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THE GENERA OF PHYTOSAURS

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ABSTRACT. The long-snouted, crocodile-like, amphibious reptiles of the late Triassic known as phytosaurs are assigned to five genera on the basis of cranial characters. The most primitive genus, *Paleorhinus*, has external nares well forward of the antorbital fenestrae, the posttemporal arch at level of the skull roof, a slender rostrum without crests, homodont dentition, a low quadrate, and no trace of a posterior squamosal process. *Mystriosuchus*, which has highly specialized posterior nares, tall quadrate, and depressed posttemporal bar, retains the primitive form of the squamosal, homodont dentition, and slender (much longer) rostrum of *Paleorhinus* from which it may be derived through *Francosuchus* (the European subgenus of *Paleorhinus*). The remaining phytosaur genera are characterized by rounded processes of the squamosal bone projecting well behind the occipital surface of the skull, and by the development of heterodont dentition and generally more robust skulls. *Angistorhinus*, the most primitive member of this lineage, retains a primitive posttemporal arch at the level of the skull deck, but is advanced over *Paleorhinus* in its posteriorly placed external nares. Its rostrum is slender and lacks crests; the dentition is only slightly differentiated. *Phytosaurus* and *Rutiodon*, the more specialized members of this group, have depressed posttemporal arches and tall quadrates. Rostra of *Rutiodon* vary from slender and uncrested in small skulls to moderately robust with high dorsal crests in the posterior half in the largest individuals; teeth vary from moderately to strongly heterodont. The squamosal processes are slender and show progressive phyletic elongation. The ratio of rostral to postrostral length varies inversely with size. *Phytosaurus* skulls are characterized by massive rostra with continuous dorsal crests and have a relatively constant rostral ratio independent of size; the squamosal processes are short and deep; dentition is strongly heterodont; considerable evidence suggests that the dorsal armor plates differed from other phytosaurs.

Among the best known and most thoroughly studied Triassic reptiles are the phytosaurs, long-snouted amphibious creatures closely comparable to modern crocodiles in size, proportions, and inferred habits. No less than 36 generic names have been proposed for fossil remains of these animals, in spite of the fact that they are a homogeneous group of limited stratigraphic range, and are known from only a few localities, all but one in the northern hemisphere.[1] A re-examination of the supposed distinctions among the 16 currently accepted genera shows that many of these differences are features reasonably attributed to changes with growth and age, or to sex. Others are artifacts of preservation or preparation of the fossils, such as curvature of the rostrum due to crushing.

When the cranial anatomy of various "genera" is critically compared in the light of the variability shown by a few samples of several individuals from contemporaneous local populations, many of the supposed taxonomic differences disappear, and a simpler and more meaningful classification emerges.

During the twenty years since my earliest attempts to identify phytosaur bones I have profited from discussions of these reptiles with the late Professor E. C. Case, with Professor Charles L. Camp, and particularly with Dr. Edwin H. Colbert, who has contributed many ideas presented here, and who most kindly read a preliminary draft of this article. Many concepts in this paper crystallized during a study of the primitive phytosaurs from Otis Chalk, Texas, in the collections of the University of Texas, Bureau of Economic Geology, for access to which I am indebted to Dr. E. H. Sellards, Dr. John T. Lonsdale, and

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[1] The Paleontologisches Institut of the University of Tübingen has a few scutes and teeth of phytosaurs collected from the Triassic of Madagascar by Prof. J. Piveteau.

especially Dr. John A. Wilson who aided in countless ways. Field work and museum study have been possible through grants from the John T. Doneghy, Jr. Research Fund of Yale University and from the Marsh Fund of the National Academy of Sciences.

I am particularly indebted to Professor Dr. Friedrich von Huene for the opportunity to study specimens at the Palaeontologisches Institut of the University in Tübingen; to Dr. Karl D. Adam for unpacking Hermann von Meyer's original specimens and other phytosaurs belonging to the Naturalien Cabinet at Stuttgart for my examination; and to Prof. Dr. R. Dehm and Dr. T. Oettingen of the Institut für Paläontologie und historisches Geologie in Munich for showing me the phytosaurs from Franconia. Drs. C. L. Gazin and Kenneth Kermack also gave valued assistance in the course of these studies. Critical comments by Professor George G. Simpson helped me clarify a number of points.

Illustrations were prepared by Miss Shirley P. Glaser and Owen Poe.

RESUME OF CURRENTLY USED CLASSIFICATIONS OF PHYTOSAURS

Huene (1922, p. 158) offered the following classification of the Parasuchia:

Fam. Desmatosuchidae Case 1920—*Desmatosuchus.*
Fam. Stagonolepidae Huene 1912—*Mesorhinus, Stagonolepis, ? Stegomus (arcuatus).*
Fam. Phytosauridae McGregor 1906—*Phytosaurus.*
Fam. Mystriosuchidae Huene 1916—*Angistorhinus, Paleorhinus, Machaeroprosopus, Rutiodon, ? Episcoposaurus, ? Parasuchus, ? Rileya, Angistorhinopsis, Mystriosuchus.*

In the same year Case gave comparative lists of the cranial characters of 6 genera of phytosaurs (1922, p. 68): *Paleorhinus, Angistorhinus, Phytosaurus* [*Machaeroprosopus*], *Mystriosuchus, Promystriosuchus,* and *Leptosuchus.* He also recognized *Rutiodon* ("*Rhytidiodon*" p. 59) and later (1929) added *Brachysuchus.*

Camp (1930, p. 147) thoroughly reviewed all phytosaurs and accepted the following forms in the suborder:

Fam. Desmatosuchidae—*Desmatosuchus, ? Episcoposaurus, Stagonolepis, ?Mesorhinus.*
Fam. Phytosauridae—*Phytosaurus, Mystriosuchus, Parasuchus, Clepsysaurus, Rutiodon, Typothorax, Heterodontosuchus, Paleorhinus, Angistorhinus, Machaeroprosopus, Promystriosuchus, Leptosuchus, Angistorhinopsis, Rileya,* and *Brachysuchus.*

Kuhn (1933, p. 16-29) substantially followed Camp's classification but included *Stegomus* among the phytosaurs and added two new European genera, *Francosuchus* (1933a) and *Ebrachosuchus* (1936).

Recognition that *Typothorax, Desmatosuchus,* and *Stagonolepis* are short-headed pseudosuchians distinct from the long-snouted phytosaurs is first clearly indicated in the classification of Romer (1945, p. 571).

Hoffstetter (1955) proposed the following grouping of genera within a single family Phytosauridae:

A. *Mesorhinus*, B. 1. *Paleorhinus*, *Francosuchus*, *Ebrachosuchus*, 2. *Angistorhinus*, *Promystriosuchus*, *Angistorhinopsis*, 3. *Brachysuchus*, 4. *Leptosuchus*, *Clepsysaurus*, *Machaeroprosopus*, *Phytosaurus*, 5. *Rutiodon*, *Mystriosuchus*.

Huene (1956, p. 456-464) accepted the restriction of the Parasuchia to the long-snouted phytosaurs and recognized the following genera:

Mesorhinus, *Promystriosuchus*, *Francosuchus*, *Ebrachosuchus*, *Angistorhinus*, *Paleorhinus*, *Leptosuchus*, *Pseudopalatus*, *Brachysuchus*, *Angistorhinopsis*, *Machaeroprosopus*, *Phytosaurus*, *Clepsysaurus*.

A slightly different assemblage is considered valid by Romer (1956, p. 597-598):

Angistorhinopsis, *Angistorhinus*, *Brachysuchus*, *Clepsysaurus*, *Ebrachosaurus*, *Francosuchus*, *Leptosuchus*, *Lophoprosopus*, *Machaeroprosopus*, *Mesorhinus*, *Mystriosuchus*, *Paleorhinus*, *Phytosaurus*, *Promystriosuchus*, *Rileya*, *Rutiodon*.

SYSTEMATIC CHARACTERS IN PHYTOSAURS

Most genera of phytosaurs have been distinguished from one another by variations in the structure of the skull. Huene, Case, and Camp have attempted to find systematic distinctions in the form of the pectoral and pelvic girdles, type of dermal armor plates, proportions of the limb bones, and form of the vertebrae. Differences certainly exist in these structures, but their use in classification is severely hampered by lack of association of parts in most species. The classification proposed here is based entirely upon cranial characters. Significant variations in other parts of the skeleton, where known, are mentioned under individual genera.

ANALYSIS OF CHARACTERS

In the following discussion various phytosaurs are referred to by the names under which they were originally described, or are commonly referred to in the literature of this family. Reference to the characters of various "genera" does not imply acceptance of these taxonomic groupings. The proposed classification is set forth later.

Case (1922, p. 68-69) tabulated contrasting characters in the skulls of phytosaurs. He did not include *Rutiodon*, perhaps considering it similar to *Mystriosuchus*, or distinguish between *Phytosaurus* of Europe and *Machaeroprosopus* of North America. In 1929 he summarized characters of *Brachysuchus* in similar form. These characters may be reviewed in the order used by Case.

1. Posttemporal arcade at the level of the top of the skull in *Angistorhinus* and *Promystriosuchus*, depressed in other genera. Case states that this arch is depressed in *Paleorhinus*; Mehl (1915, p. 159) points out that the skull is crushed in this area; in 1928 (p. 158) Mehl expressed belief that the arcade was developed to the deck level as in *Angistorhinus* and *Promystriosuchus*. Langston's (1949) figure of the type of *P. scurriensis* shows the arcade extremely thin and perhaps descending a trifle below the level of the skull roof. In *Promystriosuchus*, likewise, the posterior border is thin. It is evident that these three genera are similar in this character and more primitive than

others. *Francosuchus* is like *Promystriosuchus*; *Ebrachosuchus* like *Angistorhinus*; both have the arch essentially at skull deck level.

All other phytosaurs have the arch depressed below the level of the skull roof. commonly as a slender bar lying just above and essentially parallel to

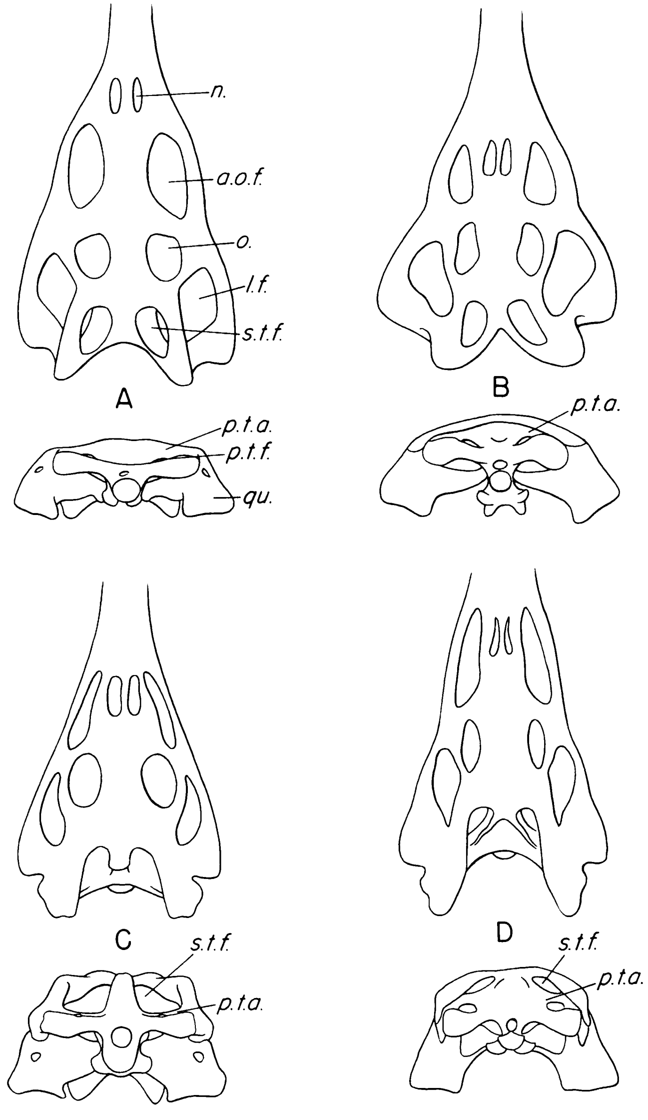

Fig. 1. Dorsal and occipital views of the posterior portion of phytosaur skulls to show variations in the posttemporal arch and superior temporal fenestra.

A. *Paleorhinus ehlersi* (Case) × 2/15.
B. *Angistorhinus alticephalus* Stovall and Wharton × 2/25 (approx.).
C. *Mystriosuchus planirostris* (Meyer) × 2/15 (after McGregor).
D. *Rutiodon lithodendrorum* (Camp) × 1/10 (after Camp).

the paroccipital process. *Mystriosuchus* shows the most extreme specialization of this arch; specimens of *Phytosaurus, Leptosuchus*, and *Machaeroprosopus* all show some variability. *Rutiodon* appears to have the arch less depressed than most others.

This feature is of equal importance to the position of the external nares in determining the relative degree of specialization of various phytosaurs. It will be noted that *Angistorhinus*, which has an advanced narial position, is most primitive in its posttemporal arch. *Paleorhinus* is primitive in both features, *Phytosaurus* and others are advanced in both.

Further diagnostic features of this area include the width of the superior fenestra, as seen from above, and the degree to which it emarginates the deck of the skull. In primitive genera such as *Paleorhinus, Promystriosuchus, Angistorhinus*, and also in *Rutiodon* and *Mystriosuchus* the superior fenestrae are broad and extend forward into the dorsal portion of the parietals. *Phytosaurus kapffi* likewise has fairly broad dorsal exposure of the fenestrae. Camp (1930, p. 20) has shown that the fenestrae become progressively narrower, and that they also indent the roof deck less in stratigraphically higher species of *Machaeroprosopus*. The extreme is reached in an undescribed skull from the Redonda formation, in which the fenestrae are confined to the occipital surface and concealed dorsally by overhanging postorbital bars.

2. Relative position of antorbital opening and external nares, which varies continuously from a primitive position of the nares well in front of the antorbital fenestra in *Paleorhinus* and *Francosuchus* to an advanced condition relatively close to the orbits, over the middle of the antorbital openings in *Phytosaurus* and *Mystriosuchus*. It can be expressed quantitatively by the orbitonasal length. Small variations, such as between specimens with the anterior border of the nares directly over the front of the antorbital fenestra and those in which the nares are slightly farther back (or the fenestra slightly forward), do not alone seem worthy of generic recognition. However, the correlation between the forward position of the nares and various features of the temporal region in *Paleorhinus, Promystriosuchus, Francosuchus*, and *Ebrachosuchus* suggests a useful qualitative separation between those phytosaurs in which the nares reach forward of the antorbital fenestra and those which do not. It may be noted that the Wyoming *Paleorhinus* and German *Francosuchus* are more extreme than *Promystriosuchus* from Texas in this respect. On the other hand, *Angistorhinus*, which retains a primitive temporal structure, is essentially as advanced as *Phytosaurus* in this feature. Unequal rates of evolution of various organs is a well recognized phenomenon, of which this is merely a further example.

3. Ratio of the prenarial length to postnarial length of skull. Case and others have specified values for various genera. Camp and, especially, Colbert (1947) discussed the variation of prenarial length with size, and showed that larger skulls of *Machaeroprosopus* have relatively shorter snouts. Figure 4 shows the variation of the ratio prenarial length:postnarial length with absolute size. Use of this ratio removes the large autocorrelation involved in the comparison of snout length to total skull length (as the rostrum makes up half or more of the

entire skull) and more clearly displays this trend. In *Leptosuchus* and the less massive species from Arizona referred to *Machaeroprosopus* (included in *Rutiodon* on the chart for reasons to be explained later) this ratio has a cor-

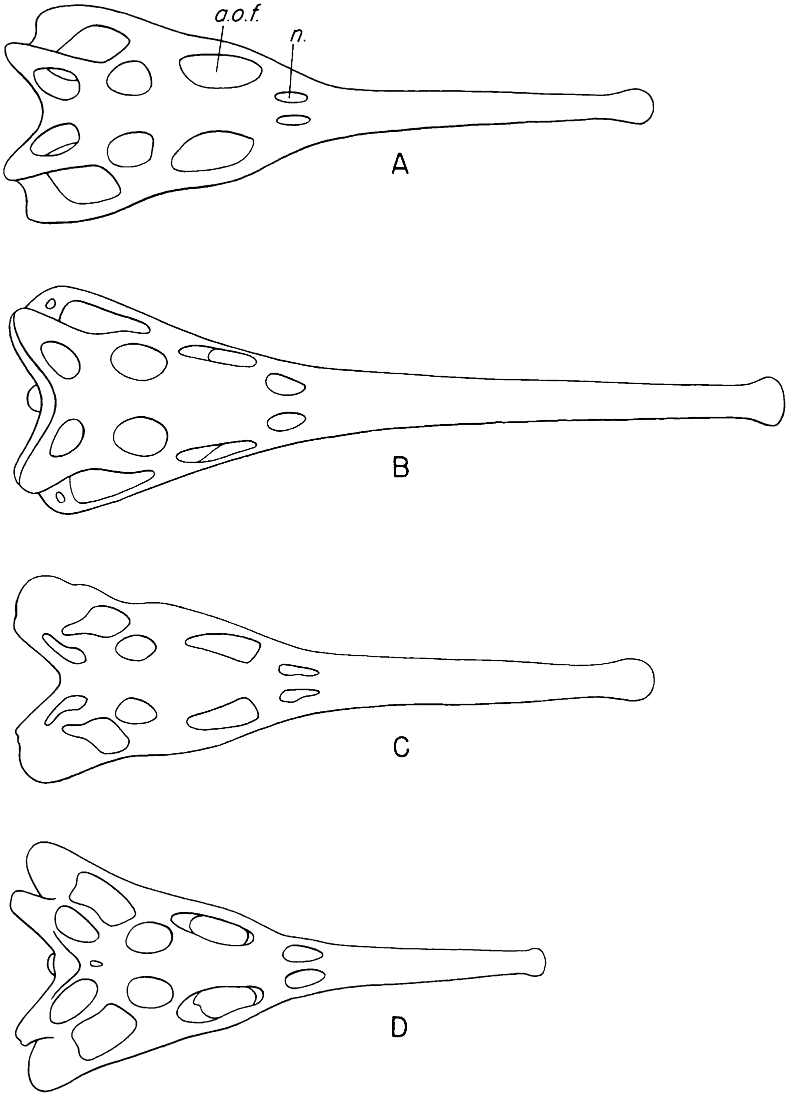

Fig. 2. Dorsal views of *Paleorhinus* skulls to show variation in position of the external nares with respect to antorbital fenestra in primitive phytosaurs.

A. *Paleorhinus ehlersi* (Case) × 2/15.
B. *Paleorhinus broilii* (Kuhn) [*Ebrachosuchus neukami* Kuhn] (after O. Kuhn) × 1/5.
C. *Paleorhinus bransoni* Mehl (after Case) × 2/35.
D. *Paleorhinus scurriensis* Langston (after Langston) × 2/15.

relation with total skull length of $r = -0.621$. In North American species of *Paleorhinus* the correlation is $r = -0.805$. This confirms Colbert's observation that the snout is relatively longer in smaller skulls. The similar slopes of trend lines for *Paleorhinus* and *Mystriosuchus* to that of *Rutiodon* show that the differential growth of snout and the remainder of the skull followed the same pattern in these genera.

The extremely large skulls of *Machaeroprosopus gregorii* Camp and *Brachysuchus megalodon* Case have rostral-cranial proportions that lie close to the projection of the trend established by the smaller *Leptosuchus* and *Machaeroprosopus* skulls. But the relatively small *Phytosaurus kapffi* (Meyer), which resembles these large species closely in many morphological details, has the same relative proportions of rostrum to the remainder of the skull as the largest American specimens. Thus four specimens of *P. kapffi* with an average total length of 757 mm have an average prenarial:postnarial ratio of 1.237; four skulls of *M. gregorii* and *B. megalodon* with lengths from 1230 to 1420 mm average 1.222 in rostral ratio. By contrast, skulls of *Leptosuchus* and *Machaeroprosopus* approaching *P. kapffi* in length have rostral ratios around 1.70. *P. kapffi* diverges markedly from the growth curve established by the smaller American species, as shown in figure 4. Such divergence might result from isolation of the American phytosaur population from that of Europe. This hypothesis fails to account for the similarity between *P. kapffi* and the large *M. gregorii* and *B. megalodon* in development of rostral crests and type of dermal armor (discussed in later paragraphs). The alternative that the *M. gregorii* group is closely related to *P. kapffi* and that this genus differs from other phytosaurs in the growth pattern of its rostrum provides a possible explanation for these features. Similar snout-length ratio of the larger specimens of *M. tenuis* and *M. lithodendrorum* to *M. gregorii* is mere coincidence, by this hypothesis. No significant difference in relative growth rate of snout and postnarial skull can be detected between *Paleorhinus* and *Rutiodon* within the size range observed. Dissimilar "initial" snout length—the result of precocious growth of the rostrum in young phytosaurs—is responsible for the marked differences in proportions between *Paleorhinus*, the *Rutiodon* group, and *Mystriosuchus*. These differences, when considered with respect to total skull length, provide a useful character for generic discrimination.

The relative growth of the rostrum (X) compared to the postnarial portion of the skull (Y) is given by the following Reduced Major Axis lines:

Paleorhinus $Y = 1.4936\,X - 231.4$ $r = +0.77$
Rutiodon $Y = 1.1769\,X - 266.7$ $r = +0.80$
(data on *Mystriosuchus* are insufficient to compute a trend).

In contrast to these, the rostral portion of the skulls of *Phytosaurus* appears to grow at nearly the same rate as (or possibly more rapidly than) the postnarial portion, the relationship being $Y = 0.7696\ X + 9.07$. ($r = +\ 0.88$).

Three of the four available skulls of *Angistorhinus* are roughly the same size: the other specimen involves restoration of the rostrum so its highly aberrant prenarial:postnarial ratio cannot be regarded as reliable. The dispersion of the values of the ratio is greater than in the *Leptosuchus-Machaeropros-*

opus sample; for the best preserved specimen the ratio lies almost on the trend line of that group. Snout proportions do not provide a means for separating *Angistorhinus* from *Rutiodon.* The similarity is suggestive of phyletic relationship between them.

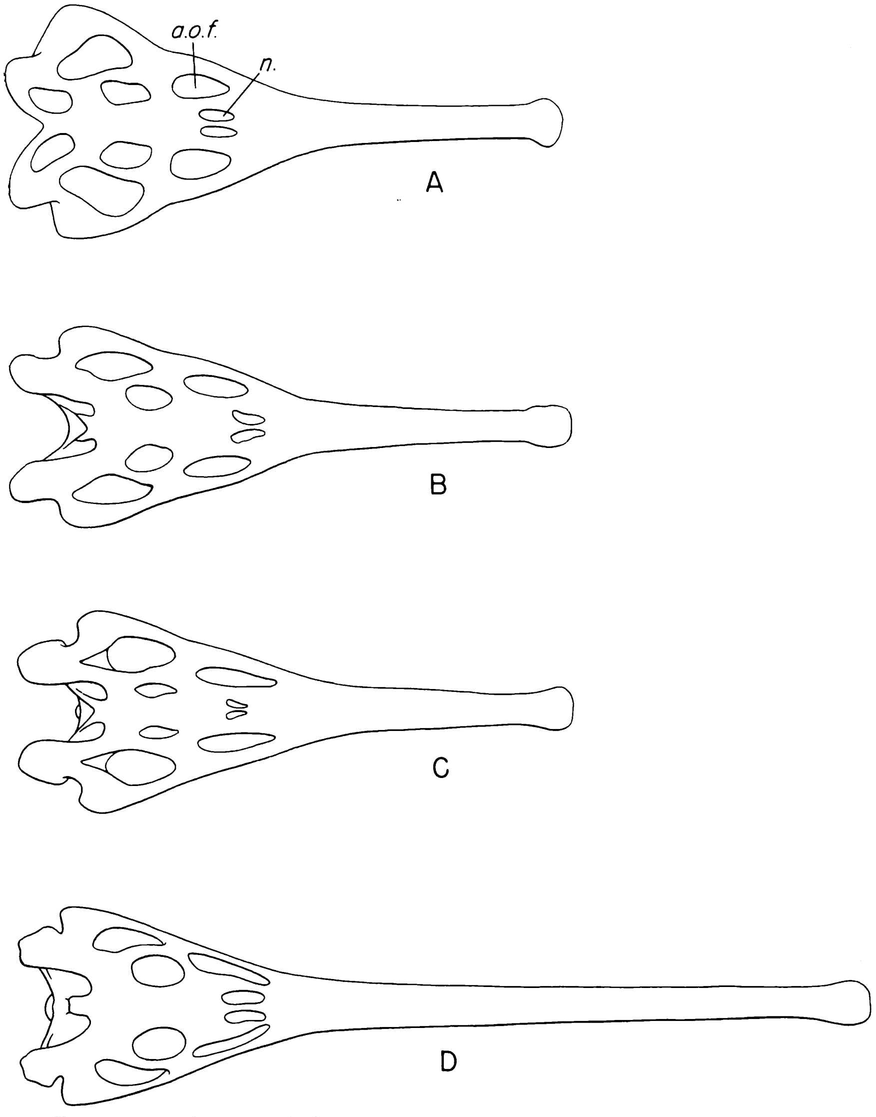

Fig. 3. Dorsal views of the skulls of phytosaurs with posteriorly placed external nares.

A. *Angistorhinus alticephalus* Stovall and Wharton × 2/25.
B. *Phytosaurus kapffi* (Meyer) × 1/10 (after Meyer).
C. *Rutiodon adamanensis* (Camp) × 1/15 (after Camp).
D. *Mystriosuchus planirostris* (Meyer) × 2/15 (after McGregor).

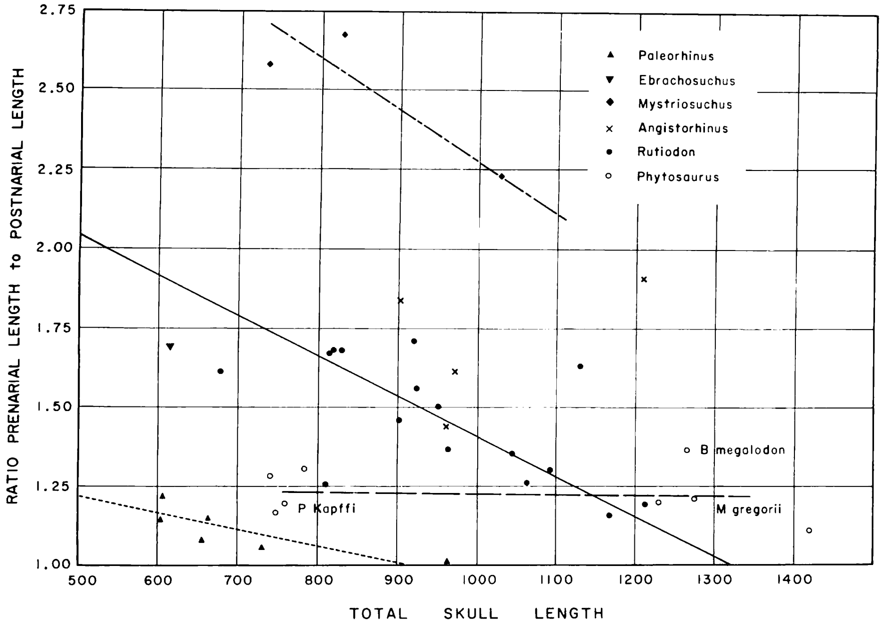

Fig. 4. Ratio of prenarial to postnarial lengths of phytosaur skulls plotted against total skull length. Data partly from Colbert (1947) and original measurements. Trend lines for *Rutiodon* and *Paleorhinus* are reduced major axis of Kermack and Haldane; those for *Phytosaurus* and *Mystriosuchus* are essentially Bartlett's best fit line.

The type skull of *Ebrachosuchus neukami* Kuhn resembles *Paleorhinus* in most details but has a significantly higher rostral:postnarial ratio. As is discussed later, this may be of systematic significance.

4. Posttemporal fenestrae small in *Paleorhinus, Mystriosuchus, Promystriosuchus,* and *Leptosuchus*; large in *Machaeroprosopus* and *Brachysuchus,* largest in *Angistorhinus.* This feature is frequently difficult to observe due to breakage in specimens. Specimens referred to "*Leptosuchus*" and "*Machaeroprosopus*" show considerable variability in the extent of contact between the posttemporal arch and paroccipital process. Although features of this area may be diagnostic for certain genera, we have not found them particularly useful.

5. Posterior bar of parietal short in *Paleorhinus, Angistorhinus* ("very short"); none in *Machaeroprosopus*; depressed and long, lying on the opisthotic in *Mystriosuchus, Leptosuchus,* and *Brachysuchus*; long in *Promystriosuchus.* The supposed distinction between *Machaeroprosopus* and other genera with depressed posttemporal arcades appears to be due to misinterpretation, as a study of better material than the type has shown. *Paleorhinus* and *Promystriosuchus* appear to differ in this respect, but only in degree, the parietal and squamosal both entering the posterior arch in each. Far more important than the relative length of the squamosal process of the parietal is the elevated or depressed condition of the posttemporal arch (see Character 1 above).

6. External nares with elevated rim in *Paleorhinus, Angistorhinus, Mystriosuchus, Promystriosuchus*; without rim in *Machaeroprosopus, Leptosuchus,* and *Brachysuchus.* Evidence suggesting that the elevation of the external nares may be a sexual character (indicating females) has been presented by Camp (1930, p. 28-29) and corroborated by Colbert (1947, p. 72). In large collections of "*Machaeroprosopus*" from Arizona and northwestern New Mexico both elevated and nonelevated nostrils occur in approximately equal numbers. Case based his analysis solely upon the type specimens of various species.

Case also noted that the internarial septum was at the level of the narial rim in some forms and depressed in others. This appears to be related to the development of the raised rim and likewise sexual.

The internal nares are behind the external in *Paleorhinus, Promystriosuchus,* and slightly so in *Angistorhinus.* This is a primitive feature of these genera; other phytosaurs have the external nares directly above the internal.

7. Squamosal not greatly extended behind in *Paleorhinus* and *Promystriosuchus*; extending backward, with strong descending hook in others (*Mystriosuchus* is somewhat intermediate). This feature definitely separates *Paleorhinus, Promystriosuchus,* and *Mystriosuchus* from *Angistorhinus* and the *Phytosaurus-Rutiodon* group.

Anderson (1936, p. 558) showed that the inner surface of the posterior squamosal process served as origin for the medial head of the adductor mandibulae externus muscle. The course of this part of the muscle is such that its greatest pull would have been exerted when the jaws were nearly closed. The posterior origin gives the muscle effective force in holding the jaws closed, important to an animal contending with struggling prey in its long jaws.

Thus we might expect to find the squamosal processes most elongate in slender-jawed types—those with the greatest relative prenarial length. As this is not so, it seems probable that extremely slender-jawed genera such as *Mystriosuchus* fed mainly on fish and had less need for holding the jaws strongly together than the more massive-snouted genera such as *Leptosuchus.*

Species with still more massive snouts, such as *Phytosaurus kapffi, Brachysuchus megalodon,* and *Machaeroprosopus gregorii* also have relatively short squamosal processes but differ from the preceding in the marked depth of this part of the squamosal, which provides an origin for a more bulky, and hence still more powerful muscle. These species were the most powerful predators of the phytosaur family, and may have fed upon land animals as well as the large metoposaurid amphibians that inhabited the Triassic ponds and streams.

8. Orbits directed upward and outward in *Paleorhinus* and *Leptosuchus,* more upward in *Angistorhinus* and *Promystriosuchus* (the latter due to crushing), and more outward than upward in *Phytosaurus* and *Mystriosuchus.*

This feature is strongly affected by crushing, and difficult to measure objectively. However, orbits of the relatively low *Paleorhinus* skulls (including the abnormally crushed type of *Promystriosuchus*) are certainly more upwardly directed than those of the deeper headed genera. Several specimens of "*Leptosuchus*" in the University of Texas collections have laterally directed orbits, and the type of *L. crosbiensis* (Case, 1922, pl. 14) has orbits well on the side of the head; perhaps Case erred in placing this in the group with upwardly rather than outwardly directed orbits. The character must be used with great caution in identifying crushed specimens.

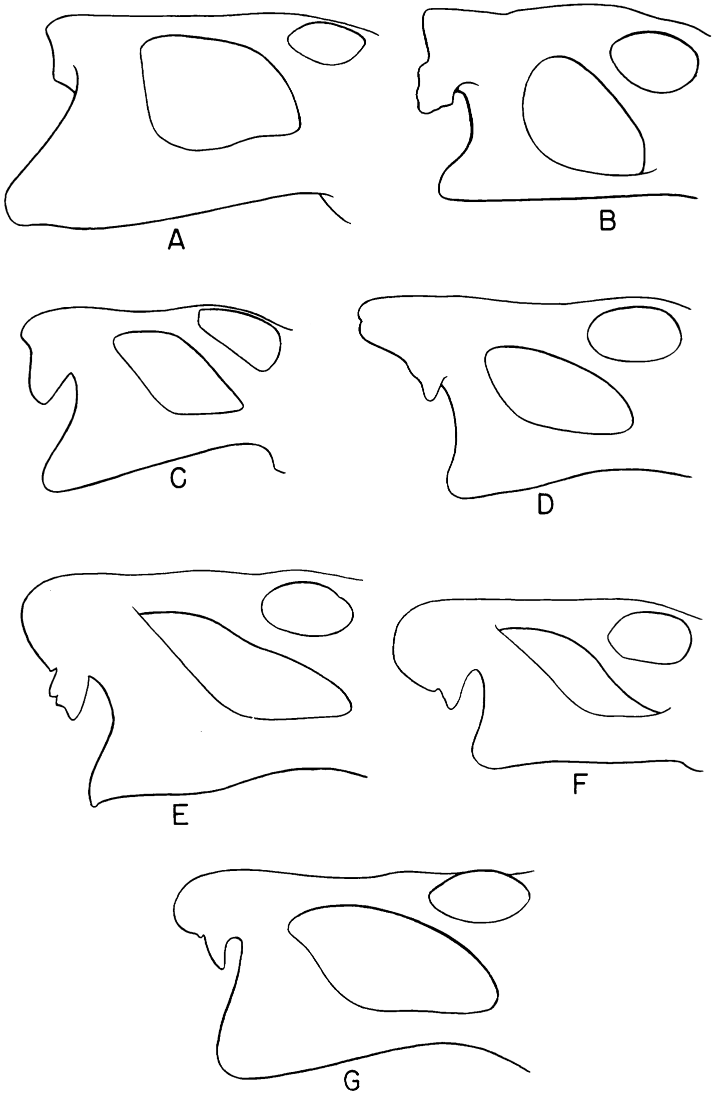

Fig. 5. Lateral view of squamosal processes of:
A. *Paleorhinus ehlersi* (Case) × 1/5.
B. *Mystriosuchus planirostris* (Meyer) (after McGregor) × 1/5.
C. *Angistorhinus alticephalus* Stovall and Wharton × 2/15.
D. *Phytosaurus kapffi* (Meyer) (after Meyer) × 1/5.
E. *Phytosaurus gregorii* (Camp) (after Camp) × 2/15.
F. *Rutiodon adamanensis* (Camp) (after Camp) × 2/15.
G. *Rutiodon tenuis* (Camp) (after Camp) × 2/15.

TABLE 1

Numbers of teeth reported in phytosaurs. Under each genus species are listed with the generic designation under which each was originally described.

Species	Pmx	Max	Total upper	Total lower	No. opp. symphysis
Paleorhinus			33-47	56-58	
Paleorhinus bransoni (type)	20	16	36	—	—
P. parvus (type)	16+?	17	33-37?	—	—
Promystriosuchus ehlersi (type)	31	16	47	—	—
P. ehlersi (4, Howard Co., Texas)	22-25	19-23	43-46	56-58	40-47
Paleorhinus scurriensis (type)	—	16	—	—	—
P. sp. (Borden Co., Texas)	20-21	19-18	39	—	—
Francosuchus broilii (type)	16?[1]	17	33?	—	—
Francosuchus sp. (Kuhn, 1936, pl. 11, fig. 4)	—	—	43	—	—
Ebrachosuchus neukami (type)	36?	20±	56-58[2]	—	—
Mystriosuchus			39-50	46-57	
Belodon plieningeri	21-26	18-24	39-50	57	—
Belodon planirostris	24	23-24	47-48	46	
Angistorhinus			36-50	47-50+	
Angistorhinus grandis (type)	23	19	42	Est 46	
A. gracilis	—	—	—	Est 49	
A. alticephalus (type)			36?		
A. alticephalus (2 Univ. Texas)	25-28	19-22	46-50	47-50	37-41
Rutiodon			39-50	42?-50	
Rutiodon carolinensis	27	15	42	Uncertain	
Leptosuchus crosbiensis (type)	23	21	44	—	—
L. crosbiensis (U.M. 8855)	—	—	—	46	31
L. crosbiensis (3, Crosby Co., Texas)	18-21	21-22	39-43	44-45	32
L. studeri (type)	20	20	40	—	—
Machaeroprosopus adamanensis	20	21	40-43	44-45	33
M. lithodendrorum (type)	21-22	23	44-45	47-49	33
M. lithodendrorum	24	22-23	—	—	32-33
M. tenuis	19-24	21-23	42-45	49-50	36
M. andersoni (type)	—	—	47-48	—	—
M. andersoni (Y.P.M.)	—	—	41-47	—	—
Angistorhinus sp. Mehl (U. Wisc. 3810)	—	—	—	42?	—
Paleorhinus sp. Toepelmann	21	21	42	—	—
Pseudopalatus pristinus	25	23-25	48-50	—	—
Phytosaurus			35-41 (46)	39-49	
Belodon kapffi	18-20	17-19	35-39	47-49	33-34
Machaeroprosopus gregorii (type)	21	21	41	47-48	34
M. gregorii A.M.N.H.	—	—	37	44	—
M. validus	—	—	37	39-40	—
Brachysuchus megalodon (type)	24	22	46	49	36
B. megalodon U.M. 14366	—	—	37-40	—	—

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[1] Possibly part of rostrum missing. See p. 673.

[2] 51 teeth ± 1 by my count, many alveoli indistinct.

9. Character of septomaxillary. Case did not distinguish between the various genera under this item, and I have not observed systematic differences.

10. Number of teeth, and whether round or sharp edged. Shape of teeth may well have diagnostic value, when due account is taken of variation in different

parts of the jaw. More data are needed on the variation in number within various species before useful generalizations can be made.

Numbers of teeth that have been reported or observed for various species of phytosaurs are given in table 1. Some distinctions which might be regarded as specific rather than generic are shown, as the greater number of teeth in Texas than Wyoming specimens of *Paleorhinus*. In general, however, various specimens referred to each genus show a wide range in numbers of teeth, so this character may well be affected by age or individual variability more than by taxonomic variation.

11. Inner edge of pterygoids (palatine on Case's first list) elevated into a ridge. Case lists this character for all genera in which the palate is known, with some variations such as "low ridge" or "rugose". The feature is not diagnostic in our present knowledge. The position of the palatine vacuity, anterior to the middle of the ectopterygoid in *Paleorhinus* and *Angistorhinus* and opposite the middle of the ectopterygoid in *Mystriosuchus*, *Promystriosuchus*, and *Leptosuchus*, likewise is of dubious value. In the University of Texas collection of *Paleorhinus* skulls from Howard County, Texas, the rear of the vacuity is in front of the middle of the ectopterygoid, and two *Angistorhinus* skulls from the same locality have the palatine vacuities well forward of the ectopterygoid. Hence this does not seem a useful feature for classification.

Perhaps the size of the palatal vacuity is more significant. *Mesorhinus*, *Francosuchus*, *Ebrachosuchus*, both the typical species of *Paleorhinus* from Wyoming and referred specimens from Texas, and *Angistorhinus*, according to Mehl's restoration (1915, fig. 2), all have fairly elongate openings between ectopterygoid, pterygoid, and palatine. The type of *Promystriosuchus* appears not to, but may be crushed. In *Mystriosuchus* the opening is of intermediate size, smaller than in the primitive genera mentioned above, but larger than in *Phytosaurus* and *Machaeroprosopus*, which have two small foramina along the posterior palatine suture.

12. Ectopterygoid overlaps the external pterygoid process below in all but *Angistorhinus*, in which it is said to meet the external edge of the pterygoid which lacks an external process. Comparison of the *Angistorhinus* skull in the Texas Memorial Museum with those of *Paleorhinus* and *Phytosaurus* does not show any difference in this structure.

13. Posterior extent of vomers. Case lacked sufficient data to fully utilize this feature in characterizing genera. He regarded *Paleorhinus* as different from others in the greater posterior extent of the vomer, which may be a valid distinction.

14. Parasphenoid process short (?) in *Paleorhinus*, long in others. Better material now available shows a long slender parasphenoid rostrum in *Paleorhinus*, which does not differ significantly from other phytosaurs in this respect.

15. Interpterygoid vacuity long and narrow in *Promystriosuchus*, short and narrow in other genera; small in *Paleorhinus*. Lees' interpretation of the

palate of *Paleorhinus* cannot be accepted in the light of more recent discoveries. *Paleorhinus* (including *Promystriosuchus*) differs from other genera in the larger and more primitive interpterygoid vacuity.

Of the 15 characters used by Case, numbers 4, 6, 9, 11, 12, and 14 do not appear to differ significantly among the various genera. The others are useful to separate the genera into two or more groups.

In later studies Case (1929, p. 43-44; 1932, p. 78) stressed an ecological subdivision of phytosaurs into a more massive and deep-headed predatory group and a lightly built, slender-snouted, fish-eating type. The analysis by Colbert (1947, p. 76) of rostral crests and robustness in *Machaeroprosopus* did not support this view, especially as applied to intermediate forms.

The interpretation of rostral length ratio, rostral crests, and form of squamosal processes presented in this paper leads to a division of the "*Phytosaurus*" group of skulls into two groups (*Phytosaurus* and *Rutiodon*) which correspond essentially to Case's Brachysuchan and Leptosuchan types (Case and White, 1934, p. 140). The gavial-like adaptation of the slender-snouted *Mystriosuchus* and *Paleorhinus* seems obvious.

Camp considered the following cranial characters particularly useful (1930, p. 60-63):

1. Anterior position of external nares in primitive genera.
2. Circular or compressed shape of external nares and thickness of narial septum (cf. also p. 146 and 149). This forms the basis for subfamily separation, along with direction of orbits, and results in the separation of *Paleorhinus* and *Promystriosuchus*, which in other respects are nearly identical. Also it separates *Angistorhinus* from *Rutiodon* and *Phytosaurus* (as used in this paper), with which it shares a large number of common features. Various specimens of *Rutiodon carolinensis* show extreme variation in both width of the septum and shape of the opening (Gregory, 1962). Much of the variability in shape results from crushing. Evidence from other skull structures does not follow the variations in nasal aperture and casts doubt on its importance.
3. Relationship of antorbital fenestra to external nares—related to number one.
4. Depression of posterior borders of the supratemporal fenestra. Camp's phylogenetic chart (p. 149) shows the specialized condition attained independently in *Angistorhinopsis*, *Phytosaurus* and *Leptosuchus*, and *Machaeroprosopus-Rutiodon-Mystriosuchus*. This is a useful character for identification but more indicative of grade of evolution than of phyletic affinity.
5. Presence or absence of squamosal process (see p. 661).
6. Position and aspect of the orbits (subject to crushing, see p. 661).
7. Specialization of palate by degree of closure of palatal vault. Some other palatal characters are listed but not stressed.

Features of elongation of rostrum and development of rostral crests were regarded as of secondary significance.

Colbert (1947, p. 67-78) reviewed and confirmed Camp's findings on the "*Machaeroprosopus*" group. He emphasized the effect of growth upon size, spacing of teeth, and proportion of rostral length to skull length; and attributed robustness and the relative elevation of the external nares to sex. Of all skull characters analyzed, he regarded only the shape of the squamosal process as especially significant for taxonomy, with subordinate importance for size, development of the postorbital-squamosal bar, and number of teeth. His comparison of the relationship of rostral length to skull length in phytosaurs and alligators provided an important basis for evaluation of morphologic differences between various specimens. The study did not extend to the more primitive phytosaurs, however.

Quadrate height: An important feature not included in Case's tabulation (though he considered it qualitatively in comparing various phytosaurs) is the relative height of the posterior part of the skull. Comparison of occipital views of *Paleorhinus* or *Francosuchus* with *Phytosaurus* or *Mystriosuchus* shows a striking contrast between the low, broad skulls of the former, and the much taller skulls of the latter genera. A quantitative measure of this character is provided by the ratio of quadrate height to width of skull table (chosen in preference to width across lower end of the quadrates because it is less subject to postmortem distortion). The accompanying table is compiled from measurements of specimens where available; and from measurements estimated from published illustrations. Dangers in the latter technique were emphasized by the discordant values for *P. kapffi* derived from McGregor's (1906) figure 4 and measurements of specimens.

The low values for *Francosuchus* and *Ebrachosuchus*, derived from Kuhn's measurements, suggest a greater difference from *Paleorhinus* than his illustrations indicate; probably the points of measurement were different from mine. An attempt to obtain values from his illustrations gave a higher ratio (.51 for *Francosuchus latus*). *Paleorhinus* lies in the range .60 to .72. *Angistorhinus* .70 to .80; the others run from .77 to 1.10, mainly clustering about 1.00.

In general tall quadrates go with depressed posterior temporal arches, *Angistorhinus* providing only a partial exception. The changes in structure and proportions of the posterior part of the phytosaur skull were associated with the evolution of the jaw musculature and undoubtedly were correlated with each other.

TABLE 2

Ratio of quadrate height to width of skull table in phytosaurs. Figures in parenthesis indicate number of observations greater than one.

Francosuchus angustifrons Kuhn	.45+
Francosuchus broilii Kuhn	.31 (Kuhn) (.51 from figure)
Ebrachosuchus neukami Kuhn	.34 ? Height doubtful
Paleorhinus ehlersi (Case) (3)	.63-.72
Paleorhinus bransoni Williston	.79
Angistorhinus alticephalus Stovall and Wharton (2)	.71-.78
Rutiodon carolinensis Emmons (2)	.50-.68+
"*Leptosuchus*" sp. Crosby County, Texas	.98
Phytosaurus kapffi Meyer (4)	.75?-1.05
Machaeroprosopus gregorii Camp	.74
Machaeroprosopus lithodendrorum Camp	.79 (Camp's figure)
Machaeroprosopus tenuis Camp	.99 (Camp's figure)
Mystriosuchus planirostris Meyer (6)	.73-1.15 mean 0.93
Mystriosuchus plieningeri (Meyer) Huene, 1911	.79

Summary of characters used: The primitive condition of nearly every skull feature is represented in *Paleorhinus. Angistorhinus* is more primitive only in possessing a broader posterior rim to the superior temporal fenestra, and is obviously more specialized in several other respects. Many cranial characters fall clearly into either primitive or specialized conditions. Taxa characterized by different combinations of primitive and specialized features are termed genera.

The following characters are of greatest systematic value. These features, except the third and fourth, appear to be independent of age or size or sex.

1. Presence or absence of posterior squamosal process.
2. Relative length and depth of squamosal process when it is present.
3. Rostrum broadening posteriorly and massive or rostrum narrow throughout most of its length. A similar distinction exists between gavials and other crocodilians. It is recognized that wide variations in the robustness of the rostrum occur among various individuals of one species; however, none of the specimens of *Angistorhinus*, *Rutiodon*, or *Phytosaurus* approach the extremely slender rostra of *Paleorhinus* and *Mystriosuchus*.
4. Teeth homodont or heterodont (probably correlated with 3).
5. Relative proportion of rostral length to postnarial length of skull, when considered in relationship to size. The way in which this proportion changes during growth is particularly significant.
6. Relative position of external nares in relation to antorbital fenestra, or more quantitatively, the distance between the external naris and orbits.
7. Posterior border of the superior temporal fenestra at level of skull roof or depressed.
8. Relative height of quadrate, as a measure of depth of the skull (probably correlated with 7).
9. Palate open or largely vaulted by pterygoids.

KEY TO PHYTOSAUR SKULLS

A. Posterior end of squamosal truncate at edge of paroccipital process, not produced posteriorly; lateral edge of upper temporal bar forming overhanging ridge between skull deck and sides; teeth homodont; orbits directed more upward than outward.

  1. Posttemporal arcade at level of skull roof; external nares over or in front of anterior end antorbital fenestra; quadrate low; palate with wide interpterygoid vacuities. *Paleorhinus*
    a) Rostral ratio <1.25; North America. Subgenus *Paleorhinus*
    b) Rostral ratio >1.50; Europe. Subgenus *Francosuchus*
  2. Posttemporal arch greatly depressed; external nares above middle of antorbital fenestra; quadrate height about equal to width skull table; interpterygoid vacuity small. *Mystriosuchus*

B. Posterior end of squamosal projecting behind contact with paroccipital process and rounded; no abrupt ridge or angle between top and lateral surfaces of skull; external nares above antorbital fenestra; teeth slightly to markedly differentiated; orbits directed outward.

1. Posterior temporal arch at level of skull roof and relatively thick; quadrate relatively low; teeth only slightly differentiated. Posterior squamosal process short, round. *Angistorhinus*
2. Posterior temporal arch depressed, thin; quadrate taller; teeth heterodont.
    a) Squamosal processes relatively elongate; upper temporal bar slender; rostra slender to moderately robust, never crested entire length; rostral length inversely proportional to size. *Rutiodon*
    b) Squamosal processes broad and round; upper temporal bars stouter; rostra massive throughout, with continuous rostral crest, never over 1.25 times postnarial length. *Phytosaurus*

GENERIC SYNONYMY

Paleorhinus Williston, 1904. Type *P. bransoni* Williston
    ? *Mesorhinus* Jaekel, 1910. Type *M. fraasi* Jaekel
    Promystriosuchus Case, 1922. Type *P. ehlersi* Case
    Francosuchus Kuhn, 1933a. Type *F. broilii* Kuhn
    Ebrachosuchus Kuhn, 1936. Type *E. neukami* Kuhn

Angistorhinus Mehl, 1913. Type *A. grandis* Mehl

Rutiodon Emmons, 1856. Type *R. carolinensis* Emmons
    Rhytidodon Cope, and other variants
    Centemodon Lea, 1856. Type *C. sulcatus* Lea
    Metarhinus Jaekel, 1910. Type *Belodon buceros* Cope
    Machaeroprosopus Mehl, 1916. Type *M. validus* Mehl
    Angistorhinopsis Huene, 1922. Type *Mystriosuchus rütimeyeri* Huene
    Leptosuchus Case, 1922. Type *L. crosbiensis* Case
    Pseudopalatus Mehl, 1928. Type *P. pristinus* Mehl

Phytosaurus Jaeger, 1828. Type *P. cylindricodon* Jaeger
    ? *Clepsysaurus* Lea, 1851. Type *C. pennsylvanicus* Lea
        see Camp, 1930, p. 142 for synonymy of *Clepsysaurus*
    Nicrosaurus O Fraas, 1866. Type *Belodon kapffi* Meyer
    ? *Heterodontosuchus* Lucas, 1898. Type *H. ganei* Lucas
    Lophoprosopus Mehl, 1915. Type *Belodon kapffi* Meyer
    Lophorhinus Mehl, 1915, *Lophosaurus* Hay, 1929, variant spellings
    Brachysuchus Case, 1929. Type *B. megalodon* Case

Phytosaurus or *Rutiodon*, indeterminate
    Compsosaurus Leidy, 1856. Type *C. priscus* Leidy
    Omosaurus Leidy, 1856. Type *O. perplexus* Leidy
    Eurydorus Leidy, 1859. Type *E. serridens* Leidy
    Palaeoctonus Cope, 1877. Type *P. appalachianus* Cope
    Suchoprion Cope, 1877. Type *S. cyphodon* Cope

Mystriosuchus Fraas, 1896. Type *Belodon planirostris* Meyer
    Belodon Meyer, 1842. Type *B. plieningeri* Meyer
    Termatosaurus Meyer and Plieninger, 1844. Type *T. alberti* idem

?*Rileya* Huene, 1902. Type *R. bristolensis* Huene = *Palaeosaurus platyodon* Riley and Stutchbury

TABLE 1

Tabular comparison of diagnostic characters of phytosaur skulls

	Paleorhinus	*Francosuchus*	*Mystriosuchus*	*Angistorhinus*	*Phytosaurus*	*Rutiodon*
Position external naris	Anterior	Anterior	Posterior	Posterior	Posterior	Posterior
Posttemporal bar	Level skull deck	Level skull deck	Greatly depressed	Level skull deck	Depressed	Depressed
Posterior squamosal process	Absent	Absent	Absent	Rounded, short	Rounded, short, deep	Rounded, elongate
Upper temporal bar	Sharp lateral ridge	Sharp lateral ridge	Sharp lateral ridge	Rounded	Rounded	Rounded
Ratio rostral length to postnarial length	Decreases with increasing size 1.0-1.2	1.7	Decreases with larger size 2.2-2.7	Trend unknown 1.4-1.9	No change with size 1.05-1.37 av. 1.23	Decreases with increasing size 1.2-1.7
Rostral crests	Absent	Absent	Absent	Absent	Massive entire length rostrum	Size dependent, confined to posterior half rostrum
Dentition	Homodont 33-47/56-58	Homodont 56-58/?	Homodont 39-50/46-57	Weakly heterodont 36-50/47-50+	Strongly heterodont 35-46/39-49	Moderately to strongly heterodont 39-50/42?-50
Quadrate	Low	Low	Tall	Moderate	Tall	Tall

SYSTEMATIC DESCRIPTIONS

Family PHYTOSAURIDAE McGregor 1906

Amphibious reptiles of crocodile- and gavial-like habitus forming the sole family of a distinctive suborder, Parasuchia, of the Order Thecodontia. Skulls with elongate rostra formed largely by premaxillaries. External nares close to midline and remote from tip of snout, between or a short distance in front of antorbital fenestrae. Lateral temporal fenestrae large. Superior temporal fenestrae primitively directed upward and confined to skull roof, but in advanced species becoming progressively directed posteriorly, confined to the occipital surface, and finally overlapped by postorbital bars. Never a bony secondary palate. Vertebrae platycoelous with centra strongly constricted between articular ends; neural spines stout, short anteroposteriorly, sometimes enlarged at tip. Coracoids rounded; clavicles and interclavicle present. Pelvic girdle primitive with platelike pubis and ischium, the former turned outward strongly at its anterior margin. Femur sigmoid. Dorsal armor of large osteoderms bearing compressed central eminences and sculpture of radial ridges, grooves, and pits. Ventral armor of small plates, articulating at least in some species.

Known geologic distribution late Triassic of Europe, India, Madagascar, and North America. A doubtful record from early Triassic of Europe ("*Mesorhinus*").

PALEORHINUS Williston, 1904

Williston, S. W., 1904, Jour. Geology, v. 12, p. 696.

Type Species: *Paleorhinus bransoni* Williston, 1904

Synonyms: *? Mesorhinus* Jaekel, 1910
Promystriosuchus Case, 1922
Francosuchus Kuhn, 1933a
Ebrachosuchus Kuhn, 1936

Types of Synonyms: *Mesorhinus fraasi* Jaekel, *Promystriosuchus ehlersi* Case, *Francosuchus broilii* Kuhn, *Ebrachosuchus neukami* Kuhn.

Included Species:
- *Paleorhinus bransoni* Williston, 1904, Popo Agie formation, Wyoming.
- *P. parvus* Mehl, 1928,[3] Pope Agie formation, Wyoming.
- *P. ehlersi* (Case, 1922), Dockum group, Texas.
  - *P. scurriensis* Langston, 1949, Dockum Group, Texas.
- *P. broilii* (Kuhn, 1933a), Blasensandstein, Germany.
  - = "*Francosuchus*" *latus* Kuhn, 1933a
  - = "*F. angustifrons*" Kuhn, 1936
  - *P. neukami* (Kuhn, 1936), Blasensandstein, Germany.
    - = *Mystriosuchus* cf. *plieningeri* Kuhn, 1936, (non Meyer, 1841), Blasensandstein, Ebrach, Germany.

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[3] No attempt is made to revise the species of the Popo Agie fauna at this time.

? *Ebrachosaurus singularis* Kuhn, 1936, (Postcranial
skeleton; doubtfully phytosaur), Blasensandstein,
Ebrach, Germany.
? *P. fraasi* (Jaekel, 1910), ? Buntsandstein,
? Bernburg, Germany.

Distinctive Characters:

1. Anterior position of external nares.
2. Posterointernal boundary of supratemporal fenestra at level of skull roof, narrow.
3. Posttemporal fenestra very small.
4. Squamosals abruptly truncate, not extending posteriorly beyond their contact with paroccipital process.
5. Laterally projecting ridge on the squamosal portion of the temporal bar forms a sharp boundary between the upper deck and sides of the skull.
6. Orbits directed relatively more upward than outward.
7. Quadrate low; ratio height quadrate to width skull deck across squamosals .31 (?) to .79.
8. Rostrum always low, slender.
9. Ratio of rostral length to postnarial length much lower for any given skull size than in other genera.
10. Teeth relatively slender, round, not enlarged or noticeably compressed in posterior part of jaws.
11. Palate with relatively large interpterygoid vacuity and elongate suborbital fenestrae.

Subgenus *Paleorhinus*

Rostra relatively shorter. North American species.

Paleorhinus was established for *P. bransoni* Williston from the Popo Agie formation in Wyoming. Mehl (1928) added a second species, *P. parvus*, based upon an incomplete mandible and the rostrum of a skull and associated postcranial bones. Although specific revision is not here undertaken, it is suspected that this may belong to a smaller individual of *P. bransoni*.

The lower part of the Dockum group in western Texas has yielded several specimens of this genus. A majority of these, including the type of *Promystriosuchus ehlersi* Case, differ from the Wyoming species in slightly smaller size, more numerous teeth, and in the position of the rear border of the external naris above rather than well forward of the anterior border of the antorbital fenestra. The fragmentary skull described as *Paleorhinus scurriensis* by Langston from the basal conglomerate of the Dockum resembles the Wyoming specimens more closely in its more anteriorly placed nares. A considerably larger skull from Borden County, Texas, may represent a distinct species of this genus.

Case (1922), in establishing the genus *Promystriosuchus* for a primitive phytosaur from Texas, distinguished it from *Paleorhinus* in the following features (numbers follow Case's list):

1. Posttemporal arcade at the level of the skull roof, depressed in *Paleorhinus*. Lees' (1907, p. 132) description of the latter genus suggests a depressed border, but in comparing *Paleorhinus* and *Mystriosuchus* (p. 147) he specifically states that the arch in *Paleorhinus* is at the upper level of the skull. Mehl (1915, p. 159) states that it is largely broken away in *Paleorhinus*, but then and later he agreed that it probably lay at skull roof level. As these arches are delicate, and the skulls often crushed, it frequently is difficult to be certain of the original configuration. The preserved parts of the *Paleorhinus* and *Promystriosuchus* skulls are so similar in this region that there can be little doubt of their identity.

2. Antorbital opening posterior to the external nares and rounded, in *Paleorhinus*, but opposite middle of the external nares and elongate oval in *Promystriosuchus*. The series of *Paleorhinus* skulls from Howard County, Texas, shows variation in the position of the nares with respect to the anterior end of the antorbital fenestra; in general the posterior end of the nares lies over the front of the fenestra. The specimen from Scurry County (*P. scurriensis* Langston) resembles *P. bransoni* in its more anterior nares. These animals differ markedly from other phytosaurs in the forward position of the external nares. They obviously are related closely to one another. To call them different genera because of slight differences in the position of nostril or size of antorbital fenestra seems unwarranted.

3. Ratio of prenarial to postnarial length, 1:1 in *Paleorhinus*, 3:2 in *Promystriosuchus*. The rostrum of Case's type specimen, at least as restored, is relatively longer than in most of the Texas material, which does not differ significantly from the Wyoming type in this respect. Values of the ratio are:

Paleorhinus bransoni	1.09
Promystriosuchus ehlersi type	1.43
Howard County specimens (4)	1.08 to 1.22
Borden County specimen	1.01

For known specimens of *Paleorhinus*, excluding the type of *P. ehlersi*: $N = 6$; $M = 1.114$; $\sigma' = 0.0713$; $V = 6.40$. The ratio for *P. ehlersi* differs significantly, ($P < 0.01$), from the mean value of the other specimens [$t = 4.431$, $N + 1 = 7$], but the crushed condition of the specimen renders the measurements and restoration doubtful, so that a scotch verdict seems reasonable. The strong similarities between these forms in most features, their occurrences in the same strata, and the absence of additional specimens with distinctive features of "*Promystriosuchus*", render it likely that they are congeneric.

5. Posterior bar of parietal short in *Paleorhinus*, long in *Promystriosuchus*. Case's interpretation of *Paleorhinus* is uncertain; Lees emphasized the length of the posterior parietal process. This region of the skull is very similar in both forms.

10. Premaxillary and maxillary teeth 36, rounded in section, in *Paleorhinus*; 47, both oval and round in *Promystriosuchus*. The Howard County, Texas, material ranges from 43 to 46 teeth, the average being 45; a larger specimen, from Borden County, Texas, has only 39. Tooth number is known to vary within about the same limits (37 to 46) in American species of *Phytosaurus*. Consequently this distinction does not seem of generic value.

The distinction in shape between the round teeth of *Paleorhinus* and round and compressed in *Promystriosuchus* is based largely upon comparison of alveolar shape, and in the absence of skulls with teeth in place cannot be regarded as a certain difference.

11. Palatines with inner edge elevated with a ridge in *Paleorhinus*, raised and rugose in *Promystriosuchus*. Rugosity of muscular attachment areas is notoriously variable with age and size of individuals; the distinction does not appear significant. In *Paleorhinus* the palatine vacuity ends anterior to the middle of the ectopterygoid; in *Promystriosuchus*, Case states that it is small and near the middle of that bone, but several other Texas specimens show the usual phytosaur condition. Case's type is crushed so these openings are obliterated by contact of palatine and maxillary.

14. Parasphenoid process short (?) in *Paleorhinus*, long in *Promystriosuchus*. The Wyoming specimen appears to be defective in this part of the palate, which accounts for the supposed difference.

15. Interpterygoid vacuity small in *Paleorhinus*, long in *Promystriosuchus*. Actually these two phytosaurs, judging from the Texas material, both differ from other genera in the relatively primitive separation of the pterygoids.

Camp separated *Promystriosuchus* from *Paleorhinus* on the basis of "orbits directed upward, nasal septum thin". As has already been pointed out, the type skull of *Promystriosuchus* is crushed and other specimens from Texas do not support this distinction.

It is thus seen that the distinctions between *Paleorhinus bransoni* and *Promystriosuchus ehlersi* are in part errors of interpretation, and partly features which in the light of present knowledge of phytosaurian variability are not of more than specific value. On the contrary, many common features set these two nominal genera apart from other phytosaurs. Together they form a distinctive, primitive generic group.

Subgenus *Francosuchus* O. Kuhn, 1933a

Rostra more elongate. European species.

In 1933 and 1936 Kuhn described the fauna of the Blasensandstein from Ebrach, Franconia, Germany. That formation is appreciably older than the fossiliferous Stubensandstein of Württemberg that produced the classic specimens of *Phytosaurus* and *Mystriosuchus*, and its phytosaurs show the same primitive position of the posttemporal arch and anterior location of the external nares which characterize *Paleorhinus*. Kuhn described his specimens as new genera, *Francosuchus* and *Ebrachosuchus*, separated from one another and from *Paleorhinus* by a large series of minute differences in proportions. My experience with collections of phytosaur skulls from single localities suggests that many of these features are normal individual variations. Comparison of Kuhn's illustrations of *Francosuchus* and *Ebrachosuchus* reveals great similarity in most features. They differ markedly however in the relatively short snout of the type skull of *Francosuchus broilii*. It should be noted that the rostrum of that skull is broken, and the small number of teeth suggests that a portion may be missing as Kuhn later recognized (1936, p. 65). Another skull (Kuhn, 1936, pl. 11, fig. 4) referred to *Francosuchus* sp. has a relatively longer snout with 43 (instead of 33) teeth on a side. If this is taken as a more reliable indication of the proportions of the animal, the difference from *Ebrachosuchus* is much less, and from *Paleorhinus* almost none. The rostrum of *Ebrachosuchus neukami* is relatively still longer and more plentifully supplied with teeth, so that it may be specifically distinct from *F. broilii*; but in view of the known variability of phytosaur rostra with growth, it does not seem reasonable to separate a genus on this character alone.

Through the kindness of Prof. Dr. R. Dehm I have had the opportunity to examine the surviving specimens of the Ebrach phytosaurs. The types of both *Francosuchus angustifrons* and *Ebrachosuchus neukami* have posttemporal arches exactly like *Paleorhinus ehlersi*, thin, vertical, at the level of the skull deck. Apparent differences suggested by published illustrations are merely effects of crushing. The type of *Ebrachosuchus* bears a lateral ridge on the postorbital bar like *Paleorhinus*. The squamosals do not form a posterior process. Crushing is partly responsible for the extremely low occiput, but the quadrates could not have been very tall. Measurements of quadrate height and hence of its ratio to skull width are not reliable. Like *Paleorhinus* the external nares are well forward of the internal, and their relationship to the front of the antorbital fenestra varies exactly as do those of various specimens of *Paleorhinus* from North America. Differences in the shape of the lateral temporal fenestra noted by Kuhn are comparable to the variations seen in *Paleorhinus* skulls from a single locality in Texas.

Other distinctions mentioned by Kuhn such as relative upturning of the orbits, amount of downturning of the tip of the rostrum, breadth of the external nares, breadth of the rostrum, relative size of the antorbital fenestra, etc., may easily be accounted for by differential crushing and individual growth differences. Kuhn (1936, p. 84) shows that both *Ebrachosuchus* and *Francosuchus* have identical development of each of 18 various primitive and advanced characters of phytosaurs utilized by Camp (1930, p. 148). Aside from the relatively longer rostrum of *E. neukami* and negligible development of surface rugosities on the interorbital region of the skulls, these specimens differ no more from North American species of *Paleorhinus* than various specimens of that genus from a single locality do among themselves.

Although the Franconia phytosaur skulls agree with *Paleorhinus* in all qualitative features of narial form and position and development of the temporal arcades, they do differ significantly in the greater length of the rostrum. This proportion is clearly shown on the graph, figure 4, and is reflected by the significant difference ($P<.001$) between the prenarial-postnarial ratio of the *Ebrachosuchus neukami* skull and those of the American species of *Paleorhinus*. This trend toward a more elongate rostrum suggests that *Ebrachosuchus* may belong to the evolutionary line leading to *Mystriosuchus*. Its geographic occurrence in Europe supports this hypothesis.

Kuhn identified a lower jaw from the Ebrach locality as *Mystriosuchus*, but as no jaws were referred to *Ebrachosuchus* or *Francosuchus*, this determination is questionable. The jaw most probably pertained to the characteristic Ebrach phytosaur, and its similarity to *Mystriosuchus* merely strengthens the probability of relationship.

Should *Francosuchus* (= *Ebrachosuchus*) be accorded generic distinction from *Paleorhinus* on the basis of the more elongate rostrum? Any decision on the taxonomic weight of a single valid distinctive character separating two geographically separated populations is subjective and arbitrary. Uniting *Francosuchus-Ebrachosuchus* with *Paleorhinus* in a single genus stresses the close relationship between these animals, which seems highly desirable. Recognizing *Francosuchus* as a subgenus seems a useful compromise which permits expression of its divergent features and relationship to *Mystriosuchus* without unduly complicating the suprageneric classification of the phytosaurs, which after all are a small and homogenous family of reptiles.

"*Mesorhinus*"—The imperfect type of *Mesorhinus fraasi* Jaekel resembles the postnarial portion of a *Paleorhinus* skull in general form and in showing traces of a posttemporal arcade at the level of the skull deck. It differs from all other phytosaurs in retaining a minute pineal foramen. Its lateral temporal fenestra is rounded like that of "*Francosuchus*" from the Blasensandstein of Ebrach. A relatively short, phytosaur-like snout has been inferred; actually the premaxillaries may not have extended much beyond the broken anterior end of the specimen. If no rostrum existed, it would be better to classify it as a pseudosuchian than a phytosaur. The posterior extent of the squamosals likewise is not determinable.

The age of the fossil also requires further corroboration; it is referred to the early Triassic Buntsandstein on the basis of a label stating that it was from Bernburg (but calling the specimen *Trematosaurus*) and some comparisons of its matrix, which Jaekel believed could be matched in the Buntsandstein. If it is truly a phytosaur and also from the early Triassic, it is by far the earliest member of the family. So many doubts exist concerning both its morphological character, and (I believe) its age and provenance, that no useful conclusions may be drawn from the specimen.

No adequate distinctions can be drawn to separate it from *Paleorhinus* on the basis of present knowledge, and it is tentatively referred to that genus.

MYSTRIOSUCHUS E. Fraas, 1896

Fraas, E., 1896, Die schwäbischen Trias-Saurier, p. 16.

Type Species: *Belodon planirostris* Meyer, 1863
Synonyms: *Belodon* Meyer, 1842, in part
? Termatosaurus Meyer and Plieninger, 1844
Types of Synonyms: *Belodon plieningeri* Meyer, *Termatosaurus alberti* Meyer and Plieninger.
Included Species: *Mystriosuchus planirostris* Meyer, 1863, Stubensandstein, Germany.
"*Mystriosuchus plieningeri* Meyer", Huene, 1911, Stubensandstein, Germany.
  ?Termatosaurus alberti Meyer and Plieninger, 1844, Rhaetic bonebed, Germany.
  Mystriosuchus ingens E. Fraas, 1896, Stubensandstein, Germany.

Distinctive Characters:

1. External nares far posterior, between antorbital fenestrae and relatively close to orbits.
2. Posterior boundary of superior temporal fenestra greatly depressed below skull roof, close to paroccipital bar.
3. Posttemporal fenestrae extremely reduced.
4. Squamosals abruptly truncate, resembling *Paleorhinus*.
5. Well defined ridge on lateral border of upper temporal bar separating top and sides of skull.
6. Orbits directed more outward than upward.
7. Quadrates relatively tall; ratio of quadrate height to width skull deck 0.73 to 1.15 in *M. planirostris* and about 0.79 in *M. plieningeri.*
8. Rostrum low and slender, but sometimes bearing local dorsal swellings.
9. Ratio of rostral length to postnarial length extreme in *M. planirostris* (2.58 to 2.67) ; moderately high in *M. plieningeri* (2.22).
10. Teeth slender, not enlarged posteriorly, round, with weakly developed keels to slightly compressed crowns in posterior part of jaw.
11. Interpterygoid vacuities small; suborbital vacuities moderate.

The outstanding features of *Mystriosuchus* are its extremely long and slender snout, delicate and nearly homodont dentition, and truncate squamosals. It has become specialized beyond the *Paleorhinus* condition in the position of its external nares, depressed posttemporal arcade, and deepened skull. Little change can be noted in the dentition beyond some increase in the number of teeth, and the squamosal area has not developed the posterior processes characteristic of other phytosaur genera. The two species contrast considerably in the degree of elongation of the snout, much in the same fashion as the Indian gavial (*Gavialis gangeticus*) and false gavial (*Tomistoma schlegelii*) differ.

Belondon plieningeri was based upon a series of broken fragments of phytosaur teeth from the Stubensandstein of Württemberg, Germany. The type specimens came from Leonburg and Löwenstein, and were figured by Meyer and Plieninger (1844, pl. 12, figs. 18-24). During the years that followed numerous specimens of reptile teeth and bones from the German Keuper were identified as *Belodon*; in 1861 Meyer separated out the dinosaur remains (*Teratosaurus suevicus* Meyer), and demonstrated for the first time the long-snouted, gavial-like character of the phytosaur skull. He founded a second species of *Belodon, B. kapffi*, upon the more massive remains and restricted the name *B. plieningeri* to the more slender-snouted specimens to which the type material in all probability belonged. Meyer recognized the identity of his *Belodon kapffi* with the remains described as *Phytosaurus* by Jaeger in 1828 but rejected the earlier name as founded upon a misconception (a not uncommon nomenclatorial practice in those days).

In 1863 Meyer described a third species, *Belodon planirostris*, with a still more elongate rostrum, from Aixheim, 90 kilometers south of Stuttgart. This species was made the type of a new genus, *Mystriosuchus*, by Fraas (1896, p. 16-17).

In 1911 Huene referred a skull from Trossingen, near Aixheim, to *Belodon plieningeri* and transferred that species to *Mystriosuchus*, apparently overlooking the implications of this determination for the generic name. (He appears to have accepted McGregor's view (1906, p. 93) that *Belodon* was a synonym of *Phytosaurus* Jaeger). As *B. plieningeri* is the type species of *Belodon*, *Mystriosuchus* would become a later synonym of that name, and according to the rule of Priority should be replaced by it.

The basis for Huene's identification of the Trossingen *Mystriosuchus* skull with *Belodon plieningeri* is not clear. In a brief visit to Stuttgart I was unable to locate the original fragments upon which *B. plieningeri* was originally based. Several specimens labeled *B. plieningeri* in Meyer's collections, including those figured in 1861 and 1863 upon which the distinctions between various species of *Belodon* were based, belong to small phytosaurs which may be, as Fraas suggested, immature individuals of *Phytosaurus kapffi*, or else may represent a separate species of that genus. They do not show the distinctive pattern of ridges and pits on the surface of the roofing bones that characterizes *Mystriosuchus*, the rostral crests when present are more like *Phytosaurus*, and the squamosal has a rounded posterior process.

If the Trossingen skull does not belong to *B. plieningeri*, the name *Mystriosuchus* remains valid, and the possibility of an undesirable and confusing transfer of the name *Belodon* from the massive *Phytosaurus kapffi* group to the slender-snouted *Mystriosuchus* through strict application of priority is eliminated.

Termatosaurus albertii Meyer and Plieninger 1844 (p. 123-125, pl. 12, figs. 25, 37, 93-94) was described from a number of isolated teeth from several localities in the Rhaetic bonebed of Württemberg; the illustrations suggest diverse animals and only one resembles a phytosaur closely. Fraas (1896, p. 17) referred these to *Mystriosuchus* as a separate species. If any of them are phytosaurs they are specifically and generically indeterminable but are almost surely remains of some of the more adequately known German forms. They should be dropped from consideration as members of this family.

The slender-snouted phytosaur from eastern North America commonly known as *Rutiodon carolinensis* Emmons has often been compared with *Mystriosuchus*. McGregor (1906, p. 58) considered generic distinction between them questionable, whereas Colbert (1947, p. 88-91) regarded *Rutiodon* as distinct and intermediate between *Mystriosuchus* and *Machaeroprosopus* (= *Phytosaurus*). Restudy of the *Rutiodon* specimens reveals that the rostrum has probably been reconstructed too long for the rest of the skull (or the skull too short for the rostrum) and that the relationships of the nares, squamosal, and posterior temporal arch are essentially identical with *Phytosaurus*. Details are given at the appropriate place.

ANGISTORHINUS Mehl, 1913

Mehl, M. G., 1913, Jour. Geology, v. 21, p. 186.

Type Species: *Angistorhinus grandis* Mehl

Referred Species: *A. grandis* Mehl,[4] 1913, Popo Agie formation, Wyoming.
A. gracilis Mehl, 1915, Popo Agie formation, Wyoming.
A. maximus Mehl, 1928, Popo Agie formation, Wyoming.
A. alticephalus Stovall and Wharton, 1936, Dockum group, Howard County, Texas.

Distinctive Characters:

1. External nares posterior, between antorbital fenestrae.
2. Posterior borders of supratemporal fenestrae at level of skull roof, thicker than in *Paleorhinus*, sometimes sculptured.
3. Posttemporal fenestrae relatively large.
4. Squamosals produced posteriorly into short rounded processes that extend well behind contact with paroccipital process.
5. Upper surface of skull rounded continuously into lateral surface over upper temporal bar.
6. Orbits directed outward as much as upward.
7. Quadrate intermediate in height between *Paleorhinus* and *Phytosaurus*: ratio of quadrate height to width skull table .71 to .78.
8. Rostrum long, stouter than in *Paleorhinus*, not known to develop crests as in *Phytosaurus*, its tip strongly downcurved.
9. Ratio of rostral length to postnarial skull length similar to *Rutiodon* (cf. fig. 4).
10. Teeth differentiated, rounded and striated anteriorly, unsymmetrically compressed, serrate edged, and spade shaped posteriorly, generally like *Phytosaurus*. Posterior premaxillary teeth slightly enlarged, but not sufficiently to cause alveolar border to flare.
11. Interpterygoid vacuity small, suborbital vacuities large in Mehl's figure.

The surface ornamentation of the skull of *Angistorhinus* is formed by short vermiculate ridges on the frontal and parietal, and coarse, irregular pits and ridges on the squamosal above the quadrate. This pattern contrasts markedly with the ornamentation of *Paleorhinus* which consists of elongate ridges in the preorbital region and simple, large, groovelike pits on the temporal bars and squamosals.

Angistorhinus shows affinity to *Phytosaurus* in the configuration of its squamosal processes and in the development of heterodont dentition. Its posttemporal arch is in some ways even more primitive than that of *Paleorhinus*, to which *Angistorhinus* does not otherwise show much resemblance. The position of the external nares is fully as "advanced" as in *Phytosaurus*. Skull depth (measured by quadrate height) and development of dentition are intermediate between the presumably primitive condition shown by *Paleorhinus* and the *Phytosaurus* type. Absence of rostral crests may also be regarded as primitive.

No features of *Angistorhinus* would bar it from direct ancestry of *Phytosaurus* or *Rutiodon*. It occurs only in the Popo Agie (from which these genera are lacking) and in the Dockum localities, Howard County, Texas, where it is

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[4] No attempt is made to revise the species of the Popo Agie fauna, which is being studied by E. H. Colbert.

associated with *Paleorhinus*. *Phytosaurus* [*Brachysuchus*] also occurs in Texas localities, so some overlap in time between *Angistorhinus* and this genus is indicated. *Rutiodon*, so far as known, is younger than *Angistorhinus*.

PHYTOSAURUS Jaeger, 1828

Jaeger, G. F., 1828, Über die fossilien Reptilien, welche in Württemberg aufgefunden worden sind: p. 22, pl. 6 figs. 3, 8-15, 17-20.

Type Species: *Phytosaurus cylindricodon* Jaeger, 1828

Synonyms:
Belodon Meyer, 1861, in part
? *Clepsysaurus* Lea, 1851
? *Centemodon* Lea, 1856
Compsosaurus Leidy, 1856
Omosaurus Leidy, 1856
Eurydorus Leidy, 1859
Palaeoctonus Cope, 1877
Suchoprion Cope, 1877
? *Heterodontosuchus* Lucas, 1898
Lophoprosopus Mehl, 1915
Lophorhinus Mehl, 1915
? *Machaeroprosopus* Mehl, 1916 [Camp 1930, in part]
Nicrosaurus O. Fraas, 1866
Brachysuchus Case, 1929

Types of Synonyms: *Clepsysaurus pennsylvanicus* Lea, *Centemodon sulcatus* Lea, *Compsosaurus priscus* Leidy, *Omosaurus perplexus* Leidy, *Eurydorus serridens* Leidy, *Palaeoctonus appalachianus* Cope, *Suchoprion cyphodon* Cope, *Heterodontosuchus ganei* Lucas, [of *Lophoprosopus*, *Lophorhinus* and *Nicrosaurus*] *Belodon kapffi* Meyer, *Machaeroprosopus validus* Mehl, *Brachysuchus megalodon* Case.

Included Species:

A full revision of the species of *Phytosaurus* is beyond the scope of this paper. In the following list various named forms that belong in the genus are listed without regard to their possible synonymy or biological validity; however, the numerous species referred to *Clepsysaurus* by Camp (1930, p. 142) and by Colbert and Chaffee (1941, p. 12-16) are not repeated nor is any attempt made to provide a complete synonymy for any species. The listing is by geographic occurrence. Original generic reference is given in brackets following the describer's name.

EUROPE

P. kapfi (Meyer, 1861) [*Belodon*], Stubensandstein, Stuttgart, Germany (= *P. cylindricodon* + *P. cubicodon* Jaeger, 1828).

ASIA

P. maleriensis (Huene, 1940) [aff. *Brachysuchus*], Maleri beds, India.

EASTERN NORTH AMERICA

P. pennsylvanicus (Lea, 1851) [*Clepsysaurus*], Brunswick formation, Upper Milford, Pennsylvania.

P. manhattanensis (Huene, 1913) [*Rutiodon*], Brunswick formation, Fort Lee, New Jersey.

P. validus (Marsh, 1893) [*Belodon*], New Haven Arkose, Simsbury, Connecticut.

SOUTHWESTERN NORTH AMERICA

P. gregorii (Camp, 1930) [*Machaeroprosopus*], Chinle formation, Round Rock, Arizona.

P. megalodon (Case, 1929) [*Brachysuchus*], Dockum group, Howard County, Texas.

P. ganei (Lucas, 1898) [*Heterodontosuchus*], Chinle formation, Clay Hills, Utah.

P. dumblianus (Cope, 1893) [*Palaeoctonus*], Dockum group, Palo Duro Canyon, Texas.

P. orthodon (Cope, 1893) [*Palaeoctonus*], Dockum group, Palo Duro Canyon, Texas.

P. superciliosus (Cope, 1893) [*Belodon*], Dockum group, Dickens County, Texas.

Distinctive Characters:

1. External nares posterior, relatively close to orbit, between antorbital fenestrae.
2. Posterior border of supratemporal fenestra depressed below level of skull roof, narrow.
3. Posttemporal fenestrae relatively large.
4. Squamosals produced posteriorly into rounded processes, deeper than long, extending somewhat behind contact with paroccipital processes.
5. Upper and lateral surfaces of skull continuously rounded across upper temporal bar.
6. Orbits directed obliquely outward and upward, less upward than in *Paleorhinus*.
7. Quadrate relatively tall; ratio of quadrate height to width of skull table from 0.90 to 1.10.
8. Rostrum massive and bearing a swollen dorsal crest throughout its length. Premaxillary border flaring laterally, the rostrum constricted at the premaxillary-maxillary suture.
9. Ratio of rostral length to postnarial length almost constant, 1.22, independent of size.
10. Teeth round anteriorly, becoming asymmetrically compressed with serrate edges posteriorly; enlarged teeth in posterior portions of both premaxillary and maxillary.
11. Interpterygoid vacuity narrow; suborbital (posterior palatine) fenestrae small.

Most recent students have been reluctant to consider the more advanced American phytosaurs congeneric with their European counterparts. The reasons which have been advanced for considering them distinct may briefly be reviewed.

Jaekel (1910, p. 219) proposed that American phytosaurs typified by *Belodon buceros* Cope be separated, as a genus *Metarhinus*, from *Phytosaurus* because of the overall shape of the skull (which differs from *P. kapffi* principally in the shorter rostral crest and considerable distortion), the arching of the prenarial portion of the snout (which is the result of crushing), the extreme posterior position of the posterior nares (which actually is not greatly different from *P. kapffi*), and the projecting squamosal process (known to vary in American species and near its maximum in *B. buceros*). In light of our present understanding of the variability of phytosaurs, only the last of these appears to be of systematic importance. When the squamosal processes of many American specimens are considered, *P. kapffi* is found to fall well within the variation of this feature. Jaekel's argument is thus unconvincing.

Mehl (1916, p. 22-23) concurred with Jaekel concerning these differences between European and American phytosaurs and added that the American species have sharp-edged, high rostral crests ending a considerable distance back of the tip, in contrast to the depressed and swollen crests of the European *P. kapffi* in which the crests reach nearly to the tip of the rostrum. He also cited supposed differences between the admittedly imperfect pterygoid of *Machaeroprosopus validus* (p. 15) and that of the phytosaurs described by Huene in 1911. His main argument for generic distinction, however, was that "not a single Triassic genus . . . is, without a reasonable doubt, recorded from both Europe and North America" (p. 23).[5]

The significance of rostral crests has been studied carefully by Camp and Colbert. The latter concluded (1947, p. 71) that their development is largely a growth character, partly controlled by sex. *Phytosaurus kapffi* appears anomalous in that its skull is appreciably shorter than the smallest American specimen on which any trace of a crest is apparent, yet it possesses the most highly developed crest known. This observation, supported by the significantly different rostral proportions and (probably) distinctive dermal armor of *P. kapffi*, affords a means for separating the European species from many, but not all, North American phytosaurs that have been referred to *Machaeorprosopus*. As will be shown below, the latter name has been applied to two separable series of species.

Mehl's argument from geographic distribution is not to be lightly dismissed. A recent re-evaluation of the faunal data (Colbert and Gregory, 1957, p. 1457) suggests that many similarities and close relationships between late Triassic vertebrates of Europe and North America have been concealed by provincial nomenclature. One of the objectives of the present study has been

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[5] Mehl proposed the genus *Machaeroprosopus*, type *M. validus* Mehl, for the American species because *Metarhinus* Jaekel 1910 was preoccupied by *Metarhinus* Osborn 1908. He regarded *Belodon buceros* Cope as a second species of *Machaeroprosopus*, closely related to *M. validus*. Unfortunately the type specimen of *M. validus* could not be located for re-examination. In form of its rostral crest it resembles *Rutiodon* as here recognized, but the squamosal processes are short, deep, and rounded like *Phytosaurus*, and the rostrum is broad and massive for the size of the skull.

to determine as far as possible upon morphological grounds the degree of relationship between European and American phytosaurs, in order to evaluate such assertions as this.

Case (1922) regarded *Machaeroprosopus* as close to *Phytosaurus*, possibly a subgenus. At the same time he established a new genus *Leptosuchus* for relatively deep- and slender-headed animals of this group; he sought to distinguish this from other American forms but did not explicitly compare it with *P. kapffi*. Later Case proposed the name *Brachysuchus* (1929) for the large, broad, and massive species, which are in fact distinguishable from his "*Leptosuchus*". During the same period Camp (1930) found sufficient intergradation among similar sorts of phytosaur skulls in the Chinle formation to lead him to refer them all to a single genus, *Machaeroprosopus*.

Camp (1930, p. 147) maintained a distinction between *Phytosaurus* and the American *Clepsysaurus* and *Machaeroprosopus* (whose synonymy he suspected but could not demonstrate) on the basis of the shape of the dermal scutes. The rectangular, overlapping plates attributed to *Belodon kapffi* by Meyer (1861, pl. 43), and Huene (1911, p. 103; 1913, p. 282) differ markedly from the non-overlapping equidimensional scutes that have been found with *Rutiodon carolinensis*, *Machaeroprosopus tenuis*, and *Leptosuchus* spp. Scutes of the *Phytosaurus* type have been found in North America (Case, 1932) but never in certain association with phytosaur skulls. This led me at one time (Gregory 1953a) to question the association of the elongate scutes with *P. kapffi*, but after examining the original collections from Heslach, Germany, I find it difficult to doubt the correctness of Meyer's identification. Instead, it seems more probable that some of the plates that I attributed to *Typothorax* (1953b), particularly Y.P.M. no. 3695 which was found a short distance from a large *Phytosaurus* cf. *gregorii* skull, are actually scutes of American species of *Phytosaurus*. North American phytosaurs with temporal fenestrae, squamosal processes, and external nares similar to those of *Phytosaurus kapffi* fall into two groups, which correspond to the "leptosuchid" and "brachysuchid" types of Case. They may be distinguished by the series of characters listed below, but some overlapping occurs among individuals of large size so that separation may not always be clear-cut. One group, including the large North American species hitherto called *Machaeroprosopus gregorii* and *Brachysuchus megalodon*, appears to be congeneric with the European *Phytosaurus kapffi*, and hereafter will be called *Phytosaurus*. The remaining forms, *Leptosuchus* and smaller species of *Machaeroprosopus*, include *Rutiodon carolinensis* as their earliest named example, and hence are properly assigned to the genus *Rutiodon*.

Comparison of *Phytosaurus* and *Rutiodon*:

1. Rostrum broad and heavy in *Phytosaurus*, the posterior premaxillary and maxillary swellings strongly developed so that the snout tapers throughout its length; crocodile-like rather than narrow and gavial-like. *Rutiodon* rostra more slender, tending to be deeper than wide, parallel sided anteriorly, the tip often strongly downcurved.

   Table 4 compares a measure of slenderness of rostra among various genera of phytosaurs.

TABLE 4

Ratio of width of rostrum at the premaxillary-maxillary suture to prenarial length. Number of measurements in brackets for each genus.

Paleorhinus	[7]	0.100-0.117
Mystriosuchus	[3]	0.067-0.117
Angistorhinus	[3]	0.099-0.130
Rutiodon	[6]	0.088-0.138
Phytosaurus		
P. kapffi	[5]	0.147-0.208
N. American species	[4]	0.129-0.171

2. Rostrum bearing a strongly elevated crest along its entire length, or with evenly descending profile from external nares to rounded tip in *Phytosaurus*. Rostral crests absent from smaller *Rutiodon* skulls, confined to posterior part of rostrum in large individuals.
3. Rostral length ratio about 1.2 in *Phytosaurus*. regardless of skull size. In *Rutiodon* ratio decreases from about 1.7 in smallest skulls to 1.2 in largest, strongly correlated with size.
4. Posterior squamosal process deep, relatively short, broadly rounded in *Phytosaurus*. Squamosal processes of *Rutiodon* more pointed, tending to project farther posteriorly, narrower.
5. Dorsal armor of overlapping. transversely broadened. rectangular plates in *Phytosaurus kapffi* and probably similar in North American species. *Rutiodon* armor of equidimentional nonoverlapping scutes.

Although large skulls cannot be separated by the rostral:postnarial length ratio alone, the dissimilar growth patterns of *Phytosaurus* and *Rutiodon* form one of the most compelling reasons for separating these genera.

The relatively short. rounded squamosal processes of *Phytosaurus* closely resemble those of *Angistorhinus* and are probably primitive. Some of the earlier species of *Rutiodon*, e.g. *R. zunii* (Camp) and *R. carolinensis* Emmons, have squamosal processes similar to *Phytosaurus*, although they do not resemble that genus in other respects. Camp (1930. p. 20) tabulated the ratio of length to height of the squamosal process in an ascending stratigraphic series of phytosaurs from Arizona. "*M.*" *gregorii* has appreciably lower values than the others and forms an exception to the otherwise progressive elongation of these processes (in species here referred to *Rutiodon*).

Parasuchus Huxley, 1870, type *P. hislopi* Huxley (ms) in Lydekker, 1885. has long been listed as a phytosaur from the Upper Triassic beds, of Maleri and Tiki. in Central India. Huene (1911. p. 41) pointed out numerous differences between the type specimen (a basicranium) and corresponding parts of other phytosaurs. Later he showed that it was a rhynchosaur, and in 1940 (p. 6-7) he was able to demonstrate its identity with *Paradapedon huxleyi* Lydekker.

Phytosaur remains from the Maleri beds include a large animal. "aff. *Brachysuchus*" *maleriensis* Huene (1940. p. 21-32), and fragments of two smaller types which Huene did not name (p. 32-36). The specimens are most unsatisfactory, for they lack critical portions for comparisons with other phytosaurs. Some or all may well pertain to *Phytosaurus* or some may represent *Rutiodon.*

Phytosaurus, as here redefined, has the greatest stratigraphic span and widest distribution of any genus of phytosaurs. In Europe *P. kapffi* is confined to the Stubensandstein. In North America *P. megalodon* (Case) occurs near the base of the Dockum group in association with *Paleorhinus* and *Angistorhinus, P. gregorii* occurs at various levels in the Petrified Forest member of the Chinle formation, and other specimens of this genus have been found in upper levels of the Dockum in northern Texas and eastern New Mexico. The large phytosaur remains from India ("aff. *Brachysuchus*" Huene, 1940) probably pertain to this genus.

RUTIODON Emmons, 1856

Emmons, E., 1856, Geological Report of the Midland Counties of North Carolina, p. 302-307, figs. A, 22, pl. 6, fig. 8, pl. 5, figs. 2, 5.

Type:	*Rutiodon carolinensis* Emmons, 1856
Synonyms:	*? Angistorhinopsis* Huene, 1922 *Leptosuchus* Case, 1922 *Machaeroprosopus* Mehl, 1916 [Camp 1930, in part] *Metarhinus* Jaekel, 1910 [not Osborn, 1908] *Pseudopalatus* Mehl, 1928 *Rhytidodon* Cope, 1866 [invalid emend.]
Types of Synonyms:	[of *Angistorhinopsis*] *Mystriosuchus rütimyeri* Huene, *Leptosuchus crosbiensis* Case, *Machaeroprosopus validus* Mehl, [of *Metarhinus*] *Belodon buceros* Cope, *Pseudopalatus pristinus* Mehl, [of *Rhytidodon*] *Rutiodon carolinensis* Emmons.

Included Species:

No attempt is made to evaluate the many nominal species of "*Leptosuchus*" and "*Machaeroprosopus*". Rather they have been sorted, in so far as possible, into the two genera *Rutiodon* and *Phytosaurus.*

EUROPE

R. rütimeyeri (Huene, 1911) [*Mystriosuchus*], Rhaetic, Niederschöntal bei Basel, Switzerland; Halberstadt, Salzgitter, Germany.

EASTERN NORTH AMERICA

R. carolinensis Emmons, 1856, Cumnock formation, Egypt, North Carolina. *Clepsisaurus leai* Emmons, 1856, Leaksfield, North Carolina. *Rhytidodon rostratus* Marsh, 1896, Gulf, North Carolina.

SOUTHWESTERN NORTH AMERICA

R. adamanensis (Camp, 1930) [*Machaeroprosopus*], Chinle formation, Petrified Forest, Arizona.

R. andersoni (Mehl, 1922) [*Machaeroprosopus*], Dockum formation, Santa Rosa, New Mexico.

R. buceros (Cope, 1881) [*Belodon*], Chinle formation, Gallina, New Mexico.

R. crosbiensis (Case, 1922) [*Leptosuchus*]. Dockum group, Crosby County, Texas.

R. doughtyi (Case, 1920) [*Phytosaurus*], Dockum group, Texas.

R. imperfecta (Case, 1922) [*Leptosuchus*], Dockum group, Crosby County, Texas.

R. lithodendrorum (Camp, 1930) [*Machaeroprosopus*], Chinle formation, Carrizo Wash, Arizona.

R. scolopax (Cope, 1881) [*Belodon*], Chinle formation, Gallina, New Mexico.

R. studeri (Case and White, 1934) [*Leptosuchus*], Dockum group, Potter County, Texas.

R. tenuis (Camp, 1930) [*Machaeroprosopus*], Chinle formation, Petrified Forest, Arizona.

? R. validus (Mehl, 1916) [*Machaeroprosopus*], Chinle formation, Tanners Crossing, Arizona.

R. zunii (Camp, 1930) [*Machaeroprosopus*], Chinle formation, St. Johns, Arizona.

Distinctive Characters:

1. External nares posterior, relatively close to orbit, between antorbital fenestrae.
2. Posterior border of supratemporal fenestrae slightly to greatly depressed below level of skull roof, narrow.
3. Posttemporal fenestrae relatively large.
4. Squamosals produced posteriorly into rounded processes of variable length, extending far behind contact with paroccipital processes.
5. Upper and lateral surfaces of skull continuously rounded across temporal bar.
6. Orbits directed obliquely outward and upward.
7. Quadrate relatively tall; ratio of quarate height to width skull table near 1.0.
8. Rostrum of variable robustness, slender in smaller skulls, massive in larger specimens. Dorsal crests only in larger specimens and confined to posterior portion of rostrum. Posterior border of premaxillary flaring laterally, the rostrum constricted at the maxillary-premaxillary suture.
9. Ratio of rostral length to postnarial length varies inversely with skull length, from about 1.7 in skulls 700 mm long to 1.1 in skulls 1400 mm long.
10. Teeth round or minutely fluted anteriorly, becoming asymmetrically compressed with serrate edges posteriorly; enlarged teeth in posterior portions of both premaxillary and maxillary.
11. Interpterygoid vacuity narrow; suborbital fenestrae small.

Rutiodon carolinensis has more often been compared to *Mystriosuchus* than to *Phytosaurus*. A re-examination of all pertinent material of this species has shown that:

1. The external nares lay between the antorbital fenestrae, although somewhat more anterior than in most species of *Phytosaurus.*
2. The posterior border of the supratemporal fenestra was thin and depressed below the skull roof. The extent of this depression is uncertain; it may have been as great or less than in species of *Phytosaurus.*
3. The squamosal extended well behind the contact with the paroccipital process in a rounded posterior process quite similar to that of *Phytosaurus kapffi.*
4. None of the specimens are adequate to show the relative lengths of rostrum and postnarial portion of the cranium. A reasonable reconstruction from several specimens indicates a considerably lower prenarial-postnarial ratio than previously has been believed, and within the known range of variation of the *Machaeroprosopus-Leptosuchus* group of southwestern U. S. A.

The rostrum of *Rutiodon carolinensis* is extremely slender for a phytosaur of this size.

These similarities are sufficient to suggest the possibility that the *Rutiodon carolinensis* specimens represent a small, possibly immature or possibly primitive, species of *Phytosaurus.* Nevertheless differences in the development of the rostral crest, squamosal processes, dermal armor, and especially in the relative growth of rostrum and postrostral portion of the skull provide adequate characters for separation of phytosaurs with this combination of basic characters into two genera. These distinctions between *Phytosaurus* and *Rutiodon* have been stated in detail under the former genus (p. 682-683) and will not be repeated here.

The large phytosaur from the Rhaetic of Germany and Switzerland was reconstructed from numerous skull fragments and made the basis of the genus *Angistorhinopsis* by Huene (1922, p. 115). There are no data on the form of the squamosal process; the supratemporal fenestra had a depressed posterior border. In general appearance this skull resembles the slender-snouted American species that Case called *Leptosuchus.* The taxonomic significance of the differences that Huene has pointed out in braincase and postcranial skeleton are as yet not understood. It is unfortunate that the genus was established upon materials for the most part lacking the parts which have been found useful in diagnosing phytosaur genera.

From the stratigraphic viewpoint the material shows that a large phytosaur with depressed posttemporal arcade, deeply excavated parietals, and posteriorly placed nostrils lived in Europe during the Rhaetic. None of these features separate it from *Rutiodon* as I understand that genus.

RILEYA Huene, 1920

Huene, F. von, 1902, Geol. u. palaeont. Abh., N.F., Band 6, p. 62.
Type Species: *Rileya bristolensis* Huene, 1902 = *Palaeosaurus platyodon* Riley and Stutchbury, 1836

Synonyms: *Palaeosaurus* Riley and Stutchbury, 1836, non Geoffroy, 1831

Included Species: *Rileya platyodon* Riley and Stutchbury. Following Huene, 1908, the phytosaurian material from Durdham Down, Bristol, England, is assigned to the type species. Specimens from the Muschelkalk at Bayreuth (Huene, 1920) and Wesseln near Bad Salzdetfurt, Germany (Huene, 1958) are referred to the genus.

Discussion: *Rileya* (aside from teeth in the original type of *Palaeosaurus platydon*) is known from only a few vertebrae and limb bones. The humerus from the Muschelkalk differs sufficiently from that from Bristol to cast doubt upon their generic identity. In the absence of diagnostic cranial parts, the relationships of this phytosaur cannot be stated.

EBRACHOSAURUS Kuhn, 1936

Kuhn, O., 1936, Palaeontographica, Band 83A, p. 85-91, pl. 11, figs. 1-3, pl. 12, fig. 2, pl. 13, fig. 4, text figs. 6-8.

Type Species: *Ebrachosaurus singularis* Kuhn, 1936, Blasensandstein, Ebrach, Germany

The closely articulating armor plates of this fragmentary specimen are somewhat suggestive of a pseudosuchian. Until the characteristics of post-cranial elements of the phytosaur skeleton have been more securely established, the relationships of this specimen (which occurs in the deposit with *Paleorhinus* skulls) will remain uncertain.

PHYLOGENETIC RELATIONSHIPS

No fossils bridge the morphological gap between the long-snouted phytosaurs and other families of Thecodontia. The structure of the temporal and antorbital fenestrae, the general form of braincase, vertebrae, and girdles, and the bony dermal armor plates all find their closest counterparts in various members of the Pseudosuchia. The elongate premaxillaries of *Chasmatosaurus* suggest a tendency toward lengthening of the snout, which might have led to the phytosaur rostrum, although the nares of that genus appear to be carried forward by rather than left behind the zone of growth. Dermal armor of the Aetosauridae so closely resembles that of phytosaurs that specimens lacking other skeletal elements are difficult to identify; vertebrae and limb girdles of these families are likewise close in structure. Aetosaurid skulls resemble those of phytosaurs principally in the round orbits; the temporal fenestrae are differently constructed in the two families, aetosaurids having considerable lateral exposure of the large superior fenestra and a relatively small and low lateral fenestra, quite opposite to the large lateral and narrow dorsal fenestrae of phytosaurs. The weak dentition of the short-snouted aetosaurs implies very different feeding habits from the long-jawed phytosaurs. Both these late Triassic families may have descended from a common early Triassic ancestor resembling *Euparkeria*, which approaches them more closely in skull structure than the armored *Ornithosuchus* and its relatives.

Paleorhinus is considered to represent the basic stock of the phytosaurs that had already developed amphibious habits and elongate jaws suitable for catching aquatic prey. Its skull is primitive for phytosaurs in the development of the temporal fenestrae, anterior position of the external nares, absence of a posterior squamosal process, and undifferentiated dentition. Presumably the relatively low skull and short quadrate are likewise primitive for the family.

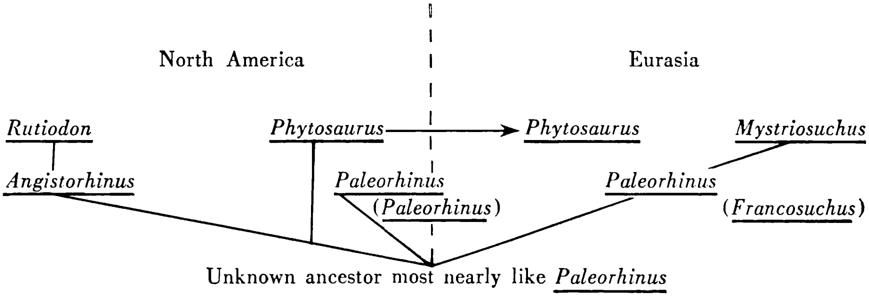
Mystriosuchus is obviously specialized similarly to *Phytosaurus* and *Rutiodon* in its tall quadrate, depressed posttemporal arcade, and posterior external nares; it resembles *Paleorhinus* in the absence of a squamosal process and in retaining a homodont dentition. *Mystriosuchus* has diverged from the primitive stock in the opposite direction from the remaining genera in the greater elongation of its slender jaws. Presumably this represents a greater specialization for feeding more strictly upon fish. The absence of a squamosal process in *Mystriosuchus*, and more especially the detailed similarity of its squamosal region to *Paleorhinus*, strongly implies that its ancestors never had acquired a posterior process. *Mystriosuchus* must therefore have descended from a *Paleorhinus*-like ancestor and acquired its similarities to *Phytosaurus* independently. The markedly longer rostra of the European *Paleorhinus* (*Francosuchus*) *neukami* compared to American species of *Paleorhinus* suggest that this species may be close to the ancestry of *Mystriosuchus* if not actually a member of that line.

Angistorhinus, *Rutiodon*, and *Phytosaurus* diverged from the primitive phytosaur stock by developing blade-like teeth in the posterior part of the jaws and by modifying the jaw musculature to exert greater pressure when the jaws were closed. These changes resulted in the development of a characteristic posterior projection of the squamosal bone. Presumably these structures enabled the reptiles to feed by cutting or tearing apart large prey. In *Phytosaurus* this adaptation was most highly developed and included considerable broadening of the posterior part of the palate and strengthening of the rostrum by a massive dorsal crest. The growth pattern of the rostrum differs from other phytosaurs.

Rutiodon displays a wide range of variation in form of the rostrum and differentiation of dentition, from relatively slender gavial-like skulls that suggest aquatic, presumably piscivorous, feeding to more massive heads with heterodont teeth similar to *Phytosaurus*. As these characteristics are correlated with size, a change in feeding habits with growth might be inferred; immature individuals with slender rostra fed principally or exclusively upon fish, but the larger animals became able to attack and feed upon tetrapods. The genus differs from *Phytosaurus* in its more slender squamosal process, shorter rostral crest, and type of dermal scutes.

Angistorhinus shows an early stage in the development of *Rutiodon* and *Phytosaurus* by its rounded squamosal processes and the beginnings of heterodont dentition. It is advanced over *Paleorhinus* in its posterior nasal opening but retains an extremely primitive posttemporal arch. The occurrence of the massive *Phytosaurus megalodon* (Case) in deposits containing *Paleorhinus* and *Angistorhinus* in Howard County, Texas, implies that generic differentiation occurred within the family at an earlier time and that structurally primitive fossils do not represent actual ancestors of all the more specialized genera. Thus *Angistorhinus* shows a stage through which *Phytosaurus* may have evolved, and might be a little-modified survivor of an actual ancestor of the latter genus. Known specimens cannot belong to the ancestral population. *Angistorhinus* could conceivably be ancestral to *Rutiodon*; the similarity is greater and they are not known to overlap in time.

These relationships may be represented by the following diagram:



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