

MEMOIRS  
OF THE  
American Museum of Natural  
History.

VOLUME IX, PART II.

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II.—The Phytosauria, with Especial Reference to  
Mystriosuchus and Rhytidodon.

By J. H. MCGREGOR.

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MYSTRIOSUCHUS AND RHYTIDODON.







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## AMERICAN MUSEUM OF NATURAL HISTORY.

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BY J. H. MCGREGOR.

PLATES VI–XI.

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## INTRODUCTION.

For the last thirty years the opinion of Huxley (1875) regarding the phyletic position of the Phytosauria or Belodonts,—namely, that they are primitive crocodiles,—has been at least tentatively accepted by most palæontologists, though Marsh, Baur, E. Fraas, and others have at various times questioned the propriety of this view and have indicated certain resemblances to other groups, especially the Rhynchocephalia and Dinosauria.

The true relationships of the group thus appearing to be somewhat problematical, it was suggested by Professor H. F. Osborn that I make a study of some phytosaurian remains in the American Museum of Natural History, which had been collected in 1894 and 1895 by Dr. W. D. Matthew in the Triassic coal-fields of North Carolina.

At the same time Professor Dr. E. Fraas, of the Royal Museum of Natural History, in Stuttgart, Germany, most generously offered to place at my disposal some newly discovered remains of the slender-snouted phytosaurian—*Mystriosuchus planirostris* von Meyer, from southern Württemberg. Since both forms were very imperfectly known their investigation seemed promising; accordingly I spent one month in the summer of 1900 in the study of the Stuttgart material, and later, at intervals studied the remains from North Carolina, which proved to be *Rhytidodon carolinensis* Emmons, a form closely allied to *Mystriosuchus*.

The earlier descriptive portions of the present paper are therefore almost entirely devoted to these two genera, both of which have the slender gavial-like type of rostrum, while in the later part I have endeavored to compare the Phytosauria in general with various other reptilian groups.

To Professor Dr. Eberhard Fraas, of the Royal Museum in Stuttgart, and to Professor H. F. Osborn, of Columbia University and the American Museum of Natural History I desire to express equally my great obligation for the use of the valuable material upon which the present work is based, and for helpful suggestion and criticism. I am also indebted to Mr. F. A. Lucas and Mr. Witmer Stone, for the loan of material from the United States National Museum and the Museum of the Philadelphia Academy of Natural Sciences, respectively.

The plates, which represent the original objects most admirably, were drawn chiefly by Mrs. L. M. Sterling and Mr. E. Christman. Of the two original figures in the photographic plate (Plate XI), that of the skull of *Phytosaurus buceros* is by Mr. A. E. Anderson, that of the partial skeleton of *Mystriosuchus*, by Dr. J. Vosseler, of Stuttgart. The text-figures are chiefly my own.

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DEPARTMENT OF ZOÖLOGY,  
COLUMBIA UNIVERSITY, NOV. 1, 1905.



## TAXONOMIC HISTORY OF THE PHYTOSAURIA.

The first contribution to the literature of this group was made by G. F. Jaeger, who in 1828 (1828) described a number of jaw fragments which had been found two years previously in the upper Keuper sandstone near Tübingen, Germany. Thinking (erroneously) that the dentition indicated a herbivorous diet, he named the genus *Phytosaurus* (plant-saurian) as the type of a new family "Phytosaurier"; and since the teeth in various fragments studied seemed to be of two distinct forms he differentiated two species,—*cylindricodon* and *cubicodon*.

As demonstrated by H. von Meyer (1844) the name "Phytosaurier" is a sad misnomer, as these reptiles were undoubtedly carnivorous. A reëxamination of the original material by von Meyer disclosed the fact that the teeth were entirely lacking, Jaeger's description being based merely upon the sandstone casts of dental alveoli; the different forms of these alveoli in the symphyseal and posterior regions of the jaw, circular and oblong respectively, forming the sole basis for his differentiation of two species. The form represented by the union of these two species was later shown by von Meyer to be the same as his *Belodon kapffi* (1861). Inappropriate as is Jaeger's family name "Phytosaurier" it has undoubted priority, and perhaps the best name for the group is Phytosauria.

The generic name *Belodon*, under which have been described most of the remains of these forms, the name which has formed the basis for the family and subordinal names Belodontidae and Belodontia respectively, dates from 1842 when it was proposed by von Meyer (1842) in reference to the arrow-head-shaped posterior teeth. The type species was *Belodon pleiningeri*. Further discoveries of the same species were described by von Meyer in 1844 and 1855.

In the last mentioned work he seems to imply some doubt as to whether all the teeth and bones of *Belodon* belong to the type species, but since the skulls were unknown and most of the bones in fragmentary condition this point could not be definitely determined. However, in his splendid series of memoirs, 'Reptilien aus dem Stubensandstein des oberen Keupers,' published 1861–1865, two other species—*Belodon kapffi* and *Belodon planirostris*—are clearly differentiated, the chief specific criteria being form of snout, character of dermal armature, and size of bones in general. In these memoirs von Meyer showed that his *B. kapffi* was the *Phytosaurus cylindricodon* + *cubicodon* of Jaeger, and also that the remains described by Pleininger in 1844 belonged to this species, instead of to *B. pleiningeri*.

These memoirs of von Meyer on *Belodon* are by far the most important contributions to the literature of the Phytosauria, and contain most minute descriptions and carefully executed lithographic plates of almost all parts of the skeleton; but the author devotes but little space to the discussion of the systematic relationships of the group.



Of British authors Huxley is the only one who has contributed notably to the knowledge of the Phytosauria and his writings are especially important on account of his masterly discussion of the question of phyletic relationships of the group, and of the evolution of the Crocodilia.

The single genus occurring in Great Britain is *Stagonolepis*, from the Triassic sandstone of Elgin, Scotland, named in 1844 by L. Agassiz, who from an examination of a number of the dermal scutes considered it a fish, a mistake which is not surprising when we recall that at that time the Elgin sandstone was regarded as belonging to the Devonian system. The reptilian nature of the remains was suspected by several naturalists even before Huxley, in 1859, (1859) demonstrated its affinities with the Crocodilia. Many years later, in 1875, appeared the famous report of Huxley's researches on 'Stagonolepis Robertsoni and on the Evolution of the Crocodilia,' in which he demonstrates the close affinity of *Stagonolepis* with *Belodon*, and places them among the Crocodilia as the most primitive group of that order, defining for their inclusion the new suborder *Parasuchia* (see page 76). Two years later, in 1877 (1877), Huxley was enabled, from the study of new material, to further elucidate the skeletal structures of *Stagonolepis*.

A possible near relation of *Stagonolepis* is *Parasuchus hislopi* Lydekker (1888) (*ex* Huxley, MS.) a form which derives its chief interest from its geographic position, namely the Maleri beds (Lower Mesozoic) of the Gondwana system at Maleri, near Sironcha, Central Provinces, India. The type specimen consists of a conjoint basioccipital and basisphenoid.

It may be mentioned here that Owen (1860) included *Belodon* in his order Thecodontia.

The earliest discoveries of phytosaurian remains in America date back to the middle of the nineteenth century. The first notes on possible phytosaurian remains were published by Isaac Lea, in the Proceedings of the Philadelphia Academy, in 1851 (1851 A and B). These articles were based on some fossil vertebræ and teeth discovered at Milford, Lehigh County, Pennsylvania, to which Lea gave the name *Clepsysaurus pennsylvanicus*.

In 1856 (1856 A and B), Lea described the tooth of a sauroid reptile, which he had found in the dark shale of the New Red Sandstone, near Phoenixville, Pennsylvania. This tooth differed from those of *Clepsysaurus* in being smaller, less attenuate, sulcate near the base, and having the trenchant edge devoid of serrations. On this single tooth Lea based a new genus, calling it *Centemodon sulcatus* (Κέντημα aculeus, ὀδούς tooth).

The name *Compsosaurus priscus* was proposed by Joseph Leidy in 1856 (1856 A) for the remains of a saurian, obtained from the coal-field of Chatham County, North Carolina, consisting of four teeth, differing in size, of compressed conical form, nearly as broad as long, slightly curved, with opposed trenchant denticulate edges, constricted at the base, and apparently inserted by a compressed cylindrical fang. These teeth are solid, the enamel striated, and in the



larger specimens the base is longitudinally ribbed. Leidy remarks a general resemblance to the teeth of *Palæosaurus* (a Dinosaur) from the English Trias, and we find him later referring to *Palæosaurus* (*Compsosaurus*) *priscus*.

Later in the same year (1856 B), Leidy proposed the name *Omosaurus perplexus*, for "an enaliosaurian, based upon a number of teeth of varied character, vertebræ, fragments of ribs and other bones, and the impression of a dermal plate, obtained from the coal-fields of Chatham Co., North Carolina, by Prof. Emmons and also by Prof. Tuomey.

"Teeth elongated conical, pointed, nearly straight, or more or less moderately curved inwardly, with opposed carinæ on the inner side, which are entire or denticulated; transverse section subcircular, flattened internally; surfaces even, or more or less distinctly fluted on the outer side or all around, and covered with minute interrupted ridges which are vertical on the even surface, oblique on the fluted surface, and divergent downward in the vicinity of the carinæ. Crown solid, enamel thin, dentine concentric, fang subcylindrical, hollowed at base. Length from 5 lines to  $1\frac{3}{4}$  inches, breadth from 2 lines to  $4\frac{3}{4}$  lines. Bodies of the vertebræ biconcave and much constricted as in *Palæosaurus* [*Compsosaurus*] and *Clepsysaurus*. . . . Dermal plate covered with radiating, bifurcating, and anastomosing ridges. Allied to *Clepsysaurus* and *Centemodon* Lea, and *probably identical with them*." (Italics mine.)

*Eurydorus serridens* is a name proposed by Leidy in (1859) on the basis of certain serrate-edged teeth, discovered at Phoenixville, Pennsylvania, the same region which had yielded Lea's *Clepsysaurus*.

E. Emmons in 1856 (1856) proposed the name *Rutiodon* (emend. *Rhytidodon* Cope) *carolinensis* (ῥυτίον plait, ὀδούς tooth), founding the new genus upon teeth from the Triassic (then supposed to be Permian) Coal Measures of the Dan River region in North Carolina. In the same report are figured a number of bones, including three successive vertebræ, about the region of transition from cervical to thoracic, part of a conjoined coracoid and scapula, a femur, and a part of an interclavicle. (This last erroneously described as a portion of the frontal bone.) Emmons, later, in his 'Manual of Geology' (1860) figures and describes a fairly complete skull of *Rhytidodon carolinensis*, a specimen thirty inches in length in which the parts posterior to the orbits are lacking. He describes the snout as subcylindrical and of one solid piece. The teeth are all fluted more or less distinctly, thus differing from *Clepsysaurus pennsylvanicus* Lea. Emmons applies rather loosely the names *Palæosaurus sulcatus* and *Palæosaurus carolinensis*, and some remains which seemed to belong to a smaller species he calls *Clepsysaurus leaii*.

In the opinion of the present writer genera and species of phytosaurians founded upon dental characters alone are very untrustworthy, owing to the great difference in form in anterior and posterior regions (a difference so great as to lead Jaeger to establish two species upon fragmentary casts from the same jaw) probable individual variation in regard to fluting of enamel, and probable variation correlated with the age of the individual.



The affinities of these American forms to the Phytosauria of Europe seem to have remained unnoted until 1866. Cope (1866) referred the remains described by Emmons to the genus *Belodon*, and later (1869) he placed the *Centemodon* of Pennsylvania in the same genus. In Cope's 'Synopsis of the Extinct Batrachia, Reptilia, and Aves of North America' (1869) he founds for the inclusion of the Belodonts a new suborder, for which he adopts Owen's ordinal name Thecodontia. He also adds a new species *Belodon lepturus*, based on material from the Phoenixville, Pennsylvania, region, which, in his opinion, differed from the previously discovered forms, in being of larger size, "in having at least three diapophyses with double articulation near the extremity instead of one [an invalid distinction], and to a different genus from the same, because several of these are cylindric in the former and broadly flattened in the latter." In this 'Synopsis' the various remains, from North Carolina and Pennsylvania, which in all had formed the basis for no less than six generic names, were all reduced by Cope to the single genus *Belodon*, since, as he states (1869, p. 58): "I can as yet find no generic characters by which to distinguish these species from the *Belodon* of Meyer, neither in the cranial, dental, pelvic, nor extremital regions." Cope considered even the specific distinctions to rest upon too slight evidence in several cases, and cuts the number of species to four (including *B. lepturus*);—*carolinensis* Emmons, teeth fluted; *priscus* Leidy, teeth not fluted; *leaii* Emmons, smaller than the other species. In addition to the specific characters here mentioned, there are other criteria, used in defining the species, which I regard as extremely untrustworthy, among such may be mentioned the proportions of vertebral centra; proportions which are frequently greatly altered by pressure. In evidence of this sort the probable error is too great, unless a very considerable number of bones is available for measurement, and in the case of the Phytosauria in question,—most of them established on a few teeth or sparse fragments of the skeleton,—I am inclined to go much farther than Cope in the reduction of the number of species. I consider it very unlikely that the Carolina and Pennsylvania material represents more than two species, and probably but one. Beyond question some of the bones and teeth which served as type specimens, belonged to carnivorous dinosaurs, probably forms allied to *Zanclodon*. The great multiplicity of generic and specific names bestowed by Lea, Emmons, and Leidy, coupled with the doubtful character of some of the meagre type specimens, renders the question of taxonomic priority somewhat difficult to answer. Cope (1869, p. 122 A) adduces evidence to show that *Clepsysaurus* Lea is a dinosaur allied to *Megadactylus*. Marsh also considers it a theropodous dinosaur of the family Anchisauridæ. Cope's reëxamination of the type tooth of Lea's *Centemodon sulcatus* rendered it also open to doubt. The material described and figured by Emmons in 1856, though attributed to several genera,—*Clepsysaurus*, *Palæosaurus*, and his new genus *Rutiodon*,—almost certainly represents but one form. Since the name *Palæosaurus* had previously been applied to a very different reptile, and as there is



doubt regarding Lea's type specimen of *Clepsisaurus*, it seems that Emmons's name *Rutiodon* has legitimate priority, and as his species *carolinensis* is well-established, the type specimen being a nearly complete skull, I retain this name (as emended by Cope) *Rhytidodon carolinensis*.

It may be recalled at this point that this American form closely resembles the *Mystriosuchus planirostris* of Württemberg in the slender gavial-like form of the snout. Cope in 1881 (1881) described two other phytosaurians, from the Triassic of New Mexico, which seem to parallel closely the two other German forms. One of these, *Belodon buceros*, the type specimen of which is a complete cranium (Plate XI), is very similar to *B. kapffi*; the other, *B. scolopax*, is not so definitely established, but seems to resemble *B. pleiningeri* in form of snout. Cope later (1893, p. 12) founded a new species, *Belodon superciliosus*, upon a few skull fragments, scutes, and teeth from the Trias of Texas. The validity of the species seems to be questionable, and it may be identical with *B. buceros*.

Among other probable Phytosauria may be mentioned two forms named and described by Cope, which are also from the New Mexican Trias,—*Episposaurus horridus* (1887, A, p. 213) and *E. haplocerus* (1892, B, p. 129). The dermal plates and remains of the endoskeleton, of these forms, so far as known, resemble the Belodonts, but as nothing is known concerning the skull, there is a possibility that this genus belongs rather to the Pseudosuchia or Aëtosauria, mentioned below.

Marsh also (1893) mentions the discovery of a specimen from the Connecticut River Sandstone (Trias) of Connecticut, which he assigns to *Belodon* as a new species, *validus*, but no description is given. He also published some very misleading observations upon a skull collected at Egypt, North Carolina, which he named as a new species, *rostratus*, of the genus *Rhytidodon*. This specimen is now in the National Museum, where I had the privilege of examining it and found it to be, without doubt, *Rhytidodon carolinensis* Emmons; probably the best preserved skull of that species known. (See figs. 12a, b, and c).

The taxonomic history of the Phytosauria would be incomplete without some mention of certain forms which, by reason of their dermal armature and some other characters, have been regarded as related to belodonts. I refer to certain genera of the suborder Aëtosauria of Nicholson and Lydekker (=the suborder Pseudosuchia of Zittel) (1890). These include *Dyoplax arenaceus* O. Fraas (1867), *Aëtosaurus ferratus* O. Fraas (1877), from the Lower and Middle Keuper of Württemberg respectively, and in North America *Typothorax coccinarum* Cope (1875, p. 84), from the New Mexican Trias. To this group is also probably to be added *Stegomus arcuatus*, known only from a natural cast of the dorsal armature discovered in the Triassic sandstone of Connecticut, and named and described by Marsh (1896) who regarded it as a Belodont. Its closer affinity with *Typothorax* was pointed out by Cope (1896, p. 123). The Aëtosauria are also possibly represented in the Trias at Elgin, Scotland, by

*Erpetosuchus* and *Ornithosuchus*, described by Newton (1894). The probable relationships of the Aëtosauria to Phytosauria are discussed on page 81.

***Mystriosuchus planirostris* E. Fraas.** = *Belodon planirostris* von Meyer.

*Belodon planirostris* was founded by von Meyer in 1861-63 (1863, p. 244), upon a fragmentary skull, a few limb-bones, and dermal scutes, which had been discovered in the Stuben Sandstone of the Middle Keuper, at Aixheim near Spaichingen in southern Württemberg. The examination of these remains disclosed the fact that the snout was much more depressed and more slender than in the species hitherto known,—*Belodon kapffi* and *B. pleiningeri*,—hence von Meyer distinguished it by the specific name *planirostris*.

Nothing further of importance was published concerning this species until 1896 when Prof. E. Fraas of the Royal Museum in Stuttgart, having obtained from the same region which had yielded the type specimens an entire skull and a number of other parts of the skeleton, published a brief description (1896) in which he showed that, in addition to distinctive features of the cranium and dermal armor this species differs from the other phytosaurians, in that the teeth are not compressed, smooth, and sharply edged anteriorly and posteriorly, but cylindrical in section and weakly grooved vertically. These characters being of more than specific value, he established it as a new genus to which he gave the name *Mystriosuchus* (μυστρίον, spoon), in reference to the spoon-like end of the snout.

Since the appearance of these brief notes the Stuttgart Museum has acquired much new and valuable material of this species, all of which Professor Fraas most generously placed at my disposal; and the descriptions and figures of *Mystriosuchus* in the present paper are based entirely upon this material.

It is of interest to note that all of the remains of *M. planirostris*, thus far discovered, have come from the same region,—Aixheim near Spaichingen in southern Württemberg. The Stuben Sandstone, of the Middle Keuper, which has yielded these fossils, is a stratum some six metres in thickness, of coarse light gray sandstone, somewhat friable when first exposed, but hardening rapidly by exposure to the air. The finest specimens of *Mystriosuchus* have come from a hillside outcrop where the stone is quarried for the purpose of crushing it to make mortar sand.

**SKULL** (Pl. VI and VII, Figs. 1-4).—The *Mystriosuchus* material in the Stuttgart Museum comprises one entire cranium with the lower jaw in place, two which lack only the distal half of the rostrum, the right half of another, and numerous fragments, so that it has been possible to make out pretty clearly most of the skull structures. In none of the specimens, however, has the matrix been entirely removed, consequently some of the deeper portions, *e. g.*, the proötic, and epipterygoid regions, are not yet perfectly known.

The skull is remarkably gavial-like in general form, the rostrum forming



two-thirds of its total length, so that this portion is relatively, as well as absolutely, considerably longer than in *Phytosaurus*. The difference in profile between *Ph. kapffi* and the present form is so well shown in Pl. XI that verbal comparison is unnecessary, but it may be remarked that in general *Mystriosuchus* with its slender rostrum bears much the same relation to the heavier *Phytosaurus* as does the modern gavia to the crocodile.

In *Mystriosuchus* the cranium is higher and narrower with the sides more nearly vertical. The greatest width of the skull, the transverse diameter through the quadrates, is, relatively to the length, almost exactly two-thirds that of *Ph. kapffi*. In the latter, the form of cranium may be described as depressed. The difference between the two, as seen from the occipital aspect, is well shown in text-figures 4 and 5.

The length of the cranium in two specimens, measured from the angle of the quadrate to the tip of the snout, is 820 mm. and 790 mm. The total length of the skull in *Ph. kapffi* is 750 mm. The length, measured from the squamosal angle is greater, but less significant for purposes of comparison, since this region is greatly produced posteriorly in the last-named species. Every part of the skull of *Mystriosuchus* is characterized by comparative delicacy of construction; in general the arcades are lighter and the openings—orbis and fenestræ—relatively larger. The relative measurements of the skulls of the two forms, based upon three crania of *M. planirostris* and two of *Ph. kapffi*, are given in the following table.

The cranial sculpture differs considerably from that of *Ph. kapffi*, which is rather a general roughness of surface; but resembles *Ph. pleiningeri*, save that it is more pronounced excepting on the rostrum. The entire upper surface of the head, especially the portions surrounding the nares, and orbits, and the frontal, parietal, and squamosal bones are sculptured with pits and short anastomosing furrows, forming no

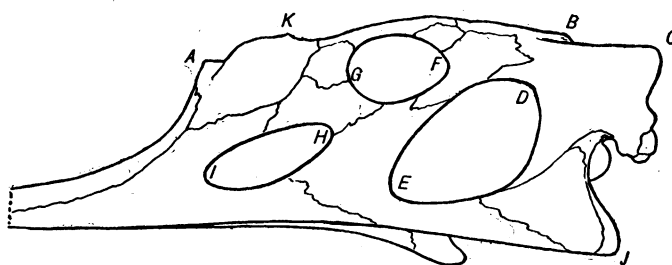


Fig. 1. Key-figure for measurements in millimeters of three skulls of *Mystriosuchus planirostris* (1, 2, and 3) and two of *Phytosaurus kapffi* (4 and 5). No. 1 is somewhat crushed laterally.

	1.	2.	3.	4.	5.
AB	220	204	?	240	227
CC	85	110	?	230	205
CJ	141	122	106	110	125
FG	60	65	62	58	61
DE	107	108	115	122	126
HI	80	82	65	99	105
JJ	167	204	224	302	317
AK	60	38	42	49	52

definite design, but giving a rugose appearance, which gradually fades out toward the snout and on the lower temporal arcade. It will be noted that the sculptured dorsal plane of the head, an area measuring about 12 by 20 cm., contains the nares and eyes, and is so elevated above the remainder of the head, that the animal was able to swim with only this small portion exposed above the

surface of the water. Inhabiting, as it did, the fresh-water lakes and streams of the middle Triassic period, its food doubtless consisted of fishes. The slender jaws and delicate teeth are evidence that it was unable to master animals of great size such as the labyrinthodonts, many of which may have fallen easy victims to the more powerful jaws of *Ph. kapffi*.

In the somewhat detailed description of the skull which follows, attention will be devoted chiefly to features in which the genus differs from *Phytosaurus* and to characters of especial morphological importance. The general form and relations of most of the bones are so clearly shown in the plates that verbal description of them in many cases seems superfluous.

*Premaxillaries*.—The total length of these elements is almost exactly two-thirds the entire skull-length, and they form practically the entire prenasal region. Their surface is smooth, save for a slight pitting near the extremity, and some scattered foramina for blood-vessels. About 5 mm. above the alveolar border on the outer face of the bone the foramina for dental vessels are placed in a continuous shallow groove.

The two bones are not coössified, and a cavity of considerable size extends through the greater part of the rostrum. There is 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. Somewhat similar ridges are seen in various long-snouted reptiles and fishes.

The premaxillaries differ from those of *Ph. kapffi*, as figured by von Meyer, in that their median dorsal processes extend farther posteriorly, nearly reaching the anterior boundary of the external nares.

The extremity of the snout is slightly widened and decurved over the tip of the mandible, beyond which it projects about 20 mm., "a condition which involuntarily recalls the beak of the pelicans and perhaps demonstrates a habit of rooting in mud for food, and catching fishes; the analogy being strengthened by the fact that in the present case the greatest development of the teeth occurs in the decurved tip of the rostrum, comparable with the sharp hook on the tip of the pelican's beak" (Fraas, 1896). The resemblance to the snout of *Lepidosteus* is still more striking.

*Maxillaries* (Pl. VI and VII, Figs. 1-3, *Mx.*).—The maxillaries do not differ in any very important respect from the same elements in *Phytosaurus* since the difference in form of rostrum in the two genera is due almost entirely to the diversity of the premaxillaries. The number of dental alveoli is here 23-24 on a side, while both species of the other genus have but 19. The difference in the form of alveoli is noteworthy: small and round in *Myriosuchus*, large and oval in *Phytosaurus*. The outer wall of the maxillary is greatly excavated by the preorbital fenestra, and a considerable portion of the floor of the cavity, and the



anterior half, or more, of its outer border, are formed by this bone, the posterior portion being bounded by the lachrymal and jugal. This preorbital fossa, plainly the homologue of the preorbital fossa of the Aëtosauria and Dinosauria, is of such size in the Phytosauria as to suggest a possible function as the lodgement of some gland, but I incline to the opinion that its sole service is to give lightness to the skull, without sacrifice of strength. In von Meyer's earliest descriptions of *Phytosaurus* skull, based on a fragment, this opening is identified as the orbit, the true orbit being mistaken for the superior temporal fossa. The palatine plate of the maxillary is narrow, about 30 mm. in width at its widest portion including the alveolar ridge. At no point do the two maxillaries approximate each other more closely than 30 mm. unless it be far forward where they are covered ventrally by the palatine processes of the premaxillaries, and here the relations cannot be discerned. The articulations of the maxillary are: on the outer surface, with the premaxillary, nasal, lachrymal, and jugal; on the palatine surface with premaxillary, possibly the anterior end of the vomer (prevomer of Broom), with the palatine, ectopterygoid and jugal.

*The Teeth.*—Since there is no difference aside from size between the premaxillary and maxillary teeth, the entire upper dentition may be described at this point. The total number of upper teeth on a side is 47, of which 23 or 24 are in the premaxillary. The most anterior three, those in the decurved terminal portion, are somewhat the largest, though not approximating in size those of *Phytosaurus*. According to Fraas (1896) the teeth diminish regularly in size and strength, proceeding backward from the tip of the snout, in contradistinction to the condition obtaining in *Ph. kapffi*. Though this diminution is very marked in the specimen upon which the observation was made, another specimen, since found, in which the maxillary teeth are well preserved, does not bear out the statement. Few of the teeth exceed 20 mm. in length of crown and some of the more posterior measure less than 10 mm. Occasionally very small teeth occur interpolated among larger ones, indicating replacement of those accidentally lost. Dentition is strictly thecodont, there being no tendency toward coalescence of alveoli into a groove. Though the teeth are more numerous in the present genus than in *Phytosaurus* their smaller size and the greater length of the entire alveolar region, render the intervals between them greater, and they are not crowded as in the latter form. One of the criteria upon which Fraas justifies the generic separation is the form of the teeth. In *Mystriosuchus* none of the teeth are flattened and none of them show any sharp edge; in this character they resemble the anterior teeth of *Phytosaurus*, and like these are very slightly curved, but differ again in that their slender conical crowns show a delicate vertical fluting, most pronounced on the outer surface, and fading out some distance from the point. (This fluting is not demonstrable in all the teeth, and is never so strongly marked as in certain teeth which have been found associated with phytosaurian remains in America.)

*Nasals* (Pl. VI and VII, Figs. 1-3, *Na.*).—Owing to the abrupt tapering of

the cranium, where it merges into the snout, the external nares of *Mystriosuchus* do not open directly upward, but slightly forward. The nasals do not extend anterior to the nares to the same extent as in *Phytosaurus*. The nasal septum is formed entirely by these elements, and is somewhat conspicuous anteriorly, as shown in the profile view of the skull, forming a 'step' from which the dorsal line of the rostrum descends abruptly. The nasals form the entire narial border. The nares are somewhat smaller than in *Ph. kapffi*, measurements of two skulls of each genus giving an average antero-posterior diameter of 40 mm. and 50 mm. respectively. The two nasal bones are not coössified; and one specimen in which the two halves—anterior portion of the skull—are slightly forced apart, shows that even the two lamina of the internasal septum remain discrete.

*Bones Surrounding the Orbit.*—The orbits are elliptical, with slightly prominent rims, and in accord with the greater lateral compression of the cranium, they do not look upward to quite so great an extent as in *Phytosaurus*, and are slightly larger than in that genus. The bones which participate in the formation of the orbital rim are so clearly figured in the plates that a very brief description here will suffice. The upper half of the rim is formed by the prefrontal, frontal, and postfrontal, the three having about equal part. The lachrymal and post-orbital bound the orbit below and posteriorly, and, at least in some specimens, the jugal also participates to a slight degree. In *Ph. kapffi*, according to von Meyer's figures, the lachrymal and postorbital are suturally united, shutting out the jugal entirely from the orbit. In *Ph. pleiningeri* this element enters the orbit to a very slight degree, while in *Mystriosuchus* its participation is somewhat greater. This must be regarded as the primitive condition, the exclusion of the jugal from the orbit undoubtedly being secondary.

All the bones in the orbital region are sculptured, especially the prefrontal, frontal, and postfrontal which are heavily rugose. The sagittal suture between the frontals is persistent.

*Bones of the Temporal Region.*—Under this heading may be included the elements which bound the latero-temporal fenestra, an irregularly oval opening which averages 110 mm. in its greatest diameter in three skulls measured. The bones framing this fenestra are the postorbital, jugal, quadrato-jugal, and squamosal. (The squamosal will be treated under "Occipital Aspect.") This portion of the skull is essentially rhynchocephalian, and resembles *Sphenodon* much more closely than it does the Crocodilia, Dinosauria, or Aëtosauria.

*Postorbital* (Pl. VI and VII, Figs. 1 and 3, *P.o.o.*).—The greater portion of the postorbital is a roughly sculptured plate, on the dorsal surface of the skull, forming the anterior portion of the broad supratemporal arcade, articulating along its inner border with the postfrontal and parietal bones, and posteriorly with the squamosal.

From the outer anterior portion of this plate a short descending bar articulates with the jugal, forming therewith the arch which separates the orbit



from the latero-temporal fenestra. The relations of this bone are thus exactly the same as in *Sphenodon*.

*Jugal* (Pl. VI and VII, Figs. 1-4, *J.*).—A striking resemblance to *Sphenodon* is seen also in the jugal. This bone is shaped like a V lying on one side, the forwardly directed apex articulating with the maxillary, and helping to form the posterior boundary of the preorbital fenestra; the lower, or horizontal limb of the V forming the infratemporal arcade, connects posteriorly with the quadratojugal, while the other limb, uniting distally with the descending process of the postorbital, separates the orbit and latero-temporal fossa, and (in somewhat varying degree) participates slightly in the formation of the ventral rim of the orbit. A remarkable feature of this bone is the great posterior development of the ventral limb, which extends backward, under the quadratojugal as far as the posterior limit of the latter, though it does not seem to have any articulation of its own with the quadrate.

*Quadratojugal* (Pl. VI and VII, Figs. 1-4, *Q. J.*).—This is a triangular plate, articulating on its inner surface with the quadrate, and overlapping by squamous suture the descending limb of the squamosal and the posterior portion of the jugal. These are the normal relations of the diapsidan quadratojugal, but here again the configuration suggests particularly the Rhynchocephalia; and it certainly exhibits less modification than in Crocodilia or Dinosauria. The outer surface of the bone is slightly roughened.

*Palatal Region.*—The strong likeness of the phytosaurian palate to that of the Rhynchocephalia has been noted by Baur, Zittel, and others, and it is safe to assert that if our knowledge of the group were limited to the palate, it would be ranked as a Rhynchocephalian. Text-figures 2 and 3, representing respectively the palatal aspect of *Mystriosuchus*, minus the rostrum, and of *Sphenodon* will serve much better than a description to elucidate the great similarity. The comparison shows that the internal nares are quite in their primitive position, and the relations of all the bones essentially similar. The palatines in *Mystriosuchus*, however, show entire lack of dentition, and a tendency toward the development of a secondary bony palate. Unfortun-

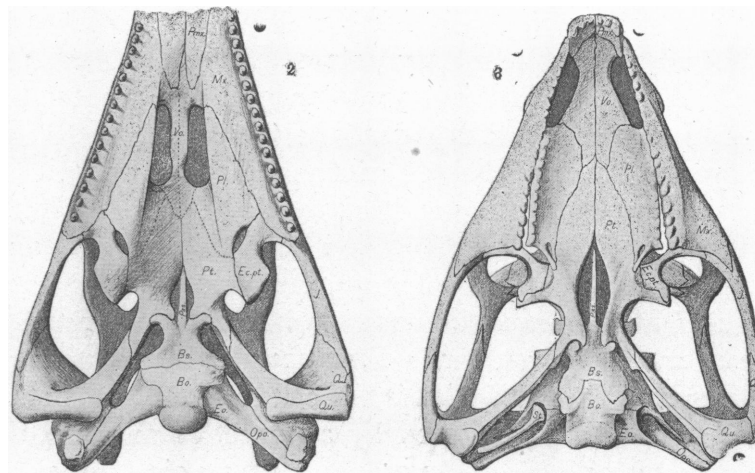



Fig. 2. Palate of *Mystriosuchus planirostris*, and Fig. 3, palate of *Sphenodon punctatus* for comparison. *Bo.*, basioccipital; *Bs.*, basisphenoid; *Ec. pt.*, ectopterygoid; *Ex.*, exoccipital; *J.*, jugal; *Mx.*, maxillary; *Opo.*, opisthotic (=paroccipital); *Pas.*, parasphenoid (vomer of Broom); *Pmx.*, premaxillary; *Pt.*, pterygoid; *Qu.*, quadrate; *Q.J.*, quadratojugal; *Vo.*, Vomer (pre-vomer of Broom).

ately, only one of the three skulls in the Stuttgart collection has the palate exposed, and in this case the surface of the bones is badly abraded, and, though the general form of the palate is clearly shown, little can be made out regarding the sutures; consequently, it has been found necessary to restore the boundaries of the bones from a study of *Phytosaurus*, aided by the excellent figures of von Meyer.

The internal nares are located directly under the external, and are very close together, resembling those of *Erpetosuchus* and *Ornithosuchus* (possible Aëtosauria) (Newton 1894), and of certain Dinosaurs. Their antero-posterior diameter is 50 mm., only two-thirds that of *Ph. kapffi*. The ventral edge of the internasal septum (vomer) is placed somewhat above the level of the palatal plate of the maxillary and the palatine, and the pterygoids, which are in sutural union in the mesial line, and are arched upward, forming a sort of narrow vault of the palate, flanked by maxillary and palatine at a lower level. A transverse section of the palate would be -shaped. The adaptive significance of this condition is plainly the formation of a space above the flat tongue, giving a breathing passage between the nares and the glottis.

This arched condition of the palate suggests two questions of great importance in their bearing upon the genetic relationships of the group, namely: (1) Do the Phytosauria exhibit the incipient formation of a secondary palate? and (2) if so is this the first step in a phyletic series, culminating in the highly modified palate of the eusuchian crocodiles? As for the first of these questions I feel that there is no escape from an affirmative answer; an examination of the palate of either *Mystriosuchus* or *Phytosaurus* shows a pair of longitudinal palatine ridges (described below under 'Palatine') which plainly represent the beginnings of a secondary palate. As to the second question, while there can be no doubt that the crocodilian palate is traceable to a similar condition, I believe that the other characters (as explained below, page 85) eliminate the Phytosauria from the line of crocodilian ancestry.

*Vomer* (prevomer of Broom) Pl. VI, Fig. 2, *Vo.*).—The vomers occupy the typical position, forming the internarial septum, and possibly a considerable portion of the anterior and posterior walls of the internal nares, but it was impossible to discover the exact limits of these bones. The two vomers are probably not coalesced, for in *Phytosaurus* the suture between them is discernible. The narrowness of the internarial septum renders it very improbable that the vomers are separated by an anterior process of the pterygoid as in some dinosaurs and in ichthyosaurs. At a point between the posterior ends of the nares the edge of the vomerine septum rises abruptly to the higher level of the vault of the pterygoids.

The vomers articulate posteriorly with the pterygoids, though the suture is not discernible. Their relation to the palatines is unknown but it is almost certain that they are in contact with these elements at the posterior border of the nares. Anterior to the nares they are overlapped ventrally by the palatal



processes of the premaxillaries and articulate with the maxillaries, though here again the suture is not demonstrable.

*Palatine* (Pl. VI, Fig. 2, *Pl.*).—The palatine, which is elongate antero-posteriorly presents two portions,—a nearly horizontal lateral plate extending forward along the entire outer border of the narial aperture, and uniting externally by suture with the maxillary, and posteriorly with the ectopterygoid. The rounded inner border projects very slightly toward the middle line, so that the palatal aspect of the cranium exhibits two elongate ridges which approximate each other within 25 mm. at the level of the anterior border of the nares, diverging gradually behind this region. These palatine ridges partly obscure the outer part of the narial cavities, and are continued anteriorly on the maxillaries, but fade out posteriorly without involving the pterygoid. Their approximation is still more marked in *Phytosaurus*, where the interval between them is but 20 mm. in the narial region. It should be explained that these ridges do not present a sharp edge, but are boldly rounded. Nevertheless it is an approximation of the palatines, ventral to the internal nares and the pterygoids, and it seems to me that it must be interpreted as a *tendency* toward the formation of a secondary palate, though there is nothing in the condition to contradict the statement, in Huxley's diagnosis of the *Parasuchia*, that "neither the palatine nor the pterygoid bones are produced into osseous plates which prolong the nasal passage and give rise to secondary posterior nares."

The inner portion of the palatine, the part posterior to the nares, and internal to the ridge, arches upward forming the sides of the 'vault' above mentioned. Its line of suture with the contiguous bones cannot be made out. It certainly articulates with the outer border of the pterygoid, and it is probable that there is also a short sutural union with the vomer and that it forms a part of the posterior narial boundary. My opinion as to its probable relations is shown in dotted lines in text-fig. 2.

*Pterygoid and Ectopterygoid* (Pl. VI and VII, Figs. 1-4, *Pt.* and *Ec.pt.*).—The pterygoid approximates very closely the primitive diapsidan condition, as exemplified in *Procolophon*, and is almost identical with the corresponding element in *Sphenodon*, except that in this form the palate is not so greatly arched. The two pterygoids uniting suturally in the middle line for a distance of 40 or 50 mm. form the arch or vault of the palate. Posteriorly they are divergent, exposing between them an interpterygoid vacuity, in which the parasphenoid (vomer of Broom) can be seen.

Posteriorly the pterygoids are firmly supported by stout knob-like processes of the basisphenoid. The quadrate process, which forms the anterior portion of the pterygoquadrate arch, appears rod-like in ventral view, but seen from behind, it has the form of a vertical plate, from 30 to 40 mm. in depth (text-fig. 5).

The anterior two-thirds of the outer border of the pterygoid unites with the palatine, but it has not been possible to determine the line of suture; the

posterior third articulates with the ectopterygoid forming together with this bone a broad lateral *ala* which projects somewhat ventrally and posteriorly, and is separated by deep notches externally and internally, from the inferior temporal arcade and the pterygoquadrate bar. In ventral view the pterygoid portion of this *ala* is largely hidden by the ectopterygoid. This last-named bone forms a short flattened bar firmly buttressed externally by the maxillary, and to a smaller extent by the jugal. Its inner anterior border is in union with the palatine by a short suture, which merges posteriorly into an oval fissure,—the *posterior palatine vacuity* or *suborbital vacuity*. The outline of this vacuity could not be clearly established in *Mystriosuchus*, but it is rather narrow and considerably smaller than in *Phytosaurus*,—apparently about  $5 \times 20$  mm. (Pl. VI, Fig. 2, *p.f.*).

*Basisphenoid and Parasphenoid* (Pl. VI, Fig. 2, *Bs.*, *Pas.*).—The basisphenoid is very heavy and broad posteriorly, its postero-ventral surface roughened for muscle attachments, while anteriorly it is narrower but gives off a pair of short, diverging pillars, with knob-like ends, forming firm supports for the pterygoid. The union with the basioccipital appears to be very firm, and the sutural line is not very distinct.

Anteriorly the diverging pillars form the posterior boundary of the interpterygoid vacuity, and deep in this vacuity can be seen the parasphenoid (vomer of Broom), which extends forward, arching above the pterygoids. At its base the parasphenoid is 7 mm. in width, slightly broader than in *Ph. kapffi*. Its ventral surface at the highest point is elevated about 3 cm. above the level of the lowest portion of the basisphenoid.

*Occipital Aspect* (Pl. VI, Fig. 4, and text-figs. 4–6).—For the sake of convenience of treatment, the bones which appear in the occipital view of the skull will be described together. To elucidate the relations of the various elements, text-figures 4, 5, and 6 are introduced, representing respectively *Phytosaurus*, *Mystriosuchus*, and *Sphenodon*. In comparing the two phytosaurians the homologies are obvious at a glance. The introduction of *Sphenodon* shows not only its general resemblance to the others, but also serves to make clear the relations of the parieto-squamosal arcade in these forms, a point which is not so obvious.

*Occipital Bones* (Pl. VI, Figs. 1–4).—The nearly round foramen magnum is bounded by the supraoccipital dorsally, the exoccipital laterally, and by the basioccipital ventrally.<sup>1</sup>

The small supraoccipital, surrounded dorsally and laterally by the parietals, has small part in the border of the foramen, less than in *Sphenodon*. Its surface is slightly concave and roughened for the attachment of muscles.

<sup>1</sup> Von Meyer (1865, Pl. XXV) gives an erroneous figure of the occiput of *Phytosaurus pleiningeri*, which represents the foramen magnum as surrounded entirely by the exoccipitals, the supra- and basioccipital being entirely excluded. The specimen from which this figure was drawn is now in the British Museum where I had the privilege of examining it, and as was to be expected, discovered that there was no warrant for the condition shown in von Meyer's figure, cracks having been mistaken for sutures.

The exoccipitals form the greater part of the boundary of the foramen magnum and contribute slightly to the formation of the occipital condyle,

rather more than in *Phytosaurus*, but less than in *Sphenodon*. Seen from behind they rise as short pillars from the condyle, articulating dorsally with the supraoccipital, and continuing latero-posteriorly into the long opisthotics or paroccipitals, which distally are surrounded above, anteriorly, and below by the squamosals. Dorsally the opisthotic supports the *greatly reduced and depressed* parieto-squamosal arcade. The exoccipital and opisthotic are firmly coalesced, and there is nothing to show the position of the suture. (Note suture in figure of young *Sphenodon*.) In lateral view the exoccipital shows two nerve foramina; the more posterior is small, about  $2 \times 3$  mm., and located very close to the condyle. This seems to be the foramen of exit for the hypoglossal nerve. Almost immediately anterior to this is a much larger vertically elongate foramen,  $6 \times 9$  mm., which must have given common exit to the vagus and the glossopharyngeal. The opisthotic portion will be further described below under "Otic Region."

The basioccipital forms nearly all of the condyle (well shown in Pl. VI, Fig. 2). In one well-preserved specimen the condyle has a transverse diameter of 30 mm. In two others it is 36 mm. and 20 mm., but both are somewhat distorted. Anterior to the condyle, as seen in the ventral aspect, the basi-

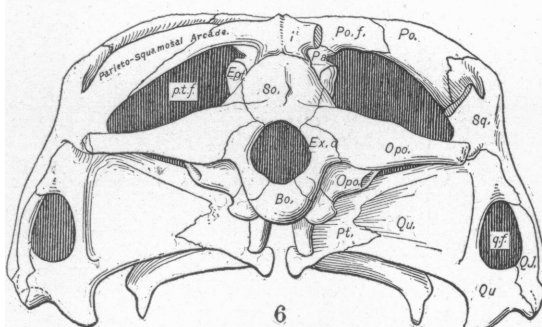
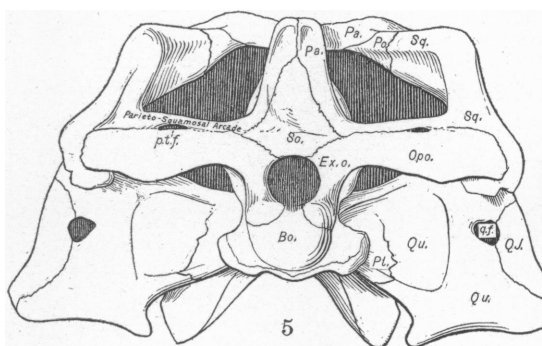
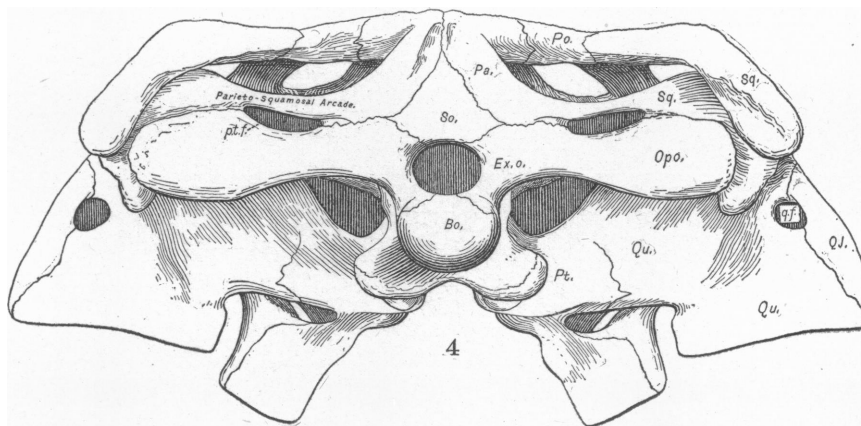


Fig. 4. Skull of *Phytosaurus kaffi*, occipital aspect; Fig. 5, *Mystriosuchus planirostris*; Fig. 6, *Sphenodon punctatus*. (In the last the right parieto-squamosal arcade is removed.) Comparison of the three figures will clearly show the reduction and depression of the parieto-squamosal arcades in the phytosaurian types, especially in *Mystriosuchus* where the posttemporal fenestra (*p. t. f.*) is almost obliterated. Figs. 4 and 5 are drawn to the same scale, one third natural size. Fig. 6 is enlarged to facilitate comparison. *Bo.*, basioccipital; *Ex. o.*, exoccipital; *Op. o.*, opisthotic or paroccipital; *Pa.*, parietal; *Po.*, postorbital; *Po. f.*, postfrontal; *Pt.*, pterygoid; *p. t. f.*, posttemporal fenestra; *q. f.*, quadrate fenestra; *Q. J.*, quadratojugal; *Qu.*, quadrate.

The basioccipital forms nearly all of the condyle (well shown in Pl. VI, Fig. 2). In one well-preserved specimen the condyle has a transverse diameter of 30 mm. In two others it is 36 mm. and 20 mm., but both are somewhat distorted. Anterior to the condyle, as seen in the ventral aspect, the basi-



occipital is very heavy, and roughened for muscular attachments. Its width across the line of union with the basisphenoid is 52 mm.

*Parietal* (Pl. VI and VII, Figs. 1, 3, 4, *Pa.*).—The dorsal plate of the parietal is very small, its surface deeply pitted and rugose, the interparietal suture persistent. An important point is the absence of a pineal foramen. A casual observation of the dorsal surface of the skull might lead the observer to think that the supratemporal fenestra was incomplete posteriorly, though its outer, anterior and inner margins are normally represented by the highly sculptured squamosal, postorbital, and parietal. The median posterior portion of the parietal seems to end suddenly over the occiput, and the parieto-squamosal arcade appears to be lacking. In fact, Marsh has stated (1896) that "the skull of *Belodon* [*Phytosaurus*] shows that the supratemporal openings characteristic of the true crocodilians are wanting." That this statement is erroneous, and that the posttemporal or parieto-squamosal arcade is present in the Phytosauria will be readily seen if the parietal (*Pa.*), squamosal (*Sq.*), and opisthotic (*Op. o.*) bones, and the posttemporal fenestræ (*p.t.f.*) be carefully compared in text-figs. 4, 5, and 6. (The drawing of *Sphenodon* represents the arcade in question only on the left side, on the right it is sawn out to demonstrate the similarity of the postorbital-squamosal arch in the three forms.)

The comparison of these figures shows plainly that both phytosaurians possess the posttemporal arcade, but that it is greatly reduced, and so depressed as to be in close contact with the supraoccipital and with the long lateral bar of the opisthotic, except for a short interval about the middle, where a posttemporal fenestra appears small (about 5 x 18 mm.) in *Phytosaurus*, but very minute—a mere vestigial fissure—in *Mystriosuchus*, where one measured 10 mm., the other 5 mm. in length. In this genus the parieto-squamosal arcade is very thin, about 3 mm. in thickness above the fossa, but in dorsal view (Pl. VI, Fig. 1) it is seen to be rather broad. The point of juncture of parietal and squamosal cannot be made out. The comparison of the two genera shows a greater and more abrupt depression in *Mystriosuchus* than in *Phytosaurus*. Depressed, as it is, it must have been covered dorsally by muscles. The reduced condition of this arcade furnishes a strong distinguishing mark of the order.

*Squamosal* (Pl. VI and VII, Figs. 1-4, *Sq.*).—This element enters largely into the formation of the supratemporal arcade. The dorsal portion is strongly sculptured, and, as above stated, it forms the outer part of the highly modified posttemporal arcade. Postero-laterally this bone is greatly developed, though less so than in *Phytosaurus*. Immediately ventral to the outer end of the opisthotic bar is a hook-like process to which a nodule of calcified cartilage adheres. This process appears to have served for the suspension of the hyoid arch, the proximal portion of which, in my opinion, is represented in the calcified nodule. A slight process having a similar function is present on the squamosal of *Sphenodon*. As seen in lateral view the squamosal articulates

with the parietal, postorbital, opisthotic, quadrate, and quadratojugal. It may be stated that this bone represents morphologically a complex of the squamosal and prosquamosal.

*Quadrate* (Pl. VI and VII, Figs. 2, 3, and 4, *Qu.*).—The articular surfaces for the mandible are slender, almost cylindrical, and placed transversely. From this articular region a transverse vertical wall extends dorsally, uniting firmly with the squamosal by suture. Internally this wall bends forward to join the pterygoid in the pterygoquadrate bar. This portion is continued upward in a thin vertical lamina. Laterally the quadrate is covered by the flat quadratojugal. A glance at text-figures 4, 5, and 6, will show, in the posterior vertical plate of the quadrate, an aperture (*q.f.*), bounded externally by the quadratojugal. The only difference is the proportionally greater size of the opening in *Sphenodon*. A similar aperture having corresponding relations occurs in Ichthyopterygia; and I believe it to be without doubt a homologous structure.

*Otic Region*.—None of the skulls was sufficiently freed from matrix to render possible a complete description of the otic complex, and the boundaries of opisthotic and proötic could not be determined. The fenestra ovale is located some 4 mm. anterior to the vagus foramen. It opens latero-posteriorly, is somewhat elongate vertically, and measures  $6 \times 9$  mm. The columella auris must have extended almost horizontally in a latero-posterior direction, and its tympanic end was placed under the notch of the squamosal, and if present it would be plainly visible in a ventral or posterior view of the skull. Prof. Fraas informed me that a delicate rod of bone, apparently the columella auris, was imbedded in the matrix in the stapedial region, but it was too fragile to be removed, and was destroyed in the preparation of the skull. The relations of the otic region resemble those of *Sphenodon* closely, also the lizards, and to a less degree the crocodiles. Both phytosaurian genera show an abrupt angle at the anterior border of the proötic, exactly as in *Sphenodon*, and this region is more like the corresponding part in *Sphenodon* than in the Crocodilia.

Unfortunately the preparation of the skulls was not sufficiently complete to permit any observations on the epipterygoid.

*Mandible* (Pl. VII, Fig. 3).—The lower jaw, with its elongate symphysis is strikingly similar to the corresponding part in the longirostral Mesozoic crocodiles. Its length is 835 mm., the symphyseal portion measuring 505 mm. or about three-fifths of the total length. It is interesting to compare these proportions with those in *Phytosaurus kapffi* as figured by von Meyer (1863, pl. xlvii), in which, of a mandible 700 mm. long only 290 mm., or about three-sevenths, are in the symphyseal portion. The symphysis is, therefore, much longer, relatively, in *Mystriosuchus*. In von Meyer's plate of the jaw of *Ph. pleiningeri*, the ratio of symphyseal length to total length is as 29 to 62, almost one-half; making one more feature in which the last-named form is intermediate between the other two. The absolute length of the symphysis is equal in

*Ph. kapffi* and *pleiningeri*, about 290 mm., but the difference in jaw proportions between the two forms seems to militate against Fraas's suggestion (1896) that both may represent the same species, *pleiningeri* being immature. If this is correct, the growth of the mandible in later life must be limited to the post-symphysial region.

The form of the mandible in lateral view is well shown in Pl. VII, Fig. 3. The symphysial portion is extremely slender, the transverse diameter 80 mm. from the extremity measuring only 22 mm. The extremity widens slightly, to accommodate the larger anterior teeth, and the bone is here a trifle deeper, forming a slight ventral convexity or 'chin' as in *Phytosaurus*.

The posterior part of the jaw is much narrower vertically than in the other genus, and in the region of the posterior teeth the ventral border is distinctly concave. The greatest vertical depth is 85 mm. A large external and a smaller internal mandibular fenestra are present, very similar to those of a crocodile. In the largest specimen measured the external fenestra is 135 mm. in antero-posterior measurement, and 30 mm. in vertical width. It is located 100 mm. from the angle of the jaw; the surangular and the dentary form its upper margin, and the angular borders it below. The two rami of the mandible do not unusually become coössified in the symphysis; in one specimen the symphysial suture is plainly visible on the ventral aspect, but is interrupted at a point 40 mm. from the tip of the jaw by a circular foramen 4 mm. in diameter, anterior to which the suture is less distinct, and there may be some coalescence of the rami. The surface of the mandible is smooth in general, but the angular is slightly rugose where the skin was closely adherent.

In view of the strongly rhynchocephalian structure of the cranium, the fact that the mandible is essentially like that of the longirostral crocodiles is of great interest. Baur (1895) showed that in Lacertilia and Crocodilia the so-called articular is a compound bone, a portion of it being of dermal origin, and representing the true angular, the so-called angular being in reality the splenial, and the bone commonly designated splenial being a 'presplenial.' This element occurs in one group of turtles (Chelyoidea), in lizards, and in the crocodiles, attaining enormous proportions in the longirostral forms of the last-named order, where it extends forward and participates in the mandibular symphysis. Baur notes that among the reptiles examined by him all in which the Meckelian cartilage is covered internally possess the presplenial. It is absent in *Sphenodon*, and reference to Howes's (1901) descriptions and figures of early developmental stages reveals no trace of it. In the *Phytosauria*, there cannot be the slightest doubt that the presplenial is present, and enormously developed, forming an internal facing of the jaw, exactly as in the crocodiles; a remarkable departure from the rhynchocephalian type, in view of the cranial resemblance to *Sphenodon*.

*Dentary* (Pl. VII, Fig. 3, *D.*).—The dentary is conspicuous on the outer surface of the jaw, and extends from the anterior extremity to a point above



the middle of the external mandibular vacuity. A considerable portion of the anterior extremity of the jaw is doubtless exclusively composed of this element as in *Ph. kapffi*, but in the hinder portion of the symphysial region, and posterior to this where the rami are separate it forms a flat plate, containing the alveolar process dorsally, but not reaching the inferior border of the jaw; its articulations are, internally and ventrally, with the splenial (= presplenial of Baur), and posteriorly with the supra-angular and the angular (= splenial of Baur). It also forms a part of the margin of the external mandibular fenestra. The outer surface is somewhat pitted and grooved for blood-vessels, the most conspicuous sculpture being a channel for dental vessels some 4 mm. to 6 mm. below the alveolar border. Since the alveolar region is a part of this bone, the mandibular dentition may be described at this point, though of necessity very imperfectly, owing to the fact that the only skull which showed the snout had the space between the upper and lower jaws still filled with matrix, so that the alveolar border could not be seen. It is possible to count 75 teeth in the mandible, but this is certainly far short of the total number. In *Phytosaurus*, both *kapffi* and *pleiningeri*, the mandibular teeth number about 52 on a side, while the upper jaw shows but 39. It is at present impossible to state whether approximately the same ratio of upper and lower teeth obtains in *Mystriosuchus*, but I incline to the opinion that in this case the numbers are about equal, since the teeth which are visible in the entire specimen, and alveoli present in several jaw-fragments, indicate that the teeth were closely similar in size and form and spacing in the corresponding parts of both jaws. Both above and below they are more closely crowded in the posterior third of the jaw. The alveoli are circular in section, never oval as in *Phytosaurus*, and are considerably greater in diameter than the contained teeth, the fangs of which must have been surrounded by a thick layer of connective tissue. In the entire specimen the posterior mandibular teeth are smaller than those nearer the extremity, but a second specimen, showing only the posterior part of the jaws, contains teeth as large as the anterior ones of the first specimen. The three anterior teeth are somewhat larger than the rest, but are not tusk-like as in *Ph. kapffi*, and are not conspicuous when the mouth is closed. The crowns of these teeth do not exceed 20 mm. in height and 7 mm. in diameter at the base. Owing to the overhang of the tip of the premaxillary, the first two upper teeth, on each side, are entirely anterior to the lower jaw. The crown of the first mandibular tooth is directed laterally, fitting in the interspace between the second and third upper teeth. A marked asymmetry is seen in the dentition of the two sides, in both jaws, owing perhaps to the mutual accommodation of upper and lower teeth, and the replacement of lost teeth. Structurally the mandibular dentition is similar to the upper above described (p. 39).

*Splenial* (presplenial, Baur; Pl. VII, Fig. 3, *Sp.*).—The form and relations of this bone, which forms the inner walls of all except the posterior 15 or 18 mm. of the lower jaw, were not clearly shown in the *Mystriosuchus* material studied,

owing to the matrix which was still present between the rami, but its essential similarity to the splenial of *Phytosaurus* cannot be questioned. In the latter genus this element closely resembles that of the longirostral Crocodilia.

The posterior border articulates dorsally with the coronoid, ventrally with the angular (splenial of Baur); while between the two is a short articulation with a long process (angular of Baur) of the articular. Anteriorly the splenial extends to within about 15 mm. of the tip of the jaw (14 mm. on the upper and 16 mm. on the lower surface), so that more than the posterior half of the mandibular symphysis is formed by this element; its relative participation must be much greater in *Mystriosuchus* where the symphysis is so much longer. The dental canal, a cavity of considerable size, extends throughout the post-symphysial portion of the ramus between the dentary and splenial bones and is largely formed by excavation of the splenial. These canals extend for some distance into the symphysial portion. Transverse sections of this region also show a small rounded median canal, between the apposed splenials, which is traceable nearly to the tip of the jaw. Comparison with the homologous bone of *Alligator* demonstrates beyond a doubt that this element is the presplenial of Baur.

*Angular* (splenial of Baur; Pl. VII, Fig. 3, *An.*).—This element is also greatly like that of the Crocodilia. It extends to the hinder extremity of the jaw, and forms the ventral border of the posterior 250 mm., being conspicuous on both inner and outer faces of the jaw. On the outer surface it forms the ventral boundary of the large external mandibular fenestra, and articulates anteriorly with the dentary and splenial (presplenial). In its hinder portion it articulates dorsally with the supra-angular and the articular. Internally it is also in sutural union along its dorsal border with the long anterior process (angular, Baur) of the articular. It forms a portion of the boundary of the internal mandibular fenestra, which is rather small.

*Supra-angular* (Pl. VII, Fig. 3, *S. an.*).—The supra-angular differs from that of the crocodiles in having a more important share in the articulation of the mandible with the cranium, the outer third of the transverse articular fossa being formed by this bone. However, its general form and relations, including its participation in the border of the external mandibular fenestra, are very crocodilian. The sculpture which ornaments the supra-angular in certain crocodilians is lacking here, indicating a heavier musculature in this region; and a conspicuous longitudinal ridge evidently represents the insertion of the masseter.

*Articular* (= articular + angular, Baur; Pl. VII, Fig. 3, *Art.*).—As this bone had not been exposed in the *Mystriosuchus* material the following description is based upon *Phytosaurus*.

Comparison with the corresponding region of *Alligator* establishes, beyond all doubt, that this element is morphologically the same in both forms, and if Baur's interpretation is correct in the case of the Crocodilia, it is no less true in

the Phytosauria that the so-called articular is a complex of the true chondrogenous (Meckelian) articular, and a dermogenous element, the angular. The chondrogenous portion is slightly excavated dorsally by the broad transverse articular fossa. (As stated above the outer third of this fossa is formed by the supra-angular.) The inner surface slightly below this fossa presents a stout process for muscle attachments, and immediately behind the inner end of the fossa is a curious spur-like process. The articular is prolonged posteriorly to the extreme end of the jaw, and at this region is slightly visible in the external view of the mandible.

The dermogenous portion (=angular, Baur) is a long flattened blade, showing much greater development than in the crocodiles, and extending forward to articulate with the splenial (=presplenial, Baur). Its ventral border is in contact with the angular (splenial, Baur), and anteriorly it forms the dorsal boundary of the small internal mandibular fenestra.

*Coronoid*.—The condition of this element has not been definitely ascertained. One of von Meyer's figures of *Phytosaurus kapffi* represents an element which has anteriorly the same relations as the coronoid in the Crocodilia, but the element is broken away posteriorly, and there is a possibility that it may be a portion of the bone last described. In view of the close parallelism obtaining in the other mandibular elements of phytosaurians and crocodiles, we may expect the conditions of the coronoid to be closely similar.

**VERTEBRAL COLUMN**.—Of the five anterior cervicals (text-fig. 7) the centra are still imbedded in the matrix, and an attempt to work them out more fully revealed the fact that they were badly disintegrated. The portion above the diapophyses is exposed, together with several of the cervical ribs, but the neural processes are broken off short, and the surface in general is in a bad state of preservation. The relative positions of these five vertebræ apparently remain undisturbed. Their aggregate length is 220 mm.

The specimen is of interest, chiefly in that it shows the atlas, which is unknown in *Phytosaurus*. The neural arches are rather widely separated dorsally, embracing between them the anterior border of the axis neural spine. They differ from those of the Crocodilia in the greater development of the antero-dorsal region. Their relation to the atlas intercentrum is obscure owing to bad preservation. The latter element presents anteriorly a concavity, which clearly forms the most important part of the articulation with the skull.

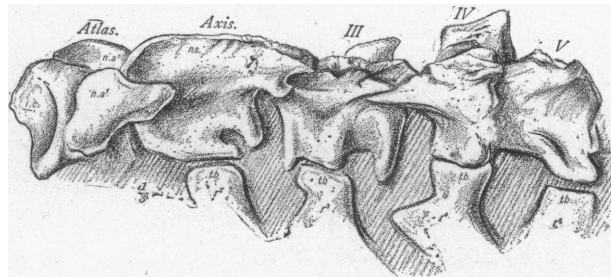


Fig. 7. Five cervical vertebræ of *Mystriosuchus planirostris* still partly imbedded in matrix.  $\times \frac{1}{2}$ . i.c., atlas intercentrum; n.a., neural arch of atlas; n.s., neural spine (broken) of axis; r., rib; tb., rib tubercle.

Concerning the axis it may be remarked that the neural spine has a very considerable antero-posterior extent, some 75 mm. in the basal portion. In



the axis of *Phytosaurus kapffi* figured by von Meyer (1863, pl. xxxviii, fig. 1,) the spine was so broken that its extent could not be determined. The transverse diameter of the axis is also much greater in the present specimen, and there can be no doubt that the one figured by von Meyer was greatly compressed in fossilization. The third, fourth, and fifth cervicals are too poorly preserved to merit special description.

The axis, and the cervicals posterior to it, all exhibit ribs, and there seem to be rather obscure traces of an atlantal rib. (From comparison with *Rhytidodon* there can be little doubt of the presence of an atlantal rib.) Of these cervical ribs only the upper surface and the tubercula are visible. At least in the ribs posterior to the axis, the outer border is produced anteriorly, giving the rib a hatchet form, as in the crocodiles and dinosaurs. In the present material the tubercula are abnormally elongated antero-posteriorly by pressure.

The cervical region of *Rhytidodon* is much better known (see page 64), and there is no reason to believe that this portion of the skeleton presents any differences of importance in the two genera.

The slab of sandstone containing ten consecutive vertebrae is illustrated in text-fig. 8. As they lie in the matrix the anterior two are somewhat displaced, and are partly covered by the right coracoid, but the remaining eight preserve very nearly their natural relations. Comparison with *Rhytidodon* leaves no doubt that the most anterior of these vertebrae is about the point of transition from cervical to thoracic, as is also indicated by the position of the shoulder girdle on the other side of the same slab. The centra are still completely obscured by matrix in all but the anterior four, and in these the parapophyses and diapophyses are not well shown. An examination of these ten vertebrae



Fig. 8. A slab of sandstone containing ten successive vertebrae, posterior cervical and anterior thoracic, of *Mystrisuchus planirostris*. Passing posteriorly the elevation and elongation of the transverse process and the tubercular rib facet are shown.

proceeding posteriorly shows several interesting points: first, the neural spines, which in the more anterior are high and rod-like, tend to become shorter and assume the form of broad antero-posterior plates in the hinder members of the series. Passing from the fifth to the tenth of the

series, there is also a marked transition in the transverse processes or diapophyses. In the fifth this process is very short, and placed low on the neural arch, quite near its base; in the tenth it is a long flattened horizontal bar, elevated almost to the level of the zygapophyses; the intervening vertebrae show the intermediate stages. Unfortunately, all these transverse processes are broken off somewhat short of the end, rendering the exact determination of their development impossible. The zygapophysial facets are less nearly horizontal than in the modern Crocodilia. The aggregate length of the last five vertebrae in the group is 250

mm., very nearly the same as the combined length of the first five cervicals. Assuming the presacral vertebræ to number not less than twenty-five or twenty-six, it is probable that the total length of this portion of the vertebral column would be 1250 mm., or a trifle over.

**THORACIC RIBS.**—The skeleton figured in Pl. XI, Fig. 49, exhibits three mid-thoracic ribs which lie very nearly in their normal relative positions, and fragments of three others. In all of these the vertebral articulation is injured, and the three first-mentioned appear like single-headed ribs, though there is no doubt of the presence of both capitulum and tuberculum in ribs of this region. The ribs are very delicate, somewhat flattened in section, those of the mid-thorax measuring about 7 mm. by 16 mm.

The material at hand contained no ribs from the posterior thoracic region. The ribs, like the vertebræ, are much more completely known in *Rhytidodon* (described below).

**SHOULDER GIRDLE** (Pl. XI, Fig. 49, and text-fig. 24).—The scapula, coracoid, and interclavicle of *Phytosaurus* have long been known, while in the case of the clavicles, though these bones were not actually found, the existence of articular surfaces on the interclavicle rendered it safe to postulate their existence. The present material fortunately shows the elements of the shoulder girdle in their natural relations (Pl. XI, Fig. 49.). The observer is at once struck by the very un-crocodilian character of this part of the skeleton, and by its resemblance to the more primitive rhynchocephalian condition, especially in the rounded form of the coracoid, the very large interclavicle and the clavicle.

The interclavicle (Pl. XI, Fig. 49, and text-fig. 9), is larger absolutely and relatively than in *Phytosaurus*. In form it resembles a very broad dagger, and is somewhat similar to the interclavicle of *Palæohatteria* and *Proterosaurus*. The total length is 370 mm., maximum width, clavicular region, 150 mm., width of neck 42 mm., width of blade (posterior portion) 83 mm. The deep fossæ with which the clavicles articulate are separated by a median ridge. The ventral surface is very slightly roughened for muscular attachment, but is not sculptured, as has been stated by one writer. The dorsal or inner face of the bone is quite smooth, and was doubtless, for the most part, in close apposition to the cartilaginous costal sternum, which has not been fossilized.

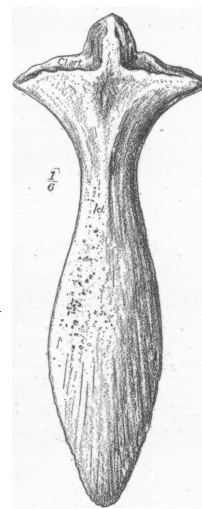


Fig. 9. Interclavicle of *Mystriosuchus planirostris*.  $\times \frac{1}{4}$ . Cl. art., groove of articulation with clavicle.

The clavicle is distinctly of the type which occurs in Rhynchocephalia and lizards,—a curved bar having slightly movable articulations with the interclavicle and with the scapula. In the skeleton figured in Pl. XI, Fig. 49, the relations of the clavicle seem to be only slightly altered from the normal. In this specimen the lateral extremity is 170 mm. from the mesial line, which would make the width from tip to tip of the two clavicles 340 mm. The

curvature of the clavicle upward and backward is such that its lateral or scapular extremity is 104 mm. above the level of the ventral face of the interclavicle, and 95 mm. posterior to the front end of this bone. The inner end of the clavicle is heavy and rod-like, and somewhat more than 50 mm. lies in the fossa of the interclavicle, a median ridge of which separates the clavicles by an interval of 10 mm. Near the middle the clavicle is flattened, thicker along its anterior border, with a rather sharp posterior edge. At its lateral end it articulates with the acromial border of the scapula for a distance of about 40 mm. The length of the clavicle, not allowing for its curvature, is 250 mm.

The coracoid, which is shown *in situ* in the skeleton figured in Pl. XI, is very similar to that of *Phytosaurus*, though a trifle smaller than the largest figured by von Meyer. There are the same rounded form and the large coracoid notch. The rounder inner margin is overlapped ventrally by the interclavicle to the extent of about 10 mm. If this represent the normal condition, as I believe it does, the two coracoids are separated by an interval of approximately 20 or 30 mm., and as the inner coracoid margin was almost certainly supplemented by a rim of epicoracoid cartilage, the cartilages of the two sides must have been in rather close approximation. The coracoid in its form, in the presence of the large coracoid notch, and in all its relations approaches much more nearly the rhynchocephalian and lacertian condition than that of the Crocodilia.

The measurements of the coracoid are : length, 147 mm.; width, 100 mm.; length of scapular articulation (from ventral surface), 33 mm.; length of glenoid fossa, 60 mm.; from lateral margin of coracoid to mesial line of interclavicle, 115 mm.; width of chest across coracoids, 230 mm.

The scapula of *M. planirostris* differs from that of *Phytosaurus* in its smaller size and the much greater relative thickness of the ventral portion. The anterior border of the ventral half is produced into a sharp crest, the acromial ridge, with which the clavicle articulates, but in the one nearly perfect right scapula in the Stuttgart collection this ridge is considerably abraded. The facet for articulation with the humerus is relatively larger than in *Phytosaurus* according to von Meyer's figures of the latter. It is highly probable that the dorsal extremity of the scapula bore a cartilaginous suprascapula.

PELVIC GIRDLE.—The material of the pelvis of this genus is limited to a left pubis and a fragment of the left ilium. The pubis is very large, almost exactly the same size as that of *Ph. kapffi* figured by von Meyer, and I am somewhat doubtful of its belonging to *M. planirostris*. A large pubic foramen, measuring 19 mm. by 30 mm., is present. The anterior end of the bone presents a thickened crest, which was probably faced with cartilage. The posterior (ischadic) border is considerably broken, but from the curvature of the portion remaining, it appears that the bone is somewhat less expanded postero-ventrally than in *Phytosaurus* or in *Rhytidodon*, so that the vacuity in the pelvic floor is probably relatively larger in the present genus. The greatest length of this bone is 158 mm.



The single fragment of the ilium, which was found with the skeleton (figured in Pl. XI) shows this element to be of more delicate construction than in *Phytosaurus*, and very much smaller than in a full-grown specimen of the latter genus. It differs in form chiefly in the greater vertical width above the acetabulum, so that the acetabulum seems to be placed lower on the bone.

FORE LIMB (Pl. XI and text-fig. 10).—The skeleton figured in Pl. XI has the left arm preserved with most of the bones very nearly in their normal relative positions; text-fig. 10 represents the same one-sixth natural size.

*Humerus* (Pl. XI, Fig. 49, *Hu.*).—The humerus resembles very closely the same bone in *Ph. kapffi*, but is smaller than the largest from that species. The proximal end has an epiphysis firmly united but still demonstrable. The head of the bone is very much flattened, and the condyle elongate. (The glenoid fossa is formed mainly by the coracoid, partly also by the scapula.) The deltoid crest extends well toward the middle of the flat under surface, being farther removed from the preaxial border than in *Phytosaurus*. The very broad distal end shows a slight cavity on the under surface for the reception of the head of the radius when the forearm is flexed. A similar cavity, having such a function, is present in *Sphenodon*. A well-marked ectepicondylar (radio-condylar) groove is present. There is less torsion of the humerus than in *Sphenodon* or in the modern crocodiles, but this may be due to pressure during fossilization.

The most complete specimen measures: length, 238 mm.; width at proximal end, 83 mm.; width at distal end, 83 mm.; thickness at middle of shaft, 33 mm. A right humerus in the collection at Spaichingen measures 210 mm. in length.

*Radius and Ulna* (Pl. XI, Fig. 49, *R.* and *U.*, and text-fig. 10).—The forearm is remarkably short, measuring only five eighths the length of the humerus. The radius is almost cylindrical, its extremities nearly round and not greatly enlarged. Its measurements are: length, 135 mm.; diameter proximal end, 28 mm.; distal end, 25 mm.; middle of shaft, 16 mm.

The ulna is much broader than the radius and flattened. An epiphysis (olecranon) on the proximal end has been broken off. The distal end being much broader than the radius doubtless forms the main support for the carpus. The postaxial border has a slight process about the middle of its length for muscle attachments. Measurements: length, 145 mm.; width proximal end, 53 mm.; distal end, 40 mm.; narrowest point, 23 mm.

*Carpus and Manus*.—Nothing is known regarding the carpus. The specimen represented in Pl. XI, Fig. 49, in which the positions of the bones of the forearm (text-fig. 10) and the metacarpals remain almost undisturbed showed no trace of carpals, nor have they been found among the bones of other Phyto-



Fig. 10. Left anterior limb of *Mystriosuchus plantrostris*.  $\times \frac{1}{6}$ . The relative positions of the bones as they lie in the matrix are accurately shown. Compare relative length of arm and forearm with corresponding parts in *Rhytidodon* as shown in Fig. 26. *dr.*, deltoid ridge; *H.*, humerus; *R.*, radius; *U.*, ulna; *rg.*, radio-condylar groove.

saurians. However, it seems quite improbable that they were cartilaginous. Though no definite statement can be made regarding the carpus, I believe that the close approximation of them etacarpals to the radius and ulna indicates that no elongate carpus could have intervened between them, such as the typical crocodilian carpus; and it seems more likely that the carpus is of the more primitive rhynchocephalian type.

Of the five metacarpals the 1st and 5th appear to be thicker than the others as they lie in the matrix; in the case of the 5th this is probably owing to rotation. The first metacarpal is slightly broken at the distal end; the others, except the 5th, may also be somewhat shortened.

The lengths of the metacarpals are: 1st, 45 mm.; 2d, 54 mm.; 3d, 48 mm.; 4th, 55 mm.; 5th, 49 mm. The fifth digit has the three phalanges in place, the lengths of which are 25 mm., 17 mm., and 11 mm. The terminal phalanx is slightly flattened at the tip. The fifth digit is separated by a considerable angle from the others, but this is probably not a natural separation.

HIND LIMB.—The only leg bones among the material of *M. planirostris* consist of a fragmentary femur, tibia, and fibula found together, a tibia lacking the distal end, and an entire left femur, the last from the Spaichingen museum.

This femur shows the S-flexure and the trochanteric ridge on the flexor surface, characteristic of the Phytosauria. It differs from the femur of *Ph. kapffi* only in its smaller size—measuring 270 mm. in length. The greatest diameter at the head is 68 mm., at the most prominent point of the trochanter, 100 mm. from the proximal extremity.

A fragmentary tibia is considerably smaller than the same bone in *Ph. kapffi*, but the shaft is relatively thick. The proximal end measures 41 mm. in width, the broken end of the shaft  $23 \times 14$  mm. Nothing is known as yet regarding the tarsus or pes of this genus. (See comparative limb measurements page 74.)

ABDOMINAL RIBS (Pl. XI, Fig. 49, *M. Ab. R.* and *L. Ab. R.*).—The abdominal ribs are arranged in three longitudinal series, a median row of  $\Delta$ -shaped elements, and on each side a lateral row of delicate spindle-shaped elements slightly bent or curved. In those of the median series the angle is sometimes produced anteriorly into a short spine bent to one side, a condition which may also occur in *Sphenodon*. As in other reptiles in which they occur the abdominal ribs are more numerous than the true segments of the body. The specimen figured in Pl. XI shows nineteen of the right lateral series beautifully preserved. Those of both median and lateral series measure about 260 mm. in length. They are slightly flattened in section.

DERMAL ARMOR (Pl. XI, Fig. 49, *D.S.*, and text-fig. 11).—The dermal armor constitutes one of the most conspicuous differences between the present form and *Ph. kapffi*. Instead of two rows of greatly elongated dorsal plates supplemented laterally by small irregular scutes *Mystriosuchus* has the back protected by four longitudinal rows of bony plates which are not greatly elongate, but

approximately square, though very irregular in outline. They are very roughly sculptured, the sculpture showing a marked tendency to center in a more pronounced longitudinal ridge or crest, especially marked on the rows of plates nearest the mesial line. This crest is comparable to the elevated bosses near the mesial border of the dorsal plates of *Ph. kapffi* and probably marks the center of ossification. The plates do not overlap those anterior to them to the same extent, or with the same regularity as in *Phytosaurus*, but there is some overlapping, and contiguous plates of the inner and outer row are in some cases firmly coössified. There is no evidence however of a similar fusion in the mesial line, between the plates of the inner rows. It is impossible to say, from examination of present material whether or not median plates were present in the cervical or caudal region, as is probably the case in *Ph. kapffi*. The inner rows of dorsal plates are as a rule of slightly greater diameter transversely than longitudinally. They measure in general from 60 to 80 mm. In Pl. XI, Fig. 49, a few of the plates are shown in the upper right-hand corner.

The ventral armor is unknown and is probably lacking except in the neck region. In this region, however, is a shield of small plates of irregular form, with interlocking serrated edges.

The best preserved of these throat-shields is shown in text-fig. 11 and in Pl. XI, Fig. 49, T. S. In this specimen 35 of the scutes are in their original relations. These are rounded, oval, or irregular in form, mostly 20 to 30 mm. in diameter, contiguous plates interlocking by means of their serrated borders and in some cases overlapping slightly. The surface is roughly sculptured. The general form of the shield is heart-shaped, the incurved posterior border conforming to the line of the clavicles, the apex proceeding forward between the jaws. A

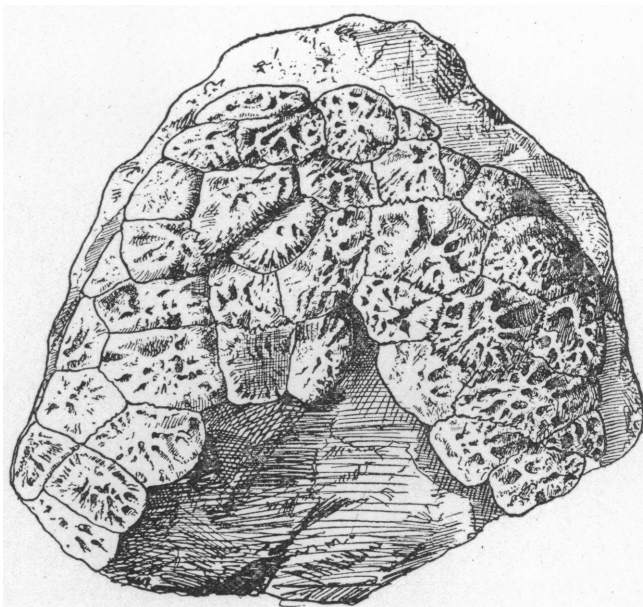


Fig. 11. Dermal throat-shield of *Mystrisuchus planirostris*.  $\times \frac{1}{2}$ . After E. Fraas.

large portion of another of these throat-shields is shown in Pl. XI, Fig. 49. In this specimen the plates average somewhat larger; a few of those from the postero-lateral region may be seen between the clavicle and the coracoid. Numerous isolated small plates of the same type, some not exceeding 10 mm. in diameter, occur among the remains; some of the scutes of *Ph. kapffi* figured by von Meyer probably belong to the ventral throat-shield, among such may be cited those in pl. xlv, fig. 4, 1863.

***Rhytidodon carolinensis* Emmons.**

The material of *Rhytidodon*, upon which the present section of this memoir is based, consists chiefly of remains collected in the Triassic coal-fields of Egypt, Chatham County, North Carolina, in 1894 and 1895 by Dr. W. D. Matthew and placed in the collection of the American Museum of Natural History. This material includes considerable parts of three skulls, and also one very immature skull, all in such fragmentary condition as to yield little new information of value, but nearly all other parts of the skeleton are represented, and it has been possible to establish pretty definitely, the morphology of nearly all parts except the carpus and tarsus.

As stated above (page 35), the differences between the German *Mystriosuchus* and the American *Rhytidodon* are slight, a true generic distinction being somewhat questionable. It is therefore particularly fortunate that the American material is rich in just those parts of the skeleton in which the German remains are poor, and *vice versa*.

SKULL (text-fig. 12 *a, b, c.*).—The material upon which are based most of my observations on the skull of this form consists of a cranium minus the rostrum

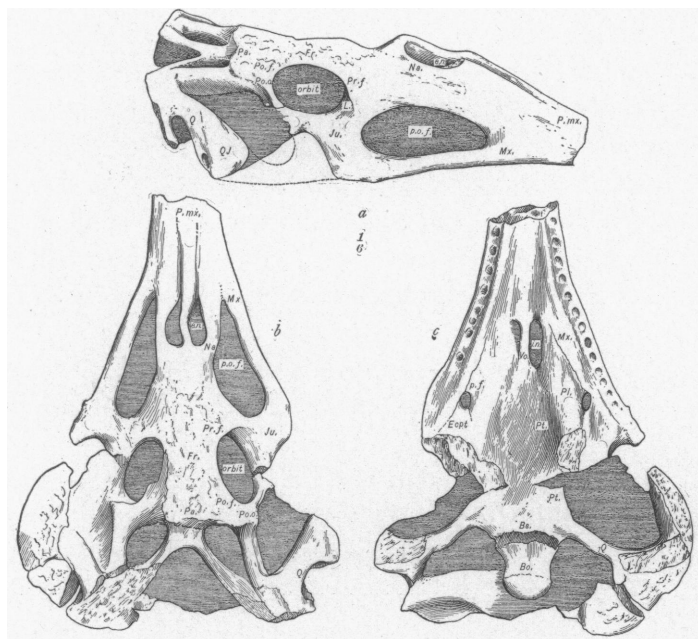


Fig. 12. Skull of *Rhytidodon carolinensis*, lateral (*a*), dorsal (*b*), and palatal (*c*) views.  $\times \frac{1}{2}$ . From a specimen in the U. S. National Museum. In this specimen the broad superficial portion of the postfronto-squamosal arcades is broken away, exposing the supratemporal fenestrae and the parieto-squamosal arcades. If uninjured, this portion of the skull would closely resemble that of *Mystriosuchus* shown in Plate VI, Fig. 1. *Bo.*, basioccipital; *Bs.*, basisphenoid; *Eopt.*, ectopterygoid; *e.n.*, external nares; *Fr.*, frontal; *i.n.*, internal nares; *Ju.*, jugal; *L.*, lachrymal; *Mx.*, maxillary; *Na.*, nasal; *Pa.*, parietal; *Pl.*, palatine; *P.m.x.*, premaxillary; *Po.f.*, postfrontal; *p.o.f.*, preorbital fenestra; *Po.o.*, postorbital; *Pr.f.*, prefrontal; *Pl.*, pterygoid; *Q.*, quadrate; *Q.J.*, quadrato jugal; *Vo.*, vomer (=prevomer of Broom).

which was collected in 1889 at Egypt, N. C. by J. B. Hatcher, and now belonging to the U. S. National Museum, where I was enabled to examine it, through the courtesy of Mr. F. A. Lucas. This is the specimen described and figured by Marsh, as the type of a new species, *R. rostratus* (1896). There is, however, no reason to believe that this skull belongs to a different species from that described by Emmons (1856) as *Rutiodon* (emend., *Rhytidodon*) *carolinensis*. The skull figured by Emmons lacked most of the region posterior to the orbits, but measured notwithstanding 30 inches (750 mm.) in

length, so that the total length of the head was probably as great as in *Mystriosuchus*, namely 820 mm. The general form of the skull, and the slender,



subcylindrical snout are very similar in both forms; that of *Rhytidodon* is perhaps slightly flatter and broader.

Marsh stated (1896): "The diagram of the skull of *Belodon* [kapffi] shows that the supratemporal openings characteristic of the true crocodilians are wanting, while in the genus *Rhytidodon* they are present and in their usual position." Marsh's first statement is of course an error, the supratemporal fenestra being present in all Phytosauria (see p. 45), but it is true that the present *Rhytidodon* skull shows this fenestra, and its posterior boundary, the parieto-squamosal bar, with unusual distinctness, owing to the fact that the expanded and sculptured surface of the postfronto-squamosal arch, which if uninjured would nearly cover the fenestra, is largely broken away, only the deeper, narrow portion remaining. (Text-figs. 12 a and b.). The displaced superficial part of this arch may be seen in the specimen crushed against the left quadratojugal. The superficial part of the postfronto-squamosal arch is broader and projects farther posteriorly than is the case in *Mystriosuchus* and in general the posterior part of the skull is relatively lower and broader, tending somewhat toward the condition of *Phytosaurus*. The character and extent of the cranial sculpture appear to be about the same as in *Mystriosuchus* (from examination of the material in the American Museum of Natural History).

The posterior border of the external nares is considerably raised, and the entire narial opening is elevated above the top of the skull, leaving a somewhat saddle-shaped depression between the nares and the orbits. In profile view the narial region does not appear quite so high as it should, owing to a depression of the narial septum toward the left side. The base of the rostrum tapers more gradually than in *Mystriosuchus*, its profile approximating that of *Ph. pleiningeri*, though throughout most of its extent, as shown by a number of fragments, the rostrum is quite as slender as in the former genus, and distally it is even more strongly decurved over the extremity of the mandible.

The palatine surface, so far as it can be determined, is very similar to that of *Mystriosuchus*, the only observable difference being in the more nearly rounded form of the posterior palatine foramina.

A cast of the entire rostral region together with the lower jaw, which I was enabled to examine through the courtesy of Dr. F. C. Paulmier, of the New York State Museum, Albany, measures, from the anterior border of the nares to the tip of the snout, 510 mm. Assuming that this specimen and that in the National Museum were of equal size, the pre-narial portion of the skull is almost exactly two-thirds its total length, the same proportion which obtains in *Mystriosuchus*. The inferior maxillary symphysis measures 390 mm., some 110 mm. less than in *Mystriosuchus*, and 100 mm. greater than in *Phytosaurus*.

It is impossible at present to state definitely the number of teeth in *Rhytidodon*. A characteristic feature of the dentition is the great size of some of the anterior teeth. The cast in the New York State Museum shows one tooth near the extremity of the lower jaw which measures 65 mm., exceeding in height

those of *Ph. kapffi*, though much more slender. Other teeth 200 mm. from the tip of the jaw have crowns 40 mm. high, thus equaling the largest of the anterior prehensile teeth in *Mystriosuchus*. Except for this cast, most of the jaw material of *Rhytidodon* shows only empty tooth sockets, but many loose teeth occur among the remains. These present such a variety of form as to render a description of the dentition of this species well-nigh impossible, and it is even somewhat doubtful whether some of them may not be teeth of carnivorous dinosaurs. It will be recalled (p. 33) that Emmons named the genus *Rutiodon* (Cope emend., *Rhytidodon*) on account of its vertically fluted teeth (1856), and differentiated it upon this character from *Clepsysaurus pennsylvanicus* Lea, in which the teeth were described as not fluted. The American Museum material from Egypt, N. C., contains teeth of the following types. (1) Teeth oval in section tapering to a point, slightly curved, very minutely serrate posterior trenchant edge, anterior trenchant edge indistinct or wanting, crown separated from fang in some instances by a slight ridge. The enamel, especially on the outer face of the tooth, shows indistinct and rather irregular vertical fluting, while the entire surface is marked by an excessively minute vertical striation, which in the jet black teeth from the North Carolina coal-fields gives a silky gloss. Some of the teeth are quite smooth and polished toward the point. Teeth of this type vary in height of crown from 14 mm. to 50 mm. the diameter of the largest at the base being  $9 \times 13$  mm. The pulp cavity is very small. (2) A second type of tooth is more nearly circular in section, more strongly curved, devoid of trenchant edges, and distinctly fluted vertically, the crown usually less than 25 mm. in height. (3) The third type has a short crown, laterally compressed, with serrate trenchant edges; tooth slightly curved with the outer face convex; enamel faintly striated. In two teeth of this type the enameled crowns measure 6 and 13 mm.

The separate discovery and description of these various forms of teeth are responsible in the main, I believe, for the differentiation by Emmons, Lea, Leidy, and others of several genera and species of Eastern North American phytosaurs, while in reality they may all belong to one species. Lea's *Clepsysaurus pennsylvanicus* (probably a Dinosaur, see p. 32) had teeth of the carinate, serrate form, with fine oblique wrinkles on the enamel,—plainly our type 1. *Rutiodon* (*Rhytidodon*), according to Emmons, differed only in having plaited, or fluted teeth, which were usually smaller and, though sometimes carinate, devoid of serrations,—our second type. The fluted teeth from the Red Sandstone of New Jersey, on which Lea founded his *Centemodon sulcatus*, were almost certainly of this species. The teeth of this type closely resemble the fluted teeth of *Mystriosuchus*. It is of great interest to note that in the present material types 1 and 2 are connected by a number of intermediate forms, and there is no reason to doubt that both belonged to the same species. The very large teeth of type 1 are apparently the anterior prehensile teeth, which in this species are probably less sharply limited to the extreme tip of the jaws. The

small trenchant teeth of type 3 undoubtedly belong to the posterior jaw region, and closely resemble the corresponding teeth of *Phytosaurus kapffi*. Emmons (1860) figured a single tooth of this type which he assigned to *Palæosaurus*. It may be noted that teeth of this third type with trenchant serrate edges resemble very closely the teeth of carnivorous dinosaurs.

It is much to be regretted that in the material at my disposal nearly all the teeth had fallen out of the jaws before fossilization so as to preclude giving a complete description of the dentition, but I believe the following can be safely postulated. In the anterior portion of both upper and lower jaws a few teeth are greatly enlarged for prehension of food; these may attain a height of 65 mm. thereby exceeding in length the corresponding teeth of *Phytosaurus* and *Mystriosuchus*. These enlarged teeth are followed by teeth of the fluted type (similar to those of *Mystriosuchus*). The more anterior of these are quite small and circular in section and not carinate; passing backward they increase in size and become gradually carinate, the fluting becomes less conspicuous, and they merge into the larger serrate carinate teeth which are oval in section, like the teeth of *Phytosaurus*. As in this genus, they become smaller in the extreme posterior part of the jaw, where the crowns are short and compressed with serrate trenchant edges. Thus it appears that the dentition resembles that of *Phytosaurus* rather than *Mystriosuchus*, except in the fluted non-carinate teeth in a portion of the jaw.

VERTEBRAL COLUMN (Pl. VIII and X, text-figs. 13-23 a).—The material in the American Museum comprises a considerable number of vertebræ, most of which are in fragmentary condition, though some forty are almost or quite entire, and serve as a basis for a pretty thorough understanding of the vertebral column. These are, however, from at least two individuals, and it is impossible to make a perfectly accurate restoration of the column with each vertebra in its serial position, or to state exactly the number of presacral vertebræ. What the study has yielded is knowledge of the atlas, the axis (from another species, page 63), the last presacral, and in general the structure of vertebræ in various regions, and the transitions in form of vertebræ and rib articulation throughout the column.

Though it is impossible to state with absolute certainty the number of presacral vertebræ, it is practically certain that it is not less than 25 nor greater than 27, and perhaps the most probable number is 26. Of these 7 to 9 are cervical (the ribs unconnected with the sternum). There are two sacrals, and the caudals probably number 40 or more, as in the Crocodilia.

The centra are very characteristic: slightly biconcave, and considerably constricted in the middle, giving them the "hour-glass form" noted by other writers.

Though having a strong general resemblance to the crocodilian vertebral column, that of the Phytosauria differs in the form of altanto-axis, and in the much greater elevation of the transverse processes in the posterior half of the

thoraco-lumbar region. The presence of movable two-headed ribs as far back as the last presacral vertebra is also a non-crocodilian character. In all these features the Phytosauria approximate dinosaurian conditions, and the resemblance to the vertebræ of dinosaurs is further strengthened by the presence of trabeculæ buttressing the transverse processes.

*Atlanto-axis* (text-fig. 13).—The material in the American Museum is the first to yield important knowledge of the phytosaurian atlas: fortunately this collection comprises a well-preserved atlas intercentrum and a left arch, both from the same specimen, and an intercentrum from a second individual.

*Atlas* (Pl. VIII, Figs. 5, 5a, 6, and 7).—The atlas intercentrum and the two arches are not coössified, but are firmly united by suture. The most noteworthy feature of the atlas is the important rôle played by the intercentrum in supporting the occipital condyle. In most reptiles, notably in the recent Crocodilia, the odontoid is an important element in the formation of the cup with which the condyle articulates, the atlas arches and intercentrum forming only the rim of the cup, but in *Rhytidodon*, and presumably in other phytosaurians, the odontoid is practically excluded from participation in the occipito-atlantal articulation. As is well shown in Pl. VIII, Fig. 5a, the anterior concavity of the intercentrum forms the ventral half of the cup, while its dorsal portion is formed by facets on the neural arches.

The atlas intercentrum as seen in dorsal view presents two roughened triangular areas, the areas of sutural union with the neural arches; posteriorly it is rounded dorso-ventrally and is in contact with the odontoid process. The entire ventral surface is flat and roughened for the attachment of ligaments. At each side, immediately below the attachment of the neural arch, is a slightly concave facet for the capitulum of the atlantal rib.

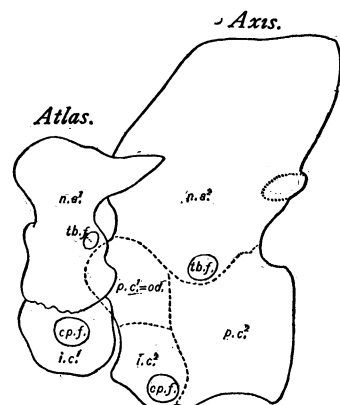


Fig. 13. Diagram to illustrate the composition of the phytosaurian atlanto-axis; based upon the atlas of *Rhytidodon* and the axis of *Heterodontosuchus*. *c.p.f.*, capitular facet; *i.c.*, intercentrum; *n.a.*, neural arch; *p.c.*, pleurocentrum; *od.*, odontoid; *t.b.f.*, tubercular facet.

The base of the neural arch where it rests upon the intercentrum is heavy, and the concave facet for the occipital condyle is very large. On the posterior and inner surface the area of articulation with the odontoid is even larger. This area is slightly concave, but is rather rough, indicating that there was little or no motion between atlas and axis. The facet for the occipital condyle is so greatly developed toward the mesial line, that the two arches meet below the neural canal, enclosing between them and the intercentrum a small triangular area, which is occupied by the tip of the odontoid process, though the latter probably does not reach the condyle. The lamina of the neural arch is expanded dorsally fore and aft, the narrow posterior processes of the two arches embracing between them the anterior



border of the spine of the axis. The arches appear to be separated dorsally by a slight interval, which was doubtless bridged by ligament.

On the outer surface of the base of the neural arch, near its posterior border, is a small elevation which may mark the attachment of the tuberculum of the atlantal rib. The surface of this elevation is broken; it may have been a small facet, or possibly only a process for the attachment of a ligament—the vestige of a rib tubercle. Its position, relative to the capitular facet on the intercentrum, strongly supports this view. As indicated above, the development of the atlantal elements shows a considerable departure from the crocodilian type as regards the structure of the occipito-atlantal articulation. It is of interest to note, on the other hand, a close approximation to the condition of the atlas of certain carnivorous dinosaurs, especially *Ceratosaurus*, in which the condyle is largely supported by the intercentrum and arches, to the exclusion of the odontoid.

No evidence of a detached neural spine comparable to the so-called “pro-atlas” of crocodiles has been found.

*Axis* (Pl. VIII, Figs. 8, 8a, 8b, and text-fig. 13).—In neither *Mystriosuchus* nor *Rhytidodon* has the axis been discovered, and it was my expectation to send the present memoir to press without any description of this very important element, when I discovered in the National Museum in Washington, an axis of the large *Heterodontosuchus ganei* Lucas (see page 94), which Mr. F. A. Lucas kindly placed at my disposal. Though this species is much larger and more powerful than *Rhytidodon*, an examination of various parts of the skeleton leaves no doubt of its phytosaurian character. Since there is no reason to believe that the axis differs essentially from that of *Rhytidodon*, it may be described here.

In the specimen the neural arches are broken off at the level of the middle of the neural canal, and the posterior third of the centrum is missing, but the important portion, the anterior two-thirds, with odontoid, intercentrum, and rib articulations, is well preserved. Both the odontoid process (=atlas centrum) and the second intercentrum are firmly coössified with the axis centrum, though the lines of fusion are still discernible with some distinctness. The middle of the axis centrum is greatly constricted from side to side, its transverse diameter being only 21 mm., while that of the intercentrum is 65 mm. The ventral surface of the centrum presents a mesial keel-like ridge.

The odontoid is a blunt process, the face of which is greatly elongated transversely, its measurements being, transverse, 48 mm., vertical, 19 mm. It is well-nigh certain that no portion of this process could have been in contact with the occipital condyle; immediately below the face of the odontoid is a transverse roughened area measuring vertically about 8 mm.—the area of union with the atlas intercentrum. Shallow depressions at the sides of the odontoid mark the surfaces of contact with the atlantal arches.

Adjoining the odontoid ventrally is the second intercentrum, which is very

large and firmly coössified with it, as well as with the axis centrum. A remarkable feature of this axis intercentrum is a broad oval face directed antero-ventrally and separated from the anterior face by a prominent transverse ridge. This antero-ventral face is roughened for the attachment of ligaments,<sup>1</sup> and greatly resembles a facet for the articulation of an osseous element.

The lateral extremities of the intercentrum are greatly produced, and bear postero-laterally the round facets for the capitula of the second rib. Close behind the rib facets may be seen the line of coalescence with the centrum.

As stated above, the neural arches are broken off short, but their bases remain, extending down over the sides of the centrum, and bearing at their extreme ventral extremities the shallow tubercular facets. The line of union of the neural arch with the centrum, and anteriorly with the odontoid is distinguishable, but the elements are firmly coalesced. It is plain, from the condition of the facets, that the axis rib had both head and tubercle well developed. The interval between the two facets measures 28 mm., anterior border of the tubercular facet is 35 mm. posterior to the level of the odontoid. These measurements are, of course, much greater than the corresponding ones for *Rhytidodon*. In the axis of *Phytosaurus kapffi*, figured by von Meyer, the neural spine is much higher than in crocodiles. The antero-posterior extent of the spine in *Mystriosuchus* is indicated in text-fig. 7.

In certain of its characters this axis is very primitive, notably in the location of the rib facets. It differs from the Jurassic crocodiles in the very firm union of odontoid and intercentrum with the centrum.

The cervical vertebræ posterior to the axis are characterized by long slender spines standing almost vertically, and by the great elevation of the zygapophyses above the centra, and by the oblique angle of the zygapophysial facets (Pl. VIII, Fig. 9, and text-figs. 14 and 14a). The centra are of smaller diameter than in the more posterior vertebræ, considerably constricted in the middle. There is a mesial ventral keel, especially prominent in the posterior half. The capitular rib facet is placed at the very anterior border of the centrum, and very near its ventral limit. The slightly prominent diapophyses are borne on the neural arches, and extend well down over the sides of the centrum, and the tubercular facets are a little anterior to the middle. The neuro-central suture is usually distinguishable. The cervicals are distinguished from those of the Crocodilia in that the zygapophyses are placed much higher and their facets are not so nearly horizontal. The diapophyses are relatively shorter, and the capitular facets nearer the anterior border of the centrum.

In a series of three consecutive cervical vertebræ, there is observable,

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<sup>1</sup>A corresponding antero-ventral face on the axis of *Phytosaurus kapffi*, figured by von Meyer (1863), appeared to me to represent a facet on the centrum for the attachment of a separate intercentrum, somewhat as in the Mosasauria, and upon first examining the axis of *Heterodontosuchus* I mistook the flattened antero-ventral surface for such a facet, but careful examination disclosed the fact that the second intercentrum is firmly coalesced with the axis centrum.

passing posteriorly, a gradual increase in size of centra and of rib facets, and a progressive widening of the space between the capitular and tubercular facets. In the most anterior the capitular facet, though placed far forward, is free from the end of the centrum; proceeding posteriorly it merges into the projecting rim of the centrum. The mid-ventral keel also becomes weaker as we pass posteriorly.

The vertebra figured in Pl. VIII, Fig. 9, and in text-figs. 14 and 14a, which is from about the middle of the neck region, has the following measurements:

Total height, 145 mm.  
Height of centrum, 40 mm.  
Length of spine above zygapophyses, 72 mm.  
Length of centrum, 36 mm.

The posterior cervicals are wanting in the present material, but it is obvious that they must have been intermediate in form between those of the mid-cervical region and the anterior thoracic type; in other words, passing from the middle to the posterior neck region the diapophyses must increase considerably in prominence, and come to occupy a higher position on the neural arch, thus separating more widely the two rib articulations.

The vertebra figured in Pl. VIII, Figs. 10 and 10a, and in text-figs. 15 and 15a, is one of the anterior thoracics. Comparing this vertebra with a mid-cervical, it is seen that the diapophyses have merged into heavy transverse processes, projecting horizontally at the level of the neural canal, while the capitular articulation, though considerably larger than in the cervical region, retains its position low on the centrum and is confluent with its anterior rim. In length this vertebra is no greater than those of the cervical region, but as may be seen from a comparison of text-figs. 14a and 15a, it is much broader and heavier and the spine is relatively short and thick with a transversely expanded extremity. At the base of the long diapophysis the bone is excavated, leaving thin buttresses supporting the process, as in dinosaurs. The capitular articulation is nearly flat, the tubercular convex. The zygapophyses are larger than those in the neck region and more nearly horizontal. The neuro-central suture is plainly visible.

The remains in the American Museum comprise six vertebræ of this type, four of which apparently belong to the same individual. A vertebra of the same type from *Phytosaurus kapffi* differs, aside from its larger size, in the much greater lateral expansion of the tip of the neural spine, which here had a width of 50 mm.; doubtless an adaptation to the support of the greatly enlarged dermal scutes of that species.

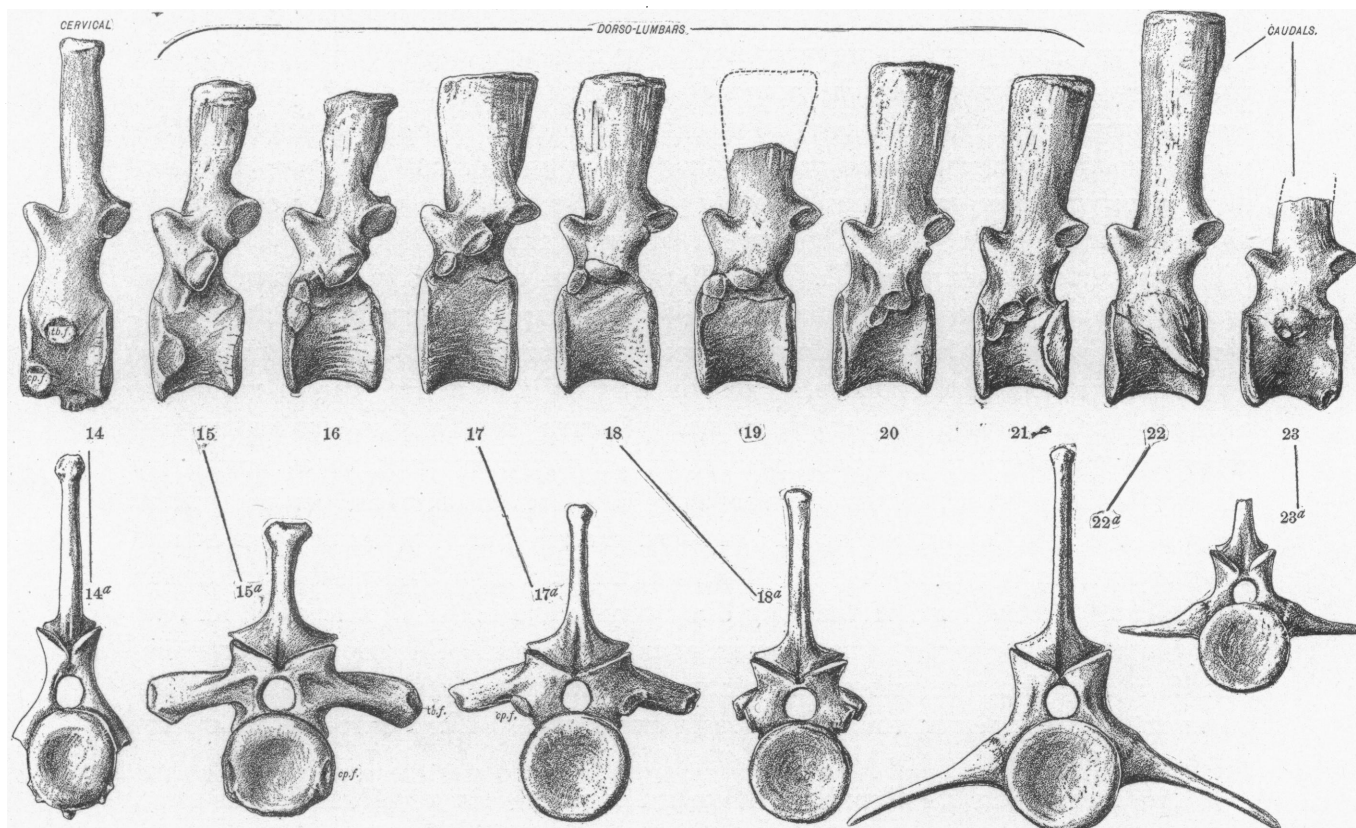
Vertebræ of nearly similar form occur in the Crocodilia; in *Alligator* the ninth, tenth, and eleventh are of this type, though differing from those of the Phytosauria in the fact that the capitular facets are placed farther back, at some distance from the anterior rim of the centrum. From the number of these

vertebræ and the number of corresponding ribs among the remains it seems highly probable that the Phytosauria had at least four vertebræ of this type.

The measurements of the vertebra figured in Pl. VIII, Fig. 10, and text-fig. 15 are as follows:

Length of centrum, 38 mm.  
Height of centrum, 42 mm.  
Total height, 120 mm.  
Width across diapophyses, 104 mm.

In the Crocodilia the transition from the type just described to the form in which the capitular facet is elevated on the transverse process is a sudden one;



Figs. 14-23a. A series of ten vertebræ of *Rhytidodon carolinensis* selected to illustrate articulation of ribs in various regions of the vertebral column.  $\times \frac{1}{4}$ . Figs. 14 and 14a represent a cervical vertebra; 15 and 15a one of the most anterior thoracics; 17 and 17a show the elevation of the capitular facet to the neural arch, a transition stage appearing in Fig. 16; Figs. 18 and 18a, 19 and 20 shows the shortening of the transverse process and depression of the rib articulation in the posterior thoraco-lumbar region. Fig. 21 is the last presacral, and shows on the centrum the facet which buttresses the sacral rib. Fig. 22 is an anterior caudal. Fig. 23 is a more posterior caudal. *cp.f.*, capitular facet; *tb.f.*, tubercular facet.

in *Alligator* the eleventh vertebra is of the first type, the twelfth of the second. In the Phytosauria there is an intermediate stage in the elevation of the capitular facet, as shown in the vertebræ of *Rhytidodon* illustrated in text-fig. 16. This vertebra was considerably crushed and broken, but careful examination shows that it is essentially similar to the one last described except that the capitular



articulation has moved to a higher position, its upper third now being on the base of the neural arch, with the neuro-central suture showing plainly across its slightly convex facet. The facet is still at the extreme anterior border of the centrum, and is vertically elongated. The long diapophysis is of more flattened form than in the most anterior thoracic. The elongate tubercular facet at its extremity is convex; its anterior end is somewhat the lower (Pl. VIII, Fig. 11).

Following this vertebra comes a series (Pl. VIII, Fig. 12, and text-figs. 17 and 17a) in which the capitular facet is still more elevated, being borne entirely on the neural arch, and occupying a position antero-ventral to the diapophysis, and forming thus a sort of 'step,' at its base. In the more anterior vertebrae of this type, the spread of the diapophyses is 95 mm., they originate high on the arch, almost at the level of the zygapophyses, and as they extend laterally they become flattened almost in a horizontal plane with the anterior border slightly depressed. The tubercular facet at the extremity is quite elongate and convex. The smaller capitular extremity is almost flat and more nearly round. These vertebrae differ from the transitional type in the greater antero-posterior extent of the neural spine, and in the still more nearly horizontal position of the zygapophyses. In the corresponding vertebrae in *Phytosaurus kapffi* (von Meyer, 1865, Pl. XXVII, Figs. 1, 2, 3), the neural spine is very short, and the transverse processes are arched upward like the spread wings of a bird, their extremities on a level with the tip of the spine. This condition is probably an adaptation to the support of the heavy dorsal armature of this form.

This type of vertebra, with both rib facets entirely on the neural arch, but distinctly separate, extends throughout the greater part of the thoraco-lumbar region, the most posterior being the third or fourth from the sacrum, so that in all there are some eight or nine vertebrae of this form. Among the material studied are ten vertebrae of this form, belonging without doubt to several individuals, but among the ten there is sufficient variety to render it certain that they comprise at least six different vertebrae.

The most conspicuous change, passing backward in the thoracic region, is the marked shortening of the diapophysis and its gradual depression toward the neuro-central suture. At the same time it is noticeable that the elongate tubercular facet on the hindmost of these vertebrae has its posterior end more depressed than the anterior, so that the long axes of the capitular and tubercular facets are almost at right angles. The two rib facets are here small and close together, and but slightly elevated above the neuro-central suture. A vertebra of this posterior thoracic type, figured in Pl. VIII, Fig. 13, and in text-figs. 18 and 18a, will serve to illustrate the transition from anterior to posterior thoracic region.

A vertebra of especial interest in its costal articulations is represented in Pl. VIII, Fig. 14. It is probably the third or fourth counting forward from the sacrum. The very short diapophysis is slightly lower than in the preceding

vertebra, barely above the neuro-central suture, and the capitular facet has descended so as to be partly on the centrum, divided by the neuro-central suture very much as in the anterior thoracic vertebra shown in Pl. VIII, Fig. 11, and text-fig. 16. (See Pl. VIII, Fig. 14, and text-fig. 19.)

The last presacral is illustrated in Pl. VIII, Fig. 16, and in text-fig. 21. Here the diapophysis is very short and depressed, and the capitular articulation has descended to the centrum, appearing as a vertically elongate facet at the anterior border. The tubercular and capitular facets, while very close together, lie in different planes and can scarcely be described as confluent. It is of particular interest to note that this vertebra bears well-developed two-headed ribs, which are movable or at most only very loosely anchylosed. In one specimen the rib of the left side is disarticulated, while on the right it is retained in place. A second specimen (in the Museum of the Philadelphia Academy of Natural Sciences) shows the rib slightly displaced, as if by pressure. It may be said that the last presacral rib is separate, but with a tendency to anchylose with the vertebra.

Another distinguishing feature of the last presacral is the presence on each side at the hinder border of the centrum of a large oblong facet, facing latero-posteriorly, which serves as a partial attachment for the secondarily expanded base of the first sacral rib, a condition which also occurs in many dinosaurs.

This last presacral is preceded by one (or possibly two) of essentially the same type, with parapophysis depressed, lying on the side of the centrum, and with separable bicipital ribs 80 or 90 mm. in length. One of these is shown in Pl. VIII, Fig. 15, and text-fig. 20.

The thoraco-lumbar region in the Phytosauria is of particular interest when compared with the corresponding part of the crocodilian skeleton. In the latter order the capitular or facet becomes elevated on the arch in the anterior part of the thorax, soon becoming a mere 'step' on the anterior border of the process which passes farther and farther outward, finally reaching the end of the process and becoming confluent with the tubercular facet, so that the hinder ribs appear to be single-headed. The Crocodilia do not exhibit the shortening of the transverse process in the lumbar region, nor the descent of the capitular facet to the centrum. In recent crocodiles the last five presacrals lack movable ribs, but in some Jurassic forms (*Teleosaurus*) all the presacrals bear ribs. In brief the more important differential characters of the thoraco-lumbar region of Phytosauria are the presence of two-headed ribs throughout, the ascent in the anterior thoracic region of the capitular facet to the arch, and its descent in the lumbar region to the centrum.

*Sacrum*.—There are two sacral vertebræ, which in size and form of centrum and height and form of neural spine are closely similar to those of the lumbar region. Though no motion between the sacrals could have been possible, they show no tendency to anchylose, and their zygapophyses are well developed. The ribs are the distinctive features of this region. They are attached to both

centrum and neural arch, but the union is not a very firm one; the sutural line is conspicuous, and in several cases the ribs have become separated.

The area of rib attachment is primarily anterior as in the lumbar region, but owing to a great secondary expansion, the base of the rib occupies the anterior three-fifths of the side of the vertebra, centrum and arch, and even extends considerably over the centrum of the vertebra next anterior, so that the centra of the last presacral and the first sacral have bevelled surfaces at their postero-lateral margins, for the accommodation of the anterior overgrowth of the bases of the two sacral ribs. These ribs are greatly expanded distally, and have convex roughened extremities for the attachment of the ilium, but the two ribs do not coalesce, and probably are not in mutual contact. They seem to be more depressed distally than in the Crocodilia. Pl. X, Figs. 40, 40a, and 40b, represent the second sacral, minus a considerable part of the neural spine, but the centrum is compressed antero-posteriorly so that Fig. 40b is somewhat misleading. The length of a well-preserved first sacral is 45 mm., width, including ribs, 160 mm.

*Caudal Vertebrae* (Pl. VIII, Fig. 17, and text-figs. 22-23a).—The *Rhytidodon* material studied contained some fourteen fairly preserved caudals, four from the base of the tail, the others near the middle. The anterior caudals bear very long spines (longer than in any other region except the cervical), one, which is entire, extending 83 mm. above the zygapophyses. The ribs, as usual in the caudal region, have moved back to the center of the vertebra, where the rather heavy rounded base arises chiefly from the centrum, but partly from the arch. The caudal ribs are all firmly anchylosed with the vertebrae, but in many of them the line of suture persists. (Since these are so plainly homologous with the presacral and sacral ribs, I consider it better to term them 'ribs' than 'transverse processes.') In the large anterior caudal (Pl. VIII, Fig. 17, and text-figs. 22, 22a), the total width, if unbroken, would be about 170 mm. Here the ribs are depressed, but farther back (text-figs. 23 and 23a) they extend horizontally. As compared with crocodilian caudals, these have the ribs placed higher and the zygapophyses are less widely separated and farther from a horizontal plane. The centra are much constricted at the middle and are slightly biconcave.

All the caudals examined, except two of the more anterior, show facets for chevrons placed near together at the posterior border of the centrum. The chevrons are of the common reptilian type, with a long spine (Pl. VIII, Fig. 18). The exact number of caudal vertebrae is unknown.

*Ribs*.—The forms of ribs are well illustrated in the series of left ribs figured in Pl. IX, Figs. 30-38.

The material examined contains fourteen cervical ribs of the form shown in Pl. IX, Figs. 31 and 31a. These are two-headed and of the hatchet form common in the cervical ribs of crocodiles and dinosaurs. The extremity is directed backward almost horizontally, overlapping the anterior part of the

succeeding rib. The tuberculum is somewhat larger than the capitulum, and is elliptical in form, due probably to crushing, since on the vertebræ both facets are approximately round. These ribs differ only in size, the posterior being larger and longer. The most posterior ones, those transitional to the anterior thoracic type, are wanting in the material studied.

The rib shown in Fig. 30 belongs, beyond question, to either the atlas or the axis, since it entirely lacks the anterior process which gives the other cervicals their hatchet form. It is straighter than the other cervicals, and seems to have been of greater length, but only the proximal half is preserved.

Pl. IX, Figs. 39 and 39*a*, represents one of the anterior thoracic ribs, from the region where the capitulum is still attached to the centrum, while the diapophysis is lengthened. A vestige of the anterior process of the cervical region is here present as a prominent crest, as in the corresponding ribs of dinosaurs and crocodiles. Ribs of this region are the heaviest and perhaps the longest; unfortunately none of them is entire.

Pl. IX, Figs. 30 to 38 inclusive, illustrate the transition in rib form and the reduction in size from the middle to the posterior thoraco-lumbar region. In these ribs both capitulum and tubercle are borne on the neural arch, and it should be noted that in every case the two articular surfaces are distinct, though the tubercle appears as a mere 'step' on the side of the rib, which, passing backward, comes gradually nearer the capitulum, as the diapophysis becomes shorter. The angle between the axes of the two heads is not shown in the plate, but may be appreciated by observing the rib facets in text-figures 18 and 19.

Pl. IX, Fig. 38, illustrates one of the last two thoraco-lumbar ribs. It will be recalled that in the corresponding vertebræ the diapophysis is very short and the capitular facet has descended to the centrum. The head and tubercle are distinct but very close together. In some cases the last presacral rib is rather weakly ankylosed to its vertebra.

The sacral and caudal ribs are discussed above in connection with the vertebræ.

SHOULDER GIRDLE (Pl. IX, Figs. 19-21*a*, and text-fig. 24).—The shoulder girdle of *Rhytidodon* is so closely similar to that of *Mystriosuchus* that verbal description here seems unnecessary, and it will suffice to indicate the points of difference as compared with the latter form, and to refer to the plates which illustrate the structures with great clearness. In general these bones in *Rhytidodon* are more delicate. The scapula is more elongate and considerably lighter. Its dorsal end was plainly tipped in life with a cartilaginous suprascapula. The lower two-fifths of the anterior border forms a narrow *crista-scapulæ*, to which the clavicle was connected by ligament. The union with the coracoid was a synarthrosis, permitting little or no motion. In this synarthrosis the scapular surface is concave, the coracoid convex. (Pl. IX, Fig. 20.)

The coracoid (Pl. IX, Figs. 21 and 21*a*) is very similar in form to that of *Phytosaurus*, and seems to be proportionally somewhat more elongate antero-



posteriorly than in *Mystriosuchus*, though absolutely smaller. The longitudinal diameter is greater than the transverse in the proportion of 7 to 5. Immediately anterior to the surface of union with the scapula is the deep coracoid incisure. Fürbringer states, regarding the Phytosauria, that "this notch was presumably closed by a bar of cartilage or a strong band of connective tissue to form a coracoid fenestra, but the scapula may also have played a considerable part in the closure. In the latter case a fenestra coraco-scapularis would be produced." It may be stated with certainty that the scapula does not participate in the closure of the notch, since the anterior border of this bone is flush with the posterior border of the notch. The roughened surface of the curved inner border of the coracoid indicates the presence of a cartilaginous epicoracoid.

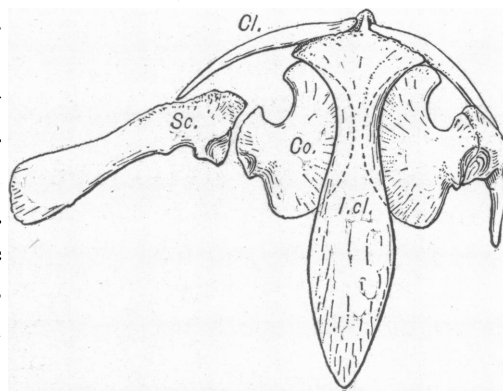


Fig. 24. Shoulder girdle of *Rhytidodon*, ventral aspect. The left scapula is shown in the normal position, the right one is displaced in order to show its form more clearly. Cl., clavicle; Co., coracoid; I.cl., interclavicle or episternum; Sc., scapula.

The clavicle (Pl. IX, Figs. 19 and 19a) is not so broad as in *Mystriosuchus*; its inner half is, indeed, almost cylindrical, but the lateral end is flattened, with a slight groove along its hinder surface to conform to the ridge of the scapula. A clavicle which lacks the distal end measures about 170 mm. in length. When entire its length was doubtless over 200 mm.

The interclavicle is represented, in the collection studied, only by a single fragment containing the middle portion of the bone, but there is no doubt of its essential similarity to the same element in the other Phytosauria.

The elements of the shoulder girdle are well represented in Pl. IX, and text-fig. 24 represents a ventral view of the restored girdle.

Some of the more important measurements of the shoulder girdle bones of *Rhytidodon* are as follows:

- Scapula, total length, 243 mm.
- Coracoid, antero-posterior, 135 mm.
- "    transverse, 97 mm.
- Coraco-scapular articular surface, 28×60 mm.

**PELVIC GIRDLE** (Pl. X, Figs. 40-43, and text-fig. 25).—The pelvis is represented by one ilium, one ischium, and two pubes, all from the same individual.

The ilium (Pl. X, Figs. 41 and 41a) is almost identical in form with that of *Phytosaurus*, but it is of course smaller and resembles that of *Mystriosuchus* in its delicate structure. The very large and very shallow acetabulum is almost entirely within the ilium. The inner face of the bone shows a roughened area of articulation with the sacral ribs. In general form and position the ilium

resembles that of certain lizards (*Varanus*, *Lacerta*). Its likeness to the crocodilian ilium is less, and it differs widely from the usual dinosaurian form.

The left pubis, shown in Pl. X, Fig. 42, is smaller than in either of the European genera, but of the same general form, heavy near the anterior border, but thin and lamelliform in its mesial and posterior portions. Antero-ventrally the border is thickened to form a crest, which probably bore a cartilaginous

epipubis. The thin mesial edges of the two pubes must have met at an angle and were connected by cartilage or connective tissue. The posterior border must have been similarly in union with the ischium. The relations of the pubic foramen are shown in the figure. The pubis takes a small part in the formation of the acetabulum.

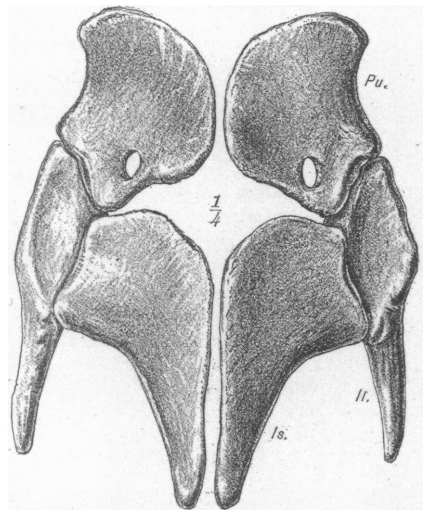


Fig. 25. Pelvis of *Rhytidodon carolinensis*, ventral aspect.  $\times \frac{1}{4}$ . Il., ilium; Pu., pubis; Is., ischium.

The very characteristic form of the phytosaurian ischium has been noted above but it is of interest to observe that in the present species this bone differs from that of *Phytosaurus kapffi* in the much broader posterior process, thus approximating the ischium of *Stagonolepis* as figured by Huxley (1877). An examination of the figure (Pl. X, Fig. 43) will show the great antero-posterior extent of this bone, its thickened posterior margin, the lamelliform anterior and mesial margin where it articulates with the pubis and with the other ischium respectively, and the ridge which marks the ventral limit of the acetabulum. Text-fig. 25, which shows the restored pelvis in ventral view, illustrates the almost solid pelvic floor, the rounded pubis and elongate ischium, with a small median pubo-ischiadic opening; a primitive condition, very different from that of Crocodilia, and which finds its closest parallel in *Palæohatteria*.

Some of the measurements of pelvic bones are:

- Ilium, total length, 185 mm.
- “ vertical depth, 82 mm.
- “ length, pubic articular surface, 45 mm.
- “ “ ischiadic “ “ 67 mm.
- Pubis, greatest diameter, 136 mm.
- “ anterior border, 85 mm.
- “ ischiadic “ 80 mm.
- “ length, antero-posterior, 110 mm.
- “ pubic foramen, 14  $\times$  18 mm.
- Ischium, antero-posterior, 162 mm.
- “ height, 120 mm.

FORE LIMB.—The American Museum collection contains one pair of humeri, one pair of ulnas, and one radius which are very probably from the same

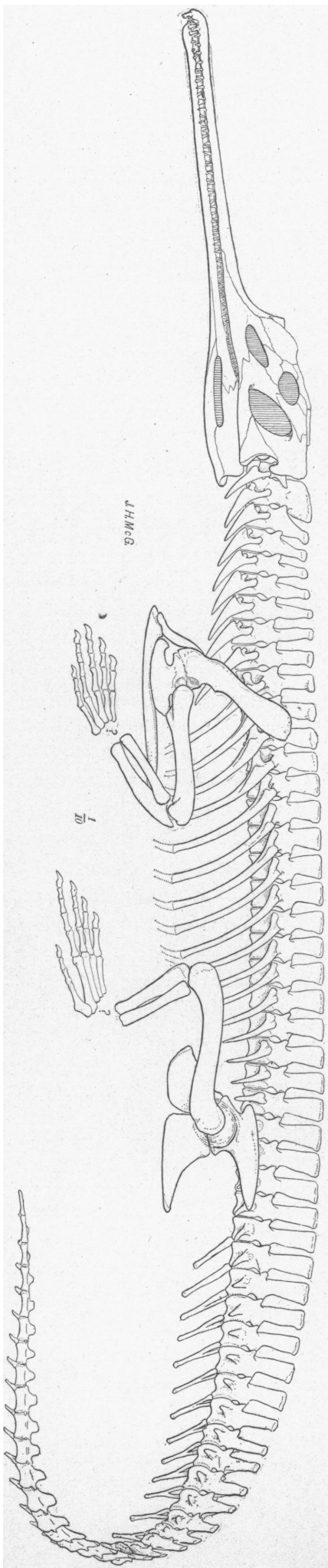


Fig. 26. Restoration of skeleton of *Rhytidodon carolinensis* with skull of *Mytilus* *plumieri*. X 15. (Since the skull is imperfectly known in the former type, and in view of the fact that the two forms are very nearly similar, and of about the same size, the author regards it as permissible to present the combination restoration.) The limbs and ribs of the right side are omitted for the sake of clearness, and the limb bones are drawn without foreshortening in order to show more clearly their relative dimensions. The carpus and tarsus are unknown, and the digital formula and the vertebral formula are somewhat doubtful.

individual. These bones are essentially similar in structure to those of *Phytosaurus* and *Mystriosuchus*, but comparison of measurements of the three genera shows certain interesting differences in proportion. In *Rhytidodon* the forearm is much longer, the relative length of humerus and radius being 100:73, while in *Mystriosuchus* it is 100:55. The lengths of the arm bones of *Rhytidodon* are humerus 242 mm., radius 177 mm., and ulna 218 mm. The slight crushing of the bones renders other measurements somewhat untrustworthy. These bones are all represented in Pl. IX, Figs. 22-24.

Nothing is known regarding the carpus. The bones of the manus will be treated with those of the pes.

HIND LIMB (Pl. X, Figs. 44, 44a, and 45).—As above stated, the material of the leg bones of *Mystriosuchus* was too fragmentary to yield important data, but in *Rhytidodon* it has been possible to examine three entire femurs, one tibia, and one fibula. A comparison of the measurement of these bones with those of *Phytosaurus kapffi* shows that in the American form, though the bones are more delicate, the leg, and especially the tibia, is longer. In general morphological characters these elements closely resemble those of *Phytosaurus*; the femur shows the S-flexure, the elongate head, and the rough trochanter on the under surface, one-third the length of the bone from the proximal end.

A comparison of measurements of leg bones of *Phytosaurus* and *Rhytidodon* gives the following results. Of *Phytosaurus* the average length of six femurs was 307 mm., of five tibias, 178 mm., of five fibulas, 182 mm., the femur-tibia ratio being about 100:58. Three femurs of *Rhytidodon* measured 311, 303, and 300 mm., an average of about 305 mm.; one tibia measured 200 mm., and one fibula 210 mm. The femur-tibia ratio is thus about 100:67. The meagre material naturally renders the ratio for *Rhytidodon* somewhat untrustworthy, but taken in correlation with the fact that the forearm is also longer in the American form, we may assume that it is not far wrong. In general it may be stated that both fore and hind leg are longer and more slender in *Rhytidodon* than in the European phytosaurs, the most marked difference being in the greater length of forearm and tibia.

MANUS AND PES.—The few bones of the manus and pes in the collection studied are figured in Pl. IX, Figs. 25-29. The largest of these, which is considerably crushed, measures 82 mm. in length, and is doubtless a metatarsal; two of the others are metacarpals or metatarsals and two are phalanges. The illustrations render description of these bones unnecessary. They cannot be said to add anything to the knowledge of the group.

On reference to the restoration (text-fig. 26), it will be observed that a fifth digit is shown in the pes. The evidence for this is the bone figured by von Meyer, 1865, pl. xxviii, figs. 12-14, and by him regarded as possibly a pelvic bone of a chelonian. The great resemblance of this bone to the flattened fifth metatarsal of *Sphenodon*, of lizards, and of *Aëtosaurus* led me to the conclusion that it was nothing else than the corresponding element of *Phytosaurus*, and as it

bears a distal as well as a proximal articular surface it must bear at least one phalanx. It was a pleasure, some time after arriving at this conclusion, to discover that G. Baur had some years previously arrived at the same conclusion, and in exactly the same manner, from an examination of von Meyer's figures.

#### RELATIONSHIPS OF PHYTOSAURIA.

In Owen's 'Palæontology,' published in 1860, the Phytosauria were placed in the order Thecodontia, which comprised a number of widely diverse reptiles, having little in common except that the teeth were set in sockets. A decade later Cope (1869) adopted the same name, but reduced it to subordinal rank, his Thecodontia being a suborder of his very heterogeneous order Archosauria, and including only the Phytosauria (Belodonts).

"In this suborder," writes Cope, "we have a singularly generalized group, combining characters of lizards, crocodiles, and Sauropterygians. The neural arch of the vertebræ united by suture and the slightly biconcave centrum resemble the last two, so also the abdominal ribs. The limbs are rather crocodilian, the position of the nares, plesiosaurian. The clavicle is lacertian, while the three vertebræ of the sacrum and the femur are between these and the Dinosauria.

"The most important characters distinguishing these animals from the Sauropterygia are the presence of an elongate sacrum and the more ambulatory form of limbs."

We see from this that in 1869 Cope's ideas regarding the affinities of the group were not very definite though tending rather toward their association with the Sauropterygia; later he accepted Huxley's view that the Phytosauria were ancestral crocodiles.

#### CRITIQUE OF HUXLEY'S OPINION.

Since Huxley was the first definitely to classify these animals, and since his ideas regarding their phyletic affinities have been so generally accepted, it may be well to preface the general discussion of relationship by a brief critical survey of his conclusions.

Professor Huxley's earliest studies of the group were based on *Stagonolepis robertsoni*, from the Elgin Sandstone of Scotland, and in 1858 in an article describing this species he asserts that "*Stagonolepis* is in the main a crocodile." His matured conclusions regarding the genetic affinities of the group were given to the world seventeen years later (1875), in the famous paper 'On *Stagonolepis Robertsoni* and on the Evolution of the Crocodilia.' In this paper Huxley points out the close relationship between *Stagonolepis* and the genus *Phytosaurus* (*Belodon*) of the German Trias, asserting that there can be no doubt that they "are members of one and the same natural group, and that this group



must be included among the order *Crocodylia*." Accordingly he erects a new crocodilian suborder, Parasuchia, for the forms in question, and divides the remaining crocodiles into two suborders: Mesosuchia, including the more generalized Mesozoic (chiefly Jurassic) genera, and Eusuchia, which comprise the highly specialized types from Cretaceous to recent. Of the suborder Parasuchia he gives the following diagnosis:

"Neither the palatine nor the pterygoid bones are produced into osseous plates which prolong the nasal passage and give rise to secondary posterior nares. Consequently the nasal chambers communicate with the mouth by apertures situated beneath the anterior part of the skull. The Eustachian passages are not enclosed by bone. The centra of the vertebræ are amphicœlous. The atlas and axis are unknown. The coracoid is short and rounded. The ala of the ilium is high, and has a large and prominent anterior dorsal angle. The acetabular margin is entire and its center projects beyond its anterior and posterior ends. The ischium is short dorso-ventrally, elongated longitudinally, and in its acetabular portion resembles that of a lizard. The characters of the manus and pes are unknown.

"There are two longitudinal series of articulated, carinated, dorsal scutes; and in *Stagonolepis* (but apparently not in *Belodon*), there is a ventral thoraco-abdominal shield, formed of not more than eight longitudinal series of articulated scutes, each of which consists of only one piece of bone.

"Genera, *Stagonolepis*, *Belodon*."

Since Huxley's ideas regarding the evolution of the Crocodylia are so well known, a very brief statement of them here will suffice.

Huxley believed that the Triassic forms comprised in his suborder Parasuchia were geologically the oldest known crocodiles, that they gave rise to the Jurassic forms which differed from them chiefly in the fact that the external nares had shifted to the extremity of the snout, and that the opening of the posterior nares had been carried backward by the formation of a secondary palate composed of projections of the palatine bones. Certain modifications in the coracoid, in the pelvis, and in some other regions occurred at the same time. For these Jurassic forms, many of which were longirostral, and some of marine habit, the suborder Mesosuchia was created. The transition from these forms to the crocodiles of modern type, the Eusuchia, entailed but slight modification, the chief change being a further backward shifting of the internal nares, and the participation of the pterygoid bones in the secondary palate. In these highly specialized forms the vertebræ are usually opisthocœlous, and the eustachian canals are enclosed by bone. Most of them are brevirostral forms. The Eusuchia are first known in the Cretaceous.<sup>1</sup> The transition from the Mesosuchia to Eusuchia is not great, and the evidence adduced by Huxley is very conclusive as to the evolution of the latter from the former. He admits that the hiatus between the Parasuchia and Mesosuchia is much greater, but concludes that, on the whole, the evidence of the evolution of the Crocodylia

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<sup>1</sup> Von Huene has recently (1902) announced the discovery of probable Eusuchian remains in the Muschelkalk.

through the three successive stages—Parasuchian, Mesosuchian and Eusuchian—is quite as cogent as the evidence in the case of the evolution of the horses. He was careful to state, however, that he did not postulate any known species of Parasuchian as ancestral to higher forms. Let us now examine the evidence upon which Huxley allied the Parasuchia with the Crocodilia. The following scheme presents his diagnosis of the order in the first column, while the second contains criticisms.

- |   |   |
|---|---|
| 1. "The transverse processes of the majority of the cervical and thoracic vertebræ are divided into more or less distinct capitular and tubercular portions; and the proximal ends of the ribs which appertain to these vertebræ are correspondingly divided into capitula and tubercula. | Also true of the Dinosauria.  |
| 2. "The dorsal ends of the subvertebral caudal bones are not united.  | Also true of many dinosaurs.  |
| 3. "The quadrate bone is fixed to the side of the skull.  | Also in Rhynchocephalia and Dinosauria. A primitive character.  |
| 4. "The pterygoid bones send forward median processes, which separate the palatines, and reach the vomers.  | Also in Rhynchocephalia and Dinosauria.   |
| 5. "There is an interclavicle, but no clavicle. [Clavicles <i>are</i> present in the Phytosauria.]  | Phytosauria have shoulder girdle of rhynchocephalian type. Clavicle is lost in true crocodiles; clavicle and interclavicle probably lost in dinosaurs.  |
| 6. "The ventral edge of the acetabular portion of the ilium is entire, or but slightly excavated.   | The phytosaurian pelvis is much more primitive than any crocodilian or dinosaurian pelvis. That of <i>Morosaurus</i> (Sauropoda) resembles it more closely than does the crocodilian type.  |
| 7. "The ischia are not greatly prolonged backward.  | The ischium of <i>Phytosaurus</i> resembles that of the Sauropod, <i>Morosaurus</i> , more closely than any crocodilian type.   |
| 8. "The pubes are directed forwards and inwards.  | In Phytosauria the pubes participate in the acetabulum, and there is a pubic foramen. <i>Morosaurus</i> shows an approximation to this condition. In the crocodiles the pubis is greatly modified, and takes no part in the acetabulum. |
| 9. "The femur has no prominent trochanter.  |   |

10. "The astragalus is not a depressed concavo-convex bone with an ascending process.

In the dinosaur *Hallopus*, the astragalus is devoid of the ascending process, and the calcaneum has a 'heel' as in the Crocodilia.

11. "There are, at fewest, two longitudinal rows of dermal scutes, one on each side of the middle line of the dorsal region of the body."

The close resemblance of dermal exoskeleton in crocodiles and phytosaurs is undeniable, but the fact may be recalled that certain Jurassic marine crocodiles possessed no scutes, and that certain dinosaurs (*Stegosaurus*) had a bony armor.

"*Stagonolepis* and *Belodon* [*Phytosaurus*]," says Huxley, "come within the order Crocodilia as thus defined, and constitute the first of the three suborders which may be distinguished on purely anatomical grounds."

In the light of present-day knowledge of the Rhynchocephalia and Dinosauria it will be noted that a combination of the characters enumerated above will give a very inclusive definition, and will go far toward embracing these two orders as well as the Crocodilia. In fact, of Huxley's eleven diagnostic characters, only one—"There is an interclavicle but no clavicle"—applies exclusively to the Crocodilia, and this only to the "true" Crocodilia, since the Phytosauria (Parasuchia) have the clavicle highly developed. Excepting the error regarding the clavicle, it must be admitted that the Phytosauria will fall within the Crocodilia as defined by Huxley; the false premise is to be found in the laxity of his definition of the order. The morphological features of the Phytosauria, on the evidence of which Huxley allied them with crocodiles, are merely the characters stated in his ordinal definition; most of these are primitive, generalized characters, excepting that relating to the dermal armor. In addition to all of these the Phytosauria have a most striking resemblance to certain crocodiles in general form of body, elongate snout, and armor, the only very conspicuous external difference, so far as known, being in the position of the nostrils. Nevertheless, there are many morphological features in the cranium and limb girdles in which the phytosaurs diverge widely from crocodiles and approach the conditions of Rhynchocephalia and Dinosauria. The close general resemblance to crocodiles I believe to be due to parallel adaptation to similar conditions of life. Their relationship to this order will be discussed more in detail below; my object at this point not being to bring negative evidence in rebuttal of Huxley's proposition, but merely to show that his evidence is insufficient to warrant the actual inclusion of the Phytosauria within the order Crocodilia.

Despite the general acceptance of Huxley's opinion as to the crocodilian nature of these animals, expressions of dissent have been heard from several quarters, and a number of palæontologists, including A. S. Woodward, Baur, Marsh, and Fraas, have made bold to question the propriety of this classification, without, however, offering any other in its stead, though nearly all who have studied these forms have noted points of likeness to Rhynchocephalia, Aëtosauria,

and Dinosauria. Even Huxley himself remarks (1877) that "It is . . . obvious that the Parasuchia, in those respects in which they differ from the Mesosuchia, approach the Ornithoscelida [Dinosauria] and the Lacertilia, especially such Lacertilia with amphicoelous vertebral centra as the existing *Sphenodon*, and the extinct *Hyperodapedon*. In fact I know of no reptiles the skull and pectoral arch of which so nearly approach the structure found in *Belodon* and *Stagonolepis*, as they do in *Sphenodon*."

In the remaining portion of the present paper I shall attempt briefly to analyze the morphological characters of the Phytosauria in their bearings upon phyletic relationship.

#### COMPARISON WITH RHYNCHOCEPHALIA.

On the rhynchocephalian side of the present comparison, we shall have recourse for the most part to *Sphenodon*, since that recent genus is so completely known. Another advantage in selecting this type is that the Sphenodontidæ, though not known to have existed earlier than the Upper Jurassic, are undoubtedly less specialized than the known Permian rhynchocephalians.

To consider first the points of difference: the elongate rostrum and the bony armor of Phytosauria are clearly adaptive structures, structures which have been secondarily acquired. The bicipital thoracic ribs also mark a divergence from the Rhynchocephalia, in which, usually, all the ribs are single headed, though two-headed ribs have been described as occurring in the cervical and anterior thoracic regions of *Champsosaurus*, and the rib of the fourth vertebra of *Sphenodon* has been described by Owen, Günther, and Baur as two-headed. The atlantal rib, which probably exists in the Phytosauria, is not known in most Rhynchocephalia, though its presence is doubtless to be regarded as a primitive character, and it is said to occur in *Palæohatteria*. The vertebral centra differ from those of *Sphenodon* in being less deeply biconcave, though not so flat as those of *Champsosaurus*, and the reduction of presacral intercentra to two in the anterior neck region is similar to the condition in *Champsosaurus*.

The thecodont teeth apparently differentiate the group from Rhynchocephalia, unless Dollo's view is correct;—namely, that the acrodont dentition is derived from a primitive thecodont type. It is of interest here to recall the slightly thecodont condition in *Champsosaurus*. (Dollo, 1891.) The absence of a presplenial (Baur) in *Sphenodon*, and its doubtful presence in any rhynchocephalian, must also be noted.

Among the structures suggesting affinity with Rhynchocephalia, are to be mentioned particularly the cranium and the shoulder and pelvic girdles. Except for the elongate premaxillaries the cranium is almost typically rhynchocephalian, and it is safe to assert that if the skull alone were known, minus the snout, the animal would have been placed without hesitation among that group. In fact the skulls of *Mystriosuchus* and *Sphenodon* are almost identical as regards

most details of morphology, as may be seen from examination of text-figs. 2 and 3.

The cranial differences are in the absence of a pineal foramen (which is lacking also in *Hyperodapedon*), the extreme prenarial development of the premaxillaries (the nares are in their primitive position, as in *Sphenodon*), the thecodont dentition, non-dentigerous palatines, and the depression of the parietosquamosal arcade in the Phytosauria; but none of these differences is of ordinal significance.

The shoulder girdle (Pl. IX, Figs. 19-21) with its rounded, notched coracoid, large clavicles, and interclavicle, is clearly of the rhynchocephalian type.

The pelvic girdle is more generalized than in *Sphenodon*, resembling that of *Champsosaurus*, and still more closely that of the very primitive *Palæohatteria*, especially in the form of ilium and ischium, and in the well-nigh complete ventral closure of the pelvis. The pelvic bones, before complete ossification, must have been almost identical in form with the corresponding structures of this genus. The small obturator foramen is represented in the young *Palæohatteria* by a notch, which probably becomes a foramen in the fully ossified pubis.

The presence of an ectepicondylar groove in the humerus cannot be regarded as of great importance in its bearing upon rhynchocephalian relationship, since different members of that order possess ectepicondylar only, entepicondylar only, or both (Osborn).

A primitive character, which is retained in great perfection is the plastron, or system of abdominal ribs, which are arranged in three series, exactly as in *Sphenodon*,—those of the median series bent at an obtuse angle, while those of the lateral series are straight.

The existence of the peculiarly modified fifth metatarsal, similar in form to that of *Sphenodon*, with a distal facet for a first phalanx is also important, as proving the presence of a fairly developed fifth digit in the pes (p.74).

To render clearer the comparison with the Rhynchocephalia, the characters of Phytosauria which show affinity, and those which seem to be divergent, may be arranged in parallel columns.

1. General morphology of cranium, thoroughly rhynchocephalian.

2. Similar union of hyoid arch with cranium.

3. More than one intercentrum in anterior cervical region. (Only one free.)

4. Two sacral vertebræ.

5. Chevrons similarly placed.

1. Elongate premaxillary rostrum (prenarial; a maxillo-premaxillary rostrum in *Champsosaurus*). A secondary character.

2. Thecodont teeth. (Teeth are slightly thecodont in *Champsosaurus*.)

3. Depressed parietosquamosal arch (secondary).



6. *Shoulder girdle of rhynchocephalian type. Clavicles and interclavicle present. Coracoids broad, rounded, with deep notch.*
7. *Pelvis very generalized in structure, resembling that of Palæohatteria.*
8. *Ectepicondylar groove (a character of doubtful value). Corresponding foramen in some rhynchocephalians (*Champsosaurus*).*
9. *Abdominal ribs (plastron) similarly arranged in three series.*
10. *Separate two-headed ribs, extending anteriorly, at least to axis (as in *Champsosaurus*).*
11. *Fifth digit of pes with flattened metatarsal, shaped as in *Sphenodon*, and with at least one phalanx.*
12. *Odontoid coössified with atlas centrum (as in *Sphenodon*).*
13. *Neural spines of thoracic vertebræ showing a tendency to bifurcate at extremity (as in *Sphenodon*).*
4. *Presplenial bone present (not certainly known to be absent in all Rhynchocephalia.)*
5. *Bicipital condition of ribs more marked, extending farther posteriorly.*
6. *Elongate transverse processes in lumbar region. (*Champsosaurus*.)*
7. *Bony dermal armor.*

## COMPARISON WITH AËTOSAURIA.

Among the Aëtosauria (=Pseudosuchia, Zittel) are here included *Aëtosaurus*, *Dyoplax*, *Typothorax* (= *Stegomus*), *Ornithosuchus*, and *Erpetosuchus*, a group of small reptiles from the Trias of Europe and North America. They are lacertiform, primitive or generalized as regards proportions of head and limbs, and are characterized chiefly by a dermal armature of bony scutes. Their resemblance to *Phytosauria* and to theropodous dinosaurs in respect to certain skull characters was long ago noted by Marsh.

The features in which Phytosauria approximate or diverge from the Aëtosaurian type, are as follows:

1. *Preorbital fenestra.*
2. *External mandibular fenestra.*
3. *Supra-, infra-, and post-temporal arcades (as in *Ornithosuchus* and *Herpetosuchus*. In *Aëtosaurus*, according to O. Fraas, the latero-temporal fenestra is closed. If so, it must be obliterated by secondary union of supra- and infra-temporal arcades, probably correlated with great size of orbit).*
1. *Elongate rostrum. (Secondary.)*
2. *External nares somewhat shifted backward, and usually surrounded by nasal bones.*

4. Pineal foramen absent.
5. Separate postfrontal and postorbital (as in *Aëtosaurus*).
6. External nares separate.
- 7 Internal nares placed well forward.
8. Dentition thecodont.
9. Parietals not coalesced, meet in suture.
10. Posterior palatine foramen small.
11. Vertebral centra biconcave. In general the number and form of presacral vertebrae.
12. Two sacrals. (Three in *Ornithosuchus*.)
13. Cervical ribs two-headed (as in *Dyoplax*).
14. Structure of shoulder girdle; coracoid, rounded clavicles, and interclavicle present.
15. Ilium and ischium of similar form to those in *Aëtosaurus*. All three pelvic bones participating in formation of the closed acetabulum.
16. Slightly S-curved femur.
17. Presence of a fifth digit in pes, with at least one phalanx. Fifth metatarsal shaped as in *Aëtosaurus*.
18. Dorsal and ventral armor of bony scutes.
3. Broad pubis with foramen,—a less specialized condition than the elongate pubis of Aëtosauria (*Aëtosaurus* and *Ornithosuchus*). The pubis of the former resembles that of *Stagonolepis* as figured by Huxley).
4. Odontoid fused with axis centrum. (Separate in *Erpetosuchus*.)

That such a preponderance of common characters indicates genetic affinity cannot be questioned, but the degree of relationship cannot be definitely postulated, until we have more knowledge of the carpus and tarsus of the Phytosauria, and of the ribs and the atlanto-axis of the Aëtosauria. Von Huene (1902) is of the opinion that the two groups are so closely united by their common characters that they should be considered as forming a single suborder, for which he adopts Huxley's name *Parasuchia*, recognizing the *Belodontia* and *Pseudosuchia* as families. He further expresses the opinion that this suborder is as sharply differentiated from the *Crocodilia* as from the *Dinosauria*.

An objection to regarding Aëtosauria and Phytosauria as groups of equal

rank is that the former, so far as known, seems to be comparatively heterogeneous, while there can be no doubt that *Phytosaurus*, *Mystriosuchus*, *Rhytidodon* (and probably *Stagonolepis*) are well within the same family.

Of the differential specializations of the two groups, the only very important ones known are the premaxillary snout of the Phytosauria, and the somewhat specialized pelvis in the (known) Aëtosauria. These differences certainly would not be considered as of more than family value in some groups, *e. g.*, in the Predentata, which contains such widely divergent types as *Iguanodon* and *Triceratops*. Therefore I see no very valid objection to grouping the Aëtosauria and Phytosauria in a single suborder, as proposed by von Huene, except that this suborder could not well be included in any recognized order. Many characters preclude its being placed among the Crocodilia or the Dinosauria. The order which it approximates most closely is the Rhynchocephalia; in fact it may be said to be differentiated from this order only by the strongly thecodont dentition and the dermal armor, but in view of the inclusiveness of the Rhynchocephalia, as generally defined, it seems best to separate the Parasuchia as a separate *order*, comprising the suborders Aëtosauria and Phytosauria, the latter including but one family, the Phytosauridæ.

#### COMPARISON WITH CROCODILIA.

The insufficiency of the evidence upon which Huxley included the Phytosauria (Parasuchia) among the Crocodilia has already been indicated (p. 75). Since the publication of Huxley's papers, a number of important points in the morphology of the group have come to light, especially regarding characters which show affinity with other orders than Crocodilia.

The general appearance of a phytosaurian, in size, form, elongate snout, and dermal armor, is essentially gavial-like, the most conspicuous difference being in the posterior location of the external nostrils (text-fig. 26). Nevertheless, a careful comparison of the skeleton with that of a crocodile will show: (1) that while there are many points of resemblance, many of them must be interpreted as due to parallel adaptive modifications; and (2) that certain crocodilian conditions could not have been derived through modification of phytosaurian structure.

In the following comparison the Mesosuchia and Eusuchia of Huxley will be treated together, since there can be no doubt as to the propriety of their inclusion in a single order.

*Characters indicating affinity with Crocodilia.*      *Characters indicating divergence from Crocodilia.*

1. General form of body, elongate rostrum, etc.

1. Rostrum formed chiefly by prenasal elongation of premaxillary, a condition which cannot have given rise to the chiefly maxillary snout of the crocodiles. The external

- nares of the crocodile have shifted forward *with* the elongation of the snout. (See discussion below.)
2. Dermal armor (very similar to that in some Mesozoic forms).
  3. Supra-, infra-, and post-temporal arcades, and supra-, latero-, and post-temporal fenestræ *present*. Post-temporal fenestra of small size.
  4. Pineal foramen absent.
  5. Internal and external mandibular fenestræ.
  6. Presplenial well-developed.
  7. Two sacral vertebræ.
  8. Dentition thecodont.
  9. Atlantal rib present.
  10. Bicipital ribs.
  11. Abdominal ribs in three series (as in some Mesozoic crocodiles).
  2. Reduction and depression of the parietosquamosal arcade.
  3. Presence of separate postfrontal and postorbital.
  4. External nares usually surrounded by nasal bones.
  5. Anterior (primitive) location of internal nares. No median union of palatines to form secondary palate.
  6. Very small posterior palatine foramina. (These openings are large in Crocodilia.)
  7. Interpterygoid vacuity present.
  8. Styliiform parasphenoid (vomer of Broom).
  9. Form of quadrate.
  10. Jugal taking little or no part in forming rim of orbit.
  11. Interparietal suture present.
  12. Presence of clavicles.
  13. Atlanto-axis. Cup for occipital condyle formed chiefly by first intercentrum (=ventral bar of the atlas).  
Odontoid very short, having but little part in articulation with condyle. Firmly co-ossified with axis centrum.
  14. Rounded form of coracoid.
  15. Pelvis. Participation of all three elements in the imperforate acetabulum. Antero-posterior elongation of ventral elements. Pelvis is almost closed ventrally. Pubis with foramen. (The pubis of *Stagonolepis* as figured by Huxley is elongate and shows no foramen.)
  16. Ectepicondylar (radiocondylar) groove on humerus.

12. Presence of interclavicle.
13. Femur slightly S-shaped, with trochanteric ridge.
17. There is strong reason to believe (from position of bones in specimen of *Mystriosuchus* shown in Plate XI) that the proximal carpals and tarsals were not elongated as in Crocodilia.
18. Fifth digit of pes not greatly reduced as in Crocodilia, having at least one phalanx.

Of this list of characters, it must be admitted that many of those cited as differential might be capable of giving rise, through modification, to crocodilian conditions. In nearly all these characters the Phytosauria are the more primitive, approximating more closely the generalized Rhynchocephalia and the Aëtosauria. There is manifest impropriety in grouping with the crocodiles an animal which has closer affinities with any other order.

Granting, therefore, that the Phytosauria cannot be placed within the crocodilian order, there still remains the question,—Can they have been ancestral to the crocodiles? This, I think, must be answered in the negative, and this mainly on account of the specialization of the snout in the Phytosauria. I do not believe that the crocodilian snout was *first* elongated and that the external nares *later* shifted forward, the constitution of the rostrum changing during the same time from chiefly premaxillary to chiefly maxillary.

In the evolution of the Crocodilia the external nares were carried forward *with* the elongation of the maxillaries and, in most cases, of the nasals, and the premaxillaries have never undergone great change. Though many of the earliest known crocodiles are longirostral, I regard it as certain that the very earliest forms were brevirostral. *Notosuchus*, from the Cretaceous of Argentina, shows little or no elongation of the snout, and yet the palate is typically mesosuchian. The little *Alligatorellus* of the French Jurassic is also an extremely brevirostral form.

Another specialization in the phytosaurian skull which militates strongly against the theory that they are ancestral to crocodiles is the condition of the post-temporal (parietosquamosal) arcade, which is greatly reduced, depressed and covered by muscles, and in dorsal view partly obscured by the posterior development of the postfronto-squamosal arcade. So inconspicuous is it that both Zittel and Marsh have erroneously described the supratemporal fenestra in these animals as open posteriorly. In the crocodiles the post-temporal arcade is not depressed, but on a level with the highest plane of the skull roof, and frequently sculptured, showing its close relation to the integument,—certainly a more primitive condition than that obtaining in the Phytosauria, and hardly derivable from it.

Certain features of the atlanto-axis also show a higher degree of specialization than in the crocodiles, though in the main this region is more primitive in the Phytosauria. The higher specialization in Phytosauria is shown in the



coalescence of the odontoid with the axis centrum, its small size, and its almost complete withdrawal from the occipito-atlantal articulation. Nothing is known of the pro-atlas, but the occurrence of such an element in Rhynchocephalia, Crocodilia, and certain Dinosauria renders its presence in Phytosauria very probable. While denying the Phytosauria a place in the line of crocodilian descent, I do not question the close genetic affinity of the two groups; but I believe that they have been evolved along two nearly parallel lines, from a common ancestor probably not more remote than early Triassic. This ancestral form must have had many rhynchocephalian characters, but had thecodont dentition, bicipital ribs, and an armor of bony scutes. The skull was normal in form, the jaws not produced into a rostrum. Such a form would fall within our definition of the Aëtosauria, though the known members of that suborder have the pelvis too highly specialized to have given rise to the Phytosauria.

It may be mentioned here that, according to von Huene, crocodilian remains, apparently Eusuchia, have recently been found in the upper 'Muschelkalk,' of Württemberg, thus antedating the earliest known Phytosauria and Aëtosauria.

#### COMPARISON WITH DINOSAURIA.

The possession of common characters by Phytosauria and Dinosauria has been noted by several writers. Marsh, as early as 1878, "pointed out that the Sauropoda were the least specialized of the Dinosaurs, and . . . gave a list of characters in which they showed such an approach to the Mesozoic Crocodiles as to suggest a common ancestry at no very remote period." Later he stated that "*Belodon* [*Phytosaurus*] of the Triassic resembles *Diplodocus*, particularly in the large antorbital vacuities of the skull, the posterior position of the external nasal apertures, as well as in other features." Marsh also pointed out certain features common to *Aëtosaurus*, *Phytosaurus*, and certain theropodous forms. A. S. Woodward (1898) also states regarding the Phytosauria that "the Triassic reptiles commonly claimed as ancestral crocodiles are capable, in the present state of knowledge, of being assigned with equal appropriateness to the Dinosauria."

It is now well-known that the Dinosauria do not form a monophyletic group, but for convenience in the comparison with Phytosauria I shall treat them as a single order. It should be stated, however, that the types showing the strongest affinity with Phytosauria are the Triassic Theropoda, especially as regards the skull and vertebræ, though these forms show great divergence in the girdles and limbs, in correlation with bipedal habit. The quadrupedal Sauropoda, as might be expected, resemble the Phytosauria more closely in the limb girdles.

In the following list the characters of Phytosauria will be compared only with relatively generalized dinosaurian structures, and certain clearly adaptive characters of the latter group will be omitted.

*Points of resemblance to Dinosauria.*

1. Supra-, infra-, and post-temporal arcades; supra-, latero-, and post-temporal fenestræ. (In some dinosaurs the post-temporal fenestra is closed.)
2. Preorbital fenestra.
3. External mandibular fenestra (as in *Ceratosaurus*). General structure of palate.
4. Fixed quadrate.
5. Presplenial present (as in *Dryptosaurus*, *et al.*).
6. No pineal foramen.
7. Thecodont dentition.
8. Form of atlas. (Resembles that of the carnivorous dinosaur *Ceratosaurus* very closely, much more so than any crocodilian atlas.)
9. Vertebral centra slightly amphicœlous (as in some Theropoda).
10. Two sacral vertebræ (as in some Theropoda; some dinosaurs have as many as 10).
11. Sacral ribs each attached to two vertebræ (as in Theropoda).
12. Bifurcation of neural spines (as in some Stegosauria).
13. Bicipital ribs, posterior ones elevated on diapophyses.
14. Rounded coracoid, with coracoid notch.
15. All three pelvic elements participate in acetabulum.
16. Fifth digit of pes present, though probably somewhat reduced. (The pes has five digits in primitive Theropoda and in Sauropoda).

*Points of difference from Dinosauria.*

1. General crocodile-like body form.
2. Elongate rostrum, anterior to external nares. (In *Diplodocus* the external nares are situated far back, almost between the eyes, but this condition has doubtless been independently evolved.)
3. Smaller number of cervical vertebræ (in Dinosauria 9 to 15).
4. Greater number of thoraco-lumbar (in Dinosauria 10 to 18).
5. Sacra not coalesced.
6. Cervical vertebræ never opisthocœlous. (This is a secondary character evolved in correlation with the long neck in dinosaurs.)
7. Presence of clavicles and interclavicle.
8. Primitive form of pelvis, with closed acetabulum. (Among the dinosaurs the pelvic type most nearly approximating that of Phytosauria is found in the Sauropoda, especially in *Morosaurus*.)
9. Presence of radio-condylar groove.
10. Dorsal and ventral armor of bony scutes. (The dermal scutes of *Stegosaurus*, *et al.*, probably have no genetic relation to those of Phytosauria.)

In comparing the Phytosauria with Crocodilia the resemblances, due to adaptation to similar habit, are so strong as to be misleading; in a comparison with Dinosauria, on the other hand, the external dissimilarities correlated with widely divergent habits of life are so pronounced as to be equally misleading. Nevertheless, if in the comparison we consider only the more generalized dinosaurian conditions, ignoring the extreme specializations, the conclusion must inevitably be that the two groups have a common ancestor not far removed. It is, indeed, not improbable that this progenitor may have been some early unknown aëtosaurian. The armor would be the only possibly disqualifying character, but the history of several ancient groups (*e. g.*, marine crocodiles) shows that armor is readily lost.

It is safe to assert that the Phytosauria, Crocodilia, and the carnivorous Dinosauria have been evolved along separate lines from a Permian or early Triassic reptile, rhynchocephalian in the main, with thecodont dentition and bicipital ribs.

#### COMPARISON WITH ICHTHYOPTERYGIA.

Very early in the course of the present study of the Phytosauria I noticed a certain resemblance to the Ichthyosauria, and further comparison has led me to the conclusion that the Phytosauria represent the nearest known relatives of the great marine fish-saurians.

That the Ichthyopterygia have been derived from some land-living reptile is unquestionable. Abundant proof of the correctness of this view has been adduced by several morphologists, most notably by Baur (1887).

Baur pointed out: (1) that the ichthyopterygian skull shows characters of the Rhynchocephalia, Phytosauria, and Dinosauria; (2) that the presence of separate postfrontal and postorbital was common to Ichthyopterygia, a few lizards and dinosaurs, the Phytosauria and the Sauropterygia; (3) that the ichthyopterygian shoulder girdle is of the lacertilian or rhynchocephalian type; (4) that the two-headed condition of the ribs is a point of resemblance to the crocodiles and dinosaurs; (5) that abdominal ribs are present as in Rhynchocephalia and Sauropterygia. From these observations Baur concluded that the Ichthyopterygia must have originated from an ancestor combining the characters of (1) the Rhynchocephalia, (2) the oldest Crocodilia (by which I think he meant the Phytosauria), and (3) the Sauropterygia.

Careful comparison with the last-named order brings to light so many fundamental points of divergence as to entirely preclude the possibility of any but the most remote genetic affinity, hence the Sauropterygia may be eliminated from consideration; but Baur was undoubtedly correct in his suggestion that the terrestrial ancestor of the Ichthyopterygia must have possessed characters of the Rhynchocephalia and the Phytosauria.

The nature and various degrees of the adaptive modifications to marine life are so well shown by comparative study of Mosasauria, thalattosuchian

crocodiles, Sauropterygia, and Ichthyopterygia among reptiles, and Pinnipedia, Sirenia, and especially Cetacea, among mammals, that it is possible to state with considerable probability of correctness the character of the proximate ancestor. If now, following Baur, we postulate the descent of the Ichthyopterygia from rhynchocephalian-like ancestors, we should look for some intermediate form, some animal not wholly aquatic, but of amphibious habit. In my opinion the Phytosauria present the nearest approximation to such a form, though no *known* phytosaurian can actually be the ancestor of the Ichthyopterygia. In the following table are enumerated in parallel columns the characters of the Phytosauria which support, and those which oppose, this view.

*Characters indicating affinity with Ichthyopterygia.*

Elongate rostrum, largely composed of premaxillaries.

External nares placed far back, separated by nasals.

Separate postfrontal and postorbital.

Separate prefrontal and lachrymal.

Internal nares separated by vomers (prevomers of Broom).

Pterygoids extending forward to unite suturally with vomers, separated posteriorly by interpterygoid vacuity. Palatines not meeting in mesial line.

Fixed quadrate.

Preorbital and external and internal mandibular fenestræ present.

Parietals separated by suture.

Supratemporal and post-temporal fenestræ.

Foramen between quadrate and quadratojugal.

Styliform parasphenoid (vomer of Broom).

Premaxillaries extending, on palatal surface, nearly back to internal nares.

Presplenial present. Homologue of the "opercula," of Ichthyopterygia, as described by E. Fraas (1890).

*Characters indicating divergence from Ichthyopterygian stem.*

Squamosal and prosquamosal bones are fused to form a complex.

Latero-temporal fenestra present. (Entirely wanting in Ichthyopterygia. Probably secondarily obliterated in correlation with increase in size of orbit.)

Pineal foramen absent.

Exoccipital and opisthotic fused to form a complex (separate in Ichthyopterygia).

Ectopterygoid present.

Pterygoids not articulating with basioccipital.

Only one free intercentrum in cervical region.

Thoraco-lumbar vertebræ far less numerous than in Ichthyopterygia.

Neural arches generally anchylosed with pleurocentra.

Centra less deeply biconcave.

Atlas centrum (odontoid) has little part in occipito-atlantal articulation. Atlantal neural arches articulate with first intercentrum. (In Ichthyopterygia the neural arches and intercentrum are widely separated by the enlarged pleurocentrum which alone forms the cup for the occipital condyle.)

Dentition thecodont. (This is also the case with the maxillary teeth of *Mixosaurus cornalianus*, one of the most primitive ichthyopterygians.)

Teeth (in some phytosaurians) corrugated vertically.

Amphicœlous vertebræ.

Distinct paired zygapophysis (as in *Shastasaurus*).

Centra (pleurocentra) of atlas and axis coalesced, as in adult *Ichthyosaurus*.

Halves of neural arch of atlas separate.

Y-shaped chevrons in caudal region (as in Triassic Ichthyopterygia).

Anterior ribs bicipital.

Atlantal rib present.

Abdominal ribs present.

Shoulder girdle with clavicle, interclavicle, rounded coracoid with notch in anterior outer border, suturally united to elongate scapula. (Scapula and coracoid shaped much as in *Ichthyosaurus communis*.)

Pelvic arch with all three elements participating in acetabulum. (The pubis and ischium of *Shastasaurus perrini* Merriam are strikingly similar to those of Phytosauria.)

Capitulum of atlantal rib on first intercentrum, tubercle on neural arch. (In *Ichthyosaurus* both are borne on the pleurocentrum.)

Passing posteriorly in the thoracic region the capitulum becomes elevated upon the neural arch, finally on the transverse process. (In the Ichthyopterygia, the anterior rib tubercles articulate with diapophyses high on the pleurocentra, close to the bases of the neural arches. Passing backward, the diapophyses descend lower and finally unite with the parapophyses.)

Rib tubercula never articulate with pleurocentra (as in Ichthyopterygia), but with neural arches.

Phytosauria possess bony dermal armor. (Like the thalattosuchian crocodiles, the ichthyosaurs may be descendants of armored ancestors.)

Of the characters differentiating Phytosauria from the ichthyopterygian stem the most important are the absence of the pineal foramen, fusion of squamosal and prosquamosal, and the single free intercentrum. These are almost the only features which show a degree of specialization sufficient to eliminate the Phytosauria from the direct ancestral line of the Ichthyopterygia, and render it necessary to postulate a common ancestor, which flourished in the lower Triassic, a form which differed from the known Phytosauria in the possession of a pineal foramen and separate squamosal and prosquamosal and separate exoccipital and opisthotic, three or more free intercentra, and perhaps a less specialized dermal armor.

In the evolution of the marine Ichthyopterygia from such a form, one of the early modifications was probably the loss of the dermal armature. A close parallel is shown in certain marine Crocodilia (*Metriorhynchus*) which have lost



their armor. The modification of the limbs to swimming paddles, and the correlated withdrawal of the pelvis from the vertebral column, is known in so many groups that it need not be outlined here. There is strong reason to believe that the girdles are derived from those of the phytosaurian type.

Strange to say, the Mixosauridæ, in which the paddles are the least specialized, have a less primitive shoulder girdle in some particulars, *e. g.*, form of scapula, than do the Ichthyosauridæ. The most primitive ichthyopterygian pelvis is that of *Shastasaurus*, the pubis of which differs from that of the Phytosauria chiefly in the fact that the pubic foramen is represented only by a deep notch. The ischium differs in being shorter antero-posteriorly. In most true ichthyosaurs the pelvis is so degenerate as to show little resemblance to any other type.

The extreme adaptation to marine habit, shown in the vertebral column and ribs of ichthyosaurs, in no way precludes their derivation from a phytosaur-like ancestor. The increase in number of thoraco-lumbar vertebræ, abbreviation of the neck region, increase in diameter and reduction in length of centra, all find a parallel in the evolution of the whales. The rib articulation (both head and tubercle articulating with the centrum) is clearly secondary, and is in correlation with the increase in diameter of the centrum, which outgrows, as it were, its rib. The absence of a latero-temporal fenestra in the Ichthyopterygia I believe to be secondary, due to the encroachment of the posterior rim of the orbit, in correlation with the enormous increase in size of the eye in adaptation to pursuit of rapidly swimming prey at great ocean depths.

#### CLASSIFICATION OF THE PHYTOSAURIA.

On account of the close affinity between the Phytosauria and Aëtosauria I have chosen to follow von Huene (1902, pp. 71-72) in his use of Huxley's term Parasuchia to include both groups, though for reasons above stated (p. 83) it seems best to rank the group as an order, instead of as a suborder as does von Huene.

#### ORDER PARASUCHIA.

Lacertiform reptiles, belonging to the diapsid division; body more or less completely encased in bony armor, the plates of which are in part metamerically arranged; dentition thecodont; external nares separate; internal nares normal (*i. e.*, no secondary palate); vertebræ amphicoelous, cervicals not exceeding 8-9, sacrals 2. Shoulder girdle complete, well-developed interclavicle; all pelvic bones participating in formation of acetabulum.

#### I.—SUBORDER AËTOSAURIA.

(= *Pseudosuchia* Zittel, 1890.)

*Aëtosaurus ferratus* O. Fraas, Middle Keuper, Württemberg.

*Dyoplax arenaceus* O. Fraas, Lower Keuper, Württemberg.

*Typothorax coccinarum* E. D. Cope, Triassic, New Mexico.

*Stegomus arcuatus* O. C. Marsh, Triassic, Connecticut.

*Ornithosuchus* E. T. Newton, Triassic, Scotland.

*Erpetosuchus* E. T. Newton, Triassic, Scotland.

## 2.—SUBORDER PHYTOSAURIA.

### Family, *Phytosauridae*.

Large diapsid reptiles, strongly resembling the Crocodilia in external form and in habit, but differing in the fact that the elongate snout is prenasal (formed almost entirely by the premaxillary bones), the nares separate, and located near the eyes, internal nares directly below external; no secondary palate. Teeth of carnivorous type, conical or with trenchant edges. Dental alveoli never become confluent to form a groove; a few anterior teeth enlarged. Post-temporal (parietosquamosal) arcade greatly depressed, reduced, and covered by muscles. Roof of skull sculptured, no pineal foramen. Large preorbital fenestra, external and internal mandibular fenestrae. Hyoid arch suspended to squamosal region of skull. Vertebrae with very slightly biconcave centra, presacrals 25–27, of which 8–9 are cervicals; sacrals 2. All presacrals bearing two-headed ribs, those of last presacral sometimes fused with vertebra.

Development of atlas intercentrum and arches excludes odontoid from participation in atlanto-occipital articulation. Odontoid and second intercentrum firmly fused with axis centrum. Capitulum of axis rib borne on intercentrum. Proximal ends of sacral ribs enlarged and attached partly to centrum of next vertebra anterior. Caudal ribs coalesced with vertebrae. Chevrons present. Shoulder girdle complete, and very primitive, with broad dagger-shaped interclavicle. Coracoids rounded, with deep coracoid notch. Pelvic bones of primitive form, all participating in formation of acetabulum; pubis rounded with pubic foramen near posterior border; pubes and ischia form an almost solid pelvic floor, with median pubo-ischiadic vacuity. Humerus with ectepicondylar (radiocondylar) groove. Femur exhibits S-flexure. Carpus and tarsus unknown (there is reason to believe that these parts are primitive, the proximal elements not elongated). Fifth digit present (at least one phalanx) in the pes. Plastron of abdominal ribs well developed, in three series, median series chevron-shaped. Dermal armature on neck, trunk, and tail, consists of sculptured bony plates, arranged metamerically on the dorsal surface, usually in four series. Ventral surface naked (?) or partly protected by a throat-shield of small scutes.

The Phytosauria were more or less aquatic, inhabiting the fresh-water lakes and rivers of the Triassic period. Their remains are known in the Trias of Germany, England, and Scotland, eastern and western North America, India, and probably South Africa. The Phytosauria of Europe and North America exhibit remarkably similar radiation, both regions yielding

species with massive body and heavy, crested snout, other species of delicate build, lighter armor, and slender gavial-like rostrum, and still other forms intermediate between the two.

*List of Genera and Species.*

1.—**Phytosaurus** (*G. F. Jaeger*) **kapffi** (*H. von Meyer*).

*Phytosaurus cylindricodon et Ph. cubicodon* G. F. JAEGER.

*Belodon kapffi* H. VON MEYER.

In this form the rostrum exhibits a heavy vertical crest (Pl. XI), the anterior teeth are cylindrical in section, the posterior flattened with serrate trenchant edges. The dorsal surface is protected by two series of transversely elongate, slightly overlapping plates, each bearing a prominent boss near its inner margin. There is also a somewhat irregular series of smaller lateral or marginal plates. Skeleton of massive construction, Skull 750 mm., in length. Stuben sandstone, Württemberg.

2.—**Phytosaurus ingens** (*E. Fraas*).

*Belodon ingens* E. FRAAS (1896).

A doubtful species, based upon a single skull which measured about 1 m. in length. Apparently very similar to *Ph. kapffi*, but of larger size. Stuben sandstone, Aixheim, Württemberg.

3.—**Phytosaurus arenaceus** (*E. Fraas*).

*Zanclodon arenaceus* E. FRAAS (1896, p. 18).

*Belodon arenaceus* FR. VON HUENE (1902, p. 62).

This species is based upon a fragment of a mandible which closely resembles *Ph. kapffi*, and may well belong to that species. The specimen is from the Feuerbacher Haide, a lower horizon than that which has yielded the other phytosaurian remains. Lower Keuper, Württemberg.

4.—**Phytosaurus pleiningeri** (*H. von Meyer*).

*Belodon pleiningeri* H. VON MEYER.

In this form the crest of the rostrum is only moderately developed. E. Fraas (1898, p. 16) regards it as a doubtful species, and suggests that it may be based upon immature specimens of *Ph. kapffi*. (See above.) Stuben sandstone, Middle Keuper, Württemberg.

5.—**Phytosaurus buceros** (*E. D. Cope*).

*Belodon buceros* E. D. COPE.

Judging from the skull (Pl. XI, Fig. 46) this species is the American counterpart of the European *Ph. kapffi*. The rostral crest appears to be somewhat less developed, near the extremity. Triassic, New Mexico.

6.—*Phytosaurus superciliosus* (E. D. Cope).*Belodon superciliosus* E. D. COPE.

Founded upon a few fragments of the skull, a few teeth, and scutes, this species must be regarded as doubtful. Triassic, Texas.

7.—*Phytosaurus scolopax* (E. D. Cope).*Belodon scolopax* E. D. COPE.

Species not very definitely established. Form of snout resembles that of *Ph. pleiningeri*. (This form may be the young of *Ph. buceros*.) Triassic, New Mexico.

8.—*Phytosaurus ganei* (F. A. Lucas).*Heterodontosuchus ganei* F. A. LUCAS (1898).

This species was based upon a fragment of the mandible, and was described as a Triassic crocodile, but a study of other parts of the skeleton, recently discovered, proves it to be a phytosaurian of enormous size. Since it is one of the more massive types I refer it to the genus *Phytosaurus*. (It would not be surprising if further study should show this to be identical with Cope's *Ph. buceros*.) Trias, Utah.

9.—*Mystriosuchus* (E. Fraas) *planirostris* (H. von Meyer).*Belodon planirostris* H. VON MEYER.

This genus differs from *Phytosaurus* in the form of the snout, which is slender, subcylindrical, with a spoonlike expansion at the extremity. The skeleton is of lighter construction throughout, and the total length was probably less than that of *Ph. kapffi*, though the skull is a trifle longer. The dorsal scutes are not elongate transversely, and those of the four series are practically similar. The throat is protected ventrally by a shield of small scutes. The teeth are more numerous than in *Phytosaurus*, are all circular in section, and exhibit delicate fluting. Stuben sandstone, Middle Keuper, Southern Württemberg.

10.—*Mystriosuchus albertii* (Th. Pleininger).*Termatosaurus albertii* TH. PLEININGER.*Termatosaurus crocodilius* F. A. QUENSTEDT.

"The isolated teeth from the Rhætic bone-bed, described as *Termatosaurus*, belong either to *Mystriosuchus planirostris* or to a very nearly related species. It is at least certain that they are belodont [phytosaurian] teeth and they may be designated as *Mystriosuchus albertii-crocodilius*." E. Fraas (1896, p. 17). An extremely doubtful species.

11.—*Rhytidodon* (*Rutiodon*) *carolinensis* (E. Emmons, 1856, pp. 307-308).

*Clepsysaurus pennsylvanicus* I. LEA (in part, 1853, pp. 185-202)

*Centemodon sulcatus* I. LEA (1856 A, p. 78).

*Omosaurus perplexus* J. LEIDY (1856 B, pp. 255-256).

*Palæosaurus sulcatus* E. EMMONS (1856, p. 318).

*Palæosaurus carolinensis* E. EMMONS (1856, p. 318).

*Compsosaurus priscus* J. LEIDY (1856 A, p. 165).

*Clepsisaurus leaii* E. EMMONS (1856, p. 299).

*Eurydorus serridens* J. LEIDY (1859, p. 110).

*Belodon carolinensis* E. D. COPE (1869, p. 59).

*Belodon priscus* E. D. COPE (1869, p. 59).

*Belodon lepturus* E. D. COPE (1869, p. 59).

*Belodon leaii* E. D. COPE (1869, p. 59).

*Rhytidodon rostratus* O. C. MARSH (1896, p. 61).

(?) *Belodon validus* O. C. MARSH (1893, p. 170).

During the last half century the phytosaurian remains in the Trias of eastern North America have served as a basis for the erection of no less than nine genera and ten species. Nearly all of this material is from the coal-fields of Chatham and Montgomery counties in North Carolina, and from the region of Phoenixville, Pennsylvania, and in most cases the species are founded upon a few teeth and scattered fragments of the skeleton.

Cope, in his 'Synopsis of the Extinct Batrachia, Reptilia, and Aves of North America' (1869), realizes the invalidity of many of these species, and unites them all in a single genus, *Belodon*, of which he recognizes four species. His inclusion of all these in a single genus was a great step in the right direction, but I am convinced, after a careful study of most of the literature and of abundant material, that the four species recognized by Cope represent in reality not more than two and probably but one species, the differentia being based upon teeth in various stages of development, and from different regions of the jaw, upon bones from mature and immature individuals, and bones which had been distorted by pressure (see pp. 32-35).

I believe, therefore, that the fifteen names given above are all synonyms, with the possible exception of *Belodon validus*, from the Trias of Connecticut, which was named, but not described, by Marsh (1893, p. 170).

For reasons above stated (p. 35) Emmons's name *Rhytidodon* (*Rutiodon*) *carolinensis* (1856) must be regarded as having priority.

The species is remarkably similar to *Mystriosuchus* of the German Trias, paralleling that form, as *Phytosaurus buceros* parallels *Ph. kapffi*; in fact the only notable points in which *Rhytidodon* differs from *Mystriosuchus* seem to be in the presence of a slight trenchant edge on some of the teeth (I suspect this will also be found in perfectly preserved teeth of *Mystriosuchus*), and in the relatively greater length of the forearm and tibia, and it is questionable whether the

differences are sufficient to warrant the recognition of two genera. Triassic North Carolina, Pennsylvania, and possibly Connecticut.

12.—**Stagonolepis robertsoni** (*T. H. Huxley*, 1859, 1875, 1877).

This form, as figured and described by Huxley, is markedly divergent in certain skeletal features from the genera above mentioned, notably in the ilium, which is much shorter, and in the pubis, which resembles that of the crocodiles. and its exact relationship to the other Phytosauria remains somewhat doubtful, Elgin Sandstone, Trias, Scotland.

13.—**Parasuchus hislopi** (*T. H. Huxley*, MS.; *Lydekker*; 1885–1888).

This species was named by Huxley on the basis of a conjoint basioccipital and basisphenoid, which resembled those of *Stagonolepis*. Maleri beds (Lower Mesozoic), India.

14.—**Episcoposaurus horridus** (*E. D. Cope*, 1887 A, p. 213).

Since nothing is known concerning the skull of this form and very little of the skeleton, its position among the Phytosauria must be regarded as tentative. It is a large species, with dermal plates resembling those of Phytosauria, but armed with spines, some of which are 85 mm. in height. Trias, New Mexico.

15.—**Episcoposaurus haplocerus** (*E. D. Cope*, 1892 A, p. 257).

Cope bases this species on fragmentary remains found associated with *Phytosaurus superciliosus*. Trias, Texas.

16.—**Rileya bristolensis** (*Fr. von Huene*, 1902, p. 62).

This species is based by von Huene on a humerus and two vertebræ from the dolomitic conglomerate of Bristol, England. The two vertebræ closely resemble those of *Stagonolepis*. Middle Keuper, Bristol, England.

17.—**Palæorhinus bransoni** (*S. W. Williston*, 1904, p. 696).

Williston founds this genus and species upon a well-preserved skull from the Popo Agie beds of the Upper Trias, of Wyoming. From the fact that the external nares are considerably more anterior than in other known phytosaurians, Professor Williston regards it as somewhat more primitive.<sup>2</sup>

<sup>1</sup> See Huxley, Quar. Journ. Geol. Soc., XXVI, p. 49 (1870).

<sup>2</sup> "Another form, represented by a complete skull of larger size, in the collection [from the Upper Trias of Wyoming] has the anterior nares apparently placed much further forward than in the present genus, or at least the beginning of the slender beak is much further forward. Yet another skull, of large size and nearly complete, has been nearly freed from its matrix. It measures 960 mm. in length; the nares are not as far forward as is the front end of the antorbital opening, though more anteriorly placed than in *B. scolopax* Cope, and the strongly deflected anterior end of the beak has three large teeth on each side. The hind teeth are flattened and serrate. Still another skull seems different from any of the foregoing."—S. W. Williston, 1904.



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## ABBREVIATIONS USED IN PLATES VI-XI.

<i>acr. r.</i> , acromial ridge.	<i>p.</i> , parapophysis.
<i>act.</i> , acetabulum.	<i>Pa.</i> , parietal.
<i>An.</i> , angular = 'splenial,' Baur.	<i>Pas.</i> , parasphenoid = 'vomer,' Broom.
<i>Art.</i> , articular.	<i>Pb.</i> , pubis.
<i>Bo.</i> , basioccipital.	<i>pb. f.</i> , pubic foramen.
<i>Bs.</i> , basisphenoid.	<i>p.c. 2.</i> , second pleurocentrum.
<i>c.</i> , capitulum.	<i>p. f.</i> , posterior palatine foramen.
<i>Ch.</i> , chevron.	<i>Pl.</i> , palatine.
<i>Cl.</i> , clavicle.	<i>Pmx.</i> , premaxillary.
<i>co. n.</i> , coracoid notch.	<i>Po. f.</i> , postfrontal.
<i>Cor.</i> , coracoid.	<i>p. o. f.</i> , preorbital fenestra.
<i>D.</i> , dentary.	<i>Po. o.</i> , postorbital.
<i>d.</i> , diapophysis.	<i>Pr. f.</i> , prefrontal.
<i>d. r.</i> , deltoid ridge.	<i>Pt.</i> , pterygoid.
<i>D. S.</i> , dorsal scutes.	<i>p. t. f.</i> , post-temporal fenestra.
<i>Ec.pt.</i> , ectopterygoid.	<i>q. f.</i> , quadrate foramen.
<i>e. m. f.</i> , external maxillary fenestra.	<i>Q. J.</i> , quadratojugal.
<i>Ex.o.</i> , exoccipital.	<i>Qu.</i> , quadrate.
<i>Fm.</i> , femur.	<i>R.</i> , radius.
<i>f. m.</i> , foramen magnum.	<i>r.</i> , rib.
<i>Fr.</i> , frontal.	<i>r. c.</i> , radial condyle.
<i>gl. f.</i> , glenoid fossa.	<i>r. g.</i> , radiocondylar groove.
<i>H.</i> , humerus.	<i>S. an.</i> , supra-angular.
<i>hy.</i> , hyoid arch, attachment to cranium.	<i>s. art.</i> , sacral articulation.
<i>i.c. 2.</i> , second intercentrum.	<i>Sc.</i> , scapula.
<i>i.cl.</i> , interclavicle.	<i>sc. art.</i> , scapular articulation.
<i>i.cl. art.</i> , interclavicular articulation.	<i>So.</i> , supraoccipital.
<i>Il.</i> , ilium.	<i>Sp.</i> , splenial = 'presplenial,' Baur.
<i>Is.</i> , ischium.	<i>Sq.</i> , squamosal.
<i>J.</i> , jugal.	<i>s. t. f.</i> , supratemporal fenestra.
<i>L.</i> , lachrymal.	<i>t.</i> , tuberculum.
<i>L. Ab. R.</i> , left abdominal ribs.	<i>Ti.</i> , tibia.
<i>l. t. f.</i> , latero-temporal fenestra.	<i>tr.</i> , trochanter.
<i>M. Ab. R.</i> , median abdominal ribs.	<i>T. S.</i> , throat shield.
<i>Mx.</i> , maxillary.	<i>U.</i> , ulna.
<i>Na.</i> , nasal.	<i>Vo.</i> , vomer = 'prevomer,' Broom.
<i>od.</i> , odontoid.	<i>X.</i> , see description of figures 5, 16, 40a, and 40b.
<i>Op.o.</i> , opisthotic (= paroccipital).	





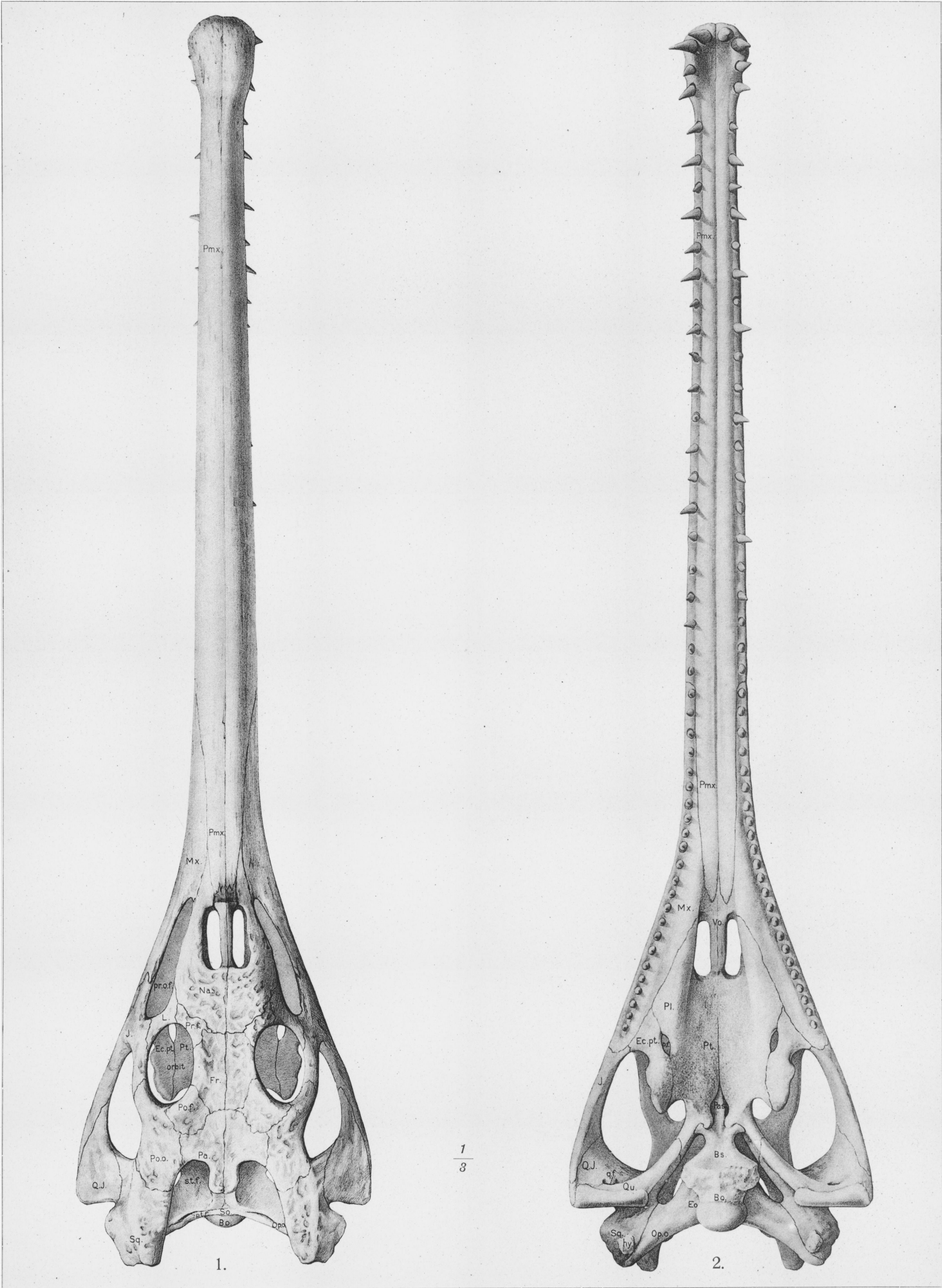
PLATE VI.

EXPLANATION OF PLATE VI.

Figures one-third natural size.

FIG. 1.—*Mystriosuchus planirostris*, skull, dorsal view.

FIG. 2.— “ “ “ palatal “



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*Mystriosuchus planirostris.*



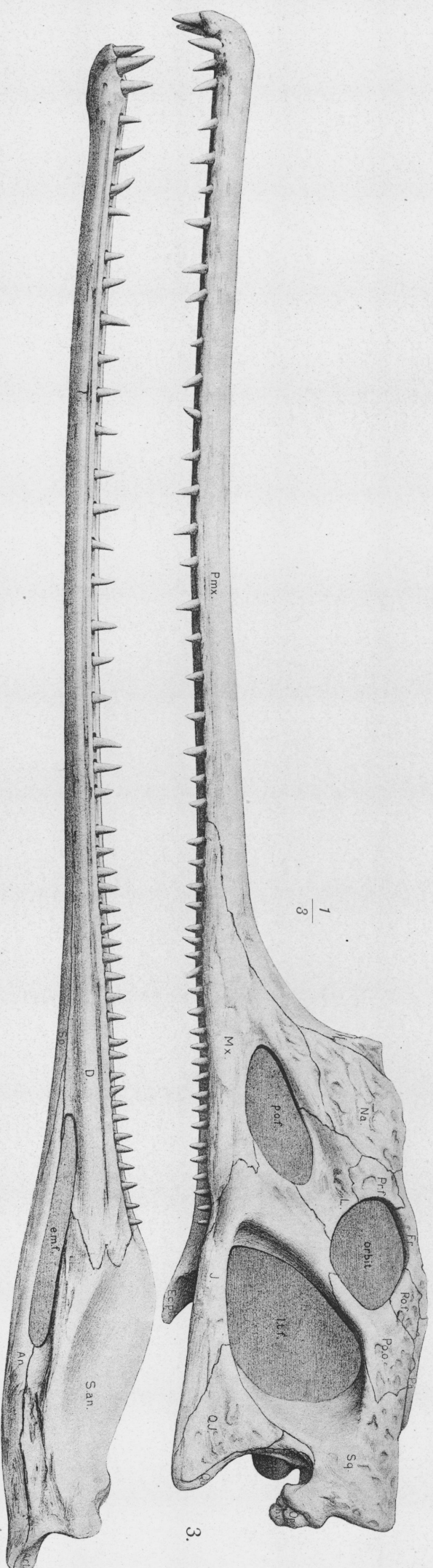
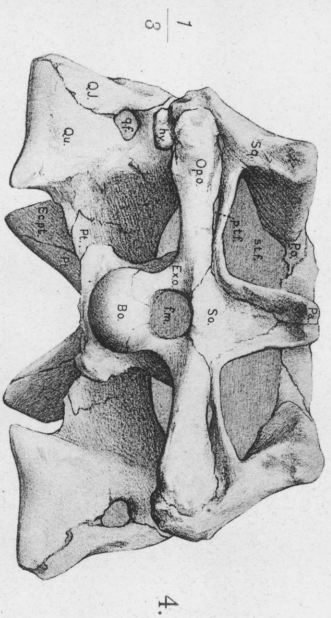
PLATE VII.

EXPLANATION OF PLATE VII.

Figures one-third natural size.

FIG. 3.—*Mystriosuchus planirostris*, skull, left side.

FIG. 4.—“ “ “ occipital view.



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*Mystriosuchus planirostris*.





PLATE VIII.

# EXPLANATION OF PLATE VIII.

Figures one-half natural size. All except 8, 8a, and 8b of *Rhytidodon carolinensis*.

FIG. 5.—*Rhytidodon carolinensis*, atlas, left side, showing at *x* and *p* the facets for articulation of tubercle and head, respectively, of the atlantal rib.

FIG. 5a.—The same, anterior view, showing socket for occipital condyle.

FIG. 6.—Left arch of same atlas, inner surface.

FIG. 7.—Intercentrum of same atlas, dorsal surface.

FIGS. 8, 8a, and 8b.—*Heterodontosuchus ganei*. (From a specimen loaned by the U. S. National Museum.) Anterior, left, and ventral views of axis. (The posterior part of the centrum and the greater part of the neural arches are broken away.) The parapophysis (*p.*) is borne on the second intercentrum, the diapophysis on the base of the neural arch. The odontoid (first pleurocentrum), the second intercentrum, second pleurocentrum, and neural arches are all firmly coössified, but the lines of union are discernible.

FIG. 9.—*Rhytidodon carolinensis*. A cervical vertebra, left side.

FIGS. 10 and 10a.—Anterior and posterior views of an anterior thoracic vertebra. The parapophysial facet, which is placed low down on the anterior rim of the centrum is not well shown. (Cf. text-figure 15.)

FIG. 11.—Mid-thoracic vertebra, left side, showing elevation of the parapophysis, which is partly above and partly below the neurocentral suture.

FIG. 12.—Posterior thoracic vertebra, left anterior view. The parapophysis is now borne entirely on the base of the neural arch, and the transverse process is smaller than in the more anterior thoracic vertebræ.

FIG. 13.—A well-posterior thoraco-lumbar vertebra, posterior view. Transverse process—greatly reduced, diapophysis and parapophysis still discrete.

FIG. 14.—Probably the third or fourth vertebra counting anteriorly from the sacrum. The parapophysis is borne partly on the base of the neural arch and partly on the centrum.

FIG. 15.—Penultimate thoraco-lumbar vertebra, anterior view. The transverse process is here greatly reduced and depressed, the parapophysis largely borne on the centrum. Parapophysial and diapophysial facets are somewhat confluent, but the double rib articulation is still apparent.

FIG. 16.—The last presacral vertebra, posterior view. In this specimen the rib (*r.*) is ankylosed on the left side, but not on the right. The bevelled surface, *x*, articulates with an anteriorly projecting flange of the first sacral rib.

FIG. 17.—An anterior caudal vertebra, anterior view.

FIG. 18.—A chevron, posterior view.

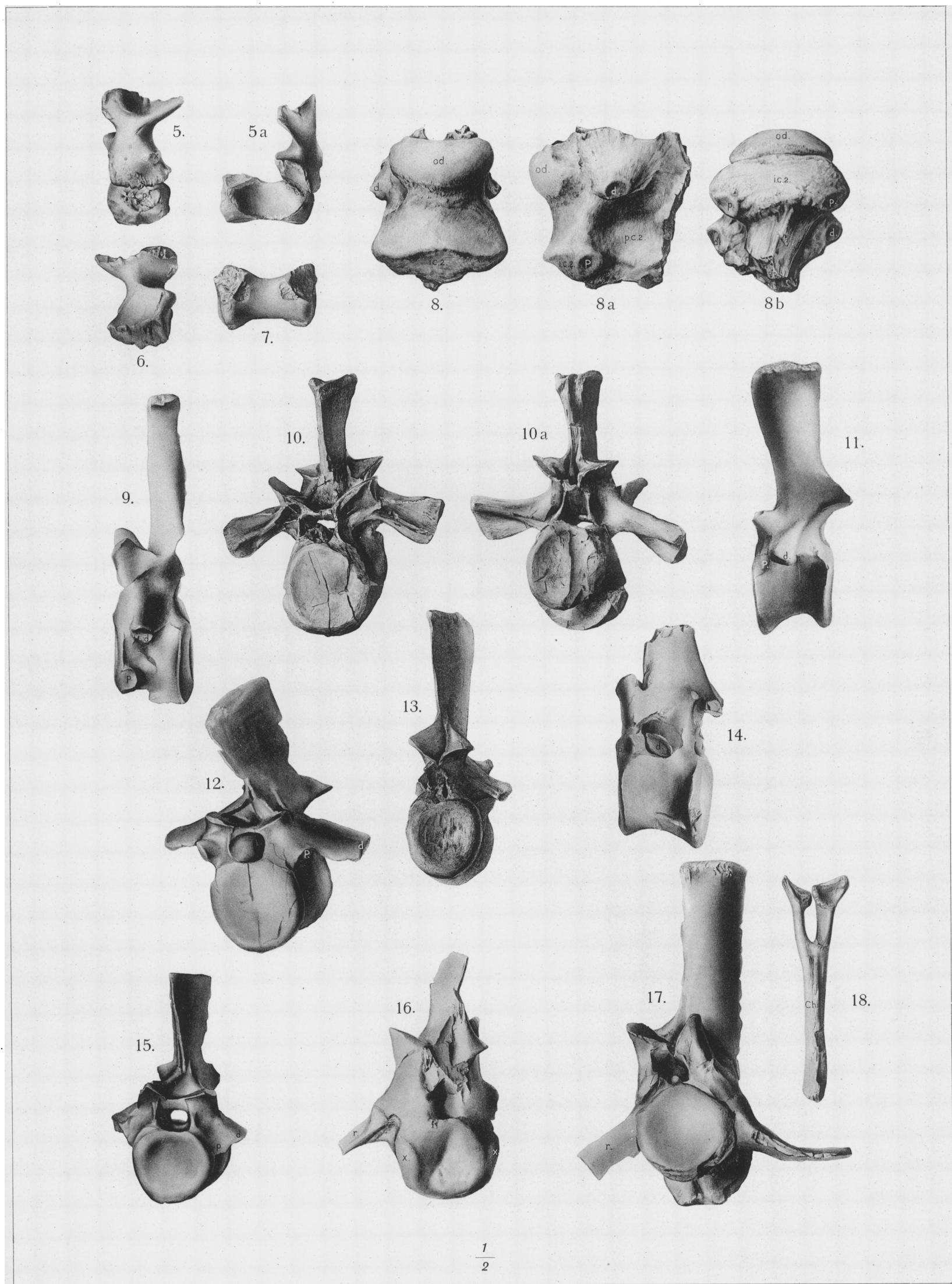




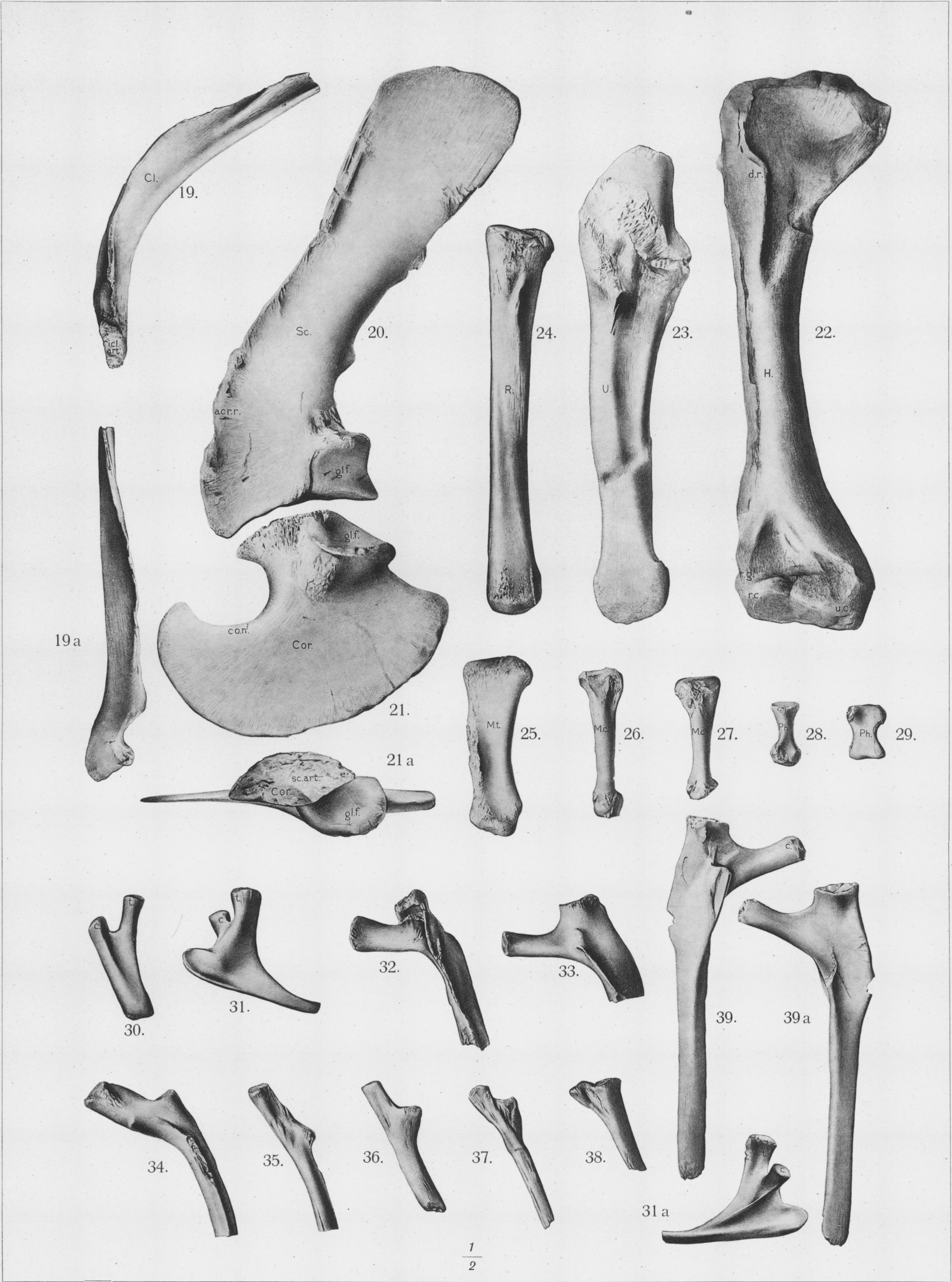
PLATE IX.

## EXPLANATION OF PLATE IX.

All figures of *Rhytidodon carolinensis*, one-half natural size.

- FIG. 19.—Left clavicle, posterior view. The lateral extremity is broken off. The surface for articulation with the interclavicle is shown (*icl. art.*) and the groove for articulation with the acromial ridge of the scapula.
- FIG. 19*a*.—The same, ventral view.
- FIG. 20.—Left scapula, outer surface.
- FIG. 21.—Left coracoid (shown in nearly natural relation to the scapula and clavicle).
- FIG. 21*a*.—The same, outer border showing scapular articulation and glenoid fossa.
- FIG. 22.—Right humerus, ventral view.
- FIG. 23.—Right ulna.
- FIG. 24.—Radius.
- FIG. 25.—A metatarsal.
- FIGS. 26 and 27.—Metacarpals.
- FIGS. 28 and 29.—Phalanges.
- FIGS. 30–38.—A series of left presacral ribs showing transition in form of proximal end.
- FIG. 30.—An atlantal (or possibly axis) rib.
- FIG. 31.—A typical cervical rib, outer surface.
- FIG 31*a*.—The same, under surface.
- FIGS. 32 and 33.—Anterior thoracic ribs, anterior view.
- FIG. 34.—A mid-thoracic rib, anterior view.
- FIGS. 35–38.—Showing progressive approximation of head and tubercle, as we pass from posterior thoracic region toward the sacrum. Fig. 38 represents one of the last presacral ribs.
- FIGS. 39 and 39*a*.—Anterior and posterior views of a right anterior thoracic rib.





Helio Alfred Dittsheim, Basle.

E. Christman, del.

*Rhytidodon carolinensis*.



PLATE X.

#### EXPLANATION OF PLATE X.

All figures of *Rhytidodon carolinensis*, one-half natural size.

FIGS. 40, 40a, and 40b.—Posterior, anterior, and ventral views, respectively, of the second sacral vertebra. In figures 40a and 40b the anteriorly protecting flange at the base of the rib is designated by *x*. (The transverse groove on the centrum in figure 40a is an artefact.)

FIGS. 41, 42, and 43 represent the pelvic bones of the left side in approximately natural relations.

FIG. 41.—Left ilium, outer view. (Drawn reversed from a right ilium.)

FIG. 41a.—Right ilium, inner view.

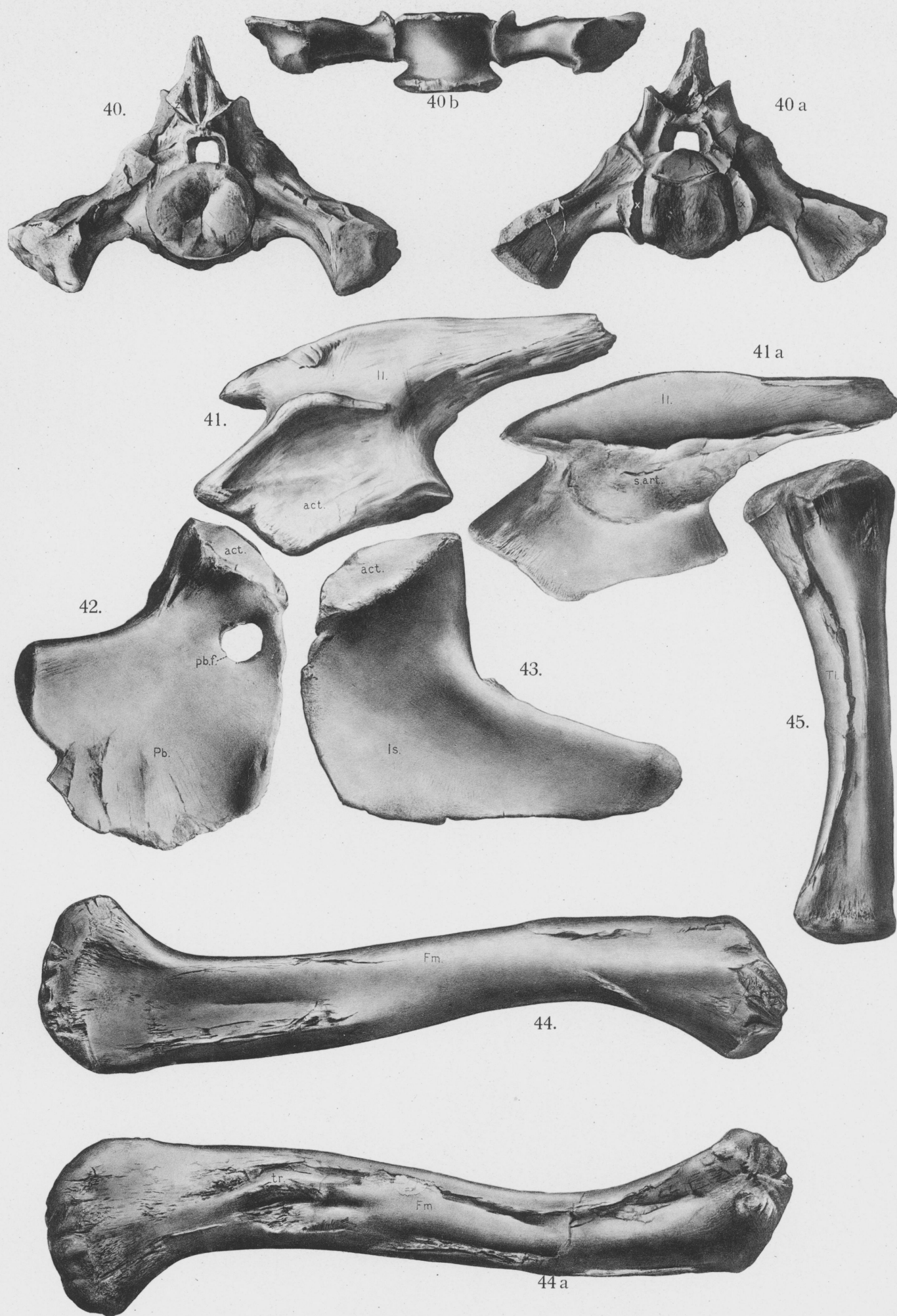
FIG. 42.—Left pubis, outer view.

FIG. 43.—Left ischium, outer view.

FIG. 44.—Right femur, antero-dorsal view.

FIG. 44a.—The same, postero-ventral view.

FIG. 45.—Right tibia.



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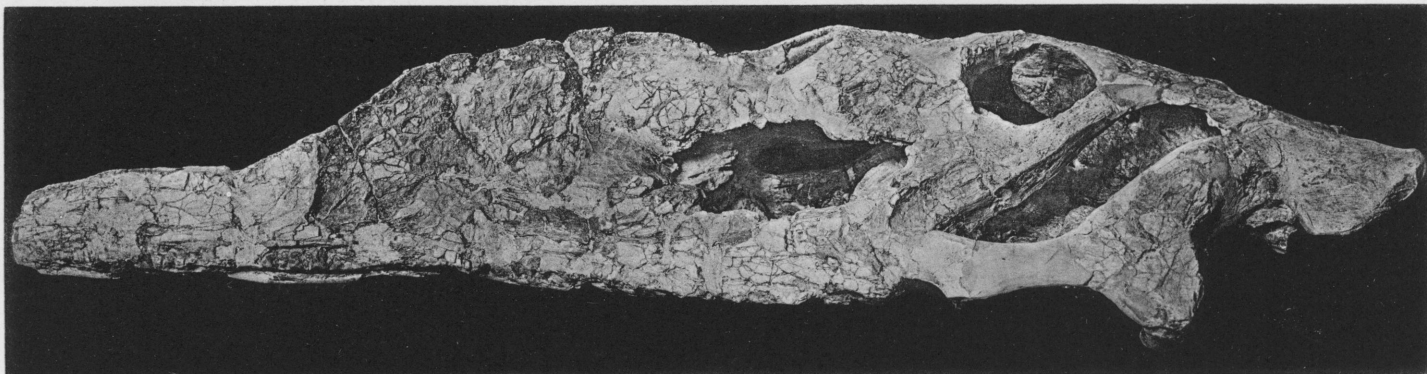


PLATE XI.

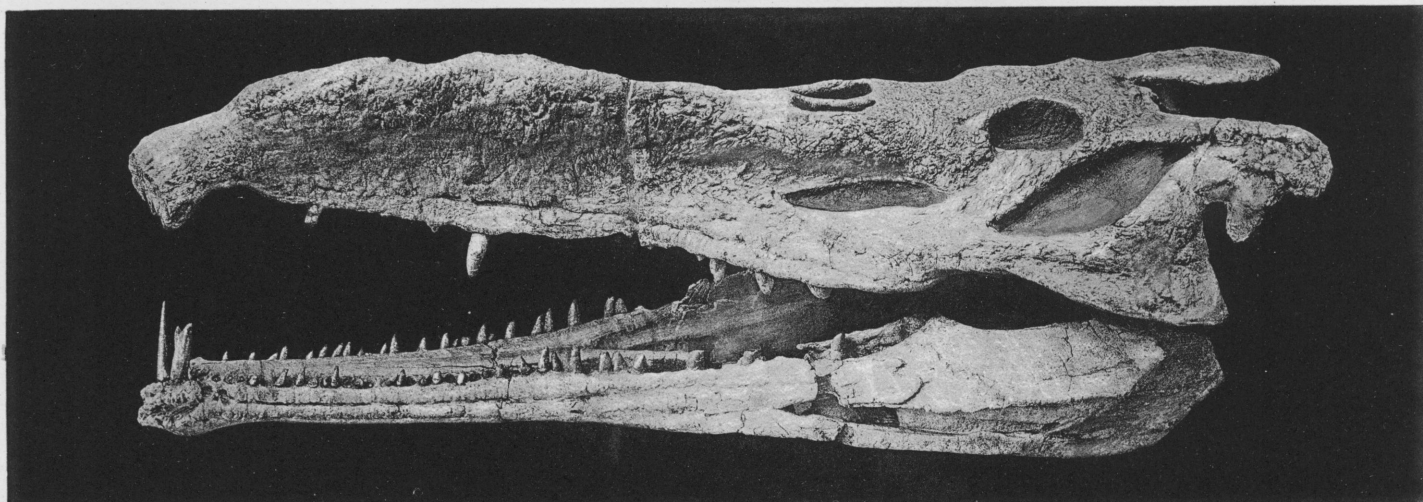


EXPLANATION OF PLATE XI.

- FIG. 46.—Skull of *Phytosaurus buceros* Cope. About one-fourth natural size.  
Photo by Mr. A. E. Anderson.
- FIG. 47.—Skull of *Phytosaurus kapffi* von Meyer. About one-fifth natural size.  
After E. Fraas.
- FIG. 48.—Skull of *Mystriosuchus planirostris* von Meyer. Over one-fifth natural size.  
After E. Fraas.
- FIG. 49.—Partial skeleton *Mystriosuchus planirostris* von Meyer. About one-eighth natural size.  
Photo by Dr. J. Vosseler.  
This specimen is of interest as showing a portion of the ventral throat shield, *T. S.*, the elements of the shoulder girdle in natural position, and twenty of the lateral abdominal ribs of the left side with their relations practically undisturbed. Eleven of the dorsal scutes, *D. S.*, are also shown.

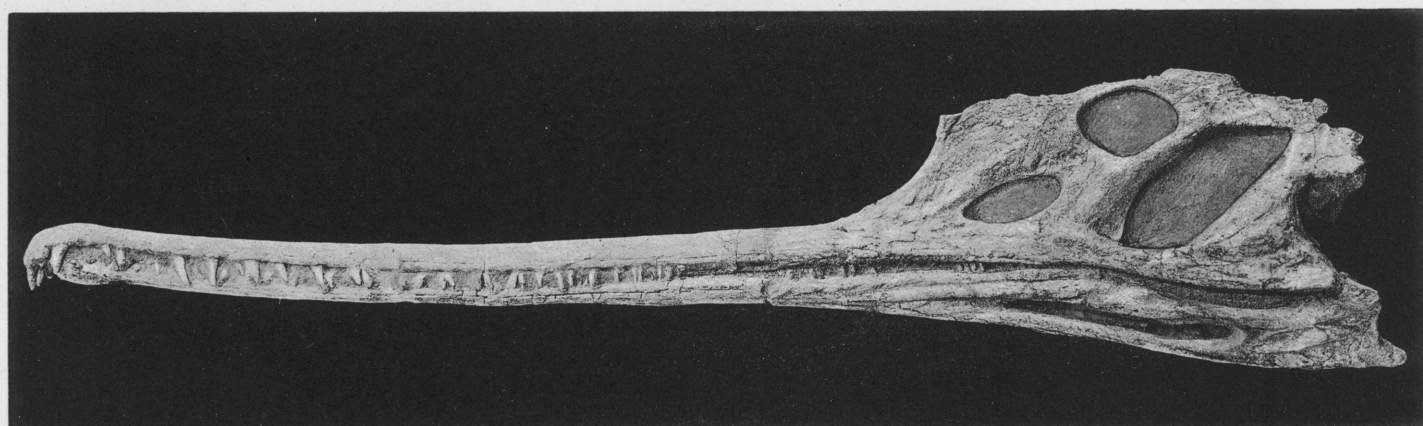


*Phytosaurus buceros.*



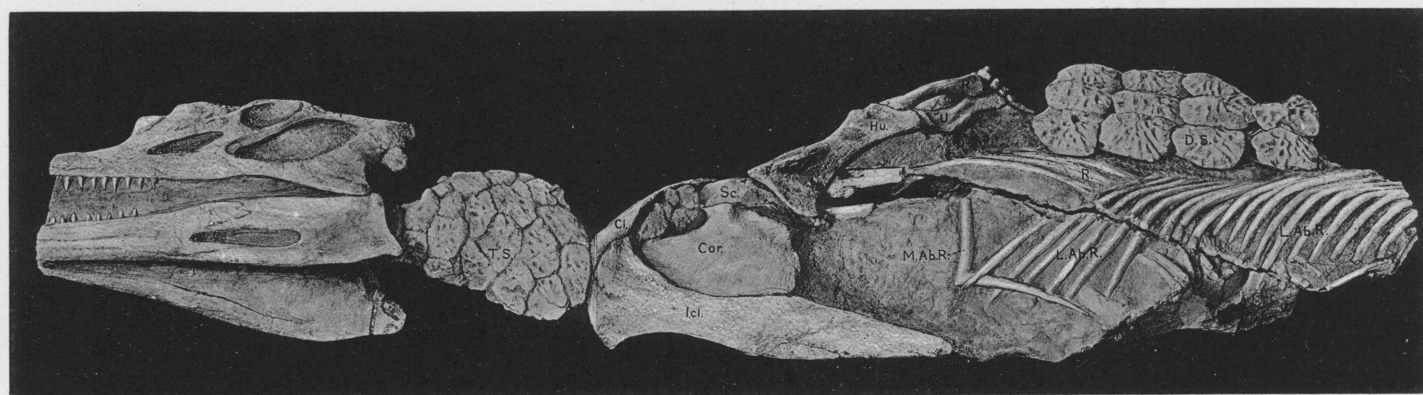
*Phytosaurus kapffi,*

after E. Fraas.



*Mystriosuchus planirostris,* von Meyer,

after E. Fraas.



*Mystriosuchus planirostris,* von Meyer.





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