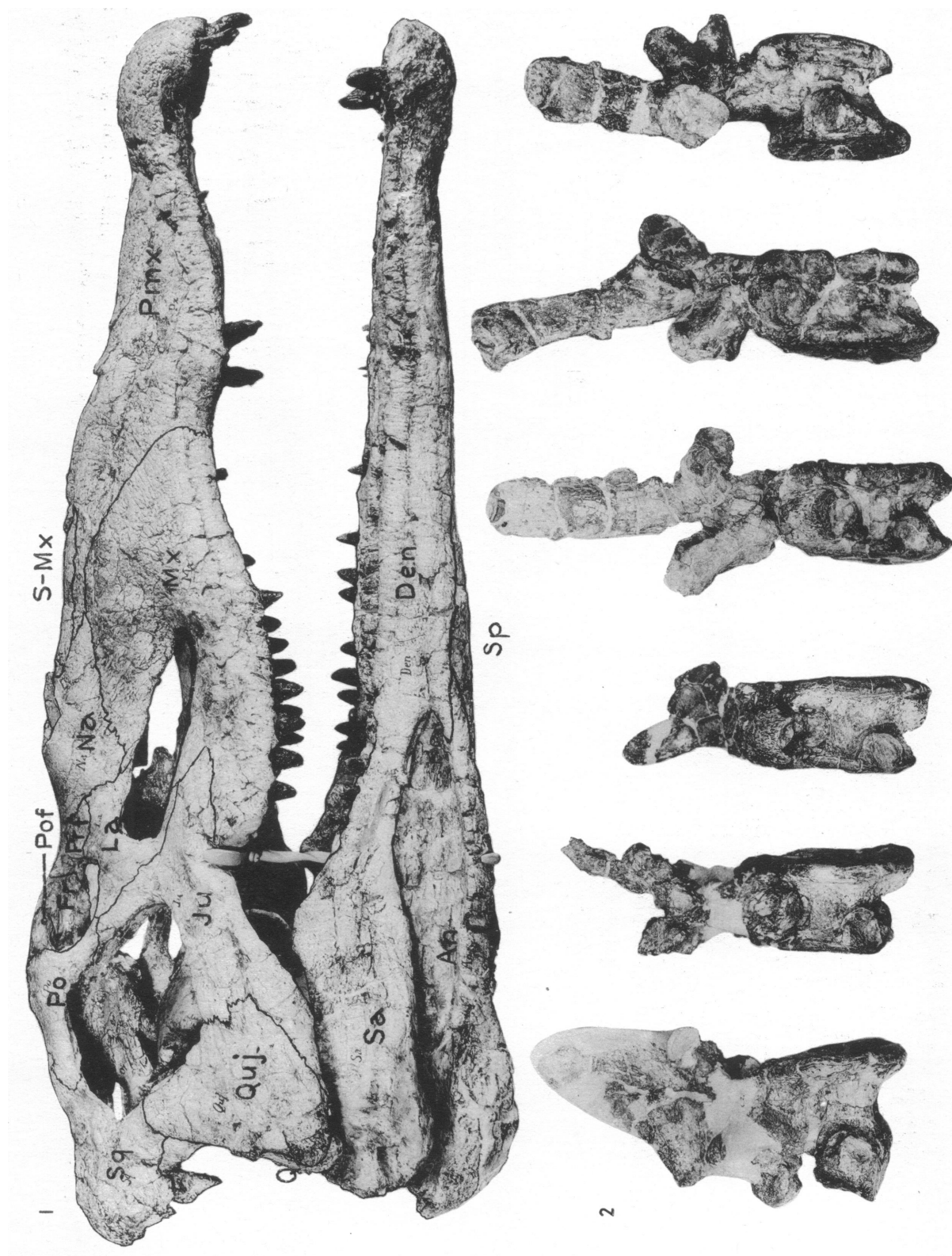


FIG. 2. Graph of prenatal length against total skull length in the genus *Machaeroprotopus*. The similarity of this graph to the graph showing a growth series in *Alligator* (fig. 3) is obvious. The numbers from 1 to 13 at the bottom of the graph identify the specimens, as follows: 1. *M. lithodendrorum*, U.C.M.P. No. 27181. 2. *M. lithodendrorum*, U.C.M.P. No. 27179. 3. *M. tenuis*, U.C.M.P. No. 27018. 4. *M. buceros*, A.M.N.H. No. 2318. 5. *M. adamanensis*, U.C.M.P. No. 27007. 6. *M. validus*, U.W. No. 3807. 7. *M. lithodendrorum*, U.C.M.P. No. 26719. 8. *M. sunii*, U.C.M.P. No. 27159. 9. *M. adamanensis*, U.C.M.P. No. 26699. 10. *M. tenuis*, U.C.M.P. No. 27149. 11. *M. lithodendrorum*, U.C.M.P. No. 26688. 12. *M. gregorii*, U.C.M.P. No. 27200. 13. *M. gregorii*, A.M.N.H. No. 3060.



*Machaeroprotopus gregorii* Camp, A.M.N.H. No. 3060. 1. Lateral view of skull and mandible,  $\times 1/7$ . 2. Lateral view of vertebrae,  $\times 1/4$ . From left to right these vertebrae are: cervicals 2, 3, 4, 5, 7; dorsal 3. Abbreviations: An, angular; Den, dentary; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Q, quadrate; Quj, quadratojugal; Sa, surangular; Sp, splenial; Sq, squamosal.

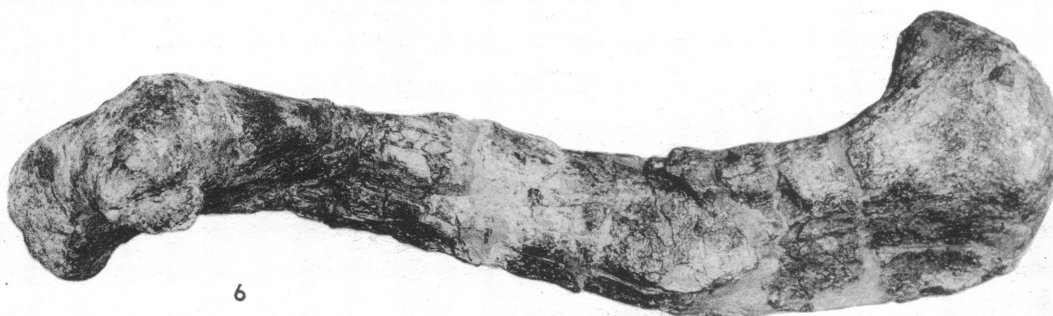
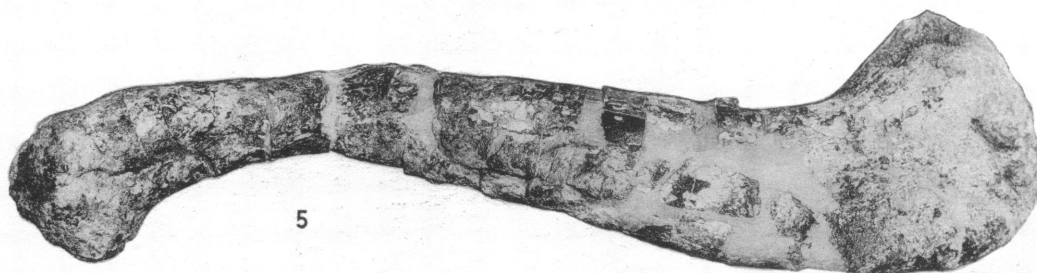
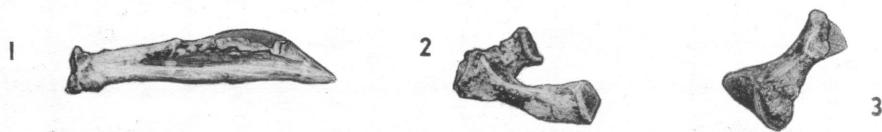


*Machaerobrosopus gregorii* Camp, A.M.N.H. No. 3060. 1. Dorsal view of skull,  $\times 1/7$ . 2. Ventral view of mandible,  $\times 1/7$ . Abbreviations: An, angular; Bo, basioccipital; Den, dentary; Fr, frontal; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Op, opisthotic; Pa, parietal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Quj, quadratojugal; S-Mx, septomaxilla; Sp, splenial; Sq, squamosal

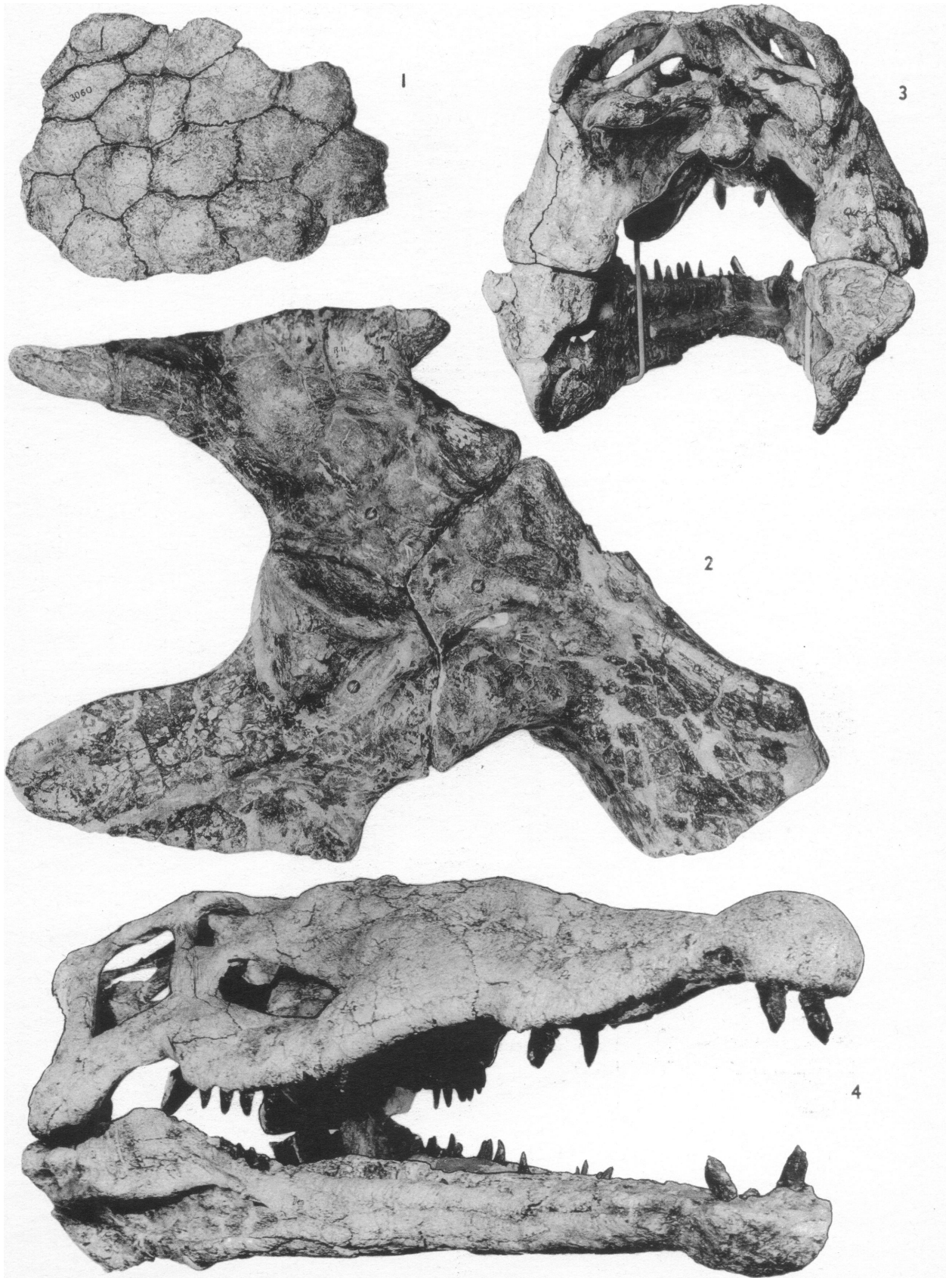




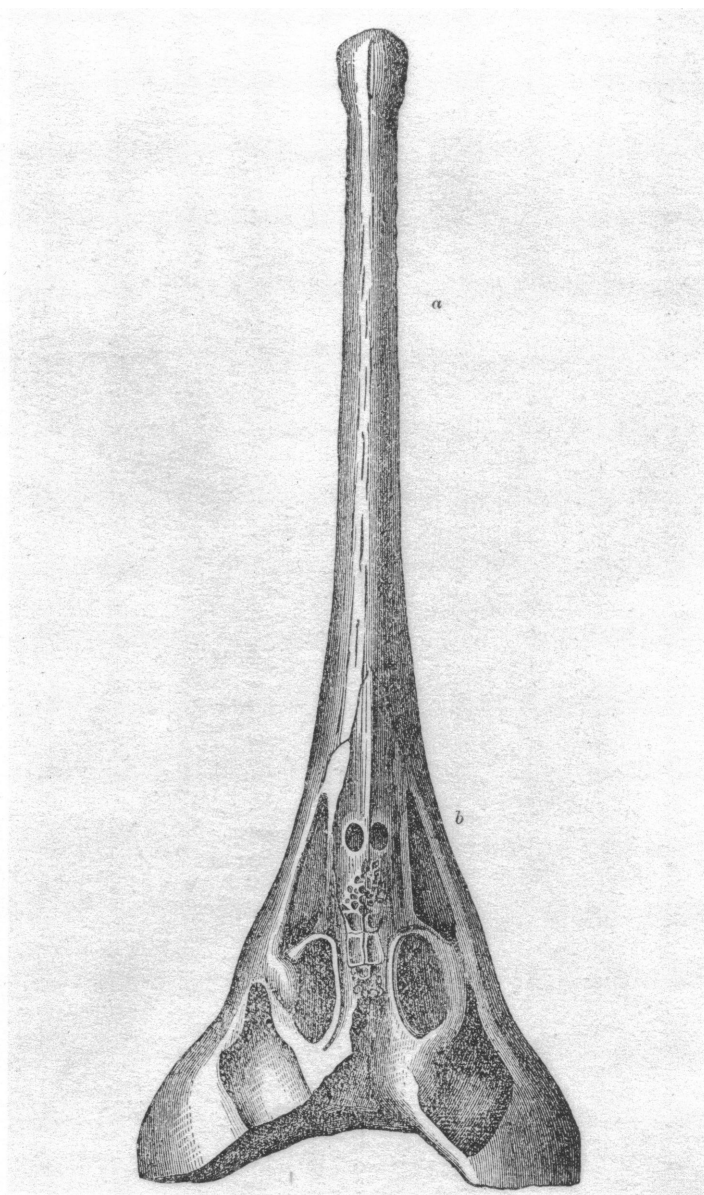
*Machaeorhynchus gregorii* Camp, A.M.N.H. No. 3060. 1. Ventral view of skull,  $\times 1/7$ . 2. Dorsal view of mandible,  $\times 1/7$ . Abbreviations: Art, articular; Bo, basioccipital; Den, dentary; Ecpt, ectopterygoid; Mx, maxilla; Op, opisthotic; Pal, palatine; Pmx, premaxilla; Pt, pterygoid; Qu, quadrate; Quj, quadratojugal; Sa, surangular; Sp, splenial



*Machaerops gregorii* Camp, A.M.N.H. No. 3060. Various elements of the postcranial skeleton, all  $\times 1/7$ . 1. Right clavicle, ventral surface. 2. Capitulum and tubercle of a rib. 3. Phalanx. 4. Right humerus, dorsal view. 5. Left femur, posterior view. 6. Right femur, anterior view

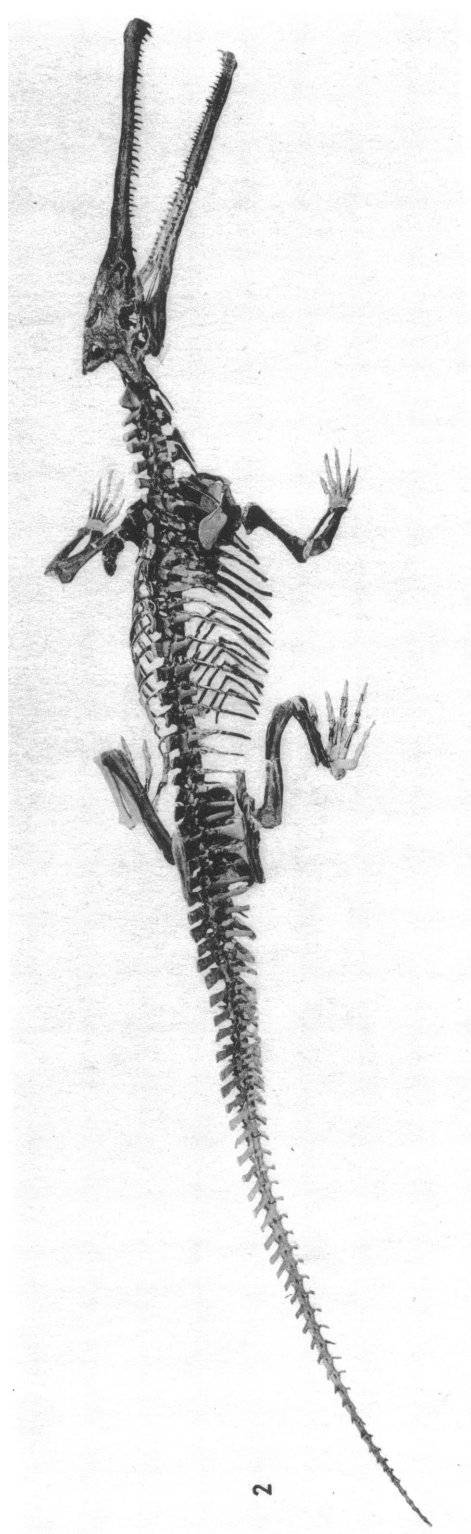
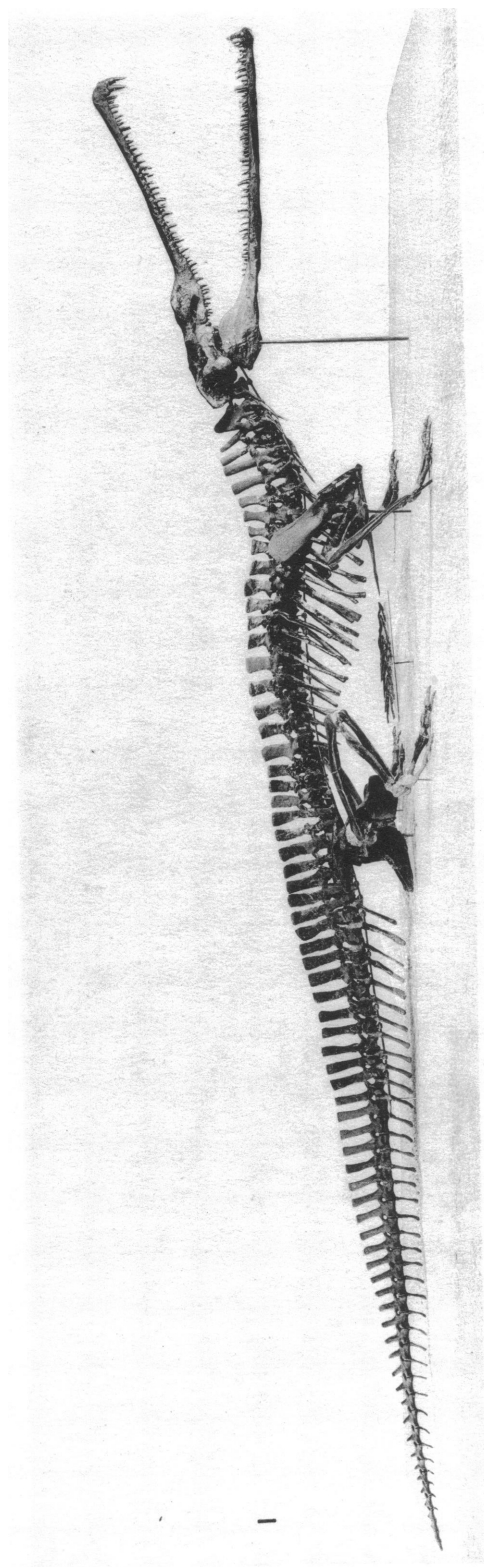


*Machaerops gregorii* Camp, A.M.N.H. No. 3060. Pelvis, skull, and dermal armor plates. 1. Armor plates,  $\times 1/4$ . 2. Right ilium, ischium, and pubis,  $\times 1/4$ . 3. Skull and mandible, occipital view,  $\times 1/7$ . 4. Skull and mandible, no scale



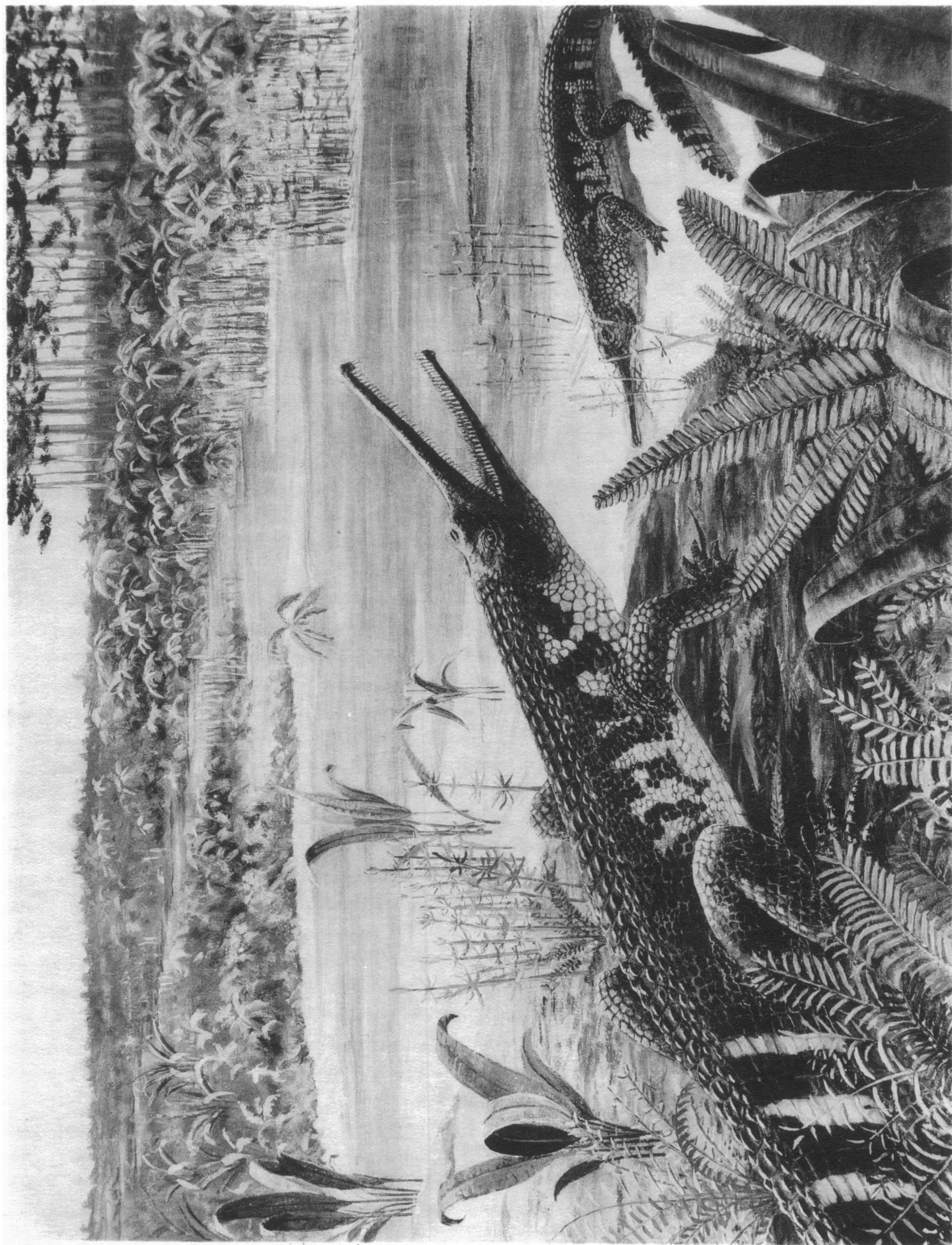
*Rutiodon carolinensis* Emmons. Williams College, Department of Geology. Skull and mandible, Dorsal view, as published by Emmons in 1860,  $\times 1/5$ . (Compare with fig. 9)





*Ruliodon carolinensis* Emmons. A.M.N.H. No. 1, composite skeleton as mounted by Charles Lang of the American Museum Paleontological Laboratory. 1. Lateral view of left side,  $\times 1/18$ . 2. Oblique dorsal view,  $\times 1/18$





*Ruitodon carolinensis* Emmons. Restoration by John C. Germann

narrow bar, namely, *M. zunii*, *M. adamanensis*, *M. gregorii*, and *M. lithodendrorum* from the lower 350 feet of the Chinle formation, the supratemporal fenestra is rather openly exposed in a dorsal view. In *M. tenuis* and

certainly more teeth in *M. tenuis* than in *M. lithodendrorum*, and more in *M. lithodendrorum* than in *M. gregorii*. The differences in the number of teeth are not to be correlated with growth or sex differences.

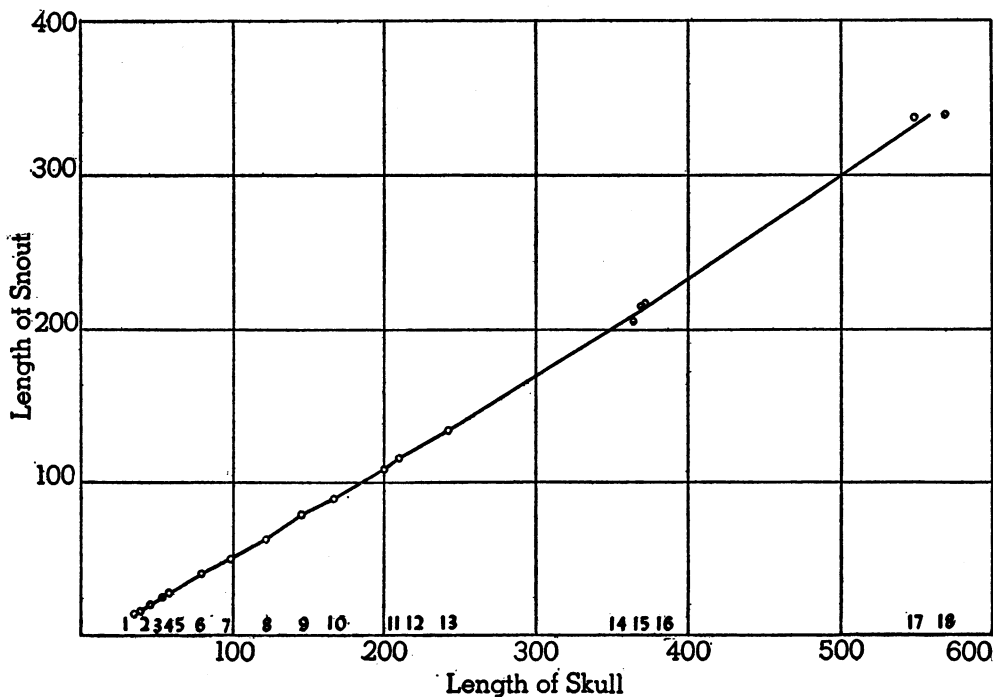


FIG. 3. Graph of the prenarial length against the total skull length in *Alligator mississippiensis*. Compare with figure 2. The numbers from 1 to 18 at the bottom of the graph identify the specimens, as follows: 1. M.C.Z. No. 13101. 2. M.C.Z. No. 13102. 3. A.M.N.H. No. 46843. 4. A.M.N.H. No. 2321. 5. A.M.N.H. No. 2320. 6. A.M.N.H. No. 7127. 7. M.C.Z. No. 13103. 8. A.M.N.H. No. 2318. 9. A.M.N.H. No. 7214. 10. A.M.N.H. No. 46844. 11. A.M.N.H. No. 40580. 12. A.M.N.H. No. 12572. 13. A.M.N.H. No. 40578. 14. A.M.N.H. No. 7119. 15. A.M.N.H. No. 15180. 16. A.M.N.H. No. 15178. 17. A.M.N.H. No. 15181. 18. A.M.N.H. (no number).

*M. validus*, from the top of the formation, the bar is wide, and as a consequence the supratemporal fenestra is largely concealed in dorsal view. These obviously are not characters of sexual or growth significance.

#### NUMBER OF TEETH

The number of teeth in *Machaeroprotopus* is perhaps of some taxonomic significance. The data are not particularly complete, and distinct lines cannot be drawn, but it would seem that the several supposed species can be distinguished to some extent by the number of teeth present. For instance, there are

#### SPACING OF TEETH

As Camp has shown, the teeth are more widely spaced and less differentiated in the small skulls than in the larger skulls. As the individual grows, the replacing teeth become increasingly larger in size, and since the prenarial region of the skull in which the teeth are located becomes relatively shorter in the sequence from young to adult, the teeth as a consequence become more crowded. Also, there is a differentiation in size and shape of the teeth in the adult that is not found in the young individual. These are clearly characters dependent upon age and

growth and are not to be correlated with sex or with species differences in *Machaeropro-*  
*sopus*.

#### ANALYSIS OF SKULL CHARACTERS IN *Machaeroprosopus*

From the foregoing discussion, it is concluded that of the various characters analyzed in the skull of *Machaeroprosopus* only certain ones can be definitely limited to one or another of the three categories of growth, sexual dimorphism, or taxonomic differentiation. Of these, four characters are of particular value, namely: proportion of prenarial to skull lengths and spacing of the teeth, definitely growth factors; relative elevation of the

other in a general systematic interpretation of the skull.

There is no doubt that the shape of the squamosal, a qualitative character, indicates a graded series of phytosaurs from the bottom to the top of the Chinle formation. The problem that confronts us is this: Does the series represent a chronocline of specific dimensions including within its confines intra-specific mutations, or is it representative rather of a vertical succession of well-defined species? This is one of those vexing questions the answer to which is not at all clearly defined. Very probably there never will be a truly satisfactory answer forthcoming. Therefore, the best we can do at the present time

TABLE 4  
ANALYSIS OF SKULL CHARACTERS IN *Machaeroprosopus*

GROWTH FACTOR	SEX CHARACTER	TAXONOMIC CHARACTER
Size (Robustness, within limits)	Robustness (Prenarial crest, within limits)	(Size, within limits)
Prenarial crest	(Posterior expansion of premaxillae, within limits)	
Posterior expansion of premaxillae	<i>Relative elevation of external nares</i>	
<i>Spacing of teeth</i>		<i>Shape of squamosal</i> (Postorbital-squamosal bar, to some extent)
<i>Proportion of prenarial length to skull length</i>		(Number of teeth, to some extent)

external nares, a sex character; and the shape of the squamosal bone, obviously a character of taxonomic significance of greater or lesser import.

The partial or complete limitation of the various characters discussed above to the categories of growth, sexual dimorphism, and taxonomic differentiation is summarized in table 4. Characters peculiar to each of the three categories are italicized. Characters of importance but not limited to a single category are in roman type; these characters are placed within parentheses within those categories where they are of lesser importance.

The analysis of skull characters in *Machaeroprosopus* having been carried to this point, the question still remains as to how these characters are to be weighed against each

is to make attempts at interpretations and to weigh them as objectively as possible.

On a preceding page, and as shown by figures 2 and 3, a comparison has been made between the length of the snout and the length of the skull in *Machaeroprosopus* and in *Alligator*. It was pointed out that these comparisons give closely parallel results in the two species, with the resultant conclusion that certain growth factors in these similar but unrelated reptiles show similar trends.

#### SKULL CHARACTERS IN *Machaeroprosopus* COMPARED WITH GROWTH CHARACTERS IN THE ALLIGATOR SKULL

This test, interesting as it may be, has used only two characters and two dimensions,

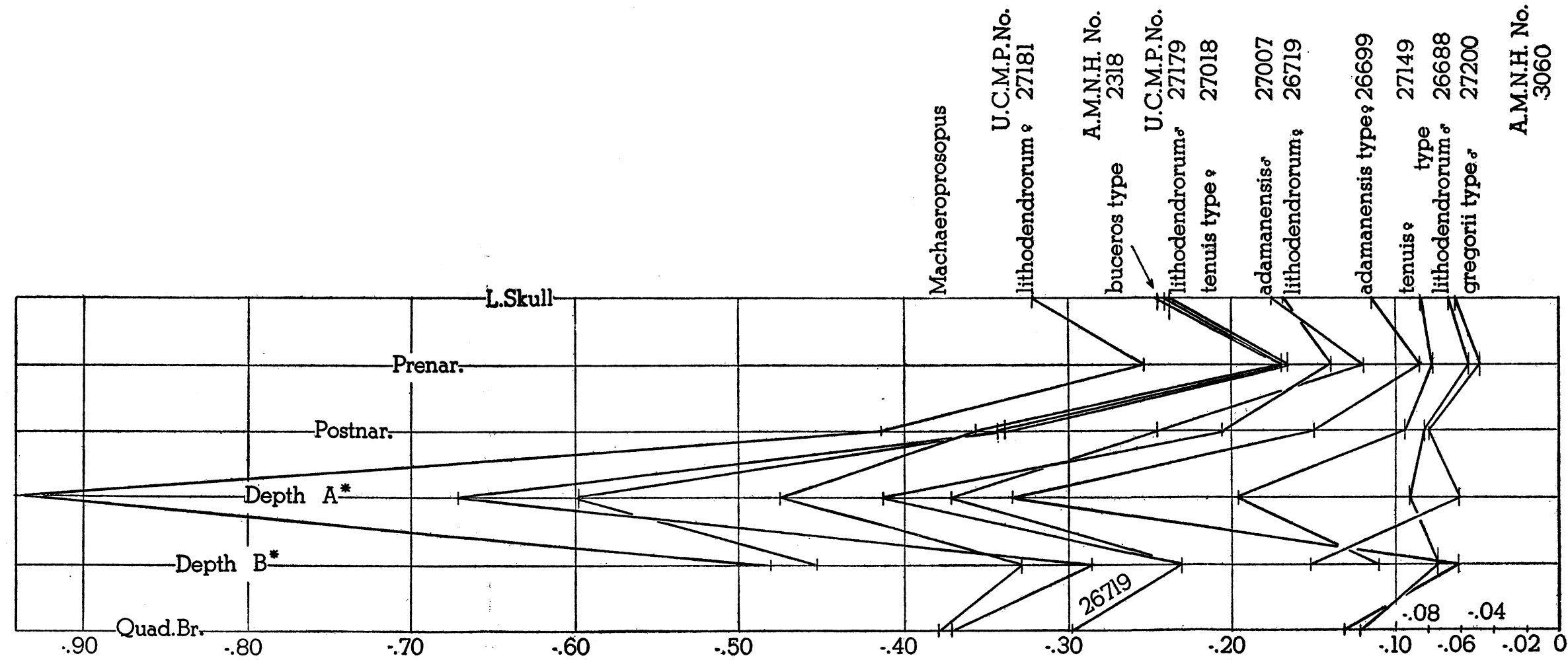


FIG. 4. Ratio diagram of certain skull dimensions in *Machaeroprotopus*. The large American Museum specimen, *M. gregorii*, A.M.N.H. No. 3060, is taken as the standard with which all the other specimens are compared. Depth A, depth of skull in front of premaxillary-maxillary suture. Depth B, depth of skull in front of nares.

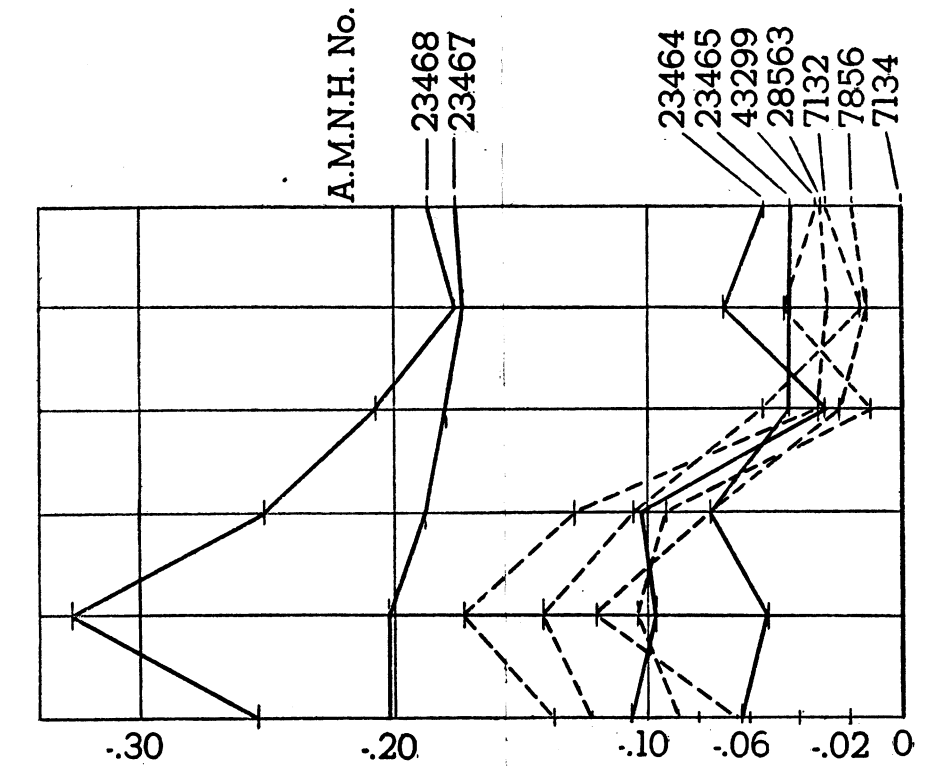


FIG. 5. Ratio diagram of certain skull dimensions in *Crocodylus niloticus* and *Crocodylus americanus*. The largest specimen of *C. niloticus*, A.M.N.H. No. 7134, is taken as the standard with which all the other specimens are compared. Compare with figures 4 and 6. Solid lines, *Crocodylus niloticus*. Dotted lines, *Crocodylus americanus*.

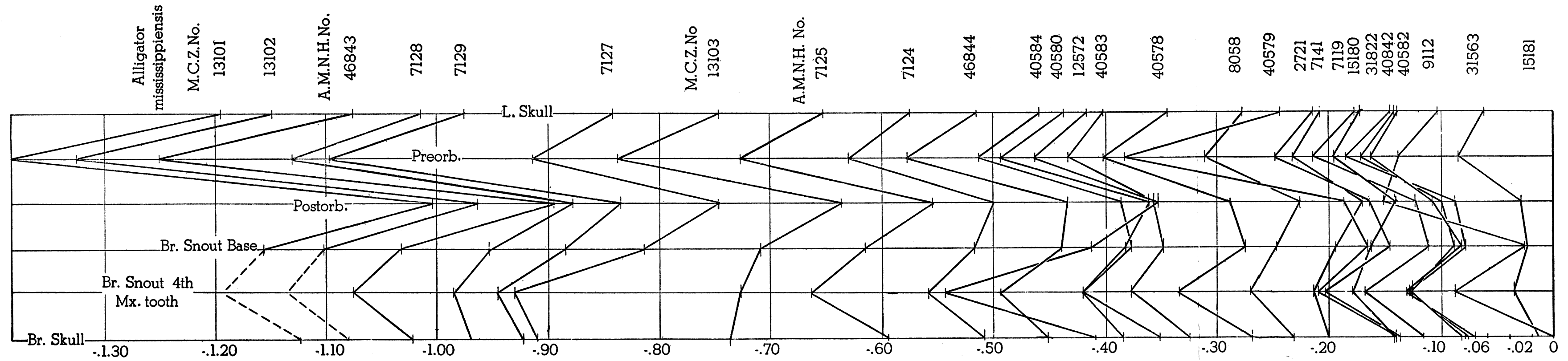


FIG. 6. Ratio diagram of certain skull dimensions in *Alligator mississippiensis*. The largest specimen, A.M.N.H. No. 15181, is taken as the standard with which all the other specimens are compared. Compare with figure 4.

namely, the skull length and the snout length. In an effort to make a more comprehensive test of certain characters observable in the Chinle phytosaurs, the ratio diagram, as devised by Simpson, has been used. By this method a number of growth characters are simultaneously analyzed, with results as shown in figures 4, 5, and 6.

Simpson (1941, p. 24) describes the method of comparing materials by the ratio diagram as follows:

"For calculation, the direct measurements are first converted to their logarithms, three decimal places generally sufficing. Some one observation is then taken as 'standard,' to represent zero difference in logarithms which corresponds with the ratio 1.00. Observations larger than this then fall to the right of it at distances determined by their ratios to it, and smaller observations similarly fall to the left. Although the differences are thus calculated from some one standard, the resulting diagram shows not only ratios to that standard but also ratios of any combinations of observations: once the diagram is made, the zero point, or ratio 1.00 point, may be placed anywhere and ratios of all other observations to that point will still be correctly represented."

In the present case the logarithms of certain skull dimensions of the large American Museum specimen, No. 3060, have been taken for the standard zero or 1.00 ratio points. Since all of the other specimens being used in the comparison are smaller than this large animal, it is obvious that their ratio points will fall on the negative or left side of the diagram, and the greater the proportionate difference, the greater the distance from the standard points to these other ratio points.

What is apparent from this diagram is that there is a progressive disparity in certain characters from the standard, as we progress from the larger to the smaller individuals. This is noticeable especially in the relationships of prenarial to postnarial lengths, and in the depth of the snout. Yet these disparities are not haphazard; they follow a definite pattern, as may be seen, and this suggests that we may be looking, at least in part, at a growth series within a species, rather than at differences between separate forms.

For a comparative test, certain measurements in a known growth series, the American alligator, have been plotted according to the same method and the same scale, using the largest individual for the standard zero or 1.00 ratio points. Here we see results suggestively similar to those obtained in plotting the Chinle phytosaurs. As the size scale is progressively descended, certain ratio points become progressively more and more separated from the standard points, according to a definite pattern. Of course this series is much more extended than that of the phytosaurs, because it includes a complete age scale, from the newly hatched individuals to aged adults, but if this point is kept in mind, the general picture is seen to be strikingly similar in the two series.

As an additional check, the same characters analyzed in the growth series in *Alligator* have been similarly analyzed by means of the ratio diagram in two species of *Crocodylus*, namely, *Crocodylus niloticus* and *Crocodylus americanus*. The results, as shown in figure 5, are not so conclusive as might be expected, in that the patterns on the ratio diagram are not strongly different in the two species. However, it can be said that the patterns do differ, in that the lines for all specimens of *Crocodylus americanus* approximate to some degree the lines for the smaller individuals of *Crocodylus niloticus*. It seems likely that if larger and more satisfactory samples were available, more definitive results might be obtained.

This chart, if its limitations are kept in mind, does show less uniformity in pattern than the charts for the growth series in a single species of *Alligator* and, what is more important, less uniformity of pattern even, than for the plotted specimens of *Machaerops*. Consequently we are led to the conclusion that the series of phytosaurs from the Chinle show, by a ratio diagram of certain growth characters, more resemblance to what is seen in the ontogenetic growth of a single species of a modern crocodilian than to two species belonging to a modern crocodilian genus. Hence this observation tends to support the previous suggestion made above, namely, that the phytosaurs from the Chinle represent, at least to a fairly large degree, a growth series within a



chronocline that probably may best be considered as a single species.

So the matter is left at the present time. No attempt is made here to designate the valid name for the species representative of *Machaeroprotopus* in the Chinle (supposing the phytosaurs of the Chinle to represent a chronocline) and the synonymy of other species names, for it is realized that there are certain considerations that may weigh against the interpretation suggested above. These are, especially, the magnitude of the

varying geologic levels and the development of certain qualitative differences in the morphology of the skull which may in the end outweigh the evidence of growth factors as presented above. In other words, while the evidence as it has been set forth is very suggestive, to make a final decision upon the basis of this evidence may be premature. Perhaps in the future, when a larger series of Chinle skulls is available, a more accurate interpretation of the problem will be possible.

## PART 2. A MOUNTED SKELETON OF *RUTIODON*

### INTRODUCTION

FOR MANY YEARS THERE WAS ON DISPLAY at the American Museum of Natural History a composite skeleton of the phytosaur *Rutiodon carolinensis*, made up of materials collected by the late Dr. W. D. Matthew in 1895 from coal workings in the Upper Triassic of Egypt, Chatham County, North Carolina. These materials, found by Dr. Matthew during the course of his protracted but futile search for the remains of Triassic mammals, are catalogued as No. 1 in the American Museum catalogue of fossil amphibians and reptiles.

It will be recalled that the fossils collected by Dr. Matthew served as the basis for Professor J. H. McGregor's monographic study of the phytosaurs, which appeared in 1906 in the Memoirs of The American Museum of Natural History. In 1911 a selection of the materials from North Carolina were combined under the direction of Mr. Adam Hermann, then Chief Preparator in the Paleontological Laboratory of the American Museum, into a plaque or slab mount. This display has been figured by von Huene (1913).

Recently, for various reasons, it was decided to dismantle this old mount and to remount the bones in a free or open mount. In the first place, the slab mount was not particularly effective, especially since the plaster background was tinted a dark grayish black, so that the bones were not very visible. Secondly, the plaque mount gave the erroneous impression that the skeleton was made up of associated bones from a single individual animal, displayed just as they had been found *in situ*; indeed, it was something of a surprise to anyone not familiar with the history of this material that this was anything other than a plaque display of a skeleton as it had been found in the rocks. Finally, it was thought that a very effective free mount could be made from the materials at hand—a mount that would reconstruct the correct pose of this phytosaur and thus one that would be of great value to the student and to the general public. Incidentally, to the best of our knowledge, this is the only free

mount of a phytosaur, or of a thecodont reptile for that matter, in North America.

The arduous task of restoring and remounting this *Rutiodon* was carried forward to successful completion by Mr. Charles Lang of the American Museum Paleontological Laboratory. The difficulties confronting Mr. Lang in the prosecution of this task cannot be too greatly emphasized. A composite mount is at best a difficult assignment. Add to that, in this instance, the fact that many of the bones were badly crushed, so that adjustments had to be made continually in order that the various elements of the skeleton might fit together more or less in the approximate natural relationships, and some idea of the problems connected with the development of this mount may be had. The manner in which Mr. Lang took the skull apart and put it together again, so that much of the crushing which previously had obscured its salient characters was removed, deserves particular mention. In short, the way in which he assembled these crushed bones from several individuals so that they make a well-articulated skeleton represents a triumph in his long career of setting up fossil skeletons.

During the construction of this mount many things were learned as to the anatomy and the pose in the phytosaurs. It is the purpose of the present contribution to discuss some of the points regarding the skeleton of *Rutiodon*, particularly as this skeleton may be compared with the skeleton in other phytosaurs and in their present-day parallels, the crocodilians.

In his monograph of 1906, McGregor presented a much abbreviated description and discussion of the skull in *Rutiodon*, even though his treatment of the postcranial skeleton was of a detailed nature. This was owing to the fact that at the time of his studies the skull in the American Museum specimen was so badly crushed as to be of little use to the student, while other available skulls were rather incomplete. Instead, McGregor described in detail the skull of the central European genus, *Mystriosuchus*, on

the assumption that this form was so close morphologically and taxonomically to *Rutiodon* that a description of the skull of one would in a general way suffice to elucidate the skull of the other genus. While this may be true, it is nevertheless a fact that there are many differences between the two genera which perhaps have not heretofore been brought out. Indeed, there is lacking a comprehensive description of the skull of *Rutiodon*.

Therefore it was decided to redescribe the skull in this genus, especially since Mr. Lang's preparation of the American Museum specimen made a proper description of this particular skull possible for the first time.

In this connection we were fortunate to have been able to borrow, through the kindness of Prof. Elwyn Perry, Chairman of the Department of Geology at Williams College, Williamstown, Massachusetts, the skull originally described and figured by Ebenezer Emmons in 1860. This specimen was never fully prepared, nor was it, in fact, adequately described or figured. Consequently with the permission of Professor Perry it was prepared by Mr. Lang, with the result that many features or characters, hitherto obscure or completely unknown, were made visible. A

new description of this important specimen forms an integral and important part of the present paper. It is felt that a description of the two skulls, the Williams College specimen and the one in the American Museum collection, should make our knowledge of the skull in *Rutiodon* reasonably complete.

At this place it might be well to say that one will find a number of variations of the name *Rutiodon* in the literature, such as *Rhytiodon*, *Rhytidiodon*, and *Rhytidodon*. These stem from Cope's emendation of Emmons' original name *Rutiodon* to *Rhytiodon*; the latter name suffered further emendations at the hands of subsequent authors. There is no reason, however, to accept any of these later emendations of the original term. Emmons, in his type description of 1856, spelled the name *Rutiodon*. This spelling is presumably an incorrect transliteration from the Greek *ῥυτις* and *ὀδὸν*, and it was because of this supposed error in transliteration that Cope made his original emendation of the word. Since, however, there are no statements in Emmons' original paper as to the derivation of the name, there is no legal basis for an emendation by a subsequent author.

## SKULL AND MANDIBLE OF *RUTIODON*

### SKULL

**PREMAXILLARIES:** In *Rutiodon* these bones are long and attenuated, and together they form the major portion of the thin, gavial-like snout or rostrum. The premaxillaries terminate anteriorly in the form of a decurved hook which carries the two anteriormost teeth on each side. This hook or beak is characteristic of many phytosaurs, but in no other genera is it so strongly developed as in *Rutiodon*. The development of this hook in *Rutiodon* with its enlarged, grasping teeth has resulted in a certain amount of broadening of the tip of the rostrum as an accommodation for the enlarged alveoli.

McGregor has described the presence in *Mystriosuchus* of a "prominent rounded ridge on each side, between the alveolar ridge and the mesial line. These ridges, meeting similar opposing ridges in the symphyseal portion of

the mandible, prevent the close approximation of the upper and lower alveolar regions, and thus serve to prevent the breaking of the teeth when the jaws are forcibly closed" (McGregor, 1906, p. 38). Similar ridges are to be seen in *Rutiodon*, and they appear to be especially well developed in the Williams College specimen.

So far as it is possible to determine sutures in the material at hand it would seem that the premaxillary of *Rutiodon* contains the alveoli for about 27 teeth. At its posterior end the dorsal surface of the bone sweeps upward, to form with the contiguous nasal bone a portion of the base of the cone-like eminence that contains the nares. Laterally the posterior end of the premaxillary is carried outward as a part of the tapering transition from the narrow rostrum to the broad postnasal region of the skull.

**MAXILLARIES:** The maxillaries are rather long, and in lateral aspect are in contact on each side with the premaxillaries, nasals, lacrimals, and jugals. According to Camp the maxillaries in *Machaeropsopus* join also the palatines, ectopterygoids, and pre-momers, but the details of these latter relationships in *Rutiodon* are not visible in the materials at hand. Each maxillary forms about one-half of the bordering edge of the antorbital opening, as is true in other genera of phytosaurs. According to McGregor the maxillaries of *Mystriosuchus* do not meet in palatal aspect, while according to Camp there is a ventral juncture of these bones in *Machaeropsopus*. This point cannot be determined in *Rutiodon*.

It would appear probable that each maxilla carries about 15 teeth, and that the alveolar border of the maxilla is approximately half as long as the alveolar border in the premaxilla. On the whole, the maxillary teeth tend to be shorter and more compressed than the premaxillary teeth, and they frequently have serrated anterior and posterior edges. Thus there is a certain amount of differentiation of function in the dentition of *Rutiodon*. The enlarged terminal premaxillary teeth are most obviously developed for grasping the prey, probably for the most part fish. Behind these enlarged teeth are the long, spike-like premaxillary teeth, also serving to help hold the food. Finally, at the posterior end of the dental series, especially in the maxillary bones, are the shorter, compressed cutting teeth that may have served to shear the food. As McGregor has pointed out, it was the separate discovery of these differentiated teeth that led Emmons, Lea, Leidy, and other early workers to describe several genera and species of phytosaurs from eastern North America.

**SEPTOMAXILLARIES:** The presence of well-developed septomaxillae is characteristic of the phytosaurs, and it is to be assumed that these bones were present in *Rutiodon*, developed perhaps in a manner similar to their expression in *Machaeropsopus*. It is not possible, however, to locate sutures on either the American Museum or the Williams College specimen that mark the limits of these bones.

**NASALS:** The nasals evidently form the

highest portion of the skull in *Rutiodon*, as they do in many of the skulls of *Machaeropsopus*. Indeed, if the effects of crushing are corrected in the American Museum and the Williams College skulls, the nasals are seen to form a large, cone-like eminence raising the narial openings above the level of the skull roof. The advantage of elevated nares such as these to an aquatic animal need not be emphasized. These bones extend forward in *Rutiodon* far beyond the anterior borders of the antorbital fenestrae—a condition similar to that in *Machaeropsopus* and noticeably different from that in *Mystriosuchus*, in which the front borders of the nasals are hardly at all anterior to the front borders of the antorbital openings. Another difference between *Rutiodon* and *Mystriosuchus* is to be found in the upward direction of the nares in the former, as compared with the anteriorly directed narial openings in the latter genus. According to Camp the role of the nasals in the formation of the nasal septum in *Machaeropsopus* is insignificant, since this structure is for the most part of septomaxillary origin.

**FRONTALS:** The frontals in *Rutiodon*, as in *Machaeropsopus*, are elongated and narrow bones. They form a portion of the superior border of the orbits.

**PARIETALS:** Although sutures are not visible in the specimens at hand, it would seem logical, because of the general similarities of the postnarial regions in *Rutiodon* and *Machaeropsopus*, to assume that the parietals were similar in the two genera. This would mean that in *Rutiodon* the parietals are rather small, thick bones, each with a divergent process extending back posterolaterally to meet a process from the squamosal, the two together forming the parieto-squamosal bar or arcade which is so characteristic of the phytosaurs. In *Rutiodon* the direction of this bar is more lateral than posterior; in *Machaeropsopus*, on the other hand, the direction of the bar is more posterior than lateral. The difference in the two genera is obviously a factor of growth, whereby the outer bones of the skull in *Machaeropsopus* have become larger in comparison with the bones of the braincase than they are in *Rutiodon*. Camp has shown that in *Machaeropsopus* there is a dome-

like excavation of the under-surface of the parietals to house the very large epiphysis of the brain, and it is probable that a similar development, to a greater or lesser degree, is to be found in other genera of phytosaurs.

**PREFRONTALS:** The prefrontal in *Rutiodon* is a well-developed bone which in lateral view is roughly rhombic in shape. It forms the anterior border of the orbit and extends forward on the face to meet the nasal in front, the frontal above, and the lacrimal below.

**POSTFRONTALS:** There is nothing definite to be said regarding the postfrontal in *Rutiodon*. In *Machaeroprotopus* this bone is small and subcircular.

**LACRIMALS:** The lacrimal is a large bone, as is generally the case in the phytosaurs, showing contacts with the prefrontal, nasal, maxilla, jugal, and postorbital. This bone forms a portion of the superior border of the antorbital fenestra, an opening which partially divides the lacrimal bone into anterior and posterior parts. Generally speaking, the shape and relationships of the bone in *Rutiodon* show strong similarities to the condition seen in *Machaeroprotopus*. For instance, both of these genera are similar in that a thin process of this bone extends back beneath the orbit, forming a part of its lower border, joining the postorbital, and in conjunction with this bone and the jugal forming the postorbital bar. This is in contrast to *Mystriosuchus*, in which the lower border of the lacrimal runs into the lower edge of the orbit and is appreciably separated from the postorbital by the jugal, therefore playing no part in the formation of the postorbital bar.

In the Williams College skull of *Rutiodon* the entrance to the lacrimal canal can be seen on the inner margin of the orbital rim, not far below the lacrimal-prefrontal suture.

**POSTORBITALS:** It is not possible with the materials at hand to be certain as to the exact limits of the postorbital in *Rutiodon*, but a careful comparison of the structure of the skull in this region with the same portions of the skull in *Machaeroprotopus* and *Mystriosuchus* would make it appear that the resemblance is with the American rather than with the European genus. Thus *Rutiodon* would appear to have the posterior portion of the postorbital attenuated as a bar, as in

*Machaeroprotopus*, although not to the degree that is characteristic of this latter genus. Indeed, in its shape this particular bone in *Rutiodon* probably is about intermediate between the condition typical of *Machaeroprotopus* and that of *Mystriosuchus*.

**JUGALS:** The shape of the jugal in *Rutiodon* is typically phytosaurian; it is a large bifid bone, the upper and lower portions of which are divided by the anterior half of the lateral temporal fenestra. As in *Machaeroprotopus*, the jugal of *Rutiodon* does not reach the border of the orbit. Posteriorly this bone runs back beneath the quadratojugal, almost reaching the articular surface of the quadrate.

**QUADRATOJUGALS:** The quadratojugals of *Rutiodon* are flat, triangular, plate-like bones, as they are in other genera of phytosaurs. They articulate with the squamosals above, the jugals anteriorly and ventrally, and the quadrates behind. Case (1920) and Camp (1930) have shown how in *Machaeroprotopus* the quadratojugal is split ventrally to receive the jugal as a thin wedge, intervening between the internal and external portions of the quadratojugal. An examination of the Williams College specimen shows that the same condition is to be found in *Rutiodon*.

**QUADRATES:** So far as can be determined, the quadrate in *Rutiodon* is a very broad bone, with a wide ascending plate that rises to meet the squamosal. The articular surface is broad laterally but narrow anteroposteriorly and convex from front to back. Mesially it is turned down rather strongly into a sort of process, which in conjunction with the same downwardly flexed process of the opposite quadrate would serve to restrain the lower jaw from slipping from side to side during the rotation of the articular upon the quadrate. Owing to the crushing which the American Museum specimen has suffered (this region is missing in the Williams College specimen), there is not much more to be seen of this bone in *Rutiodon*. As in other phytosaurs there was a pterygoid wing extending forward from the ascending portion of the quadrate, and this part of the quadrate can be seen in the United States National Museum specimen figured by McGregor in 1906.

McGregor indicates a quadrate foramen in

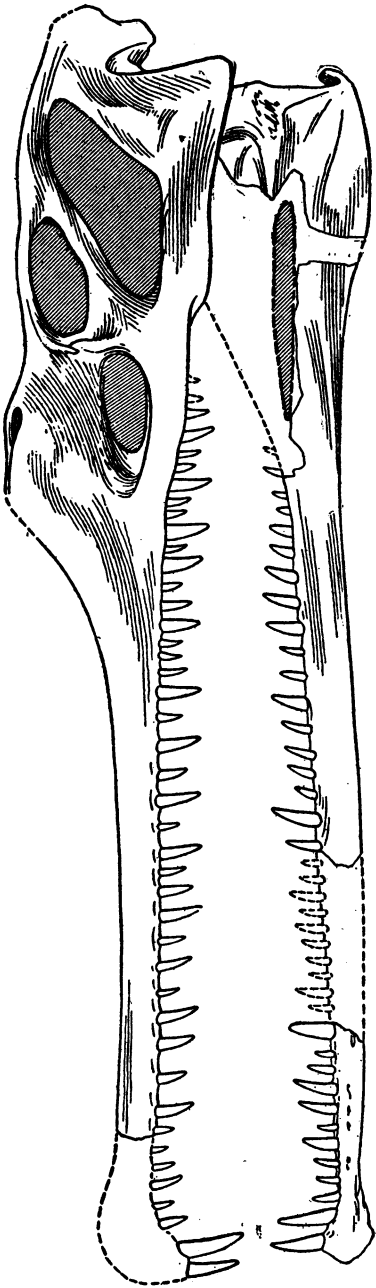


FIG. 7. *Rutiodon carolinensis* Emmons. A.M.N.H. No. 1, skull and mandible. Lateral view of left side, restored and with crushing corrected, X1/4.



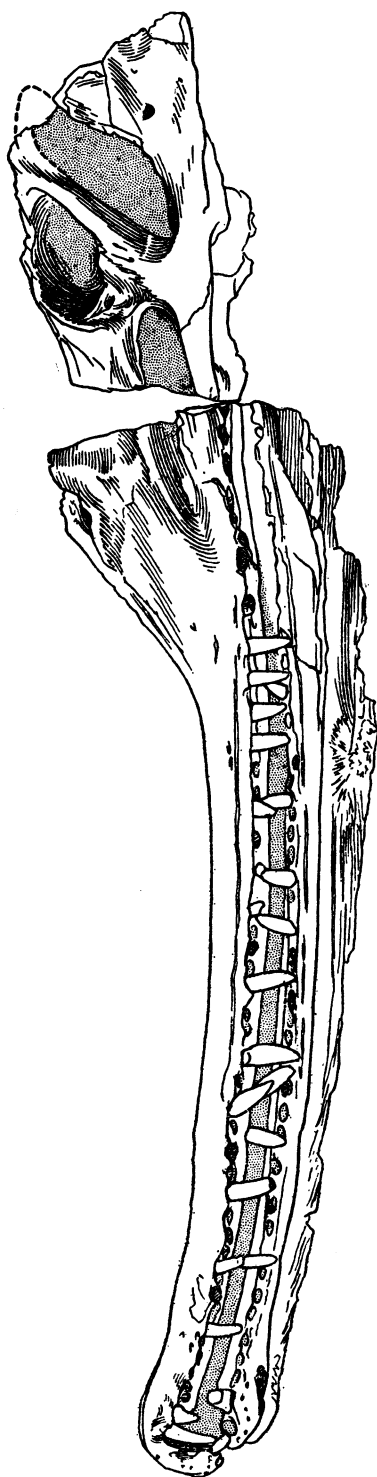


FIG. 8. *Rutiodon carolinensis* Emmons. Williams College, Department of Geology. Skull and mandible. Lateral view of left side,  $\times 1/4$ .



FIG. 9. *Rutiodon carolinensis* Emmons. Williams College, Department of Geology. Skull and mandible. Dorsal view,  $\times 1/4$ .  
(Compare with Emmons' original figure of the same specimen, pl. 8.)

*Mystriosuchus* located on the posterior surface of the ascending process of the quadrate and interrupting the suture between this bone and the quadratojugal external to it. The same foramen is shown by Camp as present in *Machaeroprotopus*. It is not visible in the *Rutiodon* materials at hand, but there is every reason to think that it was very probably present.

**SQUAMOSALS:** The squamosal is a complicated bone in the phytosaurs. Naturally this

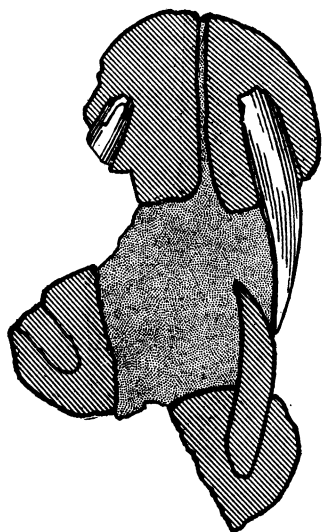


FIG. 10. *Rutiodon carolinensis* Emmons. Williams College, Department of Geology. Cross section of the skull near the anterior end showing the implantation of the teeth in the premaxillaries (above) and the dentaries (below);  $\times 1/1$ .

bone forms the posterior part of the post-orbital-squamosal bar in *Rutiodon*, as it does in other diapsid reptiles, but in addition to the anteriorly directed postorbital bar of the squamosal there is a second bar placed mesially to the one already mentioned, which serves to join the squamosal to the posterior bones of the skull roof. Exact relationships cannot be discerned in the American Museum specimen, but according to McGregor this bar in *Mystriosuchus* is composed of the squamosal plus the parietal. On the other hand, Camp shows that in *Machaeroprotopus* this process of the squamosal joins the supra-occipital and tabular, a relationship which probably holds for *Rutiodon*.

The back of the squamosal in *Rutiodon* forms the back corner of the skull and

ventrally it extends down as a sort of hook, to the inner side of which is articulated the end of the paroccipital or opisthotic. McGregor believes that this hook served as a suspensorium for the hyoid apparatus. Another process of the squamosal in *Rutiodon* extends forward as a broad sheet over the internal surface of the upper part of the quadratojugal. The relationships of this portion of the bone have been made clear in Camp's extraordinary analysis of the skull of *Machaeroprotopus*.

**TABULARS, INTERPARIETALS:** In *Machaeroprotopus* the tabulars are present as vertical plates beneath the posterior processes of the parietals, while between them and immediately above the supraoccipital is the interparietal. It is probable that the same arrangement and relationships for these bones exist in *Rutiodon*.

**PALATINES:** The American Museum specimen of *Rutiodon* is crushed in such a way that not much is to be seen of the palatine-pterygoid relationships. Therefore such osteological relationships as may be determined in this region must be worked out from the Williams College specimen, in which a portion of the palatal area is preserved. This skull shows that the palatines are strongly arched in *Rutiodon*, in which respect they may be compared with the same bones in *Mystriosuchus*. Thus, the two bones together form a narrow vault, of which the sides are formed by the vertical plates of the palatines. Lateral to this vault are the horizontal plates of the palatines, the outer borders of which join the maxillaries and ectopterygoids. It would appear that the arching of the palatines in *Rutiodon* is stronger, and that the palatal vault is narrower than is the case in *Machaeroprotopus*.

As has been shown by various authors, the arching of the palatines to form a vault is characteristic of the phytosaurs, and the significance of this development has been discussed particularly by McGregor and by Camp. As McGregor has pointed out, the vault must have afforded a passage above the flat tongue between the nares and the glottis, and Camp has suggested that there may have been "cartilaginous extensions or lappets projecting at least part way across the palatal vault, partly enclosing the air passage and

protecting the delicate bones on the roof of the vault" (Camp, 1930, p. 116). This development in the phytosaurs was an adaptation preceding and parallel to the evolution of the palate in the crocodilians, in which the passage for air between the nares and the glottis has been completely enclosed below by ventral horizontal extensions of the maxillaries, palatines, and pterygoids.

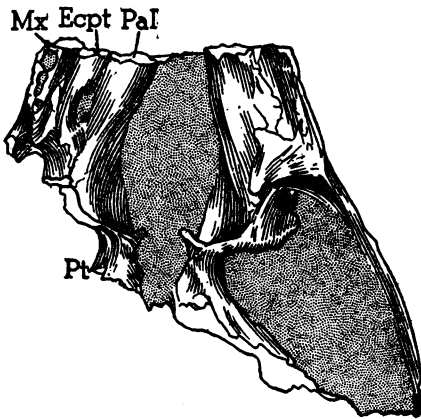


FIG. 11. *Rutiodon carolinensis* Emmons. Williams College, Department of Geology. Ventral view of palatal region,  $\times 1/4$ . Abbreviations: Ecpt, ectopterygoid; Mx, maxilla; Pal, palatine; Pt, pterygoid.

According to McGregor, a difference between *Rutiodon* and *Mystriosuchus* is to be seen in the rounder palatine foramina of the former compared with the latter genus. This supposed difference may not be so great as it appeared to McGregor. Thus, in the Williams College specimen these foramina seem to be elongated, rather than rounded as they are in the United States National Museum specimen, of which the palatal region was described by McGregor.

**PTERYGOIDS:** The phytosaurian pterygoid is a complex bone, and it has been described in detail by McGregor, and especially by Camp. In the Williams College specimen of *Rutiodon* a portion of the pterygoid may be seen adjoining the posterior part of the palatine. The pterygoids join the palatines to form the palatal vault, and the juncture of the two bones in the specimen at hand occurs along the vertical plate above and behind the strong "palatal shelf" formed by the palatine. Posteriorly, the pterygoids in this

specimen show the two surfaces for articulation between these bones and the basisphenoid, while in the left pterygoid the quadrate ramus may be seen extending posterolaterally.

**ECTOPTERYGOIDS:** Portions of these elements may be seen in the Williams College skull, lying between the maxillaries and the palatines and pterygoids. This bone forms the outer half of the boundary of the palatine foramen.

**BASISPHENOID:** This is a heavy bone in *Rutiodon*, similar in shape to the same element in *Mystriosuchus*. It, and the remaining bones of the skull to be described, are present in the American Museum specimen. Anteriorly there are two divergent processes for articulation with the pterygoids, while posteriorly it is laterally expanded at its juncture with the basioccipital. This expansion of the two bones takes the form of a pair of very heavy, roughened knobs or tubera, forming strong attachments for the neck muscles.

**BASIOCCIPITAL:** The development of the tubera, in conjunction with the basisphenoid bone, has been described above. Behind these tubera there is a constriction of the basioccipital, to form a sort of "neck," for the support of the rounded condyle. The condylar surface in *Rutiodon* is almost hemispherical in shape.

**EXOCCIPITALS:** Forming the lateral walls of the foramen magnum are the exoccipitals, separated from each other dorsally by the median supraoccipital. The exoccipitals are united suturally with the paroccipitals or opisthotics.

**OPISTHOTICS:** These bones in *Rutiodon* are large and heavy, as is characteristic of the phytosaurs. In each of these bones the lateral extremity is greatly expanded dorsoventrally, to form a long contact against the squamosal. Immediately above the opisthotic and in contact with it at the inner and outer extremities is the relatively slender squamosal bar, the two bones showing relationships with each other similar to those seen in *Mystriosuchus*, *Machaerops*, and other phytosaurs. Sutures are not visible to indicate the limits of the anterior part of the opisthotic, but the stapedial fossa, running in an anteroventral direction and terminating in the fenestra ovale, is well preserved. Ac-

According to Camp the stapedial fossa is contained within an anterior projection of the opisthotic in *Machaeroprotopus*, and it is logical to assume that the same is true for *Rutiodon*. Above this fossa and forming its dorsal surface is a strong ridge of bone which marks the approximate boundary between the opisthotic and the prootic bones above it.

**PROOTICS:** On its left side the wall of the brain case is completely preserved in the American Museum skull of *Rutiodon*, and the locations of certain foramina are clearly indicated. Thus, above the ridge of bone that forms the superior wall of the stapedial fossa, and a little anterior to the fenestra ovale, there is a well-developed foramen which must be an exit for the seventh cranial nerve. This foramen is contained within the prootic bone. Located above and slightly anterior to this last-mentioned opening, and still contained within the limits of the prootic, is the large prootic foramen, forming the exit for the fifth and sixth cranial nerves, while anterior to the prootic foramen is still another opening, which may be the hypophyseal fenestra. This opening, according to Camp, is situated at the juncture of the prootic, parasphenoid, presphenoid, and basisphenoid bones. Its identity in *Rutiodon*, as described above, is not, however, absolutely certain.

Beyond the topographical locations of these several foramina, there is nothing in particular to be said about the cranial wall in *Rutiodon*. Because of the condition of the specimen it is not possible to identify and define the other skull bones, namely, the epiotics, laterosphenoids, parasphenoid, presphenoid, and vomer. Full descriptions of these elements in *Machaeroprotopus* will be found in Camp's memoir.

#### MANDIBLE

As might be expected, the mandible in *Rutiodon* is long and slender, approximating in its proportions the mandible of *Mystriosuchus* on the one hand and that of *Machaeroprotopus* on the other. The tooth-bearing portion of the mandible is very long in this genus, since it comprises about three-fourths of the total length of the lower jaw.

In the Williams College specimen the two halves of the mandible have been shifted so that the symphyseal articulation of one side

is exposed. This indicates that the symphysis in *Rutiodon* extends far back, to about the region of the thirty-second tooth. We may compare this with the posterior boundary of the symphysis in the region of the thirtieth tooth in both *Mystriosuchus* and *Machaeroprotopus*. In spite of the similarity between these genera, so far as the morphological extent of the symphysis is concerned, there are certain differences as regards its proportional length. For instance, the symphyseal length is, so far as may be determined with accuracy, about 60 per cent of the total mandibular length in *Rutiodon*. This length is approximately intermediate between the symphyseal lengths of the other two genera mentioned, since in *Mystriosuchus* it is about 55 per cent of the total jaw length, while in *Machaeroprotopus* it varies from 40 to 48 per cent of the total jaw length. It is interesting to see that in this latter genus the relative length of the symphysis decreases as the size of the animal increases; consequently there is good reason to think that the proportion between symphyseal length and mandibular length is a variant dependent to a certain extent upon the age of the individual.

**DENTARIES:** These are very long and slender bones in *Rutiodon*. It is probable that the dentaries were essentially straight in this genus, although in the Williams College specimen they show a slight upward curvature from back to front. There is also a slight upward curvature to the rostrum in this specimen, and whether this, together with the curvature in the mandible, is to be considered as a natural condition or rather as a distortion brought about during the process of fossilization is a question difficult to decide. There is certainly a slight upward curve in the rostrum and mandible of *Mystriosuchus*, but on the other hand these regions in *Machaeroprotopus* show no such curvature.

As has been said, the symphysis in *Rutiodon* is long, and the anterior part of it is formed by the articulation of the opposing dentaries, the posterior portion being formed by the splenials. It is difficult to be sure of the anterior limits of the splenial, but the Williams College specimen would seem to indicate that, of the symphyseal union, something more than half of the length was formed by the dentaries. In *Machaeroprotopus* the

symphysis is about evenly divided between dentaries and splenials.

The end of the dentary is swollen to accommodate the enlarged terminal teeth, of which there are three on either side. It would appear that there are slightly more than 40 teeth in each dentary, so the number of lower teeth is approximately the same as the number of upper teeth.

Posteriorly the dentary is excavated by the large external mandibular fenestra, a characteristic feature in the phytosaurs.

**SPLENIALS:** The splenials in the phytosaurs, as in the crocodilians, are very large. Unfortunately it is not possible to see much of these bones in the *Rutiodon* materials at hand, but it is to be supposed that they are similar to the same bones in *Machaeroprosoopus* and in *Mystriosuchus*, which have been fully described by Camp and by McGregor.

**ANGULARS:** The angular is an elongated, low bone forming the posteroventral part of the jaw exteriorly. It is joined with the surangular above, and at the back with the articular, which rests against its inner surface.

**SURANGULARS:** The surangular in *Rutiodon* is relatively deep, and as a consequence the back of the jaw in this genus is noticeably deeper than is the case in *Mystriosuchus* or in *Machaeroprosoopus*. Like the angular, the surangular forms a flat plate on the outside of the jaw at the back, against the inner surface of which the articular rests. Presumably both the surangular and angular were excavated by the external mandibular fenestra, although this point cannot be established upon the basis of the materials at hand.

The surangular takes part in the articulation of the lower jaw, forming the outer part of the glenoid. The angular also forms the ventral border of the ramus in its posterior portion.

**ARTICULARS:** The articular in *Rutiodon* is a heavy element, expanded dorsally to carry the glenoid and projected posteroventrally into a hook at the lower corner of the jaw. The glenoid is particularly interesting in this genus, as seen in the American Museum specimen. It is not a transverse articulating surface, as in *Mystriosuchus* and many other phytosaurs, but rather it is placed at an angle, with its inner border much lower than, and

anterior to, its outer border. This position of the glenoid must be the effect, to a large extent, of distortion, because if this were the natural position the jaws would be locked shut; it is probable that the quadrate-articular joint in *Rutiodon*, as in other phytosaurs, was essentially transverse and horizontal. It should be noted, however, that the glenoid surface in *Rutiodon* is not a simple concavity but rather is in the form of two shallow pockets separated by a slight convexity in the middle of the glenoid. This forms a fairly complex articulation that probably would serve to restrict the jaws to an essentially orthal motion.

The downward projection of the articular to form a hook at the back corner of the jaw represents the development of a strong insertion for the depressor mandibulae muscle. A parallel adaptation is seen in the crocodilians, in which the articular is extended posteriorly for the accommodation of this muscle. Indeed, the arrangement of the bones in the crocodilian mandible is remarkably similar to the arrangement in the phytosaurs, a point that already has been brought out by previous authors.

The coronoid is not present in any of the *Rutiodon* material at hand.

#### GENERAL FORM AND PROPORTIONS

In both *Rutiodon* and *Mystriosuchus* the skull is characterized by its gavial-like form—in other words, by the long, attenuated snout, armed with many sharp teeth. There can be little doubt that the specialization of the upper and lower jaws in these two phytosaurs was an adaptation to fish catching, just as it is in the modern gavial of the Orient. Superficially the attenuation of the snout and the lower jaw seems to be very similar in the two phytosaurian genera, but a close examination will show that there are differences of detail that are quite distinct.

In the first place, the prenasal region in *Mystriosuchus* is appreciably longer than it is in *Rutiodon*. This fact is apparent from the accompanying diagrammatic drawing (fig. 12), in which the skulls of the two forms are compared. It will be seen that when the skulls of the two genera are reduced to a unit length, the prenasal region in *Rutiodon* is about six-tenths of the entire skull length,

while the same length in *Mystriosuchus* is almost seven-tenths of the total skull length. While the difference is not great it is sufficiently large to be readily noticeable.

As a corollary to this condition, the postnarial region of the skull in *Rutiodon* is not so compressed anteroposteriorly as it is in *Mystriosuchus*.

These differences in proportion between the prenarial and postnarial regions are reflected in various skull characters. Thus, because of the lesser proportional length of the prenarial region in *Rutiodon* as compared with *Mystriosuchus*, there is a correspondingly greater frequency of the teeth in the anterior portion of the snout, although in both genera the frequency of the maxillary teeth is about the same. Naturally similar though not identical tooth frequencies are to be seen in the lower jaws of these two genera.

In the postnarial region of the skull the differences between the two genera are readily apparent. Particularly noticeable is the rather long lateral temporal fenestra in *Rutiodon* as compared with the shortened fenestra in *Mystriosuchus*. As McGregor has pointed out, the postnarial region in *Rutiodon* is not only longer but also lower than it is in *Mystriosuchus*, and this fact also is reflected in the differing shapes of the antorbital opening and the lateral temporal fenestra in the two genera.

*Rutiodon* may be compared also with the American genus *Machaeroprotopus*, which may or may not be synonymous with *Clepsysaurus*. Whereas *Mystriosuchus* is characterized by a muzzle relatively longer and a postnarial region relatively shorter and higher than in *Rutiodon*, *Machaeroprotopus* is characterized by adaptations in a direction opposite to those of *Mystriosuchus*. Thus, in *Machaeroprotopus* the muzzle is relatively shorter and heavier than it is in *Rutiodon* while the frequency of the teeth is even greater.

In the proportions and form of the postnarial region *Rutiodon* and *Machaeroprotopus* are strikingly similar to each other. Both show similar elongations in the antorbital and lateral temporal fenestrae, and in both the shapes of the various bones that constitute this part of the skull are very much alike.

The resemblances between *Rutiodon* and

*Machaeroprotopus* in the postnarial region extend to the form and relationships of the nares. In both of these genera (and here the comparison is closest between *Rutiodon* and the smaller "female" skulls of *Machaeroprotopus*) there is a sharp upward curve of the dorsal outline of the snout, formed by the premaxillae and the nasals, from the level of the dorsal rostral surface to the level of the narial openings. While this upward curve to the nares is sharp in *Rutiodon* it is not the very abrupt upward curve that is seen in the same surface in *Mystriosuchus*.

Again, *Rutiodon* and *Machaeroprotopus* are similar in that the nares are located in the summit of a cone-like eminence formed by the nasal bones—they are at the highest point on the skull. In *Mystriosuchus*, on the other hand, the dorsal surface of the cranium behind the nares is higher than the narial openings. Therefore the outline of the top of the skull is considerably different in *Mystriosuchus* from what it is in the two American genera.

In this connection there might be mentioned the gradual tapering of the skull as seen from above, from back to front in *Rutiodon* and also in *Machaeroprotopus*, whereby the narrow rostrum merges into the narial and postnarial region. This is to be contrasted with the rather abrupt transition in *Mystriosuchus*, marked by a distinct angle between the lateral surface of the premaxillary and maxillary bones and the lateral surface of the posterior maxillary, jugal, and quadratojugal complex. This difference was noted by McGregor and was pointed out by him in his paper of 1906.

As explained above, *Rutiodon* is characterized in a most noticeable manner by the decurved tips of the premaxillaries to form a sort of "hook" on the front of the rostrum, in which are two enlarged premaxillary teeth on each side. This hooked beak armed with enlarged teeth and opposed by enlarged terminal teeth in the dentaries formed a pair of specialized pincers or tongs that must have aided the animal in grasping fish. The hook is present in both *Mystriosuchus* and *Machaeroprotopus*, but in neither of these genera is it so strongly developed as is the case in *Rutiodon*.

One very noticeable feature in the lower



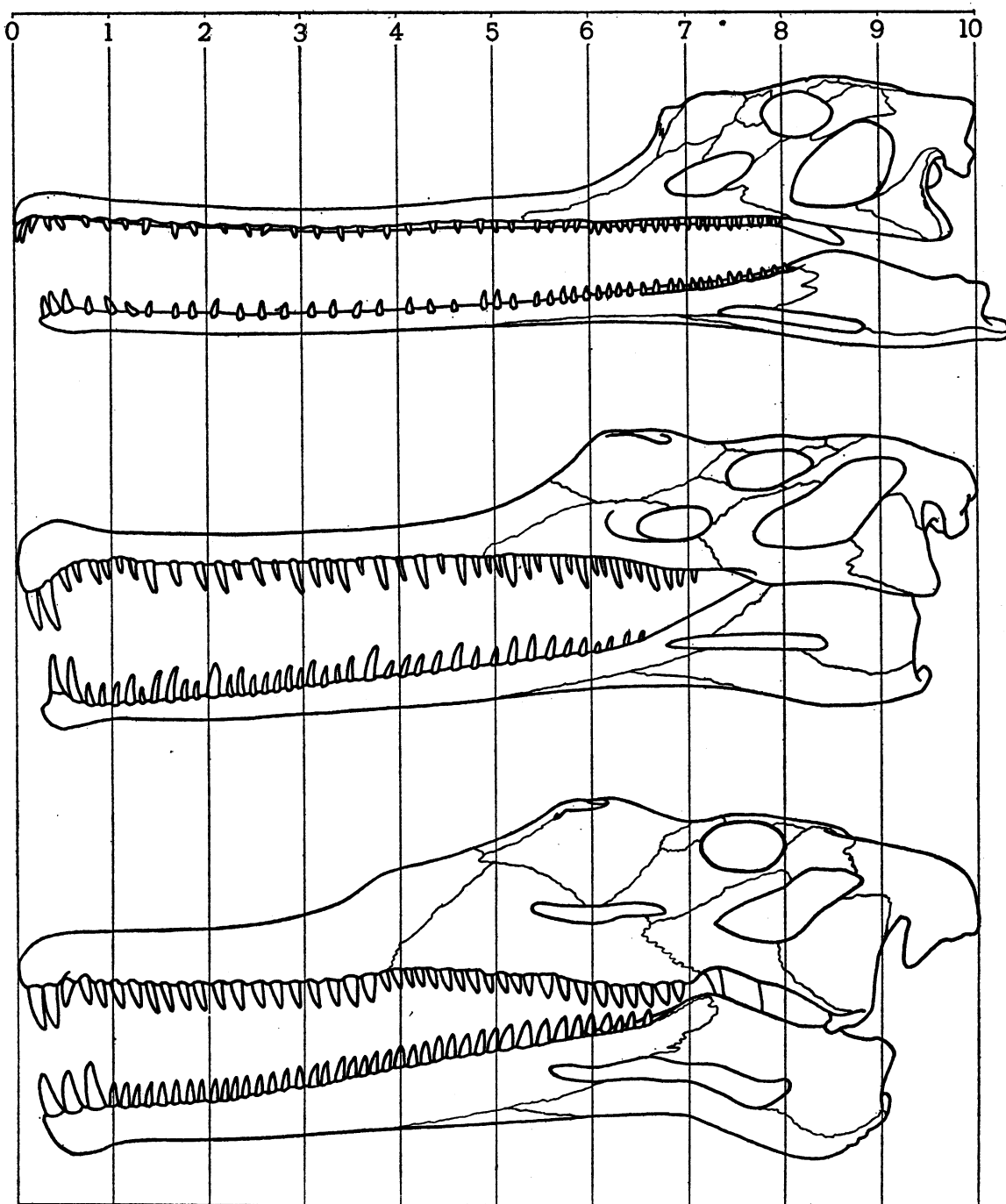


FIG. 12. A comparison of the skull and mandible in *Mystriosuchus* (above), *Ruitodon* (middle), and *Machaeroprotopus* (below). In this figure the skulls have been reduced to a unit length in order to facilitate comparisons of proportions.

jaw of *Rutiodon* is the considerable depth of the angular and surangular as seen in a lateral view, a character that has already been emphasized in the formal description of the mandible. For instance, the depth of the lower jaw beneath the glenoid of the articular is approximately 12 per cent of its total length in *Rutiodon* as compared with 7 per cent in *Mystriosuchus*, a difference that is distinctly noticeable to the eye. *Machaeroprotopus* resembles *Rutiodon* in that the back portion of the lower jaw is comparatively deep. This depth is carried forward in *Rutiodon* from the back of the jaw to the region of the coronoid, from whence the jaw tapers forward into the long and slender dentary.

It is not considered necessary to enter into a detailed description of the postcranial

skeleton at this place, since McGregor in 1906 described the vertebrae, ribs, and limbs of *Rutiodon*, and figured them in detail. His descriptions, together with the beautiful plates published in his memoir, give a comprehensive survey of the best of the materials in the American Museum collection, and further description and figures at this time would be for the most part repetitious.

It is felt, however, that some comparative measurements and ratios may be helpful, especially since these will help the reader to contrast *Rutiodon* with other phytosaurs and with certain crocodilians that paralleled the phytosaurs in a remarkable way. From these comparisons, it may be possible to establish certain trends in phytosaurian evolution as exemplified by the adaptations shown in *Rutiodon*.

TABLE 5  
COMPARATIVE MEASUREMENTS OF *Rutiodon*, OTHER PHYTOSAURS, AND  
CERTAIN CROCODYLIANS  
(Measurements in millimeters)

	<i>Rutiodon</i> A.M.N.H. No. 1	<i>Machaeroprotopus</i> Skeleton from Ghost Ranch	<i>Mystriosuchus</i> McGregor	<i>Gavialis</i> A.M.N.H. No. 15176	<i>Alligator</i> Live Specimen	<i>Tomis- toma</i> (large)	<i>Tomis- toma</i> (small) A.M.N.H. No. 48500
Skull, length	647	880	846	710	235	261	127
Prenarial length	393	488	606	—	—	—	—
Postnarial length	254	390	240	—	—	—	—
Preorbital length	486	630	681	496	119	185	91
Postorbital length	161	250	165	214	116	76	36
Skull width, quadrates	168	280	207	296	116	87	32
Skull width at premaxillary-maxillary suture	33	44	42	63	—	16	7
Mandible, length	622 <sup>a</sup>	830	835	810	—	280 <sup>b</sup>	133
Symphysis, length	340 <sup>e</sup>	370	505	454	—	134	84
Total length	3260 <sup>e</sup>	—	—	—	1510	1300	652
Presacral vertebrae, length	1055	1290	—	—	475 <sup>b</sup>	360 <sup>b</sup>	169
Caudal vertebrae, length	1560 <sup>e</sup>	—	—	—	800	640 <sup>b</sup>	309
Humerus, length	248	280	252	—	—	—	—
Radius, length	177	176	138	—	—	—	—
Manus, length	175 <sup>e</sup>	216	—	—	—	—	—
Femur, length	302	370	—	—	—	—	—
Tibia, length	194	200	—	—	—	—	—
Pes, length	240	340	—	—	—	—	—
Fore limb, length	600	700	—	—	245	170 <sup>b</sup>	—
Hind limb, length	736	740	—	—	320	235 <sup>b</sup>	—

<sup>a</sup> Estimated measurement.

<sup>b</sup> Approximate.

TABLE 6

RATIOS AND INDICES OF *Rutiodon*, OTHER PHYTOSAURS, AND CERTAIN CROCODYLIANS

	<i>Rutiodon</i>	<i>Machaeroprotopus</i>	<i>Mystriosuchus</i>	<i>Gavialis</i>	<i>Alligator</i>	<i>Tomistoma</i> (large)	<i>Tomistoma</i> (small)
<u>Skull</u>							
Total length	20	—	—	—	16	20	20
<u>Skull</u>							
Presacral length	63	68	—	—	50	73	75
<u>Prenarial</u>							
Postnarial	155	125	250	—	—	—	—
<u>Preorbital</u>							
Postorbital	302	252	413	232	103	244	253
<u>Premaxillary-maxillary width</u>							
Quadrate width	20	16	20	21	—	18	22
<u>Symphysis length</u>							
Mandible length	55	45	60	56	—	48	63
<u>Caudal length</u>							
Total length	48	—	—	—	53	49	49
<u>Presacral length</u>							
Caudal length	68	—	—	—	59	56	55
<u>Radius length</u>							
Humerus length	71	63	55	—	(47) <sup>a</sup>	—	—
<u>Manus length</u>							
Radius length	99	123	—	—	(150) <sup>a</sup>	—	—
<u>Fore limb length</u>							
Total length	18	—	—	—	16	13	—
<u>Tibia length</u>							
Femur length	64	54	—	—	(90) <sup>a</sup>	—	—
<u>Pes length</u>							
Tibia length	124	170	—	—	(136) <sup>a</sup>	—	—
<u>Hind limb length</u>							
Total length	23	—	—	—	21	18	—
<u>Fore limb</u>							
Hind limb	81	—	—	—	76	72	—

<sup>a</sup> Approximate.

## RUTIODON, OTHER PHYTOSAURS, AND CROCODYLIANS

The foregoing tables of measurements, ratios, and indices bring out some interesting facts as regards *Rutiodon*, other phytosaurs, and certain crocodilians.

One of these is the close parallelism in proportions that exists between *Rutiodon* and *Tomistoma*. Unfortunately sufficient materials were not available, nor could there be found sufficient measurements in the literature to extend the comparison to *Gavialis*, but it is very possible that a similar parallelism might be found between *Rutiodon* and the modern gavia. At any rate, the parallelism between the phytosaur and the false gavia is striking.

For instance, in various skull proportions, *Rutiodon* shows striking similarities to *Tomistoma*. These are to be seen particularly in the elongation of the skull in front of the orbits and in the narrowing of the snout, from which it might be inferred that the factors that have led to the adaptations seen in the modern, narrow-snouted, fish-eating crocodilians have been very similar indeed to those that led to the specializations seen in many of the phytosaurs. Again, the ratio of skull length to total length is identical in *Rutiodon* and in *Tomistoma*, although there is a factor of uncertainty here because of the absence of the posterior caudal vertebrae in *Rutiodon*. Therefore, the dependence that may be placed upon this comparison depends to some extent upon the accuracy with which the posterior caudal region in *Rutiodon* has been restored. At any rate, there can be no doubt that in looking at *Rutiodon* and *Tomistoma* we see two reptiles that have evolved in strikingly parallel fashion because of the parallelism in their adaptations to similar environments. The parallelism between the phytosaurs and the crocodilians has frequently been stressed by previous authors; it is when a particular phytosaur such as *Rutiodon* is compared with a particular crocodilian such as *Tomistoma* that the degree to which this parallelism exists becomes especially apparent.

Naturally there are certain proportional differences between the two genera under

consideration. Of these, two deserve particular mention. In the first place, it would seem that the crocodilian shows a relatively shorter presacral region than does the phytosaur, although the difference is not great. Secondly, there can be no doubt that the limbs are relatively longer and heavier in *Rutiodon* than in *Tomistoma*. Here we see the effects of a certain degree of higher specialization in the crocodilian as compared with his phytosaurian predecessor, the modern animal being in this respect slightly more aquatic than the Triassic form.

The morphological differences between the two genera are those differences which extend through the entire skull and postcranial skeleton and serve to show the complete distinctness of the two reptilian orders of which these genera are representatives. They have been treated thoroughly in the literature and need not be repeated here.

It may be useful, however, to continue these proportional comparisons by contrasting *Rutiodon* with certain other genera of phytosaurs. In the skull, differences are particularly apparent and have already been described. *Rutiodon* may be considered as a long-snouted phytosaur. On the other hand, it is considerably less specialized in the elongation of the snout than *Mystrisuchus*. Indeed, this last genus shows a degree of specialization that exceeds anything to be seen in any of the other phytosaurs, and thus it may be regarded as the phytosaurian fish-catcher *par excellence*.

So far as may be determined upon the basis of a composite specimen, the radius in *Rutiodon* is relatively longer as compared with the humerus than is the case in *Machaeoroprosopus*, while the manus is shorter. Similarly, the tibia is relatively longer, while the pes is shorter. It is probable that these comparisons are valid. *Mystrisuchus* is interesting because of the very short lower fore limb, an indication of the strong aquatic adaptations in this genus. Unfortunately other skeletal proportions cannot be derived in *Mystrisuchus*.

REMARKS CONCERNING THE MOUNTED SKELETON OF *RUTIODON*

Plate 9 shows the new composite mount of *Rutiodon carolinensis*, A.M.N.H. No. 1. In this mount the tip of the snout is restored from the premaxillary of another specimen in our collection. The length of the snout, as determined by the number of upper teeth, has been established from comparative studies of the American Museum and Williams College skulls of *Rutiodon*, in the latter one of which the snout is complete. A portion of the mandible is restored in its middle region, as well as certain parts of the surangulars and adjacent bones.

This skeleton has been mounted with 25 presacral vertebrae, of which the axis and numbers 8, 16, 20, and 23 are restored. This presacral count is based upon Camp's studies of the genus *Machaeroprotopus*, in which associated skeletons show this number of presacral vertebrae to be present. Seven of these presacral vertebrae are cervicals; the remainder, dorso-lumbars. There are, naturally, two sacrals. The skeleton is shown with 44 caudal vertebrae, of which the last 30 are restored. It is not possible to be certain as to the number of vertebrae in the tail, or as to the length of the tail, since there is nothing in the literature to show that the tail has ever been found in its entirety in the phytosaurs. It is felt, however, that the skeleton as restored approximates rather closely the actual length and composition of the tail in this genus.

The ribs are furnished from a great mass of ribs found at Egypt, North Carolina. Abdominal ribs were found in this material, so the ventral "basket" is included in the mount. As in other phytosaurians, the abdominal ribs consist in each case of three sections, a median V, and one lateral splint on each side.

Of the appendicular skeleton, the left ilium, the left tibia and fibula, and the right

manus are restored. In addition certain phalanges are restored in the other feet. In the manus no carpal elements have been found, and in the pes only the astragalus and calcaneum.

There are numerous bony plates in the American Museum materials. Some of these are shown on the base of the mount, but no attempt has been made to incorporate them in the skeleton in their proper places on the back.

Some attention should be called to the differences between this new mount and the restoration of *Rutiodon* shown in McGregor's monograph of 1906. In the first place, of course, there is the fact that McGregor's restoration shows a skull of *Mystriosuchus* on the *Rutiodon* skeleton, whereas the new mount has on it the skull of *Rutiodon*, as it has been fully prepared and restored. The differences between the skulls are apparent and have already been outlined above.

In the new mount there are 25 presacral vertebrae, as compared with the 26 presacral vertebrae shown in McGregor's restoration. It is felt that there cannot be much doubt that 25 is the correct number, in the light of Camp's recent studies on *Machaeroprotopus*. In this new mount there are 44 caudals, as compared with the 37 caudals in McGregor's restoration. This difference is open to argument.

A few qualitative differences might be pointed out. These are, particularly, the difference in the shape of the spine of the atlas, which in the mount is restored as a rather pointed spine, as is the case in *Machaeroprotopus*, rather than as the hatchet-shaped spine shown by McGregor, the smaller anterior cervical ribs, and the proportionately longer tibia and fibula in the mount as compared with the older restoration.

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