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The Relationships of the American Phytosaur *Rutiodon*

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The description of phytosaur remains from the Dockum Group of western Texas and eastern New Mexico has required a general revision of the genera of these gavial-like Triassic reptiles. The latter study included an evaluation of the specimens from eastern North America known as *Rutiodon carolinensis* Emmons. McGregor (1906, pp. 35, 95) compared the postcranial bones of this species with the German *Mystriosuchus* and concluded that the American form was closely related to the slender-snouted *Mystriosuchus planirostris* von Meyer. Colbert (1947) redescribed the type and other skull material in more detail, and figured a mounted composite skeleton in the American Museum of Natural History. He concluded that *Rutiodon* was a valid genus, characterized by the relatively great downward curvature of the tip of the rostrum and by the intermediate proportions of its skull between the extremely long and slender-snouted *Mystriosuchus planirostris* and the more robust, shorter-snouted *Machaeroprotopus*. Colbert emphasized the similarity in many features of the postnarial portion of the skull between *Rutiodon* and the phytosaurs from the southwestern United States commonly termed *Machaeroprotopus*.

McGregor referred all phytosaur remains from the Newark group of eastern North America, with the possible exception of *Belodon validus* Marsh, to *Rutiodon*, but placed various poorly known species from the

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southwestern United States in the European genus *Phytosaurus*. Since that time many phytosaur skulls have been described and given new names. Camp (1930) and Colbert (1947) have referred the more advanced, *Phytosaurus*-like species from the western United States to *Machaeroprotopus* Mehl and shown that the larger phytosaurs (*Clepsysaurus*) from the Newark group in Pennsylvania and New Jersey closely resemble the former and are distinct from the North Carolina species *Rutiodon carolinensis*.

One conclusion of the revision of phytosaur genera alluded to above is that the name *Machaeroprotopus* has been applied to two separable groups of species. The more massive forms, such as *Machaeroprotopus gregorii* Camp and the similar *Brachysuchus megalodon* Case, cannot be separated from the European genus *Phytosaurus* Jaeger. *Clepsysaurus* probably pertains to this group but cannot be assigned certainly without better specimens of the skull than are yet available. Other species with more slender and variably crested rostra, including Case's genus *Leptosuchus* and *Machaeroprotopus tenuis* Camp, *M. adamanensis* Camp, and others, form a separate though closely allied genus, to which the North Carolina species *Rutiodon carolinensis* Emmons apparently belongs. As the first-named member of this group, it brings to it the generic name *Rutiodon*.

Throughout this study I have benefited from frequent consultation with Dr. Edwin H. Colbert. He has also most kindly permitted me to examine all the pertinent collection in the American Museum of Natural History. Mrs. Rachel H. Nichols has aided in many ways in locating and lending specimens for study. Mr. Chester Tarka photographed the skull of the American Museum mounted skeleton. Dr. Peter Vaughn provided photographs of the skull in the United States National Museum and permitted me to examine phytosaurs in their collections. Dr. Philip S. Humphrey most generously gave the time to read the manuscript critically, and it has benefited greatly from his constructive suggestions. The drawings were prepared by Mrs. Lois Darling, and their cost was defrayed by the John Doneghy, Jr., Research Fund of Peabody Museum, Yale University.

The names of certain institutions are abbreviated, as follows:

A.M.N.H., the American Museum of Natural History
U.C.M.P., University of California, Museum of Paleontology
U.S.N.M., United States National Museum
Y.P.M., Peabody Museum of Natural History, Yale University

Rutiodon carolinensis Emmons

Rutiodon carolinensis EMMONS, 1856, Geological report of the midland counties

of North Carolina, pp. 302–307, fig. A, 22, pl. 6, fig. 8, pl. 5, figs. 2, 5.

Clepsysaurus leai EMMONS, *op. cit.*, pp. 309–313, fig. M, pl. 8, fig. 3.

Rhytidodon rostratus MARSH, 1896, *Amer. Jour. Sci.*, vol. 2, p. 61, fig. 2.

TYPE: Five striated teeth (Emmons, 1856, fig. A, p. 302).

REFERRED MATERIAL: 1. Emmons' original material, the type (five teeth), vertebral centrum (p. 304, fig. 22), vertebrae and ribs (pl. 6, fig. 8), neural spine (pl. 5, fig. 2), and fragment of interclavicle ("Frontal," pl. 5, fig. 5). [From Deep River field, North Carolina. Localities of Egypt, Farmville, Taylor Plantation, and Gulf. Teeth common at junction of Black Band and Coal Seam (p. 301).] 2. Skull lacking portion between orbits and nares and the posterior end of the roof, at present in Williams College Geological Museum (Emmons, 1860, p. 179, fig. 157; Colbert, 1947, pp. 80–88, figs. 7–11). 3. Type of *Clepsysaurus leai*, three vertebrae (Emmons, 1856, pl. 8, fig. 1, p. 310, fig. M) and other vertebrae, 14 in all, with ribs; Dan River field near Leakesville, North Carolina. 4. Teeth referred by Emmons (1856) to *Clepsysaurus pennsylvanicus* (p. 299, fig. B), to *Palaeosaurus carolinensis* Emmons (pp. 315–317, figs. F, G, H, I), and to *Palaeosaurus sulcatus* Emmons (pp. 317–318, fig. N, 1–4). 5. Femur (including supposed tibia) from gray sandstone at Germantown, North Carolina (Emmons, 1856, pp. 318–320, pl. 7, figs. 1, 2); scapulocoracoid (pl. 8, fig. 2). 6. Incomplete skull, type of *Rhytidodon rostratus* Marsh, U.S.N.M. No. 5373, Gulf, Chatham County, North Carolina (Marsh, 1896, p. 61, fig. 2; McGregor, 1906, p. 58, fig. 12). 7. Specimens from Egypt, North Carolina, in the American Museum of Natural History: A.M.N.H. No. 1, nearly complete skull on mounted composite skeleton; A.M.N.H. No. 2, skull roof (fig. 4 of the present paper); A.M.N.H. No. 3, right temporal region (figs. 2, 3); A.M.N.H. No. 4, part of rostrum from nares forward for 40 cm. (fig. 1); A.M.N.H. No. 5, skull roof. Other specimens in the American Museum of Natural History do not add significant data to those listed here. 8. Possibly portion of a jaw and rib and teeth, York County, Pennsylvania (Wanner, 1926, pl. 3). Other phytosaur remains from Pennsylvania and New Jersey have been referred to *Clepsysaurus pennsylvanicus* and *C. manhattanensis* (see Colbert and Chaffee, 1941). Perhaps Wanner's specimen also belongs to that genus.

Ebenezer Emmons based the name *Rutiodon carolinensis* (from *rutis*, "plaits," and *odous*, "tooth") on five striated teeth, the largest 1 3/8 inches (35 mm.) long and 5/16 inch (8 mm.) in diameter. The teeth bear a sharp ridge or carina on one side, but serrations are wanting. Flutings never extend to the apex, and the teeth are not labyrinthine in structure. Associated with the teeth were biconvex vertebrae with

compressed centra of hourglass shape, resembling those of *Clepsysaurus* but larger.

Emmons originally compared the North Carolina fossils with *Thecodontosaurus* and *Palaeosaurus* from the Bristol Conglomerate of England, and with *Clepsysaurus pennsylvanicus* Lea. He considered *Rutiodon* a distinct genus, because the teeth were always smaller and plaited or fluted towards the base of the crown in contrast to the smooth, lancet-shaped teeth with serrate edges of *Clepsysaurus*. Also the vertebrae were larger than any then known from Pennsylvania. A footnote to the original description acknowledges the identity of the *Rutiodon* teeth with those named *Centemodon sulcatus* by Lea (1856); the implications of this for priority of the name *Rutiodon* have been almost universally overlooked. Inasmuch as phytosaur teeth are not diagnostic for either genera or species, the identification cannot be considered certain. *Rutiodon carolinensis* has yet to be recognized certainly outside the North Carolina area. *Centemodon* is a *nomen vanum*.

In 1860 Emmons figured an imperfect large skull of this animal, the most complete phytosaur specimen to be described up to that time. He remarked (p. 175) that "The upper jaw of the *Rutiodon* is nearly cylindrical, as it is prolonged in front of the nostrils which are just anterior to the large eye-sockets, and descend vertically, like the blow-holes of a cetacean." The skull was figured in dorsal view (p. 179, fig. 157).

Marsh (1896, p. 61) figured a second skull from the Deep River area, with the name *Rhytidodon rostratus* Marsh, in comparison with the skulls of *Phytosaurus kappfi* and a crocodile, but he gave no description. This skull was briefly described and refigured by McGregor (1906, pp. 58–59, fig. 12), with a comment on the loss of much of the bone from the post-orbital bars, and a brief comparison with the skull of *Mystriosuchus*. It is refigured here (fig. 5) with additional comments on its structure.

McGregor (1906, p. 60) pointed out that all the varied types of teeth mentioned by Emmons belonged to the same animal.

Colbert (1947) gave a full description of the interorbital fragment and rostrum first figured by Emmons, and prepared a restoration. No attempt is made here to repeat his thorough description. Rather, some comparisons are made between the various specimens of *Rutiodon* and, on this basis, a new restoration has been attempted.

ANALYSIS OF SYSTEMATIC CHARACTERS OF *RUTIODON* SKULLS

The most fundamental characters for phytosaur classification are found in the position of the external nares with respect to the antorbital fenestrae.

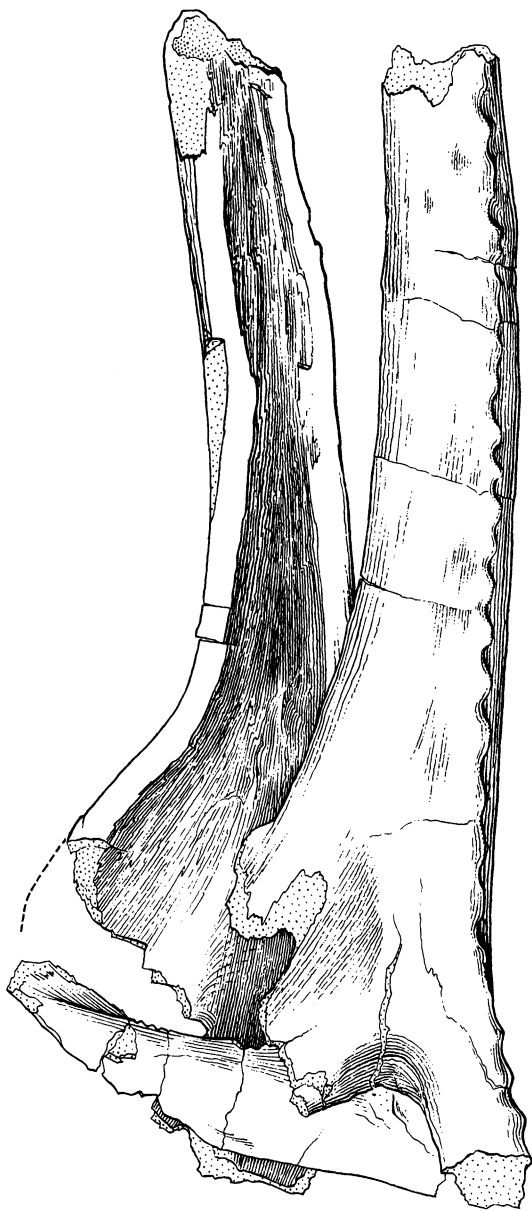


FIG. 1. A.M.N.H. No. 4. Posterior portion of rostrum and ascending process of palatine, showing position of external naris above anterior end of antorbital fenestra. $\times 1/2$.

trae, and in the development of the post-temporal arch and squamosal processes at the rear of the skull.

POSITION OF EXTERNAL NARES

In *Rutiodon* the external nares lay between the antorbital fenestrae, not anterior to them as in the primitive genus *Paleorhinus*. In the mounted skull, A.M.N.H. No. 1, the anterior border of the nares lies directly above the front of the antorbital fenestra. The same relationship is shown in the Williams College skull, in which the anterior border of the nares lies slightly anterior to the front end of the fenestrae. A.M.N.H. No. 4 (fig. 1) does not show the anterior narial border, but suggests that it lay in about the same position, either over or just anterior to the front of the antorbital fenestrae. The nares of U.S.N.M. No. 5373 lie between the anterior ends of the antorbital fenestrae but are prolonged forward by grooves so that, in the crushed, coaly material, it is almost impossible to be sure where the narial opening ended.

These four specimens indicate a remarkably constant position for the nares, which is essentially the same as that shown by *Mystriosuchus*, *Phytosaurus*, and various American species that have been called *Leptosuchus*, *Machaeropsopus*, and other names. Some specimens have the external nares relatively farther back, well behind the anterior end of the antorbital fenestra. In others, including *Phytosaurus kapffi* of Germany, the anterior borders of the nares and antorbital fenestrae lie on the same transverse line. *Rutiodon* might be termed more primitive in the tendency for the nares to extend slightly ahead of the fenestral boundary. Actually this character depends more on the variable length of the antorbital fenestra than on the position of the external nares, which seem to occupy either the primitive anterior position known in *Paleorhinus* or the posterior position found in all other genera of phytosaurs.

DEPRESSION OF POST-TEMPORAL ARCADE

Mystriosuchus and *Phytosaurus* differ from more primitive genera in the marked depression of the parietal-squamosal arcade below the level of the skull roof, so the superior temporal fenestra opens partly or entirely on the occipital surface of the skull.

In *Rutiodon* the post-temporal arch is a thin but rather deep strip of bone, the upper edge of which appears to lie close to the level of the skull roof. In the mounted skull, A.M.N.H. No. 1, the bar on the right side lies at the level of the skull roof, but the posterior part of the postorbital bar, which originally overlapped it, is broken away. On the left side the

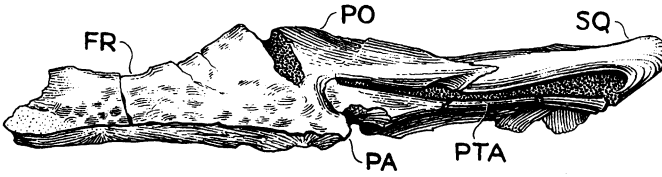


FIG. 2. A.M.N.H. No. 3. Dorsal view of right temporal region. The post-temporal arch is broken near the posterior end of the parietal deck and displaced into the anterior end of the superior temporal fenestra, which originally emarginated the rear of the skull roof. *Abbreviations:* FR, frontal; PA, parietal; PO, postorbital; PTA, post-temporal arch; SQ, squamosal. $\times 1/2$.

postorbital bar is present, but the arch is missing. On U.S.N.M. No. 5313, post-temporal arches are well preserved on both sides and appear to lie at the level of the roof. However, the posterior ends of the postorbital bars are broken away, so the appearance is again deceptive. It seems probable, indeed, that on this skull the lateral end of the post-temporal arch reached the postero-internal surface of the squamosal below the upper edge of the postorbital bar much as in A.M.N.H. No. 3. As may be seen in the medial view of that specimen (fig. 3), the bar is depressed considerably at its lateral end, although it rises to the level of the skull deck near the midline. The post-temporal arcade was narrow and deep. The temporal fenestrae extend far posteriorly, even beyond the tip of the paroccipital process. The left side of A.M.N.H. No. 2 shows that the deep, thin, posterior wall of the supratemporal fenestra meets the rear

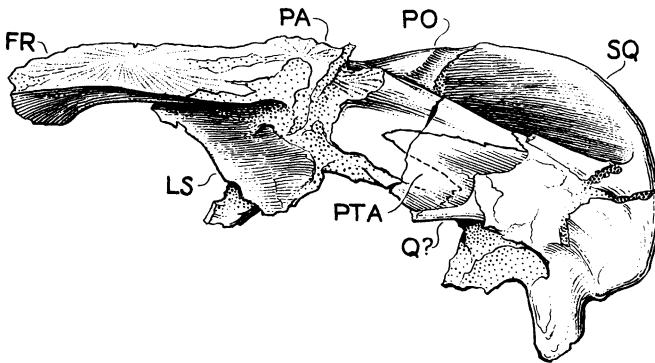


FIG. 3. A.M.N.H. No. 3. Medial view of right side of posterior end of skull roof, same specimen as shown in figure 2. Observe rounded squamosal process and post-temporal arch below level of skull roof. *Abbreviations:* FR, frontal; LS, laterosphenoid; PA, parietal; PO, postorbital; PTA, post-temporal arch; Q?, quadrate?; SQ, squamosal. $\times 1/2$.

end of the postorbital process below the level of the skull roof, much as in A.M.N.H. No. 3. The right side of this specimen also shows clearly how the lateral end of the post-temporal arch is depressed, overlapped by the posterior squamosal process, and joined to the lateral portion of the squamosal midway between the upper border and base of the downwardly projecting process for attachment of the depressor mandibulae

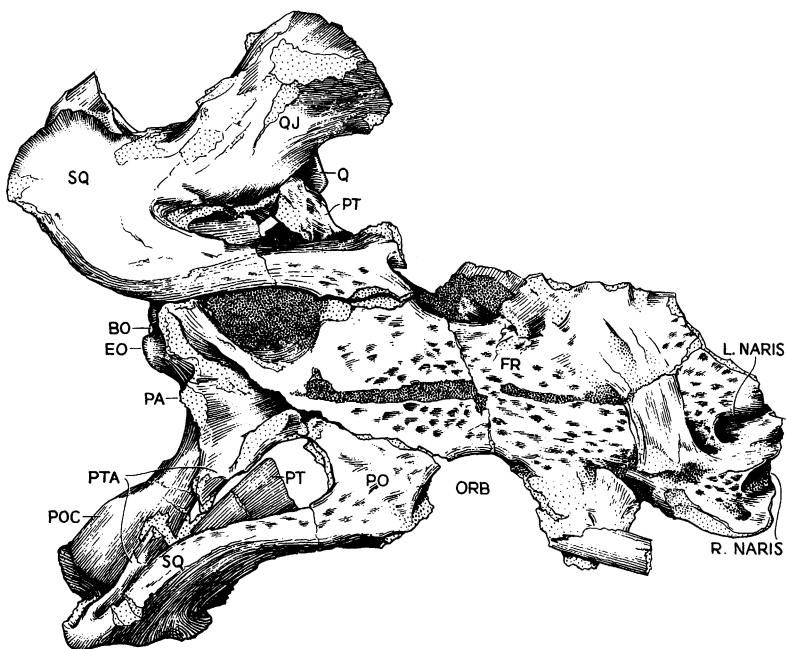


FIG. 4. A.M.N.H. No. 2. Dorsal view of postnarial portion of skull roof of a large specimen. Note rounded posterior squamosal process and depressed post-temporal arch. *Abbreviations:* BO, basioccipital; EO, exoccipital; FR, frontal; ORB, orbit; PA, parietal; POC, paroccipital process; PT, pterygoid; PTA, post-temporal (squamosal-parietal) arch; Q, quadrate; QJ, quadratojugal; SQ, squamosal. $\times 1/3$.

tendon. Such a relationship is fundamentally like that in various species of *Phytosaurus* (McGregor, 1906, fig. 4; Camp, 1930, fig. 2), although in many of these the upper surface of the post-temporal bar drops abruptly as it leaves the roof near the midline, a relationship like that in *Mystriosuchus* (McGregor, 1906, fig. 5).

Crushing and breakage are responsible for the superficial resemblance of the post-temporal arch in A.M.N.H. No. 1 and U.S.N.M. No. 5373

to that of the primitive phytosaur *Paleorhinus*. A.M.N.H. Nos. 2 and 3 indicate a more advanced condition, approaching that of typical *Phytosaurus*. Both A.M.N.H. No. 1 and the skull of *R. rostratus* (U.S.N.M. No. 5373) are broken in this area and show evidence of posterior squamosal processes like those of A.M.N.H. No. 2. The material suggests that *Rutiodon* was different from and more primitive than *Phytosaurus* in the straightness of the post-temporal arch and in its posterior termination close to the end of the squamosal process. The latter feature suggests *Angistorhinus*, which differs in having the post-temporal arcade thick, entirely at the level of the skull roof, and confluent with the upper surface of the postorbital bar. *Mystriosuchus* differs in having the arch strongly depressed throughout its length.

SHAPE OF POSTERIOR SQUAMOSAL PROCESS

Paleorhinus and *Mystriosuchus* differ strikingly from all other phytosaurs in the abruptly truncated posterior end of the squamosal bone, which extends scarcely or not at all behind the end of the paroccipital process in these two genera. *Rutiodon carolinensis* has rounded posterior squamosal processes which extend slightly beyond the paroccipital process and which resemble those of "*Machaeroprotopus*" *zunii* Camp or "*M.*" *adamanensis* Camp and those of *Angistorhinus*.

PROPORTIONS OF ROSTRUM AND SKULL IN *Rutiodon*

One of the principal features that have been used to distinguish *Rutiodon* from other phytosaurs is the form of its rostrum, which is always slender and elongate, although less so than that of *Mystriosuchus*, and never crested like that of many specimens of *Phytosaurus* and "*Machaeroprotopus*." As the temporal region of *Rutiodon* is now known to be like that of *Phytosaurus*, and the position of the nares above the antorbital fenestra is within the limits of that genus, the rostral proportions need critical examination to determine whether they differ sufficiently to warrant generic separation of the eastern North American form, or not.

When one seeks positive evidence of the proportion of rostral length to skull length in *Rutiodon*, it soon becomes evident that adequate data are totally lacking. The most nearly complete skull (A.M.N.H. No. 1) has short restored segments in both rostrum and lower jaw, so its exact length is doubtful. About 8 cm. of the rostral tip is restored. This length was determined by considerations of tooth number (E. H. Colbert, oral communication), but as other species of phytosaurs show a high varia-

bility in the number of teeth, such a criterion may not be reliable. As restored, the rostral length of 393 mm. is about 30 mm. short of the value predicted for a "*Machaeroprotopus*" skull with the same postnarial length (254 mm.).

The only complete rostrum belongs to the specimen at Williams College. This skull is broken just behind the external nares, and the fragments of the interorbital region neither makes contact with the rostrum nor shows the posterior end of the skull. The orbital length (75 mm.) is much greater than that of other *Rutiodon* skulls, and the entire specimen suggests a large and robust individual when compared with the remaining material. When the squamosal processes and orbitonasal areas of this skull are restored with the aid of A.M.N.H. Nos. 1 and 2 (fig. 8), the postnarial segment is slightly over 300 mm. Colbert (1947, p. 65) attributes to this skull a postnarial length of only 245 mm., a figure that scarcely exceeds the length of the broken interorbital block.

These estimates of the proportions of *Rutiodon* skulls both yield a ratio of 0.61 for the prenarial length to total skull length, a value similar to that of specimens of "*Machaeroprotopus*" from Arizona of comparable size. [Colbert (1947, p. 65) gives ratios of postnarial length to total length; these figures for *Rutiodon* would be (A.M.N.H. No. 1) $254: > 647 = < 0.392$ and (Williams College) $\sim 300: \sim 770 = \pm 0.390$.] They do not indicate an unusually elongate rostrum. The rather considerable difference in proportion between the *Rutiodon* and "*Machaeroprotopus*" skulls shown by Colbert (1947, fig. 12) may be merely an expression of the negative allometric growth of the snout which is shown graphically in figure 2 of the same paper.

In contrast to the similarity of the rostral proportions of *Rutiodon* and such species as "*Machaeroprotopus*" *lithodendrorum*, *adamanensis*, *tenuis*, and *buceros*, the skulls of *Phytosaurus kapffi*, although no longer than the *Rutiodon carolinensis* specimens, have rostral/total length ratios from 0.539 to 0.566. Such low values are attained by only the largest specimens of "*M.*" *lithodendrorum*, and by the massive "*M.*" *gregorii* and "*Brachysuchus*" *megalodon*. These skulls are about twice the size of the skull of *Rutiodon carolinensis* or that of *P. kapffi*. The difference in proportion suggests that *Rutiodon* and many of the species referred to "*Machaeroprotopus*" had a different pattern of skull growth from that of the European *Phytosaurus*, which might well deserve taxonomic recognition.

Differences in rostral proportions from *Mystriosuchus planirostris* (ratio of prenarial to skull length, 0.66–0.70) are obvious. *Rutiodon* has a far less elongate snout, more closely set teeth, and numerous other distinctions.

No indication of a rostral crest of any sort has been found on any specimen of *Rutiodon carolinensis*. Among the specimens of "*Machaeropsopus*" from the Chinle formation of the Colorado Plateau, crested rostra are most common on large specimens and at relatively high stratigraphic levels (Colbert, 1947, pp. 70-71). The largest known *R. carolinensis* skull is about 770 mm. in length, which is about 45 mm. shorter than the smallest phytosaur skull from the Chinle in which a rostral crest has been observed, and far below the size at which all skulls develop crests (approximately 1100 mm.). The absence of a rostral crest, therefore, does not necessarily constitute a distinction from the western species, as the eastern form may be below the size threshold for its development.

Phytosaurus kapffi, however, although similar in skull length to *R. carolinensis*, invariably has a massive crest running the entire length of its rostrum and is comparable to the largest specimens from western North America in this respect. This then is a second distinction between *Rutiodon* and *Phytosaurus*.

A third feature that has been used to characterize *Rutiodon* is the strongly down-curved tip of the rostrum. Although this feature is pronounced in the North Carolina specimens, it may also be observed in some specimens of *Phytosaurus kapffi*, some skulls of "*M.*" *lithodendrorum*, the type of "*M.*" *validus*, in *Angistorhinus*, and others. It does not seem wise to stress this as a diagnostic character.

DENTITION

The round, fluted teeth on which Emmons established *Rutiodon* are characteristic of the anterior portion of the snout, behind the enlarged grasping teeth of the rostral tip. *Paleorhinus* and *Mystrisuchus* have nearly homodont dentitions, but the most posterior teeth of both maxillary and dentary in these genera are somewhat compressed, keeled, and serrated-edged, although not of greater diameter than the round anterior teeth. *Phytosaurus* and "*Machaeropsopus*" or "*Leptosuchus*" have more highly differentiated teeth, those of the posterior part of the premaxillary being somewhat lancet-shaped, and the posterior maxillary teeth having characteristic unsymmetrically compressed crowns, broad lancet points, and serrate keels. *Angistorhinus* shows the beginning of such differentiation.

All these varieties of phytosaur teeth occur in the Deep River deposits of North Carolina. Emmons described most of the positional variants, ascribing the posterior teeth to *Clepsysaurus* and the anterior to *Rutiodon*. McGregor was perhaps the first to point out that all these types occurred in a single animal. The fluting or striation of the anterior teeth is not

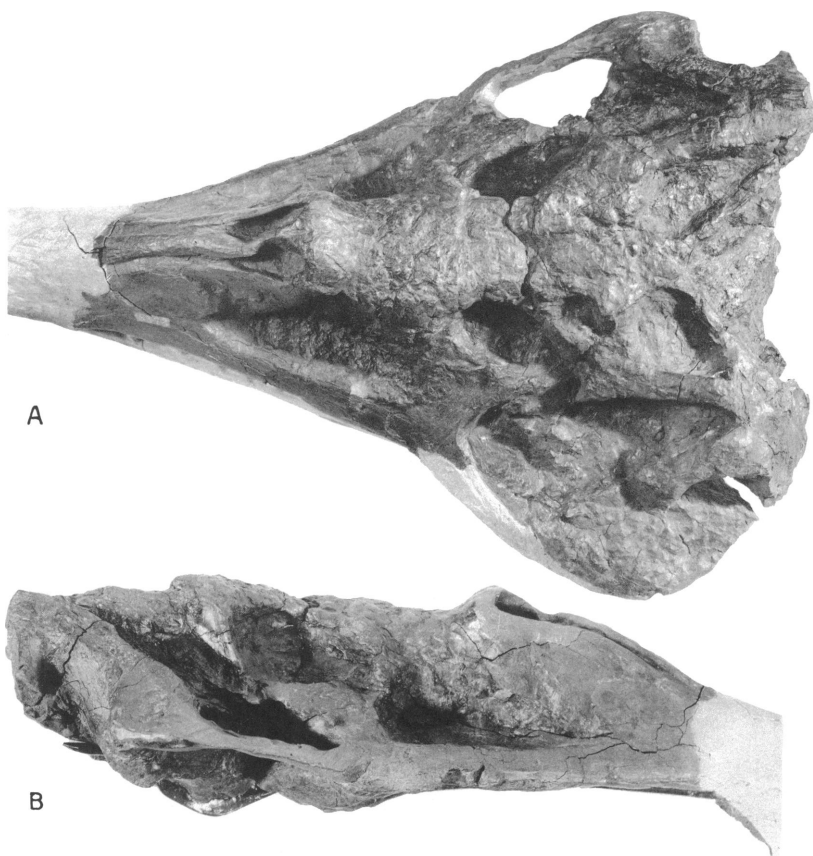


FIG. 5. *Rutiodon carolinensis* Emmons. U.S.N.M. No. 5373 (type of *Rhytidodon rostratus* Marsh). A. Dorsal view. B. Lateral view. $\times 1/2$. Photographs courtesy of the Smithsonian Institution.

confined to *R. carolinensis*; many such teeth occur in the Dockum deposits of Texas and New Mexico, associated with the usually toothless skulls of "*Leptosuchus*."

Colbert pointed out that the premaxillary teeth of *Rutiodon* were more closely spaced than those of *Mystriosuchus planirostris*. *Rutiodon* has 27 premaxillary teeth; *M. planirostris*, with its longer snout, only 23 or 24. The two skulls of *M. plieningeri* figured by von Huene (1910) have 21 and 26 premaxillary teeth, respectively. Until much more is known of both individual and age variations in tooth frequency, this difference cannot be used reliably in systematics.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF SKULLS OF *Rutiodon carolinensis*

	Williams College Skull	A.M.N.H. No. 1	A.M.N.H. No. 2	A.M.N.H. No. 5	A.M.N.H. No. 3	U.S.N.M. No. 5373
Estimated total length	[773] ^a	[652]	[792]	—	—	—
Tip of rostrum to front of external naris	475	[393]	—	—	—	—
Front of external naris to tip of paroc- cipital process	—	235E ^b	—	—	—	250±
Length of external naris	55	52	—	—	—	50
Posterior edge of naris to front of orbit	—	41/57	55±	—	—	65
Posterior edge of naris to tip of paroc- cipital process	—	—	253	—	—	218
Posterior edge of naris to tip of squa- mosal process	—	193	292/264	—	—	—
Length of orbit	75	51/62	44	52	—	65
Rear of orbit to tip of paroccipital process	—	—	141	116	100±E	97
Rear of orbit to tip of squamosal process	—	[110/100]	152	—	105E	—
Length of antorbital fenestra	—	69	—	—	—	105
Quadrate height to top of skull	—	93+	—	—	—	83
Width of skull table	—	[136-]	145	—	—	164
Width of parietals between supra- temporal fenestrae	—	20	27	—	16+ E	20
Interorbital width	43±	28	51	45	26+ E	44?
Width of rostrum at maxillary- premaxillary suture	42	33	—	—	—	—
Width of rostral constriction	30	—	—	—	—	—
Width of rostral tip	50	—	—	—	—	—
Premaxillary teeth	27	—	—	—	—	—
Maxillary teeth	15	22/33	—	—	—	—
Total number of upper teeth	42	—	—	—	—	—
Total number of lower teeth	40+	—	—	—	—	—
Teeth opposite symphysis	32	—	—	—	—	—
Length of mandibular symphysis	398	—	—	—	—	—

^a Brackets indicate restoration included in measurement.

^b E, estimated.

In summary, the dentition of *Rutiodon carolinensis* does not provide valid distinctions from *Phytosaurus* or “*Machaeroprotopus*.” Its heterodonty separates it from *Mystriosuchus* and *Paleorhinus*, but not from *Angistorhinus*, which is in about the same stage of dental differentiation.

NARIAL APERTURE

The United States National Museum skull and in all probability the Williams College specimen have the elevated, "crater-like," external nares which Camp (1930, pp. 93-94) and Colbert (1947, p. 72) regard as a sexual character that possibly indicates a female skull. The narial aperture forms a high point on the skull, behind which the skull profile



FIG. 6. *Rutiodon carolinensis* Emmons. Dorsal surface of A.M.N.H. No. 1. Note thick posterior and thin anterior portions of nasal septum. Approximately $\times 1/2$. Photograph by Chester Tarka, the American Museum of Natural History.

is concave. In the Williams College specimen, elevated nares are inferred from the slight longitudinal concavity in the preorbital region and the greater depth at the nares than at the front of the interorbital fragment. The nares of A.M.N.H. No. 1 are not so elevated, and little indication of elevation can be found in A.M.N.H. No. 2, although this latter specimen is too severely crushed to be relied upon. So far as can be judged from the few available specimens, *Rutiodon* shows the same sort of dimorphism that has been described in "*Machaeroprotopus*."

A thin bony septum divides the external nares of the Williams College skull. As Colbert (1947, p. 81) has pointed out, the absence of recognizable sutures makes it impossible to determine the relative proportions of nasals and septomaxillary in the septum. U.S.N.M. No. 5373 apparently also had a narrow septum; unfortunately the anterior portion is restored

in plaster so the original nature is uncertain. In both these skulls the anterior limits of the narial opening are obscure, the bone having been crushed together so that the slit-like remnant of the aperture is continuous with a groove along the naso-septomaxillary suture.

In contrast to these, the posterior part of the narial septum of A.M.N.H. No. 1 is 21 mm. broad and bears the same rough surface as the rest of the skull roof. Anterior to this the septum narrows to 6 mm. and is

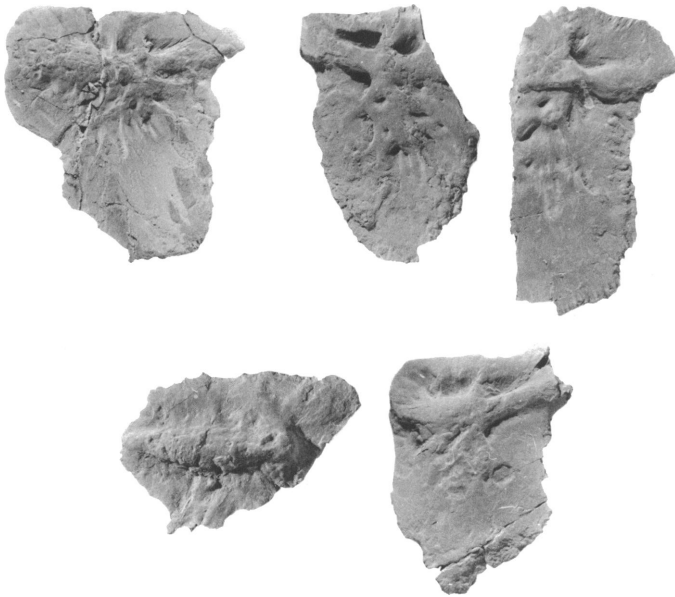


FIG. 7. *Rutiodon carolinensis* Emmons. Typical dermal scutes of A.M.N.H. No. 1. $\times 1/2$. Photographs by Chester Tarka, the American Museum of Natural History.

depressed below the level of the skull roof and is smooth. As a result, the nasal aperture itself is horseshoe-shaped. It is unlike any other specimen and presents so peculiar an appearance as to suggest an abnormality. In A.M.N.H. No. 2 the preserved posterior end of the septum is fairly stout, suggesting a thicker bone than that of U.S.N.M. No. 5373 or the Williams College skull.

Camp (1930, p. 148) regarded the thickness of the narial septum as a systematic character of high importance in the phytosaurs and made it the basis for subfamily separation of the Angistorhininae and Phytosaurinae. The several *Rutiodon carolinensis* skulls suggest that the nasal septum

tended to vary widely in thickness between individuals and that its development is not a reliable taxonomic criterion.

DERMAL ARMOR

Little emphasis has been placed upon postcranial morphology in this study. McGregor, Huene, Camp, and Case have published many observations upon and comparisons of vertebrae, girdles, limb bones, and dermal plates belonging to various phytosaurs, but no definite pattern of variation has been established. Dorsal scutes belonging to *Rutiodon* are of the roughly equidimensional, non-overlapping type bearing compressed, rounded keels similar to those of *Mystriosuchus* and "*Machaeroprotopus*" *tenuis*. This type of scute contrasts strikingly with the broad, overlapping plates associated with *Phytosaurus kapffi*, and this difference in armor, together with the skull features noted above, seems to be an adequate basis for separating *Rutiodon* from *Phytosaurus*.

In specimens from western North America both types of dermal ossifications have been found (cf. Case, 1932). An undescribed skeleton of "*Machaeroprotopus*" *tenuis* Camp (U.C.M.P. No. 27235) clearly shows the non-overlapping "mystriosuchid" type of scutes associated with a rather slender-snouted skull similar to that of *Rutiodon*. No adequate association of the overlapping, rectangular, armor plates with the large, robust skulls with full rostral crests ("*Machaeroprotopus*" *gregorii* Camp and "*Brachysuchus*" *megalodon* Case) has yet been discovered. A single scute of this type (Y.P.M. No. 3695) was found close to a skull of "*Machaeroprotopus*" *gregorii* (Y.P.M. No. 3293) near San Jon, New Mexico (Gregory, 1953, p. 12). While further discoveries to confirm the association are awaited, it seems possible to assume that relatives of both the European *Phytosaurus kapffi* and eastern North American *Rutiodon carolinensis* are present in the Dockum and Chinle formations.

RECONSTRUCTION

A reconstruction of the dorsal and lateral surfaces of the skull of *Rutiodon carolinensis* is presented in figure 8. It differs from that published by Colbert (1947, figs. 7, 12) principally in the longer and more rounded squamosal processes. The prenarial-postnarial ratio was calculated from the growth curve for various species from Texas and Arizona (unpublished data), with the use of the rostral length of the Williams College skull, the largest known *Rutiodon* specimen. The calculated postnarial length, 304 mm., is not far different from that of

A.M.N.H. No. 2, which was the main basis for the posterior portion of the skull. A.M.N.H. No. 1 and especially U.S.N.M. No. 5373 were used for a check on the depth of the facial region. As all these specimens are somewhat crushed, the restoration may indicate somewhat too low a skull.

RELATIONSHIPS OF *RUTIODON*

COMPARISON WITH *Mystriosuchus*

The details of the skull structure do not support McGregor's view that *Rutiodon* was closely related to the European *Mystriosuchus*. In particular, the rounded, posteriorly projecting squamosal processes and the absence of a sharp ridge on the lateral border of the postorbital bar separate it from that genus. The rostrum is significantly less elongate than that of *M. planirostris*, though not greatly different from that of *M. plieningeri*. As Colbert has pointed out, the skull roof of the German specimens continues to rise behind the external nares, which form the apex of the *Rutiodon* skulls. The more down-curved, hook-like tip of the rostrum and deeper posterior part of the lower jaw may also be valid distinctions between these genera. The teeth of *Rutiodon* appear to be more heterodont than those of *Mystriosuchus*. *Rutiodon* is less specialized in its less depressed post-temporal arch.

COMPARISON WITH *Paleorhinus*

The primitive phytosaur genus *Paleorhinus* differs from *Rutiodon* in the more anterior position of its external nares, in the fact that its post-temporal arch is at the level of the skull roof, in the absence of posterior squamosal processes, and in its nearly homodont dentition. It represents a distinctly more primitive stage of phytosaurian evolution which conceivably may be ancestral to *Rutiodon* and all other phytosaurs.

COMPARISON WITH *Angistorhinus*

Angistorhinus resembles *Rutiodon* in many features, notably the short, rounded, projecting squamosal processes, its slightly heterodont dentition, and the marked down-curving of the rostral hook. *Angistorhinus* is definitely more primitive in its post-temporal arch, and perhaps a trifle more advanced in the more posterior position of its external nares with respect to the antorbital fenestra. It represents a primitive stage in the line that led to forms such as *Phytosaurus* and *Rutiodon*.

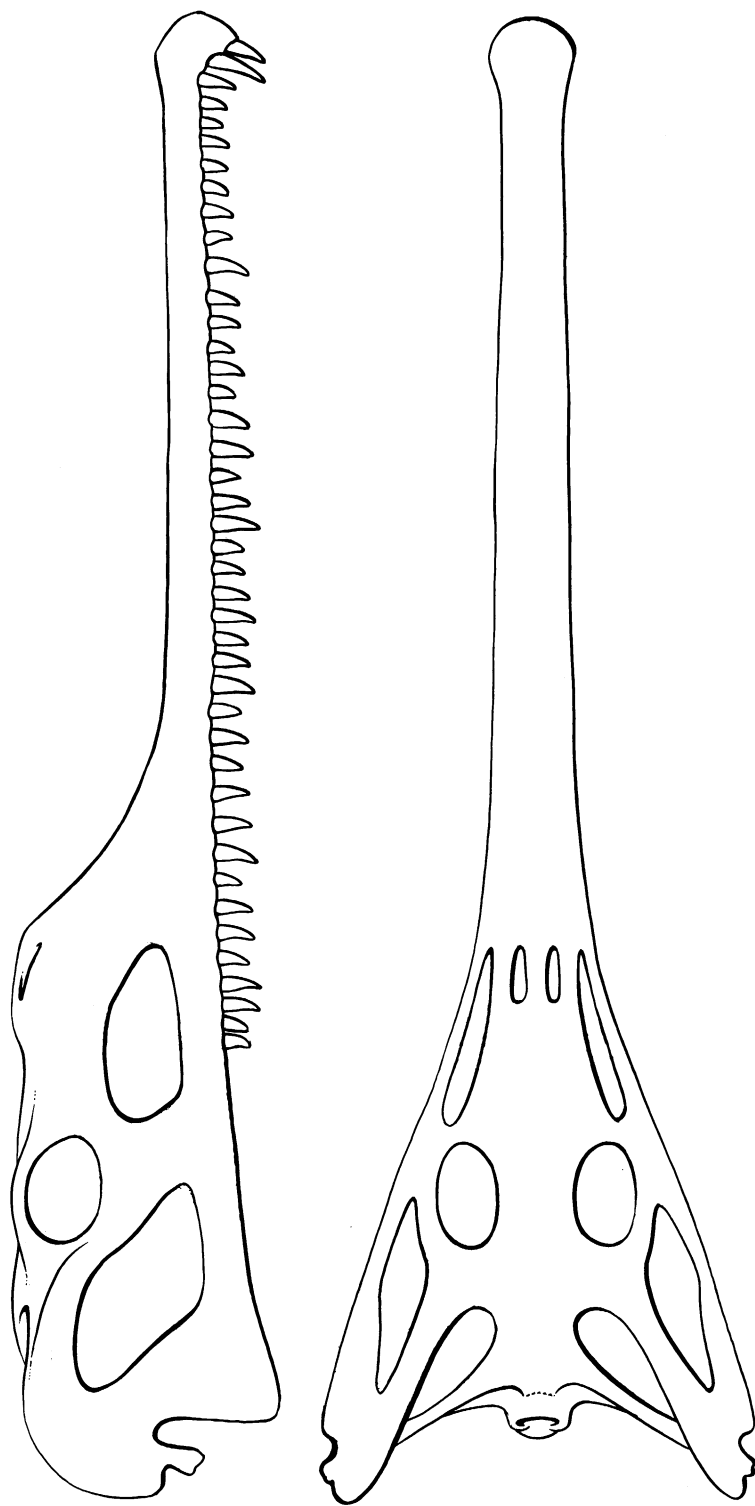


FIG. 8. Restoration of skull of *Rutiodon carolinensis* based on Williams College and American Museum specimens. *Upper*: Right lateral view. *Lower*: Dorsal view. Both approximately $\times 1/4$.

COMPARISON WITH *Phytosaurus*

As is pointed out above, the structure of *Rutiodon carolinensis* is closely similar to that of *Phytosaurus kapffi* and various American species commonly known as "*Leptosuchus*" and "*Machaeroprotopus*." Important features of agreement are found in the position of the external nares above the front of the antorbital fenestra; the rounded, projecting, squamosal processes; the heterodont dentition; and the depressed lateral end of the post-temporal arch.

Rutiodon carolinensis differs from *Phytosaurus kapffi* and such western North American species as "*Machaeroprotopus*" *gregorii* Camp or "*Brachysuchus*" *megalon* Case in the proportions of its rostrum and the absence of a rostral crest or of a posterior swelling of the alveolar border of the maxillary. Camp and Colbert have shown that all these features are at least in part correlated with size and are of doubtful taxonomic value. However, if *R. carolinensis* is compared with *P. kapffi* specimens of equal skull length, these differences in proportion are just as obvious as when the much larger skulls are examined. More important, the small *P. kapffi* skulls resemble these extremely large and massive American forms in the ratio of rostral length to skull length and in having a fairly uniform crest along the entire rostrum. The remaining species of "*Machaeroprotopus*" and "*Leptosuchus*" have variably developed rostral crests, but these crests never extend the entire length of the snout. Except for the large type specimen of "*M.*" *tenuis* Camp, none of the remaining forms has such proportionally short rostra.

Other distinctions between these massive-headed North American species and the remaining phytosaurs that have been called "*Machaeroprotopus*" or "*Leptosuchus*" include a shorter and deeper posterior squamosal process and, possibly, dermal armor of overlapping rectangular plates like that of *P. kapffi*. The squamosal processes of *Rutiodon* are not obviously different from those of the *Phytosaurus* group, perhaps because of its smaller size. The dermal armor, however, is clearly of a different type.

On these bases, then, *Rutiodon* appears to be a genus distinct from *Phytosaurus*.

COMPARISON WITH "*Leptosuchus*" AND "*Machaeroprotopus*"

If the massive "*M.*" *gregorii* and "*B.*" *megalon* are excluded, the remaining Dockum and Chinle phytosaurs (omitting *Paleorhinus* and *Angistorhinus*) form a homogeneous group in which the rostral ratio varies

inversely with skull length but, except for the type of "*M.*" *tenuis*, always is appreciably greater than in *Phytosaurus*; rostral crests are absent to well developed along the posterior third of the snout; and the squamosal processes are narrower and more projecting than in the massive skulls. Dermal armor is of the non-overlapping, "mystriosuchid" type in those specimens in which association of skull and scutes can be established.

No satisfactory basis for separating *Rutiodon* from this group is apparent; the smaller specimens in particular are extremely similar. The North Carolina specimens tend to be smaller than those from Texas and Arizona. They have less heterodont teeth, relatively short squamosal processes, a less deeply depressed post-temporal arch, and never show either a rostral crest or any flaring of the alveolar border. Some of these features may be related to small size. All of them suggest primitiveness. None is sufficiently pronounced or invariable to warrant generic separation.

In conclusion, *Rutiodon* is regarded as a valid genus, related more closely to *Phytosaurus* than to *Mystriosuchus*. Phytosaurs from western North America hitherto referred to *Leptosuchus* and various species of *Machaeroprotopus*, such as *M. adamanensis*, *M. zunii*, and *M. tenuis*, are referred to *Rutiodon*, as that generic name has many years' priority over others that have been applied to this group.

SIGNIFICANCE OF *RUTIODON* IN CORRELATION

Vertebrate fossils are associated with coal beds in the Cumnock formation of the Newark group in the Deep River basin of North Carolina, and in unnamed gray and black carbonaceous shales and sandstones associated with coals in the Dan River basin. Details of the stratigraphy are given by Reinmund (1955) and summarized by him in Reeside and others (1957, pp. 1489–1490, chart columns 75, 76). The fossils are relatively low in a thick sequence of late Triassic deposits, but no satisfactory basis is available for physical correlation with the fossiliferous Triassic deposits of Pennsylvania, New Jersey, and the Connecticut Valley.

The fauna of the Cumnock includes, besides *Rutiodon carolinensis*, a metoposaurid labyrinthodont, *Eupelor* ["*Dictyocephalus*"] *elegans* Leidy, the small advanced therapsids *Dromotherium sylvestre* Emmons and *Microconodon tenuirostris* Osborn, and the common Triassic fishes *Diplurus* and *Semionotus*. The fishes and *Eupelor* have a wide stratigraphic range in the late Triassic. *Dromotherium* and *Microconodon* are unique and likewise of limited value in correlation.

Rutiodon carolinensis, with its series of primitive characters, suggests an age later than the Popo Agie and lower Dockum faunas in which *Paleo-*

rhinus and *Angistorhinus* are the characteristic phytosaurs, and earlier than the faunas of the upper Dockum or Petrified Forest member of the Chinle formation, with their more progressive species of *Phytosaurus* and *Rutiodon*. If comparisons are made between the squamosal processes of *Rutiodon carolinensis* and the Chinle phytosaurs, it is found that the greatest resemblance is with *Rutiodon zunii* (Camp), a species that occurs low in Chinle B. The broad supratemporal fenestrae that excavate the parietal roof support this comparison.

No phytosaur skulls from more northern exposures of the Newark group are available for direct comparison with the North Carolina specimens. "*Clepsysaurus*" *manhattanensis* is a robust skeleton with many features suggestive of the large species of *Phytosaurus* from western North America. These have, however, a wide stratigraphic range, from *Phytosaurus* ["*Brachysuchus*"] *megalodon* Case in the lower Dockum, associated with the *Paleorhinus* fauna, to *Phytosaurus* ("*Machaeroprotopus*") *gregorii* from moderately high levels in the Chinle and upper Dockum. "*Clepsysaurus*" *manhattanensis* was found very low in the New Jersey section. Until adequate phytosaur skulls are obtained from the Newark deposits of New Jersey or Pennsylvania, the relative position of these beds and of those of North Carolina within the late Triassic will remain uncertain, or be established through other criteria.

Rutiodon carolinensis indicates that the age of the Cumnock formation is late Triassic and probably early but not earliest late Triassic.

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